

Substantial pulses of aquatic insects emerge from tidal freshwaters along the James River Estuary, Virginia, USA

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Abstract: Tidal freshwaters in upper estuarine reaches provide important ecosystem services but are threatened by relative sea-level rise and pollution from increased development. Tidal freshwaters are highly productive and support estuarine and riparian food webs alike. Aquatic insects are common prey subsidies crossing into riparian habitats; however, the magnitude, timing, and composition of insect emergence in tidal systems has received little attention. Our objective was to better understand the magnitude and variability of aquatic insect emergence in tidal freshwaters. To do so, we quantified insect emergence from tidal creeks and estuarine shorelines of the James River Estuary, Virginia, USA, and characterized spatial and temporal patterns in the amount of emergent biomass. We continuously monitored insect emergence from 7 April to 8 November 2019 with floating emergence traps to estimate daily emergence, then used generalized additive mixed models to analyze spatial and temporal variation in daily emergence rates. We estimated aquatic insect biomass to emerge at a mean rate (± 1 SE) of 15.6 ± 2.0 g dry mass $m^{-2} y^{-1}$, which is among the highest of previously published estimates from nontidal systems (mean ± 1 SE = 12.9 ± 6.2 g dry mass $m^{-2} y^{-1}$). Spatial variability in emergence was highly taxon specific. Diptera and Trichoptera had more biomass emerging from the subtidal than intertidal zone, Odonata biomass emerged more from tidal creeks than along the estuarine shoreline, and the amount of Trichoptera biomass increased—whereas Ephemeroptera decreased—with distance from the estuarine shoreline. The magnitude and composition of emergent taxa varied throughout the sampling period, with sequential peaks in biomass that altered the prey available to riparian consumers. Our results suggest that tidal freshwaters export substantial quantities of aquatic insects, which are valuable prey items for riparian consumers in these systems.

Key words: resource pulse, tidal freshwaters, emergent insect, EPT taxa, aquatic subsidy, Chesapeake Bay

Tidal freshwaters, found in the upper reaches of estuaries, are among the most productive ecosystems worldwide (Simpson et al. 1983, Whigham 2009). They have high biodiversity and provide important nursery grounds for migratory fish (Swarth and Kiviat 2009). Aquatically derived energy, nutrients, and prey not only support estuarine food webs but also subsidize riparian food webs (Baxter et al. 2005, Schindler and Smits 2017). Emergent aquatic insects are common prey subsidies crossing the land–water interface, and in estuaries, osmoregulatory requirements largely constrain aquatic insects to the freshwater zone (Williams and Williams 1998a). In nontidal systems, high primary productivity is related to greater insect emergence (Gratton and Vander Zanden 2009). However, there are few accounts of insect emergence from tidal freshwaters (e.g., Ramirez 2008,

Johnson and Simenstad 2015), and these only report estimates from a limited sampling duration, thus precluding a general understanding about insect emergence along the river–estuarine transition.

As a prey subsidy for riparian consumers, emergent insects can influence consumer spatial distributions and population dynamics (Polis et al. 1997). For example, availability of emergent aquatic insects leads to greater densities of spiders (Burdon and Harding 2008) and birds (Uesugi and Murakami 2007) in riparian habitats compared with nearby upland habitats. Emergent aquatic insects can account for 60 to 100% of body C in riparian web-building spiders (Collier et al. 2002, Sanzone et al. 2003) and 50 to 90% of the energy budget for some generalist bird species (Nakano and Murakami 2001). Aquatic insects are considered high-quality

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prey items because they contain essential long-chain polyunsaturated fatty acids that are sourced from autochthonous (i.e., algal) production (Hixson et al. 2015, Parmar et al. 2022). Long-chain polyunsaturated fatty acids confer benefits to consumers, such as increased immune function (Fritz et al. 2017), faster growth rates (Sabo and Power 2002), and greater breeding success (Twining et al. 2018). The flux of these essential fatty acids is ultimately determined by the abundance and composition of emergent insects (Martin-Creuzburg et al. 2017, Moyo et al. 2017).

Aquatic insect emergence varies seasonally. In temperate regions, emergence progresses in synchronized, taxonomically specific pulses during the spring and summer followed by low or negligible rates of emergence throughout the winter (Nakano and Murakami 2001, Baxter et al. 2005). The sequence of emerging taxa is generally consistent, leading to predictable compositional changes in the pulses of aquatic resources for riparian consumers throughout the emergence period (Ward 1992). However, annual variation in temperature affects emergence timing of many aquatic insects because rising water temperatures in the spring provide an environmental cue that triggers emergence (Larsen et al. 2016). For example, ephemeropterans have peak emergence in early spring but have been found to emerge earlier during years with warmer springs (Brittain 1982). As climate change advances spring onset, shifts in emergence phenology may lead to asynchrony with critical life-history periods of consumers (Durant et al. 2007), such as breeding (Shiple et al. 2022) or migration (Waller et al. 2018). More information is needed about the magnitude and timing of emergence pulses to identify potential ecological consequences of climate change on tidal freshwaters.

Aquatic insect emergence is also spatially variable because of differences in physical conditions, such as dissolved O₂, substrate, water depth, and velocity (Hynes 1970, Davies 1984). In tidal freshwaters, spatial variability may exist between intertidal and subtidal zones, longitudinally along the main estuarine channel, and between near-shore areas and adjoining tidal creeks. Aquatic insects in the intertidal zone encounter a regular risk of exposure at low tide and must be able to tolerate periodic stranding or to move with receding water—otherwise their distributions will be limited to the subtidal zone (Ward 1992). Additionally, when river discharge meets with tidal currents, the reduced velocity leads to high sedimentation rates and a silty or muddy substrate except in areas where a faster current leaves behind more sand and gravel (Diaz and Boesch 1977, Barendregt and Swarth 2013). The result of a homogeneous muddy substrate in the estuarine channel is low diversity of eurytopic insects (Diaz 1989), although it is unclear whether this low diversity is associated with low insect emergence. Furthermore, the lower tidal freshwater segment has been found to be more productive than the upper tidal freshwater segment because of a combination of allochthonous organic

matter from riverine inputs and autochthonous organic matter production (Bukaveckas et al. 2011, Tassone and Bukaveckas 2019, Bukaveckas 2022). Aquatic macroinvertebrates consume a mixture of autochthonous and allochthonous organic matter in tidal freshwaters (Hoffman et al. 2008), though they may preferentially select higher-quality autochthonous resources (Marcarelli et al. 2011). Thus, food quality may also influence the presence and abundance of emergent insects.

Our objective in this study was to better understand the magnitude and variability of aquatic insect emergence in tidal freshwaters. To do so, we quantified aquatic insect emergence from open water habitats in the tidal freshwater segment of the James River Estuary, Virginia, USA, including the subtidal and intertidal zones of tidal creeks and the estuarine shoreline. We asked how aquatic insect emergence varies spatially and temporally among open water habitat types throughout an emergence cycle. Our prior work has documented high productivity in the tidal freshwater segment of the James River Estuary (Bukaveckas et al. 2011, Wood et al. 2016); therefore, we expected high rates of aquatic insect emergence when compared with nontidal systems. We hypothesized that the subtidal zone would have greater insect emergence than the intertidal zone, but we did not have a priori expectations as to how the abundance, timing, and composition of insect emergence might differ among tidal creek and shoreline habitats.

METHODS

Study design

To address our research questions about spatial and temporal variation in aquatic insect emergence in tidal freshwaters, we conducted a field study to sample and quantify emergence over an ~8-mo period. With the goal of obtaining a robust assessment of aquatic insect emergence, we sampled and quantified emergence in 2 sites where we placed traps in 2 different tidal freshwater zones (intertidal, subtidal) and habitat placements (tidal creeks, estuarine shoreline). After identifying insects and quantifying emergence over the study period, we used visual assessment of emergence patterns over time, as well as generalized additive mixed models (GAMMs), to assess the importance of both temporal and spatial variables in explaining assemblage-wide and taxon-specific emergence.

Study sites

This study incorporated the estuarine shoreline and adjacent tidal creeks at 2 sites along the freshwater zone (salinity < 0.5 g/L) of the James River Estuary, a sub-estuary of the Chesapeake Bay (Fig. 1A). This tidal freshwater zone is a well-mixed system covering 86 km² that experiences semidiurnal tides (~70 cm) throughout the year (Bricker et al. 2007). The upper tidal freshwater segment has a deeper main

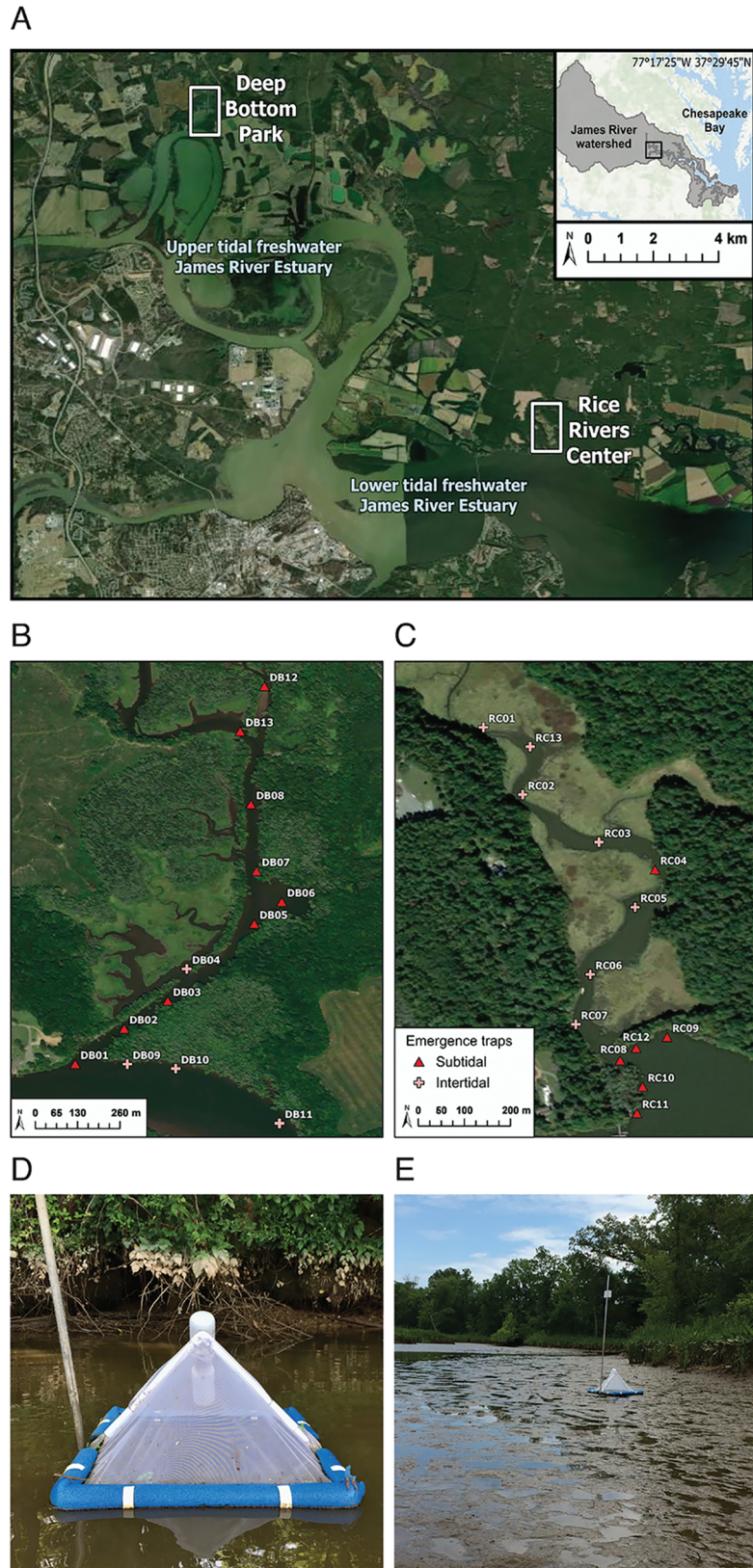


Figure 1. Locations of field sites along the tidal freshwater James River Estuary in Virginia, USA (A), and emergent insect trap placement along each tidal creek and adjacent estuarine shoreline in Deep Bottom Park (B) and the Rice Rivers Center (C). Traps placed along Bailey Creek in Deep Bottom Park were primarily subtidal (D), whereas traps placed along Kimages Creek in the Rice Rivers Center were primarily intertidal (E).

channel and less autochthonous production, whereas the lower tidal freshwater segment has a wider and shallower main channel with greater autochthonous production (Buka-veckas et al. 2011). High rates of sedimentation have led to muddy substrate in tidal creeks and along near-shore areas of the main channel. At low tide, the substrate is exposed on streambanks and shallow areas. The 2 sites differed in their placement within the tidal freshwater zone, and thus, in the degree of autochthonous resources available to aquatic insects. In the upper tidal freshwater zone, we sampled Bailey Creek and the estuarine shoreline at Deep Bottom Park (lat 37.40775, long -77.30346; hereafter, Deep Bottom) located in Henrico County, Virginia. In the lower tidal freshwater zone, we sampled Kimages Creek and the estuarine shoreline at the Virginia Commonwealth University Rice Rivers Center (lat 37.32748, long -77.20484; hereafter, Rice Center) in Charles City County, Virginia. These sites coincide with long-term monitoring of Prothonotary Warbler (*Protonotaria citrea* [Boddaert, 1783]) reproductive activity (Dodson et al. 2016), and this work is part of a broader study to assess the importance of aquatic prey in nestling diet (Rogers 2023).

Emergence sampling

At each site, we placed 4 emergence traps along the estuarine shoreline near the creek–estuary confluence (hereafter, shoreline) and 9 traps longitudinally along the creek, reaching 1050 to 1540 m from the confluence (Fig. 1B, C). We positioned all traps within 3 m of the shore (creek or estuarine) at high tide. Variation in water depth resulted in some traps resting on exposed substrate at low tide (intertidal), whereas others always remained over water (subtidal; Fig. 1D, E). Additionally, variation in streambank slope resulted in different tidal zone sampling patterns between sites. At Deep Bottom, we sampled Bailey Creek primarily in the subtidal zone and the shoreline primarily in the intertidal zone. At the Rice Center, we sampled Kimages Creek primarily in the intertidal zone and the shoreline primarily in the subtidal zone.

We continuously monitored aquatic insect emergence from 7 April to 8 November 2019, capturing all emergence events within the sampling period. We constructed floating emergence traps following Cadmus et al. (2016) with a few modifications to increase stability and allow for continuous field placement in a tidal system. We used white no-see-um mosquito netting (30.5 g/m²; Ripstop by the Roll, Durham, North Carolina) to capture small-bodied insects and reduce shading by the trap, which has been found to cause insect avoidance (Davies 1984). We tethered each trap to a 3-m metal conduit pole driven into the sediment to limit drift but allow for vertical movement with tidal changes. Traps covered a basal area of 0.4 m² and included a collection bottle containing 50 to 100 mL of 70% isopropanol to preserve insects between field collections. We accessed traps by canoe at high tide every 3 to 7 d (mean ± 1 SD: 5.1 ± 1.7 d)

to collect samples, which is within the range of collection intervals from other studies (e.g., Whiles and Goldowitz 2001, Martin-Creuzburg et al. 2017). To collect the most accurate estimate for large-bodied taxa known to avoid emergence traps (MacKenzie and Kaster 2004), we added to the sample large-bodied insects (i.e., Odonata, Ephemeroptera) that were found within the trap net but not yet in the collection bottle. We stored samples in 70% isopropanol until processing, which began after the 1st collection event and continued through August 2020.

We identified the following insects to order or suborder: mayflies (Ephemeroptera, suborders Schistonota and Pannota), stoneflies (Plecoptera), caddisflies (Trichoptera), dragonflies and damselflies (Odonata, suborders Anisoptera and Zygoptera), and aquatic flies (Diptera, suborder Nematocera) based on diagnostic morphological features (Thorpe and Covich 2001). We recorded the number of individuals in each order or suborder, dried the insects for 48 h at 60°C in a drying oven, then recorded dry mass (DM) to the nearest 0.1 mg for each sample after equilibration to room temperature. For samples containing many dipterans (>200 ind.; 47% of samples), we counted a representative sample of 100 ind. and pooled the remaining insects. We used the DM of the representative sample and the remaining pooled insects to estimate the total number of dipterans in the sample. We then standardized emergent DM and density estimates from each sample and taxon m⁻² d⁻¹ based on trap area and collection interval (mg DM m⁻² d⁻¹ and ind. m⁻² d⁻¹).

Quantifying annual emergence

We calculated annual emergent biomass and density for each taxon separately and for all taxa combined. We obtained annual estimates for each trap by summing the daily emergence estimates for all days a trap was active during the sampling period. Then, we calculated a single annual estimate of emergent biomass for our tidal freshwater system by averaging the trap annual estimates. Our annual estimates assume that emergence is negligible outside of the sampling period (9 November–6 April). We used the mean annual estimate to calculate average daily emergence rates for each taxon (i.e., a rate that assumes constant daily emergence throughout the sampling period). We compared our annual trap emergence rates with published estimates of aquatic insect emergence in nontidal systems (Table S1). From a search of the literature, we found 16 estimates from lentic systems (e.g., lakes and wetland ponds) and 20 estimates from lotic systems (e.g., streams and rivers; see references in Table S1), which captured a full emergence period for the aquatic insect community.

Temporal patterns in emergence pulses

We examined seasonality of taxon-specific emergence to characterize temporal changes in emergent insect availability for riparian consumers. We calculated the duration of the

emergence period for each taxon and the date by which 50% cumulative emergence was reached for all traps combined and for traps separated by tidal zone (intertidal vs subtidal), site (Rice Center vs Deep Bottom), and placement (creek vs shoreline). We also identified emergence pulses, which we defined as condensed timeframes during which the daily emergence rates 1) were greater than the mean daily rate derived from the annual rate and 2) reached a maximum $\geq 2 \times$ the mean daily rate. For calculation of emergence pulses, we used daily emergence rates that were averaged across all active traps regardless of spatial categories. We identified the timing of the entire emergence pulse as well as the timing and maximum rate of daily emergence during the pulse. We calculated the proportion of total emergent biomass contributed by the pulsed taxon and the proportion of the taxon's annual emergent biomass that emerged during the pulse.

To provide additional phenological context for emergence pulses, we compared emergence to rising spring water temperature. We plotted the ephemeropteran daily emergence rate at the Rice Center against daily mean water temperature using continuous (15 min) data collected at the Rice Center Research Pier (Bukaveckas et al. 2020). We summarized the variation in spring warming from 2009 to 2022 for temperatures coinciding with ephemeropteran emergence. Specifically, we plotted the day of year when the mean water temperature first reached 20.0°C.

Temporal and spatial variation in emergent biomass

To further assess temporal and spatial variation in the presence and amount of total emergent biomass and taxon-specific biomass, we used a 2-part model approach. This method is widely used for zero-inflated semicontinuous data such as ours, especially when potential differences in the variables explaining each part (i.e., presence and amount) are of interest (Liu et al. 2019). All models were GAMMs specified using the *mgcv* package (version 1.8.40; Wood 2017) in R to accommodate nonlinearity over time. Additionally, all models contained trap ID as a random effect to account for repeated measures at each trap. In the 1st part of the modeling approach, we modeled the probability of presence using a binomial distribution with a complementary log-log link, which performed better than a logit link for each taxon (Table S2; Zuur et al. 2009). In the 2nd part, we modeled the amount of emergent biomass for samples that had emergent biomass present using a lognormal distribution to account for the positively skewed, semicontinuous outcomes. We only modeled abundance for Diptera; however, we modeled presence and abundance for all other taxa.

Presence and abundance model sets followed the same process for construction. First, we accounted for nonlinearity in temporal variation by incorporating a smooth term for date classified as month (4–11) or day of year (102–312). We also included models with conditioning factors for the smooth term (i.e., tidal zone, site, placement) that may capture spatial variability in temporal emergence patterns. We

adequately sampled the entire emergence period for most taxa, resulting in emergence rates that were similarly low at the beginning and end of the sampling period. Thus, we considered time to be cyclical, and calculated the smooth term with circular cubic regression splines (option *bs* = “*cc*”) to constrain the predicted values at both ends. However, the emergence rate for Trichoptera was greater at the beginning than at the end of the sampling period. In this case, we calculated temporal variation with cubic regression splines (option *bs* = “*cr*”) to allow the beginning and end of the sampling period to differ.

Using the nonlinear temporal term with the best fit, we then added spatial variables as fixed effects in separate models, additive combinations, and interactions. Whereas the smooth terms test for differences in nonlinear patterns based on the conditioning factor, fixed effects test for differences in emergence between spatial variables over the entire sampling period (i.e., different intercepts). In addition to site, placement, and tidal zone, we included distance (to the nearest 10 m) from the confluence with the estuarine shoreline. Traps positioned at the shoreline had a distance of 0 m. Placement and distance were never included in the same model. We assessed model fit using residual plots, ranked models by Akaike's Information Criterion (AIC), and made inferences using top models ($\Delta\text{AIC} < 2$) that best fit the data (Burnham and Anderson 2002). Following implementation of GAMMs, we calculated the annual taxon-specific emergence rates separated by the spatial variables in the best-fitting model to estimate the difference in emergent biomass among spatial variables.

RESULTS

We collected 983 samples across sites but discarded 52 samples (5.3%) that were compromised by extensive trap damage, river water in the collection bottle, or decaying insect tissue from inadequate preservation. The remaining samples included 447 from the Rice Center and 484 from Deep Bottom. On average (mean ± 1 SE), 11.4 ± 0.3 traps provided data at each site on a given collection date, and individual traps sampled 190 ± 2 d or 88% of the 216-d sampling period. Overall, we collected 505,209 aquatic insects across 931 samples. Nematocera was present in 99.8% of samples, whereas Trichoptera only occurred in 52.9% of samples, Zygoptera in 31.2%, Anisoptera in 13.8%, Pannota in 11.9%, Schistonota in 9.8%, and Plecoptera in 2.1%. Dipterans constituted most total emergent biomass (86.0%), followed by Schistonota (5.5%), Zygoptera (3.9%), Anisoptera (3.1%), and Trichoptera (1.3%; Table 1). Insects identified as Pannota or Plecoptera individually made up <0.1% of total emergent biomass and, thus, were excluded from taxon-specific analyses.

For the 216-d emergence period, we calculated a mean annual emergence rate (± 1 SE) of 15.6 ± 2.0 g DM $\text{m}^{-2} \text{y}^{-1}$ (Table 1). We found that traps varied tenfold in annual emergent biomass, ranging from 4.5 to 43.0 g DM $\text{m}^{-2} \text{y}^{-1}$

Table 1. Emergent biomass and density estimates (mean \pm SE) for the 2019 sampling period (7 April–8 November 2019) averaged among traps deployed in tidal creeks and along the estuarine shoreline of the tidal freshwater James River Estuary, Virginia, USA, along with the percentage that each taxon contributed to the total. DM = dry mass.

Emergent taxon	Biomass (mg DM m ⁻² y ⁻¹)	% of total biomass	Density (ind. m ⁻² y ⁻¹)	% of total density
Diptera:Nematocera	13,449 \pm 1765	86.6	49,138 \pm 6687 (99.0%)	99.0
Ephemeroptera:Schistonota	866 \pm 308	5.5	30 \pm 10 (0.1%)	0.1
Ephemeroptera:Pannota	17 \pm 5	0.1	46 \pm 19 (0.1%)	0.1
Odonata:Anisoptera	480 \pm 90	3.1	17 \pm 3 (<0.1%)	<0.1
Odonata:Zygoptera	610 \pm 196	3.9	216 \pm 73 (0.4%)	0.4
Plecoptera	8 \pm 3	<0.1	3 \pm 1 (<0.1%)	<0.1
Trichoptera	206 \pm 33	1.3	209 \pm 42 (0.4%)	0.4
Total	15,636 \pm 1952	–	49,659 \pm 6704	–

with a median of 15.3 g DM m⁻² y⁻¹ (see Table S1 for trap estimates). Despite this variation, the tidal freshwaters sampled in this study had greater aquatic insect emergence than most published estimates from nontidal systems (Fig. 2). Nontidal lentic emergence estimates ranged from 0.1 to 2.4 g DM m⁻² y⁻¹, with a median of 1.1 g DM m⁻² y⁻¹. Nontidal lotic emergence estimates used in this comparison ranged from 0.9 to 174.0 g DM m⁻² y⁻¹, with a median of 4.2 g DM m⁻² y⁻¹. Only 3 of these studies from lotic systems reported emergence estimates greater than those presented here (Jackson and Fisher 1986, Rolauffs et al. 2001, Moyo et al. 2017).

Temporal variation in emergence

Seasonal patterns in emergence The amount of total and taxon-specific emergent biomass varied seasonally (Fig. 3A,

B). Nematocera, Trichoptera, and Zygoptera emerged throughout the entire sampling period (216 d), Anisoptera emerged for 173 d, and Schistonota had the shortest emergence duration (123 d) when all samples were considered collectively. However, emergence durations were often shorter when samples were separated spatially by tidal zone, site, or trap placement (Table 2). Taxon-specific emergence was generally lowest at the beginning and end of the sampling period, with a peak during the spring or summer (Fig. 3A). Trichoptera was an exception, having the greatest emergence estimates at the beginning of sampling. Because of our broad taxonomic grouping that combined multiple species, the amount of emergent biomass was jointly influenced by the number of insects emerging (ind. m⁻² d⁻¹) and the size of the insects emerging (mg DM/ind.; Figs S1–S5).

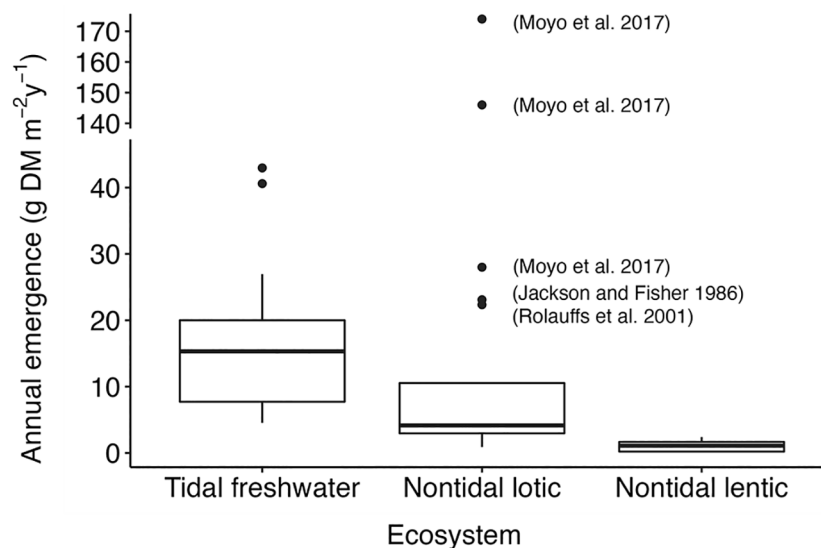


Figure 2. Comparison of annual emergence rates for tidal freshwaters from the present study with published estimates for nontidal lotic (streams, rivers) and lentic (lakes, wetland ponds) ecosystems. References are listed for lotic estimates greater than those calculated herein. Underlying data used to create figure are provided in Table S1. Boxes encompasses the 1st and 3rd quartiles, horizontal lines are the medians, whiskers extend to values 1.5 \times the interquartile range, and values beyond the whiskers are plotted individually.

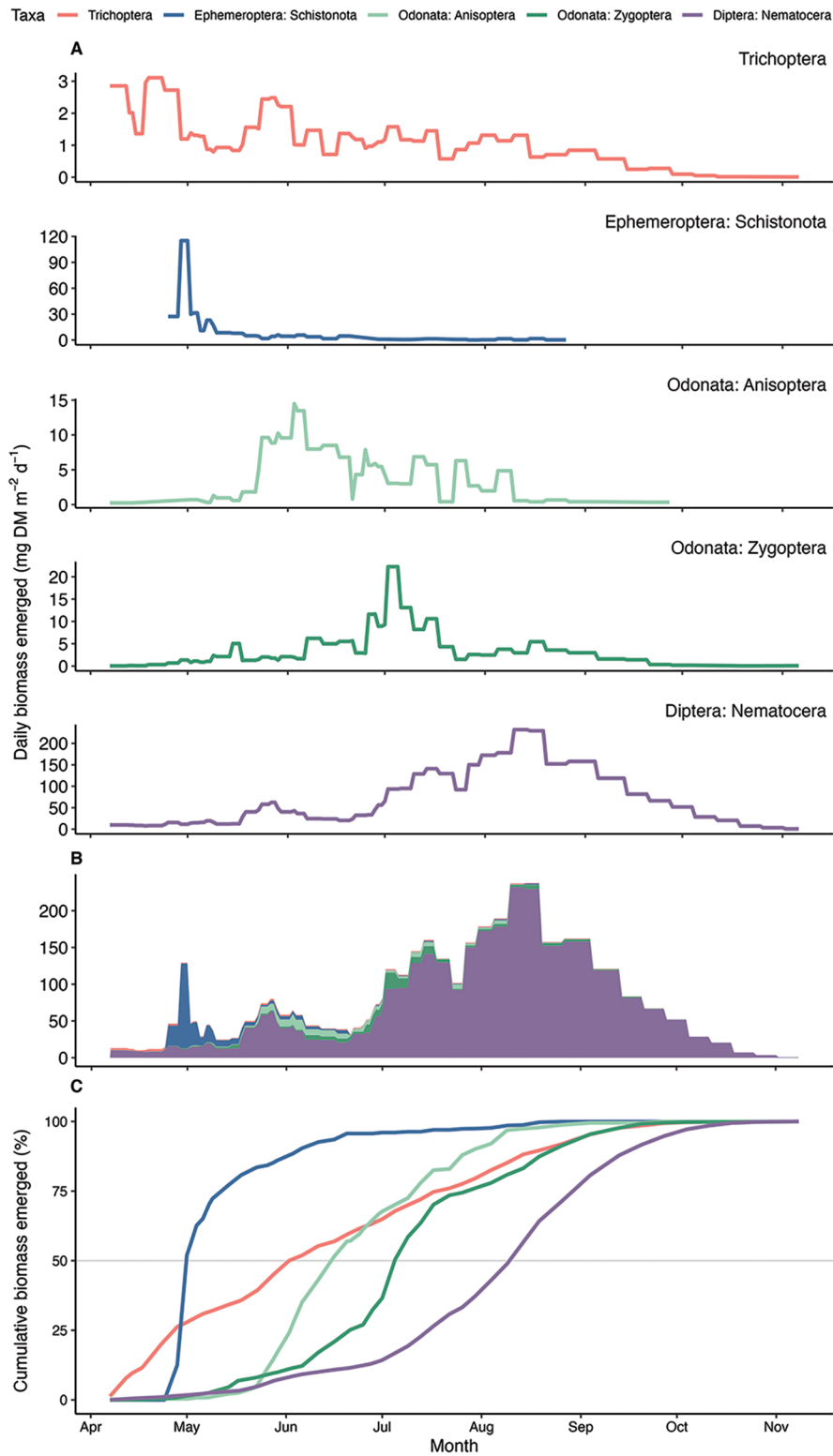


Figure 3. Temporal variation in daily emergence estimates (mg DM m⁻² d⁻¹) for each taxon representing ≥1% of total emergent biomass (A) and combined taxa (B), as well as the cumulative emergence of those taxa throughout the 2019 sampling period (7 April–8 November) in the James River Estuary in Virginia, USA (C). The gray line in Panel C corresponds to 50% cumulative emergence.

Table 2. Emergence duration (no. d) and timing of 50% cumulative emergent biomass for each taxon by tidal zone, sampling site, and trap placement. A duration of 216 d corresponds to the entire sampling period. * denotes taxa for which the most-supported generalized additive mixed models detected differences in presence or abundance (see Table S9 for model outputs).

Spatial variable	Taxon	Duration (d)	50%	Duration (d)	50%
Tidal zone		Intertidal		Subtidal	
	Diptera:Nematocera*	7 Apr–8 Nov (216)	25 Aug	7 Apr–8 Nov (216)	6 Aug
	Ephemeroptera:Schistonota	25 Apr–19 Aug (116)	1 May	Apr 25 – Aug 26 (123)	1 May
	Trichoptera*	7 Apr–8 Nov (216)	14 Jul	Apr 7 – Oct 18 (194)	26 May
	Odonata:Anisoptera	2 May–27 Sep (148)	18 Jun	Apr 7 – Sep 4 (150)	11 Jun
	Odonata:Zygoptera	19 Apr–8 Nov (203)	6 Jul	Apr 7 – Sep 13 (159)	5 Jul
Site		Deep Bottom		Rice Center	
	Diptera:Nematocera	7 Apr–8 Nov (216)	9 Aug	7 Apr–8 Nov (216)	12 Aug
	Ephemeroptera:Schistonota*	3 May–26 Aug (116)	20 May	25 Apr–19 Aug (117)	30 Apr
	Trichoptera*	7 Apr–8 Nov (216)	23 May	7 Apr–11 Oct (188)	3 July
	Odonata:Anisoptera*	7 May–4 Sep (121)	17 Jun	7 Apr–27 Sep (174)	10 Jun
	Odonata:Zygoptera*	13 Apr–4 Sep (145)	13 Jun	7 Apr–8 Nov (216)	7 Jul
Trap placement		Shoreline		Creek	
	Diptera:Nematocera	7 Apr–8 Nov (216)	11 Aug	7 Apr–8 Nov (216)	10 Aug
	Ephemeroptera:Schistonota*	3 May–14 Aug (103)	23 May	25 Apr–26 Aug (123)	1 May
	Trichoptera*	19 Apr–8 Nov (203)	26 Jun	7 Apr–18 Oct (194)	31 May
	Odonata:Anisoptera*	18 May–4 Sep (109)	16 Jun	7 Apr–27 Sep (173)	16 Jun
	Odonata:Zygoptera*	25 Apr–4 Sep (132)	14 Jun	7 Apr–8 Nov (216)	6 Jul

The greatest contributors of biomass, Nematocera and Schistonota, drove the overall seasonal pattern. Total daily emergence for all taxa was $13.8 \text{ mg DM m}^{-2} \text{ d}^{-1}$ in early April when sampling began, returned to these levels in mid-October, and was lowest in early November when sampling ended ($0.8 \text{ mg DM m}^{-2} \text{ d}^{-1}$) (Fig. 3B). Multiple emergence peaks occurred during the sampling period. The 1st peak at the beginning of May was composed primarily of Schistonota biomass, whereas peaks in June to August were composed mostly of Nematocera biomass. The largest peak occurred mid-August when total emergent biomass reached $237.9 \text{ mg DM m}^{-2} \text{ d}^{-1}$.

Phenological variation in taxon-specific emergent biomass led to seasonally changing taxonomic proportions of total emergent biomass. The sequence of taxa reaching 50% of their cumulative emergent biomass began with Schistonota (1 May), followed by Trichoptera (3 June), Anisoptera (16 June), Zygoptera (5 July), and Nematocera (10 August) (Fig. 3C). As with emergence durations, the 50% cumulative emergence date differed when separated spatially by tidal zone, site, or trap placement (Table 2, Fig. S6). Peak taxon-specific emergence occurred during an emergence pulse when the daily emergence rate was greater than the mean and the taxon contributed a greater proportion to the total emergent biomass than during the rest of the sampling period. Among taxa, these pulses varied in duration from 29 to 83 d (13.4–38.4% of the sampling period). The pulsed taxon represented 4.3 to 94.6% of all

emerging biomass during the pulse and 52.6 to 83.8% of the taxon's annual biomass emerging during the pulse (Table 3). Schistonota mayflies had the greatest synchrony in peak emergence (i.e., the greatest proportion of annual biomass emerging over the shortest peak duration).

Temperature and emergence Over the sampling period, daily mean water temperature at the Rice Center ranged from 13.0 to 32.7°C (Fig. 4A). Mean water temperature reached its maximum measurement on 20 July, indicating that 105 d (48%) of our sampling period captured rising spring temperatures. Except for Nematocera, taxa reached peak emergence before maximum values for mean temperature were reached. Schistonota emergence began when mean water temperature reached 20.0°C, then peaked during the following collection interval (29 April–1 May) when mean water temperatures was 19.0 to 21.3°C (Fig. 4B). Although our data did not show a spring trend for mean water temperature reaching 20.0°C between 2009 to 2022, there was considerable inter-annual variation for this temperature benchmark (Fig. 4C). Mean water temperature first reached 20.0°C on 24 April 14 and ranged from 22 March to 15 May.

Spatial and temporal variables explaining emergence variation

The most-supported GAMMs identified different variables as most important for explaining variation in emergent insect presence vs amount of biomass. For each taxon

Table 3. Summary of peak emergence pulses, including pulse timing and duration, the amount of taxon-specific biomass emerging during the pulse, the % of the total emergent biomass constituted by the pulsed taxon, and the % of the taxon's annual estimated biomass that emerged during the pulse. DM = dry mass.

Emergent taxon	Emergence pulse duration (d)	Biomass (mg DM/m ²)	% of total pulse emergence	% of taxon annual emergence
Diptera:Nematocera	1 Jul–27 Sep (83)	12,174	94.6	80.9
Ephemeroptera:Schistonota	25 Apr–24 May (29)	734	49.5	83.8
Trichoptera	7 Apr– 11 Jun (66)	115	4.3	52.6
Odonata:Anisoptera	23 May–17 Jul (55)	393	9.1	78.2
Odonata:Zygoptera	7 Jun–22 Jul (45)	396	9.9	61.3

modeled with GAMMs, temporal variation in presence was best explained by month conditioned on placement (i.e., creek or shoreline), whereas amount of biomass was best explained by day of year conditioned on tidal zone (for total biomass and Nematocera) or site (Trichoptera, Schistonota, Anisoptera, and Zygoptera; Tables S3–S8).

Deep Bottom vs Rice Center emergence Among presence models, site was found in the most-supported model for Zygoptera but was not included in the top model for any other taxon. The most supported model for Zygoptera contained a site \times placement interaction as a fixed effect (Tables S8, S9). Zygopterans were more likely to be present at the Rice Center than at Deep Bottom, although the extent of the difference varied between creek and shoreline traps (Fig. 5). On average, the Rice Center was 2.1 \times more likely than Deep Bottom to have zygopterans emerging at the shoreline and 7.1 \times more likely to have zygopterans emerging within the tidal creek. The exclusion of site in other top presence models suggests that site did not explain substantial spatial variability in presence of the other aquatic insects we analyzed.

Total emergent biomass and Nematocera emergent biomass were similar between Deep Bottom and the Rice Center; however, other taxa had site as a conditioning factor for the smooth term (Schistonota, Trichoptera, Anisoptera, and Zygoptera) and as a fixed effect (Anisoptera, Zygoptera, and Trichoptera), showing that site influenced the temporal pattern of emergent biomass as well as the amount of biomass emerging for these taxa (Table S9). Deep Bottom had more temporal variation and a greater peak in Anisoptera biomass, whereas the Rice Center had greater temporal variation and a greater peak in Zygoptera biomass (Fig. 6A, B). Anisopterans emerging at Deep Bottom also had a larger mean DM (54.8 ± 3.9 mg DM/ind.) than anisopterans at the Rice Center (17.0 ± 2.1 mg DM/ind.; Fig. S4). Over the sampling period, this variation resulted in 1.8 \times more Anisoptera biomass emerging from Deep Bottom and 18.3 \times more Zygoptera biomass emerging from the Rice Center. Both odonates had longer emergence durations at the Rice Center than at Deep Bottom; however, only Zygoptera exhibited a later 50% cumulative emergence at the Rice Center (Table 2).

An interaction between site and trap placement was supported for both taxa.

Site differences were more subtle for annual Trichoptera biomass (Fig. 7A), although 1.6 \times more biomass emerged from Deep Bottom than the Rice Center. Trichopterans emerged during the entire sampling period at Deep Bottom but were not detected in Rice Center samples after mid-October (Table 2). Despite the longer emergence period, the site differences in the temporal emergence patterns for Trichoptera resulted in 50% cumulative emergence that was 41 d earlier at Deep Bottom. In addition, in 1 competing model, there was an interaction between site and distance (Table S9). At both sites, emergent biomass increased as distance from the confluence increased; however, the variability in biomass emerging across distances was greater at Deep Bottom than at the Rice Center. For instance, at peak emergence, biomass emerging at the confluence was 0.6 mg DM m⁻² d⁻¹ greater than biomass emerging at 1050 m at Deep Bottom but only 0.1 mg DM m⁻² d⁻¹ greater at the Rice Center.

The pattern of Schistonota temporal variation showed a greater peak of emergent biomass at the Rice Center than at Deep Bottom (Fig. 7B), resulting in biomass estimates over the sampling period that were 3.3 \times greater at the Rice Center (Table 4). Emergence duration was similar between sites; however, the greater emergence peak at the Rice Center also resulted in 50% cumulative emergence that was 20 d earlier at that site. At both sites, the amount of Schistonota biomass also decreased as distance from the confluence with the shoreline increased; however, peak ephemeropteran emergence at the Rice Center was greater than at Deep Bottom at all distances (Fig. 7B). For instance, more ephemeropteran biomass emerged from the farthest distance (1050 m) at the Rice Center (8.1 mg DM m⁻² d⁻¹) than from the confluence at Deep Bottom (5.3 mg DM m⁻² d⁻¹).

Tidal creek vs estuarine shoreline emergence Temporal variation was conditioned on trap placement for all taxa modeled for presence (Schistonota, Trichoptera, Anisoptera, and Zygoptera), showing that creek and shoreline traps had different patterns of emergence (Table S9). Both

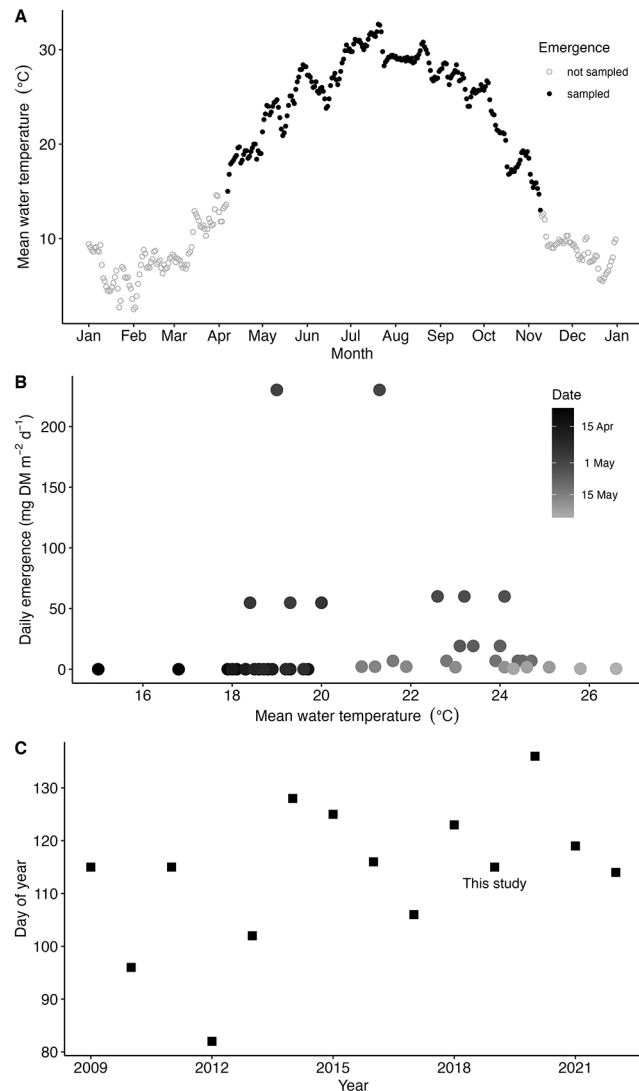


Figure 4. Daily mean water temperature at the Rice Center, James River Estuary, Virginia, USA, throughout 2019 (insect emergence was sampled 7 April–8 November 2019) (A). Biomass of Ephemeroptera: *Schistonota* emergence in relation to daily mean water temperature during rising spring temperatures (7 April–26 May are shown) (B). Day of year when daily mean water temperature first reached 20°C (C).

trap placements had an early season occurrence peak in May and mid-June; however, emergent taxa were present with the same or greater probability within the creek than at the shoreline (Fig. 5). The magnitude of this difference was taxon specific. *Schistonota* had a peak occurrence probability that was 2.1× greater in the creek (0.20 vs 0.10), and *Zygoptera* had occurrence probabilities 1.5 to 3.5× greater in the creek, whereas *Trichoptera* and *Anisoptera* had roughly similar peak occurrence probabilities. Early season presence probabilities also tended to peak earlier in the creek than at the shoreline: *Schistonota* peaked 4 d earlier, *Anisoptera* peaked 17 d earlier, and

Trichoptera peaked 22 d earlier. Additionally, in the creek, all taxa had a 2nd peak in occurrence probability during late July that was mostly absent at the shoreline (Fig. 5). The difference between creek and shoreline presence during this late-season peak was also taxon specific, with the greatest differences for *Zygoptera* (0.96 vs 0.12 at the Rice Center; 0.24 vs 0.05 at Deep Bottom).

Creek or shoreline placement also explained variation in the amount of emergent biomass for *Anisoptera* and *Zygoptera*. As fixed effects in top models for both odonates, creek or shoreline placement interacted with site (Fig. 6A, B). Over the sampling period, *Zygoptera* biomass emerging from Kimages Creek at the Rice Center was 23.4 to 34.9× greater than from Bailey Creek at Deep Bottom or the shoreline at either site. *Anisoptera* biomass emerging from the shoreline at Deep Bottom was 3.5 to 4.3× greater than from the shoreline at the Rice Center or the creek at either site (Table 4). Both odonates had longer emergence durations in the creek than at the shoreline; however, only *Zygoptera* had a later 50% cumulative emergence at the shoreline (Table 2).

Variation in *Trichoptera* and *Schistonota* biomass was better explained by distance from the confluence than by trap placement (Fig. 7A, B). *Schistonota* mayflies decreased in abundance as distance from the confluence increased, whereas trichopterans increased in abundance at farther distances. Both taxa had later 50% cumulative emergence at the shoreline than in the creek (Table 2).

Subtidal vs intertidal emergence Tidal zone appeared in the top models explaining variation in the presence and amount of *Trichoptera* biomass (Table S9). On average, *Trichoptera* was 1.9× more likely to be present in the subtidal zone than the intertidal zone. *Trichoptera* annual biomass estimates were 18.7× greater in the subtidal zone at Deep Bottom, whereas *Trichoptera* emergent biomass at the Rice Center was similar between tidal zones (Table 4). *Trichoptera* emerged during the entire sampling period in the intertidal zone but was not detected in subtidal samples after mid-October (Table 2). *Trichoptera* also reached 50% cumulative emergence earlier in the intertidal zone.

Additionally, tidal zone explained variation in the amount of *Nematocera* biomass and total emergent biomass (Table S9). More *Nematocera* and total biomass emerged from the subtidal zone than from the intertidal zone, particularly during times of peak emergence (Figs 8A, B). These differences resulted in total annual emergent biomass estimates that were 1.9× greater in the subtidal zone and *Nematocera* estimates that were 2.3× greater in the subtidal zone. The temporal patterns in emergent biomass were similar between total and dipteran biomass (Fig. 8A, B) because *Nematocera* made up most of the total emergent biomass (73.5% of intertidal biomass and 90.9% of subtidal biomass). Although dipterans emerged from both tidal zones throughout the entire emergence period, *Nematocera* reached 50%

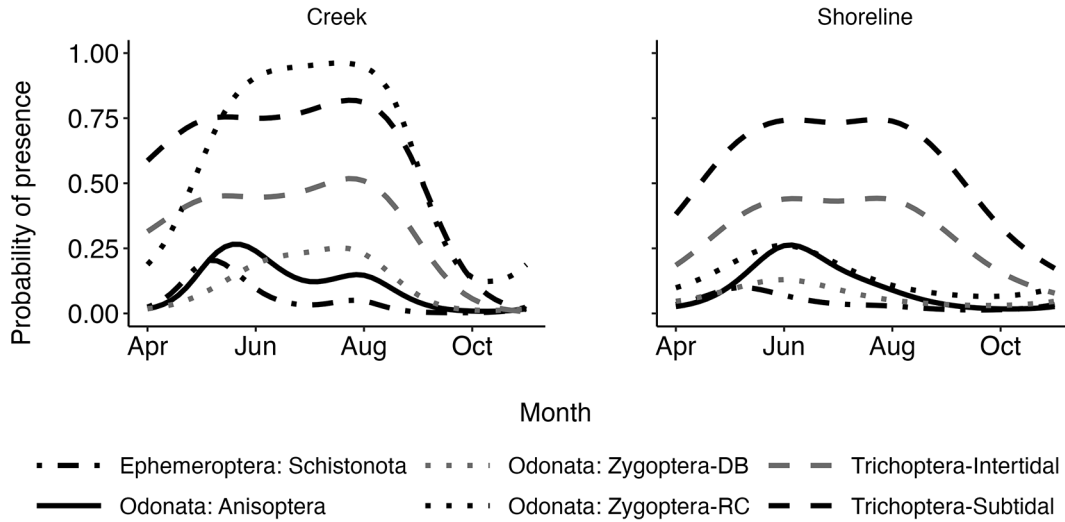


Figure 5. Fitted values depicting variation in the presence of taxon-specific emergence according to variables appearing in the top binomial generalized additive mixed models. For all taxa, temporal patterns are separated by creek or shoreline trap placement. Taxa are included multiple times when trap placement occurred in an interaction term with site or tidal zone. DB = Deep Bottom, RC = Rice Center.

cumulative emergence 19 d earlier in the subtidal zone (Table 2).

DISCUSSION

In this study, we estimated aquatic insect emergence in tidal freshwater creeks and estuarine shoreline of the James

River Estuary to identify temporal and spatial variation in emergence and compare our results with those from nontidal systems. The tidal freshwater segment of the James River Estuary has been well characterized regarding sources of organic matter supporting aquatic food webs (Wood et al. 2016, Bukaveckas 2022), though we know of no prior studies

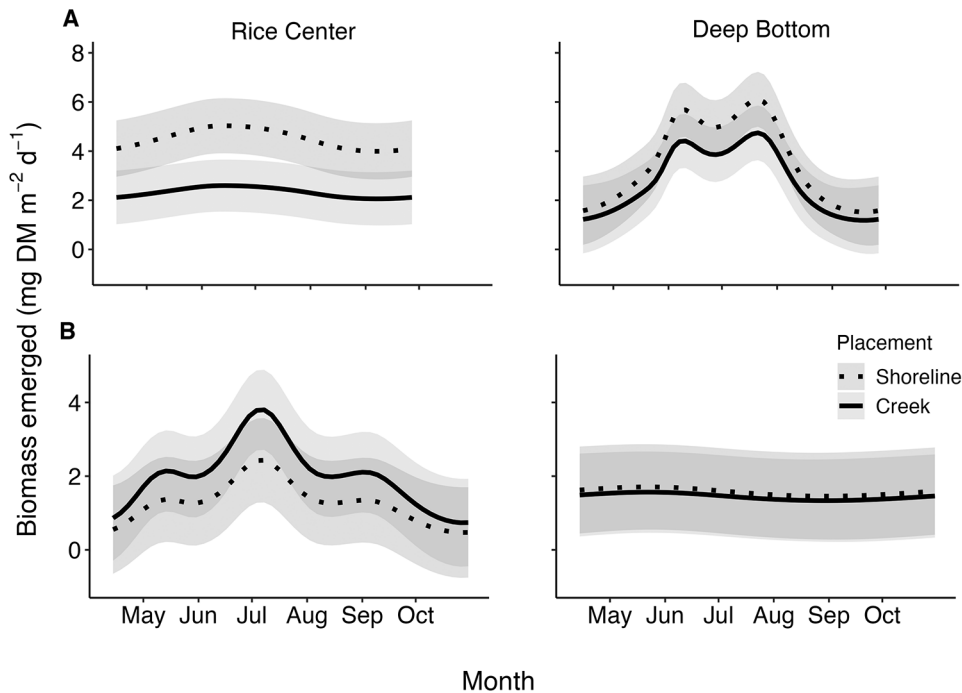


Figure 6. Fitted values (± 1 SE) depicting variation in the amount of Odonata:Anisoptera (A) and Odonata:Zygoptera (B) emergent biomass ($\text{mg dry mass [DM]} \text{m}^{-2} \text{d}^{-1}$) between trap placements along the tidal creek and along the estuarine shoreline at each sampled site. Panels are separated by variables according to the most-supported taxon-specific lognormal generalized additive mixed models.

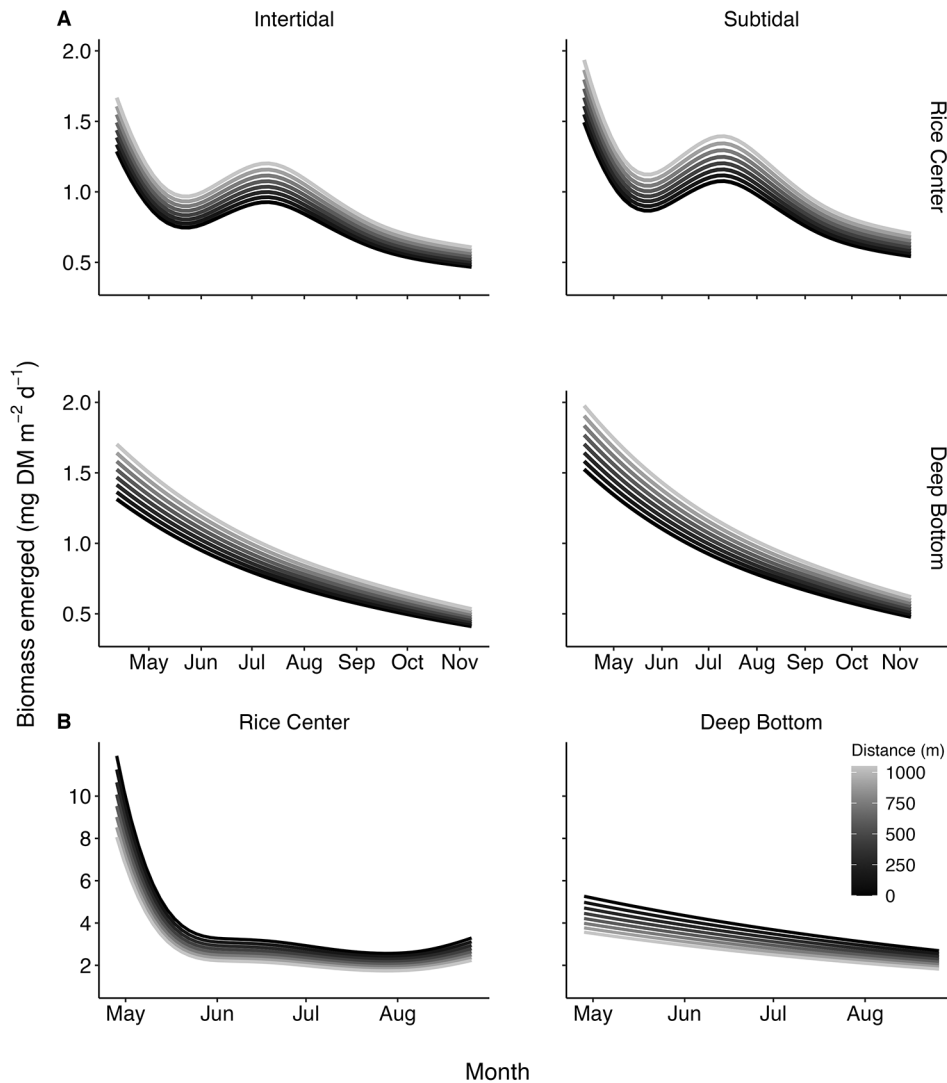


Figure 7. Fitted values depicting variation in the amount of Trichoptera (A) and Ephemeroptera:Schistonota (B) emergent biomass (mg dry mass [DM] m⁻² d⁻¹) as distance from the confluence with the shoreline increases. Panels are separated by tidal zone (A) and site (B) according to the most-supported taxon-specific lognormal generalized additive mixed models.

that have estimated aquatic insect production or emergence in this system. To our knowledge, this is also the 1st study to estimate annual rates of aquatic insect emergence from tidal freshwaters by sampling continuously over the emergence period. Other studies in tidal freshwaters have either only documented macroinvertebrate densities (e.g., Strayer and Smith 2000) or only sampled emergence during the early summer peak (Ramirez 2008, Johnson and Simenstad 2015). Our estimates of aquatic insect emergence in tidal freshwaters were greater than most estimates from nontidal systems. Most emergent biomass was attributed to Diptera; however, Ephemeroptera, Odonata, and Trichoptera were also present throughout the sampling period. Emergence was temporally and spatially variable in taxon-specific ways,

which leads to changes in prey availability for riparian consumers foraging on seasonal pulses of emergent insects.

Estimates of aquatic insect biomass emerging from tidal freshwater habitats along the James River Estuary are among the highest published to date

We found that total insect emergent biomass in the tidal freshwater habitats sampled in this study was greater than most published estimates of total emergence for nontidal lentic and lotic systems (Table S1 and references therein). Greater emergence estimates than those presented here were reported for only 3 other lotic systems, including a subtropical river (28–174 g DM m⁻² y⁻¹; Moyo et al. 2017), a

Table 4. Annual emergent biomass and density estimates (mean ± 1 SE) for the 2019 sampling period averaged among traps separated by spatial variables best supported by generalized additive mixed models, including site (Deep Bottom or Rice Center), tidal zone (subtidal or intertidal), and placement (creek or shoreline). DM = dry mass.

Emergent taxon	Intrasite variation	Biomass (mg DM m ⁻² y ⁻¹)		Density (ind. m ⁻² y ⁻¹)	
		Rice Center	Deep Bottom	Rice Center	Deep Bottom
Total emergent biomass	Subtidal	19,483 \pm 2854		62,668 \pm 9761	
	Intertidal	10,392 \pm 1482		31,920 \pm 5398	
Diptera:Nematocera	Subtidal	17,707 \pm 2390		62,244 \pm 9699	
	Intertidal	7642 \pm 1287		31,266 \pm 5409	
Trichoptera	Subtidal	161 \pm 31	356 \pm 62	219 \pm 72	306 \pm 95
	Intertidal	160 \pm 27	19 \pm 10	185 \pm 47	20 \pm 5
Odonata:Anisoptera	Creek	335 \pm 61	306 \pm 112	32 \pm 5	7 \pm 2
	Shoreline	373 \pm 211	1306 \pm 166	6 \pm 3	21 \pm 3
Odonata:Zygoptera	Creek	1639 \pm 1139	70 \pm 24	597 \pm 142	16 \pm 5
	Shoreline	70 \pm 15	47 \pm 14	15 \pm 3	9 \pm 2
Ephemeroptera:Schistonota	–	1329 \pm 577	403 \pm 165	45 \pm 18	15 \pm 6

beaver dam (18.0–26.7 g DM m⁻² y⁻¹; Rolauffs et al. 2001), and an intermittent desert stream (23.1 g DM m⁻² y⁻¹; Jackson and Fisher 1986). Collectively, the high emergence rates in these nontidal systems were explained by high primary productivity and frequent disturbance as well as high amounts of suspended organic matter and organic debris providing food and habitat for aquatic insects (Jackson and Fisher 1986, Rolauffs et al. 2001, Moyo et al. 2017).

Similar conditions in the James River Estuary tidal freshwater segment may account for the high emergence rates reported in this study. Prior work has shown that the tidal freshwater segment receives considerable organic matter inputs from both autochthonous and allochthonous sources (Wood et al. 2016, Bukaveckas 2022). Phytoplankton production in this segment of the estuary exceeds that of the adjacent riverine and oligohaline segments (Tassone and Bukaveckas 2019). Phytoplankton benefit from favorable light conditions at the transition from a deep, narrow riverine channel to a broader, shallower estuarine channel, which increases the photic-depth-to-mixing-depth ratio (Bukaveckas et al. 2011). Additionally, the transition from unidirectional (riverine) to bidirectional (tidal) flow reduces the advective loss of phytoplankton (Qin and Shen 2017). Active mixing by tidal forces acts to maintain particulate matter in suspension (Diaz 1994), which may be beneficial for filter-feeding aquatic insects. The tidal freshwater segment of the James River Estuary also retains a large proportion of allochthonous organic matter inputs because of settling of this material at the river–estuarine transition (Bukaveckas et al. 2019, Bukaveckas 2022). Stable isotope analysis has shown that benthic organic matter is predominantly of terrestrial origin and that a variety of consumers, including benthic omnivores (e.g., adult Gizzard Shad, juvenile catfish) and benthic filter feeders (e.g., *Rangia*

spp.), carry a strongly terrestrial signal (Wood et al. 2016). Our findings of high rates of aquatic insect emergence support this understanding of tidal freshwaters as exceptionally productive habitats.

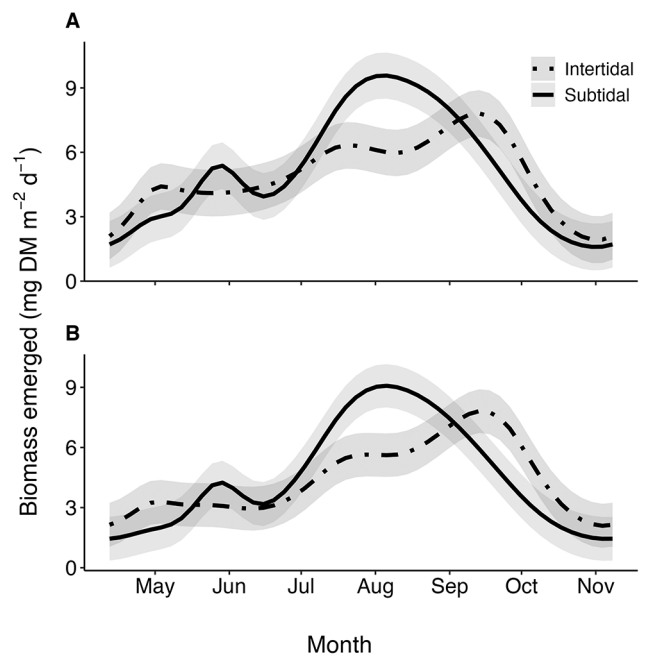


Figure 8. Fitted values (± 1 SE) depicting variation in the amount of total (A) and Diptera:Nematocera (B) emergent biomass (mg dry mass [DM] m⁻² d⁻¹) between subtidal and intertidal zones. Panels are separated according to the most-supported lognormal generalized additive mixed models.

Emergent biomass was composed mostly of dipterans

Diptera was the predominant insect order emerging at sites sampled in this study, constituting most of the biomass and density. It is common for Diptera, most often chironomids, to have the greatest density among aquatic macroinvertebrates in fluvially and tidally dominated estuarine freshwaters (Diaz 1994, Strayer and Smith 2000, Williams and Hamm 2002, Hoffman et al. 2008, Johnson and Simenstad 2015). Diptera is also the primary emergent insect order present under physically stressful conditions (Ward 1992), such as high salinity (MacKenzie 2005) or low dissolved O₂ in deeper waters (Martin-Creuzburg et al. 2017). In tidal systems, physical stress also includes the risk of desiccation and encountering temperature extremes with regular exposure (Ward 1992). Here, we found that dipteran emergence was greater in the subtidal zone where the risk of exposure is lower than the intertidal zone, which is consistent with previous work in the Hudson River Estuary showing lower chironomid macroinvertebrate density in the intertidal zone (Strayer and Smith 2000). Greater subtidal estimates may suggest that dipterans migrate with the current to avoid exposure, although species likely have a range of exposure tolerance (Brusven et al. 1974). Lower dipteran biomass emerging from the intertidal zone may also result from the presence of riparian predators, such as ground-dwelling riparian beetles and spiders, which feed on insects before their emergent stage (Paetzold and Tockner 2005).

With much of the emergent biomass dominated by Diptera, seasonal variation and peaks in total emergent biomass, as well as spatial variation by tidal zone, reflected dipteran emergence. We observed emergence peaks in May to June, but the largest peak occurred in August when the density and mean size of dipterans were greatest. These peaks may align with changes in chironomid assemblage composition because chironomid species emerge sequentially throughout the spring and summer, with larger-bodied species emerging later from warmer waters (Stagliano et al. 1998, Jonsson et al. 2015). Our observations of peak timing showed similarities with emergence phenology in other well-mixed systems, including the Columbia River Estuary in Oregon and Washington, USA, (Ramirez 2008) and a river delta wetland along Lake Michigan, Wisconsin, USA, where seiches replace lunar tides (MacKenzie and Kaster 2004). Compared with nontidal systems that reported a gradual decline in dipteran emergent biomass following a spring peak (e.g., Nakano and Murakami 2001, Twining et al. 2018), tidal freshwaters containing these late season chironomids may supply important subsidies to riparian consumers during the summer and early autumn. For example, riparian areas along United States east coast tidal rivers have been documented as important stop-over sites for migratory birds (Buler and Dawson 2014), and Great Lakes freshwater estuaries are used extensively by migrating waterfowl (Prince et al. 1992). Large densities of emerging chironomids may be refueling these migrants,

and future research could quantify consumption of chironomids within these stopover hotspots to determine the value of tidal freshwaters to migrating species.

Emergence of Ephemeroptera, Odonata, and Trichoptera

Ephemeroptera accounted for 5.6% of the total biomass emerging from tidal creeks and estuarine shoreline over the sampling period but up to ½ of the total emergent biomass during its spring emergence pulse. Most ephemeropteran biomass was composed of *Hexagenia* spp., large mayflies adapted to burrowing in the muddy substrate (Ward 1992). This finding contrasts with tidal freshwaters containing coarse-grained substrate where smaller mayflies adapted to swimming and crawling predominate (Williams and Williams 1998a, b). We found a greater emergence pulse of mayfly biomass at the Rice Center compared with Deep Bottom; however, large mayfly pulses have been reported at Deep Bottom in other years (Dodson et al. 2016), indicating that the degree of interannual variation in mayfly emergence may be substantial in tidal freshwaters. The negative relationship we found between the amount of biomass and distance from the estuarine shoreline reflected findings from MacKenzie and Kaster (2004). Placement within the creek may have provided slower water velocity compared with the estuarine shoreline (SLR, personal observation), leading to greater presence of mayflies in the creek, whereas distances close to the shoreline may have supported a greater abundance of mayflies because of adequate flow supplying suspended particulate matter.

Odonata also contributed an appreciable amount of biomass (7%) to annual emergence with some variation between and within sites. This finding contrasts with nontidal lotic systems where emergent insect communities excluded odonates (e.g., Jackson and Fisher 1986, Rolauuffs et al. 2001, Raitif et al. 2018). Many odonates burrow in fine sediment and tend to have greater abundance and diversity when well-developed aquatic vegetation is present to aid emergence (Ward 1992). Previous research has indicated a tendency for odonates to avoid emergence traps (MacKenzie and Kaster 2004). In addition, differences resulting from emergence behaviors have been found in taxonomic representation between emergence traps positioned over open water and those positioned over the streambank (Malison et al. 2010). For example, taxa that emerge by crawling onto the streambank or emergent vegetation are less likely to be represented in traps positioned over open water. Although our Odonata emergence estimates are on par with mark-recapture collections from nontidal wetlands (Gladyshev et al. 2011), our sampling of open water habitats with emergence traps and Odonata emergence behavior likely affected our estimates. For example, Kimages Creek at the Rice Center was mostly sampled at intertidal locations and had the most emergent vegetation among sampling sites and trap locations, likely resulting in

the greatest densities of damselflies and dragonflies. We attempted to account for avoidance behavior by adding to our samples any individuals found in the traps but outside of the collection bottle. However, we also observed more dragonfly exuviae inside traps than trapped individuals for several samples ($n = 16$), most of which were in intertidal creek traps at the Rice Center. Although this observation suggests we underestimated Odonata emergence, it also presents the possibility that odonates were attracted to the traps in intertidal habitats as structures to aid emergence.

Other large-bodied insect orders accounted for a small proportion of total emergence estimates. For example, Trichoptera was consistently present in $\sim 1/2$ of our emergence samples but constituted $<2\%$ of the biomass. The slightly higher contribution of Trichoptera at Deep Bottom than the Rice Center may be explained by the submerged woody debris present at this site, which provided opportunities for colonization by trichopterans (Ward 1992, Cheney et al. 2019). Our estimates of trichopteran emergent biomass from tidal freshwaters exceeded those from a nontidal wetland ($0.06 \text{ g DM m}^{-2} \text{ y}^{-1}$; MacKenzie and Kaster 2004) but were lower than those from lotic streams, where trichopterans are best represented ($2.05\text{--}3.57 \text{ g DM m}^{-2} \text{ y}^{-1}$; Jackson and Fisher 1986, Raitif et al. 2018). Both sites had negligible emergent biomass from Plecoptera, which were only collected during a short period (22–57 d) at the beginning of the sampling period. The fine substrate may have limited the abundance of plecopterans in these tidal freshwaters because few plecopteran species occur in silty habitats but instead prefer stone or cobble substrates (Ward 1992, Cheney et al. 2019). It is also possible that our traps underrepresented plecopteran emergence estimates. Plecopterans emerge by crawling out of the streambank, rather than through the water column; therefore, emergent traps may fail to capture accurate plecopteran emergence rates (Malison et al. 2010).

Pulsed emergence changes the menu for riparian consumers

Continuous sampling allowed us to capture pulsed events of several large-bodied taxa, during which these taxa represented a greater proportion of daily emergence than indicated by annual estimates. We found the timing of these emergence pulses to be sequential, agreeing with previous observations that aquatic insect composition changes predictably with increasing water temperature throughout the spring and summer (Ward 1992). In some cases, the emergence pulse was highly synchronous, with most annual biomass emerging during a short period. The most extreme example in this study occurred with *Schistonota* mayflies, for which 84% of annual biomass emerged during a 29-d period. Synchronous emergence in mayflies is well documented and thought to be an adaptive response to avoid predation

(Sweeney and Vannote 1982). However, this ephemeral emergence timing may present the risk of phenological asynchrony with consumer demand (Durant et al. 2007) because warming spring temperatures may shift the timing of aquatic insect emergence earlier (Larsen et al. 2016). Although long-term data collected at the Rice Center did not show a trend of advancing spring temperatures, mean water temperature coinciding with mayfly emergence did vary substantially over the last decade (i.e., mid-March to mid-May). At the tidal freshwater sites sampled here, emergent mayflies provide important fuel for birds early in the breeding season because they tend to align with egg laying and constitute a greater portion of early season nestling diet (Dodson et al. 2016, Rogers 2023). If mayfly emergence follows this annual variation, then in years with warmer temperatures, peak emergence may occur prior to high consumer demand (e.g., arrival of migratory birds on breeding grounds and timing of nestling rearing) and may exacerbate the difference in resources available to riparian consumers between early and late summer (Shipley et al. 2022).

Characterized as generalist feeders, riparian consumers (e.g., birds, bats, lizards) may be buffered against phenological mismatch by alternating prey items as availability changes (Dunn et al. 2011, Mallord et al. 2017). Early emerging aquatic insects may be replaced in consumer diets by late-emerging aquatic insects or by terrestrial insects. Alternative aquatic taxa may provide similar nutrition, whereas a diet switch from aquatic to terrestrial insects may lead to limitations in nutrients that are not readily obtained by consuming terrestrial insect prey (e.g., polyunsaturated fatty acids; Twining et al. 2018). For example, Tree Swallow (*Tachycineta bicolor* [Vieillot, 1808]) nestlings are fed a combination of aquatic and terrestrial insects, but nestling success is influenced specifically by the availability of aquatic insects (Twining et al. 2018). Thus, our estimates of emergent aquatic insect composition and abundance are important for assessing how pulsed aquatic resources might affect riparian consumers in tidal freshwater systems where total emergence rates remain high throughout critical life-history periods.

Implications for future research

Our emergence estimates suggest that tidal freshwaters are particularly productive ecosystems for aquatic insects compared to nontidal systems; however, the lack of data from other tidal systems precludes a robust comparison. Similar studies in other estuaries would provide a basis for assessing how emergence varies regionally among tidal freshwater ecosystems and how these differences may relate to sources of allochthonous and autochthonous inputs. Our findings may help to determine the level of sampling effort required to obtain representative estimates from these complex habitats. We document variation in aquatic insect biomass emerging from intertidal vs subtidal zones and creek vs estuarine shoreline habitats, suggesting that these are

important components of intrasystem variation. However, we note that other habitat types (e.g., deep channel and areas dominated by emergent or submerged vegetation) were not represented in our sampling design and may also be important to system-level assessments. Also, our study focused on a single year of emergence, which precludes an assessment of how interannual variability compares to spatial variability. Multiyear studies can estimate variation in abundance and emergence timing to address questions about how aquatic insects respond to climate variability and how their response may in turn affect food resources for consumers. Emergent aquatic insects not only provide energy to consumers but also supply aquatically derived and nutritionally important compounds such as polyunsaturated fatty acids. For consumers, polyunsaturated fatty acid availability depends on both insect emergence rates and species-specific lipid reserves. Future studies comparing lipid availability with consumer demand would provide a basis for assessing the potential impacts of shifts in the rate and timing of insect emergence on the growth and reproduction of riparian consumers.

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Data availability: Analyses reported in this article can be reproduced using the aquatic insect emergence data and sample metadata provided in Dryad Data Repository at doi: 10.5061/dryad.41ns1rnk1 and are available from the corresponding author upon reasonable request.

LITERATURE CITED

- Barendregt, A., and C. W. Swarth. 2013. Tidal freshwater wetlands: Variation and changes. *Estuaries and Coasts* 36:445–456.
- Baxter, C. V., K. D. Fausch, and W. C. Saunders. 2005. Tangled webs: Reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biology* 50:201–220.
- Bricker, S. B., B. Longstaff, W. Dennison, A. Jones, K. Boicourt, S. Wicks, and J. Woerner. 2007. Effects of nutrient enrichment in the nation's estuaries: A decade of change. Technical report. National Centers for Coastal Ocean Science, Silver Spring, Maryland.
- Brittain, J. E. 1982. Biology of mayflies. *Annual Review of Entomology* 27:119–147.
- Brusven, M. A., C. MacPhee, and R. Biggam. 1974. The effects of water fluctuation on benthic insects. Pages 67–79 in Hell's Canyon Controlled Flow Task Force, C. Koski, K. Bayha, and Pacific Northwest River Basins Commission (editors). *Anatomy of a river: An evaluation of water requirements for the Hell's Canyon reach of the Snake River*, conducted March 1973: A multi-agency effort. Pacific Northwest River Basins Commission, Vancouver, Washington.
- Bukaveckas, P. A. 2022. Carbon dynamics at the river–estuarine transition: A comparison among tributaries of Chesapeake Bay. *Biogeosciences* 19:4209–4226.
- Bukaveckas, P. A., L. E. Barry, M. J. Beckwith, V. David, and B. Lederer. 2011. Factors determining the location of the chlorophyll maximum and the fate of algal production within the tidal freshwater James River. *Estuaries and Coasts* 34:569–582.
- Bukaveckas, P. A., M. Katarzyte, A. Schlegel, R. Spuriene, T. Egerton, and D. Vaiciute. 2019. Composition and settling properties of suspended particulate matter in estuaries of the Chesapeake Bay and Baltic Sea regions. *Journal of Soils and Sediments* 19:2580–2593.
- Bukaveckas, P. A., S. Tassone, W. Lee, and R. B. Franklin. 2020. The influence of storm events on metabolism and water quality of riverine and estuarine segments of the James, Mattaponi, and Pamunkey rivers. *Estuaries and Coasts* 43:1585–1602.
- Buler, J. J., and D. K. Dawson. 2014. Radar analysis of fall bird migration stopover sites in the northeastern U.S. *The Condor* 116:357–370.
- Burdon, F. J., and J. S. Harding. 2008. The linkage between riparian predators and aquatic insects across a stream-resource spectrum. *Freshwater Biology* 53:330–346.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach. 2nd edition. Springer-Verlag, Berlin, Germany.
- Cadmus, P., J. P. F. Pomeranz, and J. M. Kraus. 2016. Low-cost floating emergence net and bottle trap: Comparison of two designs. *Journal of Freshwater Ecology* 31:653–658.
- Cheney, K. N., A. H. Roy, R. F. Smith, and R. E. DeWalt. 2019. Effects of stream temperature and substrate type on emergence patterns of Plecoptera and Trichoptera from northeastern United States headwater streams. *Environmental Entomology* 48:1349–1359.
- Collier, K. J., S. Bury, and M. Gibbs. 2002. A stable isotope study of linkages between stream and terrestrial food webs through spider predation. *Freshwater Biology* 47:1651–1659.
- Davies, I. J. 1984. Sampling aquatic insect emergence. Pages 161–227 in J. A. Downing and F. H. Rigler (editors). *A manual on methods for the assessment of secondary productivity in fresh waters*, number 17 in IBP Handbook. Blackwell Scientific Publications, Oxford, United Kingdom.
- Diaz, R. J. 1989. Pollution and tidal benthic communities of the James River Estuary, Virginia. *Hydrobiologia* 180:195–211.
- Diaz, R. J. 1994. Response of tidal freshwater macrobenthos to sediment disturbance. *Hydrobiologia* 278:201–212.
- Diaz, R. J., and D. F. Boesch. 1977. Habitat development field investigations, Windmill Point Marsh Development Site, James River, Virginia, Appendix C: Environmental impacts of marsh development with dredged material: Acute impacts on the macrobenthic community. Technical report. United States

- Army Engineer Waterways Experiment Station, Vicksburg, Mississippi.
- Dodson, J. C., N. J. Moy, and L. P. Bulluck. 2016. Prothonotary warbler nestling growth and condition in response to variation in aquatic and terrestrial prey availability. *Ecology and Evolution* 6:7462–7474.
- Dunn, P. O., D. W. Winkler, L. A. Whittingham, S. J. Hannon, and R. J. Robertson. 2011. A test of the mismatch hypothesis: How is timing of reproduction related to food abundance in an aerial insectivore? *Ecology* 92:450–461.
- Durant, J. M., D. Hjermann, G. Ottersen, and N. C. Stenseth. 2007. Climate and the match or mismatch between predator requirements and resource availability. *Climate Research* 33:271–283.
- Fritz, K. A., L. J. Kirschman, S. D. McCay, J. T. Trushenski, R. W. Warne, and M. R. Whiles. 2017. Subsidies of essential nutrients from aquatic environments correlate with immune function in terrestrial consumers. *Freshwater Science* 36:893–900.
- Gladyshev, M. I., A. Y. Kharitonov, O. N. Popova, N. N. Sushchik, O. N. Makhutova, and G. S. Kalacheva. 2011. Quantitative estimation of dragonfly role in transfer of essential polyunsaturated fatty acids from aquatic to terrestrial ecosystems. *Doklady Biochemistry and Biophysics* 438:141–143.
- Gratton, C., and M. J. Vander Zanden. 2009. Flux of aquatic insect productivity to land: Comparison of lentic and lotic ecosystems. *Ecology* 90:2689–2699.
- Hixson, S. M., B. Sharma, M. J. Kainz, A. Wacker, and M. T. Arts. 2015. Production, distribution, and abundance of long-chain omega-3 polyunsaturated fatty acids: A fundamental dichotomy between freshwater and terrestrial ecosystems. *Environmental Reviews* 23:414–424.
- Hoffman, J. C., D. A. Bronk, and J. E. Olney. 2008. Organic matter sources supporting lower food web production in the tidal freshwater portion of the York River Estuary, Virginia. *Estuaries and Coasts* 31:898–911.
- Hynes, H. B. N. 1970. *The ecology of running waters*. University of Toronto Press, Suffolk, Toronto, Canada.
- Jackson, J. K., and S. G. Fisher. 1986. Secondary production, emergence, and export of aquatic insects of a Sonoran Desert stream. *Ecology* 67:629–638.
- Johnson, L. K., and C. A. Simenstad. 2015. Variation in the flora and fauna of tidal freshwater forest ecosystems along the Columbia River Estuary Gradient: Controlling factors in the context of river flow regulation. *Estuaries and Coasts* 38:679–698.
- Jonsson, M., P. Hedström, K. Stenroth, E. R. Hotchkiss, F. R. Vasconcelos, J. Karlsson, and P. Byström. 2015. Climate change modifies the size structure of assemblages of emerging aquatic insects. *Freshwater Biology* 60:78–88.
- Larsen, S., J. D. Muehlbauer, and E. Marti. 2016. Resource subsidies between stream and terrestrial ecosystems under global change. *Global Change Biology* 22:2489–2504.
- Liu, L., Y. C. T. Shih, R. L. Strawderman, D. Zhang, B. A. Johnson, and H. Chai. 2019. Statistical analysis of zero-inflated nonnegative continuous data: A review. *Statistical Science* 34:253–279.
- MacKenzie, R. A. 2005. Spatial and temporal patterns in insect emergence from a southern Maine salt marsh. *The American Midland Naturalist* 153:257–269.
- MacKenzie, R. A., and J. L. Kaster. 2004. Temporal and spatial patterns of insect emergence from a Lake Michigan coastal wetland. *Wetlands* 24:688–700.
- Malison, R. L., J. R. Benjamin, and C. V. Baxter. 2010. Measuring adult insect emergence from streams: The influence of trap placement and a comparison with benthic sampling. *Journal of the North American Benthological Society* 29:647–656.
- Mallord, J. W., C. J. Orsman, A. Cristinacce, T. J. Stowe, E. C. Charman, and R. D. Gregory. 2017. Diet flexibility in a declining long-distance migrant may allow it to escape the consequences of phenological mismatch with its caterpillar food supply. *Ibis* 159:76–90.
- Marcarelli, A. M., C. V. Baxter, M. M. Mineau, and R. O. Hall Jr. 2011. Quantity and quality: Unifying food web and ecosystem perspectives on the role of resource subsidies in freshwaters. *Ecology* 92:1215–1225.
- Martin-Creuzburg, D., C. Kowarik, and D. Straile. 2017. Cross-ecosystem fluxes: Export of polyunsaturated fatty acids from aquatic to terrestrial ecosystems via emerging insects. *Science of the Total Environment* 577:174–182.
- Moyo, S., L. D. Chari, M. H. Villet, and N. B. Richoux. 2017. Decoupled reciprocal subsidies of biomass and fatty acids in fluxes of invertebrates between a temperate river and the adjacent land. *Aquatic Sciences* 79:689–703.
- Nakano, S., and M. Murakami. 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences* 98:166–170.
- Paetzold, A., and K. Tockner. 2005. Effects of riparian arthropod predation on the biomass and abundance of aquatic insect emergence. *Journal of the North American Benthological Society* 24:395–402.
- Parmar, T. P., A. L. Kindinger, M. Mathieu-Resuge, C. W. Twinning, J. R. Shipley, M. J. Kainz, and D. Martin-Creuzburg. 2022. Fatty acid composition differs between emergent aquatic and terrestrial insects—A detailed single system approach. *Frontiers in Ecology and Evolution* 10:1–13.
- Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* 28:289–316.
- Prince, H. H., P. I. Padding, and R. W. Knapton. 1992. Waterfowl use of the Laurentian Great Lakes. *Journal of Great Lakes Research* 18:673–699.
- Qin, Q., and J. Shen. 2017. The contribution of local and transport processes to phytoplankton biomass variability over different timescales in the Upper James River, Virginia. *Estuarine, Coastal and Shelf Science* 196:123–133.
- Raitif, J., M. Plantegenest, O. Agator, C. Piscart, and J. M. Roussel. 2018. Seasonal and spatial variations of stream insect emergence in an intensive agricultural landscape. *Science of the Total Environment* 644:594–601.
- Ramirez, M. F. 2008. Emergent aquatic insects: Assemblage structure and patterns of availability in freshwater wetlands of the lower Columbia River Estuary. Master thesis. University of Washington, Seattle, Washington.
- Rogers, S. L. 2023. Quantifying insect emergence in tidal freshwaters and the importance of aquatic prey in wetland-dependent songbird diet. PhD dissertation. Virginia Commonwealth University, Richmond, Virginia.
- Rolauffs, P., D. Hering, and S. Lohse. 2001. Composition, invertebrate community and productivity of a beaver dam in comparison to other stream habitat types. *Hydrobiologia* 459:201–212.

- Sabo, J. L., and M. E. Power. 2002. River–watershed exchange: Effects of riverine subsidies on riparian lizards and their terrestrial prey. *Ecology* 83:1860–1869.
- Sanzone, D. M., J. L. Meyer, E. Marti, E. P. Gardiner, J. L. Tank, and N. B. Grimm. 2003. Carbon and nitrogen transfer from a desert stream to riparian predators. *Oecologia* 134:238–250.
- Schindler, D. E., and A. P. Smits. 2017. Subsidies of aquatic resources in terrestrial ecosystems. *Ecosystems* 20:78–93.
- Shiple, J. R., C. W. Twining, M. Mathieu-Resuge, T. P. Parmar, M. Kainz, D. Martin-Creuzburg, C. Weber, D. W. Winkler, C. H. Graham, and B. Matthews. 2022. Climate change shifts the timing of nutritional flux from aquatic insects. *Current Biology* 32:1342–1349.
- Simpson, R. L., R. E. Good, M. A. Leck, and D. F. Whigham. 1983. The ecology of freshwater tidal wetlands. *BioScience* 33:255–259.
- Stagliano, D. M., A. C. Benke, and D. H. Anderson. 1998. Emergence of aquatic insects from 2 habitats in a small wetland of the south-eastern USA: Temporal patterns of numbers and biomass. *Journal of the North American Benthological Society* 17:37–53.
- Strayer, D. L., and L. C. Smith. 2000. Macroinvertebrates of a rocky shore in the freshwater tidal Hudson River. *Estuaries* 23:359–366.
- Swarth, C. W., and E. Kiviat. 2009. Animal communities in North American tidal freshwater wetlands. Pages 71–88 in A. Barendregt, D. F. Whigham, and A. H. Baldwin (editors). *Tidal Freshwater Wetlands*. Backhuys Publishers, Leiden, The Netherlands.
- Sweeney, B. W., and R. L. Vannote. 1982. Population synchrony in mayflies: A predator satiation hypothesis. *Evolution* 36:810–821.
- Tassone, S. J., and P. A. Bukaveckas. 2019. Seasonal, interannual, and longitudinal patterns in estuarine metabolism derived from diel oxygen data using multiple computational approaches. *Estuaries and Coasts* 42:1032–1051.
- Thorp, J. H., and A. P. Covich. 2001. *Ecology and classification of North American freshwater invertebrates*. Academic Press, San Diego, California.
- Twining, C. W., J. R. Shiple, and D. W. Winkler. 2018. Aquatic insects rich in omega-3 fatty acids drive breeding success in a widespread bird. *Ecology Letters* 21:1812–1820.
- Uesugi, A., and M. Murakami. 2007. Do seasonally fluctuating aquatic subsidies influence the distribution pattern of birds between riparian and upland forests? *Ecological Research* 22:274–281.
- Waller, E. K., T. M. Crimmins, J. J. Walker, E. E. Posthumus, and J. F. Weltzin. 2018. Differential changes in the onset of spring across US National Wildlife Refuges and North American migratory bird flyways. *PLoS ONE* 13:e0202495.
- Ward, J. V. 1992. *Aquatic insect ecology 1. Biology and habitat*. John Wiley & Sons, New York, New York.
- Whigham, D. F. 2009. Primary productivity in tidal freshwater wetlands. Pages 115–122 in A. Barendregt, D. F. Whigham, and A. H. Baldwin (editors). *Tidal freshwater wetlands*. Backhuys Publishers, Leiden, The Netherlands.
- Whiles, M. R., and B. S. Goldowitz. 2001. Hydrologic influences on insect emergence production from Central Platte River wetlands. *Ecological Applications* 11:1829–1842.
- Williams, D. D., and T. Hamm. 2002. Insect community organization in estuaries: The role of the physical environment. *Ecography* 25:372–384.
- Williams, D. D., and N. E. Williams. 1998a. Aquatic insects in an estuarine environment: Densities, distribution and salinity tolerance. *Freshwater Biology* 39:411–421.
- Williams, D. D., and N. E. Williams. 1998b. Seasonal variation, export dynamics and consumption of freshwater invertebrates in an estuarine environment. *Estuarine, Coastal and Shelf Science* 46:393–410.
- Wood, J. D., D. Elliott, G. Garman, D. Hopler, W. Lee, S. McIninch, A. J. Porter, P. A. Bukaveckas. 2016. Autochthony, allochthony and the role of consumers in influencing the sensitivity of aquatic systems to nutrient enrichment. *Food Webs* 7:1–12.
- Wood, S. N. 2017. *Generalized additive models: An introduction with R*. 2nd edition. CRC Press/Taylor & Francis Group, Boca Raton, Florida.
- Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed effects models and extensions in ecology with R*. Springer Science+Business Media, Berlin, Germany.