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The impact of predator exposure and anthropogenic stressors on insect emergence in stream ecosystems

Anna-Maria Vermiert^{a,*}, Iris Madge Pimentel^b, Philipp M. Rehsen^{b,c},
Jonathan Meisner^a, Alexandra N. Hollstein^a, Martin Horstmann^a,
Arne J. Beermann^{b,c}, Florian Leese^{b,c}, Linda C. Weiss^{a,c}, Ralph Tollrian^{a,c}

^a Department of Animal Ecology, Evolution and Biodiversity, Faculty of Biology and Biotechnology, Ruhr University Bochum, Bochum, Germany

^b Aquatic Ecosystem Research, Faculty of Biology, University of Duisburg-Essen, Essen, Germany

^c Centre for Water and Environmental Research (ZWU), University of Duisburg-Essen, Essen, Germany

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ABSTRACT

Emergence of aquatic insects is a vital ecological process influencing aquatic ecosystems. Predators can modify this process by inducing behavioural and developmental changes in prey species. However, these natural biotic interactions are increasingly disrupted by anthropogenic changes. Anthropogenic stressors, like freshwater salinisation and warming, pose a significant threat to lotic ecosystems worldwide, with effects that may persist even after the stressors are removed. Our study investigated the effects of fish predator exposure (*Gasterosteus aculeatus* and *Cottus rhenanus*), increased salinity (ambient vs +136 mg/L NaCl) and increased temperature (ambient vs +3.4 °C) on insect emergence in a controlled stream mesocosm experiment (*ExStream* system). We monitored the number and size of emerging insects over a 14-day stressor and recovery phase. Predator exposure and elevated salinity reduced the number of emerging insects and resulted in smaller Nematocera emerging. Increased temperature led to reduced body sizes of emerging Nematocera and increased the number of emerging individuals when interacting with increased salinity, predator exposure or both. Notably, the effects of predator exposure were diminished under increased salinity and temperature, although salinity alone reduced the impact on insect size. The stressors did not cause any lasting effect on insect emergence during the recovery phase, except tendentially the size. Our findings highlight that anthropogenic stressors can alter insect emergence and reduce the impact of fish predation, with the magnitude of these effects likely dependent on the intensity and duration of the stressor input.

1. Introduction

Insect emergence is a critical ecological process that plays a vital role in the structure and functioning of aquatic ecosystems. The emergence process represents a severe ontogenetic shift during which aquatic insects transition from an aquatic final nymphal or pupal stage to a terrestrial or aerial adult form (Lancaster and Downes, 2013). In temperate zones, emergence of individual taxa is typically seasonal and may be highly synchronous over a few days to a few months (Sweeney and Vannote, 1982). The synchronous emergence of species enhances the likelihood of finding a mate while simultaneously reducing the risk of predation by predator satiation (Corbet,

* Correspondence to: Ruhr University Bochum, Department of Animal Ecology, and Biodiversity, Bochum D-44780, Germany.

E-mail address: Anna-Maria.Vermiert@ruhr-uni-bochum.de (A.-M. Vermiert).

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1964; Sweeney and Vannote, 1982). The exact timing of emergence varies depending on the species, but it is typically triggered by environmental cues that signal good conditions for the transition (Lancaster and Downes, 2013). These cues include: water temperature, photoperiod, oxygen availability, water chemistry (salinity, pH), seasonality, resource availability and predation pressure (Connolly et al., 2004; Danks, 1978; Lancaster and Downes, 2013; Nebeker, 1971).

Predation plays an important role in shaping the emergence of insects (Hury and Wallace, 2000). This is due to the vulnerability of many aquatic species during the larval stage but especially during moulting and the pupal stage (Lancaster and Downes, 2013). Reflecting strong selective pressure, prey have evolved a suite of sensory capabilities—e.g. visual, vibrational and chemical—that allow them to detect predators (Åbjörnsson et al., 1997; Dodson et al., 1994; Peckarsky and Penton, 1989). These sensory cues can signal danger and initiate defensive strategies in potential prey, leading to shifts in behaviour (Gall and Brodie, 2009; Peckarsky, 1996), morphology and life-history (Weiss and Tollrian, 2018). For example, some insect species, particularly those with shorter life cycles, may accelerate their development, thereby reducing the time spent in vulnerable stages (Silberbush et al., 2019, 2015). In contrast, the development time can also be lengthened due to reduced activity or food intake in response to predation threats (Beketov and Liess, 2007; Benard, 2004; van Uitregt et al., 2012).

Freshwater ecosystems, however, are influenced not only by natural processes but also by the growing impact of anthropogenic stressors. Climate change, habitat loss, pollution and many other stressors can alter ecosystem conditions (Bănăduc et al., 2024), resulting in both positive and negative impacts on insects depending on the magnitude of the disturbance and species-specific tolerance thresholds (e.g., salinisation; see Cañedo-Argüelles et al., 2013). Furthermore, the intensity and duration of these disturbances may lead to effects that linger beyond the initial period of stressor exposure, persisting after the stressor removal and complicating ecosystem recovery despite restoration efforts (Vos et al., 2023). Two of the most prevalent stressors on riverine ecosystems are salinisation and warming. Freshwater salinisation results from agricultural irrigation, industrial sources, and the use of road de-icers (Cañedo-Argüelles et al., 2019; Kaushal et al., 2021). Although salinity has been proven to have detrimental effects on various insects (Cañedo-Argüelles et al., 2019), many dipterans are known to be comparatively tolerant (Castillo et al., 2018). While higher levels may reduce or even halt emergence *per se*, intermediate salinity levels have been shown to improve the emergence success (Hassell et al., 2006). In comparison, increased water temperature is caused by climate change and the removal of riparian vegetation, which reduces shaded areas (Kail et al., 2021; Woodward et al., 2010). Temperature changes can impact aquatic organisms by altering their behaviour, fitness, physiology and metabolism (reviewed in Bonacina et al., 2023). As a result, temperature shifts can lead to variations in insect body size (Atkinson, 1995, 1994), emergence timing and overall emergence numbers at the population level (Nordlie and Arthur, 1981).

Both increased salinity and temperature are discussed to affect predator-prey interactions by altering the concentration or perception of predator chemical cues in the environment. Higher salinity is hypothesised to impair the sensory abilities of insects, reducing their capacity to detect chemical cues by disrupting intracellular ion balance (Ross and Behringer, 2019). Increased temperature, in contrast, may alter the activity levels of individuals, their metabolic needs, and may also change the concentration of chemical cues in the ecosystem, potentially affecting the behaviour of both predator and prey (Draper and Weissburg, 2019).

Despite these insights, little is known about how salinisation and warming—alone or together—alter predator effects on insect emergence during periods of both stressor increase and release. This study addresses this gap by investigating the effects of fish predator exposure, increased salinity, and increased temperature on insect emergence in a controlled full-factorial mesocosm setting, examining both the number and size of emerging individuals during a stressor and a recovery phase.

We hypothesise that increased temperatures will accelerate development and lead to earlier emergence, while elevated salinity may either have no effect or may enhance emergence rates. We also predict that predator exposure will reduce the number of emerging individuals due to increased predator-induced behaviour and/or higher mortality rates. Additionally, we expect that the stressors, i.e. increased salinity and temperature, will alter the effects of predator exposure on emergence, potentially weakening the predator-induced reduction in size and/or number. Finally, we hypothesise that the impacts of these stressors will extend into the recovery phase, resulting in long-term effects on insect development that may delay or alter their emergence patterns even after the stressors are removed.

2. Material and methods

2.1. Study site

The Boye River, characterised by a carbonate-rich, sandy bottom, is classified as a lowland river (www.elwasweb.nrw.de; OFWK ID: DE_NRW_27726, accessed June 20, 2024). Since the early 20th century, it has been heavily impacted by wastewater from industries, mining, agriculture, and domestic sewage. To restore the Emscher and its tributaries, including the Boye, to a more natural state, the Emscher Restoration Project constructed a separate wastewater channel. Work at the study site began in 2017 and was completed by 2021. Prior to this, Oligochaeta dominated the river's fauna (Winking et al., 2016). Since then, the macroinvertebrate community has been recovering, aided by healthy tributary sections (Gillmann et al., 2023). This includes a thriving population of sticklebacks (Gasterosteidae), along with a few bullheads (Cottidae) and occasional sightings of species such as bleak and sunbleak (Cyprinidae), as observed during electrofishing surveys conducted by Dr C. Edler and B. Daniel (Bezirksregierung Düsseldorf, Department 51: Nature and Landscape Protection, Fisheries).

2.2. Experimental design

On March 4, 2022, we established our outdoor mesocosm system (ExStream system; Piggott et al., 2015), which consists of 64 identical flow-through mesocosms (Fig. 1), adjacent to the Boye River (An der Boy, Gladbeck, Germany; coordinates: N 51.5533°, E 6.9485°). Water from the Boye River was pumped into the system, which was set up on a scaffold, using two Pedrollo NGAm 1A-Pro pumps. To prevent debris and fish from entering, the pump intakes were fitted with protective covers featuring 5 mm diameter holes. The water was pumped to the upper level of the scaffold into four 203 L tanks. Each of these tanks was connected in the upper region via tubes to two additional tanks in a series, facilitating passive water flow (Fig. 1 B, C). In each series, the first two rear tanks functioned as sediment traps and were installed to avert extreme sedimentation and clogging of the system. The third tank in the front was designated as the header tank and connected to 16 mesocosms (Fig. 1 D) via hoses, with the water flowing gravity-driven to the mesocosms at the lower level. Each hose had a flow valve installed right before the mesocosm to maintain a controlled flow rate of approximately 2.1 L/min. There the water circulated clockwise and left through the outflow in the middle. The outflow was directed to a retention basin. To mimic the substrates of the Boye streambed, each mesocosm was filled with 1000 mL of sediment sourced from the Boye catchment (N 51.5544°, E 6.9463°; sieved through a 1 mm mesh), 100 mL of fine particulate organic matter (FPOM, N 51.5627°, E 6.9154°), 200 mL of quartz gravel (6–8 mm), and three larger stones (40–80 mm). Additionally, each mesocosm contained a coarse-meshed tube (2.5 cm diameter, 15 cm length, 5 mm mesh size) filled with approximately 7 g of air-dried alder leaf litter (*Alnus glutinosa*). The leaf litter, collected in the previous autumn and air-dried at room temperature, provided additional habitat and food for the invertebrates.

To examine the effects of fish predator exposure, elevated salinity, and temperature compared to ambient conditions, the system was designed as a full-factorial experiment. The salinity stressor and predator exposure treatments were randomly assigned across four blocks, while the increased temperature was applied directly to two of those blocks.

2.3. Predator exposure

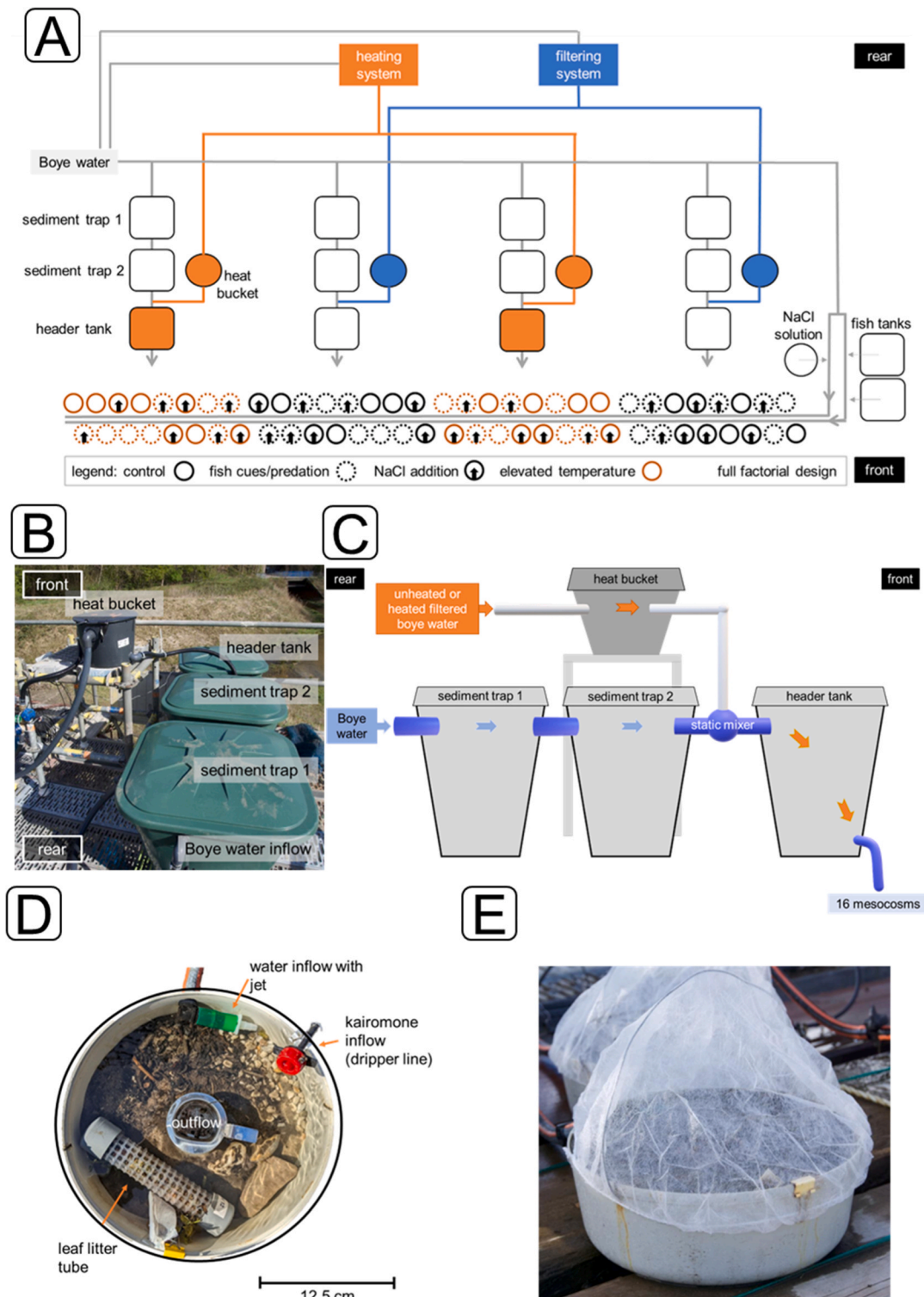
This study was conducted in compliance with the Animal Welfare Act. Two fish species were used: Sticklebacks (*Gasterosteus aculeatus*), measuring 4–7 cm, were captured through electrofishing from a natural shoal at a single location. This natural aggregation occurs in areas with abundant food and/or shelter (Keenleyside, 1955), and the use of these fish allowed for the replication of natural predator densities, taking into account shoaling behaviour and the patchy distribution of fish in natural systems. Additionally, bullheads (*Cottidae*: *Cottus rhenanus*; 3.8–7.2 cm, mean: 5.72, SD: 0.78) were collected via night fishing in the Wannebach, a tributary of the river Ruhr near Arnsberg. Both fish species were evenly distributed across two ground-level fish tanks (internal dimensions: 113 cm x 93 cm x 57.5 cm), resulting in a total biomass of approximately 480 g fish. These two species were selected to simulate predation from bottom-dwelling and mid-water feeding insectivorous fish. To simulate natural feeding behaviour and cue production, the fish were provided daily portions of insects sourced from a downstream area.

During the stressor and recovery phase, insects in the mesocosms were continuously exposed to fish-cue-enriched water (indirect predation). Water from each fish tank was pumped via Tygon hoses (standard R3603, inner diameter 6.4 mm, wall thickness 1.6 mm, outer diameter 9.5 mm) into one irrigation line using a peristaltic pump (Hei-FLOW Value 01, multi-channel pump head C8). The fish-cue-enriched water (equivalent to 100 % of predator cues) flowed at a constant rate of 32.4 L/h and was mixed with Boye water, yielding a final fish water concentration of 0.005 g fish/L (0.8 % of predator cues) in the mesocosms due to dilution. To maintain a constant water level, each fish tank was connected to a paired water tank via tubing, with a mechanical sensor triggering a pump to replenish water from the reservoir whenever the level dropped. A technical failure caused the pump to stop for one night during the stressor phase (day 12).

Additionally, on the fifth day of the stressor phase, direct predator exposure was implemented by placing bullheads into the mesocosms to increase predation pressure. Bullheads (31 in total) were taken from the fish tanks and placed in each predator-treated mesocosm. Fourteen bullheads left the mesocosms within the first six days, and an additional eight escaped by the end of the stressor phase. The remaining bullheads were also removed at the end of the stressor phase and placed back into the fish tanks. The bullheads were expected to remain in the mesocosm but likely left early due to their mating season activity (March–April; Kottelat and Freyhof, 2007). The introduction of bullheads increased fish biomass concentration in the mesocosms, relative to water flow rate, to approximately 0654 g fish/L (± 0.25 SD). At the end of the experiment, all fish were collected and returned to their original collection site.

2.4. Elevated salinity levels

The stressor salinity was implemented via a NaCl solution (refined salt tablets, Claramat, > 99.9 % NaCl, >350 g/L NaCl) stored in a 1000 L ground-level plastic tank. The solution was pumped over the salt irrigation line and a pressure-compensated dripper system into the mesocosms. Upon mixing with filtered Boye water, the NaCl solution in the mesocosms reached 136 mg/L, raising the ambient conductivity from an average of 840.63 $\mu\text{S}/\text{cm} \pm 94.20$ SD (median 853 $\mu\text{S}/\text{cm}$) to 1299.78 $\mu\text{S}/\text{cm} \pm 247.49$ SD (median 1292 $\mu\text{S}/\text{cm}$; Supplementary fig. 1). Flow rate reductions caused by clogging occasionally led to conductivity spikes beyond the intended levels. These short-term salinity peaks over 2500 $\mu\text{S}/\text{cm}$ were excluded from the calculation of the mean, median and standard deviation. The salinity increase was based on the maximum conductivity observed in the Boye system. Salt application was initially halted after a few hours on the first day due to a technical failure but resumed at the start of the second stressor day. Additionally, a 12-hour interruption occurred between days 12 and 13 due to river flooding.



(caption on next page)

Fig. 1. Setup of the ExStream system. (A) Schematic overview of the experimental mesocosm system with 64 mesocosms assigned in four randomised blocks. Stressors in the mesocosms are indicated by dotted circles (predator exposure), black arrows (increased salinity) and orange circles (increased temperature). The direction of water flow is indicated by grey arrows. Fish tank water and NaCl solution were applied via two separate irrigation lines to the mesocosms. (B) Photo and (C) Schematic overview of the sediment traps, the header tank and the heat bucket with the connections at the top level. The water flow is indicated by blue and when heated by orange arrows. The sediment trap and header tank are located on the top level of the scaffold above the mesocosms (lower level). The connection of the second sediment trap and header tank is linked to the heating system. Heated water, at approximately 50 °C, is stored in a bucket and fed into the system once the water temperature of the header tank is less than 4 °C above the water temperature of the sediment trap. (D) Circular mesocosm (volume 3.5 L; Microwave Ring Moulds, Interworld, Auckland, New Zealand) was filled with streambed substrate and a leaf litter tube. Water in the mesocosm had a clockwise flow direction and drained through the central outflow. (E) Emergence nets were placed over the mesocosms to capture the emerging insects. Adapted from Vermiert et al., (2024b).

2.5. Elevated temperature levels

The temperature increase in the mesocosms was achieved via the header tanks. Filtered Boye water was heated to around 50 °C using a heat exchange mechanism powered by a petroleum-driven heater with an internal water circuit. The heated water was pumped onto the scaffold and directed into heat buckets, where magnetic valves regulated the outflow to raise the header tanks' water temperature. The magnetic valve was connected to temperature sensors in both the heated header tanks and the ambient-temperature sediment traps, allowing for continuous monitoring and adjustment of the water temperature. The ambient temperature header tanks had the same setup as the heated header tanks, with an identical outflow from the heat buckets, but their water was filtered through a separate system unconnected to the heating unit to prevent dilution from affecting the experimental results. A more detailed description of the automatic control system used in this experiment can be found in Madge Pimentel et al. (2024b).

The ambient water temperature of the mesocosms during the stressor phase averaged 8.7 °C, ranging from a low of 3.6 °C to a high of 16.0 °C. While the targeted temperature increase in the mesocosms was + 4.0 °C, the temperature difference between ambient and warmed mesocosms averaged 3.4 °C (± 0.8 °C) accounting for heat loss during water transfer and other factors (Supplementary Fig. 2). Specifically, heating was temporarily halted on days 5, 6, 8, 13, and 14 due to high sediment loads from heavy rainfall. To avoid exceeding the bullheads' thermal limits, the maximum temperature was capped at 24 °C (Elliott and Elliott, 1995). In the recovery phase, temperatures fluctuated between 5.0 °C and 17.5 °C, with an average of 11.0 °C ± 2.9 °C.

2.6. Experimental procedures

The experiment consisted of three consecutive phases: a 20-day colonisation phase, a 14-day stressor phase, and a 14-day recovery phase (Fig. 2). In the colonisation phase, leaf litter tubes were introduced on the third day. Natural communities were formed through immigration with the inflowing water. Larger invertebrates were supplemented by multi-habitat kick-net sampling (seeding) of 51 streambed patches upstream of the Boye. The collected macroinvertebrates were added to the experimental mesocosms at similar densities using a mixing procedure adapted from Elbrecht et al. (2016). The macroinvertebrates were collected in a tank filled with Boye water and continuously stirred. Approximately 5 litres of this mixture were then scooped out and evenly distributed into eight identical jars on a potter's wheel. The contents of two jars were added to each mesocosm, with this process repeated until all mesocosms received the contents from two jars. To address high sediment loads, nets with a mesh size of 10 mm were installed in the second sediment traps four days prior to the stressor phase to prevent floating sediment particles from reaching the header tank. Additionally, sediment was cleared from the tanks several times using a pool cleaner. During this cleaning process, the flow in the mesocosms was briefly halted, preventing disturbed sediment and invertebrates from entering the mesocosms.

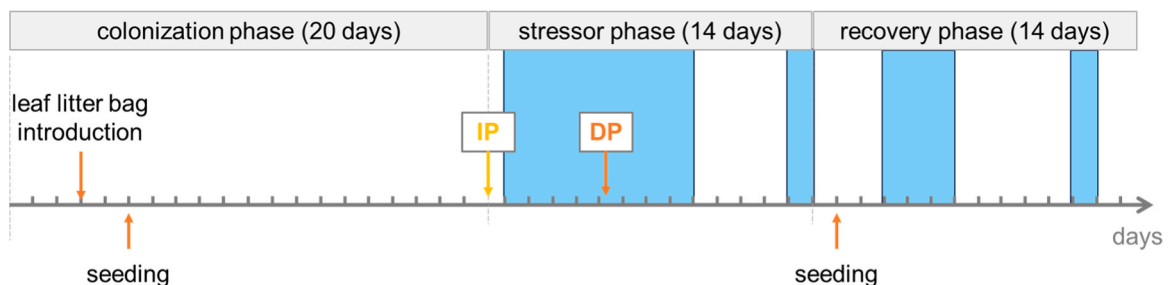


Fig. 2. Schedule for the ExStream system, starting on March 4, 2022, at 16:00 o'clock. Following setup, a 20-day colonisation phase commenced, initiating with the addition of sediment to the mesocosms and the activation of water flow. This phase included the placement of leaf litter tubes and a seeding event that introduced additional macroinvertebrates. The 14-day stressor phase began with the simultaneous introduction of salinity and temperature stressors, along with fish-cue enriched water (indirect predation - IP). On the fifth day at midnight, bullheads were additionally introduced into the predator-treated mesocosms (direct predation - DP) until the end of the stressor phase. The 14-day recovery phase commenced with the removal of the anthropogenic stressors, while fish-cue enriched water continued to be supplied. Transparent blue areas indicate the days on which emergence sampling occurred.

With the start of the stressor phase, the NaCl solution and fish-cue-enriched water were added to the mesocosms via their respective dripper systems while the water temperature was warmed in two blocks of the system. After 14 days, the salinity and temperature stressors were discontinued, marking the beginning of the recovery phase. Predator exposure continued throughout the recovery phase via the ongoing input of cue-enriched water. On the first day of this phase, a smaller seeding event was conducted with kick net sampling of 12 patches to simulate the immigration of larger invertebrates from upstream, following the same procedure as before.

To investigate both normal and anthropogenically altered predator-induced emergence behaviour during the stressor and recovery phases, emergence nets (Fig. 1 E) were installed over the mesocosms for 24 h to capture any emerging insects attempting to exit the system. Each installed net was held upright by a bent wire that connected to opposite walls of the mesocosms, creating an arch shape. Emergence samples were collected over eleven days during the stressor phase and six days during the recovery phase (Fig. 2). Once collected, the samples were preserved in 96 % ethanol. During the recovery phase, only 32 mesocosms remained from the original 64, as half were removed at the end of the stressor phase for sampling. Consequently, emergence samples were then collected from these remaining mesocosms during the recovery phase.

2.7. Sample collection and preparation

In the laboratory, the emergence nets and the ethanol in which they were stored were thoroughly inspected for emerged insects. The nets were spread over a self-made nail board and examined with a magnifying glass. Insects were identified to the lowest practicable taxonomic level by examining their morphological traits under a microscope and utilising identification keys (Bauernfeind and Humpesch, 2001; Lubini et al., 2012; Schaefer, 2018). The size of each insect was assessed in millimetres (mm) by measuring their length from head to posterior end, excluding cerci, using graph paper and rounding up to the nearest whole number. The effects of predator exposure and stressors on the counts and sizes of emerged invertebrates were then evaluated.

2.8. Data analysis

The data analysis was performed with R version 4.4.0 (R Core Team, 2024). The effects of the factors predator exposure, salinity, and temperature, as well as their interactions, were analysed for the number and body size of emerging insects. Due to the low number of emergences per day, it was not possible to compare daily emergence patterns. Therefore, the emergence count and size data were each aggregated for the stressor and recovery phase, respectively. We analysed the aggregated data by first applying deviation coding to all categorical variables, followed by using a generalised linear model (stats package; R Core Team, 2024). Given the factorial design of our study, we included main effects and interactions of the factors in the GLM. The interactions identified were classified according to the operational definitions from Piggott et al. (2015). The GLM results were further analysed for conditional effects using post-hoc comparisons among groups when a tendential or significant interaction was found (package emmeans; Lenth, 2023). The significance threshold for these results was corrected for multiple testing using the false discovery rate (FDR) adjustment method.

The total number of emerging insects was analysed without differentiating between taxa. This is due to difficulties in distinguishing them at a lower taxonomic level, as many individuals had damaged wings or small sizes. Additionally, the low abundance of most taxa would have made model construction problematic. A Poisson regression with an identity link function was used to assess main effects and interactions on an additive scale. Overdispersion in the Poisson regression models was evaluated and corrected by adjusting the standard errors using the estimated dispersion parameter through a quasi-GLM (package AER; Kleiber and Zeileis, 2008).

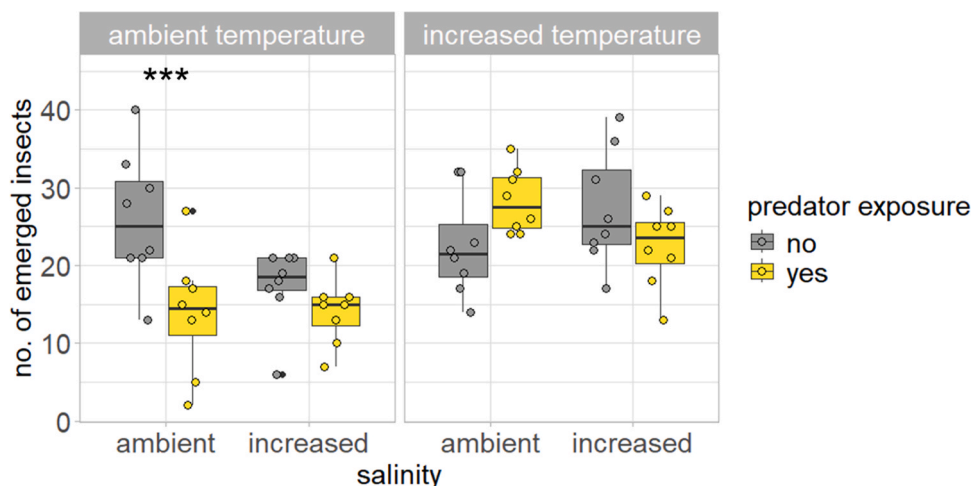


Fig. 3. The total number of emerging insects influenced by predator exposure, increased salinity, and increased temperature during the stressor phase of a field mesocosm experiment. Both stressors (salinity and temperature) were tested at two levels: ambient and increased. The experiment included 64 mesocosms ($n = 64$). Signif. code: *** $p < 0.001$.

We calculated the mean body size of Nematocera per sample, as it was the most frequently encountered taxon. Simuliidae were excluded due to their low abundance and significantly larger body size compared to the other Nematocera found. Given the right-skewed nature of the data, a Gamma distribution with an identity link function was used for model fitting.

To ensure that variability in treatment application did not bias our results, we screened for outliers using the Interquartile Range (IQR) method. As mesocosms with known variability did not produce outliers, they were retained in the analysis.

Results are presented as boxplots bisected at the median value with whiskers reaching values within the 1.5 interquartile range using ggplot (package tidyverse; Wickham et al., 2019).

3. Results

3.1. Stressor phase

3.1.1. Number of emerging insects

We recorded an average of 125 individuals per day (approximately 2 individuals per mesocosm), with a total of 1375 emerging insects observed over the 11 sampling days of the stressor phase. We identified 1342 Nematocera, with 1267 primarily classified as Chironomidae, 20 as Simuliidae and three as Psychodidae. Among the remaining insects, two belonged to the Baetidae, and 31 specimens could not be identified beyond Diptera due to damage.

Both predator exposure and increased salinity significantly reduced the number of emerging insects when compared to control conditions (predator exposure: $z = 3.900$, $p < 0.001$; increased salinity: $z = 2.660$, $p = 0.008$; [Supplementary tab 2](#)), while increased temperature had no effect.

All three factors—predator exposure, increased salinity, and increased temperature—interacted to influence the number of emerging insects ($t(56) = 3.002$, $p = 0.004$; [Fig. 3](#), [Supplementary tab 1](#), [Supplementary fig. 3](#)). Temperature increased the number of emerging insects when combined with predator exposure ($z = -4.498$, $p < 0.001$), increased salinity ($z = -3.002$, $p = 0.003$), or both ($z = -2.811$, $p = 0.005$; [Supplementary tab 2](#)). Under ambient salinity conditions, the opposite effects of predator exposure and temperature interacted positively synergistically, resulting in the highest number of emerging insects. Increased salinity disrupted this synergistic interaction ([Supplementary fig. 3](#)). This resulted in predator exposure having no effect under conditions of increased salinity, increased temperature, or both (salinity: $z = 1.176$, $p = 0.240$; temperature: $z = -1.639$, $p = 0.101$; salinity and temperature: $z = 1.368$, $p = 0.171$; [Fig. 3](#), [Supplementary tab 2](#)).

3.1.2. Size of the emerging insects

Increased temperature resulted in smaller insects emerging across all treatments ($t(56) = 2.388$, $p = 0.020$; [Fig. 4A](#), [Supplementary tab 3](#)). Predator exposure and salinity interacted negatively antagonistically ($t(56) = 2.132$, $p = 0.037$; [Supplementary tab 3](#)). Predator exposure resulted in smaller emerging Nematocera only compared to control conditions ($t = 2.357$, $p = 0.022$) and increased salinity had the same effect, but only under control conditions without predators ($t = 2.164$, $p = 0.035$; [Fig. 4B](#), [Supplementary tab 4](#)).

3.2. Recovery phase

3.2.1. Number of emerging insects

We observed an average of 167.2 individuals per day (approximately 5 individuals per mesocosm), with a total of 1003 emerging

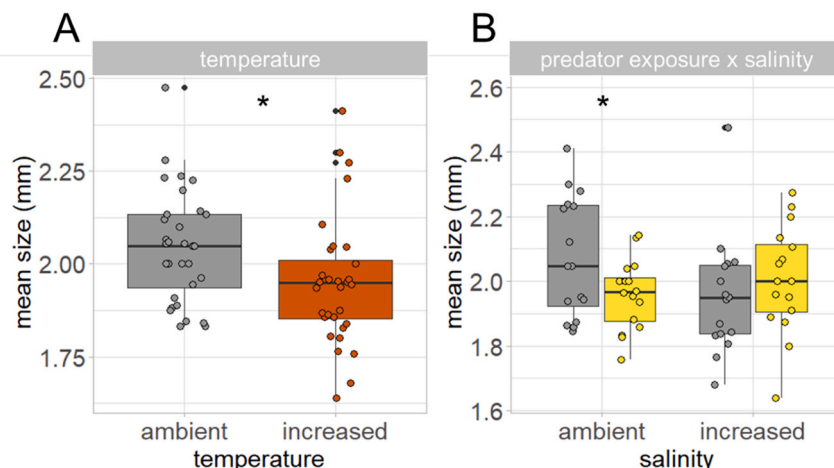


Fig. 4. Mean body size of emerging Nematocera, excluding Simuliidae, influenced by (A) increased temperature and (B) predator exposure and salinity interaction during the stressor phase of a field mesocosm experiment. Control conditions (grey), increased temperature (red), predator exposure (yellow). The experiment was conducted with 64 mesocosms ($n = 64$). Signif. codes: * $p < 0.05$.

insects recorded over the six sampling days of the recovery phase. We identified 999 Nematocera, with 997 primarily classified as Chironomidae and 1 as Simuliidae. The remaining were identified as Diptera (2), Nemouridae (1) and Baetidae (1).

Neither increased salinity, increased temperature nor their interaction influenced the number of emerging insects in the recovery phase. Only predator exposure, which was continuously applied over the recovery phase, reduced the number of emerging insects ($t(24) = 3.817$, $p < 0.001$; Fig. 5, Supplementary tab 5).

3.2.2. Size of the emerging insects

During the recovery phase the sizes were only tendentially influenced by the interaction of predator exposure, increased salinity and increased temperature ($t(24) = -1.944$, $p = 0.064$; Fig. 6, Supplementary tab 6, Supplementary fig. 4). Under increased temperature, predator exposure led to smaller insects emerging ($z = 2.147$, $p = 0.042$, Supplementary fig. 7). The synergistic interaction between predator exposure and temperature occurred only under ambient salinity.

4. Discussion

Overall, we observed a relatively low number of emerging insects each day during the sampling period in March and April. This is consistent with findings from temperate streams, where insect emergence tends to peak in late spring and early summer and emergence flux to riparian zones is generally low from autumn through early spring (Jackson and Fisher, 1986; Nakano and Murakami, 2001; Sweeney and Vannote, 1982).

4.1. Stressor phase

During the stressor phase, predator exposure reduced the number of emerging insects and led to a shift toward smaller individuals emerging within the suborder Nematocera. This decline in numbers may stem from predator-induced behavioural adaptations or direct mortality. For example, in our experiment, fish predators increased the drifting behaviour of Chironomidae larvae, reducing their numbers in the mesocosms during the 14-day stressor phase (Vermiert et al. 2024a, 2024b). Therefore, this likely contributed to the observed decrease in emerging insects. Additionally, the presence of predators may have also increased hiding and reduced activity periods. This, in turn, could have limited food intake, inhibiting growth and slowing development rates (van Uitregt et al., 2012). This could have caused a shift in the timing of synchronised emergence, potentially delaying the emergence to a later period. Otherwise, the smaller size of the emerging insects may also reflect a survival strategy. Initiating emergence earlier by accelerating development may result in a smaller body size, but it also reduces exposure time and decreases the risk of predation in the water. This phenomenon has been observed in the house mosquito *Culex pipiens*, where exposure to predator-released kairomones accelerated metamorphosis, leading to faster pupation (Silberbush et al., 2015).

Increased salinity also reduced the number and size of emerging insects, suggesting that the insects experienced osmotic stress. This pattern is consistent with previous observations in species such as *Cirrhia hians* (Herbst, 2023) and *Chironomus riparius* (Lob and Silver, 2012), where increased salinity led to reduced growth, body size, and emergence success. This occurred despite previous findings indicating that the invertebrate community in the Boye River—our study site—may have adapted to elevated salinity levels due to long-term exposure (Madge Pimentel et al., 2024a; Vermiert et al., 2024b). That emergence was still negatively affected by increased salinity, despite potential stressor adaptation and tolerance, may indicate life-stage-specific vulnerability. Pupae, in particular, are believed to have a lower salinity tolerance than larvae due to their limited capacity for osmoregulation (Berezina, 2003).

Contrary to our findings, other studies have also reported improved survival and emergence rates under moderate salinity levels, for example, in *Chironomus* sp. and *Leucorrhinia intacta*, with no growth reduction even at higher levels (Hassell et al., 2006; Zhang

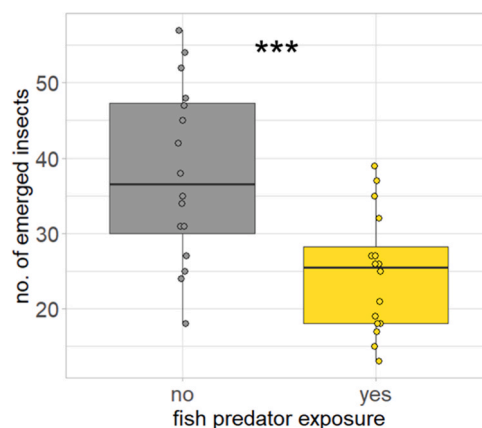


Fig. 5. The total number of emerging insects influenced by predator exposure during the recovery phase of a field mesocosm experiment. Fish predator exposure was continuously applied throughout both the stressor and recovery phases. Control (grey), predator exposure (yellow). The recovery phase included 32 mesocosms ($n = 32$). Signif. code: *** $p < 0.001$.

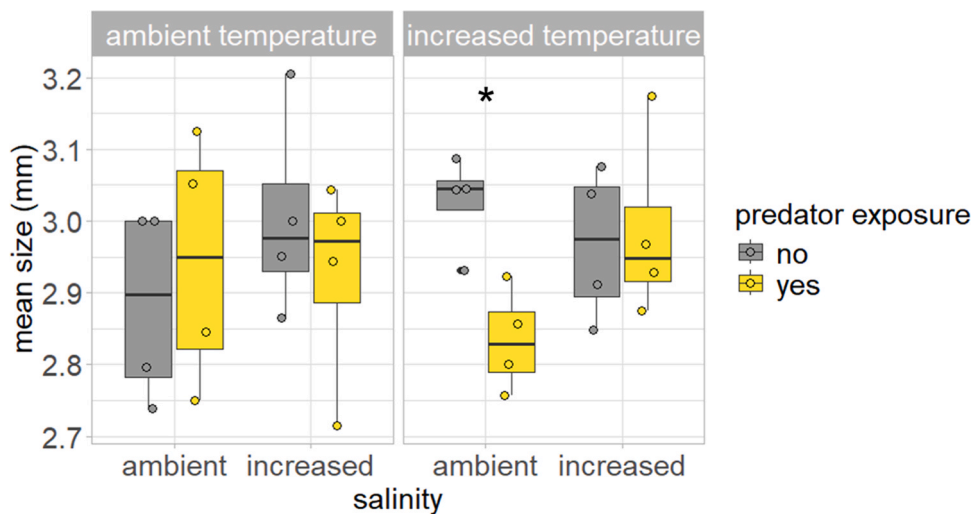


Fig. 6. Mean body size of emerging Nematocera, excluding Simuliidae, influenced by predator exposure, increased salinity, and increased temperature. Salinity and temperature were continuously applied for two weeks during the stressor phase, while predator exposure was applied throughout both the stressor and recovery phases. The recovery phase involved 32 mesocosms ($n = 32$). Signif. codes: * $p < 0.05$.

et al., 2022). These contrasting findings may have resulted from differences in species-specific responses. As our study examined the total number of all emerging insects and the body size of individuals within the suborder Nematocera, species-specific variation may have been overlooked.

In comparison, increased temperature also led to the emergence of smaller Nematocera, but did not affect the overall numbers of emerging insects, given the control conditions of the other treatments. The prevalence of smaller emerging insects may indicate accelerated development rates, leading to an earlier emergence (Atkinson, 1995; Chown and Gaston, 2010). This is supported by the observed increase in pupae in our experimental setup under elevated temperature conditions (Vermiert et al., 2024b). In contrast to our findings, other studies have found that rising temperatures can increase the insect's propensity to emerge (Piggott et al., 2015) and shorten the time to emergence (Hogg and Williams, 1996). Two interrelated factors may explain the discrepancy between these findings. First, our study was conducted during early to mid-spring, when ambient water temperatures remained relatively low (average temperature: 8.7 °C; range: 3.6 °C to 16.0 °C), even with a 3.4 °C increase. Second, the experiment was subject to natural daily temperature fluctuations, with higher temperatures occurring only during the day. Developmental times of many species are known to differ between constant and fluctuating temperatures (Hagstrum and Hagstrum, 1970) and temperature levels (Dallas and Ross-Gillespie, 2015). Combined with the relatively short duration of our experiment, the necessary thermal threshold and cumulative thermal sum (degree-day accumulation) required for development and emergence (Damos and Savopoulou-Soultani, 2012; Ward and Stanford, 1982) may have just not been met.

When interacting with other factors, increased temperature had an opposing effect to both predator exposure and increased salinity, resulting in higher numbers of emerging insects. In contrast, Jackson and Funk (2019) found that salinity toxicity increases with higher temperatures under constant temperature conditions, which should result in fewer emerging insects. The absence of this effect in our study could be due to the natural temperature fluctuations associated with the day-night cycle, which may have allowed for better salinity acclimation under higher temperatures. Moreover, higher temperatures within the optimal range can enhance metabolic rates and development, potentially improving overall survival conditions (Bonacina et al., 2023). These natural temperature fluctuations, combined with the beneficial impact of elevated temperatures, may therefore counterbalance the negative effect of increased salinity by, for example, triggering accelerated development. This appears to hold true even when predator exposure and increased salinity occur simultaneously.

Regardless of whether the stressor was increased salinity or temperature, both stressors reduced the predator effects on the number of emerging insects. This reduction in predation effects extended to body size in the presence of higher salinity levels. These findings suggest that the anthropogenic stressors salinisation and warming interfere with predator-prey interactions, possibly by either altering the prey's sensory system or reducing the effectiveness of predator cues (Draper and Weissburg, 2019; Ross and Behringer, 2019). Otherwise, the combined stress caused by their interaction with predator exposure effects could have also resulted in changed behaviour and life history traits. These observations are consistent with our previous research on drift behaviour (Vermiert et al., 2024b), where anthropogenic stressors similarly diminished predator-induced responses in prey taxa. The disruption of predation effects is likely to be caused not only by salinity and temperature but also by multiple other anthropogenic stressors. This has been observed in other studies, where changes in CO₂, pH, and the input of plastic waste disrupt biotic interactions among taxa such as *Daphnia*, Salmon, and others (Ou et al., 2015; Roggatz et al., 2022; Trotter et al., 2019; Weiss et al., 2018).

4.2. Recovery phase

Predator exposure alone continued to reduce the number of emerging insects during the recovery phase. This is not surprising, as we also introduced fish-cue enriched water throughout this phase, not treating it as a stressor to be removed, but rather as a natural component of the ecosystem. The sustained effect of predator cues suggests that their influence on insects is not merely a temporary response but exerts a continuous impact on emerging insects in stream ecosystems.

The aftereffects of anthropogenic stressors on emerging insects during a recovery phase are largely understudied and we found no literature addressing the outcome. We observed that the effects of increased salinity and increased temperature on the emergence during the stressor phase did not appear to affect the number of emerging insects and only had a tendential influence on body size during the recovery phase. It is possible that some specimens affected during the stressor phase emerged only during the recovery phase, as hatching requires time. However, the pooling of samples and seeding of new invertebrates may have mitigated this effect. Alternatively, this could suggest that the stressors' impacts were only temporary and did not extend beyond the experimental stressor phase. This is likely due to the short duration of the stressor phase, the rapid turnover rates of certain emerging insects, and the reduced sample size, which may have hindered the detection of long-term effects. Additionally, given that new invertebrates were introduced at the start of the recovery phase, any lingering effects of the stressors may have been diluted, which could also explain the limited impact observed during this period. Future studies should examine whether a longer exposure period might produce lingering effects during recovery.

5. Conclusion

In conclusion, our study shows that predator effects on emerging insects are significantly altered by the anthropogenic stressors increased salinity and temperature. Even when increased temperature did not independently influence emergence numbers, it still interacted with predation risk to disrupt or modify the emergence process. This can have far-reaching consequences for aquatic and terrestrial insect communities at both the individual and population levels. Alterations in the timing or success of emergence due to environmental stressors could lead to desynchronization with seasonal cues, such as food availability or mating opportunities, which could reduce survival and reproductive success. For instance, if insects are forced to emerge prematurely due to unfavourable conditions, they may face higher mortality risks from insufficient energy reserves, poor weather conditions, or increased predation. Conversely, delayed emergence could result in missed reproductive windows or suboptimal conditions for adult survival. Many aquatic insects have short adult lifespans focused primarily on reproduction, so disruptions in emergence timing can severely impact population viability, potentially threatening the structure and function of aquatic ecosystems.

CRediT authorship contribution statement

Alexandra N. Hollstein: Writing – review & editing, Investigation, Formal analysis. **Jonathan Meisner:** Writing – review & editing, Investigation, Formal analysis. **Philipp M. Rehsen:** Writing – review & editing, Project administration, Methodology, Investigation. **Iris Madge Pimentel:** Writing – review & editing, Resources, Project administration, Methodology, Investigation, Formal analysis. **Arne J. Beermann:** Writing – review & editing, Project administration, Methodology. **Martin Horstmann:** Writing – review & editing, Writing – original draft, Formal analysis. **Florian Leese:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Anna-Maria Vermiert:** Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis. **Ralph Tollrian:** Writing – review & editing, Writing – original draft, Supervision, Resources, Funding acquisition, Conceptualization. **Linda C. Weiss:** Writing – review & editing, Writing – original draft, Supervision, Formal analysis.

Ethics

If this manuscript involves research on animals or humans, it is imperative to disclose all approval details.

All experimental procedures involving fish in this study were conducted in accordance with European Union Directive 2010/63/EU on the protection of animals used for scientific purposes. The study was reviewed and approved by the LANUV NRW under the following permit: Animal Experimentation License AZ 81–02.04.2021.A160, with final approval (including subsequently requested amendments) granted on 01.02.2022. Every effort was made to minimize stress and suffering throughout the experiment.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) used ChatGPT in order to improve readability and correct grammar. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the published article.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2025.e03700](https://doi.org/10.1016/j.gecco.2025.e03700).

Data Availability

Data will be made available on request.

References

- Åbjörnsson, K., Wagner, B.M.A., Axelsson, A., Bjerselius, R., Olsén, K.H., 1997. Responses of *Acilius sulcatus* (Coleoptera: Dytiscidae) to chemical cues from perch (*Perca fluviatilis*). *Oecologia* 111, 166–171. <https://doi.org/10.1007/s004420050221>.
- Atkinson, D., 1994. Temperature and organism size—a biological law for ectotherms? *Adv. Ecol. Res.* 25, 1–58. [https://doi.org/10.1016/S0065-2504\(08\)60212-3](https://doi.org/10.1016/S0065-2504(08)60212-3).
- Atkinson, D., 1995. Effects of temperature on the size of aquatic ectotherms: exceptions to the general rule. *J. Therm. Biol.* 20, 61–74. [https://doi.org/10.1016/0306-4565\(94\)00028-H](https://doi.org/10.1016/0306-4565(94)00028-H).
- Bănăduc, D., Curtean-Bănăduc, A., Barinova, S., Lozano, V., Afanasyev, S., Leite, T., Branco, P., Gomez Isaza, D., Geist, J., Tegos, A., Simić, S., Olosutean, H., Cianfanglione, K., 2024. Multi-interacting natural and anthropogenic stressors on freshwater ecosystems: their current status and future prospects for 21st century. *Water* 16, 1483. <https://doi.org/10.3390/w16111483>.
- Bauernfeind, E., Humpesch, U., 2001. Die Eintagsfliegen Zentraleuropas (Insecta: Ephemeroptera): Bestimmung und Ökologie. Verlag des Naturhistorischen Museums Wien.
- Beketov, M.A., Liess, M., 2007. Predation risk perception and food scarcity induce alterations of life-cycle traits of the mosquito *Culex pipiens*. *Ecol. Entomol.* 32, 405–410. <https://doi.org/10.1111/j.1365-2311.2007.00889.x>.
- Benard, M.F., 2004. Predator-induced phenotypic plasticity in organisms with complex life histories. *Annu. Rev. Ecol. Evol. Syst.* 35, 651–673. <https://doi.org/10.1146/annurev.ecolsys.35.021004.112426>.
- Berezina, N.A., 2003. Tolerance of freshwater invertebrates to changes in water salinity. *Russ. J. Ecol.* 34, 296–301. <https://doi.org/10.1023/A:1024597832095>.
- Bonacina, L., Fasano, F., Mezzanotte, V., Fornaroli, R., 2023. Effects of water temperature on freshwater macroinvertebrates: a systematic review. *Biol. Rev.* 98, 191–221. <https://doi.org/10.1111/brev.12903>.
- Cañedo-Argüelles, M., Kefford, B.J., Piscart, C., Prat, N., Schäfer, R.B., Schulz, C.J., 2013. Salinisation of rivers: an urgent ecological issue. *Environ. Pollut.* 173, 157–167. <https://doi.org/10.1016/j.envpol.2012.10.011>.
- Cañedo-Argüelles, M., Kefford, B., Schäfer, R., 2019. Salt in freshwaters: causes, effects and prospects - introduction to the theme issue. *Philos. Trans. R. Soc. B Biol. Sci.* 374, 20180002. <https://doi.org/10.1098/rstb.2018.0002>.
- Castillo, A.M., Sharpe, D.M.T., Ghalambor, C.K., De León, L.F., 2018. Exploring the effects of salinisation on trophic diversity in freshwater ecosystems: a quantitative review. *Hydrobiologia* 807, 1–17. <https://doi.org/10.1007/s10750-017-3403-0>.
- Chown, S.L., Gaston, K.J., 2010. Body size variation in insects: a macroecological perspective. *Biol. Rev.* 85, 139–169. <https://doi.org/10.1111/j.1469-185X.2009.00097.x>.
- Connolly, N.M., Crossland, M.R., Pearson, R.G., 2004. Effect of low dissolved oxygen on survival, emergence, and drift of tropical stream macroinvertebrates. *J. North Am. Benthol. Soc.* 23, 251–270. [https://doi.org/10.1899/0887-3593\(2004\)023<0251:EOLDOO>2.0.CO;2](https://doi.org/10.1899/0887-3593(2004)023<0251:EOLDOO>2.0.CO;2).
- Corbet, P.S., 1964. Temporal patterns of emergence in aquatic insects. *Can. Entomol.* 96, 264–279. <https://doi.org/10.4039/Ent96264-1>.
- Dallas, H.F., Ross-Gillespie, V., 2015. Sublethal effects of temperature on freshwater organisms, with special reference to aquatic insects. *Water SA* 41, 712–726. <https://doi.org/10.4314/wsa.v41i5.15>.
- Damos, P., Savopoulou-Soultani, M., 2012. Temperature-driven models for onset development and vital thermal requirements. *Psyche* 2012, 1–13. <https://doi.org/10.1155/2012/123405>.
- Danks, H.V., 1978. Some effects of photoperiod, temperature, and food on emergence in three species of chironomidae (diptera). *Can. Entomol.* 110, 289–300. <https://doi.org/10.4039/Ent110289-3>.
- Dodson, S.I., Crowl, T.A., Peckarsky, B.L., Kats, L.B., Covich, A.P., Culp, J.M., 1994. Non-visual communication in freshwater benthos: an overview. *J. North Am. Benthol. Soc.* 13, 268–282. <https://doi.org/10.2307/1467245>.
- Draper, A.M., Weissburg, M.J., 2019. Impacts of global warming and elevated CO₂ on sensory behaviour in predator-prey interactions: a review and synthesis. *Front. Ecol. Evol.* 7. <https://doi.org/10.3389/fevo.2019.00072>.
- Elbrecht, V., Beermann, A.J., Goessler, G., Neumann, J., Tollrian, R., Wagner, R., Wleclik, A., Piggott, J.J., Matthaei, C.D., Leese, F., 2016. Multiple-stressor effects on stream invertebrates: a mesocosm experiment manipulating nutrients, fine sediment and flow velocity. *Freshw. Biol.* 61, 362–375. <https://doi.org/10.1111/fwb.12713>.
- Elliott, J.M., Elliott, J.A., 1995. The critical thermal limits for the bullhead, *Cottus gobio*, from three populations in north-west England. *Freshw. Biol.* 33, 411–418. <https://doi.org/10.1111/j.1365-2427.1995.tb00403.x>.
- Gall, B.G., Brodie, E.D., 2009. Behavioural avoidance of injured conspecific and predatory chemical stimuli by larvae of the aquatic caddisfly *Hesperophylax occidentalis*. *Can. J. Zool.* 87, 1009–1015. <https://doi.org/10.1139/Z09-091>.
- Gillmann, S.M., Hering, D., Lorenz, A.W., 2023. Habitat development and species arrival drive succession of the benthic invertebrate community in restored urban streams. *Environ. Sci. Eur.* 35. <https://doi.org/10.1186/s12302-023-00756-x>.
- Hagstrum, D.W., Hagstrum, W.R., 1970. A Simple device for producing fluctuating temperatures, with an evaluation of the ecological significance of fluctuating temperatures. *Ann. Entomol. Soc. Am.* 63, 1385–1389. <https://doi.org/10.1093/aesa/63.5.1385>.
- Hassell, K.L., Kefford, B.J., Nuggeoda, D., 2006. Sub-lethal and chronic salinity tolerances of three freshwater insects: *Cloeon* sp. and *Centropitulum* sp. (Ephemeroptera: Baetidae) and *Chironomus* sp. (Diptera: Chironomidae). *J. Exp. Biol.* 209, 4024–4032. <https://doi.org/10.1242/jeb.02457>.

- Herbst, D.B., 2023. Developmental and reproductive costs of osmoregulation to an aquatic insect that is a key food resource to shorebirds at salt lakes threatened by rising salinity and desiccation. *Front Ecol. Evol.* 11. <https://doi.org/10.3389/fevo.2023.1136966>.
- Hogg, I.D., Williams, D.D., 1996. Response of stream invertebrates to a global-warming thermal regime: an ecosystem-level manipulation. *Ecology* 77, 395–407. <https://doi.org/10.2307/2265617>.
- Hurny, A.D., Wallace, J.B., 2000. Life history and production of stream insects. *Annu. Rev. Entomol.* 45, 83–110. <https://doi.org/10.1146/annurev.ento.45.1.83>.
- Jackson, J.K., Fisher, S.G., 1986. Secondary production, emergence, and export of aquatic insects of a Sonoran Desert stream. *Ecology* 67, 629–638. <https://doi.org/10.2307/1937686>.
- Jackson, J.K., Funk, D.H., 2019. Temperature affects acute mayfly responses to elevated salinity: Implications for toxicity of road de-icing salts. *Philos. Trans. R. Soc. B Biol. Sci.* 374. <https://doi.org/10.1098/rstb.2018.0081>.
- Kail, J., Palt, M., Lorenz, A., Hering, D., 2021. Woody buffer effects on water temperature: The role of spatial configuration and daily temperature fluctuations. *Hydrol. Process* 35, 1–12. <https://doi.org/10.1002/hyp.14008>.
- Kaushal, S.S., Likens, G.E., Pace, M.L., Reimer, J.E., Maas, C.M., Galella, J.G., Utz, R.M., Duan, S., Kryger, J.R., Yaculak, A.M., Boger, W.L., Bailey, N.W., Haq, S., Wood, K.L., Wessel, B.M., Park, C.E., Collison, D.C., Aisin, B.Y., 'aaqob, I., Gedeon, T.M., Chaudhary, S.K., Widmer, J., Blackwood, C.R., Bolster, C.M., Devilliss, M.L., Garrison, D.L., Halevi, S., Kese, G.Q., Quach, E.K., Rogelio, C.M.P., Tan, M.L., Wald, H.J.S., Woglo, S.A., 2021. Freshwater salinisation syndrome: from emerging global problem to managing risks. *Biogeochemistry* 154, 255–292. <https://doi.org/10.1007/s10533-021-00784-w>.
- Keenleyside, M.H.A., 1955. Some aspects of the schooling behaviour of fish. *Behaviour* 8, 183–248.
- Kleiber, C., Zeileis, A., 2008. *Applied Econometrics with R*. Applied Econometrics with R. Springer New York, New York. <https://doi.org/10.1007/978-0-387-77318-6>.
- Kottelat, M., Freyhof, J., 2007. *Handbook of European freshwater fishes*. Copeia. Publications Kottelat, Cornol and Freyhof, Berlin.
- Lancaster, J., Downes, B.J., 2013. *Development. Aquatic Entomology*. Oxford University Press. <https://doi.org/10.1093/acprof:oso/9780199573219.001.0001>.
- Lenth, R.V., 2023. emmeans: Estimated marginal means, aka least-squares means.
- Lob, D.W., Silver, P., 2012. Effects of elevated salinity from road deicers on *Chironomus riparius* at environmentally realistic springtime temperatures. *Freshw. Sci.* 31, 1078–1087. <https://doi.org/10.1899/12-095.1>.
- Lubini, V., Knispel, S., Vincin, G., 2012. Die Steinfliegen der Schweiz: Bestimmung und Verbreitung. Schweizerische Entomologische Gesellschaft, Neuenburg.
- Madge Pimentel, I., Rehse, P.M., Beermann, A.J., Leese, F., Piggott, J.J., Schmuck, S., 2024b. An automated modular heating solution for experimental flow-through stream mesocosm systems. *Limnol. Oceanogr. Methods* 22, 135–148. <https://doi.org/10.1002/lom3.10596>.
- Madge Pimentel, I., Baikova, D., Buchner, D., Burfeid Castellanos, A., David, G.M., Deep, A., Doliwa, A., Hadziomerović, U., Mayombo, N.A.S., Prati, S., Spyra, M.A., Vermiert, A.-M., Beisser, D., Dunthorn, M., Piggott, J.J., Sures, B., Tiegs, S.D., Leese, F., Beermann, A.J., 2024a. Assessing the response of an urban stream ecosystem to salinisation under different flow regimes. *Sci. Total Environ.* 926, 171849. <https://doi.org/10.1016/j.scitotenv.2024.171849>.
- Nakano, S., Murakami, M., 2001. Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. *Proc. Natl. Acad. Sci.* 98, 166–170. <https://doi.org/10.1073/pnas.98.1.166>.
- Nebecker, A.V., 1971. Effect of water temperature on nymphal feeding rate, emergence, and adult longevity of the stonefly *Pteronarcys dorsata*. *J. Kans. Entomol. Soc.* 44, 21–26.
- Nordlie, K.J., Arthur, J.W., 1981. Effect of elevated water temperature on insect emergence in outdoor experimental channels. *Environ. Pollut.* 25, 53–65. [https://doi.org/10.1016/0143-1471\(81\)90114-8](https://doi.org/10.1016/0143-1471(81)90114-8).
- Ou, M., Hamilton, T.J., Eom, J., Lyall, E.M., Gallup, J., Jiang, A., Lee, J., Close, D.A., Yun, S.S., Brauner, C.J., 2015. Responses of pink salmon to CO₂-induced aquatic acidification. *Nat. Clim. Chang* 5, 950–957. <https://doi.org/10.1038/nclimate2694>.
- Peckarsky, B.L., 1996. Alternative predator avoidance syndromes of stream-dwelling mayfly larvae. *Ecology* 77, 1888–1905. <https://doi.org/10.2307/2265793>.
- Peckarsky, B.L., Penton, M.A., 1989. Early warning lowers risk of stonefly predation for a vulnerable mayfly. *Oikos* 54, 301. <https://doi.org/10.2307/3565289>.
- Piggott, J.J., Townsend, C.R., Matthaei, C.D., 2015. Climate warming and agricultural stressors interact to determine stream macroinvertebrate community dynamics. *Glob. Chang. Biol.* 21, 1887–1906. <https://doi.org/10.1111/gcb.12861>.
- R Core Team, 2024. *R: A Language and Environment for Statistical Computing*.
- Roggatz, C.C., Saha, M., Blanchard, S., Schirmacher, P., Fink, P., Verhegge, J.D., 2022. Becoming nose-blind—Climate change impacts on chemical communication. *Glob. Chang. Biol.* 28, 4495–4505. <https://doi.org/10.1111/gcb.16209>.
- Ross, E., Behringer, D., 2019. Changes in temperature, pH, and salinity affect the sheltering responses of Caribbean spiny lobsters to chemosensory cues. *Sci. Rep.* 9, 1–11. <https://doi.org/10.1038/s41598-019-40832-y>.
- Schaefer, M., 2018. *Brohmer. Fauna von Deutschland*. Quelle & Meyer Verlag GmbH & Co, Wiebelsheim.
- Silberbush, A., Abramsky, Z., Tsurim, I., 2015. Effects of fish cues on mosquito larvae development. *Acta Trop.* 150, 196–199. <https://doi.org/10.1016/j.actatropica.2015.08.001>.
- Silberbush, A., Gertler, N., Ovadia, O., Abramsky, Z., Tsurim, I., 2019. Kairomone-induced changes in mosquito life history: effects across a food gradient. *Aquat. Sci.* 81, 53. <https://doi.org/10.1007/s00027-019-0649-9>.
- Sweeney, B.W., Vannote, R.L., 1982. Population synchrony in mayflies: a predator satiation hypothesis. *Evol. (N. Y)* 36, 810. <https://doi.org/10.2307/2407894>.
- Trotter, B., Ramsperger, A.F.R.M., Raab, P., Haberstroh, J., Laforsch, C., 2019. Plastic waste interferes with chemical communication in aquatic ecosystems. *Sci. Rep.* 9, 1–8. <https://doi.org/10.1038/s41598-019-41677-1>.
- van Uitregt, V.O., Hurst, T.P., Wilson, R.S., 2012. Reduced size and starvation resistance in adult mosquitoes, *Aedes notoscriptus*, exposed to predation cues as larvae. *J. Anim. Ecol.* 81, 108–115. <https://doi.org/10.1111/j.1365-2656.2011.01880.x>.
- Vermiert, A.-M., Madge Pimentel, I., Rehse, P.M., Meisner, J., Horstmann, M., Beermann, A.J., Leese, F., Weiss, L.C., Tollrian, R., 2024a. Fish predation induces drifting and emergence in an experimental stream mesocosm system. Preprint. <https://doi.org/10.1101/2024.07.04.602120>.
- Vermiert, A.-M., Madge Pimentel, I., Rehse, P.M., Otto, T., Horstmann, M., Beermann, A.J., Leese, F., Weiss, L.C., Tollrian, R., 2024b. Salinisation and warming disrupt predator-induced drift behaviour in aquatic predator-prey interactions. Preprint. <https://doi.org/10.1101/2024.07.02.601583>.
- Vos, M., Hering, D., Gessner, M.O., Leese, F., Schäfer, R.B., Tollrian, R., Boenigk, J., Haase, P., Meckenstock, R., Baikova, D., Bayat, H., Beermann, A., Beißer, D., Beszteri, B., Birk, S., Boden, L., Brauer, V., Brauns, M., Buchner, D., Burfeid-Castellanos, A., David, G., Deep, A., Doliwa, A., Dunthorn, M., Enß, J., Escobar-Sierra, C., Feld, C.K., Fohrer, N., Grabner, D., Hadziomerovic, U., Jähnig, S.C., Jochmann, M., Khaliq, S., Kiesel, J., Kuppels, A., Lampert, K.P., Le, T.T.Y., Lorenz, A.W., Madariaga, G.M., Meyer, B., Pantel, J.H., Pimentel, I.M., Mayombo, N.S., Nguyen, H.H., Peters, K., Pfeifer, S.M., Prati, S., Probst, A.J., Reiner, D., Rolauffs, P., Schlenker, A., Schmidt, T.C., Shah, M., Sieber, G., Stach, T.L., Tielke, A.K., Vermiert, A.M., Weiss, M., Weitere, M., Sures, B., 2023. The Asymmetric Response Concept explains ecological consequences of multiple stressor exposure and release. *Sci. Total Environ.* 872. <https://doi.org/10.1016/j.scitotenv.2023.162196>.
- Ward, J.V., Stanford, J.A., 1982. Thermal responses in the evolutionary ecology of aquatic insects. *Annu. Rev. Entomol.* 27, 97–117. <https://doi.org/10.1146/annurev.ento.27.010182.000525>.
- Weiss, L.C., Tollrian, R., 2018. Predator-induced defences in crustacea. *Life Histories*. Oxford University Press, New York, pp. 303–322. <https://doi.org/10.1093/oso/9780190620271.003.0012>.
- Weiss, L.C., Pötter, L., Steiger, A., Kruppert, S., Frost, U., Tollrian, R., 2018. Rising pCO₂ in freshwater ecosystems has the potential to negatively affect predator-induced defences in Daphnia. *Curr. Biol.* 28, 327–332. <https://doi.org/10.1016/j.cub.2017.12.022>.
- Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T., Miller, E., Bache, S., Müller, K., Ooms, J., Robinson, D., Seidel, D., Spinu, V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K., Yutani, H., 2019. Welcome to the Tidyverse. *J. Open Source Softw.* 4, 1686. <https://doi.org/10.21105/joss.01686>.

- Winking, C., Lorenz, A.W., Sures, B., Hering, D., 2016. Start at zero: succession of benthic invertebrate assemblages in restored former sewage channels. *Aquat. Sci.* 78, 683–694. <https://doi.org/10.1007/s00027-015-0459-7>.
- Woodward, G., Perkins, D.M., Brown, L.E., 2010. Climate change and freshwater ecosystems: impacts across multiple levels of organisation. *Philos. Trans. R. Soc. B Biol. Sci.* 365, 2093–2106. <https://doi.org/10.1098/rstb.2010.0055>.
- Zhang, V.M., Martin, R.L., Murray, R.L., 2022. Chronic road salt exposure across life stages and the interactive effects of warming and salinity in a semiaquatic insect. *Environ. Entomol.* 51, 313–321. <https://doi.org/10.1093/ee/nvac014>.