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Biting the hand that feeds: anthropogenic drivers interactively make mosquitoes thrive

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Abstract:

Anthropogenic strestors on the environment are increasing at unprecedented rates and include urbanization, nutrient pollution, water management, altered land use and climate change. Their effects on disease vectors are poorly understood. A series of full factorial experiments investigated how key human induced abiotic pressures, and interactions between these, affect population parameters of the cosmopolitan disease vector, *Culex pipiens* s.l. Selected pressures include eutrophication, salinity, mean temperature, and temperature fluctuation. Data were collected for each individual pressure and for potential interactions between eutrophication, salinization and temperature. All experiments assessed survival, time to pupation, time to emergence, sex-ratio and ovipositioning behavior. The

results show that stressors affect vector survival, may speed up development and alter female to male ratio, although large differences between stressors exist to quite different extents. While positive effects of increasing levels of eutrophication on survival were consistent, negative effects of salinity on survival were only apparent at higher temperatures, thus indicating a strong interaction effect between salinization and temperature. Temperature had no independent effect on larval survival. Overall, increasing eutrophication and temperatures, and the fluctuations thereof, lowered development rate, time to pupation and time to emergence while increasing levels of salinity increased development time. Higher levels of eutrophication positive, impacted egg-laying behavior; the reverse was found for salinity while no effects of temperative on egg-laying behavior were observed. Results suggest large and positive impacts of arthrop genically induced habitat alterations on mosquito population dynamics. Many of these effect as exacerbated by increasing temperatures and fluctuations therein. In a world where eutrophic tich and salinization are increasingly abundant, mosquitoes are likely important benefacte s. U timately, this study illustrates the importance of including multiple and combined stressers in predictive models as well as in prevention and mitigation strategies, particularly beca se they resonate with possible, but yet underdeveloped action plans.

Keywords: Interactive effects; Habitat alteration; Mosquito; Planetary Boundary Framework; Salinization; Temperature fluctuations

Introduction

Anthropogenic pressures play a pivotal role in shaping ecosystems on a global and local scale (Foley et al. 2005; Nelson et al. 2006), and subsequently affect species abundance and composition (Barausse et al. 2011; Di Cecco and Hurlbert 2022; Eremeeva and Sushchev 2005). While most insect species are declining due to anthropogenic pressures, such as urbanization, agricultural practices, water management and climate change (Hallmann et al. 2017; van der Sluijs 2020), recent evidence shows that many mosquito species thrive under these conditions (Colón-González et al. 2021; Messina et al. 2019; Roche et al. 2015), thus showing a contrasting pattern, particularly in areas of high anthropogenic pressures (Kamdem et al. 2012; Nilsson et al. 2018; Commental changes might have a positive impact on the availability of disease transmitting organisms (hre. fter vectors), which might also influence the incidence of mosquito transmitted pathogens, such as protozoa and rthropod-borne viruses (arboviruses) (Franklinos et al. 2019; Kamdem et al. 2012; Neiderud 2015).

Research on understanding impacts of human-indu ed changes on infectious diseases has until now focused on the large-scale influence of climatic variables such as mean temperature for mosquito occurrence and precipitation for mosquito abundance (Loetti, Schweigmann, nd the morial 2011; Mottram, Kay, and Fanning 1994; Petrić et al. 2014; Reisen, Milby, and Bock 1984), while the effects of anthropogenic pressures that operate mainly on a local scale have been poorly addressed. Such local scales field of the effects of changes in land use, freshwater use, biogeochemical flows, local teraperature fluctuations, as well as the interplay between these drivers on microclimatic conditions (Reperature fluctuations, as well as the interplay between these drivers on microclimatic conditions (Reperature) (Ferraguti et al. 2016; Krol et al., 2022; Schrama et al. 2020; Versteirt et al. 2013), a comprehensive understanding of the causal relationships between mosquito population size and structure and specific landscape features is lacking (Franklinos et al. 2019; Schrama et al. 2020). Moreover, the interactions of the different pressures, which often co-occur, have not been investigated in depth (fig. 1, supplementary table 1). To understand the importance of these key anthropogenic pressures on mosquito population dynamics, which might lead to increased vulnerability to changes in (combinations of) environmental factors, in-depth experimental work is needed.



Figure 1 Overview of anthropogenic pressures as drivers on abiotic pressure. and its impacts on downstream population parameters of mosquitoes. For each of the established impacts betv eet pressures and states, it is indicated whether the association is positive (+), negative (-) or both (+/-) (based lite rature summarized in Supplementary Table 1). Question marks indicate hypothesized links and interactions of pressures with refurther work is needed.

Here, we experimentally explore the impart of salinization, temperature and eutrophication on mosquito populations (Figure 1). Freshwater use – more broadly defined as water management, thus including biogeochemical flow boundaries – mainly impacts entrophication, temperature, and salinity by a variety of pathways, such as dredging of inland water bodies (Lohrer and Wetz 2003; Smithand Huang 2010), water retention (Ceccatelli et al. 2021; Modoni et al. 2013; Zhu et al. 2015) and freshwater extraction (de Louw et al. 2013; Schmork and Mercado 1969). Land use change, in which humans transform the natural landscape impacts water bodies with respect to dissolved nutrient concentrations (potentially leading to eutrophication) and temperature via changes in sunlight in cleared areas (Franklinos et al. 2019) and albedo (Adegoke, Pielke, and Carleton 2007), respectively. Climate change, caused by greenhouse gas emissions leads to increasing mean temperatures and changes in diurnal temperature oscillations due to increasing nightly temperatures (Braganza, Karoly, and Arblaster 2004).

Each of these large-scale environmental impacts can be expected to directly affect mosquito populations. Salinization, which occurs naturally in coastal areas (Don et al. 2006; Lassiter 2021), is strengthened by climate induced sea-level rise, draining of fresh water, management of waterways and exploitation of groundwater for agriculture (Pauw, de Louw, and Essink 2012). It is known to have species specific impacts on mosquito mortality rates (Jude et al. 2012; Kengne et al. 2019; Mottram et al. 1994) and egg laying (hereafter ovipositioning) behavior (De Brito Arduino et al. 2015; Navarro et al. 2003; Silberbush et al. 2014), but landscape wide responses to changes in salinity levels are poorly characterized. Eutrophication has previously been shown to influence development speed, survival, sex-ratio (Krol et al. 2019; Merritt et al. 1992; Reisen et al. 198.¹⁷ Rejmánková et al. 2013; Schrama et al. 2018) and ovipositioning behavior (Rejmánková et al. 2013), but interactions with other stressors, e.g. larval densities of the same species (hereafter conspecific density), are not well 'epre ented.

While the effects of temperature on mosquitoes have been studied extrasively, the effects of an increases in temperature fluctuations, which is expected because of clime '/ change (IPCC 2021), are yet unknown. Temperature is known to affect mosquito development speed and' motality levels as well as sex-ratio with sex-specific effects (Loetti et al. 2011; Mottram et al. 1994; Petrić et al. 2011'b; Reisen et al. 1984), where increasing temperature generally leads to shortened development times and nigher mortality. However, the vast majority of experiments focusing on temperature have been performed by manipulating (continuous) mean temperatures (Ciota et al. 2014; Kiarie-Makara, Ngumbi, and Lee n.d.; metti et al. 2011), even though temperature fluctuations have previously been hypothesized to influence mosquito development (Alcalay et al. 2018; Couret and Benedict 2014; Mottram et al. 1994). As yet, its impact and is severely understudied (Alcalay et al. 2018; Beck-Johnson et al. 2017).

Aside from a comprehensive understanding of the isolated effects of the selected stressors, there is also a large potential for the influence of non-additive interactive effects (Tran et al. 2018). Indeed, a growing number of studies point to the ubiquity of interactive non-additive effects between stressors on population parameters (Agnew, Haussy, and Michalakis 2000; Alcalay et al. 2018; Couret and Benedict 2014; Schrama et al. 2018), but little is currently known about interactive effects. Interaction between eutrophication, larval density and temperature may manifest itself as changes in food intake per capita; interaction between salinization and temperature might increase energy expenditure for active osmoregulation via increased competition (Bradley 1987; Kengne et al. 2019). The current

lack of information on solitary and interactive effects of the selected stressors calls for a coherent and comprehensive assessment.

This study aims to evaluate and quantify the effects of eutrophication, salinization, temperature fluctuations including the interactions between eutrophication and conspecific density, temperature and eutrophication, and temperature and salinity on multiple mosquito population parameters in a series of mesocosm experiments. The cosmopolitan mosquito species *Culex pipiens s.l.* (hereafter denoted as *Cx. pipiens*) is used as a model species. Cx. *pipiens* is a known vector, e.g., for West Nile virus, Usutu virus, Sindbis virus, ...d parasites Filarioidea, Plasmodium and Hemoproteus (Bravo-Barriga et al. 2016; Gutiérrez-López et al. 2016; Hubálek 2008; Kazlauskienė et al. 2013). It has a wide habitat tolerance ranging from clean rainwater- illed containers to strongly polluted temporal waterbodies such as ground puddles and even manure tan¹..., 'Recker et al. 2013; Rejmánková et al. 2013). Wild caught individuals were used – unless mention otherwise – vithe it distinguishing between the different (sub)species of the species complex. This allowed for a more face rate estimate of the pressures on a mixed natural community.

Methods

2.1 General experimental design

All experiments were carried out in porpropylene mesocosm containers under outdoor conditions at the Living Lab field station or at the botarical gard n of Leiden University, The Netherlands. The experiments focused on semi-realistic field conditions, as the emperatures, eutrophication levels and salinities are representative of a range of larval habitats (Alcalay, Tsurim, and Ovadia 2019; Ikeshoji and Mulla 1970; Loeb and Verdonschot 2008; Oude Essink, van Baaren, and de Louw 2010; Rockett 1987; Wallis 1954). The treatments were - unless mentioned otherwise - applied to 65L black polypropylene mesocosms filled up to 30 liters and placed in a second, fully buried identical mesocosm thus providing an air-filled layer of insulation to buffer temperature fluctuations (Krol et al. 2019).

Each mesocosm was filled with tap water and then spiked with a microbial community acquired by filtering a standardized amount of water from an adjacent lake through a Φ 200 nm plankton net with Φ 53 µm collector, so

that each volume of water in the mesocosms contained a similar microbial community to that found in the same volume of water in the lake. To simulate the different levels of eutrophication standardized dried cow manure (2.4% N; 1.5% P_2O_5 ; 3.1% K_2O) was added. The mesocosms were then left to incubate for a minimum of one week so that the microbial communities could stabilize. During this period, the mesocosms were covered with shading cloth to prevent Chironomidae and Culicidae colonization. After the acclimation period, all water within the mesocosms was filtered with a Φ 300 µm sieve, to remove large particles and any remaining macro-invertebrates. Unless mentioned otherwise, *Culex pipiens* s.l. egg rafts were collected during a four-day period prior to the start of an experiment from naturally colonized black plastic buckets at the Living lab field station. Lau we were randomly selected and then added in random block design.

During the experiments all containers were covered with emergence are pecies that might compete with the prevent i) colonization by *Culex pipiens* s.l. mosquitoes and any other species that might compete with the experimental population, ii) mosquito predators from entering and iii) trap emerged adults. The water level was kept stable by daily replenishment of the evaporated volume with dechlorinated tap water after measurements were taken. The temperature in each mesocosm was recorded every chirty minutes for the duration of each experiment by a temperature logger (iButton DS1921G#F5D) net the water surface. Abiotic conditions were measured weekly using a HACH HD40 for dissolved oxygen, p.⁴ and conductivity measurements, an Aquafluor 8000-010 for chlorophyll α and turbidity measurements and a Vernier Labquest2 for ammonium, chloride, nitrate and phosphor concentrations.

2.2 Experiments

2.2.1 Eutrophication-density interaction

The experiment on interactive effects of eutrophication and larval densities took place between August and October of 2020. Eutrophication levels were chosen so as to span the entirety of the oligotrophic-hypertrophic range with levels representing a low-eutrophic water body (5 mg/L N-total), a high-eutrophic water body (20 mg/L N-total) and a hypertrophic land puddle (100 mg/L N-total) (Loeb and Verdonschot 2008). To simulate the different levels of eutrophication standardized dry cow manure (2.4% N; 1.5% P₂O₅; 3.1% K₂O) was added. Larval densities

representative of 0.1, 1 and 10 egg rafts (20, 200 and 2000 larvae, respectively) were used to study the effects of increasing conspecific competition (Agnew et al. 2000). The treatments were applied with four replicates in a random block design.

Egg laying behavior was not measured within this experiment as the effects of eutrophication could be determined from experiment 2.2.2 and the effects of larval presence had already been studied (Mwingira et al. 2020).

2.2.2 Eutrophication-temperature interaction

The experiment on the interactive effects of eutrophication and temperature k vels vas conducted in 65L black polypropylene mesocosms filled up to 30 liters between April and June o [•]202[•] . Eutrophication levels were chosen as described in section 2.2.1, additionally including a treatment represent. g rainwater (0 mg/L N-total). Temperature levels were selected around the optimal rearing temp rail re (Loetti et al. 2011) and set at 20, 25 and 30 degrees Celsius. Temperature treatments were regulated usin r 20[•] W heaters (HSaqua).

The treatments were applied with four replicates in a ran dom block design. Twenty first instar larvae were added to each of the mesocosms. The low larval density surved to exclude potential effects of density dependence (Alcalay et al. 2018). After the experiment, each mesocosm was filtered with a Φ 300 µm sieve to remove any remaining (dead) larvae and/or pupae. The emergence trape were then removed and ovipositioning choice was scored for five consecutive days.

2.2.3 Salinity and temperature interaction

The experiment on interactive effects of salinity and temperature was conducted in white 12L polypropylene mesocosms filled to 10 liters during the months of May and June of 2021. The selected salinity levels were representative for the current and expected salinity levels encountered at the Dutch coastal areas, freshwater (0 g/L chloride), brackish (0.3 g/L chloride) and saline (1 g/L chloride) conditions (Oude Essink et al. 2010).

Salinity levels were applied using a natrium chloride stock solution. Temperature levels were selected near the optimal rearing temperature (Loetti et al. 2011) and set at 27 and 30 degrees Celsius. A eutrophication level of 20

mg N-total was applied to minimize competition over resources, as determined by the experiment described in section 2.2.1. The salinity-temperature treatments were applied and 200 first instar larvae were added with three replicates in a random block design. Any pupa encountered during the experiment was counted and removed as the pupae do not eat and have a hardened exoskeleton (Becker et al. 2010), which limits their interaction with the environment (Balasubramanian et al. 2019; Mottram et al. 1994; Patrick and Bradley 2000). Consequently, data on time to emergence and sex-ratio were not collected for this experiment.

To test the effect of salinity on ovipositioning choice, 5 blocks of five 12L black mesocosms were prepared with a concentration that is representative of the range between freshwater and saltwate⁻ (0, 0.4, 1.6, 16 and 32 g/L natrium chloride). The blocks were distributed across the botanical gardens (80 meter apa) in the shade. Egg rafts were collected for five consecutive days.

2.2.4 Temperature fluctuations

The experiment on the effects of increasing levels of temper, the luctuation was executed in white 12L polypropylene mesocosms filled to 10 liters betwee the end of March and beginning of May 2021. This experiment took place during the overwintering of the natural populations, so that the ambient temperature would not overtake the experimental temperatures. During this experiment, the water temperature conditions of an average day in June were mimicked. June is commonly regarded and the optimal month for mosquito development in NW Europe as the amount of sunlight energy is maximal (Lecker et al. 2010).

To determine appropriate te. bc. *ares, water surface temperatures were monitored in three white 8L containers with an interval of 30 minutes between the months of May and July 2020. From these data a mean, minimum and maximum temperature, as well as the temporal interval between these, were derived and used to set four treatments of increasing fluctuation with the same amount of energy applied per 24 hours. These included a constant, block and curve scheme as well as a treatment with twice the amplitude of daily fluctuations, hereafter referred to as curve2 (supplementary figure 1). The treatments were temperature-controlled with thermostats and an Arduino UNO microcontroller. For this experiment *Culex pipiens pipiens* first instar larvae were obtained from culture from Wageningen University & Research, The Netherlands. The treatments were applied and 200 first instar larvae were added with five replicates in a random block design. A eutrophication level of 20 mg N-total was applied to

minimize competition over resources, as determined during the experiment on interactive effects of eutrophication and larval density (see section 2.2.1). Egg laying behavior was not measured within this experiment as temperature was determined to not affect larval habitat site selection during the experiment on interactive effects of temperature and eutrophication (see section 2.2.2).

2.3 Rearing of larvae

For the experiment on temperature fluctuations *Culex pipiens pipiens* first instar larvae were obtained from culture from Wageningen University & Research, The Netherlands.

For the remaining experiments, *Culex pipiens* s.l. egg rafts were collected during the four days prior to the start of an experiment from naturally colonized black plastic buckets at the Living lag field station. For this, the buckets were filled with 6 liters hypertrophic water (100mg N-total). The larvae weight subsequently allowed to hatch in white 12L mesocosms containing 10 liters of lake water where they weight at ambient temperature until the start of the experiment. Previous pilot studies indicated that this, type of experiments attracts *Culex pipiens* only. The collected egg rafts were distinguished from those of *Culiseta annulata* by their difference in size (Chapman et al. 2020; Sames, Schleichi, and Johnson 2005).

2.4 Measurements and life stage identification

Larval development was measured nor days a week by stirring clockwise once with a 400 mm wide Φ 200 µm sieve to create a circular water flow to prevent the larvae from diving. The sieve was subsequently used to collect the larvae by fully submerging the sieve and moving anti-clockwise twice. All collected larvae were morphologically characterized to developmental stage by using the size of the head capsule as a morphological indicator (Becker et al., 2010). The identifications were compared daily with a previously reared reference collection of *Cx. pipiens* developmental stages. The procedure was repeated up to five times until at least five, twenty or a hundred larvae were sampled for the densities of 20, 200 and 2000, respectively.

Each day, emerged mosquitoes were collected with an aspirator and sex was determined based on characteristics including, but not limited to, plumose/pilose antennae, and the length of the palps (Becker et al. 2010). The survival

rate was determined by dividing the number of adults that had emerged by the applied density. The median time to pupation was defined as the interval between the start of the experiment and the first day upon which at least 50% of the subsampled larvae had turned/developed into pupae. The median time to emergence was determined by calculating the interval between the start of the experiment and capture of 50 percent of the emerged adults. When no more pupae and adult mosquitoes were found for two subsequent days in a mesocosm, it was assumed that there were no living mosquitoes left and the mesocosm was closed off.

Ovipositioning behavior was recorded by daily counts of egg rafts per mesocosi, oer day. Encountered egg rafts were removed to minimize the positive feedback caused by their presence (B uno and Laurence 1979).

2.5 Statistical analysis

All data were analyzed in R version 4.04 (R Core Team, 2022). Differences in survival, development, sex-ratio and ovipositioning behavior between and within eutrophication and temperature levels and between levels of temperature if luctuation, were tested with general linear models comparing the number of emerged mosquitos, average a velopment stage, the number of emerged mosquitoes per sex and the number of egg-rafts respectively. Dreaded oxygen, nitrate, ammonium, and chloride levels as well as chlorophyll α concentrations were included a main effects. The effects of survival, development and ovipositioning behavior between and within salinity and temperature levels, were tested with general linear models comparing the number of emerged mosquitos, average and the number of egg-rafts respectively. Dreaded as main effects. The effects of survival, development and ovipositioning behavior between and within salinity and temperature levels, were tested with general linear models comparing the number of emerged mosquitos, average development stage and the number of egg-rafts respectively. For this, chlorophyll α and dissolved $xy_{e^{-1}}$ concentrations were included as main effects. Lastly, the effects of survival and development between and within salinity and temperature levels, were tested with general linear models comparing the number of emerged mosquitos and average development stage. For this, chlorophyll α and dissolved oxygen concentrations were included as main effects. All (16) corresponding full models are presented in Supplementary Table 2. Covariates and their interactions were stepwise removed from the full models during model optimization if not significant and if the Akaike information criterion indicated a worse fit of the data.

Results

As the aim of this paper is to shed light on the effect that anthropogenic pressures have on each of the population parameters, the results have been grouped per dependent variable. This facilitated the comparison of effects between the different pressures. Estimated regression coefficients and standard errors for each of the tests are listed in supplementary table 2.

3.1 Impact of anthropogenic pressures on absolute survival

Absolute survival rate was not impacted by different levels of temperature, temperature fluctuations, or combined effects of temperature and eutrophication within the ranges tested (p>0.1). Surv. al did however decrease under increasing temperatures within the saline treatment ($F_{(22,178)} = 1.983$, p<0.01, varti 1 $\omega^2 = 0.073$, power = 0.964). Post hoc analysis revealed significant differences in survival between the 'high st salinity at 30 degrees and lowest salinity at 27 degrees for day 7 of the experiment and between the 'r-c 'en.peratures at the highest salinity for days 7 and 10 (p<0.05 after Bonferroni correction) (Figure 1a). Survival 'lso 'ecreased with increased conspecific density ($F_{(2, 25)} = 11.613$, p < 0.001, partial $\omega^2 = 0.384$, power = 0.96 ° and decreasing amounts of food per capita ($F_{(4, 25)} = 5.745$, p = 0.002, partial $\omega^2 = 0.358$, power = 0.981°. Po t hoc analysis revealed significant differences between the oligotrophic treatment with 2000 larvae and all other tree timents (p<0.001, Bonferroni correction) as well as among the hypertrophic treatments with 20 and 200 'arv. • (p<0.05, Bonferroni correction; figure 1d).



Figure 1: Absolute survival rate across different anth opor enic pressures

Absolute survival rate depicted as the number of emerged adu's as a fraction of the initial number of larvae at the end of each experiment for A. effects of salinity at different ter $r_{t'}$ ratues, B. increasing levels of temperature fluctuation, C. effects of increasing eutrophication at different temperations at ^{-1}D . effects of eutrophication at different densities

3.2 Impact of anthropogenic pressures with time to pupation

Development time up to p pat on d creased significantly with increasing temperatures in both the salinity experiment ($F_{(1,15)} = 4.868$, p<0.05, partial $\omega^2 = 0.156$, power = 0.594; Figure 2a) and the experiment on interactive effects of eutrophication and temperature ($F_{(2,40)} = 38.57$, p<0.001, partial $\omega^2 = 0.620$, power = 1; Figure 2c) by 7 and 3 days, respectively. Additionally a trend was found for the interaction between temperature and salinity ($F_{(2,15)}$ = 2.709, p<0.1, partial $\omega^2 = 0.140$, power = 0.529). Post hoc analysis revealed that this was caused by a trend in contrasts between the temperatures within highest salinity level (p<0.06, Bonferroni correction) (Figure 2a). Increasing levels of temperature fluctuation also decreased development time up to pupation. Differences were detected between the constant and curve treatments ($\chi^2 = 2.017$, p = 0.022) and the constant and curve 2 treatments ($\chi^2 = 2.711$, Df = 3, p = 0.003) (Figure 2b). No solitary or interactive effects of eutrophication level were found (Figure 2c) except at higher densities, where decreasing amounts of food per capita resulted in longer development

times. This was true when manipulating the eutrophication level ($F_{(2, 25)} = 22.286$, p < 0.001, partial $\omega^2 = 0.556$, power = 1), density ($F_{(2, 25)} = 5.924$, p =0.008, partial $\omega^2 = 0.225$, power = 0.876) and the combination of the two ($F_{(4, 25)} = 3.012$, p = 0.037, partial $\omega^2 = 0.191$, power = 0.802). Post hoc analysis revealed significant contrasts between the oligotrophic treatment with 2000 larvae (a) and all other treatments (b) (p<0.001, Bonferroni correction; Figure 2d).



Figure 2: Median time to pup. 'ion across different anthropogenic pressures

Time to pupation in days at the c...d of each experiment for A. temperature grouped by salinity, B. increasing levels of temperature fluctuation, C. temperature grouped by eutrophication and D. eutrophication grouped by density. a, b Significantly contrasting groups.

3.3 Impact of anthropogenic pressures on time to emergence

Development up to emergence was similarly impacted as development times decreased with increasing temperatures $(F_{(3, 41)} = 230.7, p<0.001, partial \omega^2 = 0.936, power = 1; Figure 3b)$. Increasing levels of temperature fluctuations lowered development time $(F_{(3, 14)} = 230.7, p < 0.001, partial \omega^2 = 0.833, power = 1)$. Post hoc analysis indicated differences between the constant treatment (a) and all other treatments (b, c) (P<0.001, Bonferroni correction) and

between the block (b) and curve treatments (c) (p<0.05, Bonferroni correction; Figure 3a). Eutrophication did not impact development under low densities but did so under higher densities (Figure 3c). Decreasing amounts of food per capita increased time to emergence when manipulating eutrophication levels ($F_{(2, 25)} = 19.429$, p < 0.001, partial $\omega^2 = 0.520$, power = 1), density ($F_{(2, 25)} = 4.246$, p =0.026, partial $\omega^2 = 0.160$, power = 0.741) and a trend was detected when altering both ($F_{(4, 25)} = 2.297$, p = 0.087, partial $\omega^2 = 0.132$, power = 0.672). Post hoc analysis revealed significant contrasts between the oligotrophic treatment with 2000 larvae (b) and all other treatments (a) (p<0.001, Bonferroni correction; Figure 3c).



Figure 3: Median time to emergence across different anthropogenic pressures

Time to emergence in days at the end of each experiment for A. increasing levels of temperature fluctuation, B. temperature grouped by eutrophication and C. eutrophication grouped by density. a, b, c Significantly contrasting groups.

3.4 Impact of anthropogenic pressures on sex ratio

The proportion of females increased with increasing temperatures ($F_{(2, 40)} = 38.57$, p < 0.001, partial $\omega^2 = 0.620$, power = 1; Figure 4b) and between the eutrophic and hypertrophic treatments ($H_{(2)} = 9.5126$, p = 0.015; Figure 4c)

within the highest density. The sex ratio was not impacted by temperature fluctuations and density within the ranges tested (p>0.05). No other effects on sex ratio were detected.



Figure 4: Sex-ratio (SR) across different anthrop maic pressures

Male to female sex ratio (transformed as pe ura, 'ogarithm) at the end of each experiment for A. increasing levels of temperature fluctuation, B. temperature grouped by eutrophication and C. eutrophication grouped by density.

3.5 Impact of anthropogenic Pressures on ovipositioning behavior

Egg laying behavior decreased with increasing salinity ($F_{(16,63)} = 8.480$, p<0.001, partial $\omega^2 = 0.491$, power = 1). Post hoc analyses revealed a contrast between the treatments 16g/L and 32g/L and all lower salinities after day 1 of the experiment (p<0.05, Bonferroni correction). Ovipositioning behavior also increased with increasing eutrophication ($\chi^2 = 32.857$, df = 3, p < 0.001). Post-hoc analysis indicated a difference between the hypertrophic treatment (b) and all other eutrophication levels (a).





Number of egg rafts for A. temperature grouped by salinity, B. temperature grouped by eucophication. a, b Significantly contrasting groups.

4. Discussion

Anthropogenic pressures are mounting in a fast-changing work? This study assessed the life-history responses of *Cx. pipiens* to the three most prominent anthropogenically induced pressures that act directly on the mosquito larval habitat: eutrophication, temperature, and salinizatio. A series of full-factorial mesocosm experiments demonstrated that each of these pressures, together shaping the 'arval habitat, are relevant during different immature life-stages. Overall, the results suggest large and previously underestimated impacts of multiple pressures – both single and interactive – on mosquito population drink mices, well beyond the impact of changes in temperatures. However, the direction and magnitude of the effect of stressors on the investigated mosquito life history parameters, differs profoundly between the investigates, stressors. Also, while interactive effects between stressors were common, some interactions are more important 'han others. These are further discussed in the following paragraphs.

4.1 Impacts of anthropogenic pressures on mosquito survival and development time

While eutrophication and conspecific density had large, consistent effects on larval survival, exposure to different temperature regimes and differences in salinity levels only showed effect on development time. These results likely reflect different physiological processes. Eutrophication acts directly on resource competition, temperature acts on metabolic rate and salt has a toxic though sublethal effect (Balasubramanian et al. 2019; Emidi et al. 2017). Indeed, under decreasing levels of eutrophication, larval survival was markedly lower as a result of fierce competition over resources (El Husseiny et al. 2018; Merritt, Dadd, and Walker 1992; Reisen et al. 1984). This is abundantly clear

when comparing the survival under the hypertrophic treatment (45%) to that in the oligotrophic treatment (<1%). Similar effects were found when comparing the survival at the highest larval densities (40%) to the lowest densities (55%) at average eutrophication levels. This effect has been reported to be even stronger when several developmental stages are present, as mosquito larvae have repeatedly been observed to cannibalize on lower instars (El Husseiny et al. 2018; Koenraadt and Takken 2003). The effect of salinity had a negatively and stepwise effect on the larval energy budget, likely because the toxic chloride needs to be expelled actively within *Culex* larvae (Bradley 1987; Bradley and Phillips 1976; Patrick and Bradley 2000), thus slowing larval development. The higher instars seemed disproportionally more sensitive to this effect, which can be explained to the lower surface-to-volume ratio of higher instars. Within the investigated temperature ranges, which mimic o₁ tima rearing conditions, a marked effect of temperature on development time was observed, which is in line with previously reported effects that relate this to an increase in metabolic rate. Overall, the results suggest the single effects of the investigated stressors on mosquito population parameters are present in each of the mosquite his of the investigated stressors and follow directly from the physiological processes they act on.

Although the results of the interactive experiments are is r more complex, in general terms they follow a very similar pattern. An illustration of this is the interactive effect of temperature with salinity and eutrophication. As temperature increases the metabolic rate, high or temperatures can be expected to lead to speeding up the single effects of both stressors. Indeed, the experimental results show that survival rate at oligotrophic conditions was lower when larvae were exposed to for temperatures. Likewise, larval survival at higher levels of salinity was lower when larvae were exposed to for the temperatures. As these results were all collected within a relevant parameter range for the currear northern European situation, it is difficult to make any inferences outside this range. For example to delta regions in tropical areas that struggle with salinization such as the region around the Mekong delta (Bauer et al. 2022). Likewise, higher temperatures above 30 degrees Celsius (Ciota et al. 2014; Loetti et al. 2011), but it is unknown whether this might change when interacting with other stressors. One effect that might be accentuated is the masking effect, where eutrophic conditions could mask temperature stress by facilitating rapid emergence, similar to what has been observed with its effect on pesticide toxicity (Barmentlo et al. 2018). A comparable exacerbation of stressor effects by interaction with mean temperature might be present for increasing

temperature fluctuations, as these seem to further increase metabolic rates which are discussed below. Although the experiments took place during different periods of the year, no confounding effects of photoperiod on development time were expected, as most experiments were conducted before mid-summer and diapause generally sets on after August (Robich and Denlinger 2005). Additionally, diapause-associated developmental alterations take place during adulthood (Robich and Denlinger 2005; Zhou and Miesfeld 2009), whereas these experiments were limited to sub-adult development.

4.2 Impact of fluctuating temperature regimes

The impacts of higher constant temperature on larval development rate are cl ar at 1 widely acknowledged (van der Have and de Jong 1996). The experiments demonstrated similar effects b th pl or to and during metamorphosis, irrespective of nutrient availability, but strengthened by increased scill, ity. Moreover, the results show that fluctuations in temperature have large effects on larval development tube, well beyond what was expected. Larval development time, at natural temperature fluctuations, was o have age 7 days shorter than under constant temperature regime. Several authors have previously hy other lized that temperature fluctuations might have a large effect on insect growth rate (Alcalay et al. 2018; Hagsturm and Milliken 1991; Loetti et al. 2011). The experimental results also show that most of these differences are is eduring pupation (Figure 2). This is probably caused by temperature sensitivity of a multitude of enzy patic reactions around different optimum temperatures impacting enzymatic activity and thereby metabolic rate, possibly as an evolutionary adaptation in cold-blooded organisms, as has been found in insects in general (Permatical 1983; Hagstrum and Milliken 1991).

4.3 Impacts of anthropogenic pressures on sex-ratio of mosquitoes

Anthropogenic pressures may have different effects on male and female mosquitoes, thus leading to sex-specific life history trajectories (Alcalay et al. 2018). For instance, although bigger males and females both live longer (Reisen et al. 1984), comparably lower natural selection for size might push males towards early maturation, leading to smaller sizes and wing length (Alcalay et al. 2018; Loetti et al. 2011; Reisen et al. 1984; Virginio, Oliveira Vidal, and Suesdek 2015). The longer average development time of female mosquitoes may also result in prolonged exposure to stress, potentially making them more vulnerable (Hamaidia and Soltani n.d.; Schrama et al. 2018; Virginio et al. 2015). These experiments show that significantly fewer females survived under the highest density where food-

stress was most prominent. Female abundance was higher at higher temperatures, irrespective of eutrophication level, which might be due to higher development rates allowing for earlier emergence and subsequent lower exposure to competition and chemical stressors such as secondary metabolites produced by cyanobacteria. Sex ratio was not affected by temperature fluctuations or density, the latter of which indicates that cannibalism is opportunistic and does not select for certain sexes, which is in line with Loetti et al.'s (2011) notion that sexual dimorphism in growth rate only exists from the fourth larval development stage onwards. Overall, our findings indicate that expected rising temperatures and nutrient pollution will lead to a higher female survival. As females represent the sex transmitting pathogens, this may have implications for disease ansmission.

4.4 Impacts of anthropogenic pressure on egg-laying behavior of mosqui res

The results show a pronounced impact on ovipositioning behavior for the hical cues (eutrophication and salinization), but no impact of temperature. These results are in line with the notion that *Cx. pipiens* is widely known to actively seek and evaluate temporal water bodies by sensitive, geneous substances (Becker et al. 2013), bacteria (Hasselschwert and Rockett 1988), pheromones (K and Elie. 1986; Michaelakis et al. 2005) and visual cues (Ortiz Perea and Callaghan 2017). Thus, increasing levels of extrophication, and the higher levels of bacterial activity that resulted from this, were indeed preferred during orgonal activity, as females oviposited exclusively in the hypertrophic treatment. Likewise, increasing salinity knows impacted ovipositioning behavior, though it is unclear whether ovipositioning responded directly to high salt levels or whether it occurred through salt-induced changes in bacterial composition. No measurable effect of the more on ovipositioning was observed, which is unexpected as higher water temperatures in larvations have very large impact on larval development rate, suggesting that the response is primarily chemically induced rather than physically. Thus, changes in water pollution or salt content may have far ranging consequences for ovipositioning, reinforcing some of the previously observed effects on development rate and survival.

4.5 Implications

The planetary boundary framework (Steffen et al. 2015) is commonly acknowledged as a concept defining the global drivers of environmental change and the safe operating space for humanity within them. Crossing the

boundaries increases the risk of large-scale and irreversible environmental changes. There is widespread consensus that, for the vast majority of species, crossing the planetary boundaries leads to long term negative effects at the individual or population level (Wu et al. 2021). So far, evidence for the effects on infectious diseases had remained fragmented (Butler 2012). Our results indicate that mosquito species may be suffering far less or even benefiting from large scale environmental change. Furthermore, the fact that the effect of most of these stressors was exacerbated by increasing temperatures illustrates how ongoing crossing of planetary boundaries may lead to even more beneficial habitat conditions. As such, these results underscore the importance of changes in environmental conditions (Lambin et al. 2010; Schrama et al. 2020) by identifying its consisten, oattern across a range of important stressors and climatic conditions. Given the global extent and intensity of the nves igated anthropogenic pressures, these results are likely relevant for a wide array of disease vectors and provide a mechanism for the association between ecosystem degradation and disease. Overall, these results starting, suggest that the planetary boundary concept has important consequences for changes to mosquito abur Jan and likely feeds through to changes in disease risk, thus highlighting the need to further include the c in nodels and interventions. The crucial question is, however, whether the mosquitoes are better adapted to t ese changes than their predators and (invasive) competitors, whose ranges are expanded due to human activities (Co. anzo, Kesavaraju, and Juliano 2005). As such, extended work is needed on interactions with(in) biotic procluses, including interspecific competition and predation.

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Authors' contributions

SB and MS conceived the general idea for the experiments. SB set up the experiments and carried out the measurements together with EJ, AU and LK. SB carried out all statistical analysis, with feedback provided by PB and MS. EB, EJ, MS and PB contributed to the writing of the manuscript. All authors read and approved the final manuscript.

Data availability

All data will be send upon request to the corresponding author.

Competing interests

The authors declare that they have no competing interests.

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Graphical abstract



Highlights

- Impacts of interlinked anthropogenic stressors are relatively unknown
- Such stressors include land use change, freshwater pollution, and extreme weather
- Full-factorial experiments assessed stressor impacts on disease vector Culex pipiens
- The stressors and their interactions had major impacts on key mosquito life-history traits
- Results show important ramifications for mosquito populations and the pathogenic landscape