**Effect of flash flooding on mosquito and community dynamics in experimental pools**

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Abstract

Pulsed disturbances of mosquito breeding sites are likely to have a direct negative effect on mosquitoes, but may also have indirect effects due to the alteration of community structure. These altered communities may become attractive to gravid mosquitoes searching for oviposition sites when the disturbances decrease the abundance of mosquito antagonists such as competitors, which often results in an increase in mosquito food resources such as algae. However, flash flood disturbances in intermittent riverbeds can also remove mosquito food resources such as algae, so that the net effect of flash floods could be either to increase or decrease mosquito abundance.

We conducted an outdoor mesocosm experiment to assess the effects of flash floods on mosquito oviposition habitat selection and larval abundance during the post-disturbance period of community recovery. Mesocosms were artificially flooded. Mosquito oviposition, immature abundance, invertebrate species diversity, chlorophyll *a*, and abiotic parameters were monitored. Our results showed that the flash flood negatively affected phytoplankton and zooplankton, leading to a decrease of mosquito oviposition in flooded mesocosms compared to non-flooded mesocosms. More broadly, this study indicates how disturbances influence mosquito oviposition habitat selection due to the loss of food resources in ephemeral pools, and highlights the importance of considering the effects of disturbances in management, habitat restoration and biodiversity conservation in temporary aquatic habitats.

Keywords: mosquito dynamics, community interactions, flash flood disturbance, oviposition habitat selection, mesocosms, ephemeral pools

Introduction

As defined by (Resh et al. 1988), a disturbance is any discrete event in time that is characterized by frequency, intensity, and severity outside a predictable range and that disrupts ecosystem, community, or population structure and changes resources or the physical environment. The most frequent disturbances along Mediterranean river beds are floods (Fisher et al. 1982). The time required for recovery depends on the stream type and intensity of the disturbance (Hoopes 1974, Siegfried and Knight 1977). A flash flood can affect nutrient concentration and organic matter (Hershkovitz and Gasith 2013), and can potentially reduce phytoplankton and periphyton as well as invertebrate and amphibian densities and richness (de Lucena Barbosa et al., Segev and Blaustein 2014).

By disturbing community structure (Whiles and Goldowitz 2005), flash floods in ephemeral stream channels may make the rock pools an attractive breeding site for mosquitoes due to a decrease in abundance of antagonists. A decrease in competitors often results in increased mosquito food availability such as algae and bacteria. Many studies have shown that mosquito oviposition in pools is not random with regards to the presence of predators and conspecifics (Blaustein et al. 2004, Kiflawi et al. 2003b, Stav et al. 2005, Blaustein et al. 1995, Blaustein and Margalit 1994, Blaustein 1998, Walton et al. 2009). When faced with a choice of breeding sites, female mosquitoes tend to oviposit in habitats which favour offspring fitness (Spencer et al. 2002). However, from the mosquito perspective, a flash flood disturbance to temporary pools along intermittent riverbeds may result in a reduction of mosquito food resources such as algae and bacteria as well as a reduction in mosquito antagonists. Whether or not mosquitoes might preferentially oviposit into flash-flooded pools or have better larval performance will depend on whether the reduction of antagonists overrides the reduction of food resources.

Mediterranean-climate regions are located on five continents (Eurasia, Asia, Africa, South and North America, and Australia; (Boix et al. 2016). The Mediterranean climate is characterized by mild temperatures, rainy winters, and hot and dry summers (Aschmann 1973, Inbar et al. 1998), causing large water-level fluctuations (Cobelas et al. 2005, Beklioglu et al. 2007). In Northern Israel, average annual rainfall is estimated to be nearly 700 mm per year (Boix et al. 2016) and is generally distributed from November to May (Wittenberg et al. 2007, Inbar et al. 1998). Thus, sudden flooding due to sea storms, intense rainfall or river overflows may occur and may prolong periods of hydric instability of wetlands before they become isolated and gradually dry out. This hydric instability causes extreme spatio-temporal variation in the physico-chemical and species composition of these aquatic ecosystems (Quintana et al. 1998).

Rivers that naturally, periodically cease to flow are found on every continent, and these intermittent rivers, defined as temporary, ephemeral, seasonal and episodic streams and rivers, may be even more common than perennial rivers. Intermittent rivers constitute more than 30% of the total length and discharge of the global river network (Tooth 2000), and are increasing in number and length in response to climate change, land-use alteration, and water abstraction (for irrigation and/or drinking water).

Despite a seasonal pattern, flood frequencies are extremely variable in Mediterranean systems and, with the exception of summer drought, the occurrence of disturbances remains unpredictable (Quintana et al. 1998). Ephemeral stream channels, referred to as wadis, are subject to high variation in hydraulic regimes and water levels, resulting in flash floods of the river bed in winter (Segev and Blaustein 2014). Flood waters recede, resulting in formation of isolated rock pools along the wadi channel which can last from several weeks to several months (Ward and Blaustein 1994). In those temporary pools, immature mosquitoes (e.g. *Culiseta longiareolata*) and green toad tadpoles (e.g. *Bufotes viridis*) are usually numerically dominant during the winter at low elevations (Ward and Blaustein 1994), but taxa richness decreases sharply after a flood and increases as the season advances (Ward and Blaustein 1994).

We predicted that flash floods will greatly reduce richness and abundance of mosquito antagonists leading to an increase in mosquito oviposition during the post-disturbance period of community recovery. These predictions were tested by simulating flash floods in outdoor artificial mesocosms. Mosquito egg rafts, larval and pupal abundance were monitored before and after flash flood.

Materials and Methods

**Experimental design**

Assessment of mosquito oviposition habitat selection in pre- and post-flooded pools was carried out in an outdoor mesocosm (40 L plastic tubs) experiment setup on the Haifa University Campus field site (460 m asl; N32º45’41.15”; E35º1’10.27”). Twenty-four plastic tubs (length x width x height: 50 x 40 x 20 cm) were placed in the study site, tilted at 7 ±1º which is the average slope in wadis in the Northwest Mount Carmel (source: Google Earth) and filled with rain water. Zooplankton (Cladocera, Copepoda, Ostracoda), taken from nearby temporary pools (340 m asl; N32º45’18”; E35º00’54”), was added into all the pools on two occasions: 22nd December 2013 and 5th January 2014. Organic matter that consisted of a mixture of 20 g oak (*Quercus calliprinos*) leaf litter and 1.5 g rodent pellets (18% protein, 2018SC Teklad Global Diet®) per pool, were added to each pool, similar to that of (Morin 1981). Then, pools were left uncovered to allow colonization by insects prior to flooding, after which they were half-covered to keep water temperature below 25 ºC. Water level (27 L) was maintained during the course of the experiment using rain water or dechlorinated (aged) tap water.

Two different treatments (flooded, and non-flooded) were randomly assigned to the 24 pools (12 replicates per treatment). On Day 1 (10th March 2014), 12 pools were artificially flooded, while 12 pools were left unflooded, and considered as controls. The 2014 rainy season had the lowest rainfall on record (source: Israel Ministry of Transport, Meteorological Service), so natural rains did little to flood the pools. Preliminary trials were conducted for testing the simulation of flash floods to the mesocosms. Due to the lack of rainfall, the flash flood was performed with aged tap water (tap water aging in outdoor tanks at least 48h before use for dechlorination). During experimental flash floods, the tubs were flushed with 60 L of water from a holding tank over a 27 second period by opening a 5.6 cm diameter valve. We ran preliminary flushing trials with both 8 fire salamander larvae (*Salamandra infraimmaculata*) and 200 late-instar mosquito larvae (*Culiseta longiareolata*) per pool to determine flushing rates of organisms. Using 5 trials per taxon, an average of 7 of the 8 salamander larvae (SE: 0.32) (87.5%) and 155 of the 200 mosquito larvae (SE: 2.06) (77%) were flushed out. Thus, variability among trial replicates in flushing of these two taxonomic groups was very low.

**Sampling methods**

On Days 0 (pre-flooding: date 9th March), 2, and 30 (post-flooding sampling dates: 11th March and 8th April), the invertebrate community was sampled with a 11 x 8 cm plankton net (250 µm mesh size) swept through 115 linear cm of water (volume of water sampled: 10 L). Invertebrates were then emptied into a container holding 500 mL water. After one mixing, 40 mL of the 500 mL were collected with a syringe and preserved in 80% ethanol. This sampling procedure would then sample approximately 3% of the invertebrates in the mesocosms. The remaining invertebrates were transferred back into their original pools. Preserved specimens were counted under a stereomicroscope (Leica M125 stereomicroscope, Leica Microsystems, Wetzlar, Germany) and identified to the species level when possible using identification keys (Amoros 1984, Johannsen and Thomsen 1937, Pennak 1978). On each sampling date, water was collected for chlorophyll *a* (100 mL), nitrate and phosphate concentration measurements (25 mL each), and abiotic variables (temperature, pH, conductivity, and dissolved oxygen) were monitored between 10:00 and 12:00. Three times a week, egg rafts and mosquito larvae were counted in every pool and identified to species level (Rioux 1958, Harbach 1985). Egg rafts were detected visually, while larvae were sampled with an aquarium net swept (11 x 8 cm plankton net, 250 µm mesh size) into the water (volume sampled: 1.8 L), transferred into a container, counted into different classes (instars I-II, instars II-IV and pupae) before returning the contents back into the pool. Chlorophyll *a* pigments were extracted according to Lorenzen (1967) and quantified spectrophotometrically according to (Ritchie 2006), to determine phytoplankton biomass. Nitrate concentrations were measured using the Cadmium reduction method according to the American Public Health Association (APHA(Association 1992), and phosphate concentrations with the ascorbic acid method according to the US Environmental Protection Agency (USEPA 1979). At the end of the experiment, the leaf litter was collected in every pool, oven-dried at 60 °C (24 to 48 h), and weighed.

The identified taxa were categorized as either active dispersers (Culicidae, Chironomidae, Ceratopogonidae, and Ephemeroptera) or passive dispersers (zooplankton: calanoids, cladocerans, and ostracods). We expected active dispersers to recolonize the pools faster than passive dispersers, though the remaining fraction of passive dispersers after flooding could reproduce. Biomass was estimated for each taxon according to the literature (see Table S1 in Supplemental Information).

**Statistical analyses**

The effects of flash flooding on abiotic and biotic variables (temperature, pH, conductivity, dissolved oxygen, chlorophyll *a* concentrations and invertebrate taxa except mosquitoes) were investigated using analysis of variance (ANOVA). We analysed the pre-flooding data (Day 0) as a one-way ANOVA. For the data collected after the flash flood (from 2 days to 30 days after), we conducted a repeated measure ANOVA (RM-ANOVA; flooded versus not flooded). One-way ANOVA analysis was run, with the flooding treatment as the explanatory variable, when RM ANOVA showed a statistically significant time x treatment interaction effect. In the case of mosquito egg rafts and larvae, data were summed for each week. Temperature, pH, conductivity, dissolved oxygen, chlorophyll *a* concentrations and invertebrate taxa data were square root-transformed (y = √x), and mosquito data were log-transformed (y = log(x+1)) prior to analysis to approximately satisfy the assumptions of normally-distributed errors with constant variance (Levene’s test, p > 0.05).

Statistical analyses were performed using Statistica Version 2.9.0 (Statsoft).

Results

**Abiotic and biotic variables**

Table 1 summarizes the abiotic variables measured during the experiment in non-flooded and flooded mesocosms. The one-way ANOVA tests did not show any significant treatment differences on Day 0 (Table 2). After the flash flood, there were no significant differences among treatments for pH, water temperature, dissolved oxygen, phosphate and nitrate concentrations (Table 3). Water conductivity increased during the experiment, and there was a significant time x treatment interaction between non-flooded and flooded pools (*p* = 0.018; Table 3). Water conductivity was significantly higher in flooded pools than in non-flooded pools on Day 30 (F1,22=6.52, *p* = 0.018).

Concentrations of chlorophyll *a* tended to increase in all the mesocosms during the experiment (Fig. 1). One-way ANOVA did not indicate any significant differences between non-flooded and flooded pools before the flash flood (*p*=0.394; Table 2). However, RM ANOVA showed a statistically significant negative overall effect of flooding on chlorophyll *a* concentrations (*p*=0.045; Table 3).

At the end of the experiment, leaf litter quantity (One-way ANOVA, F1,22=10.76, *p* = 0.003) was significantly higher in the control pools than in the flooded pools.

**Invertebrate community**

A total of 10 different invertebrate taxa were identified in the samples collected during the study period. The aquatic invertebrate community was mainly comprised of 6 crustacean species (*Cyzicus* sp. (Spinicaudata), *Arctodiaptomus similis (*Calanoida*)*, *Ceriodaphnia quadrangula*, *Moina* sp., and *Alona* sp. (Cladocera), and *Heterocypris* sp. (Ostracoda)), and four insect taxa (*Dasyhelea* sp. (Ceratopogonidae), *Culex laticinctus* and *Culiseta longiareolata* (Culicidae), and *Chironomus* sp. (Chironomidae)). *Culiseta* *longiareolata* and *Chironomus* sp. were the most abundant insects.

Before the flash flood, the number of taxa of active and passive dispersers, and the total biomass of invertebrates in the pools, were not significantly different between the treatments (Table 2). After the flood, there were no significant differences between flooded and non-flooded pools for the taxa richness of active dispersers (Table 3, Fig. 2A). There was a significant time x treatment interaction for taxa richness of passive dispersers (*p*=0.012; Table 3); passive disperser richness tended to be higher in non-flooded pools on day 2 and higher in flooded pools on day 30 (Fig. 2B).

There was a significant time x treatment interaction for the total biomass of invertebrates (*p* = 0.002; Table 3). The total biomass of invertebrates was significantly lower in the flooded pools than in non-flooded pools two days after the flash flood (F1,22=8.58, *p*=0.008; Fig. 2C), but there was no significant difference between the flooded pools and the non-flooded pools on Day 30 (F1,22=0.88, *p*=0.359; Fig. 2C).

**Mosquito dynamics**

The main mosquito species ovipositing in the pools was *Culiseta longiareolata*.

Prior to flooding, there was little evidence for a difference in the abundance of egg rafts between flooded and non-flooded pools (*p*=0.294; Table 2). After flooding, egg raft abundance was significantly lower in the flooded pools compared to the non-flooded pools (*p*=0.047; Table 4, Fig. 3A). Egg raft abundance increased over time (*p*<0.0001; Table 4). There was no significant time x treatment interaction (*p*=0.808; Table 4).

Prior to flooding, there was no significant difference in the abundance of larvae between the flooded and non-flooded pools (*p*=0.162; Table 2). The abundance of mosquito larvae tended to increase with time in all the pools (*p*<0.0001; Table 4, Fig. 4B), but there were no significant differences between flooded and non-flooded pools (*p*=0.457; Table 4).

Discussion

We assessed the effect of flash floods on mosquito oviposition habitat selection and larval abundance during post-disturbance community recovery. Both community structure and food resources were negatively affected by the flooding, which in turn likely influenced mosquito oviposition site choice.

Composition and abundance of algal assemblages, which are important food resources for filter feeders such as mosquito larvae, are affected by multiple interactive factors such as water chemistry, light availability, temperature, current velocity, substrate type, and grazing (Stevenson 1996, Roberts et al. 2004). Water ﬂow often is the physical factor that most affects algal assemblages (Poff and Ward 1989), and extreme conditions such as floods are primary sources of environmental variability and disturbance (Stanford and Ward 1983). In our case, the flash flood negatively affected phytoplankton (chlorophyll *a* concentrations), and thus, the amount of food resources. (Fisher et al. 1988) suggested that uptake by phytoplankton was a major process responsible for nutrient removal. In our study, phytoplankton increase in the control pools did not appear to lead to decreases in nitrate and phosphate concentrations. At the end of our experiment, leaf litter quantity was significantly higher in the control pools than in the flooded pools. This suggests that the amount of substrate in the pools could have influenced nitrogen recycling by decomposer organisms and thus nitrogen availability for primary producers.

This study was performed over a period of one month in the spring. The values of the various environmental parameters measured during the survey of the mesocosms were within the range of values usually found for temporary habitats, as pH values have been found to range from 7.6 to 9 in rocky pools (Blaustein et al. 2004). (Munari et al. 2003) measured chlorophyll *a* concentrations close to 40 µg L-1 and O2 concentrations less than 6 mg L-1 in August in the Po River delta area (northern Italy) which is consistent with our observations. Due to the lack of rainfall, the flash flood was performed with aged tap water, explaining differences in conductivity between flooded pools and controls two days after. Winter and spring 2014 was one of the driest for 70 years in Israel, and provided very little precipitation. At the Haifa meteorological station, precipitation recorded from 15 December 2013 to 28 February 2014 was 54 mm while the long-term average amount for the same period is 300 mm (source: Israel Ministry of Transport, Meteorological Service). Moreover, water level gradually decreased as a consequence of natural evaporation, in particular in April (Day 30), due to the lack of additional rain water. Therefore, aged tap water was added to maintain the water level, explaining the increase of conductivity during the experiment.

**Invertebrate community**

Passive dispersers, mainly composed of zooplankton, as well as the total biomass of invertebrates, were negatively affected by the flooding. Drift of invertebrates can be active (behavioural) or passive (random). “Catastrophic” drift is caused either by natural conditions (overflow and catastrophic flooding) or by anthropogenic factors (pollution). “Catastrophic” drift can lead to structural changes in communities (Bogatov 2014). The increase in discharge and water velocity, as in spates, increases drift (Bogatov 2014, Crisp and Robson 1979, Neves 1979, Bird and Hynes 1981). As an example, (McLay 1968) showed that 50% of macroinvertebrates were washed downstream during a single spring thaw in New Zealand.

Behavioural response to flooding appears to be species-specific and related to body size (Chia et al. 1984). The ability of zooplankton to avoid washout has been tested by (Richardson 1992) both in laboratory and field conditions (in stream pools). Cladoceran species, which usually develop in environments with little turbulence and water movement (Hutchinson 1967) and which are usually considered to be poor swimmers, were mostly unable to resist flow velocities above 2.5 cm s-1. In the wadis of the Negev Desert, Israel, cladocerans are rare, likely because they cannot resist the flow (Ward and Blaustein 1994). In contrast, copepod species exhibited much greater ability to survive higher water velocities (> 7.5 cm s-1) in Richardson’s (1992) experiments, and showed strong swimming ability. In the field study, Richardson observed highest densities of ostracods in near-shore areas with high velocity, as ostracods are able to find refuge in benthic habitats, and they usually attach their eggs to the substrate (Thorp and Rogers 2010, Spencer and Blaustein 2001). However, our study should show a higher impact of flooding on the zooplankton than in Richardson’s experiment, as we used a water velocity out of the faucet of 113 cm s-1, which is 10-fold the maximum velocity tested by Richardson.

Several studies have also highlighted the negative effect of flooding on invertebrate abundance and density in streams, whether or not ephemeral. (Ward and Blaustein 1994) observed very large impacts of flash flooding on species richness in ephemeral desert pools. Indeed, flash floods washed out the inhabitants in the pools, leading to invertebrate species richness close to 0. In those pools, the authors observed insects as the dominant taxa, as some are able to avoid being washed out with the flood (Lytle 2008, Lytle and White 2007). Flash floods can cause high mortality in the juvenile aquatic stage of intermittent stream insects, but this may be compensated by life-history strategies, such as emergence that is synchronized with flood dynamics, allowing the adult stage to avoid floods (Lytle 2002). However, these life history adaptations could be impacted by flow-regime modifications due to human activities, redistributing extreme flow events to different times of the year (Lytle and Poff 2004).

**Consequences for mosquito population dynamics**

Disturbances often remove dominant species, allowing other non-dominant species to persist (Kimmerer and Allen 1982, McAuliffe 1984). Mosquitoes are pioneering species and, by definition, are better colonizers than most of their antagonists, particularly passive dispersers (Chase and Knight 2003). Thus, in our study, we expected that disturbance by flash floods would lead to increasing mosquito oviposition during post-disturbance period of community recovery. However, *Culiseta longiareolata* is vulnerable to intraspecific competition (Kiflawi et al. 2003a) and increasing food resources on which mosquito larvae feed (algae and microorganisms) can increase oviposition (Blaustein and Kotler 1993). It is thus not surprising that after the flash flood in our experiment, oviposition decreased due to the reduction of algae in the flooded pools. (Blaustein and Kotler 1993) demonstrated that oviposition by *Culiseta longiareolata* in outdoor mesocosms is increased by food supply in the aquatic habitat. (Mutero et al. 2004) demonstrated that ammonium sulphate fertiliser increased *Anopheles arabiensis* oviposition, based on the fact that gravid females use visual (such as colour, texture or brightness) and olfactory (semiochemicals) stimuli to select habitats for oviposition (Bentley and Day 1989). This suggests that *Anopheles gambiae* actively selects habitats for oviposition rather than randomly (Minakawa et al. 2004), and can avoid predator-released kairomones of *Notonecta* (Warburg et al. 2011). In our mesocosms, flash flood disturbance may have removed mosquito food resources besides mosquito antagonists. However, when flooding occurs in intermittent riverbeds, it is possible that with the water washing through the entire watershed, it might end up with more rather than less nutrients. After accumulation of riparian leaf litter and sediment in streambeds, hypoxia can lead to ammonium and phosphate release from sediments in disconnected pools (Von Schiller et al. 2011). During floods, organic matter, nutrients, and terrestrial plants that have accumulated on dry channel surfaces are transported downstream (Datry et al. 2014).

Oviposition habitat selection must be a trade-off between risk of ovipositing in an unsuitable habitat and cost of competition and predation (Spencer et al. 2002, Kiflawi et al. 2003b, Blaustein et al. 2004). When poor habitat choices are offered to *Culiseta* females, oviposition drops significantly (Kiflawi et al. 2003b). Progeny fitness will depend on food supply and presence/absence of natural enemies (Bond et al. 2005) and oviposition habitat selection is thus a balance between risk factors for the offspring (Kiflawi et al. 2003a).

Understanding how disturbances may influence oviposition habitat selection by mosquitoes can contribute to a better understanding of how community structure influences mosquito oviposition and consequently how it influences mosquito population dynamics. This knowledge could in turn help in management and biodiversity conservation of temporary mosquito breeding habitats.

Flash floods affected both the invertebrate community and food resources, which in turn influenced mosquito oviposition. More broadly, this study demonstrates how disturbances influence mosquito oviposition habitat selection due to the alteration of community structure. This highlights the importance of considering the effects of disturbances on mosquito population through community structure perturbation, in management, habitat restoration and biodiversity conservation in temporal habitats.

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Table 1.Overview of the environmental variables measured in non-flooded and flooded mesocosms at each sampling date. Mean ± standard error (n=6 for each treatment) values are presented in the table.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Abiotic Variables | Treatment | Day 0 | Day 2 | Day 30 |
| pH | Non flooded | 7.8 ± 0.13 | 7.8 ± 0.08 | 7.7 ± 0.05 |
| Flooded |  | 7.8 ± 0.12 | 7.7 ± 0.09 |
| Conductivity(mS cm-1) | Non flooded | 0.44 ± 0.04 | 0.42 ± 0.05 | 0.74 ± 0.07 |
| Flooded |  | 0.75 ± 0.02 | 0.95 ± 0.05 |
| Dissolved Oxygen (mg L-1) | Non flooded | 3.42 ± 0.44 | 4.88 ± 0.43 | 5.10 ± 0.59 |
| Flooded |  | 6.07 ± 0.34 | 5.67 ± 0.33 |
| Temperature(°C) | Non flooded | 20.0 ± 0.50 | 15.8 ± 0.47 | 18.6 ± 0.38 |
| Flooded |  | 15.8 ± 0.44 | 17.9 ± 0.44 |
| Nitrate(mg L-1) | Non flooded | 0.18 ± 0.09 | 0.09 ± 0.03 | 0.26 ± 0.18 |
| Flooded |  | 0.04 ± 0.01 | 0.07 ± 0.01 |
| Phosphate(mg L-1) | Non flooded | 0.9 ± 0.21 | 1.1 ± 0.06 | 3.7 ± 0.97 |
| Flooded |  | 1.2 ± 0.24 | 3.3 ± 1.05 |

Table 2.Results of the one-way ANOVA before the flash flood (on Day 0) on square root transformed data for the abiotic and biotic variables, and log-transformed data for the mosquito data.

|  |  |  |
| --- | --- | --- |
| Variables | *F*1, 22 | *P* |
| pH | 1.03 | 0.322 |
|  |  |
| Conductivity | 0.23 | 0.635 |
|  |  |
| Dissolved oxygen | 0.81 | 0.379 |
|  |  |
| Temperature | 0.01 | 0.926 |
|  |  |
| Nitrate | 0.88 | 0.359 |
|  |  |
| Phosphate | 1.59 | 0.221 |
|  |  |
| Chlorophyll *a* | 0.76 | 0.394 |
|  |  |
| Active dispersers | 2.75 | 0.111 |
|  |  |
| Passive dispersers | 0.10 | 0.756 |
|  |  |
| Total biomass | 4.07 | 0.056 |
|  |  |
| Egg rafts | 1.16 | 0.294 |
|  |  |
| Larvae | 2.10 | 0.162 |
|  |  |

Table 3.Results of the repeated measures ANOVA after the flash flood (from week 1 to week 4), on square root-transformed data for abiotic variables, passive and active dispersers and total biomass. *p* values appear in bold when significant (< 0.05).

|  |  |  |  |
| --- | --- | --- | --- |
| Variables |  | *F*1, 22 | *p* |
| pH | treatment | 0.01 | 0.925 |
| time | 1.09 | 0.308 |
| time x treatment | 0.00 | 0.954 |
| Conductivity | treatment | 4.14 | 0.054 |
| time | 68.95 | **0.000** |
| time x treatment | 6.59 | **0.018** |
| Dissolved Oxygen | treatment | 3.49 | 0.075 |
| time | 0.11 | 0.746 |
| time x treatment | 0.42 | 0.525 |
| Temperature | treatment | 0.32 | 0.576 |
| time | 96.30 | **0.000** |
| time x treatment | 2.23 | 0.149 |
| Nitrate | treatment | 3.72 | 0.067 |
| time | 2.00 | 0.171 |
| time x treatment | 0.120 | 0.733 |
| Phosphate | treatment | 1.59 | 0.693 |
| time | 6.51 | **0.018** |
| time x treatment | 0.08 | 0.779 |
| Chlorophyll *a* | treatment | 4.53 | **0.045** |
| time | 9.41 | **0.006** |
| time x treatment | 4.27 | **0.050** |
| Active dispersers | treatment | 0.330 | 0.572 |
| time | 17.39 | **<0.001** |
| time x treatment | 0.422 | 0.523 |
| Passive dispersers | treatment | 0.07 | 0.792 |
| time | 0.78 | 0.385 |
| time x treatment | 7.60 | **0.012** |
| Total biomass | treatment | 3.32 | 0.082 |
| time | 0.22 | 0.645 |
| time x treatment | 12.65 | **0.002** |

Table 4.Results of the repeated measures ANOVA after the flash flood (from week 1 to week 4), on log- transformed data for egg rafts and larvae of *Culiseta longiareolata*. *p* values appear in bold when significant (< 0.05).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Variables |  | df | *F* | *p* |
| Egg rafts | treatment | 1, 22 | 4.44 | **0.047** |
| time | 3, 66 | 13.94 | **<0.001** |
| time x treatment | 3, 66 | 0.323 | 0.808 |
| Larvae | treatment | 1, 22 | 0.574 | 0.457 |
| time | 3, 66 | 22.52 | **<0.001** |
| time x treatment | 3, 66 | 0.942 | 0.426 |

**Figure legends**

Figure 1. Changes in chlorophyll *a* concentrations in control and flooded pools. Mean + standard error (*n* = 12 for each treatment) are shown. The black arrow indicates the date of the flooding treatment (on Day 1).

Figure 2. Descriptors of invertebrate communities in control (non-flooded), and flooded pools. Mean values (+ SE, *n* = 12) are presented. The black arrow indicates the date of the flooding treatment (on Day 1). (A) Active disperser taxa richness (number of species); (B) Passive disperser taxa richness (number of species); (C) Total biomass of invertebrates.

Figure 3. Change in abundance (number of individual counted per swiping) of: (A) mosquito egg raft and (B) mosquito larvae in the control (non-flooded) pools and the flooded pools. Mean values (+ SE, *n* = 12) are presented. The black arrow indicates the date of the flooding treatment (on Day 1).

**Figure 1.**

**Figure 2.**

**A**

**B**

**C**

**Figure 3.**

**A**

**B**