# Effect of desiccation on mosquito oviposition site selection in Mediterranean temporary habitats

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**Abstract.** 1. Hydroperiod duration has been identified as the main factor determining the faunal composition and structure of aquatic communities in temporary habitats. It is hypothesised that desiccation will positively affect mosquito oviposition habitat selection during the post-drought period due to the lack of antagonists.

2. An experiment was carried out in outdoor mesocosms to assess whether desiccation events have post-drought effects on community richness and mosquito oviposition.

Three different treatments were randomly assigned to the mesocosms: (i) eight mesocosms were left dried for a week and then reflooded; (ii) eight mesocosms stayed dry for 4 weeks before they were reflooded; (iii) eight mesocosms were maintained at a constant water volume of 30 litres during the entire experiment as controls. Mosquito oviposition and invertebrate community richness were monitored in every mesocosm, along with environmental parameters [water temperature, pH, conductivity, dissolved oxygen, total suspended solids (TSS) and chlorophyll *a* concentration].

3. Post-drought mosquito oviposition and larval abundance were higher in the short-drought and long-drought pools than in the control. Desiccation negatively affected the biomass of the filter feeder invertebrates in both desiccation treatments. Chlorophyll *a* concentrations were higher in the long-drought pools than in controls. The negative impact of desiccation on zooplankton led to a post-drought increase in algae, associated with an increase in mosquito oviposition.

4. Despite immediate negative effect on mosquitoes, pulsed disturbances can benefit mosquitoes as they favour oviposition during the post-disturbance recovery period due to a lower abundance of mosquito antagonists and higher food resources for their offspring.

**Key words.** Community interactions, drought disturbance, ephemeral pools, mosquito dynamics, oviposition habitat selection.

# Introduction

The composition and dynamics of the communities inhabiting temporary habitats are influenced by the duration of the hydroperiod and by seasonality (Boix *et al.*, 2001). Hydroperiod has been identified as the main factor determining the faunal composition and structure of aquatic communities in these

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systems (McLachlan, 1985; Jeffries, 1994; Spencer *et al.*, 1999), and drought is often the major mortality factor for insects in temporary pools (Batzer & Resh, 1992). However, the timing of inundation also plays an important role in shaping the aquatic community (Kneitel, 2014). Drought causes considerable changes within aquatic ecosystems (Cowx *et al.*, 1984). It imposes changes in macroinvertebrate communities and functional feeding group composition (Sangiorgio *et al.*, 2007; Johnson & Colón-Gaud, 2013), and increases the importance of intraspecific and interspecific competition, which increases metamorphosis time thus delaying emergence into adulthood of aquatic insects (Blaustein & Chase, 2007). The magnitude of these changes depends on the degree and duration of the drought. Some organisms have adopted life-history traits that allow them to cope with the stressful characteristics of temporary habitats, such as resting egg stages, desiccation resistance, and ability to migrate into the hyporheic zone (Smock *et al.*, 1985; Smock, 1999; Griswold *et al.*, 2008).

Global warming is expected to increase both intermittency (i.e. alternation between flowing water periods during the wet season and dry periods, usually during hot summer months) and discontinuity (i.e. more disconnected pools) of streams. In Israel, the amount of rainfall is expected to decrease and variability of rainfall is expected to increase, leading to an increase in the frequency of extreme hydrological events (Ayalon *et al.*, 2011).

Habitat disturbances are widely assumed to promote colonisation by opportunistic species (Lozon & MacIsaac, 1997; D'antonio et al., 1999). Mosquitoes are generally opportunistic insects and are often able to colonise a habitat faster than their antagonists (i.e. competitors and predators), leading to rapid population outbreaks. However, up to now, very few studies have focused on the effect of drought episodes on mosquito population dynamics. Earlier studies have assessed the effect of drought and amount of rainfall on the composition of the adult mosquito population (Smith & Love, 1956) and mosquito species preferences (Bradshaw & Holzapfel, 1988). Others tried to correlate mosquito abundance (Aedes spp.) with rainfall episodes (Gleiser et al., 2000). Chase and Knight (2003) have evaluated the effect of hydroperiod length on mosquito abundance in three different wetland types (temporary, semi-permanent, and permanent). They demonstrated that the emergence of mosquitoes increased after a drought event due to the loss of antagonists, which usually limit mosquito abundance. These studies suggest that disturbances, in the form of desiccation events, can influence mosquito population dynamics. However, in order to understand effects of drought on mosquitoes, it is important to consider oviposition habitat selection (OHS).

When facing choices between small water bodies or larger ones, ovipositing female mosquitoes will select the smaller patches, even if these have a short hydroperiod (Bohenek et al., 2017; Westby & Juliano, 2017). When selecting breeding sites, ovipositing mosquitoes are known to avoid habitats with antagonist species in order to favour offspring fitness (Spencer et al., 2002). They may avoid competitor species for food (Blaustein & Kotler, 1993; Stav et al., 2005; Duquesne et al., 2011), or either predators or predator-released kairomones (Spencer et al., 2002; Blaustein et al., 2004; Eitam et al., 2004; Stav et al., 2005; Van Dam & Walton, 2008; Silberbush et al., 2010). Mosquitoes may thus exploit disturbed, enemy-free sites for their larvae. However, some mosquito species, such as Aedes triseriatus, can adopt avoidance behaviour at the larval stage, when facing a predator (Juliano et al., 2019). Overall, both timing and frequency of disturbances may be very important in determining the outcome of drought on mosquito populations (Mogi, 1993).

In a field mesocosm study, we assessed mosquito OHS decisions, mosquito larval performance, and invertebrate community structure alterations following simulated drought events. We hypothesised that mosquitoes would oviposit more in pools that had completely dried out and were reflooded compared with pools that retained constant water levels, because of the absence of antagonists and increased food resources, such as algae and bacteria. Mosquito OHS was assessed based on number of egg rafts laid in the experiment, during the post-drought period of community recovery.

#### Materials and methods

#### Experimental design

In March 2015, an experiment was conducted in outdoor mesocosms set up in the Hai Bar Nature Reserve, Mount Carmel, Israel (340 m asl;  $32^{\circ}45'18''$  N;  $35^{\circ}00'54''$  E). Twenty-four outdoor mesocosms (40-litre plastic tubs, length × width × height:  $50 \times 40 \times 20$  cm) were dug in the ground to mimic rock pools from Mediterranean stream beds in a  $4 \times 6$  grid design, with 50 cm between two mesocosms. The mesocosms were set up at *c*. 80 m from a large, temporary artificial pond created by the Israel Nature & Parks Authority that served as a source for colonising insects and amphibians in our mesocosms. The Mount Carmel area experiences rainy events from about mid-October to mid-April, followed by dry months in the remainder of the year. The mesocosms (pools) were naturally filled by rain from November and were left uncovered to allow colonisation by insects and amphibians.

The mesocosms were randomly assigned to one of the two treatments - two different drought or desiccation regimes - or a control (no drought). In the two desiccation treatments (shortand long-drought bouts, explained later), the pools were allowed to dry, while in the control, we maintained a constant water volume of 30 litres during the entire experiment (Fig. 1). On 14 April 2015, the 16 pools assigned to desiccation treatments had completely dried. Two weeks before the end of the hydroperiod, c. 5 litres of water were removed each week from each treated pool to ensure they would be all dry on the same day. Care was taken to avoid removing organisms along with the water, by passing the removed water through an aquarium net (mesh size =  $250 \,\mu\text{m}$ ) and returning the contents of the net to the experimental pool. As small algae, bacteria and particles could pass through the net, a quantity of 5 litres was also removed from the control pools, but then replaced with distilled water to maintain the water level. We used distilled water instead of aged tap water because of the high conductivity of tap water in the area.

The eight pools that were assigned to a short dry period (short-drought pools) were flooded again on 21 April 2015 with distilled water, 1 week after they had been completely dried out, while the remaining eight pools remained dry for 4 weeks before they were reflooded on 19 May 2015 (long-drought pools). Thereafter, the 30-litre water level was maintained with distilled water in all 24 pools. The dates of flooding were in line with the rain episodes in Israel as the last rainfall in 2015 occurred on 28-30 May.

To simulate natural conditions in northern Israel, 10 days after reflooding the long-drought pools, we allowed all 24 pools to start drying up. We monitored the post-drought period of community recovery until the water level in the pools



Fig. 1. Timing of the desiccation and flooding process in the experimental pools. Control, control pools; short drought, short-drought pools; long drought, long-drought pools.

was too low to perform the sampling. The experiment ended on 23 June 2015.

## Sampling

Sampling was performed in all pools (when not dry) every 2 weeks beginning on 4 March, then on 17 and 31 March, 14 and 28 April, 12 and 26 May, and 9 and 23 June. On each sampling date, water temperature, pH, conductivity, and dissolved oxygen were measured in every pool, between 10.00 and 12.00 hours using a pH/EC/TDS Combo testing meter (Hanna Instruments, Kehl am Rhein, Germany) and an optical dissolved oxygen meter (ProODO™, YSI Inc., Yellow Springs, Ohio). Phytoplankton chlorophyll a concentrations were determined in 100-ml water samples filtered through Whatman GF/C fibreglass filters (Whatman International, Maidstone, UK). Pigments were extracted overnight using 1.5 ml of methanol. Chlorophyll a was quantified spectrophotometrically (Spectrophotometer Nanodrop 2000C; Thermo Fisher Scientific Inc., Waltham, Massachusetts) according to Ritchie (2006) to determine phytoplankton biomass. Total suspended solids concentrations were determined in additional 100-ml water samples filtered through pre-weighed oven-dried Whatman GF/C fibreglass filters (2 h at 500 °C; 1.2 µm mesh size) and weighed according to the AFNOR (2006) method after 48 h at 105 °C.

From all 24 pools, invertebrate and anuran tadpole data were collected on each sampling date. Anuran eggs were counted in each experimental pool. Invertebrates and tadpoles were sampled by sweeping a net (dimensions  $9.5 \times 7$  cm, mesh size =  $250 \,\mu$ m) through the water (volume sampled = 8 litres) after gentle mixing, to collect both planktonic and ben-thic individuals. Invertebrates were then preserved in 80% ethanol in the laboratory. Fixed specimens were counted under

a stereomicroscope (Leica M125 stereomicroscope; Leica Microsystems, Wetzlar, Germany) and identified to species level when possible, using identification keys (Johannsen & Thomsen, 1937; Pennak, 1978; Amoros, 1984). Anuran tadpoles were counted on site and returned to the experimental pools.

Oviposition of mosquitoes was evaluated by counting the number of egg rafts laid in the pools three times a week during the experimental period and identifying them to species level after hatching. The egg rafts were collected and isolated until the eggs hatched to identify the larvae (Rioux, 1958; Harbach, 1985). The larvae were then released back into the respective tubs. Mosquito larvae relative abundance was estimated by sweeping a net (dimensions  $9.5 \times 7$  cm, mesh size =  $250 \,\mu$ m) through the water (volume sampled = 8 litres).

The identified taxa were categorised as active (insects and amphibians: Culicidae, Chironomidae, Ceratogonidae, Ephemeroptera, and the frog Hyla savignvi) or passive dispersers (zooplankton: calanoid copepods, cladocerans, and ostracods). Biomass was estimated for each taxon. Dry masses for cladocerans and calanoids were predicted from length-weight regressions of Dumont et al. (1975). Similarly, ostracod dry masses were predicted according to Widbom (1984), and dry weights of dipterans were estimated according to Sota et al. (1998), Dawson et al. (2000), Duquesne et al. (2011) and Morante et al. (2012). Dry masses of ephemeropterans were estimated according to Gupta et al. (1993). Weights of Hyla savignyi were estimated according to Stein and Blaustein (2015). The taxa were categorised as either grazers/scrapers (Ostracoda, Chironomidae, Ceratopogonidae, Ephemeroptera, and amphibian tadpoles) or filter feeders (calanoids and cladocerans). Both grazers/scrapers and filter feeders may be considered as competitive antagonists of Culiseta longiareolata larvae (Blaustein & Margalit, 1994), and filter feeders as potential competitive antagonists of Culex larvae (Stav et al., 2005).

For analysis, the sum of mosquito egg raft and larval abundances was calculated for each week and each experimental pool.

# Statistical analysis

To analyse the effect of desiccation on the different dependent variables (abiotic parameters, chlorophyll a concentrations, taxa richness, invertebrate biomass, mosquito egg raft and larval abundances) we performed a repeated-measures ANOVA. The data were divided into two stages (before and after flooding) according to the timing of desiccation and flooding: from 4 March to 14 April (before desiccation), when all 24 pools began with 30 litres of water and evaporation and water removal occurred in the two desiccating treatments; from 21 April to 23 June, when the short-drought pools were filled and maintained at 30 litres; and from 19 May to 23 June, when the long-drought pools were filled and maintained at 30 litres for 10 days and then evaporation occurred (Fig. 1). Repeated-measures ANOVA was performed and each variable was tested for the effects of desiccation duration [control (always flooded) versus short-drought (dry 1 week, then flooded), and control versus long-drought (dry 4 weeks, then flooded)], as reflooding timing was different for each treatment. Data were log-transformed  $[y = \log (x + 1))]$ before analysis to meet the assumptions of homogeneity of variance and normal distributions. A Greenhouse-Geisser correction for sphericity was used when sphericity assumptions were not met. ANOVA tests were performed using STATISTICA v.2.9.0 (Statsoft, Tulsa, Oklahoma). Significance was accepted at P < 0.05 for all tests.

Data collected before the complete desiccation and after the second flooding were used to conduct several multivariate analyses. To examine differences in invertebrate species composition among treatments, sums of each taxon were calculated for each period and a nonmetric multidimensional scaling (NMDS) was run. The dissimilarity matrix was calculated using the Bray–Curtis dissimilarity with species' presence–absence data. Species abundances were used to conduct a one-way analysis of similarity (ANOSIM) to test for treatment effects on community composition, followed by pairwise comparisons. If significant, ANOSIM results were followed by a SIMPER (similarity of percentages) test, using Bray–Curtis dissimilarity to determine the relative contribution of taxonomic groups to differences among treatments. ANOSIM and SIMPER were conducted using PAST v.1.94b (Hammer *et al.*, 2001).

We investigated the relationships among egg raft numbers for the main ovipositing mosquito species, filter feeder biomass, chlorophyll a and treatment after second flooding (19 May–23 June) using a path analysis. We hypothesised that egg raft numbers would be positively related to chlorophyll a (because pools with more chlorophyll a are expected to be more attractive to ovipositing mosquitoes) and negatively related to filter feeder biomass (because pools with more competing filter feeders are expected to be less attractive to ovipositing mosquitoes). We hypothesised that chlorophyll a would depend negatively on filter feeder biomass (because filter feeders consume phytoplankton). We hypothesised that filter feeder biomass would be reduced by drought treatments compared with the control (because filter feeders must either recolonise or emerge from refuges or resting stages after drought). We included only these *a priori* hypothesised relationships, because it would be difficult to fit more complicated models given the relatively small size of the experiment. We  $\log(x + 1)$ -transformed total egg raft numbers to deal with the mean-variance relationship expected for count data. We centred and scaled the means of filter feeder biomass and chlorophyll *a* to put their variances on similar scales. We coded treatment as two binary variables representing differences of long- and short-drought treatments from the control. We fitted the model separately for each main ovipositing mosquito species, using maximum likelihood in the sem() function in the R package LAVAAN 0.6–1 (Rosseel, 2012).

# Results

#### Abiotic parameters

Values of the abiotic parameters are summarised in Table 1. Before desiccation, there were no significant differences among treatments for pH, water temperature, dissolved oxygen and TSS (P > 0.05; Table 2). However, time × treatment interactions for conductivity before desiccation, were statistically significant for both long-drought versus control and short-drought versus control (P < 0.001; Table 2). Conductivity was significantly lower in the control pools (0.29 mS cm<sup>-1</sup>; Table 1) than in the short-drought (0.35 mS cm<sup>-1</sup>; Table 1) and long-drought pools (0.36 mS cm<sup>-1</sup>; Table 1).

After desiccation, there were no significant differences between short-drought and control pools, regarding any of the measured abiotic parameters, except for the conductivity (P = 0.009; Table 2). However, time × treatment interactions were statistically significant for pH (P = 0.005; Table 2) and dissolved oxygen (P = 0.004; Table 2). pH and dissolved oxygen were lower in the long-drought pools than in control pools after the desiccation period (Table 1).

A technical problem with the dissolved oxygen probe did not allow measurements to be taken on 4 March. Thus, measurements started on 17 March. Dissolved oxygen was significantly lower on 9 June in the long-drought pools (6.1 mg litre<sup>-1</sup>) in comparison to the control (9.8 mg litre<sup>-1</sup>, P < 0.001; Table 1).

#### Aquatic community

There was an overall significant effect of the long drought on chlorophyll *a* concentrations in comparison to control (P < 0.001; Table 3). Chlorophyll *a* concentrations were significantly higher in the long-drought pools than in controls from 26 May to the end of the experiment (Fig. 2).

Fifteen invertebrate taxa were identified during the entire experiment. The aquatic invertebrate community mainly comprised crustaceans (nine species, including calanoids, cladocerans and ostracods, with *Arctodiaptomus similis*, *Moina* sp., *Alona* sp., *Heterocypris* sp., *Cypris* sp., and *Potamocypris* sp. being the most abundant), insects (which included Ephemeroptera and Diptera), Physidae and tadpoles

Parameters	Treatment	4 March	17 March	31 March	28 April	12 May	26 May	9 June	23 June
pН	Control	$7.9 \pm 0.05$	$7.8 \pm 0.11$	8.1 ± 0.10	8.1 ± 0.10	8.1±0.13	8.6±0.18	$9.2 \pm 0.18$	$9.0 \pm 0.10$
	Short	$7.9 \pm 0.13$	$7.9 \pm 0.10$	$8.1 \pm 0.07$	$7.9 \pm 0.12$	$7.9 \pm 0.10$	$8.3 \pm 0.21$	$9.1 \pm 0.16$	$8.9 \pm 0.14$
	Long	$7.7 \pm 0.07$	$7.8 \pm 0.12$	$8.1 \pm 0.14$			$8.4 \pm 0.23$	$7.9 \pm 0.07$	$8.2 \pm 0.08$
Conductivity	Control	$0.29 \pm 0.04$	$0.30 \pm 0.03$	$0.22 \pm 0.02$	$0.25 \pm 0.02$	$0.26 \pm 0.02$	$0.21 \pm 0.01$	$0.24 \pm 0.02$	$0.32 \pm 0.04$
$(mS cm^{-1})$	Short	$0.35 \pm 0.04$	$0.43 \pm 0.04$	$0.53 \pm 0.07$	$0.17 \pm 0.02$	$0.21 \pm 0.02$	$0.16 \pm 0.01$	$0.18 \pm 0.01$	$0.22\pm0.02$
	Long	$0.36 \pm 0.05$	$0.39 \pm 0.04$	$0.45 \pm 0.04$			$0.17 \pm 0.01$	$0.24 \pm 0.02$	$0.29 \pm 0.02$
Water temperature	Control	$14.2\pm0.06$	$12.8\pm0.10$	$16.7 \pm 0.13$	$19.0 \pm 0.29$	$18.2 \pm 0.13$	$20.3 \pm 0.15$	$23.1 \pm 0.25$	$20.8 \pm 0.11$
(°C)	Short	$14.2 \pm 0.11$	$12.8\pm0.12$	$17.2 \pm 0.15$	$19.2 \pm 0.49$	$18.5 \pm 0.44$	$20.5 \pm 0.18$	$23.4 \pm 0.19$	$20.9 \pm 0.10$
	Long	$14.1\pm0.08$	$12.8\pm0.11$	$17.1 \pm 0.11$			$20.3 \pm 0.11$	$23.0 \pm 0.21$	$20.8 \pm 0.10$
Dissolved oxygen	Control		$8.5 \pm 0.47$	$8.6 \pm 0.56$	$7.6 \pm 0.36$	$7.2 \pm 0.38$	$7.3 \pm 0.31$	$9.8 \pm 0.68$	$9.9 \pm 0.69$
$(mg litre^{-1})$	Short		$8.8 \pm 0.36$	$8.9 \pm 0.44$	$6.5 \pm 0.44$	$7.2 \pm 0.55$	$7.8 \pm 0.39$	$17.3 \pm 7.68$	$10.0 \pm 0.47$
-	Long		$9.0 \pm 0.51$	$9.1 \pm 0.59$			$7.7 \pm 0.76$	$6.1 \pm 0.51$	$8.5 \pm 0.46$
TSS (mg litre <sup>-1</sup> )	Control	$16.3 \pm 2.68$		$45.1 \pm 15.09$	$62.2 \pm 23.03$		$65.7 \pm 13.72$		$46.5 \pm 7.42$
	Short	$11.3 \pm 2.36$		$101.4 \pm 29.77$	$7.0 \pm 0.90$		$34.9 \pm 9.12$		$68.3 \pm 16.35$
	Long	$25.6\pm6.32$		$53.7 \pm 10.70$			$16.1 \pm 2.32$		$65.5 \pm 13.58$

**Table 1.** Abiotic parameters measured in the experimental pools. Data are means  $\pm$  SE (n = 8 for each treatment)\*.

\*Control, control pools; short, short drought pools; long, long drought pools; TSS, total suspended solids. Cells in grey represent missing data due to the drought (28 April and 12 May for the long drought pools), due to a technical problem with the dissolved oxygen probe on 4 March, or due to the sampling frequency (every 4 weeks for the TSS).

Table 2. Results of repeated-measures ANOVA for the abiotic parameters before and after the complete desiccation of the pools.

	Before desiccation							After desiccation				
	Short drought versus control			Long c versus	Long drought versus control			Short drought versus control			Long drought versus control	
Source of variation	d.f.	F	Р	d.f.	F	Р	d.f.	F	Р	d.f.	F	P
рН												
Treatment	1, 14	0.2	0.645	1, 14	0.0	0.877	1,14	1.2	0.293	1,14	27.2	< 0.001
Time	2,28	5.5	0.010	2, 28	11.8	< 0.001	4, 56	43.3	< 0.001	1.6, 22.9	0.8	0.427*
Time $\times$ treatment	2, 28	0.2	0.789	2, 28	1.0	0.372	4, 56	0.2	0.944	1.6, 22.9	7.5	0.005*
Conductivity												
Treatment	1, 14	9.1	0.009	1, 14	8.0	0.014	1,14	9.2	0.009	1,14	0.5	0.487
Time	2,28	8.3	0.001	2, 28	2.7	0.087	4, 56	10.7	< 0.001	2,28	34.3	< 0.001
Time $\times$ treatment	2,28	44.5	< 0.001	2, 28	28.3	< 0.001	4, 56	1.3	0.291	2,28	1.4	0.272
Water temperature												
Treatment	1, 14	3.7	0.074	1, 14	2	0.149	1,14	2	0.149	1,14	0.0	0.992
Time	2,28	659.8	< 0.001	2, 28	698	< 0.001	2, 28	698	< 0.001	2,28	288	< 0.001
Time $\times$ treatment	2, 28	1.7	0.207	2, 28	1	0.354	2, 28	1	0.354	2,28	0.2	0.808
Dissolved oxygen												
Treatment	1, 14	0.5	0.505	1, 14	0.6	0.438	1,14	0.1	0.743	1,14	10.4	0.006
Time	1, 14	8.9	0.010	1, 14	9.7	0.008	4, 56	22.7	< 0.001	1.9, 27.7	5.2	0.012*
Time $\times$ treatment	1, 14	0.02	0.901	1, 14	0.00	0.984	4, 56	0.9	0.473	1.9, 27.7	6.8	0.004*
TSS												
Treatment	1, 14	2.2	0.160	1, 14	0.2	0.670	1,14	1.5	0.248	1,14	0.3	0.569
Time	1, 14	21.1	< 0.001	1, 14	18.9	< 0.001	2, 28	27.2	< 0.001	1,14	6.6	0.023
Time $\times$ treatment	1, 14	0.4	0.534	1, 14	0.8	0.385	2, 28	0.1	0.928	1, 14	0.7	0.405

\*With the Greenhouse-Geisser correction.

TSS, total suspended solids.

Bold values represent significant relationships at the 0.05 level, based on repeated-measures ANOVA.

(*Hyla savignyi*). *Chironomus* sp. and *Dasyhelea* sp. were the most abundant insects.

There were significant time × treatment interactions for active disperser richness, and for passive disperser richness after desiccation (P = 0.033 and P = 0.001, respectively; Table 3), between the short-drought pools and the controls. Active disperser richness was higher in short-drought pools than in

control pools from 12 May to 9 June (Fig. 3a). Passive disperser richness was lower in short-drought pools than in control pools from 28 April to 12 May (Fig. 3b).

Before desiccation, there was an overall significant effect of the short drought on filter feeder biomass in comparison to control (P < 0.001; Table 3), but no differences were observed between long-drought pools and control (P > 0.05; Table 3).

	Before desiccation						After desiccation					
	Short drought versus control			Long drought versus control			Short drought versus control			Long drought versus control		
Source of variation	d.f.	F	Р	d.f.	F	Р	d.f.	F	Р	d.f.	F	P
Chlorophyll a												
Treatment	1, 14	0.4	0.558	1, 14	1.7	0.207	1,14	3.4	0.087	1, 14	29.7	< 0.001
Time	2,28	0.9	0.402	2, 28	0.2	0.823	4, 56	2.5	0.049	2,28	0.225	0.800
Time $\times$ treatment	2,28	0.3	0.775	2, 28	1.2	0.321	4, 56	1.1	0.374	2,28	0.410	0.667
Active disperser richness												
Treatment	1, 14	0.1	0.822	1, 14	0.01	0.901	1,14	0.8	0.383	1, 14	0.001	0.973
Time	2,28	1.5	0.231	2, 28	0.9	0.398	4, 56	4.7	0.002	2,28	0.1	0.878
Time $\times$ treatment	2,28	1.1	0.345	2, 28	0.9	0.414	4, 56	2.8	0.033	2,28	1.8	0.178
Passive disperser richness												
Treatment	1, 14	0.004	0.951	1, 14	1.3	0.278	1,14	4.9	0.043	1, 14	0.3	0.608
Time	2,28	0.7	0.517	2, 28	1.2	0.306	2,3, 32,9	6.7	0.002*	2,28	5.9	0.007
Time $\times$ treatment	2,28	1.1	0.344	2, 28	0.6	0.541	2,3, 32,9	7.6	0.001*	2,28	2.8	0.078
Filter feeder biomass												
Treatment	1, 14	17.2	< 0.001	1,14	0.9	0.368	1, 14	14.1	0.002	1, 14	0.003	0.958
Time	2,28	0.04	0.966	2,28	4.2	0.026	3,3, 45,7	10.5	< 0.001*	2.0, 27,9	2.1	0.141*
Time $\times$ treatment	2,28	3.1	0.061	2, 28	0.3	0.756	3,3, 45,7	11.2	< 0.001*	2.0, 27,9	8.2	0.002*
Grazer/scraper biomass												
Treatment	1,14	0.01	0.926	1, 14	1.1	0.314	1, 14	0.5	0.495	1,14	7.3	0.017
Time	2,28	0.8	0.454	2, 28	0.2	0.846	4, 56	28.2	< 0.001	1,9, 26,2	2.7	$0.087^{*}$
Time $\times$ treatment	2, 28	0.3	0.738	2, 28	0.1	0.923	4, 56	3.0	0.024	1,9, 26,2	4.5	0.023*

Table 3. Results of repeated-measures ANOVA for the biotic parameters before and after the complete desiccation of the pools.

Short drought pools versus control (dissimilarity = 99.6).

\*With the Greenhouse-Geisser correction.

Bold values represent significant relationships at the 0.05 level, based on repeated-measures ANOVA.



**Fig. 2.** Chlorophyll *a* concentrations (mean + SE, n = 8) in each treatment. Control, control pools; short drought, short-drought pools; long drought, long-drought pools.

![](_page_6_Figure_1.jpeg)

**Fig. 3.** Taxonomic richness (mean + SE, n = 8) of active (a) and passive dispersers (b), in each treatment. Control, control pools; short drought, short-drought pools; long drought, long-drought pools.

Filter feeder biomass was higher in the short-drought pools than in controls from 17 March to 31 March (Fig. 2). After desiccation, time × treatment interactions were statistically significant for filter feeder biomass between the short-drought pools and the controls (P < 0.001; Table 3), and between the long-drought pools and the controls (P = 0.002; Table 3). Biomass of filter feeders was lower in the short-drought pools than in controls from 28 April to 26 May (Fig. 4a). Filter feeder biomass was lower in the long-drought pools than in controls on 26 May, but higher on 9 and 23 June (Fig. 4a).

Regarding the grazer/scraper biomass, there were no statistical differences between the treatments and control, before desiccation, (P > 0.05; Table 3). After desiccation, there were significant time × treatment interactions for the biomass of grazers/scrapers between the short-drought pools and the controls (P = 0.024; Table 3) and between the

![](_page_7_Figure_1.jpeg)

**Fig. 4.** Biomass (mean + SE, n = 8) of filter feeders (a) and grazers/scrapers (b), in each treatment. Control, control pools; short drought, short-drought pools; long drought, long-drought pools.

long-drought pools and the controls (P = 0.023; Table 3). Biomass of grazers/scrapers was higher on 9 and 23 June in the short-drought pools in comparison to the control, and lower in the long-drought pools compared with controls on 26 May (Fig. 4b).

Before desiccation, communities were not segregated in NMDS space according to treatments, and, except for two pools [pool 3 (3 litres) and pool 10 (10 litres) of the long-drought treatment group], all the pools were grouped together (stress = 0.23; Fig. 5a). However, after desiccation, communities segregated by treatment along NMDS dimension 1 (control, short-drought and long-drought; stress = 0.19; Fig. 5b).

Before desiccation, the hypothesis of no difference in taxon composition among treatments could not be rejected (ANOSIM, R = 0.096, P = 0.063), but taxon composition was significantly different among treatments after desiccation (R = 0.14, P = 0.022). In this case, SIMPER was run and indicated that ostracods and the cladoceran *Moina* contributed most to differences among these treatments (75% and 68% for short-drought and long-drought pools, respectively; Table 4). Chironomidae contributed 6.3% of the difference between short-drought pools and the control (Table 4). The ceratopogonid *Dasyhelea* (6.3%) and the clam shrimp *Cyzicus* (5.4%) contributed to differences between

![](_page_8_Figure_1.jpeg)

**Fig. 5.** Nonmetric multidimensional scaling (NMDS) plot of aquatic communities in the short-drought pools (S, circled in blue), long-drought pools (L, circled in red), and control (C, circled in green), before desiccation (from 4 to 31 March; a) and after desiccation, when all the pools are filled (from 26 May to 23 June; b).

long-drought pools and the control. The rest of the species contributed < 5% to differences in both treatments in comparison to the control.

## Mosquito oviposition habitat selection and larval performance

Four different species oviposited in the mesocosms: *Culiseta longiareolata*, *Culex laticinctus*, *Culex pipiens* and *Culex theileri*. However, the mosquito species *C. longiareolata* was the main mosquito species ovipositing in the mesocosms during

**Table 4.** SIMPER results for comparisons of desiccation treatment (control, short-drought and long-drought pools).

Taxon	Contribution	Cumulative %	Direction of difference with control
Potamocypris	23	41.5	+
Cypris	7.5	54.7	+
Moina	6.7	66.6	_
Heterocypris	4.9	75	+
Chironomus	3.4	81.3	+
Alona	2.7	86.1	_
Ceriodaphnia	2.0	89.6	+
Calanoid	1.9	93.0	_
Hyla savignyi	1.3	95.4	+
Dasyhelea	1.2	97.5	+
Cyzicus	1.2	99.6	+
Potamocypris	22	35.8	+
Moina	11.6	54.6	+
Heterocypris	8	67.7	+
Dasyhelea	3.9	74	+
Cyzicus	3.3	79.4	+
Alona	2.9	84.2	_
Cypris	2.6	88.4	+
Ceriodaphnia	2.0	91.7	+
Calanoid	1.7	94.4	_
Hyla savignyi	1.6	97.0	_
Chironomus	1.4	99.4	+

Short-drought pools versus control (dissimilarity = 99.6). Long-drought pools versus control (dissimilarity = 99.4).

the experiment (Fig. 6a). *Culex laticinctus* started to oviposit into the experimental pools later, starting from week 8 of the experiment (Fig. 7a). Due to the lack of *Culex* egg rafts before desiccation, analyses were run from week 8 to the end of the experiment.

Before desiccation, there were no significant differences among treatments in *C. longiareolata* oviposition, *C. longiareolata* larval abundance, *C. laticinctus* oviposition or *C. laticinctus* larval abundance (Table 5).

After desiccation, there were significant time  $\times$  treatment interactions between the short-drought pools and the control for *C. longiareolata* oviposition (*P* = 0.029; Table 5), *C. longiareolata* larval abundance (*P* < 0.001; Table 5), *C. laticinctus* oviposition (*P* = 0.012; Table 5) and *C. laticinctus* larval abundance (*P* = 0.036; Table 5). *Culiseta longiareolata* egg rafts were more abundant in the short-drought pools than in the control from week 8 to week 10 (Fig. 6a) and *C. longiareolata* larval abundance was higher in short-drought pools compared with control pools from week 9 to week 11 (Fig. 6B). *Culex laticinctus* oviposition was higher in the short-drought pools than in control from week 8 to week 10 (Fig. 7a) and *C. laticinctus* larval abundance was higher in the short-drought pools than in control from week 8 to week 10 (Fig. 7a) and *C. laticinctus* larval abundance was higher in the short-drought pools than in controls from week 9 to week 11 (Fig. 7b).

There was an overall significant effect of the long drought on *C. longiareolata* and *C. laticinctus* oviposition, in comparison to the control (P = 0.013 for both; Table 5). From week 12 to week 16, *C. longiareolata* egg raft abundance was higher in the long-drought pools than in the control

![](_page_9_Figure_1.jpeg)

Fig. 6. Abundance of egg rafts (a) and *Culiseta longiareolata* larvae (b) (mean + SE, n = 8). Control, control pools; short drought, short-drought pools; long drought, long-drought pools.

(Fig. 6a) and *C. laticinctus* oviposition was higher in the long-drought pools than in control pools from week 12 to the end of the experiment (Fig. 7b). There were significant time  $\times$  treatment interactions for *C. longiareolata* larval abundance between long-drought pools and control pools (P = 0.012; Table 5). *Culiseta longiareolata* larval abundance was higher in long-drought pools than in control pools from week 13 to week 16 (Fig. 6b). Time  $\times$  treatment interactions were statistically significant for *Culex laticinctus* larval abundance between long-drought pools and control pools (P = 0.001;

Table 5). *Culex laticinctus* larval abundance was higher in the long-drought pools than in control pools from week 13 to the end of the experiment (Fig. 7b).

# Path analysis

Path analyses for both *C. longiareolata* and *C. Laticinctus* showed the same qualitative patterns (Fig. 8; Table 6). There were negative but not significant relationships between

![](_page_10_Figure_1.jpeg)

Fig. 7. Abundance of egg rafts (a) and *Culex laticinctus* larvae (b) (mean + SE, n = 8). Control, control pools; short drought, short-drought pools; long drought, long-drought pools.

the two drought treatments and filter feeder abundance, and between filter feeder abundance and chlorophyll *a* (Fig. 8, dashed arrows), but very little of the variation in filter feeder abundance and chlorophyll *a* was explained by the model (Table 6,  $R^2$  values). For both mosquito species, there was a significant positive relationship between chlorophyll *a* and oviposition (Fig. 8, bold vertical arrows). The direct effect of filter feeders on oviposition was positive for both species but was significant only for *C. laticinctus* (Fig. 8b, curved bold arrow). Most of the variation in oviposition was unexplained, although the  $R^2$  values for oviposition were much higher than those for filter feeder abundance or chlorophyll *a* (Table 6,  $R^2$  values).

#### Discussion

We assessed the effect of desiccation in temporary habitats on mosquito populations during post-disturbance community recovery. Desiccation had a negative effect on invertebrate community richness and a positive effect on phytoplankton, which may have contributed to an increase of mosquito oviposition in the disturbed habitats.

## Impact of drought on communities

Most published studies of the effects of drought in freshwater communities are on lentic ecosystems, and very few

	Before desiccation in short drought			After desiccation in short drought			Before desiccation in long drought			After desiccation in long drought		
Source of variation	d.f.	F	Р	d.f.	F	р	d.f.	F	Р	d.f.	F	Р
Culiseta egg raft abundance												
Treatment	1, 14	0.4	0.532	1,14	1.5	0.241	1, 14	0.3	0.618	1,14	8.1	0.013
Time	3.9, 54.1	2.5	0.055	9,126	14.8	< 0.001	5,70	1.6	0.170	5,70	3.7	0.005
Time $\times$ treatment	3.9, 54.1	2.4	0.065	9, 126	2.2	0.029	5,70	1.0	0.413	5,70	1.2	0.315
Culiseta larval abundance												
Treatment	1, 14	2.1	0.167	1,14	2.0	0.179	1, 14	2.1	0.167	1,14	15.4	0.002
Time	5,70	14.6	< 0.001	3.2, 44.8	10.7	< 0.001	5,70	14.6	< 0.001	2.1, 30.1	11.4	< 0.001
Time $\times$ treatment	5,70	1.8	0.127	3.2, 44.8	9.6	< 0.001	5,70	1.8	0.127	2.1, 30.1	5.0	0.012
Culex egg raft abundance												
Treatment	NA	NA	NA	1,14	0.1	0.815	NA	NA	NA	1,14	8.1	0.013
Time	NA	NA	NA	5,7, 79,2	1.9	0.088	NA	NA	NA	5,70	3.7	0.005
Time $\times$ treatment	NA	NA	NA	5,7, 79,2	3.02	0.012	NA	NA	NA	5,70	1.2	0.315
Culex larval abundance												
Treatment	NA	NA	NA	1,14	1.3	0.281	NA	NA	NA	1,14	0.5	0.481
Time	NA	NA	NA	5,70	3.03	0.016	NA	NA	NA	2.5, 34.8	16.3	< 0.001
Time $\times$ treatment	NA	NA	NA	5,70	2.5	0.036	NA	NA	NA	2.5, 34.8	7.1	0.001

**Table 5.** Results of repeated-measures ANOVA for mosquito variables (*Culiseta longiareolata* and *Culex laticinctus*) before and after desiccation in the short-drought and long-drought pools\*.

\*NA, not applicable (insufficient data for analysis).

Bold values represent significant relationships at the 0.05 level, based on repeated-measures ANOVA.

concern lotic ecosystems. In the latter, stream flow variability has been identified as a major factor affecting abiotic and biotic factors that regulate lotic macrozoobenthic processes (Naiman et al., 2008; Ceola et al., 2013). Mediterranean streams are characterised by flooding and droughts. Recession of flood waters results in the formation of isolated rock pools along wadi channels, which can last from several weeks to several months, depending on the weather conditions (Ward & Blaustein, 1994). Environmental parameters such as temperature, conductivity, depth and width, and dissolved oxygen influence invertebrate distribution, genera richness, and abundance (Pires et al., 2000; Tarr et al., 2005). In our study, the difference in water conductivity between treatments before desiccation was due to the addition of distilled water in the control pools to maintain the water level. This led to low conductivity in the control pools in comparison to the short-drought and long-drought pools. pH and dissolved oxygen were significantly lower in the long-drought pools than in the controls after the desiccation period. Indeed, the 'bloom' of algae observed in the long-drought pools may have influenced pH levels and dissolved oxygen concentrations through respiration and photosynthetic activity.

In our pools, the invertebrate community was generally comprised of crustaceans and insects, the diptera *Chironomus* sp. and *Dasyhelea* sp. being the most abundant insects after mosquitoes. After the drought, dipterans colonised the pools first, with non-flying taxa (mainly zooplankton, and mainly filter feeders in our case) arriving later. This delay may have led to an increase in phytoplankton because of reduced grazing. The effect of drought is linked to intrinsic characteristics of invertebrates (Johnson & Vaughn, 1995): high recolonisation rates, delayed hatching of drought-resistant eggs, and ability to take refuge (Delucchi, 1988). Therefore, drought appears to favour dipterans, which are more tolerant of drought conditions and have more efficient recolonisation mechanisms (Extence, 1981; Pires *et al.*, 2000). However, after a drought period, Otermin *et al.* (2002) observed non-flying taxa to be more abundant as they are more resistant to drought than flying taxa.

In our study, the two drought regimes had different effects on the invertebrate community. The duration of the hydroperiod and seasonality influence the composition and dynamics of the communities inhabiting temporary habitats and determine the faunal composition and structure of aquatic communities in these systems (McLachlan, 1985; Jeffries, 1994; Boix et al., 2001). Drought imposes changes in the macroinvertebrate community, and the magnitude of the changes depends on the degree and duration of the drought (Boix et al., 2010). However, the timing of inundation has a greater and more positive impact on both species richness and density than on hydroperiod duration (Kneitel, 2014). Densities of active dispersers, such as Chironomidae and Culicidae, increased in late inundation (in spring), and more specifically in the case of short-inundation treatment (8 weeks of inundation), as compared with early inundation (in winter) and long-inundation treatment (16 weeks; Kneitel, 2014). In our study, the inundation in the long-drought pools, which was later than in the short-drought pools, led to higher concentrations of chlorophyll a, perhaps due to the late development of the filter feeders, Moina being the crustacean that was most impacted by the drought. We hypothesised that there would be a negative impact of both drought treatments on zooplankton, which are mainly herbivores, and that this would lead to an increase in algae. However, although our path analyses were consistent with this hypothesis, the relationships among these variables were not significant, and very little of the variation in filter feeder biomass and chlorophyll a was explained. Other factors that were not considered in our model may therefore be important.

![](_page_12_Figure_1.jpeg)

Fig. 8. Path analyses representing relationships between oviposition, chlorophyll *a*, filter feeders and treatment after second flooding for: (a) *Culiseta longiareolata*; (b) *Culex laticinctus*. Solid arrows represent positive relationships, and dashed arrows negative relationships. Bold arrows represent significant relationships at the 0.05 level, based on z-tests. Numbers are standardised coefficients.

able o, ram analyses for relationships among ovposition, emotophyn $a$ , interfeeder biomass and treatment after second hooding :										
Response variable	$R^2$	Explanatory variable	Coefficient	Standard error	z-score	<i>P</i> -value	Standardised coefficient			
C. longiareolata oviposition	0.37	Chlorophyll a	0.53	0.15	3.59	< 0.0005	0.59			
		Filter feeder biomass	0.24	0.15	1.59	0.11	0.26			
C. laticinctus oviposition	0.28	Chlorophyll a	0.36	0.15	2.46	0.01	0.43			

0.31

-0.16

-0.02

-0.17

0.15

0.20

0.49

0.49

**Table 6.** Path analyses for relationships among oviposition, chlorophyll *a*, filter feeder biomass and treatment after second flooding<sup>3</sup>

Filter feeder biomass

Filter feeder biomass

Long drought

Short drought

\*Models fitted by maximum likelihood using R package LAVAAN 0.6-1. Oviposition is total number of egg rafts after second flooding, log(x + 1)-transformed. Chlorophyll *a* and filter feeder biomass are centred and scaled. Root mean square errors of *c*. 0.50 for *Culiseta longiareolata* model and 0.43 for *Culex laticinctus* model. Relationships among chlorophyll *a*, filter feeder biomass and treatment are the same for both models.

# Impact of drought on mosquitoes

Chlorophyll a

Filter feeder biomass

Mosquito oviposition habitat selection is not random, and mosquitoes lay eggs selectively (Yoshioka *et al.*, 2012). Indeed, while selecting habitat to lay their eggs, females integrate environmental information on which they base ovipositing decisions

0.03

0.01

(Edgerly *et al.*, 1998), which can ultimately influence the offspring's fitness (Edgerly *et al.*, 1998). When facing choices, the female mosquito will select the habitat that is more suitable for her progeny, avoiding antagonists (competitor and/or predators; Blaustein *et al.*, 1995; Blaustein, 1998; Bond *et al.*, 2005). However, in some specific cases, the mosquito *Aedes aegypti* 

2.13

-0.80

-0.04

-0.34

0.03

0.42

0.97

0.73

0.38

-0.16

-0.01-0.08

will preferentially oviposit in habitats in which the predator Toxorhynchites theobaldi and dead conspecific larvae are present, as the ovipositing females are attracted by increasing bacterial abundance due to dead larvae (Albeny-Simões et al., 2014) Increasing the amount of food increases mosquito oviposition (Blaustein & Kotler, 1993). Pulsed disturbances of larval mosquito sites can have an immediate negative effect on mosquitoes but can also favour mosquito oviposition during the post-disturbance recovery period due to the alteration of community structure (Duchet et al., 2017, 2018). Indeed, Duchet et al. (2017, 2018) showed that altered communities become attractive to gravid mosquitoes searching for oviposition sites when the disturbances decrease the abundance of mosquito antagonists but increase mosquito food resources. In our study, the disturbed pools, and more specifically the long-drought pools, had more food resources and fewer mosquito larvae competitors, making the pools more attractive for C. laticinctus, reflected in an increase in mosquito oviposition. Our path analysis supported the hypothesis that pools with more food would be more attractive to ovipositing mosquitoes. However, extensive studies are still needed to validate this hypothesis. They should include field studies in rock pool systems where abiotic and biotic parameters may be carefully monitored in combination with measurements of invertebrate biomass and mosquito oviposition for demonstrating the role of algae dynamics on mosquito oviposition. By contrast, the direct effect of filter feeders on oviposition estimated from our path analysis was unexpectedly positive (and significantly so for C. laticinctus). This is unlikely to be because high chlorophyll a favours both high filter feeder biomass and oviposition. This pathway is already included in our analysis and would require a positive rather than a negative sign for the relationship between filter feeder biomass and chlorophyll a. An indirect mutualism also seems unlikely, because it would require mosquitoes and filter feeders to specialise on different components of the phytoplankton, rather than competing (Dethier & Duggins, 1984). However, it is possible that there is an indirect effect of some physicochemical variable not considered in the path analysis, leading to some pools having high filter feeder biomass and also being attractive to mosquitoes.

This post-drought increase in mosquito oviposition supports the observations from Chase and Knight (2003). These authors evaluated the effect of hydroperiod length on mosquito abundance and showed that emergence of mosquitoes increased after a drought event, as predators and competitors, which usually contain mosquito populations, were limited after such events. Although predators can recolonise these semi-permanent habitats following drought, mosquitoes, considered as pioneer insects, typically have much more rapid population dynamics than predators, allowing them to escape predation, leading to population outbreaks in a very short period.

In conclusion, changes to the hydrological cycle are likely under an enhanced greenhouse effect. An increased frequency of moderate to heavy rainfall events alternating with drought periods is expected in Mediterranean regions. This will increase the potential for flooding, which this study shows may have a profound effect on mosquito populations. One possible consequence is increased transmission rates for mosquito-borne diseases.

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Author contributions: CD, LB, and SM proposed and designed the study. CD performed fieldwork and data gathering with the assistance of M. Stein and SM. CD performed the data analysis with the assistance of M. Spencer and carried out the manuscript preparation. All authors contributed critically to the drafts and gave their final approval to the manuscript submitted for publication.

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