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Co-occurrence of amphibians and mosquitoes in ponds and wetlands in Switzerland

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par

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Content

Abstract

Wetland areas are decreasing in the world with a loss of biodiversity due to exploitation, agricultural expansion and sanitation. Mosquitoes are part of the trophic chains of wetlands but their ecological role is usually overlooked and reduced to their role in diseases propagation. Promoting the creation of ponds and wetlands with such uncharismatic hosts remain difficult, as trophic chains and competitors might be slower to colonize newly-created ponds. In young ponds, mosquitoes might benefit of the reduced influence of amphibian and invertebrate predators. Our hypotheses were that amphibians and invertebrate predators would decrease mosquito presence in the ponds.

In this study we sampled mosquito larvae in 79 young ponds of Western Switzerland , including the amphibian larvae (Anura and Urodela) , invertebrate predators (Odonata lavae and Coleoptera) together with physical parameters of those ponds as well as the age of the ponds, in order to determine if those factors were leading to mosquito reduced presence in such young ponds. Our results indicated that the amphibians and invertebrate predators did not influence negatively the mosquito presence in ponds, and that the presence of mosquitoes was more likely to happen in non temporary ponds. The age of the pond had slight influence on the presence of Culex mosquitoes. Such results are in opposition with the predicted hypotheses. Further studies including the density of mosquitoes as variable, as well as other aquatic predators could give more insight on the parameters influencing mosquitoes in newly created ponds.

Key words : Culex, Anopheles, Urodela, Anura, competition, predation

Résumé

Les zones humides disparaissent dans le monde entier avec une perte de diversité due notamment à l'exploitation agricole et l'assainissement. Les moustiques font partie intégrante des réseaux trophiques des zones humides, mais leur role écologique est bien souvent ignoré en regard de leur rôle direct dans la propagation de maladies. Promouvoir la création d'étangs avec des hôtes si peu charismatiques peut s'avérer difficile, notamment de par la colonisation plus lente des nouveaux étangs par les prédateurs. Dans les jeunes étangs, les moustiques pourraient bénéficier de l'influence réduite des amphibiens et prédateurs invertébrés. Nos hypothèses étaient que les amphibiens et invertébrés prédateurs réduiraient la présence des moustiques. Dans cette étude, nous avons échantillonné 79 jeunes étangs de Suisse occidentale, incluant les larves d'amphibiens (anoures et urodèles), les invertébrés prédateurs (larves d'odonates et adultes et larves de coléoptères) ainsi que des paramètres physiques et l'âge de ces étangs dans le but de déterminer quels facteurs infuencent la présence de ces moustiques dans ces derniers. Nos résultats ont indiqué que les amphibiens et prédateurs invertébrés n'influençaient pas de manière négative la présence des moustiques, et que la présence de moustiques était plus encline à se manifester dans les étangs temporaires. L'âge des étangs a eu une légère influence sur la présence des moustiques du genre Culex, très nombreux dans les échantillons. Ces résultats vont à l'encontre des hypothèses prédites. Des études ultérieures incluant la densité des moustiques en tant que variable, ainsi que d'autres prédateurs aquatiques pourraient donner plus d'indications sur les paramètres influençant les moustiques dans les étangs nouvellement créés.

Mots-clés : Culex, Anophèles, Anoures, Urodèles, competition, prédation

Introduction

Ponds for wildlife Ponds constitute important ecosystems for wildlife in many areas of the world, including Western Europe. The richness of fauna and flora in the wetlands contribute to increase the overall biodiversity of an area (Thiere et al, 2009). Wetlands are part of the natural ecosystems that decreased the most in Switzerland during the last decades, mainly due to creation of agricultural fields, peat production and overall sanitation of the land from possible diseases (Moser et al,1996; Smith & Green, 2005).

A large number of mosquito species depend on wetlands for most of their life stages, if not all of them. Mosquitoes have been studied for a long time, mostly for the ability to bring diseases among populations (Dale & Knight, 2008).

Mosquitoes play an important ecological role in wetlands due to their position in trophic chain, acting as a prey for various vertebrates and invertebrates either as larvae or adults, or as competitors for other species (DuRant & Hopkins, 2008).

Ponds are regularly dug in Switzerland in order to protect amphibians and other wetland species. The reputation of mosquitoes can refrain people to accept such new territory managements (Chase & Shulman, 2007). Promoting the construction of new ponds across the landscape is an essential step in the restoration of wetland areas (Willott, 2004 ; Tariq & Naqvi ,2009; Mokany et al, 2002; Morin, 1983). Equilibrated ponds which have already several years of existence are more likely to include a lot of different species which can have interactions with mosquitoes (Chase and Schulman 2009).

Some studies already explored the predation on mosquitoes from amphibians including either salamanders (Smith and Petranka 1987; Brodman and Dorton, 2006) or frogs (Komak and Crossland, 2000) (Mokany A, Shine R , 2003) in laboratory conditions or mesocosms created during few weeks (Rubbo et al, 2011) with no specific account of ponds age.

The predation from other aquatic predators such as Odonata species have been explored in some artificial conditions too (Stav et al, 2000).

In this study we examined the effect of the amphibian density, including Anura and Urodela larvae and adults, in young ponds less than 20 years old on the presence of mosquito larvae in natural conditions. The hypothesis was that Amphibians density would influence negatively the presence of mosquitoes in ponds. The effect of invertebrate predators including Coleoptera and Odonata underwater life stages on the mosquito presence was also evaluated in the same natural conditions. The hypothesis here was that aquatic large invertebrate predator density would decrease the possibility of mosquito larvae presence. Natural physical factors susceptible to influence the mosquito presence were monitored and analysed in the study on a third model in order to detect if one or more of them in this natural conditions of relatively recent ponds could influence mosquito larvae presence (Tariq & Naqvi, 2009).

Material and methods

Location and ponds

The study took place in western Switzerland in the canton de Vaud region around the town of Lausanne. The area is a continental plain with several deciduous and coniferous forests (46° 32' N; 6° 39' E) between 350 and 900m of altitude.

79 ponds have been successfully sampled during the survey. All the sampled ponds have an age lower than 20 years. A list of the sampled ponds with coordinates is available (Appendix 1).

A total of 100 ponds were initially chosen for the study by ArcGis map provided by KARCH members. The number of possible sampling ponds dropped to 79 as some ponds appeared to be too far from road access after some road modifications and the rest of the discarded ponds didn’t have water or disappeared in dense vegetation. This selection was made from the Ponds exploration tour conducted in the beginning of April 2015.

The samplings were conducted from mid-May to beginning of August of the year 2015, with 6 visits per pond, each of them separated by approximately 15 days. Sunny weather was preferred for sampling.

Mosquito larvae sampling and conditioning

Mosquito larvae were collected every 15 days from May to August 2015 with a small thin-wired dipper of 6x6cm in the middle range (2m long net perch) and at the side of the ponds with 5 dipping moves per sampling. During the 5 dipping moves, the dipper was placed at approximately 20cm under the surface and quickly led upwards in order to catch surface and middle-water larvae.

The sampling rate of ponds was directly correlated with the size of the pond following a protocol similar to the IBEM Pond diversity evaluation method. (IBEM protocol for aquatic invertebrates sampling .http://campus.hesge.ch/ibem p. 14). Adaptation has been made for small ponds, with 1 sampling for ponds of less than $10m^2$, 2 samplings for ponds between 10 and $20m^2$, 3 samplings for ponds between 20 and $30m^2$, and 4 samplings for ponds between 30 and $40m^2$. For ponds larger than $50m^2$, the IBEM protocol was followed.

The sampled mosquito larvae were directly placed in 20ml Eppendorf tubes containing 70° alcohol. The dead larvae were identified in Museum laboratory using binoculars with Eutaxa softwares with culicidae key. The 3rd and 4th instar larvae remained the most reliable ones for species identification. All identified larvae have been kept in the Museum of zoology of Lausanne collection in refrigerated room.

Amphibian adult and larvae counting

Amphibians have been identified and counted twice per month from May to August 2015 using a net of 45cm x 30cm with a 2m long perch. The number of samplings for each pond was the same than mosquito larvae sampling, with 5 moves per sampling. The net was placed at the bottom of the water column if possible, at 2m of the border and on the sides of the pond. Such lower placement allowed catching bottom dwelling amphibians and invertebrates. Small hatchling Urodela larvae caught with mosquito dipper during mosquito larvae sampling were counted too as they remained difficult to capture with the larger net.

The number of larvae and adults was counted each time for Urodela and Anura. Identification of the species was made on the field and all the amphibians were quickly released directly into the pond after the manipulation.

Invertebrate predators sampling

Density of invertebrate predators, including larvae of Anisoptera and Zygoptera, as well as adults and larvae of Coleoptera, was estimated by counting the number of individuals caught both during the mosquito and the amphibian samplings. Both adults and larvae were released into the pond after counting.

Pond parameters measurements

Biotic and abiotic parameters of the ponds were measured. The details of the measures of each parameter and their unity are described in the table 1.

Table 1. Biotic and abiotic variable measurements of the ponds

Parameters	Method	Unity
Biotic		
Immerged vegetation	Estimation of the percentage of pond surface showing immerged plants, particularly algae and Hydrophyta. Estimated once per month. Final value is the mean of the month values.	percentage
Emerged vegetation	Estimation of the percentage of pond surface showing emerged plants, particularly Hydrophyta including reeds. Estimated once per month. Final value is the mean of the month values.	percentage
Floating vegetation	Estimation of the percentage of pond surface covered by plants, particularly duckweed (Lemna sp.) and water lilies (Nuphar or Nymphea sp.). Estimated once per month. Final value is the mean of the month values.	percentage
Canopy cover	Spherical crown densiometer used to determine the canopy cover of the pond when placed in the middle of it. Measured once in May and once in July. Final value is the mean of both.	percentage
Forest at 50m of the pond	Calculation of forest cover in a 50m radius from the center of the pond using map calculation and field estimation. Measured once in June.	percentage
Nitrates and sulfates	Analyses conducted in laboratory of water analysis in Lausanne from 1 dl water sampled in ponds. Sampled once in August.	mg/l
Abiotic		
Permanent/ temporary pond	Factor indicating whether the pond could be dry during the year or remain in water despite summer heat, mainly with deepness and water supply. Measured at the end of the field sampling in August	Binary
Surface	Official maximum surface of the pond obtained from ArcGis maps	m^2
Flux	Factor indicating whether the pond has stagnant water or flows quietly in a certain direction. Factor measured once per month. Final value is the dominant number in the samplings.	Binary
Age	Age of the ponds known from creation date in ArcGis data	years

Sector	Factor indicating if the pond is in the same area than other ponds, in order to verify spatial distribution. This factor is detailed with map and distance between ponds, usually less than 100m.	Name
Maximum deepness	Maximum deepness of the pond measured in May before the natural volume reduction of summer.	cm

Statistical analysis

Generalized linear models (GLM) from the package CRAN in the R 3.2.5 Software (https://www.r-project.org/) were performed for each of the 3 hypothesis. One model for each hypothesis was conducted in order to limit false interactions and biased variance explanation. The 3 different models used presence/absence of mosquitoes as response variable.

The presence/absence was determined with the presence of at least one species of mosquito for the total mosquito larvae and the presence of one respective species in the 3 different genera groups (Culex, Anopheles, Ochlerotatus/Culiseta) in the pond during the whole sampling period.

The first model used amphibian density and age of the pond as explicative variables, as well as interactions between those variables. The second model used the density of predator invertebrates, age of the pond and interactions as explicative variables. The third model used the age of the pond, the immerged vegetation, emerged vegetation, floating vegetation, canopy cover, age of the pond, maximum deepness and temporary/permanent variables as explicative variables. Secondary analyses made that the fitted models were performed within the different main mosquito genus: Culex, Anopheles and Ochlerotatus/Culiseta.

.The sector of the pond was included in the 3 models as random factor in order to limit the effect of spatial correlation. The variables have been log transformed in order to perform the calculations in GLMs.

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Results

Ponds with mosquitoes and amphibians

Out of the 79 ponds, 39 indicated the presence of mosquitoes during the sampling period. 42 Ponds indicated the presence of amphibians, and 21 indicated the presence of both amphibians and mosquitoes.

Mosquito species

Several mosquito species belonging to the genus of Culex, Anopheles, Ochlerotatus, Culiseta and Aedes were identified in the samples. Some larvae remained impossible to identify due to young age, decreased quality, missing parts or uncertainty.

The most represented genus in the ponds was Culex with 634 identified larvae of 3 different species and represented the vast majority of larvae samples (Table 2). The largest samples of Culex happened in 3 small (2m^2) very young ponds (<2years old) with no predators, probably resulting from successful hatch sampled in one time with dipper. The ponds had 168, 52 and 164 Mosquito larvae with none predator of any kind.(Ponds name: Unil 2, Unil 8 and Unil 9 respectively in Appendix 1)

Table 2. Mosquito larvae species identified in the ponds per genus with total larvae number and total number of inhabited ponds.

Mosquito species	Number of larvae sampled	Number of inhabited ponds
Culex pipiens/torrentium	294	15
Culex hortensis	301	9
Culex territans	39	12
Total Culex genus	634	36
Anopheles maculipennis	17	10
Anopheles claviger	20	10
Anopheles sp.	1	1
Total Anopheles genus	38	21
Ochlerotatus punctor	5	1
Ochlerotatus communis	1	1
Ochlerotatus flavescens	1	1
Ochlerotatus cantans	6	2
Ochlerotatus sp.	4	4
Aedes gr. cinereus	2	1
Culiseta marsitans	4	1
Culiseta sp.	14	5
Total Culiseta and Ochlerotatus/Aedes genus	37	16
Total mosquito larvae	709	73

Influence of amphibians larvae on mosquito larvae presence.

The presence and density of amphibians in the ponds did not affect the overall mosquito presence in the ponds (Table 3). An outlier (density > 5) was removed from the models in order to avoid a misinterpretation from such a strong value, which appeared to really change the model and graph output if taken into account. This outlier was a very small shallow pond (< $6m^2$) In the Vivarium of Lausanne garden where the newts larvae density was particularly high when sampling (Pond name Sauvabelin 1 in Appendix 1).

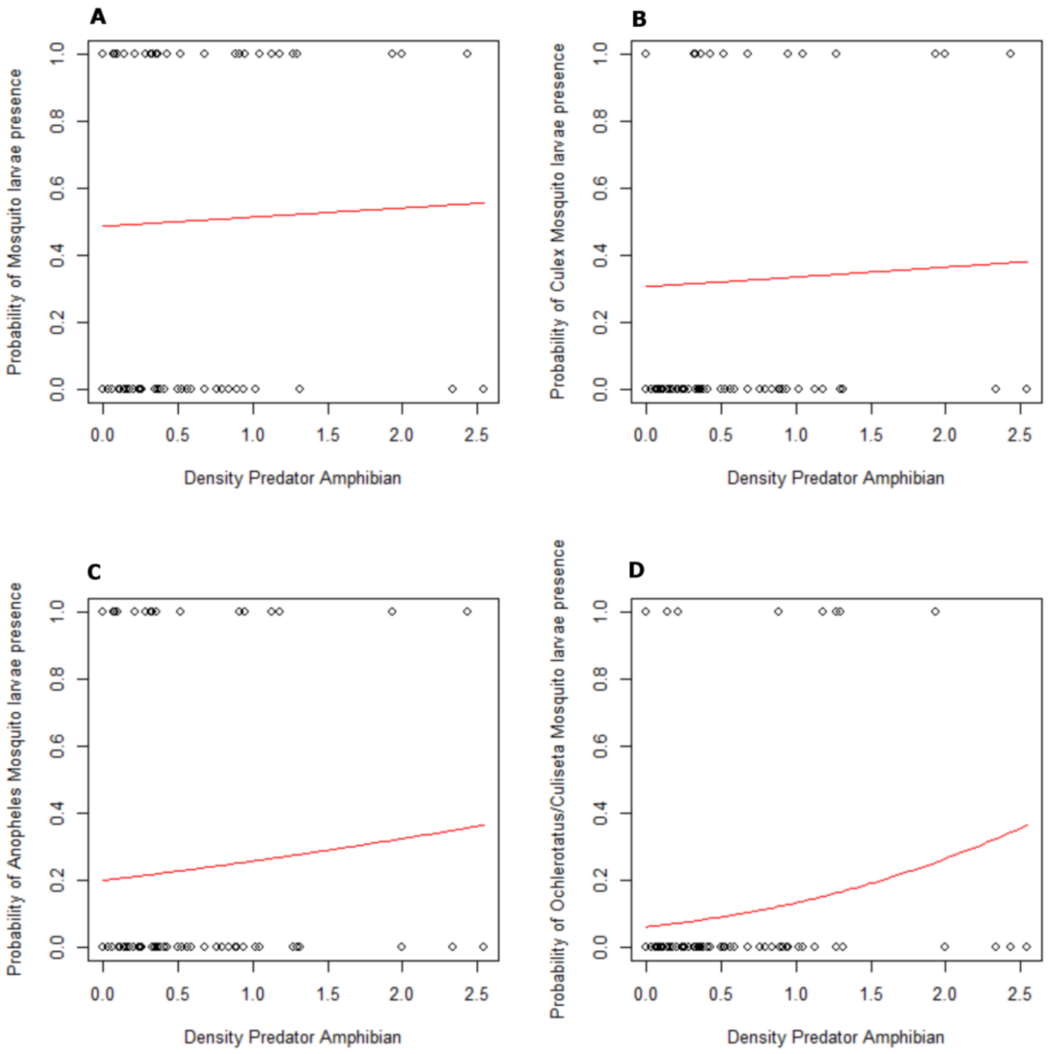
In the Culex model, a correlation between the age of the pond and density of amphibians on the presence of mosquitoes was detected (Table 3.B). The probability of mosquito presence shows a positive correlation with amphibian density in the model with only Culex genus mosquito larvae (Fig 1.B)

For the Anopheles and Ochlerotatus/Culiseta mosquito larvae models, the probability of mosquito presence appears to be similar like the Culex model and the total mosquitoe larvae model, but none significant correlation was proved within this data set (table 3.C and D.).

Table 3 : Results of the Generalised linear models (glmer) with Amphibian larvae (Anura and Urodela) density and age of the pond parameters as explicative variables and mosquito larvae presence as response variables. The sector factor was used for spatial correlation correction.

	Total larvae variables	**Sector variance**	**Df.resid**	**Std. error**	**P-value**	**AIC**
A	Age of Pond	1.458	74	0.082	0.764	110.8
	Density Amphibians	1.458	74	0.899	0.730	110.8
B	**Culex variables**					
	Age of Pond	0.094	73	0.091	**0.002 ***	94.7
	Density Amphibians	0.094	73	1.761	0.070	94.7
	Interaction Age * Density	0.094	73	0.180	**0.020 ***	94.7
C	**Anopheles variables**					
	Age of Pond	1.39^{e-20}	73	0.077	0.887	93.7
	Density Amphibians	1.39^{e-20}	73	1.685	0.584	93.7
	Interaction Age * Density	1.39^{e-20}	73	0.168	0.818	93.7
D	**Ochlerotatus/ Culiseta variables**					
	Age of Pond	0.978	73	0.161	0.603	56.3
	Density Amphibians	0.978	73	3.257	0.837	56.3
	Interaction Age * Density	0.978	73	0.309	0.703	56.3

Figure 1 : Probability of mosquito larvae presence in ponds as a function of the density of amphibian predators. **A** : Total mosquito larvae **B**: Culex mosquito larvae **C**: Anopheles mosquito larvae **D**: Ochlerotatus/Culiseta mosquito larvae. Those graphs are derived from the fitted model of the GLM.



Influence of Invertebrate predators larvae on mosquito larvae presence

The density of Zygoptera, Odonata and Coleoptera shows a correlation (p=0.04) with the presence of mosquitoes larvae in the ponds when all mosquito species are considered together (Table 4.A). The Plot in Fig 2. shows a positive correlation between the density of Invertebrate predators and the mosquitoes presence. Such similar positive correlation is observed as well in the models where each Mosquito groups are tested separately (table 4 C. and D.) but no significant correlation of the predators density was observed (Fig 4 C and D.).

In the Culex model, a correlation with the age of the pond was revealed significant (p=0.04), and the density of predators variable remains close to the P=0.05 level.

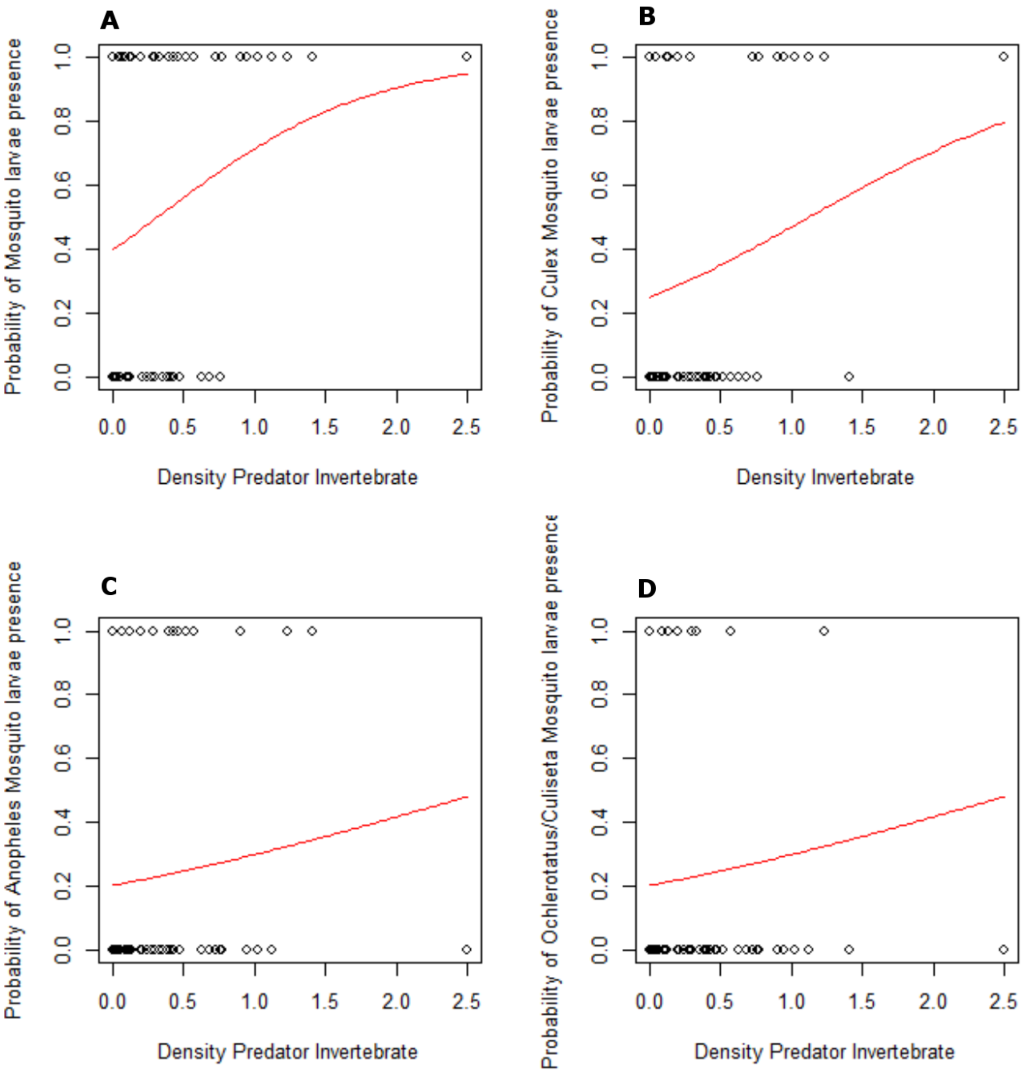
An outlier was removed (density >6) in order to avoid misinterpretation. This outlier increased the positive correlation of the graph and the significance of the model if he was taken into account in the models. It was removed for safety of the analysis.

The graphs (Fig 4) in the 4 different models indicate a positive correlation between the density of predators and the presence of mosquito larvae.

Table 4 : Results of the Generalised linear models (glmer) with Invertebrate predators (Anisoptera and Zygoptera larvae and coleoptera larvae + adult) density and age of the pond parameters as explicative variables and mosquito larvae presence as response variables. The sector factor was used for spatial correlation correction. The results are from fitted models where interactions were removed.

A	**Total Variables**	**Sector variance**	**Df.resid**	**Std. error**	**P-value**	**AIC**
	Age of Pond	1.361	74	0.083	0.6854	106.7
	Invertebrate predators density	1.361	74	1.292	**0.0402 ***	106.7
B	**Culex variable**					
	Age of Pond	0.518	71	0.072	**0.0409 ***	90.3
	Invertebrate predators density	0.518	71	1.145	0.0788	90.3
C	**Anopheles variables**					
	Age of Pond	1.37e-14	74	0.057	0.922	91.2
	Invertebrate predators density	1.37e-14	74	0.987	0.305	91.2
D	**Ochlerotatus/Culiseta Variables**					
	Age of Pond	1.126	74	0.113	0.247	56.8
	Invertebrate predators density	1.126	74	1.626	0.802	56.8

Figure 2 Probability of mosquito larvae presence in ponds as a function of the Invertebrate predators density in each pond including both Odonata (Anisoptera and Zygoptera) and Coleoptera (Adult and larvae). **A** : Total mosquito larvae **B**: Culex mosquito larvae **C**: Anopheles mosquito larvae **D**: Ochlerotatus/Culiseta mosquito larvae. Those graphs are derived from the fitted model of the GLM.



Influence of Pond Physical factors on mosquito larvae presence. The physical factors retained for the model where the immerged and emerged vegetation, the floating vegetation, the canopy cover, the age, the temporary/permanent factor and the maximum deepness of the pond. The water quality parameters (nitrates and sulfates) have been tested previously but remained to have none effect.

The only physical factors indicating a significant correlation in the models was the binomial temporary factor. This factor remained the only one kept after fitting the model (Table 5).

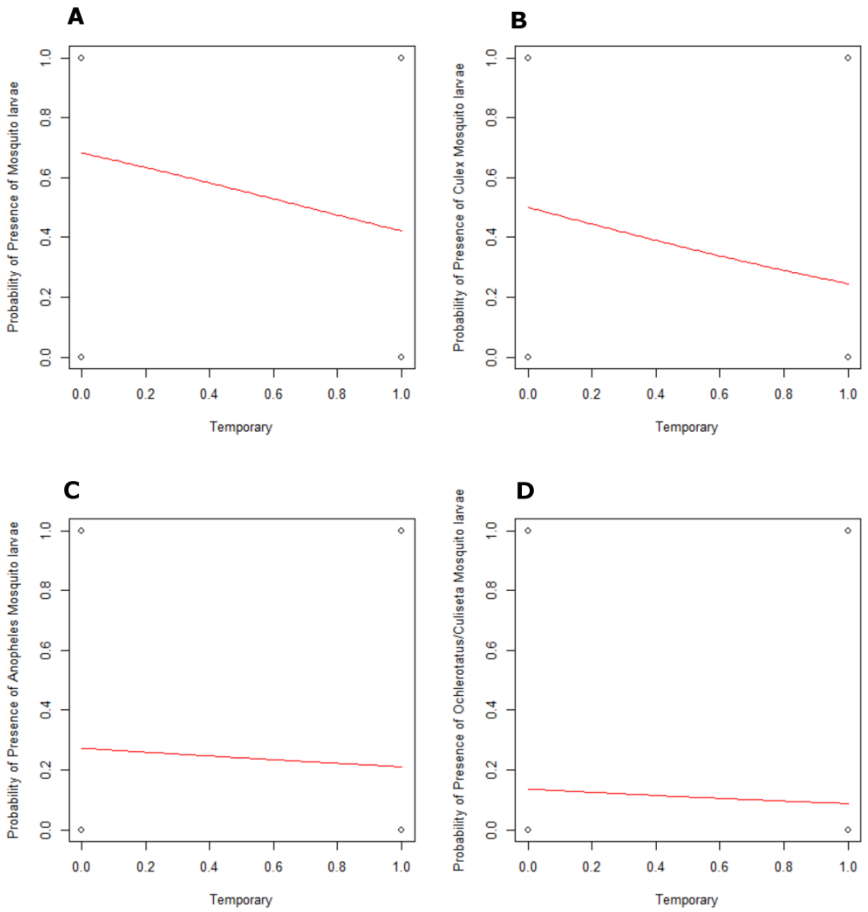
None model displayed an correlation between the temporary factor and mosquito larvae presence except the Culex one (p=0.02) (Table 5.B).

A negative correlation between temporary factor and mosquito presence was showed (Fig 3), suggesting that mosquitoes are less likely to be found in temporary ponds according to this data set.

Table 5 : Results of the Generalised linear models (glmer) with physical parameters as explicative variables and mosquito larvae presence as response variables. The sector factor was used for spatial correlation correction. The temporary factor was the only one kept after fitting the model. The results are from fitted models where interactions were removed.

	Total Variables	**Sector variance**	**Df.resid**	**Std. error**	**P-value**	**AIC**
A	Temporary	0.758	76	0.6508	0.0755	108.3
B	**Culex variable**					
	Temporary	1.023	76	0.745	**0.0229 ***	93.9
C	**Anopheles Variable**					
	Temporary	0	76	0.578	0.555	90.5
D	**Ochlerotatus/ Culiseta Variable**					
	Temporary	2.175	76	1.217	0.980	56.5

Figure 3 Probability of mosquito larvae presence in ponds when the pond is temporary (1) or not (0) **A** : Total mosquito larvae **B**: Culex mosquito larvae **C**: Anopheles mosquito larvae **D**: Ochlerotatus/Culiseta mosquito larvae



Discussion

In the results, we observed a dominance of Culex genus larvae in the samplings. In the first model, a positive correlation was observed between the Culex genus mosquito larvae presence and the interaction of amphibian density with the age of the pond. A correlation between the presence of total mosquito larvae and the age of the pond was also observed in this first model. In the second model, a positive correlation was observed between the Total mosquito larvae presence and the Invertebrate predator density. In the second model, a second correlation was observed between the Culex genus larvae presence and the age of the pond. In the third model, a correlation was observed between the Culex genus mosquito larvae presence and the temporary factor of the pond.

The important dominance of Culex mosquito larvae in the samples is congruent with the fact that it's a widespread genus in Europe able to live in a large variety of environments, including small ponds (Weitzel et al, 2011).

In the first model, the positive correlation of the higher density of amphibians with the presence of mosquitoes is in opposite with the predicted hypothesis and seems counter-intuitive, as the presence of predators or competitors usually are an obstacle for the species (Mokany et al. 2003; Rubbo et al, 2011; Fincke et al. 1997, Saha et al. 2012).

The small recent ponds with large Culex larvae number and no predators as briefly described in result section could possibly explain the observed correlation between the presence of total mosquito larvae and the age of the ponds In Culex model.

Such small recent ponds seem to act as refuges for mosquito larvae which can therefore grow up. The small size of the ponds allowed a sampling where many larvae could have been caught at the same time, increasing the effect of those ponds.

In the second model, a positive correlation suggests the possibility of none effect of invertebrate predators density on the decrease of the presence of total mosquito larvae in ponds, which is in opposite with our hypothesis where invertebrate predators would decrease the mosquito larvae number (Stav et al, 2000).

The model with only Culex mosquito larvae showed a slightly significant correlation between the age of the pond abd the mosquito presence. The other genus did not show any correlation. This result could have the same explanation with Culex genus being found in large number in some located ponds.

Factors influencing positively the mosquitoes could influence in the same way the presence and density of the amphibians and predators (Mokany et al. 2002; Blaustein & Chase, 2007). Predator minimal requirements can be very similar to their preys, such as the amount of water, number of hiding possibilities or lack of their own predators (Kumar et al, 2008).

The mosquito presence, in the opposite, could directly positively influence the presence and density of the amphibians and invertebrate predators acting as food sources (Yeoman & kimberlie, 2014; Dida et al, 2015). The presence of mosquitoes would therefore be one of the factors attracting the predators, influencing the support capacity of the pond for those larger species (Chase & Shulman, 2009; Blaustein &Sadeh, 2013).

The presence of mosquitoes in those ponds as well as the density of amphibian and invertebrate predators might be influenced by other factors which have not been measured in this data set, including other species of animals such as aquatic hemiptera predators (Blaustein et al. 2004; Silberbush & Blaustein, 2008; Toronto conservation, 2011)

The age of the ponds correlation within Culex models might have been influenced by the reduced age of the few ponds where most of Culex larvae have been sampled, increasing the correlation effect towards young ponds.

In the third model with physical parameters of the pond, the only significant correlation appeared in the Culex mosquito larvae model with the temporary factor, suggesting that Culex mosquito larvae could be more likely found in non-temporary ponds. (Brendonk et al, 2001).

Temporary ponds tend to show lower diversity as many species require more than one year to complete their cycle (Chase and Knight, 2003; Schneider 1997). Temporary ponds do represent refuges for species with short development rate (Wiggins et al, 1980; Spencer et al, 1999; Brendonck et al, 2002) but with very dry season the risk to get evaporated remains higher. Particularly small ponds with high number of mosquito larvae did profit of small volume but did dry out quickly during the season, leading to higher mortality rate. Several ponds of the study became dying places for amphibian and Odonata larvae as well, without mentioning the high temperatures leading to decreased dissolved oxygen available for animals.

Temporary ponds remain however extremely important for many amphibian and invertebrate species which do not compete successfully in permanent water places.

2015 Heatwave

2015 year displayed particularly hot summer temperatures and lack of rain (Météosuisse 2015), which might have influenced some of the species' ways to interact or laying dates and development time of species (Beck et al, 2013; Merila et al, 2000) . Early drought could have occurred in ponds which usually dry up later in the season or not at all. This condition might have influenced the availability of some species or number of individuals during the samplings, as well as vegetation cover and deepness of ponds.

A study conducted on 2 consecutive years could decrease the influence of such weather factor.

Improvements

Further possibilities to continue this study of young ponds monitoring include models where the mosquito larvae density would be the response variable, including finding appropriate models which can take into account the poisson distribution and the spatial correlation. Other models where the amphibians and invertebrate predators are the response variable and physical factors of ponds are the explicative variables could be performed in order to explore the relationships between those variables. Spatial correlation and distribution remain important to consider (Kumar and Hwang, 2005).

Dividing larger ponds in smaller units when dryness actually separates parts of the pond might give a better overview of the ponds, as some of the ponds appeared to have a large surface divided in smaller ponds during the season. The density of animals would be more accurate, as well as deepness, foliage coverage and other physical parameters, but the extremely spatially correlated ponds might increase the difficulty in statistical models run and interpretations.

Differences between laboratory, mesocosms and field conditions remain important in the understanding of predator-prey cycles. Field studies such as this one allow to have information about the real changes occurring in wetlands at the larger scale when it comes to colonization or recolonization of aquatic places.

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Appendix

Appendix 1 : List of the 79 ponds retained in this study with location coordinates.

ID etang	Sector	Coordinates
Unil 1	Unil	46° 31' 16.104" N 6° 34' 23.862" E
Unil 2	Unil	46° 31' 16.0968" N 6° 34' 24.0168" E
Unil 3	Unil	46° 31' 16.0464" N 6° 34' 23.988" E
Unil 4	Unil	46° 31' 20.2764" N 6° 34' 38.3952" E
Unil 5	Unil	46° 31' 21.7416" N 6° 34' 56.4132" E
Unil 6	Unil	46° 31' 20.82" N 6° 34' 56.6436" E
Unil 7	Unil	46° 31' 20.6148" N 6° 34' 56.9136" E
Unil 8	Unil	46° 31' 20.6328" N 6° 34' 57.7452" E
Unil 9	Unil	46° 31' 28.7976" N 6° 34' 57.5436" E
Unil 10	Unil	46° 31' 28.6392" N 6° 34' 57.1368" E
Sauvabelin 1	Sauvabelin	46° 32' 34.3788" N 6° 38' 32.2368" E
Sauvabelin 2	Sauvabelin	46° 32' 34.2888" N 6° 38' 32.7408" E
Sauvabelin 3	Sauvabelin	46° 32' 34.6308" N 6° 38' 33.2844" E
Chandelar 1	Chandelar	46° 32' 19.2624" N 6° 41' 7.1196" E
Chandelar 2	Chandelar	46° 32' 18.834" N 6° 41' 6.8064" E
Chandelar 3	Chandelar	46° 32' 18.7764" N 6° 41' 6.9576" E
Vernand dessous 1	Vernand dessous	46° 34' 12.3744" N 6° 35' 51.2484" E
Vernand dessous 2	Vernand dessous	46° 34' 12.162" N 6° 35' 50.784" E
Vernand dessous 3	Vernand dessous	46° 34' 12.324" N 6° 35' 51.324" E
Vernand dessus Ouest 1	Vernand dessus Ouest	46° 34' 30.2124" N 6° 37' 20.046" E
Vernand dessus Est 1	Vernand dessus Est	46° 34' 20.3124" N 6° 37' 37.308" E

Bois de fougères 1	Bois de fougères	46° 34' 17.5332" N 6° 38' 9.2328" E
Bois de fougères 2	Bois de fougères	46° 34' 17.4144" N 6° 38' 9.2508" E
Les Troncs 1	Les Troncs	46° 34' 29.5824" N 6° 39' 26.0748" E
Les Troncs 2	Les Troncs	46° 34' 33.7764" N 6° 39' 27.774" E
Les Troncs 3	Les Troncs	46° 34' 34.4676" N 6° 39' 27" E
Benenté 1	Les Troncs	46° 34' 36.9084" N 6° 39' 34.1064" E
Benenté 2	Les Troncs	46° 34' 37.4412" N 6° 39' 33.5664" E
Les Vuargnes 1	Les Vuargnes	46° 34' 18.4296" N 6° 41' 56.2416" E
Les Vuargnes 2	Les Vuargnes	46° 34' 18.4836" N 6° 41' 53.0772" E
Les Vuargnes 3	Les Vuargnes	46° 34' 18.2712" N 6° 41' 52.8432" E
Les Vuargnes 4	Les Vuargnes	46° 34' 17.7924" N 6° 41' 52.7676" E
Les Vuargnes 5	Les Vuargnes	46° 34' 17.472" N 6° 41' 52.5372" E
Les Vuargnes 6	Les Vuargnes	46° 34' 16.8348" N 6° 41' 52.1484" E
Côtes de Mauvernay 3	Côtes de Mauvernay	46° 34' 20.6076" N 6° 41' 37.1616" E
Côtes de Mauvernay 2	Côtes de Mauvernay	46° 34' 20.0748" N 6° 41' 37.0104" E
Corne Bochet	Corne Bochet	46° 34' 29.9748" N 6° 42' 2.3472" E
Censières 1	Censières	46° 34' 34.626" N 6° 42' 27.9936" E
Censières 2	Censières	46° 34' 34.8384" N 6° 42' 28.224" E
Censières 3	Censières	46° 34' 35.4216" N 6° 42' 28.998" E
Refuge Censières 1	Refuge Censières	46° 34' 43.5468" N 6° 42' 44.2152" E
Refuge Censières 2	Refuge Censières	46° 34' 42.5892" N 6° 42' 44.5248" E
Refuge Censières 3	Refuge Censières	46° 34' 41.9016" N 6° 42' 44.136" E
Moille Baudin 2	Moille Baudin	46° 34' 52.95" N 6° 43' 23.4948" E
Grandes Côtes 1	Grandes Côtes	46° 34' 52.626" N 6° 41' 31.9092" E
Grandes Côtes 2	Grandes Côtes	46° 34' 51.7224" N 6° 41' 31.3692" E

Grandes Côtes 3	Grandes Côtes	46° 34' 51.1932" N 6° 41' 31.2936" E
Peccau 1	Peccau	46° 33' 41.2524" N 6° 41' 23.7228" E
Peccau 2	Peccau	46° 33' 33.2856" N 6° 41' 30.3648" E
Peccau 3	Peccau	46° 33' 32.3316" N 6° 41' 32.1432" E
Peccau 4	Peccau	46° 33' 32.1192" N 6° 41' 33.0684" E
Corbessières 1	Corbessières	46° 34' 44.7132" N 6° 41' 4.1028" E
Corbessières 2	Corbessières	46° 34' 44.6592" N 6° 41' 3.8688" E
Corbessières 3	Corbessières	46° 34' 44.3964" N 6° 41' 4.0236" E
Rive Droite Talent	Talent	46° 35' 7.674" N 6° 40' 54.2892" E
Rive GaucheTalent 1	Talent	46° 35' 9.3732" N 6° 40' 53.0544" E
Rive GaucheTalent 2	Talent	46° 35' 9.8232" N 6° 40' 52.6296" E
Rive GaucheTalent 3	Talent	46° 35' 9.636" N 6° 40' 52.3992" E
Tirecul 1	Tirecul	46° 34' 52.7016" N 6° 40' 48.1872" E
Tirecul 2	Tirecul	46° 34' 52.5684" N 6° 40' 47.8416" E
Tirecul 3	Tirecul	46° 34' 52.4604" N 6° 40' 47.2224" E
Tirecul 4	Tirecul	46° 34' 52.0356" N 6° 40' 46.4484" E
Tirecul 5	Tirecul	46° 34' 51.5064" N 6° 40' 45.8724" E
Vieux Pré Noé Est 1	Vieux Pré Noé Est	46° 34' 58.4472" N 6° 40' 28.722" E
Vieux Pré Noé Est 2	Vieux Pré Noé Est	46° 34' 58.1016" N 6° 40' 29.9388" E
Vieux Pré Noé Est 3	Vieux Pré Noé Est	46° 34' 58.5372" N 6° 40' 30.9612" E
Vieux Pré Noé Est 4	Vieux Pré Noé Est	46° 34' 58.8576" N 6° 40' 31.5804" E
Vieux Pré Noé Est 5	Vieux Pré Noé Est	46° 34' 59.8656" N 6° 40' 29.3988" E
Vieux Pré Noé Ouest 1	Vieux Pré Noé Ouest	46° 34' 57.756" N 6° 40' 9.0624" E
Vieux Pré Noé Ouest 2	Vieux Pré Noé Ouest	46° 34' 57.9288" N 6° 40' 9.0048" E
Vieux Pré Noé Ouest 3	Vieux Pré Noé Ouest	46° 34' 58.0476" N 6° 40' 9.2748" E

Tridel 1	Tridel	46° 31' 58.1232" N 6° 38' 38.688" E
Tridel 2	Tridel	46° 31' 58.4436" N 6° 38' 38.7456" E
Tridel 3	Tridel	46° 31' 58.566" N 6° 38' 39.228" E
Tridel 4	Tridel	46° 31' 58.9476" N 6° 38' 39.4584" E
Tridel 5	Tridel	46° 31' 58.836" N 6° 38' 40.3188" E
Flon 1	Flon	46° 31' 49.8936" N 6° 38' 40.3836" E
Flon 2	Flon	46° 31' 51.7692" N 6° 38' 35.322" E
Moille Saugeon	Moille Saugeon	46° 34' 46.7112" N 6° 41' 55.4532" E