POLYTECH TOURS

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Rapport de stage

5ème année

Étude de la distribution spatiale du zooplancton lacustre

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Table des matières

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Présentation de l'entreprise

Le RIVE, ou le centre de recherche sur les interactions bassins versants et écosystèmes aquatiques, est un pôle de recherche basé à l'Université du Québec à Trois-Rivières. Fondé en 2009, il rassemble une équipe multidisciplinaire de chercheurs en biologie, écologie, climatologie, télédétection, hydrologie et aménagement du territoire.

Leur recherche s'articule en 4 axes principaux :

- Écologie des communautés et fonctionnement des écosystèmes
- Dynamique des hydrosystèmes
- Effets des changements environnementaux sur les hydrosystèmes et écosystèmes
- Réhabilitation, protection et gestion des écosystèmes.

L'ensemble des pôles collaborent dans de nombreux projets, notamment dans la gestion durable des littoraux du Lac Saint-Pierre, un lac en amont de Trois-Rivières qui délimite l'estuaire du Saint-Laurent.

Le RIVE accueille chaque année une cinquantaine des étudiants de maitrise et stagiaires, mettant à disposition ressources, animations et infrastructures pour les projets étudiants.

Les principales d'infrastructures appartenant au RIVE :

- Un navire de recherche
- Matériel d'échantillonnage de poissons, invertébrés, zooplancton et autre
- Laboratoires d'analyse en écologie aquatique et hydrologie
- Laboratoire d'écophysiologie animale (bassins, incubateurs et une rivière artificielle)
- Drones à capteurs embarqués (LiDAR, caméras spectrales…)

Colloque du RIVE 2017

Contenu du stage

La mission principale du stage a été l'exploration des données de la thèse de Riwan Leroux, portant sur l'impact de la stratification sur la relation de prédation poisson-zooplancton. La majeure partie du stage a ainsi consisté à l'analyse de cette base de données. À l'origine, ce stage portait sur l'étude des patrons de migrations journaliers du zooplancton cependant les méthodes développées ont révélées des résultats intéressants au sujet de la compétition interspécifique. A partir des résultats obtenus, l'écriture d'une publication scientifique a donc été commencée. Bien que sa rédaction ne soit pas terminée, une première version sera présentée dans ce rapport.

En parallèle, une assistance de terrain sur différents projets du centre de recherche a été proposé :

- Pêches électriques et caractérisation d'habitats pour des projets d'étudiants de Maîtrise
- Recensement des populations de tortue des bois (*Glyptemys insculpta*) à la sortie de leur hivernage avec le ministère des Forêts, de la Faune et des Parcs du Québec.
- Récupération d'une sonde hydroacoustique au fond d'un lac
- Observations de terrain afin de permettre la calibration et la validation de détection de végétation aquatique submergée par image satellite haute résolution

Ces missions ne seront pas traitées dans ce rapport de stage.

Spatial overlap among freshwater zooplankton taxa, their resources and predators and consequences on their population dynamics

Abstract

Large-scale studies of spatiotemporal heterogeneity among freshwater zooplankton communities have always been limited by taxonomic identification. High-frequency sampling while allowing coarse identification was made possible by an Underwater Vision Profiler (UVP), an *in situ* particle imagery device. Zooplankton spatial distribution was assessed with an UVP weekly during and after summer stratification day and night in a temperate oligotrophic lake. To identify ecological tradeoffs, spatial overlap between zooplankton and other zooplankton taxa, phytoplankton, invertebrate predators and fish predators was calculated with the Utilization Distribution Overlap Index (UDOI). Based on this overlap-index, relation between resource and independent variables were assessed through a model-selection. Population dynamics were tested with the same procedure. Results showed diversified tradeoffs pattern among zooplankton between resources, invertebrate predation and fish predation. Although spatial overlap and population dynamics analysis did not provide direct evidence of competitive exclusion, indirect impact of interspecific competition is presumed.

Introduction

Spatial stratification is one of the main drivers of biodiversity (Gamez *et* Harris, 2022; Beisner *et* Longhi, 2013), expanding available ecological niches through habitat fragmentation and resources partitioning (Schoener, 1974; Beisner *et* Longhi, 2013; Gamez *et* Harris, 2022). In temperate lakes, summer thermal stratification naturally occurs because of strong vertical temperature differences, dividing the water column in distinct layers (Kalff, 2002). This phenomenon has a significant impact on zooplankton communities, directly through its effects on vertical heterogeneity of abiotic factors (e.g. Temperature and light; Beisner *et* Longhi, 2013; Gamez *et* Harris, 2022) and indirectly through other species' distribution, consequently affecting their spatial structure (Tessier, 1986; Pinel-Alloul, 1995; Lévesque *et al.*, 2010). While predation and resources are clearly established as major drivers of zooplankton distribution among lakes (Allan, 1973; Tessier, 1986; Gignac-Brassard *et al.*, 2021), interspecific competition's contribution is less clear, probably because it is complex to quantify *in situ* and to disentangle from environmental conditions (Lynch, 1978; Hessen *et al.*, 1995a) or even from intraspecific competition (Allan, 1973; Hessen, 1990). In freshwater lakes, competitive interactions between two widespread Cladoceran genera, *Holopedium* and *Daphnia*, have been broadly studied (Allan, 1973; Tessier, 1986; Hessen, 1990; Hessen *et al.*, 1995b; Gignac-Brassard *et al.*, 2021) as they are commonly found in the same habitat (Allan, 1973; Tessier, 1986; Hessen *et al.*, 1995b) and share the same resources (Hessen *et al.*, 1995b). Whilst Daphnia is recognized as a better competitor relatively to Holopedium (Allan, 1973; Tessier, 1986; Hessen, 1990), it is more vulnerable to predation than this latter, which generates a gelatinous sheath to protect it from gape-limited predators such as fish larvae and invertebrates (Vinyard et Menger, 1980; Stenson, 1987; Dodson *et al.*, 2010). Predation pressure can therefore lead to a spatial segregation constraining *Daphnia*, allowing *Holopedium* to thrive (Tessier, 1986; Allan, 1973). Nevertheless, high-resolution spatial overlaps *in situ* between those two genera has never been studied.

Spatial overlap quantification is a powerful tool to estimate niche sharing and resource partitioning (Beisner *et* Longhi, 2013). However, such method requires a sufficient spatial resolution to correctly identify overlaps among taxa, as its relevance depends entirely on precision of data (Winner *et al.*, 2018). Because time-efficiency of traditional techniques (e.g. plankton nets) makes zooplankton high frequency sampling impractical (Stockwell *et al.*, 2002; Holbrook *et al.*, 2006), recent technologies such as optical particle counters (Stockwell *et al.*, 2002; Lévesque *et al.*, 2010) or hydroacoustics (Holbrook *et al.*, 2006) have been used to assess zooplankton spatial distribution for such study design. Even

though they allow large volume sampling, these approaches fail to capture any taxonomic resolution, relying uniquely on empirical estimations of particle size (Holbrook *et al*., 2006). In the last 30 years, *in situ* imagery capture devices have been developed to quantify distribution of floating particles with high precision while allowing some taxonomic identification (*e.g.* Picheral *et al.*, 2010). Despite its frequent use in marine ecosystems, this technique has only been seldom applied to freshwater ecosystems (*e.g.* Leroux *et al.*, 2023).

This study analyses zooplankton community's dynamics and spatial overlap with resources, predators (both vertebrate and invertebrate) in a temperate oligotrophic lake. The trophic nature of this system implies nutrient limited conditions, which is a necessary condition to study competition (Hessen, 1990). Sampling was performed on both day and night for 11 weeks, encompassing the stratified (summer) and turnover (fall) periods to test the effect of both diel periodicity in light regimes and seasonal variation in the stability of the water column. Although freshwater zooplankton's spatiotemporal structure has already been the object of other studies (Holbrook *et al*., 2002; Lévesque *et al.*, 2010), this research expands the scope of the analysis by providing a coarse, albeit reliable, taxonomic identification, thus allowing interspecific spatial overlap analysis. Using Leroux *et al.*'s (2023) data, this study aims to ***i)*** estimate spatial overlap among zooplankton taxa and between zooplankton taxa and their resources and predators, ***ii)*** determine which parameters drive the resources utilization for each taxon and finally ***iii)*** determine which parameters affect their abundance throughout the season. This study's goal is to identify different tradeoffs that zooplankton taxa adopt and their consequence on their population dynamics.

Methods

Study site

The data were sampled in lake Ledoux (46°38' N 73°15' W, Canada), a small oligotrophic temperate lake located in the Mastigouche wildlife reserve. A single fish species is present in the lake, the Brook charr (*Salvelinus fontinalis*), a cold stenothermic salmonid. The lake exhibits a summer stratification that creates a wide range of thermal habitats for zooplankton, notably providing a barrier against fish predation in the epilimnion as Brook Charr is essentially constrained in the metalimnion during this period (Leroux *et al*., 2023). Pelagic invertebrate predation is mostly represented by larvae of *Chaoborus sp.* (Diptera). Large predatory zooplankton *Leptodora* (Cladocera) is also present in the lake but has not been detected during the sampling. Many characteristics of the lake together, notably its Brook Charr population biology, are well documented as this system has been well studied in the last 30 years (e.g. Bourke *et al.*, 1993; Dykes *et al.*, 2005; Bertolo *et al*., 2011; Goyer *et al.*, 2014; Pépino *et al.*, 2017; Leroux *et al*., 2023).

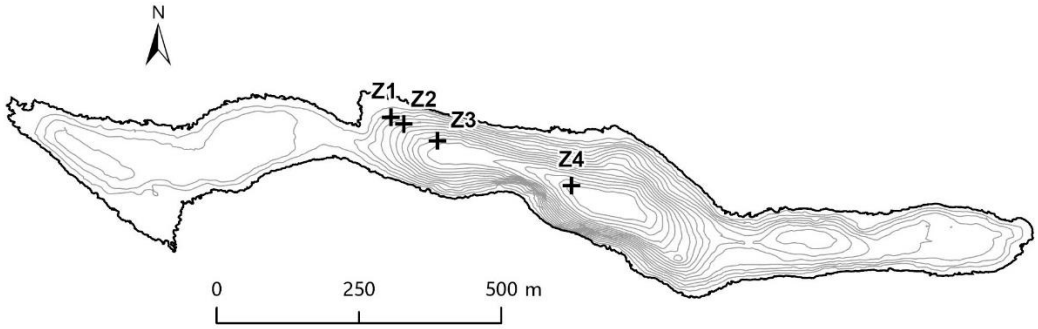

Figure 1: *Bathymetric map of Lake Ledoux indicating the position of the four sampling points (crosses) used in this study.*

Sampling

The study was conducted in summer and beginning of autumn 2018. Data were collected weekly at both noon and midnight from the 25th of July to the 8th of October. Sampling could not be performed on the 1st of October (day and night) and on the night of 6th of August due to bad weather condition, resulting in a total of 21 records. Each sampling was performed from water surface to the bottom across four vertical profiles aligned in direction the center of the lake, respectively at 40, 60, 110 and 290 meters from the shore (*fig.1*). All profiles were assessed within an hour time span to minimize spatiotemporal variance. As the amplitude of zooplankton horizontal movement is in the order of decades of meters (Burks *et al.*, 2002), the most distant point (z4) was considered as independent from the others and was used as a control.

The sampling was performed with an Underwater Vision Profiler (UVP; Hydroptic, France). The UVP samples individual particles in the water column by taking images of 22 x 18 cm (corresponding to a volume of 1.02L/image) that can be decomposed into singular vignettes, allowing a rough taxonomic recognition and biometry (Picheral *et al.*, 2010). Whereas the original version of this instrument is calibrated for relatively large particles such as marine zooplankton, the focal length of the UVP was adapted by Hydroptic to lower the detection threshold to 262µm at the expense of the sampled volume (lowered to 0.18L/image; Leroux *et al.*, 2023), thus allowing detected medium and larger sized lacustrine taxa. Temperature and fluorescence profiles were simultaneously measured from surface to bottom on each station with a FluoroProbe (bbe Moldaenke, Germany).

Data processing

All collected vignettes were processed and then identified with the Ecotaxa software (Picheral *et al.*, 2017). Due to image resolution, individuals were classified into broad taxonomic groups: Copepods, Holopediidae (exclusively *Holopedium glacialis*), other Cladocerans (Mainly *Daphnia* and occasionally Bosminidae), colonial rotifers (large colonies of *Conochilus sp.*), *Chaoborus sp*. and Others (unidentified). Zooplankton were separated into small (<1mm) and large (>1mm) individuals. Size classes were treated as separate taxon. Population density of each taxon was then averaged for every 50cm depth layer from surface to bottom. Total abundance of each zooplankton taxa, Chaoborus and phytoplankton were calculated for the 21 sampling occurrence to estimate population dynamics. The relation between each set of abundance was tested with a spearman correlation test.

Temperature and fluorescence were averaged to match the zooplankton resolution. Acting as a proxy, fluorescence was converted to phytoplankton concentration. Water density was calculated from temperature with the *water.density*() function of the R package rLakeAnalyzer (Winslow *et al.*, 2013). Vertical density difference (ΔW_{dens}) or the maximum variation of water density was then used as a proxy for stratification (*e.g.* Blais *et al.*, 2019; Woolway *et al.*, 2021) and given by the following equation:

$$\Delta W_{dens} = max\ (W_{dens}) - \min\ (W_{dens})$$

Fish vertical distribution was calculated during the whole study period with acoustic telemetry from 23 tagged individuals. Their vertical positions were captured in a 2-hour timespan before and after the UVP sampling. Similarly to zooplankton, sampled depths were aggregated to 50cm layers. Layers with less than 1% of fish presence were considered fishless. Detailed method can be found in Leroux *et al.* (2023).

Interspecific competition

Spatial overlap between pairs of zooplankton taxa was measured with the Utilization Distribution Overlap Index (UDOI). Developed by Fieberg *et* Kochanny in 2005, UDOI is proven to be robust as it is

the best performing overlap index for space-use sharing studies in multiple comparison studies (Fieberg *et* Kochanny, 2005; Robert *et al.*, 2012; Tillberg *et* Dixon, 2022). The index quantifies the degree of overlap between two different utilization distribution function (UD), which could be assimilated to a probability distribution area. Usually, UD is obtained from a habitat range estimation based on individuals' position over time. It introduces variance in the conversion from a set of locations to a UD depending on the method and the used parameters (Winner *et al.*, 2018). Furthermore, the UD estimation is exposed to heavy bias such as unmodelled autocorrelation, small sample bias and temporal bias (Fieberg, 2007; Fleming *et* Calabrese, 2017; Fleming *et al.*, 2018). UDOI was calculated directly from discretized abundance data, avoiding a supplementary conversion and therefore bypassing the aforementioned limitations. In the literature, UD is sometimes filtered by probability contours (generally 95%). Following Winner *et al.*'s (2018) guidelines, those transformation were not applied by principle of parsimony, avoiding unnecessary *ad hoc* parameters. Considering a_i the abundance of species i, $\mathrm{UD_i}$ at coordinates (x, y) is given by the following equation:

$$\mathrm{UD_i(x,y)} = \frac{\mathrm{a_i(x,y)}}{\sum_{\mathrm{n=1}}^{\infty} \mathrm{a_i(x,y)}}$$

UDOI is then calculated by multiplying the common area between species 1 and 2 (denoted $A_{1,2}$) and the sum of products of both UD at each coordinate:

$$\mathrm{UDOI} = A_{1,2} \iint_{-\infty}^{\infty} UD_1(x,y) \times UD_2(x,y)\ dx\, dy$$

UDOI was calculated separately for each zooplankton taxon with **i)** each other taxa to measure their degree of spatial overlap (and thus have a proxy of potential interspecific competition), with **ii)** phytoplankton, to estimate the potential utilization of resources, with **iii)** both vertebrate (fish) and invertebrate predators (*Chaoborus sp.*) to estimate potential predation risk.

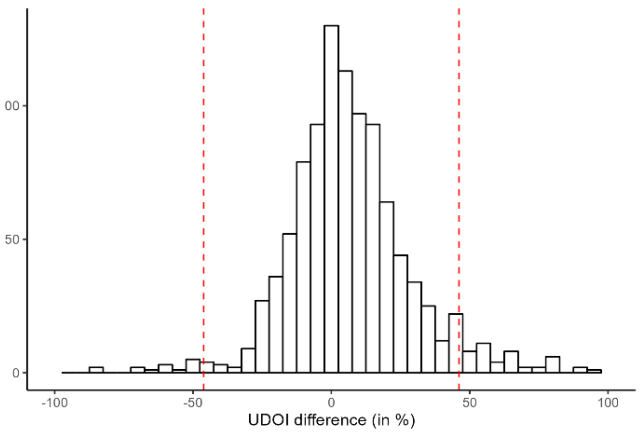

***Figure 2**: Histogram of difference between real and predicted UDOI from the cross-section simulation.*
***Red-dashed ligns** : 95% confidence interval*

To test the accuracy of the study design, UDOI between sets of two different randomly simulated normally distributed populations on a cross-section have been calculated, one following the exact resampling methodology from the same 3 transects and the other with the total population. This process was repeated 1000 times to have a significative sample. Results showed a mean difference between real and predicted UDOI of 6%, suggesting relatively unbiased results. Though, the 95% confidence intervals of difference between real and predicted reached 46% of the UDOI value (*fig.2*).

Multi-model approach

To determine which predictors would best explain the resource-coupling for each taxon, we built a set of linear models to predict the UDOI between each taxon and the phytoplankton proxy (*UDOI_Phyto*). Independent variables included **i)** the UDOI between a given taxon and *Chaoborus sp.* (*UDOI_Chaoborus*), to account for invertebrate predation, **ii)** the period of the day (day or night; *Period*), **iii)** the total phytoplankton abundance measured in the water column (*Ab_Phyto*), to account for available resources, **iv)** maximum water density difference in the water column (*ΔWdens*), acting as a proxy of stratification, **v)** time in weeks (*Time*), and **vi)** the UDOI between a given taxon and the

large individuals of the 3 main zooplankton taxa (Copepods, *Holopedium* and other Cladocerans, respectively *UDOI_LCop*, *UDOI_LHol* and *UDOI_LCla*), to account for interspecific competition. **vii)** As *Chaoborus* is a nocturnal predator, interaction between *UDOI_Chaoborus* and *Period* was also included. Variation inflation factor (VIF) was tested prior to model building with the *vif()* function of the car R-package (Fox *et al.*, 2001). As *Time* and *ΔWdens* variables were inversely correlated ($r^2 = 0.79$, $p < 0.001$), the model has been constrained to exclude the other variable if one had to be selected to avoid multicollinearity. Fish predation was not included in the model due to strong correlation with dense phytoplankton area, due to the omnipresence of both in the metalimnion. A model selection based on this list of variables was performed with the *dredge()* function from MuMIn R-package (Barton, 2010). Generated models were limited to a maximum of four terms to avoid overspecification. The obtained models were then filtered to cumulative 95% AIC weight. These models were used to obtain weighted estimates of the coefficients for each variable, for which we then calculated 95% confidence intervals. Those variables with a confidence interval excluding 0 were considered as significant.

A similar procedure was also applied to model the total abundance in the water column of each taxon (denoted *Abundance*) at a seasonal scale. The total abundance of the 3 main zooplankton taxa (Copepods, Holopedium and other Cladocerans, respectively denoted *Ab_LCop*, *Ab_LHol* and *Ab_LCla*), the abundance of *Chaoborus* (*Ab_Chaoborus*), in addition to the aforementioned terms *UDOI_Phyto*, *Ab_Phyto*, *ΔWdens*, *Time* have been used as independent variables. Interaction between *Ab_chaoborus* and *Period* was also added.

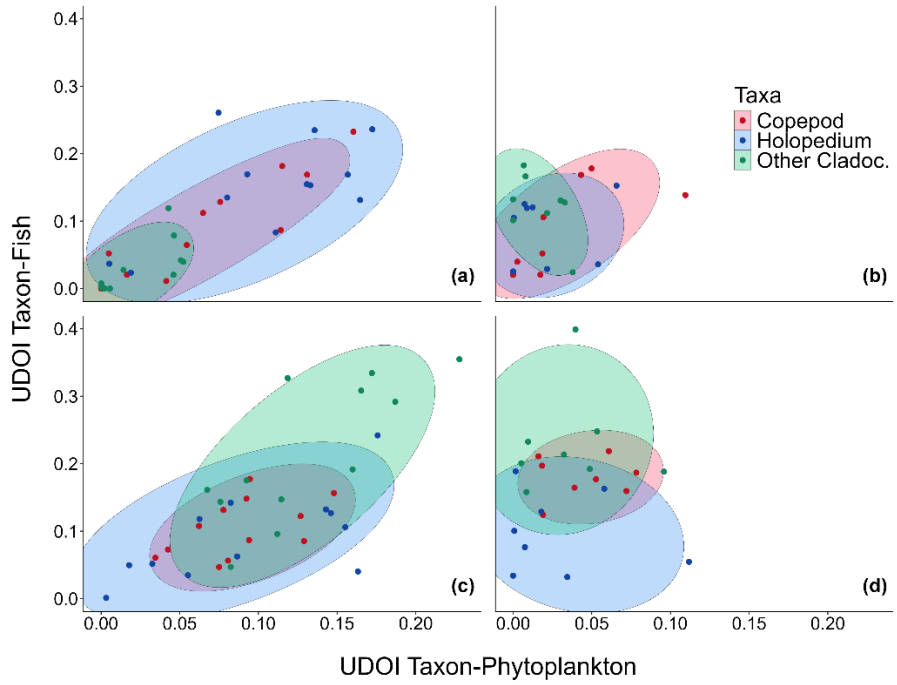

Figure 3: *UDOI between a taxon and fish according to their UDOI with resources.* ***(a)*** *Large individuals during stratification,* ***(b)*** *Large individuals after stratification,* ***(c)*** *Small individuals during stratification,* ***(d)*** *Small individuals after stratification.*

Results

UDOI values

Overall UDOI values are relatively low compared to what can be found in literature, ranging from 0 to 0.48 in certain cases of total population overlap. In particular, UDOI between zooplankton and Chaoborus did not overcome 0.12, which is substantially low even compared to other variables.

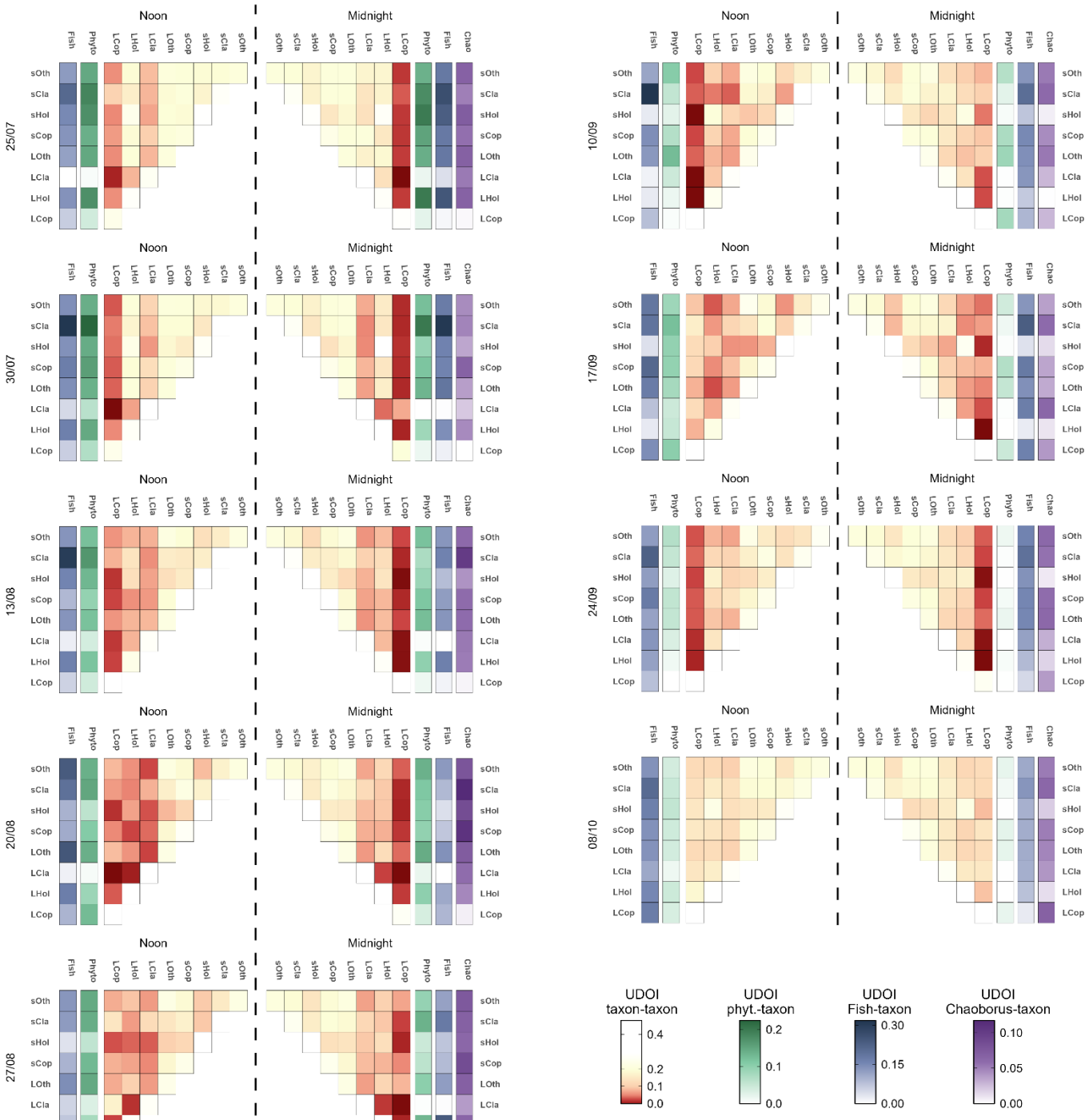

Figure 4: *Synoptic view of UDOI of zooplankton compared to Zooplankton taxa, phytoplankton, fish and Chaoborus for each taxa.*
Abbreviations: *LCop = Large Copepods, LHol = Large Holopedium, LCla = Large other cladocerans, SCop = Small Copepods, SHol = Small Holopedium, SCla = Small other cladocerans, Phyto = Phytoplankton, Chao = Chaoborus*

A clear distinction can be made between on one part small other cladocerans, small Copepods and others, both size of *Holopedium* on another part and finally large copepod and large cladocerans (*fig.4*). The prior displayed a very similar overlap pattern during all the study, with zooplankton interspecific UDOI of each taxon averaging at exactly 0.137 over the season with a very similar standard deviation (ranging from 0.062 to 0.054). In contrary, large other cladocerans and large copepods demonstrate little overlap with all other taxa with a mean UDOI = 0.085 and 0.049 respectively, which is clearly visible on fig.3. Large and small *Holopedium* had an intermediate position. However, these tendencies disappear on the last week leading to a nearly uniform pattern.

A similar dichotomy can be observed regarding environmental parameters, although patterns appear more chaotic. While no clear patterns are observed for most taxa during stratification, large other cladocerans exhibit little to no overlap with both phytoplankton and fish (*fig.3*). Drastically lower UDOI Taxon-phytoplankton after stratification coincides with a significant resource scarcity (Annex). No particular tendency stood out in regard to UDOI with *Chaoborus* except for non-existent values for large Copepods in the first 5 weeks (UDOI < 0.01) and slightly lower value for both size of *Holopedium* in the 4 last weeks.

Taxa	Variable	- CI	+ CI	Weight	adj-R^2
SCla	ΔWdens	0.46	0.87	0.98	**0.9**
	UDOI_LHol	0.29	1.25	0.98	
	Ab_Phyto	0.19	0.76	0.9	
	UDOI_LCop	0.13	0.87	0.8	
LCla	Period	-0.66	-0.11	0.97	**0.32**
SHol	Time	-1.26	-0.55	0.97	**0.68**
	UDOI_LCop	0.35	1.97	0.96	
LHol	Time	-1.19	-0.64	1	**0.79**
	UDOI_LCop	0.25	1.42	0.97	
SCop	Period	-1.25	-0.35	1	**0.79**
	Time	-0.59	-0.15	0.93	
	UDOI_Chaoborus	0.04	0.38	0.77	
LCop	UDOI_Chaoborus	0.1	1.02	0.86	**0.34**
	Period	-1.39	-0.07	0.78	

Table 1: *Results of averaged model based on UDOI of each Taxa with Phytoplankton. Variable indicate the significant variables (see method), -CI and +CI are respectively lower and upper Confidence Interval of the variable's estimate, Weight represents the Akaike weight of the variable, adj-R^2 is the adjusted R^2 of a fitted model with only the selected variable.* ***Abbreviations:*** *SCla = Small other cladocerans, LCla = Large other cladocerans, SHol = Small Holopedium, LHol = Large Holopedium, SCop = Small Copepods, LCop = Large Copepods, ΔWdens = Stratification proxy (see method), Ab_Phyto = Total abundance of phytoplankton*

Resources-coupling

Models based on UDOI with phytoplankton (*tab.1*) identified strong response to resources for small taxa and large *Holopedium* (*adj-r^2 > 0.65*), as opposed to large Cladocerans and large Copepods with significantly lower explanatory power (*adj-r^2 < 0.35*). In particular, Small other Cladocerans model showed the best results and selected relevant 6 variables (*ΔWdens*, *UDOI_LHol*, *Ab_Phyto*, *UDOI_LCop*, *Period* and *Time*) but was forced to keep the four most significant terms due the model's variable number constraint. Large and small *Holopedium* models were identical in regard to variables, with really similar intercepts. These tendencies are mainly consistent with data from z4 (*Annex 4*), although response to resources of other Cladocerans and large Copepods are even weaker, the model of the latter even failing to detect any significant relation.

Relation to stratification through the variables *Time* and *ΔWdens* were significant for all small taxa and large *Holopedium* with a positive intercept

Period was found relevant in both size of Copepod and other Cladocerans, which is supported by the pronounced diel migration of most of these taxa (*Annex 7*). Though, the negative intercept indicates a smaller overlap with resources at night, which could be related to an observed nocturnal phytoplankton depletion (*Annex 4*). Overlap with other zooplankton taxa appeared multiple time, exclusively displaying positive estimates. Though, only large Copepods and Large *Holopedium*, which are not thought as strong competitors, were found significant.

Abundance

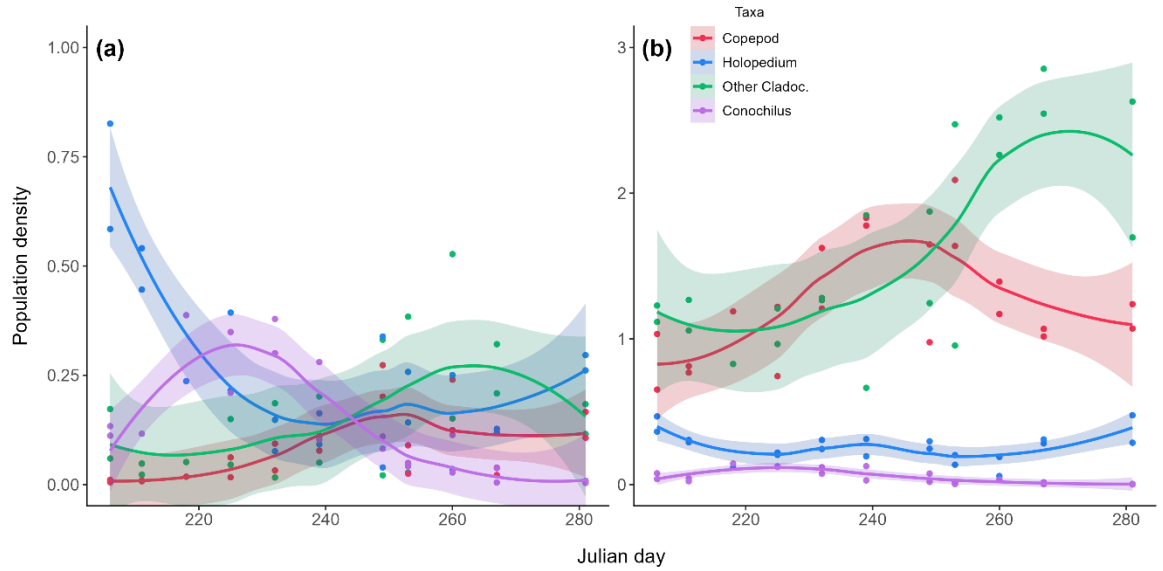

Figure 5: *Evolution of zooplankton population density in relation to time.* ***(a)*** *Large individuals* ***(b)*** *Small individuals*

Population dynamics are highlighted in *fig.5*, showing the successive predominance of large *Holopedium* in the first weeks, followed by large colonies of rotifers, small Copepods and finally small other cladocerans. General trends appear similar between large and small individuals of the same taxa, which is confirmed by significant spearman ranking test (*tab.2*) for Copepods and Other Cladocerans (*p < 0.01* for Copepod, *p <0.001* for Other Cladocerans), *Holopedium* ending up non significative with a *p-value* of 0.08. Such observations also apply to small other cladocerans' and *Holopedium*'s abundance-based averaged model as they consist mostly of their large counterparts (*tab.3*).

	Phyto	Chao	LCla	LCop	LHol	sCla	sCop
sHol	0.14	-0.02	-0.01	-0.24	0.39	0.19	-0.38
sCop	-0.19	-0.16	-0.18	0.55	-0.67*	-0.12	
sCla	-0.56*	0	0.68**	0.46	-0.26		
LHol	0.33	0.04	0	-0.58*			
LCop	-0.57*	-0.06	0.2				
LCla	-0.61*	0.39					
Chao	-0.29						

Table 2*: Matrix of Spearman correlation test among total abundance of zooplankton taxa, Chaoborus and phytoplankton. Text values are the rho coefficient, grey values represent non-significant results, black text indicates significative values, * indicate that p-value inferior to 0.01, ** indicates a p-value inferior to 0.001.*

Abbreviations: *Phyto = Phytoplankton, Chao = Chaoborus, LCla = Large other cladocerans, LCop = Large Copepods, LHol = Large Holopedium, SCla = Small other cladocerans, SCop = Small Copepods, SHol = Small Holopedium.*

Large *Holopedium* were abundant in the first week but started immediately to decrease, reaching their lowest abundance a few weeks before the turnover of the thermal stratification (occurring around the 250th day). Although this drop seems to correspond to phytoplankton abundancy decrease (fig.), spearman correlation test did not conclude significant (*p-value = 0.14*). Conversely, large Copepods and others Cladocerans, showed a negative correlation to resources. Despite spearman's results, phytoplankton abundancy did not appear in any of the abundance averaged models, even so UDOI with phytoplankton was found relevant with positive for three taxa.

Taxa	Variable	- CI	+ CI	Weight	adj-R^2
SCla	Ab_LCla	0.14	0.73	0.98	**0.63**
	ΔWdens	-1.07	-0.09	0.81	
LCla	Period	0.04	0.42	0.88	**0.33**
SHol	Ab_LHol	0.06	0.2	1	**0.47**
LHol	Ab_Chaoborus	-0.61	-0.06	1	**0.7**
	Period	0.28	0.88	1	
	UDOI_Phyto	0.18	0.51	1	
SCop	Ab_LHol	-0.63	-0.12	0.97	**0.44**
	UDOI_Phyto	0.05	1.03	0.68	
LCop	UDOI_Phyto	0.06	0.15	1	**0.68**
	Time	0.02	0.1	0.84	

***Table 3**: Results of averaged model based on Taxa's abundance. Variable indicate the significant variables (see method), -CI and +CI are respectively lower and upper Confidence Interval of the variable's estimate, Weight represents the Akaike weight of the variable, adj-R^2 is the adjusted R^2 of a fitted model with only the selected variable. **Abbreviations:** SCla = Small other cladocerans, LCla = Large other cladocerans, SHol = Small Holopedium, LHol = Large Holopedium, SCop = Small Copepods, LCop = Large Copepods, ΔWdens = Stratification proxy (see method), Ab_Phyto = Total abundance of phytoplankton*

Discussion

The results did highlight complexity and diversity of tradeoff patterns among zooplankton taxa and their evolution during and after summer stratification. No direct interactions were found between *Holopedium* and other Cladocerans in neither resources utilization or abundance. Hessen (1990) observed delayed reproductive effort between species, which could be mechanism to avoid competition. Population dynamics would favor this explanation as several weeks separate *Holopedium*'s abundance fall of other Cladocerans' rise.

Models based on overlap with zooplankton revealed two general observations. First, variables based on spatial overlap with other zooplankton taxa were found significant multiple times and consistently displayed positive estimates, which implies in theory that a taxon's presence favors another taxon's resource-coupling. As this explanation does not make much sense in our context, this can be interpreted as a convergence towards resources. Furthermore, the absence of negative intercepts supports the absence of competitive exclusion in zooplankton communities (Allan, 1973; Lynch, 1978; Goulden *et al.*, 1982; Hessen, 1990; Hessen *et al.*, 1995b). Second, diel periodicity seems to have a negative impact on Copepods and other Cladocerans resources overlap. This result was expected as the large individuals of each Taxa were observed to migrate towards the hypolimnion for Copepods and the epilimnion for other Cladocerans (Annex) while phytoplankton generally peak in the metalimnion (fig). This result can also be attributed to an important phytoplankton nocturnal depletion phenomenon, which has already been observed and attributed to intense diurnal zooplankton grazing (Frempong, 1981; Levesque *et al.*, 2010). This pattern should be reinforced by low diurnal predation context (Levesque *et al.*, 2010), which is consistant with nocturnal predation pression of *Chaoborus*.

Logically, abundance variations seem to depend primarily on resources as three taxa show correlations to phytoplankton abundance through spearman test and three taxa showed positive relation overlap with phytoplankton through model selection. No taxa were found negatively related to another, further hinting towards an absence of competitive exclusion. It should be noted nonetheless that resources were solely represented by phytoplankton, which is quite reductive as zooplankton are capable to feed on a wider variety of food sources (*e.g.* bacteria; Hessen, 1990; Hessen *et al.*, 1995b).

Other Cladocerans

Although other Cladocerans included Bosminidae, large individuals have been identified to be predominantly *Daphnia* (Leroux et al., 2023). Unsurprisingly, other cladocerans showed low overlap with both resources and fish on the first 6 weeks, which suggest a spatial segregation during summer stratification due to its vulnerability to predation. Furthermore, resource-coupling models systematically performed poorly, which substantiate that resources are not a powerful driver to *Daphnia*'s distribution. Abundance however was demonstrated negatively correlated to phytoplankton, converging with Tessier's (1986) results on *Daphnia*'s increase was associated with decline of ressources. In fact, *Daphnia* has been observed to maintain reproductive effort despite resource rarefaction, leading to a population growth regardless of food rarefaction (Goulden *et al.*, 1982). Reinforced by the lag time between egg production and growth, this leads to population extansion primarly composed of small individuals (Goulden *et al.*, 1982; Tessier, 1986), which also corroborate with our results as small individuals are 10 times more abundant than large one during that event.

Holopedium

Unlike other taxa, the taxonomic identification was unambiguous (*i.e.* composed by only one species), which explain the similarities of UDOI and models between large and small individuals. Both abundance and resource-coupling models did highlight a strong relation between *Holopedium* and phytoplankton, the prior clearly emphasizing the relation between its population dynamics the decline of resources despite the inconclusive spearman correlation test. As the production of *Holopedium*'s gelatinous capsule is hypothesized to be energetically costly (*Tessier*, 1986; Hessen *et al.*,1995b), resources are an important driver of its success. This capsule offers him predatory protection in return, granting him an advantage over other competitors such as *Daphnia*. This tradeoff would supposedly imply that *Holopedium*'s population dynamics would depend of phytoplankton abundance. However, this study did not show significant results in that regards, but found instead that *Holopedium*'s abundance is better explained by its spatial overlap phytoplankton and Chaoborus' distribution. Though, overlap with phytoplankton seems to depend mainly on stratification, as the overlap with large Copepods does not seem relevant in our context. Despite its gelatinous capsule, *Chaoborus* abundance seemed to negatively influence large *Holopedium's* abundance. Although unexpected, similar result had been observed by Gignac-Brassard *et al.* (2021) and Drouin *et al.* (2009), which subtantiate that *Holopedium* can still be preyed uppon by large *Chaoborus* individuals.

Copepods

With the exception of the last week, large Copepods consistently showed little overlap with other zooplankton taxa due to their generally deep position within the lake. They also displayed a pronounced reverse vertical diel migration. As expected, Copepods did not demonstrate response to fish predation as they are known to have a rapid swimming escape mechanism (Buskey *et al.*, 2002). Phytoplankton did not appear significant in the phytoplankton-related model due to low explanatory power. Unlike Daphnids and *Holopedium*, Copepods are selective filter-feeders (*Friedman et Strickler*, 1976; *DeMott*, 1986) and have been found to be sensitive to food quality (*Gignac-Brassard et al.*, 2021). This physiological trait might allow them to be more efficient foraging like marine snow and therefore allow them to thrive with low resource (Hessen, 1989). Yet their abundance displayed a clear relation with both abundance and overlap with phytoplankton. The impact of *Chaoborus* on Copepods also

stood out multiple times as well, which has already been described in litterature (Neill, 1990; Reid *et* Williamson, 2010; Gignac-Brassard *et al.*; 2021). *Chaoborus*' presence has been observed to induce a lower depth distribution in freshwater Copepods as well as a reverse diel vertical migration (Neill, 1990) or even uncouple with resources (Gignac-Brassard *et al.*; 2021) which might explain the distinctive spatial pattern of large copepods in Lake Ledoux. Thus, the distribution of large copepod might not depend on resources because of their selective filtering ability, but may be a response to invertebrate predation. Though, phytoplankton availability and disponibility appear to have an impact on their adundance.

Methods and limitations

The used of Abundance as a proxy of a zooplankton species fitness is suboptimal, as there is a time lag until the response is visible (Goulden *et al.*, 1990). Egg fitness is known to better indicator as it reflects of instantaneous fitness (Hessen, 1990) but the resolution of the UVP does not permit such precise operation. Also, the effect of wind and current were not considered, though their impact has been shown to be limited in small lakes (Lévesque *et al.*, 2010).

Chaoborus displayed a very low and fragmentary distribution throughout the study (annex1). This chaotic distribution could be related avoidance of the UVP, supposedly swimming away by detecting turbulence created by the instrument (pers. comm., Leroux, 03/2024). This hypothesis could also explain that *Leptodora* remained undetected. Instrument avoidance could therefore explain the low *Chaoborus* abundance and considerably affect the overlap values. Regardless, relations were still detected, comforting the relevance of these results.

Unlike standard calculated Utilization Distribution function, this study's UD were not modified and are therefore discontinuous due to the chaotic nature of distribution of zooplankton distribution *in situ*. Due to its particular set-up, it is unreasonable to compare UDOI values obtained in literature. Anyhow, UDOI already has strong bias when comparing different studies due to its non-standardized nature (Fieberg *et* Kochanny, 2005).

The UDOI simulation have proved that the sampling design allowed unbiased overlap estimate despite covering less than 5 % of the total simulated cross-section. However probably due that low coverage, the 95% confidence intervals of difference between real and simulated UDOI are rather large (46%) demonstrating significant variance in the results. The two-dimensional design of the simulation can also be criticized as environments complexity comes from their three-dimensional natures (Gamez *et* Harris, 2022).

Despite a really low sample size (n=21), models-averaging approach demonstrated relatively high explanatory power. However, the low sample size induced variable estimates with really large 95% confidence intervals which often resulted in exclusion of seemingly stable variables (*i.e.* little variation in their estimate but had a confidence interval just beyond the 0 threshold). Furthermore, models systematically selected the simplest model with a $\Delta AICc < 2$ (difference with the best AICc value), suggesting that our approach tends to be conservative. Although Doorman *et al.* (2018) did not recommend the use of parametric methods (such as AICc weight) for model averaging purposes, they also demonstrated that all the current methods lead to similar results. Also, suggested methods like Model stacking and cross-validation were not possible with such low sample size.

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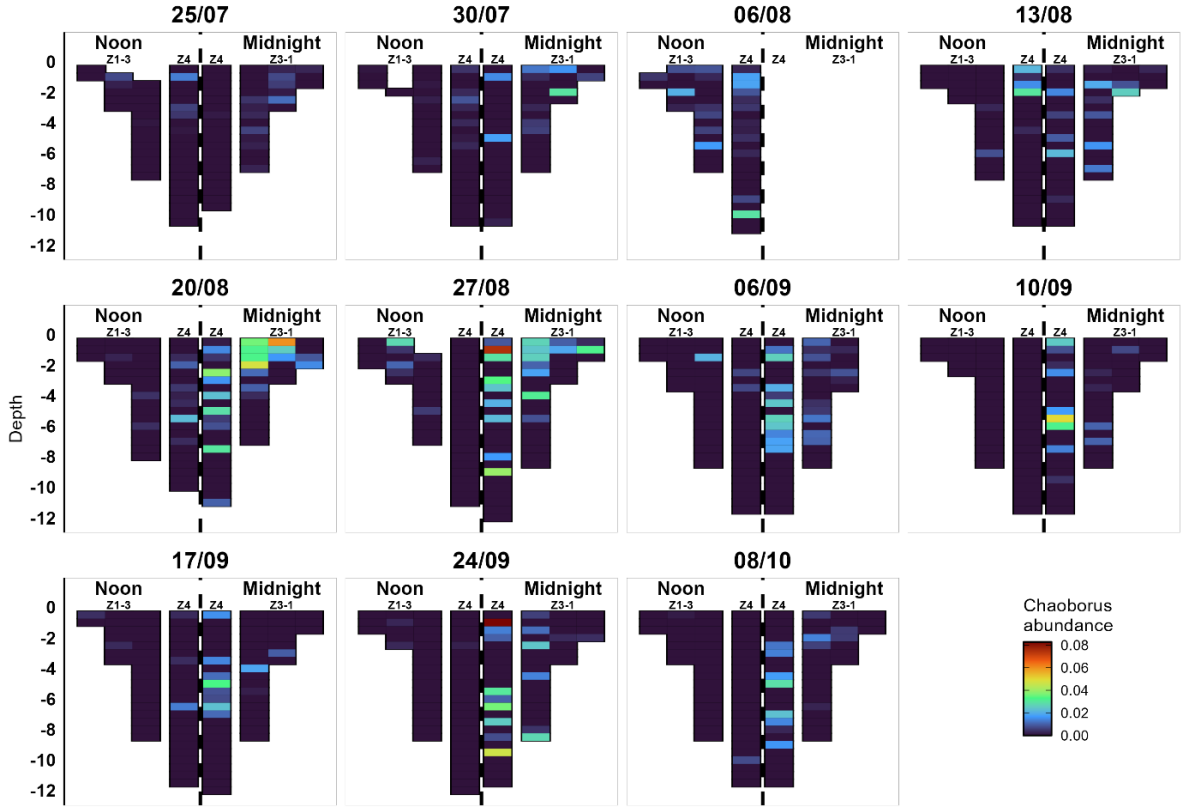
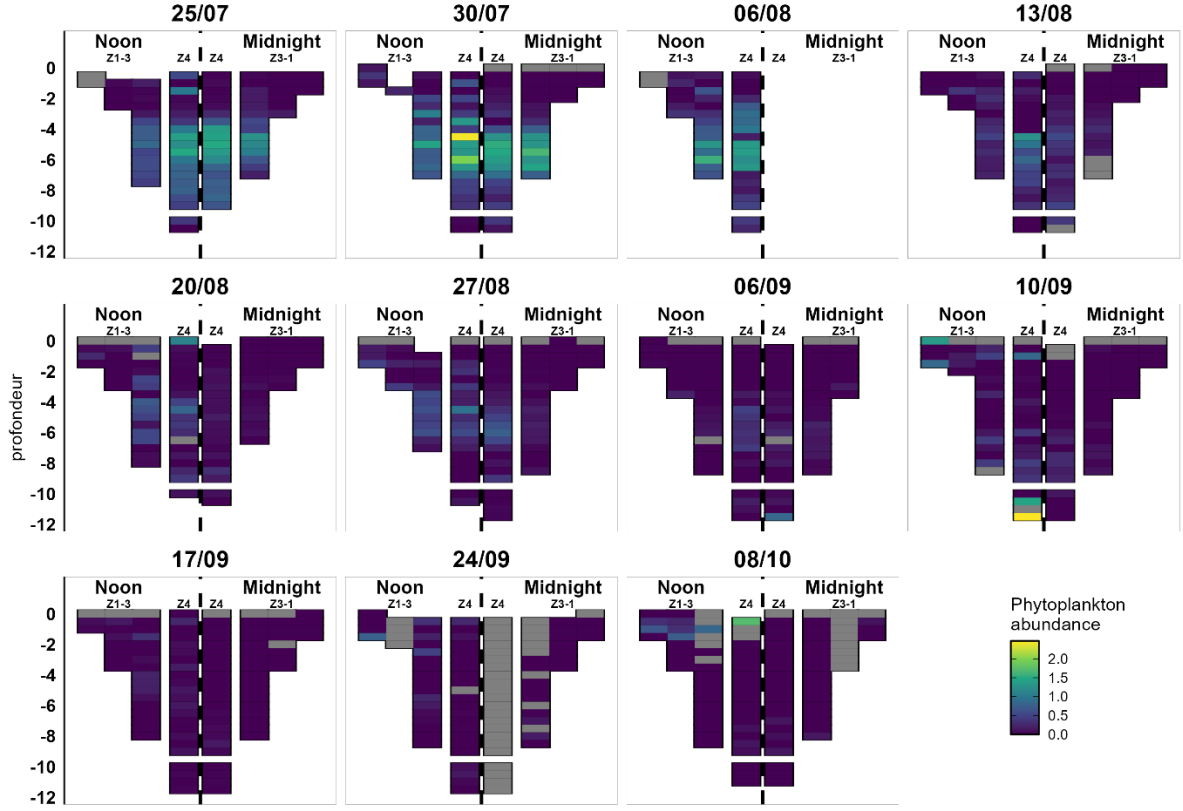
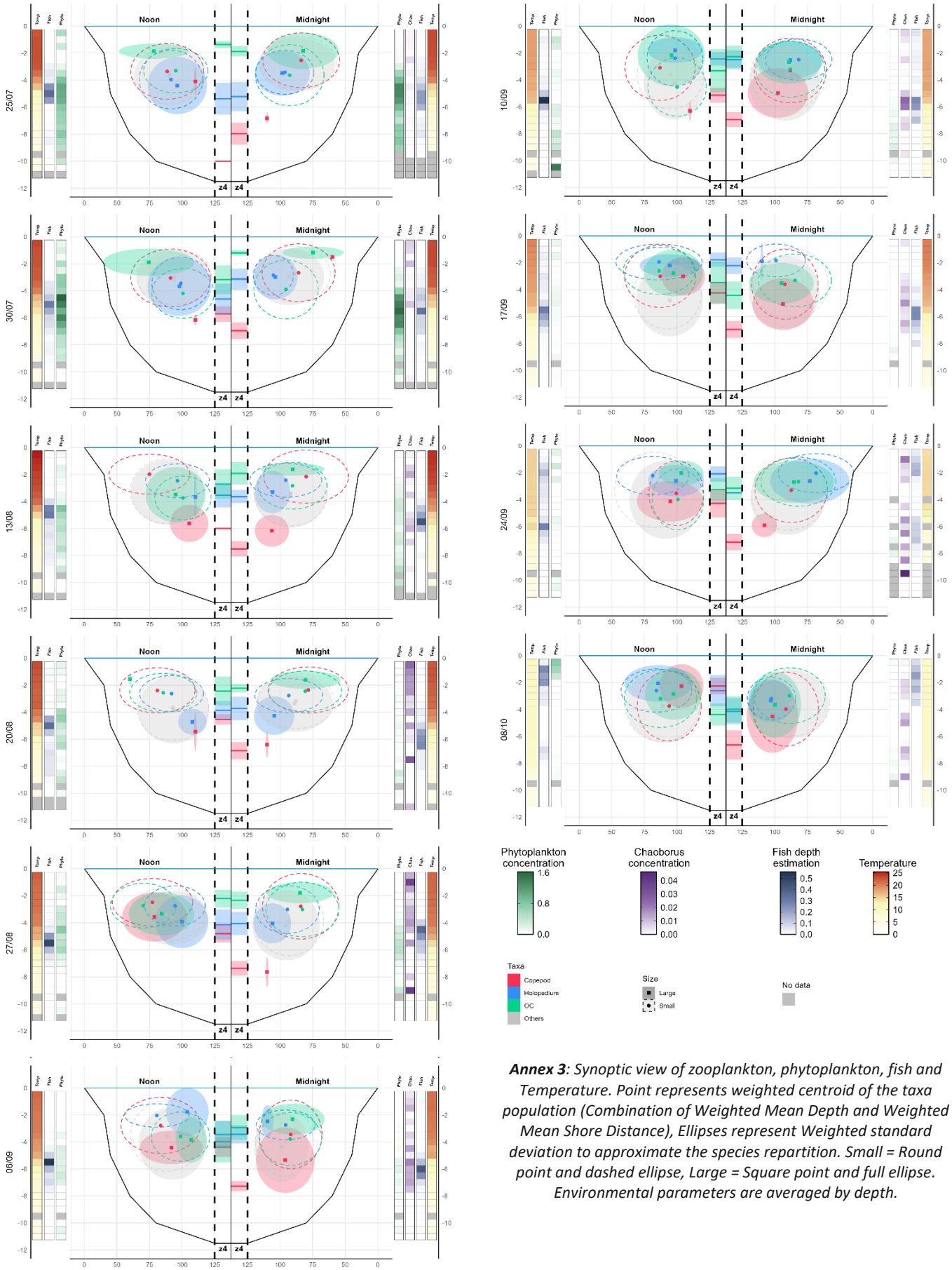
ANNEXES



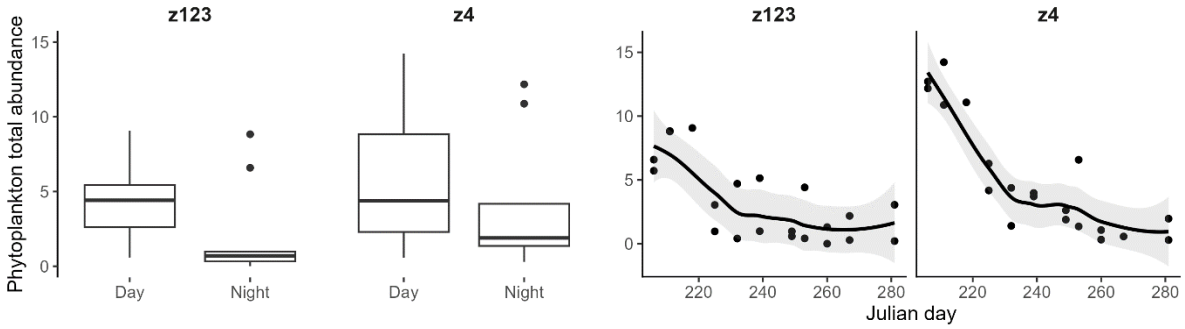
***Annex 1**: Heatmap of Chaoborus distribution throughout the study*



***Annex 2**: Heatmap of Phytoplankton distribution throughout the study*



***Annex 3**: Synoptic view of zooplankton, phytoplankton, fish and Temperature. Point represents weighted centroid of the taxa population (Combination of Weighted Mean Depth and Weighted Mean Shore Distance), Ellipses represent Weighted standard deviation to approximate the species repartition. Small = Round point and dashed ellipse, Large = Square point and full ellipse. Environmental parameters are averaged by depth.*



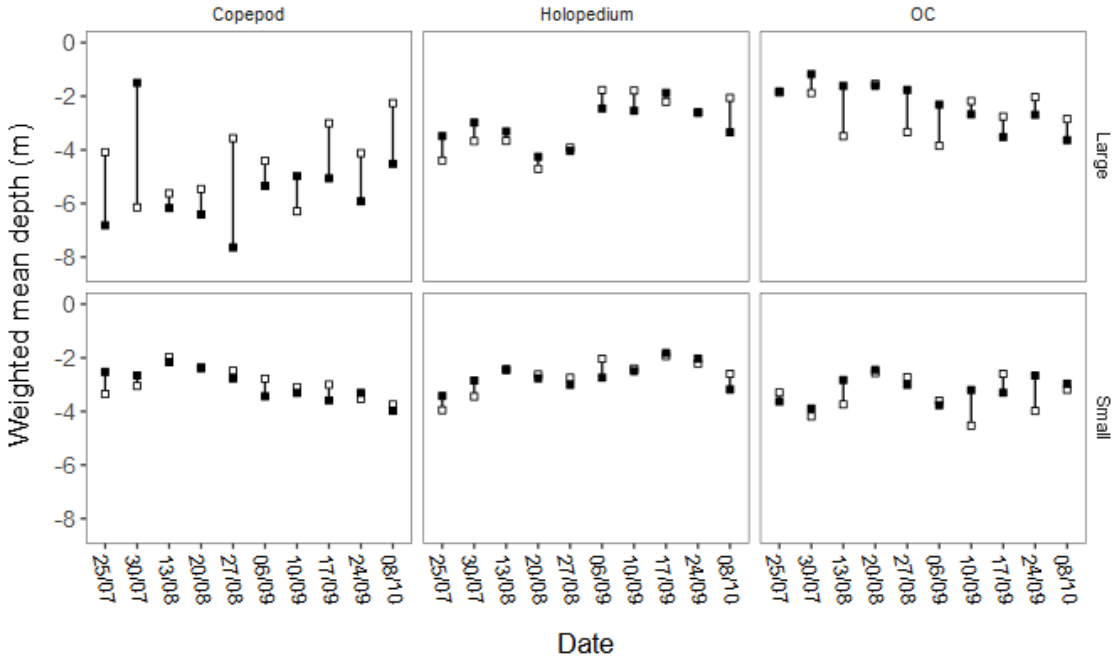
Annex 4: *Phytoplankton abondance throughout the study*

Taxa	Variable	- CI	+ CI	Weight	adj-R^2
SCla	UDOI_LCop	0.59	1.63	1	**0.88**
	UDOI_LHol	0.28	1.38	0.98	
	Time	-1.29	-0.59	0.98	
	UDOI_LCla	-1.28	-0.04	0.67	
LCla	UDOI_LHol	0.01	0.75	0.71	**0.16**
SHol	UDOI_LHol	0.05	0.82	0.7	**0.74**
	Ab_Phyto	0.12	0.87	0.68	
	Time	-1.52	-0.03	0.49	
LHol	Time	-1.5	-0.6	0.97	**0.75**
	UDOI_LCop	0.02	1.66	0.71	
SCop	Time	-0.93	-0.39	0.71	**0.72**
LCop		-	-	-	-

Annex 5: *Results of averaged model based on UDOI of each Taxa with Phytoplankton. Variable indicate the significant variables (see method), -CI and +CI are respectively lower and upper Confidence Interval of the variable's estimate, Weight represents the Akaike weight of the variable, adj-R^2 is the adjusted R^2 of a fitted model with only the selected variable.*
Abbreviations: *SCla = Small other cladocerans, LCla = Large other cladocerans, SHol = Small Holopedium, LHol = Large Holopedium, SCop = Small Copepods,, LCop = Large Copepods, Ab_Phyto = Total abundance of phytoplankton*

Taxa	Variable	- CI	+ CI	Weight	adj-R^2
SCla	Ab_Chaoborus:Period	0.1	1.91	0.12	**0.2**
LCla	Period	0	0.23	0.82	**0.22**
SHol	Ab_LCla	-0.15	-0.05	1	**0.92**
	Ab_LHol	0.19	0.29	1	
	Ab_Phyto	-0.1	-0.02	0.97	
LHol	UDOI_Phyto	0.12	0.32	1	**0.73**
	Ab_LCla	0.03	0.3	0.78	
SCop	Ab_Phyto	-0.53	-0.11	1	**0.49**
	Wdens	0.07	0.39	0.71	
LCop	Time	0.03	0.09	0.95	**0.7**
	UDOI_Phyto	0.01	0.06	0.88	

Annex 6 *: Results of averaged model based on Taxa's abundance for z4 profile. Variable indicate the significant variables (see method), -CI and +CI are respectively lower and upper Confidence Interval of the variable's estimate, Weight represents the Akaike weight of the variable, adj-R^2 is the adjusted R^2 of a fitted model with only the selected variable.*
Abbreviations: *SCla = Small other cladocerans, LCla = Large other cladocerans, SHol = Small Holopedium, LHol = Large Holopedium, SCop = Small Copepods, LCop = Large Copepods, ΔWdens = Stratification proxy (see method), Ab_Phyto = Total abundance of phytoplankton*



Annex 7 *: Diel vertical migration of zooplankton taxa throughout the study.*
Full square *= Night,* ***Empty square*** *= Day*

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Alan Fritsch
2023-2024

Étude de la distribution spatiale du zooplancton lacustre

Résumé : A l'aide d'imagerie de particules *in situ*, la distribution spatiale du zooplancton d'un lac oligotrophique a été étudiée lors de la stratification estivale. À partir de ces données, le recouvrement spatial entre chaque taxon du zooplancton et leurs compétiteurs (autres zooplanctons), leurs ressources (phytoplancton) et leurs prédateurs (poisson et invertébrés) a été calculé à l'aide de l'Index de recouvrement de fonction de répartition (UDOI). La relation entre et l'abondance de chaque taxon et de ces valeurs de recouvrement a été testé à l'aide d'une approche multi-modèle.

Mots Clés : Limnology, Zooplankton, Spatial overlap, UVP, Interspecific competition, UDOI

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