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Title: Are zooplankton communities structured by taxa ecological niches or by hydrological features?

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Abstract:

This study aimed to clarify the mechanisms that structure zooplankton communities in a lowland river network. 14 stations on the Scheldt upper river basin (France/Belgium) were sampled during 4 campaigns in 2014-2015.

Firstly, a niche analysis of zooplankton taxa was conducted for April and September 2014 using the Outlying Mean Index (OMI) ordination technique. Then, application of Hutchinson’s niche and of Hubbell’s neutral theories to zooplankton community of the river network were tested for April and June 2015. We subsequently tested whether the taxa ecological preferences revealed were reflected in the April and June 2015 zooplankton spatial distributions.

In April 2015 zooplankton community dissimilarity (Bray-Curtis distance) was more influenced by environmental conditions than by hydrological distance, in accordance with niche theory. In June 2015, a stronger influence of neutral processes was suggested by an important role of hydrology. In 2014 samples, 17 over 32 taxa presented significant marginality relying on the considered environmental parameters. This specialization was reflected in the 2015 community patterns, particularly in April. During this month, local environmental parameters were more influencing than hydrology, probably related to a higher environmental heterogeneity than in June 2015.

Although zooplankters are often considered to be generalists and opportunists, mainly dependent of river hydrology, these results showed that even for passive dispersers in highly

connected systems, niche processes contribute to community structuring by local filtering. Determination of species niche parameters is thus important to understand observed community patterns but also changes in species distribution relative to environmental and hydrological changes.

Introduction:

Understanding the mechanisms that determine species distribution in relation with environmental conditions is a central topic in community ecology. In particular, community spatio-temporal patterns have been related to species habitat preferences through Hutchinson's niche theory (Hutchinson, 1957). According to Hutchinson's theory, a species ecological niche can be defined as an n-dimension hypervolume delimiting environmental limits in which species can survive and develop. According to the niche theory, local conditions act as species filters. Thus, similar physico-chemical conditions may involve similar community compositions, and investigations of habitat preferences (i.e. ecological niche) of taxonomic units can be useful to understand their distribution patterns (Dolédec et al., 2000). By contrast, the neutral theory (Hubbell, 2001) suggests that all taxa have similar fitness regarding processes of birth, death, dispersal and speciation, and that ecological drift and stochastic events structure communities. The neutral concept thus supports the importance of spatial configuration influencing dispersal while environmental conditions are supposed to play a minor role in structuring communities.

Gravel et al. (2006) argue that rather than being opposite concepts, niche and neutral theories may be viewed as the two "extremes of a continuum". Niche and neutral models are thus complementary, and their relative importance in controlling community dynamics can vary (Leibold and McPeck, 2006; Chase and Myers, 2011). In metacommunity studies, niche-based control and neutral models can both be applied. Leibold et al. (2004) proposed a framework for the metacommunity concept and reviewed the different approaches that can help understanding its structuring. Indeed, a metacommunity can be defined as a set of local communities linked by dispersal and interaction of individuals (Leibold et al., 2004; Alonso et al., 2006; Soininen et al., 2007a). Hence, when similar communities are observed in similar environmental conditions, niche processes are likely dominant in structuring communities. By contrast, in the case of neutral model dominance, community composition will be rather independent of environmental conditions, and mainly related to spatial configuration

(distance between observations) involved in dispersion processes. In this case, the similarity between communities is expected to decrease when distance between them increases (distance-decay of similarity, see Hubbell, 2001; Soininen et al., 2007b; Morlon et al., 2008).

According to Soininen et al. (2007b), the distance-decay of similarities can be influenced by 3 major causes: 1) the variability of environmental conditions which increase niche processes (nearest communities can be more similar than distant communities because they share similar environmental conditions) ; 2) the degree of isolation of communities, since dispersal barriers can affect the dispersal rate of organisms ; 3) the dispersal ability of organisms: dispersal limitation increases the dissimilarity between distant communities.

Zooplankton plays an essential role in pelagic energy fluxes by ensuring the transfer between the phytoplanktonic primary producers and higher trophic levels (Carpenter et al., 1985; Park and Marshall, 2000; Tackx et al., 2003). Through the trophic cascade, zooplankton dynamics, community composition and resulting biomass can have repercussions on other ecological compartments, either on prey (e.g. phytoplankton) or predators (e.g. fish) (McQueen et al., 1989; Beaugrand et al., 2000; Carpenter et al., 2001; Sommer and Sommer, 2005). The understanding of zooplankton community distribution in pelagic systems is complex because of the multiple abiotic and biotic factors that influence their abundance and composition (Pinel-Alloul et al., 1995; David et al., 2005; Mialet et al., 2010; 2011; Chambord et al., 2016). Due to their limited swimming capacities regarding strong currents (Riandey et al., 2005; Dur et al., 2007; Devreker et al., 2010), zooplankters are particularly sensitive to physico-chemical factors of their environment, but are also highly dependent of hydrodynamics and climate properties (in particular precipitation - Kimmel et al, 2006 ; Primo et al., 2009). Moreover, their central position in pelagic foodwebs makes them highly dependent of bottom up and top-down processes (Carpenter et al., 1985; Stibor, 1992; Walz, 1997; Shurin, 2001).

Many studies have investigated the mechanisms that structure zooplankton spatial distribution in freshwater systems. In particular, zooplankton distribution patterns have been studied in relation to the metacommunity concept in lentic systems. Cottenie et al. (2003) aimed for example to quantify the relative roles of local environmental factors and of spatial configuration in structuring zooplankton metacommunities in a series of interconnected ponds. They suggest that, despite the high degree of dispersal in the system, local environmental factors may be strong enough to allow striking differences between different

pond communities. Soininen et al., (2007a) also showed in boreal wetland interconnected ponds that both spatial configuration and local environmental factors drove zooplankton and phytoplankton community structure.

Since river networks form complex dendritic systems, the degree of connectivity, directionality and hydrological constraints influence ecological processes and community distributions (Grant et al., 2007; Brown and Swan, 2010). For example, Brown and Swan (2010) investigated metacommunity patterns of benthic macroinvertebrates in three river networks (Youghiogheny, Savage, and Casselman Rivers - Maryland, USA), and found that headwater communities which are more isolated are mainly structured by local environmental conditions while in mainstreams the influence of dispersal is stronger.

In the Ying River (China) it has been demonstrated that local communities of zooplankton are influenced by both local environmental conditions and spatial configuration (Zhao et al., 2017). The authors showed that the relative importance of both processes was dependent of hydrological conditions, since during the low flow season local communities were more isolated from each other and thus more influenced by different local conditions than during the wet season. Because the hydrological river regime is directly related to the quantity of water collected in the drainage basin, seasonality indeed strongly influences dispersion processes and therefore community structuring. On the other hand, man-made dams and other ecological barriers influence residence times of water masses and reduce connectivity of such systems (Ward and Stanford, 1983; Merritt and Wohl, 2006; Cote et al., 2009).

The present study aims to investigate whether, in a low flowing and highly channelized freshwater hydrological network (i.e. the upper Scheldt basin), zooplankton abundance / composition is influenced by niche or neutral processes. In other words, we investigate the influence of ecological factors versus spatial configuration on zooplankton metacommunity structure.

The study has been conducted in a two steps procedure, based on two temporally distinct datasets. First, zooplankton taxa ecological preferences in the study area were investigated from April and September 2014 data. A multivariate method of niche analysis (Outlying Mean Index : OMI analysis) was performed, allowing to characterize niche position and breadth of each taxonomic unit in a multivariate space. Then, we tested whether zooplankton distribution was related to taxa niche or to spatial configuration in April and June 2015.

Methods

Data acquisition

Study area

The Scheldt River has its source in Northern France near Gouy (49° 59' 13" N 3° 15' 59" E), runs through Belgium and flows into the North Sea at Vlissingen, the Netherlands (51° 25' 51" N 3° 31' 44" E) (Fig. 1).

The Scheldt basin is characterized by important industrial and agricultural activity, and is also densely populated. The study area is a part of the Scheldt watershed located crossing the French-Belgian border. It encompasses the non-tidal freshwater part of the Scheldt, upstream from Gent, and some tributaries being part of its watershed: the Lys River with its tributary Deûle, the Scarpe River with its tributary Sensée (Fig. 1, Table 1). The area is dominated by agricultural landscapes, but includes agglomerations such as Lille (220 000 inhabitants), Douai or Valenciennes (40 000 inhabitants each). Facilitated by the low relief of the basin (altitude of the Scheldt source: 100 m above sea level), the hydrological network has been strongly channelized for navigation purposes, and is regulated by many dams and sluices. All the sites considered in this study are on channelized stretches, except Crévecoeur sur Escaut. As a consequence, current velocity in these systems is relatively low (about 1 m sec⁻¹; Prygiel & Coste, 1993).

In the basin, discharge varies seasonally, in relation with pluviometry (Fig. 2, Meire et al., 2005). Regular data on discharge are available at Melle, which is located downstream the study area (Fig. 1). All the sites have been sampled for zooplankton and environmental factors at 4 occasions: April and September 2014 and April and June 2015. This allowed to perform a repeated sampling of the April spring situation, and to cover two other seasonal conditions: early summer and fall.

Compared to the daily discharges recorded at Melle over a 10 years period (2005-2015: median = 21.37 m³.sec⁻¹), the year 2014 presented higher median discharge (24.19 m³.sec⁻¹) and the year 2015 lower median discharge (14.96 m³.sec⁻¹). Therefore, and even if April was sampled both in 2014 and 2015, the 4 sampling periods were all conducted under hydrologically different conditions: April 2014 during a medium-high flow (23 to 60 m³.sec⁻¹ at Melle), September 2014 during a medium-low flow (10 to 24 m³.sec⁻¹), April 2015 during

medium flow (17 to 25 m³.sec⁻¹), and June 2015 took place during a very low flow (4 to 6 m³.sec⁻¹) (Fig. 2).

Zooplankton sampling

Fifty liters of sub-surface water were collected at each site using a pump and filtered through 50 µm mesh plankton net. The collected zooplankton was narcotized with carbonated water and fixed with formaldehyde (4 % final concentration), and finally stained with erythrosine in the laboratory.

Subsamples were taken for counting and identification of organisms at the most precise taxonomic level possible under binocular microscope, to obtain zooplankton abundances at each site. The minimum number of individuals counted was 500 per sample. In order to exclude the influence of rare taxa, only taxa present in more than 5% of the observations were retained for statistical analysis.

Environmental data

Simultaneously with each zooplankton sampling, the following environmental factors were measured in subsurface natural water.

Temperature, conductivity and dissolved oxygen concentration (O₂) were measured using a multi parameter sensor (WTW, Multi 3430).

Suspended Particulate Matter (SPM) concentrations were quantified by filtration of 250 to 1200 mL of sub-surface water, depending on the SPM concentration (ranging between 3 and 80 mg L⁻¹, leading to clogging of the filter after more or less volume had been filtered), onto pre-weighed Whatman GF/C filters (porosity: 1.2µm). As a rule of thumb, filters were dried (45 °C) during 24 hours, briefly cooled in a desiccator (5 minutes maximum) and weighed. The same filters were burned at 500°C for 5 hours (inspired from: Lardies & Wehrmann, 1996 ; Abelho and Graça, 1998 ; Heiri et al., 2001), and re-weighed to obtain ash concentration. Organic Matter (OM) concentrations were calculated as the difference between SPM and ash concentrations.

110 to 1080 mL water samples were also filtered on Whatman GF/C filters for the determination of chlorophyll *a* (Chl*a*) concentrations (also depending on SPM concentration), which were then extracted in 2 % ammonium acetate solution and quantified by reversed

phase HPLC, following the method of Wright and Jeffrey (1997). Details of the methodology are given in Majdi et al. (2011).

Using 100 mL subsurface unfiltered water samples filtered through 0.2 μm cellulose nitrate filters, total Phosphorus (P_{tot}) concentrations were determined with the ammonium molybdate spectrophotometric method, Nitrite (NO_2^- -N), Nitrate (NO_3^- -N) and Orthophosphate (HPO_4^{2-} -P) concentrations were determined by Ion Chromatography analyses (Dionex Ics-5000+, Dionex Corp., Sunnyvale, CA, USA).

Data analysis

Comparison of environmental factors during sampling campaigns

Mean values for all environmental factors measured among all stations were calculated for each sampling campaign. Mean values were then, for each factor, compared between the four sampling periods by a Mann-Whitney test ($p < 0.05$).

Assessment of the ecological niche of zooplankton taxa from 2014 data

Taxa ecological preferences were characterized using niche analysis (quantification of niche breadth and marginality) considering samplings carried out in April and September 2014 together.

To explore the niche characteristics of zooplankton taxa, an Outlying Mean Index (OMI) analysis was used (Dolédec et al., 2000), based on both taxa abundance and environmental 2014 data (conductivity, temperature, Chl a , O_2 , SPM, OM/SPM, P_{tot} , NO_2^- -N, NO_3^- -N and HPO_4^{2-} -P concentrations).

OMI analysis provides, for each taxon, a value of marginality and tolerance. The marginality (expressed as “Outlying Mean Index”: here referred as “omi”) of a taxonomic unit corresponds to the distance between the mean habitat conditions used by the taxa and the mean habitat conditions of the sampling area (i.e. taxa with a high omi value have a marginal habitat relative to the average conditions of the sampling area). The Tolerance index (Tol) corresponds to the niche breadth, which measures the range of taxa distribution across habitat conditions. Taxa with lower tolerance can be considered more as specialists than those with high tolerance, being rather generalists. The residual tolerance index (Rtol) corresponds to the proportion of variance in the taxon niche unexplained by environmental parameters: thus low

value of R_{tol} indicates a strong correlation between explanatory variables and the taxon distribution.

In order to reduce the influence of dominant taxa, abundances were $\log(x+1)$ -transformed prior to analysis (Clarke and Warwick, 2001). A random permutation test with 999 permutations was used to test the statistical significance of the marginality of each taxon.

Testing the relationship between zooplankton community structure and both ecological and spatial distance from 2015 data

Relative influences of environmental forces and dispersal processes on community structuring were assessed by comparing pairwise community similarity of sites with the distance separating them. As distances, we considered pathways along the river network (hereafter called “hydrological distance”), and dissimilarity of environmental conditions (hereafter called “ecological distance”).

Hydrological distances (in km along the river network) were calculated between each couple of sampling sites using QGIS 2.6.1 software (QGIS Development Team, 2014).

The ecological distance (i.e. the environmental dissimilarity between each pair of sites) was obtained for April 2015 and for June 2015 by applying, for both periods, a procedure of PCA-HAC (Principal Component Analysis - Hierarchical Ascendant Classification) coupling to the environmental factors (conductivity, temperature, Chl a , O $_2$, SPM, OM/SPM, P $_{tot}$, NO $_2^-$ -N, NO $_3^-$ -N and HPO $_4^{2-}$ -P concentrations). The following procedure was used for this PCA-HAC coupling:

A PCA was applied to the environmental factors. PCA scores were then extracted from the first Principal Components (PCs) accounting for more than 90% of total variance, in order to obtain linearly independent variables. A hierarchical classification based on Ward’s method (Ward, 1963) was applied to the PCA scores using the Euclidean distance as in Anneville et al. (2002), in order to obtain a distance-matrix between samples based on environmental factors.

Mantel tests (Mantel, 1967) were used to investigate correlations between community dissimilarity between sites (Bray-Curtis distance on zooplankton abundances) and both ecological distance matrices and hydrological distance matrices, for the periods of April 2015 and June 2015.

Influence of environmental factors on zooplankton community structure in 2015:

The spatial structure of zooplankton community in relationship with the environmental factors was studied separately for each of the sampling campaigns of April and June 2015.

For each sampling period, data were centered and standardized by species, abundances were $\log(x+1)$ transformed, and a Redundancy analysis (RDA) was performed by using environmental factors as explanatory variables and zooplankton taxa abundances as response variables.

Results :

Environmental conditions

In April 2014, discharge at Melle ranged between 23 and 60 $\text{m}^3 \cdot \text{sec}^{-1}$ and corresponds to a medium flow in comparison with the median discharge of this year. In April 2015, discharge was lower (between 17 and 25 $\text{m}^3 \cdot \text{sec}^{-1}$) than in April 2014 although it was also near the annual discharge median. Rainfall at Lille was also lower in April 2015 than in April 2014 (respectively 31 and 51 mm). September samplings occurred at medium-low discharge, at the end of a large peak flow, and pluviometry was 49 mm at Lille. At this period, discharge at Melle ranged between 10 and 24 $\text{m}^3 \cdot \text{sec}^{-1}$. In June 2015, very low discharge values at Melle were observed, ranging between 4 and 6 $\text{m}^3 \cdot \text{sec}^{-1}$. Rainfall reached 38 mm at Lille in June 2015.

$\text{NO}_2\text{-N}$ and $\text{PO}_4\text{-P}$ concentrations were both significantly higher in April 2014 ($0.19 \pm 0.06 \text{ mg} \cdot \text{L}^{-1}$) than in April 2015 ($0.05 \pm 0.05 \text{ mg} \cdot \text{L}^{-1}$) (Mann & Whitney, $p < 0.001$). Other environmental factors were not significantly different between these two periods (Mann & Whitney, $p < 0.05$) (Fig. 3).

Temperature was the only environmental factor that significantly differed between September 2014 and June 2015, with $18.22 \pm 1.64 \text{ }^\circ\text{C}$ in September and $19.56 \pm 1.85 \text{ }^\circ\text{C}$ in June (Mann & Whitney, $p < 0.05$).

Differences in Temperature, Chl a and O_2 concentrations occurred between April and September 2014: temperature was lower in April ($14.28 \pm 1.37 \text{ }^\circ\text{C}$) than in September while O_2 and Chl a were both higher in April ($10.64 \pm 1.57 \text{ mg} \cdot \text{L}^{-1} \text{ O}_2$ and $32.98 \pm 34.55 \text{ } \mu\text{g} \cdot \text{L}^{-1}$ Chl a in April 2014 versus $7.97 \pm 1.92 \text{ mg} \cdot \text{L}^{-1} \text{ O}_2$ and $8.06 \pm 6.13 \text{ } \mu\text{g} \cdot \text{L}^{-1}$ Chl a in September - Mann & Whitney, $p < 0.05$).

In 2015, temperature was also higher in June (19.56 ± 1.85 °C) than in April (14.49 ± 1.22 °C) and it was also the case for NO₂-N concentrations (0.05 ± 0.05 mg.L⁻¹ in April, 0.22 ± 0.11 mg.L⁻¹ in June). O₂ and Chl_a concentrations were higher in April (12.55 ± 2.66 mg.L⁻¹ O₂ and 24.39 ± 18.57 µg.L⁻¹ Chl_a) than in June (8.28 ± 1.92 mg.L⁻¹ O₂ and 11.24 ± 11.03 µg.L⁻¹ Chl_a).

Conductivity (863 ± 133 µS.cm⁻¹), SPM (27 ± 17 mg.L⁻¹), OM (10 ± 4 mg.L⁻¹), NO₃-N (6 ± 2 mg.L⁻¹) and P_{tot} (0.24 ± 0.14 mg.L⁻¹) did not significantly differ across sampling periods (Mann and Whitney, $p < 0.05$).

Zooplankton composition

A total of 39 taxa were identified at the highest possible taxonomic level across all 14 stations and 4 sampling periods (Table 2), and 7 of them were found in less than 5% of samples, and are thus not included in statistical analyses. Rotifers dominated the communities with 84 % of total abundance, over all sites and sampling periods. Copepods represented 13% and cladocerans 2%.

Considering all samples, the most abundant taxon was the rotifer *Brachionus calyciflorus*, representing 24 % of total zooplankton abundance. *Synchatea* spp. represented 23%, *Keratella* spp. 18 % and *Polyarthra* spp. 5 %. Copepod nauplii were also an important part of the community, accounting for 11% of total abundance, and for 82% of copepod abundance.

In April 2014, rotifers represented 89% of total abundance in average, with a mean abundance of 230 ind.L⁻¹. Five sites had rotifer abundances superior to 300 ind.L⁻¹: Crévecoeur, Nivelles, Berchem, Warcoing and Neuville. However, 16 ind.L⁻¹ crustaceans in average were found in samples at this season, which is lower than at other sampling periods (Mann & Whitney, $p < 0.05$).

September 2014 was the sampling period with the lower mean total abundance (in average 80 ± 41 ind.L⁻¹) compared to other sampling periods (in average 225 ± 263 ind.L⁻¹ for the 3 other periods). Only Férin presented more than 100 ind.L⁻¹, but rotifers were significantly less abundant at this period (Mann & Whitney, $p < 0.05$). However, crustaceans abundances remains at the same level than at other sampling periods, and with particularly high nauplii abundances (in average 27 ind.L⁻¹ Nauplii).

In April 2015, rotifers were particularly abundant at 3 sites: Berchem, Warcoing and Zingem (in average 837 ind.L⁻¹ in the 3 sites; 144 ind.L⁻¹ in other sites). Crustaceans were dominated by nauplii (85% of crustaceans), and their abundance were lower in Berchem, Warcoing and Zingem (10 ind.L⁻¹ in average) than in other sites (50 ind.L⁻¹ in average).

The maximal total abundance was reached at Nivelles in June 2015, with more than 1100 ind.L⁻¹ (Fig. 4), mainly due to the rotifer *Synchatea* spp. which was highly abundant in this sample. Except this peak, in June 2015, rotifers abundances (140 ind.L⁻¹) were comparable to those of April 2014 and 2015, and crustaceans reached 50 ind.L⁻¹, which is higher than the average abundance of other periods.

Zooplankton taxa ecological niches

17 taxa over 32 showed a significant marginality as a result of the OMI analysis based on April and September 2014 data ($p < 0.05$; Table 3). Residual tolerance (Rtol) for these taxa ranged between 43 and 81%, showing an important proportion of variability unexplained by the environmental parameters considered. *Trichotria* spp. and *Monomatta* spp. showed the highest marginality and lowest tolerance values. Nauplii had low omi indicating non-marginal niches, and high tolerance indicating a wide niche breadth. It was also the case for *Brachionus calyciflorus*, *Polyarthra* spp. and *Keratella cochlearis*.

The two first axes of the OMI analysis accounting respectively for 64% and 21% of the total explained variability are presented in the Fig. 5. The first axis corresponded to an opposition between O₂ and Temperature / NO₂-N. Axis 2 was positively associated with NO₃-N concentrations and negatively with P_{tot} and conductivity. Chla was both positively associated to axis 1 and negatively associated to axis 2 (Fig. 5a).

According to their niche position and breadth along axis 1 (Fig. 5b.), *Brachionus leydigii*, *Asplanchna* spp., *Brachionus calyciflorus*, *Monomatta* spp., *Brachionus urceolaris*, *Filinia longiseta*, *Kellicotia* spp., and *Trichotria* spp. presented a niche specialized in high O₂ and Chla concentrations, contrarily to Calanoid copepodites and *Brachionus quadridentatus* associated to temperature and NO₂-N concentration. Along the second axis (Fig. 5c), only *Trichotria* spp. presented a specialization for NO₃-N concentration, while *Brachionus calyciflorus* and *Brachionus leydigii* showed a significant specialization for sites with high Chla and P_{tot} concentrations.

Zooplankton similarity in relation to ecological and physical distances:

Mantel tests showed a light significant relation between zooplankton community dissimilarity and ecological distance in April 2015 ($P < 0.05$), while they showed a significant relationship between community dissimilarity and hydrological distance in June 2015 ($P < 0.05$ - Table 4).

Influence of environmental factors on zooplankton community structure in 2015:

The two first axes of the RDA analysis on April 2015 samples explained 39% of total variance in zooplankton abundance data, and the two first axes of the RDA conducted on June 2015 samples explained 38% (Fig. 6).

In April 2015, axis 1 was positively correlated to $\text{NO}_3\text{-N}$ concentrations while it was negatively related to OM, O_2 , Chl a and P_{tot} . Axis 2 corresponds to an influence of temperature and $\text{NO}_2\text{-N}$ (on its negative part).

Several rotifer taxa were associated to the negative part of axis 1, and in particular *Brachionus calyciflorus* (B. cal), *Filinia longiseta* (F. lo), *Keratella quadrata* (K. qua), and *Keratella cochlearis* (K. co), contrarily to *Monomatta* spp. (Mono) which was rather associated with $\text{NO}_3\text{-N}$ concentrations. Along the second axis, copepods (including nauplii) are found in association with temperature.

In June 2015, Conductivity is opposed to OM and SPM concentrations along the first axis and the second axis was mainly related to an opposition between nutrient concentrations versus oxygen and Chl a .

Most of crustaceans (except copepod nauplii) were associated with conductivity, while most abundant rotifers (*B. calyciflorus*, *K. cochlearis*, *K. quadrata*) were rather related to OM and SPM. *Brachionus quadridentatus* and *B. urceolaris* were related to O_2 and Chl a .

Discussion:

Many studies showed that zooplankton community structures in riverine systems are closely related to hydrology (Pace et al., 1992; Reynolds et al., 2000; Baranyi et al., 2002).

According to the River Continuum Concept (RCC, Vannote et al., 1980), water residence times are too short to allow zooplankton development in headwaters. However, this concept has been reconsidered in particular by taking into account the discontinuities that can occur along a watercourse and that alter upstream-downstream effects (the Serial Discontinuity Concept, Ward & Stanford, 1983; 1995), or the consideration of 4 dimensional structure of hydrological networks (Ward, 1989) and the interactions with floodplain (flood pulse

concept, Junk et al., 1989). At the scale of the entire basin, from source to mouth, the influence of the salinity gradient and of tidal effects in structuring zooplankton communities along the Scheldt continuum have been highlighted in Le Coz et al. (2017). The data presented in le Coz et al (2017) and in the present paper show that, contrarily to the RCC concept, zooplankton communities in the upstream Scheldt basin are substantial in abundance. Clearly, hydrological conditions in this lowland basin allow their growth and reproduction. Thus the relative contribution of hydrology and of ecological factors in explaining their distribution patterns within this non-tidal hydrological network needed deeper consideration.

The present study aimed to understand the mechanisms that structure zooplankton communities in the upstream lowland river network of the Scheldt basin, considering neutral and niche models. Taxa ecological preferences were first investigated based on April and September 2014 data.

Among the 32 taxa identified, 17 (i.e. 53%) had a significant marginality in April and September 2014, meaning that environmental conditions had a significant influence on these taxa. However, most of them had a high value of residual tolerance, indicating that a high proportion of variability in taxa niche was not explained by the considered environmental factors. Obviously, other factors should be considered, since zooplankton respond to multiple biotic and abiotic factors. A high degree of unexplained heterogeneity is indeed generally described in zooplankton community studies (Pinel-Alloul et al., 1995; Cottenie et al., 2003; Soininen et al., 2007a; Zhao et al., 2017). However, this study did not aim to search for explanatory variables for zooplankton distribution patterns but rather to test whether taxa ecological preferences were reflected in the community distribution, despite the influence of hydrological connectivity (i.e. spatial configuration).

As a result, the environmental factors used in the OMI analysis explained between 18.7 and 55.5% of inertia for each taxon. The OMI analysis showed that most rotifer taxa considered had low marginality and high tolerance and were thus rather generalists, in particular considering some very abundant taxa: *Brachionus calyciflorus* (B.cal), *Keratella cochlearis* (K.co) or *Keratella quadrata* (K.qua). This was also the case for copepod nauplii.

Nevertheless, the analysis permitted to distinguish a degree of specialization among rotifer taxa. Taxa with high marginality but low tolerance can be considered as the most specialized. *Trichotria* spp. (Trt) was the taxon with the lowest residual tolerance (44.5%) so the chosen

environmental factors measured in this study are the most influencing for this taxon compared to other taxa. *Trichotria* spp. had a relatively high marginality and low tolerance and a preference for high O₂, Chla and NO₃ concentrations. *Monomatta* spp. (Mono) was also specialized for high O₂ and Chla concentration conditions. But its higher associated residual tolerance (69.4%) indicates that other non-investigated parameters may contribute to its niche inertia. Other taxa can display both low marginality and low tolerance, as it was the case for *Alona* spp. (Alo). *Alona* spp. occurred near average conditions of the study area, but had low tolerance, so that a change of conditions could disadvantage its development. As *Monomatta* spp., *Alona* spp. had high residual tolerance and may be influenced by non-considered factors.

Niche parameters of taxa obtained from April and September 2014 were then used to interpret the community patterns obtained from sampling campaigns of April and June 2015.

Results of Mantel tests between Bray-Curtis distance among zooplankton communities and environmental or hydrological distances suggest that zooplankton distribution patterns are associated to different processes in April and in June 2015. In April 2015, Bray-Curtis dissimilarity of pairwise zooplankton communities presented a significant relationship with ecological distance. Thus, at this period of medium base flow, zooplankton community structuring was rather influenced by environmental conditions (related to niche processes). In June 2015, zooplankton community pairwise dissimilarity was on the contrary significantly related to hydrology, a pattern suggesting that nearest zooplankton communities are more similar, and thus that the spatial configuration of sites is more structuring for zooplankton than local environmental conditions (following the neutral theory), despite a lower flow than in April 2015. Such a change in mechanisms structuring zooplankton communities could lead to several alternative interpretations:

- 1) The change of hydrological conditions between April and June 2015 changed the degree of connectivity between stations: In the Ying River, Zhao et al (2017) showed that at the low flow season, the increase of isolation between communities increases niche processes. In the Ying River, the climate is semi-humid, and dry and wet seasons are strongly marked (more than 60% of annual precipitation falls between June and September). In the Scheldt basin, the discharge was higher in April than in June 2015 at Melle, but monthly precipitations at Lille, closer to the sampling sites, were higher in June compared to April 2015. The hypothesis of a higher dispersal due to a higher current velocity in June is

therefore unlikely considering discharge at Melle, but more accurate hydrological data is necessary to rule on this question.

2) If environmental conditions between sites differ sufficiently, environmental filtering can be strong enough to overwhelm hydrological influence (Cottenie et al., 2003). In the present study, certain measured environmental factors indeed presented a much higher coefficient of variation among sites in April 2015 than in June (e.g. coefficient of variation for $\text{NO}_2\text{-N}$ concentration was 109% in April and 51% in June). Thus, a higher heterogeneity of certain environmental factors across sites in April potentially increased the effect of environmental filtering on the zooplankton community structuring.

3) The degree of isolation between sites may have changed because of anthropogenic manipulation of hydrological barriers. For example, Zhao et al. (2017) showed that, in the Ying River (China), the presence of dams influences metacommunity structure by creating dispersal barriers and quasi-lentic areas, and by modifying environmental conditions. In the studied area, opening and closing of sluices depends on boat traffic which can be relatively important (Prygiel et al., 2015), and thus the degree of isolation can vary in time and among sites situated on different rivers of the watershed.

As a result of these different patterns in April and June 2015, the comparison between 2014 niche parameters and 2015 community structure is most relevant for April 2015, since in June 2015 community distribution is probably more influenced by hydrology.

The RDA results performed on April 2015 data showed that the environmental factors that influenced taxa ecological niche in 2014 were the same as those revealed to influence community distribution in April 2015 : in particular O_2 , Chla P_{tot} , $\text{NO}_3\text{-N}$, and temperature. The ecological preferences found for most taxa in 2014 were reflected in the RDA conducted in April 2015. For example, *Brachionus calyciflorus*, *Filinia longiseta* and *Keratella quadrata* were associated in the OMI analysis on 2014 data to O_2 , Chla, OM and P_{tot} concentrations. The April 2015 RDA shows an influence of these environmental factors on these taxa distribution, which is thus probably related to ecological preferences.

However, some taxa did not show the expected response according to their 2014 niche parameters: *Notholca* spp showed for example a preference for higher oxygen concentration in opposition with temperature, but is found in April 2015 poorly influenced by temperature

and negatively associated with oxygen. For this taxon, it is likely that niche separation is more related to seasonal effect and cannot be assessed on single period.

On the June 2015 RDA, environmental factors influence on zooplankton structure is more difficult to interpret in the light of taxa niches. Only *Brachionus quadridentatus* is associated with Chl a and O $_2$ as predicted by its niche. If, as the Mantel tests suggest, zooplankton are rather influenced by spatial configuration and thus hydrological conditions in June, the segregation between crustaceans and rotifers / nauplii could be related to different sensitivity to currents or to dispersal abilities of these different size-classes of organisms.

The use of April and September 2014 data for characterization of taxa niches allowed to covering a broad range of within growth season conditions to detect the niche parameters, and to consider the expression of seasonal effects in our results. Indeed, three of the considered environmental factors were significantly different between April and September 2014 (temperature, Chl a , O $_2$), and the first axis of OMI analysis was associated with an opposition between April and September. Ecological niches described here are thus probably partly temporally separated, and related to zooplankton seasonal successions (Laprise and Dodson, 1994 ; Talling et al., 2003 ; Li et al., 2000 ; Le Coz et al., 2017). On the other hand, the results of RDA processed on April 2015 data showed that taxa ecological preferences are also reflected in spatial structure of metacommunities within a unique sampling period, and thus that this niche separation is not only seasonally but also spatially expressed.

Due to their inherent incapacity to counteract currents, zooplankters disperse passively, and at relatively high rates (Shurin et al., 2008, Havel and Shurin 2004), even if dispersal rates of organisms remain taxa-dependent and may thus vary with community composition (Bohonak and Jenkins, 2003, Shurin et al., 2000; Louette and De Meester 2005). Cottenie et al. (2003) quantified dispersal of zooplankton in a set of highly interconnected ponds, and found a high influence of homogenizing communities by dispersal. Nevertheless, local environmental conditions were so different among ponds that environmental filtering overwhelmed dispersal processes in structuring communities. Indeed, even if dispersal capacities are substantial, establishment success of organisms will depend on local (abiotic and biotic) environmental conditions of its new habitat in relation to its competitiveness and ecological niche (Shurin, 2000; Louette and De Meester, 2005). When at the same time heterogeneity of environmental conditions is strong and niche overlap among communities is weak, conditions are met to observe a differentiation between local communities. For these reasons, understanding the

ecological preferences of taxa constituting the community is a necessity, even if hydrology is known as a major driver of zooplankton communities in river networks.

Conclusions:

The present study showed influence of both neutral and niche processes on zooplankton communities in a lowland river system. At the scale of the upper non-tidal Scheldt river basin, passive dispersers such as zooplankton presented, for certain taxa, ecological preferences influencing metacommunity structure. These results attest the interest of considering zooplankton communities in upstream rivers where they are still poorly documented.

Many zooplankton taxa in this study have neither a marginal niche nor a narrow niche breadth. Nevertheless, the employed method allowed identifying the key taxa for which ecological preferences clearly influenced their distribution. These taxa can be considered as indicators of conditions close to their ecological preferences. Brachionids for example are described in literature as indicators of eutrophic conditions, and of rich-*Chla* environments (Sládeček, 1983; Bērziņš and Pejler, 1989; Attayde and Bozelli, 1998), and our results confirm that this ecological preference can influence their spatial and temporal distribution patterns. The strong influence of O_2 , *Chla* and P_{tot} concentrations on the rotifer distribution is not surprising, since rotifers are known to be bottom-up controlled and dependent of primary production (Hansen et al., 1997; Walz, 1997).

Including other environmental factors in such analysis could permit to find other specializations of taxa. Several authors indeed recommend the inclusion of zooplankton as bio-indicators in water quality assessment, and in particular in the European Water Framework Directive evaluation (Moss, 2007; Jeppesen et al., 2011; Haberman and Haldna, 2014). Better knowledge on the ecology of these zooplankton potential indicator taxa may thus be useful in this context, and understanding the mechanisms that influence them is a necessity. Niche analysis could provide integrative data for understanding both taxa ecology and community response to spatial or temporal environmental changes, and could become more powerful by increasing the size of the datasets considered. We think that this perspective can be extended to various taxa and ecosystems.

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Accepted Article

Table 1: Geographical position, Codes as used in analyses and sampling dates and of the 14 sites.

Site	Geographical coordinates		Code	Sampling dates			
				April 2014	September 2014	April 2015	June 2015
Aire sur la Lys	50°38'45,1" N	2°24'34,8"E	ASL	08/04/2014	03/09/2014	23/04/2015	15/06/2015
Berchem	50°47'36,71"N	3°30'16,74"E	BER	07/04/2014	07/09/2014	22/04/2015	16/06/2015
Brebières	50°20'08,3" N	3°01'17,8"E	BRE	09/04/2014	02/09/2014	16/04/2015	19/06/2015
Crèvecoeur sur l'Escaut	50°05'36,7"N	3°14'35,2"E	CSE	09/04/2014	02/09/2014	20/04/2015	18/06/2015
Don	50°32'48,8" N	2°55'14,7" E	DON	08/04/2014	03/09/2014	21/04/2015	15/06/2015
Erquinghem -Lys	50°40'37,8" N	2°50'08" E	EL	08/04/2014	03/09/2014	23/04/2015	15/06/2015
Férin	50°19'24,1" N	3°04'18" E	FER	09/04/2014	02/09/2014	16/04/2015	19/06/2015
Fresnes sur Escaut	50°25'33,0"N	3°34'52,7"E	FSE	10/04/2014	05/09/2014	17/04/2015	18/06/2015
Neuville sur Escaut	50°18'05,9"N	3°21'01,1"E	NSE	09/04/2014	02/09/2014	20/04/2015	18/06/2015
Nivelle	50°28'11,6"N	3°27'58,1"E	NIV	10/04/2014	05/09/2014	17/04/2015	17/06/2015
Wambrechies	50°41'10"N	3°03'10"E	WAM	08/04/2014	04/09/2014	21/04/2015	17/06/2015
Warcoing	50°41'8.04"N	3°20'49.66"E	WAR	07/04/2014	07/09/2014	22/04/2015	16/06/2015
Wervicq	50°46'36"N	3°02'35"E	WER	07/04/2014	04/09/2014	21/04/2015	17/06/2015
Zingem	50°53'36,30"N	3°40'50,07"E	ZIN	07/04/2014	07/09/2014	22/04/2015	16/05/2015

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Table 2: Zooplankton taxa observed in the study area and their percentage of total zooplankton abundance, considering all sites and sampling occasions. Taxa present in less than 5% of observations (in less than 3 observations) are indicated in grey.

	code	abundance (%)		code	abundance (%)
Rotifera					
<i>Brachionus calyciflorus</i>	B.cal	24.04 %	<i>Cephalodella</i> spp.	Cep	0.19 %
<i>Synchaeta</i> spp.	Syn	23.41 %	<i>Notholca</i> spp.	Not	0.15 %
<i>Keratella cochlearis</i>	K.co	13.81 %	<i>Lecane</i> spp.	Lec	0.12 %
Bdelloida	Bdel	8.33 %	<i>Brachionus quadridentatus</i>	B.qu	0.08 %
<i>Polyarthra</i> spp.	Pol	5.34 %	<i>Brachionus rubens</i>	B.ru	0.07 %
<i>Keratella quadrata</i>	K.qua	4.19 %	<i>Kellicottia</i> spp.	Kel	0.06 %
<i>Brachionus angularis</i>	B.an	2.48 %	<i>Trichotria</i> spp.	Trt	0.05 %
<i>Filinia longiseta</i>	F.lo	0.53 %	<i>Monommata</i> spp.	Mono	0.04 %
<i>Brachionus leydigii</i>	B.le	0.36 %	<i>Keratella valga</i>	K.va	0.02 %
<i>Asplanchna</i> spp.	Aspl	0.34 %	<i>Trichocerca</i> spp.	Trc	0.01 %
<i>Euchlanis</i> spp.	Euc	0.33 %	<i>Brachionus diversicornis</i>	B.di	0.01 %
<i>Brachionus urceolaris</i>	B.ur	0.29 %	<i>Testudinella</i> spp.	Tes	<0.01 %
<i>Lepadella</i> spp.	Lep	0.24 %	<i>Mytilina</i> spp.	Myt.	<0.01 %
Copepoda			Cladocera		
copepod nauplii	Nauplii	10.77 %	<i>Bosmina</i> spp.	Bos	1.24 %
cyclopoid copepodite	Cyc.C	1.54 %	<i>Chydorus</i> spp.	Chy	0.69 %
calanoid copepodite	Cal.C	0.32 %	<i>Daphnia</i> spp.	Dap	0.20 %
cyclopoid adult	Cyc	0.30 %	<i>Alona</i> spp.	Alo	0.12 %
calanoid adult	Cal	0.19 %	<i>Ceriodaphnia</i> spp.	Cer	0.03 %
harpacticoid	Har	0.08 %	<i>Pleuxorus</i> spp.	Pleu	0.01 %
			<i>Illicryptus</i> spp.	Ill	0.02 %

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Table 3: Niche parameters of the zooplankton taxa (April and September 2014 samplings): Inertia, Outlying Mean Index (OMI), tolerance (Tol), residual tolerance (Rtol) and p.value. Refer to Table 1 for taxa codes.

taxa	inertia	omi	Tol	Rtol	omi (%)	Tol (%)	Rtol (%)	P.value
B.le	11.28	2.35	3.51	5.42	20.8	31.1	48.1	0.01
B.qu	9.96	2.04	1.25	6.67	20.5	12.5	67	0.01
B.ur	10.61	1.64	2.00	6.96	15.5	18.9	65.6	0.01
Har	9.23	0.83	1.67	6.73	9	18.1	72.9	0.01
Cal.C	9.76	0.72	2.26	6.78	7.3	23.2	69.5	0.01
Alo	8.75	0.49	1.14	7.12	5.6	13.1	81.3	0.01
Cal	10.60	0.31	2.68	7.61	2.9	25.3	71.8	0.01
B.cal	10.56	0.14	3.42	7.00	1.3	32.4	66.3	0.01
Nauplii	10.00	0.01	2.89	7.10	0.1	28.9	71	0.01
Trt	7.45	3.39	0.74	3.31	45.6	10	44.5	0.02
Mono	10.59	2.72	0.52	7.35	25.7	4.9	69.4	0.02
Dap	9.85	0.79	2.44	6.63	8	24.7	67.3	0.03
K.co	10.17	0.02	2.81	7.33	0.2	27.6	72.1	0.03
K.qua	10.39	0.07	2.92	7.41	0.7	28.1	71.2	0.04
Kel	11.30	1.73	3.00	6.57	15.3	26.6	58.2	0.05
Not	10.65	1.03	1.34	8.28	9.6	12.6	77.8	0.05
F.lo	10.93	0.27	2.75	7.91	2.5	25.1	72.4	0.05
Pol	10.14	0.01	3.04	7.09	0.1	29.9	69.9	0.06
B.ru	9.37	1.48	0.82	7.07	15.8	8.8	75.5	0.07
Syn	10.31	0.05	3.02	7.24	0.5	29.3	70.2	0.08
Ill	13.60	2.44	2.44	8.72	17.9	18	64.1	0.1
Chy	9.93	0.16	1.41	8.36	1.6	14.2	84.2	0.1
Aspl	9.78	0.27	2.22	7.28	2.7	22.8	74.5	0.13
Cyc.C	9.92	0.01	2.43	7.48	0.1	24.5	75.4	0.13
B.an	10.10	0.01	2.14	7.95	0.1	21.2	78.7	0.19
Lec	9.58	0.56	0.93	8.09	5.8	9.7	84.5	0.3
Cyc	10.03	0.05	1.74	8.24	0.5	17.4	82.1	0.32
Cep	10.47	0.23	1.75	8.48	2.2	16.7	81	0.42
Euc	10.10	0.19	1.17	8.75	1.8	11.5	86.6	0.61
Trc	12.13	2.35	1.23	8.54	19.4	10.2	70.4	0.64
Bos	9.87	0.03	2.80	7.03	0.3	28.4	71.3	0.66
Bdel	10.01	0.01	0.90	9.10	0.1	9	90.8	0.8

Table 4: Results of Mantel tests run to compare zooplankton based-distances between samples and successively: environmental based-distances, and hydrological distance. P-values are determined with a Monte Carlo permutation test using 999 permutations.

	April 2015	June 2015
Bray-Curtis distance and ecological distance	$r=0.21$ $p=0.03$	$r=0.03$ $p=0.39$
Bray-Curtis distance and hydrological distance	$r=0.10$ $p=0.14$	$r=0.37$ $p=0.006$

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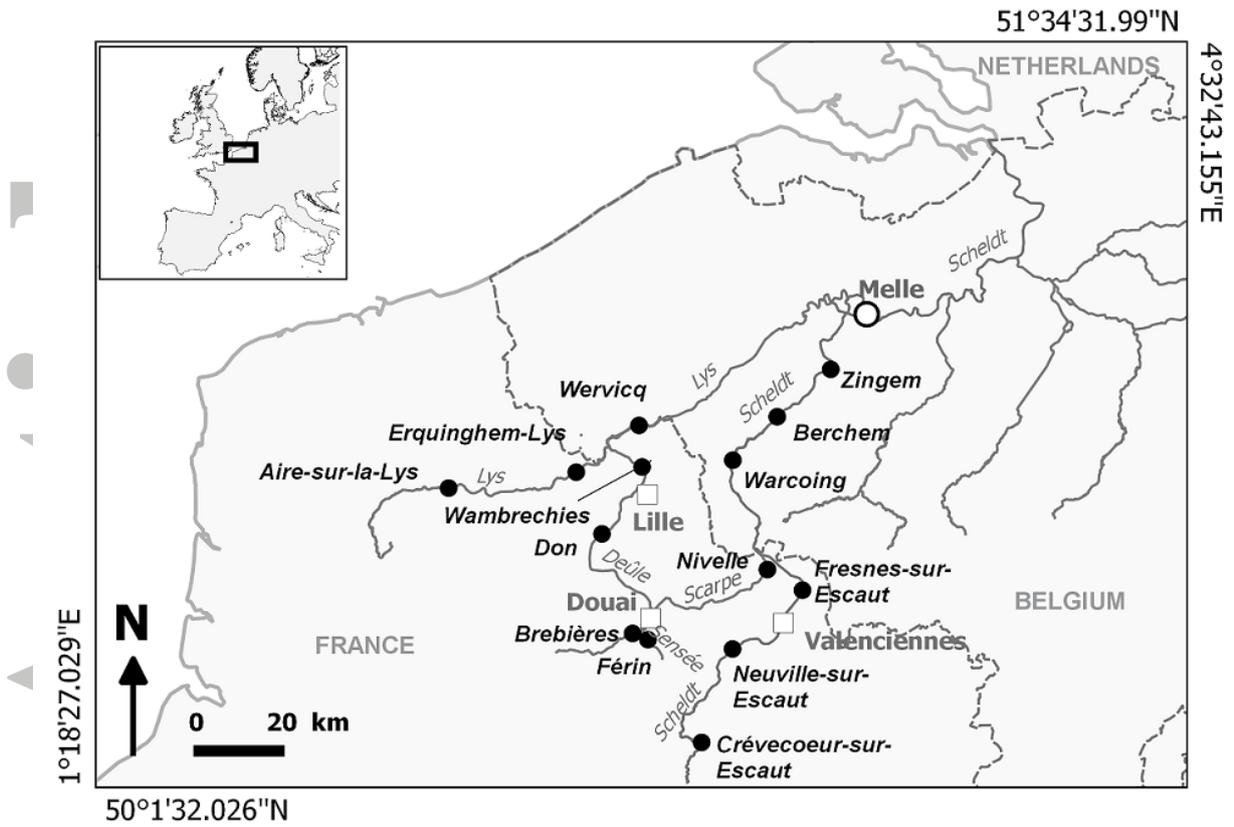


Figure 1: Location of sampling sites (black dots) in the upstream basin of the Scheldt. Melle is the limit of the tidal influence. White squares are cities.

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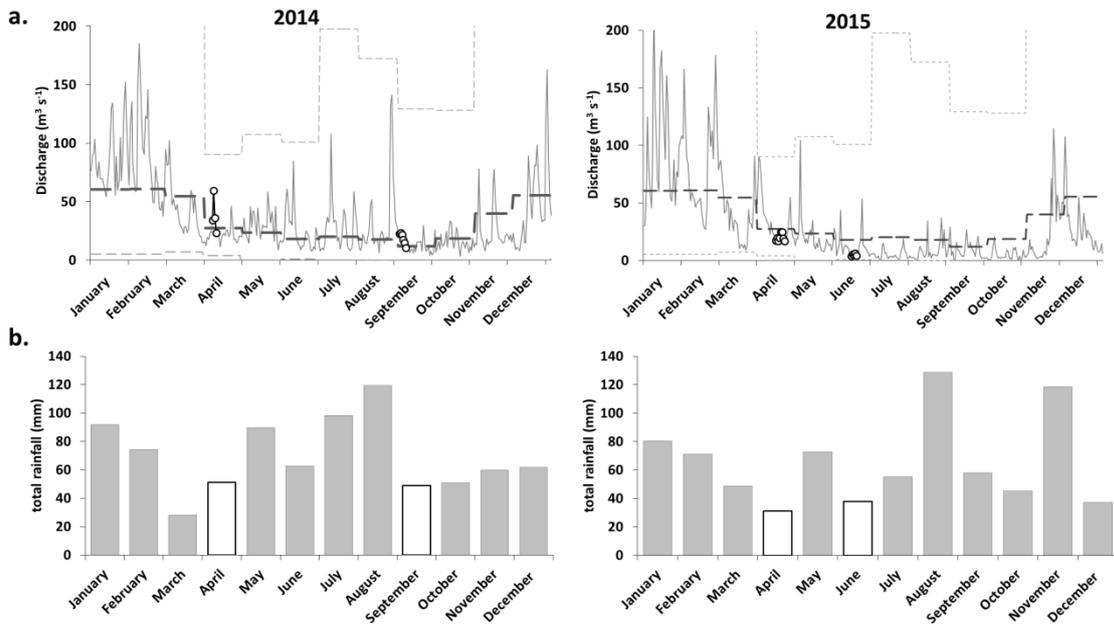


Figure 2: Hydrological conditions in the upper Scheldt basin: (a) Daily discharge at Melle (see Fig.1) in 2014 and 2015. Sampling periods correspond to the thicker white dots. Mean, minimal and maximal discharge calculated for each month over 10 years (2005-2015) are represented for each year by dotted lines. (b) Monthly cumulative rainfall at Lille in 2014 and 2015. Sampling months are indicated by the white bars.

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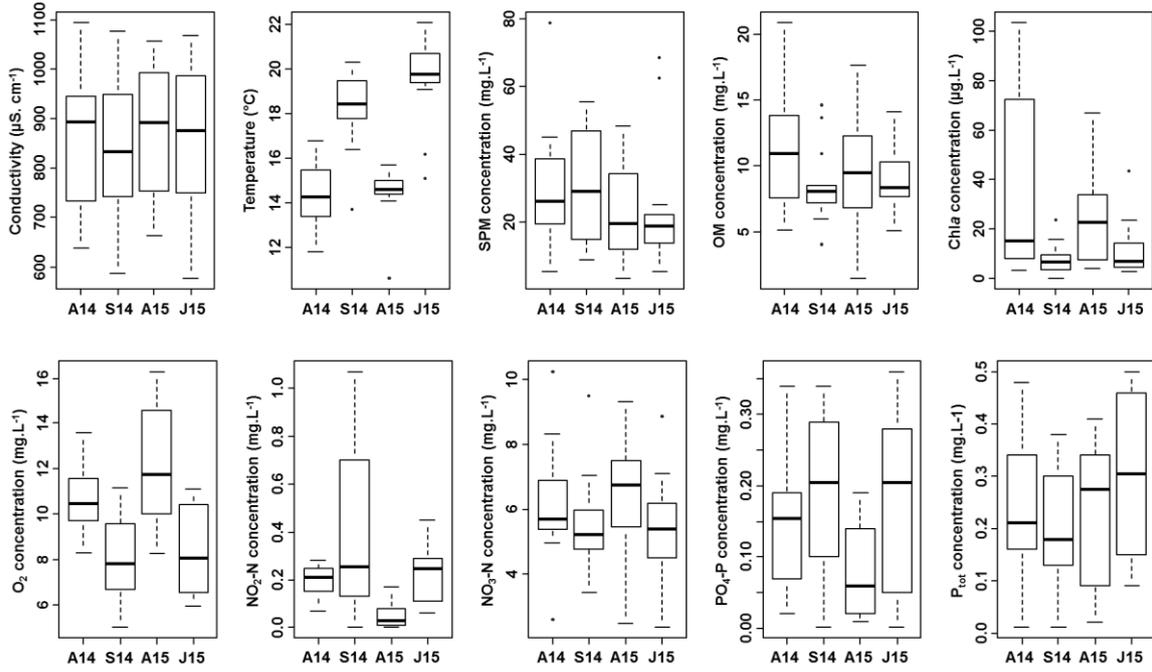


Fig. 3. Box-and-whisker plots describing the distribution of environmental conditions within sampling periods (A14: April 2014; S14: September 2014 ; A 15: April 2015 ; J15: June 2015).

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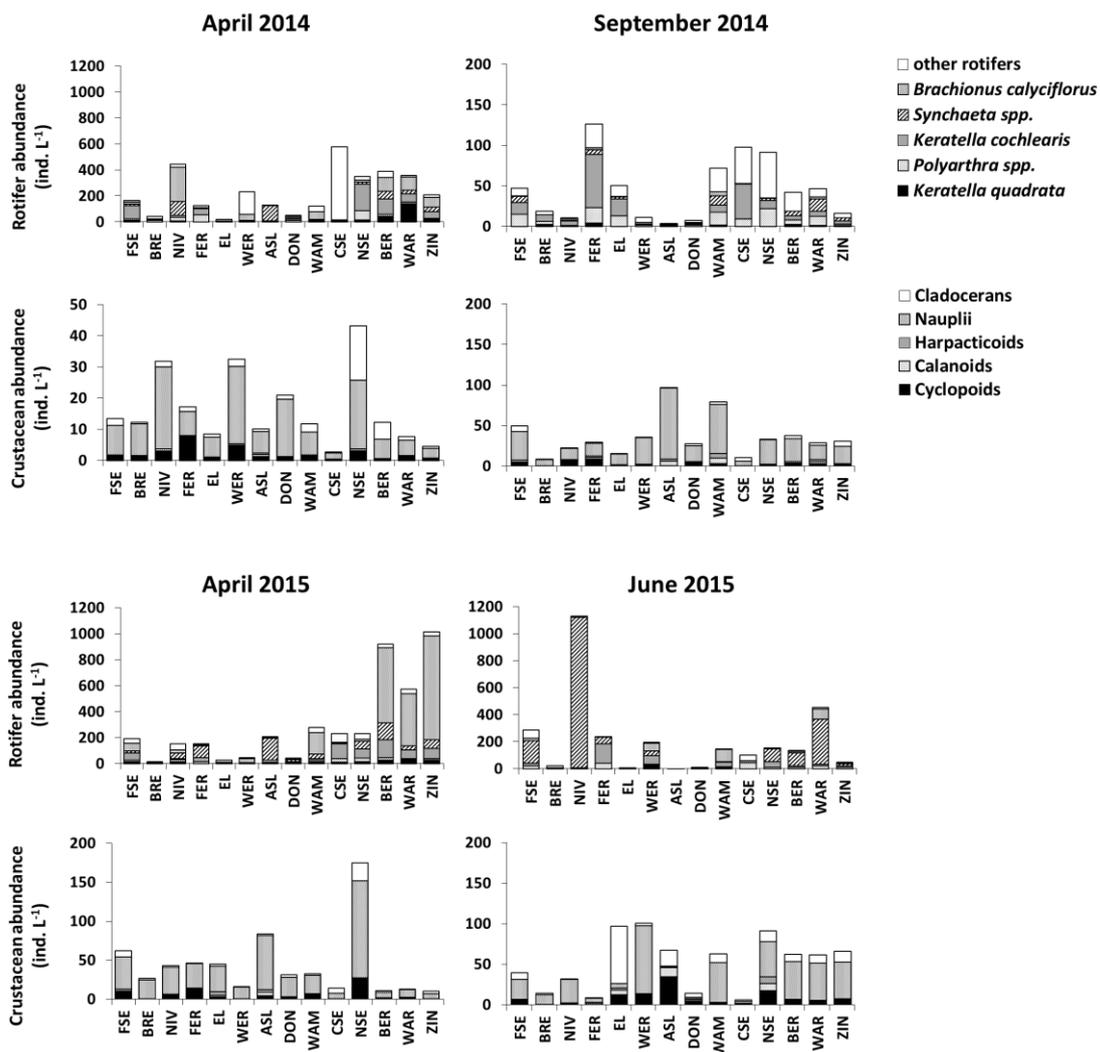


Figure 4: Abundance of rotifers (upper figure), and crustaceans (lower figure) for all sampling stations and at each sampling occasion. For readability reasons, Y-axis scales are different for rotifers and crustaceans.

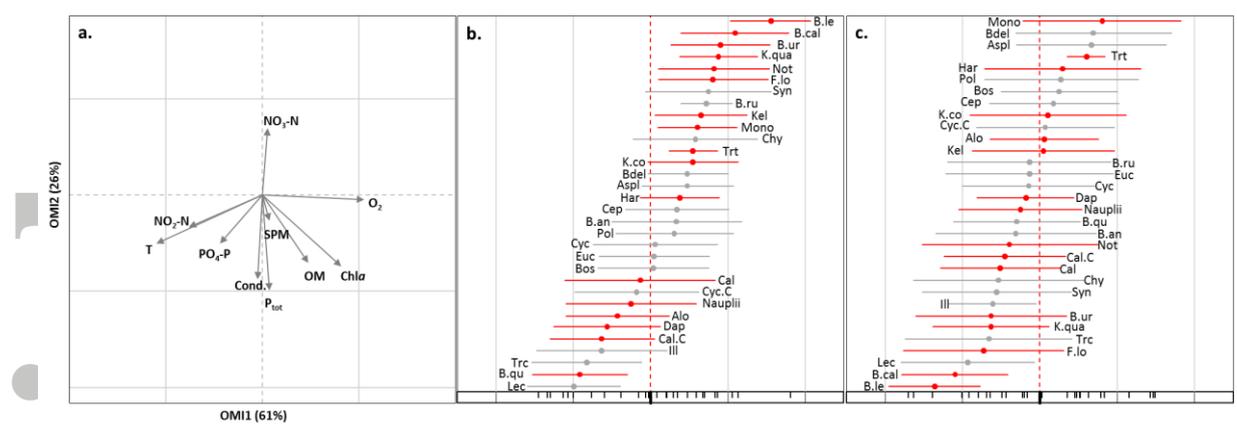


Figure 5: Results of the OMI analysis: Canonical weights of environmental (a) and taxa weighted average position (dots) and niche breadth (horizontal lines) along the first (b) and second (c) axis. Taxa in red presented significant deviation from mean conditions.

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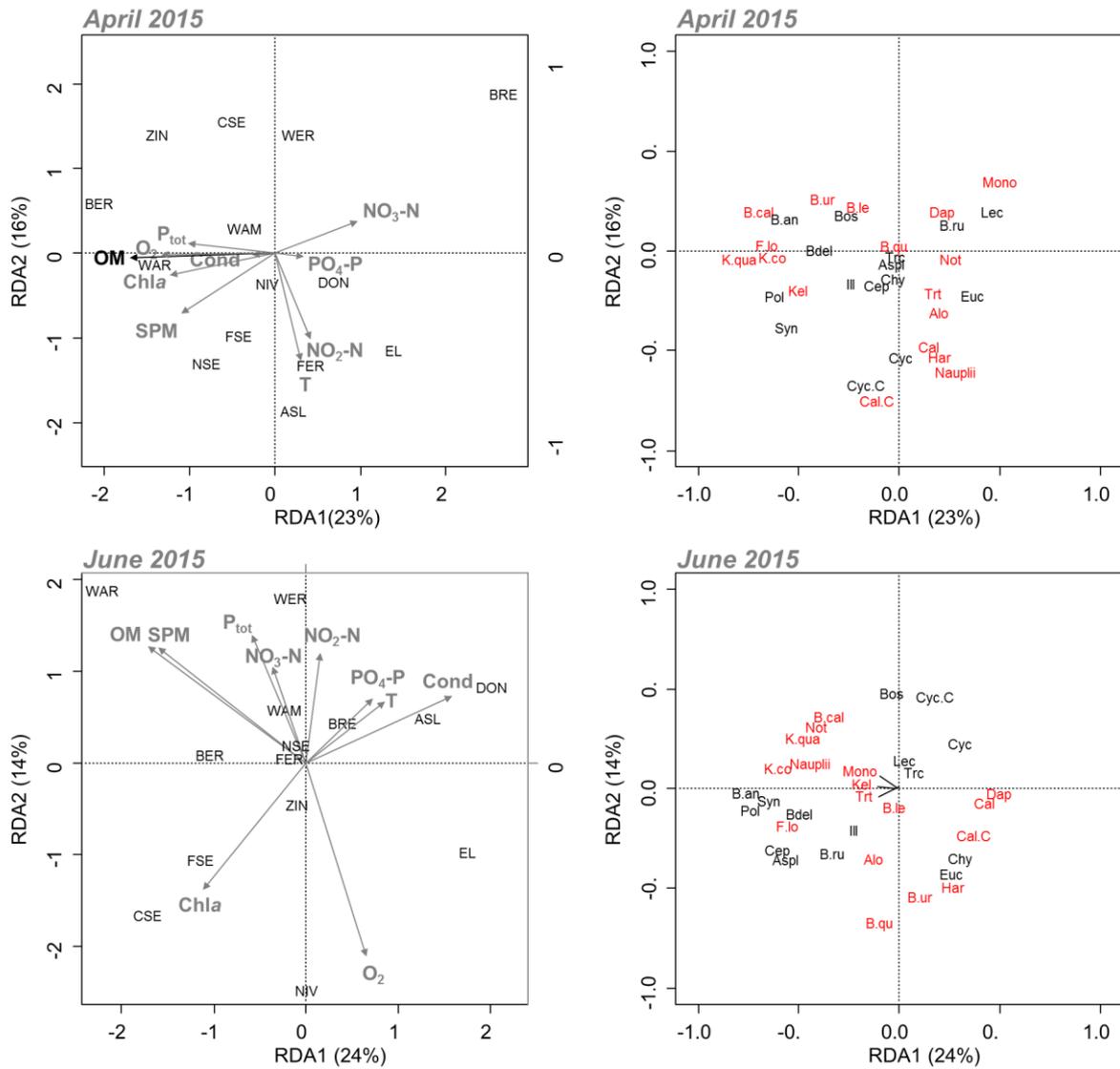


Figure 6: Ordinations of April 2015 and June 2015 RDA analyses: Axis 1 and 2 biplots for environmental parameters and sampling sites (left), and for taxa (right). For taxa abbreviations see Table 1. Taxa which showed significant marginality according to OMI analysis in 2014 are shown in red.

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