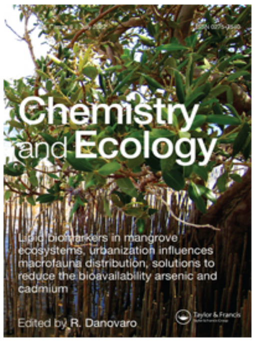

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Limited plankton community shifts over winter inundation events in Austral temporary wetlands

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ABSTRACT

Plankton are key components of wetland ecosystems, comprising different food web levels. In the present study, we assessed temporal plankton diversity patterns in three temporary wetland systems over winter inundation periods. We examined taxon relationships with environmental variability associated with wetland inundation phase changes, over six consecutive sampling events (i.e. T1–T6; or until the ponds dried). Fifty-nine phytoplankton species belonging to 36 genera were identified across the three wetlands, with 21, 22 and 19 taxa being identified for Wetlands 1, 2 and 3, respectively. Twenty-five zooplankton taxa were also identified across the three wetlands. Significant differences in environmental variables were found across sampling events. Ammonium, conductivity, dissolved oxygen, water temperature, turbidity, nitrates (NO_3–N) and zooplankton abundances were identified as important variables structuring phytoplankton communities, whereas, NO_3–N, phosphates and chlorophyll-*a* concentration were identified as important environmental variables for zooplankton. No significant differences were, however, observed in plankton community structure over time or among wetlands. Accordingly, hydroperiod phases did not have any significant influence on the plankton taxa richness in this study, in contrast to other seasons in the region and other parts of the world. The present study highlights that where temporary wetlands are characterised by both summer and winter inundation events, community succession dynamics may be seasonally distinct and require sampling in both periods to fully understand propagule and emergent community dynamics.

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1. Introduction

Temporary wetland systems are widespread in subtropical and arid regions [1]. These environments are characterised by their temporary inundation with water, and are integral

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components of many terrestrial landscapes, supporting biodiversity and sustainable livelihoods [2–5]. As in most aquatic environments, planktonic and benthic components comprise much of the base of the food web in these ecosystems. However, finer-scale community succession dynamics are poorly described for these systems. As a result, drivers of primary and secondary productivity dynamics, and community phenology in relation to the variable stages of inundation are still poorly understood in certain regions.

Plankton components comprise different food web levels in aquatic ecosystems, including temporary wetlands [1,6,7]. Within wetland systems at smaller scales, plankton community patches with distinct life forms contribute to wider environmental heterogeneity and support other aquatic life [8]. Plankton taxa accordingly comprise a large diversity of ecological strategies that vary with wetland environmental conditions, i.e. from small, fast-growing phytoplankton taxa adapted to short hydroperiod phases, to large slow-growing organisms adapted to more stable conditions [9,10]. Temporary wetlands are, however, extreme environments given that they do not permanently hold water. Planktonic species that occur in these environments are typically fast-growing, early maturing and are capable of diapause at some stage of their life cycle to facilitate survival through dry periods.

Given the nature of temporary wetlands, plankton have a particularly close relationship with the hydrological condition, and can also directly or indirectly affect overall community structure [11,12]. Hydroperiod, for example, is driven by the amount of water available, which has direct implications for physicochemical characteristics of the water, particularly for those components prone to dilution effects [13–15]. Turbidity, conductivity, pH and other water quality parameters are heavily affected by hydroperiod dynamics, with implications for resident and colonising biotic communities. Variation in the hydroperiod has also an important role in determining the relative importance of active dispersal, growth rates or desiccation-tolerance for survival [16–20]. Periods of high water can result in abiotic homogenisation or decreased beta diversity for certain taxonomic groups, as a consequence of higher connectivity between aquatic habitats [13]. Whereas zooplankton (i.e. particularly rotifers) alpha diversity increases at high or intermediate water levels [19,20], microcrustaceans (e.g. cladocerans, copepods, ostracods) can show an opposite pattern [21].

Temporary wetland studies are often equivocal in the relative importance of abiotic and biotic variables structuring plankton communities [16,17,19,20,22,23]. Despite their ecological importance and wetland management concern, research on plankton community structuring has been given little attention in Austral systems. The role of the season of inundation in structuring community succession dynamics is especially underexplored. In certain regions, temporary wetlands can fill in either summer or winter months, but phenological dynamics associated with different seasons have been unexamined. Most regional temporary wetland assessments have been conducted in warmer sub-tropical environments, marked by seasons characterised by rainfall dynamics (e.g. summer rainfall) [24–27]. Although evidence supports the fundamental role of dynamic water levels (i.e. hydroperiod) in wetland diversity distribution, little is known about seasonal hydroperiod effects on plankton communities, particularly in winter. Such investigations are not only relevant for regions that historically receive both winter and summer rainfall, but have implications for other regions projected to experience shifting rainfall conditions associated with climate change.

Plankton diversity spatial patterns in the current study were addressed based on a taxonomical approach, and by assessing the taxon relationships with environmental variability associated with hydroperiod changes during a winter inundation event. Studying the plankton communities in temporary wetland systems can provide insights into community- and organismal-level responses to hydroperiod phases, and consequent biodiversity dynamics [16,17]. The current study used Austral wetlands in a semi-arid region to: (i) investigate whether the diversity of phytoplankton and zooplankton differs among wetlands and over hydroperiod, and (ii) determine the main zooplankton diversity of wetlands. This was done during winter inundation events. We hypothesised that community succession patterns in plankton community composition would be low over the hydroperiod phases, characterised by a lack of hexapod colonisation. As such, we hypothesised that the plankton community would comprise the bulk of the food web, with strong coupling between phytoplankton and zooplankton irrespective of hydroperiod phase (filling, intermediate and desiccation).

2. Materials and methods

2.1. Study sites

The study was conducted between 2 August and 5 September 2016 in three temporary wetlands over the course of their entire winter inundation event. The temporary wetlands (i.e. Wetland 1 (−33.283660, 26.490212), 2 (−33.284102, 26.488651), and 3 (−33.250715, 26.436976)) were situated near the town of Makhanda (formerly Grahamstown) in the south-eastern temperate region of South Africa (Figure 1). Hydroperiods in these endorheic temporary wetlands are thought to be driven by direct rainfall dynamics. As such, hydroperiod phases are highly variable and determined by the amount of rainfall in the small catchment areas around the wetlands [28,29]. The region has mean winter and summer daily temperatures of 12.3°C and 20.3°C, respectively. The mean annual rainfall is approximately 680 mm and is evenly distributed over the entire region [30]. Sampling was conducted at six discrete time periods from three sites over the course of each wetland’s winter inundation event (or until they completely dried). The first sampling event took place on 2 August 2016 (T1), one week after a large rainfall event that partially filled the dry wetlands during to the prevailing drought (i.e. ongoing from year 2015 to present) conditions in the region, with sampling events two (T2), three (T3), four (T4), five (T5) and six (T6) being conducted on 8, 15, 22, 29 August and 2 September 2016, respectively as the wetlands slowly dried out. Within 2.5 weeks of the first sampling event, Wetland 1 dried up, followed by Wetland 2 between weeks 4 and 5, and finally, Wetland 3 dried after week 6.

2.2. Environmental variables

Portable CyberScan Series 600 probes (Eutech Instruments, Singapore) were used to measure dissolved oxygen (DO), total dissolved solids (TDS), conductivity, pH, salinity and water temperature from three random locations within each wetland per sampling event. Water depth at the deepest point of each wetland was measured using the graduated rod. Furthermore, 500 mL water samples ($n = 3$) were collected and placed on ice for

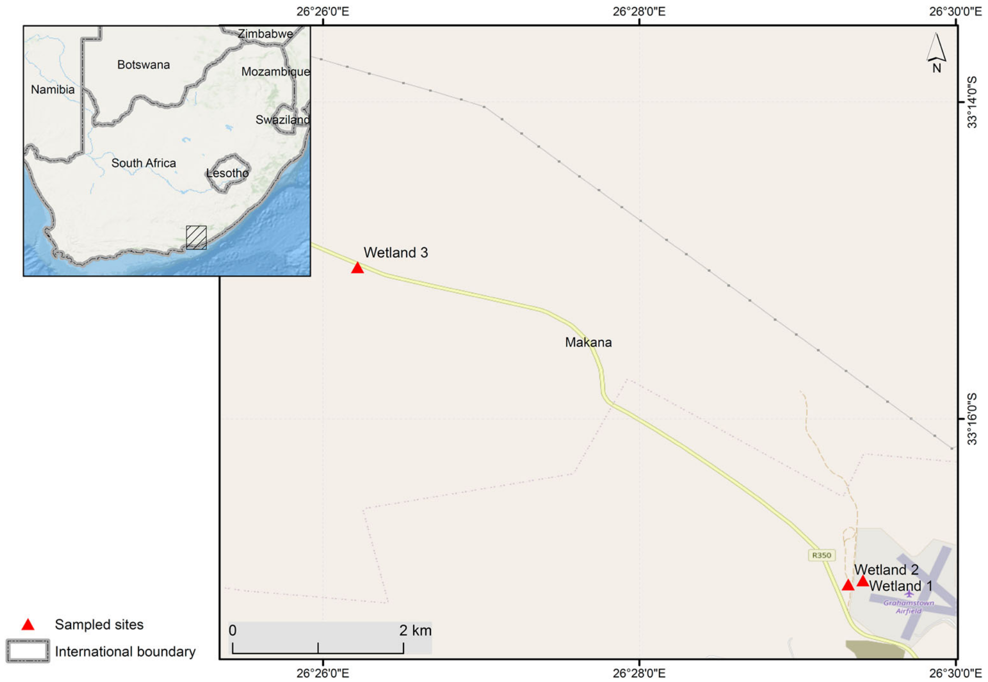

Figure 1. Location of the three study wetlands near the town of Makhanda, Eastern Cape Province of South Africa.

later determination of nutrient (ammonium (NH_4^+), nitrates (NO_3–N), phosphates (PO_4^{3-})) concentrations in the laboratory using a HI 83203 multi-parameter bench photometer (Hanna Instruments Inc., Rhode Island). Ammonium was analysed using the Nessler colorimetric method (HANNA HI93715-01 method; photometer range of 0–10 mg L^{-1} ± 0.05 mg L^{-1} accuracy as NH_4^+), nitrate using the cadmium reduction colorimetric determination of nitrate as nitrogen (HANNA HI93728-01 method; photometer range of 0–50 mg L^{-1}, ± 0.5 mg L^{-1} accuracy as NO_3–N) and phosphates using an adaptation of the ascorbic acid method (HANNA HI93713-01 method; photometer range of 0–30 mg L^{-1}, ± 1 mg L^{-1} accuracy as PO_4^{3-}). Water for nutrient determination was vacuum filtered through 0.7 µm glass fibre filters. Size fractionated chlorophyll-*a* (chl-*a*; microphytoplankton – 20 µm nylon filter mesh size, nanophytoplankton – 2 µm cellulose membrane filter mesh size, picophytoplankton – 0.7 µm glass fibre filter mesh size) concentrations were determined using a Turner 10 AU fluorometer according to Froneman [31].

2.3. Plankton collection

Horizontal phytoplankton tows were performed at each site and sampling event using a 32 cm diameter, 20 µm mesh plankton net for 3 mins for each wetland and sampling event, and fixed in Lugol's iodine solution. The volume of sampled water that passed through the net was then estimated by $V = (\prod r^2 d)/K$, where V = volume of water filtered by the plankton net, r = radius of the mouth of the net, d = distance of the net pulled through and K is the proportion of net under water. Sampling was conducted by the same personnel at each site to ensure that the total volume sampled was comparable. After two days, the undisturbed phytoplankton samples were concentrated by decanting the supernatant, taking care not to disturb the settled phytoplankton material at the bottom. The remaining precipitate was then vigorously mixed and phytoplankton taxa were identified according to the Utermöhl method [32] under a phase-contrast light Olympus microscope. All phytoplankton were identified to genus and/or species level according to John et al. [33].

Zooplankton were also collected by towing a 32 cm diameter, 63 μm mesh size plankton net horizontally through the water column approximately 1–2 cm from the bottom for 3 mins at each site and sampling event. The samples were preserved in 70% ethanol for later processing in the laboratory under a dissecting microscope. All zooplankton were identified to the lowest taxonomic resolution using keys by Day et al. [34,35], Fernando [36] and Suárez–Morales et al. [37].

2.4. Data analysis

A measure of phytoplankton and zooplankton community species turnover, corresponding to the internal heterogeneity within each ‘wetland community’ i.e. the Whittaker β-diversity (or intra-habitat diversity) was calculated. This index may be calculated as $\beta W = \gamma/\text{mean } \alpha$ [38]. A PERMANOVA was conducted to test for significant differences in selected environmental variables, phytoplankton and zooplankton community data among temporary wetlands (1, 2, 3) and sampling times (T1–T6). To assess how the environmental and biological parameters grouped according to wetland and sampling times, a cluster analysis and group average method were performed using PRIMER v6 add-on package PERMANOVA + [39]. Using Euclidean distance similarity, cluster analysis was employed for measured environmental variables. For phytoplankton and zooplankton, separate cluster analyses, using Bray Curtis distance similarities were constructed. A two-way ANOVA analysis using SPSS version 16.0 for Windows software [40] was performed to assess differences in environmental variables using wetlands and sampling times as factors. Diversity indices (i.e. Simpsons, Shannon–Weiner), species richness and evenness were calculated using the whole dataset of phytoplankton and zooplankton taxa in PAST version 2.0 [41].

The relationships between biotic (i.e. phytoplankton, zooplankton) relative abundances and environmental variables along the three wetlands over time were explored using the unimodal Canonical Correspondence Analysis (CCA – phytoplankton) and constrained linear Redundancy Analysis (RDA – zooplankton) methods. The CCA and RDA methods were based on significant ($p < 0.05$) forward-selected environmental variables using 9999 Monte Carlo Permutations [42]. To eliminate the influence of extreme values on ordination scores, phytoplankton and zooplankton taxa abundances were square-root transformed, whereas environmental variables were log ($x + 1$) transformed, with the exception of pH, before analysis.

3. Results

3.1. Environmental variables

Significant differences in environmental variables across sampling events (PERMANOVA, Pseudo-F = 45.798, $p = 0.0001$) and wetlands (PERMANOVA, Pseudo-F = 62.815, $p = 0.0001$), as well as a significant wetland × time interaction (PERMANOVA, Pseudo-F =

Table 1. Two-way ANOVA results for environmental variables across the different wetlands over the hydroperiod phases.

	Time		Wetland		Time × Wetland	
Variable	F	*P*	F	*P*	F	*p*
Temperature	435.04	<0.001	578.55	<0.001	318.47	<0.001
Conductivity	147.79	<0.001	267.13	<0.001	23.48	<0.001
DO	20.49	<0.001	15.00	<0.001	3.23	0.030
Turbidity	35.22	<0.001	914.12	<0.001	60.72	<0.001
pH	73.08	<0.001	77.91	<0.001	29.75	<0.001
Salinity	217.99	<0.001	364.37	<0.001	58.92	<0.001
TDS	135.64	<0.001	140.54	<0.001	54.85	<0.001
Water depth	39.80	<0.001	14.49	<0.001	21.35	<0.001
Ammonium (NH_4^+)	15.23	<0.001	11.57	<0.001	0.81	0.531
Nitrate (NO_3–N)	24.97	<0.001	86.75	<0.001	14.74	<0.001
Phosphate (PO_4^{3-})	63.08	<0.001	18.94	<0.001	18.07	<0.001
Secchi depth	41.73	<0.001	17.51	<0.001	22.42	<0.001

7.486, $p = 0.0001$), were observed. Particularly, in Wetland 1, levels in most environmental variables increased from T1 to T2 before the wetlands dried out, with a similar pattern also being observed for Wetland 2 from T1 to T4 (Table S1). However, water depth and Secchi disk decreased over the course of the inundation event in both wetlands. In Wetland 2, NH_4^+ and NO_3–N did not show any clear patterns. In Wetland 3, water temperature, conductivity, salinity, TDS and NH_4^+ increased from T1 to T6, with DO, turbidity, water depth, NO_3–N and PO_4^{3-} decreasing over the course of the inundation event (Table S1). Using two-way ANOVA, significant differences were observed for time ($p < 0.05$) and wetlands ($p < 0.05$) for all environmental variables (Table 1).

The clustering was based on similarities in environmental variables for the three study wetlands. Cluster analysis showed three groups, with *Group 1* containing Wetland 3

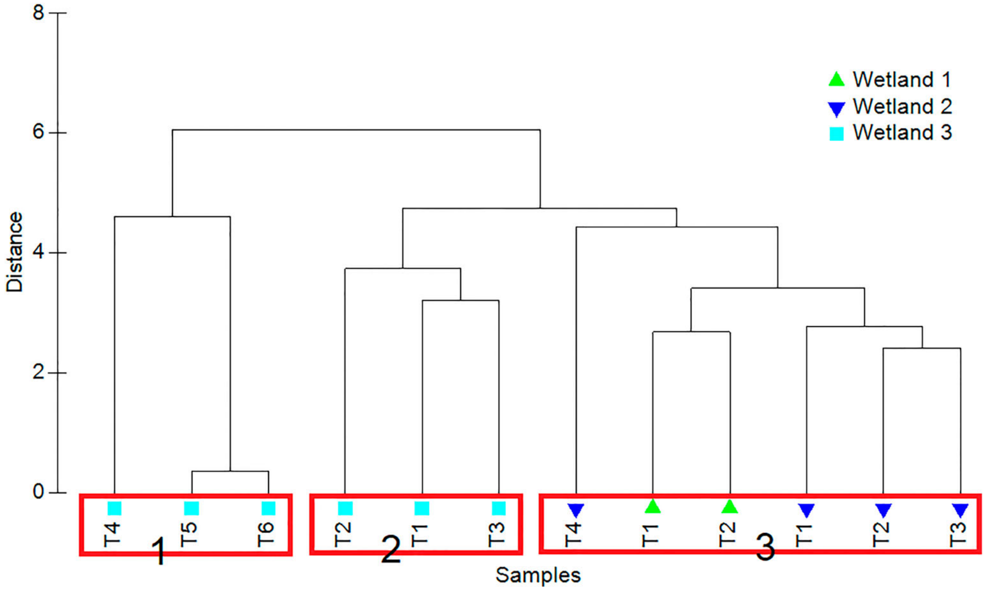

Figure 2. Cluster analysis of environmental variables from three study wetlands near the town of Makhanda over the hydroperiod phases (T1–T6). Red boxes comprise significantly similar community groups.

during T4–T6 sampling times, *Group 2* having Wetland 3 at T1–T3 sampling times, and *Group 3* containing the Wetlands 1 and 2 at all sampling times (Figure 2).

The total chl-*a* concentration was generally high in Wetland 2 (mean range 1.2–100.9 mg m^{-3}) and low in Wetland 3 (range 0.8–4.9 mg m^{-3}; Figure 3(a,c,e)). Total chl-*a* concentration was found to significantly differ among wetlands (ANOVA, $F = 3.22$, $p = 0.023$) and over time (ANOVA, $F = 3.50$, $p = 0.046$), with Tukey's post-hoc analysis indicating significant differences ($p = 0.020$) between Wetland 2 and Wetland 3. Wetland 1 was dominated by nanophytoplankton, with macrophytoplankton increasing from 2% (T1) to 25.1% (T2; Figure 3(b)). Nanophytoplankton also dominated Wetland 2 at T1 (55.6%) and T2 (57.6%), with picophytoplankton being the second most dominant i.e. T1 (41.3%) and T2 (41.5%). However, at T3 and T4 picophytoplankton dominated in Wetland 2 (Figure 3(d)), exceeding nanophytoplankton after T1 and T2. For Wetland 3, picophytoplankton was generally the most abundant group in T1 (49.9%), T2 (56.5%), T4 (56.2%) and T5 (48.9%), while nanophytoplankton slightly dominated in T3 (49.1%) and T6 (41.5%) (Figure 3(f)).

3.2. Phytoplankton

Fifty-nine species belonging to 36 genera were identified across the three wetlands, with 21, 22 and 19 taxa being identified for Wetlands 1, 2 and 3, respectively (Table S2). The highest species richness was observed in Wetland 2 and Wetland 3, ranging from 13 to 22 (mean 18.5) and 15–19 (mean 17.2), respectively. Phytoplankton community structure was largely spatio-temporally similar, as it was found to not be significantly different among wetlands (PERMANOVA, Pseudo-$F = 0.943$, $p = 0.505$) or over time (PERMANOVA, Pseudo-$F = 0.871$, $p = 0.637$). Phytoplankton diversity indices in Wetland 1 decreased from T1 to T2, with Wetland 2 and Wetland 3 having variable patterns over time (Table S2). No significant differences (Kruskal–Wallis, $p > 0.05$) were observed in phytoplankton diversity indices for wetlands and time. The corresponding Whittaker β-diversity values for phytoplankton taxa in wetlands 1, 2 and 3 were 2.59, 2.21 and 2.52, respectively.

Cluster analysis indicated two groups: *Group 1* consisted of Wetland 3 (T2 and T4) and *Group 2* had all other wetlands sampling times (Figure 4). *Group 1* was mostly characterised and dominated by *Closterium* sp., *Epithemia adnata*, *Euglena velata*, *Gomphonema venusta* and *Fragilaria crotonensis*, whereas, *Group 2* was characterised by *Teilingia granulata*, *Staurastrum chaetoceros*, *Anabaena* sp., *Cyclotella* sp., *Merismopedia* sp., *Navicula cryptocephala*, *Nitzschia acicularis*, *Chroococcus* sp., *Achnanthes* sp., and *Lepocinclis fusiformis* (Table S2).

3.3. Zooplankton

No significant differences were observed in zooplankton community structure among wetlands (PERMANOVA, Pseudo-$F = 0.794$, $p = 0.608$) or over time (PERMANOVA, Pseudo-$F = 1.338$, $p = 0.265$). Twenty-five zooplankton taxa were identified, with Cladocera resting eggs (i.e. ephippium) and nauplii also being identified for selected times (Table S3). Nine Rotifera, 5 Copepoda, 4 Cladocera and 2 Branchiopoda, including 1 of each of the Amoeba, Prostigmata, Nematoda and Ostracoda groups, were found. Mean

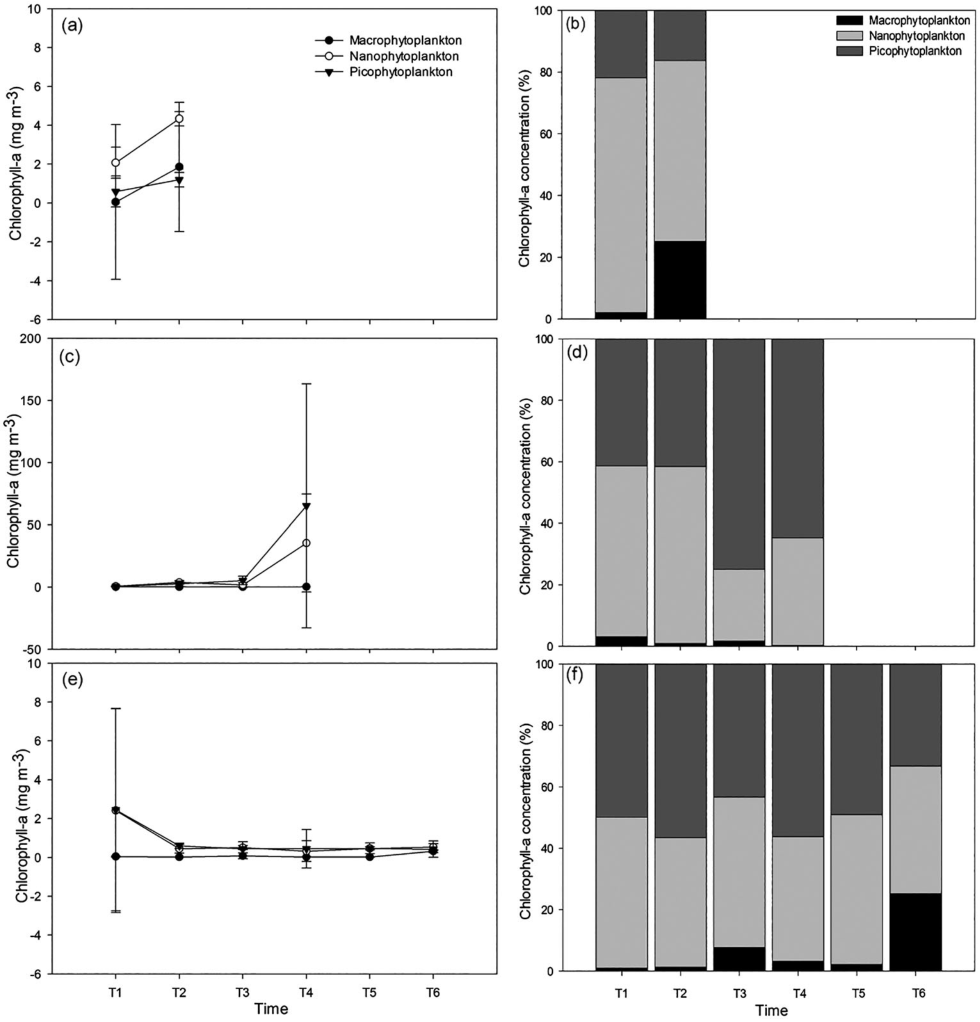

Figure 3. Size-fractionated chlorophyll-*a* (a,c,e) concentrations (± standard error; *note differences in scale*) and (b, d, f) proportions among the three wetlands (Wetland 1 (a, b); Wetland 2 (c, d), Wetland 3 (e, f)) over time (T1–6) in a warm temperate Austral system over the hydroperiod phases.

taxa richness (mean range 7–7.6), Shannon–Weiner (mean range 1.61–1.72), Simpson (mean range 0.74–0.79) and evenness (mean range 0.72–0.80) diversity indices were similar among wetlands. Variable patterns were observed in the diversity indices over time for Wetlands 2 and 3, whereas for Wetland 1 the zooplankton taxa decreased (Table S3). No significant differences (Kruskal–Wallis, $p > 0.05$) were observed in zooplankton diversity indices for wetlands and time. The corresponding Whittaker β-diversity values for zooplankton taxa in Wetlands 1, 2 and 3 were 2.71, 2.47 and 2.39, respectively.

Based on cluster analysis, two groups were identified. *Group 1* consisted of Wetland 3 T2, Wetland 1 T1 and Wetland 2 T1 and T2, characterised by *Mesocyclops* sp., nauplii, *Diaphanosoma excisum*, Ostracoda, *Keratella* sp. and *Metadiaptomus capensis*. Whereas *Group 2* consisted of all the other sampling times for the three wetlands, which were

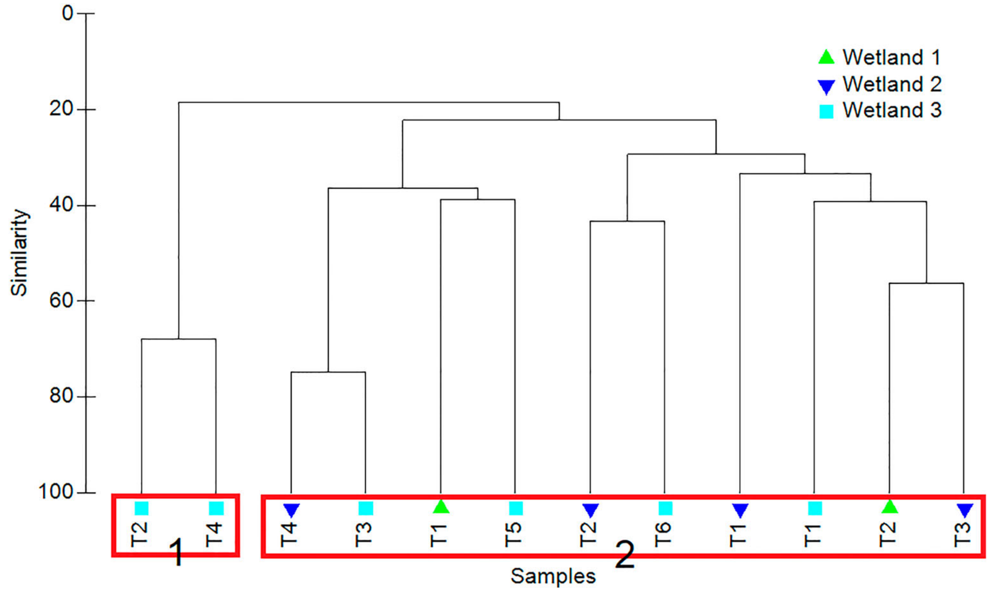

Figure 4. Cluster analysis of phytoplankton communities from three study wetlands near the town of Makhanda over the hydroperiod phases (T1–T6). Red boxes comprise significantly similar community groups.

characterised mostly by *Microcyclops* sp., *Paradiaptomus lamellatus*, *Lovenula raynerae* and *Daphnia lumholtzi* (Figure 5).

3.4. Relationships between plankton and environmental variables

Considering the relationship between phytoplankton communities and environmental variables, CCA axis 1 (22.5%) and 2 (44.1%) explained 63.6% of the total variation. Ammonium (NH_4^+), conductivity, DO, water temperature, turbidity, NO_3–N and zooplankton abundances were identified as important variables structuring phytoplankton communities (Figure 6(a)). Wetland 3 samples (T2–T5) were separated from the rest of the sites along CCA axis 1, with NH_4^+, conductivity, DO and NO_3–N being important environmental variables in structuring these sites, and were characterised by species such as *St. chaetoceros*, *Anabaena* sp., *Co. contractum*, *F. crotonensis* and *E. adnata* (Figure 6(a)). Wetland 1 (T1–T2), Wetland 2 (T1–T4) and Wetland 3 (T1, T6) were associated with water temperature, turbidity and zooplankton abundances, and characterised by species such as *Achnanthes* sp., *Cyclotella* sp., *Merismopedia* sp. and *N. cryptocephala* (Figure 6(a)).

Based on RDA analysis, the following environmental variables were found to have a significant (Monte Carlo test, $p < 0.05$) impact on zooplankton communities: NO_3–N, PO_4^{3-} and chlorophyll-*a* concentration. The first two axes of the species-environmental variables plot accounted for 41.3% of the total variation in the zooplankton community, with RDA axis 1 and 2 explaining 24.1% and 17.2% of the zooplankton taxa variation due to the measured environmental variables, respectively (Figure 6(b)). The RDA axis 1 separated the sites according to wetlands, with Wetland 3 (T1, T3–T6) and Wetland 2 (T4) being

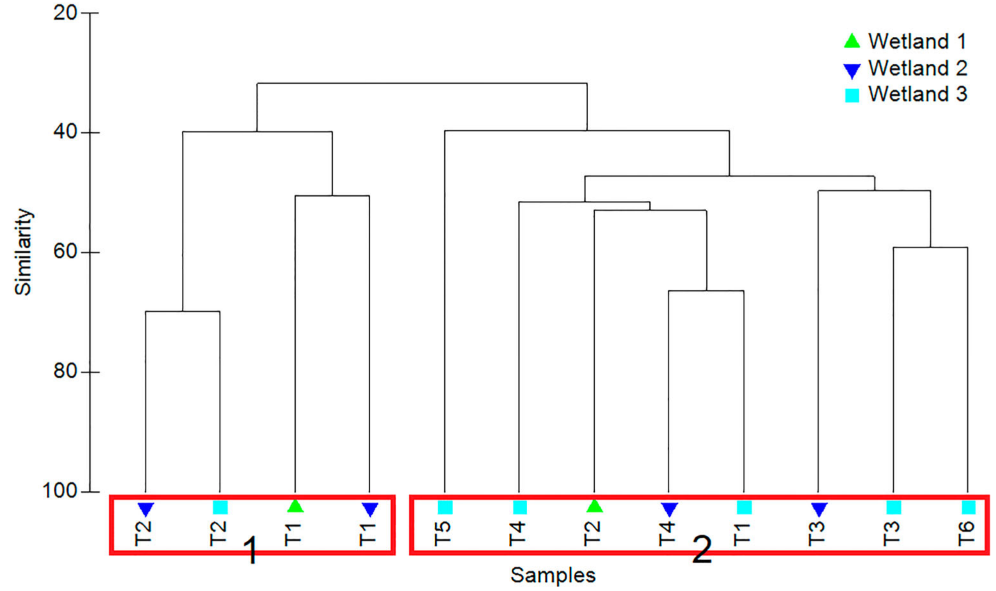

Figure 5. Cluster analysis of zooplankton communities from three study wetlands near the town of Makhanda over the hydroperiod phases (T1–T6). Red boxes comprise significantly similar community groups.

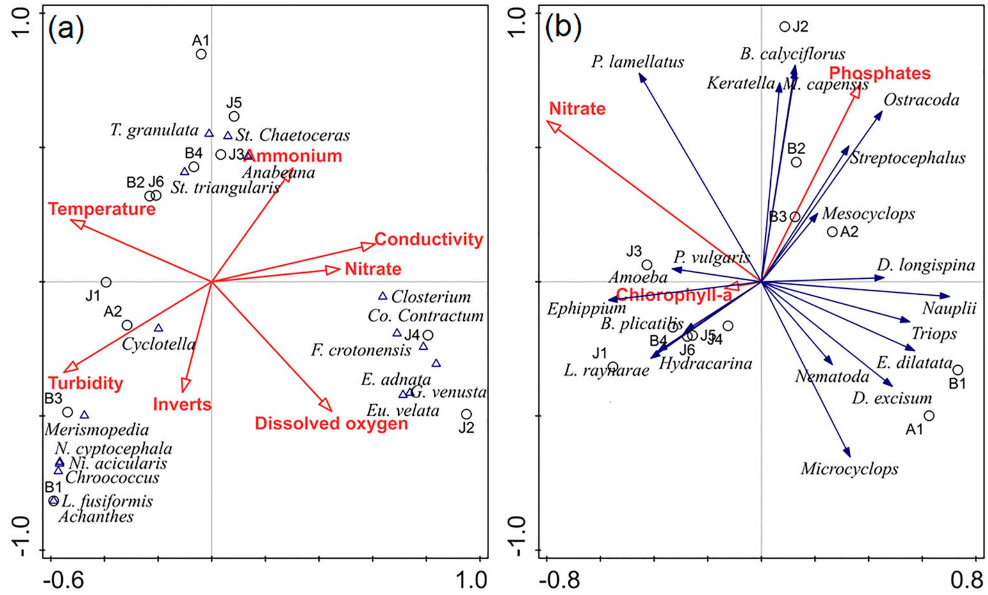

Figure 6. (a) Canonical correspondence analysis ordination biplot of phytoplankton taxa and (b) redundancy analysis ordination biplot of zooplankton taxa associated with significant environmental variables collected among the three wetlands throughout the study sampling times. Abbreviations: A1 (T1)–A2 (T2): Wetland 1; B1 (T1)–B4 (T4): Wetland 2; J1 (T1)–J6 (T6): Wetland 3, nitrate – NO_3–N; phosphates – PO_4^{3-}; ammonium – NH_4^+.

separated from the rest of sampling times/wetlands and being dominated by *L. raynerae*, *P. vulgaris*, Hydracarina and Amoeba. These sites were structured mostly by chlorophyll-*a* and NO_3–N concentration, whereas, Wetland 1 (T1, T2) and Wetland 2 (T1–T3) and Wetland 3 were separated by the *x*-axis from the rest of the sites (Figure 6(b)).

4. Discussion

Species diversity within temporary wetland ecosystems is affected by abiotic and biotic variables and processes operating at multiple spatial and temporal scales. However, such investigations within particular climate types and biogeographic regions are lacking [15,18]. The current study aimed to investigate temporal plankton diversity trends over inundation events in three proximal wetlands and potentially identify temporo-spatial drivers of community dynamics. We observed that plankton community structure was not significantly different among wetlands and over time, therefore showing no clear spatial or temporal structuring.

There was rapid wetland colonisation by emerging, internally recruited invertebrates immediately after the first inundations with water. Only four Cladocera species were identified in the current study. In comparison to other studies, the Cladocera richness was low [13,29,43,44]. It is important to note that The wetlands differed temporally, however, in terms of Cladocera richness, with *Daphnia excisum* being found only in Wetland 1 and the inundation events being relatively short in this system (as low as two weeks in one system). Most of the Cladocera taxa observed are common in both permanent and temporary wetland systems, with the exception of *Daphnia magna*. Two copepod species (i.e. *Lovenula raynerae*, *Paradiaptomus lamellatus*) have been found to be the most dominant species in wetlands of the Makhanda region (TD, *personal observation*) [29]. There was, however, poor immigration by semi-aquatic hexapods, in contrast to what has been observed in previous studies from the region when conducted in summer [29,45,46], and other regions [47]. These other studies were, however, also characterised by longer hydroperiods. Indeed, hydroperiod length in temporary wetlands has been identified as a major driver of community succession through immigrating macroinvertebrate taxa [47]. Similarly, Wilcox [48] highlighted that large, long-lived wetland systems generally attract larger numbers of macroinvertebrates compared to smaller wetland systems. While in the present study shorter hydroperiods were observed, it is also imperative to note that the study was conducted during the colder winter month of August, a time of year insect activity is characteristically low in the region.

The Whittaker β-diversity indices showed relatively intermediary values, with McCune et al. [49] highlighting that Whittaker β-diversity values of < 1 are low and > 5 high. Both the phytoplankton (Whittaker β-diversity range 2.21–2.59) and zooplankton (Whittaker β-diversity range 2.39–2.71) data suggested a relatively homogenous distribution within sites. This observation was similar to Fonseca et al. [43], who observed that lower or intermediary Whittaker β-diversity values were common across regions, and two potentially countervailing factors – dispersal and selection – of microorganisms are predominant. Plankton communities tend to have wider geographic ranges (i.e. often considered to be cosmopolitan) compared to large taxa such as vertebrates and plants, due to their ability to produce resting stages which facilitate their dispersal by animals or wind, as well as potentially poorly constrained biogeography historically. Given their geographic proximity, such uniformity among sites is not unexpected given the ready dispersal of biological material among discrete systems, and particularly for adjacent systems in Wetlands 1 and 2. Ephemeral wetland systems play an important role for macroinvertebrate taxa, acting as growth and reproduction sites due to abundance of food and low predation pressure [13], but are highly varied in their hydroperiod duration.

Several environmental factors were found to be important in driving the variation in plankton diversity or community composition of wetlands (see Figure 6), suggesting that plankton communities did not show a strong spatial structuring and niche-based control (i.e. instead of showing a strong structuring by environmental variables). The ordination analyses highlighted environmental variables accounted for approximately 63.6% and 41.3% of phytoplankton and invertebrate community structuring, respectively. Other studies [13,44] have also shown high variation in environmental variable structuring with respect to phytoplankton and zooplankton taxa. Therefore, the prevalence of wetland taxa or species with a low dispersal probability could be a reason for the importance of local environmental variables. Zooplankton taxa are passively dispersed and depend largely on diapause to override unfavourable environmental conditions and only emerge when conditions are favourable [50]. We note that for the zooplankton community, there were no marked differences between the filling, intermediate and desiccation phases, and this is in contrast to several studies, such as Gilbert et al. [51]. However, the contribution of the lack of hexapod colonisation to this observation, and seasonal hydroperiod dynamics, cannot be overlooked when making such comparisons. The Makhanda region is characterised by both winter and summer rainfall and summer hydroperiod community dynamics may be considerably different.

Based on the CCA analyses, phytoplankton community structure was significantly influenced by water temperature, nutrients (i.e. NH_4^+, NO_3–N), conductivity, DO, turbidity and zooplankton abundances. Water temperature has been highlighted in several studies [13,44,52] to significantly influence phytoplankton reproduction and growth via the regulation of their physiological mechanisms. An increase in turbidity was found to have a significant effect on the phytoplankton community through increased nutrient availability, which could have been a result of bioturbation by benthic invertebrate taxa such as the *Triops* sp. and/or sediment particle resuspension during the wetland filling process, which was supported by the high nutrient concentrations recorded in the wetlands [51]. The effect of increased turbidity can also cause a marked reduction in light penetration, which severely affects aquatic ecosystem primary productivity, and this could help explain the low phytoplankton biomass observed in the study. It should be noted that phytoplankton biomass is principally dependent on nutrient levels together with other environmental variables [44,51,52]. Potapova and Charles [53] and Mangadze et al. [54] highlighted that conductivity levels explained a significant amount of phytoplankton variation, similar to our study.

Zooplankton communities were found to be significantly influenced by nutrients (i.e. PO_4^{3-}, NO_3–N) and chl-*a* concentration according to the RDA analysis. Norlan et al. [55] highlighted that in wetland systems where zooplankton communities dominated, very low phytoplankton biomass (i.e. chl-*a* concentration) was recorded, and this might explain the low phytoplankton biomass observed during our study. There was exceptionally high chl-*a* concentration during the last sampling time (T4) for Wetland 2, which was attributed to an *Euglena* spp. algal bloom observed at the time of sampling and the absence of the larger Cladocera spp. which could have controlled the phytoplankton biomass. The presence of more predacious Paradiaptomidae copepods than grazer copepods could have influenced the biomass observed at T4.

Conclusions

This study highlights that in regions where temporary wetlands are characterised by both summer and winter inundation events, community succession dynamics may be distinct depending on the season of inundation. Phenological dynamics observed in other studies conducted in summer, may not be applicable for winter inundation events. The hydroperiod phase did not seem to have any significant influence on the plankton taxa richness in this study, in contrast to many other studies in the region and in other parts of the world. As such, there were no marked differences between the filling, intermediate and desiccation hydroperiod phases, as has been observed in many other temporary wetland studies. This suggests that regions that will experience shifting seasonal climatic conditions and rainfall dynamics may experience fundamental changes in phenological dynamics in temporary wetland ecosystems. This was presumably a result of the study being conducted primarily in a colder winter month, although the role of hydroperiod length cannot be overlooked.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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Permitting and ethics approval

Samples were collected under permit number CRO 43/16CR, issued by the Department of Economic Development, Environmental Affairs and Tourism. No ethical approval was required since research involved planktonic organisms only.

Data availability statement

The datasets generated and/or analysed during the current study are publicly available in the supplementary files.

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