Effects of Inundation on Water Chemistry and Invertebrates in Floodplain Wetlands

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Abstract

Floodplain wetlands play a significant role in the storage of sediment and water and support high levels of nutrient cycling that lead to substantial primary production and high biodiversity. This storage, cycling and production system is driven by intermittent inundation. In regulated rivers the link between channel flows and floodplain inundation is often impacted with reduction in the frequency and duration of inundation. Managed floodplain inundation is us being used as a tool to help restore floodplain wetland processes and rehabilitate river systems. However, the use of managed water for the environment remains contentious and it is important to quantify the outcomes of re-introducing water to floodplain wetland systems. We examined the effects of environmental floodplain watering on water chemistry and three groups of invertebrates, including benthic and pelagic invertebrates and macroinvertebrates, in wetlands on the Gwydir River system in the north of the Murray-Darling Basin. We hypothesised that wetlands that were inundated for longer periods of time would have altered water chemistry and support a greater richness and abundance of invertebrates, thus altering their assemblage structures. Water chemistry and the assemblage structure of all three invertebrate groups in the wetlands was significantly influenced by the time since connection (TSC) to their respective rivers and therefore inundation period. The microinvertebrate abundance of was positively associated with TSC, but not macroinvertebrates. This suggests that the duration of connection between the channel and floodplain is important in maintaining the ecology and food webs in the wetlands.

Introduction

Wetlands occupying river floodplains play a significant role in nutrient cycling and the storage of sediment and water in the landscape. They also support substantial primary production and high biodiversity, which is sustained by intermittent inundation (Junk et al., 1989; Tockner et al., 2000). Following inundation of dry floodplain wetlands nutrients are released from sediments stimulating primary and secondary production (Lake et al., 2006; McInerney et al., 2017). Invertebrates occupy an important role in floodplain wetlands linking aquatic and terrestrial carbon sources and nutrients to higher trophic levels such as fish and waterbirds (Boon & Shiel, 1990; Lindholm & Hessen, 2007). Following the inundation of a wetland invertebrate density and biomass can increase through emergence from egg banks, aerial colonisation and recruitment through breeding (Jenkins & Boulton, 2003; Siziba et al., 2013). High productivity and invertebrate abundance can be achieved within weeks following inundation (Lindholm & Hessen, 2007; Growns et al., 2020a). The link between inundation and increased productivity exists for both microinvertebrates (defined here as animals belonging to the Orders Cladocera and Ostracoda, Subclass Copepoda and Phylum Rotifera) and macroinvertebrates (all other invertebrate aquatic taxa) (Angeler et al., 2000; Baber et al., 2004; James et al., 2008; Chessman & Hardwick, 2014; Balkic et al., 2018).

Biotic and environmental factors influence the succession of different microinvertebrate groups following inundation (Dias et al., 2016). In relatively undisturbed wetlands rotifers generally increase in abundance immediately following inundation but decline in response to increases in the abundance of cladocerans...
Rotifer declines maybe due to either competition for food resources or direct physical interference of the cladocerans (Gilbert & Slemberger, 1985; Gilbert, 1988; Dias et al., 2016). Lindholm and Hessen (2007) noted a temporal succession of three species of cladocerans following flooding but then rapid declines in each species and suggested overgrazing of phytoplankton was the cause. However, in disturbed wetlands following increases in turbidity or turbulence rotifers can become dominant (Gabaldon et al., 2017; Zhou et al., 2018). A generalised temporal succession does not exist for macroinvertebrate (Batzer, 2013). However, successions have been demonstrated (Moorhead et al., 1998; Jeffries, 2011). It has been suggested that the colonisation traits of different groups is likely to influence the sequence of arriving taxa. For example, diapausi ng groups such as certain molluscs can colonise quickly while groups that rely on aerial colonisation, such as Odonata, may establish later (Datry et al., 2017; Pires et al., 2019).

Increasing demand for freshwater during the last century has severely affected wetland ecosystems to the point that they represent some of the most seriously degraded environments in the world (Lemly et al., 2000; Vorosmarty et al., 2010; Davidson et al., 2018). Most of the world’s river systems and associated wetlands are now subject to human impacts (Tonkin et al., 2019). Since the mid 20th century, rivers and their wetlands have experienced significant pressure due to changes in hydrology, habitat degradation, and loss of biodiversity (Prieditis, 1999; Masing et al., 2000; Tourenq et al., 2001). The degradation of wetlands requires increasingly sophisticated approaches to the management of rivers that feed these ecosystems (Thompson et al., 2019). An important tool which has emerged has been the delivery and management of environmental flows to restore, protect or enhance environmental outcomes both in-channel and in associated floodplains (Arthington et al., 2018; Whipple & Viers, 2019). While there has been considerable progress in the science underpinning environmental flows there remain substantial gaps in our understanding (Poff & Zimmerman, 2010; Davies et al., 2014). The sharing of limited water resources between anthropogenic users and biodiversity conservation remains a contentious issue (Graham, 2009). It is thus important that the benefits of increased allocation of water to wetland flooding is further documented, so that the benefits can be considered against the potentially associated socioeconomic costs (Chessman & Hardwick, 2014).

In this study we examined the effects of environmental flows on water chemistry and three groups of invertebrates, including benthic and pelagic invertebrates and macroinvertebrates, in wetlands on the Gwydir River system in the north of the Murray-Darling Basin. We hypothesised that wetlands that were inundated for longer periods of time would have altered water chemistry and support a greater richness and abundance of invertebrates, thus altering their assemblage structures. In addition, we also hypothesised that invertebrates would follow clear temporal successional pathways following inundation.

### Methods

#### Study area
We tested our hypotheses in the Gwydir Wetlands State Conservation Area which covers an area of 9712 ha some of which has been listed under the RAMSAR Convention since 1999 (Fig. 1). All major tributaries join the Gwydir River upstream of Moree, while downstream the channels form an inland delta of extensive floodplains. The river divides into two watercourses comprising the Gingham Watercourse to the north and the Lower Gwydir River to the south. Apart from infrequent larger flooding events, the majority of the water in the wetlands is delivered from managed water released from an upstream impoundment (Copeton Dam). The remainder of the water comes from smaller flows from minor upstream unregulated tributaries.

The Gwydir River downstream of Copeton Dam is one of the most flow-altered rivers in the northern Murray-Darling region (Sheldon et al., 2000; Growns, 2008). One of the main impacts of the damming has been the reduction in major flood events that would otherwise inundate extensive areas of the Lower Gwydir floodplain (Bennett & Green, 1993; Wilson et al., 2009). Prior to the building of the Dam, the wetland areas were flooded 17% of the time over 93 years, but now flooding occurs only 5% of the time due to diversions and a 70% reduction in flows large enough to reach the Gwydir wetlands (Keyte, 1994; Kingsford, 2000).

Since the stabilisation of the Raft, a natural accumulation of felled timber and sediments which effectively dams the river approximately 20km west of Moree, more water is naturally diverted into the Gingham Channel (Pietsch, 2006; Environment Climate Change and Water, 2011), in which channel depth and width and estimated bankfull discharge are smaller than on the Lower Gwydir Channel (Department of Water and Energy 2007).

**Sampling and processing**

Invertebrates and water chemistry were sampled seasonally on twenty sampling occasions between 2014 and 2019 at four sites from each wetland system (Fig. 1). However, not all sites could be sampled on those twenty sampling occasions as sometimes they were dry.

Benthic microinvertebrates were haphazardly sampled by following the methods of King (2004) by combing five cores (50 mm diameter x 20 mm long with 250 mL volume of water) from immediately above the sediment surface for each site. Replicates were separated by a minimum of 20 lineal metres. The composite sample was allowed to settle for a minimum of 15 minutes and then the supernatant was poured through a 63 µm sieve. The retained sample was washed into a labelled jar and stored in ethanol (70% w/v with Rose Bengal stain) until laboratory analysis. Pelagic microinvertebrates were sampled by haphazardly taking 10 replicates of 10 L of the water column at each site. Samples were poured through a 63 µm mesh net and preserved in ethanol (70% w/v with Rose Bengal stain) until laboratory analysis.

Macroinvertebrates were collected following the Standard Operating Procedures in Hale et al. (2014). Briefly, sampling involved sweeping a 250 um mesh net through water for a length of 10 m and preserving the sample in ethanol.
For processing, microinvertebrate samples were sieved through a 250 and 63 µm mesh. All invertebrates collected in the 250 µm sieve were identified and counted. Invertebrates in the smaller sieve size were subsampled if very abundant by taking 1 ml aliquots from the material suspended in 20 ml of ethanol and identifying and counting until a minimum of 100 animals had been counted. Each subsample was sorted on a Bogorov tray (Bogorov, 1927) under a stereo microscope at up to 400x magnification. Abundances were then calculated by multiplying the subsample abundance by the reciprocal of the proportion of sample processed. Cladocerans and Rotifera were identified to family level, ostracods to class, copepods, conchostracans and arachnids to order, tardigrades and nematodes to phyla and notostracans to species.

Macroinvertebrate samples were processed by putting each sample through a 1 mm and 250 µm sieve. The 1 mm fraction was picked for all animals and identified. The 250 µm fraction was subsampled using a Marchant (1989) type subsampler. This involved placing the fraction in container with 100 cells, filling with water and vigorously shaking until the contents were evenly distributed. The contents of individual cells were pipetted into a Bogorov tray and the animals counted and identified until either 100 animals had been counted or 20% of the sample processed. Macroinvertebrates were identified to Family level with the exception of Chironomidae that were identified to subfamily level, Arachnida to Class and Oligochaeta to sub-order.

Eleven water chemistry variables indicators were measured at the time of invertebrate sampling using the methods outlined in Commonwealth of Australia (2019). Briefly, in-situ spot measurements of water column temperature (TEMP), pH, turbidity (TURB), specific conductivity (Cond) and dissolved oxygen (DO) were taken using an electronic meter. Water nutrient samples including dissolved organic carbon (DOC), total nitrogen (TN), total phosphorus (TP), nitrate-nitrite (NOx) and soluble reactive phosphorus (SRP) were collected and analysed following standard methods. Chlorophyll a (Chla) was sampled by filtering as much water as possible (100–1,000 mL) through a glass microfiber grade GF/C filter and analysed using spectrophotometry.

**Hydrology**

Water levels at the sites in the wetlands were not recorded, however, the length of time the wetlands were inundated or time since connection (TSC) between wetland sites and the corresponding river channels was estimated using data from the nearest Water NSW telemetered gauge (Fig. 1). Specifically, for sites on the Gingham Watercourse connection was identified when the discharge at Gingham @ Tillaloo gauge exceeded 10 ML/d or when the Gingham @ Waterhole gauge water level began to increase. In the Lower Gwydir River sites connection were identified when Gwydir @ Millewa gauge water levels rose above 1.5m.

**Data analysis**

The influence of TSC, wetland and site within wetland on water chemistry and the richness, abundance and assemblage structure of benthic and pelagic microinvertebrates and macroinvertebrates was tested using permutational analysis of variance (PERMANOVA) (Anderson, 2001). To examine a potential
temporal succession of different microinvertebrate groups with TSC we also tested its influence on the percentage abundances of Cladocera, Copepoda and Rotifera. Wetland areas were defined as fixed factors, site was defined as a random factor nested within wetland. TSC was fitted as a covariate. All data were log transformed prior to analysis and the water chemistry variables normalised. Bray Curtis dissimilarity was calculated between samples for the assemblage structure and Euclidean distance for the water chemistry data and univariate biotic variables and used as input into the PERMANOVA analyses. Probabilities of differences between factors were calculated following 9999 permutations of the data. Where significant relationships between TSC and water chemistry variables and invertebrate assemblages were detected we displayed the spatial variation among samples using non-metric multidimensional scaling ordinations (nMDS) (Clarke, 1993). Water chemistry variables or taxa that had correlations of greater than 0.5 with either axis were displayed as vectors in two dimensional ordination space. Significant relationships with univariate variables were display in scatterplots and trend lines fitted with linear regression. All analyses were conducted in the PERMANOVA + add on to PRIMER (Anderson et al., 2008).

Results

A total of 734,528 benthic microinvertebrates from 38 taxa, 133,902 pelagic microinvertebrates from 40 taxa and 17,918 macroinvertebrates from 75 taxa were estimated from the collected samples. Time since inundation significantly explained between 1.2% and 4.5% of the variation in both water chemistry and invertebrate assemblage structure (Table 1). However, there was a significant interaction between TSC and wetland for water chemistry and the assemblage structure of both microinvertebrate groups. These interactions indicate that the response to TSC differed between wetlands. TSC explained more variation for these three variables for the Gingham wetland compared with the Lower Gwydir wetland (Table 2).
Table 1
Pseudo-F values and probabilities of different sources of variation on water chemistry and taxonomic richness, abundance and assemblage structure of three groups of wetland invertebrates. The amount of variation explained by significant sources of variation is indicated in parentheses.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Source of variation</th>
<th>Time since connection (TSC)</th>
<th>Wetland (W)</th>
<th>Site within W</th>
<th>TSC x W</th>
</tr>
</thead>
<tbody>
<tr>
<td>Water chemistry</td>
<td></td>
<td>2.3* (1.2%)</td>
<td>12.3***</td>
<td>ns</td>
<td>2.8** (9.2%)</td>
</tr>
<tr>
<td>Benthic microinvertebrate</td>
<td>assemblage</td>
<td>2.5* (1.8%)</td>
<td>ns</td>
<td>ns</td>
<td>2.6* (10.1%)</td>
</tr>
<tr>
<td></td>
<td>richness</td>
<td>7.3* (10.1%)</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>abundance</td>
<td>10.7** (15.3%)</td>
<td>ns</td>
<td>2.2*</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>% Cladocera</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>% Copepoda</td>
<td>8.0** (7.4%)</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>% Rotifera</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Pelagic microinvertebrate</td>
<td>assemblage</td>
<td>5.3*** (4.5%)</td>
<td>5.6*** (21.1%)</td>
<td>ns</td>
<td>2.3* (8.2%)</td>
</tr>
<tr>
<td></td>
<td>richness</td>
<td>ns</td>
<td>ns</td>
<td>4.4** (33.2%)</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>abundance</td>
<td>9.4** (11.8%)</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>% Cladocera</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>% Copepoda</td>
<td>9.5** (6.4%)</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>% Rotifera</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Macroinvertebrate</td>
<td>assemblage</td>
<td>2.7** (2.1%)</td>
<td>6.7*** (33.8%)</td>
<td>2.2*** (7.8%)</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>richness</td>
<td>ns</td>
<td>ns</td>
<td>5.7*** (30.7%)</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>abundance</td>
<td>ns</td>
<td>ns</td>
<td>4.3** (21.3%)</td>
<td>ns</td>
</tr>
</tbody>
</table>

* - p < 0.05, ** - p < 0.001, *** - p < 0.0001
Table 2
Pseudo-F values and probabilities of the influence of time since connection on water chemistry and assemblage structure of two microinvertebrate groups in different wetlands. The amount of variation explained by significant sources of variation is indicated in parentheses.

<table>
<thead>
<tr>
<th>Wetland</th>
<th>Variable</th>
<th>Gingham</th>
<th>Lower Gwydir</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Water chemistry</td>
<td>10.7*** (15.2%)</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>Benthic microinvertebrate assemblage</td>
<td>6.3*** (10.2%)</td>
<td>2.4* (6.3%)</td>
</tr>
<tr>
<td></td>
<td>Pelagic microinvertebrate assemblage</td>
<td>12.2*** (17.5%)</td>
<td>ns</td>
</tr>
</tbody>
</table>

* - p < 0.05, *** - p = 0.0001

Six water chemistry variables including COND, DO, pH, TURB, TN and TSS had vectors in ordination space lying in a similar direction to TSC suggesting they were positively associated with increased length of inundation (Fig. 2). In contrast, the vector of SRP lay in an opposite direction to the vector of TSC suggesting concentrations of this nutrient decreased with increased time since inundation. Four macroinvertebrate taxa including Hydrophilidae, Planorbidae, Dytiscidae and Coenagrionidae had vectors in ordination space lying in a similar direction as TSC. The direction of these vectors suggested that increased TSC had positive effects on some macroinvertebrate taxa thus altering assemblage structure. In contrast, there did not appear to be any macroinvertebrate taxa negatively affected by TSC. Five pelagic microinvertebrate taxa in the Gingham wetland including Brachionidae, Filiniidae, Asplanchnidae, Synchaetidae and Sididae had vectors lying in a similar direction as TSC indicating a positive influence. Similarly, four benthic microinvertebrate taxa in the Gingham wetland including Brachionidae, Synchaetidae, Filiniidae and Notommatidae had vectors in a similar direction as TSC. In the Lower Gwydir wetland TSC had positive associations with three taxa including Lecanidae, Cyclopoida and Euchlanidae.

TSC was significantly related to the abundance of both microinvertebrate groups, the taxonomic richness of benthic microinvertebrates and the percentage of Copepoda, explaining between 7.4% and 15.3% of the variation (Table 1). There were no significant interactions between TSC and wetland for these univariate indices suggesting the relationship was the same between wetlands. TSC had positive associations with the abundance of both microinvertebrate groups and richness of the benthos and negative relationships with the percentage of Copepoda (Fig. 3).

Discussion

Relationships between time since connection and water chemistry and invertebrates
Water chemistry and the assemblage structure of all three invertebrate groups in the wetlands was significantly influenced by the time since connection to their respective rivers and therefore inundation period. Water chemistry was affected by an increase in six variables, including the nutrient TN and a decrease in the nutrient SRP. Our observed increase in TN may be associated with its release from terrestrial litter accumulation over time (Baldwin & Mitchell, 2000; McInerney et al., 2017). An increase in TP may not have been documented here as SRP decreased presumably by uptake from aquatic plants. Changes in other water chemistry variables associated with the length of inundation have been demonstrated by other studies, however, the results are often inconsistent. For example, McInerney et al. (2017) showed a decrease in pH over time but Waterkeyn et al. (2008) showed an increase. Differences in the water chemistry changes between studies maybe due to underlying differences in geology, soil and vegetation.

We expected that the assemblage structure of all three invertebrate groups would change with increased inundation time due to increases in richness and abundance and successional change in taxa. Although assemblage structure changed only the abundances of the microinvertebrates increased with TSC. While this finding is consistent with a few studies (Sheldon et al., 2000; Puckridge et al., 2010), the lack of change in richness is in contrast with the majority of wetland/hydrological permanence studies (Rundle et al., 2002; Tarr et al., 2005; Hanson et al., 2009; Vanschoenwinkel et al., 2009; Hassall et al., 2011; Chessman & Hardwick, 2014). The differences between studies may be due to the differences between wetlands, such as depth, surface area or climate which may alter the effects of water regime or hydroperiod. As expected, the abundances of microinvertebrates increased with increasing TSC but we did not demonstrate increases in macroinvertebrates. It is unclear why there is a difference in response to TSC. However, the microinvertebrate groups feed directly on bacteria or algae which are likely to respond to changes in water chemistry with TSC, while macroinvertebrate taxa occupy a range of feeding strategies including predation, gathering, shredding, scraping and filtering (Merritt et al., 2019). Macroinvertebrate predators are known to structure local assemblages through prey depletion (Wallace & Webster, 1996; Downing, 2005). In lentic habitats, the effect of predators on prey assemblages may be heightened because prey emigration is limited (i.e., leaving the pool may lead to desiccation or terrestrial predation) (Washko & Bogan, 2019).

The response of water chemistry and the microinvertebrate assemblages to TSC differed between the two wetlands, the relationship being stronger in the Gingham wetland. Growns et al. (2020b) demonstrated that soil from the Gingham wetland produced a greater density and nutritional value of invertebrates compared with the Lower Gwydir wetland. They suggested that the differences between the wetlands was due to differences in water regime, with the Gingham system naturally receiving more water (Pietsch, 2006; Environment Climate Change and Water, 2011). It is possible that the stronger response of water chemistry and microinvertebrates to TSC in the Gingham wetland is due to it receiving more water. However, other factors may influence wetland invertebrates and chemistry, for example, wetland plant diversity can directly affect the occurrence and distribution of aquatic macroinvertebrates (Cheruvelil et al., 2002; Thomaz et al., 2008; Dibble & Thomaz, 2009).
Management implications

We have established a direct link between TSC and the water chemistry and invertebrate assemblages in the Gwydir wetlands, including the abundance of microinvertebrates. Our measure of water period, TSC, is an estimate of the length of time the river channels are connected to the wetlands. This suggests that the length of time river flows, including managed environmental flows occur at a certain river height is important in maintaining the ecology and food webs in the wetlands. It is unclear the optimal amount of time these types of flows should be provided, however, our results suggest the longer the TSC the greater the environmental benefits for aquatic invertebrates.

Other aspects of the water regime of wetlands include the frequency of flows, extent and depth and variability (Boulton et al., 2014). Further research is required to examine the relationships between these hydrological aspects and the ecology of the Gwydir wetlands to provide more management options to help maintain and restore their conservation values into the future.

Declarations

Acknowledgments

The New South Wales National Parks and Wildlife Service is thanked for providing approval to sample invertebrates in their National Parks and RAMSAR sites.

Data Availability Data collected as part of the Long Term Intervention Monitoring Program is available from the Australian Department of Agriculture, Water and Environment. Contact details are available from https://www.environment.gov.au/.

Code Availability Not applicable.

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Ethics Approval Not applicable.

Consent to Participate Not applicable.

Consent for Publication Not applicable.

Conflicts of Interest/Competing Interests The authors declare that they have no conflict of interest.

Authors contributions WT organised the field work, processed samples and identified the invertebrates. IG analysed the data and wrote the draft manuscript. MS calculated the hydrological variables and proof read the draft manuscript. DR received the funding for and managed the project. PF received the funding for the project and proof read the draft manuscript. All authors read and approved the final manuscript.
References


**Figures**
Figure 1

Map of the study area with sampling locations indicated by black circles. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.
Figure 2

Non-metric multidimensional ordinations of water chemistry and invertebrate assemblages significantly influenced by time since connection.
Figure 3

Scatterplots of invertebrate variables significantly associated with time since connection. The general trend is demonstrated by a line fitted by linear regression.