FLOOD PLAIN INFLUENCES ON METABOLIC ACTIVITY IN THE SOUTH AUSTRALIAN SECTION OF THE MURRAY RIVER DURING THE 2010/11 FLOOD

Roderick L Oliver and Zygmunt Lorenz

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The following Associate organisations contributed to this report:

Enquires should be addressed to: Goyder Institute for Water Research
Level 1, Torrens Building
220 Victoria Square, Adelaide, SA, 5000
tel: 08-8303 8952
e-mail: enquiries@goyderinstitute.org

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Executive summary

There are two broad sources of organic material that support the food webs of river ecosystems; internal supplies generated by the primary production of aquatic autotrophs (autochthonous sources), and external supplies of terrestrially produced organic material carried in from the surrounding catchment (allochthonous sources). The organic materials are delivered in many different forms each containing an array of organic compounds of different composition, energy content and nutrient status. The mix of organic materials supplied and their utilisation within the food web play an important role in determining the total biomass of secondary producers that can be supported, and the characteristics of the trophic links that underpin community structure and diversity. Understanding these interactions can help managers set flow and water quality targets for sustaining food webs of suitable composition to provide food resources to populations of fish and waterbirds that are of direct concern to the public.

Photosynthesis and respiration are the metabolic processes responsible for the formation and breakdown of organic material. The balance between photosynthesis and respiration within the river channel identifies the fluxes of energy through the entire channel food web. Environmental conditions influence river metabolism across a wide range of time scales from sub-daily changes in incident irradiance to inter-annual variations in weather patterns. Less well recorded are the decadal changes in response to droughts and floods, especially where flow is further modified by regulation as in the Murray River. This component of the Goyder Murray Flow Ecology project measured metabolic conditions in the Murray River channel in response to the 2010/11 drought-breaking flood.

Metabolism measurements have been made periodically along the Murray River channel since 1998 in order to quantify the effects of environmental conditions on gross primary production (*GP*), community respiration (*CR*) and net ecosystem production (*NP*). These estimates have been based on day-night changes in oxygen concentration measured continuously in the river over 24-36h periods. Metabolism measurements describe the quantity of utilisable organic carbon (food resources) supporting river channel food webs, the sources of supply, and the distribution of metabolic activity between compartments, such as planktonic versus benthic.

Prior to the flood the metabolic rates in the South Australian section of the Murray River were similar to those measured upstream at other sites along the river and they responded to changes in water velocity in similar ways. As the SA section of the river is comprised of an almost continuous series of weir pools metabolism was more variable than observed in flowing river reaches and small

negative *NP* values were common indicating that weir pool sites accumulated organic material either from upstream or from their local catchment. In flowing sections the rates of *GP* and *CR* were relatively small and closely balanced so that the negative *NP* rates were close to zero. Based on these characteristics it is considered that prior to the flood river metabolism in flowing sections was largely driven by phytoplankton photosynthesis and the respiratory breakdown of phytoplankton cells, but with a small external organic carbon contribution evident within the weir pools. This is consistent with patterns observed further upstream.

This situation changed dramatically in response to the flood. Planktonic *GP* remained at similar levels throughout whereas the open water *GP* was larger than the planktonic rates and on occasions larger than had previously been observed for open water measurements. These continuing and sometimes high rates of *GP* were unexpected because the poor light penetration and the increased water depth within the river channel during the flood were not supportive of high rates of photosynthesis. A detailed analysis of the oxygen measurements showed that the photosynthesis peaks in oxygen concentration were not being generated within the river channel but in the shallower waters of the floodplain. The oxygen signal was then transported into the river channel by the returning floodwaters and moved downstream with little further enhancement by photosynthesis, but with modification of the peaks due to respiration within the channel and gas exchange at the air-water interface. Travel time analyses of the oxygen peaks indicated that they were generated in two major floodplain areas, Chowilla and Barmera, with little influence observed from smaller floodplain areas in between. These findings indicate that significant photosynthesis is occurring on major floodplains but the transport of this production to the river channel depends on whether the photoautotrophic organisms are attached or not, and if grazers of attached forms are transported by the flood waters. Chlorophyll-a measurements on river samples indicated that the planktonic plant biomass was high, peaking at 85 mg m^{-3} chlorophyll-a and that phytoplankton growing in the flood waters were making a substantial contribution to the organic carbon load returning to the river.

The reduced oxygen concentrations that occur in rivers during floods are usually attributed to the respiratory metabolism of organic material transported from the floodplain back into the channel. The most active material is considered to be reactive dissolved organic carbon (DOC) as it is easily transported and its composition is more amenable to assimilation by microbial cells. In contrast, particulate organic carbon (POC) may be difficult to transport and less suitable for assimilation depending on particle size and composition. The compositional suitability of DOC and POC for metabolic breakdown is influenced by prior weathering and metabolism on the floodplain. Because respiration rates can vary greatly in response to the organic matter composition and the composition of the biotic community, loss rates preferably are measured *in situ.* Downstream

reductions in DOC concentration were analysed to estimate the rate of decline and this was attributed to respiratory breakdown. It was found that the rates of DOC decline accounted on average for 50% of the measured planktonic respiration rates. Planktonic respiration rates were four times higher during the flood than prior to the flood so the contribution from the respiratory breakdown of DOC was significant. However, the DOC respiration accounted for only 15% of the open water respiration rates with other planktonic respiration accounting for a further 15%. The remaining 70% of the open water respiration was attributed to non-planktonic sources.

The large proportion of the respiration associated with non-planktonic sources was unlikely to be due to the breakdown of carbon accumulated by attached phototrophs as conditions were unsuitable for photosynthesis during the flood period. Alternatively the organic carbon supply driving the non-planktonic respiration might be due to sedimentation of organic material entering the river from the floodplain, including phytoplankton growing in the flood waters or allochthonous organic carbon from the floodplain. However, it is also possible that there was a large non-planktonic respiratory activity on the floodplain and that oxygen depleted water was transported back to the river. Evidence for this floodplain link was the large reduction in the non-planktonic respiratory rates that occurred when receding flood waters disconnected from the floodplain.

On balance it is suspected that a large component of the respiratory reduction in oxygen that was observed in the river channel during the flood was due to oxygen drawdown in water moving across the floodplain and returning to the river. This corresponds with the observations that significant proportions of the primary production were occurring in waters on the floodplain. The significance of this respiratory activity to the river channel food webs then depends on whether the organisms utilising the organic materials are transported to the channel. If the respiratory activity was due to processes occurring on the floodplain, perhaps driven by metabolism in the flooded soils drawing down oxygen in the overlying flood waters, then this component of the respiration would not necessarily represent a corresponding source of organic carbon to the river channel and its importance to river food chains will depend on other forms of connection. Such connections include the movement of river organisms onto the floodplain during floods, later wash-in by rainfall runoff, or the occurrence of follow up floods. Under these situations, estimating the food resources delivered to rivers during floods based solely on the decline in oxygen concentration within the river channel would over estimate the supply of organic carbon to the system.

Following the major flood the rates of metabolism declined to levels similar to those prior to the flood. There were slightly increased respiration rates evident during the final two samplings that suggested a small store of residual organic carbon had been transported into the river by the flood

but this was smaller than expected and its role is yet to be fully explored. However, this increased activity might also have been due to a small secondary flood peak which further perturbed the system close to the final project measurements. Continuing measurements would have been necessary to monitor the return of the river to pre-flood conditions.

Identification of the sites of major floodwater metabolism is important information for the management of the system. In the South Australian section of the Murray River the two large floodplain areas of Chowilla and Barmera were identified as major sites for phytoplankton photosynthetic production. These floodplains were also important sources of organic matter and suspected to be major sites of oxygen depletion and so likely to represent a site of major food supply where organic material is transformed into microbial biota. The extent to which the organisms growing on the floodplain represent food resources for the food webs of the river channel is more difficult to quantify. Part of the phytoplankton biomass that formed on the floodplain was transferred to the river channel. The contribution to primary production of attached photoautotrophs on the floodplain has not been determined from the data but is expected to be relatively small because of the flood conditions. The transfer of heterotrophic organisms growing on the floodplain into the river channel could not be assessed from this data but other projects have collected information that could provide information on this question and further joint analyses are warranted. In either case it is unlikely that all of the potential food resources formed on the floodplain will be transferred back to the river channel. This supports the need for access to the floodplain by organisms during times of flood to maximise opportunities to harvest food resources associated with the floodplain. Overall the results highlight the importance of the dynamic connection between the river and floodplain and especially connections to significant flooded areas.

Introduction

Background

There are two broad sources of organic material that support riverine food webs; internal supplies generated by the primary production of aquatic autotrophs (autochthonous sources), and external supplies of terrestrially produced organic material carried in from the surrounding catchment (allochthonous sources), (Vannote et al. 1980; Thorp and Delong 1994; Oliver and Merrick 2006). External material is transported into the river by rainfall runoff, flooding, wind dispersal and by direct litter fall. The organic materials are delivered in many different forms; as intact organisms, as non-living particulate organic matter (detritus), and as dissolved organic matter. Each of these categories contains an array of organic compounds of different composition, energy content and nutrient status. The mix of organic materials supplied and their utilisation within the foodweb determines the relative roles of herbivores, carnivores, detritivores and decomposers in system metabolism (Moore *et al*. 2004; Dodds and Cole 2007). Consequently, the quantities and types of organic material that are derived from the different internal and external sources play an important role in determining the total biomass of secondary producers that can be supported, and the characteristics of the trophic links that underpin community structure and diversity (Lefevre et al. 2008; Hampton et al. 2006). The food chains that form the trophic connections dictate the energy flow pathways through the food webs and influence populations of higher organisms (such as fish and waterbirds) that are reliant on the aquatic ecosystems for food supplies. These higher organisms are generally more valued by the community and their population distributions are used by natural resource managers to assess ecosystem condition and to set management targets. However, management of the conditions that support these populations requires an understanding of their requirements for food resources and of the trophic links and energy supplies that underpin the production and delivery of their food supplies.

In floodplain-rivers like the Murray, it is expected that river-channel food resources will be subsidised by organic materials transported from the floodplain (Vannote *et al*. 1980; Oliver and Merrick 2006). However, like many rivers that are regulated to supply irrigation, industrial and urban users, flooding in the Murray River has been significantly reduced and the channel increasingly isolated from the floodplain (Maheshwari *et al*. 1995). Despite recognition of this disconnection, the effects on the supplies of organic material and on metabolic activity within river channels have only recently been investigated in any detail in Australian rivers (Oliver and Merrick 2006; Howitt et al 2007; Burford et al 2008; Oliver and Lorenz 2010). Little is known of the importance of different sources of organic material to river channel energy supplies and the effects of hydrological

fluctuations in changing the sources of supply, or the influence of these changes on river food web structures that are critical in transferring energy to fish and bird populations (Bunn *et al*. 2003; Vink *et al.* 2005; Doi 2009). Consequently the requirements for energy capture, transformation and transfer to meet natural resource management targets are largely unknown and rarely considered in analyses of environmental flow allocations or hydrological delivery patterns.

Metabolism measurements have been made periodically along the Murray River channel since 1998 in order to quantify the effects of environmental conditions on river metabolism (Oliver and Merrick 2006; Oliver and Lorenz 2010). Environmental conditions influence river metabolism across a wide range of time scales from sub-daily changes in incident irradiance to inter-annual variations in weather patterns. Less well recorded are the decadal changes in response to droughts and floods. During the period 2000-2010 the Murray Darling Basin suffered a severe drought (Murphy and Timbal 2008) and the metabolism measurements during this period were strongly influenced by the regulated flows within the river channel (Oliver and Merrick 2006; Oliver and Lorenz 2010). The drought ended in the spring and summer of 2010-2011 with widespread heavy rainfall throughout the Murray Darling Basin resulting in an extended period of flooding along the Murray River. This event presented a rare opportunity to assess the ecological responses of the river system to flooding after an extended dry period. In response the Goyder Institute in South Australia, along with collaborating organisations (CSIRO, SARDI, University of Adelaide and Flinders University) developed the Murray Flood Ecology Project to gather information on these responses both on the flood plain and in the river channel. This section of the project investigated the changes in river metabolism associated with the flood flows.

River metabolism

Photosynthesis and respiration are the metabolic processes responsible for the formation and breakdown of organic material. The balance between photosynthesis and respiration within the river channel identifies the fluxes of energy through the entire channel food web (Odum 1956). Gross primary production (*GP*) is the total carbon fixed into organic material by photosynthesis, and in the river channel contributions can come from phytoplankton, biofilms and submerged macrophytes. Community respiration (*CR*) is the loss of carbon due to the metabolism of organic materials to provide cellular energy and nutrients, and all living organisms within the river channel contribute to this process. The respiration of organic material provides the energy and structural components for organisms to grow and a comparison of respiration rates between sites indicates the extent to which organic material is being utilised. An increased respiration rate suggests a larger utilisation and incorporation of organic carbon into cellular material (Dodds and Cole 2007). However this correspondence is not straightforward as different organic compounds are respired in different ways

and release different amounts of energy. Also different compounds provide different mixtures of elements and carbon depending on their composition and this will influence the growth responses of consumers depending on their nutrient requirements. Despite these difficulties, broad scale comparisons can be made between respiration rates to provide an overview of relative energy utilisation between sites and over time (Dodds and Cole 2007).

The difference between *GP* and *CR* is the net ecosystem production (*NP*) and this describes the balance between the production and breakdown of organic material. In general when *NP* is positive then the organic content has increased, and if it is negative then the organic carbon content has decreased. However, in an interconnected and flowing river system changes in *NP* may not be due solely to processes at the sampling site. Organic materials produced by primary production in one part of the river can be transported by flow and respired in a different part, or may even be exported totally from the river system to coastal waters before being respired. As a result, the respiratory activity at a sampling site can exceed *GP* if the quantity of metabolisable organic carbon is subsidised by transported supplies, either from inside or outside of the river channel. Conversely, if organic material formed through primary production is exported from a measuring site prior to respiratory breakdown, then the resulting positive *NP* will not necessarily indicate an accumulation of organic material. To address these issues, measurements need to be made at sufficient spatial and temporal scales to assess the influences of imports, exports and transport, and to capture the changing balance in *NP* in response to daily, seasonal and annual alterations in factors such as light, flow and temperature.

Objectives

Previous analyses of measurements along the Murray River have demonstrated the major role of phytoplankton in river metabolism during periods of regulated flows, with only small contributions from attached organisms such as macrophytes and benthic biota (Oliver and Merrick 2006; Oliver and Lorenz 2010). This situation was expected to change in response to flooding as the flux of external organic carbon carried in by flood waters from the floodplain causes substantial changes in the immediately metabolisable food supplies within the river channel resulting in increased respiration rates. The load of organic carbon was expected to be especially large after the period of prolonged drought during which organic carbon accumulated on the floodplain. Such conditions can lead to “blackwater” events where the delivery of large loads of organic carbon from the floodplain to the river channel reduces oxygen concentrations to very low levels that are detrimental to a range of biota including fish, invertebrates and amphibians (Howitt et al 2007). It was also expected that less reactive forms of particulate organic material carried into the channel might be stored as residual organic carbon supplies within the bottom sediments and that these could provide a

continuing subsidy of organic material to support enhanced metabolism following the flood. Residual sediment supplies could provide a background food resource supporting prolonged heterotrophic growth that might be critical to maintaining food web complexity and energy flow during periods of constrained autochthonous supply.

It was hypothesised from these scenarios that:

- Prior to the flood, during extended periods of regulated flows, river respiration within the South Australian section of the Murray River would be supported by supplies of organic carbon from phytoplankton as observed previously upstream, with only minor contributions from allochthonous floodplain sources.

- During the flood, large contributions of dissolved and fine particulate organic material transported from the floodplain into the river channel would increase respiratory activity within the water column.

- During the flood the increased flows, increased water depth, and high colour and turbidity within the water column would restrict phytoplankton production and consequently phytoplankton respiration.

- During the flood there would be large amounts of coarse particulate organic material from the floodplain settling within the channel and contributing to metabolic activity within the river sediments.

- Following the flood planktonic metabolism would return to levels similar to pre-flood conditions, but there would be a continuing, enhanced metabolism within the sediments due to the storage and metabolism of settled organic material.

Interpretation of the data collected during the flood period relied heavily on the availability of a longer term data set from CSIRO that described the fluctuations in metabolic activity during periods of more stable flows (Oliver and Merrick 2006; Oliver and Lorenz 2010).

Materials and Methods

Study sites

River metabolism was measured in the main channel of the Lower River Murray in South Australia (Figure 1). Six sites were selected to provide data on longitudinal changes in metabolism especially in relation to individual floodplain areas, and to contrast alterations in flow velocity due to the presence of weirs and their associated pools.

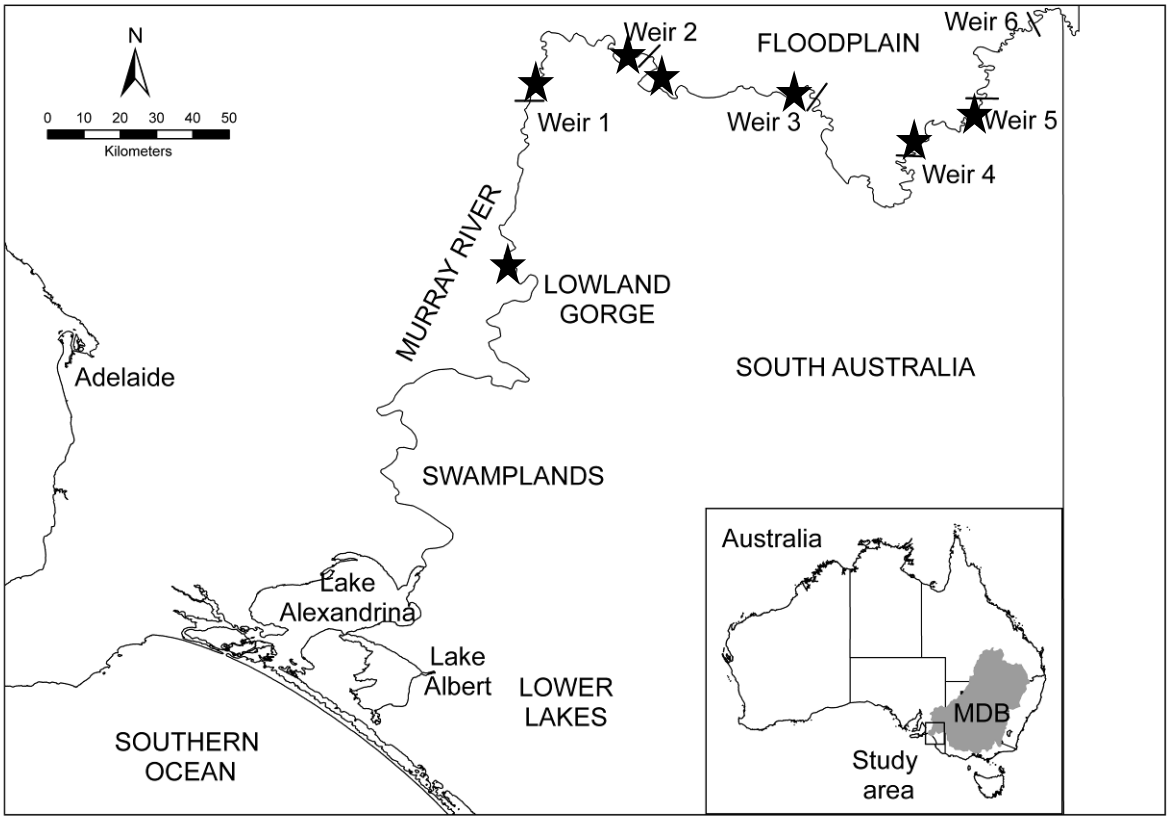


Figure 1. The Lower River Murray and geomorphic regions in South Australia; inset shows extent and position of the Murray-Darling Basin in Australia. Sampling sites are marked by stars.

The choice of sites was also influenced by the availability of metabolism measurements from the South Australian section of the River Murray prior to the flood. These data were collected as part of a project funded by the CSIRO Water for Healthy Country Flagship. The sampling sites are listed in Table 1 along with the months and years of sampling. A site not sampled during the flood period (Weir 2 Upstream) was included to provide extra pre-flood data. Each of these sampling sites is associated with a nearby measurement of river discharge. During the flood a number of the flow stations were inoperative as a result of high water levels and in these cases the nearest suitable station was used.

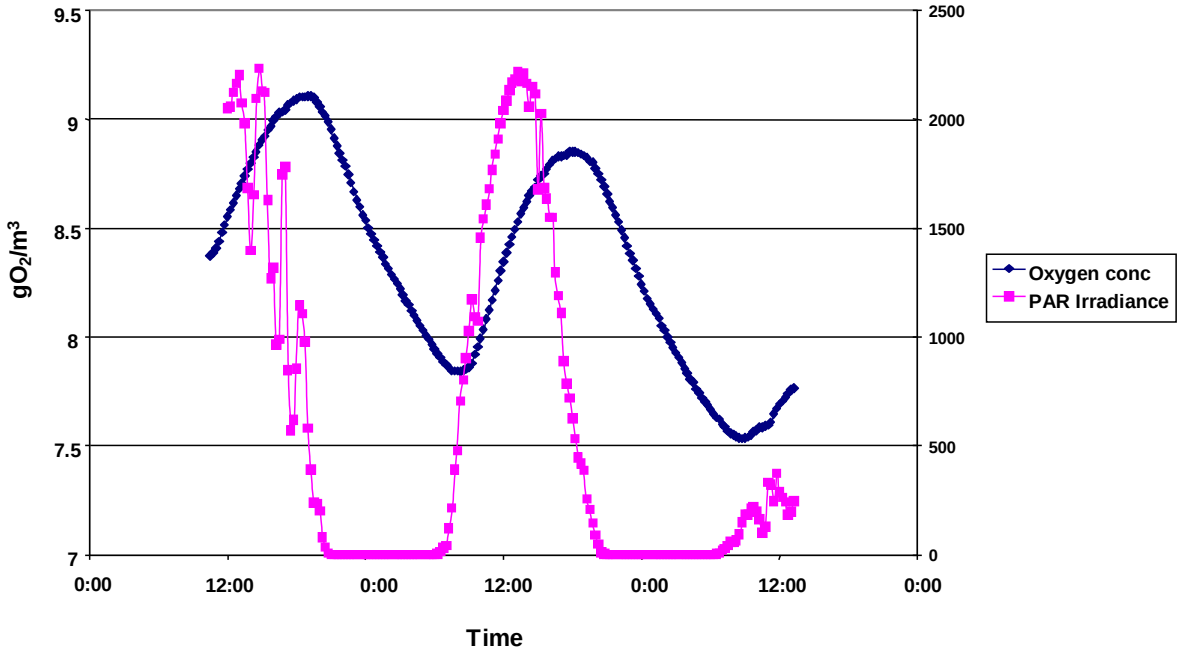
Site	Prior sampling occasions	Flood sampling occasions	Notes
Lock 5 Downstream	Feb, April, Sept 2006; Feb, April, Oct 2007; April 2008; May 2010	Feb, May, Dec 2011	
Lock 4 Upstream	Feb, Mar, Sept 2006; Feb, Oct 2007; April 2008	Feb, May, Nov 2011	
Lock 3 Downstream	Oct 2007; April 2008	Feb, May, Nov 2011	
Lock 2 Downstream		Feb, May, Nov 2011	No prior data
Lock 2 Upstream	Oct 2007; April 2008		No flood data
Lock 1 Upstream		Mar, May, Dec 2011	No prior data
Swan Reach	Nov 2009	Mar, May, Dec 2011	

Table 1. Sampling sites and sampling times in South Australia prior to and during the flood period.

Metabolism measurements

River metabolism was estimated from analyses of the daily time series of dissolved oxygen concentrations and light intensities (Figure 2) (Odum 1956; Young and Huryn 1996; Oliver and Merrick 2006). Oxygen is generated during photosynthesis and consumed during respiration so the net oxygen concentration change during the daylight period estimates *NP* as photosynthesis and respiration are occurring simultaneously. Overnight, when photosynthesis is not occurring, the decline in oxygen concentration due to respiration provides an estimate of *CR*. The *GP* is then calculated from these two measurements by correcting the daytime *NP* measurement for the estimated reduction in oxygen due to *CR*.

Dissolved oxygen concentrations within the river channel were measured using oxygen sensors fitted to recording sondes (Figure 3). These were suspended in the water column at two to three locations along a 3 km river reach for a minimum of 36 h and measured the total system metabolism. The component of metabolism due to planktonic organisms was determined by



enclosing water samples in clear, tubular, Perspex incubation chambers that extended over the depth of the illuminated surface layer (the euphotic zone). The depth of the euphotic zone was defined as the depth of penetration of 1% of the surface irradiance. Submersible pumps clipped to the outside of the incubation tubes circulated water up through the sealed chamber, past an oxygen electrode at the top, and then back around through clear external plastic tubing. Diel chamber incubations were run in parallel with the total open water channel measurements. The difference between total and planktonic metabolic rates is due to the metabolism of non-planktonic organisms such as benthic and sedimented microalgae, but because the identity of these organisms is generally unknown it is referred to here as non-planktonic metabolism (Figure 3).

Figure 2. Example time series of river oxygen concentrations measured in the open water using data recording sondes and the associated changes in incident photosynthetically active radiation (PAR, µmole photons $m^{-2}s^{-1}$).

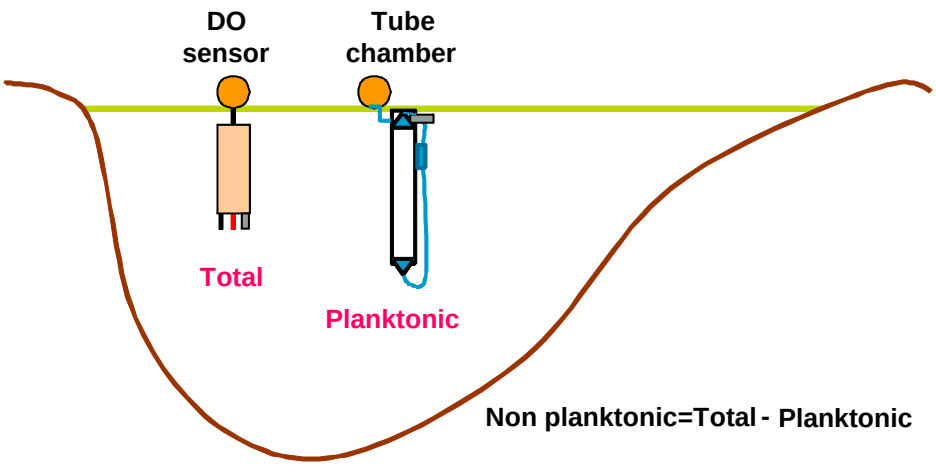


Figure 3. Metabolism measurement techniques

Metabolic rates in the closed chambers were calculated directly from concentration changes in the dissolved oxygen time series. More complex analyses were required for the open water measurements because changes in oxygen concentration depend not only on the rates of photosynthesis and respiration, but also on gas exchange at the air-water interface. The rate of gas exchange and the metabolic parameters were estimated by fitting the experimental data with a numerical model (Oliver and Merrick 2006).

The rates of dissolved oxygen concentration change (dO/dt) within the river were considered due to photosynthesis, respiration and exchange of oxygen at the air-water interface as depicted by Equation 1 (Young and Huryn 1996; Oliver and Merrick 2006):

$$dO/dt = AE_t^{\ p} + kD + CR \qquad \text{Equation 1}$$

Here $AE_t^{\ p}$ describes the dependence of integral gross photosynthetic production (*GP*) on irradiance intensity (Kosinski 1984; Young and Huryn 1996), *A* and *p* being coefficients, and E_t being the incident photosynthetically active radiation (*PAR;* µmole photons $m^{-2}s^{-1}$) at time *t*. The exponent *p* provides for the possibility that the integrated gross primary production shows a saturating response to irradiance through the day (Kosinski 1984). Atmospheric gas exchange was estimated as the product of a re-aeration coefficient *k* ($time^{-1}$) and the oxygen deficit *D.* The deficit is the difference between the saturation oxygen concentration and the measured oxygen concentration in the water (Odum 1956; McCutchan *et al.* 1998). Saturated oxygen concentrations were calculated from the water temperatures measured at five minute intervals using formulae from the International Oceanographic Tables (1973) but without a salinity correction. The last term in the oxygen balance equation is the community respiration rate *CR*.

Measured changes in oxygen concentrations and the matching calculated saturated oxygen concentrations were used to estimate dO/dt and *D*, while E_t was obtained from a recording light sensor deployed on location. A three dimensional curve fitting routine (*Sigma Plot*) was applied with these time series to estimate average values for *CR*, *k*, *A* and *p*. Equation 1 was then re-arranged to give *GP* ($AE_t^{\,p}$) and values calculated for 10 minute time intervals and summed over the day (Oliver and Merrick 2006; Oliver and Lorenz 2010). This step enabled temperature responses for *R* and *k* to be introduced into the equation to investigate their effect.

Additional measurements

In parallel with the oxygen time series the incident photosynthetically active radiation (*PAR*) was recorded at five minute intervals. Measurements were also made of changes in light intensity with depth in the water column to estimate the vertical attenuation coefficient. Water samples were collected for chlorophyll analyses, for phytoplankton enumeration and identification, and for organic carbon analyses.

Rates of river discharge do not provide a consistent basis for comparing the biogeochemical or physical influences of flow rate because the important hydrodynamic characteristics are related to water velocity. The water velocity generated by a particular discharge is dependent on the cross-sectional area of the flow and is a function of channel shape. Cross-sections at each sampling site were estimated either from direct survey measurements made during previous studies or from analyses of historical depth surveys from the Murray Darling Basin Authority (Oliver and Lorenz 2010). These measurements were related to the nearest suitable gauging station so that cross-sectional area could be calculated as a function of discharge. In this way hydraulic characteristics including mean water depth, wetted perimeter and water velocity could be estimated at each site from the discharge.

Results

Flow histories and metabolism measurements

Since 1998 river metabolism has been measured periodically along the length of the Murray River. This has resulted in an over-lapping progression of sampling sites moving downstream and including sites within SA at Locks 2, 3, 4 and 5 between 2006 and 2008 (Oliver and Merrick 2006; Oliver and Lorenz 2010) (Figure 4).

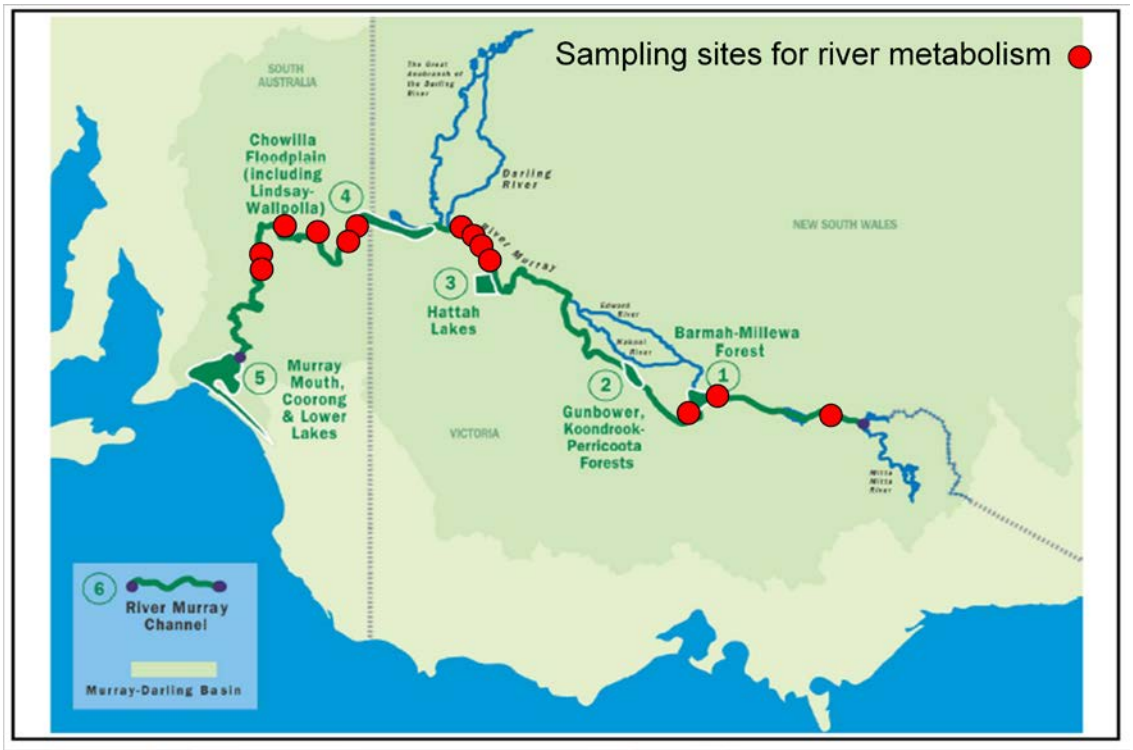


Figure 4. River metabolism sampling sites along the Murray River for the period 1998-2011. The map shows the five floodplain icon sites designated by the MDBA (Map modified from the Ministerial Council Communique, Nov 2003 from the MDBA website).

Prior to the first set of measurements during 1998-99 there had been a decade with almost annual floods, some of which were extensive (Figure 5). There was a minor flood prior to the 1998-99 sampling although it followed a period of two years without floods. However, during the decade when most of the metabolism measurements were made there was a major reduction in flood occurrences, especially during 2000-2010 when the Murray Darling Basin was in drought (Figure 5). During the first sampling period the river channel remained largely at bank full during spring-summer due to irrigation flows (Irrig) released from major upstream storages. The next set of

measurements were made in 2006-2007 and followed a four year period during which there were no floods. Channel flows were again dictated by irrigation demands with bank full levels common in spring and summer (Irrig). As the drought continued even irrigation flows declined as stored water reserves dwindled and the 2008-2009 measurements covered a time of reducing discharge resulting in drought like flows within the channel (Drought).

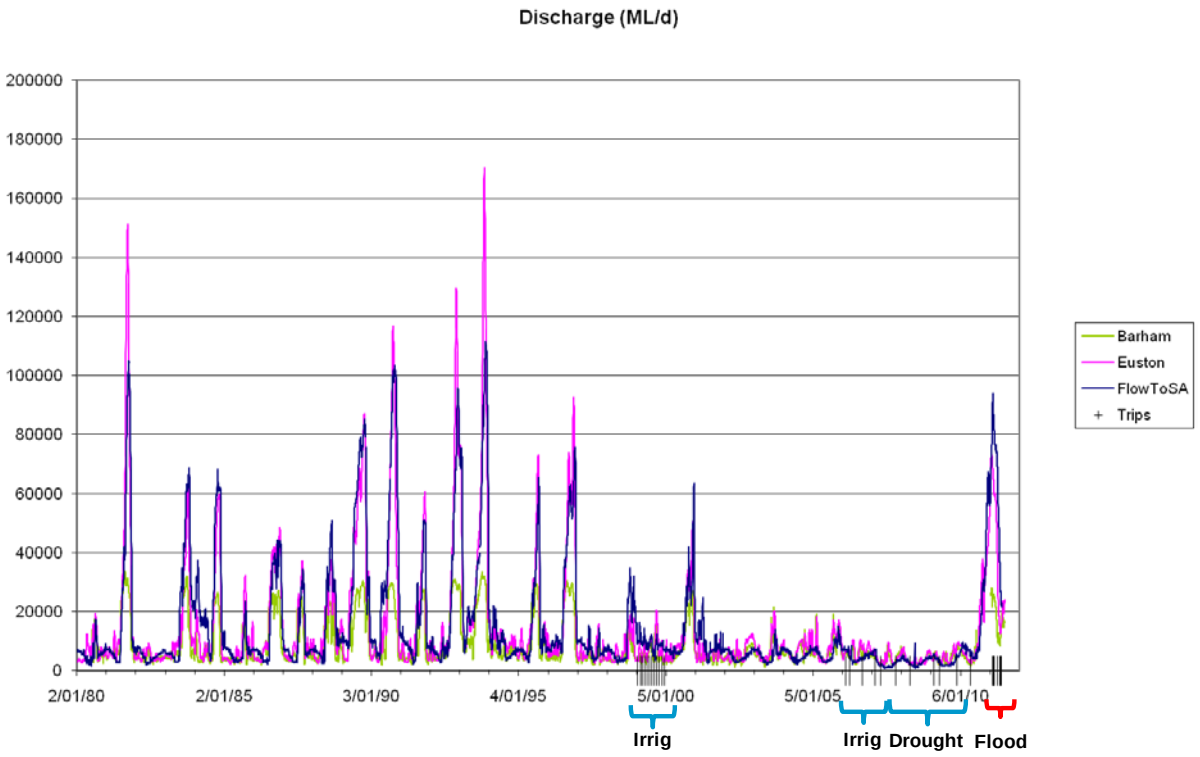


Figure 5. Murray River hydrographs at three gauging stations from 1980-2011 showing discharge prior to and during periods when river metabolism measurements were made. Sampling trips are indicated by vertical lines crossing the x-axis. The sampling times are categorized into periods of irrigation flows (Irrig), drought flows (Drought) and flood flows (Flood) as described in the text.

Then in 2010-2011 significant rains marked the end of the Millennium Drought and caused flooding through-out the Murray Darling Basin culminating in large and extensive floods in the Murray River. Although this flood occurred over large areas of the floodplain the peak flow in the mid-reaches of the river (Euston) was of moderate size compared to major floods prior to 2000 (Figure 5). However, the peak flow to South Australia was similar to flow peaks prior to the drought. The Goyder Institute Project covered the period from February to December 2011, recording information from near the peak of the flood and in the months following.

Comparing metabolism measurements along the river

An overview of the various sets of metabolism measurements standardised to rates per unit surface area show distinct differences between the hydrological periods of irrigation flows, drought flows and flood flows (Figure 6). During the 1998-99 period when flows were largely dominated by irrigation supply and measurements were restricted to upstream, flowing sections of the river, the production and respiration rates were relatively small (Figure 6). During the period between 2006 and 2009 some of the sampling sites were in South Australia (SA) and measurements were made not only at flowing river sites but also in weir pools where flow velocities are diminished. A wider range of metabolic rates was observed from this set of sites, and this is particularly evident in the open water measurements (Figure 6). During the flood in 2010-11 metabolism measurements were restricted to SA and so the measurements for this region of the river are extracted from Figure 6 and compared in Figure 7 to more clearly show the details.

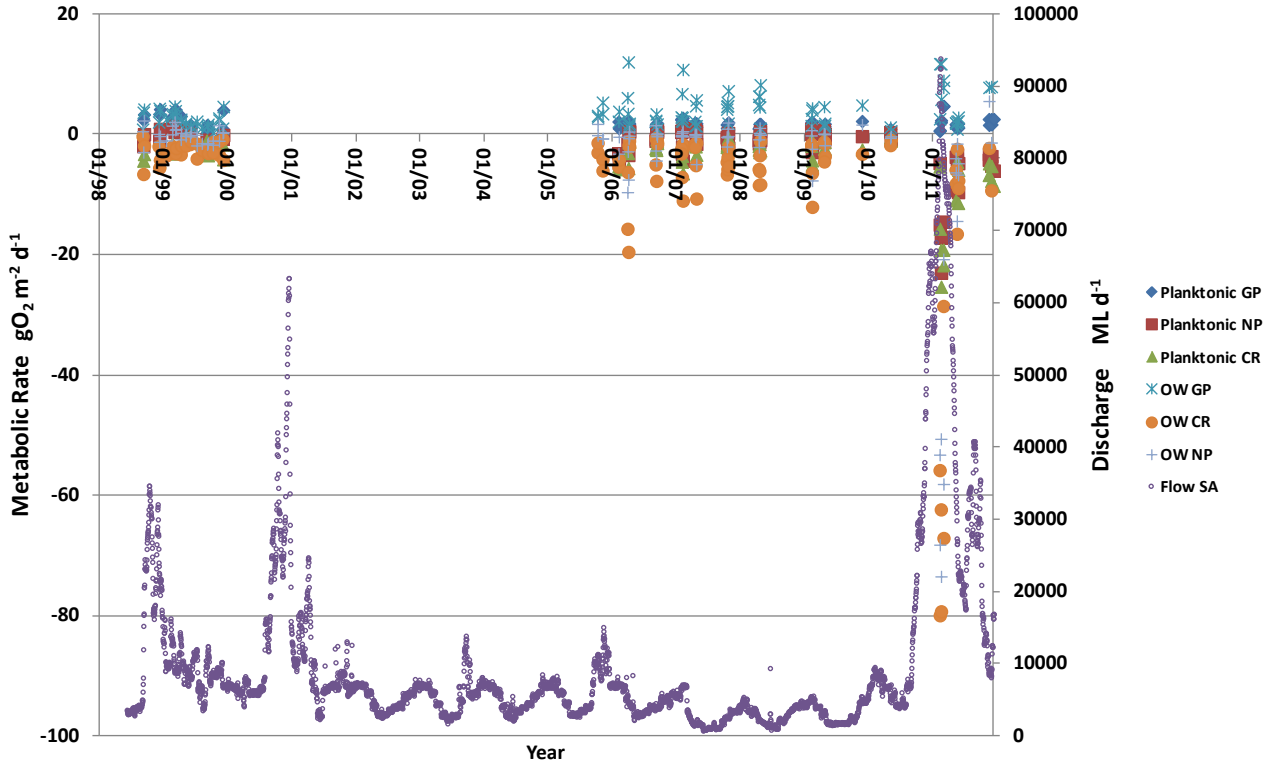


Figure 6. Areal rates of gross photosynthesis (GP), Community Respiration (CR) and net production (NP) for the open water (OW) of the river channel and for the plankton at all sampling sites and times along the Murray River measured during different hydrological conditions, indicated here by the flow to South Australia.

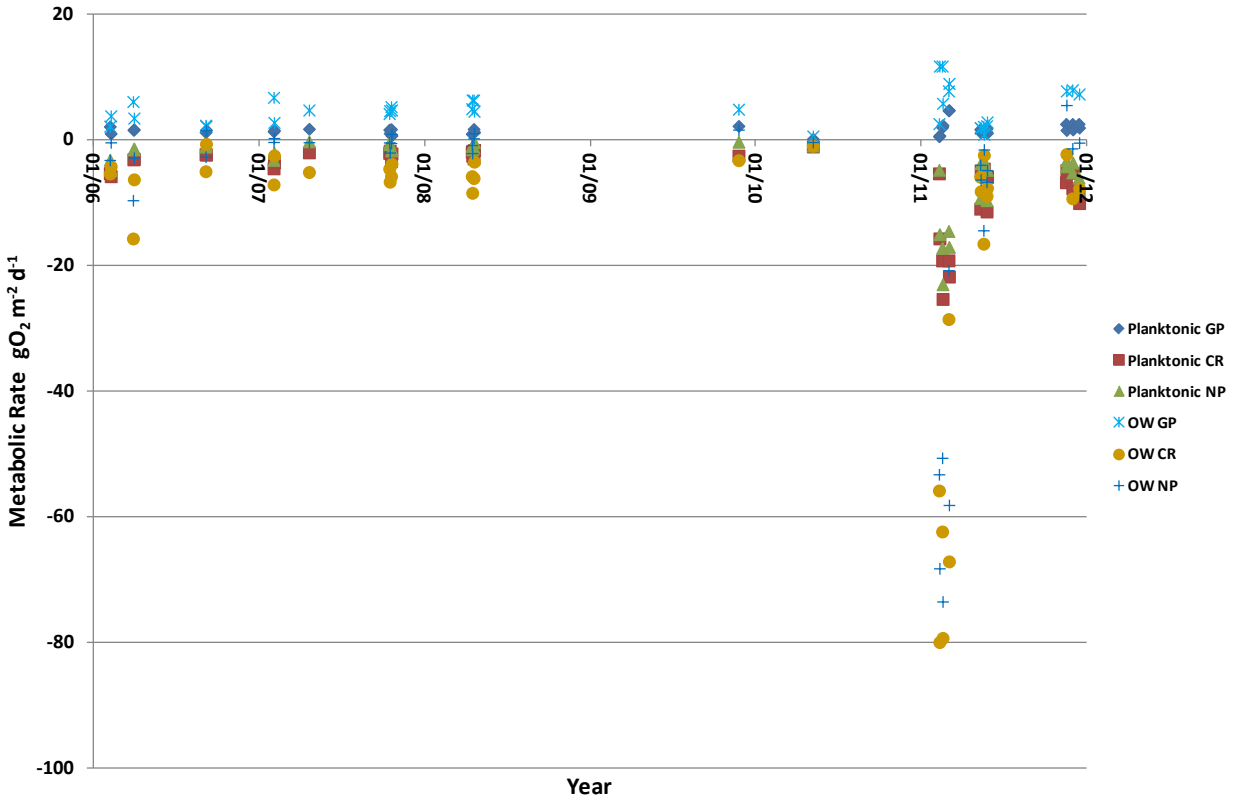


Figure 7. Areal rates of gross photosynthesis (*GP*), Community Respiration (*CR*) and net production (*NP*) for the open water of the river channel (*OW*) and for the plankton, over time for all sampling sites in South Australia.

There were very large changes in metabolism in response to the flood with marked increases particularly in the rates of respiration in both the open water and plankton samples (Figure 6 and Figure 7). After the passage of the flood metabolic rates returned to levels similar to those observed prior to the flood The large respiration rates observed during the peak of the flood were expected as flood waters carry organic material from the floodplain back into the river, supporting an increased heterotrophic metabolism. However, it was surprising to observe at the peak of the flood that the open water production exceeded that of the plankton and in some cases was larger than any previous measurements. This occurred despite light penetration into the water column being low due to the high turbidity of the flood waters. The poor light and high flow conditions were not expected to be conducive to production by phytoplankton or macrophytes, so it was unclear initially where the open water *GP* was being generated.

Water velocity and metabolic patterns

The long time-series of metabolic measurements includes results from a range of different conditions and encompasses flowing river sites and weir pool sites (Figure 6). This makes it difficult to identify important environmental influences on river metabolism from the sequential data series. Water velocity is expected to affect metabolic rates through its influence on water depth, turbulent mixing and water quality attributes. The data collected from all sites prior to the flood period (1998-2010) show a consistent response to water velocity with open water *GP* and *CR* closely balanced above velocities of 0.2 m s^{-1} (Figure 8). This equivalence does not occur on every sampling occasion, but averaged over time the difference between the two, which is the *NP*, is not significantly different from zero. At higher velocities *NP* is slightly positive for the plankton but zero for the open water measurements as indicated by the trend lines (Figure 8). This indicates that phytoplankton production is the major source of organic carbon being metabolised in flowing sections when flows are within channel.

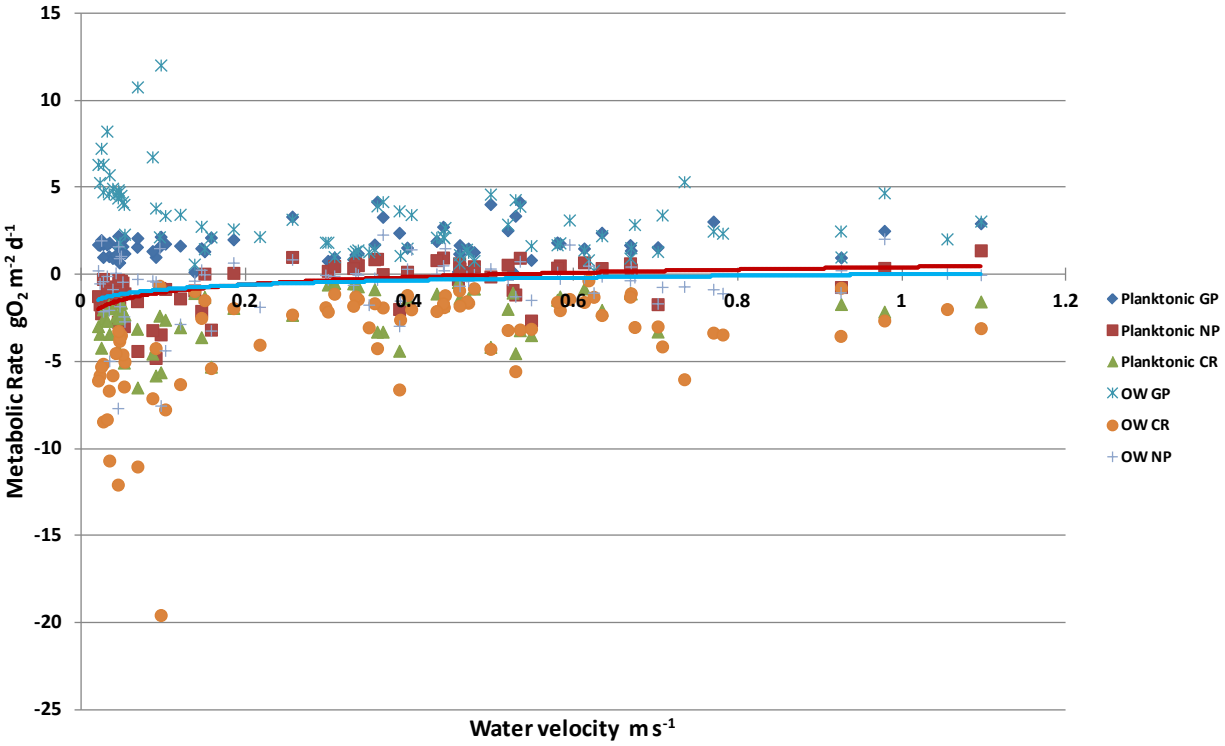


Figure 8. Areal rates of gross photosynthesis (*GP*), Community Respiration (*CR*) and net production (*NP*) for the open water (*OW*) and for the plankton occurring at different water velocities at all sampling sites and times along the Murray River prior to the flood period ie. prior to May 2010. The trend lines for *NP* values match the colours for *OW* and Planktonic rates.

Velocities below 0.15 m s^{-1} are representative of weir pool sampling sites and as velocity declines below this level there is a trend to increasing *GP* and *CR* (Figure 8). A relatively greater increase in the respiration rate results in a negative *NP* indicating an external supply of organic material to these sites (Oliver and Merrick 2006; Oliver and Lorenz 2010).

The difference between the total rate of metabolism measured in the open water (*G*P, *CR* or *NP*) and the corresponding rate measured in plankton chambers estimates the non-planktonic metabolic rates. The non-planktonic rates are often attributed to metabolism by organisms growing on the bottom sediments or attached to surfaces within the water column, but this interpretation depends on having relatively well mixed and uniform conditions. Under complicated flow patterns or rapidly changing environmental conditions metabolic signals generated elsewhere in the water column can be transported to the sampling site giving misleading results. For example, it is possible that plankton samples enclosed within the incubation tubes and collected over a short-time interval may not be representative of the total flow past the open water sensors. However, the consistent shapes of the oxygen concentration curves measured in the water column indicated that in general there were no significant fluctuations in the metabolic characteristics of the flowing systems during the incubation periods except in particular, identifiable circumstances that will be discussed later.

In the flowing river sections contributions from non-planktonic sources were generally found to be small (Figure 9) and planktonic metabolism dominated the system (Oliver and Merrick 2006). In these sections *GP* was attributed to photosynthesis by phytoplankton in the water column whereas respiration, although predominantly in the water column, often had a proportion associated with the non-planktonic compartment and this was attributed to respiration within the bottom sediments. As the open water *NP* in the flowing reaches was on average not significantly different from zero (Figure 8), it was concluded that the organic material captured by phytoplankton photosynthesis was fully respired in the system, some by the phytoplankton themselves and their grazers within the water column, and some by benthic organisms making using of sedimented plankton. The zero *NP* suggests that within these river sections all the available organic material is utilised and as a result the system is energy constrained (Oliver and Merrick 2006).

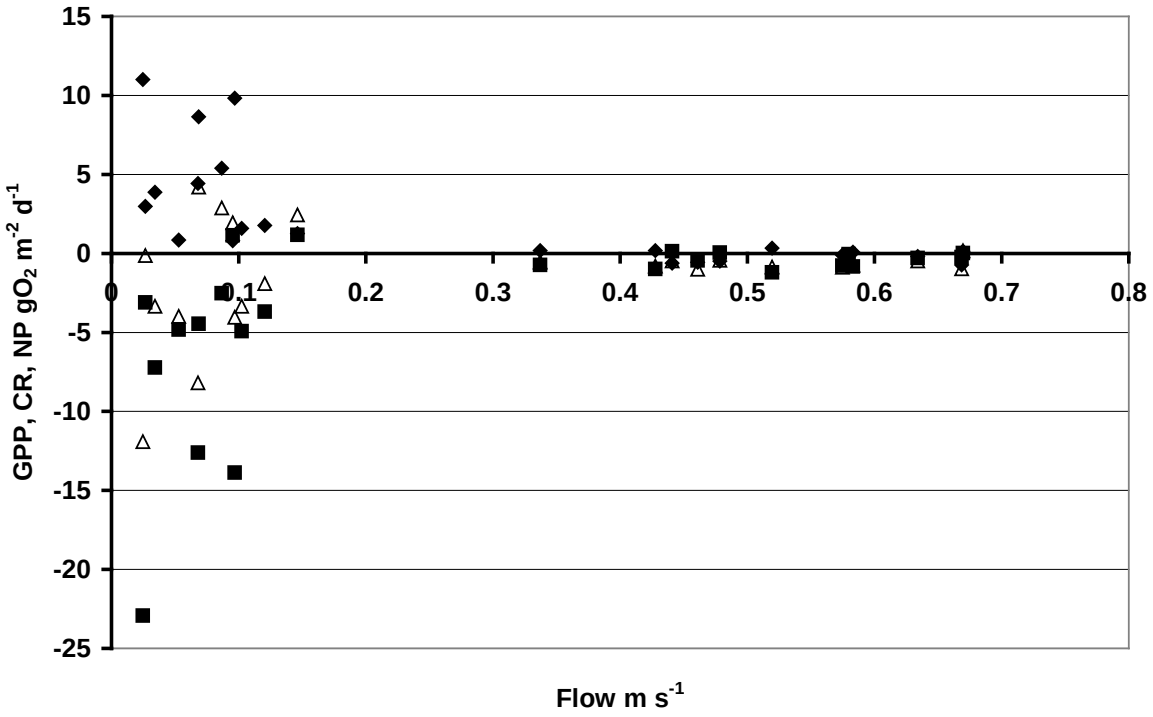


Figure 9. Areal non-planktonic *GPP* (♦), *CR* (■) and *NEP* (Δ) displayed on a flow velocity axis for all sites from the 2006-07 sampling period.

In contrast it was found that in weir pools and slow flowing river sections the non-planktonic contributions to metabolism increased (Figure 9) and in some cases were the largest contributors to *GP*, *CR* and *NP* (Oliver and Lorenz 2010). The metabolic rates were highly variable but often *NP* was negative, indicating that some weir pools were collecting external supplies of organic carbon (Figure 9). This organic material may have been carried in by the river from upstream and concentrated within the weir pools, or it could have been sourced from the vegetated zones around the weir pools, it is not known yet which of these scenarios is correct. Occurrences of negative net production in the weir pools was not associated with similar observations at sampling sites immediately downstream of the weirs, suggesting that the supply of organic material to the weir pools was not being transported downstream. It appears that the weir pools are isolated patches of enhanced metabolic activity (Oliver and Lorenz 2010).

Metabolic patterns in the South Australian Murray River

A plot of metabolism data against velocity for all the available South Australian sites includes samples collected during the flood period (Figure 10). In South Australia long stretches of the river consists of weir pools with low flow rates. Metabolic rates during the non-flood periods are similar to earlier measurements taken along the river system except that *NP* is often negative even at

higher velocities suggesting a source of external material as observed for weir pools elsewhere along the river. Rates of metabolism changed significantly in response to the flood with greatly increased respiration rates measured during the high flow velocities. As described previously, there were also some surprisingly high rates of open water *GP* observed during the flood peak, despite the high turbidity and high flows.

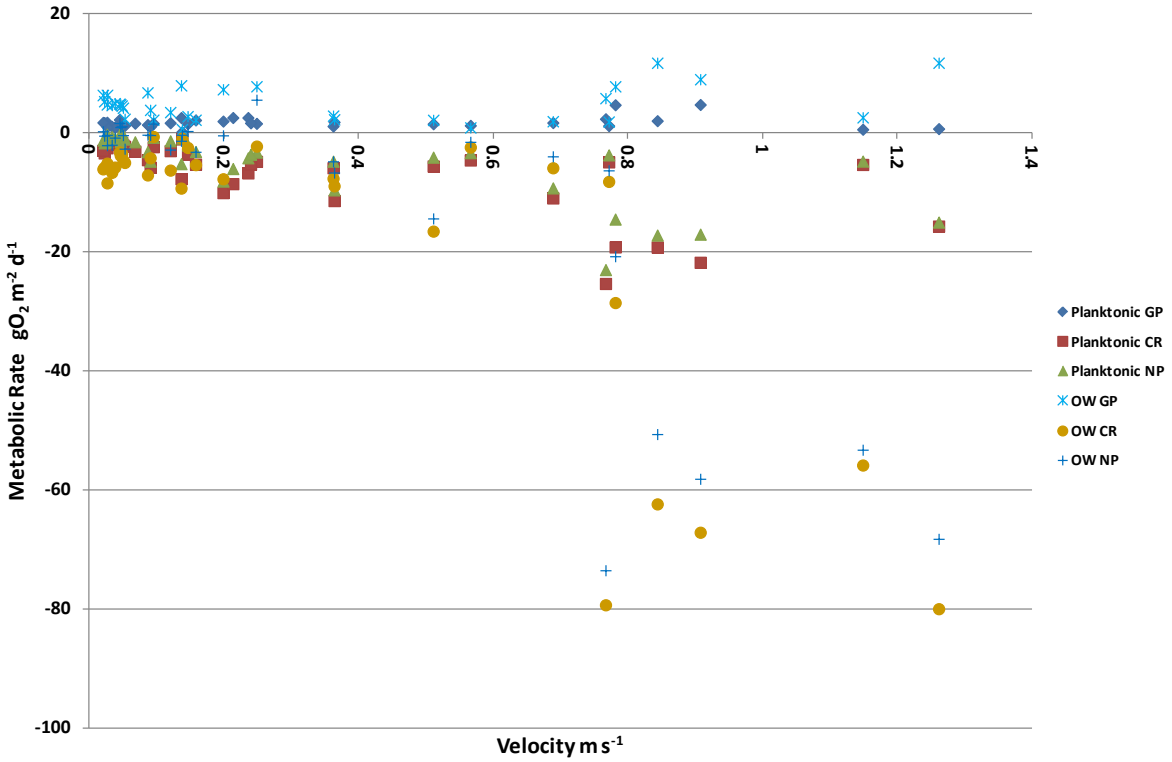


Figure 10. Areal rates of gross photosynthesis (GP), Community Respiration (CR) and net production (NP) for the open water (OW) of the river channel and for the plankton at different water velocities for all sampling sites and times in South Australia.

Focusing on samples collected during and after the flood it is apparent that metabolic activity declines quickly as flow reduces, the decreasing velocities in Figure 11 indicating increasing time after the flood peak (Figure 7). Very high respiratory rates and negative *NP* values for the open water measurements occurred at velocities above ca. 0.75 ms^{-1} but reduce remarkably at velocities below this. The high respiration rates were considered due to flood supplies of organic material driving heterotrophic activity but these were apparently not sustained as the flood receded.

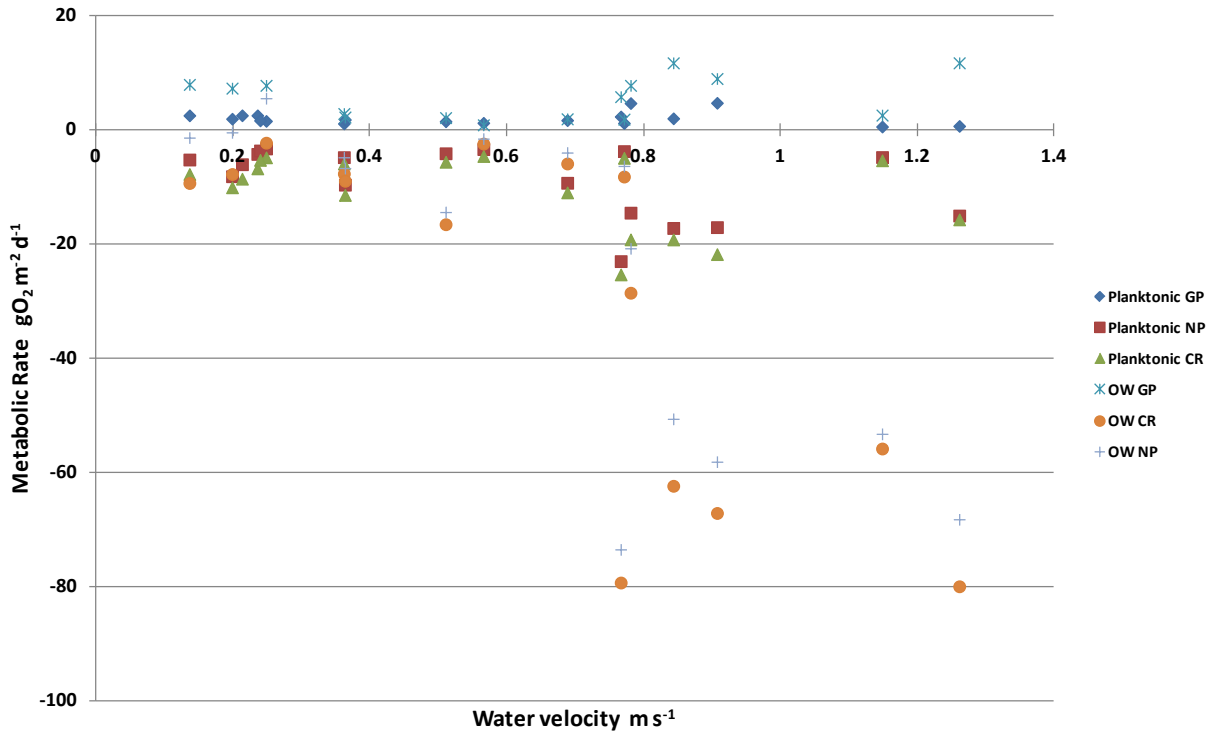


Figure 11. Areal rates of gross photosynthesis (GP), community respiration (CR) and net production (NP) for the open water (OW) of the river channel and for the plankton in South Australian sampling sites at different water velocities. Data is from February 2011 onwards which was during and following the major flood peak.

The time between measurements of the high respiration rates and the reduced rates was three months during which period discharge decreased from ca. 78,000 ML d^{-1} to 50,000 ML d^{-1} (Figure 6). Discharge continued to decline to 17,500 ML d^{-1} in early July before again increasing to a second, smaller flood which peaked at a flow of 41000 ML d^{-1} in August (Figure 6). No metabolism measurements were made during the period of this second flow peak but measurements were available from before and after the peak. The measurements after the peak were made in November- December 2011, almost one year after the commencement of the major flood and when discharge was back to regulated flows between 8000 and 14000 ML d^{-1} (Figure 6). However, because the second flow peak in August reduced slowly through to November, water velocities of 0.2 m s^{-1} or less that are typical of weir pools and the South Australian sites generally, had only occurred for a period of a few weeks prior to the final metabolism measurements (Figure 6).

The measurements taken either side of the second flow peak showed a continuing decline in the rates of metabolism, with the final sets approaching the metabolic rates measured at the South Australian sites during the prolonged drought period and prior to the major flood. Planktonic *NP* remained slightly more negative despite the open water *NP* approaching close to zero (Figure 7).

The non-planktonic metabolism in the South Australian section of the Murray River prior to the flood showed characteristics similar to those observed elsewhere along the river. Measurements made in SA weir pools, such as upstream of Lock 4, showed highly variable metabolic rates with non-planktonic production and respiration often making sizeable contributions to metabolic activity and with net production often being negative (Figure 12). This is similar to the results from weir pools along the Murray River. In contrast at the flowing sites in SA, such as downstream of Lock 5, the non-planktonic contributions to metabolic activity were smaller and comparable with results from flowing sites along the Murray River (Figure 12). Because the non-planktonic metabolism is calculated from the open water and planktonic measurements, non-planktonic *NP* and *CR* declined immediately the flood peak passed, in line with the reduction in the open water rates.

Respiration and organic carbon sources

During the flood both open water and planktonic respiration rates increased but much greater increases occurred in the open water rates suggesting a large non-planktonic contribution to the respiration. At the peak of the flood the open water respiration rates averaged ca. 70 $gO_2m^{-2}d^{-1}$, whereas the planktonic rates averaged ca. 20 $gO_2m^{-2}d^{-1}$ (Figure 7). As the rates of *GP* were only a small fraction of the respiration rates the *NP* was large and negative.

One interpretation of these results is that the high respiration rates during the flood were due to the transfer of organic material from the floodplain to the river channel. Some of this was dissolved organic matter or fine particulate material and this remained in suspension and caused the increase in planktonic respiration. But a large proportion of metabolisable organic material was delivered as large particles that were sufficiently dense to sink to the sediments and drive the large respiration rates associated with the non-planktonic sources. This explanation seems conceptually straightforward but there are problems with the interpretation. In general, reactive dissolved organic carbon (DOC) from floodplain sources is considered to be most readily utilised by heterotrophs (Battin et al 2008). Terrestrial particulate organic carbon (POC) from the floodplain is considered less available for use, often because it has been weathered and metabolised while resident on the floodplain and also because of its reduced surface area (Battin et al 2008). However, if large amounts of particulate material are transferred then large total respiration rates are possible even if the rates per unit of organic material are low. But under these conditions it might be expected that if there was a large store of particulate organic material in the sediments, enhanced non-planktonic respiration rates would continue for some time following the recession of the flood.

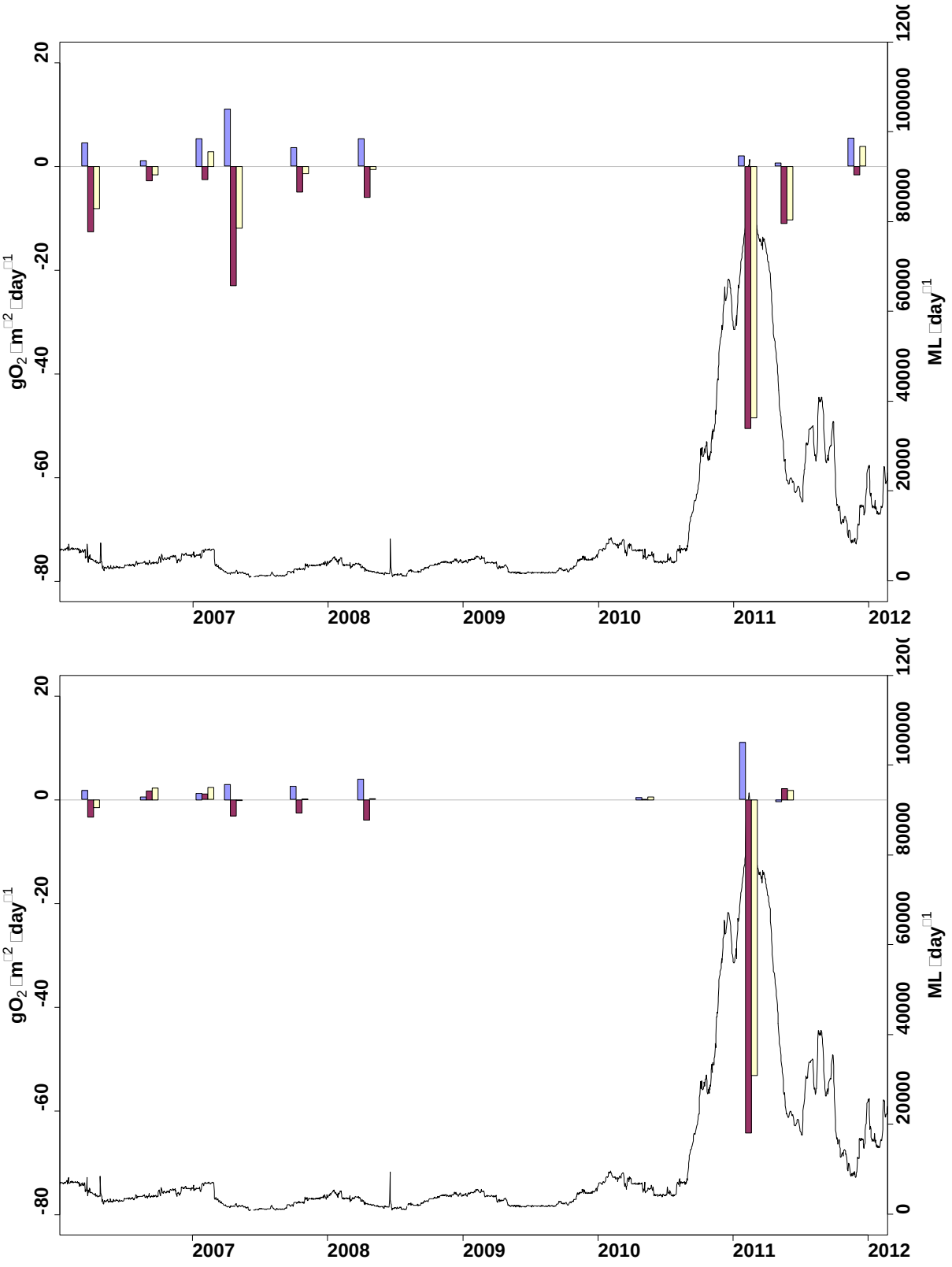


Figure 12. Non-planktonic rates of *GP* (blue bars), *CR* (red bars) and *NP* (yellow bars) measured in the weir pool upstream of Lock 4 (top) and in the river downstream of Lock 5 (bottom) in South Australia before, during and after the flood flows shown by the discharge hydrograph.

Instead, respiration rates declined as the flood receded and when water velocities fell below ca. 0.75 m s^{-1} they returned to levels similar to those observed prior to the flood (Figure 11). The discharge associated with the 0.75 m s^{-1} flow velocity is about 35,000-45,000 ML d^{-1} and this is the discharge level where significant inundation of the floodplain commences. These results suggest that the non-planktonic metabolism may be occurring not in the river channel itself but in waters on the inundated flood plain and that the return of this water into the channel directly influences the oxygen concentration in the river. This would mean that the low oxygen concentrations within the river channel do not necessarily indicate the magnitude of the supply of organic material to the channel that is utilised as an energy source.

A similar critical discharge level can be derived from the time series of dissolved organic carbon (DOC) and dissolved oxygen obtained from the MDBA monitoring data (Figure 13). Although DOC increases as flow increases it is not until discharge exceeds ca. 20,000 ML d^{-1} that significant oxygen depletion occurs within the channel. Similarly DOC declines as the flood recedes but oxygen concentrations only attain saturation levels as the discharge approaches 20,000 ML d^{-1}. There appears to be a close association between the extent of floodplain inundation as represented by increasing discharge and the DOC concentrations and dissolved oxygen concentrations in the river channel. These data could be interpreted to suggest that as DOC increases there is enhanced respiratory activity in the river that draws down the oxygen concentration. However, it cannot be determined from simple comparisons of the data whether it actually is the increase in DOC concentration that causes the oxygen depletion. The DOC is expected to cause increased respiration within the water column but the measured planktonic rates that include this contribution accounted for less than a third of the total open water respiration rates.

To assess the influence of dissolved organic carbon on respiration rates within the river channel the rates of DOC decline were determined from the calculated travel times and changing DOC concentrations. Calculations were made for the period of increasing flood conditions when peaks of DOC were observed travelling downstream. The estimated rates of DOC decline were then compared with the measured respiration rates converted from oxygen to carbon equivalents.

During the period 19th-28th October 2010 the rate of decline in DOC between Lock 9, Lock 5 and Morgan was 0.31 $gCm^{-3}d^{-1}$. The rate across these same sites during the period 18th-24th January 2011 was 0.35 $gCm^{-3}d^{-1}$. The planktonic rate of respiration was measured on 9th February 2011 at Lock 4 which is mid way through the series of sites, and when converted from oxygen to carbon units assuming a 1:1 molar ratio for respiratory metabolism yielded a value of 0.36 $gCm^{-3}d^{-1}$. Respiration measurements were also made over the following week at Locks 5, 3 and 2 and yielded higher rates

than at Lock 4. The average respiration across these sites for the period 9th-17th February was 0.86 $gCm^{-3}d^{-1}$. These comparisons suggest that the respiratory breakdown of DOC is similar to or less than the measured planktonic respiration rate and is unlikely to account for the large open water respiration rates. The proportion of the DOC metabolism that is occurring in the water column or the sediments cannot be determined from these analyses.

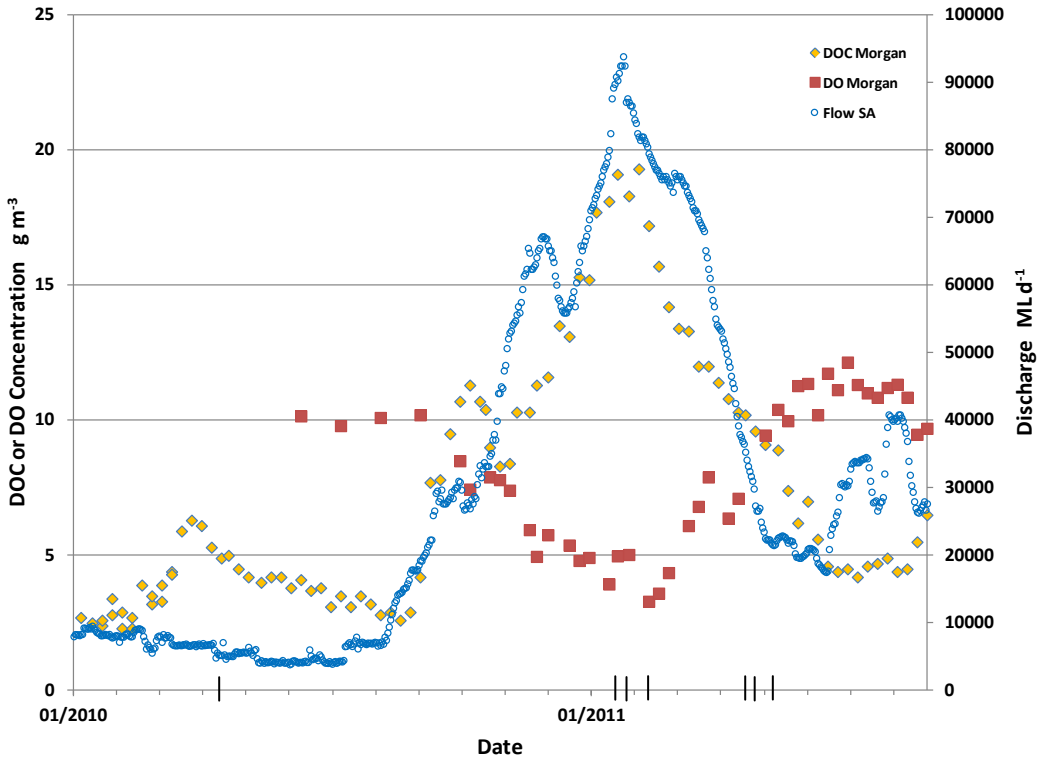


Figure 13. Changes over time in the discharge to SA and the concentrations of dissolved oxygen and dissolved organic carbon measured in the Murray River at Morgan in South Australia. Vertical lines on x-axis indicate times of metabolism measurements.

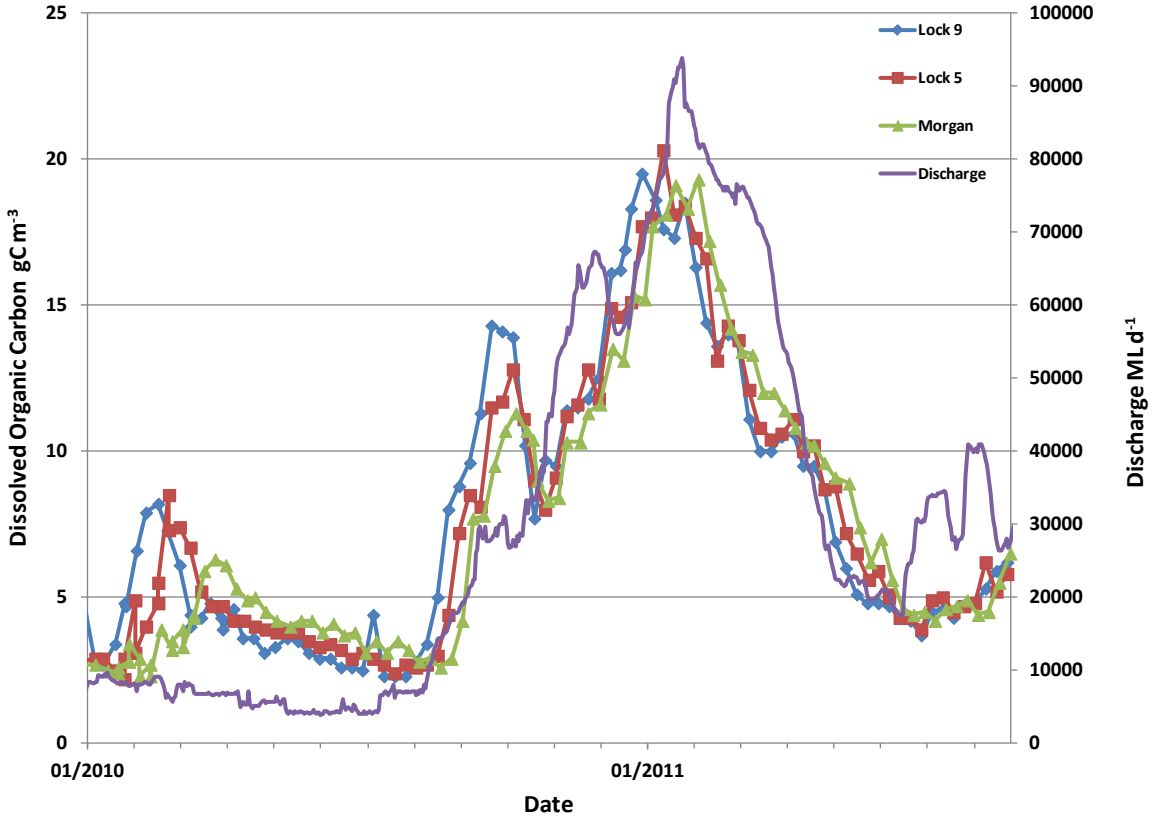


Figure 14. Time series of dissolved organic carbon concentrations and river discharge at Lock 9, Lock 5 and Morgan prior to and during the 2010-2011 flood peak. Data provided from the MDBA monitoring program.

Floodplain-channel interactions influence metabolism

Two unexpected metabolic responses were observed in the data collected during the flood in South Australia. The first was the continuing, and at times enhanced rates of open water *GP* which exceeded the planktonic rates suggesting that it was from a non-planktonic source. This would normally be considered due to attached plants and biofilms. However, the highly turbid and fast flowing conditions in the river channel at the time of the flood were not conducive to photosynthesis by plankton or attached plants and the continuing and enhanced open water production appeared anomalous. In addition, very high respiration rates during the flood appeared to be predominantly associated with non-planktonic metabolism rather than the metabolism of dissolved organic material in the water column as was expected. Although the non-planktonic respiration may have been associated with a large load of sedimenting particulate organic material that was labile and rapidly respired, this seems unlikely as it is difficult to identify a likely source of such material from the floodplain. Furthermore, the rapid decline in respiration rate as the flood receded does not

strongly support this suggestion but rather indicates an association with processes occurring on the floodplain. Interpretation of these results required a return to the original metabolism measurements and the day-night changes in oxygen concentration as typified in Figure 2.

The time series of oxygen concentrations at Locks 5, 4, 3 and 2 (Figure 1) during the sampling of the flood peak showed a downstream increase in the average oxygen concentration of the water column around which daily oscillations due to photosynthesis and respiration were apparent (Figure 15). The average concentration increased from 2 gO_2 m^{-3} at Lock 5 to 2.25 gO_2 m^{-3} at Lock 4 and then to 3 gO_2 m^{-3} at both Locks 3 and 2. This progression suggests a source of organic material at the upstream site driving a metabolic decline in oxygen concentration which is then moderated downstream. This progression might reflect the river channel morphology as large floodplains occur in the river reaches containing Locks 4 and 5 but are reduced downstream, especially below Lock 3 where the river enters a confined gorge section.

The diel oxygen curves for Lock 5 (Figure 15) show the expected sinusoidal response in concentration with time. There is a daytime sunlight driven increase and then decrease in photosynthetic oxygen production and an overnight decline in oxygen concentration due to community respiration. However, a comparison with the changing light intensity shows a surprising situation. Usually the increasing oxygen concentration commences at sunrise and the shift to an almost linear respiratory response begins at sunset (Figure 2). At Lock 5 the data shows that photosynthesis is continuing into the night and that the period of rapidly increasing oxygen concentration is occurring in the afternoon during falling light conditions. It appears that the oxygen time series is ca. 4h out of alignment with the light series (Figure 15). As there is a 24h periodicity in the measurements this means that respiration rates are also out of alignment.

At Lock 4 the diel change in oxygen concentration is not as large with a concentration range of 0.25gO_2 m^{-3} compared with the 0.75gO_2 m^{-3} range at Lock 5 (Figure 15). However, the oxygen time series is again out of alignment with the light series, this time by ca. 10h. The measurements made at Lock 5 and Lock 4 overlap but as the sites were measured in reverse order to the flow direction only a partial sequence can be formed (Figure 15). Measurements at the next two downstream sites, Locks 3 and 2 were made a week later and were not expected to be continuous with the measurements upstream at Locks 5 and 4. However the oxygen concentration patterns were similar with two major oxygen peaks 24h apart misaligned with the light series (Figure 15). In addition the major peaks at Locks 3 and 2 were separated by a smaller oxygen peak that fell between them during the first night of the time series.

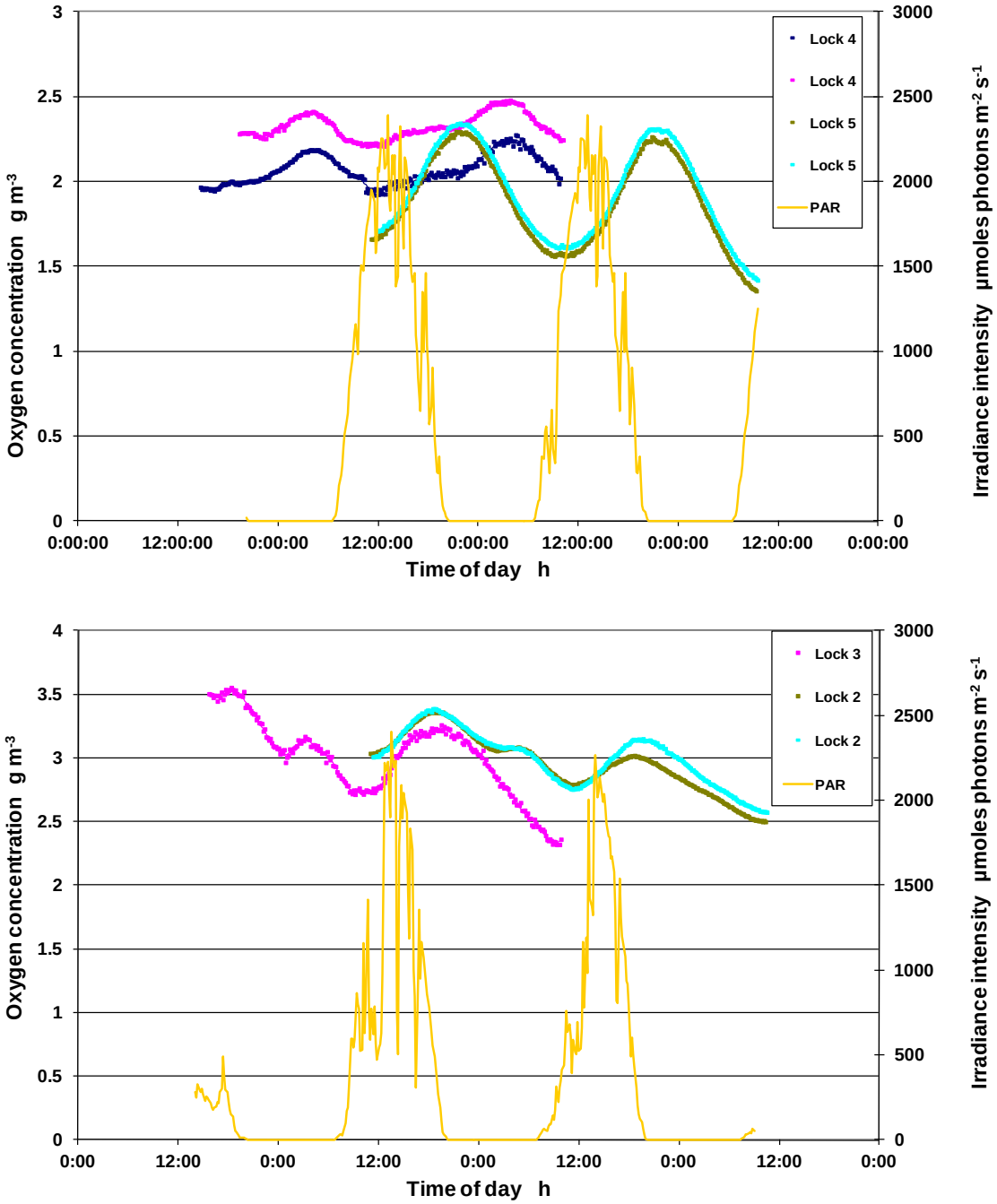


Figure 15. Time series of oxygen concentrations and incident irradiance at Locks 5 and 4 between the 8th-11th February (upper figure), and Locks 3 and 2 between 15th-18th February (lower figure) during the flood peak sampling in 2011.

This same multiple-peak pattern occurred at both Locks 3 and 2 with the downstream site offset further from the light series. The small oxygen peak that occurred between the two larger peaks did not reappear after the second large peak at either site, even though the same period of the

following night was recorded. Such a major reduction in what is considered to be an oxygen peak due to *GP* suggests a large reduction in the light conditions. This provides a further clue to what is happening, as the first (partial) irradiance curve for this sampling period shows significantly lower levels of incident irradiance (Figure 15).

Usually photosynthesis responds similarly over the longitudinal flow section sampled during the open water sensor deployment, with the whole flow section increasing and decreasing in response to light so that there are no single, distinct oxygen peaks that move downstream. Single peaks could occur if there were parcels of water that contained higher concentrations of actively photosynthesising phytoplankton than either upstream or downstream flanking parcels of water sampled during the same measurement period. If these passed by the sensor at night they might appear as phase shifted oxygen peaks. However, this explanation does not account for these observations as conditions within the channel were not conducive to photosynthesis as demonstrated by the low rates in the planktonic chambers. Also such periodic concentrations of phytoplankton are unlikely to occur neatly at 24h intervals as do the major and minor peaks at the four sets of locks (Figure 15). Alternatively, an upstream reach of the river channel with a high concentration of attached autotrophs could generate an oxygen peak as the water flowing over at different times of the day picked up the different rates of photosynthesis. However, this is also an unlikely cause of these observations as the conditions within the channel were not conducive to high rates of photosynthesis by attached plants or biofilms. The most likely explanation for the observed phase shift in peaks is that photosynthesis occurred on the floodplain and the oxygen signal was carried into the channel by returning flood waters.

To investigate this suggestion further, estimates of water velocity were used to calculate the travel time between sampling sites and these were compared with travel times estimated from the displacement of the oxygen peaks from the irradiance time series. A realignment of the oxygen time series with the immediately prior light series provided a first estimate of the potential travel time of the oxygen peaks. In a second step, this time period was increased by 24h increments to account for the possibility of multiple days of travel to match water velocity estimates. A comparison was also made between the relative heights of series of oxygen peaks separated by 24h and the time series of daily incident irradiance, as these patterns also need to correspond. Using these pieces of information it could be shown that the most likely sources of photosynthesis producing the oxygen peaks were individual extensive floodplain areas upstream of the sampling sites.

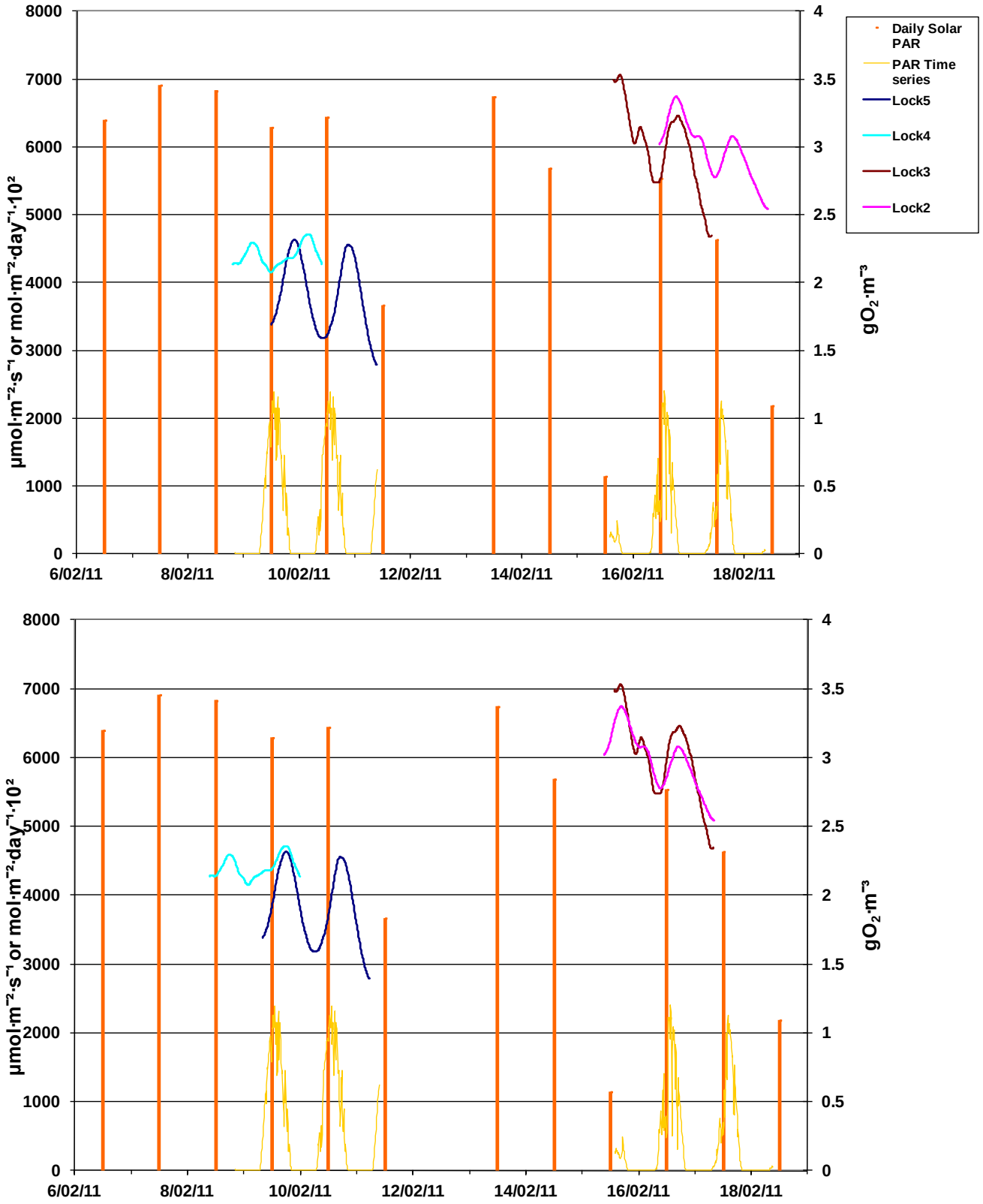


Figure 16. Daily solar photosynthetically active radiation (PAR) and the time series of PAR and oxygen concentrations during metabolism measurements at Lock 5, 4, 3, and 2. Upper graph shows oxygen curves as measured, lower graph shows oxygen curves shifted to align with prior light period. Daily PAR values multiplied by 10^2 to fit on axis scale.

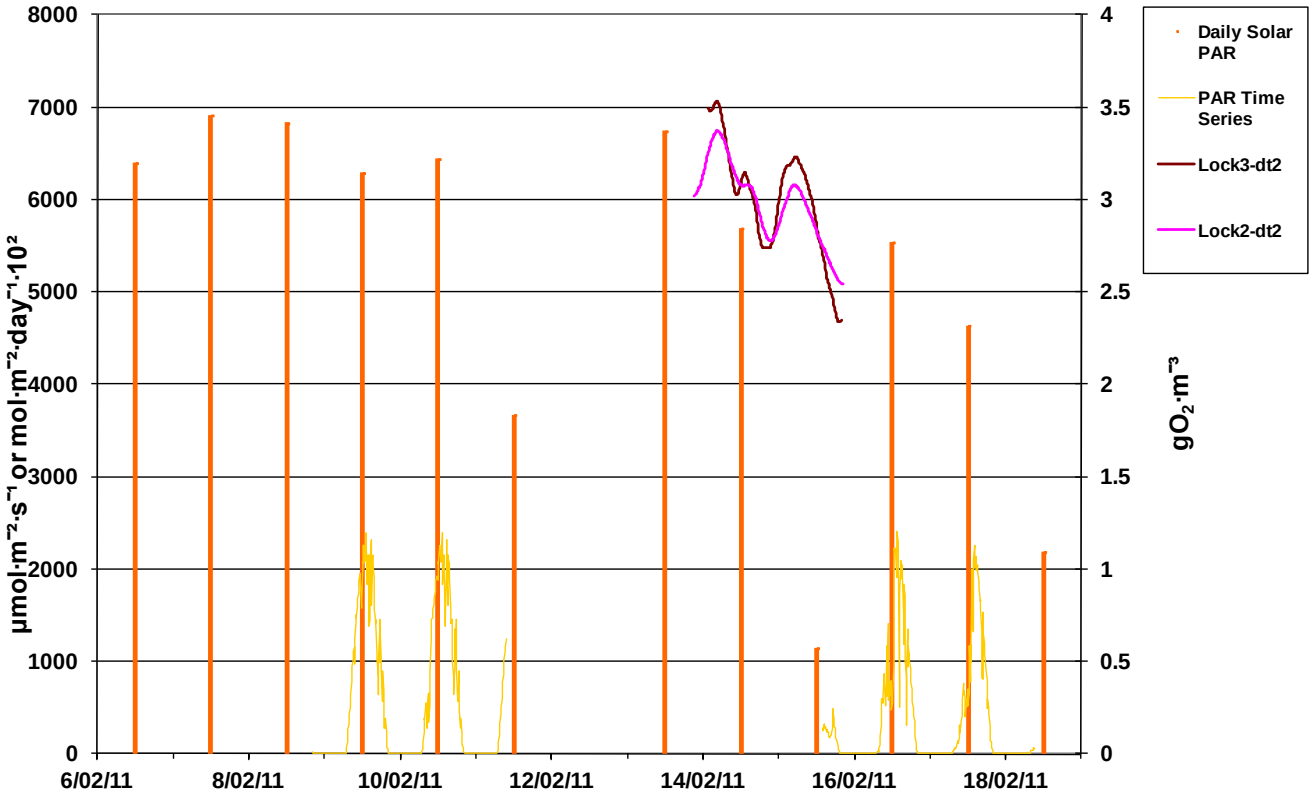


Figure 17. Daily solar photosynthetically active radiation (PAR) and the time series of PAR and oxygen concentrations during metabolism measurements at Lock 3 and 2. The oxygen curves were shifted to align minor peaks with appropriate prior light periods. Satellite estimates of daily irradiance values were obtained from Bureau of Meteorology and converted to PAR. They are multiplied by 10^2 to fit the axis scale.

A diagrammatic representation of these calculations is shown in Figure 16 and Figure 17. In the upper graph of Figure 16 the original time series of the oxygen curves are contrasted with satellite estimates of the daily total PAR (Bureau of Meteorology 2011), and corresponding time series of PAR measured during the actual sampling period. In the lower figure the oxygen curves are shifted to align the major oxygen peaks with the prior light period. In Figure 17 the oxygen curves from Locks 3 and 2 were shifted further back to align the minor intervening peaks with the appropriate daily light estimates. The minor peak appeared between the two major peaks but did not reappear following the second major peak and this was attributed to the very low light intensity measured on the 15/02/2011 (Figure 17).

Site	Time Shift 1 (h)	Time Shift 2 (h)	Distance 1 (km)	Distance 2 (km)	
Lock 5 DS	**4**		**17**		
Lock 4 US	**10**		**44**		
Lock 3 DS	**2**	**38**	**6**	**134**	
Lock 2 DS	**26**	**62**	**78**	**197**	

Table 2. Travel times and distances of oxygen peaks estimated from the time shift required to align the peaks with the previous light conditions where single sets of peaks were observed (Shift 1) or earlier light conditions for multiple sets of peaks (Shift 2).

These calculations indicated that the oxygen peaks at the various sampling locations had travelled different amounts of time from their sources (Table 2). By combining these travel times with estimates of water velocity it was calculated that the oxygen peaks measured at Lock 5 had travelled from 17km upstream while those at Lock 4 had travelled from 44 km upstream (Figure 18). The major oxygen peaks at Locks 3 and 2 came from the same source site as each other which was 2 and 26km upstream of each lock respectively (Figure 18). The secondary peaks at Locks 3 and 2 also came from the same source site as each other, but in this case it was 38 and 62km respectively upstream and was coincident with the source site of the major peaks measured at the Lock 4 US sampling site (Figure 18). The upstream source sites for Lock 5, Lock 4 and the minor peaks at Locks 3 and 2 were all associated with the extensive Chowilla floodplain. The source site for the major peaks at Locks 2 and 3 were associated with a second major floodplain area of shallow lakes and wetlands upstream of these locks at Barmera. The reduced floodplain area between sites 2 and 3 is due to the confinement of the river channel to a gorge section.

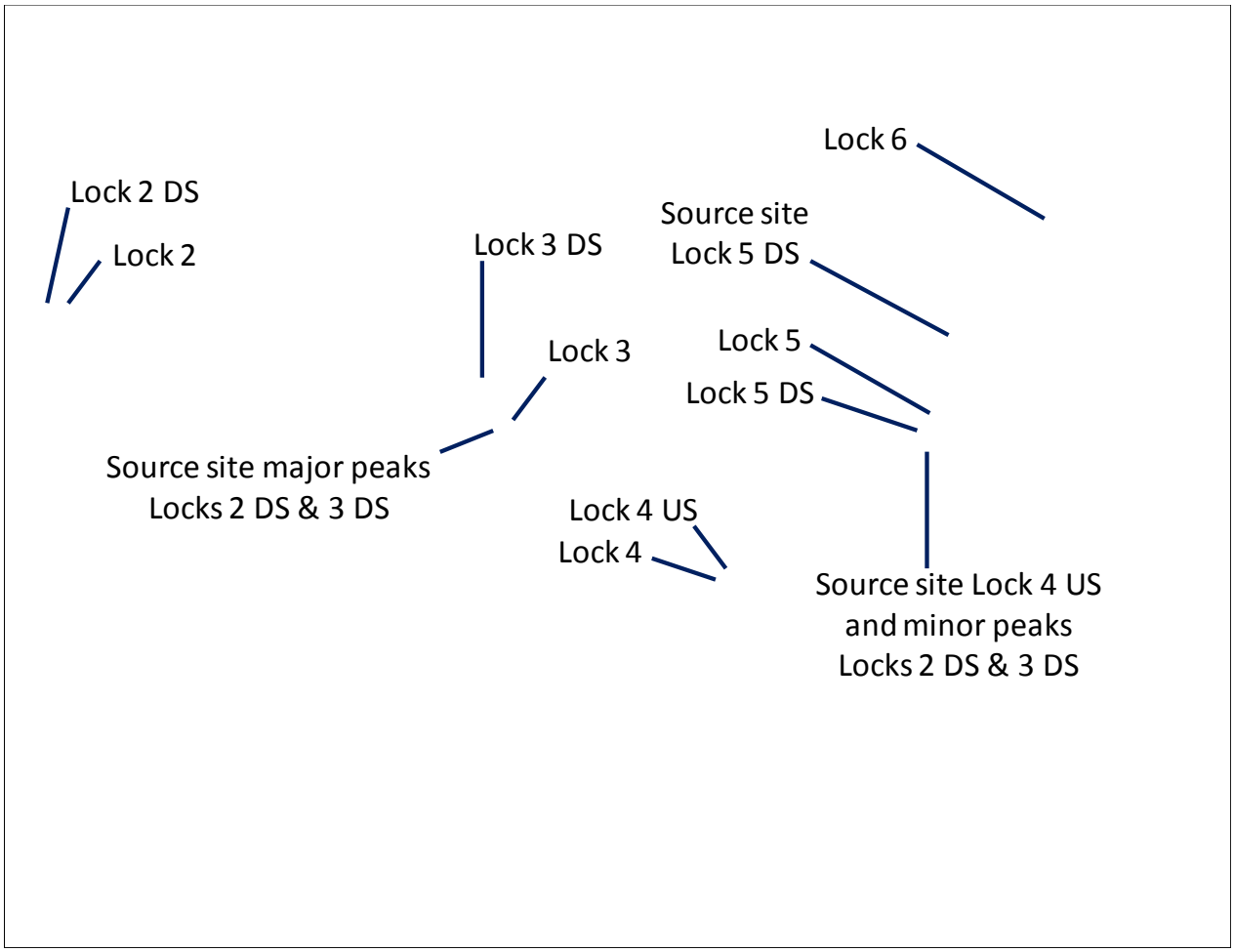


Figure 18. Locations of source sites for oxygen peaks observed travelling along the Murray River during the 2010-2011 flood as described in the text. Also shown are locations of Locks, sampling sites and the maximum recorded floodplain extent from the flood of 1956.

The time shifted peaks in photosynthesis provide an explanation for the unexpectedly high *GP* measurements made during the flood. It seems that the peaks in oxygen were not generated within the river channel, but instead were produced in the shallower waters on the flood plain and the oxygen enriched water was transferred back to the river channel. These oxygen peaks then travelled downstream, slowly diminishing in size due to respiration and gas exchange, and moving progressively further out of alignment with the irradiance that generated their formation.

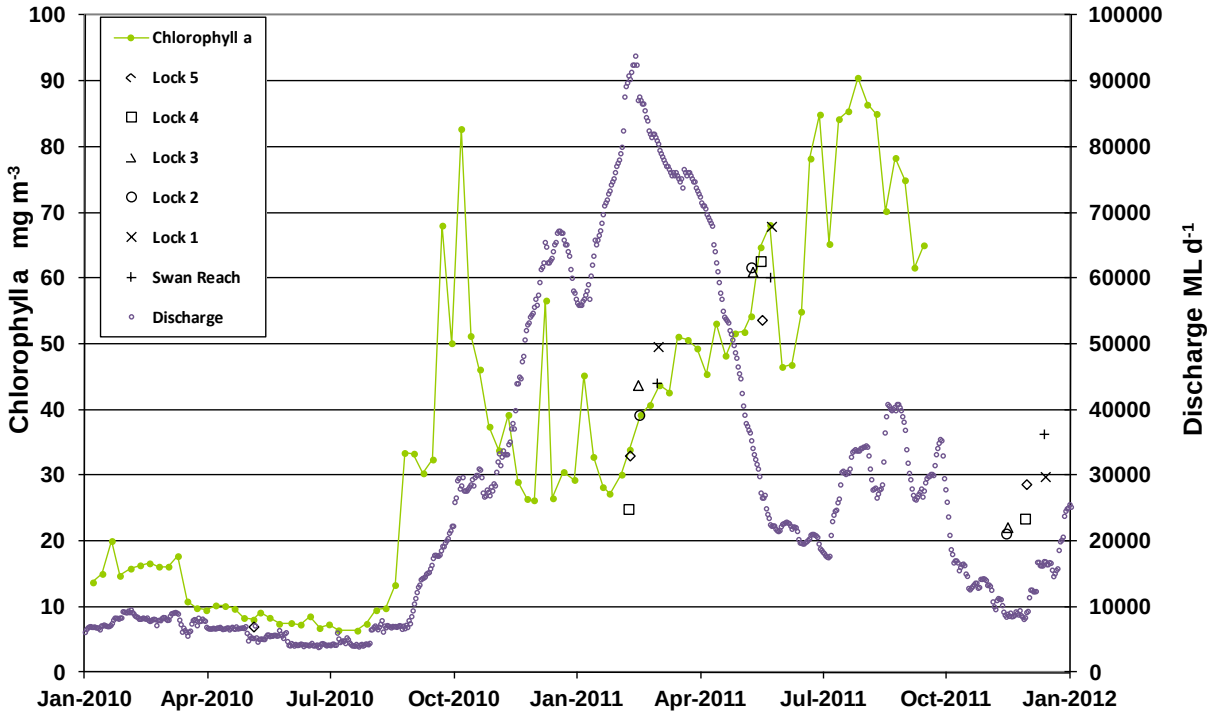


Figure 19. Chlorophyll a concentrations monitored at Morgan by the MDBA, and concentrations determined during metabolism measurements at sampling sites (symbols) compared with the river discharge to South Australia.

If the autotrophic organisms that generated these signals are attached on the floodplain then the estimates of photosynthesis do not correspond to production within the river, but rather to production that remains on the floodplain. If plankton generated the oxygen signal then organic material could be transferred along with the oxygen peak to provide a source of organic material to the channel. Analyses to identify particulate organic matter transfer from the floodplain are ongoing. However the organic matter associated with micro-photoautotrophs is indicated by the chlorophyll a concentrations monitored by the MDBA (Figure 19). At the start of the flood as flows increased to a quarter of the discharge peak chlorophyll concentrations increased to 85 mg m^{-3} then fell back to 35 mg m^{-3} until the peak of the flow arrived. As the peak receded and flow decreased, chlorophyll concentrations increased up to 85 mg m^{-3}. It is unlikely that the large concentrations of phytoplankton grew within the river channel where conditions were not conducive and residence times short, so the growth and production occurred on the floodplain. This demonstrates that significant amounts of autotrophic material were transferred from the floodplain to the river.

Discussion

Metabolism in the lower Murray River

Prior to the flood the metabolic rates in the South Australian section of the Murray River were similar to those measured upstream at other sites along the river and they responded to changes in water velocity in similar ways. As the SA section of the river is comprised of an almost continuous series of weir pools metabolism was more variable than observed in flowing river reaches and small negative *NP* values were common indicating that the weir pool sites accumulated organic material either from upstream or from their local catchment. In flowing sections the rates of *GP* and *CR* were relatively small and closely balanced so that the negative *NP* rates were less than those observed in weir pools. Based on these characteristics it is considered that prior to the flood river metabolism was largely driven by phytoplankton photosynthesis and the respiratory breakdown of phytoplankton cells, but with a small external organic carbon contribution evident within the weir pools. This is consistent with patterns observed further upstream along the river.

This situation changed dramatically in response to the flood. Planktonic *GP* remained at similar levels throughout whereas the open water *GP* was larger than the planktonic rates and on occasions larger than had previously been observed for open water measurements. These continuing and sometimes high rates of *GP* were unexpected because the poor light penetration and the increased water depth within the river channel during the flood were not supportive of high rates of photosynthesis. A detailed analysis of the oxygen measurements showed that the photosynthesis peaks in oxygen concentration were not being generated within the river channel but in the shallower waters of the floodplain. The oxygen signal was then transported into the river channel by the returning floodwaters and moved downstream with little further enhancement by photosynthesis, but with modification of the peaks due to river channel respiration and gas exchange at the air-water interface. Travel time analyses of the oxygen peaks indicated that they were generated in two major floodplain areas, Chowilla and Barmera, with little observable influence from smaller floodplain areas in between. These findings indicate that significant photosynthesis is occurring on the floodplains during the flood but the transport of this production to the river channel will depend on whether the photoautotrophic organisms are attached or not, and whether grazers of attached forms are transported by the flood waters.

Planktonic chlorophyll-*a* analyses were used to estimate the concentration of micro-photoautotrophs in the water column. Apart from occasional summer blooms the chlorophyll concentration in the SA Murray River is commonly between 10-20 mg m^{-3}. At the start of the flood as flows increased to a quarter of the discharge peak chlorophyll concentrations increased to 85 mg m^{-3}

then fell back to 35 mg m^{-3} until the peak of the flow arrived. As the peak receded chlorophyll concentrations increased inversely with flow up to 85 mg m^{-3}. Conditions within the river channel were not suitable for growth of these high and sustained chlorophyll concentrations and they most likely developed in the waters on the floodplain and were transferred back to the channel. This represents a significant source of organic material to the river channel. Whether these planktonic organisms account for most of the production taking place on the floodplain requires further analyses. It is possible that attached aquatic plants and benthic micro-photoautotrophs increase across the inundated floodplain and account for part of the photosynthesis signal but without a transfer of organic material to the river.

The reduced oxygen concentrations that occur in rivers during floods are usually attributed to the respiratory metabolism of organic material transported from the floodplain back into the channel. The most active material is considered to be reactive dissolved organic carbon (DOC) as it is easily transported and its composition is more amenable to assimilation by microbial cells. In contrast, particulate organic carbon may be difficult to transport and less suitable for assimilation depending on particle size and composition. Particulate organic carbon forms a surface for microbial activity or small particles can be consumed directly by larger organisms including aquatic invertebrates. The respiratory breakdown of DOC or POC by micro-organisms and aquatic invertebrates increases their growth rates and is expected to provide an enhanced source of food and energy to the lower trophic levels of aquatic foodwebs. These are critical food resources for aquatic ecosystems and have important influences on food web structure and functioning so it is important to obtain a better understanding of their delivery and usage in the river channel.

The compositional suitability of DOC and POC for metabolic breakdown is influenced by prior weathering and metabolism on the floodplain. Because respiration rates can vary greatly in response to the organic matter composition and the composition of the biotic community, loss rates preferably are measured *in situ.* Downstream reductions in the DOC concentration were analysed to estimate the rate of decline and this was attributed to respiratory breakdown. It was found that the rates of DOC decline accounted on average for 50% of the measured planktonic respiration rates. Planktonic respiration rates were four times higher during the flood than prior to the flood so the contribution from the respiratory breakdown of DOC was not insignificant. However, the DOC respiration accounted for only 15% of the open water respiration rates with other planktonic respiration accounting for a further 15%. The large remainder of the open water respiration was attributed to non-planktonic sources.

The non-planktonic respiration is usually considered due to metabolism by attached organisms within the river channel or to respiration of organic material that has sedimented to the bottom. Attached organisms are unlikely to have been productive during the flood period and so sedimented particulate organic material was considered likely to be the source of the organic carbon driving the non-planktonic respiration. However, if this sedimented particulate organic carbon was the debris of terrestrial material weathered and metabolised on the floodplain then the mass specific rate of breakdown is expected to be slow and a large quantity would need to be transported to account for the large oxygen depletion rates. In these circumstances the respiration of this material might be expected to continue after the passage of the flood. Instead respiration rates quickly declined as the flood receded resulting in both open water and planktonic respiration rates being only slightly greater than they were prior to the flood. It is possible that reactive forms of particulate organic carbon were transported from the floodplain and were rapidly respired within the bottom sediments, but the terrestrial source for such an organic carbon supply is not obvious.

An alternative source of organic material for the non-planktonic respiration could paradoxically have been phytoplankton. The high concentrations of phytoplankton during the flood could have led to a continual sedimentation of cells to the bottom of the river channel where their breakdown caused the major oxygen reduction within the river. As phytoplankton cells are rapidly broken down there would not be an extended period of respiration following the flood and this was observed in the data. However as the flood receded the phytoplankton concentration increased significantly and the water velocity declined and so the amount of phytoplankton sedimenting would have been expected to increase leading to increased respiration in the sediments. This was not observed and instead non-planktonic respiration rates declined suggesting that phytoplankton sedimentation was not a major contributor at this time. Conditions during the flood were quite different to those following and so it is possible that phytoplankton sedimentation was an important contributor to the non-planktonic respiration and represents a major pathway for organic carbon transfer into the river foodwebs during a flood, but the magnitude of this contribution cannot be assessed from the data without further analyses.

On balance it is suspected that a large component of the respiratory reduction in oxygen that was observed in the river channel during the flood was actually due to oxygen drawdown in water moving across the floodplain and returning to the river. This corresponds with the observations that significant proportions of the primary production were occurring in waters on the floodplain. The significance of this respiratory activity to the river channel foodwebs then depends on whether the organisms utilising the organic materials are attached or planktonic. If the respiratory activity was due to processes occurring on the floodplain, perhaps driven by metabolism in the flooded soils

drawing down oxygen in the overlying flood waters, then this component of the respiration would not necessarily represent a corresponding source of organic carbon to the river channel. Under these situations, estimating the food resources delivered to rivers during floods based solely on the decline in oxygen concentration within the river channel would over estimate the supply of organic carbon to the system. In the future, continuous measurements of oxygen at selected stations along the river would provide greater ability to interpret the processes and interactions observed (Izagirre et al 2008).

Conclusions

It was found that during the flood significant proportions of *GP* and *CR* estimated from measurements within the river channel were actually the result of processes occurring on the floodplain. The flood caused large increases in phytoplankton production which mostly occurred on the floodplain with significant quantities of cells transported to the river channel. It was estimated that of the increased respiration measured in the river channel, one third was due to processes within the water column including the breakdown of dissolved organic carbon transported from the floodplain and the respiration of phytoplankton that were also transferred from the floodplain. However, the specific location or organic carbon sources responsible for 70% of the respiration measured within the river channel could not be conclusively identified. This might be due to the respiration of organic material collected within the bottom sediments of the river in which case it would be of direct importance to the river food web. Alternatively it might be due to processes on the floodplain de-oxygenating the passing flood waters without contributing the organisms utilising the carbon supply to the river channel, in which case its importance to river food chains will depend on other forms of connection. Such connections include the movement of river organisms onto the floodplain during floods, later wash-in by rainfall runoff, or the occurrence of follow up floods. It is likely that there are contributions from both sedimented organic material and floodplain respiration.

Identification of the sites of major floodwater metabolism is important information for the management of the river system. In the South Australian section of the Murray River the two large floodplain areas of Chowilla and Barmera were identified as major sites for phytoplankton photosynthetic production. These floodplains were also important sources of organic matter and suspected to be major sites of oxygen depletion and so likely to represent a site of major food supply where organic material is transformed into microbial biota. The extent to which the organisms growing on the floodplain represent food resources for the food webs of the river channel is more difficult to quantify. Part of the phytoplankton biomass that formed on the floodplain was transferred to the river channel. The contribution to primary production of attached

photoautotrophs on the floodplain has not been determined from the data but is expected to be relatively small because of the flood conditions. The transfer into the river channel of heterotrophic organisms growing on the floodplain could not be assessed from this data, but other projects have collected data that could provide information on this question and further joint analyses are warranted. In either case it is unlikely that all the potential food resources formed on the floodplain are transferred back to the river channel. This supports the need for access to the floodplain by organisms during times of flood to maximise opportunities to harvest food resources that develop there. Overall the results highlight the importance of the dynamic connection between the river and floodplain and especially to significant areas of flooding such as Chowilla and Barmera.

Following the major flood the rates of metabolism declined to levels similar to those prior to the flood. There were slightly increased respiration rates evident during the final two samplings that suggested a small store of residual organic carbon had been transported into the river by the flood but this was smaller than expected and its role is yet to be fully explored. However, this increased activity might alternatively have been due to a small secondary flood peak which further perturbed the system close to the final project measurements. Continuing measurements would have been necessary to monitor the return of the river to pre-flood conditions.

The results suggest that high rates of oxygen depletion in rivers during floods cannot be directly interpreted as increased supplies of organic material to the river channel and may lead to an over estimate of the supply of energy to the channel. Consequently a reduction in floods may be more significant than currently perceived as smaller supplies of organic material are delivered to the river on each occasion. Improving our understanding of these interactions will help to better identify the importance of internal and external supplies of organic carbon and the role of floods in delivering enhanced food supplies to the river channel.

Further analysis of the data would provide more insight into the effects of the flood as time did not allow for all measurements to be completed and incorporated into this report. In addition further exploration of the characteristics of the flood waters using remote sensing would help identify larger scale connections between the distributions of organisms and metabolic activity. There are clearly links between the extent of inundation and the metabolic and biotic responses and the means to explore these connections are available.

References

Battin, T.J., Kaplan, L.A., Findlay, S., Hopkinson, C.S., Marti, E., Packman, A.I., Newbold, J.D. and Sabater, F. (2008) Biophysical controls on organic carbon fluxes in fluvial networks. Nature Geosci 1(2), 95-100.

Bunn SE, Davies PM,Winning M. 2003. Sources of organic carbon supporting the food web of an arid zone floodplain river. Freshwater Biology 48: 619–635.

Bureau of Meteorology 2011 Daily Global Solar Exposure Climate Data. Commonwealth Government of Australia. Data source created on Wed 24 Aug 2011 06:29:56.

Burford, M.A., Cook, A.J., Fellows, C.S., Balcombe, S.R., Bunn, S.E. (2008) Sources of carbon fuelling production in an arid floodplain river. Marine and Freshwater Research, 59(3): 224-234.

Dodds, W.K. and Cole, J.J. (2007) Expanding the concept of trophic state in aquatic ecosystems: It's not just the autotrophs. Aquatic Sciences 69(4), 427-439.

Doi, H. (2009) Spatial patterns of autochthonous and allochthonous resources in aquatic food webs. Population Ecology 51(1), 57-64.

Hampton SE, Scheuerell MD and Schindler DE (2006) Coalescence in the Lake Washington story: Interaction strengths in a planktonic food web. *Limnology and Oceanography* 51, 2042–51.

Howitt, J.A., Baldwin, D.S., Rees, G.N. and Williams, J.L. (2007) Modelling blackwater: Predicting water quality during flooding of lowland river forests. Ecological Modelling 2 0 3, 229–242.

International Oceanographic Tables. 1973. Volume 2. Prepared under the supervision of the Joint Panel on Oceanographic Tables and Standards. National Institute of Oceanography of Great Britain, Wormley, Surrey and Unesco, Paris.

Izagirre, O., Agirre, U., Bermejo, M., Pozo, J.s. and Elosegi, A. (2008) Environmental Controls of Whole-Stream Metabolism Identified from Continuous Monitoring of Basque Streams. Journal of the North American Benthological Society 27(2), 252-268.

Kosinski, R. .J. (1984) A comparison of the accuracy and precision of several open-water oxygen productivity techniques. *Hydrobiologia,* **119,** 139-148.

Lefevre E, Roussel B, Amblard C and Sime-Ngando T (2008) The molecular diversity of freshwater picoeukaryotes reveals high occurrence of putative parasitoids in the plankton. PLoS ONE 3(6): e2324.

McCutchan, J. H., Lewis, W. M., and Saunders, J. F. (1998). Uncertainty in the estimation of stream metabolism from open-channel oxygen concentrations. *Journal of the North American Benthological Society* **17**, 155-64.

Maheshwari, B.L., Walker, K.F. and McMahon, T.A. (1995) Effects of regulation on the flow regime of the river Murray, Australia. Regulated Rivers: Research & Management 10(1), 15-38.

Moore, J.C., Berlow, E.L., Coleman, D.C., de Ruiter, P.C., Dong, Q., Hastings, A., Johnson, N.C., McCann, K.S., Melville, K., Morin, P.J., Nadelhoffer, K., Rosemond, A.D., Post, D.M., Sabo, J.L., Scow, K.M., Vanni, M.J. and Wall, D.H. (2004) Detritus, trophic dynamics and biodiversity. Ecology Letters 7(7), 584-600.

Murphy, B.F. and Timbal, B. (2008) A review of recent climate variability and climate change in southeastern Australia. International Journal of Climatology 28(7), 859-879.

Odum H.T. (1956). Primary production in flowing waters. *Limnology and Oceanography,* **1,** 102-117.

Oliver RL and Lorenz Z. (2010) 'Flow and metabolic activity in the channel of the Murray River'. In: Saintilan, N. and Overton, I.C. (eds) (2010). 'Ecosystem Response Modelling in the Murray-Darling Basin'. CSIRO Publishing, Canberra, Australia.

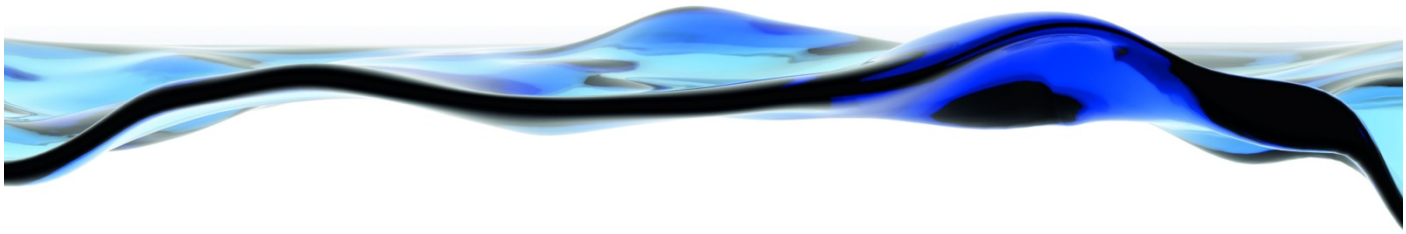
Oliver, R. L. & Merrick, C. (2006) Partitioning of river metabolism identifies phytoplankton as a major contributor in the regulated Murray River (Australia). *Freshwater Biology* **51**, 1131–48.

Thorp J.H. and Delong M.D. (1994) The riverine productivity model: an heuristic view of carbon sources and organic processing in large river ecosystems. *Oikos,* **70,** 305-308.

Vannote R.L., Minshall G.W., Cummins K.W., Sedell J.R. and Cushing C.E. (1980) The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences,* **37,** 130-137.

Vink, S., Bormans, M., Ford, P.W. and Grigg, N.J. (2005) Quantifying ecosystem metabolism in the middle reaches of Murrumbidgee River during irrigation flow releases. Marine and Freshwater Research 56(2), 227-241.

Young R.G. and Huryn A.D. (1996) Interannual variation in discharge controls ecosystem metabolism along a grassland river continuum. Canadian Journal of Fisheries and Aquatic Sciences, 53, 2199-2211.



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