Distribution and persistence of temporary wetland habitats in arid Australia in relation to climate

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Abstract The distribution and area of temporary wetlands across the arid zone of Australia are highly variable. Any change in their distribution or extent due to climate change and/or extraction of water has the potential to adversely impact dependent biota. Satellite imagery was used to determine the spatial and temporal distribution of wetlands across arid Australia over an 11-year period. Synoptic climate data were examined to identify the weather systems that caused wetland filling events. Simple threshold models relating rainfall to wetland filling for seven large regions of Australia were developed to examine patterns of wetland filling over the last 100 years. These data were used to examine the climatic processes that drive wetland filling and the likely impacts of climate change on wetland distribution. The strongest climatic influence on wetland filling in the arid zone was tropical weather systems. Their influence extended into southern regions and their effects were often widespread. Variation in wetland area in all regions of the arid zone was high. The Lake Eyre Basin experienced more large flood events than other regions and had the most large, persistent wetlands that remain unregulated by humans. Hindcasting of past filling events indicated that there was a general pattern of frequent wetland filling across inland Australia in the 1910s, 1950s and 1970s, and less frequent wetland filling in the late 1920s, 1930s and 1960s. Furthermore, there appeared to be no period greater than 12 months over the previous 95 years when there was no predicted wetland filling in the arid zone. Wetland ecosystems dependent on a few infrequent heavy rainfalls are clearly vulnerable to any change in frequency or magnitude of these events. Climate change that results in a drying or reduced frequency of large flood events, exacerbated by extraction of water for agriculture, could be catastrophic for some biota, particularly waterbirds, which use a mosaic of wetland habitat at broad spatial scales.

Key words: climate change, El Niño–Southern Oscillation, temporary wetlands, tropical weather systems, waterbirds.

INTRODUCTION

Rainfall in the arid interior of Australia is highly variable in timing, duration and intensity, even when compared with other arid regions of the world (Stafford Smith & Morton 1990). Consequently, Australian rivers have greater variation in flow and flooding patterns than elsewhere on the globe (Williams 1981; Puckridge et al. 1998). These variable flows combine with low topographic relief to isolate many standing waters from each other spatially and temporarily (Williams 1981). The two greatest threats to fauna dependent on these temporary wetlands are global climate change and the development of water-extracting industries. In North America, numbers of waterfowl are predicted to decline by more than half by 2060 in response to declines in wetland abundance due to climate change (Sorenson et al. 1998; also see Bethke & Nudds 1995). In Australia, most endemic waterbirds are known to frequent the arid zone (Frith 1982; Marchant & Higgins 1990; Briggs 1992) and upwards of 8 million waterbirds were estimated to utilize the wetlands of the arid interior in 1995, a dry year (Kingsford & Halse 1998). In an already highly variable environment (Stafford Smith & Morton 1990), increases in rainfall variation have the potential to cause sudden rather than incremental change in some populations if the return period for heavy rainfall events exceeds the reproductive lifespan of individuals or results in extraordinary drought-induced mortality. The extraction or diversion of water has already had adverse impacts on Australia’s dryland rivers (Walker 1985; Kingsford & Thomas 1995; Kingsford 2000). A major difficulty for managers in deciding how to respond to these threats is uncertainty about current levels of water availability, how these compare to previous decades and likely scenarios for the future. The key to understanding these issues is knowledge of the

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current distribution and persistence of wetlands and the weather and climatic forces that drive wetland-filling events.

The many thousands of temporary wetlands found in the arid zone of Australia range in size from a few square metres to thousands of square kilometres and support a diverse biota (Williams 1998a,b). These standing waters can be terminal water bodies filled by major drainage systems (e.g. Lake Eyre), lakes filled by local drainage (e.g. Lake Gairdner and Lake Torrens) or creeks and overflow lakes associated with major drainage systems, which are filled by flood events, such as those that occur along Cooper Creek and the Darling, Paroo and Warrego Rivers (Bowler 1982, 1986; Kotwicki 1986; Kingsford & Porter 1991, 1993, 1994; Timms 1993, 1997, 1998a,b, 1999; Knighton & Nanson 1994; Walker et al. 1995; Seddon et al. 1997; Kotwicki & Allan 1998; Puckridge 1998). Flood events range in duration from minutes to months as floodwaters flow quickly down dry drainage lines or traverse many hundreds of kilometres of river channel in the larger drainage basins.

The modelling of hydrological processes in arid environments is made difficult by a number of practical and theoretical problems. The major practical problem is a paucity of data with which to develop or verify a model (Pilgrim et al. 1988; Kotwicki & Allan 1998). In addition, most hydrological models of runoff and stream flow are deterministic and assume homogeneity of abiotic and biotic characteristics in catchments. Hydrological processes in arid environments are highly variable in time and space and the coefficients of variation in runoff characteristics in Australian catchments tend to increase with increasing catchment size (Finlayson & McMahon 1988). When stream-flow data have been used to construct hydrological models for the arid zone, the applicability of the model remains site specific (e.g. Knighton & Nanson 1994; Puckridge et al. 1999). Because of the paucity of hydrological data, the modelling of surface flows over larger regions of the arid zone is dependent on rainfall data, or some derivative thereof (Bowler 1986; Kotwicki 1986).

In the present paper we analyse the distribution of temporary wetlands across the arid zone of Australia and the climatic influences that drive wetland filling in order to determine the likely impacts of climate change on wetland distribution and waterbird populations. First, the spatial and temporal distribution and areas of wetlands across inland Australia were determined from satellite imagery. Second, these data were used to identify wetland filling events (positive changes in wetland area) and synoptic climate data were examined to identify the weather systems that caused filling. Third, a simple threshold model was developed to examine patterns of wetland filling across inland Australia since 1889 in each of seven arid regions. Finally, the likely impacts of climate change on wetland distribution and waterbird populations are discussed.

**METHODS**

**Spatial and temporal distribution and areas of wetlands**

The study area was 5.4 million km² or 71% of the Australian mainland (Fig. 1). Wetlands were mapped using Advanced Very High Resolution Radiometer (AVHRR) satellite imagery. The AVHRR data have a single channel in the visible red (channel 1, 0.58–0.68 μm), near infrared (channel 2, 0.725–1.10 μm) and mid-infrared (channel 3, 3.55–3.93 μm) parts of the electromagnetic spectrum and two channels in the thermal infrared (channels 4 and 5; 10.3–11.5 μm and 11.5–12.5 μm, respectively). The coarse resolution of these data (1.1 km) means that the smallest picture element or pixel has an area of 120 ha and only wetlands larger than this in area could be mapped reliably.

Data from AVHRR with consistent radiometric processing and complete continental coverage are not yet available for Australia (McVicar & Jupp 1998). There are two major sources of archived AVHRR data in Australia, CSIRO Marine Laboratories in Hobart and the Department of Land Administration (DOLA) in Perth. Data from both sources have been archived since 1981 but a comprehensive archive of imagery does not exist for dates prior to September 1986. For data sourced from CSIRO Marine Laboratories, Hobart, wetlands were mapped by using an algorithm that compares the spectral signature of water in each picture element or pixel to that of known water bodies (Roshier 1999). The resultant image has a distribution of digital values with zero mean and minimum variance, where target matches score unity and pixels with none of the target feature have negative values (Research Systems et al. 1996). Pixels that partially match the target return a value between zero and one. These digital values can be related directly to proportion of the target in each pixel and can therefore be used to estimate area.

For data sourced from DOLA in Perth, negative Normalized Difference Vegetation Indices (NDVI) were used as a proxy for water (Fleming 1993; Verdin 1996; Roshier 1999). The NDVI are derived from visible red light and near-infrared radiation (NIR) channels in satellite data and tend to enhance features that have higher NIR reflectance and lower red light reflectance. The index is \((\text{NIR} – \text{red})/(\text{NIR} + \text{red})\) and takes values between –1 and +1. Open water features tend to have negative values, bare soil takes values near zero and vegetation takes positive values (McFeeters 1996).
The results of these classifications are a single array of picture elements or pixels, with each pixel having a value that denotes the degree to which the spectral signature of that pixel in the original image corresponds to the spectral signature of water. These data were converted to concentric contours in a Geographic Information System (GIS) and a single contour was selected to approximate the wetland boundary (Roshier 1999). Contours at the wetland boundary are close together and the contour selected is that which reliably represents the water boundary without including areas of damp soil or salt (see Roshier 1999 for details).

No single satellite image gave Australia-wide coverage, because of limitations of geographical extent of satellite coverage and cloud cover. To generate a composite view of water distribution for a period, images were selected that gave cloud-free views of continental Australia from any date within a month-long sampling period. The results from cloud-free regions in each image were combined in a GIS to form a composite view of wetland distribution for each month-long sampling period. Where data were available for an area on two or more dates within each month-long sampling period, the maximum extent of water was used.

Satellite data were analysed for sampling periods 6 months apart over the 11-year period from September 1986 to September 1997. In addition, between March 1987 and December 1990 data were processed for June and December of each year to correspond with waterbird surveys in the north-west of NSW (Kingsford et al. 1994). Thus, we analysed satellite imagery from 31 month-long sampling periods.

To determine wetland persistence, water distribution for each sampling period was represented by a binary map of 1-km grid cell size showing areas of wetland. Where the wetland distribution for a sampling period overlapped with a wetland from an earlier sampling period, a cumulative count (0–31) in each grid cell in the region of overlap occurred and data from all sampling periods were consolidated into a single map. For catchments in the study area with missing or incomplete wetland distribution data, the wetland persistence data were corrected for number of observations.

Wetland filling and climatic influences

Historical rainfall data for the period 1889–1995 (Bureau of Meteorology, Melbourne) were interpolated to a $1/4° \times 1/4°$ grid by the Queensland Centre for Climate Applications (Queensland Department of Primary Industries, Brisbane) and mean monthly rainfall was calculated for regions within the study area with similar drainage patterns and climatic influences.

Monthly rainfall totals used in the present paper represent spatially averaged rainfall for a region in that month. The boundaries of these regions were based on the boundaries of drainage divisions (AUSLIG

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**Fig. 1.** Study area (all shaded areas) and climatic regions used in this study. Regions were based on a combination of AUSLIG 1:250000 digital drainage data and prevailing weather patterns.
colder air from higher latitudes is ‘cut-off’ by warmer
which form as a middle-level tropospheric feature when
the least well-known weather systems are cut-off lows,
systems, or some combination of these types. Of these,
subsequent rain depressions, cut-off lows, frontal
ical troughs), strong monsoonal, tropical cyclones and
of the regions. Weather systems were broadly classified
ments to wetland area, weather systems or climatic
between samplings identified. For all positive incre-
positive increments to wetland area in the 3 or 6 months
area. Wetland area in each region was summed and
larger wetland filling events are more readily associ-
leading to wetland filling is somewhat subjective.
or climatic phenomena as the source of surface runoff
phenomena explained positive increments to wetland
area in each of the regions. Identifying a weather event
phenomena as the source of surface runoff
leading to wetland filling is somewhat subjective.
Larger wetland filling events are more readily associ-
related to wetland filling
mean sea level pressure maps, together
with descriptions of synoptic systems (Bureau of
Meteorology classifications of major weather systems
seen in the accompanying synoptic charts in their
Monthly Weather Review (Bureau of Meteorology
1986–1995). It was felt that this approach, together
with the experience of P. H. Whetton and R. J. Allan
as climate scientists in determining synoptic types, was
quite sufficient to deduce the major climatic controls
influencing wetland filling. More sophisticated synoptic
typologies could have been used but they would
not have produced any more incisive determination of
the major weather systems operating at the scale of the
present study.
In order to examine the likely temporal distribution
of wetland filling events implied by historical rainfall
data, changes in wetland area were regressed on mean
monthly rainfall for each region to produce a simple
threshold model of wetland filling. Rainfall data were
not available for the full period of the study and these
analyses are restricted to dates prior to December 1995.
Because it was not clear how much antecedent rainfall
was required to initiate wetland filling in the different
regions, wetland area was regressed on regional rain-
fall averaged for 3- and 6-month periods prior to the
month of observation. The 3-monthly data were only
available for the period from March 1987 to March
1991. The models developed using the 6-monthly data
were derived from up to 26 data points separated by
3- and 6-month time periods. Thus, not all these data
were independent as some 6-monthly intervals over-
lapped each other. Data points were not dropped to
eliminate this lack of independence as the data were
insufficient in some climatic regions.
There are reasons to expect that the relationship
between wetland area and the preceding 3- or 6-
monthly rainfall may not be linear. In particular,
decreases in wetland area will be dependent on previous
wetland area and increases will be affected by catch-
ment characteristics. However, in the absence of any
theoretical justification for a particular non-linear
relationship, a linear relationship was assumed. In each
regression model the y-intercept estimated the amount
of rainfall, averaged over the whole region, that was
needed to produce a positive increment to wetland area.
This estimate, or threshold, was used to generate time-
series of wetland filling events in each region for the
period 1889–1995 by using interpolated monthly
totals derived from historical rainfall records (as
described previously).

RESULTS

Spatial and temporal distribution and area of
wetlands

Total surface water area in the study area varied by
an order of magnitude during 11 years, from less
than 315 000 ha in September 1986, June 1987 and
September 1994 to 3305 000 ha in June 1989 (Fig. 2). Some drainage basins rarely contained water bodies large enough to be detected using AVHRR satellite data or were dry, while others experienced several major floods. The extent of the flooding was sometimes extraordinary. In March 1991, more than 1800 000 ha of the floodplains of Cooper Creek and the Diamantina and Georgina Rivers were inundated. Six months later, the total wetland area in the Lake Eyre Basin had declined to 155 000 ha. This cycle of flooding and drying in the Lake Eyre Basin occurred four times in 11 years (Fig. 2). Most other regions in the arid zone experienced only one or two major flooding events. For instance, a major flood occurred in southern parts of Western Australian after Cyclone Bobby crossed the coast in February 1995 and another major flood occurred in the Northern Territory in March 1993 after heavy monsoon rains.

Persistence of wetlands

While many drainage features were inundated only once in 11 years, some wetlands contain water most of the time, even in the driest parts of the continent. Lakes Koolivoe and Mipia on the fringes of the Simpson Desert, some of the Coongie Lakes in northern South Australia and Lakes Wyara and Numalla in southwestern Queensland hold surface waters with similar regularity to water bodies with modified water regimes resulting from damming or increased inflows (Appendix I).

Among persistent wetlands (i.e. those with water present on more than 50% of sampling dates) only 24 (44%) have water regimes unmodified by human activities (i.e. those not dammed or with artificially increased inflows). Nonetheless, the maximum possible surface area of wetlands with unmodified water regimes exceeds that of wetlands with a modified water regime by 7.8 times. The largest unregulated wetland, Lake Eyre, filled only once in 11 years when an intense tropical rain depression bought widespread rain to inland Australia in March 1989.

Of the persistent wetlands in the Murray–Darling Basin that are large enough to be detected using the methodology used here, few remain unmodified (Fig. 3). The exceptions are Lake Tyrrell in Victoria, Narran Lake and Lake Teryaweya in New South Wales, and Lake Bullawarra in Queensland (Appendix I). Assuming that all wetlands with a modified water regime are filled to their natural shoreline, the maximum possible surface area of modified wetlands in the study area is 135 500 ha. This represents less than 5% of the wetland area in the study area during periods of greatest wetland extent, for example June 1989 and March 1997. A similarly uneven geographical distribution exists for unmodified persistent water bodies. Most of these are located in the Lake Eyre Basin and the adjacent catchment of the Paroo River (Fig. 3). A notable exception is Lake Gregory in north-western Western Australia.

Wetland filling and climatic influences

Changes to wetland area in each of the regions were pulsed over the 3- and 6-month intervals used in the analysis (Fig. 4). In particular, between December 1990 and March 1991, wetland area in the Upper Eyre region increased 10-fold after heavy rains from tropical weather systems, before declining to its preflood level 6 months later. Some of these wetland-filling events resulted from single large weather systems, such as the tropical system that brought widespread rain to the Upper Eyre, Lower Eyre, Torrens and Cobham regions in March 1989. At other times the wetland filling resulted from rainfall over an extended period. For example in December 1992 and January 1993, frontal
systems combined with tropical weather systems to bring 190 mm of rainfall to the Cobham region in 5 weeks (Fig. 4). In most regions wetland area is highly variable and aseasonal, changing by orders of magnitude in the 3 or 6 months between estimates (Fig. 4). Wetland area can be near its peak for a decade or near its lowest in any month of the year.

Most weather systems that contributed to wetland filling in the study area were tropical in origin or an interaction of tropical and mid-latitude weather systems (Table 1). For Upper and Lower Eyre, Darling, Cobham and Northern Deserts all wetland filling was associated with tropical weather systems. Frontal weather systems were most influential in: (i) the

Table 1. The number of wetland filling events resulting from different types of weather systems during the period 1986–1995 in each region

<table>
<thead>
<tr>
<th>Weather system type</th>
<th>Upper Eyre</th>
<th>Lower Eyre</th>
<th>Darling</th>
<th>Murray</th>
<th>Cobham</th>
<th>Torrens</th>
<th>Northern Deserts</th>
<th>Southern Deserts</th>
<th>Gascoyne</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Tropical</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tropical systems</td>
<td>5</td>
<td>6</td>
<td>5</td>
<td>2</td>
<td>5</td>
<td>3</td>
<td>6</td>
<td>5</td>
<td>3</td>
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<tr>
<td>Tropical cyclone or rain depressions</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Strong monsoon</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Sub-total</td>
<td>6</td>
<td>6</td>
<td>5</td>
<td>2</td>
<td>5</td>
<td>5</td>
<td>8</td>
<td>7</td>
<td>5</td>
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<tr>
<td><strong>Tropical–mid-latitude</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tropical systems + frontal systems</td>
<td>3</td>
<td>6</td>
<td>1</td>
<td>3</td>
<td>4</td>
<td>5</td>
<td>5</td>
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<td>1</td>
</tr>
<tr>
<td>Cut-off low</td>
<td>2</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Cut-off low + tropical system</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>0</td>
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<tr>
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<td>6</td>
<td>9</td>
<td>1</td>
<td>3</td>
<td>5</td>
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<td>8</td>
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<td><strong>Mid-latitude</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
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<tr>
<td>Frontal system</td>
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<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>3</td>
<td>2</td>
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<tr>
<td>Cut-off low + frontal system</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Sub-total</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td><strong>Total wetland filling events</strong></td>
<td>12</td>
<td>15</td>
<td>6</td>
<td>7</td>
<td>10</td>
<td>15</td>
<td>16</td>
<td>15</td>
<td>9</td>
</tr>
</tbody>
</table>

Fig. 3. Wetlands that are highly or moderately persistent (water present on more than 67 and 50% of sampling dates (1986–1997), respectively) in the study area ( ), based on data in Appendix I. Basin boundaries are marked as solid lines.
Fig. 4. (——) Wetland area and (■) monthly rainfall totals for the period 1986–1997. Note that: (i) rainfall data were not available after 1995; (ii) there are different scales on the y-axis for wetland area; and (iii) there was a 6-month interval between samplings after March 1991. (a) Upper Eyre; (b) Lower Eyre; (c) Darling; (d) Murray; (e) Torrens; (f) Northern Deserts; (g) Southern Deserts; (h) Gascoyne; (i) Cobham. The solid lines are discontinuous because cloud cover prevented the determination of wetland area from satellite data during these periods.
Southern Deserts region; and (ii) in the Torrens, Lower Eyre and Northern Deserts regions, where they combined with tropical weather systems to bring widespread rain (Table 1).

Linear regression models of change in wetland area in each region plotted against rainfall showed that for the nine relationships that were significant, the $y$-intercept was between 15 and 23 mm, with most less than 20 mm (Table 2). Based on these regressions a conservative threshold of 20 mm mean monthly rainfall in the previous 3 months was used to model wetland filling events since 1889 using historical rainfall data. No attempt was made to model wetland filling for the Murray and Darling regions as no reasonable model relating wetland filling and rainfall could be constructed using the available data.

Hindcasting of filling events using a threshold of 20 mm mean monthly rainfall (Table 2) indicated that the distributions of probable wetland filling events varied with region (Fig. 5). For the Northern Deserts and Gascoyne regions there appear to have been an almost annual occurrence of wetland filling events, with the longest period between events being 2 years. For the Lower Eyre, the driest region, there may have been periods up to 8 years with no wetland filling event. In contrast, the pattern of wetland filling in the Upper Eyre region was relatively regular, with the longest period between predicted wetland filling events being 4 years in the late 1920s. Across the regions there was a general pattern of frequent wetland filling in the 1910s, 1950s and 1970s, and less frequent wetland filling in the late 1920s, 1930s and 1960s.

Although the distribution of wetland filling events predicted by the model varied between regions, there appeared to be no period greater than 12 months over the previous 95 years when there was no predicted wetland filling in the whole arid zone. The only periods when most of the regions would have had few wetlands flooded were in the mid-1930s and mid-1940s. At these times the model predicts that wetland filling events occurred only in the Northern Deserts region. At other times when the eastern part of the study area was dry (i.e. late 1920s, late 1950s and late 1960s) the Gascoyne and Northern Deserts regions were likely to have had flood events. Conversely, when the Gascoyne, Northern and Southern Deserts regions in the western part of the study area were dry in the early 1890s, the model predicts that there were wetland filling events in the east.

**DISCUSSION**

**Wetland distribution**

The results of the present study show that large areas of the arid zone are inundated at frequent but irregular intervals. Even at the driest times in the 11 years studied, the region had substantial areas of wetland and the large flood events recorded in the arid parts of study area are likely to be typical but irregular features of these ecosystems. While the distribution of wetlands in time and space is highly variable, some temporary wetlands were highly persistent. These were mainly located in the Lake Eyre Basin and the adjacent Paroo River catchment.

The Lake Eyre Basin is unique in the Australian context because it is so large (1140 000 km$^2$) and is internally draining. Its northern parts extend into the tropics and the rivers that drain it have a very high ratio of floodplain area to total catchment area (Graetz 1980) and shallow gradients (Puckridge 1998). As a result, flow velocities of flood waters down these catchments are low (Kotwicki 1986) and flood transmission times are long (Knighton & Nanson 1994). Therefore, most rivers within the basin inundate large areas of their floodplain despite the Lake Eyre Basin having the lowest mean annual runoff of any major drainage basin in the world (Kotwicki & Allan 1998). These

<table>
<thead>
<tr>
<th>Region</th>
<th>3-monthly rainfall increments</th>
<th>6-monthly rainfall increments</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$y$-intercept</td>
<td>Coefficient of determination ($r^2$)</td>
</tr>
<tr>
<td>Upper Eyre</td>
<td>18.8</td>
<td>0.79** ($n = 12$)</td>
</tr>
<tr>
<td>Lower Eyre</td>
<td>15.4</td>
<td>0.72** ($n = 16$)</td>
</tr>
<tr>
<td>Darling</td>
<td>–</td>
<td>NS</td>
</tr>
<tr>
<td>Murray</td>
<td>–</td>
<td>NS</td>
</tr>
<tr>
<td>Cobham</td>
<td>–</td>
<td>NS</td>
</tr>
<tr>
<td>Torrens</td>
<td>17.0</td>
<td>0.38* ($n = 14$)</td>
</tr>
<tr>
<td>Southern Deserts</td>
<td>15.2</td>
<td>0.51* ($n = 14$)</td>
</tr>
<tr>
<td>Northern Deserts</td>
<td>–</td>
<td>NS</td>
</tr>
<tr>
<td>Gascoyne</td>
<td>–</td>
<td>NS</td>
</tr>
</tbody>
</table>

*P < 0.05; **P < 0.01; NS, not significant.
characters combine with spatial variability in topography and hydrology to produce a diverse range of wetland habitats and biotic assemblages (Puckridge 1998). Most persistent wetlands identified here have been recognized as significant 'refugia for biological diversity in arid and semiarid Australia' (Morton et al.

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Fig. 5. Based on a rainfall threshold, time series of periods when increases in wetland area are likely to have occurred in each region (bands). Bands represent periods when spatially averaged rainfall exceeded 20 mm per month over the previous three months. (a) Upper Eyre; (b) Lower Eyre; (c) Cobham; (d) Torrens; (e) Southern Deserts; (f) Northern Deserts; (g) Gascoyne.
1995). The only large persistent lake from the current study not identified as a refuge for biodiversity is Lake Rebecca in Western Australia.

Climatic processes

The irregular, episodic nature of wetland filling events in the study area and the strong influence of tropical weather systems at mid-latitudes are indicative of a process being driven by something other than local climatic forces. The El Niño–Southern Oscillation (ENSO) is a strong influence on the climate of eastern Australia (see Nicholls 1988; Allan et al. 1996; Sturman & Tapper 1996; Whetton et al. 1997). Several authors have proposed a relationship between the discharge of inland rivers and the behaviour of the ENSO phenomenon in Australia. Inflows into Lake Eyre have been shown to be most often associated with the La Niña phase of the ENSO phenomenon (Allan 1985, 1989; Isdale & Kotwicki 1987; Kotwicki & Isdale 1991; Kotwicki & Allan 1998; Puckridge et al. 2000). The ENSO phenomenon provides a strong influence on tropical cyclone patterns in the Australian region (Hastings 1990; Evans & Allan 1992). Flooding events in the Lake Eyre Basin have been linked to extreme rainfall events resulting from the passage of tropical cyclone remnants or more isolated synoptic events occurring in conjunction with enhanced monsoonal conditions (Allan et al. 1986; Allan 1990). The ENSO events also affect the discharge of rivers in the Murray–Darling Basin (Whetton & Baxter 1989; Simpson et al. 1993a,b; Whetton et al. 1993), resulting in large interannual variations in flow (Whetton & Baxter 1989). In terms of interannual variability in discharge, three of the major rivers in the study area, the Diamantina and Darling Rivers and Cooper Creek, are among the most variable large river systems on earth (Puckridge et al. 1998).

There is widespread speculation about the likely impacts of climate variability and changes in the behaviour of ENSO (e.g. Allan 1993; Whetton et al. 1993, 1996; Allan et al. 1996; Allan 2000). During the first half of the 1990s, a ‘protracted’ El Niño event led to concerns that the ENSO phenomenon was being enhanced by the greenhouse effect on the climate system (Trenberth & Hoar 1996). However, other work has indicated that similar types of ENSO episodes (El Niño and La Niña) have occurred in both the historical and palaeoclimatic records (Harrison & Larkin 1997; Rajagopalan et al. 1997; Allan & D’Arrigo 1999; Wunsch 1999). In addition, evidence for a change in the climatic regime over the Pacific basin since the mid-1970s being possibly an enhanced greenhouse influence (Trenberth & Hoar 1997), with rainfall in Australia being higher for given values of the Southern Oscillation Index (Nicholls et al. 1996), has been compounded and complicated by growing evidence for the importance of decadal–multidecadal climatic features in shaping patterns of variability and change (Power et al. 1999a,b; Allan 2000). Recent climate modelling shows an El Niño-like mean state and a predominance of decreases in mean rainfall due to enhancement of the greenhouse effect (Hulme & Sheard 1999; Cai & Whetton 2000). However, rainfall increases cannot be confidently excluded and some modelling results suggest that the heaviest rainfall events may increase in intensity even when mean rainfall decreases (Walsh et al. 2000).

While the implications of low-frequency climate variability and change on rainfall in the Australian region remain uncertain, even small changes in rainfall patterns will change wetland availability in the study area. A relatively small increase in annual rainfall of 10% would increase mean annual inflows into Lake Eyre from 4 to 6 km$^3$ and transform it into a permanent water body (Kotwicki & Allan 1998). With time, such changes would likely produce a concomitant increase in abundance of some species, particularly fish and fish-eating waterbirds. For waterfowl (ducks, geese and swans) the presence of a large permanent wetland may increase survival or negate the need to move elsewhere during dry periods but would be unlikely to produce the food resources needed for a marked increase in abundance. For Australian waterfowl, food resources are generally most abundant in the weeks and months following inundation (Frith 1959; Braithwaite & Frith 1969; Maher & Carpenter 1984; Briggs & Maher 1985; Crome 1986; Lawler & Briggs 1991) and are unlikely to be limiting at these times. For there to be a marked increase in waterfowl abundance in inland Australia it is likely that the frequency of flooding of temporary wetlands would also need to increase.

Typically it is assumed that the response of individual species to low frequency climate variability and change is to alter their range limits or their abundance (Schneider & Root 1996). This model of change conceptualizes the response as incremental, with steady alterations of range (Parmesan 1996; Parmesan et al. 1999) or changes in the timing of migration or breeding (Sparks & Carey 1995; Sparks & Yates 1997; Crick & Sparks 1999; Sparks 1999) with increases in temperature. This model of species responses to climate change has developed from observations of temperate environments of the Northern Hemisphere where ecosystems are generally highly productive and subject to strong seasonal effects. The impacts of climate change on Australia’s arid zone biota are unlikely to be as predictable and are potentially more damaging (see Jones & Pittock 1997).

Given that most flooding events in inland Australia are tropical in origin, the most significant climatic change for waterbirds may be alterations to the frequency, path and intensity of tropical systems, particularly cyclones, across inland Australia. Although there is some evidence based on climate modelling that
tropical cyclones may become more intense under enhanced greenhouse conditions, changes in frequency and tracks remain quite uncertain (Walsh et al. 2000). If the intervals between flooding events increase, opportunities to breed for species that depend on the temporary wetlands of the inland, such as the banded stilt (Cladorhynchus leucocephalus), become increasingly infrequent. This species is reliant on the passage of the remnants of tropical cyclones over the arid inland to fill one of the many shallow lakes, as occurred at Lake Torrens in 1989 (Williams et al. 1998) and Lake Ballard in 1992 (Minton et al. 1995). Breeding colonies of this species are prominent because of their large size but have rarely been recorded. Since 1900 there have been 14 major breeding events and only 27 breeding records in total, mostly in Western Australia (Marchant & Higgins 1993; Minton et al. 1995). Any decrease in the frequency of large flood events in arid Australia could further limit the opportunities for this and other waterbird species to breed. Furthermore, habitat modification in the south-east of the continent (Briggs 1994) may reduce options for other species to adjust their distribution on a drying continent.

**Limitations to analyses**

There are a number of caveats on the findings presented here. Firstly, the quality of the rainfall record in each region over the full period has changed from time to time with consequences for the grided mean monthly rainfall data used here. However, these changes would have to be consistently biased and of large magnitude to affect the results significantly. Furthermore, the distribution of rainfall recording stations is sparse in some regions of the study area and the errors associated with the interpolated rainfall data vary across the study area and are of unknown magnitude.

Secondly, the period for which data were available to establish a rainfall/wetland filling relationship was short. The threshold resulting from regressions of increments to wetland area on rainfall may differ significantly if a larger data set was used. Thirdly, correction of wetland area for evaporation would improve the rainfall/wetland filling relationship but there were insufficient data for this to be done.

Nonetheless, the concordance between the results presented here and other published studies of wetland filling in one part of inland Australia, the Lake Eyre Basin, is high (see Kotwicki 1986; Kingsford et al. 1999). The adequacy of the methodology for examining landscape scale changes in wetland distribution is illustrated by the relationship between wetland filling and rainfall in the Cobham region. This region has no major drainage systems and wetlands are largely filled by local runoff. In the period 1987–1995 there were nine sampling periods for which rainfall exceeded the 20 mm per month threshold used in the model. Seven corresponded with an increase in wetland area, one with no change and another with a decline. On two other occasions there were small increases in wetland area (< 700 ha) on rainfalls less than the threshold.

While this highlights the complexities of modelling hydrological processes in arid environments, the simple threshold model used in this analysis provides a reasonable approximation of wetland filling within the arid zone of Australia.

**ACKNOWLEDGEMENTS**

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**REFERENCES**


APPENDIX I

Location, size and recurrence of inundation (%) at 31 sampling dates between September 1986 and September 1997 for wetlands, or parts thereof, in the study area.

<table>
<thead>
<tr>
<th>Water body</th>
<th>Location</th>
<th>Max. area (ha)</th>
<th>Recurrence of inundation (%)</th>
<th>Comments*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Waranga Basin</td>
<td>36°33'S, 145°06'E</td>
<td>5717</td>
<td>100.0</td>
<td>Dammed</td>
</tr>
<tr>
<td>Lake Pamamaroo (ML)</td>
<td>32°16'S, 142°27'E</td>
<td>6390</td>
<td>96.5</td>
<td>Dammed and increased inflows</td>
</tr>
<tr>
<td>Lake Cawndilla (ML)</td>
<td>32°28'S, 142°13'E</td>
<td>9311</td>
<td>95.6</td>
<td>Dammed and increased inflows</td>
</tr>
<tr>
<td>Lake Ballyrogan</td>
<td>33°29'S, 145°58'E</td>
<td>6289</td>
<td>97.3</td>
<td>Dammed and increased inflows</td>
</tr>
<tr>
<td>Lake Hindmarsh</td>
<td>36°02'S, 141°54'E</td>
<td>13447</td>
<td>95.5</td>
<td>Increased inflows</td>
</tr>
<tr>
<td>Lake Tandure (ML)</td>
<td>32°16'S, 142°32'E</td>
<td>2252</td>
<td>95.2</td>
<td>Increased inflows</td>
</tr>
<tr>
<td>Lake Menindee (ML)</td>
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<td>Dammed and increased inflows</td>
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<td>Lake Victoria</td>
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<td>92.9</td>
<td>Dammed and increased inflows</td>
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<tr>
<td>Lake Wyara (PR)</td>
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<td>89.7</td>
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<td>Lake Cowal</td>
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<td>Lake Numalla (PR)</td>
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</tr>
<tr>
<td>Lake Mipia (LEB)</td>
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<td>2051</td>
<td>85.2</td>
<td>Dammed and increased inflows</td>
</tr>
<tr>
<td>Barren Box Swamp</td>
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<td>3201</td>
<td>85.2</td>
<td>Dammed and increased inflows</td>
</tr>
<tr>
<td>Yanga Lake</td>
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<td>85.2</td>
<td>Increased inflows</td>
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<td>Lake Moolaan</td>
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<td>82.6</td>
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<td>Kow Swamp</td>
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<td>81.8</td>
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<td>Lake Koolinvoe (LEB)</td>
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<td>81.6</td>
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<tr>
<td>Hume Reservoir</td>
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<td>70.3</td>
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<td>Kangaroo Lake</td>
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<td>68.1</td>
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<td>Lake Bonney</td>
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<td>296</td>
<td>66.8</td>
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</tr>
<tr>
<td>Dry Lake</td>
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<td>590</td>
<td>65.5</td>
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<td>Lake Tyrell</td>
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<td>15421</td>
<td>65.2</td>
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<td>Lake Eyre North (LEB)</td>
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<td>750628</td>
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<td>Lake Burrendong</td>
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<td>64.3</td>
<td>Dammed</td>
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<tr>
<td>Lake Buloke</td>
<td>36°16'S, 142°37'E</td>
<td>5515</td>
<td>63.5</td>
<td>Dammed</td>
</tr>
<tr>
<td>Lake Bullawarra</td>
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<td>862</td>
<td>62.9</td>
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<td>Lake Balaka (ML)</td>
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<td>Lake Nettlegeoe</td>
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<tr>
<td>The Marsh</td>
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<td>691</td>
<td>61.0</td>
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<td>Narren Lake</td>
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<td>5176</td>
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<tr>
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<td>58.7</td>
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<td>6381</td>
<td>58.3</td>
<td>Dammed</td>
</tr>
<tr>
<td>Lake Cargelligo</td>
<td>33°17'S, 146°24'E</td>
<td>1032</td>
<td>55.5</td>
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<tr>
<td>Lake Yantabangee (PR)</td>
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<td>1396</td>
<td>55.2</td>
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<td>Lake Cowan</td>
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<td>75725</td>
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<td>Lake Benancee</td>
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<td>747</td>
<td>55.2</td>
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<td>Green Lake</td>
<td>36°26'S, 144°50'E</td>
<td>425</td>
<td>52.9</td>
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<tr>
<td>Lady Blanche Lake</td>
<td>27°01'S, 140°21'E</td>
<td>1243</td>
<td>51.9</td>
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<tr>
<td>Tala Lake</td>
<td>34°34'S, 143°43'E</td>
<td>667</td>
<td>51.8</td>
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<tr>
<td>Lake Bijuje</td>
<td>32°13'S, 142°36'E</td>
<td>1384</td>
<td>51.7</td>
<td>Increased inflows</td>
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<tr>
<td>Mullawoolka Basin</td>
<td>30°30'S, 143°49'E</td>
<td>2076</td>
<td>51.6</td>
<td>Increased inflows</td>
</tr>
</tbody>
</table>

Comments refer to whether damming regulates the wetland or has increased inflows due to water diversion, or partly used as water storage for mining. ML, PR and LEB designate whether the water body is associated with the Menindee Lake Scheme, the Paroo River or the Lake Eyre Basin, respectively. *Based on personal communications from R. Kingsford, S. Briggs and by reference to resource management agencies.