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Synthesis of a new conceptual model to facilitate management of ephemeral deflation basin lakes

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Abstract

Ephemeral deflation basin lakes are widespread throughout arid and semiarid regions of the Murray–Darling Basin in Australia. Although they are diverse, productive habitats, the water resources development has generally caused significant declines in their ecological condition. Managers are currently trying to protect or restore these systems, however, without an adequate theoretical framework on which to base management decisions. This is because the existing conceptual models provide little insight into the effects of any component of the flow regime except flooding. This paper reviews the effects of flooding and drying on lakes, using the information and conclusions therein to propose a conceptual model that identifies five stages in the flooding and drying cycle. This conceptual model incorporates elements of the Flood Pulse Concept, Trophic Cascade models and the Geomorphic–Trophic model, as they apply to these highly variable water systems.

Key words

birds, fish, hydroperiod, invertebrates, water quality, wetlands.

INTRODUCTION

Ephemeral deflation basin lakes (EDBLs) are widespread throughout the arid and semiarid regions of the Murray–Darling Basin, Australia, where evaporation exceeds rainfall. Ephemeral deflation basin lakes are important both as wetlands and as components of the larger floodplain ecosystem (Ward 1989; Ward & Stanford 1995). They support diverse and productive plant and animal communities and provide, for example, critical nursery habitat for native fish (Puckridge 1999), as well as breeding and feeding habitat for birds (Kingsford *et al.* 2004). In addition to these natural values, EDBLs represent a valuable resource for human activities, as many are used to grow crops, to store water and/or as recreational areas. A considerable body of evidence suggests that water resource and agricultural development on arid zone EDBLs have generally had detrimental impacts on net ecosystem productivity and diversity (Kingsford 2000a; Kingsford *et al.* 2004).

Ephemeral deflation basin lakes are lowland river floodplain environments that fluctuate between terrestrial and aquatic states. The hydrology of these systems leads to the development of wetland and terrestrial annual vegetation on the dry bed of the lake, surrounded by a fringe of perennial vegetation – similar to the low groundwater recharge, drought wetlands described by the Wetland Continuum (Euliss *et al.* 2004). In the Murray–Darling Basin, the water resources management has significantly altered the hydrological regime of many EDBLs, such that they can be classified into three broad categories as follows: (i) those that are not affected by water resources development; (ii) those that are dry more frequently than under natural conditions; and (iii) those that remain wet for longer periods or more frequently than under natural conditions – ~35% of the River Murray wetlands, according to Pressey (1990) and Seddon *et al.* (1997). Alterations to natural hydrological patterns can strongly impact biotic and abiotic processes.

It is generally agreed that both wet and dry periods are important for maintaining ecosystem integrity in ephemeral wetlands (Boulton & Lloyd 1992; Boulton & Jenkins 1998). Disturbances, such as flooding and drying, drive the aquatic and terrestrial successional processes and facilitate the biotic and abiotic exchanges between elements of the floodplain and the riverine environment (cf. Flood Pulse Concept, Junk *et al.* 1989). Because of this

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reality, EDBLs are potentially sites of high productivity and diversity within arid zone floodplain ecosystems. As a consequence, management of these systems has implications for their productivity and diversity at a landscape scale.

While the pressure placed on resource managers to achieve both environmental and water resources objectives has increased, the knowledge required to achieve these objectives is not readily available. This situation exists despite an increasing body of knowledge concerning various aspects of the ecology of floodplain systems. The current knowledge on these aspects is fragmented, and is not integrated within a conceptual framework appropriate to EDBLs, encompassing aspects of both wet and dry lake phases. As an example, although the Flood Pulse Concept (Junk *et al.* 1989) predicts that the loss of flooding is expected to have a detrimental effect on wetland condition, there are no similar conceptual models to predict the effect of the loss of drying episodes.

To attempt to construct an heuristic conceptual model of EDBLs, the existing conceptual models of ephemeral lake ecology were examined, and combined with our knowledge of the ecological impacts of lake drying and inundation. Although the subsequently developed conceptual model focuses on EDBLs in the Murray–Darling Basin, it also is likely to be at least partially applicable to EDBLs found in semiarid regions throughout the world.

EDBLs in the Murray–Darling Basin

The majority of EDBLs in the Murray–Darling Basin occur in western New South Wales. Based on a survey of lakes in this region, Seddon and Briggs (1998) identified 567 deflation basin lakes larger than 100 ha. Although numerous smaller deflation basins have been identified and mapped (Kingsford *et al.* 1998), very little information exists for the majority of lakes in the region. Seddon *et al.* (1997) compiled a database of lake attributes, publishing literature for EDBLs larger than 100 ha in western New South Wales. And, although not restricted to EDBLs alone, similar information about smaller Murray–Darling Basin wetlands, and wetlands considered important from a conservation perspective, also has been compiled (ANCA 1992).

In western New South Wales, depressions (which become EDBLs) are formed on the floodplain by the eastward movement of bed material by wind and wave action from the prevailing westerly winds. Sand dunes or lunettes formed by the deposition of these eroded bed materials commonly occur on the eastern margin of lake basins. Lake beds generally consist of fertile clay soils deposited by successive flooding events and differ markedly from the soils on surrounding higher ground (Bowler 1990; Pressey 1990). Ephemeral deflation basin lakes receive water intermittently from their riverine supply during periods of high flow, or from local rainfall. Under natural conditions, EDBLs are subjected to episodes of rapid flooding, followed by more protracted periods of evaporative drying. The periodicity of these wet/dry phases varies considerably among EDBLs. Some lakes receive water from annual high river levels, filling frequently, while other might remain dry for many years. In fact, some might never fill if their supply channels have been disconnected or obstructed. Although variations in groundwater interactions among lakes also might have impacts on surface water hydrological regimes, little information concerning these processes is presently available. Despite their geomorphological similarity, EDBLs are heterogeneous, with the flood frequency, flood duration, salinity and water source varying greatly among lakes (Seddon & Briggs 1998).

The periodicity of flooding and drying is not well documented for most EDBLs. Records exist for some of the more actively managed storages, examples being Lake Victoria (Hope 2000) and the Menindee Lakes (Green 1997), and for those on the Darling Anabranch (Withers 1994) and Talyawalka Creek (Withers 1996). However, similar records are not usually maintained for rainfall-filled lakes, which are often excluded from management strategies because they do not occur on the floodplains of gauged rivers. Nevertheless, it has become evident over the last two decades that all EDBLs are extremely vulnerable to water resources development (Kingsford 2000b; Roshier *et al.* 2001).

Existing conceptual models

Appropriate conceptual models can greatly assist in the management of EDBLs for sustainable use, and for the protection of their environmental values. They can be used as a basis for developing management strategies, as well as for designing monitoring programs to evaluate the possible environmental outcomes of management interventions. There are several conceptual models concerning lake ecology currently available to scientists and managers that could be used to guide the management of EDBLs. However, because all of the current conceptual models are derived from lakes or tropical rivers in the Northern Hemisphere, they might not be appropriate in an Australian context.

Alternate stable states

The first of these conceptual models views lakes as oscillating between stable states of macrophyte

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domination or phytoplankton domination (Scheffer *et al.* 1993; Casanova *et al.* 1997; Bachmann *et al.* 1999). Each of these states is influenced by the distribution and concentration of nutrients and sediments. The loss of macrophytes has the effect of eliminating habitat for a range of invertebrates (Diehl & Kornijow 1992; Schriver *et al.* 1995; Burks *et al.* 2001), thereby altering trophic structure. In some instances, varying water levels has led to the loss of macrophytes and a change in state (Coops *et al.* 2003). In other instances, hydrological variation has stimulated the macrophyte community (Poiani & Johnson 1993; Casanova 1994; Blanch *et al.* 1999). For this reason, although the concept of alternative stable states does not provide managers with a comprehensive framework on which to formulate hydrological strategies, it does provide guidance on nutrient management and erosion.

Trophic cascade

The trophic cascade or food-web models also might have some relevance in regard to managing EDBLs. These models suggest that lake productivity and community composition are determined by a combination of top-down and bottom-up forces, such that changes in the fish community can influence algal abundance and water quality (Carpenter *et al.* 2001). While food-web manipulations have successfully facilitated improvements in water quality and in reducing algal blooms (Carpenter & Kitchell 1988; Carpenter *et al.* 2001), there are nevertheless some situations in which they are not appropriate. Trophic cascades appear to be weakened, for example, as the food web or habitat becomes more complex (Shapiro 1990; Lazzaro 1997), or where other stresses (e.g. sedimentation) are an environmental factor (Phillips *et al.* 1999). As the trophic cascade models have not considered water regime, they have only limited utility for managers concerned with the effects of water resources development.

Flood Pulse Concept

The third conceptual model is the Flood Pulse Concept, which states that the flood pulse stimulates productivity (Junk *et al.* 1989; Lewis *et al.* 2000b). The Flood Pulse Concept was formulated to describe the ecology of river–floodplain ecosystems rather than to describe individual wetlands. Floods are considered important in determining the productivity and diversity of lake communities. Thus, alteration of flooding regimes has had a detrimental impact on Australian wetlands (Briggs *et al.* 1998; Kingsford 2000a). A major limitation of the Flood Pulse Concept is that it emphasizes the flood pulse, with no reference to either long-term flow regimes or other important hydrological events such as drying (Walker *et al.* 1995; Puckridge *et al.* 2000). Thus, the Flood Pulse Concept provides advice for only one component of the water regime common in ephemeral lakes.

Geomorphic–Trophic Model

The fourth conceptual model is the Geomorphic–Trophic Model. This model suggests that variations in biogeochemical and biotic processes between floodplain lakes can be largely understood, and predicted on the basis of morphometric and hydrological factors. The Geomorphic–Trophic Model has been utilized for Orinoco floodplain lakes, wherein lake shape affects turbidity and, in turn, the biotic community (Lewis *et al.* 2000a). The model also has been utilized for Arctic lakes, whereby lake shape affects the persistence of fish during the winter freeze (Hershey *et al.* 1999). Lake shape also affects diversity, with positive correlations being reported between the lake surface area and the diversity of zooplankton (Dodson 1992; Dodson *et al.* 2000), fish (Barbour & Brown 1974; Browne 1981) and molluscs (Browne 1981). The increased diversity with lake surface area appears to be an example of the species–area relationship, although the mechanism producing these patterns has received little attention (Douglas & Lake 1994).

Lake morphology also affects productivity, with shallow lakes usually being more productive (Hamilton & Lewis 1990; Serruya 1990; Perin *et al.* 1996). The mechanisms underlying this pattern include mixing and stratification, oxygenation, the relative contribution of the littoral zone, and nutrient inputs (Hamilton & Lewis 1990; Serruya 1990; Perin *et al.* 1996). Although a relationship exists between lake depth and lake hydroperiod, it is possible that the observed patterns of productivity in ephemeral lakes are large because ephemeral lakes tend to be shallower than permanent lakes of similar volume. However, this hypothesis does not explain why water resources development has such detrimental effects on EDBLs.

The above summary demonstrates that no existing conceptual models adequately describe the relationship between water regime and lake ecology in ephemeral systems. The lack of such a conceptual model is because, in part, of the lack of data regarding the changes that occur in lakes as they undergo cycles of drying and flooding. There is a growing body of information, however, about the ecology of floodplain and ephemeral wetlands.

Ecological impacts of lake drying

The drying of a lake is brought about by a combination of draining, evaporation and groundwater infiltration, with the relative importance of each process varying among lakes and drying stages. Most of the available literature on drying concerns lakes and wetlands in which evaporation

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is the dominant process. As lakes and wetlands evaporate, a number of predictable changes usually occur, examples being the concentration of nutrients, salt and organisms, and an increased turbidity (Talling 1992; Thormann *et al.* 1998). Increases in algal abundance and changes in algal species composition also have been reported (Talling 1992; Ibanez 1998).

Another common feature of drying lakes is that biotic interactions such as predation and competition increase (Schneider & Frost 1996; Golladay *et al.* 1997; Tockner *et al.* 1999; Wantzen *et al.* 2002). These changes are usually linked to a declining availability of habitat (Golladay *et al.* 1997) and increases in the proportion of predatory taxa (Lake *et al.* 1989; Batzer & Wissinger 1996; Corti *et al.* 1997; Moorehead *et al.* 1998). This trend, however, is not universal (Timms & Boulton 2001). Increases in predator abundance have been explained primarily in terms of the progressive colonization of ephemeral lakes and wetlands by predators (Wiggins *et al.* 1980; Lake *et al.* 1989; Jeffries 1994).

Although the number of predatory taxa in a lake increases with drying, the situation is complicated by the changes that occur in habitat availability as a result of drying. Top-down control has been proven to be more important in shallow lakes (Jeppesen *et al.* 1997). As lakes dry and become shallower, predation might become more intense without additional colonization by predatory taxa. As an example of the way in which predator pressure might change, deep lakes offer fish refuge from avian predation. This refuge is eventually lost, however, and while some fish might attempt to find their way back to deeper refuges, many remain isolated (Kahl 1964; Kushlan 1976). Without a refuge, the fish community might undergo dramatic population reduction as avian predation becomes more effective (Kushlan 1976; Scholz *et al.* 1999). The reduction in fish numbers might offer invertebrate predators (e.g. notonectids and dytiscid beetles) an opportunity to proliferate (Boulton & Lloyd 1991; Jeffries 1994; Brendonck *et al.* 2002).

During the final stages of drying, the concentration of nutrients and salts can be extreme, fluctuations in water quality can increase, the buffering capacity of the water volume diminishes, and the lake is more exposed to weather (Talling 1992; Balla & Davis 1995; Podrabsky *et al.* 1998). When the lake finally dries, there is typically a well-established vertical zonation of terrestrial flood-dependent vegetation surrounding an area of dry cracked mud, where salt levels are too high, or drying conditions too extreme, to allow development of vegetation. Drought-resistant propagules of microinvertebrates (Boulton & Jenkins 1998; Jenkins & Boulton 1998) and plants (Brock 1998; Nicol 2004) remain within the sediments, awaiting cues for germination. Other animals (e.g. yabbies and frogs) might find refuge in burrows or in moist habitats under litter (Wiggins *et al.* 1980; Boulton 1989).

Drying also consolidates lake-bed sediments (van der Wielen, 2003). Although this process is affected by the duration of the dry phase, upon re-inundation it can decrease the sediment resuspension rates and increase the particle settlement rates. The reduced turbidity has the significant effect of increasing the light penetration into the water column (van der Wielen, 2003).

Ecological impacts of the loss of lake drying

There is little doubt that drying is a major disturbance. Many taxa, however, have found ways of surviving even prolonged periods of drying such as drought. In many ephemeral systems, the loss of a dry phase has led to significant changes often perceived as deleterious. Bird density and diversity, for example, are known to decline with the removal of a dry phase (Briggs *et al.* 1994; Kingsford *et al.* 2002; 2004), as the original community composition shifts towards a composition with a greater proportion of piscivorous species (Kingsford *et al.* 2002). Invertebrate productivity (Brinson *et al.* 1981; Maher & Carpenter 1984; Briggs & Maher 1985) and diversity (Leslie *et al.* 1997; Boulton & Jenkins 1998) also have been shown to decline in response to the loss of wetland drying. The loss of a dry phase has been associated with an increased abundance of introduced fish species such as carp (*Cyprinus carpio*) (Gehrke *et al.* 1995; Boulton & Jenkins 1998; Gehrke *et al.* 1999). The vegetation community also undergoes significant changes, including the loss of lignum (*Muehlenbeckia cunninghamii*) and red gums (*Eucalyptus camaldulensis*) (Walker & Thoms 1993; Thornton & Briggs 1994), as well as changes to the macrophytic community structure (Brock & Casanova 1991; Poiani & Johnson 1993; Walker *et al.* 1994). While much less is known about changes to ecological processes, it would appear that the loss of a dry phase leads to an increased importance in anaerobic decomposition of organic matter (Brinson *et al.* 1981; Boon *et al.* 1996).

In regulated water systems, a greater proportion of the water volume in such lakes is drained for consumptive use. This has ecological implications for regulated lakes, by facilitating the export of nutrients and salt, as well as such organisms as algae and microinvertebrates. Although this study is not aware of data that allow determination of the specific effects of these changes on lake ecology, it is likely that it has an effect on the post-flood nutrient pulse. An accelerated drawdown might alter the rate of solute concentrations in a lake, thereby depriving some

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microinvertebrates of the cues required to stimulate the onset of resting stages (Kalk & Schulten-Senden 1977; Ricci 2001). There is no evidence to date from Australian studies to support this hypothesis (Sinclair-Knight-Merz 2002).

Ecological impacts of lake flooding

Floods are highly variable phenomena. This is particularly the case in Australia where flood frequency, magnitude, timing and duration are all highly unpredictable (Puckridge *et al.* 1998). Flood effects can vary with timing (Boulton & Jenkins 1998; Nielsen *et al.* 1999), depth (Briggs *et al.* 1993a; Leeper & Taylor 1998), mode of flooding (Quinn *et al.* 2000) and floodwater water quality (Leeper & Taylor 1998; Rabalais *et al.* 1998; Lewis *et al.* 2000a). Despite such variations, however, some effects are common to all floods.

Floods are generally associated with a pulse of nutrients and organic matter. Nutrients and organic matter are released from dried sediments (Qui & McComb 1996; Baldwin & Mitchell 2000), vegetation (Furch & Junk 1997), and other organic material (Dumont 1992) and/or they are imported from upstream or the floodplain by the floodwater (Hillbricht-Ilkowska 1999; Tockner *et al.* 1999; Lewis *et al.* 2000a). Floods also are associated with increases in the abundance or productivity of invertebrates (Hart 1985; Junk 1997; Lewis *et al.* 2000a), macrophytes (Brinson *et al.* 1981; Poiani & Johnson 1993; Nielsen & Chick 1997), fish (Holcik 1996; Poizat & Crivelli 1997; Gutreuter *et al.* 1999; Puckridge *et al.* 2000) and birds (Briggs & Thornton 1999; Kingsford *et al.* 1999). Based on the Flood Pulse Concept, the pulse of nutrients and organic matter drives the observed increases in the plant and animal productivity. If these impacts were the only effect of floods, however, responses similar to those of eutrophication might be expected. Although moderate eutrophication has been associated with increased productivity (Growns *et al.* 1992; Carpenter *et al.* 1998), there are virtually no studies suggesting that eutrophication and flooding have the same ecological impacts and outcomes.

This study suggests that a nutrient pulse is just one of at least three changes that occur when ephemeral wetlands are flooded. The second change is expansion of aquatic habitat and habitat complexity. At small spatial scales, complex habitat patches are created through either inundation of terrestrial vegetation, or by stimulating macrophyte growths. Numerous studies have found that this type of spatially complex habitat provides refuge for a range of prey organisms, thereby allowing development of more diverse and abundant invertebrate communities (Boulton & Lloyd 1991; Dumont 1992; Balla & Davis 1995; Leslie *et al.* 1997; Battle & Golladay 2001). The inundated vegetation might provide both a refuge habitat and a source of organic carbon, in fuelling a highly productive community (Lewis *et al.* 2000a; Battle & Golladay 2001), and while plants that can live on both land and water (e.g. lignum and red gums) continue to provide spatial complexity as long as they are inundated, many terrestrial grasses and herbs decompose and offer only ephemeral habitat for aquatic invertebrates (Battle & Golladay 2001). Although some lake beds might support the growth of submerged or emergent macrophytes, this possibility is highly variable and depends on a range of environmental factors.

At a larger spatial scale, floods can create a mosaic of habitat types, including deep pools, large shallow water areas, and vegetated islands (Kingsford *et al.* 2002). These habitats are important for different groups of organisms. As an example, vegetated islands provide important breeding habitat for birds (Briggs *et al.* 1993b), whereas shallow water provides important feeding habitat for wading birds (Kingsford *et al.* 1999).

The third important change that occurs during the flooding of an ephemeral wetland involves alterations to the predator community (Lake *et al.* 1989; Batzer & Wissinger 1996; Battle & Golladay 2001). The use of lake-bed sediments as a dry refuge means that microinvertebrates can rapidly colonize after a flood event: many predators, though not all invertebrate predators (Brendonck *et al.* 2002), take longer to colonize and reproduce. This contention is supported by studies that record a slow accumulation of predators in ephemeral lakes, and the presence of predator-intolerant species during early flooding stages (Jeffries 1994; Collinson *et al.* 1995; Batzer & Wissinger 1996; Timms 1997). The initial scarcity of predators immediately after flooding gives the microinvertebrate community the opportunity to take maximum advantage of the increased autotrophic and heterotrophic productivity associated with a flood, as predicted by the trophic cascade model (Carpenter & Kitchell 1988).

Ecological impacts of the loss of lake flooding

In view of the effects of floods on nutrient dynamics, aquatic habitats and community composition, it is not surprising that many of the dramatic changes associated with the loss of flooding have been reported. These include changes in the species composition of floodplain vegetation (Bren 1992; Brereton 1994; Nielsen & Chick 1997), and declines in invertebrate diversity (Boulton & Lloyd 1991; Jenkins & Boulton 1998), fish (Kingsford

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2000a; Gehrke & Harris 2001) and birds (Kingsford & Thomas 1995; Leslie 2001; Kingsford *et al*. 2004). As a consequence, the effects of water resources development on the flooding characteristics are a major challenge facing managers of EDBLs (Walker *et al*. 1997; Kingsford 2000a).

CONCEPTUAL MODEL OF EDBL FUNCTION

Based on this study, it is believed that EDBLs undergo cycles of flooding and drying, in which there are five phases that begin and end with a dry lake bed (Fig. 1), as follows:

1. The first phase occurs after a dry or partially dried lake is flooded (Fig. 1b). It is characterized by high habitat diversity and complexity, high productivity and relatively few aquatic predators. This combination of characteristics allows for the development of an abundant, diverse consumer community.

2. During the second phase (Fig. 1c), the fish abundance increases while habitat complexity decreases. As the flood water begins to recede, vegetation (e.g. lignum) is stranded on the floodplain. Inundated grasses also begin to degrade and decompose, further reducing the habitat complexity.

3. As a lake contracts further, organisms become concentrated and the numbers of predators increase (Fig. 1d), exerting a significant top-down pressure on the invertebrate community.

4. When a lake becomes too shallow to serve as a refuge for fish, avian predation becomes an important structuring force (Fig. 1e), producing a trophic cascade that causes invertebrate numbers to increase. This process continues until the physical conditions become too harsh.

5. The lake finally dries, becoming an important terrestrial habitat for a range of plants and animals (Briggs *et al*. 2000).

This conceptual model suggests that the Flood Pulse Concept, trophic cascade/food-web models, and Geomorphic–Trophic Model all have some application to ephemeral lakes and the role of drying. As discussed above, although floods create aquatic habitats and increase productivity, the ecosystem relies on dry phases to facilitate the accumulation of organic matter, as well as

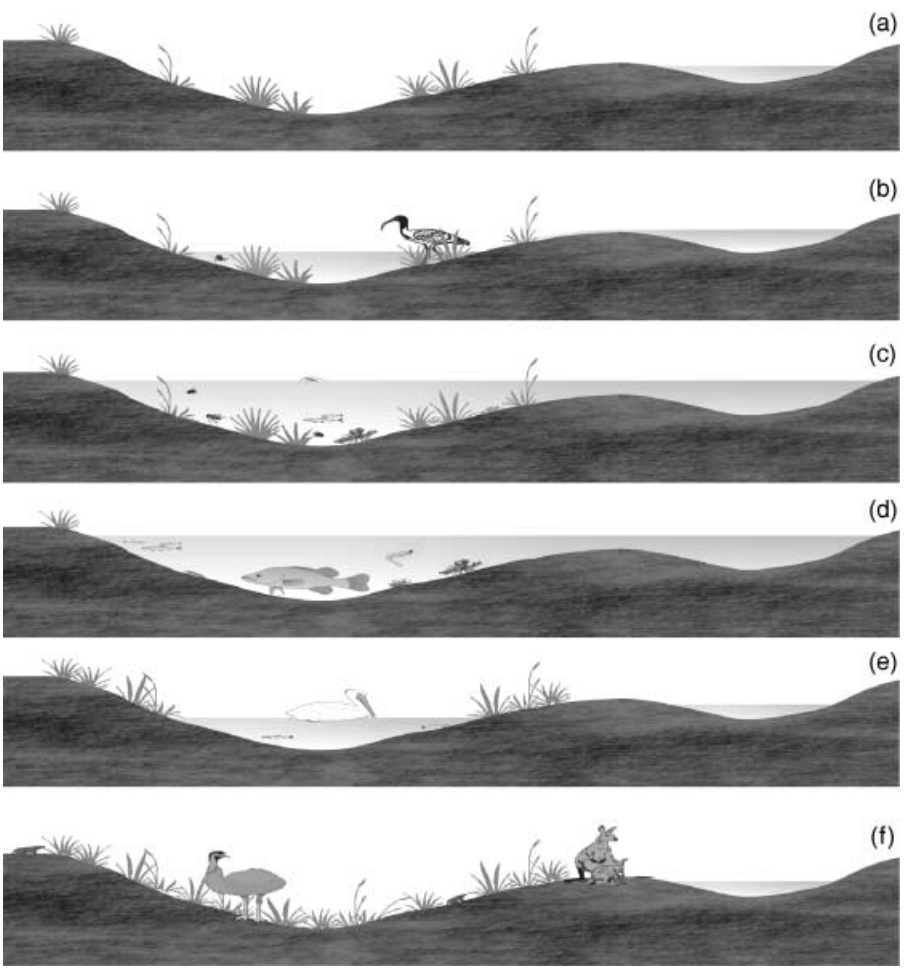

Fig. 1. Illustration of the five stages of lake filling and drying. (a) Dry lake bed with forbs and grasses; (b) shallow flooding creates a heterogeneous, nutrient-rich aquatic habitat with few aquatic predators; (c) established lake with established invertebrate and fish communities; (d) late-flooding cycle with low habitat heterogeneity, and well established predatory fish community; (e) drying lake in which avian predation dominates; (f) dry lake, providing productive habitat for terrestrial plants and animals.

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the generation of habitats important for fuelling the subsequent increased productivity once flooding occurs. Although the trophic cascade/food-web models appear to have some applications, the effects of predators change over time – predators first accumulate within the lake and, as the lake subsequently dries, the influence of avian predation increases. From this perspective, the Geomorphic–Trophic Model also has some application, because some of the observed changes appear to be driven by the changes occurring in lake shape during the five phases of the flooding and drying cycle.

It is recognized that the knowledge base upon which this conceptual model is founded is incomplete – there might be regions for which the model might be partially or totally inappropriate. We believe that this synthesis of the available information, however, will provide a valuable reference point for researchers, as well as a useful tool for managers who currently lack adequate scientific information on which to base their management decisions regarding these productive and diverse systems.

Management implications

The management of EDBLs should consider the different roles and nature of the flooding event, the drying and the connectivity. Any change to the depth or duration of flooding can have significant impacts on a lake ecosystem, first by affecting the ability of each organism to colonize the lake, and then by altering trophic relationships. These changes already have been widely recognized as significant degrading forces in Australian wetlands (Puckridge 1999; Kingsford 2000a,b).

The loss of a dry phase also has been recognized as a major degrading force for lakes (Briggs 1988). The conceptual model presented herein suggests that permanent inundation allows the accumulation of predatory species, with the potential to exclude predator-intolerant species. This situation can, in turn, force a lake into a trophic configuration in which its productivity and diversity are reduced. The loss of a dry phase also might lead to the loss of habitat heterogeneity, with similar effects on production and diversity. This conceptual model suggests that, although rehabilitation might not require complete drying, restoration of a hydrological cycle that produces changes in trophic structure and the development of vegetation on the lake bed will be important considerations in managing these systems.

Finally, the conceptual model presented herein indicates that changes to the nature of the connection between the lake and the source of its colonists (e.g. river or floodplain) will have an impact on the ecology of a lake by affecting the ability of aquatic organisms to colonize the lake. This observation also has implications for the lake's trophic structure.

This conceptual model attempts to describe the ecology of individual wetlands, and implies that any change to the hydrological cycle is likely to lead to changes in the condition of wetlands. The consequences of these changes must be viewed from the perspectives of both the individual wetland and the broader landscape that would have contained wetlands with a diversity of hydrological regimes. While this review reveals that we have made progress in attempting to understand how ephemeral wetlands function, much additional information is needed before we will have a thorough understanding of the impacts of hydrological changes at larger spatial and temporal scales. Thus, the model presented herein should be viewed as a means of improving our ability to predict the outcomes of water resources development on individual wetlands, while also providing guidance for attempts to restore or rehabilitate the wetlands.

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REFERENCES

Australian Nature Conservation Agency (ANCA). (1992) *A Directory of Important Wetlands in Australia*. ANCA, Canberra, Australia.

Bachmann R., Hoyer M. & Canfield D. (1999) The restoration of Lake Apopka in relation to alternative stable states. *Hydrobiologia* **394**, 219–32.

Baldwin D. S. & Mitchell A. M. (2000) The effects of drying and re-flooding on the sediment and soil nutrient-dynamics of lowland river-floodplain systems: A synthesis. *Regul. Rivers: Res. Manage.* **16**, 457–67.

Balla S. & Davis J. (1995) Seasonal variation in the macroinvertebrate fauna of wetlands of differing water regime and nutrient status on the Swan Coastal Plain, Western Australia. *Hydrobiologia* **299**, 147–61.

Barbour C. & Brown J. (1974) Fish species diversity in lakes. *Am. Nat.* **108**, 473–89.

Battle J. & Golladay S. (2001) Water quality and macroinvertebrate assemblages in three types of seasonally inundated limesink wetlands in southwest Georgia. *J. Freshwat. Ecol.* **16**, 189–207.

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Batzer D. & Wissinger S. (1996) Ecology of insect communities in nontidal wetlands. *Annu. Rev. Entomol.* **41**, 75–100.

Blanch S., Ganf G. & Walker K. (1999) Tolerance of riverine plants to flooding and exposure indicated by water regime. *Regul. Rivers: Res. Manage.* **15**, 43–62.

Boon P., Virtue P. & Nichols P. (1996) Microbial consortia in wetland sediments: A biomarker analysis of the effects of hydrological regime, vegetation and season on benthic microbes. *Mar. Freshwater Res.* **47**, 27–41.

Boulton A. & Lloyd L. (1991) Macroinvertebrate assemblages in floodplain habitats of the lower River Murray, Australia. *Regul. Rivers: Res. Manage.* **6**, 137–51.

Boulton A. J. (1989) Over-summering refuges of aquatic macroinvertebrates in two intermittent streams in central Victoria. *Trans. R. Soc. S. Aust.* **113**, 23–34.

Boulton A. J. & Jenkins K. M. (1998) Flood regimes and invertebrate communities in floodplain wetlands. In: *Wetlands in a Dry Land: Understanding for Management* (ed. W. D. Williams), pp. 137–46. Environment Australia, Biodiversity Group, Canberra, Australia.

Boulton A. J. & Lloyd L. N. (1992) Flooding frequency and invertebrate emergence from dry floodplain sediments of the River Murray, Australia. *Regul. Rivers: Res. Manage.* **7**, 137–51.

Bowler J. M. (1990) The last 500 000 years. In: *The Murray* (eds N. Mackay & D. Eastburn), pp. 95–110. Murray-Darling Basin Commission, Canberra, Australia.

Bren L. J. (1992) Tree invasion of an intermittent wetland in relation to changes in the flooding frequency of the River Murray, Australia. *Aust. J. Ecol.* **17**, 395–408.

Brendonck L., Michels E., De Meester L. & Riddoch B. (2002) Temporary pools are not 'enemy-free'. *Hydrobiologia* **486**, 147–59.

Brereton G. (1994) *Summary Report: Macquarie Marshes Management Strategy – Stage 1: Biophysical Investigations.* Department of Water Resources, Dubbo, New South Wales, Australia.

Briggs S., Thornton S. & Hodgson P. (1993a) Dissolved and particulate organic carbon in two wetlands in southwestern New South Wales, Australia. *Hydrobiologia* **264**, 13–19.

Briggs S., Thornton S. & Tongway D. (1993b) Characteristics of river red gums used by nesting waterbirds. *Aust. Birds* **27**, 12–20.

Briggs S., Lawler W. & Thornton S. (1998) Relationships between control of water regimes in River Red Gum wetlands and abundance of waterbirds. *Corella* **22**, 47–55.

Briggs S., Seddon J. & Thornton S. (2000) Wildlife in dry lake and associated habitats in western New South Wales. *Rangel. J.* **22**, 256–71.

Briggs S. V. (1988) Guidelines for management of inland wetlands in southern New South Wales. *Wetlands Aust.* **8**, 1–2.

Briggs S. V. & Maher M. T. (1985) Limnological studies of waterfowl habitat in southwestern New South Wales. II. Aquatic macrophyte productivity. *Aust. J. Mar. Freshwat. Res.* **36**, 59–67.

Briggs S. V. & Thornton S. A. (1999) Management of water regimes in river red gum *Eucalyptus camaldulensis* wetlands for waterbird breeding. *Aust. Zool.* **31**, 187–97.

Briggs S. V., Hodgson P. F. & Ewin P. (1994) Changes in populations of waterbirds on a wetland following water storage. *Wetlands Aust.* **13**, 36–48.

Brinson M., Lugo A. & Brown S. (1981) Primary productivity, decomposition and consumer activity in freshwater wetlands. *Annu. Rev. Ecol. Syst.* **12**, 123–61.

Brock M. A. (1998) Understanding plant germination, establishment and reproduction for wetland vegetation. In: *Wetlands in a Dry Land: Understanding for Management* (ed. W. D. Williams), pp. 131–6. Environment Australia, Biodiversity Group, Canberra, Australia.

Brock M. & Casanova M. (1991) Vegetative variation of *Myriophyllum variifolium* in permanent and temporary wetlands. *Aust. J. Bot.* **39**, 487–96.

Browne R. (1981) Lakes as islands: biogeographic distribution, turnover rates, and species composition in the lakes of central New York. *J. Biogeogr.* **8**, 75–83.

Burks R., Jeppesen E. & Lodge D. (2001) Littoral zone structures as *Daphnia* refugia against fish predators. *Limnol. Oceanogr.* **46**, 230–7.

Carpenter S. & Kitchell J. (1988) Consumer control of lake productivity. *Bioscience* **38**, 764–9.

Carpenter S., Cole J., Hodgson J. *et al.* (2001) Trophic cascades, nutrients, and lake productivity: Whole lake experiments. *Ecol. Monogr.* **71**, 163–86.

Carpenter S. R., Caraco N. F., Correl D. L., Howarth R. W., Sharpley A. N. & Smith V. H. (1998) Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecol. Appl.* **8**, 559–68.

Casanova M. T. (1994) Vegetative and reproductive responses of charophytes to water-level fluctuations in permanent fluctuations in permanent and temporary wetlands in Australia. *Aust. J. Mar. Freshwat. Res.* **45**, 1409–19.

Casanova M. T., Douglas-Hill A., Brock M. A., Muschal M. & Bales M. (1997) Farm ponds in New South Wales, Australia: relationship between macrophyte and phytoplankton abundances. *Mar. Freshwat. Res.* **48**, 353–60.

Collinson N. H., Biggs J., Corfield A. *et al.* (1995) Temporary and permanent ponds: An assessment of

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the effects of drying out on the conservation value of aquatic macroinvertebrate communities. *Biol. Conservation* **74**, 125–33.

Coops H., Beklioglu M. & Crisman T. L. (2003) The role of water-level fluctuations in shallow lake ecosystems – Workshop conclusions. *Hydrobiologia* **506**, 23–7.

Corti D., Kohler S. L. & Sparks R. E. (1997) Effects of hydroperiod and predation on a Mississippi River floodplain invertebrate community. *Oecologia* **109**, 154–65.

Diehl S. & Kornijow R. (1992) Influence of submerged macrophytes on trophic interactions among fish and macroinvertebrates. In: *The Structuring Role of Submerged Macrophytes in Lakes* (eds E. Jeppesen, M. Sondergaard, M. Sondergaard & K. Christofferson), pp. 24–45. Springer, New York.

Dodson S. (1992) Predicting crustacean zooplankton species richness. *Limnol. Oceanogr.* **37**, 848–56.

Dodson S., Arnott S. & Cottingham K. (2000) The relationship in lake communities between primary productivity and species richness. *Ecology* **81**, 2662–79.

Douglas M. & Lake P. S. (1994) Species richness of stream stones: an investigation of the mechanisms generating the species-area relationship. *Oikos* **69**, 387–96.

Dumont H. (1992) The regulation of plant and animal species and communities in African shallow lakes and. *Wetlands* **25**, 303–46.

Euliss N. H., Jr, LaBaugh J. W., Fredrickson L. H. *et al.* (2004) The wetland continuum: A conceptual framework for interpreting biological studies. *Wetlands* **24**, 448–58.

Furch K. & Junk W. (1997) Physicochemical conditions in the floodplains. In: *The Central Amazon Floodplain: Ecology of a Pulsing System (*ed. W. Junk), pp. 69–108. Springer-Verlag, Berlin.

Gehrke P. & Harris J. (2001) Regional-scale effects of flow regulation on lowland riverine fish communities in New South Wales, Australia. *Regul. Rivers: Res. Manage.* **17**, 369–91.

Gehrke P., Brown P., Schiller C., Moffat D. & Bruce A. (1995) River regulation and fish communities in the Murray-Darling Basin. *Regul. Rivers: Res. Manage.* **11**, 363–75.

Gehrke P., Astles K. & Harris J. (1999) Within-catchment effects of flow alteration on fish assemblages in the Hawkesbury-Nepean River system, Australia. *Regul. Rivers: Res. Manage.* **15**, 181–98.

Golladay S., Taylor B. & Palik B. (1997) Invertebrate communities of forested limesink wetlands in southwest Georgia, USA: habitat use and influence of extended inundation. *Wetlands* **17**, 383–93.

Green D. (1997) *The Effects of Regulation on the Ecology of the Menindee Lakes.* Ecological Services Unit, Department of Land and Water Conservation, Buronga, New South Wales, Australia.

Growns J., Davis J. & Cheal F. (1992) Mulitvariate pattern analysis of wetland invertebrate communities and environmental variables in Western Australia. *Aust. J. Ecol.* **17**, 275.

Gutreuter S., Bartels A. D., Irons K. & Sandheinrish M. B. (1999) Evaluation of the flood-pulse concept based on statistical models of growth of selected fishes of the Upper Mississippi River system. *Can. J. Fish. Aquat. Sci.* **56**, 2282–91.

Hamilton S. & Lewis W. J. (1990) Basin morphology in relation to chemical and ecological characteristics of lakes on the Orinoco River floodplain, Venezuela. *Arch. Hydrobiol.* **119**, 393–425.

Hart R. C. (1985) Seasonality of aquatic invertebrates in low-altitude and Southern Hemisphere inland waters. *Hydrobiologia* **125**, 151–78.

Hershey A. E., Gettel G. M., McDonald M. E. *et al.* (1999) A geomorphic–trophic model for landscape control of arctic lake food webs. *Bioscience* **49**, 887–97.

Hillbricht-Ilkowska A. (1999) Shallow lakes in lowland river systems: role in transport and transformations of nutrients and in biological diversity. *Hydrobiologia* **409**, 349–58.

Holcik J. (1996) Ecological fish production in the inland delta of the Middle Danube, a floodplain river. *Env. Biol. Fishes* **46**, 151–65.

Hope J. (2000) *The Lake Victoria Shore: Understanding Change in the Landscape*, Vol 2. Murray-Darling Basin Commission, Canberra, ACT.

Ibanez M. (1998) Phytoplankton composition and abundance of a central Amazonian floodplain lake. *Hydrobiologia* **362**, 79–83.

Jeffries M. (1994) Invertebrate communities and turnover in wetland ponds affected by drought. *Freshwat. Biol.* **32**, 603–12.

Jenkins K. M. & Boulton A. J. (1998) Community dynamics of invertebrates emerging from reflooded lake sediments: flood pulse and aeolian influences. *Int. J. Ecol. Environ. Sci.* **24**, 179–92.

Jeppesen E., Jensen J., Sondergaard M., Lauridsen T., Pedersen L. & Jensen L. (1997) Top-down control in freshwater lakes – the role of nutrient state, submerged macrophytes and water depth. *Hydrobiologia* **342**, 151–64.

Junk W. (1997) *The Central Amazon Floodplain: Ecology of a Pulsating System*. Springer, New York.

Junk W. J., Bayley P. B. & Sparks R. E. (1989) The flood pulse concept in river-floodplain systems. Proceedings of the international large river symposium in D. P.

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Dodge, editor. *Can. J. Fish. Aquat. Sci. Spec. Publ.* **106**, 110–27.

Kahl M. (1964) Food ecology of the wood stork (*Mycteria americana*) in Florida. *Ecol. Monogr.* **34**, 97–117.

Kalk M. & Schulten-Senden C. (1977) Zooplankton in a tropical endorheic lake (Lake Chilwa, Lilawi) during drying and recovery phases. *J. Limnol. Soc. S. Afr.* **3**, 1–7.

Kingsford R. (2000a) Ecological impacts of dams, water diversions and river management on floodplain wetlands in Australia. *Aust. Ecol.* **25**, 109–27.

Kingsford R. (2000b) Protecting rivers in arid regions or pumping them dry? *Hydrobiologia* **427**, 1–11.

Kingsford R. & Thomas R. (1995) The Macquarie Marshes in arid Australia and their waterbirds: a 50 year history of decline. *Environ. Manage.* **19**, 867–78.

Kingsford R., Boulton A. & Puckridge J. (1998) Challenges in managing dryland rivers crossing political boundaries: lessons from Cooper Creek and the Paroo River, central Australia. *Aquat. Conserv. Mar. Freshwat. Ecosyst* **8**, 361–78.

Kingsford R., Curtin A. & Porter J. (1999) Water flows on Cooper Creek in arid Australia determine 'boom' and 'bust' periods for waterbirds. *Biol. Conservation* **88**, 231–48.

Kingsford R., Jenkins K. & Porter J. (2002) *Waterbirds and Effects of River Regulation on Menindee Lakes of the Darling River. Consultant Technical Report.* Department of Land and Water Conservation, Buronga, New South Wales, Australia.

Kingsford R. T., Jenkins K. M. & Porter J. L. (2004) Imposed hydrological stability on lakes in arid Australia and effects on waterbirds. *Ecology* **85**, 2478–92.

Kushlan J. (1976) Wading bird predation in a seasonally fluctuating pond. *Auk* **93**, 464–76.

Lake P. S., Bayley I. A. E. & Morton D. W. (1989) The phenology of a temporary pond in western Victoria, Australia, with special reference to invertebrate succession. *Arch. Fur Hydrobiol.* **115**, 171–202.

Lazzaro X. (1997) Do the trophic cascade hypothesis and classical biomanipulation approaches apply to tropical lakes and reservoirs. *Verh. Internat. Verein. Limnol.* **26**, 719–30.

Leeper D. & Taylor B. (1998) Insect emergence from a South Carolina (USA) temporary wetland pond, with emphasis on the Chironomidae (Diptera). *J. N. Am. Benthol. Soc.* **17**, 54–72.

Leslie D. (2001) Effect of river management on colonially-nesting waterbirds in the Barmah–Millewa forest, southeastern Australia. *Regul. Rivers: Res. Manage.* **17**, 21–36.

Leslie A., Crisman T., Prenger J. & Ewel K. (1997) Benthic macroinvertebrates of small Florida Pondcypress swamps and the influence of dry periods. *Wetlands* **17**, 447–55.

Lewis W., Hamilton S., Lasi M., Rodriguez M. & Saunders J. III (2000a) Ecological determinism on the Orinoco floodplain. *Bioscience* **50**, 681–93.

Lewis W., Hamilton S., Lasi M., Rodriguez M. & Saunders J. (2000b) Ecological determinism on the Orinoco floodplain. *Bioscience* **50**, 681–92.

Maher M. & Carpenter S. M. (1984) Benthic studies of waterfowl breeding habitat in south-western New South Wales. II. Chironomid populations. *Aust. J. Mar. Freshwat. Res.* **35**, 97–110.

Moorehead D., Hall D. & Willig M. (1998) Succession of macroinvertebrates in playas of the Southern High Plains, USA. *J. N. Am. Benthol. Soc.* **17**, 430–42.

Nicol J. (2004) *The Effect of Water Resource Development on the Propagule Banks of Arid Deflation Basin Lakes.* Adelaide University, Adelaide, Australia.

Nielsen D. L. & Chick A. J. (1997) Flood-mediated changes in aquatic macrophyte community structure. *Mar. Freshwat. Res.* **48**, 153–8.

Nielsen D. L., Hillman T. J. & Smith F. J. (1999) Effects of hydrological variation and planktivorous competition on macroinvertebrate community structure in experimental billabongs. *Freshwat. Biol.* **42**, 427–44.

Perin S., Pick F., Lean D. & Mazumber A. (1996) Effects of planktivorous fish and nutrient additions on primary production of shallow versus deep (stratified) lake enclosures. *Can. J. Fish. Aquat. Sci.* **53**, 1125–32.

Phillips G., Bramwell A., Pitt J., Stansfield J. & Perrow M. (1999) Practical application of 25 years' research into the management of shallow lakes. *Hydrobiologia* **395/396**, 61–76.

Podrabsky J., Hrbek T. & Hand S. (1998) Physical and chemical characteristics of ephemeral pond habitats in the Maracaibo basin and Llanos region of Venezuela. *Hydrobiologia* **362**, 67–78.

Poiani K. & Johnson W. (1993) A spatial simulation model of hydrology and vegetation dynamics in semi-permanent prairie wetlands. *Ecol. Appl.* **3**, 279–93.

Poizat G. & Crivelli A. J. (1997) Use of seasonally flooded marshes by a fish in a Mediterranean wetland: timing and demographic consequences. *J. Fish Biol.* **51**, 106–19.

Pressey R. (1990) Wetlands. In: *The Murray* (eds N. Mackay & D. Eastburn), pp. 167–81. Murray-Darling Basin Commission, Canberra, Australia.

Puckridge J. (1999) The role of biology in the hydrology of dryland rivers. In: *A free-flowing River: the Ecology of the Paroo River* (ed. R. T. Kingsford), pp. 97–112.

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NSW National Parks and Wildlife Service, Hurstville, New South Wales, Australia.

Puckridge J. T., Sheldon F., Walker K. F. & Boulton A. J. (1998) Flow variability and the ecology of lowland rivers. *Mar. Freshwat. Res.* **49**, 55–72.

Puckridge J., Walker K. & Costelloe J. (2000) Hydrological persistence and the ecology of dryland rivers. *Regul. Rivers: Res. Manage.* **16**, 385–402.

Qui S. & McComb A. J. (1996) Drying-induced stimulation of ammonium release and nitrification in reflooded lake sediments. *Mar. Freshwat. Res.* **47**, 531–6.

Quinn G., Hillman T. & Cook R. (2000) The response of macroinvertebrates to inundation in floodplain wetlands: a possible effect of river regulation? *Regul. Rivers: Res. Manage.* **16**, 469–77.

Rabalais N., Turner R., Wiseman W. J. & Dortch Q. (1998) Consequences of the 1993 Mississippi River flood in the Gulf of Mexico. *Regul. Rivers: Res. Manage.* **14**, 161–77.

Ricci C. (2001) Dormancy patterns in rotifers. *Hydrobiologia* **446/447**, 1–11.

Roshier D., Whetton P., Allan R. & Robertson A. (2001) Distribution and persistence of temporary wetland habitats in arid Australia in relation to climatic influences. *Aust. Ecol.* **26**, 371–84.

Scheffer M., Hosper S. H., Meijer M.-L., Moss B. & Jeppesen E. (1993) Alternative equilibria in shallow lakes. *Trends Ecol. Evol.* **8**, 275–9.

Schneider D. & Frost T. (1996) Habitat duration and community structure in temporary ponds. *J. N. Am. Benthol. Soc.* **15**, 64–86.

Scholz O., Gawne B., Ebner B., Ellis I., Betts F. & Meredith S. (1999) *The Impact of Drying on the Ecology of Menindee Lakes. Technical Report.* Cooperative Research Centre for Freshwater Ecology, Canberra, Australia.

Schriver P., Bogestrand J., Jeppesen E. & Sondergaard M. (1995) Impact of submerged macrophytes on fish-zooplankton-phytoplankton interactions: Large-scale enclosure experiments in a shallow eutrophic lake. *Freshwat. Biol.* **33**, 255–70.

Seddon J. & Briggs S. (1998) Lakes and lakebed cropping in the Western Division of New South Wales. *Rangel. J.* **20**, 237–254.

Seddon J., Thornton S. & Briggs S. V. (1997) *An Inventory of Lakes in the Western Division of New South Wales.* National Parks and Wildlife Service, Lyneham ACT.

Serruya C. (1990) Overview: an appraisal of concepts. In: *Large Lakes: Ecological Structure and Function* (eds M. Tilzer & C. Serruya), pp. 663–73. Springer-Verlag, New York.

Shapiro J. (1990) Biomanipulation: The next phase – making it stable. *Hydrobiologia* **200/201**, 13–27.

Sinclair-Knight-Merz (2002) *Menindee Lakes Aquatic Fauna: Integration Report for Menindee Lakes ESD Project.* Buronga, New South Wales, Australia.

Talling J. (1992) Environmental regulation in African shallow lakes and wetlands. *Rev. Hydrobiol. Trop.* **25**, 87–144.

Thormann M., Bayley S. & Szumigalski A. (1998) Effects of hydrologic changes on aboveground production and surface water chemistry in two boreal peatlands in Alberta: Implications for global warming. *Hydrobiologia* **362**, 171–83.

Thornton S. A. & Briggs S. V. (1994) A survey of hydrological changes to wetlands of the Murrumbidgee River. *Wetlands Aust.* **13**, 1–13.

Timms B. & Boulton A. (2001) Typology of arid-zone floodplain wetlands of the Paroo River (inland Australia) and the influence of water regime, turbidity, and salinity on their aquatic invertebrate assemblages. *Arch. Hydrobiol.* **153**, 1–27.

Timms B. V. (1997) Study of coastal freshwater lakes in southern New South Wales. *Mar. Freshwat. Res.* **47**, 249–56.

Tockner K., Pennetzdorfer D., Reiner N., Schiemer F. & Ward J. V. (1999) Hydrological connectivity, and the exchange of organic matter and nutrients in a dynamic river-floodplain system (Danube, Austria). *Freshwat. Biol.* **41**, 521–36.

Walker K. F. & Thoms M. C. (1993) Environmental effects of flow regulation on the River Murray, South Australia. *Regul. Rivers: Res. Manage.* **8**, 103–19.

Walker K. F., Boulton A. J., Thoms M. C. & Sheldon F. (1994) Effects of water-level changes induced by weirs on the distribution of littoral plants along the River Murray, South Australia. *Aust. J. Mar. Freshwat. Res.* **45**, 1421–38.

Walker K. F., Sheldon F. & Puckridge J. T. (1995) An ecological perspective on large dryland rivers. *Regul. Rivers: Res. Manage.* **11**, 85–104.

Walker K. F., Puckridge J. T. & Blanch S. J. (1997) Irrigation development on Cooper Creek, Central Australia – Prospects for a regulated economy in a boom-and-bust ecology. *Aquat. Conserv. Mar. Freshwat. Ecosyst.* **7**, 63–74.

Wantzen K., Machado F., Voss M., Boriss H. & Junk W. (2002) Seasonal isotopic shifts in fish of the Pantanal wetland, Brazil. *Aquat. Sci.* **64**, 239–51.

Ward J. V. (1989) The four-dimensional nature of lotic ecosystems. *J. N. Am. Benthol. Soc.* **8**, 2–8.

Ward J. W. & Stanford J. A. (1995) Ecological

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connectivity in alluvial river ecosystems and its disruption by flow regulation. *Regul. Rivers: Res. Manage.* **11**, 105–19.

van der Wielen M. (2003) Drying cycles as a switch between alternative stable states in wetlands. *Verh. Internat. Verein. Limnol.* **28**, 1448.

Wiggins G., MacKay R. & Smith I. (1980) Evolutionary and ecological strategies of animals in annual temporary pools. *Arch. Hydrobiol. suppl.* **58**, 97–206.

Withers M. (1994) *Flooding and Water Conservation in the Great Anabranch of the Darling River.* Springwood Station, Wentworth, New South Wales, Australia.

Withers M. (1996) *The Talyawalka Creek and Associated Lakes.* Springwood Station, Wentworth, New South Wales, Australia.

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