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Environmental changes affect ecosystem services of the intermittent Lake Cerknica

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ABSTRACT

Lake Cerknica is an intermittent wetland with seasonal water level fluctuations. This paper discusses the possible changes of ecosystem services due to altered ecosystem functions caused by regional climate change. For this purpose, the lake's water regime was analysed and biomass production of common reed (*Phragmites australis*), the prevailing species, was related to ambient temperatures and water level. The effect of the latter was also examined for reed transpiration rate and plant diversity. The results revealed a gradual loss of seasonality of floods and droughts. High water level in winter months and temperatures at the beginning as well as the end of vegetation period were found to have a significant influence on reed biomass. The plant diversity research in six subsequent years in three different aquatic habitats revealed trends of a decrease due to increased water depth during the vegetation period. The complexity of the system and consequently ecosystem services might also be affected due to changes of other processes, which revealed to be related to water level; namely transpiration rate, plant mycorrhizal colonisation and soil mineralisation.

1. Introduction

Ecosystem processes enable system regulation and provide different goods and services. The concept of ecosystem services deals with benefits that humans gain from natural processes and ecological functions (Costanza et al., 1997). Ecosystem services are supporting, provisioning, regulatory and cultural. The Millennium Ecosystem Assessment (World Resource Institute, 2005) focused on services of different ecosystems, stressing their overall decline. Wetlands are among the most endangered systems (Cronk and Fennessy, 2001) even though they have a great influence on human well being, offering a majority of important services. Beside habitat destruction and pollution, climate change presents an additional threat to habitat structure and function.

Ecosystem processes depend on biotic community complexity (Lawton, 1994; Tilman and Downing, 1994), however changes in time as meteorological rhythms and trends are also important for ecosystem functioning (Millán et al., 2009). In many cases a positive relation among services and biodiversity was shown (Costanza et al., 2007). Lake Cerknica is a unique karst wetland, where seasonal alternations of floods and dry periods play an indispensable role in energy through-flow, turnover of matter and providing habitats for numerous organisms (Gaberščik et al., 2003; Gaberščik and Urbanc-Berčič, 2003a). Basic biogeochemical processes are similar to those in other natural systems classified as water level fluctuating ecosystems (Odum, 1971). Water level fluctuations present physical disturbances maintaining the ecosystem in an early, relatively productive stage of development. They interfere with a process of succession and in this way support the ecosystem's long-term stability. This state is defined as "pulse" or "water level fluctuation climax". For a long time, more or less regular changes with a long aquatic phase in the cooler part of the year have provided favourable conditions for a diverse community. Habitats are mainly delineated by a range of changes in water regime and soil properties, resulting in a specific vegetation pattern (Martinčič and Leskovar, 2003). Different studies of processes in intermittent wetlands revealed that water level during vegetation period (from May to September) as well as the intensity, timing and extent of floods and droughts affect primary production, life cycles of animals, i.e. spawning of fish and nesting of birds, as well as mineralisation and decomposition (Boulton and Brock, 2001; Dinka et al., 2008). In the past life cycles of the majority of organisms in Lake Cerknica were intimately coupled to water level fluctuations, which were more or less regular. Primary producers were well adapted to water level changes (avoiding unfavourable conditions, being cosmopolites, having persistent stadia or amphibious character). Since 1950s the trends of increasing temperatures and duration of solar radiations were observed in central Slovenia. The precipitation rate showed slight decrease (Zupančič, 2003; ARSO, 2008; Ipavec and Kajfež-Bogataj, 2008). As a consequence in the last decades flood and drought events in Lake Cerknica are becoming more and more scattered and irregular; therefore the conditions for plant growth are changing. Altered conditions also affect other organisms and ecosystem in

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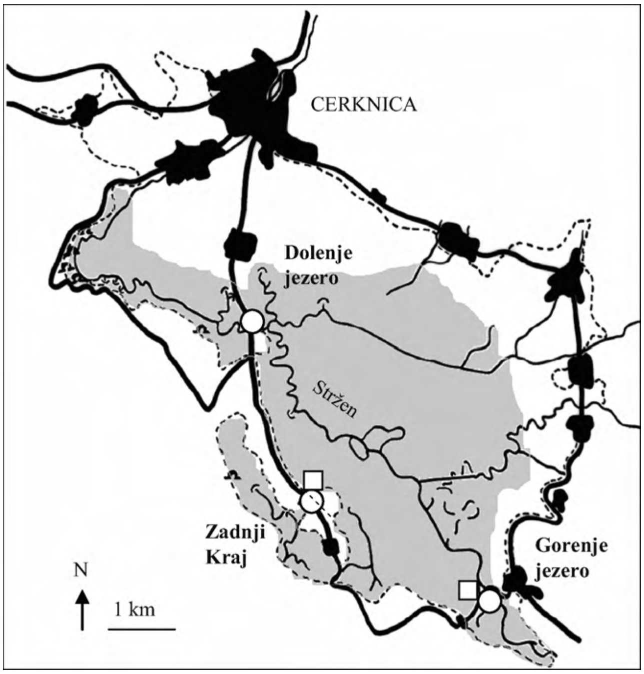

Fig. 1. Map of Lake Cerknica. Circles indicate three locations of water level and biodiversity measurements, while squares indicate locations of two experimental reed stands.

whole. Since ecosystems do not respond linearly to such pressures, ecosystem changes are hard to predict (Scheffer et al., 2001; Burkett et al., 2005).

In this paper, a direction of possible changes of some ecosystem services of Lake Cerknica due to regional climate changes will be discussed on the basis of recent measurements of the ecosystem processes and published data.

2. Materials and methods

2.1. Site description

Lake Cerknica is *locus typicus* for intermittent lakes, appearing at the bottom of a karstic valley named Cerkniško polje (38 km^2). Due to abundant precipitation in spring and autumn, the polje changes into a lake 20–25 km^2 in size. Floods last on average 260 days a year and the dry period usually starts in late spring (Kranjc, 2003). The intermittent water regime of Lake Cerknica creates specific conditions that differ from flooded areas elsewhere (Martinčič, 2003).

2.2. Abiotic parameters

Data sets for water levels at two locations, namely Gorenje Jezero and Dolenje Jezero, were provided by the Environmental Agency of the Republic of Slovenia. The correlation between the two locations was very high ($r = 0.979$, $p = 0.001$) therefore only the latter was used for analyses. Temperature sets are publicly available (http://www.arso.gov.si/vreme/podnebje). Environmental conditions during the transpiration measurements were measured at the site. Locations of the measurements are presented in Fig. 1.

2.3. Biomass assessment

Common reed (*Phragmites australis*) was sampled in 1986, 1987, 1997, and 2002–2007 in two types of stands: (1) "ecotonal" stands thriving along a stream at Gorenje Jezero that become part of the lake during the aquatic phase and (2) "littoral" stands near Zadnji Kraj, which are part of extensive reed stands growing in up to 1.5-m deep water in the aquatic phase (Fig. 1 and Table 1). Each year, five 0.25 m^2 squares were sampled (Dykyjová et al., 1973). The dry mass of samples was measured after 24 h of oven drying at 105 °C.

2.4. Ecophysiological measurements

Transpiration rate of reeds was measured in three subsequent vegetation periods from 2004 to 2006 in 2–3 week intervals in reed stands at Gorenje Jezero. Measurements were performed with a portable infrared gas analyser (ADC, LCA 4, UK) and were carried out on clear days at noon by sun time (PPFD more than 1100 $\mu mol\ m^{-2}\ s^{-1}$) at ambient conditions.

2.5. Plant diversity measurements

Between 2001 and 2006, plant species presence and abundance was monitored in three aquatic habitats. Sampling plots of approximately 500 m^2 were surveyed. The survey was undertaken in peak season in the beginning of July. Relative abundance was evaluated using a five degree scale (Kohler and Janauer, 1995). On the basis of the presence and abundance of species, the Shannon–Wiener index of plant diversity (H') was calculated. For the purpose of plant diversity study water level was occasionally measured also at Zadnji Kraj (data not shown).

2.6. Statistical analysis

Correlations between biomass data, different process measurements and water levels and temperatures in months the most important for primary production was investigated by calculating two-way Pearson's correlation coefficients and applying different regression models. Normal distribution was tested with Kolmogorov–Smirnov and Shapiro–Wilks tests. All statistical analyses were performed with SPSS for Windows 13.0.

3. Results

3.1. Water level fluctuations and water accumulation

Average water level fluctuations in Lake Cerknica show two peaks – in spring and late autumn, which are connected to the

Table 1
The characteristics of research locations: DJ, Dolenje Jezero; ZK, Zadnji Kraj and GJ, Gorenje Jezero.

Location	Habitat type	Water level (m)		Soil organic matter content	Soil wetness during drought
		Min	Max[b]		
DJ	Main stream	0.5	3.7	<10%	Wet, locally free water
ZK	Central lake area	0	1.5	<10%	Usually dry
GJ	Flood plain of main stream	0 (0.5[a])	0.7 (2.0[a])	<25%	Water saturated or wet, occasionally dry

[a] Measured in the main stream.
[b] At normal floods.

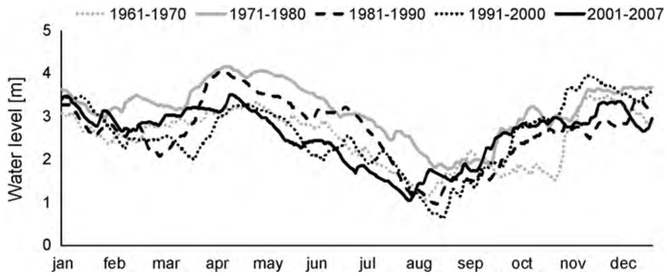

Fig. 2. Ten-year averages of daily water level changes at Lake Cerknica for the periods of 1961–1970, 1971–1980, 1981–1990, 1991–2000 and 2001–2007.

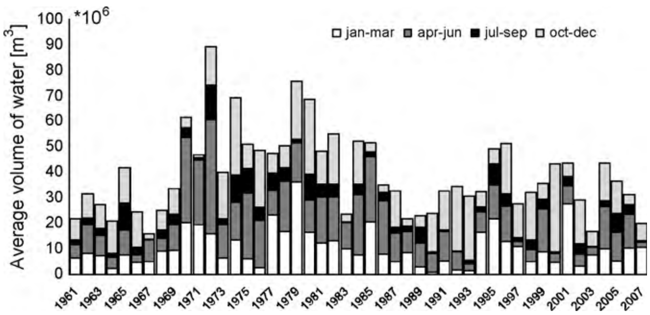

Fig. 3. Changes of average volume of water in Lake Cerknica since 1961.

temporal distribution of precipitation. The 10-year averages of Lake Cerknica water level in the last 4 decades have revealed a gradual loss of seasonality (Fig. 2). On the basis of volume/water level ratio, the average volumes of water for 3-month periods January–March, April–June, July–September and October–December were calculated for each year (Fig. 3). Water accumulation in the lake at the beginning of growth period (April–June) was rather high in 1970s and 1980s and is becoming very variable in last two decades. The amount of accumulated water was the lowest in the period from July to September and especially in some years when the main stream Stržen became a narrow and shallow brook.

3.2. Reed biomass production

Reed biomasses of the "littoral" and the "ecotonal" stands measured in 1986, 1987, 1997, and 2002–2007 were very variable (Fig. 4) as were the water level changes (Fig. 5). The productivity of "ecotonal" stand was higher in comparison to "littoral" one. Yearly primary production of "ecotonal" reed stands, which were occasionally flooded, was negatively related to the December and January water levels prior to growing season (Table 2), while for "littoral" stand no significant correlation was obtained.

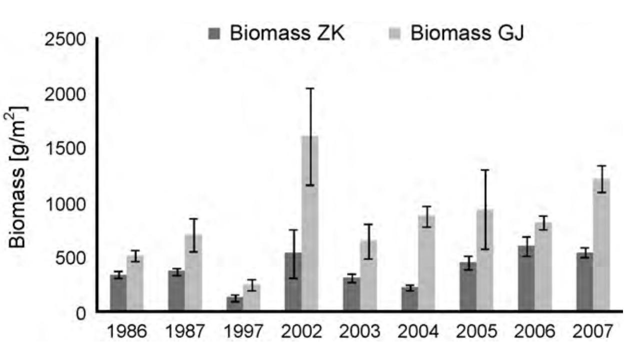

Fig. 4. Reed biomass at Lake Cerknica, at two locations: Zadnji Kraj (ZK) and Gorenje Jezero (GJ).

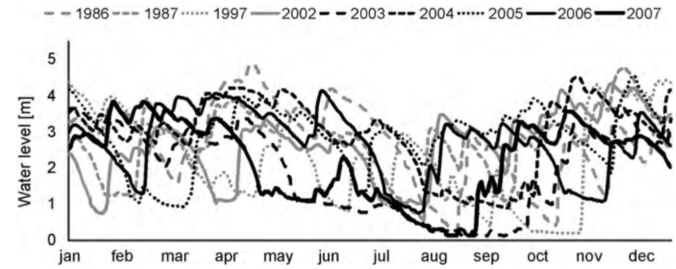

Fig. 5. Water level changes of Lake Cerknica in the years of reed biomass measurements: 1986, 1987, 1997, 2002–2007.

Table 2
The relationship between reed biomass production (ZK, Zadnji Kraj; GJ, Gorenje Jezero) and average monthly water level (WL) or temperature (*T*).

	WL, December (prev. y.)	WL, January	*T*, October (prev. y.)	*T*, April	*T*, July
Biomass, ZK					
Pearson	−0.392	−0.596	0.733	0.669	0.716
p	0.296	0.090	0.016*	0.049*	0.030*
Biomass, GJ					
Pearson	−0.742	−0.697	0.745	0.557	0.340
p	0.022*	0.037*	0.013*	0.119	0.371

Only months with significant associations are presented. Two-way Pearson correlation.
* $p < 0.05$.

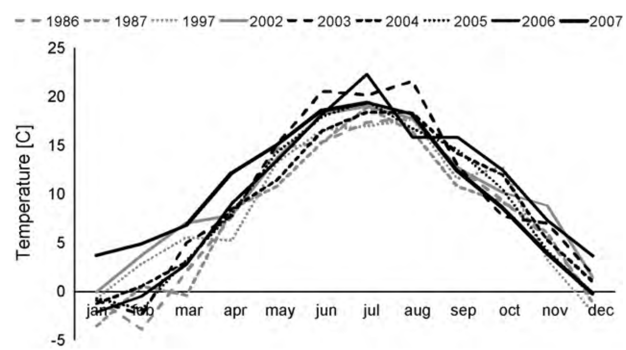

Fig. 6. Air temperature changes at the nearest weather station Postojna in the years of reed biomass measurements: 1986, 1987, 1997, 2002–2007.

The effect of temperatures (Fig. 6) on reed biomass production was more pronounced at Zadnji Kraj, than at Gorenje Jezero (Table 2). Temperatures in October in the previous year were positively related to biomass production at both locations. The correlation between biomass and temperatures at the very beginning of the growing season and in July was significantly positive. The latter was possibly a consequence of the fact that in years with high temperatures in July, the droughts were not very severe (Fig. 5).

An additional parameter affecting primary production is the frequency of water level fluctuation. In 1997, when frequent water level changes occurred, the lowest biomass was measured at both locations (Figs. 4 and 5).

3.3. Transpiration rate

The measurements of reed transpiration rate revealed great differences under contrasting hydrological conditions. Lower rates were measured in deeper water while during water drainage the transpiration rate increased (Fig. 7). No clear relationship was obtained when testing the potential influence of ambient temperatures (data not shown).

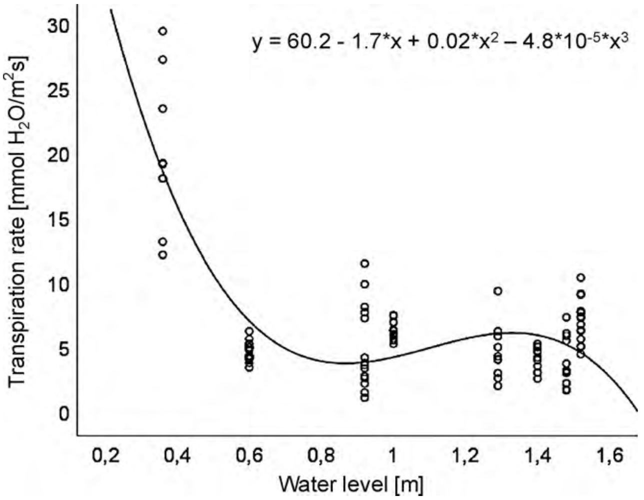

Fig. 7. Transpiration rate of common reed in relation to water level at Gorenje Jezero.

3.4. Plant diversity and vegetation

The plant diversity was studied in six subsequent years in three different aquatic habitats of Lake Cerknica. Shannon–Wiener diversity indices revealed changes in species composition as shown by indices ranging from 2.97 to 3.29 at Gorenje Jezero (in main stream), from 3.12 to 3.26 at Zadnji Kraj and 3.08 to 3.50 at Dolenje Jezero (in main stream). Variable water regime exerted lesser effect on the presence of macrophytes and more pronounced effect on the abundance of single species, which was why the plant diversity remained rather high. Even though we did not obtain a significant correlation with the water level changes, the trends showed a decrease in plant diversity occurring mainly due to temporarily increased water depth during the vegetation period.

4. Discussion

4.1. Ecosystem processes and services

Goods and services which support our lives are based on ecosystem processes. The most important processes in Lake Cerknica as well as in many other wetlands are: production of biomass, involvement in the water cycle, material degradation, decomposition and mineralisation. Complexity of the processes depends on organism diversity and performance which in Lake Cerknica is regulated by water level fluctuations (Gaberščik and Urbanc-Berčič, 2003b; Costanza et al., 2007). Many organisms of the area have a direct value for humans, such as fish and other wildlife (Povž, 2003; Polak, 2003), while the majority of others fulfil a very important ecological role contributing to the resilience and succession of the ecosystem (Gaberščik et al., 2003; Schulze et al., 2005).

4.2. Water level fluctuations and water accumulation

Data analyses showed that in the last four decades the water fluctuation pattern is becoming more and more irregular. The period from 1961 to 1970 differs from this pattern, because at the end of the 1960s man-made changes to the sink cave entrances (Smrekar, 2003) interfered with regular water level fluctuations. Lake Cerknica has an extensive karst watershed collecting water from an area of 475 km^2 (Kranjc, 2003). Thus it acts as a water supply reservoir, providing an important source of drinking water and influencing the regional climate. During an average flood, water covers an area of 20 km^2, which is about 28 million m^3 of water. If the water raises for an additional 2.5 m the flooded area increases to 24 km^2, which is about 76 million m^3 of water (Smrekar, 2003). The results showed large differences in the amount of accumulated water in the area, as well as large differences in different times of the year. The amount of water is crucial in the vegetation period since it is essential for plant activity. In the first part of vegetation period the availability of water was very variable, while in the second part it was the lowest due to reduced rainfall and high potential evapotranspiration rate (Kranjc, 2003).

4.3. Reed biomass production

Reed stands contribute the most to the primary production of the lake ecosystem (Martinčič and Leskovar, 2003). Common reed is a cosmopolitan species that may be temporarily exposed to flooding or to drought ranging from few days to several months (Mauchamp and Méthy, 2004). Deep water might affect the performance of reed by constraining oxygen supply to the below-ground parts of the plant (White and Ganf, 2002). Under such conditions reed produces fewer but taller stems, maintaining positive carbon balance (Dinka and Szeglet, 2001).

Reed biomass differed among years and locations. The enhanced production of "ecotonal" reed was negatively related to the water levels in the winter months of the previous year. We presume a possible reason is the occurrence of waves and formation of ice cover, followed by a decrease in water level. Waves and broken ice may damage reed culms and prevent oxygen transfer into the underground parts, affecting early growth in spring. The decline in reed production due to reduced oxygen supply to roots has already been shown in Lake Constance (Stark and Dienst, 1989) and Lake Bled (Urbanc-Berčič and Gaberščik, 1995). This relation was not obtained in "littoral" reed. At this location pressures are much more complex, because severe drought might occur in summer (at low water level) while deep water might disturb reed growth at the beginning of the growth season. Previous research of physiological condition of reeds also showed the presence of stress due to the short-term water level fluctuations and deep water in spring which might additionally affect the success of plants (Gaberščik et al., 2000; Dinka et al., 2008).

For "littoral" reed at Zadnji Kraj a closer relation was found between reed biomass production and temperatures. A possible reason why this relation was absent for "ecotonal" reed (except for autumn temperatures in previous year) could be that reed stands at Gorenje Jezero which are located along a main stream, have a water supply from a karst spring originating in the vicinity. Research showed that underground water buffers seasonal temperature extremes, therefore monthly water temperature fluctuations of karst tributaries to the lake were rather low (Gaberščik et al., 1994). A significant positive relationship between temperatures and reed biomass at both locations was found for autumn temperatures in the previous year. Common reed as a perennial species benefits from high temperatures in October, since this means the prolonging of the vegetation period, allowing for longer transport of assimilates, proteins and valuable bioelements into storage organs (Larcher, 2003). Measurements of light use efficiency in September showed almost no decline in carbon assimilation potential in early senescing leaves (unpublished data). The correlation between biomass and temperatures at the very beginning of the growth season and in July was significantly positive. The latter was possibly a consequence of the fact that in years with high temperatures in July, the droughts were not very severe. Temperature plays an important role in the plant life cycle influencing photosynthesis, respiration and transpiration as well as growth and development. High spring temperatures are also very important, quickly warming up shallow water. This is of primary importance for early vegetative development of plants in temperate climate, since active cell division and expansion of aboveground organs are initiated at temperatures about 10 °C (Larcher, 2003).

4.4. Transpiration rate

Water flow across the soil–plant–air continuum is affected by different biotic and abiotic factors. The principal factors are water availability and ambient temperatures. Another factor, which affects this continuum, is water depth causing disturbances in oxygen supply to the below-ground parts (White and Ganf, 2002). Our measurements of reed transpiration rate were in line with these findings, since lower rates were measured in deeper water while during water drainage the transpiration rate increased. No significant relationship was obtained when testing the relation with ambient temperatures (data not shown).

4.5. Plant diversity and vegetation

The occurrence, reproduction and distribution of plant species and structure of plant communities in intermittent habitats are determined by short-term changes such as the duration of inundation, water depth and soil water retention capacity (Barrat-Segretain et al., 1999; Riis and Hawes, 2002; Capers, 2003; Gaberščik et al., 2003; Warwick and Brock, 2003; Urbanc-Berčič et al., 2005). The life history of plants is closely related to intermittent water regime even though extreme conditions might disturb their growth and development. With increased stress for organisms, adaptations are becoming more and more costly, which results in changed vegetation patterns. Lower plant diversity and abundance in selected aquatic habitats was probably the consequence of three reasons: (1) pronounced water masses movements, (2) increased turbidity, and (3) because of the fact that in deep water the development of amphibious plants with more "terrestrial" character was disturbed.

Changes in vegetation pattern are occurring also in other habitats. Vegetation of Lake Cerknica is characterised by wetland communities, among which the community *Phragmitetum australis* is the most abundant (Martinčič and Leskovar, 2003). The survey of habitat types in 2007 and 2008 revealed that tall sedges (*Carex elata*) are spreading into previously monospecific reed stands. All these changes indicate a possibly altered ecosystem function and role in the landscape.

4.6. Other processes

Alternation of wet and dry periods at Lake Cerknica also influences other processes. The most important consequence of the intermittent water regime is the exchange of anaerobic and aerobic processes in the sediments (Urbanc-Berčič and Gaberščik, 1999, 2003). At the beginning of the dry period decomposition of organic matter is accelerated by the access of oxygen. Further drying decreases mineralisation by killing microorganisms (Boulton and Brock, 2001). During the wet period, nutrients are released and together with light and water provide a basis for germination and abundant growth of photoautotrophs (Brock and Casanova, 1997; Gaberščik et al., 2000). Previous research showed a significant positive correlation between soil water content and microbial activity of organic soils ($r = 0.73$, $p \geq 0.001$) (Urbanc-Berčič and Gaberščik, 2004).

Plants developed several adaptations to overcome changes in water regime, which enhance the survival under stress conditions caused by the lack of water and nutrients. Amphibious character and mycorrhizal colonisation, facilitating efficient nutrient uptake and diminishing the effects of water stress, are two of them (Smith and Read, 1997). Mycorrhizal colonisation in terrestrial specimens of amphibious plants was significantly higher than in submerged ones (Kržič et al., 2006). Mycorrhizal colonisation in plants of aquatic environment is believed to decline with water depth or flood duration due to anoxic conditions (Stevens and Peterson, 1996; Miller, 2000).

4.7. Implication to ecosystem services

In central Slovenia the average temperature increase since 1850 was more than 1.5 °C. The precipitation rate showed only slight decrease, but temporal distribution and short-term rates are changing (Zupančič, 2003; ARSO, 2008; Ipavec and Kajfež-Bogataj, 2008). However, even an apparently irrelevant change in a relevant factor can impact ecosystem complexity in long-term (Boero et al., 2004). Meteorological changes together with decreased landscape water retention capacity due to human activity (regulation of tributaries) (Smrekar, 2003) negatively affected the amount of water accumulated in the area as well as its distribution during the year. Loss of seasonality affected plant life cycles and their production which is related to the water level. High water level in winter months and high temperatures at the beginning as well as the end of the vegetation period revealed to have the most negative effect. Even though the data analysis did not show a significant relation between water level and reed production during the vegetation period it is likely that the trend of lower water accumulation as well as increased frequency of floods in late spring

Table 3
Changes in studied ecosystem processes, pressures and expected trends in ecosystem services due to changes of water regime (↓ decrease; ⥯ not defined).

Service provided	Supporting processes	Pressure	Expected trend in service provided
Water accumulation	System water retention capacity[a]	Stream regulations, extreme water level fluctuations, prolonged droughts, high frequency of water level changes, increased temperatures	↓
Local climate regulation	Evaporation, transpiration rate, albedo	Increased temperatures, prolonged droughts, deep water	↓
Biomass production	Photosynthesis, light use efficiency[b], decomposition processes, mycorrhiza[c]	Loss of seasonality, extreme water level fluctuations, prolonged droughts, deep water in winter, high frequency of water level changes	⥯
Nutrient cycling and retention	Decomposition[b], mycorrhiza[c]	Prolonged droughts and floods	⥯

Supporting references:
[a] Smrekar (2003).
[b] Urbanc-Berčič and Gaberščik (2003, 2004).
[c] Kržič et al. (2006).

and summer might have negative effect on long-term success of reeds. On the other hand we presume that prolonged vegetation periods may be beneficial for reed allowing for longer transport of assimilates into the storage organs in autumn and supporting quicker growth in spring. A decrease in plant diversity with increased water depth was detected in aquatic habitats. The complexity of the system and consequently ecosystem services will also be affected due to changes of other processes related to water regime, namely transpiration rate, plant mycorrhizal colonisation and soil mineralisation. Table 3 summarizes the studied and reviewed data indicating the important processes in the ecosystem, their implication to ecosystem services and the trends of possible changes. These effects might be mitigated by proper management that includes restoration of tributaries, which is the task of an ongoing LIFE Nature Project. Findings presented in the paper might also imply to other aquatic ecosystems, since the changes in temperature and the amount of precipitation and therefore water level fluctuations are becoming a reality. However additional complex analyses of Lake Cerknica, i.e. using conceptual framework proposed by Prato (2008) are needed for detailed assessment of the ecosystem changes.

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