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Extreme hydrological events destabilize aquatic ecosystems and open doors for alien species

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A B S T R A C T

The number of alien species invasions steadily grows worldwide, as well as the frequency of extreme climatic/hydrological events (ECEs/EHEs). ECEs and the invasion of alien species are among the main reasons for catastrophic transformations of aquatic ecosystems, watersheds, and human activities worldwide. Along with other negative results ECE may facilitate biological invasions. The objective of this review paper is to summarize how extreme climatic events may improve the likelihood of successful invasions in aquatic ecosystems and analyze some of the mechanisms. The morphometric characteristics of water bodies and their positions in the landscape connectivity may influence lake processes. ECE may result in an extreme ecological response – destabilization of an ecosystem and abrupt shift towards an alternative new state. Lakes' peculiarities mediate the effect of ECE influences on a lake ecosystem and determine whether the ecosystem response will be catastrophic or not. Different ecosystem alternative stable states have different levels of ecosystem immunity to invasions. ECEs can destabilize ecosystems and push them towards a tipping point where an ecosystem is most vulnerable. In a destabilized ecosystem near tipping point, ecosystem immunity is sharply decreased and the 'door' for alien species opens. The invasion process has several steps, and ECEs influence all of them. We are beginning to understand the association of ECE with invasions; to gain a deeper understanding of this we should integrate and coordinate the joint efforts of climatologists, hydrologists, limnologists, ecologists and biologists in this direction.

1. Introduction

Extreme hydrological events (EHE), caused by extreme climate events (ECE) due to sharp variability in regimes of temperature, precipitation and winds, as well as the invasions of alien species are among the main reasons of catastrophic transformations of aquatic ecosystems, watersheds, and human activities worldwide (Ward and Masters, 2007; Jentsch and Beierkuhnlein, 2008; Richardson, 2011; Yabi and Afouda, 2012; Zhang et al., 2015). Invasive alien species (IAS) are now regarded as one of the major threats to the biodiversity of the planet system and its ability to meet the needs of the people (Richardson, 2011). As an example, annual monetary impacts of invasive species on an economy are estimated at €120 billion in the USA and at least €12 billion in Europe (Vilà et al., 2009; Pimentel, 2011; Bonanno, 2016). Drastic reorganizations of aquatic ecosystems as a result of invasions of planktonic and benthic IAS are noted in different regions (Richardson, 2011). As an example, *Artemia sinica* (Anostraca) were introduced intentionally into the Tibetan lake Dangxiong Co in 2004 and as a result, by 2014, an entirely new ecosystem had formed in the lake (Jia et al., 2015). In this lake, species and trophic structure of the community completely changed, the clarity of the lake doubled, stratification of the water column and types of sediments changed, and many more birds started to use the lake surface for feeding. In another case, in 2009, Lake Mendota (USA) was invaded by the spiny water flea (*Bythotrephes longimanus*), originating from Russia, which now feeds on the native zooplankton species *Daphnia pulicaria* (Walsh et al., 2016). *Daphnia* helped 'clean' the lake by eating abundant amounts of algae but today Lake Mendota's daphnia are falling prey to the spiny water flea before they can reduce algal abundance. Complicating matters is agricultural fertilizer that goes into the lake. These conditions, with high-fertilizer and low-daphnia abundance, have led to a dramatic decline in water clarity and a sharp rise in algal blooms. The loss of water clarity has been valued

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at US$140 million (US$640 per household) (Walsh et al., 2016).

Extreme climatic events (ECE) may lead to EHE (floods, droughts, etc.) with more harm for ecosystems and people (Ward and Masters, 2007; Yabi and Afouda, 2012; Zhang et al., 2015). Frequency and size of EHE fluctuate through the Holocene (Brown et al., 2000). Currently an increase in frequency of ECE/EHE are marked in different parts of the world and further increase is predicted (Jentsch and Beierkuhnlein, 2008; Smith, 2011; Chen et al., 2014; Yu and Li, 2015; Lelieveld et al., 2016). Unique data from human observations of ice freeze dates (1443–2014) for Lake Suwa (Japan), and of ice breakup dates (1693–2013) for the Torne River (Finland) showed increasing frequency of years with warm extremes and reduction of strong inter-decadal quasi-periodic rhythms in long-term dynamics (Sharma et al., 2016). These trends are most pronounced after 1900. Using data from the Hydrometeorological Centre of Russia (Rosgydromet, 2015) changes in severe weather events in Russia in 1996–2014 (Fig. 1) can be seen; the regression equation was calculated by the authors of this article. The frequency of these events grew almost linearly during the period, an increase of 2.5–3 times. Over the past six decades a reliable increase of extreme daily precipitation was observed in both dry and wet regions, and the climate models also demonstrate this trend (Donat et al., 2016). Gradual climate changes and ECE led to abrupt changes in the lake areas and salinity (Liu et al., 2013; Shadrin and Anufriieva, 2013; Yan and Zheng, 2015).

Grave dangers may arise from the interaction of ECE and IAS; the scientific community is gradually recognizing this (Masters and Norgrove, 2010; Smith et al., 2012). In spite of these dangers, the ecological effects of ECE/EHE are among the main gaps in our knowledge of ecosystem ecology (Jentsch and Beierkuhnlein, 2008; Smith, 2011). Along with other negative results ECE/EHE may facilitate biological invasions (Smith, 2011; Diez et al., 2012). The main objective of our paper is to summarize how ECEs may improve the likelihood of successful invasions of alien species in aquatic ecosystems and analyze some of the mechanisms.

2. The responsiveness of the lakes to ECE

Lake processes and their variability depend on the morphometric characteristics of water bodies and their positions in the landscape connectivity (Brylinsky and Mann, 1973; Shadrin, 1985; Duarte and Kalff, 1989; Staehr et al., 2012). This dependence includes the lake responses on the ECEs (sharp changes in regimes of temperature, precipitation, and winds). Wind provides mixing energy for lakes and alters turbulent fluxes of heat but landscape geomorphology and forest development influence winds and their mixing effects (Tanentzap et al., 2008; Jia et al., 2015). As an example, winds influence water exchange of marine lakes with the seas; a change of a direction of prevailing winds may lead to catastrophic fluctuations in lake salinity and biotic composition (Shadrin and Anufriieva, 2013).

The morphometric dimensionless index of a lake – MI ($MI \sim L/h$, where L – the shoreline length and h – the mean depth) may influence some important abiotic and biotic characteristics of a lake (Shadrin, 1985, 2003; Hakanson, 2010). For example, the influence of lake size on diel temperature variability of surface waters was analyzed using data from 100 lakes (Woolway et al., 2016). It was shown that in summer there is a strong negative relation ($p < 0.001$) between a range of daily temperature variations and a lake's area and volume of water. Same daily variations of air temperature led to different responses in lake water temperature.

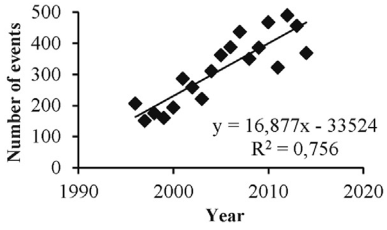

Fig. 1. Dynamics of hazardous hydrometeorological events in Russia from 1996 to 2014 (on data from Rosgydromet, 2015).

Consider for example, the dependence of the pond desiccation tolerance during drought. Water volume (V) in a reservoir is equal to $S * h$, where S – the water surface area, and h – the average depth of the reservoir. The evaporation of the water in the reservoir is positively proportional to the surface area of the reservoir. Consequently, the specific rate of loss of water in it will be equal to $S/V = 1/h$. The fall of the water level in the lake will be proportional to $1/h$, as well as the rate of a salinity increase in salt lakes. Deep lakes with underdeveloped coastlines are the least susceptible to catastrophic response to drought, heavy rains, floods and other ECE. Local, regional and global ECE may have different impacts on water bodies, which in particular are defined as morphometry of reservoirs and their position in the system of landscape connectivity.

There are two faces of ECE (Smith, 2011). 1. ECE is unusual, severe or unseasonal rare hydro-meteorological extremes of historical distribution – the range that has been seen in the past is not connected with traits of the individual lakes. 2. ECE may result in EHE and an extreme ecological response – destabilization of an ecosystem and an abrupt shift towards an alternative new state. Lakes' peculiarities (morphometry, position in landscape, etc.) mediate the effect of ECE influence on a lake ecosystem and determine whether the ecosystem response will be catastrophic or not. It is suggested that MI may be used as a measure of inertia potential of a lake's responses to external impacts, including ECE/EHE and IAS (Shadrin, 1985, 2003; Gomoiu et al., 2002). It should be noted that these issues are still poorly understood and are questions for future studies.

3. Resistance to invasion and alternative ecosystem states

Ecosystems have different susceptibility to invasions by alien species such as ecosystem invisibility (Rejmánek, 1989; Williamson, 1996; Lonsdale, 1999; Richardson and Pyšek, 2006); in particular, the asymmetry of flows of invasive species between water bodies (Gomoiu et al., 2002). For example, flow rates of successful invasive species are much higher from the Black Sea to the Caspian Sea than in the opposite direction. This is also typical for the exchange of invasive species between the Caspian and Baltic Seas. It has been proposed to name the resistance of ecosystems to invasions of exotic species 'ecosystem immunity' (Shadrin, 2000; Takahashi, 2001; Gomoiu et al., 2002; Hillel and Rosenzweig, 2005). Currently 'ecosystem immunity' is mostly a metaphor, and we need to move towards a more strong definition and quantification of it.

Ecosystem immunity is not constant over time; it is largely determined by the stage of development of the community/ecosystem. All ecosystems are undergoing constant change, and they may be in different alternative stable states (Dent et al., 2002; Beisner et al., 2003; Petraitis et al., 2009). There are certain regularities in the ecosystems' dynamics. In ecosystem dynamics there are coherent and incoherent stages; each of the stages in turn includes two phases; together C. Holling (1973, 2001) proposed to call 'the adaptation cycle'. During an adaptive cycle an ecosystem alternates between a long coherent stage of aggregation/growth (r) and conservation (K) and a shorter incoherent stage that creates opportunities for innovation – Ω (release or collapse/

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