Climate-induced hydrological changes and the ecology of freshwater biota: A review

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ABSTRACT

Climate change is believed to pose adverse effects to biodiversity of aquatic systems, both in boreal and tropical areas. the tropical freshwater systems are expected to suffer more severe impacts of climate change, from heavy floods or extended drought than do the boreal areas. Unfortunately, next few decades species extinction is suggested as dark future as we lack researches uncovering how climate change threats the aquatic biota. Therefore, a comprehensive understanding of biota' performance in face of climatic pressures, will guide the further necessary researches. This paper presents a review on the available researches addressing ecological effects of the most influential climatic parameters, flood and drought, on freshwater biota.

Abstrak

Perubahan iklim dipercaya lebih memberikan pengaruh terhadap biodiversitas pada sistem perairan baik pada belahan bumi utara maupun tropik. Biota pada sistem perairan tawar tropik diperkirakan mengalami lebih banyak dampak akibat perubahan iklim, mulai dari banjir besar atau kekeringan yang lebih panjang dibandingkan yang terjadi pada daerah bumi utara. Sayangnya, kepunahan spesies pada beberapa dekade ke depan dinyatakan sebagai masa depan yang gelap, karena tidak adanya ahli yang mengkaji tentang bagaimana perubahan iklim bisa mempengaruhi biota perairan. Sebab itu, pemahaman menyeluruh terhadap bagaimana kemampuan biota perairan menghadapi tekanan iklim akan menjadi panduan bagi peneliti yang berkepentingan di masa datang. Tulisan ini menyajikan telaah terhadap penelitian-penelitian yang ada terkait pengaruh ekologi dari parameter iklim yang paling berpengaruh, banjir dan kekeringan pada biota perairan tawar.

Keywords: Freshwater ecosystem, climate change, flood, drought, biota' performance

INTRODUCTION

The results of anthropogenic activities has been shown and predicted to have major effects on biodiversity at global, regional, and local scales, although global change constitutes a number of different forms of (Sala et al. 2000). Changes in climate and climate variability would, somehow, significantly affect natural ecosystems, and may pose additional threats to ecosystems. Furthermore, the effect of climate change on biodiversity has been predicted to cause the extinction of 15 - 37% of the Earth's terrestrial species in the next 50 years (Thomas et al., 2004). A similarly dark prognosis has been suggested for freshwater species in the next few decades (Xenopoulos et al., 2005).

Freshwater ecosystems are vulnerable to global change. Important global climate variables that are expected to change in the next decades with respect to freshwater habitat are air temperature and precipitation (Mitchell et al. 1990). Changes in these variables will affect water temperature, water quantity and water quality variables of freshwater environments which are the three primary linkages between climate and freshwater organisms (Regier and Meisner 1990).

Climate change pushes species out of their ecological

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synchrony and environmental landscape. This influences not only species distributions or community structure, but also the services they provide to ecosystems. Understanding how species' performances change along with the environmental gradients is important, particularly in aquatic systems, where shifts in habitat quality associated with environmental perturbations threaten the integrity of aquatic biota (Strayer et al., 2004).

The magnitude of impacts from global change and responses of aquatic ecosystems differ between boreal and tropical areas. In the tropics, the annual air temperature variation is smaller, but there is a large and predictable annual precipitation variation (Lowe-McConnell 1987). The seasonal precipitation cycle produces wide ranges in river flow rates and water levels, which directly alters the amount of freshwater habitat available for biota and indirectly alters many critical characteristics of that habitat (eg, O2 levels, turbidity, food availability, etc.).

The increase in global temperature is predicted to cause more vigorous hydrological cycle, with changes in precipitation and evapotranspiration rates. Warming accelerates land-surface drying as heat goes into evaporation of moisture and this increases the potential incidence and severity of droughts, which has been observed in many places worldwide (Dai et al. 2004). In tropical systems, evaporation and evapotranspiration often already exceed precipitation in the dry season (Irion and Junk 1997). In weather systems, convergence of increased water vapour leads to more intense precipitation and the risk of heavy rain or snow events, but may also lead to reductions in duration and/or frequency of rain events, considering that the total amounts are not predicted to change significantly (Trenberth, 2005). In such cases, the tropical areas are expected to suffer more severe impacts of climate change, from heavy floods or extended drought than do the boreal areas.

Despite an increase in research into this topic, there remains a lack a comprehensive understanding of the consequences of extreme precipitation fluctuation, outside the normal seasonal changes, on the ecology of freshwater biota. The aim of the present article is to complement the existing information by reviewing current knowledge of climate change effects, paying particular attention to the hydrological regime and resilience of the freshwater biota.

Key climate-related parameters

Aquatic ecosystems are vulnerable to changes in quantity and quality of their water supply, and it is expected that climate change will have a pronounced effect on global freshwater through elevated temperature and alterations in hydrological regimes with great global variability. Aquatic organisms have to adapt to a variety of environmental factors simultaneously; however, temperature, water quantity and water quality are regarded as the most fundamental climate-related factors.

In tropical regions, fluctuations in rainfall often represent the strongest seasonal variation, and change the environment to an extent comparable to temperature in temperate areas (Jacobsen and Encalada 1998). Variation in rainfall that affects stream discharge is among the most important sources of natural disturbances (Taylor et al. 1996). Flow regimes range from spates or peak flows during the wet season to zero flow in the dry season. The shape and size of river channels, the distribution of riffle and pool habitats and the stability of the substrate are largely determined by the interaction between the flow regime and local geology and landform (Newbury and Gaboury 1993). The complex interaction between flows and physical habitat becomes the major determinant of the distribution, abundance, and diversity of stream and river organisms (Nilsson and Svedmark 2002). It is reported that effects of climatic variability on hydrology can be particularly devastating, causing changes in water chemistry, stream size, water temperature, streambed structure, streambed substrate and stream flow (Medeiros and Maltchik, 2001; Starks et al., 2014). Such environmental variation can dramatically alter the living conditions and aquatic habitats within the water, affecting much of the aquatic fauna inhabiting streams (Moyle and Vondracek. 1985; Taylor and Warren, 2001).

Impacts of flood on biota

Water flow in aquatic ecosystem is often subject to high temporary variability. Temporary variability may be caused by high precipitation events in the catchment area. Hydroperiod and flood frequency (Medley and Havel 2007), as well as high water flow (Godlewska et al. 2003) have been recognized as significant factors structuring communities. This suggests that hydrology has a significant effect on both species richness and community structure of biotic communities in rivers, streams, floodplain ponds and lakes. Flood events often act as disturbances that interrupt the succession in plankton communities (Mulyaert et al., 2001). A short flood may have effects on the plankton ecosystem that last for weeks. However, the responses of the plankton communities differ from site to site, suggesting that it is dependent of other biotic and abiotic factors. Some groups of plankton may respond positively or negatively, while some others do not show clear response; e.g. Chlorophyll a concentration and abundance of bacteria, oligotrich ciliates and crustacean zooplankton did not respond significantly to the flood event (Mulyaert and Vyverman, 2006).

Flood waters transport large amounts of suspended solids and nutrients into lakes and/or the sea. An increase in concentration of suspended matter in a lake leads to greater light attenuation and, thus, to a decrease in primary production (Lloyd et al., 1987). High concentrations of abiogenic turbidity can limit phytoplankton photosynthesis and therefore restrict biomass development (Holst and Dokulil, 1987; Dokulil, 1994). In most cases, an increase in nutrient input will cause a rapid increase in algal biomass, especially in oligotrophic lakes (Thomas, 1973). However, in several lakes, an impoverishment of the algal standing stock and a decrease in the phosphorus concentration are observed following events involving the discharge of suspended sediment into the lake, despite the fact that the turbid inflow transports a large load of particulate phosphorus into the lake (Sampl, 1986). This is due to phytoplankton sedimentation after a flood, as the phytoplankters and suspended matter coagulate (Elber and Schanz 1990), resulting in a decrease in primary production and phytoplankton biomass. Negative responses can also occur under condition of prolonged floods, because flood pulse can dilute nutrients, resulting in a significantly lower phytoplankton biomass build up (Keckeis et al., 2003; Mihaljević et al., 2009).

Grobbelaar (1992) and Dokulil (1994) suggest that the ratio of mixing to euphotic depth is one of the most important factors affecting overall productivity in turbid waters. Under such water conditions, the aphotic portion is large, compared to the euphotic zone, and determines the relative time spent in the dark by the algae. In contrast, nutrients are of secondary importance, because it influence productivity only when a more favourable underwater light regime prevails, for example, prior to the flooding and increased turbidity. Energy available for phytoplankton growth is dependent on the availability of underwater light, which depends on the critical mixing depth, fluctuating light intensities and algal circulation patterns.

Godlewska et al. (2003) reported shifts in phytoplankton distribution from hypolimnion into the whole water column) and species composition during floods. This is likely caused by high water flow eliminated large species of cladocerans and copepods and favoured development of rotifers. However, in certain cases plankton animals concentrated at different depths in the water column before and after the flood, because they were transported to different locations by the currents. Dirnberger and Threlkeld (1986) suggest that, during the flood period, most zooplankton populations declined and the distribution of remaining individuals deepened. The changes in distribution may result from trying to maximize foraging while minimising the risk of predation (Gliwicz 1986).

Floods can also have positive impacts on planktonic communities. Dispersal among patches is important to the long-term viability of species in metapopulations, and flood connections can enhance the vagility of certain species (Jenkins, 1995). Immigrants with differential competitive ability can be introduced into communities and release local communities from competitive exclusion, shifts local dynamics and enhance long-term persistence (Leibold et al., 2004). "Normal" flooding can introduce new species (Havel et al., 2000), but extreme flooding can wash out entire populations (Baranyi et al., 2002). Turbulence, which increases in high flood, can also reduce grazing rate (Miquelis et al., 1998) and food selectivity of zooplankton (Vanderploeg, 1994).

Increased discharge into rivers leads to increased drifts. Downstream invertebrate drift is a normal feature in lotic systems and facilitates the recolonization of denuded areas of a stream (Brittain and Eikeland, 1988). However, flooding may have an important role in regulating the distribution, abundance and coexistence of macroinvertebrate (Resh et al., 1988). Significant reductions in macroinvertebrate density have been recorded after scouring floods (Robinson et al., 2004), while moderate disturbance may encourage diversity in many systems (Smith and Brown, 2006). In regulated river reaches below dams, it was reported that sudden increases in flow can cause catastrophic downstream drift (Layzer et al., 1989).

The most frequently reported effect of sedimentation associated with floods is an increase in drift density (Doeg and Milledge, 1991; Suren and Jowett, 2001), which may account for the loss of individuals and species in response to a loss of suitable habitat and changes to the food web (Rabeni et al., 2005). In addition, high water flow can also be acute for invertebrates; Doeg and Koehn (1994) identified a reduction in total number of benthic macroinvertebrate taxa and abundance, after a flushing event that increased suspended solid concentration. Pruitt et al. (2001) reported that total suspended solids concentrations greater than 284 mg/l resulted in biological impairment of invertebrate communities, while a concentration of 58 mg/l or less during storm flow provided an adequate margin of safety and were protective of aquatic invertebrates. Variability in tolerance to suspended solids could be explained by sediment particle characteristics, water temperature, species differences and other stressors that might have synergistic effects (Bash et al., 2001). In addition, the degree of turbidity associated with flood events has been known to affect the response of benthic invertebrate to flood. Some studies report that the magnitude of response of macroinvertebrate community to the flood is most severe in the non-turbid, upper main river and tributaries, where benthos community is dominated by the most sensitive Ephemeroptera, Plecoptera and Trichoptera species (Miserendino, 2009).

Sediment transport and deposition are processes that are a natural part of the stream environment and play a major role in structuring stream habitats. However, streams are vulnerable to increased sedimentation brought about by altered land uses in the surrounding catchments, with detrimental effects on benthic stream communities. The exacerbation of erosion and sedimentation may be particularly striking in the tropics (Newcombe and MacDonald, 1991; Wood and Armitage, 1997) where extreme climatic conditions can prevail and aquatic systems are increasingly under threat. How sediment affects aquatic ecosystems vary depending on the shape, size and density of the particles; their potential for microbial colonization; the velocity, temperature, flow and turbulence of the water (Hellawell, 1986); and the presence of associated factors, such as nutrients (Lemly, 1982). Increased levels of sedimentation can bury macroinvertebrates and their habitats (Wood et al., 2001; Wood et al., 2005) leading to shifts in the structure of the habitat and its associated fauna (Ryder, 1989).

Sedimentation has been shown to induce behavioural macroinvertebrate response that actively avoid substratum coated with excessive fine sediment (McClelland and Brusven, 1980; Connolly and Pearson, 2007). It is predicted that the upland fauna will be more sensitive to sedimentation, because it will naturally experience lower exposure to sedimentation than the lowland fauna; such different responses have been demonstrated in the mesocosm as well as in-situ experiments (Connolly and Pearson, 2007). Fine sediment deposition can cause shifts in the community structure through the loss of sensitive species, particularly those requiring coarse substrata for attachment or feeding, and through increases in the abundance of burrowing animals, such as some Chironomidae and Oligochaeta (Hellawell, 1986). Sedimentation can also affect the filter feeders, scrapers and collector through ingestion of inorganic when feeding, with a negative effect on nutrition and growth (Ryder, 1989). Fine silt deposit trapped by periphyton can reduce photosynthesis (Yamada and Nakamura, 2002), and thus algal availability to grazers (Donohue and Irvine, 2004). There may also be indirect effects of sedimentation transmitted through top-down effects of predators, such as fish and crayfish (Schofield et al., 2004). However, several studies have shown that changes in abundance rather than diversity are commonly associated with sedimentation (Lenat et al., 1981, Wagener and LaPerriere, 1985).

In large lenthic ecosystems, water level fluctuation is more important than flow regime. Such effects on ecosystems are very complex, and the biological effects in lakes are greatest in shallow water and littoral areas, where even small changes in water levels can result in the conversion of large areas of a standing-water environment in air exposed habitats (Leira and Cantonati, 2008). The potential effects of lake-level changes have been judged by impacts at the physical level, i.e. transparency, sedimentation patterns, erosion; at the species level, i.e. target species, and by indicators at the ecosystem level, i.e. carrying capacity and biodiversity (Leira and Cantonati, 2008). The fluctuation of water level can alter the lake morphometry and transform the characteristics of the sedimentation zone (erosion, transportation, accumulation; Håkanson, 1977), thereby water-level drawdown enhances sediment erosion and has the potential to fundamentally change littoral sediment and biogeochemical characteristics (Furey et al., 2004). The water level fluctuation cause changes in the littoral area available for benthic macroinvertebrate. The loss of littoral vegetation due to inundation or the establishment of emergent species from seeds during low water is always accompanied by changes in invertebrates and amphibians (Eulis et al., 2004).

The functioning of shallow lakes and floodplains is supposedly very sensitive to water level changes and littoral plant communities in shallow lakes located in semi-arid to arid regions appear to be particularly susceptible to water-level fluctuations (Beklioglu et al., 2006). High water level can facilitate the expansion of submerged vegetation to the benefits of many benthic invertebrates.

The effects of water level fluctuation on benthic macroinvertebrate can directly affect changes in the structure and dynamics of taxa that cannot withstand dry periods and lead to a limiting of their distribution at low water levels (Bowers and de Szalay 2004; Leira and Cantonati, 2008; Rossa and Bonecker, 2003. Indirect effects emerge through alteration of habitats (e.g. substrate composition, periphyton growth, resuspension versus sedimentation). Particularly important are those habitats with cobbles and macrophytes that provide an extensive suitable habitat for periphytic algae, which are their major food source, egg-laying and tube building, and also provide a refuge from predation (Scheifhacken et al., 2007). However, different zooplankton groups seem to show different sensibility to water level and are distinctly affected by floods (Ortega-Mayagoitia et al., 2000).

Fishes are particularly susceptible to changes in environmental conditions. Flow plays a critical role in the lives of fish with critical life events linked to flow regime (Bunn et al., 2002; Janáč et al., 2010). Numerous studies have shown that changes in stream flow associated with extreme variations in precipitation can alter fish communities and habitats. Many fish species display a preference for particular types of habitat such as pools, riffles, or backwater areas. While habitat structure is generally considered to be a good predictor of fish assemblage, habitat instability associated with variations in stream flow will disturb resident fish communities (Gelwick et al., 2001). Therefore, sudden or long-term variations in discharge arising from, for example, extended droughts or large storms, can be particularly devastating, causing changes in water chemistry, stream size, water temperature, streambed structure and substrate as well as stream flow (Medeiros and Maltchik, 2001). Extreme discharge associated with storm events can dramatically alter channel morphology and benthic habitat, which may have significant effects on fish communities. Such environmental alteration can dramatically alter living conditions and aquatic habitats

within the water, affecting much of the aquatic fauna inhabiting streams (Moyle and Vondracek, 1985; Taylor and Warren, 2001).

Crosa et al. (2009) reported that a large volume of sediment associated with reservoir flushing has decreased fish density and biomass; a greater mortality recorded for juveniles will likely result in long-term impairment of the age-structures fish populations. Juveniles' mortality due to flushing was also reported (Garric et al., 1990) along with damage to the gill epithelium (Petz-Glechner et al., 2003). High level of sediment can cause mortality of sensitive fish species (Lloyd, 1987; Newcombe and MacDonald, 1991), whilst prolonged lower levels of suspended solids and turbidity can result in chronic weight-loss due to inability to feed efficiently (Sigler et al., 1984). Stream fish can become stranded on gravel bars or trapped in off-channel habitats when flow decreases rapidly. Susceptibility to stranding is a function of behavioural response to changing flows, and this varies with species, body size, water temperature, time of year and day, substrate characteristics, and the rate of flow reductions (Bradford, 1997). Mature fish may be able to shift into temporarily suitable habitats to compensate for periodic reductions in quality or availability of habitat (Bunt et al., 1999).

Variables, such as sediment load, pH, dissolved oxygen, and various nutrients, frequently change during increased flow associated with storm events and is reported to affect fish (Winemiller et al., 2000, Ostrand and Wilde, 2002). Winemiller et al. (2000) reported that diversity and abundance of freshwater fish populations correlate positively with total dissolved nitrogen, nutrient concentration, and food resources in the water. Gelwick et al. (2001) found positive correlations between common measures of assemblage structure (diversity and abundance) and dissolved oxygen and salinity, whereas the change in chemical composition was minor (Keaton et al. 2005). On the other hand, extreme storm events that lead to flooding can introduce new species into assemblages and create new habitats (Winemiller et al., 2000), or increase availability of shelter and allochthonous food sources, and enrich water with nutrients carried from adjacent areas or present in flooded organic or inorganic material (Agostinho et al., 2004). Nevertheless, floods can dilute the aquatic biota by increasing water depth, reducing the availability of food resources, especially mobile ones. As a result, the hydrological cycle affect interspecific relations, particularly predation and competition. The flooding regime seems to favour piscivores, since floods are associated with the reproductive success of many of their prey species. However, due to their diluting effect, floods also reduce the density of prey species as well as provide increased shelter resulting in reduced prey availability (Luz-Agostinho et al., 2008).

Drought and freshwater biota

In contrast with the effects of floods, there have been relatively few studies of stream faunal dynamics after droughts (Lake, 2000). If floods amplify hydrological connectivity, droughts disrupt hydrological connectivity. With the onset of drought, falling water levels reduce the habitat availability for most aquatic biota, exposing marginal areas (Stanley et al., 1997), breaking surface water contact between the stream and its riparian zone, and reducing the hydraulic heterogeneity of flow. Changing water levels are another stressor on lake and littoral communities. Water level fluctuation in lakes are dominant forces controlling the functioning of lacustrine ecosystems (Wilcox and Meeker, 1992; Poff et al., 1997). It plays an important role in the lake's physical processes (e.g. the geomorphologic processes of erosion and sedimentation) (Leira and Cantonati, 2008). With falling water levels, lentic habitats may increase in extent and new types of habitats may be created, that favour some species. As drying proceeds, the threshold of cessation of surface flow is reached.

Droughts can have direct and indirect impacts on stream biota. Direct impacts are those caused by loss of water and flow, and habitat reduction and reconfiguration, whereas indirect impacts are those associated with changes in phenomena such as interspecific interactions, especially predation and competition, and the nature of food resources. The direct and indirect impacts of drought can greatly reduce population densities, species richness and alter life-history schedules, species composition, patterns of abundance, type and strength of biotic interactions (e.g. predation and competition), food resources, trophic structure and ecosystem processes. Resh (1992) found that a severe drought eliminated a population of the caddisfly, Gumaga nigricula. Following water flow reduction, many aquatic biota cannot move and become trapped and concentrated in lingering pools (Boulton et al., 1992; Matthews 1998; Matthews and Marsh-Matthews, 2003). Stream connectivity becomes differentially disrupted by the cessation of upstreamdownstream longitudinal links, and the weakening of lateral links between the stream channel and riparian zone, including floodplains, and vertical links between the surface, hyporheic zone and groundwater.

Information about the effect of droughts on invertebrates and fish are more abundant than that of micro- and macroalgae, macrophytes and riparian plants (Holmes, 1999; Matthews, 1998; Peterson, 1996; Yount and Niemi, 1990). During drought, flow may cease with stretches of rivers turning into isolated pools, where biota become concentrated with very high densities of invertebrates (Boulton and Lake, 1992; Miller and Golladay, 1996) and fish (Labbe and Fausch, 2000; Matthews, 1998; Matthews and Marsh-Matthews, 2003). Different isolated pools may harbour different assemblages of biota and with time, such pools can diverge from each other in their community structure (Meyerhoff and Lind 1987; Power et al., 1985; Stanley et al., 1997). During extreme drawdown events in reservoirs, the water quality changes significantly. Drawdown events cause changes to nutrient dynamics and, ultimately, lead to periods of high algal biomass; in one case leading to the formation of a potentially toxic cyanobacterial bloom (Naselli-Flores, 2003).

Physicochemical conditions shift rapidly with flow cessation with possible adverse effects on the benthos. When flow decreases, the capacity of the stream to transport organic matter decreases and cause an increase in detritus coverage. With flow cessation and the emergence of isolated pools, the abrupt change in physicochemical conditions impose a threshold on the ecosystem (Acuna, 2005). Organic matter or detritus and sediments are accumulated in pools, and reduce physical reaeration causing a decrease in dissolved oxygen concentrations and an increase in nutrient concentrations (Caruso, 2002; Stanley et al., 1997; Towns, 1985).

At the onset of drought, tolerant species can grow rapidly, leading to a density peak soon after flow cessation, although this density peak dropped rapidly in response to changes caused by flow cessation (Boulton and Lake, 1992; Towns, 1985). The most probable causes of these adverse effects are deoxygenation (Labbe and Fausch, 2000; Stanley et al., 1997) and toxicity of certain leachates from leaf decomposition (Boulton and Lake, 1990, 1992; Chergui et al., 1997; Towns, 1985, 1991). As streams dry and the surface water shrinks to unshaded pools, the build-up of nutrients, high temperatures and solar radiation can precipitate blooms of algae (Dahm et al., 2003; Freeman et al., 1994; Winder et al., 2012). The algae may create large diel changes in oxygen concentration (Matthews, 1998) and with rising water temperatures, such pools may become lethal for aquatic biota such as fish (Acuna, 2005; Matthews, 1998). Simultaneously, deoxygenation may occur in pools too, threatening biota (Golladay et al. 2002; Labbe and Fausch, 2000; Stanley et al., 1997).

Low discharge conditions during drought can limit habitat resources and mobility (Lohr and Fausch, 1997) and can have marked effects on community composition, diversity, size structure of populations, spawning, and recruitment of fish (Lake, 2003; Ledger et al., 2012; Poff et al., 2001). Droughts also results in intense aggregations of fish and possible competition for food and/or space, because fish are confined to small areas and usually at considerably higher densities, thus potentially increasing competition. Poff and Ward (1989) considered that such biotic interactions contribute relatively little to community structure in rivers. However, during periods of low flow, and the attendant reduction of habitat area or volume, biotic interactions could become temporarily important (Cowx et al., 1984; Matthews, 1988). Fish population structure can also be changed by drought (Resh et al., 2013), reducing spawning and recruitment (Cowx et al., 1984; Davies et al., 1988). Pires et al. (1999) note that some species are well adapted to natural droughts, however major native species are considered to be more sensitive to stream fragmentation and hydrological alteration (Parkin et al., 2014). In addition, habitat degradation and, possibly, the introduction of exotic species contribute to marked variability in species composition.

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