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ABSTRACT

Floods and droughts are key driving forces shaping aquatic ecosystems. Climate change may alter key attributes of these events and consequently health and distribution of aquatic flora and fauna. Improved knowledge of natural biological responses to different types of floods and droughts in rivers would allow us to better predict the ecological consequences of climate change-induced flow alterations. This review highlights that in unmodified ecosystems, the intensity and direction of biological impacts of floods and droughts vary, but the overall consequence is an increase in biological diversity and ecosystem health. To predict impact of climate change, physical metrics allowing to quantitatively link the physical disturbance attributes to the directions and intensities of biological impacts is needed. The link between the physical change and character of biological response is provided by the frequency of occurrence of the river wave characteristic – i.e. the event's predictability. The severity of impacts of floods is largely related to river wave amplitude (flood magnitude), and of droughts to river wave length (drought duration). Presented analysis of three rivers in Poland demonstrates how river wave characteristics for floods and droughts can be captured with flow duration statistics, and with help of habitat models and Uniform Continuous Under Threshold duration techniques, respectively.

Kewords: river wave concept, biological response, extreme events, disturbance, hydromorphology, climate change, river ecosystems, river floods, river droughts, warming.

INTRODUCTION

Global climate change is expected to modify patterns of hydrological events in many regions of the world (Glaser et al. 2010, Garner et al. 2015, Blöschl et al., 2017, Bormann et al. 2017, Markovic et al. 2017), affecting water temperature (Markovic et al. 2013, Van Vliet et al. 2013), and changing the temporal distribution of river flows (Blöschl et al. 2017). Since flow is considered a master variable shaping riverine ecosystems, such changes are expected to cause substantial shifts in the composition of aquatic communities (Guse et al. 2015, Rolls et al. 2016). This could lead to massive extinctions or to the creation of new traits and adaptations (Myers et al. 2017). The changes may vary depending on climate change magnitude and geographic location.

Understanding functional relationships between flow patterns and biological consequences is of the outmost importance for planning adaptation measures to climate change and for sustainable river management. Defining elements of the hydrological regime directly responsible for shifts in community composition is necessary. Subsequently, the attributes determining the direction and magnitude of the shift can be identified.

It is widely recognized that extreme events such as floods and droughts are a major driving force behind the composition of aquatic biotas (e.g. Poff et al. 2007, Sukhodolov et al. 2009, Wolter et al. 2016, Poff 2018). However, not all floods and droughts are the same, and therefore different events have different consequences. Knowledge of the directions and intensities of natural biological responses to different types of floods and droughts would allow to better understand and predict the consequences of natural and anthropogenic alterations.

To be precise in predictions useful for climate adaptation planning it is necessary to identify the appropriate quantitative metrics of disturbance that correlate with biological responses. Thus, the role that floods and droughts play in biological cycles needs to be better understood. Specifically, the following questions need to be answered:

- What are the functional mechanisms between physical patterns and biological response?
- Which attributes of floods and droughts are most closely related to population shaping phenomena?
- Which of these attributes are most sensitive to climate change effects?

While there is a substantial body of literature relating to various aspects of floods and droughts, the information is disjointed and not synthesized in a fashion that allows to fully understand the driving forces and mechanisms leading to biological responses. Therefore, the purpose of this paper is to:

- provide a systematic overview of the topic based on a review of the recent literature;
- identify practical, quantitative metrics that may be used to estimate the climate-induced modifications of flow patterns that determine biological response.

The paper concludes with an application of the identified metrics in three case studies for rivers in Poland.

FLOODS AND DROUGHTS AS ECOLOGICAL DISTURBANCE PROCESSES

For the ecology of a system, floods and droughts are considered physical disturbances, i.e. stochastic events forcing normal system environmental conditions substantially away from the mean (Stanford and Ward, 1983, Puckridge et al. 1998, Death et al. 2015, Fuller et al. 2019). Physical disturbance is a natural component of aquatic ecosystems, and aquatic biotas are adapted to deal with these disturbances (Resh et al., 1988; Fisher & Grimm, 1991; Lake, 2000, Lytle & Poff 2004, Van Looy et al. 2019).

Lake (2000) described three types of disturbance: pulse, press and ramp, which trigger three different processes that alter populations. A pulse disturbance causes an instantaneous alteration in animal or plant densities and possibly diversity, while a press disturbance causes a sustained change in abundance or composition. Ramps have been defined as disturbances that increase in strength (and often spatial extent) over time (Lake, 2000). Obviously, these definitions refer to a temporal scale experienced by individual organisms, and for aquatic organisms at the spatial scale of the reach. At this scale, floods are most often pulse or press disturbances, and droughts tend to be ramps. At coarser temporal scales all disturbances may be considered as pulses (Poff, 1992; Lake, 2003).

HABITAT CHANGES

Functionally, disturbance changes the quantity and quality of habitat available, which can directly modify community composition as well as affect biotic interactions (Fisher et al., 1982; Grossman et al., 1982, 1998; Reice, 1985; Frissel et al. 1986, Junk 2005, Parasiewicz et al., 2012, Winemiller et al. 2014, Gurnell et al. 2016, Leigh & Datry 2017). The processes triggered by floods or droughts can create two types of changes: concurrent i.e. occurring only during the event; and post-event changes that persist after the event for a considerable time (Pearsons et al. 1992, Bork & Kranz 2008, Death et al. 2015, Leigh & Datry 2017).

HABITAT CHANGES CAUSED BY FLOODS

Floods affect habitat elements such as stream substrate composition, stability, refugia, river channel cross-section and planform morphology, and the flow regime (Poff, 1992; Lake, 2000; Lake, 2007). However, as floods are pulse disturbances, their effects are most strongly related to the magnitude of the event (Molles, 1985; Grimm and Fisher, 1989, Pearsons et al. 1992, Wetter et al. 2010, Stolz et al. 2013, Herget et al. 2015). The effects of flooding may vary from minor geomorphological changes caused by small spates or freshets, to alteration of the entire structure of the stream channel caused by extended, powerful high discharge events (Costa and O'Connor, 1995; Bork & Kranz 2008, Dotterweich 2008, Hauer & Habersack 2009). Wolman and Miller (1960) showed that floods of bankfull discharge cause most geomorphological change because they have significant stream power and occur relatively frequently. Out-of-season floods are acknowledged to create more significant changes to river morphology than those that occur during typical wet seasons (Lytle, 2003; Giller, 2005, Wetter et al. 2010).

Concurrent changes

At the onset of a natural flood event, the increasing discharge raises flow velocities, and the thalweg of the river channel deepens and widens (Figure 2). Subsequently mobilization and deposition patterns reverse: pools are scoured and deposition takes place at the riffle areas, with little difference in water depth and velocity between pools and riffles (velocity-reversal phenomenon, Keller and Florsheim, 1993; Thompson et al., 1999, Hogan and Church, 1989). The temperature can either increase (e.g. in consequence of warm thunderstorms) or decrease (e.g. snowmelt waters), but it generally becomes more diverse across a cross-sectional profile (Tockner et al., 2000).

The extent of habitat change is also a function of river type and morphology (e.g., Tockner et al., 2000; Magoulick and Kobza, 2003). In constrained rivers, floods raise flow velocity and shear stress, creating major changes in channel morphology through the scouring and filling of the streambed (Gordon et al., 2004; Vezza et al., 2014). In lowland rivers with extensive floodplains, flood energy is more easily dissipated and water velocity and shear stress may not increase significantly. Nutrients previously deposited on the floodplain are also mobilized, affecting water quality and potentially greatly increasing rates of primary production (Edwards et al., 2012, Davis et al. 2018). Floods fill wetlands, anabranches and flood runners with a slow-moving flow that recedes slowly, and deposits sediments and organic particles upon the floodplain.

Post disturbance effects

Floods reshape the distribution and composition of habitat. The consequences may range from spatial rearrangement of habitats, but maintaining a similar quantitative distribution, to complete destruction of habitat for some species and creation of habitats for others (Arthington et al., 2005; Roghair et al., 2002). In some cases, the morphology of the channel returns to pre-flood conditions (dynamic equilibrium), but this depends on lower flows being sufficiently powerful to move sediments. Thus, recovery is partly determined by river and sediment type.

HABITAT CHANGES CAUSED BY DROUGHTS

Droughts can be divided into those that cause predictable, seasonal press disturbances and less predictable, protracted ‘ramp’ disturbances (Humphries and Baldwin, 2003). Droughts can either be periodic, seasonal or supra-seasonal events. Seasonal droughts are press disturbances, whereas supra-seasonal droughts are ramps marked by an extended decline in rainfall (Lake, 2003). Droughts tend to be more spatially extensive than floods, which are frequently limited to individual basins (Edwards et al., 2012).

Concurrent changes

During a drought, precipitation, runoff, soil moisture, groundwater levels and stream flow decline sequentially (Changnon, 1987; Grigg, 1996; Dahm et al., 2003). Similar to floods, there are both direct and indirect effects on stream habitat during the drought. Direct effects include loss of habitat area for aquatic organisms and loss of stream connectivity (Lake, 2003, Magoulick & Kobza 2003, Matthews & Marsh-Matthews 2003, Marshall et al. 2016, White et al. 2016).

Loss of habitat is caused by a lack of flow replenishment from upstream and may be exacerbated by evaporation and loss of water into the ground. Indirect effects include deterioration of water quality caused by increased concentration of organic matter that occur despite lower overall input of nutrients (Dewson et al., 2007; Golladay and Battle, 2002; Zielinski et al., 2009). The ratio of inorganic to organic nutrients declines, potentially causing a shift in stream metabolism (Dahm et al., 2003). Due to reduced sediment transport capacity, fine particles and organic matter are deposited on the river bed and into interstitial spaces (McKenzie-Smith et al., 2006). An increase in the density of aquatic organisms, as well as growth of algae and cyanobacteria feeding on the concentrated nutrients, may lead to oxygen depletion and potentially hypoxic conditions (Suren et al., 2003). During hot periods, a continuous increase of water temperature is sometimes accompanied by reduced inflow of cooler groundwater and consequent loss of thermal refugia (Elliot, 2000; Torgersen et al., 1999) and lower oxygen solubility. Higher temperatures increase decomposition rates and thus, further reduce oxygen concentrations. During cold weather periods, droughts may lead to lowering of water temperature, ice and frazil ice formations. Frazil ice tends to scour river bottoms causing morphological change (Lake, 2003). Overall, habitat area and quality decline during droughts.

Post disturbance effects

Long-term changes depend on drought intensity, duration and the ability of the ecosystem to recover. The changes are mostly of a morphological and/or chemical nature, and among others are consequences of ice-induced scour or sedimentation. Growth of macrophytes and riparian vegetation during droughts can create new morphological patterns after the event (Gurnell 2014, Gurnell et al. 2016a, 2016b). However after drying, the bare ground undergoes important chemical changes, increasing phosphate retention and re-oxidisation of sulphur that may lead to acidification after re-wetting (Baldwin and Mitchell, 2000; Lamontagne et al., 2006).

BIOLOGICAL RESPONSE

There are two generally recognized forms of biological response to disturbance: resistance (the capacity of the biota to withstand the disturbance) and resilience (the capacity to recover from the disturbance) (Lake, 2000). A third type of response is opportunistic utilization of habitats that are created by the disturbance, such as spawning or feeding habitats (e.g., Grift et al., 2001; Welcomme, 1979, Gorski et al. 2010, 2011, Phelps et al. 2015, Van Looy et al. 2019). Resistance is observed concurrently with disturbance events, while resilience is expressed during the post-disturbance phase. Opportunism can be observed in both phases. Figure 1 represents this concept for the example of floods.

Figure 1 here

Biological responses are triggered by changes in habitat area and quality that fall outside the normal range. Physico-chemical habitat quality attributes are related to flow velocity, water depth, substrate stability, temperature and water quality. These factors affect organisms at the scale at which they perceive their environment (i.e. river element and hydraulic unit; see Gurnell et al 2014). Once the factors exceed the typical suitable range they cause resistance reactions that include: changes in habitude (i.e. organisms occupy sub-optimal habitats when favorable habitats are lost), behavior (e.g. the drag-minimizing body posture and adhesive anchoring observed in some invertebrates (Schnauder et al. 2010) or body size related swimming performance (Wolter & Arlinghaus 2003, Radinger & Wolter 2014)) and a search for areas offering refuge (Lancaster and Belyea, 1997; Meffe, 1984). Resilience is driven by the availability of refugia, connectivity and the organism’s fecundity and flexibility of life history strategy (Arlinghaus & Wolter 2003, Klemetsen et al. 2003, Wolter et al. 2016, Van Looy et al. 2019). Opportunism is a function of species being able to take advantage of circumstances during the disturbance.

BIOLOGICAL RESPONSE TO FLOODS

Concurrent response

Floods increase the overall wetted area, although much of this area may be uninhabitable due to high velocities, suspended solids or chemical loads (e.g., Moffett, 1936; Hoopes, 1974). This is followed by change of habitude from, for example, foraging to refuge seeking (Bolland et al. 2015). In rivers without floodplains, the consequence is a reduction of abundance and diversity of macroinvertebrates and juvenile fish (Bischoff & Wolter 2001). Adult fish may also be affected by displacement and injury caused by moving debris and bed instability, or by a shortage of food (Jensen and Johnsen, 1999; Lusk et al., 1998; Weng et al., 2001, Hogberg & Pegg 2015). Extreme events may scour eggs and prevent hatching (Peterson et al. 2000, Carline and McCullough, 2003; Cowx and de Jong, 2004; Phillips et al., 1975, Dusterhoff et al. 2017).

In terms of opportunism, salmonids for example are well adapted to high velocities and use floods to reach spawning grounds that are not accessible or suitable during lower flows (DeVries, 1997). Inundation of the floodplains of low gradient rivers causes a net increase in habitat area for many fish species, and offers refuge and foraging habitat (Schwartz & Herricks 2005, Beesley et al. 2014). The available flooded areas will also determine fish productivity, growth and survival and, accordingly, density of juvenile year classes, especially in spring (Copp 1989, Holčík 1996, Coops et al. 2008, Gorski et al. 2010, 2011, 2013, 2014). The additional influx of nutrients supports rapidly-growing populations of macroinvertebrates (Hickey and Salas, 1995). Allochthonous inputs and high autochthonous floodplain production dominate ecological processes (Humphries et al., 2014, Davis et al. 2018). This creates an abundance of prey for fish (Allen, 1993; Junk et al., 1989). The abundance of phytophilous and phytolithophilous species increases due to higher food and shelter availability (Jurajda et al., 2004, Schomaker & Wolter 2011). However, such a situation is less common during winter floods.

Post-disturbance effects

Overall the most important consequence of flooding is shift of the species composition towards fish species that are better adapted to, or even dependent on, floodplain habitats (Bayley, 1991; Jurajda et al., 2006; Maher, 1994; Leitman et al., 1991, Bischoff & Wolter 2001, Schomaker & Wolter 2011). Due to high mobility of aquatic organisms, the recolonization of highly disturbed areas rapidly takes place, although the rate is strongly dependent on availability and quality of refugia (Magoulick and Kobza, 2003; Townsend, 1989) and species-specific dispersal ability (Radinger & Wolter 2015, Radinger et al. 2017, 2018).

Furthermore, species composition and densities after recovery depend on many morphological changes caused by floods (Elwood and Waters, 1969).

BIOLOGICAL RESPONSE TO DROUGHTS

Concurrent response

Reduction of habitat area during drought conditions is not only due to a smaller wetted area, but also to reduced habitat suitability (e.g. due to excessive temperatures or nutrients). Many fish change their behavior, adjusting to the new conditions (Elliot, 2000, 2006; Davey et al. 2006, Dekar and Magoulick, 2007). For organisms that prefer shallow and low-velocity zones (e.g. invertebrates and juvenile fish), or that are tolerant to high temperature and low oxygen, the amount of suitable habitat may initially increase (Reid et al. 2013). As wetted area further declines, the densities of these organisms increase (Matthews et al. 1994, Dewson et al., 2003; McIntosh et al., 2002). Soon food availability declines and predation increases. The numbers of invertebrates decline and fish assemblage structure changes as a consequence (Arthington et al., 2005; Wood et al., 2000, White et al. 2016).

In perennial streams, the richness of macroinvertebrate species declines due to the loss of habitat diversity. In contrast, the same phenomenon leads to local increases in fish species richness in remnant pools. However, this is an artefact of relocation of fish from dried up areas (Pires et al., 2010). Again, predation by fish and other vertebrates becomes a limiting factor for macroinvertebrates (Labbe and Fausch, 2000; Maceda-Veiga et al., 2009).

Since large portions of aquatic zones become terrestrial, sedentary and sessile species such as freshwater mussels are at risk of stranding, desiccation and predation. The temperature increase in expanding shallow margins also exposes such organisms to thermal shock (Castelli et al., 2012).

Long lasting effects

The overall consequence of drought is a change in species composition towards drought-tolerant, small-bodied species, i.e. those for which habitat conditions have actually improved (e.g. Boix et al, 2010, Schomaker & Wolter 2011, Ruhí et al. 2015, Leigh & Datry 2017). As drought persists and water quality exceeds critical thresholds, the numbers of individuals rapidly declines (Extence, 1981). For fish, the timing of drought is important, as it may affect sensitive life history stages such as spawning or egg incubation. This shapes community composition in future years by potentially causing the failure of entire year classes. Fish and macroinvertebrates can recover quickly from short-term droughts, but the availability of refugia during the drought is critical for this (Covich et al., 2003; Fenoglio et al., 2006; Matthews and Marsh-Matthews, 2003). If cease-to-flow conditions occur, populations may go locally extinct unless aquatic dispersers have made it to permanent water. Populations can be re-established by subsequent high-flow events. Recovery from longer-term droughts that span multiple years is slower because of the smaller pool of surviving organisms. The impacts of supra-seasonal droughts are difficult to predict because of our limited experience of these events (Lake, 2007, Ruhí et al. 2015).

WHAT AFFECTS THE INTENSITY AND DIRECTION OF BIOLOGICAL RESPONSE?

The above sections allow recognition of a general pattern of biological response. Floods and droughts may lead to a change in aquatic community composition, impacting upon the organisms less adapted to the disturbance and promoting those better adapted. During flooding, the mechanisms leading to these changes are drift, injury, dislocation, and concurrent and post-disturbance habitat modifications. However, the flood is not solely a damaging disturbance, but also a major regenerator of biodiversity and production. Drought in contrast leads at coarse scales to net loss of populations through habitat limitation, predation and food shortages. Consequently, a general observation is that predictable floods tend to increase fish species richness, abundance and biomass, whereas droughts lead to a decline (Figure 2).

Figure 2 here

Still, the conceptual model in Figure 2 is generic and some studies have found different results for individual cases (Piniewski et al 2016). One of more significant covariates causing such deviations is the morphological variability of rivers and floodplains. The presence of refugia has a direct effect on survival of animals, and is therefore important for the speed and scale of recolonization. Spatial variability not only mitigates deleterious impacts by providing refugia, but also by offering a diversity of habitats that increase richness, abundance, biomass, recruitment and productivity prior to any disturbance. Habitat shifts also occur for aquatic biota, caused by changes in discharge and resulting changes in flow velocities, shear forces and water levels (e.g. Wolter et al. 2016). For example, in lowland floodplain rivers, the occurrence of hydraulically inhospitable habitats (i.e. very fast flowing) is compensated for by the creation of vast areas of attractive spawning and larval rearing habitats on the floodplain (Gorski et al. 2010, 2011, van de Wolfshaar et al. 2011, Stoffels et al. 2015). In high-gradient rivers, floods create access to tributaries, effectively expanding accessible habitat area (e.g. Sukhodolov et al. 2009).

The intensity of biological response also depends upon factors such as geographic location and seasonality. For example, a drought of the same magnitude will have different consequences in northern and southern Europe. In some Mediterranean streams, adaptation to climatic regimes means that fish can survive much more severe droughts that would be lethal to any northern organisms (Horne et al., in review).

Similar differences in response are seen with the timing of disturbance. For example, in many rivers of the northern hemisphere severe flooding in summer has different biological consequences than during the spring (spawning) time. Since summers are characterized by low-flow conditions, many animals utilize habitat for rearing and growth, with extensive nursery habitats (Olaya-Marin et al., 2013). Unpredictable floods (e.g. unseasonal or happening with higher frequency than in the past) have been documented as having very deleterious effects on fish assemblages (Bischoff & Wolter 2001,George et al. 2015, Hogberg & Pegg 2015).

Consequently, the intensity of biological responses to disturbance events depends on their predictability; populations become adapted to the conditions that are most common, and the frequency of occurrence in the past is a driver of the predictability.

Predicting impact of climate change on ecologically-relevant flow regimes

A recent work projecting hydrologic response to future weather data derived from various IPCC global circulation models for the state of New Hampshire, USA provides some insight on how the climate change could modify hydrologic patterns (Bjerklie and Sturtevant, 2017). This state wide analysis documented a common pattern characterised by an increase of higher flows over cold season and lower flows during spring and summer. The study also projected increased variability of flows, with changes to the magnitude of baseflows (groundwater inflow) varying depending on elevation and micro-climatic factors related to location. The variability of the flow response to climate changes within the state is demonstrated by comparing flow duration curves of a relatively small coastal river the Oyster River and the larger Pemigewassett River (Bjerklie et al., 2015). Although both of them follow the described trend it is more pronounced in the Pemigewassett River. The Oyster River has little topographic relief and sandy soils, while the Pemigewassett River is located in the upland and more mountainous terrain (Bjerklie et al., 2015).

The question about the way in which predicted river flow changes will mediate climate change signal on biota is rather complex due to many confounding factors. The majority of the model-based climate change impact studies deal with ‘ecologically relevant’ flow regimes (Dhungel et al. 2016, Döll & Zhang 2010, Laizé et al. 2013, Morales-Marin et al. 2019, O'Keeffe et al. 2018, Piniewski et al. 2014, Stagl and Hattermann 2016, Van Vliet et al. 2013, Vigiak et al. 2018) whereby ‘ecological relevance’ is usually assessed based on available literature. This approach is better suited for large-scale analyses: from global (Döll &

Zhang), through continental (Laizé et al. 2013, Van Vliet et al. 2013) to national (Dhungel et al. 2016) and large river basin scale (O'Keeffe et al. 2018, Stagl and Hattermann 2016). Predicted effects of climate change on riverine biota are only implicit in such studies. For example, O'Keeffe et al. (2018) reported a projected increase in high flow frequency in the Vistula and Odra basins in Poland, which could be beneficial for northern pike due to more frequent floodplain inundation and better river-floodplain connectivity. On the other hand, abnormally high streamflow could wash away the fish and eggs.

In a more complex approach, but typically applied at finer spatial scales, climate change forcing is propagated through a modelling cascade consisting of a hydrological model loosely coupled with a habitat suitability or a species distribution model (Jaeger et al. 2014, Kakouei et al. 2018, Kuemmerlen et al. 2015, Morid et al. 2016, Muñoz-Mas et al. 2016, Mustonen et al. 2018, Viganò et al. 2015, Woznicki et al. 2016). For example, Jaeger et al. (2014) predicted a higher frequency of zero-flow days in an intermittent stream in Arizona, United States, which would inevitably lead to more channel fragmentation and a reduced network-wide hydrological connectivity during spawning of native fish.

Yet higher level of complexity can be achieved by including a hydraulic model in the modelling chain, yet such approaches are typically applied only at small catchment scales (Guse et al. 2015, Papadaki et al. 2016). Papadaki et al (2016) showed that the West Balkan trout is likely to expect a deterioration in habitat quantity and quality in summer months in a mountainous stream in Greece. In contrast, Guse et al. (2015) reported variable changes in habitat suitability for fishes in a small stream in northern Germany in response to climate change. They also predicted a dampened effect of climate change on stream hydraulics compared to the effects on discharge itself.

DISCUSSION

Our review underlines the importance of floods and droughts as a master driving force of the riverine ecosystems that shape the biotic communities. Each of these events creates immediate and long lasting modification of habitat conditions for riverine flora and fauna.

This in turn causes specific biological response that leads to change of composition of aquatic communities, also in short and long term.

The response may be in form of resistance, change of habitude and resilience. The intensity and direction of biological impact may vary depending on location and particular climatic and physiographic setting of the watershed. The variety of impact will further diversify if we include other human-induced alterations to riverine ecosystems. For example, a good demonstration of the consequences of dam construction is presented in a study on the Tana River in Kenya (Langat et al 2019).

Nevertheless, the expected overall long term consequence of natural floods and droughts regime is an increase in biological diversity and ecosystem health. Hence, floods and droughts can be seen as “rejuvenating” events essential for ecological equilibrium. Therefore, sudden and dramatic alteration of floods and droughts pattern as expected in climate change perspective may cause dramatic changes in the structure and composition of aquatic communities. Quantification of these changes is therefore key to prediction of biological consequences of climate change. To capture these modifications descriptive pattern metrics, which are directly related to biological response need to be identified.

As presented by Humphries et al. (2014) in the River Wave Concept, river flow may be conceptualized as series of waves varying in shape, amplitude, wavelength, and frequency. Floods are crests and droughts are the troughs of the wave and define its overall characteristics. These attributes can be used as hydrologic metrics to characterize the pattern of disturbance events.

As presented above the aquatic organisms evolved around the hydrologic events that are predictable and therefore more common. Hence, the event frequency is a wave metric most closely related to disturbance predictability and consequently intensity of biological response. It is in a reverse relationship i.e. the higher the natural frequency, the higher the probability the less intense the biological alteration (Figure 3).

The relationship between the metrics of event intensity and frequency is generally described by a power law (Bak, 1996). In undisturbed ecosystems the disturbances of large magnitude or duration are much less frequent and vice versa. Consequently, events of extreme magnitude and/or duration (floods or droughts) can be expected to have a much stronger biological effect, in that they may even cause a depletion or expansion of populations. The smallest and most frequent events commonly cause a change of habitude, as the migration to refuge sets on (Figure 3).

Figure 3 here

According to Lake (2000), floods are pulse disturbances and the response to floods is most often of a pulse type. However, extreme floods that create dramatic hydromorphologic change will cause a press response. In both cases, flood magnitude is a stronger driver than event duration.

Since floods are generally pulse disturbances, the key attributes related to biological response are flood **frequency** and **magnitude**. Consequently, there is a functional relationship between these two metrics and the intensity of biological impact of floods. In regions where the hydrologic response to climate change is towards increasing frequency of high flow events, resulting in significant change to the flow regime, the channel will try to widen and deepen its cross-section to accommodate the more frequent flooding. The time frame for the river to adjust to a more stable geometry is intricately associated with the time for instream habitat to adjust. If the response also includes larger flood events, adjustments to the channel morphology may also include changes to the planform structure of the river network, including changes to the meandering pattern and associated riverine floodplain features such as wetlands and ponds. Additionally, changes in flood frequency and magnitude will markedly change the amount of woody debris entering the river channel, and the amount of sediment transported to downstream areas. Subsequently, the relative alteration of flood magnitude and frequency that is caused by climate change is intricately tied to, and can be indicative of, biological response to climate change.

Since droughts are presses and ramps, the response is also a ramp. Here, the key driver of biological response is **drought duration** (Figure 4). In addition, increased **frequency** even of small disturbance events can also be a cause of ramp responses. For example, increased frequency of smaller drought events that happen during supra-seasonal droughts will further affect the physical condition of fauna and may lead to catastrophic consequences.

Figure 4 here

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