

# Hydrological controls on pelagic food structure—From shunts to chemostats as caused by runoff magnitudes and frequency of episodes

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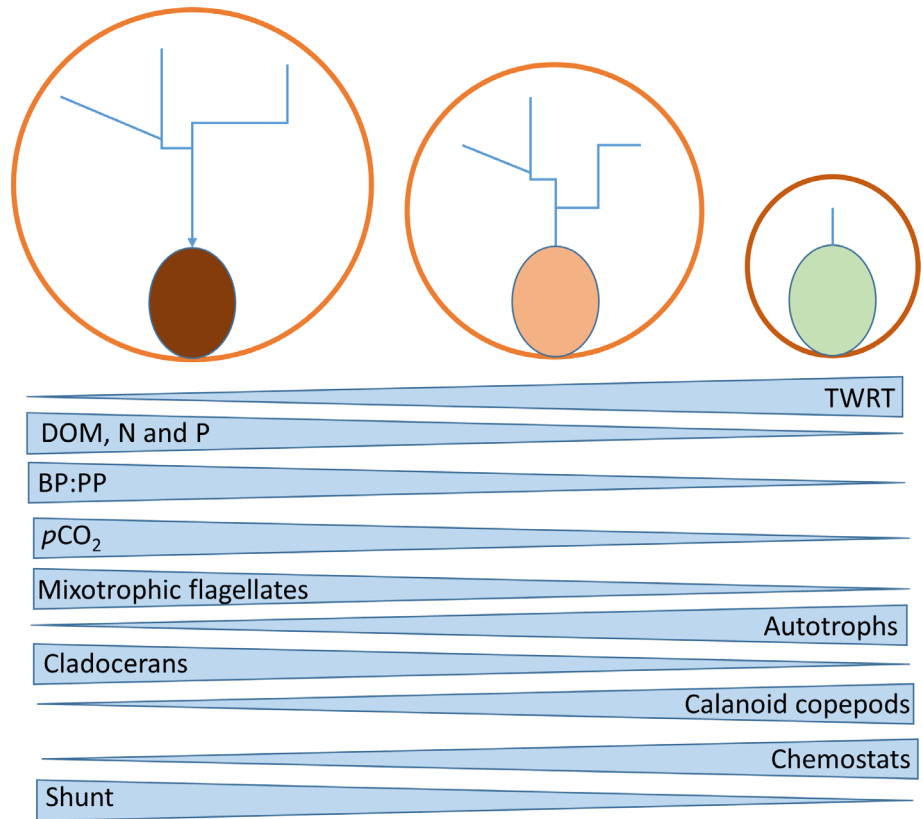
Hydrological high flow events, or episodes, are pulses of water that shape the pelagic food webs of lakes. These episodes promote hydrologically-driven terrestrial inputs of dissolved organic matter (DOM) and nutrients (nitrogen (N) and phosphorus (P)) that influence lake productivity. At northern latitudes, episodes have typically occurred during spring snowmelt events (Andreasson, Bergström, Carlsson, Graham, & Lindström, 2004). However, the timing, frequency, and magnitude of spring flood episodes are changing in response to climate change (e.g., earlier occurrence of events with lesser frequency and magnitude; Andreasson et al., 2004; Creed, Hwang, Lutz, & Way, 2015) and are increasingly surpassed by extreme rainfalls in summer and early autumn (Creed, Hwang, et al., 2015; Min, Zhang, Zwiers, & Hegerl, 2011; Westra et al., 2014). In addition to changes in water delivery rhythm, northern lakes are facing hydrological intensification (e.g., wetter conditions in wet area, dryer conditions in dry areas; Huntington, 2006) which influence the delivery of terrestrial DOM and nutrients, and lake water retention times.

Change in magnitudes of water input (runoff), and its seasonal rhythm (episodes) affect whether lakes act as “shunts” (less resistance, faster flow of water shunted from land to lake, and through the lake, where the residence time and thus degree of processing of constituents in the lake water are reduced) or “chemostats” (more resistance, slower flow of water from land to lake, and through the lake, where the residence time and degree of processing of constituents in the lake water are increased). These terms have been used for streams and rivers (Creed et al., 2015; Raymond, Saiers, & Sobczak, 2016) but can be applicable to lakes as well. The potential consequences of the changing nature in water input may drive lakes from autochthonous

(chemostats) to allochthonous (shunts) DOM dominance, or the opposite, with cascading effects throughout the pelagic food web. Here I will illustrate how the “shunt vs. chemostat concept” can be viewed in different time frames (e.g., annually or seasonally) and how this impacts the pelagic food web structure of northern lakes.

The annual turnover of water in lakes is defined by the theoretical water residence time (TWRT; lake volume divided by output water losses). In boreal landscapes, the TWRT is highly related to the catchment to lake area ratio (CA:LA) (Seekell et al., 2014; Kothawala et al., 2014) at least in a given region since CA correlate quite well with lake volume (cf. Sobek, Nisell, & Fölster, 2011). This means that the TWRT increases with decreasing CA:LA (i.e., short TWRT when CA and runoff is high relative to the lake size and its volume.). The CA:LA and the TWRT to a large extent determine lake DOM and nutrient concentrations in boreal lakes (Figure 1). From numerous lake studies in northern Sweden (see references in Figure 1) we know that short TWRT (high CA: LA) promotes shunt lakes where allochthonous DOM and nutrient concentrations are high, light conditions poor, with high bacterial (BP) to phytoplankton production (PP) ratios (BP:PP ratios) and  $p\text{CO}_2$  concentrations, and where the phytoplankton community is dominated by flagellates (usually mixotrophs) capable of ingesting bacteria (Isaksson, Bergström, Blomqvist, & Jansson, 1999). In shunt lakes, the proportions of unselective filtering and bacteria feeding cladocerans (Vrede & Vrede, 2005) are further increased within the zooplankton community. With longer TWRT (lower CA:LA) lakes becomes increasingly more of a chemostat, with lower allochthonous DOM and nutrient concentrations, better light conditions, lower BP:PP ratios and  $p\text{CO}_2$  concentrations, and increasingly higher

**FIGURE 1** Changes in CA:LA and TWRT, promoting shifts from shunt to chemostat lakes, impacting DOM and nutrient delivery and pelagic food web structure of northern oligotrophic boreal lakes (data from Blomqvist, Jansson, Drakare, Bergström, & Brydsten, 2001; Jansson, Bergström, Drakare, & Blomqvist, 2001; Algesten et al., 2003; Bergström, Jansson, Drakare, & Blomqvist, 2003, Drakare, Blomqvist, Bergström, & Jansson, 2003; Bergström, 2009 and unpublished data; Deininger, Faithfull, & Bergström, 2017; Deininger, Faithfull, Karlsson, Klaus, & Bergström, 2017)



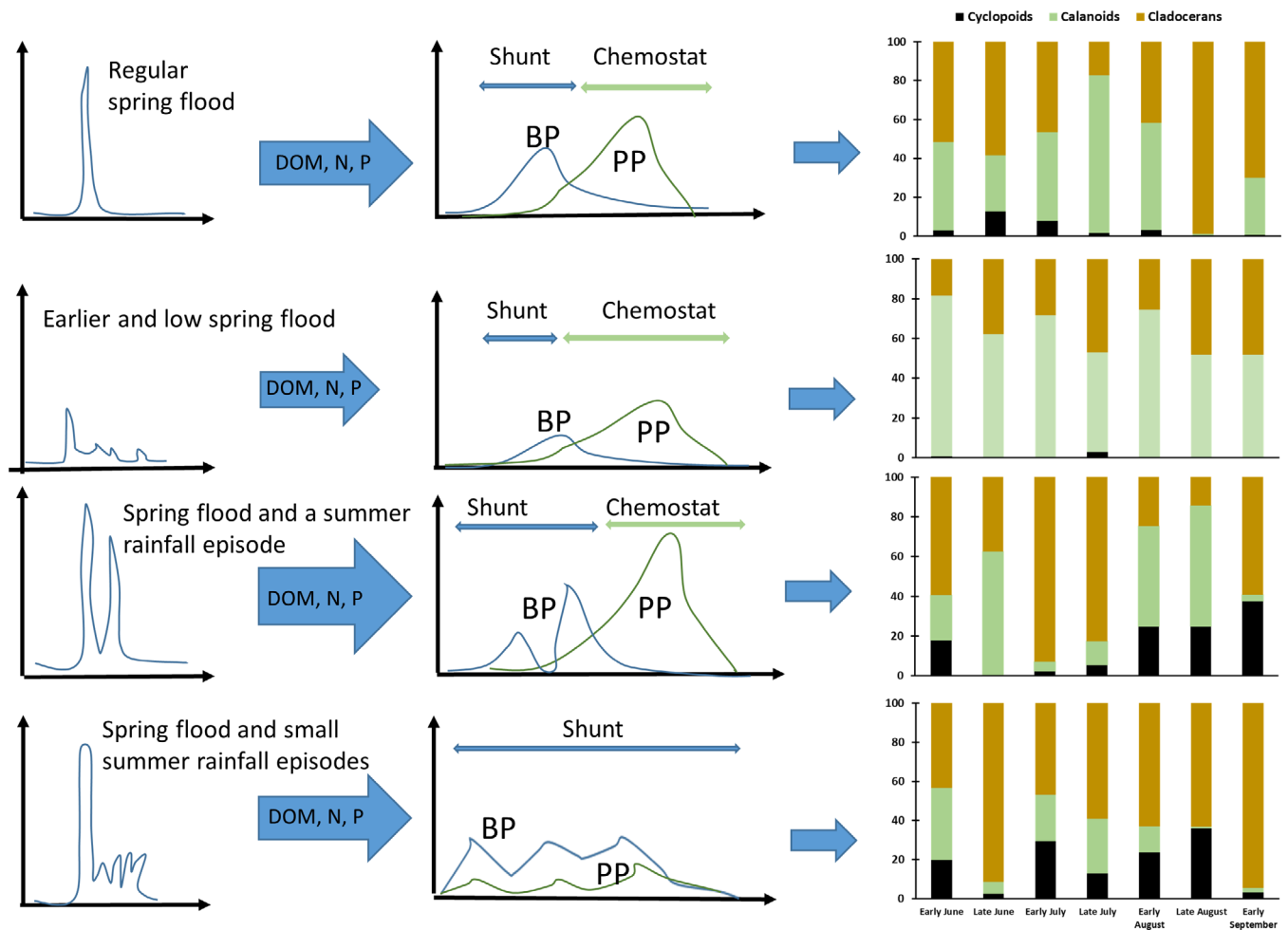
phytoplankton- and autochthonous DOM production. In chemostat lakes, the proportions of larger autotrophs and autotrophic flagellates are further increased within the phytoplankton community, and calanoid copepods feeding selectively on phytoplankton (Sommer & Sommer, 2006) often dominate the zooplankton community. Thus, shifts from shunt to chemostat, which is highly linked to hydrology and TWRT, very much shape the pelagic food web structure in lakes.

The patterns recognized in Figure 1 are based on comparative studies among lakes when CA:LA and TWRT gradually change. However, our knowledge on how the pelagic food web structure in a given system, where CA:LA is constant, is impacted when the water delivery rhythm changes seasonally is much more limited. A question which also arises when comparing lakes is whether the change is gradual (as illustrated in Figure 1) or if there are thresholds in TWRT where lakes more suddenly shift from shunt to chemostat or the reverse. In a previous study we identified two “break-off points” in TWRT (100 and 200 days) where the external control on lake bacterial communities dropped as a result of longer TWRT and reduced bacterial import (Lindström, Forslund, Algesten, & Bergström, 2006). More research is needed into whether similar and sudden break points also exist for separating shunt from chemostat lakes, and their associated pelagic food web structures, presumably by examining lakes distributed along gradients of increased TWRT and reduced terrestrial DOM and nutrient loading in regions where climate and N deposition is similar. We know that the vast majority of the Swedish lake population has TWRT between 1–100 days (78%), and very few have TWRT of >200 days (ca 12%) (Lindström et al., 2006). Thus, most Swedish lakes should act as shunts and be dominated by allochthonous DOM

(cf. Kothawala et al., 2014). Weyhenmeyer, Norman, and Tranvik (2016) also modelled that a majority of Sweden's freshwaters will become browner following increased flushing of DOM from terrestrial systems due to a predicted 32% increase in precipitation to 2030 under the worst case climate scenario, and that the relative change in “browness” would be the most severe in lake with TWRT >6 years. This suggests that few lakes in the Swedish boreal landscape will shift from chemostats to shunts with cascading impacts on pelagic food web structure due to increased precipitation and terrestrial DOM and nutrient loading. Instead, the majority of the Swedish boreal lakes will become increasingly more “shunted.”

It could be that precipitation episodes and the seasonal rhythm of water flux in a given system impact whether lakes function as shunts or chemostats. If northern lakes have a biological memory that is “hardwired” to spring floods, the diminution of these events and more frequent interruptions by extreme summer rainfall episodes might create disruptions between supply and organism demands at different trophic levels in the pelagic food web. We can assess these seasonal changes in hydrology and their potential impacts on pelagic food web structure using data from Lake Ötrasket and Lake Övre Björntjärn (see Figure 2 and associated references) which according to their TWRT (0.1 years, high CA:LA) can be classified as shunt lakes. Again, the hydrology will determine the magnitude of DOM and nutrient delivery to the lakes; however, in this case we will assess different rhythms of water, DOM and nutrient delivery (cf. Figure 2).

During a **regular spring flood** year, DOM and nutrient loading is linked to the size of the spring flood, which also determines the WRT of the epilimnion which in this case increases with number of days



**FIGURE 2** Different episode rhythms, and DOM and nutrient delivery, that promote shifts from shunt to chemostat conditions over summer impacting pelagic food web structure of boreal lakes of short TWRT (0.1 years) (data from Bergström & Jansson, 2000; Jansson et al., 2001; Bergström et al., 2003; Drakare, Blomqvist, Bergström, & Jansson, 2002; Bergström, 2009 and unpublished data; Deiningen et al., 2017, b)

after the spring flood event. Over the summer the lake will shift from a shunt to a chemostat, with high BP:PP ratios in early summer caused by delivery of fresh DOM and limiting nutrients, where limiting nutrients in DOM primarily are allocated to bacteria due to their innate superiority in inorganic nutrient uptake compared to phytoplankton (Currie & Kalff, 1984). As the number of days after the spring flood event increases, easily degradable substrates in DOM are depleted and BP declines. Limiting nutrients are now allocated to phytoplankton causing increased PP and declining BP:PP. In late summer, PP will be higher than BP since phytoplankton can produce more carbon per limiting nutrient than bacteria (C:N:P stoichiometry by weight: phytoplankton 41:7:1 (Redfield, 1958) vs. bacteria 20:6:1 (Caron, Porter, & Sanders, 1990)). Total basal production (the sum of BP and PP; cf. Jansson, Karlsson, & Blomqvist, 2003) is therefore highest in late summer when PP dominates during periods of long epilimnion WRT and when the lake starts to function as a chemostat. This sets up special conditions for phytoplankton development, where mixotrophs dominate the phytoplankton community in connection with high BP, which switches to higher proportions of

autotrophs later in summer (not illustrated in Figure 2). Zooplankton community composition and their resource use is very much linked to this pattern in basal production and the phytoplankton community composition, with larger proportions of cladocerans of high allochthony in early summer, and greater proportions of selectively feeding calanoids of high autochthony in late summer (Berggren, Ziegler, St-Gelais, Beisner, & del Giorgio, 2014; Karlsson et al., 2012).

Under a situation of an **earlier spring flood of much lower magnitude**, DOM and nutrient delivery will be reduced and the epilimnion TWRT will increase, promoting a longer chemostat period over summer. The BP in connection to the earlier spring flood will be lower and of shorter duration. The PP will start earlier and extend for a longer period of time over summer. The paradox of this is that the total basal production might not be much lower compared to the spring flood event, despite lower DOM and nutrient input, since limiting nutrients in this case are allocated to phytoplankton during a longer period of time in summer. These changes are also reflected in the phytoplankton- and zooplankton community composition, which will

have high proportions of autotrophs and calanoid copepods, respectively, throughout the summer.

Under a situation of *a spring flood and a summer rainfall episode*, BP will increase again after the rainfall episode due to delivery of fresh DOM and nutrients. The PP will be pushed, occurring after the rainfall episode later in summer over a shorter duration, and with a higher peak as caused by greater DOM and nutrient delivery. Total basal production will be higher with a substantial proportion performed by bacteria. Hence, the lake will be shunted several times, and chemostatic behaviour when PP production dominates will occur late in summer with reduced duration. The phytoplankton and the zooplankton community will return to high proportions of mixotrophs and cladocerans after the summer rainfall episode, and autotrophs and calanoids will become more abundant late in summer in connection to the PP peak.

Under a situation of *a spring flood followed by frequent smaller rainfall episodes*, such as under a rainy summer, the lake will be shunted throughout the summer, with BP production exceeding PP which will be very low. The phytoplankton- and zooplankton communities will be dominated by mixotrophic flagellates and cladocerans, respectively. An important aspect to consider is that spring floods are caused by snow melt which does not affect incoming light, whereas high flow episodes in summer are related to rainfall events when light conditions usually are poor. Hence, protracted summer rainfall events will have a twofold negative impact on PP, by increasing competition for limiting nutrients and reducing the light conditions in lake water. However, warming and consistent trends toward reduced lake ice-cover (Magnuson et al., 2000) combined with earlier and smaller spring flood events (Andreasson et al., 2004; Creed, Hwang, et al., 2015) may on the other hand improve light conditions in lakes promoting enhanced PP (Weyhenmeyer, Westoo, & Willen, 2008).

Hence, data from these two shunted lakes (Figure 2) suggest close cascading effects between the rhythm of the water, the DOM and nutrient delivery, and the structure of the pelagic food web. As expected small organisms with short generation times (bacteria, flagellates) respond quickly to changes in epilimnetic water retention times and are benefitted relatively to larger organism with longer generation times (larger phytoplankton) when lakes are being shunted. Thus, moving from spring floods to situations of spring floods of low magnitudes, whether or not one or more summer rainfall episodes occur, are not causing "collapses." Instead, strong changes in timing and magnitudes in BP and PP production occur in summer, linked to DOM and nutrient delivery which zooplankton quickly adapt to. Since shunt lakes usually are humic (Figure 1), with low benthic algal production (Ask et al., 2009), it remains to be evaluated how these changes in the seasonal rhythm of water input and DOM and nutrient delivery, which shape the pelagic food web structure (Figure 2), might impact fish which rely increasingly more on pelagic food resources when lake DOM concentrations increase (Karlsson et al., 2009). Although the quantity of basal resources (BP + PP) might not change much for zooplankton when comparing a summer with a low spring flood vs. a summer with a distinct spring flood event, it will be very different in quality. For example, bacteria lack essential fatty acids (Müller-

Navarra, 2008) and are not fed upon by calanoid copepods (Sommer & Sommer, 2006). A bacterial based pelagic food web is longer and of lower trophic transfer efficiency compared to a phytoplankton based food chain (Jansson, Persson, De Roos, Jones, & Tranvik, 2007). The functionality of the lakes will further be impacted, with transition between CO<sub>2</sub> or biomass producers driven by changes in hydrology. The relative importance of internal nutrient recycling (Levine & Schindler, 1992; Sterner & Hessen, 1994) and external nutrient loading for phytoplankton nutrient limitation will also be impacted (Bergström, Karlsson, Karlsson, & Vrede, 2015; Downing & McCauley, 1992), regardless of whether a lake's hydrological connection with its catchment is enhanced or suppressed.

We need to assess to what extent these patterns and changes in pelagic food web structure recognized for northern Swedish lakes (Figures 1 and 2) are applicable to lakes in other areas within and beyond the boreal zone. Lakes are exposed to different hydrology and seasonal rhythms of water, and supplied with different quantities and qualities of DOM (DOM: nutrient stoichiometry, aromaticity) that will impact pelagic food webs. Annual water retention times have been shown to be negatively related to DOM turnover across inland waters (Catala'n, Marce', Kothawala, & Tranvik, 2016; Zwart, Sebestyen, Solomon, & SE., 2017), and extreme precipitation episodes have been recognized as "hot moments" of carbon turnover that promote heterotrophy in lakes (Zwart et al., 2017) similar to what has been shown for humic Lake Örträsket (Bergström, 2009; Bergström & Jansson, 2000; Drakare et al., 2002; Jansson, Bergström, Blomqvist, Isaksson, & Jonsson, 1999). However, the extent to which TWRT can be used to identify a lake's pelagic food web structure, whether thresholds in TWRT that account for shifts between chemostatic and shunting behaviour are similar between arctic, boreal and temperate regions, and the precise form of such shifts remain unknown.

If we are facing smaller spring floods and more frequent summer rainfall episodes, then we also need to assess the cascading effects on pelagic food web structures on a seasonal basis, and evaluate if changes in "hot moments" in what we would regard as shunt lakes promote similar impacts and shifts in pelagic food web structure when assessing lakes at local, regional, national or continental scales. In northern landscapes, external DOM and nutrient delivery to lakes is highly related to terrestrial primary production and hydrology (Hope, Billet, & Cresser, 1994; Jansson, Hickler, Jonsson, & Karlsson, 2008). However, changes in hydrology (promoted by precipitation increases) in areas with similar terrestrial primary production may also cause dilution of lake DOM concentrations but at the same time increase lake water retention times (Larsen, Andersen, & Hessen, 2011). Much less research has been focused on the specific impact of lake water retention time on pelagic food webs relative to the role of changes in lake DOM. This should be possible to assess in areas with large precipitation gradients and little change in terrestrial landscape cover. When these questions have been resolved, then we may advance even further in applying the "shunt to chemostat" concept to lakes and separate the impacts of hydrology from those associated with the quantity and quality of DOM delivery on pelagic food web structure and lake productivity.

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