Plenary Lecture

Ecological impacts of excessive water level fluctuations in stratified freshwater lakes

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Abstract

Water levels of lakes fluctuate naturally in response to climatic and hydrological forcing. Human over-exploitation of water resources leads to increased annual and interannual fluctuations of water levels, at times far beyond natural amplitudes and/or at altered time schedules. Climate change models predict increased occurrence of extreme events (flooding, extended droughts), which will further magnify the seasonal and multiannual amplitude of water level fluctuations in lakes. A relatively wide literature base already exists for shallow lakes, demonstrating that excessive water level fluctuations impair ecosystem functioning, ultimately leading to shifts between clear-water and turbid states. Evidence is gradually building in the published literature demonstrating that deep (stratified) freshwater lakes also respond adversely to excessive water level fluctuations. Analysis of existing data suggests that at moderate disturbance levels littoral habitats are affected, and hence their biota is also impacted. At further disturbance levels, ecosystem destabilization symptoms are observed, including weakening of keystone species, proliferation of nuisance and invasive species, loss of biodiversity, and increased internal nutrient loading. Ultimately, eutrophication symptoms are manifested, especially large and more frequent cyanobacterial blooms, without increased external nutrient loading. Examples from a range of subtropic and temperate freshwater lakes and reservoirs demonstrate that both top-down and bottom-up processes promote those symptoms. The response of aquatic ecosystems, particularly deep lakes, to water level fluctuations is an under-studied field of crucial importance to the management of water resources, where limnologists have a leading role to play in the near future.

Key words: climate change, deep lakes, habitat complexity, internal nutrient loading, Lake Constance, Lake Kinneret, littoral, littoral-pelagic coupling, stratified lakes, water level fluctuations

Introduction

Water levels of lakes fluctuate naturally as a result of seasonal or long-term imbalance between the amounts of water entering (by inflow, precipitation, runoff, and groundwater) and leaving the lake (by evaporation and outflow). The magnitude of those fluctuations depends on factors such as the morphology of the lake and its watershed, the ratio of their areas, intensity of rainfall events, and rates of delivery of rainfall or ice-melt water to the lake, as well as on factors determining water losses such as outflow fluxes or wind speed and air temperature that impact evaporation. Lakes fluctuate seasonally between maximum levels, usually at the end of the rainy season or snowmelt, and minimum levels at the end of the dry season. In regions where precipitation occurs year-round, 2 or more water level peaks are common (e.g., White et al. 2008). Natural water level fluctuations (WLF) in freshwater stratified lakes of the temperate and subtropical regions are typically up to 1.5 m annually and up to 3 m multiannually (Table 1), although exceptions with considerably greater natural fluctuations do occur. The multiannual amplitude of fluctuation is greater than the annual amplitude because it is determined by exceptionally dry and wet events.

These natural fluctuations are an inherent feature of lake ecosystems, essential for the survival and well-being of

Table 1. Range of natural annual and interannual water level fluctuations in a selection of natural lakes. Data shown are for periods of no human intervention in lake hydrology.

Lake, location	Period	Annual amplitude, avg ± SD (max), m	Max amplitude (multi-annual), m	Reference/source of data
Constance, Germany	1950–2010	1.53 ± 0.36 (2.52)	3.0	Wantzen et al. 2008a
Biwa, Japan	1990–2009	0.76 ± 0.25 (1.4)	1.5	Japan Min. of Infrastructure, Transport & Tourism
Van, Turkey	1944–1974	0.5 ± 0.18 (1.0)	2.2	Kadioglu et al. 1997
16 Canadian Lakes*	1980–2003	0.3 ± 0.15 (1.3)	~2.0	White et al. 2008
Kinneret, Israel	1926–1932	1.1 ± 0.19 (2.0)	2.0	Israel Hydrological Services

* Laurentian Great Lakes region

many species that have evolved to suit their life cycle to those fluctuations, and needed for a range of ecosystem services (Gasith and Gafny 1990, Wantzen et al. 2008b). However, extreme or untimely WLF have undesirable effects for the biota, the ecosystems, and man (Bond et al. 2008).

The water balance of both natural and man-made lakes is modified by water abstraction and diversion into or out of lakes, or by hydrological modifications to their catchments or outflows. Human exploitation of water resources leads to increased annual and interannual fluctuations of water levels, at times far beyond natural amplitudes. A range of natural features of the water level regime are often impacted, not only the amplitude of fluctuation but also the timing of the minimum and maximum water levels and the rates of water level increase and decline (Wantzen et al. 2008a). In addition to drawdown and other forms of water exploitation, climate change models predict increased occurrence of extreme events such as flooding and extended droughts (IPCC 2007), which will further magnify the seasonal and multiannual amplitude of WLF in lakes and alter their temporal dynamics (Magnuson et al. 1997).

The majority of research on the impacts of excessive WLF on lake ecosystems was conducted in shallow lakes and wetlands (Leira and Cantonati 2008). This is not surprising because small water level changes in shallow lakes are translated to significant proportions of the total surface area and total amount of water in those lakes, and naturally the ecological implications are quite distinct. A relatively wide literature base already exists for shallow lakes, generally demonstrating that excessive water level fluctuations as well as severely reduced fluctuations impair ecosystem functioning, ultimately leading to shifts between clear-water and turbid states (Coops et al. 2003, Beklioglu et al. 2007). An ecological regime shift in the large and shallow Lake Võrtsjärv, Estonia, in 1977–1979 was attributed to changes in water levels (Noges et al. 2010). Excessive WLF are expected to have more critical impacts on the structure, function, and biodiversity of wetlands communities than impacts due to temperature

increases resulting from climate change (Hulme 2005, Abrahams 2008). Reduced amplitude of natural WLF is also considered undesirable, as suggested by experience from Netherlands shallow lakes (Coops and Hosper 2002).

Deep lakes are defined here as those deep enough to stratify seasonally. In deep lakes the impacts of WLF are not as noticeable as in shallow lakes (Nowlin et al. 2004), and only the littoral zones change visibly. Changes to the entire ecosystem are less evident and difficult to identify as being related to WLF; thus, the existing literature base on the ecological impacts of WLF in deep lakes is considerably smaller than for shallow lakes. Our objective was to summarize the current knowledge on water level fluctuations and their impacts on ecosystem functioning in deep lakes and to critically assess whether WLF beyond natural levels contribute to their destabilization and eutrophication. We restricted our overview to deep freshwater lakes and reservoirs from the subtropic and temperate zones. We focused on lakes for which long-term records and studies existed and compared natural lakes where the fluctuations are small with managed lakes where they are more extreme. Given pending water shortages predicted in some areas, natural lakes may not be spared drastic water level fluctuations in the future.

The extent of WLF in lakes and reservoirs

The annual and interannual WLF of 3 deep natural lakes (Biwa, Constance, and Kinneret) and 3 man-made stratifying reservoirs (Arancio, Shasta, and Hartbeespoort) over the last 20 years were compared by plotting the actual water level minus the multiannual mean for each water body, thus standardizing the values as fluctuations around a 20 yr mean, set at zero (Fig. 1). Of the 3 natural lakes, Biwa (Japan) shows the smallest fluctuations and Kinneret (Israel) the largest. Lake Biwa had notable minima (about −1 m) in 1994, 1995, and 2002. Lake Constance (Germany) experienced a distinct flooding event in 1999 (2.2 m), followed by draught and exception-

ally low water level in 2005 (−1 m). Lake Kinneret water levels showed the greatest annual fluctuations, as well as the largest multiannual trends and fluctuations. Those fluctuations were due to the semiarid climate and the use of this lake as a main source of drinking water. For decades its management was aimed at maximizing the storage capacity by excessive withdrawal in dry years to make room for lake fill-up in exceptionally wet years. The 20 yr record for Kinneret (Fig. 1) includes 2 extended periods of water level drawdown (1993–2002 and 2004–2009) as well as 2 extreme refill events (winter 1991–1992: 4.0 m rise; winter 2002–2003: 4.7 m rise). The overall multiannual amplitude was 6 m, as opposed to natural maximum amplitude of 2 m recorded in the 1920s, before the lake's outflow was dammed (Table 1).

Man-made reservoirs tend to experience greater WLF than natural lakes. Hydropower reservoirs often undergo annual WLF of tens of meters; an example is Lake Shasta in California, with annual mean fluctuations of 18.4 m and multiannual amplitudes of 47 m (Fig. 1). Another example is Serra Serrada Reservoir in Portugal, with mean annual fluctuations of ~10 m (Geraldes and Bovida 2005). Lake Arancio in Sicily, which stores irrigation water, has a mean annual fluctuation of 3.3 m with maximum multiannual amplitude of 20.5 m. Hartbeespoort Dam in South Africa has been kept at relatively fixed water levels since the mid-1990s, with annual fluctuations of 1.5 m, although in the early 1990s it too was lowered by nearly 10 m (Fig. 1). Lakes Hume and Burragorang, both drinking water storage reservoirs in Australia, have experienced long-term water level drawdown of tens of meters as a result of extended droughts (Baldwin et al. 2008, Vilhena et al. 2010).
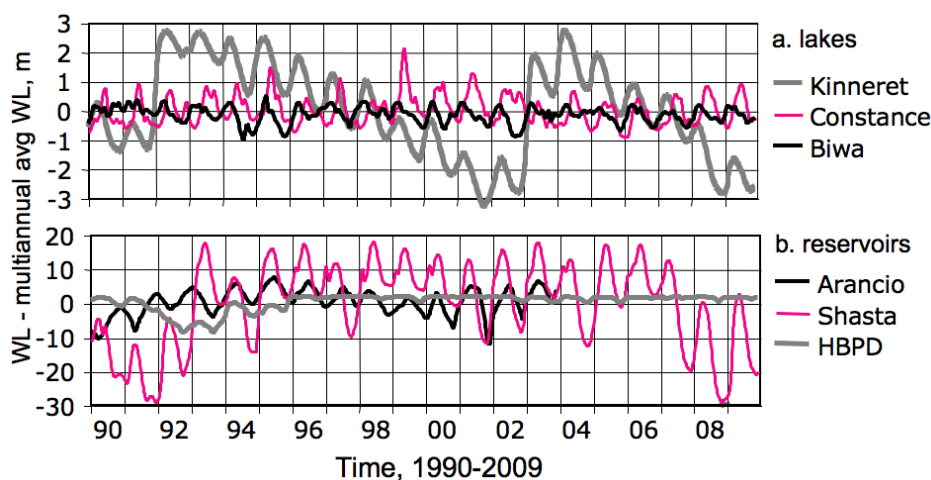
The littoral zone and its physical complexity

The littoral zone of deep lakes is the first to be adversely impacted by excessive WLF. The littoral, comprising the geophysical environment and its biota, is generally defined as the belt of shallow water around the shoreline of a lake to the maximum depth at which light still reaches the bottom sediments to allow macrophytic growth. This depth varies from lake to lake, usually about 1–5 m. The littoral zone shifts its location with changes in water level, such that the physical substrates underlying the water or emerging from it, both abiotic and biotic, alternate between being exposed and inundated. The abiotic substrates vary in particle size, from continuous rock surfaces; through boulders, stones, and gravel; to sand, silt, and clay (Hofmann et al. 2008). To this category, human activities add vertical walls, paved or tarred surfaces, and other forms of constructed shores. Biotic substrates are usually live or dead plant material ranging from bushes, tree trunks, and roots to submerged, floating or emergent macrophytes.

Lake shorelines are transitional habitats or ecotones because they constitute habitats for both terrestrial and aquatic organisms and as such produce high biodiversity in comparison with the pelagic water (Schmieder 2004). Furthermore, due to the variety of physical structures, the littoral is much more diverse in habitats than the aquatic habitat of the pelagic zone. Consequently, a diverse assemblage of microorganisms, algae, and microinvertebrates colonizes the littoral. Macroinvertebrate and fish grazers, predators, and birds, exploit these rich food resources. The structured substrates, whether abiotic or biotic, also comprise refuge for prey organisms and are often used as preferred fish spawning sites (Gafny et al. 1992). Many fish inhabit the littoral for parts of, if not their entire, life cycle.

The diverse species inhabiting littoral habitats have evolved with adaptations to the natural regime of WLF; alternation of the natural fluctuation regime exerts an obvious stress on the biota. In contrast with the species richness of the shorelines of lakes with natural WLF, lakes experiencing extreme WLF of tens of meters annually (e.g., Lake Shasta; Fig. 1) typically have barren shorelines. Under extreme WLF, and especially if the minimum and maximum water levels are

Fig. 1. The annual and interannual water level (WL) fluctuations of 3 natural lakes (upper panel), Biwa (Japan), Constance (Germany), and Kinneret (Israel), and 3 man-made reservoirs (lower panel), Shasta (California), Arancio (Sicily), and Hartbeespoort Dam (HBPD, South Africa) over the last 20 years. Data shown are the actual water level minus the multiannual mean for each water body, thus standardizing the values as fluctuations around a 20 yr mean, set at zero.

different from year to year, both the terrestrial and aquatic organisms have low chances of survival (Smith et al. 1987). Similarly, the littoral fauna and flora of lakes with extreme WLF may be strongly depressed and consist of a restricted number of ephemeral species, such as insect larvae.

The littoral tends to be more productive than the pelagic zone (Wetzel 2001). Sala and Güde (2006) concluded that the overall contribution of the littoral zone to degradation of organic matter in Lake Constance was comparable to that of the total pelagic water body, even though the littoral comprised <10% of the lake surface. In Lake Kinneret, chlorophyll concentrations and fish abundance are generally greater in the lake periphery than in its pelagic zone (Ostrovsky et al. 1996).

Littoral habitat diversity increases with physical complexity. Sand and silt bottoms provide low structural complexity, offering no refuge and less food resources than stones and boulders, which provide intermediate complexity, while diverse macrophyte assemblages and tree roots offer greater complexity and are inhabited by a greater diversity of life forms (Gasith and Gafny 1998, Meerhoff et al. 2007, Brauns et al. 2008). Artificial structures constructed by man, such as walls, driveways, and paved surfaces, minimize or completely eliminate natural habitat complexity. Gasith and Gafny (1990) pointed out 20 years ago the importance of littoral habitat complexity and suggested that the littoral of deep lakes constitutes a potentially limiting resource.

Habitat complexity changes with the regime of WLF and depends to some extent on the slope of the shoreline; regions of shallow slopes experience a greater magnitude of change than those with steep slopes. Hofmann et al. (2008) explained how wave action in interaction with changing water levels act to transport small particles to deeper waters, thus exposing boulders at the higher water level mark and accumulating sand and silt at lower levels. Gasith and Gafny (1990) found that the percent of shoreline covered by small particles (sand, clay, and silt) in Lake Kinneret increased from 6% at a high water level to 49% when the water level was 3 m lower. As the proportion of small particle size increased, the proportion of gravel, stones, and boulders declined, and thus also littoral habitat complexity.

Macrophytes

In deep lakes macrophytes are restricted to littoral zones. Besides being primary producers themselves and food for grazers and decomposers, they comprise a component of the physical structure. Different macrophyte species provide habitats with different food, cover, and structure for the aquatic biota (Wilcox and Meeker 1992). Water level drawdown as well as excessive flooding and/or altered timing of the minimum and maximum water levels lead to

loss of macrophyte species and abundance as their physiological capabilities are surpassed. An extreme example is from Lake Sevan in Armenia, where a multiannual drop of the water level by 19.5 m resulted in the loss of most of the macrophyte vegetation, followed by a shift in primary producer dominance to planktonic algae (Parparov 1990). Wilcox and Meeker (1992) reported that both larger (2.7 m) and smaller (1.1 m) than natural (~1.6 m) WLF in northern Minnesota lakes resulted in lower species diversity of macrophytes, with implications to the rest of the biota. The reduced structural diversity led to diminished habitats for invertebrates, reduced availability of invertebrates as food for fish and water birds, reduced winter food supplies for muskrats, and reduced feeding efficiency for adult northern pike, yellow perch, and muskellunge. In Lake Constance, 24% of reed beds were lost in an exceptional flood in 1999 with water level rising about 1 m higher than the normal annual maximum (Dienst et al. 2004). In Lake Biwa, 70% of the reed beds were lost with artificial lowering of the water level by only 0.3 m (Yamamoto et al. 2006). Water level fluctuations alone explained 88% of the variation in the occurrence of the native macrophyte *Typha* in Lake Ontario marshes (Wei and Chow-Fraser 2006). Hill et al. (1998) found that regulated lakes were less diverse, contained more exotic species, and were usually devoid of rare species when compared to unregulated water bodies. Smith et al. (1987) recorded that reservoirs used for hydropower that experienced regular, large fluctuations were devoid of littoral macrophytes.

Invertebrates

Increases in WLF cause significant losses to the littoral invertebrate communities. Aroviita and Hamalainen (2008) investigated invertebrate species richness in 11 regulated and unregulated Finish lakes and found that greater taxon richness was associated with natural amplitude of WLF. Baumgartner et al. (2008) found that WLF explained most of the variability in macroinvertebrate fauna in Lake Constance. White et al. (2008) reported that species richness of macroinvertebrates in Sparkling Lake, Wisconsin, declined in years when water levels were higher or lower than the long-term mean.

In Lake Kinneret, the abundance of the native mollusks *Melanopsis costata*, *Melanoides tuberculata*, and *Theodoxus jordani* declined dramatically after the unusually large water level rise of winter 2002–2003 (J. Heller, Hebrew University of Jerusalem, May 2008, pers. comm.), opening a niche for the establishment of invasive species. An aquarium snail, *Thiara scabra*, was first seen in the lake in 2005 (Meinis and Meinis 2008). By summer 2010 this invasive species was the dominant mollusk around the entire lake, with the native species seen only rarely

(A. Dolev, Kinneret Limnological Laboratory, pers. comm.). The consequences of this recent invasion for the fauna and flora of Lake Kinneret and for its ecosystem functioning are still unknown but should unravel themselves in the near future.

Fish as littoral–pelagic links

Many fish use the littoral zone at spawning and as juveniles but the pelagic as adults (Winfried 2004); hence, their life cycle and reproduction depends on littoral resources. Such species provide a littoral–pelagic link and loss of their littoral habitat may have cascading effects influencing the entire lake ecosystem (Gasith and Gafny 1990, Gasith et al. 1996). Loss of reed beds at low water levels in Lake Biwa led to reduced survival of larvae of the cyprinid fish *Cyprinus carpio* and *Carassius* spp. (Yamamoto et al. 2006). In years of strong autumn water level drawdown in Lake Constance, the young (age-0) of the benthic fish *Lota lota* migrated into pelagic waters at an earlier age than typical for the species, possibly due to shortage of littoral resources (Fischer et al. 2004). Fischer and Ohl (2005) conducted outdoor mesocosm experiments to test the impact of loss of shelter resulting from water level decline on the behavior and growth of 2 benthic fish species. The responses were species-specific.

While macrophytes often provide a preferred spawning ground for many fish species, littoral stones provide spawning grounds for others. *Acanthobrama terraesanctae* (cyprinidae), a zooplanktivore and the most abundant fish in Lake Kinneret, comprising more than 80% of all pelagic fish, spawns in winter when water levels rise and adheres its eggs to freshly inundated (i.e., epiphyton-free) stones in shallow (<50 cm) water (Gafny et al. 1992). Ostrovsky and Walline (2000) correlated its reproductive success with rates and magnitude of water level rise; years of exceptional water level rise were followed by population explosions of this species, as indicated by hydroacoustic surveys. Their explanation for this correlation was that the availability of substrate for attaching the eggs was hugely increased relative to years of more typical WLF. Furthermore, newly inundated terrestrial plants were much more abundant in years of extreme water level rise than under the typical WLF regime; in Kinneret, terrestrial plants proliferate in the exposed shores during years of unusually low water level and are inundated when the levels rise (Gafny and Gasith 2000). These inundated plants provided the fish larvae emerging from the eggs with ample shelter from predators, increasing their survival rates. Preference of epiphyton-free substrates for adhering eggs was reported for other fish species, such as *Abramis brama* (cyprinid) from Lake Constance (Probst et al. 2009), yellow perch (Fisher et al. 1996), and American smelt (Rupp 1965). It is clear that the life cycle of such species is tightly coupled to changes in water levels.

Changes in the littoral impact the pelagial: evidence from Lake Kinneret

Evidence from Lake Kinneret demonstrates that changes in the littoral cascade to the pelagic zone, eventually impacting the entire ecosystem and its water quality. The enormous reproduction success of the zooplanktivore fish *Acanthobrama terraesanctae* in years of exceptional water level rise in Lake Kinneret, described above, led to an 8–10-fold increase in the total number of fish in the lake, as seen by acoustic surveys. Such population explosion events happened twice: once following a 4.0 m rise in water level in winter 1991–1992 and again following a 4.7 m rise in water level in winter 2002–2003 (Fig. 2). In both cases there was a time lag between the water level rise and
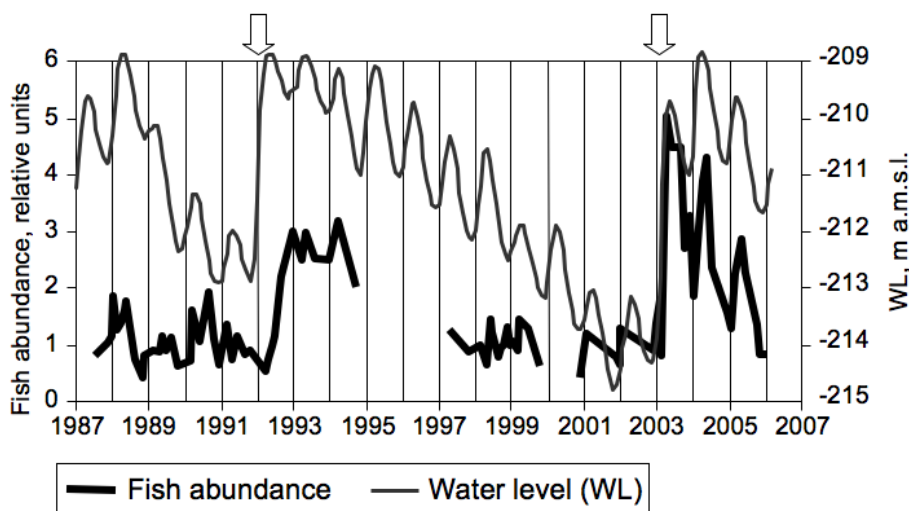

Fig. 2. Time series of water level and fish abundance in Lake Kinneret. The fish abundance data were collected by means of a 70-kHz EY-M echo sounder during 1987–1994 and a 120 kHz DE5000 echo sounder during 1997–2006. Because the 2 instruments were not calibrated against each other, the fish abundance data are presented in relative units (computed as the ratio of the actual fish abundance to the mean abundance over the sampling period prior to the rapid rise in water level). Arrows above the figure mark the 2 events of 4 m (winter 1991–1992) and 4.7 m (winter 2002–2003) rise in water level, which were followed by a huge increase in the number of the fish.

the rapid rise in fish abundance, which reflected the time needed for the newly hatched fish to reach the lowest sizes detectable acoustically. In both cases, the *A. terraesanctae* population explosion was followed by a crash of the zooplankton population, which was attributed to increased fish predation pressure (Ostrovsky and Walline 2000, Gal and Anderson 2010). The 1–2 year time lag between the appearance of the exceptionally abundant fish cohort and the crash of the zooplankton fitted the time required for this cohort to attain its maximal biomass and production rate (Ostrovsky and Walline 1999). In such years, the fish growth rate is slower and they have poor body condition attributed to food scarcity (Ostrovsky and Walline 2000). Interestingly, in both cases of fast rise in water level and

fish explosion, a year after the zooplankton crash the lake experienced its biggest ever blooms of N2-fixing cyanobacteria (Fig. 3a:, a bloom of *Aphanizomenon ovalisporum* in summer 1994 (Pollingher et al. 1998, Hadas et al. 1999) and a bloom of *Cylindrospermopsis raciborskii* in summer 2005 (Zohary and Shlichter 2009, Alster et al. 2010), both invasive species that were never reported to occur in the lake prior to 1994. Those summer–fall blooms attained filament abundance and biomass never matched again in the 40 yr phytoplankton record for Lake Kinneret. While the processes leading to those blooms are still unclear, the repetition of the same series of events on both occasions of exceptional water level rise suggests a possible link
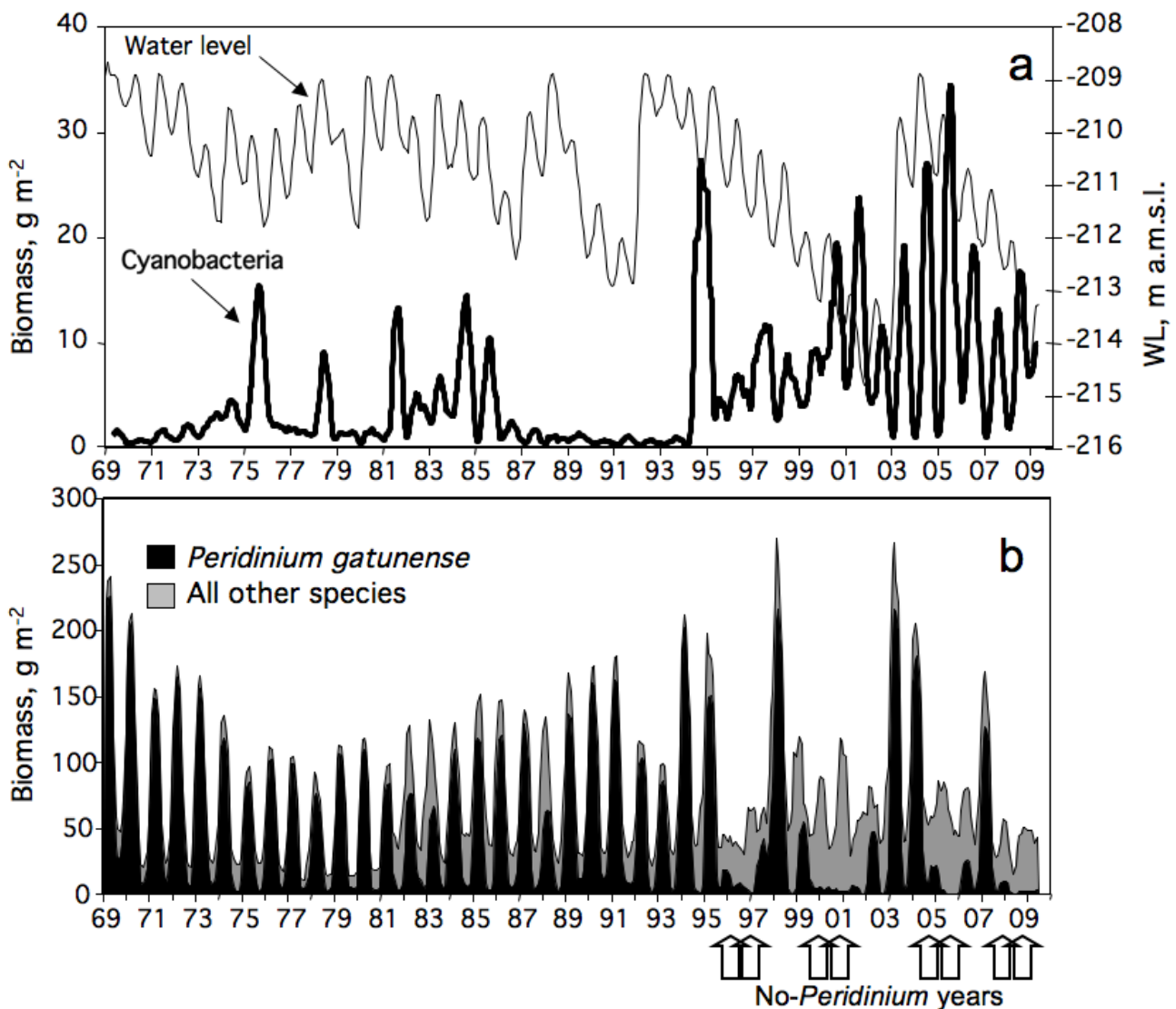

Fig. 3. Monthly mean, depth-integrated cyanobacterial (a) or *Peridinium gatunense* and all other phytoplankton species (b) wet-weight biomass (g m^{-2}) in Lake Kinneret, 1969–2009. Data shown are running means of 5 consecutive months. The time series of Kinneret water levels (WL) is also shown in (a). Arrows below X-axis indicate years of no *P. gatunense* bloom.

between the fish population explosion, zooplankton decline, and cyanobacterial blooms.

Additional interesting and potentially related data from Lake Kinneret is the record of phytoplankton abundance. Until the mid-1990s, the dinoflagellate *Peridinium gatunense* dominated phytoplankton biomass, peaking every year in spring and declining in summer, when a low-biomass, species-rich assemblage flourished (Pollingher 1986, Zohary 2004). Since the mid-1990s, *P. gatunense* has failed to develop regular massive blooms. During the last 6 years, 2005–2010, a bloom developed only in 2007 (Fig. 3b). Because *P. gatunense* is a keystone species, this is a major change to the functioning of Lake Kinneret. Roelke et al. (2007) interpreted this change as a shift of alternate stable state that took place in 1993–1994 following the first event of excessive water level rise, fish population explosion, and zooplankton crash. Concurrent with the loss of *P. gatunense* blooms, the commercial catch of the highly priced native cichlid fish, *Sarotherodon galilaeus*, declined from a multiannual catch of ~300 tons to an all-time minimum of 8 tons in 2008. This fish feeds mostly on *P. gatunense* (Gophen and Landau 1977, Zohary et al. 1994). The decline of the cichlid catch was also associated with its over-fishing at low water levels, when large spawning individuals were an easy target for fishermen (Ostrovsky 2005), and the loss of its major spawning grounds as water levels declined.

These observations from Lake Kinneret suggest that changes in the littoral may cascade to the pelagic system with impacts on the entire food web and on water quality. Certainly, more research is needed to better understand how changes in the littoral of deep lakes impact the pelagic system.

As a result of these observed changes to the pelagic system, the management strategy for Lake Kinneret was altered in 2008. It was understood that man-induced extreme WLF lead to changes that eventually promote eutrophication and impair water quality. The new strategy is to limit the extent of WLF, reduce the exploitation of water from the lake, and instead generate new water by desalination.

Summary of impacts of excessive WLF on the biota

Excessive water level drawdown or fluctuations impact the littoral and its inhabitants, mostly as a result of loss of habitat complexity via shifts from stony to sandy substrates, decline in macrophyte species diversity, and ultimately death and complete loss of macrophytes. As a result, the abundance of species inhabiting the ecosystem declines, and in extreme cases they are even lost. Instead, invasive generalist species with physiological capabilities that render them more competitive under the new conditions often take advantage of the opening niches and proliferate, causing homogenization and loss of biodiversity. New pathogens and parasites are often introduced with the invasive species (Meinis and Meinis 2008). The establishment of invasive species further pushes aside the native species and leads to reduced species diversity and loss of ecosystem functions, such as littoral food resources and decomposition products, spawning sites, and refuge from predators. These losses further enhance the loss of native and keystone species in a feedback loop (Fig. 4).

Processes promoting internal nutrient cycling

Low and declining water levels in lakes are usually associated with low inflows and therefore low external nutrient loading, which is supposed to lead to oligotrophication and improved water quality. However, other processes act to increase the internal loading of nutrients as water levels decline and fluctuate beyond natural and may outweigh the impacts of reduced inflows.

Internal loading processes in lakes are tightly associated with stratification and the thermal structure of lakes, which in turn depend on meteorological and hydrological factors and their interactions. Key determining processes include radiative and turbulent heat exchanges at the air–water interface, energy storage within the lake, and net energy flowing into or out of the lake. Meteorological factors such as radiation, air temperature, precipitation, and evaporation affect the surface temperature, while winds provide the mechanical energy required to mix the heat downward. Hydrological factors such as inflow and outflow cause local temperature changes by inducing horizontal movement and
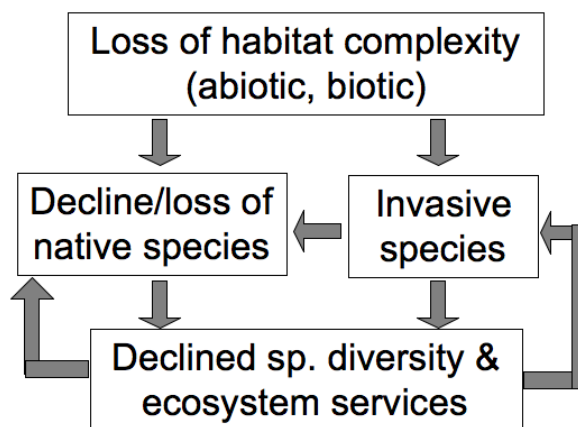

Fig. 4. Conceptual diagram of the pathways from loss of littoral habitat complexity to reduced species diversity and loss of ecosystem functions.

mixing of the lake waters. Solar radiation penetrates into the water column, affecting the heating of the uppermost layers.

Thermocline depth is determined primarily by wind and solar radiation (Magnuson et al. 1997). Water level draw-down by excessive abstraction from the epilimnion happens independently of wind regime and solar radiation, and therefore thermocline depth and epilimnion thickness should remain unchanged. Lake morphometry plays an important role; in lakes with steep slopes, the loss of lake volume will be mostly at the expense of the hypolimnion, which will shrink in thickness and size (Serruya and Pollingher 1977). Hambright et al. (1997) demonstrated that this indeed happened in Lake Kinneret as its water level was drawn down. In lakes with gentle slopes, the complex processes responsible for boundary mixing (e.g., internal seiching, upwelling, and downwelling) may become more important at low water levels, especially in small- and medium-sized lakes. In such systems, the excessive decrease in water level may cause an increase in intensity and relative importance of boundary mixing and thus affect the entire thermal regime. One can hypothesize that in such cases the thickness of the epilimnion and metalimnion will increase if other meteorological and hydrological variables remain unchanged, but this requires field verification. Nevertheless, the real impact of water level fluctuation on boundary processes may also depend on different variables of thermal and hydrological regime, such as water circulations, inflow and outflow dynamics, and location of water intake and withdrawal (e.g., epilimnetic vs. hypolimnetic). The role of these processes and their influence on biogeochemical processes in lakes are still poorly understood.

Wetzel (2001) pointed out that lakes with small hypolimnia tend to be more eutrophic than lakes of similar size but with large hypolimnia. Lake Sevan is a classical example portraying a large increase in primary productivity with a 19.5 m decrease in water level (Parparov 1990). At low water levels in Lake Kinneret, the organic matter produced in the epilimnion sank into a hypolimnion of smaller volume, and the hypolimnetic concentrations of decomposition products of this organic matter were higher than at high water levels (Serruya and Pollingher 1977, Hambright et al. 1997). Translocation of settling organic particles via the metalimnion and benthic boundary layer is a major mechanism responsible for concentrating of organic material produced all over the lake toward the shrunken hypolimnion (Ostrovsky and Yacobi 2010). In cases of anoxic hypolimnia, another likely factor contributing to higher hypolimnetic concentrations of decomposition products released from the anoxic sediments is the larger aspect ratio between the hypolimnion–bottom interface area and the hypolimnetic volume at lower water levels. Data from 4 decades of monitoring in Lake

Kinneret (Fig. 5) demonstrate that hypolimnion thickness is significantly related to water levels whereas epilimnion thickness is not. Furthermore, hypolimnion concentrations of total phosphorus (TP), ammonium (NH_4), and hydrogen sulfide (H_2S) increase with declining water levels, while no correlation can be found between the epilimnion concentrations of the constituents and water levels (Fig. 5).

Highly concentrated nutrients that remain in the hypolimnion are not available to the primary producers in the illuminated upper layers., Various processes related to WLF may also lead to changes in diapycnal and boundary mixing, however, and thus affect the upward flux of hypolimnetic nutrients and their supply into overlying water layers. These include boundary mixing (Imberger 1994, MacIntyre et al. 1999) and, at extreme water level drawdown, also full mixing events (Naselli-Flores 2003, Baldwin et al. 2008); or uplifting and mixing of the hypolimnion by large cold inflows that plunge under an existing hypolimnion (Vilhena et al. 2010).

Boundary mixing is the process of enhanced mixing near the lateral boundaries of a lake. A major cause for boundary mixing is wind-induced internal waves shoaling at the sediment–water interface (Imberger 1994, Lorke 2007). Basin scale internal waves are a known feature of many stratified lakes, especially large ones. Like sea waves that break at the sea shore, internal waves at the depth of the thermocline break when they hit the sloping boundary of a lakebed, causing turbulent mixing and sediment resuspension (Gloor et al. 1994, Ostrovsky and Yacobi 1999), and thus entrainment of nutrients contained in the uppermost sediment layer and the interstitial water. The turbulent mixing sets up horizontal intrusions of water of intermediate density into the lake interior (Imberger and Patterson 1989). MacIntyre et al. (1999) reported that high winds caused boundary mixing that led to vertical fluxes of nutrients across the nutricline in monomictic Mono Lake, California. They calculated that ammonium fluxes due to boundary mixing were sufficient to support daily rates of primary production in the deep chlorophyll maximum throughout the lake. Lake Kinneret has internal wave activity all summer (Hodges et al. 2000, Antenucci et al. 2000), when westerly winds push the uppermost water from one side of the lake to the other so that the deeper water uplifts on one side of the lake then oscillate as the winds calm down. Internal waves in Kinneret may exceed 10 m and cause intensive boundary mixing (Ostrovsky et al. 1996, Lemckert et al. 2004). Ostrovsky et al. (1996) attributed the localized higher abundance of chlorophyll and planktivorous fish in near-shore waters of Lake Kinneret to enhanced upward nutrient fluxes caused by energetic boundary mixing.

Boundary mixing induced by internal wave activity occurs at the depth of the thermocline, swiping the

"washing zone" (Ostrovsky et al. 1996), the region between the upper and lower points of the wave hitting the boundary. As water levels of a lake decline from year to year, its thermocline will be displaced and the associated boundary mixing activity will impact a different (lower) belt of bottom sediments, supplying new nutrients that would have remained buried if the water level had not changed. This is a hypothesis, awaiting field confirmation from a current research project, taking place in Lake Kinneret by I. Ostrovsky and W. Eckert. Direct measurements of sedimentation fluxes during a series of drought years in Lake

Kinneret showed that the large decline of water levels caused massive resuspension of particulate material at the lake periphery and its redeposition toward the lake center. Moreover, at very low water levels, resuspension of particulate matter was detected even in the deepest part of the lake, which could be associated with increases in horizontal velocities at the lake bottom when hypolimnion thickness was small (Ostrovsky et al. 2006). Expanding the peripheral washing zone to the lake center can be one possible mechanism responsible for the increased concentrations of nutrients in the hypolimnion.
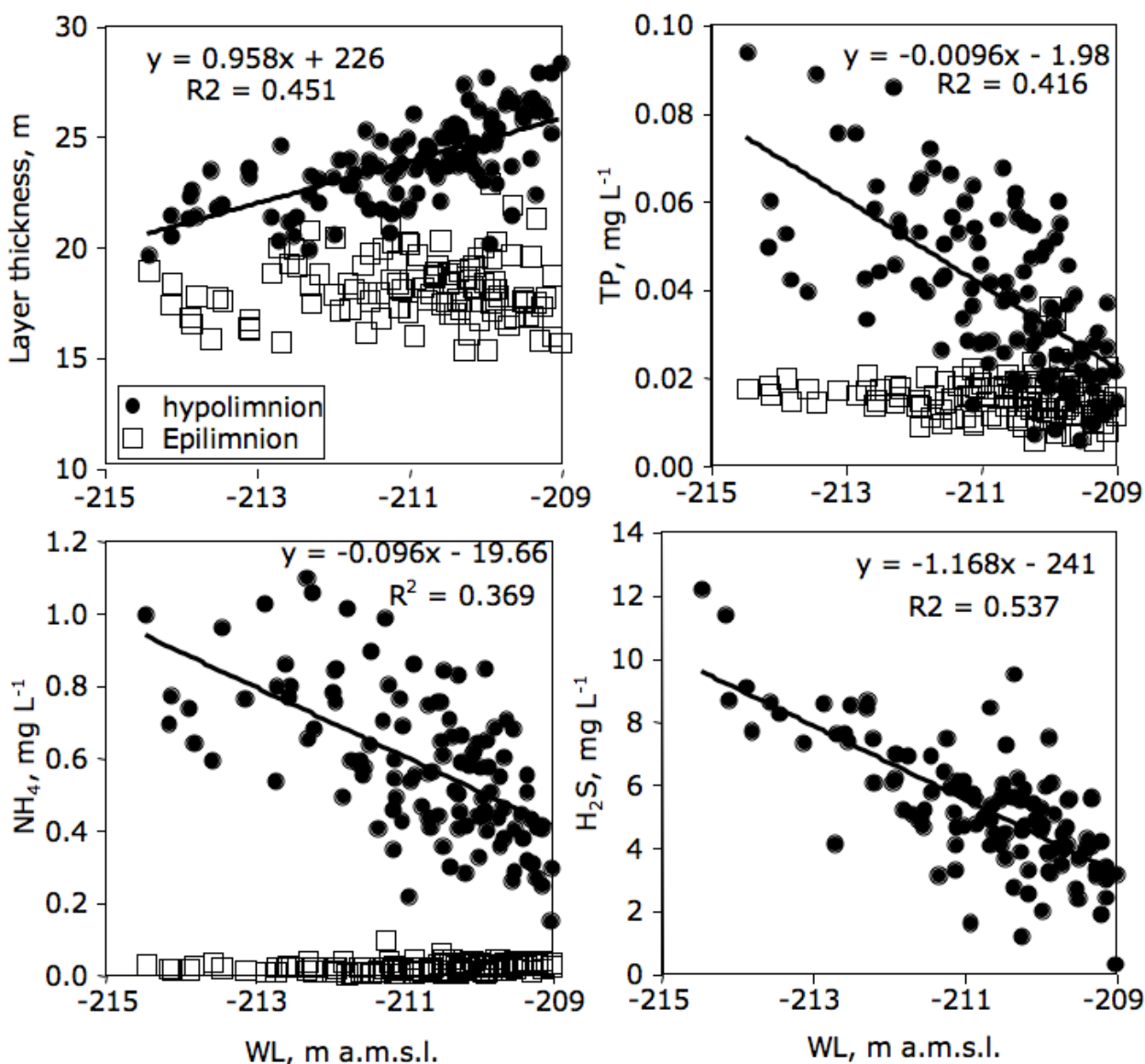

Fig. 5. The relationships between Lake Kinneret water levels (WL) and hypolimnion (circles) or epilimnion (squares) thickness (m) or concentrations of: NH_4, TP, or H_2S, 1969–2007. Data are monthly mean values for Jul, Aug, and Sep (3 data points each year). Epilimnion nutrient determinations were made weekly on water samples from 1, 3, 5, and 10 m; hypolimnion determinations were made weekly on water samples from 30, 35, and 40 m.

Extreme drawdown of lakes, by more than 10 m, can lead to extreme changes in the thermal structure of the water column. Lake Arancio is a hypertrophic monomictic reservoir with a maximum depth of 29 m, from which water is abstracted in summer for irrigation. From June to October 2001, its water level was reduced by 15 m, as opposed to an average annual drawdown of only 3.3 m. This huge water level reduction caused in July what Naseli-Flores (2003) referred to as "breaking" of the thermocline; strong winds caused mixing of the entire water column in the middle of summer when the lake is supposed to be strongly stratified. The result was enrichment of the epilimnion with hypolimnetic nutrients at a time of year when light and water temperature are maximal and optimal for cyanobacterial growth. This led to a rapid shift in phytoplankton species composition and the establishment of a major bloom of toxic cyanobacteria (Naselli-Flores and Barone (2005). The excessive drawdown has converted the monomictic lake into a polymictic one. Similarly, mid-summer holomixis events were reported by Baldwin et al. (2008) to occur in Lake Hume, an Australian reservoir, after its drawdown to 11 m (vs. max depth of 41 m). As in Lake Arancio, massive cyanobacterial blooms developed in response to the deep mixing.

Extreme and fast lake refill events lead to similar consequences as those of extreme and fast drawdown events, especially if the refill begins at particularly low water levels. Lake Burragorang in Australia is a large, deep reservoir that supplies drinking water to Sydney. Its maximum depth at the dam is 105 m and its mean depth is 27.4 m. Droughts with declining river inflows over the region have led to a multiannual drawdown of its water level; in 2007 it was 25 m lower than at full capacity. An exceptionally large inflow in July 2007 refilled the lake by 8.6 m and was followed by a major cyanobacterial bloom. Two other fast refill events that took place in the past occurred at higher water levels and did not lead to cyanobacterial blooms. Vilhena et al. (2010) compared the dynamics of these refill events by examining field data and running model simulations. They demonstrated that the 2007 inflow was cold and plunged to the bottom of the reservoir, lifting the old hypolimnion and causing it to partially mix with the epilimnion and trigger the bloom. They concluded that higher water levels provide higher hydrodynamic resistance against the inflow, decreasing the underflow velocity and the energy available to generate upward circulation, hence decreasing the chances for bloom development.

These examples of extreme lake refill (Kinneret and Burragorang) or drawdown events (Arancio and Hume) over a short period of time led to extreme ecological responses culminating in nuisance cyanobacterial blooms. It is probably those extreme events that have the greatest ecosystem destabilization effects.

Summary and conclusions

The water level regime of many lakes is likely to change in the near future as a result of increasing demands and global climate changes (IPCC 2007). The current literature review suggests that, as much as possible, increased WLF should be avoided. The changes likely to occur in stratified lakes as a function of increasing the degree of WLF beyond natural (Fig. 6) include both top-down and bottom-up effects. With increasing WLF the littoral zones of deep lakes will be affected first, their habitat diversity will decline, and consequently also species richness and abundance. This will increase the chances of establishment and proliferation of alien generalist species (mostly top-down effects), which will further reduce species diversity. With further increase of WLF beyond natural, littoral resources will diminish completely, leaving the pelagic system devoid of littoral services such as food resources, hiding places (from predation), and fish spawning sites. Internal nutrient cycling processes (bottom-up effects) may compensate for the reduced external nutrient loading in dry years with low inflows. Extreme reduction of water levels may convert monomictic lakes into polymictic ones, in which mid-summer full water column mixing events lead to cyanobacterial blooms. "Extreme" is a relative term that may have to be determined for each lake, taking into consideration its geographic location, morphology, trophic
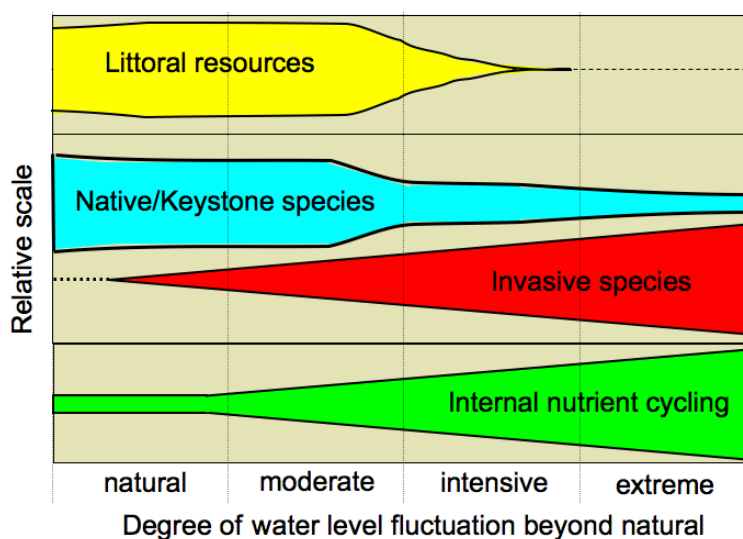

Fig. 6. Conceptual diagram of the changes likely to occur in stratified lakes as a function of increasing the degree of water level fluctuation beyond natural.

status, resilience, and type of disturbance to the natural water level regime.

Lakes are often viewed as closed systems that hardly interact with their terrestrial surroundings. Consequently, lake studies, monitoring programs, and ecosystem models tend to focus on the pelagic system and to disregard the littoral. This contribution highlights the importance of the littoral zones to the functioning of deep lakes and suggests that it should not be ignored. Additional research is needed regarding the coupling of the littoral, benthic, and pelagic systems to further our understanding of how changes in the littoral zone impact the pelagic zone of deep lakes. This study further highlights the need for studies quantifying the contribution of boundary mixing, resuspension, and other possible mechanisms of internal nutrient cycling to the nutrient budgets of lakes subjected to water level fluctuations beyond natural.

The response of aquatic ecosystems, and particularly of deep lakes, to water level fluctuations is an under-studied field of crucial importance to the management of water resources, where limnologists have a leading role to play in the near future. This review is based on literature from the subtropical and temperate zones; information from the tropics and from subarctic and arctic lakes is particularly scarce.

Excessive WLF are usually not single stressors on lakes but rather one of multiple stressors such as warming, salinization, land use practices, nutrient loading, introduction of exotic species, and over-exploitation of fish, which jointly lead to eutrophication. As claimed by Jeppesen et al. (2009, 2010), in the future, lower nutrient thresholds will be needed to obtain clear water conditions and good trophic status in lakes.

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