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Factors affecting the occurrence of littoral vegetation in a reservoir with storage function

Ph.D. Thesis

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Annotation

This Ph.D. thesis focuses on the characteristic of littoral vegetation in reservoirs with a storage function and on the factors that may affect it. The current state of the littoral vegetation in different types of biotopes was detected by a detailed survey of the littoral in Lipno reservoir. Complexes of environmental factors characteristic for different types of biotopes were described. The dynamics of littoral vegetation in response to changes in water level fluctuations was monitored in a protected bay during three years. Based on the results, the vegetation zonation was described in the eulittoral zone of an aquatic ecosystem with irregular fluctuations in water levels. The thesis also deals with the use of a breakwater structure to protect littoral vegetation in erosion exposed biotopes. The results of all three studies are used as a basis for proposals for supporting the development of littoral vegetation in the eulittoral zone in reservoirs as defined in the Water Framework Directive.

Declaration [in Czech]

Prohlašuji, že svoji disertační práci jsem vypracovala samostatně, pouze s použitím pramenů a literatury uvedených v seznamu citované literatury.

Prohlašuji, že v souladu s § 47b zákona č. 111/1998 Sb. v platném znění souhlasím se zveřejněním své disertační práce, a to v úpravě vzniklé vypuštěním vyznačených částí archivovaných Přírodovědeckou fakultou elektronickou cestou ve veřejně přístupné části databáze STAG provozované Jihočeskou univerzitou v Českých Budějovicích na jejích internetových stránkách, a to se zachováním mého autorského práva k odevzdanému textu této kvalifikační práce. Souhlasím dále s tím, aby toutéž elektronickou cestou byly v souladu s uvedeným ustanovením zákona č. 111/1998 Sb. zveřejněny posudky školitele a oponentů práce i záznam o průběhu a výsledku obhajoby kvalifikační práce. Rovněž souhlasím s porovnáním textu mé kvalifikační práce s databází kvalifikačních prací Theses.cz provozovanou Národním registrem vysokoškolských kvalifikačních prací a systémem na odhalování plagiátů.

České Budějovice, 22.4.2013 ....
Monika Krolová

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List of papers and author's contribution

The thesis is based on the following papers (listed chronologically):

I. **Krolová M**., Čížková H., Hejzlar J. 2012. Depth limit of littoral vegetation in a storage reservoir: A case study of Lipno Reservoir (Czech Republic). Limnologica 42: 164-174 (IF=1.527).
Monika Krolová carried out field measurements, vegetation monitoring, soil sampling and analysis, data assembly, statistical analysis and had a major share on writing the manuscript.

II. **Krolová M.**, Čížková H., Hejzlar J. and Poláková S. (*in press*). Response of littoral macrophytes to water level fluctuations in a storage reservoir. Knowledge and Management of Aquatic Ecosystems (IF=1.520).
Monika Krolová carried out field measurements including vegetation monitoring, soil sampling, measurement of water transparency, water and soil temperature, redox potential and pH, data assembly and had a major share on writing the manuscript.

III. **Krolová M.** and Hejzlar J. (*manuscript in preparation*). Protection and support of littoral macrophyte stands by breakwaters on differently exposed shores of Lipno Reservoir.
Monika Krolová carried out field measurements, vegetation monitoring, soil sampling and analysis, data assembly, statistical analysis and had a major share on writing the manuscript.

Contents

INTRODUCTION

1.1 Introduction: The importance of aquatic macrophytes in reservoirs

The presence of well-developed vegetation of aquatic macrophytes positively influences the overall character of the aquatic ecosystem and water quality (Carpenter and Lodge 1986; Moss 2008). Their presence is therefore considered an important component of evaluation of the aquatic ecosystem quality in the Water Framework Directive (WFD; Directive 2000/60/EC), which induces legislative conditions to improve the ecological status of waters in the European Union.

Among various types of water bodies, storage reservoirs usually have poorly developed littoral vegetation (Lindström 1973; Baxter 1977; Moss 2008). In addition to physicochemical factors (Hutchinson 1975; Barko and Smart 1981) and biotic interactions (Carpenter and Lodge 1986) that commonly shape aquatic plant communities of standing waters in general, littoral stands of reservoirs are affected by reservoir management (Kennedy and Thornton 2001; Kennedy 2005). Especially important is the impact of the large annual amplitude of water level fluctuation (Lidström 1973; Baxter 1977; Furey et al. 2004; Moss 2008). In comparison with other types of water bodies, little attention has been paid to the development of littoral vegetation in reservoirs. This is probably because reservoirs are unnatural and have definite management priorities, which limits the possibilities of restoration measures.

The aim of this review is to assess the current state of knowledge of the dynamics of littoral vegetation in different types of biotopes, with emphasis on biotopes of reservoirs, and to highlight important factors that influence the state of littoral vegetation.

1.2 The littoral zone and its ecological functions

The littoral zone is the shore region of lakes and lowland rivers where the sediments lie within the photic zone, and where the shallow water flora is frequently dominated physically by macrophytes (Kalff 2002). It extends down the bottom profile to the point where insufficient light penetrates to support net plant growth and it includes the water column above the bottom. Its extent varies seasonally because of changes in light penetration through the water column caused by changes in phytoplankton crop or the colour of incoming water and it includes the swampy regions at the margin. The littoral is divided into two zones: eulittoral and infralittoral. The eulittoral zone is costal and it is influenced by wave activity and water level fluctuation in the course of the year. This zone is developed in most reservoirs with extensive water level fluctuation. The infralittoral zone is the most important area in the water ecosystems with stable water levels (Hutchinson 1967; Wetzel 1983).

A typical zonation of littoral vegetation in shallow lakes with good water transparency is characterized by the presence of well-developed littoral vegetation (Hanson et al. 1990; Scheffer et al. 1992; James and Barko 1994; Weisner et al. 1997; Welch et al. 2003). Well-developed littoral vegetation is composed of emergent, floating-leaved, free-floating and submerged species (Hutchinson 1967; Sculthorpe 1985) (Fig. 1). Emergent macrophytes species (such as *Typha latifolia, Phragmites australis, Cyperus papyrus*) are anchored by a root and rhizome system in flooded or waterlogged soil. Their underground parts are therefore in an anaerobic environment where they cope with a lack of oxygen, but they are able to grow in the water column from <50 cm to ca 150 cm (Sculthorpe 1985). Their above-ground parts are at least partially located in the atmosphere and they take up mainly atmospheric CO_2 during photosynthesis. Macrophytes with floating leaves are firmly connected to the bottom substrate by means of roots and rhizomes (Wetzel 1983). Macrophytes with floating leaves occur in flooded habitats, where the height of the water column ranges from 0.25 to 3.5 m (Sculthorpe 1985).

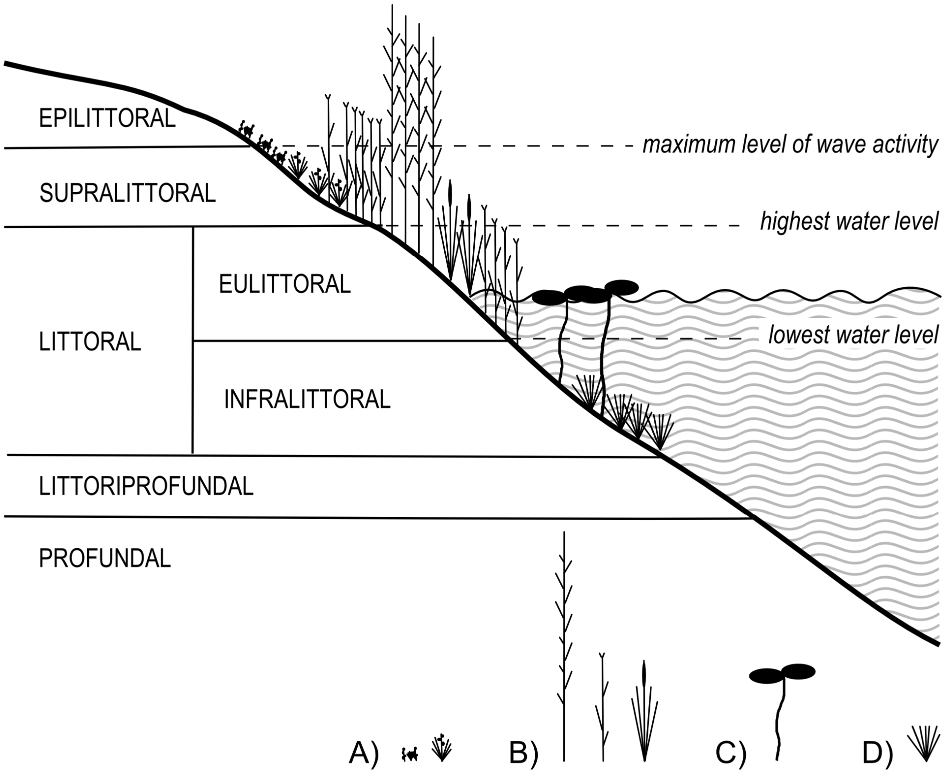

Figure 1: The bottom of a lake basin is separable from the free open water. The epilittoral zone lies entirely above the water level and is uninfluenced by spray; the supralittoral zone also lies entirely above the water level, but is subject to spraying by waves. The eulittoral zone encompasses that shoreline between the highest and lowest seasonal water levels. The eulittoral zone and the infralittoral zone collectively constitute the littoral zone. The infralittoral zone is characterized by distribution of macrophytic vegetation (emergent, floating-leaved and submerged species). The littoriprofundal is occupied by scattered photosynthetic algae and bacteria. The remainder of exposed fine sediment free of vegetation is referred to as the profundal zone (Hutchinson 1967). Legend: A) terrestrial species; B) emergent species; C) floating-leaved species; D) submerged species.

Photosynthetic exchange of CO_2 takes place predominantly between the upper side of the leaves and the atmosphere. Submerged macrophyte species are a heterogeneous group including predominantly submerged species of higher plants, but also filamentous and multicellular algae (*Cladophora, Charales*) (Wetzel 1983). Mostly, but not always, they are anchored by rhizomes, roots or rhizoids in the substrate. They occur in water depths of up to 10-11 m (Sculthorpe 1985). Photosynthetic fixation of CO_2 takes place in the water column.

Macrophytes have numerous functions in aquatic ecosystems. Rooted species stabilize bottom and shores, and thus protect them against wave erosion (Welch et al. 2003; McComas 2003). All macrophyte species support sedimentation of particles and reduce turbidity (Vermaat et al. 2000) that decreases light intensity in the water column. Macrophytes can be important for nutrient cycling and biochemical cycles (for example organic carbon production, phosporus mobilisation and transfer of other trace elements) (Jeppesen et al. 1998). Submerged plant parts create a habitat for periphyton, (Carpenter and Longe 1986), consisting of bacteria and algae. Periphyton is significantly involved in food chains and helps phosphorus removal from the water column (Dodds 2003). Littoral vegetation creates a suitable environment for invertebrates (Stansfield et al. 1997; Scheffer 1999; Welch et al. 2003; Cronin et al. 2006), some vertebrates, such as frogs (Martín et al. 2005), and early developmental stages of fish. They also form habitats for fish predators (Perrow et al. 1999; Balon 1975; Aarts and Nienhuis 2003; Čech et al. 2009) as well as for many bird species (Lauridsen et al. 1993; Janda et al. 1996; van Vessen and Trucker 1997).

1.3 The effect of environmental factors on littoral vegetation in lentic esosystems

The distribution of macrophytes in nature ecosystems is largely determined by physicochemical factors (Hutchinson 1975) and biotic interactions (Carpenter and Londge 1986). The physicochemical factors include: light, temperature, transparency of the water column, substrate quality and erosion factors such as waves, water level fluctuation and ice. Biotic interactions include: food, competitive and other relations between plants and animals.

Solar radiation is of fundamental importance to the plant component of any ecosystem as a pre-requisite for photosynthesis. Low transparency in the water column is a limiting factor for the presence of submerged macrophyte species (Hanson et al. 1990; Scheffer et al. 1992; James and Barko 1994; Weisner et al. 1997; Kalff 2002; Welch et al. 2003). Many submerged species are adapted to low light intensities (for example shade-adapted leaves are finely divided) (Hutchinson 1975). Water transparency can be very low owing to (1) the presence of phytoplankton, (2) the resuspension of fine bottom material by wave action (Kalff 2002), (3) shade vegetation on the shores (Sculthorpe 1967) and (4) fish activity (Welch 2003).

Freshwater ecosystems are usually considered to be more stable in terms of temperature variation than terrestrial ecosystems (Sculthorpe 1967). However, the thermal variability of water can differ greatly among ecosystems, depending on several parameters. In large ponds and lakes, the depth and volume of water can lead to seasonal stratification of temperature during the growing season. In most situations, the epilimnion coincides with the photic zone, where plant growth is possible (Sculthorpe 1967). In lakes with high light penetration, the maximum depth at which macrophytes occur is limited by temperature. In small water bodies with short hydraulic residence time, water temperature is potentially influenced by the size of the water body but also by the temperature of any water input (Bornette and Puijalon 2012).

The spreading and production of macrophytes in the littoral depends on the availability of nutrients in the sediment (Dykyjová and Úlehlová 1978) and in water (Bornette and Puijalon 2011). The amount of available nutrients in the bottom substrate is influenced by its texture and especially by the content of silt and clay particles. A larger proportion of these particles increase the substrate capacity to retain nutrients and other substances (Brady and Weil 2002). The physical texture of the substrate of freshwater ecosystems varies greatly according to water movements, transport and deposit of fine sediment, as well as biological processes of organic matter production, accumulation and degradation (Bornette and Puijalon 2011). Fine particles favour macrophyte development (Furey et al. 2004). Submerged macrophyte species predominantly occur in shallow lakes with the presence of fine particles in the substrate (Madsen et al. 1996; Weisner et al. 1997; Melzer 1999; Van Geest et al. 2003).

Aquatic macrophytes are negatively affected by the mechanical effects of wave activity, which is the primary cause of erosion, transport and accumulation of sediment in water bodies (Weisner 1987; Weisner et al. 1997), which in turn modifies the nutrient availability for plant stands. Vegetation is often mechanically disturbed in wave exposed habitats (Hutchinson 1975; Spence 1982; Keddy 1983). The height of waves generated by winds is determined by wind speed, wind duration, fetch distance and bottom depth (Nordstrom and Jackson 2012). As a result, the vegetation is generally less productive in wave exposed than in sheltered littoral zones, and distributions of emergent and floating-leaved macrophyte species have been found to shift landward with increasing wave exposure (Hutchinson 1975; Spence 1982). Erosion is promoted by bottom freezing and thawing during winter (Vilmundardóttir et al. 2010), which in turn destroys some macrophyte species, especially submerged ones (Hutchinson 1975; Ostendorp 1995; McComas 2003). Water level fluctuations also adversely affect macrophyte growth through erosion and degradation of the substrate due to the washing out of fine particles and nutrient-rich components (Furey et al. 2004; Hutchinson 1975).

Aquatic and littoral macrophyte species are often involved in the food chains of many animal species. Littoral species are commonly grazed by water birds (Weisner et al. 1997; Perrow et al. 1997) and herbivorous fish (Brönmark and Hansson 1998; McComas 2003). Periphyton serves as an important food source for herbivorous freshwater invertebrates (Straškraba 1959). Intensive grazing may lead to a reduction or complete disappearance of certain species of aquatic plants, such as submerged plant species (Weisner et al. 1997). Populations of various plant species behave very similarly in the ecosystem, regardless of their taxonomic relations (Dykyjová 1989). Aquatic species compete with one another for light and nutrients available in the water column (Brönmark and Hansson 1998). This leads to interspecific competition, which may result either in the adaptation of the species, or to the replacement of the population of one species by the population of another one; the suppressed species may either disappear from the locality or may be forced to change its niche (Odum 1971; Hutchinson 1975).

1.4 Specific features of reservoirs that affect macrophytes

The character of littoral vegetation in the reservoirs is determined, to a large extent, by specific features of these artificial water bodies. These include mainly the age of the ecosystem, shore morphology and amplitude of fluctuations in water level.

Reservoirs represent new, emerging ecosystems, only several decades (or at most centuries) old, which in many cases have not yet reached the climax stage (Whittaker 1953; Odum 1971). The zonation of littoral vegetation in artificial ecosystems starts to shape after flooding, when most terrestrial species die (Heteša and Marvan 1984). Among the terrestrial species, only those survive that are able to cope with flooding and a subsequent lack of oxygen in the soil and its consequences (Armstrong 1979). Initially, submerged species expand after flooding (eg. Krahulec and Lepš 1994). Their development is possible owing to (1) the large amounts of nutrients released by the decomposition of terrestrial plant species and (2) high transparency in the water column, which is due to the intense predation of phytoplankton by zooplankton in the absence of fish in the initial stage of a reservoir (Heteša and Marvan 1984; Krahulec and Lepš 1994). Fish populations develop after a certain time, creating a predation pressure on zooplankton, which supports, along with the presence of nutrients, the development of the phytoplankton and deterioration of light conditions in water (Jeppesen et al. 1998). As a result, submerged macrophytes are competitively displaced by the phytoplankton (Kalff 2002).

An important factor that influences the presence of littoral vegetation in artificial water bodies is the shore morphology (van Geest et al 2003). When a new lake is formed by damming a stream, its shape will usually be different from that of most natural lakes (Hutchinson 1957). Reservoirs are predominantly built in deep valleys, which results in their greater depths, steeper banks, and lesser extent of shallows suitable for development of littoral communities compared to natural lakes. Whereas natural lakes are normally deepest somewhere near the middle, river reservoirs are almost always deepest just upstream from the dam (Baxter 1977). The morphology (depth, area, shore slope and exposure), age of reservoir, climatic conditions and ice cover formation of the littoral influences the extent of shoreline erosion (Vilmundardóttir et al. 2010). The erosion processes in the littoral zone affect the substrate quality, hence influencing the abundance and composition of macrophytes (Furey et al. 2004). The mechanical effects of accumulated water are manifested by waves, landslides and ice formation (Nordstrom and Jackson 2012). The littoral vegetation may not create in extreme conditions such as irregular flooding or macrophyte destruction by waves. Banks resist the erosion better if they are covered with vegetation. On the contrary, where littoral macrophyte species are missing, the coast can be heavily eroded (McComas 2003).

Man-made reservoirs with a water storage function also differ from natural lakes by an increased water level fluctuation, which is associated with the reservoir management (Kennedy and Thornton 2001; Kennedy 2005). Hellsten et al. (1996) and Partanen and Hellsten (2005) have shown that the presence and diversity of littoral vegetation in reservoirs depend on the seasonal timing of water level changes. The structure of littoral vegetation is determined by the fluctuation of water level (Hejný and Husák 1978; Hejný and Segal 1998). Large water level fluctuations caused by the management of a reservoir restrict the development of littoral vegetation, which is therefore developed less well than in lakes (Lidstrom 1973; Baxter 1977; Furey et al. 2004; Moss 2008). Periodical drying of the bottom negatively affects the submerged species and the species with floating leaves. On the other hand, it can promote the development of the species of bare bottoms and amphibious species (Hutchinson 1975).

AIMS OF THE STUDY

In storage reservoirs, the factors determining the development of littoral stands are largely associated with management practices and other human impacts. However, little is known about how combinations of these factors relate to reservoir management. Further characteristic of vegetation dynamics in the eulittoral zone during several vegetation seasons can provide further information about how littoral vegetation copes with large seasonal fluctuations in water level. Understanding the dynamics of littoral vegetation can contribute to the knowledge needed to maximize the ecological potential of reservoirs, as defined by the Water Framework Directive (WFD 2000).

The overall aim of this study was, therefore, to evaluate the limits of development of littoral vegetation for a selected reservoir with storage function.

The specific objectives of the study were:

I to assess the species composition and cover of littoral vegetation as related to typical combinations of environmental factors in various types of littoral biotopes;

II to characterize the seasonal and inter-annual changes in the structure and diversity of vegetation in a sheltered littoral biotope as related to temporal changes in key environmental factors;

III to assess the effects of a simple breakwater as a measure of protecting littoral vegetation from wave action on erosion-exposed sites;

IV to infer management possibilities that could lead to improved ecological conditions in the littoral zone in the sense of the EU Water Framework Directive.

DESCRIPTION OF STUDY SITES AND METHODS

3.1 Study sites

The Lipno Reservoir was selected for detailed assessment of complex factors that may influence littoral macrophyte communities. The Lipno Reservoir is a river impoundment (total volume: 306 million m^3; flooded area: 47 km^2; max. depth: 22 m; mean water residence time: 0.6 yr) situated in South Bohemia, Czech Republic. The reservoir is multi-purpose and has been used for hydropower, flood protection, flow control in the River Vltava, recreation and water supply for the Loučovice waterworks (Dolejší 1996). The central part of the reservoir is situated in a flat part of the landscape, where the flooded area extends into considerable distances from the original riverbed. The downstream part of the reservoir is stuck in the valley created by the eroding river. This segment is characterized by the steep slope of banks and by rocky outcrops. The width of the littoral zone and the character of littoral biotopes vary according to differences in morphology in particular segments of the banks.

3.2 Methodological approach

Study I deals with Objective I and includes an overall characterization of the littoral zone in the Lipno Reservoir. The spatial distribution of littoral macrophyte species was analysed in relation to key environmental factors. The study was conducted at 115 sites, each 50 m long, along the whole reservoir perimeter at regular 1-km intervals. The sites were surveyed for species composition and cover, shore morphometry (the slope of shore and bottom, the erosion step and the fetch length), characteristics of substrate, transparency of water, and for anthropogenic impacts.

Study II deals with Objective II. In Study II, the bay of Vřesná was selected for the analysis of littoral macrophyte dynamics as a model area sheltered from wave action and supporting well-developed littoral vegetation. Temporal changes were characterized in the zonation of littoral vegetation, in relation to key environmental factors. In order to describe the situation appropriately, the terminology used in limnology for the description of littoral zonation (Hutchinson 1967; Wetzel 1983; Figure 1) was combined with the concept of ecophases developed in wetland botany by Hejný and Husák (1978) and later modified by Hejný and Segal (1998). An ecophase represents a complex of environmental conditions determined by the current water level at a biotope at a given time. The concept of ecophases makes it possible to categorize the current hydrological conditions on particular sites and evaluate the effect of their sequences on the vegetation over time. Plant species composition and cover, water level, soil and water temperature, water transparency, and substrate characteristics were measured along a transect across the littoral zone during three growing seasons (2007-2009).

Study III corresponds to Objective III. Study III was an experiment aimed at testing the use of simple breakwaters in order to support littoral vegetation in erosion exposed biotopes. Breakwaters and control areas without breakwaters were located in three biotopes exposed to different extent of water erosion. The horizontal structure of littoral vegetation, plant species composition and cover, as well as the sediment structure before and at the end of the experiment were measured at each site. The experiment was conducted in the course of six years (2006-2011).

Objective IV was achieved through synthesis of all data acquired in the research in relation to literature data.

Similar methodology of data collection and characterization of littoral vegetation was used in all studies.

MAIN RESULTS

The study of macrophytes along the whole perimeter of the reservoir has shown significant relationships between the occurrence of macrophytes and shore morphology, exposure to waves, and human impacts. Most of the Lipno perimeter was characterised by a wide eulittoral zone (i.e. the shoreline region between the highest and the lowest seasonal water levels) with a tenuous cover of terrestrial hydrophilic, amphibious, and/or emergent macrophytes (Table 1, Table 2 and Figure 7 in Study I), and a low proportion of silt, clay, and organic fractions in the substrate (Figure 4 in Study I). Infralittoral submerged and floating-leaved macrophytes were restricted to a few sites within the mouths of the main and side tributaries where high transparency was maintained by clear inflow water and water level was independent of reservoir pool fluctuations (Table 2 in Study I). Water transparency was low (1–2 m) compared to annual changes of water level (2 to >3 m) (Study I). Anthropogenic impacts resulted in low cover regardless of site morphology (Figure 4 in Study I) and low cover of macrophytes (Figure 3 in Study I). Multivariate statistical analysis (DCA, CCA) confirmed relationships between the occurrence of macrophyte species and morphological and substrate characteristics of the shore (Figure 8 in Study I). The CCA ordination diagram (Figure 8 in Study I) shows the distribution of species in relation to different site characteristics. Amphibious, floating-leaved, and submerged species were confined to sheltered sites with tributaries. Such sites were characterized by low shore slopes, low erosion steps, low fetch lengths, and relatively high amounts of fine particles and organic matter in the substrate. Emergent species occurred in all types of biotopes of littoral zone in the Lipno Reservoir. Terrestrial trees and shrubs occurred on steep slopes above the erosion step.

The tree-year monitoring of seasonal changes in the dynamics of littoral vegetation has shown that the eulittoral zone is divided into three sub-zones: the upper eulittoral with a stable community of perennial species with high cover, the middle eulittoral with relatively rich emergent and amphibious species present at low cover values, and the lower eulittoral devoid of permanent vegetation (Table II; Figure 2; Figure 5 and Figure 6 in Study II). The cover and species composition in particular sub-zones were primarily influenced by the duration and timing of flooding (Figure 3 in Study II), followed by nutrient limitation and strongly reducing conditions in the flooded organic sediment (Table I in Study II).

The effects of breakwaters on macrophyte growth in the eulittoral zone were assessed in Study III. Simple breakwaters made of wooden poles and additionally amended with strings of fabric supported the retention of fine particles in the substrate (Figure 5 in Study III). Nevertheless, the breakwaters proved relatively inefficient in supporting littoral vegetation (Figure 3 in Study III), especially in areas that were shaded by shrub and tree layers, without the presence of nutrients in the substrate and without vegetation in the upper eulittoral zone. Other important factors in erosion exposed areas included fluctuations in water level (Figure 2 and 4 in Study III) and ice phenomena (Figure 6 in Study III).

DISCUSSION

5.1 Main factors affecting macrophyte growth

Low water transparency is an important factor limiting the presence of submerged macrophyte species, as has previously been shown in lake studies (Hanson et al. 1990; Scheffer et al. 1992; James and Barko 1994; Weisner et al. 1997; Welch et al. 2003). Study I confirmed a low water transparency in the Lipno Reservoir (ranging between 0.3 and 2 m). As the depth of the photic zone is smaller than the annual amplitude of water level fluctuation (of up to 3.5 m), the low transparency may be the main reason for the absence of infralittoral zone in the reservoir. Littoral vegetation is therefore confined to the eulittoral zone, which is determined by the maximum and minimum water level.

Water level fluctuation significantly affects the presence and growth of macrophytes in the littoral zone in lakes as well as and in reservoirs (Keddy and Reznicek 1986; Wantzen et al. 2008). The large annual amplitude of water level fluctuation in Lipno Reservoir results in a wide eulittoral zone (Study I.; Krolová et al. 2010), which, nevertheless, supports only sparse vegetation in some places. Vegetation was also poorly developed in some shallowly flooded parts of the eulittoral, where light light penetrated down to the bottom (Study II). This may be due to periodical drying and freezing of the substrate in the eulittoral zone, which not only damages the bottom (Nilsson 1981; Björk 1994; Hellsten 2001), but also prevents the development of submerged macrophytes (Hutchinson, 1975; McComas 2003; Study I).

Hill et al. (1998) proposed a response model to water level fluctuations, which took into account both intra-annual and inter-annual variation in water level as a predictor of plant communities that should occur along shorelines. They argue that a hypovariable water level fluctuation leads to species loss owing to interspecific competition while hypervariable fluctuation causes loss of species as a result of unfavourable environmental conditions and exceeded regeneration capacities of the populations. According to their model, the Lipno rReservoir ranks among hypervariable water bodies with low species richness and high risk of invasion by exotic species. However, this model requires further improvement as it does not consider the varied responses of different plant species to such disturbances (Casenova and Brock 2000; Van der Valk 2005), related to their functional strategies (Bornette and Puijalon 2011). Study II complements the above knowledge by associating the plant species composition and cover in the eulittoral zone to the seasonal pattern of water level fluctuation. The use of the concept of ecophases *sensu* Hejný and Segal (1998) has proved to be a useful tool for delimitation of sub-zones within the eulittoral (upper, middle and lower), which differ in the plant species composition and cover. The results indicate that the character of vegetation is consistent with the ecophase prevailing in the particular sub-zone in summer.

Even within a single water body, there are a variety of biotopes differently favourable for aquatic macrophytes. These differences between various biotopes are largely determined by differences in shore morphology (cf. Chapter 1.3 and references therein). Study I demonstrates this phenomenon for the Lipno Reservoir. The structure of littoral vegetation in Lipno is crucially influenced by the combination of factors that include the slope of shores/bottom and wave exposure (the fetch length). Sheltered sites with tributaries represent the most valuable habitats with respect to the development of littoral vegetation (Study I).

5.2 Management options

When the eulittoral zone is flooded, it becomes part of the aquatic ecosystem and can fulfil the same ecological functions as the infralittoral zone (cf. Chapter 1.3 and references therein). According to Study II, the typical annual pattern of water level fluctuations in the Lipno Reservoir shows a seasonal maximum in early spring, when the whole eulittoral zone is usually flooded. Similar annual dynamics can be expected in other reservoirs in temperate climate that are fed with water from melting snow.

This seasonal maximum in water level coincides with the time when phytophilous fish (such as *Esox lucius, Blicca bjoerkna, Scardinius erythrophthalmus*) spawn in macrophyte stands (Balon 1975; Aarts and Nienhuis 2003). It can be concluded that the eulittoral zone can take over the ecological function of the infalittoral. This may be important especially in water bodies where the infralittoral zone is not developed, such as the Lipno Reservoir. However, observations of the bay of Vřesná cover only a three-year time period. Further monitoring is therefore necessary to verify this conclusion.

The most valuable littoral biotopes, where vegetation is well developed, are worth preferential protection. Hellsten and Riihimäki (1996) and Just et al. (2009) recommend protecting littoral areas in bays in the first place. Study I elaborates this recommendation by drawing attention to sites with tributaries. The delimitation of the most favourable sites with respect to development of littoral vegetation belongs to the most important results of this thesis. According to Study II, the periodical flooding/drying of the eulittoral zone can support the growth of some plant species, especially annuals and species of bare bottoms. Regeneration and rooting of emerged species and the support of annual macrophyte species can be promoted in sheltered sites if the lower part of the eulittoral zone is not flooded in the second half of the season (August to October). If this observation is confirmed by further studies, it can be considered as an ecological measure promoting the development of vegetation in the eulittoral zone as it is not in conflict with management priorities in reservoirs with storage function.

Littoral vegetation does not develop well along shores with steep slopes and inappropriate exposure, which are often found in reservoirs (cf. Chapter 1.3, 1.4 and references therein). This has also been confirmed by Studies I and III. In addition, Study III indicates that mechanical protection of macrophytes in the eulittoral zone by breakwaters can be effective only in places where basic ecological conditions for the development of littoral vegetation are fulfilled. These include substrate containing nutrients and good light conditions (without shading, for example, by trees and shrubs). Another pre-requisite for a successful protection of littoral stands is a correct location of the breakwater, which should be placed in the middle eulittoral. On heavily eroded sites, construction of more complex breakwaters (e.g. breakwaters with fabric strings), which prevent loss of fine sediment particles, can be complemented with addition of nutrient rich substrate and macrophyte plantation (Iseli 1993; Ostendorp et al. 1995b; Zhen 2002).

The EU Water Framework Directive (WFD; Directive 2000/60/EC) requires occurrence of littoral macrophytes on all suitable sites of any water body, which reflects the understanding of the high ecological importance of macrophyte stands in aquatic ecosystems (Moss 2008). Because of large water level fluctuations, the eulittoral zone in reservoirs can be extensive and can cover large areas. If flooded during the vegetation period, the eulittoral zone can fulfil similar ecological functions as the infralittoral zone. The presence of vegetation in the eulitoral zone should therefore be included as a positive factor in the assessments of the ecological potential of reservoirs (cf. also Study II, Discussion). Encouraging the development of vegetation in the eulittoral zone, e.g. by modest seasonal regulations of reservoir management (cf. Study II), can further improve the ecological potential of reservoirs.

CONCLUSIONS

I The quality and character of littoral vegetation are determined by water transparency, morphology of the reservoir, and the extent of water level fluctuations. Acting in combination, these factors form different types of biotopes. Erosion-exposed biotopes, characterized by steep slopes of shores/bottom and large fetch lengths, are not favourable for the development of littoral vegetation. Conversely, sheltered biotopes, especially those with tributaries, represent the most valuable habitats with respect to the development of littoral vegetation. These habitats host developed littoral communities with submerged and floating-leaved macrophyte species, along with rich stands of emergent species.

II The structure of littoral vegetation in the eulittoral zone in the sheltered biotopes is affected by irregular changes in water level and by the substrate quality. Three sub-zones were distinguished within the eulittoral zone in the bay of Vřesná in the Lipno Reservoir: (i) the upper eulittoral with a stable plant community formed by a small number of perennial plant species forming high cover in the zone of occasional flooding (less that 30% of the time), (ii) the middle eulittoral with a relatively high richness of emergent and amphibious species present at fairly low cover values in the zone of moderate flooding (30–50% of the time), and (iii) the lower eulittoral devoid of permanent vegetation in the zone of predominant flooding (50–80% of the time).

III In areas exposed to intense erosion, devoid of fine particles in the substrate, and/or shaded eulittoral zones, littoral vegetation cannot be effectively supported by using simple breakwaters. Simple strung breakwaters work well on retention of fine particles in the substrate, but may not be sufficient for retaining the finest mineral and organic fractions containing nutrients. If nutrients are retained in the substrate, the area protected by breakwaters can be expected to support the development of vegetation.

IV Sheltered biotopes with tributaries, where the eulittoral zone is wide and suitable for macrophytes, should be protected in reservoirs. The promotion of vegetation in the eulittoral zone can help reservoir managers to improve the ecological potential in the sense of the EU Water Framework Directive, especially in reservoirs where the shore morphology allows macrophyte growth. A relatively modest regulation of reservoir water level during the growing season, which does not contradict major reservoir purposes, can support the formation of eulittoral macrophyte stands and their ecological functioning in the aquatic ecosystem.

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RESEARCH ARTICLES

Paper I

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Depth limit of littoral vegetation in a storage reservoir: A case study of Lipno Reservoir (Czech Republic)

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Abstract

Controlling factors for the occurrence of littoral macrophyte species were investigated in Lipno Reservoir (area: 46.5 km^2; z_{mean}: 6.6 m; z_{max}: 22 m; water residence time: 0.6 yr), a dam impoundment with moderately fluctuating water level (amplitude up to 4 m) which is used for hydropower and downstream flow augmentation. The options of supporting littoral macrophyte growth for improving the reservoir's ecological potential were evaluated according to the European Water Framework Directive's definitions. Macrophytes were examined at 115 sites, each 50 m long, along the whole reservoir perimeter at regular 1 km intervals. Sites were surveyed for their phytocoenology, shore morphometry, pedological characteristics of substrate, transparency of water, and anthropogenic impacts. Most of the sites were characterised by a wide eulittoral zone with a tenuous cover of terrestrial hydrophilic, amphibious, and/or emergent macrophytes and a low proportion of silt, clay, and organic fractions in the substrate. Infralittoral submerged and floating-leaved macrophytes were restricted to a few sites within the mouths of the main and side tributaries where transparency was maintained by clear inflow water independent of reservoir pool fluctuations. Water transparency was low (1–2 m) compared to annual changes of water level (2 to >3 m). Multivariate statistical analysis (DCA, CCA) confirmed relationships between the occurrence of macrophyte species and morphological and substrate characteristics of the shore. Improvement of macrophyte cover and establishment of vital infralittoral zones requires improvements in water transparency and changes in reservoir operation, i.e. limiting the range of water level fluctuation to less than ca 1 m.

Paper II

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Response of littoral macrophytes to water level fluctuations in a storage reservoir

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ABSTRACT

Lakes and reservoirs that are used for water supply and/or flow regulations have usually poorly developed littoral macrophyte communities, which im- pairs ecological potential in terms of the EU Water Framework Directive. The aim of our study was to reveal controlling factors for the growth of lit- toral macrophytes in a storage reservoir with fluctuating water level (Lipno Reservoir, Czech Republic). Macrophytes occurred in this reservoir only in the eulittoral zone *i.e.*, the shoreline region between the highest and the lowest seasonal water levels. Three eulittoral sub-zones could be distin- guished: the upper eulittoral with a stable community of perennial species with high cover, the middle eulittoral with relatively high richness of emer- gent and amphibious species present at low cover values, and the lower eulittoral devoid of permanent vegetation. Cover and species composi- tion in particular sub-zones were primarily influenced by the duration and timing of flooding, followed by nutrient limitation and strongly reducing conditions in the flooded organic sediment. Our results stress the ecolog- ical importance of eulittoral zone in reservoirs with fluctuating water levels where macrophyte growth can be supported by targeted management of water level, thus helping reservoir managers in improving the ecological potential of this type of water bodies.

Key-words: ecophases, eulittoral, European Water Framework Directive, littoral macrophytes, water level fluctuation

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Paper III

Krolová M. and Hejzlar J. (*manuscript in preparation*). Protection and support of littoral macrophyte stands by breakwaters on differently exposed shores of Lipno Reservoir.

Protection and support of littoral macrophyte stands by breakwaters on differently exposed shores of Lipno Reservoir

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Abstract

In reservoirs with high water level fluctuation, littoral macrophyte stands are often absent on the erosion-exposed shores. The poorly developed aquatic ecosystem at these sites/habitats indicates low ecological potential in sense of the EU Water Framework Directive. The aim of this study was to (1) describe the littoral macrophyte vegetation and their habitats on differently erosion-exposed shores of Lipno Reservoir, (2) assess factors that impair the vegetation development, and (3) verify positive effect of simple wooden breakwaters on this vegetation. Three breakwaters were installed in the eulittoral zone with homogeneous morphology but different fetch length. Changes in littoral macrophyte vegetation under breakwater treatment were evaluated in 2006–2011. Species composition, distribution and cover as well as water level fluctuation and sediment structure were assessed at the breakwater- and control-sites. The results showed that simple breakwaters can be effective only if basic requirements for the growth of littoral macrophytes are met, i.e. the presence of nutrients in substrate and sufficient light without shading by trees. This type of breakwaters was not effective in heavily erosion-exposed areas with largely degraded substrate. In such sites, it is necessary to consider whether the protection by more complicated breakwaters that can prevent losses of fine particles from the substrate together with addition of nutrient-rich substrate and planting macrophytes would be feasible.

Keywords *Breakwater structure · Shoreline erosion · Littoral vegetation · Water level fluctuation · Wave activity*

Introduction

The presence of well-developed littoral vegetation influences positively the aquatic ecosystem and water quality (Carpenter and Londge 1986, Just et al. 2003, Moss 2008). Macrophytes as primary producers supply food to the first consumers in trophic chains (Gross et al. 2001), provide habitats and refuges for periphyton, zooplankton, other invertebrate species, and vertebrates, such as fish (Balon 1975, Aarts and Nienhuis 2003) and frogs (Strayer and Findlay 2010, Bornette and Puijalon 2011). They play an important role in biochemical cycles, e.g. by storing nutrients in their biomass and influencing food webs of the aquatic ecosystem (Jeppesen et al. 1998).

Man-made lakes are used for different purposes, such as hydropower, water storage, flow augmentation, irrigation, flood protection, fish production, and recreation. Many of these uses may generate water level fluctuations, shift the transition zone between land and water, and accelerate erosive processes along the shoreline. Erosion-exposed areas of water bodies have usually high slope of shores with a large fetch length (Moss 2008, Krolová et al. 2012). Growth of littoral macrophytes and vegetation development at these sites is prevented by unfavourable conditions induced by wave action (Weisner 1987, Weisner et al. 1997), frost and ice phenomena (Nilsson 1981, Björk 1994), bottom degradation (Madsen et al. 2006, Madsen et al. 1996, Nordstrom and Jackson 2012) sediment resuspension or reduced water transparency (Kalff 2002).

To mitigate erosive processes along the shoreline, anti-erosion barriers (breakwaters) from wooden structures, large stones (McComas 2003) or planted trees (Smith et al. 1986, Šlezingr 2007, Míča and Šlezingr 2008) have been used. These measures have usually little supporting effect to littoral macrophyte vegetation even if erosion was diminished because of persisting poor nutrition conditions due to the degraded substrate at the erosion-damaged shores. For restoration of macrophyte stands at such sites, transplanting of native macrophytes together with nature sediment (Jansen 1993, Ostendorp et al. 1995, Hermann et al. 1993) or addition of nutrient-sufficient substrate (Iseli 1993, Zhen 2002) was often needed after the shores had been protected against erosion.

The aim of this study was to investigate factors that control littoral vegetation development on erosion-exposed sites of the shore of a reservoir with fluctuating water level and to test if simple woody breakwaters can be effective in protection of the shore against erosion and under which conditions they can support littoral macrophyte vegetation development. In erosion-exposed areas of water bodies, the breakwaters were supposed to reduce wave activity and consequently support growth and reproduction of macrophytes.

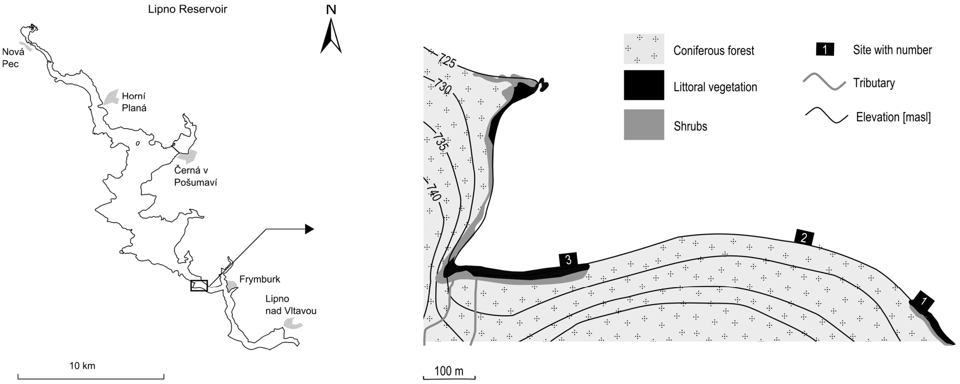

Fig. 1- Situation drawings of Lipno Reservoir and study sites.

Methods

Study area

Lipno Reservoir (Fig. 1) is a large dam impoundment situated on the upper reaches of the Vltava River in the foothills of the Šumava Mountains (coordinates of dam: 48°38'00"N−14°14'15"E; surface area: 48 km^2; volume: 306 mil. m^3; mean water residence time: 0.6 yr; maximum water level: 725.6 masl). The reservoir was built as the uppermost part of the Vltava cascade of hydropower reservoirs and was first filled in 1960. The major reservoir´s purposes include hydropower, flow augmentation, and flood control but the reservoir is also largely used for recreation and sport fishing. The reservoir is operated within an annual cycle of filling and emptying. The maximum reservoir pool is in the spring; during the winter period, the pool is intentionally decreased to increase the flood control capacity before the snow melt; in the summer and autumn months the water level depends on flow conditions: a high water level almost without fluctuations occurs in years of high flow conditions but large drops in water level (up to >3 m) are common in years of subnormal flow (Fig. 2).

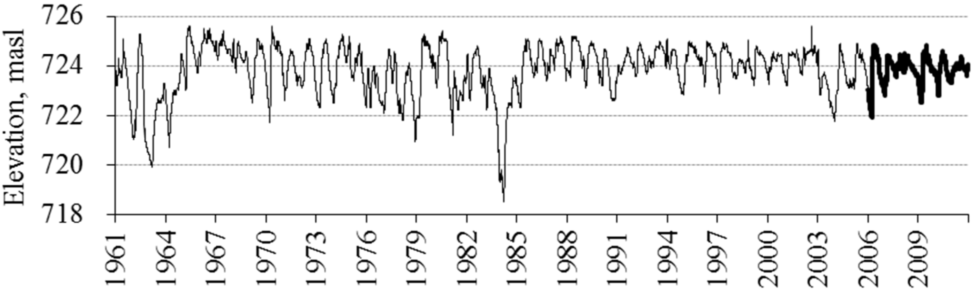

Fig. 2. Water level fluctuation in Lipno Reservoir during 1961−2011. Period 2005−2011 is marked with thick line to show period of breakwater installation. (Data of the Vltava River Basin Authorities, State Enterprise).

In Lipno Reservoir, littoral macrophytes occur only in the eulittoral that is delimited by the range of water level fluctuations and has characteristic macrophytes zonation. The shore protected against erosion contains of 3 zones: (i) *upper eulittoral* in range of 724.3−725.6 masl (flooded during <20% of time during 2005−2011) that hosts dense hydrophilic vegetation of grasses and *Carex*; (ii) *middle eulittoral* in range of 723.9−724.3 masl (flooded 25−50% of time), with a low cover of a community of perennial and annual emerged species, amphibious species and bare bottom species; (iii) *lower eulittoral* in range of 723.5−723.9 masl (flooded 50−75% of time), with sporadic occurrence of bare bottom macrophyte species (Krolová et al. *in press*). This zonation of macrophytes exists also on the erosion-exposed shores, but the dense vegetation of the upper eulittoral recede to the uppermost margin of the reservoir (725.6 masl) and the communities of the middle and lower eulittoral are much rarer, species-poorer and covering smaller area (Krolová et al. 2012, Krolová et al. *in press*).

Table 1. Morphology characteristics of the study sites: geographic coordinates (WGS84; N, latitude; E, longitude); elevation; fetch length of wind action; height of erosion step (HES); shore slope; areas of breakwater protected and control areas.

Site	Coordinates		Elevation [masl]		Fetch length [km]	HES [cm]	Slope [°]	Break water area [m^2]	Control area [m^2]
	N	E	min	max					
1	48°39'27"	14°08'37"	724.2	724.5	2.5	10	4.4	54	50
2	48°39'31"	14°08'26"	723.9	724.4	8.5	30	5.7	53	69
3	48°39'29"	14°08'04"	723.6	724.0	1.0	5	4.6	57	54

Breakwaters

Breakwaters were installed along the erosion-exposed shore of Lipno Reservoir nearby Frýdava village during 2006–2011 in three locations with similar morphology but largely differing in fetch length and hence differently exposed to erosion and with different conditions for littoral vegetation development (Fig. 1, Table 1). The breakwaters were installed within the eulittoral but at different elevations according to the expected highest potential for protection and support of littoral vegetation (elevations at Sites 1, 2, and 3 corresponded to the upper, middle, and lower-to-middle eulittoral, respectively; cf. Table 1). The construction of breakwaters was from wooden poles (diameter 10 cm, length 150 cm) that were closely spaced (distances 10 cm) and fixed in the bottom. The final length (ca 15 m) and shape of each breakwater was inferred from the site-specific activity of waves. The construction of breakwater at Site 1 was modified by adding a 30-cm stripe of non-woven geotextile in October 2009 in order to stop continued losses of fine particles from the substrate. Two monitoring areas were located and marked with fixed points on each site − a breakwater protected area behind the breakwater and a control area of a similar size and vegetation cover next to each breakwater protected area.

Characterisation of littoral vegetation

Littoral macrophytes vegetation was examined in autumn at the beginning and the end of the study period 2006–2011. Species composition, plant cover of individual species and total vegetation cover were quantified at each monitoring area and, in addition, qualitative descriptions of the vegetation above and below the breakwater area were done. The plant cover of individual species was determined using the Braun-Blanquet combined abundance-dominance scales (Dierschke 1994) but extended in category 2 to subcategories 2a and 2b: r (rare), + (cover negligible), 1 (less than 5%), 2a (5–15%), 2b (15–25%), 3 (25–50%), 4 (50–75%), 5 (75–100%). Nomenclatures of vascular plants were unified according to Kubát et al. (2002).

Substrate structure

Five samples of substrate (0.5 l) were taken from the surface (0 to 10 cm) layer of the bottom in each breakwater protected and control area.

Sampling and samples analysis were performed in 2006 and 2011. Substrate particle size, determined by dry sieve and wet sedimentation methods (Brady and Weil 2002), was divided into three categories: gravel (>2 mm; dry sieve); sand (0.06–2 mm; sedimentation); silt and clay (<0.06 mm; sedimentation).

Statistics analysis

Changes in selected characteristics (substrate particle size distribution, vegetation cover values in 1-m^2 squares of the monitoring areas, flooding regime) of the breakwater protected and control areas on each site between 2006 (before the installation of breakwaters) and 2011 (shore protected by breakwaters for five years) were tested by repeated measures ANOVA. The data on the substrate particle size distribution and the vegetation cover were logarithmically transformed to ensure normality. The analyses were performed in STATISTICA 10.0.

Results

Effects of breakwaters on littoral vegetation

In general, littoral macrophyte vegetation on the studied sites consisted of six species. Quantitative changes in the vegetation characteristics prior (autumn 2006) and after (autumn 2011) installations of breakwaters are shown in Table 2 and Fig. 3.

Site 1

In 2006 (prior installation of breakwater), a dense cover of *Phalaris arundinacea* and *Carex acuta* with *Salix* sp. bushes consisting of young individuals only was present above elevation 724.7 masl. In the upper eulittoral zone, where the breakwater and control monitoring areas were located, we observed markedly eroded substrate and low cover of macrophyte vegetation formed from clusters of *Phalaris arundinacea* and solitary seedlings of *Salix* sp. and *Taraxacum* sp. (Table 2, Fig. 3). A zone of a lower cover of *Eleocharis acicularis* was present below the breakwater in the middle eulittoral.

In 2011, we observed a significant (F = 4.3, df = 1, p = 0.045) increase in total area of vegetation in the breakwater protected area, which was mainly caused by an expansion of Phalaris arundinacea (Table 1, Fig. 3). We also recorded an increase in species number, when two species, Carex acuta and Equisetum fluviatile, emerged in low cover yet. The zone of Eleocharis acicularis below the breakwater was not recorded.

The character of the littoral vegetation, their areas and cover were not significantly changed in the control area in 2011. Similar to the breakwater protected area, species number increased, when a small plant stand of *Carex acuta* appeared in 2011 (Fig 3).

Site 2

The littoral macrophyte vegetation was sparse at this site both in the middle eulittoral where the breakwater protected and control areas were situated and also in the upper eulittoral, apparently in connection with the shading by a ca 20-m high forest stand on the shore that was composed of *Picea abies*, *Betula pendula*, *Alnus gluttinosa*, and *Salix* sp. Trees and shrubs of this forest stand were rooted above the erosion step (724.9−725.20 masl) and their branches overhung above the eulittoral zone. In 2006, the characteristics of littoral macrophyte vegetation were the same both in the breakwater protected and control area (Table 2, Fig. 3).

In 2011, we observed only tiny, insignificant changes in the total areas and density of cover of littoral macrophyte vegetation or emerged species both in the breakwater protected and control areas. An increase of species number occurred in the breakwater protected area as *Eleocharis acicularis* established a narrow (ca 10-cm wide) and thin strip across the study area parallel to the elevation contour of 724.3 masl (Table 2, Fig. 3).

Site 3

In 2006, the macrophyte vegetation in the breakwater protected and control areas (that were situated into the middle and lower eulittoral at this site) were created by clusters of *Phalaris arundinacea* at their upper margin and by *Eleocharis acicularis* at lower elevations (Table 2, Fig. 3). The upper eulittoral above the study areas was grown by a dense community of dominant species *Phalaris arundinacea* and *Carex acuta* and with willow bushes *Salix* sp. above the elevation of 724.2 masl.

In 2011, the character of littoral macrophyte vegetation changed markedly in parallel both in the breakwater protected and control areas. The cover of emergent macrophyte species represented by *Phalaris arundinacea* significantly increased (F = 12.36, df = 1, p = 0.0016; Fig. 3) in contrary to *Eleocharis acicularis (*amphibious species) that did not change. Interestingly, species number decreased as *Carex acuta* disappeared from both study areas.

Flooding and water level fluctuation

The flooding regime at the three sites was different (F = 173, df = 6, p <0.0001) as a result of their location in different elevations (Table 1, Fig. 4). Comparing the regime among the study sites it is evident that flooding periods prolonged from Site1 to Site 3. All sites were flooded at least in spring.

Table 2. Macrophytes at localities of breakwaters and controls area between 2006 and 2011. Legend: B – breakwater protected area; C – control area; Group – functional group according to habitat preference (T – hydrophilic terrestrial, E – emergent, A – amphibious, Sh – shrub).

		Site 1				Site 2				Site 3			
		B		C		B		C		B		C	
Year		2006	2011	2006	2011	2006	2011	2006	2011	2006	2011	2006	2011
Total area of littoral vegetation [m^2]		16	23	4	2	0.5	0.02	0.5	0.02	57	57	54	54
Area of emergent species [m^2]		16	23	4	0.2	0.5	0.02	0.5	0.02	7	19	11	26
Total cover of littoral vegetation [%]		35	60	30	30	3	5	3	1	45	60	45	55
Cover of emergent species [%]		25	50	30	30	3	3	3	1	30	40	35	35
Number of species		3	5	2	3	1	2	1	1	3	3	2	2
Species	Group	Cover of species by Braun-Blanquet scale											
Carex acuta L.	E	–	1	–	1	–	–	–	–	1	–	2a	–
Eleocharis acicularis	A	–	–	–	–	–	1	–	–	2b	2b	2a	2a
Equisetum fluviatile L.	E	–	+	–	–	–	–	–	–	–	–	–	–
Phalaris arundinacea (L.) Roth.	E	2a	2b	2a	2a	1	1	1	1	2b	3	2b	3
Salix sp.	Sh	+	+	+	+	–	–	–	–	–	–	–	–
Taraxacum sp.	T	1	1	–	–	–	–	–	–	–	–	–	–

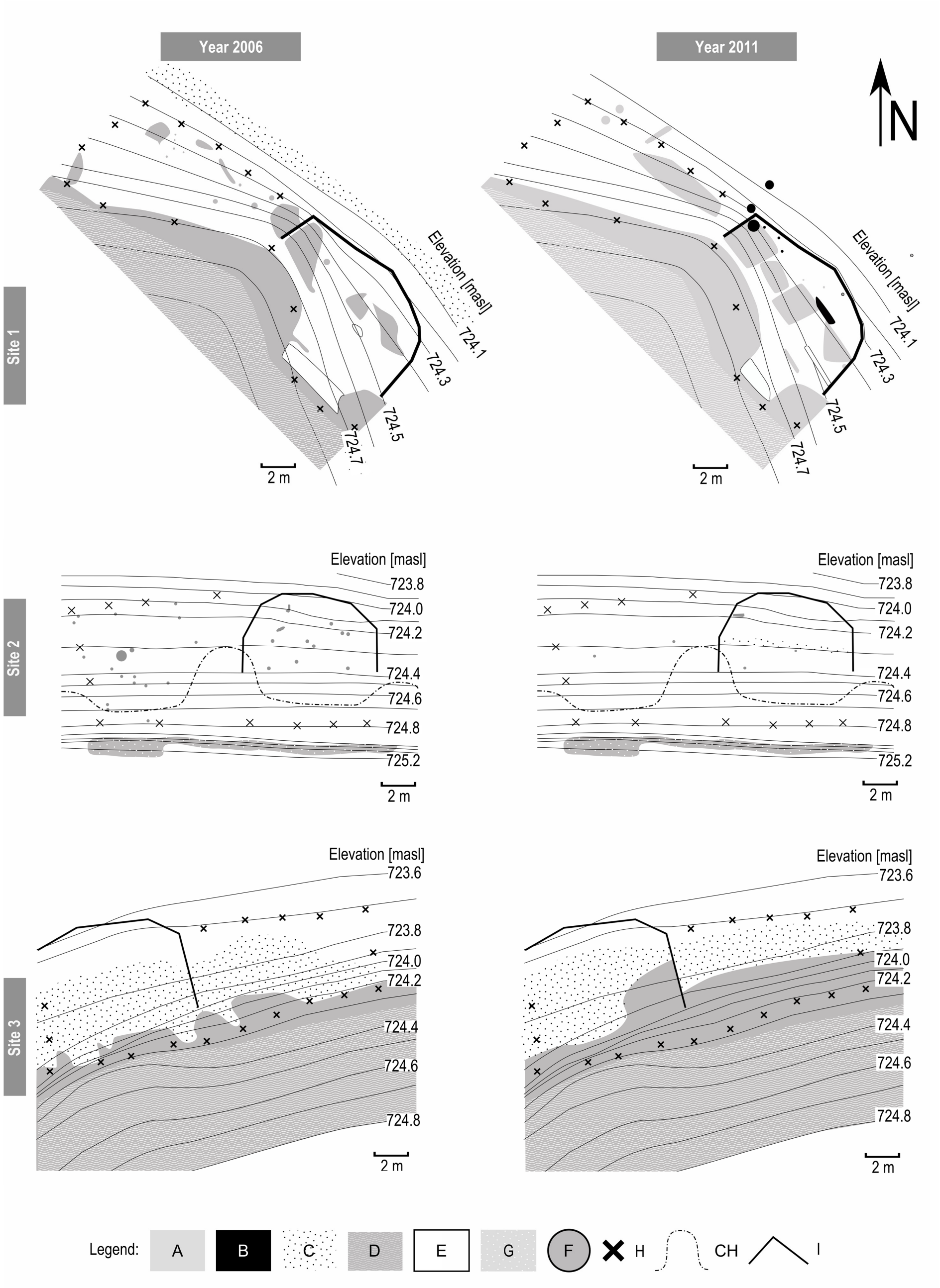

Fig. 3. Maps of littoral vegetation at study sites in 2006 and 2011. Legend: A – *Phalaris arundinacea*, B – *Carex acuta*, C – *Eleocharis acicularis*, D – *Phalaris arundinacea*, *Carex acuta* and *Salix*.sp E – *Taxacum* sp., F – *Equisetum fluviatile*, G – *Phalaris arundinace* and terestrial species, H – control point of monitored area, CH – shading of locality, I – breakwaters.

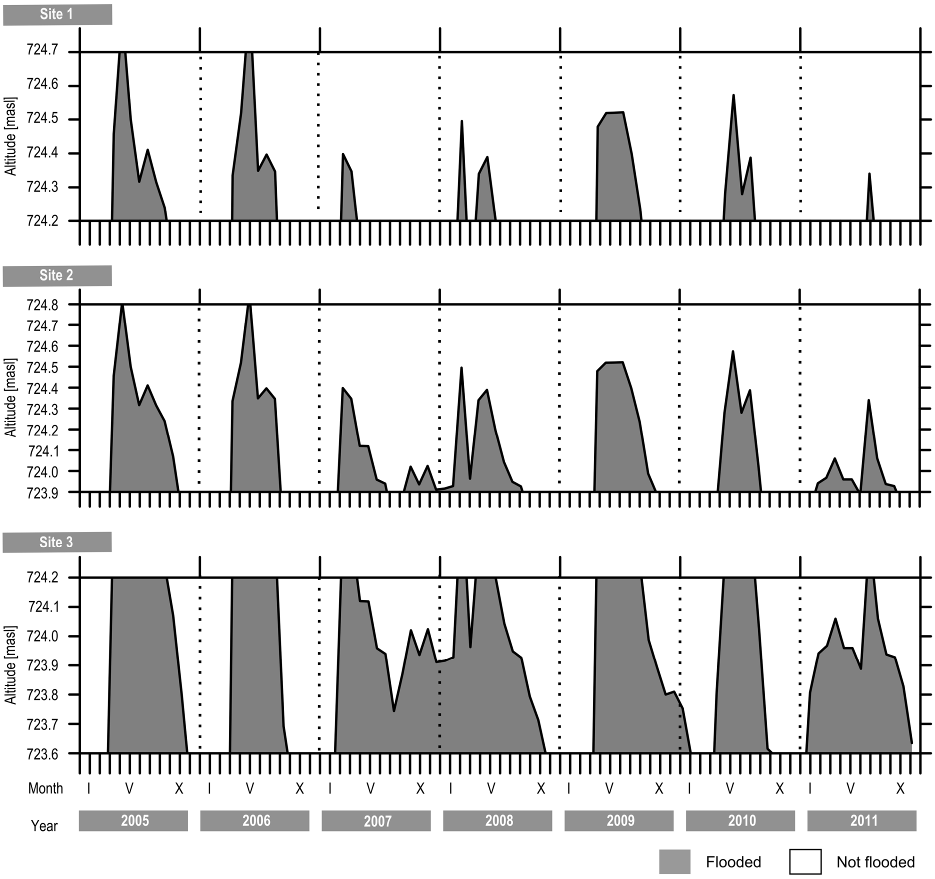

Fig. 4. Water level fluctuations at study sites during 2005–2011. Daily data of water level in Lipno Reservoir were provided by the Vltava River Basin Authorities, State Enterprise.

Character of substrate

The results of the particle size analysis of substrate samples from the study sites are in Fig. 4. The substrate at Sites 1 and 2 was heavily degraded as indicated by the almost missing silt and clay fraction (<0.06 mm) and the predominance of the gravel and sand fractions. The sand fraction was largest also at Site 3 but the substrate here contained also ca 15% of silt and clay fraction. A fraction of sand (0.06–2 mm) was accumulated (F = 12.308, df = 1, p = 0.004) at the locality No 1 protected by a breakwater during the observation. No significant changes in substrate structure occurred when protected by breakwater.

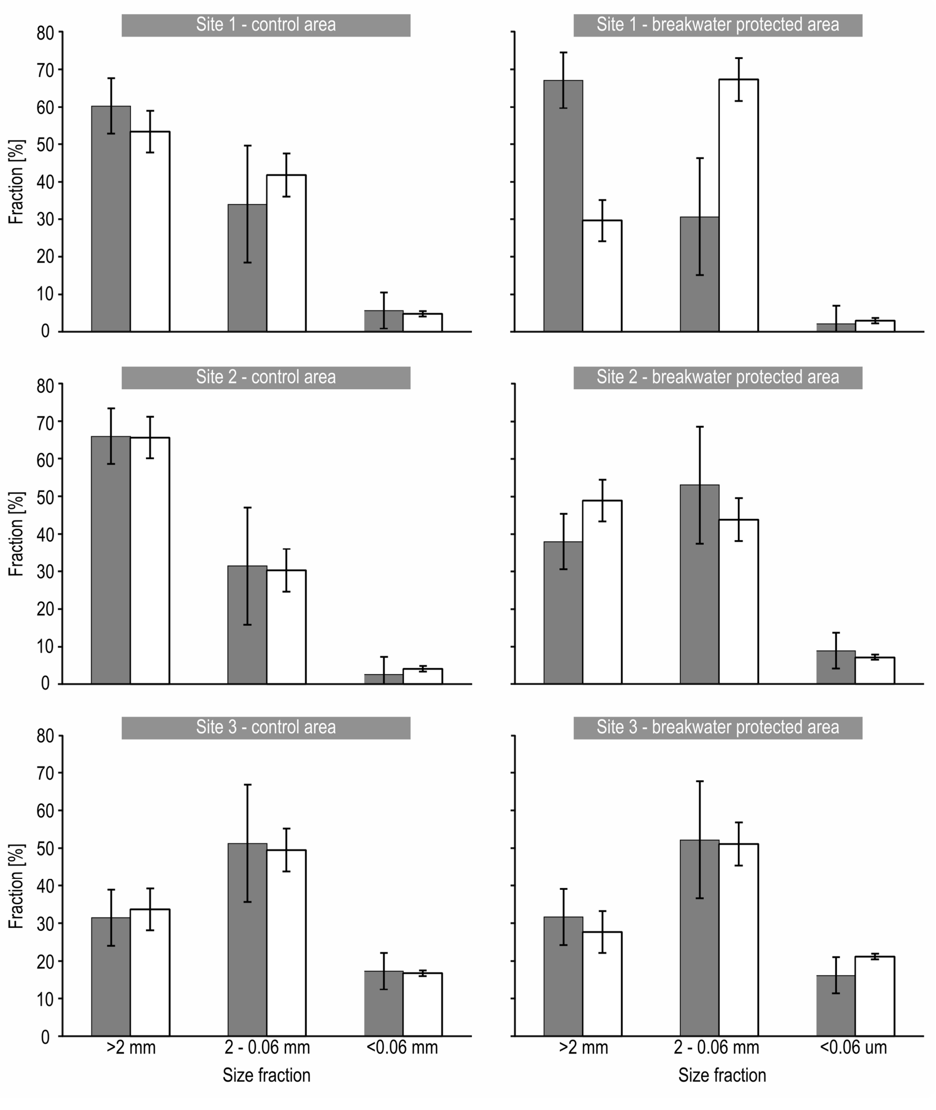

Fig. 5. Comparison of particle size fractions in the substrate at study sites.

The ice phenomena participated at erosion degradation of the substrate as wave activities. An example of such an event was observed in the lower zone at the locality No 1 in the spring of 2009 (Fig. 6). The preceding winter period was relatively dry and cold, with a 2-month period of continuous frosts (from the end of December till the beginning of March). The water level in the reservoir was gradually lowered (by ca 2 m) until the snow and ice melting in early April. The soil that froze during the drawdown became unstable in the following melt period and an erosion furrow approximately 1.5–2 m wide, 30 cm deep and at least 1 km long was formed parallel with the shoreline.

Fig. 6. Bottom damage after ice melt during a drop in water level in the eulittoral zone of Lipno Reservoir near Site 1 in spring 2009.

Discussion

Littoral vegetation at study sites

The development of macrophytes at the study sites corresponded mainly to a gradient of erosion incidence that was largest at Site 2, mean at Site 2, and smallest at Site 3 and was also influenced by the shading that was marked at Site 2. These factors were reflected in the zonation of macrophytes that has been formed on the shores of Lipno Reservoir due to water level fluctuation. The typical zonation of macrophytes with three zones in the eulittoral (Krolová et al. *in press*) was developed only at the least erosion exposed Site 3. A strong erosion hindered growth of littoral vegetation at Sites 1 and 2. At Site 1, the zone with emergent species (*Phalaris arundinacea*, *Carex acuta*) and shrubs (*Salix* sp.) typical for the upper eulittoral was shifted by 0.5 m up compared to the typical zonation (above the erosion step at elevations 724.7−724.8 masl) and littoral macrophyte vegetation was almost absent at the elevations of middle and lower eulittoral subzone. At Site2, the erosion step was even higher at elevation 724.9−725.2 masl and littoral vegetation of upper eulittoral subzone was not present, apparently due to shading by trees and shrubs (Fig. 3; Lellák and Kubíček 1991).

The combination of two factors, namely water level fluctuation and wave activity, leads to erosion and losses of fine particles from the substrate in the eulittoral and it supports the occurrence of macrophytes that are adapted to these conditions (periodical flooding and poor nutrient conditions in the substrate). The emergent species of *Phalaris arundinacea* was typical for this zone at elevations ca 723.8−725.6 masl. This species doesn't spread into lower elevations because it is not able to survive a long-time flooding (Rice and Pinkerton 1993, Krolová et al. *in press*). *P. arundinacea* is also known for its resistance in habitats that are highly eroded, for example, due to the mechanical effects of a river flow (Grime et al. 1988).

Another widespread species at the monitored sites was *Eleocharis acicularis* that was frequently present down to elevation ca 723.4 masl at the erosion exposed shore of Lipno Reservoir (Krolová et al. 2010). This species is resistant to water level fluctuations, undiscerning to the quality of substrate and has a very good to regeneration ability after damage (Duras et al. 2007). This species is typical for reservoirs with water level fluctuation and was also observed for example in reservoirs Lučina, Žlutice, Klíčava, Karhov (Duras et al. 2007), and Nýrsko (Hejzlar et al. 2005, Štěrba 2006).

Efficiency of breakwaters

The breakwaters efficiency in terms of recovery of degraded substrate and support of macrophyte growth was not high. Some effect could be recognised only at Site 1. Our assumption that the amendment of the breakwater with a stipe of geotextile will increase retention of fine particles and thus increase nutrient content in the substrate was not verified; the results of substrate analysis showed (Fig. 5) that the content of nutrient-rich silt and clay particles <0.06 mm (Brady and Weil 2002) remained unchanged and the littoral vegetation consisted of species that have low demand for nutrients. We ascribe the significant increase in total vegetation cover mainly to the mechanical protection against the wave activity (Bornette and Puijalon 2011) in conjunction with less flooding of the area in recent years (Fig. 4). It can be assumed that if the breakwater was supplemented by substrate with nutrients, littoral vegetation would spread more, as in the cases described in other studies (e.g., Iseli 1993, Ostendorp et al. 1995, Zhen 2002).

The low efficiency of the breakwater at Site 2 can be explained mainly by the heavily degraded substrate due to the strong erosion activity of waves and water level fluctuation (Björk et al. 1972, Coops and Hosper 2002, Vilmundardóttir et al. 2010). The absence of macrophytes was influenced by both nutrient limitation and tree shading of the locality. The presence of *Eleocharis acicularis* should be considered most likely as an episodic event. The low cover in the line (parallel to the water level) suggests that this species might be carried from other nearby localities shortly before the survey.

Site 3 was covered by littoral macrophyte vegetation already at the start of the study, apparently because this shore is relatively well protected against the activity of waves (with the low fetch length; see Table 1 and Fig. 1). Another favourable characteristic of this site in terms of the growth of macrophytes is its location in a valley and the fact that the soil is moistened by seepage of groundwater at many sites. The simple breakwater does not bring a great benefit in this area because macrophytes are not exposed by a strong wave activity but their presence is probably predominantly regulated by water level fluctuations, flooding and drying.

Erosion, shading and suitable placement of breakwaters

The measured results show that the development of littoral vegetation is influenced by a combination of factors and their interactions. It is obvious that erosion is the main limiting factor for the development of littoral macrophytes at Sites 1 and 2 because the substrate there does not contain fine particles rich in nutrients (Fig. 5) that are necessary for the development of macrophytes (Madsen et al. 1996, van Geest et al. 2003, Furey et al. 2004). Erosion and erosion degradation of substrate are primarily dependent on the exposure of a locality (the fetch length and the direction of wind; Vilmundardóttir et al. (2010)). The result of the exposition of a locality is the extent of erosion zone at the shores that is related to the magnitude of generated waves. For example, the calculated heights of waves at Sites 1, 2 and 3 according to ČSN 75 0255 (1988) at wind speed 20 m s^{-1} (the occurrence of such wind speed repeats every 10 years according to the 1994−2011 data set from the nearby weather station of the Czech Hydrometeorological Institute at Černá v Pošumaví) are 0.9, 1.5 and 0.8 m, while they are 0.4, 0.6 and 0.2 m at wind speed 10 m s^{-1} (with an average occurrence of 2 days per year), and 0.2, 0.3 and 0.1 m at wind speed 5 m s^{-1} (with an average occurrence of ca 30 days per year). The differences between the calculated wave heights correspond well with the position of erosion step at each locality, e.g., the erosion step is by 0.3 m higher at the most erosion exposed Site 2 than in less exposed Site 1.

Water level fluctuations are another important factor in the erosion of shores (Björk et al. 1972, Coops and Hosper 2002). The erosion of shores is a long-term process and results from the entire reservoir history. It is evident from Fig. 2 that from the 1960s to 1980s the reservoir was exposed to even higher water level fluctuations than in the past decades and also the seasonal maximum of water level was higher. Hence, the erosion of shoreline apparently reached higher elevation at this period and the current state of erosion is its consequence yet.

The construction of simple breakwaters has no meaning for conditions with a combination of multiple unsuitable factors, e.g., an exposure of locality to a large fetch length together with shading by trees and shrubs (like at Site 2). In such case, the support of the development of littoral vegetation is very difficult. Conversely, localities that contain eroded substrate but that are not highly exposed to erosion, have good light conditions, and also developed littoral vegetation is present in the upper eulittoral (like at Site 1) can have a potential for the successful support of littoral macrophyte vegetation by using simple erosion protection measures. However, breakwaters should be always designed to prevent the washing out of fine particles from the substrate, like was our pile breakwater amended by geotextile (at Site 1).

The correct location of breakwaters at suitable elevation in relation to the range of water level fluctuations in reservoir is by our opinion of a great importance. The development of seasonally flooded vegetation of the middle eulittoral is most valuable for the aquatic ecosystem (Carpenter and Lodge 1986, Krolová et al. *in press*) and therefore the protection and support of macrophytes in this zone should be preferred. This zone is flooded in Lipno Reservoir with frequency 20–50% of time. As the flood line occurs very often within this zone, the probability of heavy erosion events due to strong winds that occur with low frequencies but have critical consequences for shore erosion is largely increased. The breakwater in the middle eulittoral can also protect the upper eulittoral. On the other hand, it would be not very sensible to locate breakwaters in the lower eulittoral, mainly because the growth of macrophytes here does not primarily respond to erosion but to water level fluctuations.

Conclusions

The development of littoral macrophytes at the erosion exposed shores in Lipno Reservoir is limited due to erosive effects of wave activity and ice phenomena that interact in combination with water level fluctuation caused by the reservoir management.

Mechanical protection of macrophytes in the eulittoral zone by a simple breakwater can be effective at locations where basic conditions for the development of littoral vegetation are met, such as the presence substrate with sufficient nutrient contents, good light conditions without shading (for example by trees and shrubs), and a correct locating the breakwater within the eulittoral zone (especially in the middle eulittoral that has the greatest significance for the functions in the aquatic ecosystem).

The use of a simple breakwater in areas highly exposed to wave activity with strongly degraded substrate due to long-lasting erosion and with tree shading is not suitable. In erosion exposed places, it is necessary to consider whether the protection by more advanced breakwaters that can prevent losses of fine particles from the substrate along with the addition of nutrient-rich substrate and planting of macrophytes, would help or if it would be better to leave these exposed areas without littoral vegetation and focus only on mechanical protection of shores.

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