Cladoceran stratigraphy in two shallow brackish lakes with special reference to changes in salinity, macrophyte abundance and fish predation

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Abstract

Sub-fossils of Cladocera and Foraminifera were used to reconstruct changes since 1870 in the trophic dynamics of two brackish lakes, Glombak and Han Vejle, located in the Vejlerne nature reserve, Denmark, a site of international conservation importance. After creation of the lakes in the mid-1870s following land reclamation, the two lakes have developed quite differently; today Glombak is turbid, while Han Vejle is clear. In both lakes, stratigraphic changes in the assemblages of foraminifers and cladocerans indicate an abrupt shift from marine to brackish conditions at the end of the 19th century, coinciding with land reclamation. However, the composition of the fossil invertebrate assemblages in the 20th century implies differences in the exposure to salinity, in fish predation and in habitat diversity. In Glombak, the cladoceran record suggests relatively saline conditions in the first quarter of the last century and high macrophyte abundance followed by lower salinities and subsequently a major decrease in macrophyte abundance and an increase in fish predation during the past ca. 40 years. By contrast, in Han Vejle low salinity, high abundance of macrophytes and only minor changes in fish predation seem to have prevailed throughout most of the 20th century. The results are consistent with recent contemporary data, the few historical records, as well as with trends in the records of diatoms and macrofossils. This study highlights the potential of using crustacean remains as indicators of long-term changes in the trophic dynamics of brackish lakes.

Introduction

During the past century, many brackish and freshwater shallow temperate lakes throughout Northern Europe have shifted from a clearwater to a turbid state due to an increase in nutrient loading (Moss 1994). However, detailed information on long-term developments, past conditions and biological responses to eutrophication is limited, as most studies of trophic dynamics in brackish systems include only modern day observations, or are based on short-term field enclosure studies. Contemporary studies conducted so far indicate that freshwater and brackish lakes respond differently to changes in nutrient concentrations. In freshwater lakes, lakes remain in a clear state as long as submerged macrophytes are abundant even at high nutrient concentrations due to a number of positive feedback mechanisms, but shift to a turbid state once the plants are lost. In brackish lakes, nutrient enrichment leads to a turbid state even when submerged macrophytes are abundant (Moss 1994; Jeppesen et al. 1997b). A higher predation pressure on cladocerans by planktivorous fish and invertebrates, lack of refuge...
within the vegetation even when plants are abundant (Jeppesen et al. 1994; Søndergaard et al. 2000) and enhanced cladoceran sensitivity to increasing salinities (Aladin 1991; Frey 1993) may explain the limited top-down control of phytoplankton by cladoceran grazers in nutrient rich turbid brackish lakes (Jeppesen et al. 1994, 1997b). However, the trophic dynamics of brackish lakes are far from fully understood.

Substantial differences also exist between brackish and athallassic saline lakes. In brackish lakes, salinity is typically characterised by a homogeneous ionic composition dominated by Na and Cl, whereas salinity in athallassic saline lakes is characterised by a more heterogeneous ionic composition of the major cationic species Na, K, Mg, Ca and the anionic species Cl, SO$_4$, HCO$_3$, CO$_3$ (Frey 1993). As cladocerans exhibit different physiological tolerances to the various ionic components (Aladin 1991; Bos et al. 1996), studies from saline lakes cannot be directly transferred to brackish lakes (Moss 1994).

Given the general lack of long-term records from brackish lakes and the adverse transference of knowledge obtained from long-term studies from saline and freshwater lakes to brackish lakes, application of paleolimnological techniques may provide insight into past ecological responses to environmental changes in brackish lakes. Paleoecological studies in freshwater lakes demonstrate that cladoceran remains are useful indicators for eutrophication-related changes in predation by planktivorous fish (Kitchell and Kitchell 1980; Sanford 1993; Hann et al. 1994; Jeppesen et al. 1996, 2002b, 2003) and for changes in the relative importance of different habitats such as macrophytes, sediments and the pelagic zone (Whiteside 1970; Frey 1986; Hann 1990; Jeppesen et al. 2001; Shumate et al. 2002).

This paper presents the results of a paleolimnological investigation of two Danish artificial brackish lakes, Glombak and Han Vjele. The objective was to elucidate whether cladoceran remains could be used to describe the historical changes in the ecological state of the two lakes, which have evolved simultaneously but along different trajectories, one became turbid (Glombak), while the other (Han Vjele) remained in a clearwater state. Changes in $^{210}$Pb-dated sediment records of the community structures of cladocerans and foraminifers are compared with existing information on changes in land use, salinity and water level. In addition, the changes in cladoceran community structure are compared to diatom habitat information from subfossil assemblages. Emphasis is placed on the differences in past trophic structure and salinity of the two lakes to explain the present distinct states of water transparency.

**Study sites**

The study lakes are located in the Vejlerne nature reserve situated in northwest Jutland, Denmark (Figure 1). The reserve is the largest bird sanctuary in Northern Europe and is recognised internationally in the Ramsar Convention and under the EC Bird Directive as a Special Protection Area. The reserve covers about 6000 ha and includes shallow brackish lakes, tidal meadows and extensive reed beds. The total surface area of lakes comprises approximately 2500 hectares.

Before damming, the reserve area consisted of shallow branches of the Limfjord. In the mid-1870s, farmland was created via land reclamation involving damming and drainage of the area. However, the reclamation failed and finally stopped around 1916, and swamps of reeds, meadows and brackish lakes evolved extensively. In 1965, a new and more effective central sluice system and channels were established, which caused a lowering of the local water table (ca. 10–30 cm) and an increased risk of saltwater intrusion into the eastern part of the reserve (COWI 2000). During the 20th century, nutrient loading has increased as a consequence of more intensive agricultural practices in the surrounding areas (Jakobsen and Sorensen 1993; Hald 1998; COWI 2000).

Glombak (57°3’29”N and 9°6’62”E, 94 ha, mean depth 0.4 m) is situated about 0.5 km from the central sluice and has a local catchment area of 522 ha (Figure 1). However, Glombak receives inlet water from the larger Selbjerg Vjele (446 ha) via the Krap Channel. Selbjerg Vjele has a catchment area of 2,680 ha and is primarily influenced by nutrient loading from agricultural fields (COWI 2000; Jeppesen et al. 2002a). Thus the total catchment area of Glombak is 3202 ha. Until 1965, outlet water of Glombak was discharged into the Limfjord by self-regulating sluices, but since 1965 the central sluice has controlled the outlet. *Phragmites* reed swamps surround Glombak to the north and east, while meadows are found to the west and south.

Han Vjele (57°9’26”N and 9°5’64”E, 36 ha, mean depth 0.5 m) is located approximately 7 km from the central sluice (Figure 1). Originally the lake was part