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Submersed macrophytes as a food source for wintering waterbirds at Lake Constance

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Abstract

We investigated the relationship between Charophytes and herbivorous waterbirds in the littoral zone of Lake Constance by quantifying their seasonal dynamics. The waterfowl extensively consumed Charophyte vegetation in shallower areas (<1 m water depth) at the beginning of the winter season, while deeper regions were only used in late winter. By the end of winter, the waterfowl had almost completely depleted the available Charophyte biomass down to a water depth of approximately 2 m (relative to average mean water level (AML)). Enclosure experiments revealed that senescence processes had a negligible influence on Charophytes biomass loss until early February. Coot, Red-crested Pochard and Pochard are the main avian Chara consumers in winter. Despite their great influence on biomass in winter, their influence on subsequent Charophyte regeneration is probably limited in Lake Constance, since Charophytes as typical pioneer species produce innumerable diaspores forming dense Charophyte meadows at a depth of between 1 and 4 m every year.

Keywords: Submersed macrophytes; Waterfowl; Herbivory; Food resource; Bird migration; Fulica; Netta; Aythya

1. Introduction

Submersed macrophytes constitute a nutritional basis for herbivorous organisms, including invertebrates, fish and birds, in the littoral zone of lakes. While many invertebrates only consume periphyton, several insects, isopods, decapodes, crustaceans and molluscs consume submersed macrophytes (see Lodge, 1991; Lodge et al., 1998 for reviews).

In Lake Constance, for example, the main herbivorous invertebrate, *Acentria ephemerella*, shows exponential population growth during the vegetation period and causes severe damage to submersed macrophyte stands (Gross et al., 2002). Submersed macrophytes also constitute a significant proportion of the diet of fish such as Roach (*Rutilus rutilus*), Rudd (*Scardinius erythrophthalmus*) and Orfe (*Leucisus idus*) (Prejs, 1984). Körner and Dugdale (2003) reported that herbivorous Roach plays an important role in preventing the re-establishment of submersed macrophytes in a shallow lake. Finally, the varying seasonal influence of herbivorous waterbirds on the biomass of submersed macrophytes can be substantial (Anderson and Low, 1976; Santamaria and Rodriguez-Girones, 2002; Søndergaard et al., 1996; Szijj, 1965; van Donk, 1998; van Donk et al., 1994). Waterfowls' herbivory may lead to a reduced biomass the following season (Anderson and Low, 1976). Søndergaard et al. (1996) reported that herbivorous waterfowl can also play a role in preventing re-establishment of submersed macrophytes in a shallow lake, thus keeping it in a macrophyte-free, turbid state.

The influence of herbivores on submersed macrophytes' abundance and species composition in limnic habitats has, in contrast to terrestrial areas, long been considered negligible (Lodge, 1991). However, during the last decades the abundance of many herbivorous waterbirds has greatly increased in North and Central Europe. This applies to the Mute swan (*Cygnus olor*), Pochard (*Aythya ferina*), and Red-crested Pochard (*Netta rufina*), while the abundance of Coot (*Fulica atra*) has remained relatively constant (Rose, 1994). As a consequence, the influence of herbivorous waterbirds on the submersed vegetation in shallow bodies of water is increasing. More recent investigations showed seasonally dependent macrophyte biomass losses caused by Coot (Søndergaard

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et al., 1996; van Donk, 1998; van Donk et al., 1994) and depletion of Potamogeton turions by swans (Santamaria and Rodriguez-Girones, 2002; Nolet, 2004).

At Lake Constance (latitude: 47°39′N, longitude: 9°18′E) increased eutrophication in the early 1960s led to a marked change in submersed macrophytes species composition and abundance (Lang, 1981; Schmieder, 1997, 1998). Following the extinction of several Charophyte species during the 1970s (Lang, 1981; Schmieder, 1998), Red-crested Pochard was largely absent in subsequent years (Schuster et al., 1983). Subsequent re-oligotrophication since the early 1980s led to a steady recovery of Charophytes in Lake Constance. This development was mirrored by Red-crested Pochard numbers. Whereas in the 1950s many thousands of Red-crested Pochard individuals could be counted regularly in lower Lake Constance (Szijj, 1965), these populations had almost vanished by the 1970s and 1980s (Stark et al., 1999). In recent years, aggregations of up to 20 000 individuals have been recorded at Lake Constance, concentrated mainly at the study sites (Bauer et al., 2002).

The objective of our investigation was to quantify the loss of Charophyte biomass in the littoral zone of Lake Constance (Lower Lake) during winter, due to herbivory by Red-crested Pochard and other herbivorous waterfowl. In addition to avian consumption, we investigated the naturally occurring senescence process during winter in order to assess the relative influence of waterbirds on macrophyte biomass. Furthermore, the influence of water depth on consumption was studied.

2. Methods

2.1. Bird counts

Observation teams counted waterfowl using the ‘‘Look-See’’ method (Bibby et al., 2000) at chosen sites on Zeller See on randomly selected days within each 10-day period from October to April. As in international waterbird counts, the observers visited a site and made a count of every waterbird species present (Gilissen et al., 2002). During the daytime each study site was checked for birds with binoculars and telescopes (magnification of 10× and 30×, respectively). Additional nocturnal observations were accomplished using a long-range infrared system (Inframetrics IRTV 445L Lorris).

2.2. Design

For this study we chose two sites on the south shore of Zellersee, lower Lake Constance (total surface area 62 km^2, IGKB, 2004), where up to 10 000 Red-crested Pochard (1.6 ind./ha) wintered in recent years. To investigate the influence of herbivorous waterbirds as well as the senescence process, submersed vegetation was sampled monthly inside and outside of enclosure cages at two depths (1.5 and 2 m AML). Scientific divers set up a total of 56 cages (28 at each water depth) at intervals of 10 m in dense homogenous Charophyte meadows of 100% cover. Samples were also taken at 1 m water depth. However, no cages were placed here, since experience had shown that the water level decreases rapidly in winter (Fig. 1) and danger of wave action displacing cages is high. Enclosure cages were anchored to the ground with approximately 70 cm long pegs. The cages (60 cm in diameter and 70 cm high) were made of wire netting with a mesh size of 5 cm to exclude diving birds from entering, but at the same time to avoid shading effects by algae growing on the mesh during the study period.

2.3. Sample collection and processing

At each sampling scuba divers collected Charophytes from four randomly chosen cages per depth level using a cutting frame (30 cm × 30 cm). The cut Charophyte biomass was transferred quantitatively into perforated plastic bags and given to staff in the accompanying boat. In addition, four plant samples at the same depth levels were taken randomly outside of the cages at distances between 1 and 5 m from the cages in order to avoid potential edge effects of the cages. After sampling the cages were removed. Following centrifugation with a hand centrifuge, fresh weight was determined on board the boat with a spring balance, to record initial variance between the different samples. In the lab, the samples were dried in an incubator at 85 °C for 48 h, and immediately weighed.

On 4 February 2002, it became apparent that Charophyte samples collected in the exclosure cages had a high abundances of macroinvertebrates and small fish. Before the samples were processed further, the fish were classified and returned to the lake. Macroinvertebrates from two samples (one each from 4 and 15 February 2002) were separated in the laboratory, classified, dried and weighed in order to estimate the proportion of macroinvertebrates in the Charophyte samples.

Due to strong north-easterly winds, sampling on 15 February was impaired by extremely turbid water. Some of the exclosure cages could not be relocated and quantitative transfer of the Charophyte samples into the plastic bags was not always possible.

2.4. Statistical analyses

The variance in Charophyte biomass inside and outside the cages at different depths during the study period was analysed with a three-way ANOVA procedure including interactions among the independent variables. Biomass dry weight was set

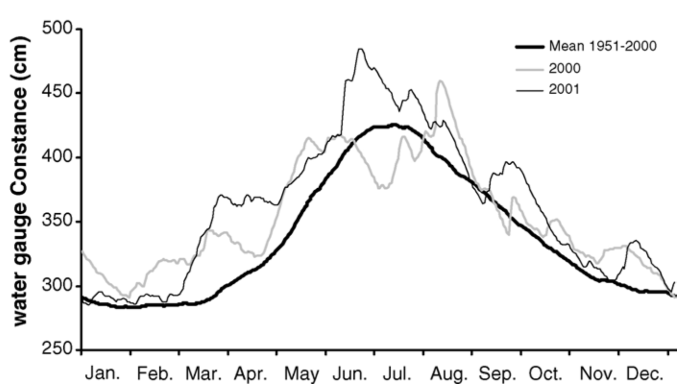

Fig. 1. Annual water level fluctuations at Lake Constance (water gauge Constance) in the years 2000 and 2001 compared to the mean of 1951–2000.

as a dependent variable and month, inside/outside, and depth as independent variables. Analyses were done with S-PLUS (v. 6.0, Mathsoft Inc., Seattle, WA).

3. Results

3.1. Waterbird counts during the study period

A steady increase in waterbirds was noted at the study sites from the beginning of the study period at the end of September 2001 until December (Fig. 2). The herbivore population decreased abruptly after the shallow water zone froze over at the end of December, but soon recovered after the ice had melted. Therefore, in February this resting and feeding area was again used intensively by some 20 000 wintering waterbirds.

The population of omnivorous Coot decreased greatly during the freezing period from December to January. Coot numbers recovered afterwards and reached some 15 000 individuals in February 2002 (Fig. 2a). Populations of Pochard (Fig. 2b) and Tufted duck (*Aythya fuligula*, Fig. 2c) at Zellersee showed the same profile as the Coot, with an increase up until December (maximum 10 000 Tufted ducks and 20 000 Pochards), followed by a decrease during the ice cover. However, February numbers did not reach pre-freezing levels. Night surveys with infrared optics revealed similar bird numbers in the study area; some of these were foraging.

Several aggregations of Red-crested Pochards were present at lower Lake Constance during the whole winter. However, due to disturbances (including sampling) the actual study sites were only visited sporadically, so that the high abundances were only observed once (Fig. 2d). They reached their maximum, totalling about 10 000 individuals, at the shallow Lower Lake in December 2001 (Fig. 2d) and almost disappeared at the beginning of ice cover in late December.

3.2. Changes in Charophyte biomass during the study period

At the beginning of the study in October a homogenous Charophyte meadow of *Chara contraria* and *Chara globularis* covered the littoral area at a water depth between 0.5 and 4 m. Biomass at different depths ranged from 1240 ± 155 (S.D.) g dry weight (DW) m^{-2} at 2 m to 1610 ± 424 g DW m^{-2} at 1.5 m water depth (Fig. 3b). At 1 m water depth, a continuous decrease of Charophyte biomass occurred from 1350 ± 212 g dry weight (DW) m^{-2} on 18 October 2001, down to 0 ± 0 g DW m^{-2} on 15 February 2002 (Fig. 3b). At deeper levels, Charophyte biomass initially increased slightly then decreased continuously from December onwards at a depth of 1.5 m, but only from February 2002 at a depth of 2 m. At 1 m the influence of waterbird consumption was immediately visible despite the comparatively low numbers of birds present (Fig. 2). The decrease in Charophyte biomass at a depth of 1 m in October and November was largely due to the foraging activities of Coots and Pochards. Large aggregations of herbivorous waterbirds, particularly Red-crested Pochard, were recorded at the study sites from the end of November onwards. Their increasing effect on Charophyte biomass became apparent in the increasing difference between the biomass inside and outside the enclosures (Fig. 3).

At a depth of 1.5 m the biomass outside the enclosures decreased continuously (Fig. 3b). Biomass did not decline significantly inside the enclosures (Fig. 3a), but rather increased initially at this water depth up to early February, and subsequently decreased slightly. The samples from 15 February represent outliers due to unfavourable sampling conditions.

At a depth of 2 m, biomass decrease only started after the freezing period. However, by early March the Charophytes were totally depleted. Within the enclosures biomass remained relatively constant at this depth, with the exception of samples

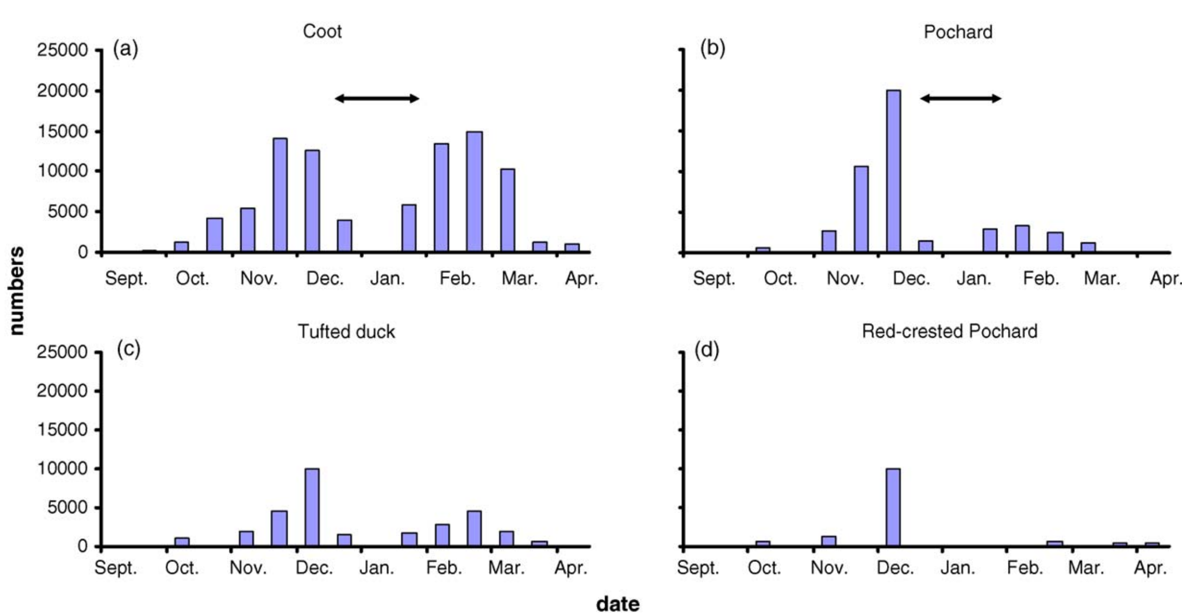

Fig. 2. Population size of Coot (a), Pochard (b), Tufted duck (c), and Red-crested Pochard (d) at Lake Constance (Zeller See) from September 2001 to April 2002, daytime counts. Icecover in December and January is indicated by arrows.

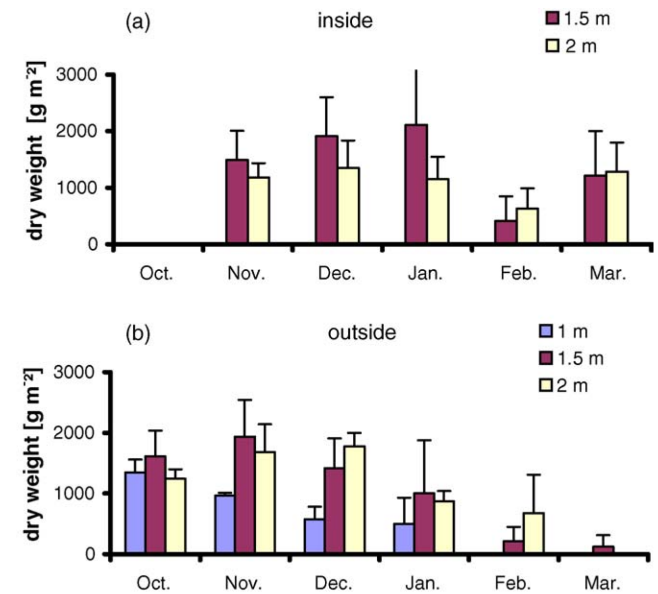

Fig. 3. Temporal changes in Charophyte biomass inside (a) and outside (b) the enclosures at different depth levels (mean values ± S.D. ($n = 4$), depth in relation to mean water level).

taken on 15 February, which were generally extremely low (Fig. 3a). At the end of winter, Charophyte biomass outside the enclosures was totally depleted down to a depth of approximately 2 m.

At all depths Charophyte biomass outside the enclosure cages varied significantly over time, depth and inside/outside of the enclosures (Table 1, data from 15 February not included). Significant interactions between inside/outside and month showed that charophyte biomass development over time was significantly different inside and outside of the enclosures, supporting the assumption of herbivorous consumption by waterfowl. The scuba divers reported that in some areas Charophyte vegetation was completely absent, except inside the enclosures. Significant interaction was also detected between depth and inside/outside, supporting the observation that Charophyte biomass was first consumed in shallow regions before birds grazed in deeper areas of the littoral zone. Interactions between depth and month and between all three variables were not significant.

After the ice cover, large numbers of macroinvertebrates were observed within the samples from 4 and 15 February.

Table 1
Three-way ANOVA table of the three factors: month, depth and inside/outside enclosure cages

	d.f.	Sum of squares	Pr(F)
Month	4	95505.6	<0.001
Depth	1	13190.4	0.011
Inside/outside	1	24086.8	<0.001
Month × depth	4	6044.4	0.537
Month × inside/outside	3	41955.2	<0.001
Depth × inside/outside	1	29992.3	<0.001
Month × depth × inside/outside	3	3414.1	0.621
Residuals	69	132211.1	

Macroinvertebrates accounted for 33% and 28% of the total biomass of 986 and 1035 g DW m^{-2}, respectively. Taxonomical analysis of the macroinvertebrate community showed large proportions of detrivorous *Asselus aquaticus*, indicating that the senescence process proceeded in the enclosure stands from February onwards.

4. Discussion

In this study we demonstrate the close relationship between the seasonal dynamics of Charophytes and herbivorous waterbirds in the littoral zone of lower Lake Constance during the winter period. The available dense Charophyte vegetation covering the littoral zone was completely depleted down to a depth of 2 m. As our enclosure experiment showed, macrophyte senescense had only a negligible influence on the decrease of Charophyte biomass.

As in other studies, herbivory by wintering waterbirds played the major role in macrophyte biomass loss (Kiørboe, 1980; van Donk, 1998), whereas waterfowl herbivory in summer is considered to be rather low (Søndergaard et al., 1996; van Donk, 1998; Mitchel et al., 1994). In particular, Coots have mutually exclusive territories during the nesting period (Glutz von Blotzheim et al., 1973), thus reducing feeding pressure on macrophytes per unit area. In addition, bird densities are much higher during the migration and wintering period due to the presence of Nordic populations. However, even low densities of Coot might prevent re-establishment of macrophytes in a shallow lake, resulting in the lake remaining in a macrophyte-free, turbid state (Søndergaard et al., 1996).

At the beginning of the investigation in October, Charophyte vegetation did not show any evidence of herbivory, such as ripped off branches or disturbed Charopyhte meadow homogeneity. From the end of October onwards, large numbers of Charophyte-feeding Red-crested Pochard appeared in the study area, constituting the main consumers of Charophyte biomass. Schuster et al. (1983) reported that during the eutrophication period Red-crested Pochards abandoned their traditional resting and foraging sites for new sites on lower Lake Constance, exactly corresponding to the remaining Charophyte stands, according to Lang (1981).

In contrast to Red-crested Pochards, maximum numbers of Coot were recorded after the freezing period in January. Since vegetation in the shallowest parts of the littoral zone was already depleted, Coot and Pochard were forced to dive deeper for the remaining Charophyte stands. In February and March the Charophyte biomass, including macroinvertebrate components, was mainly consumed by omnivorous Coots, whereas Red-crested Pochards were virtually absent.

Waterfowl were encountered in the study area both during the day and at night. Unlike other parts of Lake Constance (compare Bauer et al., 1992) this area was not subject to many disturbances during the winter period, thus the waterbirds could also resort to diurnal foraging.

In our study, Charophyte biomass in the littoral zone was only depleted down to a depth of 2 m, whereas Szijj (1965) included diving depths of more than 4 m during the 1960s.

This may have been due to Charophytes being restricted to a smaller area during that time (Lang, 1981; Schmieder, 1998), so that the available biomass had to be used optimally.

However, all littoral areas of the lower Lake are currently covered with dense Charophyte vegetation from 0.5 m down to a water depth of 4–5 m (Schmieder, 1997, 1998). Therefore, enormous food resources are available for Red-crested Pochard and other Charophyte consumers in shallow areas above a depth of 2 m. Presumably because plentiful resources are easily available, the herbivorous waterbirds were not forced to dive for Charophytes below depths of 2 m.

Significant differences in biomass changes at different depths suggest that easily accessible Charophytes (at shallow water levels) are consumed first, before resources at deeper levels are exploited. This behaviour is well suited to falling water levels during the winter season. It is difficult to infer from this study as to what extend the wintering waterbirds can consume the total amount of macrophyte biomass available at the lake. However, it can be assumed that the birds prefer to relocate rather than expend more energy on deeper dives, as long as enough food resources are easily available in shallow areas. Depletion-driven habitat switching was reported by Nolet et al. (2002) in a swan-pondweed-sugar beet field system. However, other factors may affect feeding behaviour, such as state-dependency, predation risk, protein requirements (Nolet et al., 2002) and disturbance (Bauer et al., 1992).

In February, a high proportion of macroinvertebrates was found in the Charophyte samples, most of them detrivores, indicating that the Charophytes senescence process was in fully underway. This indicates that compared to herbivory, senescence is not a factor in Charophytes biomass loss in Lake Constance until February.

Herbivory by waterbirds during the vegetation period, or on bulbs in winter can have a strong influence on the following generation of submersed macrophytes (van Wijk, 1988; Walser, 1995; Nolet, 2004). However, in Lake Constance the influence of wintering waterbirds on the subsequent generation of Charophytes is probably limited, since Charophytes as a typical pioneer species produce innumerable diaspores that are able to germinate rapidly in the following vegetation season (Krause, 1997, p. 49). Mechanisms of overcompensation and grazing optimisation, as suggested by Nolet (2004), can be excluded in this case. Nutritional resources for Charophyte-feeding wintering waterfowl at lower Lake Constance seem to be limited only by the extent of the littoral zone and occasional freezing periods.

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