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Effects of water level management on autumn staging waterbird and macrophyte diversity in three Danish coastal lagoons

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Abstract. Many Danish wetlands frequently experience algae blooms and oxygen deficiencies because of eutrophication caused by enhanced nitrogen and phosphorous levels. As a consequence, wetland managers have focused on improving water quality, but often without considering the suitability of wetlands for waterbirds. In this study, managers improved water quality in two Danish lagoons by opening a floodgate to the sea. We studied the responses of autumn staging waterbirds and submerged vegetation, to resultant higher water replacement rates and water levels. A third lagoon with no change in management was studied for comparisons. Lagoons with rise in water levels experienced declines in bird species diversity, a decline in benthivore species abundances and an increase in herbivore species abundances. Macrophyte biomass increased but seagrass diversity was low due to high salinity. The lagoon with no changes in management control had high and stable waterbird diversity and bird-days spent was increasing during the study period. Explanations for this were diverse typography and low water levels. Furthermore, the macrophyte community was more diverse due to low salinity. In order to improve both water quality and to increase waterbird diversity in the managed lagoons, we suggest water levels should be managed actively during peak migration in autumn. This could secure more shallow-water areas to waders and create better congruence between appropriate water levels and timing of peak bird migration in autumn. The rest of the year the floodgate should be left open in order to secure a high water quality.

Introduction

The diversity and variety of wetland habitats along the 7000 km coastline of Denmark offers ideal foraging opportunities for migrating and wintering waterbirds. Indeed, more than three million waterbirds have been counted during national surveys, and Danish waters are considered to be among the most important staging and wintering areas for waterbirds in the Western Palearctic (Laursen et al. 1997).

During the last century, however, Danish wetlands have suffered from severe loss of habitat (Gyalokay 1987) and increasing pressures from physical development and recreational use (Madsen 1998a). Furthermore, with a population density of 125 persons/km^2 and with 60% of the land area under cultivation, Denmark has one of the more densely populated and intensively cultivated landscapes in Europe, where phosphorous from household sewage and nitrogen and phosphorous from agricultural fertilizers is carried by groundwater and streams or enters directly into lakes and estuaries. As a consequence, many Danish wetlands frequently experience algae blooms and oxygen deficiencies (Andersen et al. 2004). In order to improve water quality, The Action Plan on the Aquatic Environment was adopted in 1987, followed by a second and third plan in 1998 and 2003, respectively (Conley et al. 2002; Ministry of Food, Agriculture and Fisheries 2004). Furthermore, the EU-Water Framework Directive was adopted in 2000, establishing a framework for community action in the field of water policy (European Community 2000). As a consequence, the majority of wetland managers during recent decades have been highly concerned about the water quality of Danish wetlands (Cowiconsult 2000; Jeppesen et al. 2002; Ringkøbing Amt 2003; Andersen et al. 2004).

The action plans have focused on reducing phosphorous and nitrogen runoff to streams, lakes, lagoons and estuaries. In lakes and lagoons, a number of management tools have been applied to improve water quality, such as enhancing water dilution (Cowiconsult 2000; Jeppesen et al. 2002), increased rates of water replacement (Ringkøbing Amt 2003) or increasing salinity in the water (Andersen et al. 2004). The two former approaches normally result in elevated water levels, potentially influencing the amount of food available for non-diving waterbirds (Clausen 2000). Water depth exploited by different species at foraging sites often correlate with neck length (Pöysä 1983) or with culmen and tarsus lengths (Baker 1979). Consequently, in deeper waters, food is only available to larger species (Madsen 1988; Clausen 2000). Furthermore, tools for water quality improvement can have an effect on salinity if used in brackish areas. Submerged aquatic vegetation (SAV) communities change in species composition along a salinity gradient (Verhoeven 1979), as do the feeding potential for herbivorous waterbirds. Plant species preferring fresh or slightly brackish waters (e.g. Charophytes and *Potamogeton* species) is generally high quality food compared to the high salinity tolerant *Ruppia* species (compare van Eerden et al. 1997; Holm 2002).

For managers, it should be possible to optimize wetlands to support a large number of waterbird species, synchronous with a rise in water quality. Because of the interspecific differences in habitat use between waterbird guilds, the management goal should be to provide the greatest diversity of water depth (Colwell and Taft 2000; Isola et al. 2000; Taft et al. 2002) or to syncronize optimal water levels with species' migration phenologies. In addition, it might be possible to control salinity in some of the managed wetlands and thereby the quality and quantity of food resources for herbivorous waterbirds.

In this study, we quantified waterbird community structure during 1994–2002 on three brackish lagoons concurrent with changes in water levels, salinity and macrophyte distribution and biomass. In two areas, managers have improved water quality by enhancing water replacement rates starting in 1998. A third lagoon has experienced no change in management during the study period. We investigate and compare waterbird responses and diversity among areas during autumn. Furthermore, in 1999 we compared plant communities in the three areas and determined foodstocks for herbivorous waterfowl by quantifying macrophyte biomasses. Concurrently, we evaluate the management of the three habitats with reference to autumn staging and wintering waterbirds.

Materials and methods

Definitions of water depths, water levels and feeding depths

The term 'water depth' refers to the depth in the lagoon relative to DNN ('Danish Ordnance Datum', a fixed vertical point). The shallowest parts of the lagoons therefore may have areas lying above DNN $= 0$ and consequently water depths in such areas are expressed as negative values (Figure 1). The term 'water level' refers to the height of the water table relative to DNN, and this will fluctuate depending on precipitation, evaporation, air pressure and wind conditions. The term 'feeding depth' is the combination of the water depth and the fluctuating water level. Thus, if a bird feeds at a patch where the water depth is $+30$ cm and the water level is -12 cm, both relative to DNN, then the feeding depth will be 18 cm.

Study area

The study was carried out on three shallow brackish lagoons: Agger Fjord (3.17 km^2), Thyborøn Fjord (1.94 km^2), and Harboør Fjord (1.95 km^2). These are located on the peninsulas of Agger Tange and Harboør Tange in the western part of Denmark, between the North Sea and the Limfjorden (56°43′ N 8°14′ E) (Figure 1). The lagoons were created in 1949–1957 when establishing new embankments along the peninsulas (Tortzen 1966). The lagoons are designated as Ramsar sites under the Convention of Wetlands of International Importance especially as Waterfowl Habitat (Jensen 1996). Furthermore, they are designated Special Protection Areas under the EU Directive for the Conservation of Wild Birds (Jensen 1996). Since 1996, they have been part of the newly established reserve network in Denmark, which cover important wintering and staging sites (Madsen et al. 1998). Except for the hunting protected embankment, the areas surrounding the lagoons are mainly reed beds and salt marshes, where hunting is allowed from September to December.

On Agger Tange, a floodgate connects Agger Fjord with Limfjorden (Figure 1). The floodgate is permanently closed during summer and autumn, where the water levels are affected primarily by precipitation and evaporation (Holm 2002). During winter and early spring the floodgate is open for run-off from the

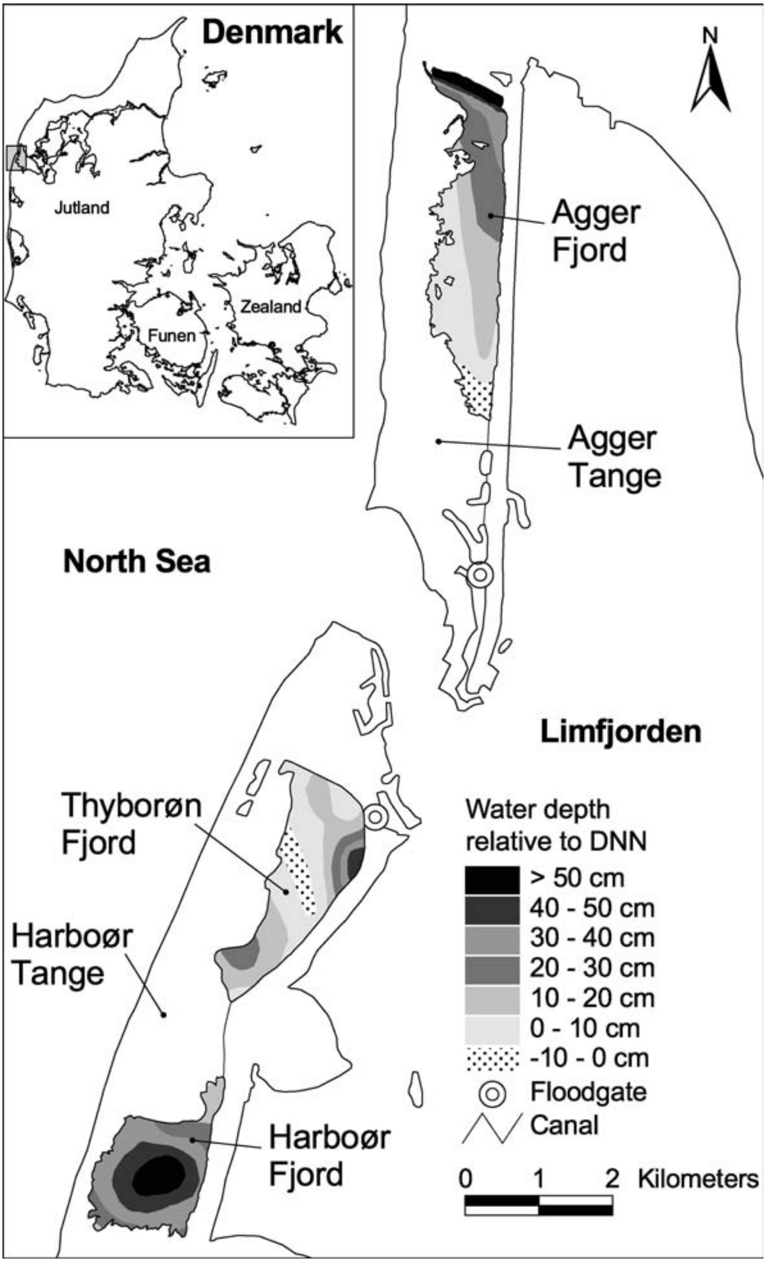

Figure 1. The study area existing of the two peninsulas, Harboør Tange and Agger Tange. The brackish lagoons investigated were Agger Fjord, Thyborøn Fjord and Harboør Fjord. The two canals shown connect Agger Fjord with a floodgate and Harboør Fjord with Thyborøn Fjord. Water depth relative to DNN (Danish Ordnance Datum, a fixed point) is also shown.

lagoon to the sea. The submerged macrophyte community in Agger Fjord is composed of five different species. The two dominant species are bearded stonewort *Chara canescens* and common stonewort *Chara vulgaris*, which are mainly distributed in the parts of the lagoon that do not dry out in the summer. Horned Pondweed *Zannichellia palustris* covers the deepest areas. In shallow areas, Beaked Tasselweed *Ruppia maritima* and Sago Pondweed *Potamogeton pectinatus* dominates. Salinity is below 7.5‰ (Table 2). Ancillary data suggest water levels, salinities and vegetation structure at Agger Fjord were maintained at steady levels throughout the study period.

A canal connects Harboør Fjord to Thyborøn Fjord and a floodgate connects Thyborøn Fjord with Limfjorden (Figure 1). This floodgate was closed until 1998, resulting in low water levels and large dry mudflats with no vegetation at both Thyborøn and Harboør Fjords. Because of very high concentrations of phytoplankton, phosphorous and nitrogen, the local county authorities tested improvements to water quality by permanently opening the floodgate in 1998. The open passage to the sea has resulted in improved water quality at both lagoons, but also in high and fluctuating water levels (Figure 2) (Ringkjøbing Amt 2003).

Throughout the study period there was no vegetation in Thyborøn Fjord, but annual maximum salinity decreased after change in management. The high maximum salinity in 1995 was due to low water replacement and high evaporation (Ringkøbing Amt 2003). On Harboør Fjord, annual maximum salinity

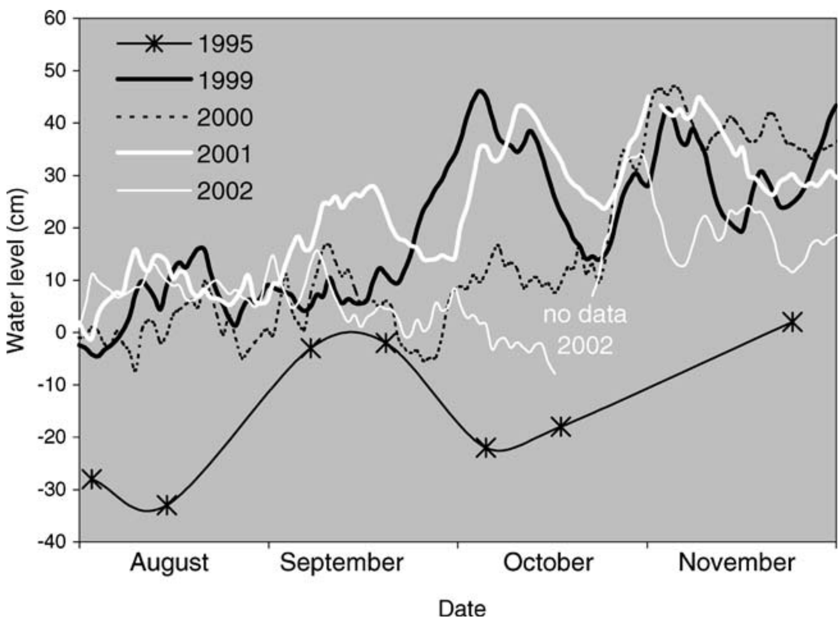

Figure 2. Variation in water levels on Harboør Fjord in 1995 and 1999–2002.

values increased because of influx of seawater after change in management. There were no changes in mean salinities in both lagoons in the study period. Vegetation cover and biomass on Harboør Fjord were low before the floodgate was opened in 1998, due to permanent low water levels and a smaller area covered with water (Ringkøbing Amt 2003; aerial photos from 1994 to 1995). From 1999 onwards, a new steady state emerged with a larger stock of vegetation dominated by Spiral Tasselweed *Ruppia cirrhosa* (Figure 4).

Just like Agger Fjord, new hunting regulations were imposed in the surroundings of Thyborøn and Harboør Fjords in 1996. In contrast to Agger Fjord and many other new reserves (Madsen 1998b; Bregnballe et al. 2004; Clausen et al. 2004) quarry waterbirds have been non-responding, except in 1999 when an experimental reserve resulted in significant increases in numbers of staging Green-winged Teal in Harboør Fjord and common snipe *Gallinago gallinago* on adjacent marshes (Bregnballe et al. 2004).

Monitoring of lagoons

Samples were taken along transect lines 13–14 September 1999, 28–29 October 1999 and 12–13 January 2000. To quantify water depth, macrophyte distribution and biomass, two transects were laid out across Agger Fjord, three across Thyborøn Fjord and four across Harboør Fjord. Lines ran parallel and 500 m apart, and sample stations were 100 m apart along transects. Depending on the water level of each lagoon, transects were walked or sailed, and the predetermined positions of sample stations located to the nearest meter by a Philips AP MK10 DGPS Professional navigator. Water levels in the lagoons relative to DNN were recorded to the nearest cm at least once a week between August and November.

At each sample station, percent vegetation cover was estimated to the nearest 5% in a radius of approximately 5 m, and the water depth was measured to the nearest cm with a folding scale. The SAS/GRAPH G3GRID procedure with spline smoothing (using default settings, SAS Institute Inc. 1990) was subsequently used to interpolate depths in remaining areas of lagoons.

At intervals of 500 m along the transect lines, a sample station was marked and six biomass samples were taken. Each sample was taken using a 15 cm wide circular core-sampler penetrating 20 cm down into the sediment, then transferred to a sieve (1 mm mesh size) where the sediment were washed out and the resulting material was stored in plastic bags. In the laboratory, samples were sorted into species and into live and dead material. For Sago Pondweed, samples were also sorted into above- and below-ground biomass. All samples of live material were dried to constant weight at 70 °C in an oven and weighed. An estimate of the biomass/m^2 of each plant species at each sample station was calculated by multiplying the average dry weight of the six samples with the percentage of the average leaf cover of each plant species on the same sample station. This estimation method is based on the assumptions that (i) plants are distributed uniformly, and (ii) proportional coverage has a linear relationship with biomass (Petersen and Noer 1993; Percival et al. 1996; Therkildsen 2000).

Salinity was measured in two sites on Thyborøn Fjord, two sites on Harboør Fjord and four sites on Agger Fjord when collecting macrophyte samples.

A Mann–Whitney *U*-test was used to compare our readings of water levels and salinities with 1995-measurements made by county authorities. Macrophyte biomass and leaf cover data were normalized using logarithmic and arcsine transformation, respectively (Zar 1984). Changes in vegetation biomasses and leaf coverages between sample dates were subsequently investigated using one- and two-way analysis of variance (ANOVA) (Zar 1984). Tukey's q-test was used as multiple comparison procedure. $p < 0.05$ was considered significant.

Bird counts

Waterbirds, i.e. Anseriformes, Charadriiformes, Gruiformes, Ciconiiformes, Podicipediformes, Gaviiformes and Pelecaniformes, were censused one to two times per month August–November, 1994 to 2002 (Table 1). The three study areas were counted on the same day. The total number of species per year were found and a average for 1994–2002 was calculated. In 1999, waterbirds were counted more frequently at two to five times per month. Numbers of ducks, waders, swans, geese, coots, grebes, cormorants and herons were included in the analysis. Gulls and terns were left out because they primarily used the areas for roosting. Waterbird species were divided into functional (trophic) guilds based on feeding type (Table 1, following Ysebaert et al. 2000). Green-winged Teal *Anas crecca*, Mallard *Anas platyrhynchos*, Pintail *Anas acuta* and Shoveler *Anas clypeata* feeding on seed material and small macrofauna were considered as omnivores. The remaining dabbling duck species, swans, Coot *Fulica atra* and geese were considered as herbivores. All waders and the shelduck *Tadorna tadorna* were considered as benthivores. Diving ducks except mergansers were considered diving benthivores. Grebes, cormorants, herons, and mergansers were considered as piscivores.

To express changes in use of the areas, bird-days for each functional guild were calculated for each year as average number of birds counted each month multiplied by the number of days in the month. Peak counts were used to express the highest number of birds observed each year. Furthermore, distributions of three herbivorous species, Coot, Eurasian Wigeon *Anas penelope* and Green-winged Teal were mapped in 1999 by drawing the position of flocks on detailed maps (scale 1:25,000). Mapping took place at Agger and Harboør Fjords. For analysis, a 250 m × 250 m grid was superimposed on the maps. Where flocks of birds were distributed in more than one grid cell, numbers were apportioned between grid cells, assuming that there was an even distribution of

Table 1. Species list of the waterbirds observed on Agger Fjord, Thyborøn Fjord and Harboør Fjord during the study period (1994–2002).

Common name	Scientific name	Functional guild	Agger Fjord		Thyborøn Fjord		Harboør Fjord	
			Peak 1994–1998	Peak 1999–2002	Peak 1994–1998	Peak 1999–2002	Peak 1994–1998	Peak 1999–2002
Little Grebe	*Tachybaptus ruficollis*	Piscivore	14	5				13
Great Crested Grebe	*Podiceps cristatus*	Piscivore	24	39	1	16	16	48
Red-necked Grebe	*Podiceps grisegena*	Piscivore	1				1	3
Slavonian Grebe	*Podiceps auritus*	Piscivore	3					1
Black-necked Grebe	*Podiceps nigricollis*	Piscivore		3				2
Great Cormorant	*Phalacrocorax carbo*	Piscivore	110	185	66	592	63	57
Grey Heron	*Ardea cinerea*	Piscivore	18	23	10	10	53	17
Mute Swan	*Cygnus olor*	Herbivore	340	739	252	26	675	924
Bewick Swan	*Cygnus columbianus*	Herbivore	87	14	2	45		90
Whooper Swan	*Cygnus cygnus*	Herbivore	48	63	11	10	4	161
Bean Goose	*Anser fabalis*	Herbivore			2			
Pink-footed Goose	*Anser brachyrhynchus*	Herbivore	20	135	1		13	120
Greylag Goose	*Anser anser*	Herbivore	350	2230	39	304	25	22
Canada Goose	*Branta canadensis*	Herbivore	1	5				
Barnacle Goose	*Branta leucopsis*	Herbivore		1				
Light-bellied Brent Goose	*Branta bernicla hrota*	Herbivore	52		91	39	330	34
Dark-bellied Brent Goose	*Branta bernicla bernicla*	Herbivore	1	1	13	2	13	6
Shelduck	*Tadorna tadorna*	Benthivore	320	270	746	166	439	5
Eurasian Wigeon	*Anas penelope*	Herbivore	2190	2350	607	1649	1300	2850
American Wigeon	*Anas americana*	Herbivore				1		
Gadwall	*Anas strepera*	Herbivore	11	4			16	
Green-Winged Teal	*Anas crecca*	Omnivore	814	3510	98	223	221	830
Mallard	*Anas platyrhynchos*	Omnivore	487	1172	54	214	261	115
Pintail	*Anas acuta*	Omnivore	840	1135	14	15	100	55
Garganey	*Anas querquedula*	Herbivore		1	13			1

Shoveler	*Anas clypeata*	Omnivore	16	58	4	2		8
Pochard	*Aythya ferina*	Diving benthivore	362	580		1	129	241
Tufted Duck	*Aythya fuligula*	Diving benthivore	170	155	3		45	878
Greater Scaup	*Aythya marila*	Diving benthivore	1				5	16
Long-tailed Duck	*Clangula hyemalis*	Diving benthivore	1					
Common Scoter	*Melanitta nigra*	Diving benthivore		2		4		
Goldeneye	*Bucephala clangula*	Diving benthivore	155	178	125	206	65	116
Smew	*Mergus albellus*	Piscivore	1					
Red-breasted Merganser	*Mergus serrator*	Piscivore	8	8	25	16	1	
Coot	*Fulica atra*	Herbivore	2835	2745	97	604	720	1660
Oystercatcher	*Haematopus ostralegus*	Benthivore	16	3	36	25	28	
Avocet	*Recurvirostra avosetta*	Benthivore	40	56	2		38	
Ringed Plover	*Charadrius hiaticula*	Benthivore	188	137	33	12	43	11
Kentish Plover	*Charadrius alexandrinus*	Benthivore	1					
Golden Plover	*Pluvialis apricaria*	Benthivore	850	2100	260	105	1700	370
Grey Plover	*Pluvialis squatarola*	Benthivore	26	24	76	23	73	7
Lapwing	*Vanellus vanellus*	Benthivore	220	235	25	38	213	55
Knot	*Calidris canutus*	Benthivore	167	195	26		114	6
Sanderling	*Calidris alba*	Benthivore	54	4	20	2		
Little Stint	*Calidris minuta*	Benthivore	226	47	20	13	17	3
Temminck's Stint	*Calidris temminckii*	Benthivore	1	1	1			
Curlew Sandpiper	*Calidris ferruginea*	Benthivore	86	24	9	5	18	9
Dunlin	*Calidris alpina*	Benthivore	2810	1535	1410	446	2948	158
Ruff	*Philomachus pugnax*	Benthivore	98	141	30	61	6	4
Snipe	*Gallinago gallinago*	Benthivore	22	24	119	130	16	23
Woodcock	*Scolopax rusticola*	Benthivore	1		1			
Black-tailed Godwit	*Limosa limosa*	Benthivore	48	19	1	7	7	
Bar-tailed Godwit	*Limosa lapponica*	Benthivore	58	78	206	36	215	4
Whimbrel	*Numenius phaeopus*	Benthivore			1	2	6	
Eurasian Curlew	*Numenius arquata*	Benthivore	4	61	51	58	8	6

Table 1. Continued.

Common name	Scientific name	Functional guild	Agger Fjord		Thyborøn Fjord		Harboør Fjord	
			Peak 1994–1998	Peak 1999–2002	Peak 1994–1998	Peak 1999–2002	Peak 1994–1998	Peak 1999–2002
Spotted Redshank	*Tringa erythropus*	Benthivore	9	15	12	5	2	1
Redshank	*Tringa totanus*	Benthivore	122	91	59	129	179	61
Greenshank	*Tringa nebularia*	Benthivore	62	27	10	7	12	14
Green Sandpiper	*Tringa ochropus*	Benthivore	2	1	1	1	1	4
Wood Sandpiper	*Tringa glareola*	Benthivore	8	15	10	16	1	1
Common Sandpiper	*Tringa hypoleucos*	Benthivore	1	2	10			1
Ruddy Turnstone	*Arenaria interpres*	Benthivore	1			11	1	
Red-necked Phalarope	*Phalaropus lobatus*	Benthivore	6	1	2	1	1	

For each species the functional guild and peak numbers is shown. Peak numbers are shown from before and after change in floodgate management.

birds within flocks. The number of bird-days per grid unit was calculated for each species.

To examine changes in waterbird species diversity with time, the Shannon–Wiener index of diversity (H') was calculated for each year (Zar 1984):

$$H' = -\sum_{i=1}^{k}(p_i)(\log p_i),$$

where k is the number of species and p_i is the proportion of total sample belonging to the ith species. To test the null hypothesis that waterbird diversities betweenlagoons were equal, a t-test was performed (Hutcheson 1970). In addition, the Shannon–Wiener index of evenness (J') was calculated (Zar 1984):

$$J' = \frac{H'}{H'_{\max}}$$

J' expresses the observed diversity as a proportion of the maximum possible diversity.

In the calculations of diversity indexes we only include one count per month, the count nearest to the 15th, because this 'mid-monthly' count was carried out in all years, and a sub-sample of counts based on these therefore may be considered directly comparable.

Between-year changes in bird-days and indexes were investigated by using Spearman Rank Correlation coefficients r_s (Zar 1984).

Results

Feeding depths 1999–2000

Between September 1999 and January 2000, water levels at Agger Fjord gradually increased 48 cm (Table 2). Feeding depths for waterbirds ranged from +5 to +53 cm in shallow areas and from +65 to +113 cm in deeper areas. At Thyborøn Fjord, feeding depths for waterbirds between September 1999 and January 2000 ranged from 0 to +65 cm in shallow areas and from +60 to +136 cm in deeper areas. Compared with 1995 (Table 2), opening the floodgate in 1998 had resulted in a significant ($p < 0.05$) increase of +28 cm in mean water level and feeding depth experienced by waterbirds. Feeding depths at Harboør Fjord between September 1999 and January 2000 ranged from +3 to +53 cm in shallow areas and from +65 to +123 cm in deeper areas. Compared with 1995 (Table 2), opening of the floodgate in 1998 had resulted in a significant ($p < 0.05$) increase of +53 cm in mean water level and feeding depth experienced by waterbirds. In 1999–2000 salinity was not significantly different from other years ($p > 0.05$) (Table 2).

Table 2. Maximum, minimum and mean values for depth, water level (1995 and 1999) and salinity (1995 and 1999-2001), respectively.

	Agger Fjord			Thyborøn Fjord			Harboør Fjord		
	Max	Min	Mean (±SE)	Max	Min	Mean (±SE)	Max	Min	Mean (±SE)
Depth (cm DNN)	50	−10	13.5 ± 15.1	62	−9	12 ± 16.6	65	3	36.0 ± 14.1
Water level 1995 (cm relative to DNN)	–	–	–	7	−23	− 7.2 ± 12.5	2	−33	− 21.0 + 12.0
Water level 1999 (cm relative to DNN)	63	15	43 ± 13.9	74	−2	21 ± 18	50	0	32.0 ± 15.5
Annual salinity 1995 (‰)	–	–	–	39.2	17.2	29.2 ± 22.9	25	8.5	14.5 ± 5.69
Annual salinity 1999 (‰)	7.22	2.2	4.5 ± 2.5	32.7	19	27.3 ± 3.35	34.3	6.2	13.5 ± 7.34
Annual salinity 2000 (‰)	–	–	–	35.6	13	26.1 ± 4.91	36.1	7.3	15.7 ± 8.72
Annual salinity 2001 (‰)	–	–	–	32.5	17.7	26.8 ± 3.87	33.1	6.9	14.9 ± 6.64

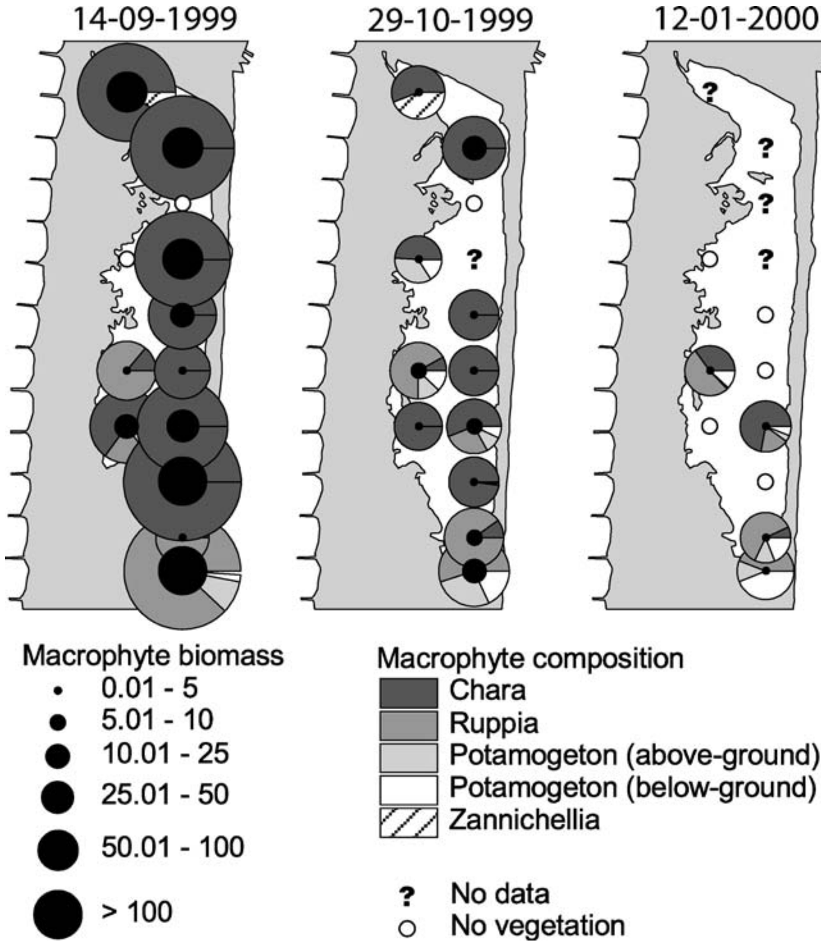

Figure 3. Distribution of submerged macrophyte communities and seasonal variation in macrophyte biomass between 14 September 1999 and 12 January 2000 at Agger Fjord. Because of high water levels, some data were not collected in October and January.

Macrophyte cover and biomass 1999–2000

Mean leaf cover percentage at Agger Fjord was 37.9 ± 30.5% in September, 11.4 ± 13.8% in late October, and 2.5 ± 2.5% in January (all values mean ± SD). Percentage leaf cover differed between all sample months ($F_{2,114} = 39.89$, $p < 0.0001$). There was a significant positive correlation between the depth and the percentage of macrophyte cover in September ($R^2 = 0.42$, $p < 0.0001$). Up to 95% of the total macrophyte biomass were composed of *Chara* spp. and *Ruppia maritima* (Figure 3). Total macrophyte biomass differed among all months ($F_{2,158} = 53.75$, $p < 0.0001$). In September, the quantity of *Chara* spp. was very scattered within the *Chara*-dominated

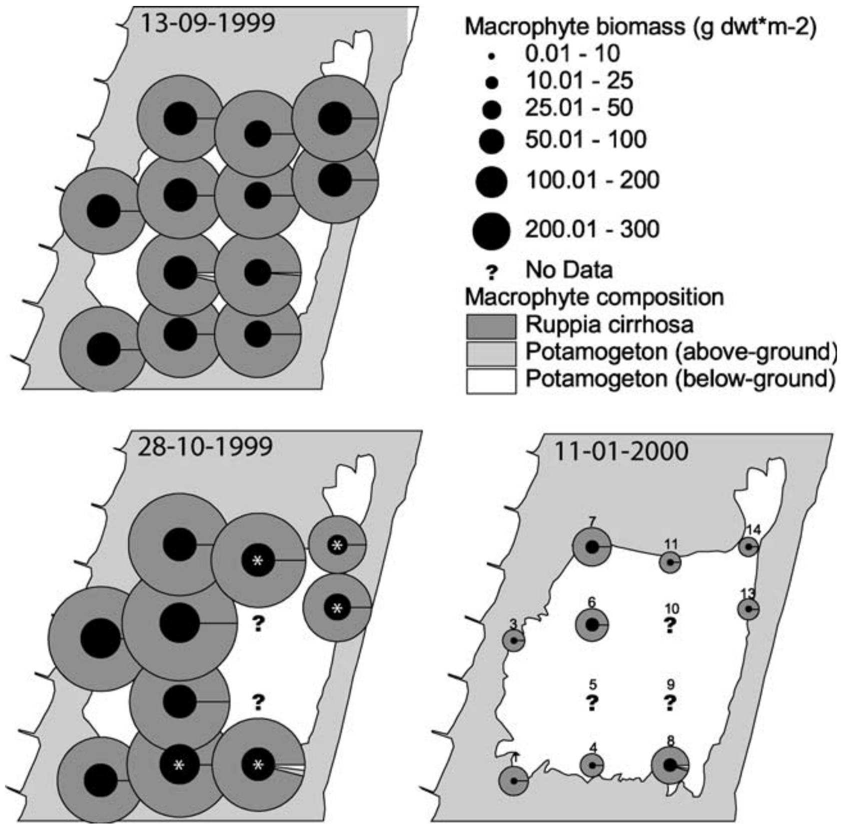

Figure 4. Distribution of submerged macrophyte communities and seasonal variation in macrophyte biomass between 13 September 1999 and 11 January 2000 at Harboør Fjord. Station numbers is shown for 11 January 2000. Significant changes in macrophyte biomass at individual stations between 13 September and 28 October 1999 are highlighted with an *. An increase in biomass due to growth was seen at station 4, 8 and 11. A decrease in biomass due to waterfowl grazing was seen at station 13 and 14. Because of high water levels, some data were not collected in October and January.

areas, with stations containing biomasses between 0 and 100 g/m^2, lying in layers up to 30 cm thick (pers. obs.). In October and January, macrophyte biomass was more evenly distributed.

In Harboør Fjord, there was a seasonal change in leaf cover percentage in the sampling period ($F_{2,72}$ = 50.07, p < 0.0001): January samples (mean ± SD: 32.1 ± 25.4), were significantly smaller than both September (89.6 ± 17.6) and October (93.4 ± 16.2). Leaf cover did not differ between October and September, when most areas of the lagoon had 100% cover of submerged macrophytes. Throughout the sample period, more than 98% of the total macrophyte biomass in Harboør Fjord was composed of *Ruppia cirrhosa* (Figure 4). January samples of standing biomass were significantly smaller than both October and September ($F_{2,159} = 272.67$, $p < 0.0001$), although detached Spiral Tasselweed was found lying at the bottom near the shore in January (pers. obs.). There was no difference in total macrophyte biomass between September and October. Among stations, however, there was a significant increase in macrophyte biomass from September to October at stations 4, 8 and 11, and a significant decrease in biomass at stations 13 and 14 (Figure 4).

Herbivorous waterbird distribution 1999–2000

During autumn 1999, the majority of the mapped bird species initially fed on the shallower south and western parts of the lagoon, gradually moving out to slightly deeper areas in the central parts of the lagoon. Two of the three mapped species avoided the deepest northern end of the lagoon, which was only exploited by the diving Coot (Figures 1 and 5). In Harboør Fjord, number of bird-days spent by Coot, Eurasian Wigeon and Green-winged Teal was greatest at station 13 and 14. All species used the deeper middle part of Harboør Fjord less or avoided it (Figure 5).

Waterbird abundance, species richness and diversity 1994–2002

An average of 40 waterbird species was observed on Agger Tange during 1994–2002 (Table 3). The most abundant bird species were Green-winged Teal, Coot and Dunlin *Calidris alpina* (Table 1). For each of the functional guilds on Agger Tange, there was no correlation between time and number of bird-days (benthivore: $r_s = 0.000$, $p > 0.05$, diving benthivore: $r_s = 0.150$, $p > 0.05$, herbivore: $r_s = 0.566$, $p > 0.05$, omnivore: $r_s = 0.333$, $p > 0.05$, diving benthivore: $r_s = 0.366$, $p > 0.05$). However, there was a significant increase in peak numbers ($r_s = 0.666$, $p < 0.05$) and in the total number of bird-days ($r_s = 0.683$, $p < 0.05$) from 1994 to 2002 (Figure 6). The Spearman rank correlation coefficient r_s showed no change in the comparison of species diversity H' ($r_s = 0.216$, $p > 0.05$) and evenness J' ($r_s = 0.333$, $p > 0.05$) (Figure 7).

On Thyborøn Fjord, an average of 28 waterbird species were observed during 1994–2002 (Table 3). Between 1994 and 1998, the most abundant species were dunlin and shelduck, both benthivorous species (Table 1). Between 1999 and 2002, the most abundant species were Eurasian Wigeon and Coot, which both are herbivorous waterfowl. We found no change in peak-numbers ($r_s = 0.550$, $p > 0.05$) and the total number of bird-days ($r_s = -0.133$, $p > 0.05$) between 1994 and 2002 (Figure 6). However, a significant increase in bird-days was found in the diving benthivore guild ($r_s = 0.666$, $p < 0.05$). No change was found at Thyborøn Fjord for diversity H' ($r_s = 0.200$, $p > 0.05$) or evenness J' ($r_s = 0.316$, $p > 0.05$) (Figure 7).

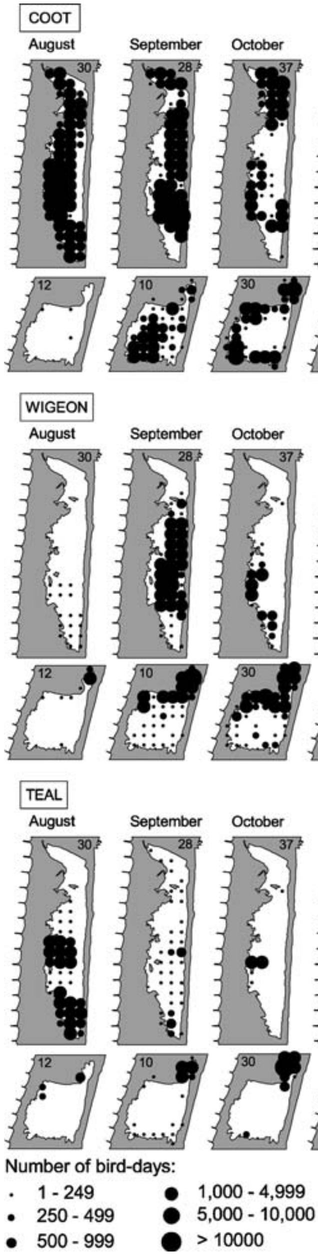

Figure 5. Seasonal changes in distribution of three of the four most common species associated with aquatic vegetation, August–November 1999. Similar plots for the forth common species, Mute Swan, are given by Holm (2002). For each species the distribution at Agger and Harboør Fjord is expressed as the number of bird-days in 250 m×250 m grid squares. The average water level in DNN (Danish Ordnance Datum, a fixed point) when counting the birds is given on each map. The three species are the omnivore leaf-eating diving Coot, the herbivore leaf- and seed-eating non-diving Eurasian Wigeon and the omnivore seed-eating non-diving Green-winged Teal.

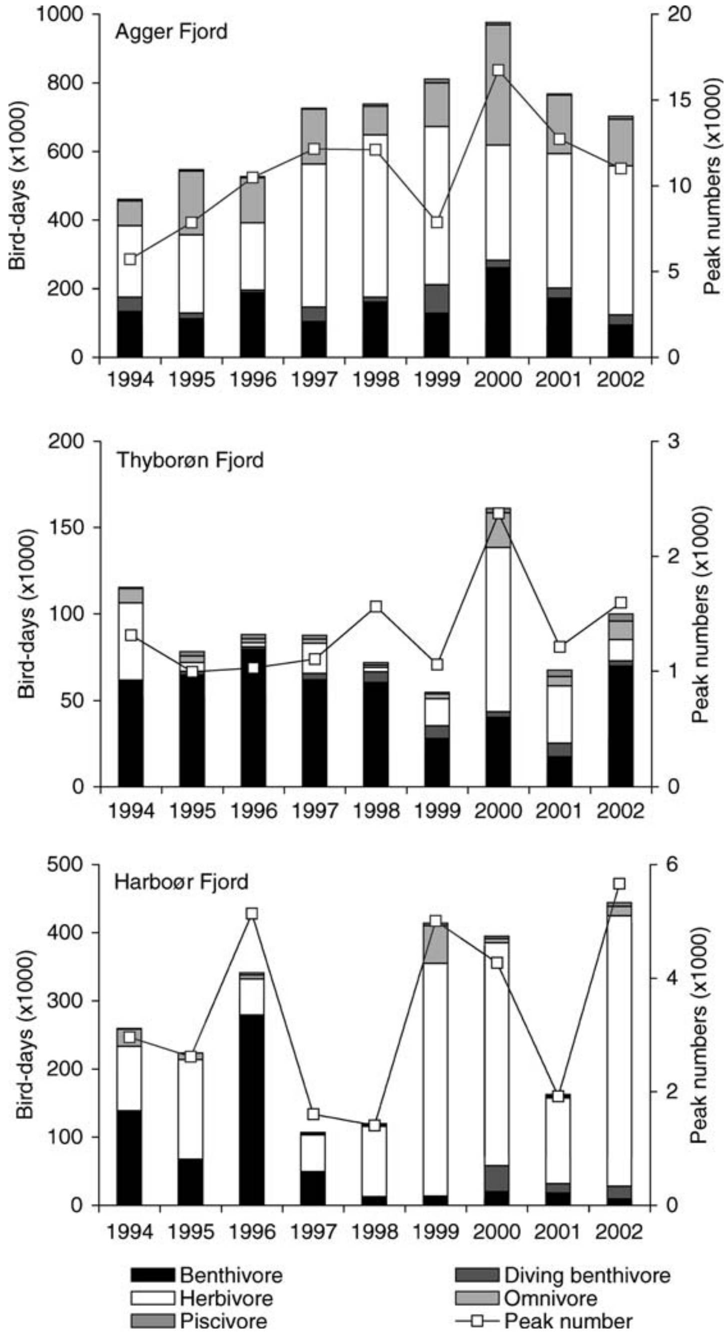

Figure 6. Annual variation in numbers of birds in Agger Fjord (upper), Thyborøn Fjord (middle) and Harboør Fjord (lower), expressed by the number of bird-days of functional guilds, and the peak number recorded in the lagoons within an autumn season.

An average of 27 waterbird species were observed on Harboør Fjord (Table 3). Between 1994 and 1998, the most abundant species were Dunlin and Golden Plover *Pluvialis apricaria*, both benthivorous waders (Table 1). Between 1999 and 2002, the most abundant species were the herbivorous Eurasian Wigeon and Coot. We found no difference in peak-numbers ($r_s = 0.233$, $p > 0.05$) and the total number of bird-days ($r_s = 0.366$, $p > 0.05$) between 1994 and 2000 (Figure 6). However, a significant decrease in bird-days was found in the benthivore guild ($r_s = -0.816$, $p < 0.05$), and a significant increase in bird-days for the piscivore ($r_s = 0.783$, $p < 0.05$), diving benthivore ($r_s = 0.683$, $p < 0.05$), and herbivore ($r_s = 0.650$, $p < 0.05$) guilds. A significant decrease was found at Harboør Fjord for both diversity H' ($r_s = -0.683$, $p < 0.05$) and evenness J' ($r_s = -0.733$, $p < 0.05$) (Figure 7).

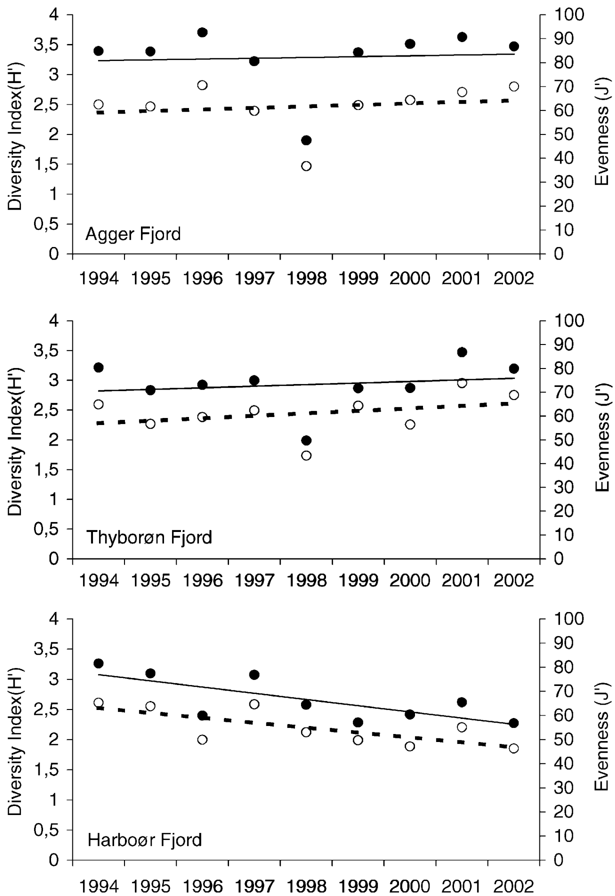

Figure 7. Annual variation and trends in Shannon–Wiener Diversity Index H′ (—) and Evenness J' (- - -) in Agger Fjord (upper), Thyborøn Fjord (middle) and Harboør Fjord (lower).

Among sites, Agger Tange had the highest diversity index for all years ($p < 0.001$).

Discussion

Comparing macrophyte communities

Studies have documented that distribution of seagrass is strongly related to physiology and growth characteristics, including water depth and salinity (Santamaria et al. 1996; Robbins and Bell 2000). Both factors are likely to affect the macrophyte diversity and composition of the two vegetation communities on Agger Fjord and Harboør Fjord. Because of the high salinity in Harboør Fjord (Table 2), the macrophyte community has low diversity and is dominated by *Ruppia cirrhosa*, which can cope with the highly saline water coming from the Limfjorden (Verhoeven 1979). Contrary, Agger Fjord has a low saline and more diverse macrophyte community with freshwater *Chara* species dominating the deepest areas, as found in studies by Moore (1986) and Santamaria et al. (1996) . In the parts of the lagoon that dry out in the summer, *Potamogeton pectinatus* and *Ruppia maritima* dominates, probably because their seeds are resistant to cold and drought (Kiørboe 1980; Verhoeven 1980; Kantrud 1990).

Maintaining a diverse aquatic plant community can be beneficial to migrating and wintering waterbirds because the many species have different macrophyte preferences (Benedict and Hepp 2000). Many omnivorous species feed on seeds whereas herbivores feed on the leaves, tubers or rhizomes of the plants. For the latter species differences in foraging quality, i.e. the nutritious value between plant species, is of foremost importance. Holm (2002) found a large difference in foraging quality between the dominant plants in the two lagoons. *Ruppia cirrhosa* in Harboør Fjord contains large amounts of hemicellulosis and cellulosis, which are hard to digest for waterfowl and hamper the digestion of the content of the plant cells (Prop and Vulink 1992). Thus, *Ruppia cirrhosa* is low quality food, which is utilized most efficiently by herbivorous birds with a long retention time. The *Chara* species in Agger Fjord has low contents of structural carbohydrates and the high proportion of easily metabolizable components such as protein and non-structural carbohydrates, which makes *Chara* high quality food. Therefore, herbivorous waterbirds are expected to derive more energy from the *Chara* species in Agger Fjord than from the same amount of *Ruppia cirrhosa* in Harboør Fjord, which may be one of the main reasons why waterbirds choose Agger Fjord in preference to Harboør Fjord. This interpretation is supported by Noordhuis et al. (2002), who also found that several waterbird species had a strong preference for Charophytes.

Macrophyte length is limited by water depth in shallow waters and light availability in deeper waters, and the highest biomass would therefore usually be found at intermediate depths (Verhoeven 1979). Our seasonal data on macrophyte biomasses and mappings of waterbirds, however, demonstrate that waterbird grazing especially of the non-diving herbivores took place in the shallowest waters until depletion (Figures 1 and 5). In Agger Fjord this happened despite the abundance of submerged vegetation initially was highest at deeper waters. The explanation behind this is that most non-diving waterbirds, probably independent of size, prefer to forage at low depths provided sufficient food is available. When feeding in the shallow birds can feed by dipping their head and necks only (neck-dipping), whereas if they feed at deeper waters they might have to feed by tilting the whole body forward (up-ending). The latter feeding method both results in lower food intake rates, as demonstrated experimentally for ducks by Guillemain and Fritz (2002), and higher energy expenditures, as found in a study of Bewicks's Swans *Cygnus columbianus bewickii* feeding on *Potamogeton pectinatus* (Nolet et al. 2002). Holm (2002) likewise found, that Mute Swans *Cygnus olor* in Harboør Fjord avoided deep areas and only foraged in shallow waters near the shore, despite the fact that they would be able to reach vegetation in the deepest part of the lagoon by up-ending. Furthermore, the greatest decrease in biomass during autumn 1999 on Harboør Fjord was seen in the northern bay, where the shallowest water was found.

Comparing bird species diversity

The development in the total number of bird-days spent on Thyborøn Fjord and Harboør Fjord was not affected by the change in floodgate management in 1998. There were, however, changes in bird-days spent by the different functional guilds. Bird-days spent by diving benthivores increased in both lagoons. Furthermore, herbivorous and piscivorous species increased their use of Harboør Fjord, while benthivorous species decreased their use. There was no decrease in benthivorous species' use of Thyborøn Fjord (Figure 6), probably due to a low water level on Harboør Tange in October 2002 (Figure 2), which extended the time with available food for waders. In both lagoons the most abundant species changed from being benthivores to herbivores after opening of the floodgate, this happening despite the fact that no submerged vegetation was found in Thyborøn Fjord. The change in guild-dominance in the latter area most likely represents the decline in benthivores in combination with the increased amount of submerged vegetation in nearby Harboør Fjord, which attracted herbivorous species to the lagoon system on Harboør Tange generally. Although these changes were a benefit for herbivorous waterbird numbers, they had a negative effect on overall waterbird diversity on Harboør Fjord, probably because of the decrease in the diverse group of benthivorous species (Figure 7). Although vegetation often benefits density and abundance of prey for benthivorous birds, e.g. oligochaetes and chironomids (Safran et al. 2000), a decline in benthic fauna density between 1995 and 2001 was found for both lagoons on Harboør Tange (Hedeselskabet 2001). Increased feeding depth and less food availability were presumably the reasons why benthivore species were forced to exploit other areas. Therefore, instead of having a shallow watered reserve for waders, the change in management with its associated rise in water level regime made a reserve for herbivorous waterfowl. In comparison, Agger Fjord, with no change in management, had a high carrying capacity for most functional guilds during all 9 years and waterbird diversity was much higher.

Factors affecting bird numbers and species diversity

The great difference in diversity and the number of waterbirds between the lagoons is probably due to the dissimilarity regarding abiotic factors such as topography (i.e. water depth), water level, and salinity, which influence biotic factors such as macrophyte composition, biomass and quality. Agger Tange has great depth diversity, with large areas drying out in summer providing habitat suitable for waders. Earlier studies have shown that numbers of small waders increase with increasing availability of areas with water depth of 0–5 cm (Isola et al. 2000; Collazo et al. 2002). The large shallow watered areas below 20–30 cm DNN are suitable for feeding dabbling ducks and the deep areas provide habitat for diving species. Furthermore, there are undisturbed islands that provide protected habitats for roosting birds and provide a shelter for preening and molting Mute Swans (Holm 2002).

Thyborøn Fjord has the same depth diversity and feeding depths as Agger Fjord but contained approximately six times less waterbirds during autumn. This difference may partly be explained by a smaller size (surface area 61% of Agger Fjords), most likely in combination with the absence of suitable food such as submerged vegetation and benthic fauna, as found by Hedeselskabet (2001).

In contrast to the other lagoons, Harboør Fjord has a more uniform depth profile, with few shallow watered areas and large flooded areas with depths above 30 cm relative to DNN. Prior to the 1998 change in water table management, and with a mean water level of −21 cm (in 1995), the lagoon contained large areas of sands suited for waders, and a central part with less than 20 cm water coverage throughout most of the year. Although such areas have suitable feeding depths for waterbirds, the length (i.e. biomass) of the dominant submerged macrophyte, *Ruppia cirrhosa*, is limited by water depth (Verhoeven 1979). Therefore, under that management regime, food densities may have been below a threshold of 10–20 g/m^2 where herbivores are thought to be able to cover their daily energy requirements (Nolet and Drent 1998). From 1999 onwards, feeding depths increased and the majority of food for herbivores was only available for species like the long necked Mute Swans (Holm 2002) and diving Coots. Dabbling ducks could only reach the food in the shallow northern bay of Harboør Fjord where grazing was significant at station 13 and 14 (Figure 4). When not in the bay, Wigeon fed by kleptoparasiting Mute Swans (pers. obs.), implying low macrophyte availability. Green-winged Teal

Table 3. Maximum, minimum and mean values for numbers of waterbird species, diversity H' and evenness J', respectively, measured in Agger Fjord, Thyborøn Fjord and Harboør Fjord 1994–2002.

	Agger Fjord			Thyborøn Fjord			Harboør Fjord		
	Max	Min	Mean (±SE)	Max	Min	Mean (±SE)	Max	Min	Mean (±SE)
Waterbird species	45	31	40.2 ± 4.46	34	22	28.1 ± 4.11	35	24	29 ± 3.16
Waterbird diversity H'	3.71	1.89	3.29 ± 0.54	3.21	1.99	2.93 ± 0.41	3.26	2.27	2.66 ± 0.38
Waterbird evenness J'	70.6	36.7	61.7 ± 10.1	73.8	43.3	61.1 ± 8.72	65.2	46.3	55 ± 7.66

used the shallow watered areas in the bay only for roost in daytime and were probably foraging elsewhere at night (Madsen and Holm 2002).

Management implications

Agger Fjord support greater flocks of birds than Harboør Fjord, despite the plant food stocks here being lower, indicating that shallow watered wetlands with great depth diversity can support a greater number and diversity of waterbirds than deep wetlands, probably due to food accessibility. A study by Colwell and Taft (2000), found a similar correlation between water depth and the number and density of bird species. Greatest diversity and densities of many waders and waterfowl is found to occur when wetlands average 15–20 cm depth (Colwell and Taft 2000; Isola et al. 2000). Agger Fjord is shallow watered and in a low saline steady state, with a diverse macrophyte community. The waterbird diversity is high and stable, and the peak number and bird-days spent is increasing. Hence, there should be no major change in floodgate management on Agger Fjord, but one might consider opening the floodgate for runoff slightly earlier in autumn. This could make vegetation found at deeper waters more accessible to waterbirds in late autumn and mid-winter.

The initiative taken by the County Authorities to improve water quality in Thyborøn and Harboør Fjords by enhanced water replacement made no change in waterbird diversity on Thyborøn Fjord, but caused waterbird diversity to decrease on Harboør Fjord. However, the initiative restored vegetation in Harboør Fjord and indeed proved beneficial for piscivorous, diving benthivorous and herbivorous, but unfavorable for benthivorous waterbirds. The quantity of food for herbivorous in Harboør Fjord is very large, indicating that this lagoon could support large flocks of herbivorous waterbirds throughout the autumn. Under the present management, most of this food is, however, unavailable for the birds. In order to provide a reserve suitable for larger numbers of waterbird species and individuals, we propose water levels on Harboør Tange should be managed actively in autumn to avoid extreme high waterlevels. This might be done by closing the floodgate 3–4 months in autumn in a situation where water levels has fallen to a level where the upper mudflats in Thyborøn Fjord become exposed, but without drying out patches with submerged macrophytes in Harboør Fjord. We guess the optimal water level is approximately 0 cm relative to DNN, at which there would be areas suitable to both waders and short-necked herbivorous waterbirds. The optimal water level could be more firmly identified by modeling, combining elements of the small wader habitat maximization model of Collazo et al. (2002) with the herbivore food availability models of Clausen (2000) and Therkildsen (2000). This approach would identify a water level that benefits both groups, without sacrificing the other. The rest of the year the floodgate should be open in order to secure a high water quality. This would create a synchronicity between water level and bird migration in autumn. Furthermore, it would fulfil the requirements in The Action Plan on the Aquatic Environment, the EU Water Framework Directive and the requirements of the EU Birds Directive.

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