

Effects of lake restoration on breeding abundance of globally declining common pochard (*Aythya ferina* L.)

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Abstract Common pochard *Aythya ferina* are rapidly declining globally, partly due to water quality change at breeding habitats. Lake restoration at two southern Danish lakes (external nutrient loading reduction, bream *Abramis brama* and roach *Rutilus rutilus* removal and stocking of pike *Esox lucius*) improved water clarity and submerged macrophyte cover. Nesting pochard on one lake increased from 2.3 females per annum pre-treatment to 13.9 afterwards and from 22.7 females to 99.6 post-treatment at a second. Numbers fell from 27.7 to 11.3 at a third untreated lake with consistently high water clarity, but

which was colonised and became dominated by holly-leaved naiad *Najas marina*, which provides no food resources for breeding pochard. Linear modelling (controlling for serial autocorrelation) showed statistically significant effects of annual summer measurements of suspended solids (negative) and Secchi depth (positive) on pochard abundance at both restored lakes and chlorophyll (negative) at one of those lakes, but no effects at the third. Breeding pochard numbers also correlated positively with submerged macrophyte cover at one restored lake with adequate data. Results support the hypothesis that lake restoration to improve water quality enhances conditions for locally breeding pochard, as long as restored conditions secure appropriate submerged macrophyte communities for nesting pochard.

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Introduction

Globally, many nutrient-rich, shallow water bodies have shifted from clear water states, with dense submerged macrophytes and piscivorous fish populations to turbid waters dominated by phytoplankton algae and plankton- and benthos-feeding fish due to human enrichment from sewage disposal and

agricultural runoff (Moss, 1990; Scheffer et al., 1993; Jeppesen et al., 1998). Despite reductions in external phosphorus and nitrogen loadings and consequent reductions in phytoplankton biomass (Søndergaard et al., 2003; Jeppesen et al., 2005), such turbid states often resist restoration to clear water lake systems (e.g. van der Molen & Portielje, 1999; González Sagrario et al., 2005). Chemical or biological inertia preventing/delaying improvements (Moss, 1990; Rip et al., 2006; Ibelings et al., 2007) may necessitate additional physical, chemical and biological restoration interventions that have been developed and implemented with varying degrees of success (e.g. Søndergaard et al., 2007, 2008). Improved light penetration encourages macrophyte growth, reducing sediment resuspension. Plants compete for nutrients with phytoplankton and provide zooplankton refuges, further amplifying water quality/clarity improvements (Moss, 1990; Schriver et al., 1995). Removing benthos-feeding fish (reducing sediment resuspension) and encouraging zooplankton (enhancing their grazing effects on phytoplankton) can restore macrophytes and thereby re-establish clearer water states, combating environmental problems associated with turbid water lakes (Hansson et al., 1998; Søndergaard et al., 2008; Jeppesen et al., 2012).

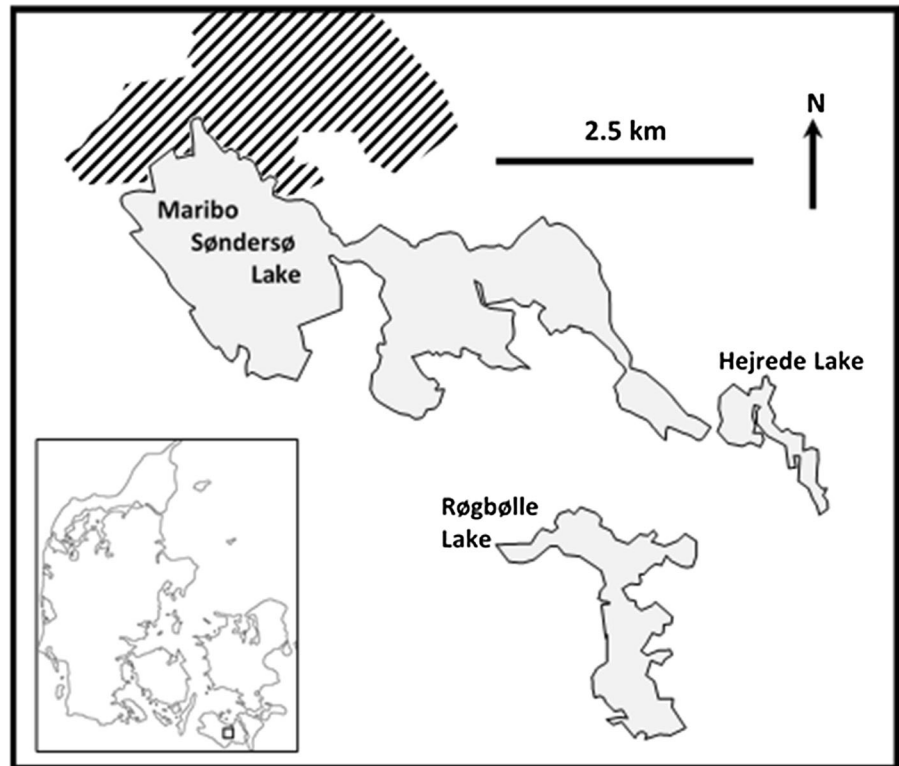
Denmark has restored many shallow nutrient-rich lakes to improve water quality in the last 30 years (Liboriussen et al., 2007a, b; Søndergaard et al., 2008) by removing planktivores (especially roach *Rutilus rutilus* (Linnaeus 1758) and bream *Abramis brama* (Linnaeus 1758), Søndergaard et al., 2008; Jeppesen et al., 2012) and stocking predatory fish (mostly northern pike *Esox lucius* Linnaeus 1758, Skov & Nilsson, 2007). Reductions of 20–50% in chlorophyll, total phosphorus/nitrogen and suspended solids have occurred 8–10 years after removal of planktivorous and benthivorous fish, with significant and enduring effects on summer Secchi depth and suspended solids, enabling recolonization by submerged macrophytes (van den Berg et al., 1998; Liboriussen et al., 2007a, b; Søndergaard et al., 2008). Despite dramatic changes in freshwater ecosystem function, studies of broader biodiversity benefits from restoration programmes are rare (Hilt et al., 2017), despite reported benefits to wintering and breeding waterbird communities (e.g. Noordhuis et al., 2002; Liboriussen et al., 2007b; Hansson et al., 2010).

Formerly common and widespread, breeding common pochard *Aythya ferina* (Linnaeus 1758) (hereafter pochard) have rapidly declined across Europe, where they winter in greater numbers supplemented by birds nesting further east in Eurasia. A halving of the population in three generations (22.8 years) in the late 20th century changed its status from IUCN Least Concern Status to Vulnerable (Nagy et al., 2014; BirdLife International, 2015a, b; IUCN, 2015). Changes in water quality, benthos, fish management and loss of submerged macrophytes were considered responsible for breeding pochard declines in 12 out of 17 European countries (Fox et al., 2016), despite lacking site-specific evidence of relationships between lake water quality, submerged macrophytes and breeding pochard abundance. Breeding pochard are important biodiversity indicators of shallow, relatively eutrophic waters, especially those retaining a clear water column, dense beds of charophytes and species such as fennel pondweed *Potamogeton pectinatus* L. which feature prominently in the diet (Cramp & Simmons, 1977). Pochards are protected under international conventions and laws and are a key hunted quarry species (Hirschfeld & Heyd, 2005). For this reason, we urgently need to understand factors causing the abandonment of pochard breeding habitat and find management interventions to restore them to waterbodies where changes in water quality, benthos, fish management and submerged macrophytes are responsible for their loss (Fox et al., 2016). We therefore assessed lake restoration effects on two of three separate basins in the Maribo Lakes system on the island of Lolland, in southern Denmark (54°45'N, 11°32'E; Fig. 1) on local nesting pochard abundance. We compared asynchronous temporal changes in basin water quality (specifically submerged vegetation cover) with local pochard breeding densities using a linear modelling approach to determine whether lake restoration projects, generally aimed to fulfil broader water quality objectives, can benefit this increasingly rare and declining diving duck species.

Study area and methods

Maribo Søndersø Lake (860 ha) is mostly < 2 m deep, with 22 islands, islets and abundant reed beds (Liboriussen et al., 2007b). In the early 1800s, the lake received untreated sewage and effluent from

Fig. 1 Map showing location of Maribo Lakes on Lolland, southern Denmark (inset) and the size and relative locations of Maribo Søndersø, Hejrede and Røgbølle Lakes in relation to Maribo town (cross hatched)



Maribo town on its northwest edge, subsequently diverted away from the lake because of health concerns. From 1900, the Maribo sugar beet factory discharged wastewater into the lake, a considerable source of organic pollution and phosphorus, until stopped c.1962. There has been no subsequent industrial pollution and the major sources of input come from agriculture and the sparse rural population of the catchment. These historical factors combined to cause highly turbid, poor water quality and no submerged vegetation in the late 1980s, with a fish fauna dominated by roach and bream, with few pike and perch *Perca fluviatilis* Linnaeus 1758. The local county coordinated a restoration plan in 1989, implementing sewage treatment from Maribo and villages in the catchment, removal of 132 tonnes of roach and bream in the following 14 years, the introduction of 618,000 pike fry during 1994–1997 (65–235 individuals ha⁻¹ stocking⁻¹) and restricting the take of perch and pike from the lake. The lake water level was raised by c. 30 cm to increase shallow flooded areas and regulated to maintain constant water levels.

Hejrede Lake (53.4 ha) is between 0.9 and 3.5 m deep with a catchment of 24.4 km², while Røgbølle

Lake (201 ha) is between 1.0 and 4.0 m deep with a catchment of 11.4 km². Both lakes flow into Maribo Søndersø Lake. Hejrede Lake is linked via a pump-station, up-graded in the late 1990s to reduce the annual fluctuation in water levels from more than 1 m magnitude to within 0.15 m. Røgbølle Lake has a natural outlet to Maribo Søndersø Lake but its water levels can be regulated to a minor extent. Little remedial management activity was undertaken at Hejrede Lake during the early 1990s, as the local fisherman removed large bream and roach during his ongoing commercial fishing activities; however, the timing and magnitude of the fish removal here was not quantified. In addition, a natural fish kill occurred during the winter of 1995/1996 due to a prolonged 4-month period of ice cover. There was no organised fish removal in Røgbølle Lake, but the fish kill in winter 1995/1996 also occurred to a lesser extent (because of clearer and deeper water). All three lakes, their emergent vegetation and immediate areas associated with their catchment are protected as a European Union Special Protection Area and Ramsar Wetland of International Importance for their breeding and staging waterbird populations (MESN, 1995).

Measures of water quality and surveys of submerged macrophytes

The Danish national aquatic environmental monitoring programme provided the chemical data presented here from the ongoing programme started in 1989, based on well-defined and comparable sampling and analytical procedures (Svendsen et al., 2005). For water chemistry, biweekly samples were taken during summer (1 May–1 October). Analyses of total phosphorus, total nitrogen, suspended solids and chlorophyll *a* were based on a depth-integrated sample from the photic zone sampled at a mid-lake station. All chemical analyses were performed using standard analytical procedures; see Søndergaard et al. (2005) for full details. In addition, Secchi depth was measured with a standard Secchi disc. Note that these data were not available for every year (see Fig. 2 for gaps).

Macrophyte cover data from Maribo Sønderlø Lake were derived from a regional programme based on surveys undertaken during 1992, 1998 and 2003. Macrophyte cover was assessed throughout the lake, based on morphometry in a number of sub-areas, each

assigned to 0.5 m depth zones within which macrophyte coverage was estimated using a hydroscope, rake or by diving, depending on water depth (Storstrøms Amt, 1993, 1999, 2004). Total lake coverage for each species was calculated by scaling up from the results from the sub-areas. Subsequently macrophytes were monitored under the Danish national monitoring programme in 2004 and 2007 (Svendsen et al., 2005) based on a series of transects, which were subsequently converted to macrophyte percentage coverage by averaging the average percentage cover for each transect. Only macrophyte species constituting more than 0.05% bottom coverage within transects in 2004 and 2007 were used in this analysis. Both surveys generated estimates of vegetation cover for each of these five monitoring years at Maribo Sønderlø Lake, which we used to compare to breeding pochard abundance in these years.

Annual assessment of breeding pochard abundance

Breeding abundance was determined using the methods described in Koskimies & Väisänen (1991), but

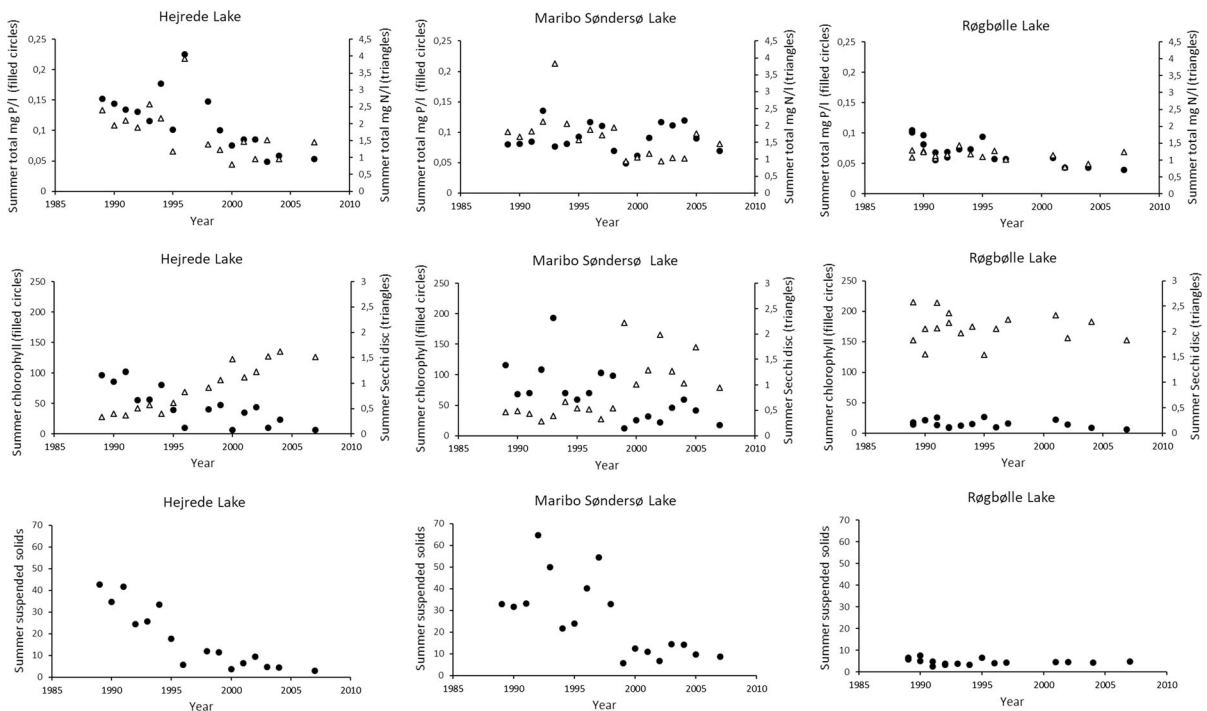


Fig. 2 Plots of annual determinations of summer total nitrogen and phosphate (mg l^{-1} , upper row of graphs), chlorophyll *a* and Secchi depth determinations (middle row) and suspended solids

(lowest row) from Hejrede, Maribo Sønderlø and Røgbølle Lakes, 1989–2007. See methods for full details

using counts of numbers of female pochard (unattended, paired and associating with multiple males, hereafter “breeding pochard”) rather than pairs. This involved consistent registration from the same observation points strategically positioned around each of the lake basins by author Hans Erik Jørgensen during thorough surveys undertaken in the period 25 April–20 May each year, i.e. just prior to or during the beginning of the laying period in Denmark (Cramp & Simmons, 1977). Surveys were carried out in most years from 1977 until 2007, except 1978, 1981–1983, 1990 and 2006, while data were missing from other years in some of the lakes when full counts were not possible (see “Results”). The annual numbers of females present on each waterbody were generally slightly higher than the numbers of females seen subsequently with broods, due to nesting failure and cryptic behaviour during brood rearing, but are an accurate and consistent assessment of females settling and attempting to breed annually at the site. We do not report breeding success here because hatching may take place over an extended period and the highly mobile broods were typically reared in areas of dense emergent vegetation, making true assessment of reproductive output difficult and settling females our best estimate of the breeding population.

Statistical methods

We used linear regression models that accounted for potential autocorrelations (Proc AUTOREG in SAS 9.3 SAS Institute, Cary, NC) to test changes in lake parameters between 1989 and 2007 (i.e. year vs. lake parameters), and the relationship between lake parameters and the $\log_{10}(x + 1)$ transformed number of breeding pochard females. We did this because autocorrelation is likely to arise from sequential annual measurements of parameters at the same lake. We generated Durbin–Watson d statistics for all parameters to test for the presence of autocorrelation at lag 1 in the residuals (prediction errors) from each regression analysis. As a rule of thumb, values of $d = 2$ indicate no autocorrelation, values of $d > 3$ and < 1 give cause for concern about the influence of serial autocorrelation (Field, 2009). To analyse the relationships between vegetation cover and the $\log_{10}(x + 1)$ transformed number of breeding pochard females, we used a Spearman correlation (Proc CORR) to test the correlation between number of

breeding pochard and cover for each of the submerged macrophyte species. We only included those plant species, which were registered in all 5 years by submerged macrophyte monitoring (1992, 1998, 2003 and 2004 and 2007) and which contributed more than 0.05% cover in the latter two years.

Results

Total nitrogen and phosphorus, water clarity, chlorophyll and suspended solids

Following remediation treatments, levels of total nitrogen fell at Hejrede and Maribo Søndersø Lakes and total phosphorus fell in Hejrede Lake, whilst there was no change in total nitrogen at Røgbølle Lake, although total phosphorus fell over the study period (Table 1, Fig. 2). Water clarity improved at Hejrede and Maribo Søndersø Lakes, with increases in Secchi disc depth and significant declines in summer chlorophyll and suspended solids during 1989–2007 (Table 1, Fig. 2). Declines in suspended solids to relatively stable lower levels were especially (but asynchronously) evident at Hejrede and Maribo Søndersø Lakes with tipping points in 1996 and 1999, respectively (Fig. 2). Secchi depth and suspended solids showed no change at Røgbølle Lake, although summer chlorophyll fell, as water clarity was sustained prior to the start of and throughout the entire study period.

Changes in submerged macrophytes

Submerged macrophytes coverage increased at Maribo Søndersø Lake by 90% between summer 1998 (less than 10%, see Fig. 3) and 2003 and extended to all but the deepest lake sections (Fig. 3). Species richness increased from 10 submerged macrophyte species in 1998 to 29 in 2003, including eight charophytes and 17 higher plant species. The Danish Red-listed holly-leaved naiad *Najas marina* L. was first reported at Røgbølle Lake in 2001 but quickly spread throughout the entire lake. Much of the bottom was dominated by rigid hornwort *Ceratophyllum demersum* L. in 1997, which was only codominant by 2004, with solid stands of *Najas* (Orbicon, 2006). By the summer of 2006, *Najas* dominated the bottom vegetation throughout the lake, completely displacing

Table 1 Linear regression models (accounting for autocorrelation in parameters between years) for site-specific changes in summer lake parameters between 1989 and 2007 at Maribo Søndersø, Røgbølle and Hejrede Lakes

Lake	Parameter	Durbin–Watson d	T value	P value	Estimate
Hejrede	Chlorophyll	1.51	10.20	< 0.0001	– 4.082
Søndersø	Chlorophyll	1.96	8.20	< 0.0001	– 4.948
Røgbølle	Chlorophyll	1.92	4.02	0.004	– 0.478
Hejrede	Secchi disc	1.95	6.14	< 0.0001	0.065
Søndersø	Secchi disc	2.15	5.67	< 0.0001	0.055
Røgbølle	Secchi disc	1.63	0.24	0.812	0.002
Hejrede	Suspended solids	1.94	6.01	< 0.0001	– 1.813
Søndersø	Suspended solids	1.88	4.35	< 0.0001	– 2.122
Røgbølle	Suspended solids	1.95	10.82	0.421	– 0.023
Hejrede	Total phosphorus	1.63	6.33	< 0.0001	– 0.006
Søndersø	Total phosphorus	1.86	2.91	0.005	– 0.004
Røgbølle	Total phosphorus	1.81	7.24	< 0.0001	– 0.003
Hejrede	Total nitrogen	2.07	2.95	0.007	– 0.061
Søndersø	Total nitrogen	2.05	4.22	< 0.0001	– 0.059
Røgbølle	Total nitrogen	1.91	0.19	0.850	– 0.002

The Durbin–Watson d statistic tests for the presence of autocorrelation at lag 1 in the residuals (prediction errors) from each regression analysis. As a rule of thumb, values of $d = 2$ indicate no autocorrelation, $3 < d < 1$ give cause for concern about the influence of serial autocorrelation (Field, 2009), hence we accept these models in the absence of high levels of serial autocorrelation in any of them

charophytes and substantially reducing the area of *Potamogeton pectinatus* and *Ceratophyllum demersum* (Orbicon, 2006 and see below).

Numbers of breeding pochard

Numbers of female pochard at Hejrede Lake increased from 0 to 4 annually (mean 2.3) prior to 1997 to between 5 and 20 nesting birds (mean 13.9) between 1998 and 2007 (Fig. 4). Numbers at Maribo Søndersø Lake increased from an average of 22.7 (range 15–36) to 99.6 (20–205) birds before and after 1997, whereas numbers on Røgbølle Lake declined from 27.7 (5–45) nesting birds to 11.3 (4–20) during the two periods (Fig. 4) despite consistently good water quality throughout the study period (Fig. 5, see below). Numbers at the two newly restored lakes responded rapidly to the shift from turbid to clear water systems that occurred after 1996 at Hejrede Lake and in 1999 at Maribo Søndersø Lake, both following summers with declining suspended sediment.

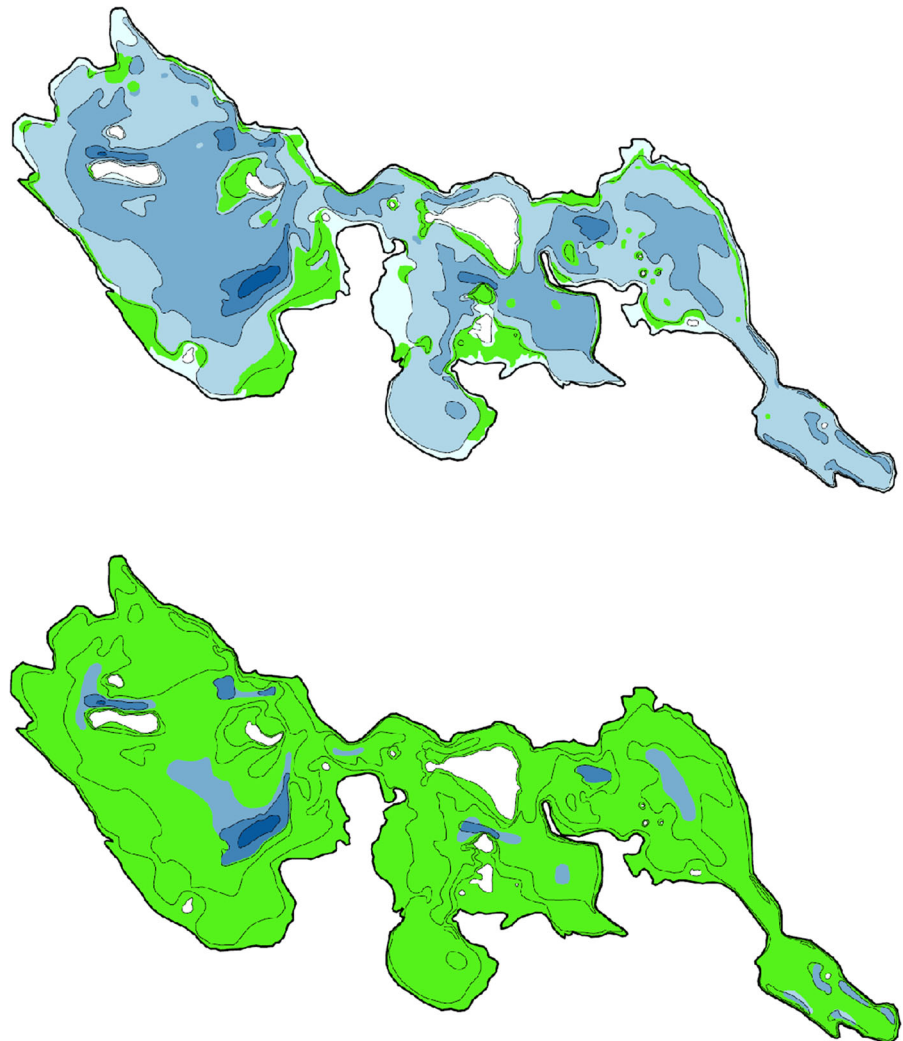
Relationships between numbers of breeding pochard, water parameters and macrophytes

Annual breeding pochard numbers on Hejrede and Maribo Søndersø Lakes significantly increased with declining suspended solids, increased Secchi disc measurements and declining summer chlorophyll at Maribo Søndersø (Table 2 and see Fig. 5 for biplots). Annual breeding pochard abundance showed no such relationships at Røgbølle Lake. At Maribo Søndersø Lake, submerged macrophyte covers of all species were positively correlated with pochard numbers, although only four to five of the nine Spearman correlations attained statistical significance (Table 3).

Discussion

This study is the first to demonstrate the recovery of breeding pochard abundance associated with lake restoration management to re-establish submerged macrophyte communities. As at many Danish lakes, removal of large numbers of bream and roach combined with nutrient loading reduction in eutrophic

Fig. 3 Distribution of continuous submerged bottom vegetation cover in Maribo Søndersø Lake (green shading) in 1998 (upper) and 2003 (lower). Successively darkening shades of blue indicate water depths at one metre intervals for information (taken from Liboriussen et al., 2007b)

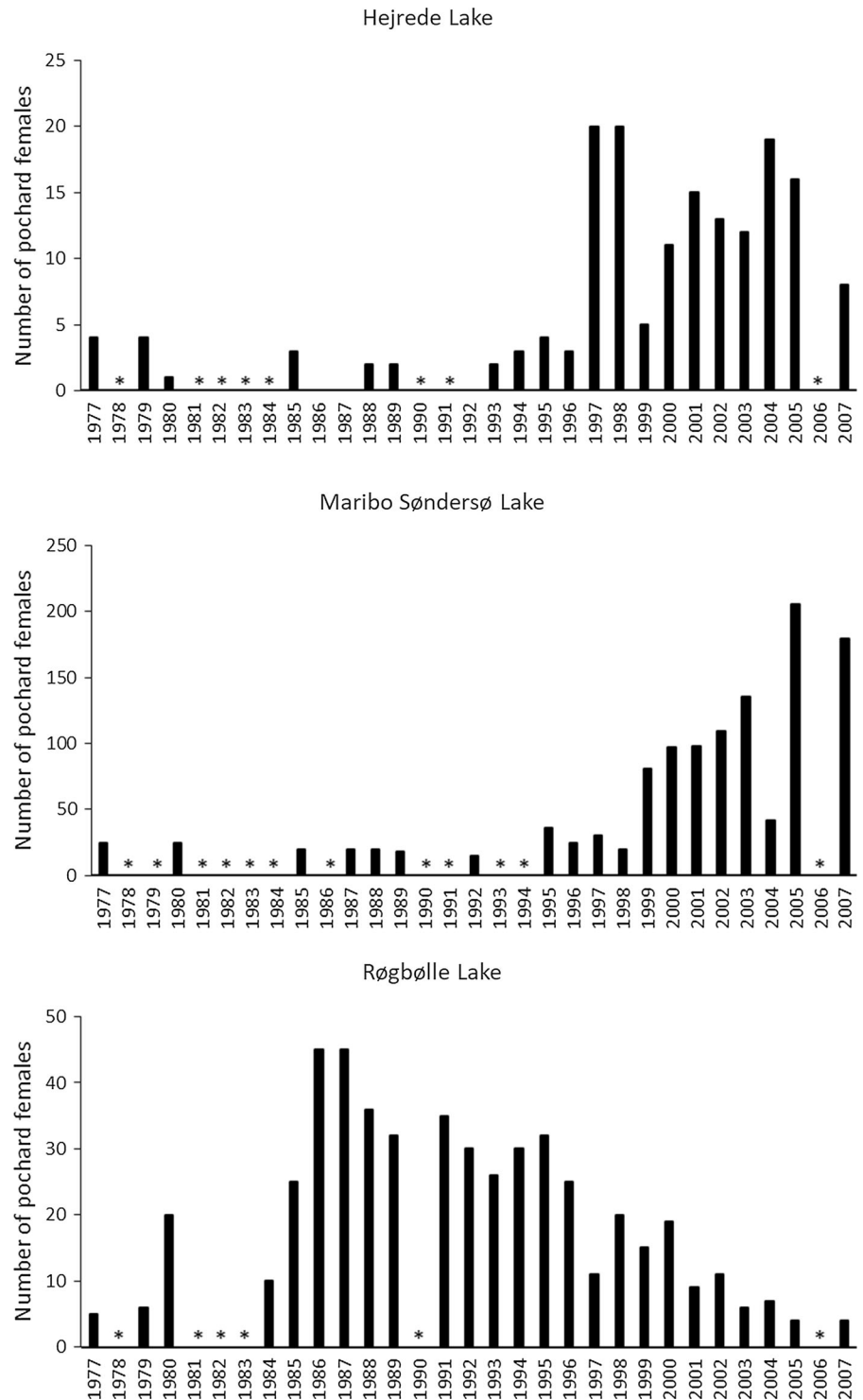


lakes improves water clarity and development of abundant submerged macrophytes (Søndergaard et al., 2008; Jeppesen et al., 2012). This, in turn, benefits top consumers such as breeding pochard, as demonstrated here at Maribo Søndersø and Hejrede Lakes, although it was not possible to determine whether this response was due to expansion of the vegetation cover or its presence as substrate and cover for invertebrates, since pochard are known to feed on both the macrophytes and the invertebrates within their canopy (Cramp & Simmons, 1977). However, it is well demonstrated that macroinvertebrate density increases substantially with increasing macrophyte coverage (Marklund et al., 2001; Boll et al., 2012).

Reduced wastewater incursion into the lakes prior to the onset of the present study had reduced internal

loading prior to bio-manipulation (Søndergaard et al., 2003), maintained throughout the study. Year-round elevated water levels of 30 cm in Maribo Søndersø Lake may have had a contributory effect. The systematic removal of bream and roach annually throughout the study shifted the fish community from one dominated by large planktivorous and benthivorous fish to one with increasing proportions of predatory pike and, to a larger extent perch. These factors combined permitted macrophyte development. In 1999, sudden increases in Secchi depth coincided with declines in chlorophyll and suspended solids and changes in water chemistry parameters. The 2003 vegetation survey showed almost all of Maribo Søndersø Lake was covered by submerged macrophytes, almost completely lost under the previous

Fig. 4 Numbers of breeding female pochard *Aythya ferina* registered at Hejrede, Maribo Søndersø and Røgbølle Lakes, 1989–2007. Asterisks indicate years when no counts were undertaken or considered inadequate to generate annual totals. See also methods for full details



ecological regime (shown by the 1998 survey). At Hejrede Lake, reductions in external loadings and in biomass of bream and roach also improved water

clarity and the slightly earlier return of nesting pochard was highly correlated with measures associated with these changes.

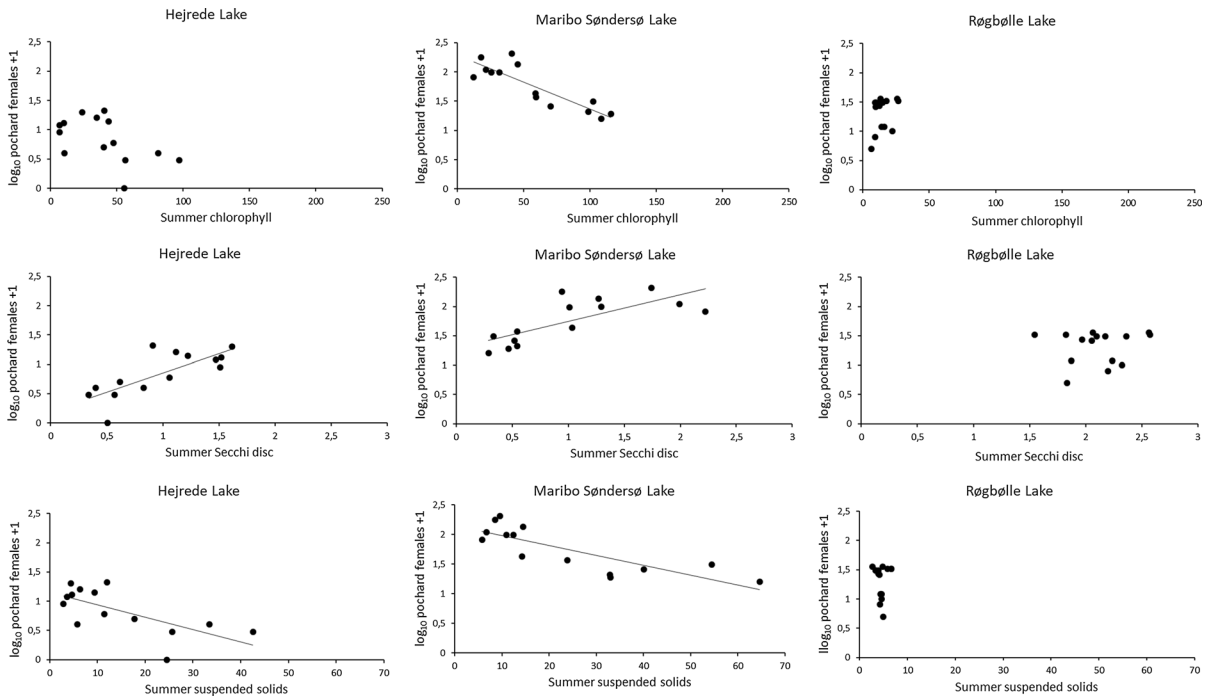


Fig. 5 Relationships between annual base 10 logarithmically transformed numbers of breeding female pochard *Aythya ferina* ($x + 1$) and summer determinations of chlorophyll (upper row

of graphs), Secchi depth determinations (middle row) and suspended solids (lowest row) from Hejrede, Maribo Sønderø and Røgbølle Lakes, 1989–2007. See methods for full details

Table 2 Linear regression models (accounting for autocorrelation in parameters between years) of the base 10 logarithmically transformed number of breeding pochard *Aythya ferina* ($x + 1$) in relation to summer water chlorophyll, suspended solids, Secchi disc depth, total P and total nitrogen determinations for each of the Maribo Lakes

Lake	Parameter	Durbin–Watson d	T value	P value	Estimate
Hejrede	Chlorophyll	1.68	1.06	0.303	− 0.003
Sønderø	Chlorophyll	1.95	8.99	< 0.001	− 0.007
Røgbølle	Chlorophyll	2.02	0.00	0.997	9.6×10^{-6}
Hejrede	Secchi disc	2.48	5.73	< 0.001	0.632
Sønderø	Secchi disc	1.98	5.92	< 0.001	0.222
Røgbølle	Secchi disc	2.08	0.88	0.388	0.046
Hejrede	Suspended solids	2.77	5.50	< 0.001	− 0.027
Sønderø	Suspended solids	1.98	4.26	< 0.001	− 0.009
Røgbølle	Suspended solids	2.02	0.02	0.985	0.0002
Hejrede	Total phosphorus	2.11	0.60	0.553	− 0.845
Sønderø	Total phosphorus	2.00	4.03	< 0.001	− 5.174
Røgbølle	Total phosphorus	2.03	0.27	0.789	0.377
Hejrede	Total nitrogen	1.91	1.44	0.166	− 0.098
Sønderø	Total nitrogen	1.89	6.84	< 0.001	− 0.122
Røgbølle	Total nitrogen	2.02	0.66	0.518	0.072

See Table 1 for explanation about Durbin–Watson statistic

In contrast to Hejrede and Maribo Sønderø Lakes, Røgbølle Lake had retained clear water column characteristics, which had not necessitated restoration activities. It sustained low total phosphorus,

suspended solids, summer chlorophyll and a clear water column throughout (Figs. 2, 5). In this state, Røgbølle Lake supported 30–40 nesting female pochard throughout the 1980s and early 1990s, but

Table 3 Spearman correlation between extent of submerged plant percentage cover (for species constituting more than 0.05% cover in 2004 and 2007) and base 10 logarithmically

transformed number of breeding pochard on Maribo Søndersø Lake based on survey data from 1992, 1998, 2003, 2004 and 2007 (see methods for full details)

Species names	R_s	P	N
<i>Ceratophyllum demersum</i> L.	0.90	< 0.05	5
<i>Ceratophyllum submersum</i> L.	0.87	0.05	5
<i>Chara globularis</i> Thuiller	0.90	< 0.05	5
<i>Chara tomentosa</i> L.	0.90	< 0.05	5
<i>Chara vulgaris</i> L.	0.80	0.10	5
<i>Nitella flexilis</i> (L.) C. Agaradh	0.67	0.22	5
<i>Nittelopsis obtusa</i> (Desvaux in Loisel.) J. Groves	0.56	0.32	5
<i>Potamogeton pectinatus</i> L.	0.60	0.28	5
<i>Potamogeton pusillus</i> L.	0.90	< 0.05	5

P values are for one-tailed tests following Proc corr in SAS 9.3 SAS Institute, Cary, NC

numbers declined to less than 10 in the 2000s (Fig. 4 compared to less than 30 pre- and 50–200 pochard pairs post restoration at Maribo Søndresø Lake). *Ceratophyllum demersum* was the dominant submerged vegetation type at Røgbølle Lake, with much *Potamogeton pectinatus* until at least 2004 (Storstrøms Amt, 1993, 1997, 1998, 2004, 2005). *Najas marina* was first reported at Røgbølle Lake in 2001 (Storstrøms Amt, 2004, 2005) although highly likely present undetected many years prior to this. This species spread rapidly, dominating the submerged vegetation throughout the lake by 2006, completely displacing charophytes and substantially reducing the area of *Potamogeton pectinatus* and *Ceratophyllum demersum* (Orbicon, 2006). Røgbølle Lake differed considerably from the two adjacent restored lakes in terms of water quality change and its colonisation by *Najas*, which spread aggressively and displaced submerged plants known to be attractive to breeding pochard (especially *Chara* and *Potamogeton* spp., Cramp & Simmons 1977). Investigations have found significantly lower densities of fish fry in *Najas* stands, which is because the above substrate biomass develops rapidly from July onwards and supports little cover for invertebrates during the period of nesting and brood rearing for pochard (Orbicon, 2006). *Najas marina* remains extremely rare in both other lakes and has certainly not achieved dominance over large proportions of the lake bottoms as at Røgbølle. *Najas marina* shows allelopathic activity (Gross et al., 2003), displacing other submerged macrophyte species in

studied freshwater systems (e.g. Mazej & Germ, 2008). At Røgbølle Lake, dense stands of this species developed above sediment biomass too late for pre-breeding female or post-hatching duckling pochard, potentially explaining declines in nesting pochard there in contrast to increases at the two neighbouring restored lakes (Orbicon, 2006). We therefore hypothesise that recent declines in pochard in later years at Røgbølle Lake was related to *Najas* colonisation, but acknowledge that there were signs of pochard decline before the plant was detected at the site.

Despite major between-year fluctuations in water clarity measures in Hejrede and Maribo Søndersø Lakes, these correlated well with breeding female pochard abundance throughout the study period, providing strong support for the hypothesis that a clear water column and a rich bottom flora in these eutrophic shallow lakes systems provide far better nesting and brood rearing conditions than did the same lakes in their previous turbid state, as long as the bottom flora is of suitable species composition. In particular, the positive relationships with some of the *Chara*, *Potamogeton* and *Ceratophyllum* species, known species favoured by foraging pochard (Cramp & Simmons, 1977), emphasise the link between extent of suitable foraging opportunities and breeding pochard numbers. This was not the case at Røgbølle Lake, where the increasingly *Najas* dominance might have contributed to the reduction in its attractiveness over the same period.

These results also provide more support for the argument that pochard declines throughout its breeding range are at least partly due to trophic shifts in shallow nutrient-rich lakes from clear to turbid water systems, which seem to be the case for autumn staging pochard, which also respond to similar improvements in water quality at two Swedish lakes (Andersson & Nilsson, 1999) in one case in response to submerged vegetation (Milberg et al., 2002). Most encouragingly, these results show that bio-manipulation of fish communities potentially reinstate conditions of improved water quality to restore breeding pochard numbers, although the apparent effects of *Najas marina* also confirmed that establishment of suitable submerged macrophyte communities is essential to secure maximum numbers of nesting pochard.

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References

- Andersson, G. & L. Nilsson, 1999. Autumn waterfowl abundance in Lake Ringsjön, 1968–1996. *Hydrobiologia* 404: 41–51.
- BirdLife International, 2015a. European Red List of birds. Office for Official Publications of the European Communities, Luxembourg.
- BirdLife International, 2015b. *Aythya ferina* (Common Pochard) – European Red List Status. Accessible at: http://www.birdlife.org/datazone/userfiles/file/Species/erlob/summarypdfs/22680358_aythya_ferina.pdf (last accessed 27 June 2016).
- Boll, T., D. Balayla, F. Ø. Andersen & E. Jeppesen, 2012. Can artificial plant beds be used to enhance macroinvertebrate food resources for perch (*Perca fluviatilis* L.) during the initial phase of lake restoration by cyprinid removal? *Hydrobiologia* 679: 175–186.
- Cramp, S. & K. E. L. Simmons, 1977. Handbook of the birds of Europe, the Middle East and North Africa (the Birds of the Western Palearctic); Vol. 1, Ostrich to Ducks. Oxford University Press, Oxford.
- Field, A. P., 2009. Discovering Statistics Using SPSS: and Sex and Drugs and Rock ‘n’ Roll, 3rd ed. Sage, London.
- Fox, A. D., A. Caizergues, M. V. Banik, M. Dvorak, M. Ellermåa, B. Folliot, A. J. Green, C. Grüneberg, M. Guillemain, A. Håland, M. Hornman, V. Keller, A. I. Koshelev, V. A. Kostyushin, A. Kozulin, Ł. Ławicki, L. Luigujõe, C. Müller, P. Musil, Z. Musilová, L. Nilsson, A. Mischenko, H. Pöysä, M. Šćiban, J. Sjeničić, A. Stipnicec, S. Švažas & J. Wahl, 2016. Recent changes in the abundance of breeding common pochard *Aythya ferina* in Europe. *Wildfowl* 66: 22–40.
- González Sagrario, M. A., E. Jeppesen, J. Gomà, M. Søndergaard, J. P. Jensen, T. L. Lauridsen & F. Landkildehus, 2005. Does high nitrogen loading prevent clear-water conditions in shallow lakes at moderately high phosphorus concentrations? *Freshwater Biology* 50: 27–41.
- Gross, E. M., D. Erhard & E. Iványi, 2003. Allelopathic activity of *Ceratophyllum demersum* L. and *Najas marina* ssp. *intermedia* (Wolfgang) Casper. *Hydrobiologia* 506–509: 583–589.
- Hansson, L.-A., H. Annadotter, E. Bergman, S. F. Hamrin, E. Jeppesen, T. Kairesalo, E. Luokkanen, P.-Å. Nilsson, M. Søndergaard & J. Strand, 1998. Biomanipulation as an application of food-chain theory: constraints, synthesis, and recommendations for temperate lakes. *Ecosystems* 1: 558–574.
- Hansson, L.-A., A. Nicolle, C. Brönmark, A. Hargeby, Å. Lindström & G. Andersson, 2010. Waterfowl, macrophytes, and the clear water state of shallow lakes. *Hydrobiologia* 646: 101–109.
- Hilt, S., S. Brothers, E. Jeppesen, A. J. Veraart & S. Kosten, 2017. Translating regime shifts in shallow lakes into changes in ecosystem functions. *Bioscience* 67: 928–936.
- Hirschfeld, A. & A. Heyd, 2005. Mortality of migratory birds caused by hunting in Europe: bag statistics and proposals for the conservation of birds and animal welfare. *Berichte zum Vogelschutz* 42: 47–74.
- Ibelings, B. W., R. Portielje, E. H. R. R. Lammens, R. Noordhuis, M. van den Berg, W. Joosee & M. L. Meijer, 2007. Resilience of alternative stable states during the recovery of shallow lakes from eutrophication: Lake Veluwe as a case study. *Ecosystems* 10: 4–16.
- IUCN, 2015. The IUCN Red List of Threatened Species, Version 2015-4. Available at: www.iucnredlist.org (last accessed 27 June 2016).
- Jeppesen, E., M. Søndergaard, M. Søndergaard & K. Christoffersen (eds), 1998. The Structuring Role of Submerged Macrophytes in Lakes. Springer, New York.
- Jeppesen, E., M. Søndergaard, J. P. Jensen, K. E. Havens, O. Anneville, L. Carvalho, M. F. Coveney, R. Deneke, M. T. Dokulil, B. Foy, D. Gerdeaux, S. E. Hampton, S. Hilt, K. Kangur, J. Köhler, E. H. R. R. Lammens, T. L. Lauridsen, M. Manca, M. R. Miracle, B. Moss, P. Nöges, G. Persson, G. Phillips, R. Portielje, S. Romo, C. L. Schelske, D. Straile, I. Tatrai, E. Willén & M. Winder, 2005. Lake responses to reduced nutrient loading – an analysis of contemporary long-term data from 35 case studies. *Freshwater Biology* 50: 1747–1771.
- Jeppesen, E., M. Søndergaard, T. L. Lauridsen, T. A. Davidson, Z. Liu, N. Mazzeo, C. Trochine, K. Özkan, H. S. Jensen, D. Trolle, F. Starling, X. Lazzaro, L. S. Johansson, R. Bjerling, L. Liboriussen, S. E. Larsen, F. Landkildehus & M. Meerhoff, 2012. Biomanipulation as a restoration tool to combat eutrophication: recent advances and future challenges. *Advances in Ecological Research* 47: 411–487.
- Koskimies, P. & R. A. Väisänen, 1991. Monitoring Bird Populations: A Manual of Methods Applied in Finland. Zoological Museum, Finnish Museum of Natural History,

- University of Helsinki. Accessible at https://www.luomus.fi/sites/default/files/files/04b_waterfowl_round_counts.pdf.
- Liboriussen, L., M. Søndergaard & E. Jeppesen (eds), 2007a. Søresuarering i Danmark. Del I: Tværgående analyser. Technical Report 636. Danmarks Miljøundersøgelser, Aarhus Universitet.
- Liboriussen, L., M. Søndergaard & E. Jeppesen (eds), 2007b. Søresuarering i Danmark. Del II: Eksempelsamling. Technical Report 636. Danmarks Miljøundersøgelser, Aarhus Universitet.
- Marklund, O., I. Blindow & A. Hargeby, 2001. Distribution and diel migration of macroinvertebrates within dense submerged vegetation. *Freshwater Biology* 46: 913–924.
- Mazej, Z. & M. Germ, 2008. Competitive advantages of *Najas marina* L. in a process of littoral colonization in the lake Velenjsko jezero (Slovenia). *Acta Biologica Slovenica* 51: 13–20.
- MESN, 1995. EF-fuglebeskyttelsesområder og Ramsarområder: kort og områderbeskrivelser. Miljø- og Energiministeriet Skov og Naturstyrelsen, København.
- Milberg, P., L. Gezelius, I. Blindow, L. Nilsson & T. Tyrberg, 2002. Submerged vegetation and the variation in the autumn waterfowl community at Lake Takern, southern Sweden. *Ornis Fennica* 79: 72–81.
- Moss, B., 1990. Engineering and biological approaches to the restoration from eutrophication of shallow lakes in which aquatic plant communities are important components. *Hydrobiologia* 200: 367–377.
- Nagy, S., S. Flink & T. Langendoen, 2014. Waterbird trends 1988–2012 Results of trend analyses of data from the International Waterbird Census in the African-Eurasian Flyway. Report by Wetlands International, Ede, the Netherlands. Accessible at: http://www.wetlands.org/Portals/0/TRIM%20Report%202014_10_05.pdf (last accessed 29 May 2015).
- Noordhuis, R., D. van der Molen & M. van den Berg, 2002. Response of herbivorous water-birds to the return of *Chara* in Lake Valuwemeer, The Netherlands. *Aquatic Botany* 72: 349–367.
- Orbicon, 2006. Stor najade i Røgbølle Sø og dens indflydelse på de biologiske forhold 2006. Report by Orbicon, Åbyhøj, Denmark to Storstrøm County.
- Rip, W. J., N. Rawee & A. de Jong, 2006. Alteration between clear, high-vegetation and turbid, low-vegetation states in a shallow lake: the role of birds. *Aquatic Botany* 85: 184–190.
- Scheffer, M., S. H. Hosper, M. L. Meijer, B. Moss & E. Jeppesen, 1993. Alternative equilibria in shallow lakes. *Trends in Ecology and Evolution* 8: 275–279.
- Schriver, P., J. Bøgestrand, E. Jeppesen & M. Søndergaard, 1995. Impact of submerged macrophytes on fish-zooplankton-phytoplankton interactions – large-scale enclosure experiments in a shallow eutrophic lake. *Freshwater Biology* 33: 255–270.
- Skov, C. & P. A. Nilsson, 2007. Evaluating stocking of YOY pike *Esox lucius* as a tool in the restoration of shallow lakes. *Freshwater Biology* 52: 1834–1845.
- Søndergaard, M., J. P. Jensen & E. Jeppesen, 2003. Role of sediment and internal loading of phosphorus on shallow lakes. *Hydrobiologia* 506: 135–145.
- Søndergaard, M., E. Jeppesen & J. P. Jensen, 2005. Water Framework Directive: ecological classification of Danish lakes. *Journal of Applied Ecology* 42: 616–629.
- Søndergaard, M., E. Jeppesen, T. L. Lauridsen, C. Skov, E. H. Van Nes, R. Roijackers, E. Lammens & R. Portielje, 2007. Lake restoration in Denmark and the Netherlands: successes, failures and long-term effects. *Journal of Applied Ecology* 44: 1095–1105.
- Søndergaard, M., L. Liboriussen, A. R. Pedersen & E. Jeppesen, 2008. Lake restoration by fish removal: short and Long-term effects in 36 Danish lakes. *Ecosystems* 11: 1291–1305.
- Storstrøms Amt, 1993. Bundvegetationen i Maribo Sønderø og Røgbølle Sø 1992. Report from Bio/consult as.
- Storstrøms Amt, 1997. Vegetationsundersøgelser i Røgbølle Sø 1996. Report from Bio/consult a/s, Åbyhøj, Denmark.
- Storstrøms Amt, 1998. Vegetationen i Røgbølle Sø 1997. Report from Bio/consult a/s, Åbyhøj, Denmark.
- Storstrøms Amt, 1999. Vegetationen i Maribo Sønderø 1998. Report from Bio/consult a/s, Åbyhøj, Denmark.
- Storstrøms Amt, 2004. Vegetationen i Maribo Sønderø 2003. Report from Bio/consult a/s, Åbyhøj, Denmark.
- Storstrøms Amt, 2005. Vegetationen i Maribo Sønderø 2004. Report from Bio/consult a/s, Åbyhøj, Denmark.
- Svendsen, L. M., L. van der Bijl, S. Boutrup & B. Norup (eds), 2005. NOVANA. National Monitoring and Assessment Programme for the Aquatic and Terrestrial Environments Programme Description, Part 2. NERI Technical Report No. 537. National Environmental Research Institute, Aarhus, Denmark. http://www.dmu.dk:80/NR/rdonlyres/5EC5E735-724E-4769-A560-D53613C89536/0/FR537_www_S_H.pdf.
- van den Berg, M., M. Scheffer, H. Coops & J. Simons, 1998. The role of Characean algae in the management of eutrophic shallow lakes. *Journal of Phycology* 34: 750–756.
- van der Molen, D. T. & R. Portielje, 1999. Multi-lake studies in the Netherlands: trends in eutrophication. *Hydrobiologia* 409: 359–365.