Arch. Hydrobiol. **162** 2 143–165 Stuttgart, February 2005

Pond or lake: does it make any difference?

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With 7 figures and 5 tables

Abstract: To investigate the importance of lake size, we analysed the chemical and biological characteristics of nearly 800 Danish lakes ranging from 0.01 to 4200 ha. Most of the lakes were shallow (median depth = 1.5 m) and eutrophic (lake water mean total phosphorus = 0.26 mg P l^{-1} and mean chlorophyll-a = 60 µg l^{-1}). Phosphorus and nitrogen concentrations were unaffected by lake size, but positively related to agricultural exploitation. Lakes < 1 ha showed a higher variability in phosphorus concentrations, but had a lower chlorophyll yield per unit of both nitrogen and phosphorus, which is indicative of less importance of nutrients in small lakes. Fish were absent in most lakes smaller than 0.1 ha and mean fish biomass was markedly lower in lakes < 1 ha than in lakes > 1 ha. The absence of fish did, however, not result in higher abundance of *Daphnia*, suggesting a higher impact by invertebrate predators in small lakes. Taxon richness of both zoo- and phytoplankton was weakly related to lake size, whereas the number of submerged macrophyte and fish species increased steadily with lake size. Also species richness of macrophytes increased with increasing alkalinity. The low impact of lake size on the species richness of several taxonomic groups suggests that ponds and small lakes are important biodiversity components in the agricultural landscape.

Key words: catchment, phosphorus, phytoplankton, fish, zooplankton, macrophytes, biodiversity.

Introduction

Research into the role of environmental factors such as nutrient loading and other anthropogenic stresses for lake water quality has focused traditionally on relatively large lakes (WETZEL 2001). Small lakes or ponds covering only few hectares or less have received less attention despite their numerical prevalence

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DOI: 10.1127/0003-9136/2005/0162-0143 0003-9136/05/0162-0143 $ 5.75

and rich biological diversity (BIGGS et al. 1999, OERTLI et al. 2002, WILLIAMS et al. 2003). In Denmark, for example, lake research has concentrated on lakes > 5 ha, although these constitute only 0.5 % of the 120,000 Danish lakes > 0.01 ha. The existing pond studies have mainly been directed towards specific taxa, such as amphibians and odonates (OERTLI et al. 2002), macrophytes (PALMER et al. 1992, VAN GEEST et al. 2003) or the nutrient retention capacity of wetland ponds (JOHNSTON 1991, NAIRN & MITSCH 2000). Thus, while a broad ecological understanding has been gained in recent decades of human influence on large lakes, the overall ecological function of ponds has been less well elucidated (PALIK et al. 2001, TESSIER & WOODRUFF 2002). There is no doubt, however, that data from pond systems including interactions between the pelagic and the littoral zone and the benthic-pelagic coupling may provide useful insight into the function of particularly shallow and relatively small lakes. Still, comparative ecological studies along a gradient in lake size are few (e. g. TONN & MAGNUSSON 1982, WELLBORN et al. 1996, TESSIER & WOODRUFF 2002), which renders it difficult to determine the extent to which existing knowledge from large lakes may be applied to small lakes or ponds and vice versa.

The discrimination between large lakes and small lakes or ponds is difficult to establish as the lake size gradient comprises an environmental continuum without any clear delimitation (WELLBORN et al. 1996). However, several factors suggest that the two lake types differ. Small lakes and ponds: 1) have closer contact with the adjacent terrestrial environment and a relatively greater littoral zone (PALIK et al. 2001) and thus higher terrestrial-aquatic interchange of both organisms and matter; 2) are potentially more isolated from other wetlands and have a more insular nature compared with the often large catchments and riverine inflows of large lakes; 3) exhibit a potential lack of fish owing to winter fish kill and summer dry out. Fish may potentially have strong cascading effects on multiple levels in both larger and small lakes (WELLBORN et al. 1996, JEPPESEN et al. 1997); 4) exhibit an increased importance of invertebrate predators taking over the role of fish when absent (YAN et al. 1991, HOBÆK et al. 2002); 5) have a shallow and wind-protected morphometry, implying that submerged and floating-leaved macrophytes potentially cover large parts of or even the whole lake area under favourable conditions; 6) have relatively stagnant water favouring certain species of flora and fauna and often also a relatively more heterogeneous environment, the overall biological diversity measured per unit of area thus being higher in small lakes and ponds (GEE et al. 1997, OERTLI et al. 2002); and 7) have a relatively low water volume and low input of water resulting in enhanced benthic-pelagic coupling and greater impact by the sediment on the water's content of nutrients (TESSIER & WOODRUFF 2002). High benthic-pelagic coupling may explain why phytoplankton is less often limited by phosphorus in small lakes (BARICA 1974, LIM et al. 2001, WAISER 2001).

The need for acquiring knowledge has become increasingly obvious following the initiation of a multitude of restoration projects in wetlands and ponds in recent decades with the aim to mitigate the loss of wetlands and to protect flora and fauna, including waterfowl populations (ZEDLER 2000, ANGELER et al. 2003). In Denmark, after a century with dramatically decreasing numbers of particularly small lakes following land reclamation from intensified agriculture and a growing population, about 700 small lakes and ponds are now created yearly (Danish Forest and Nature Agency 2002). In this study we have collated existing morphological, physical, chemical and biological data from 796 Danish lakes of different sizes, ranging from 0.012 ha to 4200 ha. The aim was to elucidate the overall changes in chemical conditions and biological structure along a gradient of lake size.

Methods

Study lakes

Survey data from a total of 796 lakes distributed all over Denmark were included in the analyses. Chemical data were available from more lakes than biological data. Only six lakes were > 1000 ha, while 56 were between 100 and 1000 ha, 169 between 10 and 100 ha, 478 between 1 and 10 ha, 55 between 0.1 and 1 ha and 32 were < 0.1 ha. A majority of the lakes were shallow (median mean depth = 1.5 m) and only 10 % had a mean depth > 6 m. Most lakes were situated in intensively agri-cultivated areas with considerable anthropogenic impact.

Sampling and analyses

Data were collated mainly by the local counties using standard sampling techniques and analyses (KRONVANG et al. 1993). For lakes smaller than 5 ha, sampling was typically conducted once or only a few times during the summer season, while most larger lakes were sampled once monthly or more frequently during summer. In the latter case, mean summer values (1 May–1 October) were calculated for each year and in case of data from several years, these were averaged to obtain one value for each lake.

Water for chemistry and plankton analyses was collected as surface samples from a mid-lake station. Water used for chemical analyses of dissolved forms was filtered on Whatman GF/C-filters. Chemical parameters and chlorophyll-a (CHLA) were analysed according to standard procedures (JESPERSEN & CHRISTOFFERSEN 1987, SØNDERGAARD et al. 1992). Organic-bound nitrogen (Org-N) was calculated as the difference between total nitrogen (TN) and the inorganic nitrogen fractions [ammonia (NH_4) and nitrate + nitrite (NO_3)]. Quantitative measurements of the fish stock were expressed as CPUE (catch per unit effort) using standardised 42 m long multiple mesh-sized gill nets with 14 different mesh sizes, ranging from 6.25 mm to 75 mm (MORTENSEN et al. 1991, JEPPESEN et al. 2004). The nets were typically set in late afternoon and retrieved the following morning after 18 hours, except for lakes < 0.5 ha, where the nets were retrieved after one hour to avoid a significant reduction in the fish stock. In lakes >5 ha, 6–24 nets were used, while one or a few nets were used in lakes <5 ha. Zooplankton and phytoplankton were fixed in Lugol's iodine and identified down to the lowest feasible taxonomic level, usually genus or sometimes species level. Presence/absence, and in some lakes also relative abundance (%-coverage of lake area), of submerged macrophytes were recorded during maximum abundance in July or August. Coverage was grouped into the following categories: 0–1, 1–5, 5–25, 25–50, 50–75 and 75–100 % of total lake area.

GIS and statistics

GIS (Geographical Information System) data were used to categorize lakes of different sizes and to relate lake data with land use characteristics in the nearest surroundings. As an example representing a typical geological and land use landscape of Denmark, this analysis was conducted on data from the island of Funen only (2,985 km^2 representing 7 % of Denmark), including approximately 11,000 lakes ranging in size from 0.01 to 317 ha. GIS data were used to define land use within a distance of 25, 50, 100 and 500 m of lake shores, and the results were subsequently correlated with water quality variables. Land use was classified according to five major categories: residential, cultivated, pasture/forest (natural grassland, forest, heath), wetlands (bogs, meadows, etc.) and "others".

Statistical analyses were performed using SAS (SAS Institute 1989). Canonical correspondence analyses (CCA) on submerged macrophyte communities and environmental variables were performed using SAS statistics and conducted according to TER BRAAK & SMILAUER (1998). We only conducted CCA analysis on submerged macrophytes, however, as complete data sets for other biological variables (zooplankton, fish and phytoplankton) were too scarce, particularly for small-sized lakes. We also performed linear regression using proc GLM or proc REG and proc NLIN for non-linear regression. Regression analyses were performed on log-transformed data.

Results

Physical and chemical variables

Mean depth in lakes increased significantly with increasing lake area, from about 1 m in the smallest lakes to 3 m in the largest lakes (Fig. 1, Table 1). Water colour decreased steadily from a median value of 150 mg Pt l^{-1} in lakes <0.1 ha to about 20 mg Pt l^{-1} in lakes >100 ha. pH increased by about one unit from the smallest to the largest lakes, while silica and total alkalinity only varied slightly along the size gradient. Both Secchi depth and suspended solid concentrations increased significantly with increasing lake size, but the correlation was weak.

A majority of the lakes were eutrophic and had a total phosphorus concentration (TP) above 0.1 mg P l^{-1} (Fig. 2). Neither TP, soluble reactive phospho-

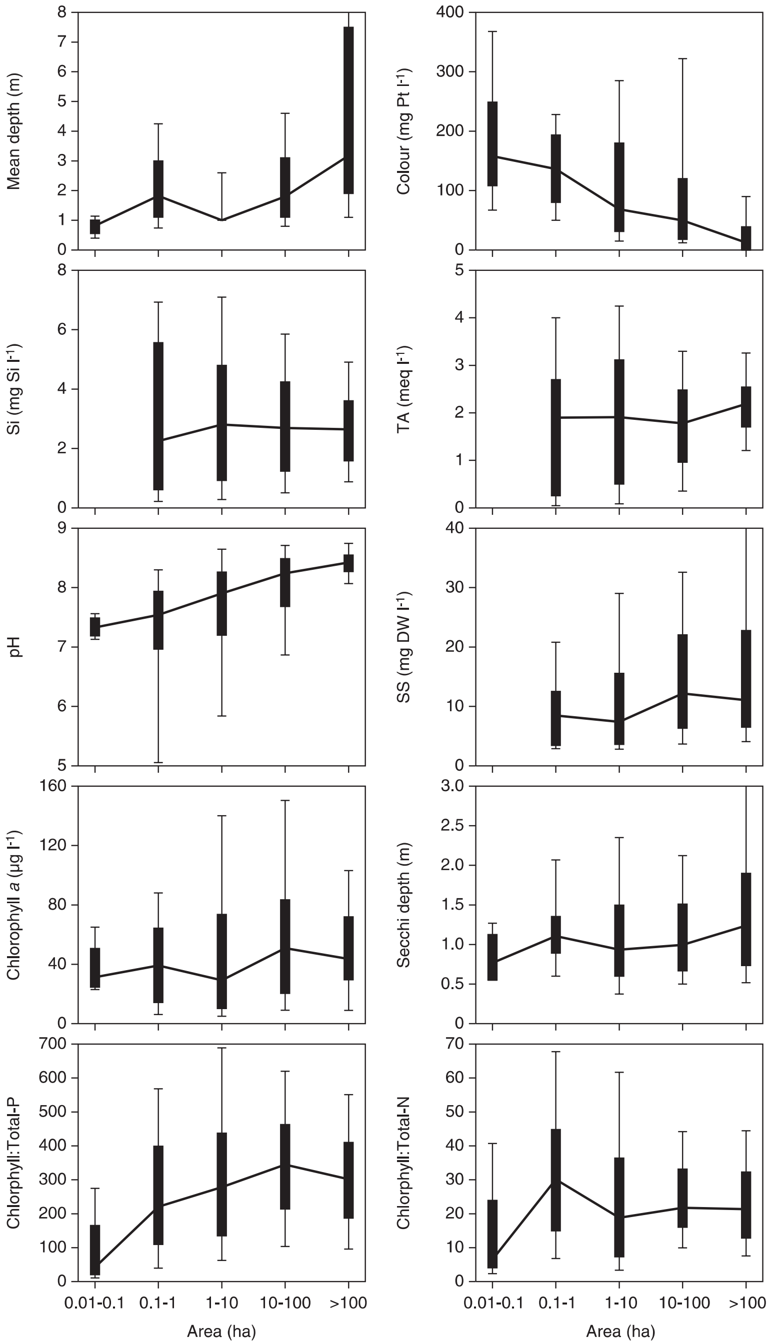

Fig. 1. Physical and chemical variables along a lake size gradient shown as box-plots. Each box shows 25 and 75 % percentiles, the horizontal line the mean value, and the top and bottom of the thin line depict the 90 and 10 % percentiles.

Table 1. Linear regression between physical-chemical characteristics and lake area and depth (on log transformed data). The right part of the table shows a multiple regression including both area and depth (proc REG, forward selection, entry level = 0.1). N = number of lakes, p = level of significance and r^2 = coefficient of determination with + or –, indicating a positive or negative relationship. For the multiple regression R^2_a and R^2_d are the partial correlation coefficients for area and depth, respectively.

	Area			Depth			Area & depth			
Variable	N	p	r^2	N	p	r^2	N	p	R^2_a	R^2_d
Mean depth	698	<0.001	+0.25	–	–	–	–	–	–	–
Colour	187	<0.001	−0.10	187	0.001	−0.10	171	0.001	0.13	–
TP	777	0.48	–	683	0.007	−0.01	682	0.007	0.01	0.01
SRP	579	0.63	–	488	0.38	–	487	>0.1	–	–
SRP/TP	576	0.07	–	486	0.001	+0.04	485	0.001	–	0.04
Total N	775	0.04	+0.01	681	0.02	−0.01	680	0.02	0.02	0.01
NO_3	602	<0.001	+0.13	510	0.001	+0.04	508	0.001	0.14	–
NH_4-N	571	0.04	+0.01	479	0.33	–	478	>0.1	–	–
Si	454	0.07	–	393	0.009	−0.02	392	0.009	0.03	0.02
TA	641	0.03	+0.01	556	0.20	–	556	0.027	0.01	–
pH	714	<0.001	+0.05	627	0.007	+0.01	626	0.001	0.07	–
Susp. solids	566	<0.001	+0.05	513	0.049	−0.01	512	0.001	0.05	0.06
CHLA	702	<0.001	+0.02	627	0.11	–	626	0.001	0.02	0.03
CHLA : TP	699	0.001	+0.01	624	0.51	–	623	0.002	0.02	–
CHLA : TN	699	0.01	+0.01	624	0.56	–	623	0.010	0.01	0.01
Secchi depth	689	0.004	+0.01	615	0.001	+0.16	614	0.001	0.01	0.16

rus (SRP) nor the SRP : TP ratio changed significantly with lake size, but the upper 10 and 25 % fractiles of TP were higher in the smallest lakes. TN increased slightly with lake size, while nitrate + nitrite concentrations (NO_3) differed, particularly between lakes < 10 ha and lakes > 10 ha, mean NO_3 being 0.57 mg N l^{-1} (SD = 1.2, n = 384) and 1.26 (SD = 3.2, n = 220), respectively. Ammonia increased slightly with lake size, but very high concentrations were found mostly in lakes < 1 ha. Correspondingly, Org-N was particularly low in lakes <0.1 ha. The TN : TP ratio did not vary along a size gradient.

In a multiple regression including both depth and area, some of the chemical variables like suspended solids, Secchi depth, TP, TN and silica (Si) correlated significantly to both area and depth; the correlation was generally weak, however (Table 1). For Secchi depth the correlation was much stronger to depth (partial R^2 = 0.16) than to area (partial R^2 = 0.01). Some of the variables, colour, NO_3, pH, total alkalinity (TA) and the CHLA : TP ratio related significantly only to area.

In the multiple regression using TP, TN, area and depth as explainable variables, particularly suspended solids and CHLA were highly correlated (r^2 = 0.41–0.43) to TP (Table 2). The correlation to Secchi depth was negative, but this result should be interpreted with caution as Secchi depth cannot be

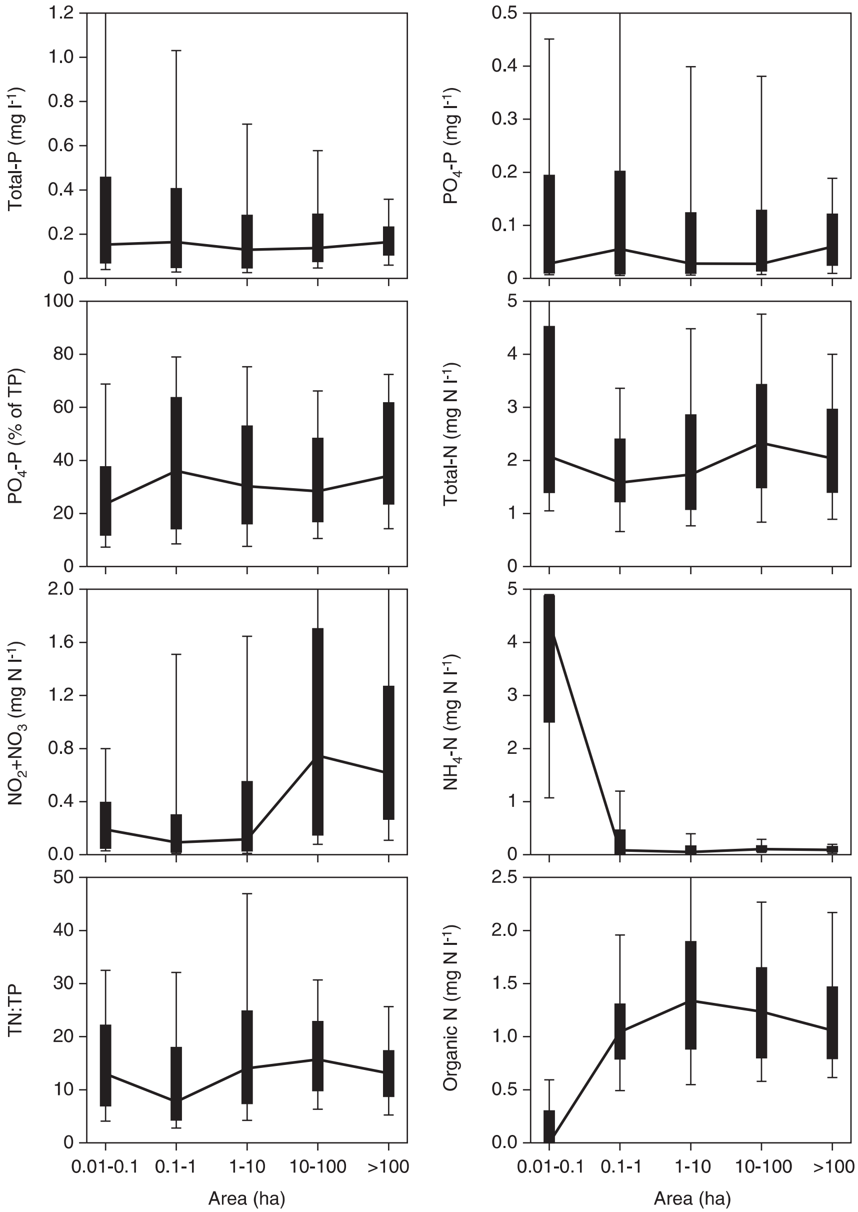

Fig. 2. Nitrogen and phosphorus concentrations along a lake size gradient shown as box-plots. See also legend to Fig. 1.

measured correctly in many of the shallow lakes (> maximum depth). TN, area and depth were significantly related to CHLA and suspended solids also, but the correlation was generally weak. Inclusion of water colour reduced the

Table 2. Multiple regression between CHLA, suspended solids, pH, Secchi depth and TP, TN, lake area and lake depth (on log transformed data, proc REG, forward selection, entry level = 0.1). N = number of lakes, p = level of significance and R^2 = multiple coefficient of determination and r^2 = coefficient of determination (for the model or as the partial correlation coefficient) with + or –, indicating a positive or negative relationship.

Variable	N	Model	TP		TN		Area		Depth	
		R^2	p	r^2	p	r^2	p	r^2	p	r^2
CHLA	623	0.47	0.001	+0.43	0.001	+0.02	0.001	+0.01	0.028	–0.00
Susp. solids	512	0.48	0.001	+0.41	0.001	+0.04	0.001	+0.02	0.001	–0.02
pH	611	0.13	0.001	+0.07	>0.1	–	0.001	+0.06	>0.1	–
Secchi depth	596	0.46	0.001	–0.31	0.001	–0.02	>0.1	–	0.001	+0.12

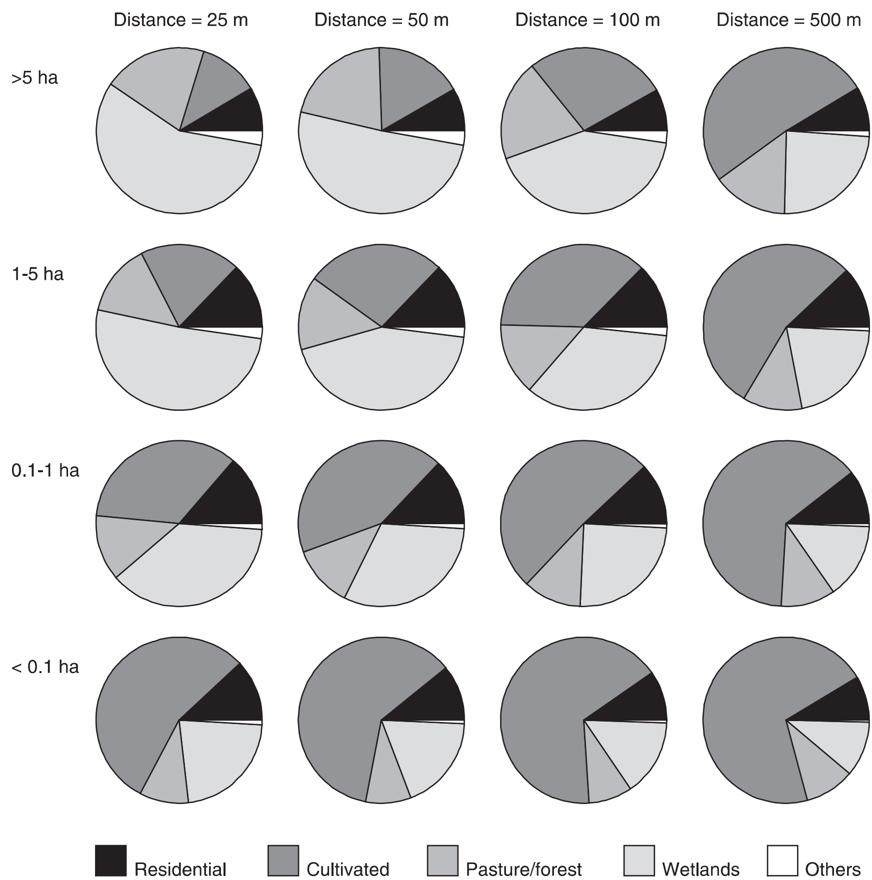

Fig. 3. Land use in catchments of all lakes and ponds on the island of Funen (total number of lakes = ca. 11,000). The lakes are divided into 5 size classes and the calculations performed for 4 zones surrounding the lakes (25, 50, 100 and 500 m). Data from the AIS system (NIELSEN et al. 2000).

Table 3. Correlation analyses (Spearman) between land use (within 25 m of the lake) and lake water measurements from lakes on the island of Funen. r = correlation coefficient with + or –, indicating a positive or negative relationship and p = level of significance.

Variable	TP		TN		CHLA		Secchi		Alkalinity		pH	
	p	r	p	r	p	r	p	r	p	r	p	r
Residential	0.005	+0.11	+0.21	–	+0.76	–	+0.11	–	<0.001	+0.32	<0.001	+0.36
Cultivated	<0.001	+0.16	+0.002	+0.12	+0.04	+0.08	+0.79	–	<0.001	+0.36	<0.001	+0.32
Wetlands	<0.001	+0.22	<0.001	+0.20	<0.001	+0.20	<0.001	−0.26	+0.44	–	+0.44	–
Pasture/forest	<0.001	−0.26	<0.001	−0.22	<0.001	−0.17	<0.001	0.27	<0.001	−0.33	<0.001	−0.36

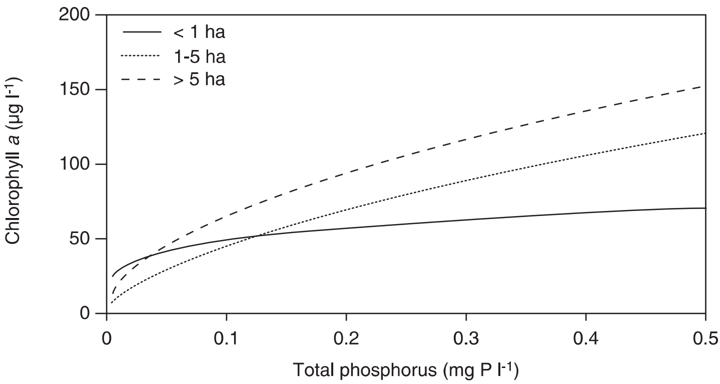

Fig. 4. The relationship between total phosphorus and chlorophyll-a in lakes of different areas. Parameter estimates (proc nlin, SAS) using CHLA = a xTP^b: lake area <1 ha (n = 41): a = 57, b = 0.18; lake area = 1–5 ha (n = 363): a = 211, b = 0.64; lake area >5 ha (n = 236): a = 125, b = 0.41.

number of lakes to 129, but CHLA was not significantly ($p > 0.1$) related to colour in a multiple regression including also TP, TN, area and water depth.

Land use around the lakes and its relation to nutrient concentrations

Cultivated areas and wetlands were the most common land types surrounding the lakes and ponds (Fig. 3), and the proportion of cultivated land increased from 10–50 % for lakes >5 ha to between 55 % and 70 % for lakes <0.1 ha. For all size classes, the cultivated share increased with increased size of the surrounding zone. This pattern was most clear for lakes >1 ha, and for lakes >5 ha the percentage of cultivated land increased from 10 % if a 50 m zone around the lake was included, to 50 % using a 500 m zone. Corresponding to the increased share of agricultural areas, particularly the size of wetland area decreased. In a single factor analysis TP, TN, CHLA, total alkalinity (TA) and pH were significantly and positively related to the agricultural exploitation of the catchment zone, but negatively so to the share of pasture/forest (Table 3).

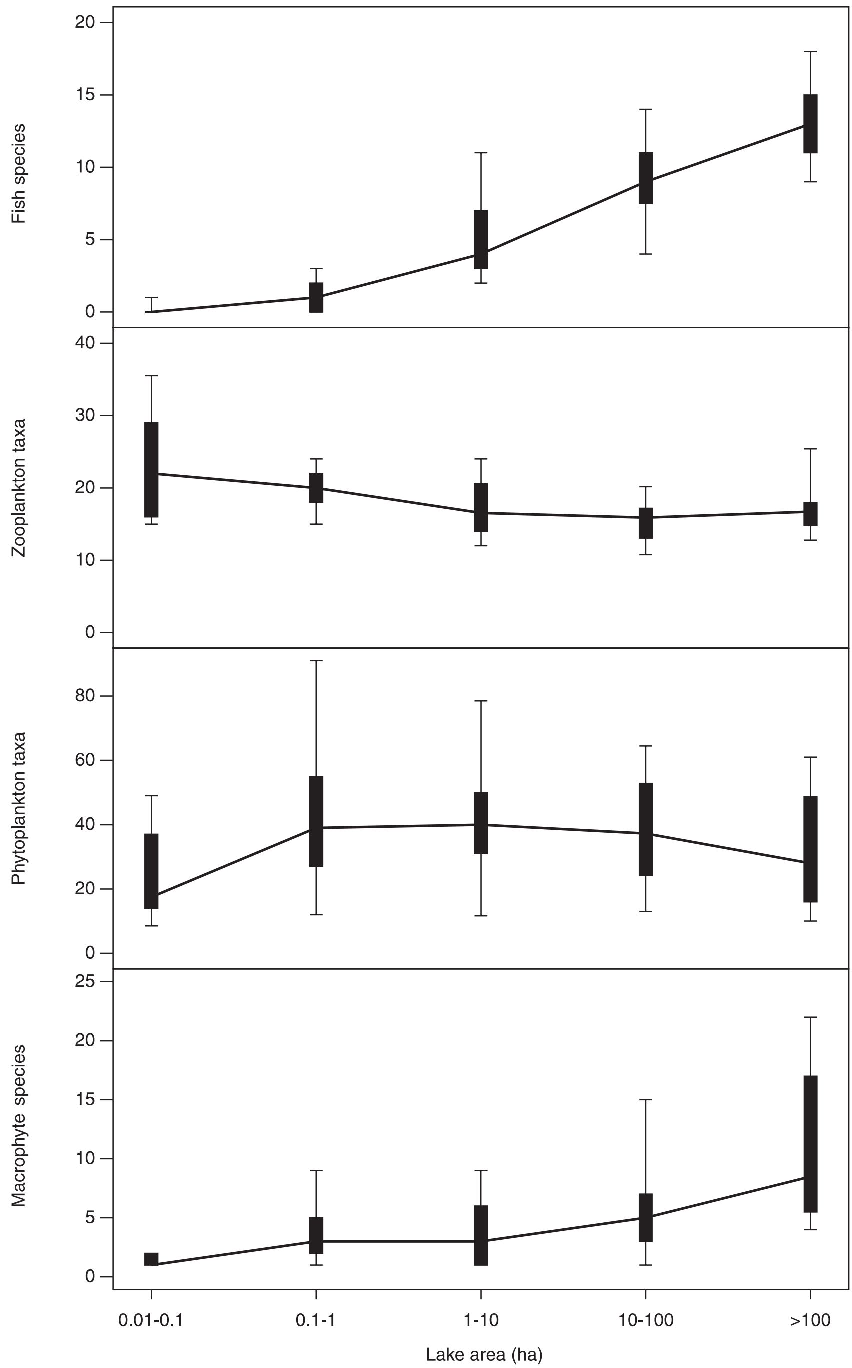

Fig. 5. Species and taxa numbers of fish, zooplankton, phytoplankton and submerged macrophytes along a lake size gradient shown as box-plots. See also legend to Fig. 1.

Phytoplankton

CHLA varied considerably, but increased significantly with lake size. The CHLA : TP and CHLA : TN ratios both correlated significantly and positively with lake area, and the ratios were markedly lower in lakes < 0.1 ha than in larger lakes (Fig. 1). The overall lower CHLA in the smaller lakes was also reflected in a non-linear model relating CHLA to TN and TP (Fig. 4).

The number of phytoplankton taxa recorded ranged between 20 and 40 in most lakes (Fig. 5). Highest numbers occurred in lakes between 1 and 100 ha, with median numbers about 40, but only 20 in lakes < 0.1 ha and 30 in lakes above 100 ha. The number of taxa was significantly but weakly ($p < 0.007$, $R^2 = 0.06$, $n = 363$) unimodally related to both area and TP.

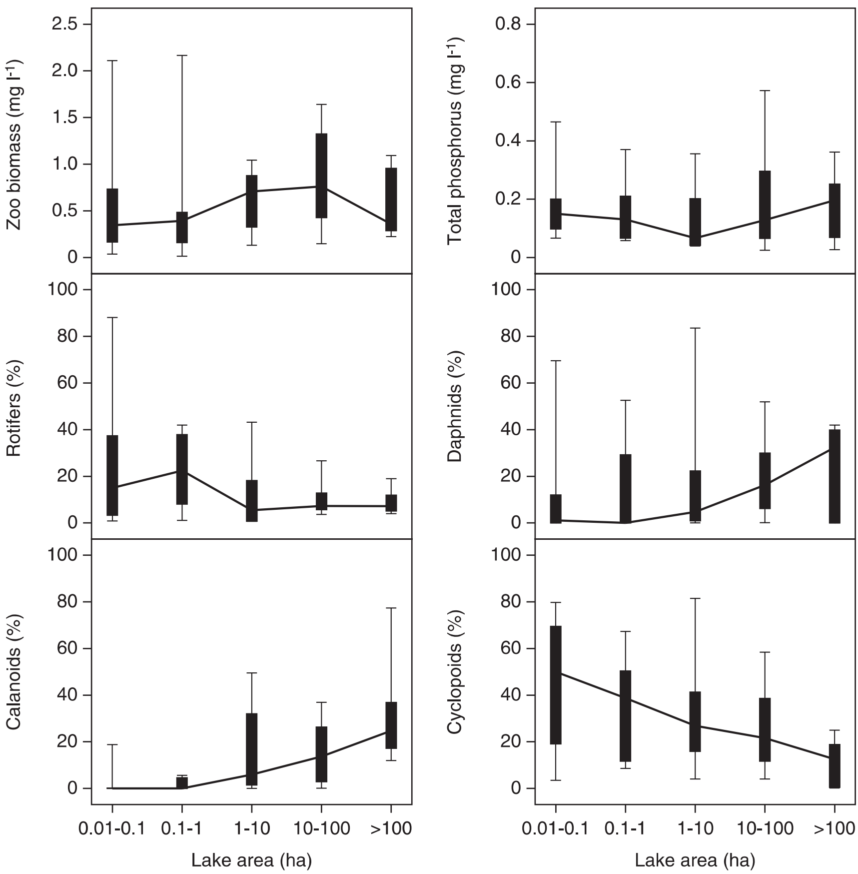

Fig. 6. Zooplankton biomass, relative biomass proportion of cyclopoid copepods, rotifers, *Daphnia* spp. and calanoid copepods relative to lake area shown as box-plots. See also legend to Fig. 1.

Zooplankton

Zooplankton biomass was relatively unaffected by lake size, but tended to be lowest in the smallest lakes (Fig. 6). In a multiple regression (n = 116), biomass was significantly ($p < 0.0001$, $R^2 = 0.26$) positively related to TP ($p < 0.0001$) and depth ($p < 0.002$). Taxon richness of zooplankton in the lakes ranged typically between 15 and 25, with a tendency to a higher richness in lakes smaller than 1 ha (Fig. 5). Thus, in a multiple regression taxon richness was weakly negatively related to lake area ($p < 0.0001$, $R^2 = 0.15$, n = 121), while TP and mean depth were not. The share of cyclopoid and calanoid copepods of the total biomass decreased and increased, respectively, with increasing lake size, but independently of TP and depth. In a multiple regression the share of cyclopoids was significantly ($p < 0.0001$, $R^2 = 0.22$, n = 116) negatively related to area ($p < 0.04$) and depth ($p < 0.01$) and positively so to TP ($p < 0.03$). By contrast, the shares of *Daphnia*, rotifers and calanoids were related to area only. The share of *Daphnia* ($p < 0.003$, $R^2 = 0.22$, n = 116) and cala-

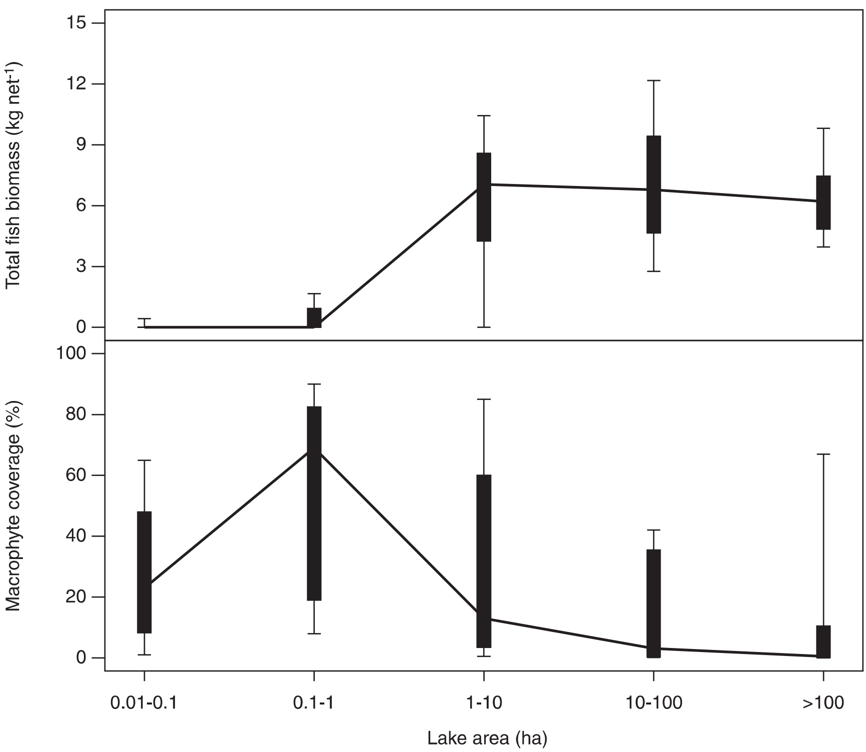

Fig. 7. Total biomass of fish (CPUE, n = 113) and coverage of submerged macrophytes (% of total lake area, n = 132) in relation to lake area shown as box-plots. See also legend to Fig. 1.

noids ($p < 0.0001$, $R^2 = 0.16$) increased slightly with area and rotifers ($p < 0.0001$, $R^2 = 0.16$) decreased.

Fish

Most of the lakes <0.1 ha were fishless and the median number of fish species recorded in lakes between 0.1 and 1 ha was only about one as many lakes in this category were also fishless (Fig. 5). Fish richness increased steadily up to a median number of 12 species in lakes >100 ha. A multiple regression revealed that both area ($p < 0.0001$), mean depth ($p < 0.04$) and TP ($p < 0.03$) contributed significantly and positively to species richness of fish ($R^2 = 0.79$, n = 86). Correspondingly, total catch by standard fishing with multiple mesh-sized gill nets [catch per unit effort (CPUE), weight-based] was generally low in lakes < 1 ha, but increased steeply in the category 1–10 ha, the values recorded for many of these lakes still being low, however (Fig. 7). For lakes between 10 and 100 ha, CPUE values were similar to those of large lakes. Using all data in a multiple regression, CPUE was strongly linked to area ($p < 0.0001$) and to TP ($p < 0.002$, $R^2 = 0.70$, n = 109), but if only lakes larger than 10 ha are considered, only TP remains significant ($p < 0.0004$, $R^2 = 0.15$, n = 83). The most common fish species recorded were roach (*Rutilus rutilus*), perch (*Perca fluviatilis*), pike (*Esox lucius*), rudd (*Scardinius erythrophalmus*), bream (*Abramis brama*) and eel (*Anguilla anguilla*).

Submerged macrophytes

The number of macrophyte species ranged from 0 to 23 (Fig. 5). Species number was highest in the largest lakes, increasing from a mean number of 1.1 in lakes between 0.01 and 0.1 ha to 10.6 in lakes larger than 100 ha. (Table 4). Apart from area, the distribution of macrophytes was particularly ordered along an alkalinity and a depth gradient (Table 5). Species number was lower in lakes with low alkalinity than in lakes with high alkalinity: number of macrophyte species = 2.6 x area$^{0.16}$ in lakes with alkalinity below 0.2 meq l^{-1} and 2.6 x area$^{0.24}$ in lakes with alkalinity above 0.2 meq l^{-1} (proc NLIN, SAS).

Table 4. Estimated number of submerged macrophyte species in lakes at two levels of alkalinity (TA) and at three levels of total phosphorus (TP). Number of species = a x area^b, where area = lake area in ha. Proc NLIN, SAS was used.

TP	TA ≤0.2 meq l^{-1} (n = 59)		TA >0.2 meq l^{-1} (n = 87)	
	a =	b =	a =	b =
0–25 µg P l^{-1}	4.26	0.23	3.60	0.33
25–50 µg P l^{-1}	3.01	0.16	3.13	0.30
50–100 µg P l^{-1}	1.97	0.19	2.55	0.11

Table 5. CCA-analyses of submerged macrophytes using the forward selection procedure. F ratio is the sum of all canonical eingenvalue and λ the eigenvalue.

Parameter	λ	F-ratio	P value
Area	0.47	1.91	0.049
Alkalinity	0.42	1.76	0.006
Chlorophyll-a	0.28	1.2	0.229
Mean depth	0.33	1.43	0.047
Total nitrogen	0.23	0.98	0.495
Total phosphorus	0.1	0.4	0.986

The relative coverage of submerged macrophytes was highest in lakes < 10 ha, with a mean coverage of 31 %, 52 % and 35 % in lakes < 0.1, 0.1–1 and 1 to 10 ha, respectively (Fig. 7). In lakes between 10 and 100 ha coverage decreased to 7 % and to 3 % in lakes > 100 ha. There was a weak, but significant relationship between TP and coverage ($p = 0.04$, $R^2 = 0.06$).

Discussion

In the vast majority of the study lakes, the nutrient concentrations were high and well above the levels expected to occur in lakes situated in natural areas without anthropogenic influence. They were, however, comparable with levels found in other studies of lakes affected by agricultural run-off (Bennion & Smith 2000, Nairn & Mitch 2000, Schell et al. 2001). The increasing agricultural dominance of lake surroundings found with decreasing lake size emphasises that small lakes in the agricultural landscape have a high risk of impact from nearby farming activities. This is also indicated by the positive relationship found between land use and nutrient concentrations in the lakes. Therefore, nutrient concentrations in small lakes and ponds in an agricultural landscape can be strongly impacted by catchment activities, even though they are often devoid of surface inflows.

Many of the small lakes and ponds had high nutrient concentrations, particularly of total phosphorus and ammonia (Fig. 2). Similarly, Bennion & Smith (2000) in a study of shallow ponds in south-east England found high inter-annual variability in phosphorus, which tended to be highest in the most enriched water. Possibly, this reflects the high impact by the sediment on seasonal nutrient concentrations, which tend to be most important in eutrophic and shallow waters with a large sediment to water interface (Waiser 2001, Søndergaard et al. 2003). The importance of internal processes is high in small lakes as these usually have no surface outflows and all phosphorus entering the lakes will be retained and potentially recycled within the lake. For nitrogen, the higher nitrate concentrations recorded in lakes > 10 ha likely reflect higher hydraulic loading, including surface inflows rich in nitrate, and the fact that nitrogen retention is strongly affected by the hydraulic retention time (Oecd 1982). Thus, nitrogen in small lakes with low hydraulic flushing will eventually be removed from the systems through denitrification. This might also explain why small lakes generally have higher submerged macrophyte coverage than larger lakes, as also found by Van Geest et al. (2003). Low nitrogen concentrations have a positive impact on the potential presence of submerged macrophytes and their biodiversity (Moss 2001, Sagrario et al. 2005). Thus, macrophytes in small lakes may benefit from a small catchment, because of low nitrogen concentrations.

The generally high phosphorus concentrations of both TP and SRP in lakes < 1 ha was not reflected in the chlorophyll concentrations, and the chlorophyll-a yield per unit of phosphorus was particularly low in lakes < 1 ha. Correspondingly, pH decreased markedly with lake size, which indicates reduced primary productivity as alkalinity was almost unaffected by lake size. In some small lake types, low CHLA may relate to reduced light availability because of shading from trees (Palik et al. 2001) or the higher humic content generally seen in the smaller lakes (Klug 2002); however, CHLA did not correlate significantly with water colour in the multiple regression including also TP, TN lake area and depth. Strong control of phytoplankton by zooplankton in the absence of fish, as observed in large lakes at low zooplanktivorous fish abundance (Mazumder 1994, Mazumder & Havens 1998, Quiros 1998) might also be an important factor. This effect could be even further enhanced by the high coverage of macrophytes in the smallest lakes. Thus, Leibold (1999) found a positive relationship between the densities of zooplankton and plants in 31 fishless ponds, and Paterson (1993) recorded large numbers of microcrustaceans in association with macrophytes. Our zooplankton data do not, however, support the view that zooplankton has any strong control on phytoplankton, as indicated by low biomass in the small lakes, although we cannot exclude that zooplankton biomass was underestimated as sampling was undertaken during the day (Burks et al. 2002). A high grazing impact and filtration rate may alternatively arise from sessile filtrators or macrophyte associated filter-feeding microcrustaceans, such as *Sida* (Stansfield et al. 1997), or macroinvertebrates when macrophytes are present and fish absent (Brönmark & Vermaat 1998). We have no data to support this, but the generally higher coverage of submerged macrophytes in lakes < 10 ha implies a higher potential influence. Although the mechanisms are not fully elucidated, our findings overall suggest a lesser nutrient control on phytoplankton abundance in small lakes compared with larger lakes, and support the view that major shifts in the functional coupling of grazers and phytoplankton occur across a size gradient (Tessier & Woodruff 2002).

In the absence of fish, invertebrate predators may become an important factor structuring the food web, which may explain why we found a relatively low zooplankton biomass also in the small lakes normally without fish. For example, HOBÆK et al. (2002) in a study of 36 mainly small Norwegian lakes found that lakes without pelagic fish predators had a distinct zooplankton assemblage normally confined to ponds and that these lakes appeared to be dominated by the predatory phantom midge *Chaoborus*. Similarly, YAN et al. (1991) found that *Chaoborus* regulated the zooplankton communities in acidified fish-free lakes. Other invertebrates, such as notonectids, may also contribute to reduce zooplankton abundance (SHURIN 2001, STEINER & ROY 2003). Cascade-like effects caused by day-night migration by zooplankton, as usually recorded in the presence of fish, have been observed also in fishless, small lakes in the presence of a species of predatory backswimmers (*Buenoa* sp.) (GILBERT & HAMPTON 2001).

The occurrence of alternative predators in the small fishless Danish lakes is supported by the zooplankton composition. Although poor *Daphnia* performance in fishless ponds may also owe to abiotic conditions and resource effects (STEINER & ROY 2003), the proportion of cyclopoid copepods and rotifers was high and low for *Daphnia*, which normally indicates high predation pressure. This suggests that invertebrate predators play a significant role in the fishless small lakes, which compensates for the lack of fish predation. Furthermore, the function of submerged macrophytes as a refuge for large-bodied zooplankton shown from larger lakes (BURKS et al. 2002) may be less important in small lakes, as indicated by BURKS et al. (2001) who showed that in the presence of dragonfly nymphs (*Epitheca cynosura*), *Daphnia* were effectively eliminated within 24 hours regardless of macrophyte presence. An alternative explanation of the low proportion of *Daphnia* may be diel vertical migration, where *Daphnia* hide near the bottom or in the littoral zone during the day to avoid predators, as has been observed in other fishless ponds (GILBERT & HAMPTON 2001), or that low water depth in small lakes leads to higher predation, as the predation risk tends to increase with declining depth (JEPPESEN et al. 1997).

The absence of fish or low biomass in the smallest lakes and their presence in larger lakes is probably the single-most important structuring factor for changes observed in the biological communities along the size gradient. WELLBORN et al. (1996) termed this transition between permanent fishless habitats and habitats with fish "predator transition", because very distinct community types are produced. In our study, most lakes with an area < 0.1 ha were without fish. Similarly, an investigation of 20 ponds < 0.1 ha located in western Denmark showed that fish were present in only 17 % of the ponds (E. KANSTRUP, County of Ringkjøbing, unpubl. results), and in another Danish investigation including 83 ponds (mean size 0.06 ha, range: 0.0025–0.34 ha) HENRIKSEN (2000) found fish in only 8 % of the ponds.

Water depth is probably the most important factor regulating fish survival during cold winters or during droughts (TONN & MAGNUSSON 1982), and a cold winter or a dry summer may have a long-lasting effect in small lakes and ponds. As the lakes in our study also include a depth gradient parallel to the size gradient, it is difficult to disentangle the role of these two variables. However, except for Secchi depth and the SRP : TP ratio, the chemical variables were related better to area than to depth, suggesting area to be a primary factor. Data on biological variables are much more limited, but for submerged macrophytes area also seems more important than lake depth. The presence/absence of fish and the rapidity of colonisation of fish or other organisms following a fish kill also depend highly on the extent of the lake's contact with other wetlands and the frequency of dispersal events (PONT et al. 1991, SHURIN 2001, HOBÆK et al. 2002, COHEN & SHURIN 2003). Even relatively small ponds may hold a fish stock if the spreading potential from adjacent wetlands and streams is favourable. Especially fast colonizers such as three-spined stickleback (*Gasterosteus aculeatus*) are known to rapidly invade new wetlands where they quickly reach a significant population size (BERG & MÆHL 1998). Sticklebacks often have a highly negative impact on large-sized zooplankton in previously fish-free ponds (PONT et al. 1991). In lakes with frequent occurrence of winter kill, connectedness is also important for the fish structure (TONN & MAGNUSSON 1982). The small lakes included in our study exhibiting the greatest species number (7–8 species) were lakes connected with other lakes via streams (SØNDERGAARD et al. 2002).

Species richness relative to lake size has been a frequent subject of debate, and the general finding is that species richness increases along a size gradient according to island biogeographic predictions (TONN & MAGNUSSON 1982, DODSON 1992, ALLEN et al. 1999, OERTLI et al. 2002). Other factors like lake depth (KELLER & CONLON 1994), pelagic primary productivity (DODSON et al. 2000) or phosphorus concentrations (JEPPESEN et al. 2000) may also influence species richness and often exhibit unimodal relationships (DODSON et al. 2000). Overall, our study showed that taxon richness of zoo- and phytoplankton varied only slightly along a size gradient, whereas species richness of fish and submerged macrophytes increased markedly with lake size, as shown in other studies (AMARASINGHE & WELCOMME 2002, BAZZANTI et al. 2003).

The weak effect of lake size on zooplankton taxon richness is in accordance with SCHELL et al. (2001), whereas DODSON et al. (2000) found a significant positive relationship between lake area and species richness of rotifers and cladocerans. However, the latter study only included five lakes < 10 ha and might not be comparable with the lakes in our study. COTTENIE & DE MEESTER (2003) have suggested that local environmental variables related to the clearwater/turbid state alternative equilibria are more important for cladoceran species richness than connectivity of ponds. The weak area dependency for phytoplankton diversity is in accordance with the finding of DODSON et al. (2000) and to ROJO et al. (2000), who suggested that phytoplankton dynamics are more complex in ponds than in lakes owing to the large number of interacting factors.

For submerged macrophytes, area was the most important factor explaining species richness, but alkalinity was also important as in other mainly larger lakes (FRIDAY 1987, RØRSLETT 1991), explained by increased occurrence of elodeids with increasing alkalinity (VESTERGAARD & SAND-JENSEN 2000). Like fish, macrophyte species richness may also be influenced by the distance between ponds, as shown for vascular plants in a study by MØLLER & RØRDAM (1985) and a study of neighbouring waterbodies by LINTON & GOULDER (2003).

The on-off appearance of fish in small lakes may for specific taxonomic groups challenge the expected increased richness with increasing size. Thus, the absence of fish in small lakes would enable a more diverse community of macroinvertebrates to occur, and this may explain the weak or missing effect of lake size in our study. Also, biodiversity relative to lake size can be expected to be higher in small lakes and ponds where the littoral habitat heterogeneity interfaces with pelagic regions (WETZEL 2001). SHURIN (2001) concluded that fish facilitated invasion of more zooplankton species than they excluded, but species richness along a lake size gradient might differ among different taxonomic groups. In a study of 80 Swiss ponds sized between 6 and 94,000 m^2 (median area = 1800 m^2) OERTLI et al. (2002) found that pond size was only important for species richness of odonates and concluded that a set of small-sized ponds may host more species than a single large pond of the same total area. Moreover, from a comparison of river, stream, ditch and pond biodiversity of macrophytes and macroinvertebrates, WILLIAMS et al. (2003) concluded that individual ponds varied considerably in biodiversity, but that ponds at the regional level contributed most to biodiversity by supporting more unique species.

In conclusion, lake size makes a difference. Taxon richness clearly changes for some taxonomic groups such as macrophytes and fish, whereas other groups remain unimpacted. In many aspects, however, ponds and lakes are relatively similar. The small Danish lakes and ponds situated in lowland and highly agri-cultivated areas usually exhibit high nutrient concentrations and frequently turbid water. However, in small lakes high nutrient concentrations do not necessarily lead to high phytoplankton biomass as in larger lakes owing to the effects of other controlling factors.

Acknowledgements

We are grateful to the Danish counties for access to data and to the Danish Forest and Nature Agency for financial support to this project. We thank Carlsbergfondet for its financial support to finalising this paper. The technical staff at the National Environmental Research Institute, Silkeborg, are gratefully acknowledged for their assistance. Field and laboratory assistance was provided by J. Stougaard-Pedersen, B. Laustsen, L. Hansen, L. Nørgaard, K. Jensen and K. Thomsen. GIS data was made available by Inge-Lise Madsen. Layout and manuscript assistance was provided by A. M. Poulsen and T. Christensen.

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Submitted: 9 April 2004; accepted: 5 October 2004.