Ann. Limnol. - Int. J. Lim. 48 (2012) 225–240
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DOI: 10.1051/limn/2012016

Mass invasion of non-native *Elodea canadensis* Michx. in a large, clear-water, species-rich Norwegian lake – impact on macrophyte biodiversity

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Received 12 October 2011; Accepted 23 March 2012

Abstract – The impact of *Elodea canadensis* on aquatic macrophyte biodiversity in (Lake) Steinsfjord has been studied through extensive lake-wide surveys and photographic sampling. *E. canadensis* greatly expanded in Steinsfjord since its appearance in 1978 and still dominated the macrophyte community in 2004. The areal distribution of *E. canadensis* peaked within 6 years from invasion and has remained relatively stable since; however, stands no longer reach the water surface. *E. canadensis* significantly increased its depth range, but the cover-weighted mean depth remained unchanged, suggesting that 3–4 m is its optimal depth in Steinsfjord. Species richness has not changed significantly since the earliest survey in 1936–38. However, species composition has changed remarkably, from isoetid dominance in 1936–38 to a diverse community dominated by *Najas flexilis* in 1979–80 to a less diverse community dominated by *E. canadensis* in 2004, with *Potamogeton berchtoldii* and *Myriophyllum alterniflorum* as lake-wide subdominants. Regardless of their abundance at the onset of the *E. canadensis* invasion, taxa whose cover-weighted mean depth overlapped with *E. canadensis*'s in 1979–80 greatly reduced their abundance in 2004, shifted to deeper or shallow water or disappeared from sampling stations. Our survey indicates that *E. canadensis* may be the reason for the decrease of *N. flexilis*, likely through depletion of CO_2 in the water column and reduced nutrients in sediments. The abilities to survive and grow in periodically exposed shallow areas, combined with minor herbivory by waterfowl, are likely important factors for the increase of *M. alterniflorum* in Steinsfjord's shallow waters.

Key words: Aquatic macrophytes / invasive species / species composition / depth distribution / *Najas flexilis*

Introduction

Introduction of new species in a habitat may bring about dramatic changes in the original, native community. Although colonization success depends also upon habitat characteristics (Knapton and Petrie, 1999; Lonsdale, 1999; Ali and Soltan, 2006), species accidentally or intentionally introduced by humans often originate from distant areas (alien, exotic, or non-native species), and may rapidly get established. Although the mechanisms behind successful colonizations remain poorly known (*e.g.*, Coleman and Levine, 2007), the establishment of invaders typically causes a decline in native species performance (Madsen *et al.*, 1991; Corbin and D'Antonio, 2004).

Canadian waterweed (*Elodea canadensis* Michx.) is a North American native that is exotic and invasive in Europe. Since its first European record in 1836, *E. canadensis* has greatly expanded from its original invasion area in Britain (Simpson, 1984) to colonize many running and standing waters of temperate Europe. *E. canadensis* may form extensive clonal patches, and thanks to viable stem fragments, disperses quickly to new sites (Bowmer *et al.*, 1984; Barrat-Segretain *et al.*, 1999). The species may thrive in a variety of habitats, from relatively oligotrophic to eutrophic, and from clear to humic or turbid water (Collins *et al.*, 1987; Grime, 1988). *E. canadensis* is typically favored by high water-column and/or sediment nitrogen and phosphorus concentrations (Glänzer *et al.*, 1977; Ozimek *et al.*, 1993; Thiébaut, 2005).

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Potential for colonization of new areas seems to be augmented by movement of boats and fishing equipment between localities (Stuckey, 1979; Johnstone *et al.*, 1985; Nichols, 1994). However, despite its rapid spread and high invasiveness, *E. canadensis* appears to be past its colonization peak in Europe, being gradually replaced by the congeneric *Elodea nuttallii* (Planch.) H. St. John as the dominant invasive exotic in many areas (Simpson, 1984; Thiébaut *et al.*, 1997; Barrat-Segretain, 2001). *E. nuttallii* may begin to be replaced by another invasive hydrocharitacean species, *Lagarosiphon major* (Ridl.) Moss, in the U.K. (Josefsson, 2011).

Long-term monitoring data from (Lake) Steinsfjord, including information on water quality, phytoplankton, macrophytes, nutrient inputs and waterfowl populations, make the lake particularly well suited for studying the ecological impact(s) of *E. canadensis* on the lake ecosystem. Aquatic macrophyte data from Steinsfjord include extensive surveys since 1936–38 (Baardseth, 1942). Our photograph-based, quantitative 2004 survey was carried out at the same sites and with the same methods as the 1979–80 survey (Rørslett, 1983), and was preceded by preliminary semi-quantitative registrations in 1996 (Mjelde and Johansen, 1997) and 2003.

We have studied the impact of the *E. canadensis* invasion on the taxonomic composition and diversity *sensu latu* of the Steinsfjord aquatic macrophyte community, with an emphasis on *Najas flexilis,* one of the most endangered species in Norway (Kålås *et al.*, 2010). Our study focuses on the quantitative data from the photographic surveys; however, information from the 1936–38 survey was included whenever applicable to provide a ~ 70-year history of the Steinsfjord macrophyte community along with changes in lake characteristics. Our investigation is a contribution within a broader-scope project aimed at ecosystem-scale impacts of the *E. canadensis* invasion on water chemistry, waterfowl, phytoplankton and macrophytes (Berge *et al.*, unpublished data).

Lake description

Lake Steinsfjord is situated in the southeastern lowland area of Norway, with surface area of 13.9 km^2 and mean depth of 9.9 m. It is a moderately alkaline and slightly mesotrophic lake. Water chemistry data show no significant change in trophic status between the two photographic surveys in 1979–80 and 2004 (Berge *et al.*, unpublished data). The sparse water chemistry data from 1936–38 suggest oligotrophic conditions (Baardseth, 1942). The nutrient content in the sediment had decreased by 5–30% from 1979–80 to 2004, and in 2004 the total phosphorus content varied between 0.30 and 0.59 mg g^{-1} in the 0–5 cm upper layer of the sediment (Berge *et al.*, unpublished data).

Steinsfjord was dammed for drinking water purposes in 1906. However, the water-level change was minor (~ 1 m) and seems to have had no ecological effects (Berge, 1986, 1989). In the period 1979–2004, the maximum variation in the median water level did not exceed 50 cm, except for the years 1991 and 1992 when the water level was lowered due to construction work on the outlet dam. Low precipitation and decreased flow in spring caused low water level also in 1996 and 1997. The spring (April–May) water level in such years and in 2003 was 20–30 cm lower than normal. Summer water levels seem to have been stabilized in the last 5–6 observation years, while low water levels seem to appear more often in winter in the same period.

E. canadensis was first observed in Norway in 1925, with an accelerated spreading to nearly 60 southern Norwegian lakes in the last 25 years (Mjelde, 1997). The main watercourse upstream of Steinsfjord has been heavily infested with *E. canadensis* since the early 1960s (Rørslett *et al.*, 1986) and *E. canadensis* was first observed in Steinsfjord in 1978 (Rørslett, 1983), first in the southern and western parts of the lake. From these localities, *E. canadensis* spread rapidly within the lake and by 1982 it covered ~ 72% of the 0–6 m depth area (Berge, 1989). An update study in 1996 showed a decrease in macrophyte biodiversity since 1979–80, such period including the most aggressive, initial lake-wide colonization by *E. canadensis*. For the periods between these surveys we have sparse data about the condition of *E. canadensis*. However, based on scattered information it seems that extensive stands of *E. canadensis* reached the water surface through at least 1985–87 (Mjelde and Johansen, 1997).

Following the rapid colonization of *E. canadensis*, mass populations of waterfowl invaded the lake every autumn, during their annual migration cycles (Berge *et al.*, unpublished data). From the < 10 typically observed in the pre-*E. canadensis* autumn period, 800–1000 individuals of waterfowl were observed from the *E. canadensis* peak period (late 1980s–early 1990s) until the late 1990s, consisting of around 450 individuals of mute swans (*Cygnus olor* (Gmelin)), 400 wigeon (*Anas penelope* L.), 350 whooper swans (*Cygnus cygnus* L.) and < 10 coot (*Fulica atra* L.) (Larsen, 2006). However, in the last 5–6 years the number of all these species, except for coot, has decreased markedly to a total of ~ 200 individuals (autumn counts) in 2005. Coot reached its peak in 2002 with nearly 180 individuals (Larsen, 2006).

Materials and methods

Field survey and photo analysis

The macrophyte community in Steinsfjord was surveyed quantitatively in the summers of 1979–80 (except for some pictures at station A taken in 1976) at seven sampling stations, with an emphasis on gentle-slope habitats (Fig. 1). Underwater photographs were taken by SCUBA divers at several randomly chosen plots from ~ 0.5 m of depth (equipment structure not allowing photographs in shallower water) to below the observed maximum colonization depth. The photographs were taken with a camera mounted on a square metal frame with an area of 0.25 m^2.

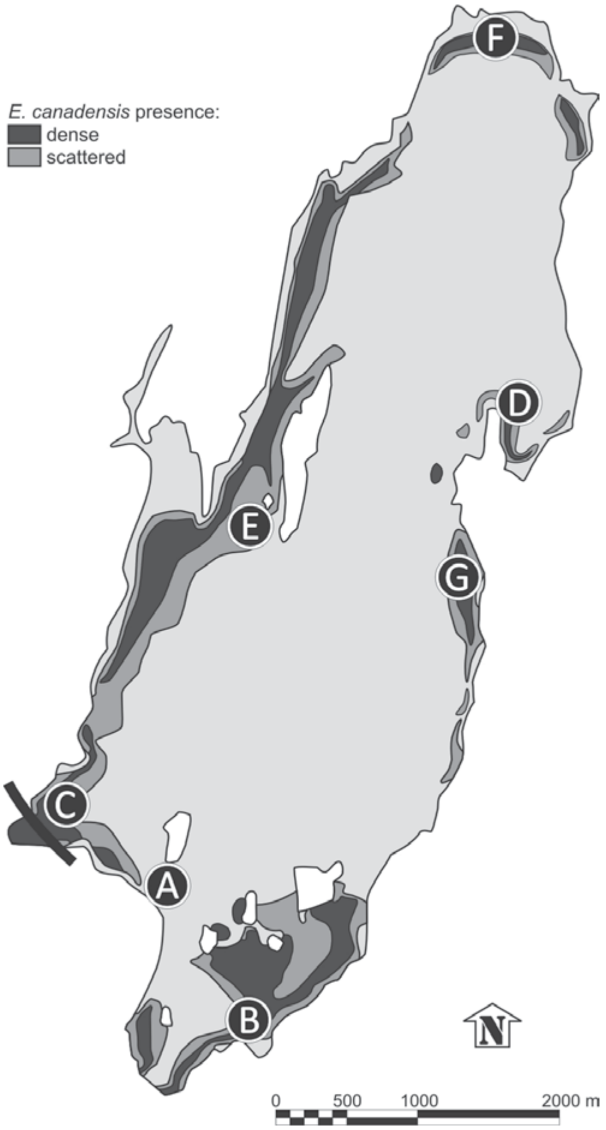

Fig. 1. Lake Steinsfjord. The letters indicate the stations for the 1979–80 and 2004 photographic surveys. The area cover of *E. canadensis* in 2004 is shown on the map, while other years can be seen in Berge *et al.* (unpublished data).

A total of 646 photographs were obtained. For each sample, depth and abundance of macrophyte species and sediment type were determined. Abundance was calculated as the percentage of the 0.25-m^2 area covered by each macrophyte taxon (%cover). Taxa were identified at the species level, except for the taxon of filamentous algae, which included *Cladophora aegagropila* (L.) Trevisan and unspecified chloro- and cyanophytes. Total vegetation %cover was obtained as the sum of the %cover values of the individual taxa in each photograph. Details about the photographic method and vegetation results are in Rørslett (1983) and Rørslett *et al.* (1978).

The photographic survey in 2004 was carried out with identical methods and at the same sampling stations as in 1979–80, producing a total of 789 photographs. Vegetation-devoid photos (most of which below the maximum macrophyte colonization depth) were excluded from calculations and statistics, leaving a total of 623 viable photos for 1979–80. In 2004, "exploratory" photographs in areas below maximum colonization depth and with bare mud were avoided. Therefore, all pictures taken in 2004 were used in the analysis, and sampling randomness was maintained within the depth of vegetation colonization for both periods. All depths given relate to the median water level calculated from daily average levels from the period 1955–2004.

Two major semi-quantitative surveys were carried out between the 1979–80 and 2004 photographic surveys. Aquatic macrophytes were recorded at different localities in the lake in 1996 (Mjelde and Johansen, 1997) and again in August–September 2003 using an aqua scope and collected by raking from the boat. Distribution patterns from these surveys were compared, when possible, with those obtained in 1936–38 during the presence–absence survey reported in Baardseth (1942). Presence–absence-based frequency of occurrence in observational plots of selected species was compared with the 1936–38 frequency data, obtained with the same method. However, Baardseth (1942) provided partially elaborated data for 1936–38, thus precluding statistical analysis, and the comparison with our more recent data remained semi-quantitative.

Species names were abbreviated as genus initial followed by the first three letters of species names (*e.g.*, E.can = *Elodea canadensis*) in some indices, graphs and tables.

Statistical analysis

Photographs were sorted by sampling period, station and depth interval. Individual photographs within each such category were treated as replicate quadrats.

Lake-wide depth distribution for total vegetation and selected macrophyte species was estimated by pooling all quadrat data from the seven sampling stations into 0.25-m depth intervals, producing smoothed line curves of depth-based average %cover ± standard error, which expressed (relative) abundance (*e.g.*, Canham and Thomas, 2010; Bonar *et al.*, 2011).

Two-factor analysis (such as two-way analysis of variances (ANOVAs)) could not be performed because of uneven sample size (*e.g.*, Zar, 2009). Even when one-way ANOVAs could be applied, we opted for two-tailed, paired *t* tests to maintain an ecologically more meaningful site-by-site comparison. Because of a higher cumulative chance of Type I errors related to our choice of statistical comparison, we limited our analysis to the pair-wise comparisons that seemed warranted from an ecological viewpoint; for example, deep-water species were compared with other deep-water species. Also, Fisher's combined probability test (Fisher, 1954), testing the null hypothesis that all the individually tested H_0s are true, applied to the largest such family of *t* tests (*i.e.*, the one with the highest chance of committing at least one analysis-wide Type I error) gave a highly significant combined $P = 0.0063$ ($\chi^2 = 95.67$, d.f. = 46), indicating that our approach, though imperfect, was acceptable (Quinn and Keough, 2002; Gotelli and Ellison, 2004). Bonferroni-like corrections have been avoided on the grounds of being excessively conservative, being based on unrealistic assumptions, and/or not providing an adequate balance between pros and cons (Gotelli and Ellison, 2004).

Statistical analysis included comparisons of spatial distributions between sampling periods by means of two-tailed *t* tests, and within-year multiple comparisons of species abundance (as %cover) using the Student–Newman–Keuls (SNK) test for species richness analyses. All analyses were performed with arcsine-transformed %cover data. The Anscombe formulation [$x' = \arcsin\sqrt{(x + 3/8) \cdot 4/7}$ with x expressed as %cover/100] was used because of frequent extreme %cover values (near zero and 100%: Zar, 2009). Significance levels for SNK tests were pre-set at $P \leq 0.05$. Among taxa multiple comparisons were limited to the major lake-wide taxa.

In order to allow a direct comparison with the earliest dataset (1936–38), distribution data for selected taxa were expressed as frequency of occurrence in observational plots (*i.e.*, photograph-based quadrats in 1979–80 and 2004) in relation to depth. Comparisons with 1936–38 data remained qualitative, as statistical analyses could not be performed on such frequency data.

Species richness (defined as number of species S: *e.g.*, Maurer and McGill, 2011) was calculated as mean number of macrophyte species per photographic quadrat; replicates were sorted by wide depth category (shallow: < 2 m; intermediate: 2–4 m; deep: > 4 m). Temporal changes between sampling periods were analyzed by means of two-tailed *t* tests on log-transformed data, using Bartlett's formula [$x' = \log_{10}(x + 1)$] (Zar, 2009). Additional *t* tests for selected data subsets also were performed on log-transformed data. Given the different methods employed and the partially elaborated data provided by Baardseth (1942), photograph-based richness could not be compared with sample-based richness from the 1936–38 survey.

The mean depth (cover-weighted) ($\boldsymbol{T_i}$) (in m), for a taxon i has been calculated as

$$T_i = \frac{\sum_1^{n_i} (\%\text{cover}_i \times \text{depth}_i)}{\sum_1^{n_i} (\%\text{cover}_i)}$$

where n_i is the number of quadrats in which taxon i has been observed, %cover$_i$ is taxon-specific abundance (expressed as %cover), and depth$_i$ (in m) is for each nth quadrat (Rørslett, 1983). Differences between sampling periods were tested with two-tailed *t* tests on log-transformed data using sampling stations as replicates.

Results

Species richness

A total of 32 aquatic macrophyte species were recorded in Steinsfjord in 2003–04 (Table 1), compared to 37 species in 1979–80 (Rørslett, 1983) and 33 species in 1936–38 (Baardseth, 1942).

Quadrat-based species richness (S) ranged from 0 to 6 species per photograph; however, 1–3 species were recorded in most cases (86.9% and 92.3% of the total number of plant-present photographs in 1979–80 and in 2004, respectively). In general, average S per photograph was lowest in deeper waters (Fig. 2 and Table 2). Average S significantly decreased since 1979–80 at mid-depths (2–4 m), but increased in shallow and deeper waters (< 2 and > 4 m, respectively) (Table 2).

Species composition

In 1936–38, the most frequent species were isoetids (*Littorella uniflora* and *Isoetes lacustris*), plus *Myriophyllum alterniflorum, Chara globularis, Nitella opaca* and *Potamogeton perfoliatus*. The most frequent species in 1979–80 were *N. flexilis, E. canadensis, N. opaca, Potamogeton berchtoldii* and *M. alterniflorum*, while *E. canadensis, M. alterniflorum, P. berchtoldii, N. opaca* and *C. globularis* were most frequent in 2003–04. Each of the first three species in each sampling period exceeded 25% frequency (Table 1).

Some species reported from earlier surveys were not recorded in 2004. Most of these were reported as rare in 1936–38 and/or in 1979–80, and can have been overlooked in the last survey. However, two relatively common taxa in 1979–80, the red-listed species *Potamogeton pusillus* and *Nitella confervacea* ((Brébison) A. Braun) (= *N. batrachosperma* ((Reichenbach) A. Braun), also were not retrieved in 2004. The most apparent change, besides the explosive invasion of *E. canadensis,* is the increased abundance of *M. alterniflorum* and *P. berchtoldii*, and the strong decrease in abundance for *N. flexilis* and *C. globularis* (despite an increase in frequency), which were among the most common species in 1979–80.

In spite of a fairly common distribution at four stations in 2003–04, the importance of *Callitriche hermaphroditica* had decreased compared to 1936–38 and 1979–80. In 1936–38, this species had a scattered distribution, but with some larger stands in shallow areas down to 1.1 m depth (Baardseth, 1942). In 1979–80, *C. hermaphroditica* was one of the most common species in the lake. The species was not recorded at all in the 1996 update survey (Mjelde and Johansen, 1997). Conversely, *C. globularis* and *Potamogeton crispus* expanded their presence from three to five or six sampling stations, respectively, from 1979–80 to 2004. *P. crispus* was observed for the first time in Steinsfjord in 1896 (Baardseth, 1942) and in 1936–38 the species was widely, but patchily, distributed in the lake.

Depth distribution

Although statistical analysis was not possible on frequency data, long-term temporal decreases in abundance are particularly evident for the isoetids *L. uniflora* and *I. lacustris* (Fig. 3). The frequency of *L. uniflora* seems

Table 1. Aquatic macrophytes in Lake Steinsfjord in 1936–38, 1979–1980 and 2003–04. When available, frequency of occurrence (as percent of replicate observations in which each species occurred) is given. All species from the lake are included. * = recorded 1979–80 in sampling stations not visited in 2003–04; x = species present, but abundance not quantified.

Growth form/species	1936–38	1979–80	2003–04
ISOETIDS			
Elatine hydropiper L.	x	x	x
Eleocharis acicularis (L.) Roemer & Scultes	x	1.4	0.9
Isoetes echinospora Durieu	x	0.3	x
Isoetes lacustris L.	x	2.5	0.3
Limosella aquatica L.	x	x	x
Littorella uniflora (L.)Ascherson	x	2.6	4.2
Lobelia dortmanna L.	x	0.2	x
Ranunculus reptans L.	x	0.2	x
Subularia aquatica L.	x	0.9	x
Tillaea aquatica L.	x	x	
ELODEIDS			
Batrachium eradicatum (Laest.)Fr.	x	x	x
**Batrachium floribundum* (Bab.)Dumort		x	x
Callitriche hermaphroditica L.	x	15.9	2.3
**Callitriche palustris* L.	x	x	
Elodea canadensis Michx		20.7	91.6
**Hippuris vulgaris* L.	x	x	
Juncus bulbosus	x		
Myriophyllum alterniflorum DC.	x	15.4	33.0
Najas flexilis (Willd.) Rostkov & W.L.E. Schmidt		23.1	1.3
Potamogeton alpinus Balbis	x	x	x
Potamogeton berchtoldii Fieber	x	17.8	28.0
Potamogeton crispus L.	x	2.2	5.1
Potamogeton gramineus L.	x	0.2	0.8
**Potamogeton* × *nitens* Weber	x	x	
Potamogeton perfoliatus L.	x	5.0	2.8
Potamogeton pusillus L.		10.1	
Stuckenia filiformis (Pers.) Börner			x
**Utricularia intermedia* Hayne	x	x	
Utricularia minor L.		0.2	x
Utricularia cf. ocroleuca R.W.Hartm.			x
Utricularia vulgaris L.	x	1.6	x
NYMPHAEIDS			
Persicaria amphibia (L.) Gray	x	x	x
**Potamogeton natans* L.	x	x	
Sagittaria sagittifolia L.	x	x	0.1
Sparganium angustifolium Michx		x	x
Sparganium emersum Rehmann	x	x	x
**Sparganium angustifolium* × *gramineum*	x		
**Sparganium angustifolium* × *emersum*	x		
LEMNIDS			
Lemna minor L.	x	x	x
Lemna trisulca L.			0.3
CHAROPHYTES			
Chara globularis Thuill.	x	10.7	5.3
Nitella confervacea ((Brébison) A. Braun)		3.4	
Nitella opaca Ag.	x	20.7	9.8
total number of species	33	37	32

to have rebounded in 2004 from the historical minimum of 1979–80, while *I. lacustris* has remained a rare taxon in Steinsfjord. Both species also have markedly reduced their maximum lake-wide colonization depth since 1936–38. *P. perfoliatus* also has declined in frequency since the maximum in 1936–38 (Fig. 3). Maximum frequency of occurrence for *P. perfoliatus* has remained roughly stable at around 20% since 1979–80. General patterns in frequency of occurrence for *M. alterniflorum* have remained stable since 1936–38, with the highest frequencies consistently observed in shallow-to-intermediately-deep waters (Fig. 3). *M. alterniflorum* also had declined in 1979–80, but it has rebounded dramatically since, with frequency in 2004 higher than in 1936–38.

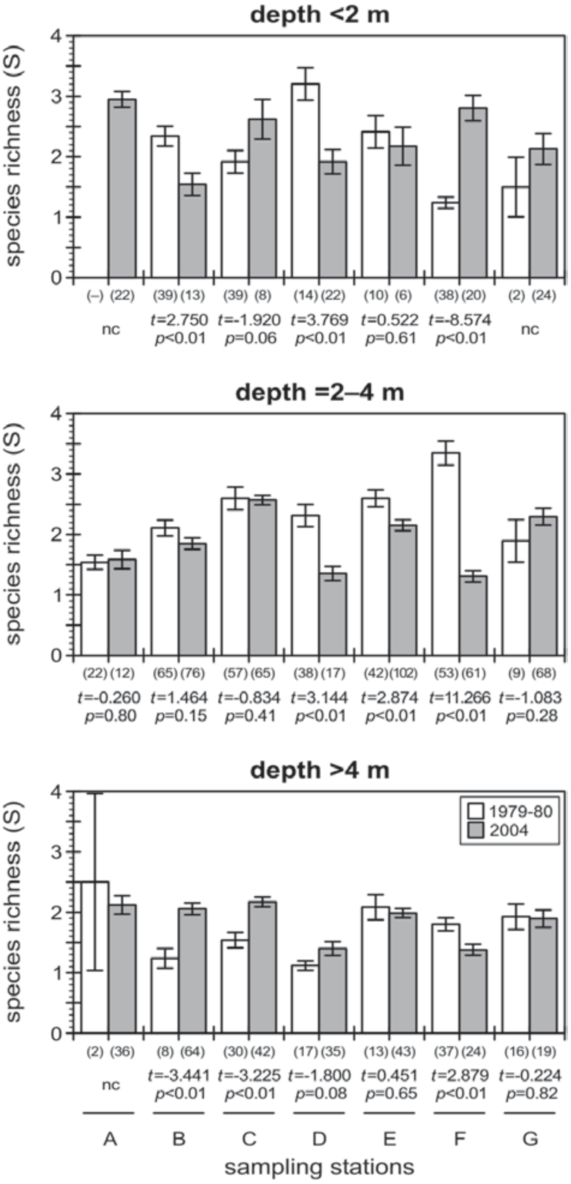

Fig. 2. Average species richness, S (number of taxa ± standard error) in each photograph, at each sampling station and sampling period (1979–80 and 2004), at three selected depth ranges: shallow (<2 m), intermediate (2–4 m) and deep (>4 m). Number of replicate photographs per category is given in parentheses below each bar. Results for each between-year pairwise comparison (two-tailed t tests with d.f. $= n_1 + n_2 - 2$) also are given; "nc" = not calculable (n_1 and/or $n_2 < 3$).

The photograph- and abundance-based distribution patterns have been analyzed in detail for total vegetation and the major taxa, and are reported hereafter. Taxa are listed in descending order of general, lake-wide importance (dominance or abundance) in 1979–80 and/or 2004.

Total vegetation

Total vegetation abundance (as mean %cover) increased significantly from 1979–80 at almost all depths (Fig. 4 and Appendix Table A1 available online), while the lower colonization depth remained at ~6–6.5 m (two-tailed t test using sampling stations as replicates: $t_{1979\text{-}vs.\text{-}2004} = 0.409$, d.f. $= 12$, $P = 0.69$). Total abundance (as %cover) increased from a 1979–80 peak at ~30–50% at intermediate depths to a steady ≥70% through the first ~4.5 m of depth in 2004 (Fig. 4). However, the mean depth of total vegetation has remained stable at ~3.25 m (two-tailed t test: $t_{1979\text{-}vs.\text{-}2004} = 0.039$, d.f. $= 12$, $P = 0.97$).

Elodea canadensis

In 1979–80, the abundance of *E. canadensis* was marginal at most stations. In 2004, *E. canadensis*'s abundance (as %cover) had markedly increased at all stations and most depths. Lake-wide temporal increases in %cover were significant in the 1.5–5.5 depth range, and were especially pronounced at depths ≥2 m (Fig. 4). *E. canadensis* had also significantly expanded its upper and lower colonization depth by 2004 (two-tailed t tests using sampling stations as replicates: upper limit: $t_{1979\text{-}vs.\text{-}2004} = 2.604$, $P = 0.03$; lower limit: $t_{1979\text{-}vs.\text{-}2004} = -3.143$, $P < 0.01$; d.f. $= 11$ for both). However, the stands in shallow water have decreased in cover since the peak development in 1981–84. The decrease was especially pronounced in Steinsvika (large bay west of station E), in whose inner parts stands were almost completely absent in 2004. *E. canadensis*'s mean depth has remained unchanged at ~3.2–3.3 m since its early colonization in 1979–80 (Fig. 6), and virtually coincided with the mean depth for total vegetation in both sampling periods (paired two-tailed t tests $t_{1979\text{–}80} = -0.198$, d.f. $= 5$, $P = 0.85$; $t_{2004} = 0.577$, d.f. $= 5$, $P = 0.59$).

Myriophyllum alterniflorum

The lake-wide depth distribution pattern of *M. alterniflorum* has remained roughly consistent since 1936–38, with abundance peaks in the 1–3 m depth range (Fig. 4). Although still a widespread species, *M. alterniflorum* exhibited a relatively low lake-wide abundance in 1979–80 (Fig. 4). *M. alterniflorum*'s frequency rebounded to pre-eutrophication levels in 2004 (Fig. 3), and significantly increased in abundance in the 1–3 m depth range (Fig. 4). Accordingly, *M. alterniflorum*'s mean depth has remained unchanged at just above 2 m since 1979–80 (Fig. 6), in spite of a significant increase in its downward distribution by 2004 (Fig. 4). *M. alterniflorum*'s mean depth has remained consistently shallower than *E. canadensis*'s since 1979–80, with the difference more marked in 2004 (higher significance level than for 1979–80 in Fig. 6).

Potamogeton berchtoldii

The importance of *P. berchtoldii* (as %cover) was low in 1979–80 at all but two sampling stations. *P. berchtoldii*'s importance had decreased markedly at these two stations by 2004, but it had increased at all other stations, resulting in a lake-wide increase in %cover (significant in the 3–4 m

Table 2. Species richness (S) as average number of species per photograph ± standard error, all sampling stations combined, in 1979–80 and 2004. Differences among depth intervals were tested with SNK ($P \leq 0.05$), and differences between sampling periods were tested with pairwise, two-tailed t tests (d.f. = $n_1 + n_2 – 2$) on log-transformed data.

	Depth intervals						
	< 2 m		2–4 m		> 4 m		Comparison among depth intervals
Sampling periods	n	avg ± std err	n	avg ± std err	n	avg ± std err	
1979–80	142	2.01 ± 0.09	225	2.51 ± 0.08	123	1.67 ± 0.07	Complete SNK separation at $P \leq 0.05$
2004	115	2.33 ± 0.10	224	2.08 ± 0.07	231	1.91 ± 0.05	Complete SNK separation at $P \leq 0.05$
Between-year comparison		$t = -2.782$, $P < 0.01$		$t = 3.769$, $P < 0.01$		$t = -2.393$, $P = 0.02$	

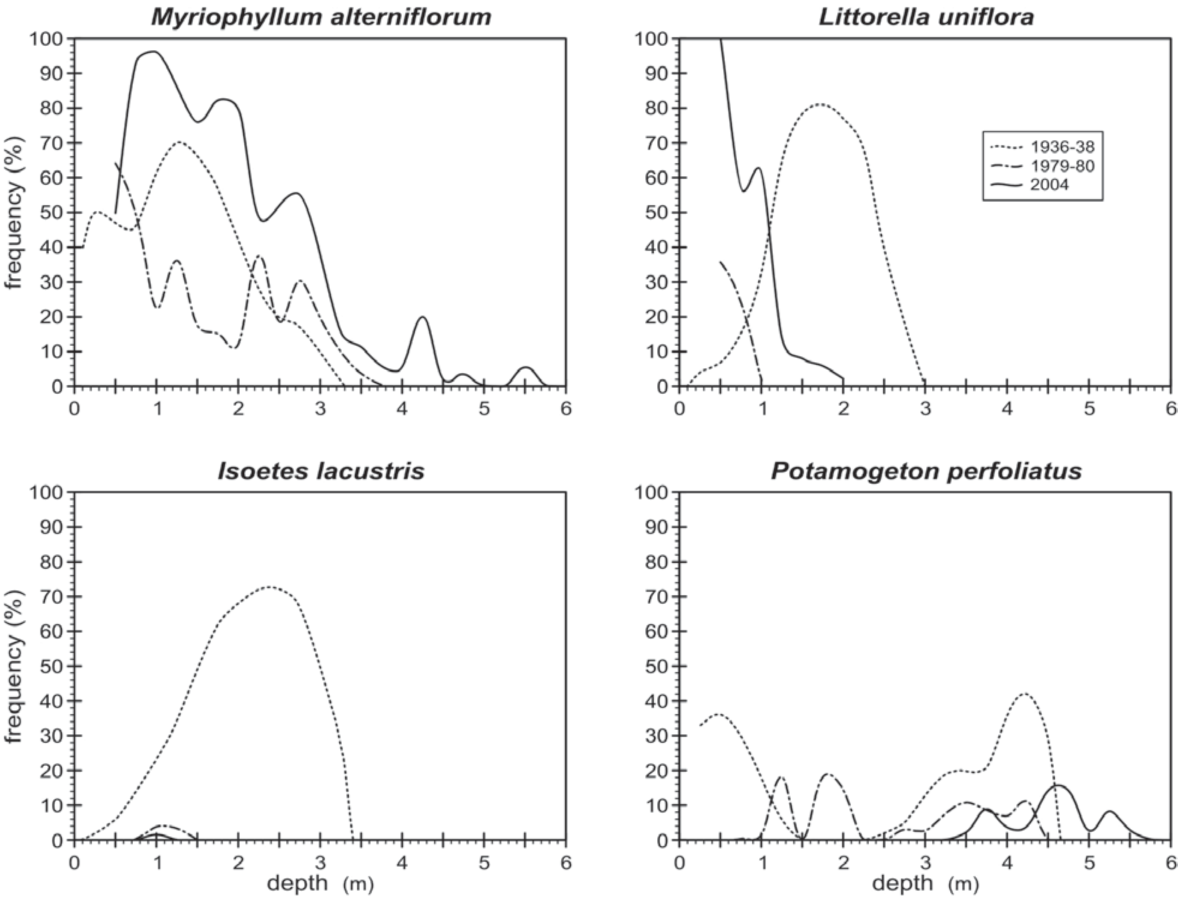

Fig. 3. Lake-wide depth distribution as frequency of occurrence (as % of total observational plots) of selected taxa in 1936–38, 1979–80 and 2004. 1936–38 distributions from Baardseth (1942).

depth range: Fig. 4). *P. berchtoldii*'s presence in the deeper waters of Steinsfjord was less uniformly distributed in 1979–80 than in 2004. *P. berchtoldii*'s mean depth changed from a complete overlap with *E. canadensis*'s and *M. alterniflorum*'s in 1979–80 to being significantly lower (*i.e.*, deeper) than *E. canadensis*'s (Fig. 6) and *M. alterniflorum*'s in 2004 (two-tailed t tests: $t_{1979–80} = 1.378$, d.f. = 10, $P = 0.20$; $t_{2004} = 6.535$, d.f. = 12, $P < 0.01$). *P. berchtoldii*'s lower colonization depth also moved further down from *M. alterniflorum*'s in 2004 (two-tailed t tests: $t_{1979–80} = 1.847$, d.f. = 10, $P = 0.09$; $t_{2004} = 2.152$, d.f. = 12, $P = 0.05$).

Najas flexilis

Although it was not observed in the first semi-quantitative survey (Baardseth, 1942), *N. flexilis* was the most common macrophyte species in 1979–80 based on number of occurrences per replicate photo, having been observed in 149 out of the 623 pictures. *N. flexilis*'s cover peak at ~3.5 m depth in 1979–80 (Fig. 4) corresponded to its mean depth (Fig. 6), which in 1979–80 was similar to the mean depths of *E. canadensis* (Fig. 6) and *P. berchtoldii* (two-tailed t test: $t = 1.399$, d.f. = 9, $P = 0.20$), but was significantly lower (*i.e.*, deeper) than that of *M. alterniflorum*

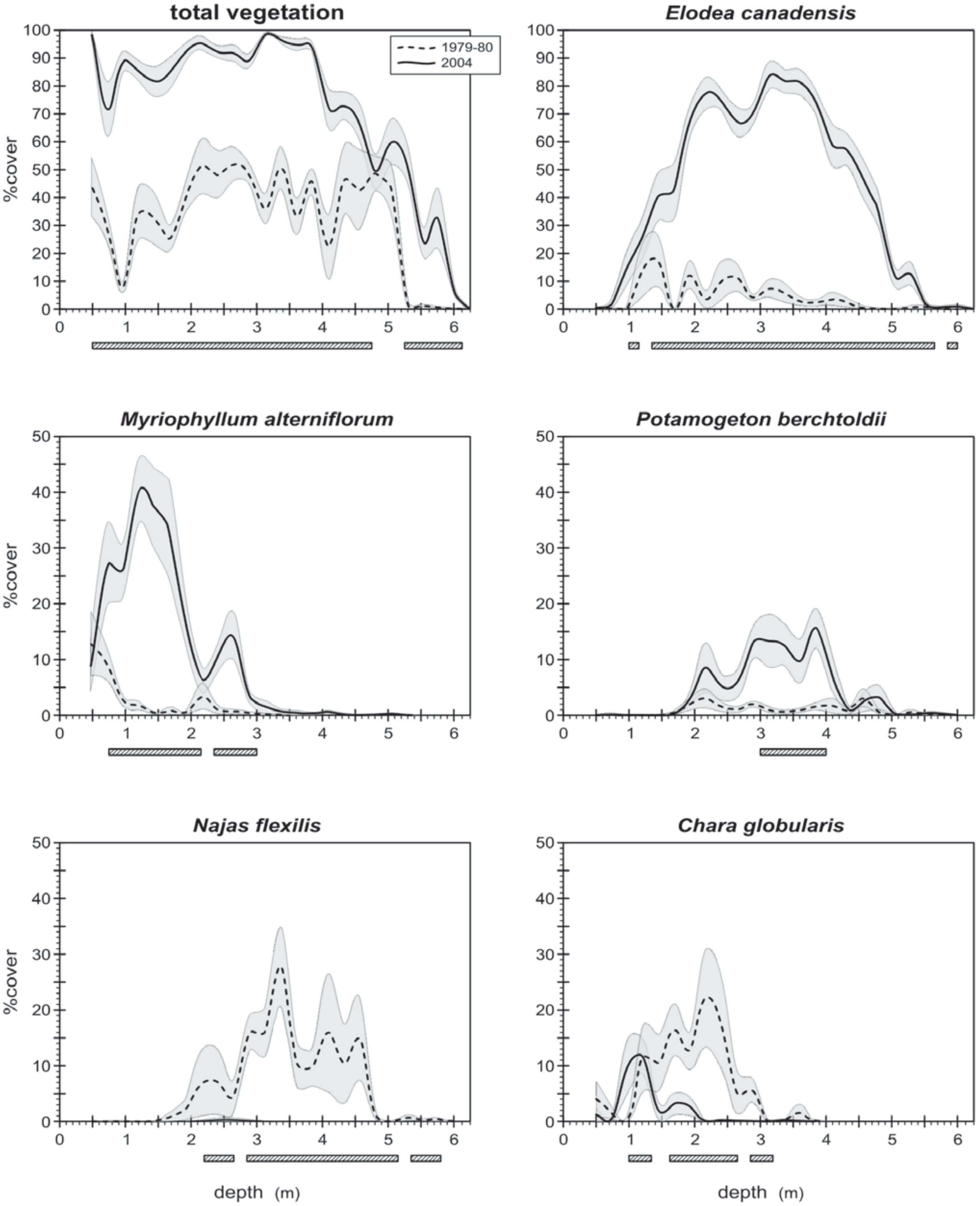

Fig. 4. Lake-wide depth distribution (line and shaded area: %cover average ± standard error) for total vegetation and major taxa in 1979–80 and 2004. Scale for taxa that were subdominant (on a lake-wide basis) in 1979–80 and/or 2004 is at 50%. Hatched area below each graph represents statistically significant between-year %cover average values according to two-tailed paired *t* tests ($P \leq 0.05$) on arcsine-transformed data (d.f. = $n - 1$). Detailed *t* test analysis is in Appendix Table A1 available online.

($t = 3.304$, d.f. = 9, $P < 0.01$). *N. flexilis* greatly decreased by 2004, having being found at low %cover at only one station (Fig. 4). Occurrence at a single station precluded quantitative comparisons in 2004; however, *N. flexilis*'s depth range in 2004 was fully contained in *E. canadensis*'s and *M. alterniflorum*'s, and overlapped partly with *P. berchtoldii*'s, the other major co-dominant in 2004.

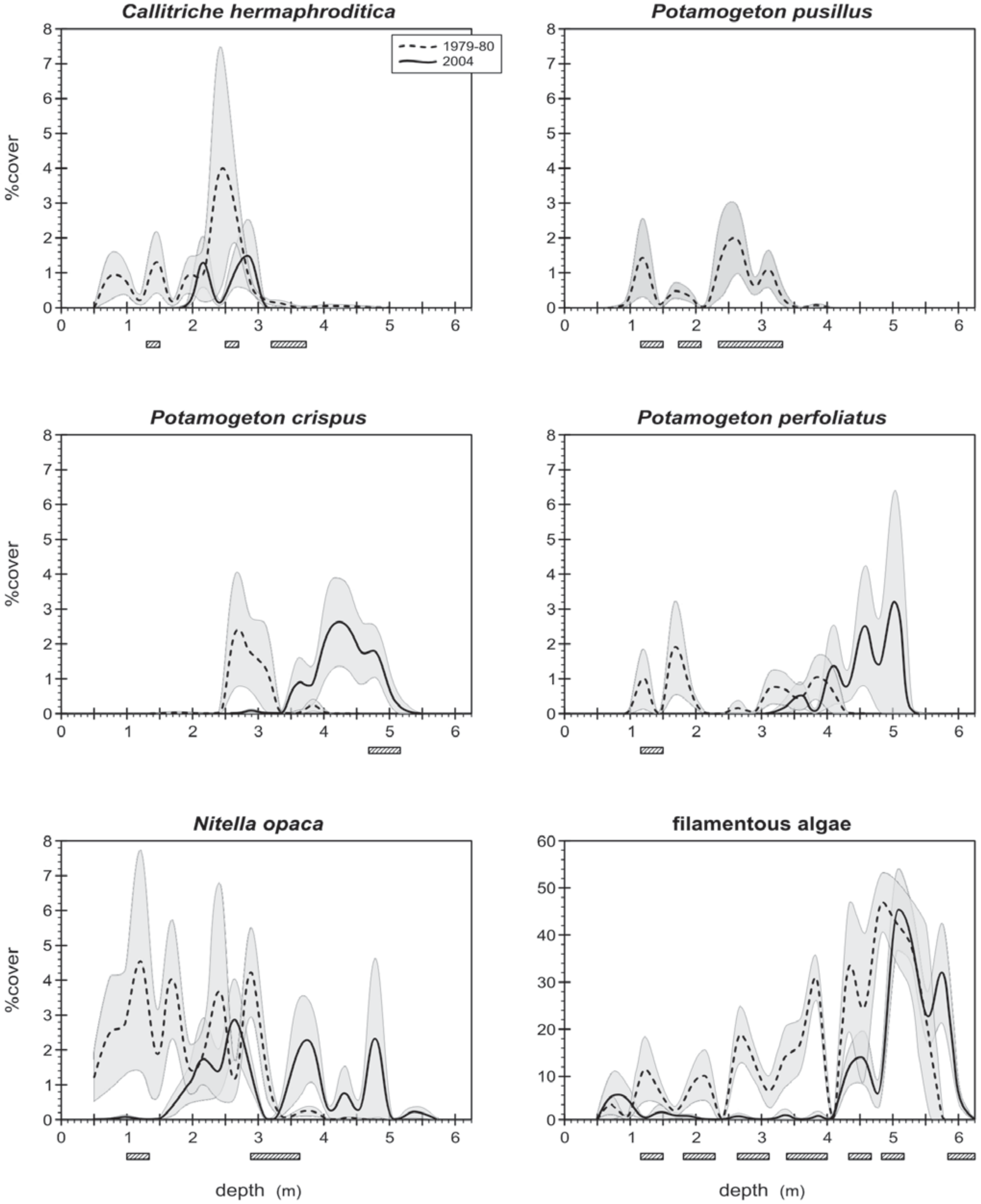

Fig. 5. Lake-wide depth distribution for uncommon species (scale = 8%) and for filamentous algae in 1979–80 and 2004. Explanations as in Figure 4. Detailed *t* test analysis is in Appendix Table A2 available online.

Chara globularis

C. globularis was the least abundant of Steinsfjord's subdominant species, with a 22% cover peak at 2.25–2.50 m of depth in 1979–80 (Fig. 4). The 1979–80 depth distribution of *C. globularis* was similar to that in 1936–38 (from data in Baardseth, 1942) despite the different survey methods. The lake-wide distribution of *C. globularis* was more widespread in 2004, *C. globularis* having been found at all but one sampling station in 2004, but only at three stations in 1979–80. However, %cover of *C. globularis* had decreased markedly by 2004 (Fig. 4). The upward shift in

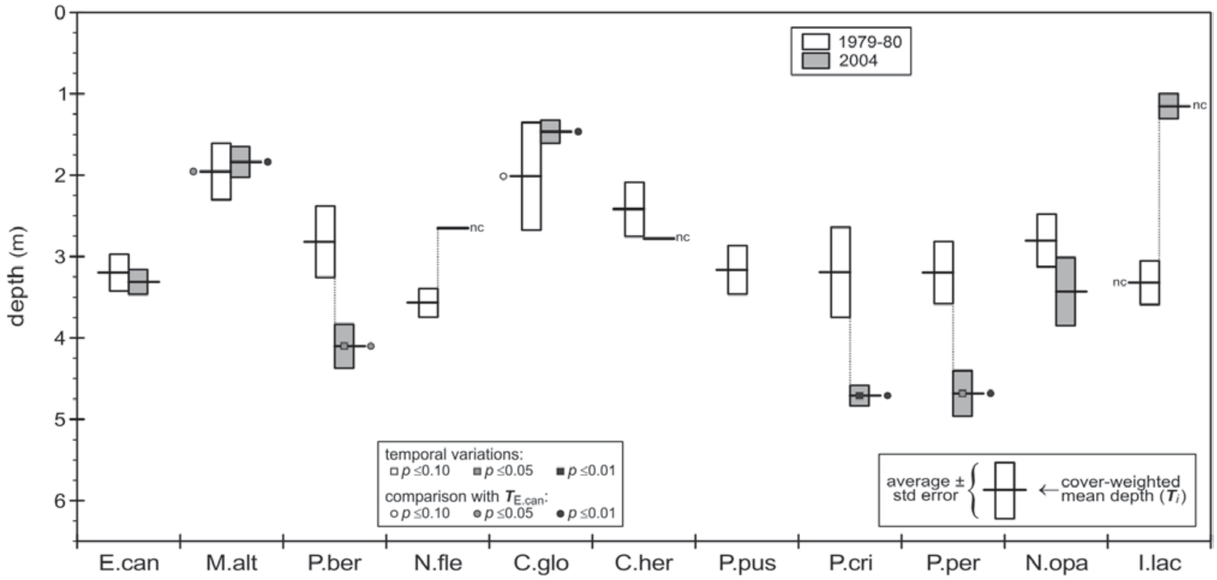

Fig. 6. Cover-weighted mean depth (averaged over seven sampling stations ± standard error), for *E. canadensis* and selected species in Steinsfjord, in 1979–80 and 2004. Symbols for statistically different changes in temporal variations are inside the bars and comparisons with same-period mean depth of *E. canadensis* ($T_{\text{E.can}}$) are reported laterally; nc = not calculable ($n < 3$) (only for comparisons with $T_{\text{E.can}}$). Species are listed from commonest to rarest. Species names: E.can = *Elodea canadensis*, M.alt = *Myriophyllum alterniflorum*, P.ber = *Potamogeton berchtoldii*, N.fle = *Najas flexilis*, C.glo = *Chara globularis*, C.her = *Callitriche hermaphroditica*, P.pus = *Potamogeton pusillus*, P.cri = *Potamogeton crispus*, P.per = *Potamogeton perfoliatus*, N.opa = *Nitella opaca*, I.lac = *Isoetes lacustris*. Detailed *t* test analysis is in Appendix Table A3 available online.

C. globularis's mean depth remained qualitative (Fig. 6 and Appendix Table A3 available online), but *C. globularis*'s mean depth had further shifted upward away from *E. canadensis*'s by 2004 (Fig. 6). Similarly, *C. globularis*'s mean depth moved above *M. alterniflorum*'s in 2004, albeit non-significantly, after an initial full overlap in 1979–80 (two-tailed *t* tests: $t_{1979\text{–}80} = 1.010$, d.f. = 7, $P = 0.99$; $t_{2004} = 1.491$, d.f. = 11, $P = 0.16$).

Callitriche hermaphroditica

Despite a relatively unchanged depth distribution since 1936–38 (Baardseth, 1942), *C. hermaphroditica* had markedly decreased in abundance by 2004 (Fig. 5 and Appendix Table A2 available online), when it was found at only one photographic station and at an additional area (in 2003) in very shallow water at low abundance. The single-station occurrence in 2004 precluded temporal and within 2004 statistical comparisons of mean depths. However, the 2004 depth range of *C. hermaphroditica* was fully (*E. canadensis* and *M. alterniflorum*) or partially (*P. berchtoldii*) contained in those of the major (co)dominant species, with whose mean depth *C. hermaphroditica* overlapped in 1979–80 (Fig. 6; other results not shown).

Potamogeton pusillus

P. pusillus was widespread and relatively common in Steinsfjord in 1979–80, (Fig. 5), with a mean depth at ~3.2 m (Fig. 6). *P. pusillus*'s mean depth fully overlapped with *E. canadensis*'s (two-tailed *t* test: $t_{1979\text{–}80} = 1.146$, d.f. = 5, $P = 0.30$) and *P. berchtoldii*'s ($t_{1979\text{–}80} = 0.745$, d.f. = 5, $P = 0.49$), and overlapped marginally with *M. alterniflorum*'s in 1979–80 ($t_{1979\text{–}80} = 2.411$, d.f. = 5, $P = 0.06$). *P. pusillus* was not recorded in the 2004 photographic survey.

Potamogeton crispus *and* P. perfoliatus

P. crispus and *P. perfoliatus* had a scattered distribution and were uncommon in both photographic surveys, but exhibited a shift to deeper water from 1979–80 to 2004 (Fig. 5). *P. perfoliatus* had similar bimodal depth distributions in 1936–38 and 1979–80, with two maxima of occurrence in shallow and moderately deep waters, while the 2004 distribution pattern was unimodal, with a single peak in deeper waters (Figs. 3 and 5). *P. crispus*'s distribution remained weakly bimodal in both photographic surveys (Fig. 5). As a result of the general downward shift, *P. crispus*'s and *P. perfoliatus*'s mean depths became significantly different from *E. canadensis*'s in 2004 after an initial overlap in 1979–80 (Fig. 6). Similarly, these two pondweeds moved further away from *M. alterniflorum* after an initial partial overlap in 1979–80 (two-tailed *t* tests for mean depth: *P. crispus*: $t_{1979\text{–}80} = 2.129$, d.f. = 2, $P = 0.17$; $t_{2004} = 7.075$, d.f. = 5, $P < 0.01$; *P. perfoliatus*: $t_{1979\text{–}80} = 2.016$, d.f. = 4, $P = 0.11$; $t_{2004} = 8.658$, d.f. = 4, $P < 0.01$).

Nitella opaca

N. opaca remained a widespread but marginal presence with a scattered occurrence both in 1979–80 and 2004 (Fig. 5). Its depth range was the widest among the less common taxa (Fig. 5). Although the downward shift in mean depth remained statistically not significant, *N. opaca*'s depth range became completely included in *E. canadensis*'s in 2004 (Figs. 4 and 5). *N. opaca*'s mean depth had moved below *M. alterniflorum*'s (two-tailed t tests: $t_{1979\text{–}80} = 1.665$, d.f. = 11, $P = 0.12$; $t_{2004} = 3.788$, d.f. = 11, $P < 0.01$) but had remained within those of *E. canadensis* (Fig. 6) and *P. berchtoldii* by 2004 ($t_{1979\text{–}80} = 0.042$, d.f. = 11, $P = 0.97$; $t_{2004} = 1.389$, d.f. = 11, $P = 0.19$).

Filamentous algae

Filamentous algae maintained their wide depth range since the early *E. canadensis* colonization in the late 1970s, but their abundance was greatly reduced in the ˜1.5–4-m range by 2004 (Fig. 5). The temporal change in mean depth of filamentous algae from 3.5 to 4.6 m remained qualitative (two-tailed t test: $t_{1979\text{-}vs.\text{-}2004} = 1.376$, d.f. = 11, $P = 0.20$), but their mean depth moved significantly below *E. canadensis*'s by 2004 ($t_{1979\text{–}80} = 0.445$, d.f. = 10, $P = 0.67$; $t_{2004} = 2.070$, d.f. = 12, $P = 0.06$). The chlorophyte *C. aegagropila* dominated the taxon of filamentous algae in deeper waters, and made up the bulk of the total vegetation at such depths.

Discussion

The slightly mesotrophic condition of clear-water (Lake) Steinsfjord combined with the relatively large lake size (Rørslett, 1991; Jones *et al.*, 2003) may be the reason for the temporally stable high species richness of macrophytes.

E. canadensis greatly expanded its presence in Steinsfjord since 1979–80, and has dominated the community of submerged vegetation through 2004. Although the peak in areal distribution occurred within a decade from invasion, the colonization area of *E. canadensis* has remained relatively stable for the past decade or so. The "typical" pattern of *E. canadensis* colonization, "explosion", domination and decline (*e.g.*, Nichols and Lathrop, 1994; Simberloff and Gibbons, 2004) seems to have taken a longer-than-average time in Steinsfjord. *E. canadensis* fully colonized Steinsfjord in ∼ 6 years, and showed only a slight decline since its 1982–85 peak biomass, in contrast to sharper and faster declines reported elsewhere (*e.g.*, Simberloff and Gibbons, 2004). Lake size may account for the slow colonization and subsequent decline in Steinsfjord, as most other studies of invasive macrophytes have been carried out in more "typical" smaller and shallower lakes (*e.g.*, Nichols, 1994; Nichols and Lathrop, 1994), where the area for initial colonization is smaller, and the number of possible refuge areas is lower (Jones *et al.*, 2003).

Since early colonization, *E. canadensis* has significantly increased its depth range both upward and downward; however, its mean depth has not changed since early colonization, suggesting that 3–4 m is its optimal depth for growth, at least in Steinsfjord. *E. canadensis*'s initial and stable biomass peak at 3–4 m in Steinsfjord aligns with similar observations of *E. canadensis*'s "preference" for such intermediate depths (*e.g.*, Collins *et al.*, 1987; French and Chambers, 1996). However, surface mats have not appeared in Steinsfjord since the peak period in the mid-1980s, and plant shoots have become shorter (Berge *et al.*, unpublished data). The nutrient level in the sediment seems to be a major factor for the growth of *E. canadensis* in Steinsfjord (Rørslett *et al.*, 1986, Berge *et al.*, unpublished data), aligning to similar findings for the closely related *E. nuttallii* in Lake Biwa and Lake Kizaki in Japan (Nagasaka, 2004, and references herein). However, the extensive grazing of waterfowl during and after the peak of *E. canadensis* is expected to have contributed to the depletion, by removing plants (and associated nutrients) from the lake through sustained herbivory. This hypothesis is supported by diet studies of the most important waterfowl species in Steinsfjord in the last 20 years: *E. canadensis* comprises 95–100% of the diets of mute swan (*C. olor*), coot (*F. atra*) and wigeon (*A. penelope*), and ∼ 50% of the diet of whooper swan (*C. cygnus*) (Larsen, 2006). Also, Perrow *et al.* (1997) found that grazing on species such as *E. canadensis* may determine macrophyte abundance and community structure in subsequent growing seasons.

Absence or low presence of *E. canadensis* in very shallow waters has been reported earlier (Forest, 1977; Nichols and Shaw, 1986; Collins *et al.* 1987; French and Chambers, 1996) and may be associated with a combination of factors, including changed nutrient level in the sediment and grazing pressure from waterfowl. Lowered water level and corresponding periodic draining of the upper littoral zone in the mid 1990s may have had an additional effect. The variation in the median water level in the growing season, at approximately 80 cm, is expected to have minor importance for the distribution of species in deeper areas. However, periods with considerable low water in spring (for instance, in 1996–97 and 2003) caused freezing and ice-erosion of the sediment and on-site vegetation, which may have affected the *E. canadensis* stands in shallow water.

Rørslett (1983) noticed a reduction in *Lobelia dortmanna* from 1936–38 to 1979–80. Our photo survey does not cover the very shallow areas this species prefers, but we recorded a scattered distribution of the species during the 2003 update survey from the boat, which is a further decrease since 1979–80. The main decrease, in both frequency- and cover-based depth distribution, for *I. lacustris* and *L. uniflora* took place before the invasion of *E. canadensis*, and seems to be caused by mild eutrophication (as pointed out by Skogheim and Rognerud, 1976; Rørslett, 1983) or competition with elodeids.

We found no significant whole-lake decrease in species richness for the period 1979–2004; most of the taxa found in 1979–80 could still be found in 2004. Some of the 1979–80 taxa not retrieved in 2004 were observed at localities that today are physically disturbed or changed in different ways, *e.g.* road construction. However, the photograph-based decrease in average species richness corresponded to the range of maximum *E. canadensis* abundance in 2004 (*i.e.*, the 2–4-m depth interval), suggesting that *E. canadensis*'s invasiveness may have led to a decline in local biodiversity through displacement of some species.

The only taxa whose spatial distributions greatly overlapped with *E. canadensis* in 2004 were *M. alterniflorum* and *P. berchtoldii*, in addition to the less abundant *N. opaca*. *M. alterniflorum* and *P. berchtoldii* had in 2004 mean depths which were shallower and deeper, respectively, than *E. canadensis*'s, though their depth ranges overlapped with that of *E. canadensis*. Both *M. alterniflorum* and *P. berchtoldii* are among the most common species in Norway, and have wide ecological amplitudes, growing into extensive stands also in oligotrophic lakes and rivers (Lindstrøm *et al.*, 2004), suggesting low nutrient demands. Compared to other plants (see later), they may therefore be less affected by the sediment nutrient depletion caused by *E. canadensis* (Berge *et al.*, unpublished data). Nutrient uptake from sediments is increasingly more important than foliar uptake in nutrient-poorer waters (Carignan and Kalff, 1980; Rattray *et al.*, 1991; Robach *et al.*, 1995), suggesting the potential for strong underground competition among rooted species in Steinsfjord. Sharp declines in abundance for some species since 1979–80 (*N. flexilis, P. pusillus* and *C. hermaphroditica*) suggest that such species may be at a competitive disadvantage against *E. canadensis, M. alterniflorum* and *P. berchtoldii. N. flexilis, P. pusillus* and *C. hermaphroditica* appeared unable to move away from *E. canadensis*'s mean depth, with which they fully overlapped in 1979–80, supporting this hypothesis.

As distinct from *E. canadensis*, *M. alterniflorum* can grow in a terrestrial state above the water level (Preston and Croft, 1997), and is therefore a strong competitor of *E. canadensis* in Steinsfjord's shallow areas, which occasionally are artificially drained. In addition, a number of studies have reported the effect from waterfowl grazing on submerged macrophytes (*e.g.*, Lauridsen *et al.*, 1993, Weisner *et al.*, 1997, Rodríguez-Villafañe *et al.*, 2007), and Crawley (1983) had proposed that selective grazing by waterfowl could affect species composition and even succession. Weisner *et al.* (1997) showed pronounced grazing effect on *Potamogeton pectinatus* L. and no effect on *Myriophyllum spicatum* L. in (Lake) Kranksjön in Sweden. They suggested that selective grazing could explain the increase of *M. spicatum* in the lake. Rodríguez-Villafañe *et al.* (2007) also found that *M. alterniflorum* is a "non-preferred" species by herbivorous waterfowl. Even though *M. alterniflorum*'s "preference" for shallow waters (Collins *et al.*, 1987) and *E. canadensis*'s for mid-depths (Collins *et al.*, 1987; French and Chambers, 1996; this study) suggest an inherent spatial partitioning to some degree, *E. canadensis* can also grow in shallow waters (*e.g.*, Bowmer *et al.*, 1984; Kłosowski *et al.*, 2011). We suggest that the heavy herbivory on *E. canadensis* in Steinsfjord may have led to an enhanced competition benefit for *M. alterniflorum* in shallow areas. The ability to survive and grow in areas being occasionally drained, combined with minor herbivory by waterfowl, are likely important factors for the increase of *M. alterniflorum* in Steinsfjord's shallow areas.

The subdominant taxa whose cover-weighted mean depth overlapped with *E. canadensis* at the onset of its colonization in 1979–80, either shifted to deeper water (*P. berchtoldii*, *P. perfoliatus* and *P. crispus*) or apparently went locally (near) extinct (*P. pusillus*, *N. flexilis* and *C. hermaphroditica*). This seems to have happened despite the fact that some of these taxa had higher cover than *E. canadensis* in 1979–80. In addition, some species with mean depth in the area covered by mass stands of *E. canadensis* in 2004 (*C. globularis* and *I. lacustris)* seem to have moved further up, and have greatly reduced their depth range. Marginal or non-existing overlap between *N. flexilis*'s or *P. pusillus*'s and *M. alterniflorum*'s mean depth, but full overlap with *E. canadensis*'s and *P. berchtoldii*'s in 1979–80 (ongoing for *N. flexilis* in 2004), suggest that competition may have been much higher with the then spreading *E. canadensis* than with the long-established *M. alterniflorum*. *N. flexilis* and *P. pusillus* therefore appear to have been brought to local (near) extinction by *E. canadensis* rather than by *M. alterniflorum*. The latter species may have been more heavily (co)involved in the dramatic reduction of *C. hermaphroditica* (whose mean depth in 2004 continued to overlap with those of all major taxa) and in the marginalization of *C. globularis* (and possibly also *I. lacustris* and *L. uniflora*) to much shallower waters. Full inclusion of *N. flexilis*'s depth range within *E. canadensis*'s and *M. alterniflorum*'s ranges, and partial overlap with *P. berchtoldii*'s range in 2004, suggest that *N. flexilis* may have continued to experience a competitive disadvantage against all major (co)dominant taxa in Steinsfjord through 2004.

In 1979–80, *N. flexilis* was well established in the 2.5–4.5 m depth range. In this depth area, the *E. canadensis* plants are erect and non-branching, therefore having a lower shading effect on *N. flexilis* than the canopy stands with heavily branching plants; the latter have never been seen in waters deeper than 2 m. In addition, the typical shoot heights of *E. canadensis* at these depths were less than 1 m in 2004 (Berge *et al.*, unpublished data). We therefore suggest that shading effects from *E. canadensis* are not the main reason for the decline of *N. flexilis*, though some shading effect may exist also in stands of only erect plants (Pokorný *et al.*, 1984; Wingfield *et al.*, 2004). In Scotland, *N. flexilis* is found only in mesotrophic water (Wingfield *et al.*, 2004), which perhaps indicates that both eutrophication and oligotrophication have a negative effect on *N. flexilis*. The very slight recent oligotrophication in Steinsfjord, with a decrease in water-column total phosphorus concentration from 11–12 $\mu g\ L^{-1}$ in 1979–80 to 8–9 $\mu g\ L^{-1}$ in 2003–04, and a corresponding increase in Secchi depth from around

5.5 to 6 m (Berge *et al.*, unpublished data), also can hardly explain the reduction in abundance suffered by *N. flexilis* in the same time frame. *E. canadensis* growth patterns are highly variable, but this species is able to start growing early in the spring (Nichols and Shaw, 1986), sprouting from old stems, and may pre-empt the available nutrient pool in the sediment (Craine *et al.*, 2005). This could have enabled *E. canadensis* to greatly expand its presence in Steinsfjord at the expenses of other species. The 30% reduction in sediment nutrients since 1979–80 (Berge *et al.*, unpublished data) suggest that *E. canadensis* is the reason for the decrease of *N. flexilis* in Steinsfjord, *N. flexilis* obtaining the bulk of its nutrients from the sediments (Moeller *et al.*, 1988). Dramatic seasonal (May–October) decreases in phosphorus and especially nitrogen concentrations were observed in the top 5 cm of sediments in a dense littoral macrophyte stand dominated by *E. canadensis* by Pokorný *et al.* (1984). Diminished nutrient content in the sediment by *E. nuttallii* was also linked to the displacement of native species in Lake Kizaki (Nagasaka, 2004), supporting our hypothesis of competition by *E. canadensis* through absorption of sediment nutrients.

In addition, the mass invasion of *E. canadensis* in Steinsfjord raised the water-column pH to 8.5 (summer average) *via* extensive photosynthesis (Rørslett *et al.*, 1985, 1986), and to a maximum pH of 10.2 inside the *E. canadensis* stands (Berge, 1986). In water with such pH values, no free CO_2 can be found (Golterman *et al.*, 1978). *N. flexilis* is an obligate CO_2 user (Wetzel, 1969), and is not able to use HCO_3^-, which instead can be utilized by *E. canadensis* (Ondok *et al.*, 1984). Intense photosynthesis in *E. canadensis*-dominated stands can lead to CO_2 depletion in the water column (Ondok *et al.*, 1984), thus impairing growth for the CO_2-obligate *N. flexilis*. The depletion of water-column CO_2 by *E. canadensis*, coupled with the likely competition for sediment nutrients, support our hypothesis that *E. canadensis* may be the main reason for the decrease of *N. flexilis* in Steinsfjord.

E. canadensis is also known to produce allelochemicals (*e.g.*, Erhard and Gross, 2006), and some close-range allelopathy between *E. canadensis* and sensitive target species, *e.g. N. flexilis*, also may have occurred, though this mechanism is even more difficult to prove than some form of direct competition for nutrients or space (Gross *et al.*, 2007). However, given the high number of taxa that shifted their distribution range and mean depth around *E. canadensis*, pre-emptive competition for nutrients and space by the early-growing *E. canadensis* is more likely to be the primary factor behind the takeover of the Steinsfjord macrophyte community by *E. canandensis*.

Among the less abundant species, the pondweeds *P. perfoliatus* and *P. crispus* seem to have survived the invasion of *E. canadensis* by moving to deeper water. *P. perfoliatus* had approximately the same frequency-based depth distribution in 1936–38 and 1979–80, with two maxima of occurrence which were supposed to be due to two different genotypes (Baardseth, 1942; Rørslett, 1983). If the hypothesis of the two genotypes is true, the shallow-water type seems to have disappeared or markedly reduced by 2004, with *P. perfoliatus* persistence in Steinsfjord possible thanks to its deeper-water genotype. Although Secchi depth has not changed dramatically since the peak of eutrophication in the 1970s (Berge *et al.*, unpublished data), the downward expansion and/or increased abundance below 3 m of depth in 2004 of many taxa, including *N. opaca*, the shallow-water dweller *M. alterniflorum*, the pondweeds *P. berchtoldii* (a subdominant in 2004), *P. crispus* and *P. perfoliatus*, suggest some amelioration in the light conditions at such depths. Berge (1986) and Rørslett *et al.* (1986) directly related year-to-year variations in underwater light conditions to seasonal variation in the then peaking biomass of *E. canadensis* in Steinsfjord, strongly suggesting that *E. canadensis* has a positive effect on water transparency. Short-range anti-algal allelopathy by *E. canadensis* (Erhard and Gross, 2006) supports Berge *et al.*'s (1986) ecosystem-scale findings, though other mechanisms are likely (co)involved. *E. canadensis* may have suppressed the biomass of benthic filamentous algae in its "preferred" depth range of 3–4 m, either by allelopathy, shading, or both. Seedlings of rooted macrophytes such as pondweeds may have thus being partially released from competition (for light, nutrients, or simply space, as *E. canadensis* does not form thick bottom mats as most filamentous algae do), leading to some relatively diversified growth at such depths. Regardless of the mechanisms involved, increased quadrat-based species richness (S) in deeper waters (4–6 m) in 2004 also supports the hypothesis that the mass invasion of *E. canadensis* in Steinsfjord has brought about some positive effects along with the negative effects on many individual taxa, especially at mid-depths.

The reported maximum colonization depth for *I. lacustris* in Scandinavian lakes is 7 m, and is estimated to be equal to 6–10% of the surface irradiance (Rørslett and Brettum, 1989). Based on the typical Secchi depth readings and light intensity in Steinsfjord (Blikstad Halstvedt, unpublished data), Mjelde (unpublished data) suggests that *I. lacustris* has a maximum colonization depth of 3.5–5 m depth in Steinsfjord. Therefore, the observed lower limit of *I. lacustris*'s depth range at 1.5 m in 2004 is unlikely to be due to light limitation, as also argued by Rørslett (1983). After the decline prior to 1979 (see earlier), the isoetids may have been prevented from rebounding by *E. canadensis*'s explosive expansion.

The presence of *C. globularis* in Steinsfjord changed little from 1936–38 to 1979–80. After 1979–80, the sharp decline in abundance (as %cover) below 1.5 m depth concomitant with an increase in shallow areas, an increased lake-wide frequency of occurrence (as %frequency), and a significant upward departure from the mean depth of *E. canadensis* and *M. alterniflorum*, suggest that both *E. canadensis* and *M. alterniflorum* have exerted some competitive pressure on *C. globularis*.

Summary and conclusions

The present study shows that *E. canadensis* has had a marked impact on the aquatic macrophyte community in Steinsfjord. Species composition has changed remarkably, from a diverse community dominated by *N. flexilis* in 1979–80 to a 2004 community dominated by *E. canadensis* at depths > 2 m, with *P. berchtoldii* and *M. alterniflorum* as subdominants. Most other macrophyte species have decreased in importance by 2004.

In particular, species whose cover-weighted mean depth overlapped with *E. canadensis*'s in 1979–80 had reduced their abundance in 2004, and either shifted to deeper or shallow water, or (almost) disappeared from the sampling stations. This seems to have happened despite some of these species having had a higher presence than *E. canadensis* in 1979–80. One of the strongly reduced species is the red-listed species *N. flexilis*. Our study indicates that *E. canadensis* is likely to be the reason for the decrease of *N. flexilis*, and maybe of other species such as *C. hermaphroditica* and *P. pusillus*, mainly through depletion of free CO_2 in the water column and/or of nutrient content in the sediment. The shallow-to-intermediate-depth subdominant *M. alterniflorum* may have contributed to the marginalization of other shallow-water species such as *C. globularis*, *I. lacustris*, and maybe *C. hermaphroditica*. The ability to survive and grow in areas that are occasionally drained, combined with minor herbivory by waterfowl, are likely important factors for the increase of *M. alterniflorum* in Steinsfjord's shallow areas at the expenses of *E. canadensis*.

Acknowledgements. This project was supported by the Norwegian Research Council (project No. 154270/S30). Constructive criticism from two reviewers substantially improved the manuscript.

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