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Aquatic macrophytes as tools for lake management

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Abstract

Aquatic macrophytes can serve as useful indicators of water pollution along the littoral of lakes. In Bavaria, the submerged vegetation of about 100 lakes has been investigated by SCUBA diving over the past decade to evaluate the state of nutrient pollution. All lakes are marl lakes located in the northern calcareous alps and the prealpine region. The lakes differ in size, morphology, water residence time, nutrient loading, trophic status, recreational activities, and other characteristics. In all cases the entire shoreline of the lakes has been investigated. Among the investigated lakes are the three biggest Bavarian lakes, i.e. Lake Chiemsee, Lake Starnberg and Lake Ammersee. Mapping of the submerged vegetation occurred in four different depth zones, and variable shoreline sections. The length of each section was determined by the uniformity of the vegetation; as it changed, a new section was designated. Within each section and zone species were recorded and abundance of all observed macrophytes was estimated semi-quantitatively on a five-point scale. Nine different groups of macrophytes were recognised, including, in total, 45 different species of macrophytes. On the basis of this catalogue of indicator species, in combination with the abundance of the species, a 'macrophyte index' was devised, which ranges from 1 (unpolluted) to 5 (heavily polluted). Six groups of values of the macrophyte index, each represented by a different colour or grey-scale (in this publication), are presented to allow a clear illustration of the results. Important information for the successful restoration of lakes in Upper Bavaria has been obtained from the distribution patterns of the submerged vegetation. Many unknown waste water inflows or diffuse sources could be detected due to abrupt changes in the macrophyte index. Furthermore, the success of waste water removal by 'ring canalisation', resulting in a re-oligotrophication of many Bavarian lakes can be followed by changes in the macrophyte index.

Introduction

Aquatic macrophytes in the littoral zones of lakes have two fundamental properties which make them attractive as limnological indicators. In the first instance, they react slowly and progressively to changes in nutrient conditions, in contrast to bacteria and microalgae, i.e. over several years. Macrophytes therefore function as integrators of environmental conditions to which they are subjected and thus can be used as long-term indicators with high spatial resolution.

Secondly, the littoral zone may experience patterns of nutrient (and pollutant) concentrations (Dave, 1992; Drake & Heaney, 1987), caused by natural or artifical inflows as well as by diffuse, non-point sources. The latter are difficult to localize and quantify but even chemical analysis of point sources is often neglected in limnological routine work. Since most important nutrient loading occurs in the land–water ecotone, programmes for the restoration of lakes are dependent on reliable data which give insight into quality and quantity of nutrient loading. Early investigations in Scandinavia have shown that aquatic macrophytes reflect the nutrient status of their immediate habitat by their presence/absence and abundance and thus can be effectively used as biological indicators (Suominen, 1968; Uotila, 1971).

In Central European lakes, the disappearance of a number of species as a consequence of rapid eutrophication has been recorded over the past three decades (Lachavanne & Wattenhofer, 1975; Lang, 1968; Melzer, 1981). Concern over the widespread effects of species loss, in comparison with historical records, and realisation of the need to understand precise impacts of nutrient pollution in the littoral zone in order to direct restoration, led to the development of a method for macrophyte community evaluation

Methods

Mapping of macrophytes

Mapping of the submerged vegetation of lakes can be done with the help of mechanical equipment, however, investigation by SCUBA diving is more precise. The entire shoreline of about 100 calcareous lakes in Upper Bavaria has been mapped by divers to obtain comprehensive and reliable data on the distribution of submerged macrophytes. To improve exactness, mapping occurred in four different depth zones: 0–1 m, 1–2 m, 2–4 m and >4 m. By this procedure depth preferences of single species and changes of maximal depth distribution of macrophytes along the shoreline could both be evaluated.

Mapping was carried out in shoreline sections of variable breadth. The boundaries of each section were determined by the uniformity of the vegetation; as this changed, a new section was designated. The breadth of a mapping section ranged between 2 km at maximum and 20–30 m in the case of small point sources. Within a mapping section and depth zone all macophyte species (spermatophyta, bryophyta and charophyta) were recorded and abundance estimated on a five-point scale following Tüxen & Preising (1942), where 1= very rare, 2= infrequent, 3= common, 4= frequent and 5= abundant. However, the scale is not linear and so the abundance value was cubed ($y = x^3$) to develop a ‘macrophyte index’ (see below).

The occurrence of macrophyte species reflects the degree of nutrient enrichment within a shoreline section. A catalogue of nine ‘indicator groups’ of macrophyte species (Table 1) exhibiting different sensitivity towards nutrient enrichment was developed from the lake survey. In total 45 species of submerged macrophytes and free floating plants were included. Species allocated to ‘indicator group’ 1 are restricted to oligotrophic lakes, while those in ‘indicator group’ 5 are restricted to eutrophic, nutrient-rich lakes or sections of lakes. The remaining seven groups represent transitions between these two extremes.

Macrophyte index

The ‘macrophyte index’ (MI) was calculated separately for each surveyed section, using the 45 indicator species. It is based on the values of ‘indicator group’ (I) of the species (a–z) and the ‘quantity’ (Q) of these species. MI is calculated by the following formula:

$$\mathrm{MI} = \frac{\sum_{a-z} I_{a-z} \cdot Q_{a-z}}{\sum_{a-z} Q_{a-z}},$$

where MI = macrophyte index; I_{a-z} = indicator group of the species a-z; Q_{a-z} = quantity of species a-z.

Six classes of the macrophyte index were designated, each representing different degrees of nutrient pollution. These six classes are assigned different colours (shown as grey scale, Table 2) to allow a clear illustration of the results. The application of the macrophyte index in a series of case studies demonstrates its value in directing cost-effective restoration.

Results

Osterseen lakes

The Osterseen lakes are situated south of Lake Starnberg, into which they drain, are 20 individual lakes which offer the ideal site for a ‘natural experiment’ and illustrate the kind of survey data which was enabled the macrophyte index to be constructed. The lakes are connected in series with each other by natural channels. Water flows through them from south to north. Anthropogenic influence is concentrated around the southern-most lakes, at the beginning of the lake chain. Natural self-purification as well as dilution occurs along the chain and the nutrient levels gradually decline. Mean total phosphorus concentration of the southern-most Lake Waschsee is 80 μg l^{-1} P, this of the following lake 65 μg l^{-1} P, that of the third 40 μg l^{-1} P. Phosphorus concentrations drop below 15 μg l^{-1} P in the northern lakes. Lake Lustsee is a lake in the north of the area without through flow. It possesses many nutrient-poor groundwater inlets and as a consequence total phosphorus concentrations are below 10 μg l^{-1} P. This results in a high Secchi-disk transparency (annual mean >10 m). The northern lakes are characterized by a flora typical for nutrient poor lakes. Here *Chara hispida, C. aspera, C. tomentosa, C. intermedia, C. contraria, Potamogeton coloratus, Utricularia ochroleuca, U. minor* and *U. australis* prevail. In Lake Lustsee *Chara* meadows cover the surface of the sediment down to 17 m, the deepest point of the lake.

Exclusively restricted to the southern lakes, as well as to Lake Fischkaltersee in the south-east are

Table 1. Classification of 45 submerged and free-floating macrophyte species into nine indicator groups

Group 1.0	Group 1.5	Group 2.0	Group 2.5	Group 3.0	Group 3.5
Chara hispida	*Chara aspera*	*Chara delicatula*	*Chara contraria*	*Chara vulgaris*	*Myriophyllum verticillatum*
Chara polyacantha	*Chara intermedia*	*Chara tomentosa*	*Chara fragilis*	*Myriophyllum spicatum*	*Potamogeton berchtoldii*
Chara strigosa	*Utricularia minor*	*Potamogeton alpinus*	*Nitella opaca*	*Potamogeton filiformis*	*Potamogeton lucens*
Potamogeton coloratus			*Nitellopsis obtusa*	*Potamogeton perfoliatus*	*Potamogeton praelongus*
Utricularia ochroleuca			*Potamogeton gramineus*		*Potamogeton pusillus*
			Potamogeton natans		
			Potamogeton × *zizii*		

Group 4.0	Group 4.5	Group 5.0
Fontinalis antipyretica	*Callitriche cophocarpa*	*Ceratophyllum demersum*
Hippuris vulgaris	*Elodea canadensis*	*Zannichellia palustris*
Lagarosiphon major	*Elodea nuttallii*	*Potamogeton mucronatus*
Potamogeton pectinatus	*Potamogeton crispus*	*Sagittaria sagittifolia*
	Potamogeton obtusifolius	*Lemna minor*
	Ranunculus circinatus	*Spirodela polyrhiza*
	Ranunculus trichophyllus	*Potamogeton nodosus*

Table 2. Relationship between index class, degree of nutrient status and assigned colour

Index class	Degree of nutrient enrichment	
1.00–1.99	Slight	Dark blue
2.00–2.49	Low	Pale blue
2.50–2.99	Moderate	Green
3.00–3.49	Immense	Yellow
3.50–3.99	Heavy	Orange
4.00–5.00	Massive	Red

macrophyte species designated to 'indicator groups' 4.5 and 5.0, respectively (*Elodea canadensis, Potamogeton crispus, Ceratophyllum demersum, Zannichellia palustris* and *Lemna minor*). Floristic transitions between these two extremes are to be found in the middle group of lakes. Mapping of macrophytes was carried out in 1974, 1981 and 1994, respectively. In Figure 1 only the results of the most recent investigation are shown. With the exception of the southern-most lakes changes in macrophyte index in between the years were negligible. Lakes Waschsee, Schiffhüttensee and Sengsee in the south and Lake Fischkaltersee in the south-east were exposed to a substantial nutrient enrichment until 1983. As a consequence, values of the macrophyte index in 1974 and 1981 were higher.

Until 1983 waste water from the village of Iffeldorf, situated in the south of the Osterseen lakes area between Lake Waschsee and Lake Fischkaltersee, was cleaned insufficiently by underground-seepage. From that time on it has been collected by a canal and pumped to a treatment plant ouside the catchment area of the lakes. In addition, the intensity of agriculture was reduced in the surroundings of the lakes which were declared a natural conservation area after 1981. Results of the macrophyte mapping provided decisive information for these restorative measures. The remaining nutrient gradient within the chain of lakes is clearly reflected by macrophyte index. Although nutrient enrichment of the southern lakes was reduced, additional efforts have to be undertaken to obtain total improvement.

Lake Starnberg

Lake Starnberg (5636 ha, 2998 $\times$ 10^6 m^3, length of shoreline 49.2 km, max. depth 128 m, average depth 73 m) is located 25 km south of Munich. In this lake submerged macrophytes clearly indicated that meso-eutrophic conditions prevailed by the end of the 1970s (Figure 2, left). In 1979 the construction of a 'ring canal' for sewage, surrounding almost the entire lake, and reducing waste water pollution by 95%, was completed. In that year mapping of the macrophytes recorded the lake's status. Species of indicator group 3.5 (*Potamogeton pusillus*), 4.0 (*Potamogeton pectinatus*), 4.5 (*Ranunculus circinatus*) and 5.0 (*Zannichellia palustris*) occurred frequently. Maximum abundance of these species was demonstrated for parts of the west bank between the villages Unterzeismering and Niederpöcking. The macrophyte index for these sections indicated 'immense', and 'heavy' nutrient enrichment. Species indicating moderate or low nutient pollution only occurred infrequently. These species exhibited maximum growth in the southern part of the lake. Along parts of the east bank no 'macrophyte index' could be evaluated due to exteme morphology resulting in sparse growth of plants.

Figure 2 (right) reflects the changed situation after 1979. The situation improved markedly up to 1989, especially along the formerly enriched section between Unterzeismering and Niederpöcking. In 1989 shorter shoreline sections could be used than in 1979, which led to a higher resolution. The cases where 'heavy' and 'massive' nutrient enrichment still occurred could be traced to point sources. The Rötlbach and Seeseitenbach brooks were polluted by fish ponds. On the bank of one small section near Unterzeismering is a camp-site with direct waste water inflow into the lake. Within the villages of Bernried, Tutzing, Feldafing and Niederpöcking there are overflows of the ring canal which discharge into the lake in cases of overload caused by heavy rainfall. The water authorities which financed the macrophyte mapping successfully carried out further measures to remove these remaining sources of pollution.

Lake Chiemsee

Lake Chiemsee is the largest lake in Bavaria (7990 ha, 2048 $\times$ 10^6 m^3, length of shoreline 63.9 km, max. depth 73.4 m, average depth 25.6 m). Recovery of the lake by the completion of a ring canal started in 1986 did not begin until in 1991. The macrophyte vegetation had been mapped 1 year earlier. Figure 3 shows the diverse pattern of nutrient enrichment revealed by the macrophyte index. Massive enrichment occurred in the south-east bay where the river Tiroler Ache flows into the lake. 90 tonnes of phosphorus were imported annually by this river at the time of macrophyte

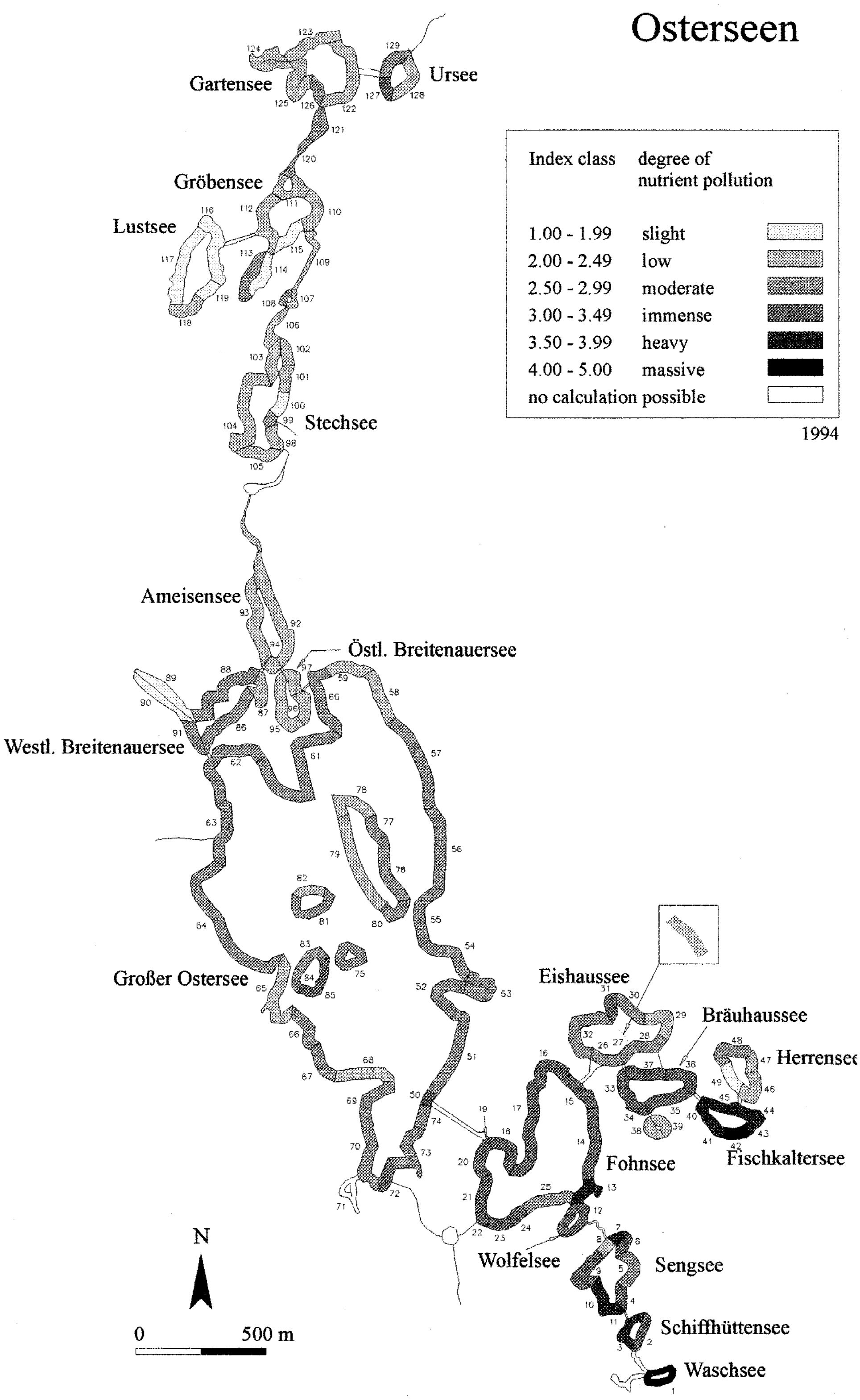

Figure 1. Macrophyte index of the Osterseen Lake area.

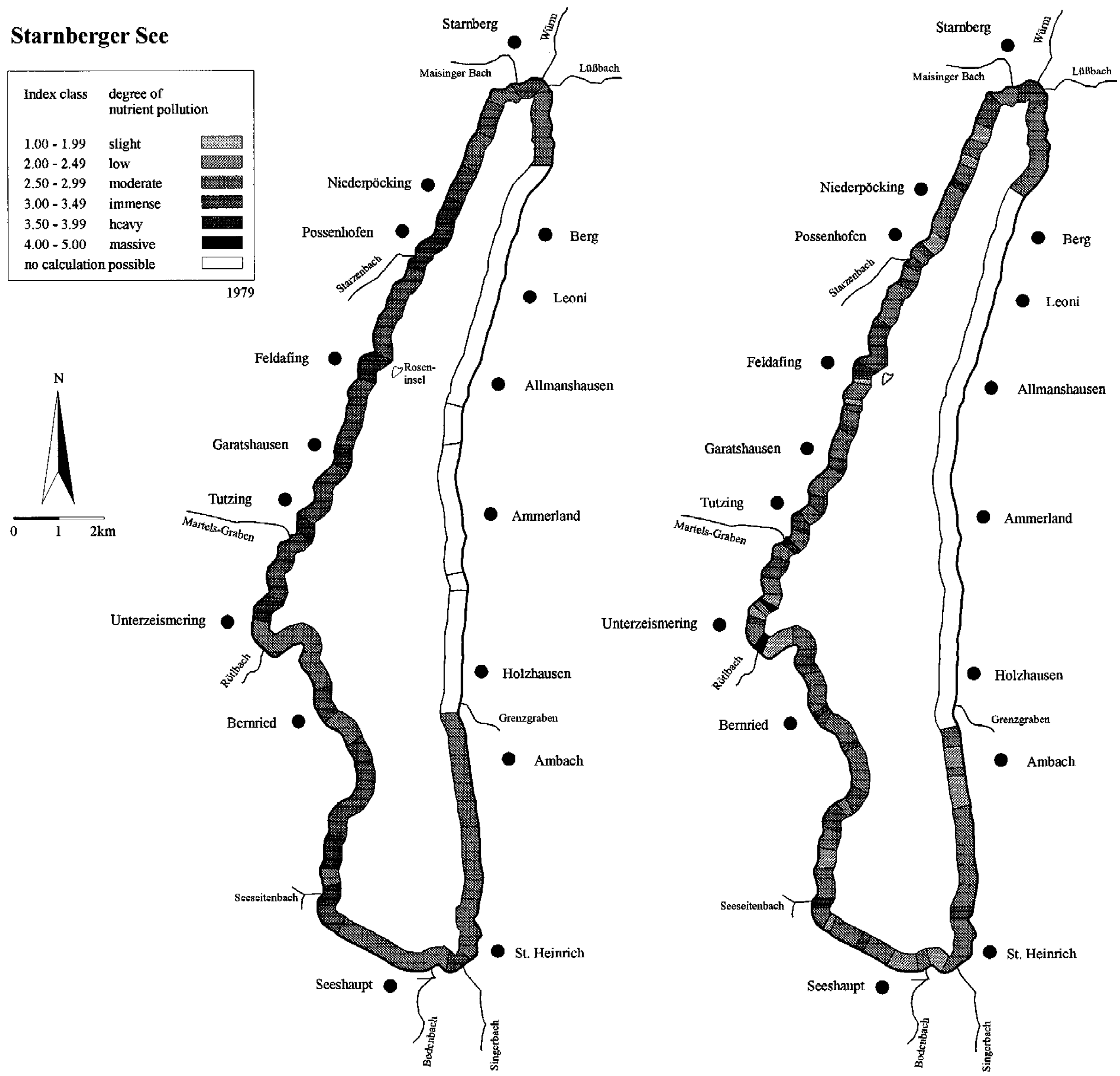

Figure 2. Macrophyte index of Lake Starnberg, 1979 (left) in comparison to 1989 (right).

mapping. The eastern parts of the lake were negatively influenced by this nutrient import. Massive enrichment was also caused by the inflow of all other rivers and brooks, except Krebsbach brook which is mainly fed by groundwater. The river Alz in the north is the outlet of the lake.

A low and moderate nutrient enrichment was registered for Herreninsel island, which is relatively sparsely populated. However, in three sections nutrient pollution was higher due to inflow of drainage ditches. In contrast Fraueninsel island is densely populated, although to reduce nutrient enrichment a sewage treatment plant with chemical phosphorus elimination had been constructed in 1976 with its effluent led into the hypolimnion. However, the effluent pipe was broken at 2 m depth and the (unknown) leakage was detected by macrophytes indicating ‘heavy’ and ‘massive’ enrichment. These species grew in a circle around this point source in the north-west section of the island.

In the area of the village Prien approximately 30 unknown pipes could be deteced due to changes in the composition of macrophytes. These pipes carried

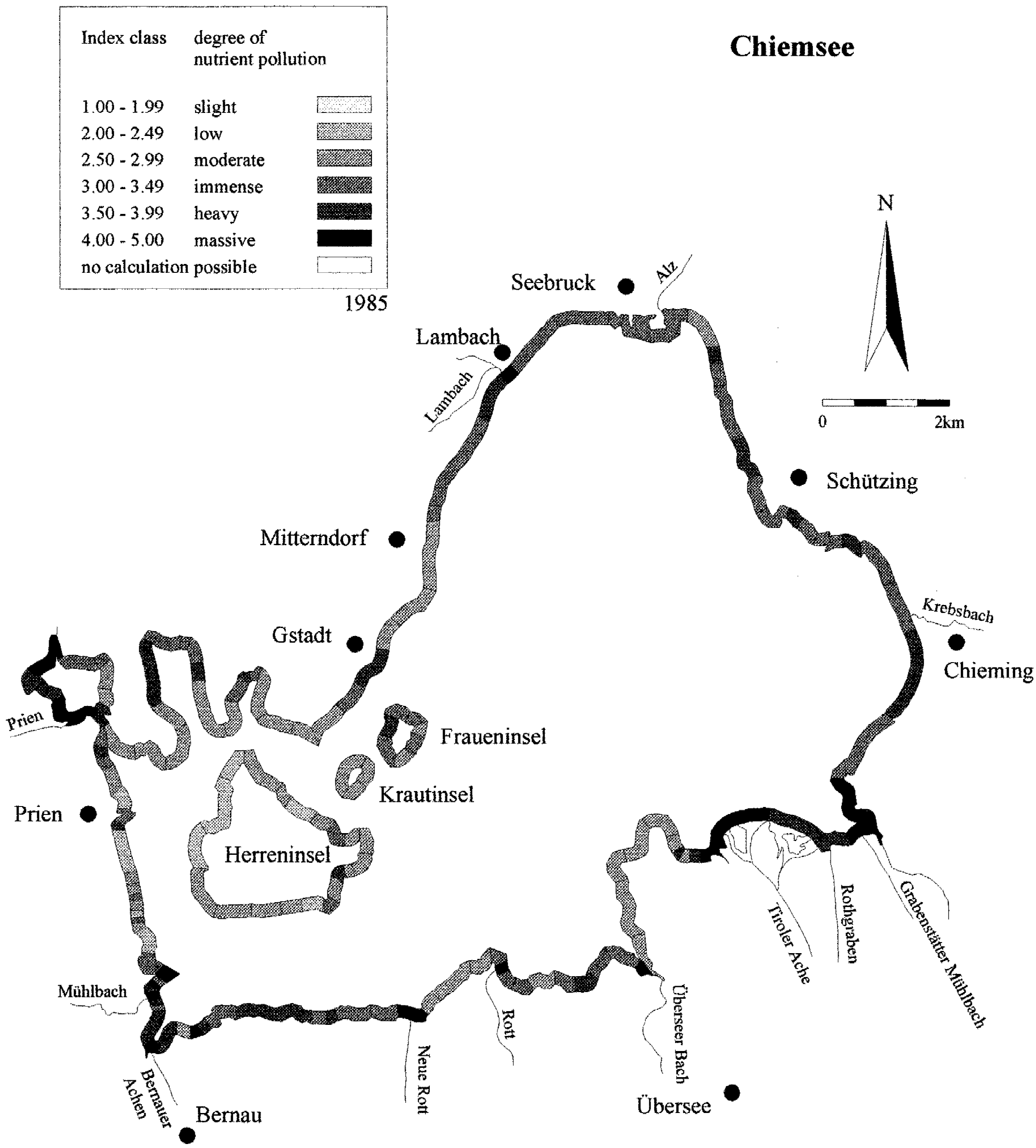

Figure 3. Macrophyte index of Lake Chiemsee.

either mechanically purified waste water, surface run-off or drainage water into the lake. In the area of the village Gstadt as well as in other sections nutrient-rich groundwater inlets caused by seepage of waste water were recognized by the growth of *Zannichellia palustris*. The success of the restoration of Lake Chiemsee following discovery and rectification of these varied sources will be revealed by re-survey in 1998.

Discussion

Natural lakes in Upper Bavaria are glacial in origin. They are all located in the alpine foothill plateaux and the northern calcareous Alps and therefore are hard-water lakes. In such lakes a characteristic flora exisits, differing from that occuring in soft water lakes. Although changes in the composition of the submerged macrophyte flora due to eutrophication have been reported in both types of lakes (Lang, 1968; Roelofs, 1983), the different vegetational characteristics restrict application of macrophyte index to calcareous lakes.

The macrophyte index can be applied to lakes of the southern calcareous Alps (Melzer, unpubl. data), although investigations of calcareous lakes in north Germany (Trapp, 1995) and north-east Germany (Krausch, 1964; Melzer, unpubl. data), respectively, have shown that some species exhibit a different behavior towards nutrient pollution. One example is *Ceratophyllum demersum*. In Bavarian lakes this species (indicator group 5) is restricted to highly polluted lakes or sections of lakes where it forms typical free-floating mats (Succow & Kopp, 1985). However, it grows well in oligo- and mesotrophic lakes of north and north east Germany, where this rootless species is loosely attached to the substrate and descends to greater depths depending on lake trophy (Trapp, 1995). *Ceratophyllum demersum* may even occur together with *Chara* species, for example in Lake Stechlin (Krausch, 1964), a combination which has never been observed in Bavarian lakes.

Comparison of observations between the two areas indicate that differences in nutrient tolerance also exist for *Myriophyllum spicatum*, *Potamogeton pectinatus* and some *Chara* species. It is not clear whether this contrasting behaviour results from differences in climate, in biotic interactions or in the physico-chemical properties of the lakes. From recent investigations it is known that aquatic macrophytes may genetically vary within a habitat, for example *Vallisneria americana* along a depth profile in Detroit River (Lokker et al., 1994). Different genotypes within a lake have also been shown for *Phramites australis* (Neuhaus et al., 1993). *Phragmites australis* is mainly propagated vegetatively (Sculthorpe, 1967) as are many submerged macrophytes and this property would support the formation of genetically uniform clones. Whether the observed differences in ecological behaviour can be traced back to genetically varying ecotypes is not yet known.

Thus, as a consequence of the regionally differing behaviour of some species, an overall application of the macrophyte index is not possible without a screening of the composition of characteristic macrophyte communities and a re-evaluation of the ‘indicator groups’.

The question arises whether macrophyte distribution really expresses anthropogenic nutrient enrichment, or whether the occurrence of eutrophic species is a result of a natural aging and nutrient enrichment of lakes. Many observations affirm the former question. In the case of Lake Starnberg there are two lines of supporting evidence.

Firstly, a survey of the macrophyte flora by mechanical means was carried out at the turn of the century (Brand, 1896). At that time, water transparency was high with a minimum of 5 m during summer (Ammann, 1912). Without doubt this was due to low nutrient concentrations. Charophyte species of ‘indicator groups’ 1.0; 1.5 and 2.0, respectively (*Chara hispida*, *C. aspera*, *C. tomentosa* and *Nitella syncarpa*) formed extensive meadows reaching down to a depth of about 20 m. These species were extinguished completely by 1978. On the other hand, *Potamogeton mucronatus* and *Zannichellia palustris*, the only two species indicating ‘massive’ nutrient enrichment (‘indicator group’ 5) in Lake Starnberg in 1978 were absent in 1896 (Melzer, 1981).

Secondly, from 1978 onwards anthropogenetic nutrient enrichment dropped continuously due to waste water removal. Total phosphorus concentrations in the lake were reduced from 25 to 30 μg l^{-1} P in 1978 to half that value by 1991 (Henschel & Melzer, 1992). In 1989 a second survey of the macrophyte flora showed a marked increase in abundance of charophytes, and decline of eutrophic species. *Chara hispida, C. tomentosa* and *Nitella syncarpa* have not yet reappeared in the lake, however. These species have been replaced by *Chara contraria*, *Chara globularis* and *Nitellopsis obtusa*. Future investigations must show if the former species, requiring a lower nutrient status than the latter (Table 1) will return to the lake in the course of its continuing re-oligotrophication.

Lake Chiemsee and the Ostersee lakes also invalidate the hypotheses that macrophyte distribution solely expresses the natural aging and corresponding nutrient accumulation of a lake. In lake Chiemsee point sources cause striking changes in macrophyte composition and in the Osterseen lakes which are all of the similar age and morphology an anthropogenic gradient in nutrient enrichment developed within the chain of lakes and as a consequence different vegetational elements established. Those typical for eutrophic lakes have diminished since enrichment was reduced. Such changes in macrophyte flora are not exceptional, and are mirrored in other hard-water lakes. Examples are lake Constance (Schmieder, pers. comm.), lake Lugano (Lachavanne et al., 1992) and lake Botshol in the Netherlands (Simons et al., 1994). In all cases nutrient reduction of the lakes was followed by a recovery of charophytes.

Despite the current knowledge of recovery from several countries, the mechanisms of enrichment-controlled changes in macrophyte vegetation are not fully understood. These changes may depend on direct or indirect nutrient effects in which a uniform reaction among species is unlikely. Different strategies in nutrient uptake and assimilation lead to diverse reactions. In contrast to terrestrial plants, aquatic macrophytes are able to assimilate nutrients via both roots and shoots. For example, acquisition of phosphorus by roots is between 50 and approximately 100% (Bristow & Whitcombe, 1971; Carnigan, 1982; Carnigan & Kalff, 1980; Twilley et al., 1977), in which the proportion may vary seasonally (Smith & Adams, 1986). However, some genera (e.g. *Ceratophyllum, Utricularia*) are rootless and uptake is restricted to the shoot. Nitrogen assimilation is not only split between root and shoot uptake but moreover depends on the form of inorganic nitrogen in sediment and water. In general, ammonia prevails in sediment while nitrate does in water. In the latter, however, ammonia increases with eutrophication. In *Myriophyllum spicatum* a suppression of nitrate uptake has been observed with ammonia concentrations in the ambient water down to 30 μg l^{-1} (Nichols & Keeney, 1976), although, this reaction may not be general. Different species of Lemnaceae deviate in their capacities of nitrate uptake and nitrate reductase activities when exposed to increasing concentrations of ammonia (Melzer & Müller, 1983). A high diversity in the capacity of nitrate uptake and nitrate reductase activities of different coexisting macrophyte species in a river, exposed to identical ambient nutient conditions has also been shown (Melzer & Kaiser, 1986). These findings support the assumption of specific nutritive strategies of submerged plants and they may explain differences in the reaction of plants following changes in nutrient enrichment.

Nutrients in sediment as well as water are increased by eutrophication and, as a consequence, sediment fractions of total phosphorus and nitrogen, together with diatom records, are often used to evaluate the history of lake trophy (Christie & Smol, 1993; Reavie et al., 1995). However, little is known about the time course of nutrient enrichment or depletion in littoral sediments following eutrophication or restoration of lakes. It may be assumed that, after successful control of pollution, a decrease of nutrients in littoral sediments occurs, albeit with some delay. The relatively slow reaction in qualitative and quantitative aspects of macrophyte composition may be traced back to this separation in nutrient status of water and sediment.

Other important environmental factors in lakes also have uneven effects upon macrophytes, e.g. light (Dale, 1986; Vant et al., 1986); epiphytes (Blindow, 1987; Sand-Jensen & Sondergaard, 1981); intra- and interspecific competition (Agami & Waisel, 1985; Moen & Cohen, 1989), and herbivory (Bailey, 1988; Lodge, 1991). Despite the diverse reactions of single species to such environmental conditions, the similarity in the reaction of macrophyte species to nutrients, at least in one lake district, probably indicates their overall limiting effect on growth. This forms the basis for the macrophyte index and its successful application to lake management.

References

Agami, M. & Y. Waisel, 1985. Inter-relationships between *Najas marina* L. and three other species of aquatic macrophytes. Hydrobiologia 126: 169–173.

Ammann, H., 1912. Physikalische und biologische Beobachtungen an oberbayerischen Seen. Thesis, Königl. Techn. Hochsch. München.

Bailey, R.C., 1988. Correlations between species richness and exposure: freshwater molluscs and macrophytes. Hydrobiologia 162: 183–191.

Blindow, J., 1987. The composition and density of epiphyton on several species of submerged macrophytes – The neutral substrate hypothesis tested. Aquat. Bot. 29: 157–168.

Brand, F., 1896. Über die Vegetationsverhältnisse des Würmsees und seine Grundalgen. Bot. Centralbl. 65: 1–13.

Bristow, J.M. & M. Whitcombe, 1971. The role of roots in the nutrition of aquatic vascular plants. Am. J. Bot. 58: 8–13.

Carnigan, R., 1982. An empirical model to estimate the relative importance of roots in phosphorus uptake by aquatic macrophytes. Can. J. Fish. Aquat, Sci. 39: 243–247.

Carnigan, R. & J. Kalff, 1980. Phosphorus sources for aquatic weeds: water or sediments? Science 207: 987–989.

Christie, C.E. & J.P. Smol, 1993. Diatom assemblages as indicators of lake trophic status in southeastern Ontario lakes. J. Phycol. 29: 575–586.

Dale, H.M., 1986. Temperature and light: The determination factors in maximum depth distribution of aquatic macrophytes in Ontario, Canada. Hydrobiologia 133: 73–78.

Dave, G. 1992. Sediment toxicity and heavy metals in eleven lime reference lakes of Sweden. Wat. Air Soil Pollut. 63: 187–200.

Drake, J.C. & S.I. Heaney, 1987. Occurence of phosphorus and its potential remobilization in the littoral sediments of a productive English lake. Freshwat. Biol 17: 513–523.

Henschel, T. & A. Melzer, 1992. Die limnologische Entwicklung des Starnberger Sees im Fortgang der Abwasserfernhaltung unter besonderer Berücksichtigung der Makrophytenvegetation, Informationsber. Bayer. Landesamt f. Wasserwirtsch. München 3/92: 1–117.

Krausch, H.-D., 1964. Die Pflanzengesellschaften des Stechlinsee-Gebietes. I. Die Gesellschaften des offenen Wassers. Limnologica 2: 145–203.

Lachavanne, J.-B. & R. Wattenhofer, 1975. Contribution à l'étude des macrophytes du Léman. Commission internat. pour la protection des eaux du Léman et du Rhône contre la pollution, Geneva: 1–147.

Lachavanne, J.-B., J. Perfetta & R. Juge, 1992. Influence of water eutrophication on the macrophyte vegetation of Lake Lugano. Aquat. Sci. 54: 351–363.

Lang, G., 1968. Vegetationsveränderungen am Bodenseeufer in den letzten hundert Jahren. Schrift. Ver. Gesch. Bodensees 86: 295–319.

Lodge, D.M. 1991. Herbivory on freshwater macrophytes. Aquat. Bot. 41: 195–224.

Lokker, C., D. Susko, L. Lovett-Doust & J. Lovett-Doust, 1994. Population genetic structure of Vallisneria americana, a dioecious clonal macrophyte. Am. J. Bot. 81: 1004–1012.

Melzer, A., 1981. Veränderungen der Makrophytenvegetation des Starnberger Sees und ihre indikatorische Bedeutung. Limnologica 13: 449–458.

Melzer, A. & R. Kaiser, 1986. Seasonal variations in nitrate content, total nitrogen, and nitrate reductase activities of macrophytes from a chalk stream in Upper Bavaria. Oecologia 68: 606–611.

Melzer, A. & M. Müller, 1983. In vivo-nitrate reductase activities of different species of Lemnaceae and comparison with endogenous nitrate depletion. In Proceedings of the International Symposium on Aquatic Macrophytes Sept. 1983 Nijmegen: 139–144.

Moen, R. A. & Y. Cohen, 1989. Growth and competition between *Potamogeton pectinatus* L. and *Myriophyllum exalbescens* Fern. in experimental ecosystems. Aquat. Bot. 33: 257–270.

Neuhaus, D., H. Kühl, J.-G. Kohl, P. Dörfel & T. Börner, 1993. Investigation on the genetic diversity of *Phragmites* stands using genomic fingerprinting. Aquat Bot. 45: 357–364.

Nichols, D.S. & D.R. Keeney, 1976. Nitrogen nutrition of *Myriophyllum spicatum*: uptake and translocation of ^{15}N by shoots and roots. Freshwat. Biol. 6: 145–154.

Reavie, E.D., R.I. Hall & J.P. Smol, 1995. An expanded weighted-averaging model for interferring past total phosphorus concentrations from diatom assemblages in eutrophic British Columbia (Canada) lakes. J. Paleolimnol. 14: 49–67.

Roelofs, J.G.M., 1983. Impact on acidification and eutrophication on macrophyte communities in soft water lakes in the Netherlands, I. Field observations. Aquat. Bot. 17: 139–155.

Sand-Jensen K. & M. Sondergaard, 1981. Phytoplankton and epiphyte development and their effect on submerged macrophytes in lakes of different nutrient status. Int. Rev. ges. Hydrobiol. 6: 529–552.

Sculthorpe, C. D., 1967. The Biology of Aquatic Vascular Plants. Edward Arnold, London.

Simons, J., M. Ohm, R. Daalder, P. Boers & W. Ripl, 1994. Restoration of Botshol (The Netherlands) by reduction of external nutrient load: recovery of a characean community, dominated by *Chara connivens*. Hydrobiologia 275/276: 243–253.

Smith, C. S. & M. S. Adams, 1986. Phosphorus transfer from sediments by *Myriophyllum spicatum*. Limnol. & Oceanogr. 31: 1312–1321.

Succow, M. & D. Kopp, 1985. Seen als Naturraumtypen: Petermanns Geogr. Mitt. 3: 161–170.

Suominen, J. 1968. Changes in the aquatic macroflora of the polluted Lake Rautavesi, SW-Finland. Ann. Bot. Fenn. 5: 65–81.

Trapp, S., 1995. Wasserpflanzen Bremer Seen und ihr Verhältnis zur Gewässergüte. Abh. Naturw. Verein Bremen 3: 165–177.

Tüxen, R. & E. Preising, 1942. Grundbegriffe und Methoden zum Studium der Wasser- und Sumpfpflanzengesellschaften. Dtsch. Wasserwirtsch. 37: 10–17 & 57–69.

Twilley, R. B., M. M. Brinson & G. J. Davis, 1977. Phosphorus absorption, translocation, and secretion in *Nuphar luteum*. Limnol. Oceonogr. 22: 1022–1032.

Uotila, P., 1971. Distribution and ecological features of hydrophytes in the polluted Lake Vanajavesi, S-Finland. Ann. Bot. Fenn. 8: 257–295.

Vant, W. N., R. J. Davies-Colley, J. S. Clayton, & B. T. Coffey, 1986. Macrophyte depth limits in North Island (New Zealand) lakes of differing clarity. Hydrobiologia 137: 55–60.