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Littoral macrozoobenthos biomass in a continuous habitat series

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Abstract

The macrozoobenthos, especially large-sized benthos as notably important fish food, were studied in a limited area of Lake Inari, one of the largest lakes in Finland. Samples were collected along the selected shoreline, where new samples were taken at standard 2 m depth each time the habitat changed. Many morpho-edaphic factors and the covering of vegetation were measured simultaneously with the benthic samples in each habitat. Based on the stepwise regression analysis, an equation

$$\text{logMZB} = \frac{358.23 - 0.24Exp + 0.65Sed}{100}$$

explained 73% of the macrozoobenthos biomass (MZB) in the habitat series, where the exposure of the habitat (Exp) and the water content of the sediment (Sed) fitted the model best.

Introduction

There have been found many factors affecting the littoral macrozoobenthos (MZ), for example, abiotic factors exposure, slope, bottom quality, water level fluctuation (Brittain & Lillehammer, 1978; Särkkä, 1983; Raspopov et al., 1988; Rasmussen, 1988; Palomäki & Koskenniemi, 1993; Palomäki, 1994), eutrophication (Dermont et al., 1977), acidification (Johnson et al., 1993), fish and invertebrate predation (Strayer & Likens, 1986). The relationship between the macrozoobenthos biomass (MZB) and fish abundance is, however, not at all clear (Ramcharan et al., 1995). The aim of this study was to identify more precisely the important morpho-edaphic variables maintaining the structure of habitat types and explaining the variation in the macrozoobenthos biomass. All the factors were measured within a limited area. Thus the spatial variation in e.g. water quality and transparency were minimal. Only a few studies using this approach have been carried out before this, because there are still great difficulties to measure quantitatively the bottom quality and to find the general classification methodology for classifying the habitats in the littoral (Barton & Hynes, 1978; Brittain & Lillehammer, 1978; Streit & Schoener, 1978; Dall et al., 1984, 1990).

This study seeks to answer the following two questions:

1. Which morpho-edaphic factors describing the habitat structure are effective on the macrozoobenthos biomass in the habitat series of the middle part of Lake Inari?

2. Does the vegetation, which is richest in summer, have an effect on the macrozoobenthos biomass?

This study is a part of the Lake Inari Research Project co-ordinated by the Lapland Regional Environment Centre. The main purpose of this project is to promote fishing and fishery management and to better describe the ecosystem of Lake Inari.

Table 1. Characteristics of Lake Inari, Northern Finland

Drainage area, km^2	14575
Lake area, km^2	153
Metres above sea level	119
Max. depth, m	98
pH	6.8–7.3
Color, mg Pt/l	10–36
Secchi disk value, m	3–10
Tot. phosphorus, μg/l	4–7

Study area, material and methods

Study area

Lake Inari is an oligotrophic clear water lake in Finnish Lapland (68°58′ N, 27°52′ E, Table 1). The drainage area is very sparsely populated and almost in a natural state. Due to the clear water, the littoral illuminated area constitutes 35% of the total area of Lake Inari. The water level has been slightly regulated since 1941 with a yearly fluctuation of 1.38 m. Stony, steeply sloping shores are usually without higher vegetation, but in sheltered shores several *Carex* species may form dense belts.

The study area is situated in the central part of the lake (Figure 1), where water quality is near the mean of the whole lake (Airaksinen & Heinonen, 1976). The study area as a part of a larger area for habitat quality estimation in Lake Inari was aerially photographed in September 1993 at a height of 650 m (black and white film/400 ASA/6 × 7 cm; 55 mm objective, 1:1600 scale cf. Palomäki, 1992) by Lentokuva Vallas Ltd.

The term habitat has been defined in accordance with Goodall (1986) and Southwood (1988). Habitat is a structure based on the abiotic factors, not on vegetation or animals. The beginning point of the habitat series in Lake Inari was randomly chosen, including 27 habitats situated one after another along a 10 km stretch of shore line. The characteristics of the sites at the depth of 2 metres (from the long-term mean water level) were measured from the aerial photographs and a map (1:50 000) and during the field study (Table 2). The impact of wave action, represented by two variables, were measured from the map. Effective fetch (Lf) was measured according to Håkanson (1981) and exposure by the angle opening from the site to the offshore according to the method developed by Palomäki (1992). The slope from the shore line to the sampling site and the uppermost depth of sedimentation were measured from the aerial photographs. The penetrometer cone L3 (the heaviest and most pointed cone, Håkanson & Jansson, 1983) was used as an indication of the softness of the bottom (see Weisner, 1992). The water content of the sediment was determined by the penetration of the cone (Håkanson & Ahl, 1976; Håkanson & Jansson, 1983).

Sampling procedures

Samples were taken on August 10, 1993 from the soft bottoms with an Ekman grab (17 × 17 cm) and from the stony bottoms with a pump (SCUBA, Whale Gusher 25) outlining the sample area (20 × 20 cm) with a metal frame. The three sampling points in each habitat were chosen randomly.

The samples were sieved (1.0 × 1.0 mm mesh size) immediately after the sampling and preserved in 70% ethanol, and the animals were sorted from the sieved residues in the laboratory using a black and white dish. After four months (see Leuven et al., 1985), the total macrozoobenthos biomasses (wet weight) were weighed (Sauter AR 1014) to the nearest mg, after drying the animals some seconds with blotting paper.

Comparison of the methods

Material was collected on September 15 and 16, 1993 with an Ekman grab and with a pump from an area of 50 m^2 with a sandy-muddy bottom close to the habitat series (Figure 1). The sampling methods were the same as in the earlier sampling of the habitat series, except that the replicates consisted of 10 pump samples and 20 Ekman samples. Furthermore, 10 Ekman samples were sieved through both 1.0 and 0.5 mm meshes to find out the amount of macrozoobenthos biomass (MZB) lost by using only 1.0 mm mesh. The benthos caught in the finer sieve (0.5 mm) represent the whole macrozoobenthos (SFS 5076). The food items of the fish consist mainly of the large-sized invertebrates (e.g. Tuunainen, 1970).

The ww biomass of the Ekman samples ranged from 346 to 13 356 mg m^{-2} (1.0 mm sieve), i.e the highest value was 39-fold compared to the lowest one. The ww biomass values of the pump samples varied from 4275 to 12 350 mg m^{-2}, i.e the difference was only 3-fold. When proceeding in the sampling order, the cumulative mean biomass value of the Ekman samples after the 3rd replicate was 97% of the mean value of the whole sampling series (20 replicates). It was only slightly lower (85%) in the pump sampling series

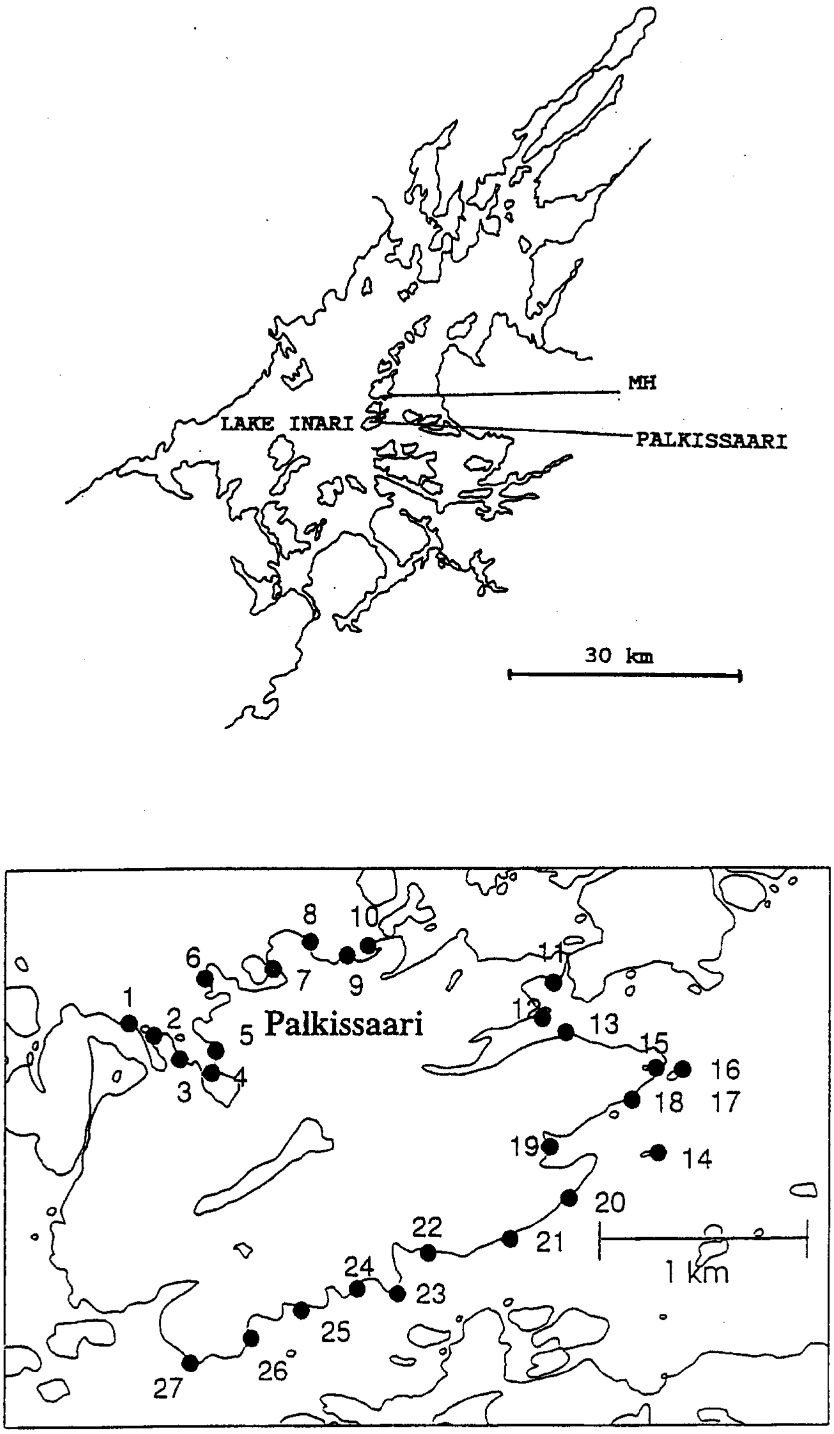

Figure 1. Lake Inari and the habitat series studied. Number 1,2,....= number of the habitat in the habitat series; MH = habitat where the method material was sampled.

Table 2. Data collected from the habitat series. E = Ekman sampler, P = Pump.

Dependent variable:

MZB Macrozoobenthos biomass, mg ww/m^2
Based on a comparison of the sampling methods, the macrozoobenthos biomass collected with an Ekman sampler was corrected by 30%.

Independent variables:

A. Fetch, km (Håkankson, 1981)

B-C, Exposure. The bay (or cape) where the habitat was situated opens to the offshore with an angle, which was measured as degrees (Palomaki, 1992)
-angular degree, when the lenght of the angle side= 0.5 km (B)
-angular degree, when the lenght of the angle side= 1.0 km (C)

D. Slope, % (Håkanson, 1981) measured from the shore line to the habitat at a depth of 2 metres

E. Uppermost depth (m) of sedimentation as shown by aerial photographs

F. Penetration depth (cm) of the penetrometer cone L3 (the heaviest and most pointed cone Håkanson & Jansson 1983) into the sediment

G. Water content (%) of the sediment (based on the classification of sediment types by Håkanson & Ahl, 1976, Håkanson & Jansson, 1983)

H. Vegetation: Classification based on the points number: 1=no vegetation, 2=vegetation present near the sampling station, 3=shoots in the samples

I. Vegetation cover of the habitat, %

Habitat	E/P	MZB	A	B	C	D	E	F	G	H	I
1	P	725	1.4	215	121	11.7	2.8	1	1	1	0
2	E	6277	1.4	47	44	8.3	2.7	7	55	2	5
3	E	17597	0.2	53	46	6.7	1.6	9	93	2	20
4	E	4993	0.2	35	26	5.0	1.4	7	80	2	14
5	E	7959	0.1	47	31	12.8	1.2	11	93	3	32
6	P	2925	1.5	215	111	23.4	3.4	1	1	1	0
7	E	12307	0.1	29	28	1.8	0.5	16	93	2	38
8	P	2075	1.0	131	49	17.6	2.5	7	65	2	0
9	E	11813	0.5	149	62	3.3	2.4	57	93	3	37
10	P	500	0.8	137	67	15.6	2.0	1	1	1	0
11	E	6524	0.3	108	21	6.4	1.5	36	55	2	31
12	P	3925	1.2	90	33	15.6	2.5	4	15	2	0
13	E	8847	0.7	114	8	23.4	2.3	12	80	2	0
14	E	1483	4.4	251	185	8.3	2.5	1	15	1	0
15	E	26147	0.2	25	25	3.7	1.6	12	93	1	20
16	P	1700	5.0	227	185	37.5	2.3	1	5	1	0
17	P	2125	1.5	161	64	37.5	2.3	1	5	1	0
18	E	890	3.4	239	195	8.3	2.1	1	55	1	0
19	E	4844	1.2	53	46	9.4	2.7	7	35	1	16
20	P	1525	2.1	215	185	10.2	2.8	1	1	1	0
21	E	1236	2.6	239	123	11.7	1.8	1	5	1	0
22	E	1977	1.6	137	77	11.7	2.3	1	5	1	0
23	P	1400	1.5	227	87	17.6	2.3	1	1	1	0
24	E	890	0.8	172	131	10.0	2.4	8	15	1	0
25	E	5734	1.2	131	105	7.8	2.0	5	65	1	22
26	P	4750	0.9	137	105	8.3	2.0	1	15	3	2
27	P	1075	2.4	215	185	70.3	2.3	1	1	1	0
Mean	..	5268	1.4	141	87	15.0	2.2	10	39	..	9
S.D.	..	5927	1.2	75	59	14.0	0.6	14	37	..	13

Table 3. Statistically significant (<0.05) correlation coefficients between the factors measured in each station. Significances *: p<0.01. See full descriptions of all variables A-I in the Table 2.

	Fetch (A)	Exp r=0,5 (B)	Exp r=1.0 (C)	Slope (log D)	Sed-line (E)	Penetro. (F)	Sed-% (G)	Veget. Obs. (H)	Veget. Cover (I)
log MZB	−0.57*	−0.77*	−0.67*	−0.54*	−0.45	0.53*	0.81*	0.59*	0.73*
A	–	0.74*	0.81*	0.44	n.s.	−0.43	−0.55*	−0.52*	−0.55*
B	–	–	0.84*	0.50*	0.53*	−0.42	−0.71*	−0.51*	−0.61*
C	–	–	–	n.s.	0.41	n.s.	−0.60*	−0.52*	−0.51*
log D	–	–	–	–	0.50*	−0.50*	−0.62*	n.s.	−0.68*
E	–	–	–	–	–	n.s.	−0.59*	n.s.	0.65*
F	–	–	–	–	–	–	0.58*	0.56*	0.74*
G	–	–	–	–	–	–	–	0.59*	0.76*
H	–	–	–	–	–	–	–	–	0.53*

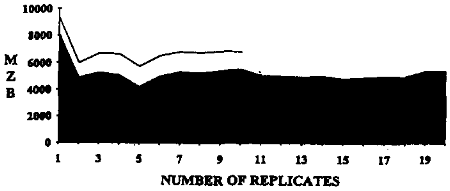

Figure 2. Changes in the cumulative mean value of the macrozoobenthos biomass (MZB mg ww/m^2, 1.0 mm sieve) when the number of replicates increases in the method material. Black column = Ekman samples, White column = pump samples.

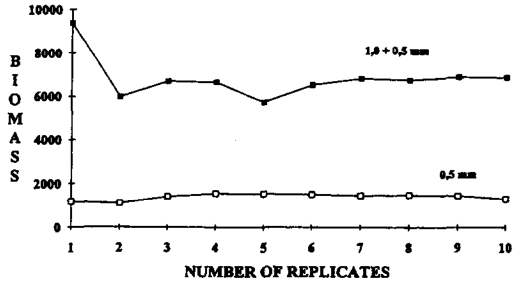

Figure 3. Cumulative mean value of the total macrozoobenthos biomass (black squares, all animals on the 1.0 and 0.5 mm sieves, mg ww/m^2) and of the 'mesofauna' biomass (white squares, animals on a 0.5 mm sieve, mg ww/m^2) when the number of replicates increases in the methodological data set.

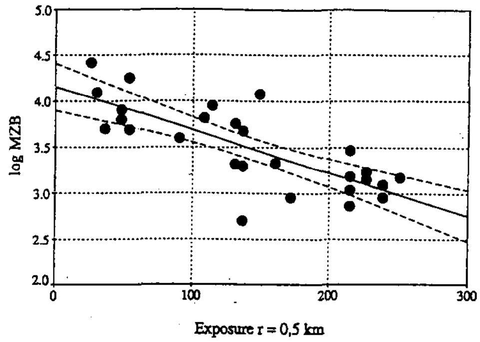

Figure 4A.

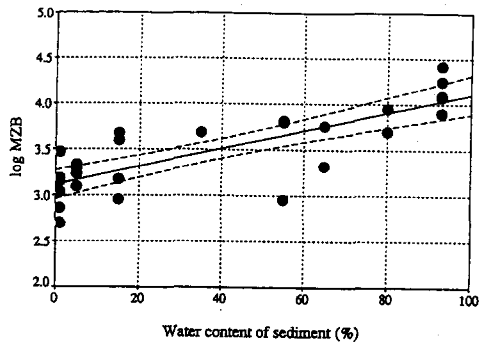

Figure 4B.

Figure 4. Relationships between MZB (log mg ww/m^2) and the two most powerful independent variables in the habitat series studied (A: exposure, r^2=0.59, B: water content of sediment, r^2=0.65).

(Figure 2). Three replicates seem to give a sufficient precision to describe the level of the biomass in habitats of this kind.

Only 19% of the macrozoobenthic animals was lost by using the 1.0 mm sieve compared to the finer mesh (0.5 mm). Thus, a sieve with 1.0 mm mesh turned out to be quite effective (Figure 3). It was further notable, that the cumulative mean value of the biomass on the finer sieve remained at the same level even when the number of samples increased. The biomass retained on the 1.0 mm sieve seems also to constitute most of the total biomass range.

The pumping method seems to collect macrozoobenthic animals more effectively than the Ekman

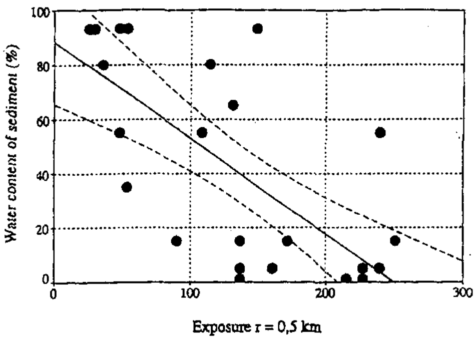

Figure 5. Relationship between the sediment water content (%) and exposure (variable B) (r^2=0.51).

Table 4. Macrozoobenthos biomass (mg ODW/m^2) VI and VIII 1977 (Palomäki, 1981, 1994) in the two shore types, which are situated very near Palkissaari in Lake Inari. Max. marked.

Shoretype	Sandy, bold		Detritus, slope	
Month	VI	VIII	VI	VIII
Depth, m				
1	150	100	600	500
2	200	300	**900**	**600**
3	**600**	300	650	400
5	500	**400**	400	200
8	250	200	250	300
10	100	50	–	–

grab (Figure 2) showing in average 30% greater biomass values than those obtained with the Ekman grab. However, the differences were not significant (Sign test, M=3, n = 10, p = 0.340), and these two methods can hence be used parallel to each other.

Statistics

The relationships between the ecological variables of the habitats were evaluated using a standard regression technique and the slopes were tested with the F-test. Multivariate statistical analysis (stepwise regression analysis, forward selection) was used to account for the interactions between several factors of the habitats and the littoral MZB. The normality of the distribution of all the variables was tested, and log-transformation was used when necessary.

Results

The MZB was clearly negatively correlated with the exposure (r = 0.5 km), positively correlated with the water content of the sediment and more weakly correlated with the covering of vegetation (Table 3). The biomass was lowest on stony and hard bottom, and highest in the habitats with soft sediment. The biomass also decreased along with increasing exposure. According to the regression studies, the water content of the sediment explained 65% of the total biomass. Correspondingly, exposure alone explained 59% of the MZB

$$(\text{Figure 4A} : \log \text{MZB} = \frac{415.44 - 0.47\ \text{Exposure}}{100},\ p < 0.001,$$

and

$$\text{Figure 4B} : \log \text{MZB} = \frac{311.63 + 0.99\ \text{Sediment water content}}{100},\ p < 0.001).$$

The exposure and the sediment water content correlated with each other (Table 3), but not strongly (Figure 5). The stepwise regression analysis based on these two independent variables established a model,

$$\log \text{MZB} = \frac{358.23 *** - 0.24 \text{Exp} * + 0.65\ \text{Sed} ***}{100},$$

where

MZB = macrozoobenthos biomass mg ww m^{-2};
Exp = exposure (r = 0.5 km, measured as degrees);
Sed = water content of the sediment (%);
* = Statistical significance in the F-test, in which the F-values were 46.5 (Sed) and 6.6 (Exp).

This model explained 73% of the MZB, which can be considered a relatively good value for the coefficient of determination obtained using stepwise regression analysis.

Discussion

The benthos biomass is generally greatest in the littoral area of lakes. The variation in biomass is great because of the mosaic nature of the shore area (Rasmussen, 1988). The variation can be decreased to better analyze the factors affecting the variation.

Morpho-edaphic factors

Wave action is a great factor disturbing the benthos in littoral. Fetch is one of the most important factors describing wave height and the energy regime at the sediment-water interface (Smith & Sinclair, 1972; Smith, 1979; Hodgins et al., 1983). Fetch was not, however, the best factor to describe MZB in this study. A stronger correlation was found between the opening angle of the shore line and the MZB in the habitat series. The angle (the shape of the shore line) shows the probability of wave action (especially frequency) at the shore line during the ice-free season.

Another strong positive correlation was found between the sediment water content and the MZB. This variable was one of the factors representing the habitat structure and sit seems to have a close relationship with all the other factors (Table 3). The slope and the washing of the rich sediment have been found to be closely related (Rasmussen, 1988). The strong relationship between the sediment water content and the slope supports this viewpoint (Håkanson, 1977; Duarte & Kalff, 1986).

However, the vegetation can partly also prevent the washing of the sediment (Raspopov et al., 1988; Coops et al., 1991). The correlation between the exposure (factor 2A) and the sediment water content was also strong. The observations concerning this relation do not however clearly support this. In general, the bottom is minerogenic in open habitats, but not always organogenic in sheltered habitats. Bottoms consisting of detritus, peat, sand, silt, gravel, pebbles, stones. etc. occur in sheltered bays. At least the slope, the vegetation and the shore material (especially if the place is situated in a ridge area) have a marked effect on the sediment water content. However, any testing of this hypothesis requires a larger material collected from sheltered areas. The above mentioned findings affected the decision to choose the factors 2A (exposure) and 6 (sediment water content) to be used in building a model based on stepwise regression analysis.

On the basis of the results of the stepwise regression analysis, the most important factors affecting the MZB appeared to be the sediment water content and exposure. The results can be interpreted to indicate that if the water content in the sediment increases, the animals have more space in the vertical direction and possibly more algal food, e.g benthic algae, which do vertical migrations in the sediment during the day (see e.g. Wetzel, 1975). Benthic algae are a very important food resource for benthos (Strayer & Likens, 1986).

The water level regulation is one of the factors disturbing the littoral macrozoobenthos (Palomäki & Koskenniemi, 1993). Disturbance lowers the animal number but also often changes the characteristics of the habitat type. The relationships between the littoral MZB and the factors making up the habitat seem to be remarkably parallel to the results obtained by Grimas (1961, 1965) from strongly regulated Swedish lakes. He found water level regulation to cause erosion especially in sheltered areas, which began to resemble the open areas, causing a decrease in the benthos biomass.

Vegetation

One important factor is the effect of the vegetation and its ability to prevent wave attacks and flushing of the rich organic sediment. However, the fact that vegetation is not always present in the same form (alive or as litter) in the littoral, may be of notable seasonal importance for the macrozoobenthos via the habitat structure. The direct effect of the vegetation on the MZB was found to be slight in Lake Inari in the growing season, when vegetation was richest. More exact descriptions of MZB in sheltered habitats are needed. Water quality (especially tot. P), explains less accurately the variation of MZB than the physical factors (Rasmussen, 1988; Palomäki, 1994), which were studied very carefully. In addition to the physical factors structuring the habitat, there are the biotic interactions (Southood, 1988; Ramcharan et al., 1995), which were examined only in a cursory way (vegetation-macrozoobenthos).

Wave action moves MZ biomass to the deeper littoral (Palomäki & Koskenniemi, 1993). Water level fluctuation disturbs MZ especially in the sheltered shores, causing a decrease of MZB, together with bottom freezing in winter (Palomaki & Koskenniemi, 1993). The environment, e.g. bottom quality, changes very often in the regulated lakes (Grimas, 1961). The number of sheltered habitats in Lake Inari is great due to the large number of islands and islet (over 3000 islands). In spite of the disturbing factors (water level regulation, bottom freezing, wave action) and owing to the clear water (algae production), the MZ can produce great masses in deeper littoral. This was observed in the earlier study of Lake Inari (Table 4, Palomäki, 1990). So it seems that a slight regulation in the water level of Lake Inari not cause a great decrease of MZB (see Palomäki, 1994).

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References

Airaksinen, E. & P. Heinonen. 1976. Inarinjarven tutkimus vuonna 1974. (Data on the water quality in Lake Inari in the year 1974, English summary). National Board of Waters, Finland. Report 103: 1–59.

Barton, D. R. & H. B. N. Hynes, 1978. Seasonal study of the fauna of bedrock substrates in the wave zone of lakes Huron and Erie. Can. J. Zool. 56: 48–54.

Brittain, J. E. & A. Lillehammer, 1978. The fauna of the exposed zone of Ovre Heimdalsvatn: methods, sampling stations and general results. Holarctic Ecol. 1: 221–228.

Coops, H., R. Boeters & H. Smith, 1991. Direct and indirect effects of wave attack on helophytes. Aquat. Bot. 41: 333–352.

Dall, P. C., C. Lindegaard, E. Jonsson, G. St. Jonsson & P. M. Jonasson, 1984. Invertebrate communities and their environment in the exposed littoral zone of lake Esrom, Denmark. Arch. Hydrobiol. Suppl. 69, Mon. Beitr.: 477–524.

Dall, P. C., C. Lindegaard & P. M. Jonasson, 1990. In-lake variations in the composition of zoobentos in the littoral of Lake Esrom, Denmark. Verh. int. Ver. Limnol. 24: 613–620.

Dermott, R. M., J. Kalff, W. C. Leggett & J. Spence, 1977. Production of *Chironomus, Procladius* and *Chaoborus* at different levels of phytoplankton biomass in Lake Memphremagog, Quebec-Vermont. J. Fish. Res Bd Can. 34: 2001-2007.

Duarte, C. & J. Kalff, 1986. Littoral slope as a predictor of maximum biomass of submerged macrophyte communities. Limnol. Oceanogr. 31: 1972–1080.

Goodall D. W, 1986 Biotope structure and pattering. In: Kikkawa, J. & D.J. Anderson (eds), Community ecology. Pattern and process, Blackwell Sc. Publ., London: 30–40.

Grimås, U., 1961. The bottom fauna of natural and impounded lakes in northern Sweden (Ankarvattnet and Blasjon). Rep. Inst. Freshwat. Res. Drottningholm 42: 183–237.

Grimås, U., 1965. Effects of impoundment on the bottom fauna of high mountain lakes. Acta Univ. Upsalensis (Abstracts of Uppsala Dissertations in Science) 51: 1–24.

Holdings, D. O., P. H. Leblond & D. A. Huntley, 1983. Shallow water wave calculations. Can. Contract Rep. Hydrogr. Ocean Sci. 10: 1–75.

Håkanson, L., 1977. The influence of wind, fetch and water depth on the distribution of sediment in Lake Vänern, Sweden. Can. J. Earth Sci. 14: 397–412.

Håkanson, L., 1981. Lake morphometry. Springer Verlag, Berlin, Heidelberg, New York, 78 pp.

Håkanson, L. & T. Ahl, 1976. Vättern - recenta sediment och sedimentkemi. Natl. Swed. Environ. Prot. Board, SNV PM 740 Uppsala, 164 pp.

Håkanson, L. & M. Jansson, 1983. Principles of lake scdimentology. Springer Verlag, Berlin, 316 pp.

Johnson, R., T. Wiederholm & L. Eriksson, 1993. Classification of littoral macroinvertebrate communities of Swedish reference lakes. Verh. int. Ver. Limnol. 25: 512–517.

Leuven, R. S. E. W, T. C. M. Brock & H. A. M. Druten, 1985. Effects ot preservation on dry- and ash-free weight biomass of some common aquatic macro-invertebrate. Hydrobiologia 127: 151–159.

Palomäki, R., 1992. Oulujarven rantatvvppien ja rantahabitaattien suhteellisten osuuksien arviointi. (Estimation of the proportions of the shore types and shore habitats in Lake Oulujarvi). Vesi-ja ympäristöhallituksen monistesarja 385: 1–31 (in Finnish).

Palomäki, R., 1981. Inarijarven siikamuodot ja niiden ravinnonvalinta. Pro gradu -tutkielma, Dept. of Biology, Univ. of Jyväskvlä, 101 pp (in Finnish).

Palomäki, R., 1990. Lievän järvisäännostelyn vaikutukset eriyyppisten jarvien ranta-alueen pohjaeläimistoon (in Finnish). Licentiate's dissertation, Dept. ot Biology, Univ. of Jyvaskylä, 90 pp.

Palomäki, R., 1994. Response by macrozoobenthos biomass to water level regulation in some Finnish lake littoral zones. Hydrobiologia 286: 17–26.

Palomäki, R. & E. Koskenniemi, 1993. Effects of bottom freezing on macrozoobenthos in the regulated Lake Pyhajärvi. Arch. Hydrobiol. 128: 73–90.

Ramcharan, C. W., D. J. McQueen, E. Demers, S. A. Popiel, A. M. Rocchi, N. D. Yan, A. H. Wong & K. D. Hughes, 1995. A comparative approach to determining the role of fish predation in structuring limnetic ecosystems. Arch. Hydrobiol. 133: 389-416.

Rasmussen, J. P, 1988. Littoral zoobenthic biomass in lakes, and its relationships to physical, chemical, and trophic factors. Can. J. Fish. aquat. Sci. 45: 1436–1447.

Raspopov, I. M., T. D. Slepukhina, I. F. Vorontzov & O. N. Dotzenko, 1988. Wave effects on the bottom biocoenoses in the Onega Lake bays. Arch. Hydrobiol. 112: 115–124.

Smith, I. R., 1979. Hydraulic conditions in isothermal lakes. Freshwat. Biol. 9: 119–145.

Smith, I. R. & I. J. Sinclair, 1972. Deep-water waves in lakes. Freshwat. Biol. 9: 387–399.

Southwood, T. R. E., 1988. Tactics, strategies, templets. Oikos 52: 3–18.

Strayer, D. & G. E. Likens, 1986. An energy budget for the zoobenthos of Mirror Lake, New Hampshire. Ecology 67: 303–313.

Streit, B. & P. Schroder, 1978. Dominierende Benthosinvertebraten in der Gerollbrandungszone des Bodensees: Phänologie, Nahrungsokologie und Biomasse. Arch. Hydrobiol. Suppl. 55: 211–234.

Särkkä, J., 1983. A quantitative ecological investigation of the littoral zoobenthos of an oligotrophic Finnish lake. Ann. Zool. Fennici 20: 157–178.

Tuunainen, P., 1970. Relations between the benthic fauna and two species of trout in some small Finnish lakes treated with rotenone. Ann. Zool. Fennici 7: 67–120.

Weisner, S. E. B., 1990. Patterns in water depth penetration of emergent vegetation in eutrophic temperate lakes. Manuscript in Dissertation: 67–83.

Wetzel, R. G., 1975. Limnology. Saunders College Publishing, Philadelphia, 743 pp.