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# Body size and substrate association of littoral insects in relation to vegetation structure

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## Abstract

Variation in substrate association types and maximum size of aquatic insects were studied in a vegetated littoral zone of three lake basins. The basins differed from each other in trophic status, biomass of benthivorous fish, and abundance of macrophytes. Four types of substrate association – swimmers, crawlers, semisessiles and burrowers, respectively – were assumed to represent decreasing vulnerability to fish predators. Large-sized species were also hypothesised to be more vulnerable to fish predators. The distributions of species traits were examined in relation to vegetation density. Inferring from "predation hypothesis" opposite selection pressures on the species traits were expected along the vegetation density. Dense macrophyte beds were thought to be dominated by invertebrate predators and open water by fish predators, since the predation efficiency of fish decreases in complex environments. In the case of invertebrate predator domination, large size and higher activity should be favoured traits among the prey species. Distribution patterns of modes of the two studied traits were explored separately for predatory and non-predatory insects. As expected, swimmers and large-sized crawlers were characteristic of the insect assemblages of dense macrophyte beds. The densities of Odonata, Corixidae, Dytiscidae, Ephemeroptera and Sialidae were higher among macrophytes than in open water, where these insect taxa were possibly depleted by fish. On the other hand, the small-sized and fairly immobile Chironomidae were the most abundant group in open water. These results support the existence of a predator transition zone among littoral vegetation, ranging from domination of invertebrate predation among the dense beds to that of fish predation in open water.

## Introduction

Habitat complexity correlates positively with increasing abundance of macrophytes in the littoral zone. Dense macrophyte stands are associated with a higher number of available niches and a more abundant assortment of food for both benthic invertebrates and fish. Yet, the predation efficiency of fish generally decreases in complex environments (Gilinsky, 1984; Hershey, 1985; Winfield, 1986; Diehl, 1988, 1992). These factors together often result in a higher diversity and abundance of benthic invertebrates among macrophytes than on bare bottoms (Crowder & Cooper, 1982; Gilinsky, 1984; Gregg & Rose, 1985; Beckett et al., 1992; Diehl, 1992).

In his review, Strayer (1991) concluded that the effects of vertebrate predation on size structure are probably weaker in lacustrine zoobenthos than in zooplankton owing to the availability of physical refuges and the widespread occurrence of morphological and behavioural defences in benthic invertebrates. However, Blumenshine et al. (2000) found the size distribution of the macroinvertebrate community to change along the gradient of consumption rate by fish. Similar effects on the littoral macroinvertebrate assemblages by the predation of fish have been documented experimentally e.g. by Crowder & Cooper (1982) and Diehl (1992). Both studies suggested that the size structure of invertebrates is related to fish predation rather than to vegetation. Cardinale et al. (1998) found that, in coastal wetlands, large-sized macroinvertebrate taxa inhabited mainly the shoreward parts of vegetation, and this distribution pattern was suggested to be mediated by the different risks of fish predation throughout the wetland.

In most aquatic systems, fish are the top predators, searching for prey by swimming actively. Fish usually prefer larger and mobile prey, which are more conspicuous to a visual predator (McPeek, 1990; Wellborn et al., 1996). In contrast, many invertebrates such as the larvae of Odonata are mainly "sit-and-wait" predators and can capture only prey that come close to them (Corbet, 1980; Wellborn et al., 1996). Even many highly mobile invertebrate predators prefer sessile or sluggish prey because they are easier to capture (Allan et al., 1987). Many invertebrate predators are also limited to small-sized prey, because of their inability to handle large prey (Lampert & Sommer, 1997). Thus, in benthic communities subject to high fish predation, low activity and small body size should be the favoured traits among prey species. In contrast, high activity and large body size should be favourable traits when invertebrate predators are dominant (Nilsson, 1981; Crowder & Cooper, 1982; Hildrew et al., 1984; Henrikson, 1988; Blois-Heulin et al., 1990; Bechara et al., 1993; Wellborn et al., 1996). Although there are numerous studies on the effects of vertebrate *vs.* invertebrate predation on benthic macroinvertebrate assemblages, most of these studies are experimental or deal with lotic systems.

In this paper, the effect of the structural complexity, created by macrophyte vegetation, on body size and substrate association (activity) of aquatic insects were studied in three basins of the large Saimaa lake system in eastern Finland. These basins differed from each other with respect to water nutrient content and fish biomass. We aimed to examine spatial patterns in body size and activity of invertebrate prey along the gradient of vegetation density in order to see if they are consistent with patterns predicted from the controlled studies of predator–prey interactions. We expected bare bottoms or the locations with sparse vegetation to be dominated by small-sized and inactive taxa under the domination of fish predators. By contrast, the vegetated zone with high habitat complexity was thought to be dominated by large-sized and active taxa. Divergent selection pressures assumed to be directed at invertebrate prey under domination of fish or invertebrate predators are summarized in Figure 1. This study is part of a comprehensive analysis of the effects of eutrophication and anthropogenic activities on littoral biodiversity and community structure in the Saimaa lake system and in the brackish Archipelago Sea (http://fibre.utu.fi).

## Materials and methods

Benthic macroinvertebrates, macrophytes and fish were sampled in the vegetated littoral zone of three separate basins of the Saimaa lake system (Table 1). A more detailed description of the basins is given in Tolonen et al. (2001). The field work was conducted within a period of 9 days at the end of July 1997.

### *Sampling of macrophytes and aquatic insects*

In each basin, macrophytes and aquatic insects were sampled from three transects perpendicular to the shoreline. Each transect was divided into three depth zones. The shallowest zone was 0–0.5 m in depth. The second zone extended from a depth of 0.5 m to the outer edge of emergent or floating-leaved macrophyte vegetation (PLI, pelagic-littoral interface, Cardinale et al., 1997). The third zone ranged from the PLI to a depth of 3 m. In Lake Puruvesi, submerged macrophytes extend down to a depth of 6–7 metres because of the clarity of water. In the other two basins, the bottom of the deepest zone was completely devoid of rooted plants.

All plant stems were collected from three 0.25 or 1 $m^2$ square plots per depth zone (smaller squares were used in dense stands). In the laboratory all the plants were identified, counted, and the stems were dried and weighed. Benthic macroinvertebrates were sampled from transects in the same manner as macrophytes: three samples per depth zone. Quantitative samples were taken with a centrifugal pump (Robin PTG-201T). A stiff plastic pipe with a 143 $cm^2$ metal funnel was attached to the entrance hose of the pump. The sample consisted of an area of 1590 $cm^2$ inside a round metal frame (20 cm high) fixed to a 0.45 mm

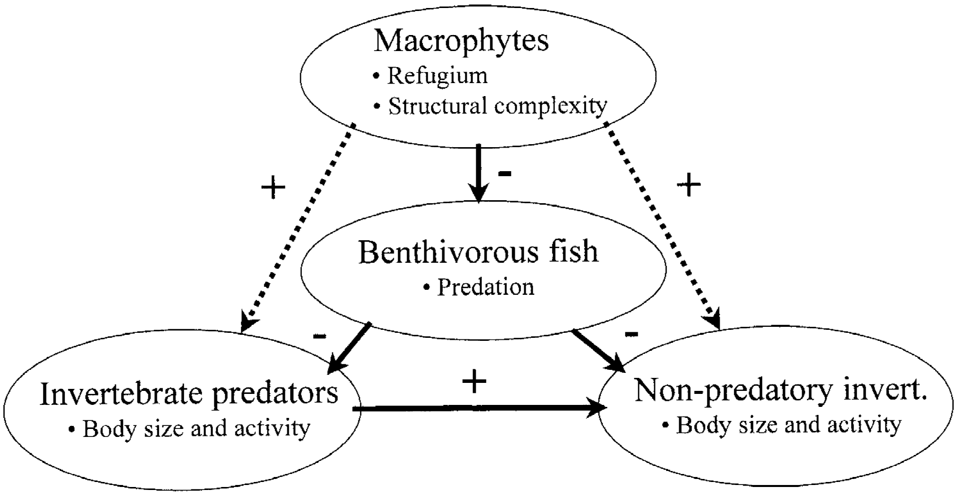

*Figure 1.* Dense macrophyte cover has a negative effect on fish predation and thus, indirectly may increase body size and activity of both predatory and non-predatory invertebrates. Increased invertebrate predation favours larger body size and higher activity in their prey, the non-predatory invertebrates. In the diagram, indirect effects are marked with dotted arrows

*Table 1.* Limnological and morphological characteristics of the vegetated littoral zone of three basins of Saimaa lake system with catch-per-unit-of-effort (CPUE) as an index of fish biomass. Macroinvertebrate and macrophyte transects were placed to the 0–3 m depth. Means and standard errors (±SE) of the variables are presented

| | L. Puruvesi | L. Pyhäselkä | L. Haukivesi |
|---|---|---|---|
| Surface area (km$^2$) | 415 | 263 | 514 |
| Length of the transects (m) | 422.0 ± 173.4 | 345.0 ± 62.5 | 111.0 ± 25.1 |
| Total phosphorus ($\mu$g l$^{-1}$) | 4.7 ± 0.3 | 11.3 ± 0.7 | 23.0 ± 1.2 |
| Total nitrogen ($\mu$g l$^{-1}$) | 299.3 ± 5.9 | 421.0 ± 19.6 | 511.7 ± 29.2 |
| Colour (mg Pt l$^{-1}$) | 8.3 ± 1.7 | 66.7 ± 6.7 | 40.0 ± 0.0 |
| pH | 7.5 ± 0.0 | 7.0 ± 0.0 | 7.4 ± 0.0 |
| CPUE of benthivorous fish (g) | 263.3 ± 36.1 | 226.6 ± 74.5 | 935.8 ± 101.7 |
| Total CPUE (g) | 1004.1 ± 172.3 | 1101.2 ± 285.6 | 2376.6 ± 210.2 |
| Perch (% of CPUE) | 57.6 | 37.3 | 27.4 |
| Roach (% of CPUE) | 26.7 | 37.7 | 42.4 |
| Other cyprinids (% of CPUE) | 13.6 | 6.1 | 19.7 |
| Others (% of CPUE) | 2.1 | 18.9 | 10.5 |

mesh net mantle long enough to extend above the water surface. After the frame and mantle had been slid over the vegetation and pushed into the sediment, the entire enclosed water column was stirred vigorously with the plastic pipe to loosen animals from the plants. Finally the sediment inside the frame was sampled by the funnel. Thus, the samples included both the benthic and the epiphytic animals. The samples were sieved through a 0.5 mm mesh and preserved in 70% ethanol. In the laboratory, the samples were sorted on white trays, and invertebrates were preserved in ethanol. Later on, insects were counted and identified to species when possible. The wet mass of insect groups (Chironomidae, Ephemeroptera, Odonata, Trichoptera, others) was weighted after animals were soaked for ten minutes in water and laid shortly on filter paper to remove excess water (SFS 5076 1989).

### *Sampling of fish*

The biomass of fish in each study site was estimated by the catch-per-unit-of-effort (CPUE) method by testfishing with multimesh gillnets (1.5 m 30 m) with 10 mesh sizes (10, 12, 15, 20, 25, 30, 35, 45, 55 mm) in each net. The size of a single mesh panel was 1.5 m 3 m. The nets used were modifications of the Nordic multimesh gillnet (Kurkilahti & Rask, 1996). Three littoral sites were fished per basin. The gill-netting was carried out once at each site and the nets were examined after 24 h. At each site, two nets were placed at a bottom depth of 1.5–2 m and two nets at a depth of 2–3 m. The nets were set parallel to the shoreline.Diets of fish were not analysed. Thus, the benthivorous fish were separated roughly by their diet preferences at a given size (e.g. Brabrand, 1985; Bergman, 1991; Horppila, 1994; Persson & Hansson, 1999; Vuorimies & Tolonen, 1999; Horppila et al., 2000; Tolonen et al., 2000; Vinni et al., 2000).

### *Species traits, community metrics and statistical analyses*

The size distribution of invertebrate assemblages may change seasonally due to the cohort dynamics of different species. Therefore, the relative ranking of mean body sizes in open *vs.* vegetated habitats may be reversed at different times (Diehl & Eklöv, 1995). In order to minimize the effects of phenology, and because identified invertebrates were not measured, we used maximum size (average maximum size of aquatic stage) to express the size of aquatic insects. While the actual body size at any time is affected by season, the maximum size of an individual is not. However, the distribution of maximum size is affected by temporal changes in assemblage composition, because the maximum size is directly linked to the taxonomic structure. A single species specific measure for body size is commonly used to quantify the size distribution in terrestrial communities and has also been applied previously to aquatic systems (Cyr et al., 1997, see however Blumenshine et al., 2000 for criticism). For the insect taxa with aquatic larvae only, the average maximal dry mass (mg), i.e. the maximum size, was calculated from body length (mm) of the final larval stage. In Coleoptera with aquatic adult stages, the maximum size was calculated for the adult stage, and a full-grown larva was thought to have the same mass as the adult. Body lengths and parameter values of the dry mass equations ($W = a L^b$) were obtained from the literature. A median of the reported range was used as a body length for the taxa. For each sample, an average maximum body mass of insects was calculated. Similarly, the mean actual body mass was also calculated by dividing the total wet mass of insects in a sample by the number of individuals.

Using information from the literature, the taxa were additionally grouped into four classes by their association with the substrate: burrowers, semisessiles, crawlers and swimmers, which were thought, in this order, to represent increasing activity. Taxa with temporary attachment to the substrate (Richoux, 1994; Tachet et al., 1994; Usseglio-Polatera, 1994) were classified as semisessiles. The climbers and sprawlers of Merritt & Cummins (1996) were grouped with the crawlers, and the clingers (usually net-spinners or tube-builders) with the semisessiles. The classification of taxa according to their affinities for different substrate association was performed by the fuzzy coding approach (Chevenet et al., 1994). In this system, any taxon can represent several modalities within the studied traits to a variable degree (0–3). For detailed information of substrate association, parameter values and body lengths used in dry mass equations, and average maximum size of each taxa, the readers are invited to contact corresponding author.

Logarithmic ($\log_{10}$ x +1) transformations were made for estimates of abundances, biomass and environmental variables, in order to normalize their distributions. Differences between basins in the CPUEs obtained by testfishing were compared by One-Way ANOVA. *Post hoc* comparisons were performed by the Tukey test. Since the biomass of macrophytes was not distributed normally, even after transformation, the nonparametric Kruskal-Wallis test was used to compare biomass values between basins and depth zones. Macrophytes were grouped into four different growth forms: emergents, floating-leaved, elodeids and isoetids. For different predatory and non-predatory insect taxa, the density was compared in relation to two factors – basin and vegetation density category (stem density: $<10$, 10–50 and $>50$ $m^{-2}$) – by multivariate analysis of variance (MANOVA). The isoetid growth forms were not included in stem density because of their small size, low stature and minor contribution to the structural complexity of the habitats. Despite their high density in some study plots, the biomass of isoetids was always low (Table 2). Relations between the species traits of insects and the environmental variables: depth, macrophyte biomass, vegetation density, biomass of benthivorous fish and density of large insect predators (maximum size $>3$ mg), were explored by redundancy analysis (RDA, Van den Wollenberg, 1977; ter Braak & Prentice, 1988) using abundances and CANOCO for Windows version 4.0 (ter Braak

*Table 2.* Dry mass (g m$^{-2}$) of four life forms of aquatic palnts in different basins and depth zones (Mean ± SD)

| | Emergents | Floating-leaved | Elodeids | Isoetids |
|---|---|---|---|---|
| **L. Puruvesi** | | | | |
| 0–0.5 m | 195.4 ± 196.9 | 0.2 ± 0.3 | 3.8 ± 5.0 | 0.2 ± 0.4 |
| 0.5–2 m | 35.5 ± 28.3 | 1.0 ± 1.5 | 11.8 ± 9.2 | 11.4 ± 12.6 |
| 2–3 m | 0.0 | 0.0 | 8.3 ± 7.0 | 7.6 ± 12.1 |
| **L. Pyhäselkä** | | | | |
| 0–0.5 m | 520.6 ± 354.1 | 12.4 ± 14.6 | 4.3 ± 5.4 | 2.0 ± 4.6 |
| 0.5–2 m | 88.4 ± 11.9 | 8.8 ± 13.1 | 0.9 ± 1.0 | 0.2 ± 0.5 |
| 2–3 m | 0.0 | 0.0 | 0.0 | 0.0 |
| **L. Haukivesi** | | | | |
| 0–0.5 m | 98.0 ± 67.5 | 3.6 ± 4.2 | 0.1 ± 0.1 | 0.0 ± 0.1 |
| 0.5–2 m | 8.9 ± 6.9 | 24.5 ± 10.3 | 0.0 | 0.0 |
| 2–3 m | 0.0 | 0.0 | 0.0 | 0.0 |

& Smilauer, 1997). The significance of the eigenvalues of the first canonical axis and all axes together were tested by means of 1000 Monte-Carlo permutations. In the RDA, taxa were divided into five size classes: $<$0.3 mg, 0.3–3 mg, 3-10 mg, 10–50 mg and $>$50 mg according to their maximum size. RDA was performed separately for predatory and non-predatory taxa. Many aquatic insects may be omnivorous, but the taxa were classified as either predatory or non-predatory according to their main feeding mode and trophic position. The relationships between vegetation and the maximum size of aquatic insects were tested by nonparametric Spearman's correlation analysis.

## Results

### *Fish biomass*

CPUE of benthivorous fish differed between the basins ($F$ = 27.24, df = 36, $p < 0.001$). The mean CPUE was about three times higher in Lake Haukivesi than in Lake Puruvesi ($p < 0.001$, Tukey test) and Lake Pyhäselkä ($p < 0.001$) (Table 1), while there was no difference between the latter two basins (p = 0.942). In all basins, perch, *Perca fluviatilis* L. and roach, *Rutilus rutilus* (L.) constituted most of the catch.

### *Macrophyte vegetation*

In all basins, *Phragmites australis* (Cav.) was the dominant emergent species. In addition, *Equisetum fluviatile* L. and *Eleocharis palustris* (L.) were common in Lake Puruvesi. The abundance of floating-leaved species, such as *Nuphar lutea* (L.), *Polygonum amphibium* L. and *Sparganium* spp. increased with water nutrient content. The isoetids, *Isoëtes* spp., *Lobelia dortmanna* L., *Subularia aquatica* L. and *Littorella uniflora* (L.), and the elodeid *Myriophyllum* spp. were abundant in the clear water lake Puruvesi. The elodeid *Potamogeton perfoliatus* L. was the only submersed species common in Lakes Pyhäselkä and Haukivesi.

The biomass of emergent macrophytes differed significantly between depth zones ($\chi^2$= 57.17, df = 2, $p < 0.001$, Kruskal-Wallis) and basins ($\chi^2$ = 7.11, df = 2, p = 0.029), being highest in shallow water (Table 2), and peaking in Lake Pyhäselkä, the basin with an intermediate level of nutrients. The biomass of floating-leaved plants also differed significantly between basins ($\chi^2$ = 9.39, df = 2, $p$ = 0.009) and depth zones ($\chi^2$ = 25.24, df = 2, $p < 0.001$). The biomass was highest in the most eutrophic basin (Lake Haukivesi), and in the middle zone. The isoetids were most abundant in the oligotrophic Lake Puruvesi, and their biomass decreased with increasing trophic status of the basin ($\chi^2$ = 17.05, df = 2, $p < 0.001$). The biomass of elodeids was also highest in Lake Puruvesi, but the difference between basins was not significant ($p$ = 0.079). Neither the biomass of isoetids ($p$ = 0.312) nor that of elodeids ($p$ = 0.238) differed between depth zones. Like the total biomass of macrophytes, the vegetation density (stems m$^{-2}$, isoetids not included) correlated negatively with water depth in all basins (L. Puruvesi: $r_s = -0.76$; L. Pyhäselkä: $r_s = -0.85$; L.

*Table 3.* Densities (ind. $m^{-2} \pm SD$) of some key taxa, and total density of predatory and non-predatory taxa in three study basins and three macrophyte density categories ($<$10, 10–50 and $>$50 stems $m^{-2}$). Statistical significance ($p < 0.05$, MANOVA) between basins and vegetation density are denoted by letters b and v, respectively. Significant interaction term is denoted by asterisk (*)

| | L. Puruvesi | | | L. Pyhäselkä | | | L.Haukivesi | | |
|---|---|---|---|---|---|---|---|---|---|
| | <10 | 10–50 | >50 | <10 | 10–50 | >50 | <10 | 10–50 | >50 |
| Corixidae (b, v) | 0.0 | 23.1 ± 60.2 | 8.4 ± 7.6 | 0.0 | 1.6 ± 4.4 | 42.2 ± 82.0 | 0.5 ± 1.8 | 0.0 | 0.0 |
| Dytiscidae (b) | 0.7 ± 2.1 | 3.7 ± 6.3 | 10.5 ± 20.2 | 5.2 ± 16.3 | 2.4 ± 3.3 | 32.3 ±48.8 | 0.0 | 0.0 | 0.0 |
| Odonata (v) | 0.0 | 10.5 ± 23.1 | 21.0 ± 12.4 | 14.7 ± 50.8 | 11.8 ± 16.6 | 71.0 ± 63.8 | 0.0 | 3.9 ± 6.6 | 12.6 ± 0.0 |
| Sialidae | 0.0 | 10.5 ± 23.4 | 15.7 ± 25.1 | 5.2 ± 18.2 | 0.0 | 6.3 ± 9.6 | 0.5 ± 1.8 | 4.4 ± 7.4 | 0.0 |
| Tanypodinae (v) | 188.0 ± 135.2 | 104.8 ± 82.1 | 88.0 ± 8.0 | 170.9 ± 111.8 | 81.8 ± 89.6 | 79.1 ± 68.6 | 206.0 ± 133.4 | 88.0 ± 123.3 | 31.4 ± 17.8 |
| *Total predators* | 226.4 ± 140.4 | 184.5 ± 132.8 | 156.5 ± 33.3 | 296.3 ± 146.3 | 183.5 ± 117.1 | 287.3 ± 156.9 | 245.1 ± 135.5 | 126.5 ± 132.8 | 58.7 ± 20.8 |
| Ephemeroptera (b, v) | 6.3 ± 9.9 | 35.1 ± 36.9 | 57.6 ± 66.5 | 66.0 ± 72.6 | 48.0 ± 29.3 | 176.1 ± 186.8 | 10.5 ± 14.8 | 20.8 ± 20.9 | 62.9 ± 62.3 |
| Trichoptera NP (b, v) | 0.7 ± 2.1 | 6.3 ± 7.1 | 4.2 ± 5.1 | 32.0 ± 52.6 | 32.2 ± 20.6 | 31.4 ± 44.5 | 7.9 ± 10.8 | 21.8 ± 23.8 | 6.3 ± 8.9 |
| Chironomidae NP (b) | 185.2 ± 287.7 | 84.4 ± 69.8 | 93.3 ± 32.2 | 819.7 ± 656.1 | 796.3 ± 690.3 | 557.9 ± 435.5 | 324.9 ± 219.1 | 407.3 ± 550.7 | 188.7 ± 71.2 |
| *Total Non-predators (b)* | 195.5 ± 291.7 | 133.9 ± 90.8 | 161.9 ± 68.7 | 936.2 ±661.6 | 881.9 ± 691.4 | 782.9 ± 456.4 | 348.0 ± 223.8 | 457.6 ± 556.2 | 257.8 ± 17.8 |

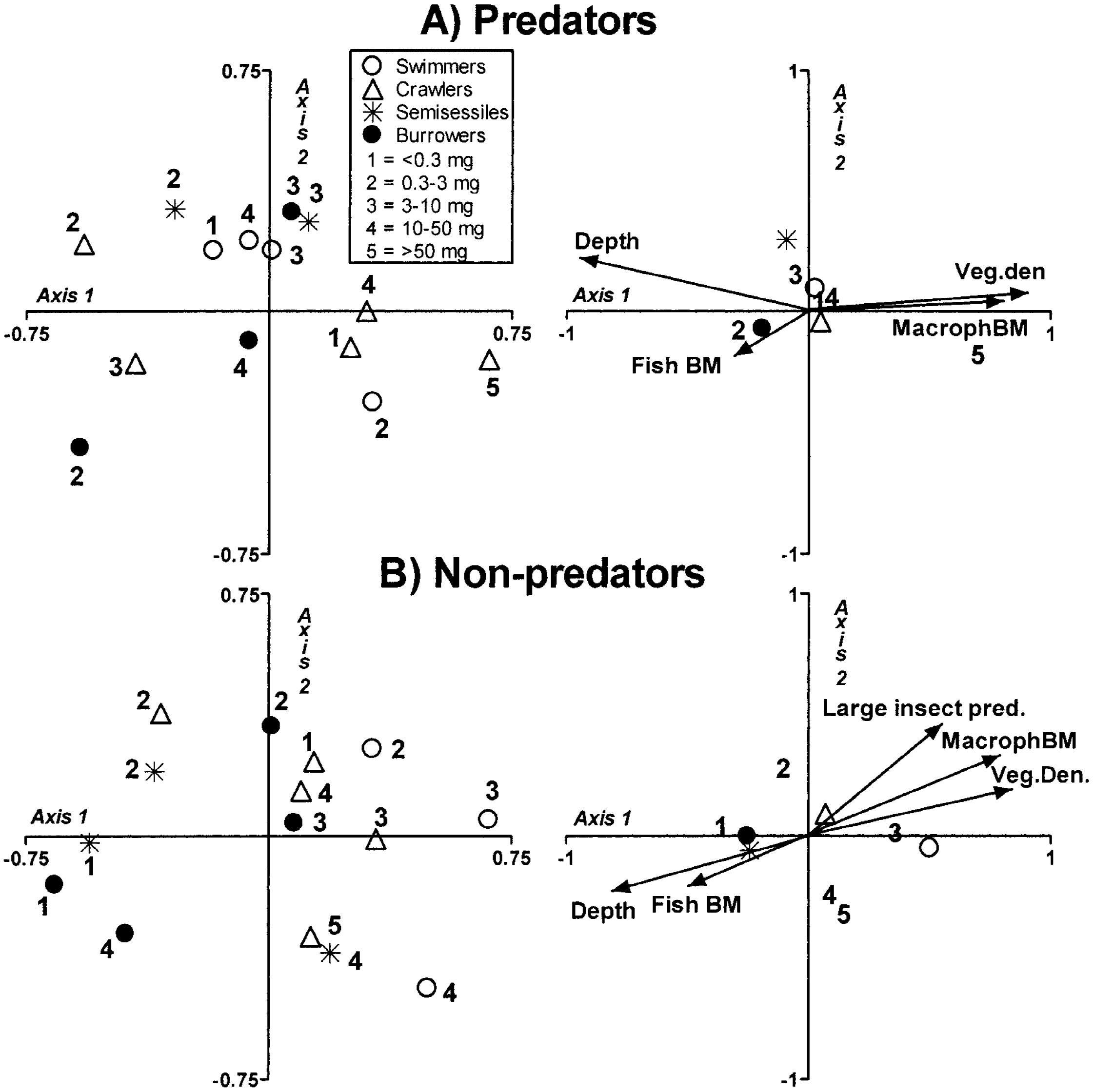

*Figure 2.* RDA-ordinations of environmental factors in relation to the traits representing different types of substrate association and potential size of insects. On the right, the gravity centres (averages) of both studied traits are presented with environmental factors. (A) Predatory insects and (B) Non-predatory insects.

Haukivesi: $r_S = -0.67$; in all three cases $n = 27$ and $p < 0.001$).

### *Aquatic insects and environmental variables*

Of the insect predators, Tanypodinae (Chironomidae) were most abundant on bare bottoms or the bottoms with low vegetation density (Table 3). On the other hand, Odonata, Corixidae and Dytiscidae were common in dense vegetation. The density of Odonata, Corixidae and Tanypodinae differed significantly between the categories of macrophyte density ($p \leq 0.004$). The abundances of Corixidae and Dytiscidae differed significantly among basins. Corixids were rare and dytiscids were not found at all in Lake Haukivesi.

Among non-predatory taxa, densities of Ephemeroptera, Trichoptera, Chironomidae and all taxa in total differed significantly among basins (Table 3). The abundances of Ephemeroptera and Trichoptera were significantly affected by macrophytes. Ephemeroptera was positively associated with vegetation dens-

*Table 4.* Results of redundancy analyses. CPV = cumulative percentage variance

| | Predators | | | | Non-predators | | | |
|---|---|---|---|---|---|---|---|---|
| Axes | 1 | 2 | 3 | Total variance | 1 | 2 | 3 | Total variance |
| Eigenvalues | 0.168 | 0.058 | 0.032 | 1.000 | 0.186 | 0.062 | 0.036 | 1.000 |
| Species-environment correlations | 0.847 | 0.641 | 0.531 | | 0.756 | 0.725 | 0.678 | |
| CPV of species data (%) | 16.82 | 2.62 | 5.8 | | 18.6 | 24.9 | 28.5 | |
| CPV of species-environment relation (%) | 59.9 | 80.7 | 92.1 | | 57.0 | 76.0 | 87.0 | |
| Sum of all canonical eigenvalues | | | | 0.280 | | | | 0.327 |
| INTER-SET CORRELATIONS | | | | | | | | |
| Depth | –0.76 | 0.13 | –0.07 | | –0.57 | –0.15 | 0.25 | |
| Macrophyte BM | 0.65 | 0.02 | 0.02 | | 0.56 | 0.23 | –0.23 | |
| Vegetation density | 0.73 | 0.05 | –0.02 | | 0.60 | 0.13 | –0.26 | |
| Benthivorous fish BM | –0.21 | –0.10 | 0.38 | | –0.34 | 0.11 | –0.30 | |
| Density of large insect pred. (>3 mg) | | | | | 0.40 | 0.33 | 0.07 | |

ity. Trichoptera was most abundant in intermediate densities of vegetation.

In the RDA of both predatory and non-predatory taxa, the eigenvalues of the first canonical axes and all axes together were highly significant ($p < 0.001$) (Table 4). In the RDA-ordination of predators, sampling depth, vegetation density and the total biomass of macrophytes correlated strongly with the first axis (Fig. 2a). The site-specific biomass of benthivorous fish was not strongly associated with either of the first two axes. Large-sized crawlers, e.g. Odonata, and some swimmers, like Corixidae, were clearly associated with shallow water and high vegetation density. The smallest size-class of crawlers was perhaps unexpectedly placed in a shallow littoral zone. This size-class consisted of Tanypodinae: *Conchapelopia* spp. and *Labrundinia longipalpis*. Along the gradient of depth and vegetation density, the gravity centres of substrate attachment types and size-classes were placed in an expected order, except for the smallest size-class (Fig. 2a). However, the maximum size of only crawlers correlated strongly with macrophyte density (Table 5). Although not statistically significant, the correlation coefficients of semisessiles and burrowers were positive indicating that larger taxa tended to be associated with shallow water and abundant vegetation.

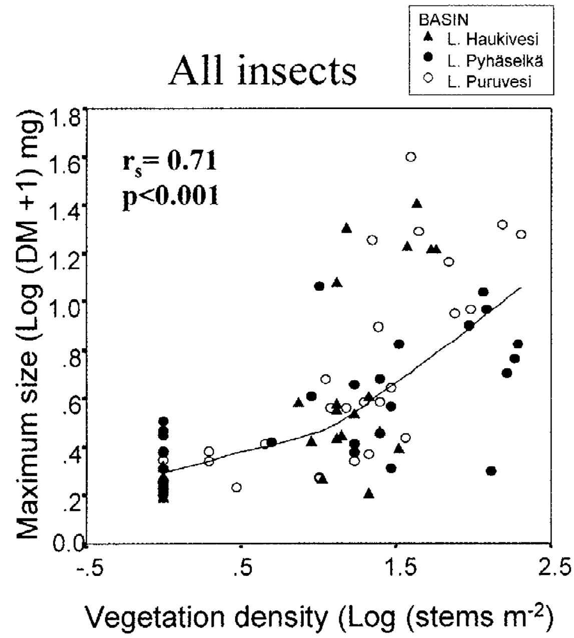

*Figure 3.* Potential size (potential dry mass, log x +1 transformed) of all insects in relation to the vegetation density. An individual sample is represented by a single data point. Trend line was fitted by LOWESS-procedure (Cleveland, 1979) smoothing 80% of the samples.

In the RDA-ordination of non-predatory taxa (Fig. 2b), the first ordination axis was associated with the vegetation density, the macrophyte biomass, sampling depth and density of large insect predators (potential size >3 mg). However, the gradient along which the abundance of large insect predators varied deviated from the course of the first two axes and was placed between them. The gravity centres of substrate association modes were arranged in an expected order in relation to the horizontal littoral gradient. Burrowers and semisessiles (mainly Chironomidae) were characteristics of deeper waters with scarce vegetation. Swimmers (e.g. Baetidae and Siphlonuridae mayflies) were

*Table 5.* Spearman correlation coefficients ($r_s$) between vegetation density and potential size of predatory and non-predatory insects. Coefficients are also presented individually for each substrate association type

| | Predators | | | Non-predators | | |
|---|---|---|---|---|---|---|
| | $r_s$ | $n$ | $p$ | $r_s$ | $n$ | $p$ |
| Swimmers | –0.10 | 54 | 0.468 | 0.52 | 63 | <0.001 |
| Crawlers | 0.62 | 80 | <0.001 | 0.39 | 80 | <0.001 |
| Semisessiles | 0.33 | 28 | 0.091 | 0.27 | 76 | 0.020 |
| Burrowers | 0.17 | 65 | 0.186 | –0.01 | 80 | 0.956 |
| Total | 0.68 | 80 | <0.001 | 0.45 | 81 | <0.001 |

strongly associated with shallow water and high macrophyte biomass. The different size-classes, however, were not arranged as expected, but generally the large-sized taxa seemed to be associated with vegetation. With the exception of burrowers, the maximum size of all substrate association modes of non-predatory insects correlated positively with the vegetation density. Excluding predatory swimmers, the strength of association increased with increasing vulnerability of the substrate association type to fish predation (Table 5). Furthermore, the maximum size of all predatory and non-predatory taxa, as well as, that of all insects together (Fig. 3) were positively associated with plant density. There was an apparent threshold density of approximately 10 stems m$^{-2}$, above which the maximum size of insects tended to increase (Fig. 3). In addition to the patterns found in the maximum sizes, the mean wet mass of insects (actual size) in the samples correlated positively with vegetation density ($r_s = 0.34$, $n = 81$, $p = 0.002$). Furthermore, for all taxa together, the actual body size correlated positively with maximum size ($r_s = 0.58$, n = 81, $p < 0.001$).

## Discussion

Macrophytes often play an important role in regulating the predator-prey interactions, and community and size structure of littoral invertebrates (Jeppesen et al., 1998). Our results suggest that in oligo-mesotrophic lakes with a well-developed macrophyte zone, distributions of two studied species traits, maximum size and substrate association, change along the gradient of vegetation density horizontally from shore to open water. The observed distribution patterns are consistent with those predicted by predation hypothesis (Fig. 1).

Naturally, the distribution patterns of aquatic insects observed by us can be affected by other factors as well. Usually the shallow water of temperate lakes is a zone of high disturbance due to the ice cover, water level fluctuations and wave activity. High ice-induced mortality of less mobile taxa could cause a similar horizontal distribution pattern of substrate association modes to that predicted by the "predation hypothesis". However, the generally high survival rate of frozen insect larvae (Olsson, 1981; Andrews & Rigler, 1985; Palomäki & Koskenniemi, 1993), their behavioural ice avoidance capability (Olsson, 1983; Andrews & Rigler, 1985; Oswood et al., 1991) and the high colonization potential of aquatic insects (e.g. Voshell & Simmons, 1984), may reduce the effects caused by physical disturbance. Moreover, our study sites were relatively sheltered from wave disturbance, and there was a two and a half month ice-free period before the sampling. The biomass of insects was also highest in the shallow water zone (<0.5 m) affected most by ice in winter. Furthermore, water chemistry (nutrients, pH, oxygen) also change along the horizontal gradient of vegetated shores (see Sarvala et al., 1982; Cardinale et al., 1997; Tolonen et al., 2001). Thus it is hard to estimate the relative contributions of biotic and abiotic factors to the rise of observed patterns in the distribution of studied species traits.

Some studies indicate that adult perch and cyprinids remain in open water, while stands of macrophytes are avoided due to the risk of predation by pike (*Esox lucius* L.) (Eklöv & Hamrin, 1989; Laffaille et al., 2001). On the other hand, the use of vegetated habitats by benthivorous fish may be increased by the presence of piscivores in open water (Eklöv & Hamrin, 1989; Eklöv & Diehl, 1994; Diehl & Eklöv, 1995; Persson & Eklöv, 1995; Holopainen et al., 1997), and thus the effects of piscivores on habitat use by their prey fish may cascade further down the food chain (Diehl & Eklöv, 1995). In any case, the predation effect by benthivorous fish is stabilized by structural complexity, and the effects of fish predation on the abundance, body size, diversity and community structure of macroinvertebrates are less pronounced in vegetation than in open water (Crowder & Cooper, 1982; Gilinsky, 1984; Diehl, 1992; Diehl & Eklöv, 1995; Diehl & Kornijów 1998). Partly because of the fish sampling scheme, we could not directly connect the abundance of fish with the gradient of vegetation density. The gillnet fishing was carried out in relatively deep (>1.5 m) and open water with no or only sparse vegetation. Thus, the role of fish predation in the observed patterns of species traits in aquatic insects is inferential only. However, large and mobile taxa, e.g. Odonata, Dytiscidae, Baetidae, Siphlonuridae, Corixidae and Phryganeidae which are sensitive to fish predation (Nilsson, 1981; Bendell & McNicol, 1987, 1995; Henrikson, 1988; Brett, 1989; McPeek, 1990; Rask et al., 1996; Zimmer et al., 2000; Tolonen et al., 2001), inhabited macrophyte beds only and were virtually absent from the open water zone, which in turn was dominated by small-sized and cryptic forms, primarily Chironomidae (see also Hargeby et al., 1994; Eklöv, 1997; Cardinale et al., 1998). Several experimental and manipulative studies (Crowder & Cooper, 1982; Morin, 1984; Mittelbach, 1988; Gilliam et al., 1989; Blois-Heulin et al., 1990; Diehl, 1992; Bechara et al., 1993; Blumenshine et al., 2000) have also indicated that benthivorous fish can reduce the number of large-sized and active taxa and change the invertebrate community to comprise more small and cryptic forms.

Based on the model of Lodge et al. (1988), Strayer (1991) proposed that benthic assemblages of unproductive environments should be dominated by small-sized fauna, since they are more effective in exploiting small and sparsely distributed patches of high-quality food. Large-sized taxa should be able to dominate only in productive environments. In accordance with the productivity model, large body size could be favourable to benthic invertebrates in dense vegetation beds with plenty of high quality food in the form of decaying macrophytes, root exudates and bacteria associated with plant roots (Ságová-Marecková, 2002), periphytic algae and retained allochtonous detritus. In contrast, less nutritious open water zone could be favourable to small-sized animals.

The size structure of littoral macroinvertebrate assemblages has also previously been examined (Mittelbach, 1981; Hanson et al., 1989; Rodríguez & Magnan, 1993; Blumenshine et al., 2000; Zimmer et al., 2001), but the novelty of the present study lies in the fact that it explores the distribution of maximum size, in addition to actual size. Maximum size may be more sensitive for detecting environmental effects than actual body size, since the maximum size, like other species traits, is related to the taxonomic structure of the community. In contrast to Rodríguez & Magnan (1993), Hanson et al. (1989) noticed a considerable seasonal variation in the size structure of benthic invertebrates. Although both these size-related approaches are influenced by phenology, the distribution of maximum size may be less affected by seasonality and reflect long term processes and demographic events rather than a momentary situation represented by actual body size. Although the structuring forces of predation are directed at the actual body size of invertebrates, the maximum size structure may be more closely related to evolutionary adaptations e.g. in antipredatory behaviour. In addition, the use of a single measure of body size for species is practical, as labourious length measurements are not required. Our results gave some inferential evidence that aquatic insect communities may be structured by the top-down forces of both invertebrate and vertebrate predation. In our RDA-ordinations, a gradient was found along which those taxa (swimmers and large crawlers) most sensitive to fish predation were separated from other forms. This gradient was associated with the horizontally changing variables, such as the biomass and density of macrophytes, and water depth. However, further studies are needed to gain a better understanding of size-related processes in benthic food-webs, and the contribution of fish, lake trophic state and various disturbances to the structure of littoral macroinvertebrate communities.

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