

## **Biomass size distributions as a tool for characterizing lake fish communities**

J. J. DE LEEUW\*<sup>†‡</sup>, L. A. J. NAGELKERKE\*<sup>‡</sup>, W. L. T. VAN DENSEN\*, K. HOLMGREN<sup>§</sup>, P. A. JANSEN<sup>¶</sup> AND J. VIJVERBERG<sup>‡</sup>

*\*Wageningen University, Department of Animal Sciences, Fish Culture and Fisheries Group, P. O. Box 338, 6700 AH Wageningen, The Netherlands, ‡Netherlands Institute of Ecological Research, Centre for Limnology, Rijksstraatweg 6, 3631 AC Nieuwersluis, The Netherlands, §Institute of Freshwater Research, National Board of Fisheries, 7893 Drottningholm, Sweden and ¶Norwegian University of Science and Technology, Department of Zoology, 7034 Trondheim, Norway*

*(Received 4 January 2003, Accepted 10 September 2003)*

Biomass size distributions (BSDs) can be useful tools to (1) summarize complex information about fish community structure in a condensed graphical form, facilitating the characterization of freshwater fish communities, (2) compare the position of fish communities along environmental gradients and (3) elucidate major trophic interactions in freshwater fish communities. Biomass size distributions are presented by taxonomic and trophic group, for a selection of fish communities from 35 Scandinavian and eight Dutch lakes. They were used for the analysis of taxonomic and trophic shifts in the fish communities along a large environmental gradient, with productivity (expressed as total phosphorus concentration, TP) as its most important component. Regression analysis of fish community variables (such as proportion of cyprinids, or biomass of benthivores) were consistent with the semi-quantitative conclusions drawn from BSDs, regarding taxonomic and trophic shifts with changes in TP in both Scandinavian and Dutch lakes, especially an increase in the amount and size of benthivorous fishes with increasing TP-levels. In addition, differences in mortality and growth rates were shown to partly explain differences in BSDs. Biomass size distributions thus provide an integrative tool for qualitative and quantitative comparisons among fish communities.

© 2003 The Fisheries Society of the British Isles

**Key words:** European lakes; fish community; productivity; size distribution.

### **INTRODUCTION**

Analysis of fish community structure is widely considered as an integrative indicator of the ecological status of water bodies since Karr (1981) launched his index of biotic integrity. Aspects of the fish community that contribute to community structure are species composition, species abundance, size (or age)

<sup>†</sup>Author to whom correspondence should be addressed at present address: Netherlands Institute for Fisheries Research, P. O. Box 68, 1970 AB IJmuiden, The Netherlands. Tel.: +31 255 564 646; fax: +31 255 564 644; email: [joep.deleeuw@wur.nl](mailto:joep.deleeuw@wur.nl)

structure and trophic composition. Comparisons of fish community structure among water bodies or among years are indicative of ecological status or ecological changes. Most studies have been limited to only one or only a few fish community characteristics. For example, Hanson & Leggett (1982) describe the increase of total fish biomass with productivity. Other authors have described taxonomic shifts with productivity level changes (Colby *et al.*, 1972; Gascon & Leggett, 1977; Hartmann, 1977; Leach *et al.*, 1977; Marshall & Ryan, 1987; Persson *et al.*, 1991). In addition, studies of size distribution and abundance, by means of biomass size spectra have been described since the 1970s, starting with Sheldon *et al.* (1972), who found general patterns in the distribution of biomass over size classes, ranging from bacteria to whales. These size spectra were mainly used to study trophic interactions within aquatic communities, such as planktonic communities (Gaedke, 1992, 1993), whole marine ecosystems (Sprules *et al.*, 1991; Pope *et al.*, 1994), and whole pelagic freshwater food webs (Thiebaut & Dickie, 1993), and for the study of the influence of environmental variables, such as productivity, on fish communities (Sprules *et al.*, 1991; Boudreau & Dickie, 1992; Pope *et al.*, 1994; Cyr *et al.*, 1997) or acidification (Holmgren, 2001). There are few studies, however, that use size distribution, taxonomy and size-related trophic characteristics simultaneously, to evaluate the trophic interactions within aquatic communities (Persson *et al.*, 1991; Holmgren, 2001).

In this study, information on distribution of biomass over size classes and taxonomic or trophic groups was combined by constructing biomass size distributions (BSDs). The use of these BSDs as an integrative indicator for ecological status, in which complex information about fish community structure is summarized in a condensed form, was explored, thus facilitating the characterization of freshwater fish communities.

To evaluate the use of BSDs, freshwater fish communities were compared in northern European lakes, along a large environmental gradient in which climatic, productivity and elevation factors act simultaneously, and most probably interactively. Despite the complexity of the environmental gradient, productivity was considered as one of the most important factors influencing the fish community, since it directly and indirectly affects food conditions for fishes. The studied lakes varied from ultra-oligotrophic Scandinavian mountain lakes to hypertrophic Dutch lowland lakes. The BSDs were compared qualitatively, based on overall shape differences indicating mean size, dominant size groups, and dominant taxonomic and trophic groups. To evaluate the information-value of the BSDs, a quantitative analysis of the same variables was also performed. Finally, the influence on BSD shape of system-specific growth and mortality rates of two dominant species, perch *Perca fluviatilis* L. (planktivore to piscivore) and bream *Abramis brama* (L.) (planktivore to benthivore) was explored.

## MATERIALS AND METHODS

### LAKES

Two Norwegian (data from 1996 to 1997), 35 Swedish (data from 1996 to 1997), and eight Dutch (in total 16 data sets from varying periods per lake) freshwater lakes

were used (Appendix I). The data sets of four of the Dutch lakes span long time periods (22–27 years), within which productivity (expressed as total phosphorus concentration, TP,  $\mu\text{g l}^{-1}$ ) changed drastically. Therefore, these time periods were divided in shorter time periods (6–11 years) in which TP was more or less constant.

## FISH SAMPLING

The Norwegian and Swedish lakes were sampled using standardized gillnet fishing procedures with multi-mesh Nordic series (Appelberg *et al.*, 1995). The nets consisted of 12 panels ( $1.5 \times 2.5$  m each) with mesh sizes from 5 to 55 mm (knot to knot), based on geometric series with a factor 1.25. The pooled selection curve was flat for 1+ year and older fish (Kurkilahti *et al.*, 1999), so no selectivity corrections were made. The Dutch lakes were monitored using bottom trawlnets with a 3 m beam and a codend stretched mesh size of 10–12 mm. The trawlnets were towed by boats at a speed of  $1\text{--}2 \text{ m s}^{-1}$  (hauls of 10 min). In the shallow Dutch lakes (<10 m deep), there is no temperature stratification and most fishes, including small planktivores, are concentrated in the lower water layers. Owing to lack of or sparse vegetation, low water transparency (Secchi disc depths usually <1 m) and daytime fishing (most fishes concentrated near the bottom) late in the season (autumn), trawling procedures were highly standardized and most 0+ year fishes and a large fraction of larger fishes were caught. Biomass of a few pelagic species and species living nearshore (both small proportions of total fish biomass) were underestimated.

## BIOMASS SIZE DISTRIBUTIONS OF TAXONOMIC AND TROPHIC GROUPS

Biomass size distributions were constructed on the basis of length–frequency data of catches. Fish total lengths ( $L_T$ ) were measured and converted into individual wet body mass using species-specific length–mass relationships. Total biomass per size class was estimated by summation of the body mass of all individuals per size class. For lakes that were sampled by bottom trawls, biomass was estimated directly ( $\text{kg ha}^{-1}$  swept area). For lakes that were sampled by gillnets, biomass was estimated from the catch per unit effort (CPUE), which is supposed to be proportional to fish biomass ( $\text{g m}^{-2}$  gillnet area  $\text{night}^{-1}$ ). Size was expressed as  $\log_2$  individual mass classes, which condenses large size classes relative to the more detailed presentation of small size classes. This has the advantage that the BSD becomes more ‘stabilized’, since large size classes are usually rare in fish communities and therefore subject to large variation in the catch. Through ‘lumping’ large specimens over wider length ranges, this variation becomes less erratic.

Species were grouped at the taxonomic level of families (salmonids, coregonids, cyprinids, esocids, osmerids and percids). Trophic groups were classified as planktivores, benthivores (including detritivores) and piscivores based on species- and size-specific diet studies (Appendix II). Herbivory is rare in the study lakes and disregarded further. This classification reflects the average trophic category. It does not account for flexibility in shifting between food types, although this can play a role in species such as bream (Lammens *et al.*, 1985) and perch (van Densen *et al.*, 1996).

Graphical presentations of BSDs are shown for the largest possible productivity gradient, leaving out some lakes with overlapping TP: both Norwegian lakes were selected, Swedish lakes were sorted by TP and subsequently, one lake was randomly selected for each concentration, Dutch lakes were sorted (all 16 data sets) by TP leaving out two lakes that were similar to others (*i.e.* Hollandsch Diep, which was similar to Haringvliet, and Wolderwijd, which was similar to Veluwemeer).

## FISH COMMUNITY VARIABLES IN RELATION TO PRODUCTIVITY

In order to compare the information from the BSDs with a quantitative analysis of the fish community variables, the relationships of (1) biomass of different taxonomic groups, (2) proportion of different taxonomic groups, (3) biomass of different trophic groups

(zooplanktivores, benthivores and piscivores), (4) proportion of different trophic groups and (5) mean body mass ( $M$ , weighted by the number of fish per size class) with TP were analysed. In order to describe these relationships the following simple curves were fitted to all of the above data: (1) linear, (2) log, (3) exponential, (4) power and (5) quadratic curves. Only the significant ( $P < 0.05$ ), or marginally significant ( $0.05 < P < 0.1$ ) curves are shown. Regression analyses were performed with the SAS statistical package software.

In principle, all lakes were used for these analyses. For the Swedish lakes, however, the 0-values for a particular taxon were excluded from the quantitative analyses if the lake for which the 0-value was recorded was situated outside the natural range of that taxon. This means that 0-values for coregonids, cyprinids, esocids and percids from lakes at an elevation  $>500$  m were excluded. For the Netherlands the data sets of two lakes, Hollandsch Diep and Haringvliet, in 1973–1979 were excluded, because in this period these lakes were in transition from a marine to a freshwater environment.

The Scandinavian and Dutch lakes were analysed separately, since the sampling methods differed. Gillnets are generally biased towards larger sizes (Hamley, 1975). Small-meshed trawlnets are highly efficient for catching small fishes, but tend to be less efficient for larger specimens. When taking these biases into account, however, qualitative, graphical comparisons between Scandinavian and Dutch lakes could still be made.

## GROWTH AND MORTALITY AFFECTING BIOMASS SIZE DISTRIBUTIONS

Growth data of two characteristic species of the northern-temperate lakes, perch (growth based on opercular bone readings: Netherlands Institute for Fisheries Research, unpubl. data) and bream (scale readings; Cazemier, 1982), were used to explain how particular, moderate differences in BSDs could already be explained from differences in growth and mortality. From the minimum and maximum growth rates (averages from most contrasting lakes) of perch and bream and a range in mortality rates ( $Z = 0.4$  considered as natural mortality;  $Z = 1.0$  considered as mortality under commercial fishing pressure), the theoretical ranges of BSDs were explored, under the assumption of constant recruitment, growth and mortality.

## RESULTS

The biomass size distributions (BSDs) give a semi-quantitative impression of the structure of fish communities, both for taxonomic (Fig. 1) and trophic groups (Fig. 2). Diversity of the fish community, relative contribution of different taxonomic and trophic groups to the total biomass, and average size classes are presented in unison. This enables the simultaneous comparison of all fish community variables between lakes, also (with some caution) between Scandinavian and Dutch lakes. Comparison of the lake fish communities based on the quantitative analyses (Fig. 3) gave similar results to the comparison of BSDs.

## TAXONOMIC SHIFTS

The BSDs show the overall differences in the taxonomic composition of the fish communities (Fig. 1) at the family level. Scandinavian lakes exhibited a shift along the productivity gradient. Lakes with the lowest TP ( $< 8 \mu\text{g l}^{-1}$ ) were dominated by salmonids [Arctic char *Salvelinus alpinus* (L.) and brown trout *Salmo trutta* L.]. Percids [especially perch and, to a smaller extent, ruffe *Gymnocephalus cernuus* (L.)] and coregonids (*Coregonus* spp.) became abundant in the lakes with TP of  $8\text{--}13 \mu\text{g l}^{-1}$ . Cyprinids [mainly roach *Rutilus rutilus* (L.)]

and esocids (pike *Esox lucius* L.) also contributed substantially to the total fish biomass in these communities. Where TP were  $>13 \mu\text{g l}^{-1}$ , cyprinids (especially bream) became more dominant, and coregonids disappeared. Note, however, that there were exceptions to this general pattern (e.g. Rödningträsket, which had a TP of  $20 \mu\text{g l}^{-1}$ , and a fish community which was entirely composed of salmonids). Statistical analysis corroborated this general pattern: the proportion of the total fish biomass per taxonomic group increased significantly with TP for cyprinids, decreased significantly for salmonids and percids, and showed a maximum (at a TP of  $15 \mu\text{g l}^{-1}$ ) for esocids in Scandinavian lakes (Fig. 3).

Dutch lakes were not as diverse as Scandinavian lakes, and they did not show significant qualitative or quantitative relationships between TP and the taxonomic composition of the fish communities (Fig. 3). In almost all cases there was a high biomass of cyprinids (mostly bream and roach). Dutch lakes mainly differed in the relative abundance of percids and osmerids [smelt *Osmerus eperlanus* (L.)]. The above relationships were all consistent with those in the BSDs (reflected by the relative surface area of the different taxonomic groups; Fig. 1).

### TROPHIC SHIFTS

Most Scandinavian and Dutch lakes were dominated by benthivorous fishes (Fig. 2). Only in Scandinavian lakes of intermediate productivity levels (TP of  $8\text{--}13 \mu\text{g l}^{-1}$ ) were piscivores dominant, while Dutch lakes with many small percids or osmerids were dominated by zooplanktivores.

In Scandinavian lakes, the catch per unit effort (CPUE) of planktivores increased significantly with TP, while the increase of the proportion of planktivores was marginally significant (Fig. 3). Both increases were caused by the growing importance of planktivorous (small) cyprinids and coregonids. The increase of the CPUE of piscivores with TP was marginally significant, and in most cases due to the increase of pike. The proportion of benthivores was at a minimum at an intermediate TP of *c.*  $13 \mu\text{g l}^{-1}$ , reflecting the relatively large biomass of benthivorous salmonids in the lower TP regions, and increasing amounts of benthivorous roach and perch at higher TP.

In Dutch lakes, both biomass and the proportion of benthivores increased significantly with TP (Fig. 3), mainly because of the increase of large, benthivorous bream (*>c.* 25 cm), with high individual body mass. The increase of the biomass of piscivores was only marginally significant, and explained by the increase of pikeperch *Stizostedion lucioperca* (L.). The proportion of planktivores decreased significantly. Most of this decrease was due to the relative increase of large-bodied, mainly benthivorous, bream. The above relationships were all consistent with those in the BSDs (reflected by the relative surface area of the different trophic groups; Fig. 2).

### SIZE ASPECTS

In Dutch lakes with a relatively large biomass of small percids and osmerids, the peak biomass was usually found in body mass classes of 0–4 (Figs 1 and 2). This is markedly smaller than the body mass classes at peak biomass in the other Dutch lakes (body mass classes 8–11). Scandinavian lakes had their peak biomass usually at intermediate body mass classes (4–9).

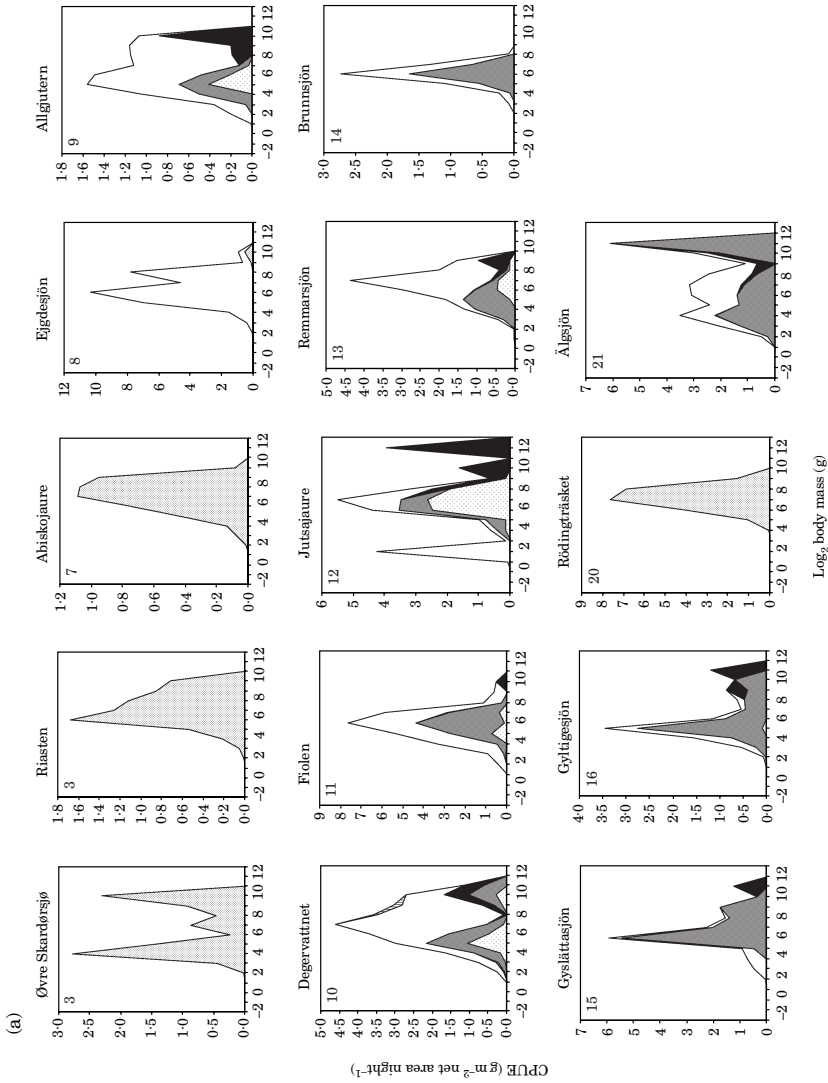


FIG. 1. Continued Overleaf.

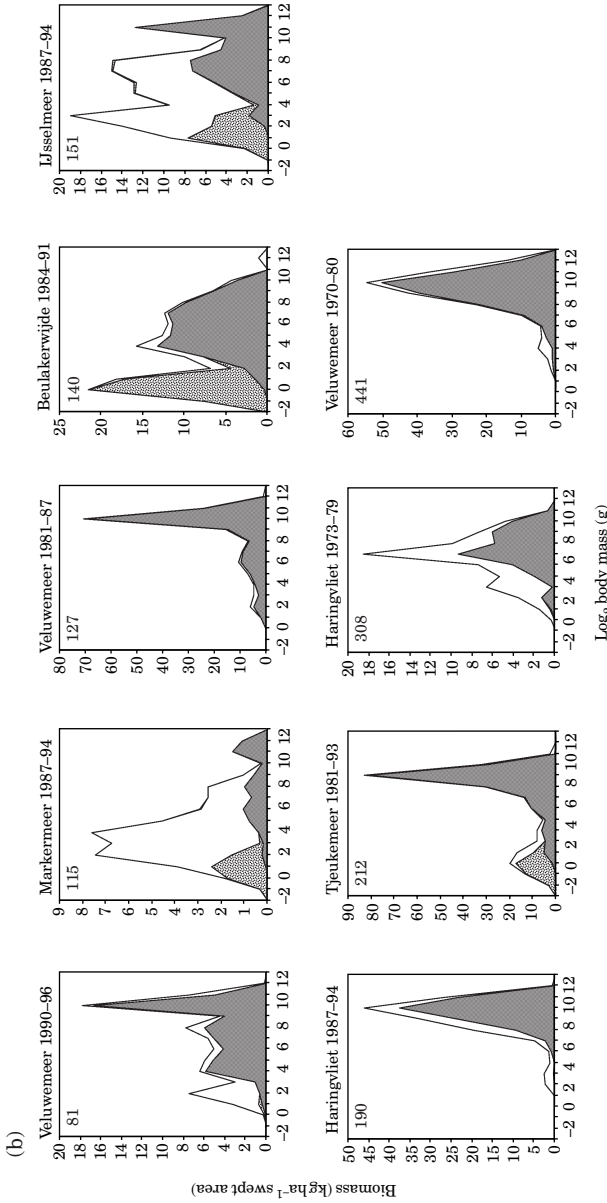


FIG. 1. Biomass size distributions of taxonomic groups (▨, other; □, percid; ▤, osmerid; ■, esocid; ▩, cyprinid; ▧, coregonid; ▨, salmonid) in (a) Scandinavian, and (b) Dutch lakes, along a productivity gradient. Total phosphorus concentrations ( $\mu\text{g l}^{-1}$ ) are indicated in the graphs. Note that Scandinavian lakes were sampled with gillnet surveys, while Dutch lakes were sampled by trawl surveys.

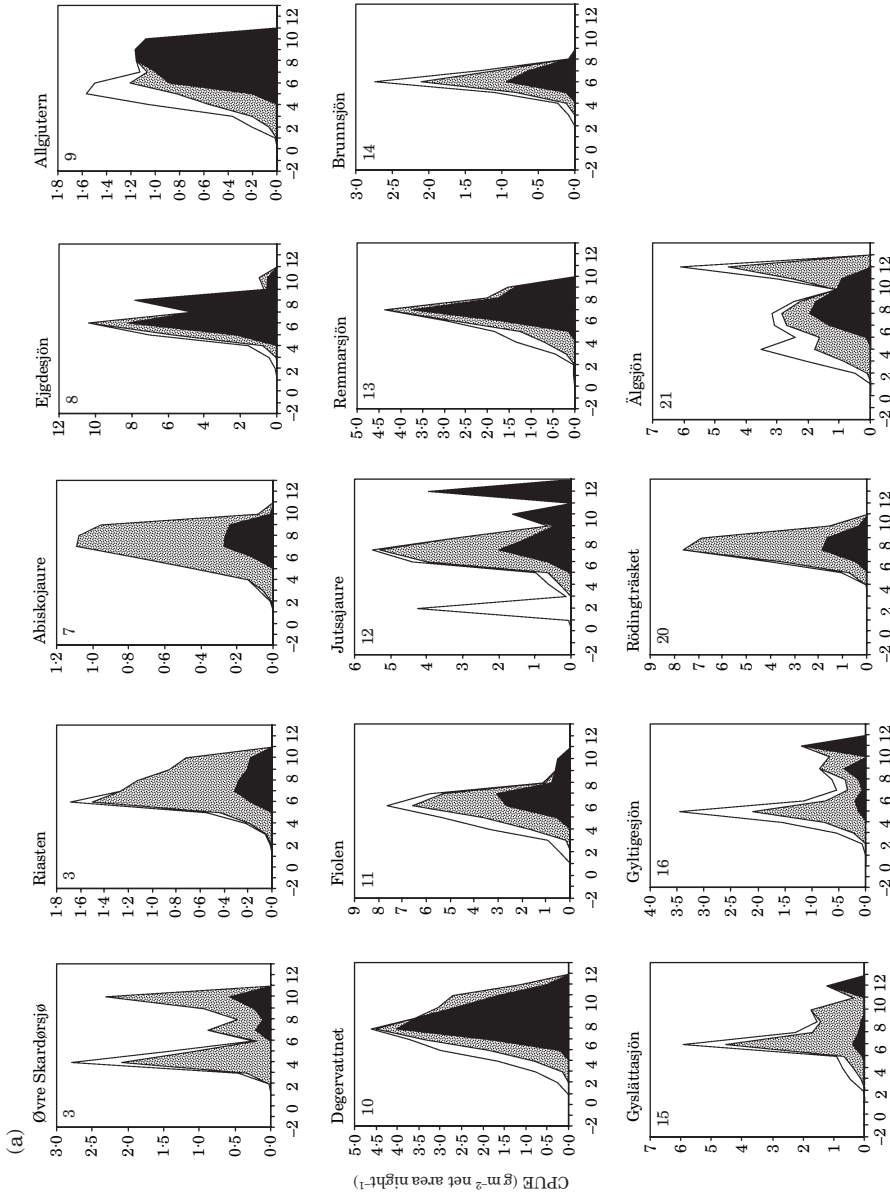


FIG. 2. Continued Overleaf.

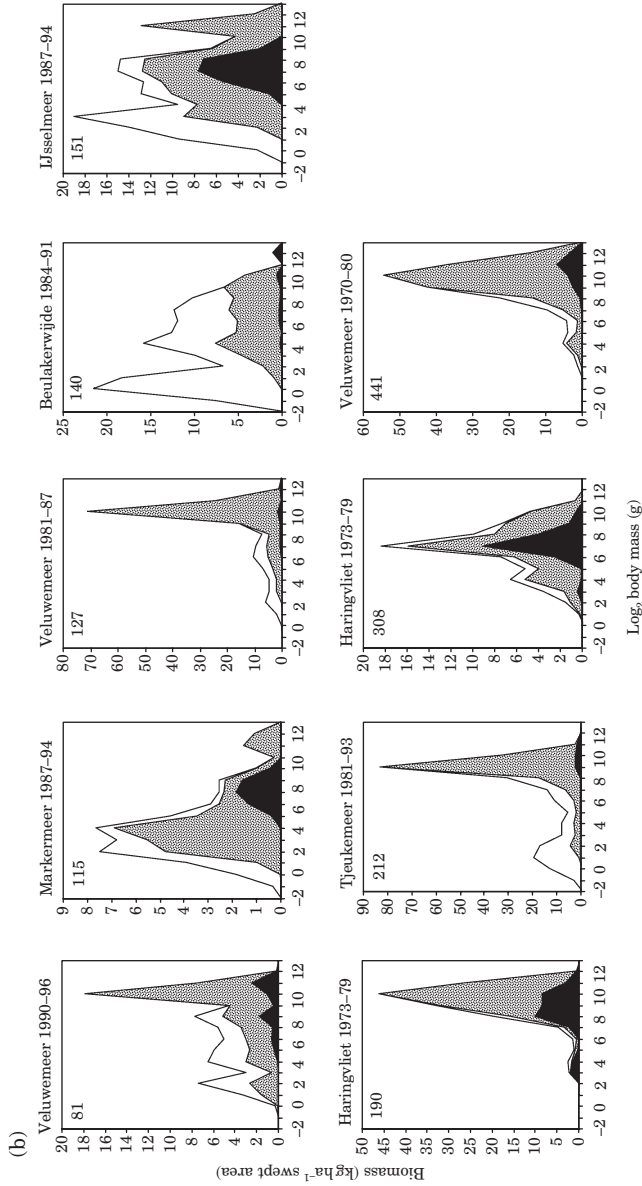


FIG. 2. Biomass size distributions of trophic groups (□, planktivores; ▨, benthivores; ▩, piscivores) in (a) Scandinavian, and (b) Dutch lakes, along a productivity gradient. Total phosphorus concentrations ( $\mu\text{g l}^{-1}$ ) are indicated in the graphs. Note that Scandinavian lakes were sampled with gillnet surveys, while Dutch lakes were sampled by trawl surveys.

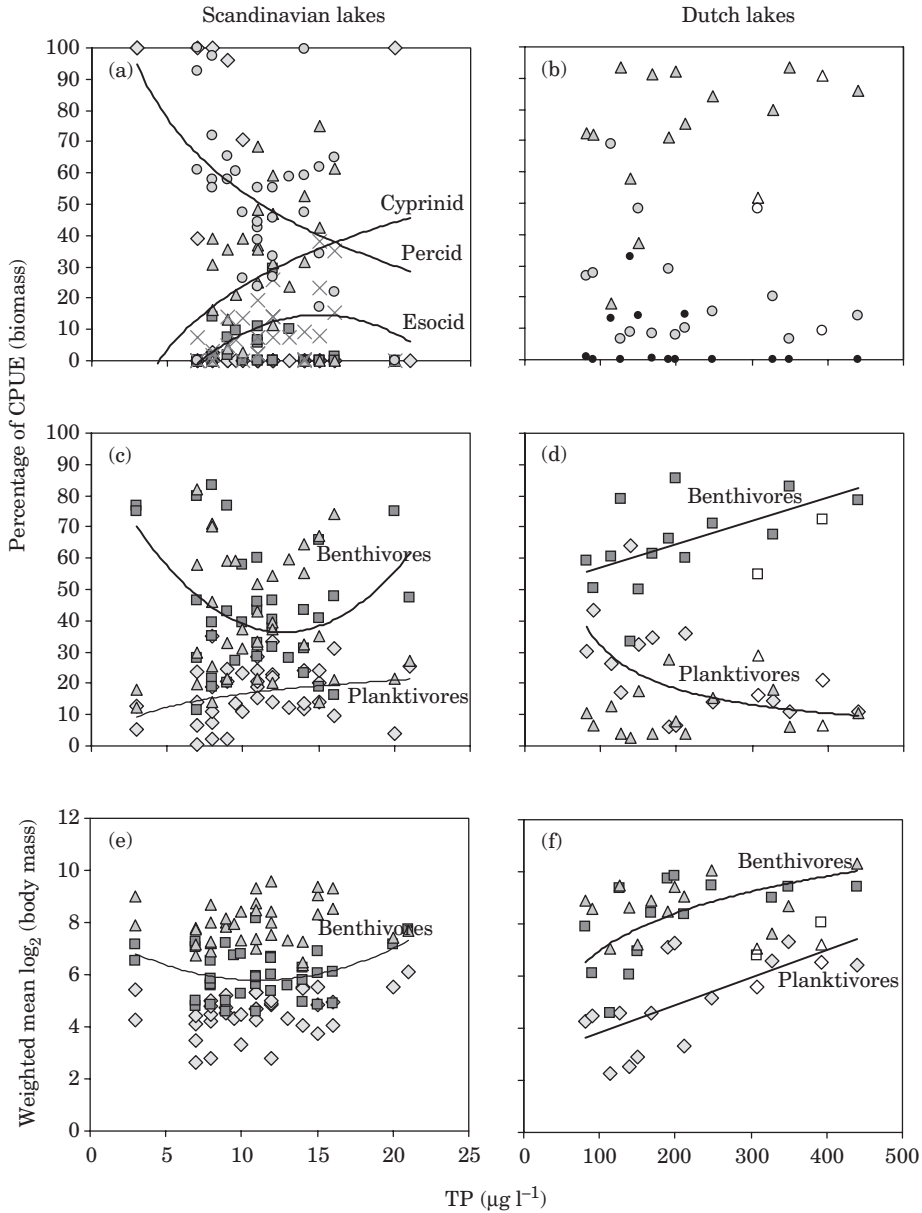


FIG. 3. The fraction of total CPUE and biomass of (a), (b) taxonomic groups ( $\diamond$ , salmonid;  $\blacksquare$ , coregonid;  $\blacktriangle$ , cyprinid;  $\bullet$ , osmerid;  $\times$ , esocid;  $\circ$ , percid) and (c), (d) trophic groups ( $\diamond$ , planktivores;  $\blacksquare$ , benthivores;  $\blacktriangle$ , piscivores), and (e), (f) the weighted mean body mass ( $\bar{M}$ ) of trophic groups as a function of total phosphorus content of (a), (c), (e) Scandinavian and (b), (d), (f) Dutch lakes. —, significant ( $P < 0.05$ ) and - - -, marginally significant ( $0.05 < P < 0.1$ ) relationships. Note that the open symbols (Haringvliet and Hollandsch Diep in 1973–1979) were not included in the regression analysis, since these lakes were in the transition from a marine to a freshwater habitat.

In Scandinavian lakes, the  $\bar{M}$  of planktivores increased significantly with TP (Fig. 3), caused by the increasing size of cyprinids (mostly roach and bream)

and percids (mostly perch). In Dutch lakes, the  $M$  of planktivores increased with TP, which was mainly caused by the increase of the average size of bream. This species can use zooplankton until it reaches a  $L_T$  of *c.* 25–30 cm, in contrast with other cyprinids that only use zooplankton up to sizes of *c.* 15–20 cm  $L_T$  (Lammens *et al.*, 1985). The simultaneous decrease of the biomass of planktivorous small-bodied cyprinids, percids and osmerids further enhanced the overall increase in average size. The overall  $M$  of planktivores appeared to be larger (with marginal significance) in Dutch lakes than in Scandinavian lakes (Wilcoxon test,  $P < 0.09$ ).

The  $M$  of benthivores had a marginally significant quadratic relationship with TP in Scandinavian lakes, with a minimum value at a TP level of *c.*  $11 \mu\text{g l}^{-1}$  (Fig. 3). This was caused by the decrease of large, mainly benthivorous salmonids, and the increase of smaller-bodied cyprinids. In Dutch lakes, the  $M$  of benthivores increased significantly with TP (Fig. 3), which was almost exclusively caused by the increase of large, benthivorous bream. Overall, the  $M$  of benthivores was significantly larger in Dutch lakes than in Scandinavian lakes (Wilcoxon test,  $P < 0.0001$ ). Taking into account that gillnets tend to be biased towards larger fishes and trawlnets towards smaller fishes, the real size difference between fishes of Scandinavian and Dutch lakes is probably even larger. The difference in  $M$  was clearly reflected in the BSDs (Figs 1 and 2), by the position of the highest peaks.

#### POPULATION DYNAMICS VARIABLES AND SIZE DISTRIBUTIONS

To assess to what extent growth and mortality affect BSDs, the effects of population dynamics of perch and bream on BSDs was explored. Bream and perch were chosen, because they are most widespread in Dutch and Scandinavian lakes, respectively. Moreover, their population dynamics are well-studied. Length at age data of slow and fast growing perch and bream (minimum and maximum growth rates of either species in the studied lakes), were used to calculate the instantaneous individual body mass increment  $G$  (Fig. 4):  $G = dM/M dt = \ln(M_2 M_1^{-1})$ , where  $M$  is individual body mass. The survivorship of size class  $M_1$  to  $M_2$  is  $(M_2 M_1^{-1}) - ZG^{-1}$ , where  $Z$  is instantaneous mortality rate. The biomass ratio of adjacent size classes can therefore be written as:  $B_{M_2} B_{M_1}^{-1} = (M_2 M_1^{-1})^{1-ZG^{-1}}$ , where  $B$  is the biomass of a particular size class. It follows that the peak biomass in the BSD (the inflection point where  $B_{M_2} = B_{M_1}$ ) is found at the body mass where growth rate equals mortality rate ( $G = Z$ ).

Simulated BSDs for slow and fast growing perch and bream at instantaneous mortality rates of  $Z = 0.4$  (approximating natural mortality) and  $1.0$  (commercial fishing pressure), respectively, are also given (Fig. 4). Growth rates of perch were found to be more variable than those of bream, especially at early ages. Peak body masses differ 2–3 body mass classes between fast and slow growing conditions. At higher mortality rates (*e.g.*  $Z = 1.0$ ), the peak body mass of the size distributions shifts to the lower size classes.

The above simulation only holds under the assumption of constant rates of growth, mortality and recruitment. If these assumptions are approximately met,

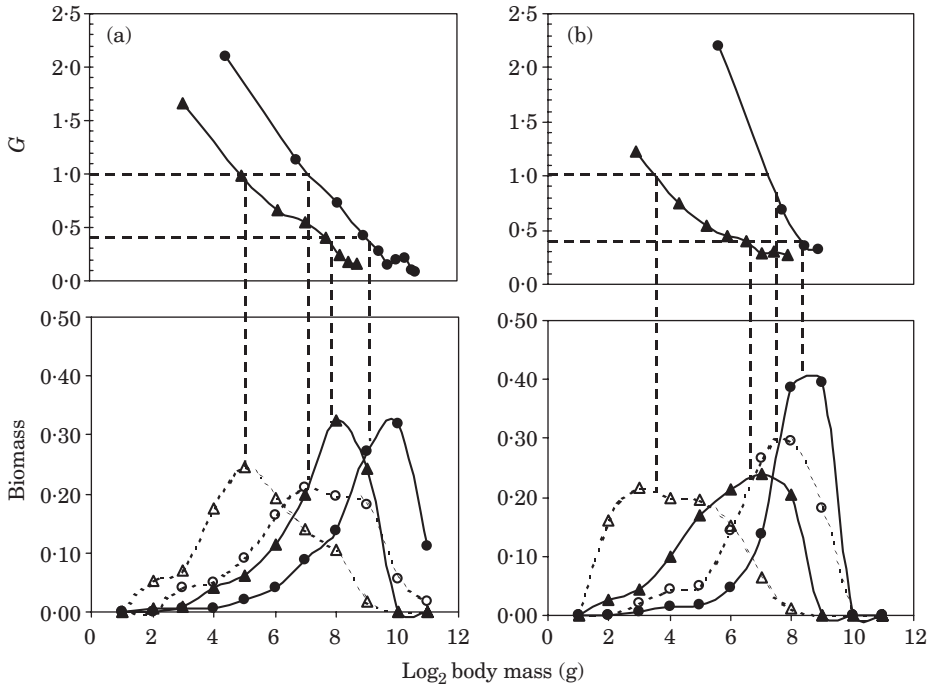


Fig. 4. Size-dependent growth rates ( $G$ ,  $\text{year}^{-1}$ ) and the effects of growth rate on biomass size distributions (BSD) under low ( $\blacktriangle$ ,  $\bullet$ :  $Z=0.4$ ) and high mortality rates ( $\triangle$ ,  $\circ$ :  $Z=1.0$ ) for (a) bream and (b) perch.  $\bullet$ ,  $\circ$ , highest lake-average growth rates and  $\blacktriangle$ ,  $\triangle$ , lowest lake-average growth rates observed. Horizontal lines indicate where  $G=Z$  (0.4 and 1.0, respectively), corresponding with the top of the BSD (vertical lines).

however, it is possible to infer growth differences from the body mass classes at which the peak biomass is found. For example, the peak biomass of cyprinids (almost exclusively bream) in Beulakerwijde in 1984–1991 was at a body mass class of 5–6 (Fig. 1), while in Veluwemeer in 1970–1980 it was a body mass class of 10. There is no fishing pressure on bream in either of these lakes, so it can be assumed that mortality rates will be rather similar in both lakes (*c.*  $Z=0.5$ : Ministry of Transport, Public Works and Water Management, unpubl. data). The differences in peak body mass class between Beulakerwijde and Veluwemeer therefore suggests a much slower growth in Beulakerwijde than in Veluwemeer. This would also mean that a shift of peak biomass of 4–5 body mass classes (with a total of 14 body mass classes), could be entirely caused by growth differences alone. In cases where no assumptions on rates of mortality and growth can be made, shifts in peak biomass are indicative of changes in population dynamics, but interpretation of the shifts requires analyses of growth and mortality data.

## DISCUSSION

This study shows that biomass size distributions (BSDs) can be used as integrative indicators for the ecological status of fish communities. The

semi-quantitative results from the BSDs (relative surface areas of taxonomic or trophic groups and position of biomass peaks) are consistent with the detailed quantitative results from the regression analysis of the same variables. Additionally and simultaneously, BSDs can give a first indication of population dynamics variables such as growth and mortality.

The observed shifts in biomass of the major taxonomic groups along the productivity gradient, as apparent from the BSDs, are consistent with earlier studies (Colby *et al.*, 1972; Hartmann, 1977; Leach *et al.*, 1977; Marshall & Ryan, 1987; Persson *et al.*, 1991). Salmonids dominate in ultra-oligotrophic waters and percids in mesotrophic waters. Cyprinid-dominated communities prevail under eutrophic and hypertrophic conditions. Major shifts in the taxonomic composition (on the family level) of fish communities were not observed in Dutch lakes, probably because they are at the extreme end of the productivity gradient.

In addition to taxonomic differences, BSDs reflect trophic shifts of fish communities, such as the simultaneous increase in abundance and size of benthivores in Dutch lakes (Figs 2 and 3) with increasing TP. This shift is caused by a complex of taxonomic, size and population dynamics differences. First, there is the shift towards a dominance of cyprinids with increasing productivity levels. Once they reach a certain size, most cyprinids become benthivorous and stay so to a large extent (although, under certain environmental circumstances, they can still switch back to planktivorous feeding behaviour; Lammens *et al.*, 1985). The increase in the average size with TP mainly results from bream (the largest abundant cyprinid in Dutch waters) growing to a larger size in water bodies with a high TP. Since large bream ( $>30$  cm  $L_T$ , *i.e.* size classes  $>9$ ) is almost exclusively benthivorous (Appendix I), this suggests that growth conditions, and thus benthic food conditions, must be good (Cazemier, 1982) in water bodies with high TP. This is generally the case (Rasmussen, 1988, 1993), but there are also many hypertrophic lakes, such as Dutch Tjeukemeer, that have a poor benthic fauna, because of wave-exposure (Lammens, 1986), or unfavourable substratum conditions (Cazemier, 1982). In such cases, bream still has to rely heavily on zooplankton (Lammens *et al.*, 1985), which, in the presence of more efficient planktivores such as smelt, can lead to decreased growth of bream, resulting in bream in poor condition with a maximum length of *c.* 30 cm (size class 9) (Lammens *et al.*, 1985). A large biomass of smelt combined with relatively small-bodied bream indicates poor growth conditions for bream, probably caused by a lack of zoobenthos. Slow growth is reflected by peak biomass at smaller sizes (Fig. 4). The BSDs of Beulakerwijde in 1984–1991 and Veluwemeer in 1970–1980 (Fig. 1) show this simultaneous occurrence of smelt with relatively small-bodied cyprinids at peak biomass.

The above illustrates the integrative quality of the BSDs. Many aspects of fish community structure can be evaluated simultaneously (species and trophic diversity; relative importance of taxonomic or trophic groups; average sizes of taxonomic or trophic groups), thereby providing a tool for summarizing complex information, which can be helpful in tracing the status of the underlying processes that structure fish communities, such as trophic interactions, growth

and predation mortality. In other words, BSDs form a fingerprint of individual fish communities.

With due caution these fingerprints can be used for qualitative comparisons between fish communities where direct quantitative comparisons are difficult or impossible, because of differences in sampling methodology (as is the case for the Dutch and Scandinavian lakes). For example, it is difficult to compare the relative abundance and average size of cyprinids and percids in Scandinavian and Dutch lakes directly, but qualitatively it can be stated that percids are relatively more abundant in Scandinavian lakes, and that cyprinids are larger in Dutch lakes, keeping in mind that the number of large fishes is most probably underestimated in the trawl surveys of the Dutch lakes. These qualitative results may lead to more quantitative questions on differences of cyprinid and percid abundance and size between Scandinavian and Dutch lakes, and to a new, clearly focused, survey aimed at these questions. Such qualitative comparisons are often the only possibility for the comparison of historical fish communities with present data. Since historical data of fish communities become more important for the identification of reference situations of fish communities at high ecological status, the BSD methodology provides a tool, not only for the characterization of fish communities, but also for the comparison with (historical) reference situations. The recent development of using multivariate techniques can further enhance the application of BSD for quantitative ecological quality assessments (Nagelkerke & van Densen, 2001).

This study was funded by EC-FAIR CT96-1957. We kindly thank the Netherlands Institute for Fisheries Research, the Norwegian University of Science and Technology, the Swedish Institute of Freshwater Research, the Netherlands Ministry of Transport, Public Works, and Water Management and the Netherlands Institute of Ecology for use of water quality and fish monitoring data. We thank J. van Oostenbrugge, P. van Zwieten and two anonymous referees for valuable comments on this manuscript. Publication 3188 NIOO-KNAW Netherlands Institute of Ecology, Centre for Limnology, Nieuwersluis, The Netherlands.

## References

- Appelberg, M., Berger, H.-M., Hesthagen, T., Kleiven, E., Kurkilahti, M., Raitaniemi, J. & Rask, M. (1995). Development and intercalibration of methods in Nordic freshwater fish monitoring. *Water, Air and Soil Pollution* **85**, 401–406.
- Boudreau, P. R. & Dickie, L. M. (1992). Biomass spectra of aquatic ecosystems in relation to fisheries yield. *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 1528–1538.
- Cazemier, W. G. (1982). The growth of bream (*Abramis brama* L.) in relation to habitat and population density. *Hydrobiological Bulletin* **16**, 269–277.
- Colby, P. J., Spangler, G. R., Hurley, D. A. & McCombie, A. M. (1972). Effects of eutrophication on salmonid communities in oligotrophic lakes. *Journal of the Fisheries Research Board of Canada* **29**, 975–983.
- Cyr, H., Downing, J. A. & Peters, R. H. (1997). Density–body size relationships in local aquatic communities. *Oikos* **79**, 333–346.
- van Densen, W. L. T., Ligtvoet, W. & Roozen, R. W. M. (1996). Intra-cohort variation in the individual size of juvenile pikeperch, *Stizostedion lucioperca*, and perch, *Perca fluviatilis*, in relation to the size spectrum of their food items. *Annales Zoologici Fennici* **33**, 495–506.

- European Union (2000). Directive 2000/60/EC of the European Parliament and of the Council establishing a framework for the Community action in the field of water policy. *Official Journal OJL* **327**.
- Gaedke, U. (1992). Identifying ecosystem properties: a case study using plankton biomass distributions. *Ecological Modelling* **63**, 277–298.
- Gaedke, U. (1993). Ecosystem analysis based on biomass size distributions: a case study of a plankton community in a large lake. *Limnology and Oceanography* **38**, 112–127.
- Gascon, D. & Leggett, W. C. (1977). Distribution, abundance and resource utilization of littoral zone fishes in response to a nutrient/production gradient in Lake Memphremagog. *Journal of the Fisheries Research Board of Canada* **34**, 1105–1117.
- Hamley, J. M. (1975). Review of gillnet selectivity. *Journal of the Fisheries Research Board of Canada* **32**, 1943–1969.
- Hanson, J. M. & Leggett, W. C. (1982). Empirical prediction of fish biomass and yield. *Canadian Journal of Fisheries and Aquatic Sciences* **39**, 257–263.
- Hartmann, J. (1977). Fischereiliche Veränderungen in kulturbedingt eutrophierenden Seen. *Schweizerisches Zeitschrift für Hydrologie* **39**, 243–254.
- Holmgren, K. (2001). Biomass-size distribution of the aquatic community in limed, circumneutral and acidified reference lakes. *Water, Air, and Soil Pollution* **130**, 1751–1756.
- Karr, J. R. (1981). Assessment of biotic integrity using fish communities. *Fisheries* **6**, 21–27.
- Kurkilahti, M., Appelberg, M., Hesthagen, T. & Rask, M. (1999). Selectivity of Nordic multimesh gillnet for five freshwater fish species. In *Nordic Multimesh Gillnet-Robust Gear for Sampling Fish Populations* (Kurkilahti, M., ed.), pp. 1–22. Helsinki: Riistan-Ja Kalantutkimus.
- Lammens, E. H. R. R. (1986). Interactions between fishes and the structure of fish communities in Dutch shallow, eutrophic lakes. PhD Thesis, Wageningen Agricultural University, Wageningen, The Netherlands.
- Lammens, E. H. R. R., Nie, H. W., de Vijverberg, J. & van Densen, W. L. T. (1985). Resource partitioning and niche shifts of bream (*Abramis brama*) and eel (*Anguilla anguilla*) mediated by predation of smelt (*Osmerus eperlanus*) on *Daphnia hyalina*. *Canadian Journal of Fisheries and Aquatic Sciences* **42**, 1342–1351.
- Leach, J. H., Johnson, M. G., Kelso, J. R. M., Hartmann, J., Nümann, W. & Entz, B. (1977). Responses of percid fishes and their habitats to eutrophication. *Journal of the Fisheries Research Board of Canada* **34**, 1964–1971.
- Lessmark, O. (1983). *Competition between Perch (Perca fluviatilis) and Roach (Rutilus rutilus) in South Swedish Lakes*. Lund: University of Lund, Sweden.
- Marshall, T. R. & Ryan, P. A. (1987). Abundance patterns and community attributes of fishes relative to environmental gradients. *Canadian Journal of Fisheries and Aquatic Sciences* **44**, 198–215.
- Nagelkerke, L. A. J. & van Densen, W. L. T. (2001). The utility of multivariate techniques for the analysis of fish community structures and the design of monitoring programmes. In *Proceedings of Monitoring Tailor-made III: International Workshop on Information for Sustainable Water Management, Nunspeet, The Netherlands* (Timmerman, J. G., Cofino, W. P., Enderlein, R. E., Jülich, W., Literathy, P., Martin, J.-M., Ross, P., Thyssen, N., Turner, R. K. & Ward, R. C., eds), pp 323–323. Lelystad, The Netherlands. [http://www.iwac-riza.org/IWAC/IWAC\\_Site.nsf/Publications?OpenPage&Start=1&Cou](http://www.iwac-riza.org/IWAC/IWAC_Site.nsf/Publications?OpenPage&Start=1&Cou)
- Persson, L., Diehl, S., Johansson, L., Andersson, G. & Hamrin, S. F. (1991). Shifts in fish communities along the productivity gradient of temperate lakes—patterns and the importance of size-structured interactions. *Journal of Fish Biology* **38**, 281–293.
- Pope, J. G., Shepherd, J. G. & Webb, J. (1994). Successful surf-riding on size spectra: the secret of survival in the sea. *Philosophical Transactions of the Royal Society of London B* **343**, 41–49.
- Rasmussen, J. B. (1988). Littoral zoobenthic biomass in lakes, and its relationship to physical, chemical, and trophic factors. *Canadian Journal of Fisheries and Aquatic Sciences* **45**, 1436–1447.

- Rasmussen, J. B. (1993). Patterns in the size structure of littoral zone macroinvertebrate communities. *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 2192–2207.
- Sheldon, R. W., Prakash, A. & Sutcliffe, W. H. J. (1972). The size distribution of particles in the ocean. *Limnology and Oceanography* **17**, 327–340.
- Sprules, W. G., Brandt, S. B., Stewart, D. J., Munawar, M., Jin, E. H. & Love, J. (1991). Biomass size spectrum of the Lake Michigan pelagic food web. *Canadian Journal of Fisheries and Aquatic Sciences* **48**, 105–115.
- Thiebaut, M. L. & Dickie, L. M. (1993). Structure of the body-size spectrum of the biomass in aquatic ecosystems: A consequence of allometry in predatory–prey interactions. *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 1308–1317.

APPENDIX I. Lake characteristics. Scandinavian lakes were sampled by gillnet surveys, and total catch per unit effort (CPUE,  $\text{g m}^{-2}$  net night $^{-1}$ ) is indicated; Dutch lakes were sampled by trawnet surveys and estimated biomass ( $\text{kg ha}^{-1}$ ) is indicated. TP, total phosphorus concentration. Data were compiled by the Norwegian University of Science and Technology, the Swedish Institute of Freshwater Research, the Netherlands Ministry of Transport, Public Works, and Water Management, and the Netherlands Institute of Ecology

Country	Lake	Years	Altitude (m above sea level)	Area (ha)	Mean depth (m)	Maximum depth (m)	Secchi disc depth (m)	TP ( $\mu\text{g l}^{-1}$ )	Total fish biomass or CPUE ( $\text{kg ha}^{-1}$ or $\text{g m}^{-2}$ net night $^{-1}$ )	
Norway	Øvre Skardørsjø	1996–1997	1118	50	9	32	18.0	3	9.7	
	Riasten	1996–1997	805	500	12	42	12.0	3	4.5	
Sweden	Abiskojaure	1996–1997	488	282	–	35	11.4	7	4.7	
	Hjärtsjön	1996–1997	274	137	3.4	7	5.8	7	37.1	
	Øvre Skärsjön	1996–1997	219	169	6.1	32	3.2	7	12.2	
	Västra Skälsjön	1996–1997	233	43	6.6	19	9.5	7	20.3	
	Ejdesjön	1996–1997	143	85	6.4	28	6.9	8	33.9	
	Lien	1996–1997	156	165	7.3	28	3.7	8	14.2	
	Nedre Särnamansjön	1996–1997	951	38	2	5	5.0	8	15.2	
	Stora Härsjön	1996–1997	89	251	15.7	47	5.1	8	15.0	
	Ulvsjön	1996–1997	25	6	2.7	4	5.0	8	9.0	
	Allgjutern	1996–1997	131	18	11.7	40	5.9	9	9.3	
Dagarn	Bösjön	1996–1997	582	113	4	18	4.9	9	12.3	
	Dagarn	1996–1997	130	155	5.1	13	–	9	15.4	
	Degervattnet	1996–1997	212	158	5.1	18	4.5	10	24.7	
	Stora Envättern	1996–1997	62	37	5	11	4.3	10	32.2	
	Tryssjön	1996–1997	344	29	7.4	19	3.0	10	7.2	
Fräcksjön	Fiolen	1996–1997	226	156	3.9	10	5.1	11	26.1	
	Fräcksjön	1996–1997	58	28	4.1	15	3.2	11	13.3	

## APPENDIX I. Continued

Country	Lake	Years	Altitude (m above sea level)	Area (ha)	Mean depth (m)	Maximum depth (m)	Secchi disc depth (m)	TP ( $\mu\text{g l}^{-1}$ )	Total fish biomass or CPUE ( $\text{kg ha}^{-1}$ or $\text{g m}^{-2}$ net night $^{-1}$ )
	Stengårdshultasjön	1996–1997	224	498	8.6	26	2.6	11	20.8
	Stensjön (north)	1996–1997	268	59	4.3	9	3.3	11	24.8
	Stensjön (south)	1996–1997	35	39	8.4	21	4.0	11	15.9
	Jutsajaure	1996–1997	422	113	–	10	3.3	12	25.8
	Skärgölen	1996–1997	72	16	7	13	4.4	12	13.3
	Långsjön (south)	1996–1997	141	67	4.3	17	2.7	12	14.4
	Stora Skärsjön	1996–1997	60	32	3.9	12	4.3	12	27.9
	Remmarsjön	1996–1997	234	140	5	14	2.6	13	14.8
	Brunnsjön	1996–1997	98	10	5.3	13	0.83	14	5.7
	Gipsjön	1996–1997	376	67	4.9	14	1.8	14	6.5
	Rotehogstjärnen	1996–1997	121	16	3.6	9	2.2	14	27.1
	Gyslättsjön	1996–1997	224	32	2.3	9	1.8	15	15.6
	Källsjön	1996–1997	232	27	7.7	17	2.2	15	15.4
	Mäsen	1996–1997	101	43	9.6	22	4.4	15	8.8
	Gyltigesjön	1996–1997	66	40	7	19	1.7	16	10.9
	Harasjön	1996–1997	163	61	2.3	9	1.9	16	22.1
	Rödingträsket	1996–1997	351	108	2.5	9	1.8	20	21.5
	Älgsjön	1996–1997	49	36	2.5	7	1.8	21	27.9
Netherlands	Markermeer	1987–1994	0	70 000	3.2	6	0.45	115	36.2
	Beulakerwijde	1984–1991	0	1300	1.5	3	0.34	140	139.7
	Ijsselmeer	1987–1994	0	112 000	4.2	9	0.56	151	110.0
	Tjeukemeer	1981–1993	0	2088	1.5	3	0.35	212	255.1
	Wolderwijd	1990–1996	0	2670	1.3	3	0.45	90	128.1
		1981–1987	0	2670	1.3	3	0.35	168	133.7
		1970–1980	0	2670	1.3	3	0.32	248	89.8

Haringvliet	1987–1994	0	8500	7	30	1.30	190	141.1
	1973–1979	0	8500	7	30	1.29	308	66.8
	1981–1986	0	8500	7	30	1.25	327	109.4
Hollandsch Diep	1987–1994	0	4000	6	25	0.72	199	180.6
	1981–1986	0	4000	6	25	0.61	359	181.8
	1973–1979	0	4000	6	25	0.85	393	66.8
Veluwemeer	1990–1996	0	3240	1.3	3	0.44	81	75.5
	1981–1987	0	3240	1.3	3	0.37	127	167.1
	1970–1980	0	3240	1.3	3	0.25	441	201.8

APPENDIX II. All recorded fish species and their generalized (and simplified), length-based, trophic group assignment for Scandinavian and Dutch lakes. This generalization is based on Lammens (1986), Lessmark (1983) and the Netherlands Ministry of Transport, Public Works, and Water Management, the Netherlands Institute of Ecology, and the Swedish Institute of Freshwater Research (unpubl. data)

Scientific name	Common name	$L_T$ (cm)	Percentage of food		
			Zooplankton	Macrofauna	Fishes
<i>Oncorhynchus mykiss</i> (Waldbaum)	Rainbow trout	0–10	50	50	
		10–20		100	
<i>Salmo trutta</i> L.	Brown trout	>20		75	25
		0–10		100	
<i>Salvelinus alpinus</i> (L.)	Arctic char	10–20	25	75	
		>20		75	25
<i>Coregonus albula</i> L.	Vendace	0–10	50	50	
		10–20		100	25
<i>Coregonus</i> sp.	Whitefish	>20	100	75	
		0–10	100		
<i>Thymallus thymallus</i> (L.)	Grayling	10–20	50	50	
		>20		100	
<i>Osmerus eperlanus</i> (L.)	Smelt	0–10	50	50	
		10–20		100	25
<i>Esox lucius</i> L.	Pike	>20	100	75	
		<5	100		
<i>Rutilus rutilus</i> (L.)	Roach	>5	100		100
		0–7	100		
<i>Leuciscus leuciscus</i> (L.)	Dace	7–15	50	50	
		>15	25	75	
		0–10	100	50	
		10–15	50	50	
		>15	25	75	

<i>Leuciscus idus</i> (L.)	Ide	<10	100	100
		>10		100
<i>Phoxinus phoxinus</i> (L.)	Minnow	<10	75	25
		>10	100	50
<i>Scardinius erythrophthalmus</i> (L.)	Rudd	0-10	100	50
		>10	50	75
<i>Tinca tinca</i> (L.)	Tench	0-7	100	100
		7-15	50	75
		>15	25	100
<i>Gobio gobio</i> (L.)	Gudgeon		100	
<i>Alburnus alburnus</i> (L.)	Bleak	0-10	100	50
<i>Blicca bjoerkna</i> (L.)	White bream	10-15	50	75
		>15	25	100
		<10	100	75
<i>Abramis brama</i> (L.)	Bream	10-20	75	50
		20-30	50	100
		>30	100	
<i>Abramis ballerus</i> (L.)	Blue bream	0-10	100	50
		10-15	50	75
		>15	25	100
<i>Carassius carassius</i> (L.)	Crucian carp	<10	100	
<i>Cobitis taenia</i> L.	Spined loach	>10		100
<i>Anguilla anguilla</i> (L.)	Eel			100

## APPENDIX II. Continued

Scientific name	Common name	$L_T$ (cm)	Percentage of food		
			Zooplankton	Macrofauna	Fishes
<i>Lota lota</i> (L.)	Burbot	<10 >10	100		100
<i>Pungitius pungitius</i> (L.)	Nine-spined stickleback		100		
<i>Gasterosteus aculeatus</i> L.	Three-spined stickleback		100		
<i>Perca fluviatilis</i> L.	Perch	<10 10–15 15–18 >18	50	50	50 100
<i>Stizostedion lucioperca</i> (L.)	Pikeperch	<5 >5	100		100
<i>Gymnocephalus cernuus</i> (L.)	Ruffe	<5 >5	33	67	100
<i>Cottus gobio</i> L.	Bullhead			100	100
<i>Cottus poecilopus</i> Heckel	Siberian sculpin			100	100