The Roach Population in the Hypertrophic Bautzen Reservoir: Structure, Diet and Impact on *Daphnia galeata*

**Uwe Kahl, Hendrik Dörner, Robert J. Radke, Annekatrin Wagner & Jürgen Benndorf**

With 7 Figures and 4 Tables

**Key words:** Roach, population structure, diet, biomanipulation, *Daphnia galeata*

**Abstract**

The structure and diet of the roach (*Rutilus rutilus*) population in the hypertrophic Bautzen Reservoir was examined from April to November 1998. Under the long-term impact of high predation pressure by piscivorous fish, a very heterogeneous population structure of roach had developed. Only a few age classes were dominant while other age classes were nearly absent. The proportion of males decreased with increasing age to 4% of the total abundance of one age class, which nevertheless seemed to have no negative effect on reproductive success. Food analysis revealed that the diet consisted of a high proportion of algae and macrophytes. The collapse of the *Daphnia galeata* population in early summer 1998 forced the roach to switch to benthic food resources [macroinvertebrates and fish: chironomids, molluscs and ruffe (*Gymnocephalus cernuus*)] in early June. Total consumption of age-2 and age-4 roach, the two most dominant year classes, was calculated by a bioenergetics model. Additionally, consumption of age-0 roach was estimated by assuming a fixed daily food consumption rate. The results suggest that daily consumption by these age groups, which never exceeded 0.2% of total biomass of the *D. galeata* population, had a negligible impact on the population of daphnids in Bautzen Reservoir during the period studied.

**Introduction**

Cyprinids affect water quality by consuming zooplankton, by their excretory products and by releasing nutrients from the sediment as an effect of their feeding activities (Horppila 1994). Roach (*Rutilus rutilus*) play a key role, particularly in eutrophic lakes, because of their ability to utilize almost any kind of food sources, especially in situations of strong competition (Persson 1983a; Brabrand 1985). As a consequence of this ability roach frequently dominate in eutrophic and hypertrophic waters (Hartmann 1977a, b; Kubecka 1993).

With the aim of water quality improvement, a whole-lake biomanipulation experiment was initiated in 1981 in the hypertrophic Bautzen Reservoir (Benndorf 1990, 1995). The enhancement of the piscivorous fish stock by stocking with pikeperch (*Sander lucioperca*), pike (*Esox lucius*), eel (*Anguilla anguilla*) and wels (*Silurus glanis*) in combination with catch restrictions, led to strong top-down control of the food web. As a consequence of this food web manipulation, the proportion of piscivorous fish in the total fish biomass increased to 68% in 1997 (Benndorf et al. 1998), while the total fish biomass decreased to less than 50% of the initial biomass. Consequently, the fish stock in Bautzen Reservoir in biomass terms is not dominated by cyprinids, but by percids, in contrast to the general expectation for eutrophic or hypertrophic lakes without food web manipulation (Hartmann 1977a, b; Kubecka 1993).

The aim of this study was: i) to describe the age and size structure of a roach population which had developed under a long-term high predation pressure of mainly pike and pikeperch (Schultz et al. 1992), ii) to detect whether selective predation pressure on male roach could be the cause for the drastic decline of the proportion of males in the roach population of Bautzen Reservoir as described by Schultz (1996) and iii) to evaluate the predation pressure on daphnids by estimating the consumption of the remaining roach population.

**Methods**

Age-1 and older roach were caught with gill-nets (mesh sizes 12, 15, 18, 22, 25, 32, 40, 50, 60 and 70 mm) set overnight in the littoral (area of sediment resuspension, 1–6 m) and pelagic zone (7–11 m) on April 20, August 19 and November 15 in 1998. Each fish was weighed to the nearest gram and measured [total length (TL) and maximum body depth] to the nearest millimeter. Sex was determined
and the opercular bone was removed for age determination. A random sub-sample of 100 roach per gillnet were taken on April 20 and of 50 on August 19 were taken for age determination. Nominal catches were standardized to catch per unit effort (CPUE) according to equation 1:

\[
CPUE = \frac{C_N \times \frac{A_s}{A_N}}{t}
\]  

with: CPUE - catch per unit effort; \(C_N\) - nominal catch; \(A_s\) - area of standard net (100 m²); \(A_N\) - area of net used (m²); \(t\) - time of exposure (h).

The CPUE of the pelagic zone was weighted by factor 7.33 according to the proportion of pelagic zone volume versus littoral zone volume. Additionally, roach were caught weekly from May 11 to June 22 and on July 6, July 20 and August 10 with a bottom trawl (10 mm mesh size in the cod end, three horizontal hauls per date and zone) at night in the littoral and pelagic zone and by beach seineing in the evening. A flowmeter was used to calculate the water volume fished by the trawl. To estimate the abundance of roach in Bautzen Reservoir the number of fish caught per unit volume was multiplied by the total volume of the respective area (littoral or pelagic zone).

The nominal catch and the abundance estimate for every sampling date are given in Table 1. The abundance of each age group was calculated by applying its proportion in the total population, determined from the gill-net catches on April 20 and August 19, to the respective abundance estimate. In the case of age group 1 only the August data were used as this age group was not caught representatively in April with the mesh sizes used. Age-0 roach were sampled once a week between May 11 and June 8 at night by using two bongo-nets (MEHNER et al. 1997, 1998a). On June 8, age-0 roach were sampled by using a small otter trawl as described by MEHNER et al. (1998a). Fish abundance was calculated in the same way as for trawls (Table 2).

Diet of roach caught by trawl and beach seine was pooled for food analysis. The content of the anterior part of the gut (pharynx - first bend) was filtered through 100 µm gauze and analysed under a stereo microscope. The food items were counted and if possible measured to the nearest 0.1 mm. Individual biomasses of the food items measured were backcalculated by using the equations given by MEHNER et al. (1995) and H. Voigt (Inst. of Hydrobiology, unpubl. results). The proportion of the non-measurable food items was estimated visually. The consumption estimate was calculated with the help of a bioenergetics model (KITCHELL et al. 1977; HANSSON et al. 1997). The underlying parameters were taken from HÖRPIULA & PELTONEN (1997). The consumption estimate was made only for the period between May 11 and June 8, before and during the collapse of the daphnid population (S. HOLSMANN, Inst. of Hydrobiology, unpubl. data). Consumption rates

### Table 1. Nominal catches of roach in the littoral and pelagic zone by trawl fishery in Bautzen Reservoir with abundance estimates (number of individuals) in 1998.

<table>
<thead>
<tr>
<th>Date</th>
<th>Number of roach caught in the littoral</th>
<th>Number of roach caught in the pelagial</th>
<th>Estimated total abundance</th>
</tr>
</thead>
<tbody>
<tr>
<td>11 May</td>
<td>28</td>
<td>61</td>
<td>298135</td>
</tr>
<tr>
<td>18 May</td>
<td>118</td>
<td>193</td>
<td>787881</td>
</tr>
<tr>
<td>25 May</td>
<td>76</td>
<td>46</td>
<td>281080</td>
</tr>
<tr>
<td>2 June</td>
<td>51</td>
<td>19</td>
<td>258766</td>
</tr>
<tr>
<td>8 June</td>
<td>112</td>
<td>4</td>
<td>168482</td>
</tr>
<tr>
<td>15 June</td>
<td>90</td>
<td>13</td>
<td>172701</td>
</tr>
<tr>
<td>22 June</td>
<td>94</td>
<td>71</td>
<td>300182</td>
</tr>
<tr>
<td>6 July</td>
<td>94</td>
<td>28</td>
<td>195532</td>
</tr>
<tr>
<td>20 July</td>
<td>51</td>
<td>39</td>
<td>166684</td>
</tr>
<tr>
<td>10 August</td>
<td>89</td>
<td>25</td>
<td>247893</td>
</tr>
<tr>
<td>Mean</td>
<td>80</td>
<td>50</td>
<td>287733</td>
</tr>
<tr>
<td>Standard error</td>
<td>9</td>
<td>17</td>
<td>58070</td>
</tr>
</tbody>
</table>

### Table 2. Abundance, mean individual wet body mass and proportion of daphnids in the diet of age-0 roach in the littoral and pelagic area in May and June 1998 in Bautzen Reservoir. L - littoral; P - pelagial; standard error in parenthesis; *) no SE because only one trawl was performed.

<table>
<thead>
<tr>
<th>Date</th>
<th>Sampling area</th>
<th>Abundance (Ind m⁻³)</th>
<th>Mean wet body mass (mg Ind⁻¹)</th>
<th>Proportion of daphnids in the diet (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>11 May</td>
<td>L</td>
<td>0</td>
<td>3.18 (0.36)</td>
<td>72</td>
</tr>
<tr>
<td></td>
<td>P</td>
<td>0</td>
<td>1.40 (0.07)</td>
<td>0</td>
</tr>
<tr>
<td>18 May</td>
<td>L</td>
<td>5.33 (0.12)</td>
<td>3.18 (0.36)</td>
<td>72</td>
</tr>
<tr>
<td></td>
<td>P</td>
<td>1.11 (0.09)</td>
<td>1.40 (0.07)</td>
<td>0</td>
</tr>
<tr>
<td>25 May</td>
<td>L</td>
<td>2.18 (0.07)</td>
<td>9.25 (1.49)</td>
<td>19.1</td>
</tr>
<tr>
<td></td>
<td>P</td>
<td>0.40 (0.08)</td>
<td>5.38 (0.59)</td>
<td>95.1</td>
</tr>
<tr>
<td>02 June</td>
<td>L</td>
<td>3.31 (0.37)</td>
<td>36.79 (2.04)</td>
<td>15.0</td>
</tr>
<tr>
<td></td>
<td>P</td>
<td>0.45 (0.08)</td>
<td>10.99 (1.61)</td>
<td>63.6</td>
</tr>
<tr>
<td>08 June</td>
<td>L</td>
<td>1.01 (*)</td>
<td>108.78 (2.60)</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>P</td>
<td>0.09 (0.04)</td>
<td>113.42 (3.54)</td>
<td>0</td>
</tr>
</tbody>
</table>

### Table 3. Mean water temperatures over the whole water column in May and June 1998 and respective days of simulation used for the calculation of roach consumption.

<table>
<thead>
<tr>
<th>Date</th>
<th>Day of simulation</th>
<th>Water temperature (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>11 May</td>
<td>1</td>
<td>15.7</td>
</tr>
<tr>
<td>18 May</td>
<td>8</td>
<td>16.4</td>
</tr>
<tr>
<td>25 May</td>
<td>15</td>
<td>15.0</td>
</tr>
<tr>
<td>02 June</td>
<td>23</td>
<td>17.4</td>
</tr>
<tr>
<td>08 June</td>
<td>29</td>
<td>19.4</td>
</tr>
</tbody>
</table>

### Table 4. Mean individual initial and end wet weight (ww) of roach used for the calculation of roach consumption in the period from May 11 to June 15. Number of roach per sampling date and age group (n). Standard error in parenthesis.

<table>
<thead>
<tr>
<th>Age</th>
<th>Initial mass (g ww)</th>
<th>End mass (g ww)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>May 11</td>
<td>May 18</td>
</tr>
<tr>
<td>2</td>
<td>20.7 (1.4)</td>
<td>6</td>
</tr>
<tr>
<td>2</td>
<td>19.3 [back-calculated]</td>
<td>24.9 [back-calculated]</td>
</tr>
<tr>
<td>4</td>
<td>104.5 (5.5)</td>
<td>35</td>
</tr>
</tbody>
</table>
per individual and day were calculated for age-2 and age-4 roach—which formed 70% of roach population biomass—and then multiplied by the estimated abundance of the age group and the proportion of daphnids in the diet of the respective age group. Mean water temperatures (total water column) used in the model calculations are shown in Table 3. Initial and final wet body mass of roach are given in Table 4. Because of low numbers caught on May 11 and June 8, initial and final wet body mass for age-2 roach were backcalculated assuming a linear increase in body mass of 0.2 g d\(^{-1}\). This daily growth rate was derived from the mean mass increase of this age class between May 18 and June 15. Since the physiological parameters given by Höppli & Peltonen (1997) are not applicable to age-0 roach, consumption of this group was estimated by making a few simple assumptions: First, total biomass of the age-0 roach population was calculated by using the abundance estimates and the mean individual biomass values of the respective dates (Table 2). Second, assuming that roach of this size have a daily ration of 100% of their own body mass (Marmulla & Rosch 1990) and knowing the proportion of daphnids in the gut (Table 2) the consumption of age-0 roach was calculated. With the total daily consumption rates of these three age classes the predation pressure on D. galeata was then estimated for the period between May 11 and June 8 with reference to the standing crop of the daphnids (S. Hulsmann, Inst. of Hydrobiology, unpubl. data).

**Results**

**Population structure**

Length-frequency distribution of age-1 and older roach was very heterogeneous (Fig. 1). In April, roach with a total length between 10 and 12 cm were dominant, whereas in August roach of a length between 12 and 16 cm dominated, and in November roach between 24 and 28 cm total length were dominant. The length-frequency distribution is reflected in the age distribution (Fig. 2), showing that the roach population (without young-of-the-year) of Bautzen Reservoir was numerically dominated by only three age groups (age-1, 2 and 4). In April the proportion of age-2 roach was 83% but decreased to 17% of the total catch in November, while the age-4 roach dominated with a proportion of 62% at that time. The distribution of biomass showed dominance by four year old roach (42% to 69%) over the whole study period (Fig. 3). The proportion of two year old roach, which were dominant in abundance in April and August, was 23% and 30%, respectively. The total biomass proportion of the remaining age groups never exceeded 10%.

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**Fig. 1.** Length-frequency distribution of roach caught by gill-netting in Bautzen Reservoir in April, August and November 1998.

**Fig. 2.** Age distribution of roach caught by gill-netting in Bautzen Reservoir in April, August and November 1998.
Sex ratio was determined for the age groups 1–4 and pooled for the older age groups (Fig. 4, data for each age group pooled over the sampling period). Age-2 roach showed a sex ratio of 1. The proportion of males in the age group 1 was 36% and in the age group 3 it was 65%. However, both proportions were not significantly different from 50% (chi-squared-Test, $\alpha = 0.05$) because of small sample size, while age-4 roach with a proportion of males of 35% showed a significant difference from 50%. The proportion of five year old and older male roach was only 4% and also significantly different from 50%. Fig. 5 shows the shift of the sex ratio of the age-4 roach during the period of study in 1998. The proportion of males was 43% in April, 19% in August and 22% in November. The latter two values were significantly different from the April value (chi-squared-Test, $\alpha = 0.05$). Thus, the decline of the proportion of males must have taken place between April and August.

Significant differences in body depth between males and females were only found in the four year old roach in April and August (t-Test, $p < 0.05$), with female body depth (56.7 mm ± 5.5 mm SD and 73.9 ± 5.1 mm SD) deeper than that of the males (51.1 ± 5.0 mm SD and 55.7 ± 4.8 mm SD).

**Diet and impact on Daphnia galeata**

The diets of a total of 441 age-1 and older roach were analysed. Because of the small sample size of some age groups the data were pooled in three groups (group 1: age-1 + age-2, group 2: age-3 + age-4, group 3: age-5 and older). In general, diet of roach in the Bautzen Reservoir contained plant material such as coccal and filamentous algae and parts of macrophytes in addition to a wide spectrum of animal food. Apart from daphnids, other crustaceans such as Alona, Bosmina, Chydorus, Leptodora and, in a few cases, copepods (Cyclops) were found. The benthic diet component mainly consisted of chironomids, but molluscs, mites and the eggs and larvae of other insects were also found. Older age groups were partly piscivorous. Specifically, roach of the age group 1 and 2 showed a wide spectrum of food (Fig. 6) which was dominated by algae and macrophytes (up to 87% of prey biomass). Daphnia galeata was rarely ingested by this age group (not exceeding 10%). The diet of the three and four year old roach was dominated by algae and macrophytes (47% to 95%). Daphnids were only found in the diet in May at proportions of 9% to 34%. From June onwards, benthic organisms were ingested predominantly (up to 53%) amongst algae and macrophytes. On June 15, age-0 ruffe (Gymnocephalus cernuus, TL = 20 mm) was found in the diet of this age group. The diet of five year old and older roach contained mainly algae and macrophytes (up to 100%) and daphnids were found only in May. In June and July, ruffe (TL = 12-56 mm) was an important part of the diet (up to 96%). Benthic organisms and zooplankton were of little importance in the diet of this age group.
The estimated consumption of *D. galeata* by age groups 0, 2 and 4 is shown in Fig. 7. The maximum biomass (wet weight) of *D. galeata* consumed by age-0 roach was 194 kg day$^{-1}$ on June 2, by age-2 roach it was 26 kg day$^{-1}$ on May 11. Age-4 roach had consumed the highest amount of daphnid biomass (up to 212 kg day$^{-1}$ on May 25). The biomass consumed by these age groups on May 25 corresponds to 0.15% d$^{-1}$ of the standing crop of *D. galeata* in Bautzen Reservoir and reflects the maximum consumption detected during the time of our study (Fig. 7). On all other days of the study the proportion of biomass of the total *D. galeata* population consumed by these roach age groups was less than 0.1%.

### Discussion

#### Population structure

While roach populations usually consist of a mixture of age classes with many fish up to 10 years or more in age (TOWNSEND & PERROW 1989), the roach population in Bautzen Reservoir exhibited a very heterogeneous structure. The age distribution shows that only few year classes (1994, 1996) were dominant while other year classes were nearly absent. An underestimation of certain year classes due to gill net selectivity seems unlikely as the shift of the size classes as a result of growth during the time of the study is well documented (Fig. 1). It can be generally stated that the growth of roach in Bautzen Reservoir is very fast compared to other lakes (e.g. WYATT 1988; SCHULTZ 1992; RADKE 1998). Accordingly, age group 4, which forms the major part of the roach stock by biomass, had a mean total length of 261 mm and a mean body depth of 65 mm at the time of our study. Roach of this size are probably only vulnerable to predation by pike and were seldom found in the diet of pikeperch, the most important piscivore in Bautzen Reservoir (SCHULTZ et al. 1992). Consequently, the predation pressure of piscivores is restricted to younger age groups (0 to 3), and it can be predicted that only age groups reaching the size refuge with a sufficient number of individuals will be dominant over the following years.

![Fig. 6](image-url)  
**Fig. 6.** Relative proportion (by biomass) of food components in the diet of roach caught by trawl net fishing in Bautzen Reservoir in 1998. "Other zooplankton" includes other cladocerans and copepods, "zoobenthos" includes chironomids (larvae and pupae), molluscs, mites, eggs and larvae of other insects. Data of littoral and pelagic catches were pooled. Numbers of guts analysed are indicated above bars.

![Fig. 7](image-url)  
**Fig. 7.** Consumption of *Daphnia galeata* (kg wet weight) by roach age group 0, 2 and 4 (vertical bars) and daily uptake of daphnids by roach age 0, 2 and 4 (expressed as a proportion of the total population biomass of the daphnids, circles) in Bautzen Reservoir from May 11 through June 8 in 1998. Values of consumption estimates refer to the total volume of the water body of the reservoir.
Our results concerning sex ratios corroborate those of an earlier study by SCHULTZ (1996) in Bautzen Reservoir. Figs. 4 and 5 indicate a decline of the proportion of males. It should be taken into account though that it shows the instantaneous state of the sex ratio at a small time scale. A study following the fate of the proportion of males within a distinct year class over a longer time period could give clearer evidence of a change of the sex ratio. Body size of prey is a decisive factor for prey selection of gape-limited piscivorous fish such as pikeperch (HAMBRIGHT et al. 1991; VAN DENSEN 1988). From this it could be deduced that male roach should be selectively preyed upon by piscivorous predators if they had a smaller body depth than the females of the same age group. For younger roach this hypothesis is refuted because of a lack of significant differences in the body depth between males and females within the age groups 1 to 3. It is unlikely that predation was the main reason for the decline of the 4 year old males because a significant decline could only be detected in the period between April and August and not thereafter (Fig. 5). Though we have no direct evidence for the increased mortality of four years old males during or after the spawning period in early May, the catch data make this hypothesis seem reasonable. An effect of estrogenic substances can be excluded, as visually detectable hermaphrodites only made up 0.02% (SCHULTZ 1996) and 0% (this study) of the adult population. Furthermore, the very low proportion of males older than four years probably does not negatively affect reproduction and consequently does not lead to a restriction in recruitment success as postulated by MEHNER et al. (1994), because reproduction of the small roach population in the years 1994 and 1996 was sufficiently high to produce very large year classes.

Diet and impact on *Daphnia galeata*

Results of the diet analysis were pooled for all roach caught by trawl and beach seine, as diel migration is typical for cyprinids (BOHL 1980; BRABRAND et al. 1990). This is supported by HORPPILA (1994) who found that roach caught in the pelagic area had macrophytes and invertebrate larvae in their diet, which had been consumed in littoral areas. In addition, Bautzen Reservoir is not distinctly structured by macrophytes, so it can be assumed that roach feed on the zooplankton of the whole lake. The diet of roach in Bautzen Reservoir contained a high proportion of algae and macrophytes. This corresponds well with many other studies of roach in eutrophic lakes (PERSSON 1983a, b; BRABRAND 1985; JAMET et al. 1990; HORPPILA 1994). Such feeding behaviour is not only a consequence of the availability of algae and macrophytes in the environment, but also a consequence of a lack of animal food and resulting food competition (PERSSON 1983a; BRABRAND 1985; PERSSON & GREENBERG 1990). Algae and macrophytes have little energy that can be used by roach compared to animal food (HOFER et al. 1985). Nevertheless, the roach showed a positive energy budget even with a diet based entirely on plant material. The lower energy yield from plant material is compensated partially by an increased ingestion of this food resource. However, growth is reduced compared to a diet based on animal food (HOFER et al. 1985).

In general, the proportion of zooplankton in the diet of roach decreases with increasing age and size (e.g. JAMET et al. 1990; HORPPILA 1994). While age-0 roach caught in the pelagic zone followed this general pattern, those caught in the littoral zone and age-1 to age-2 roach had a smaller proportion of daphnids in their diet in May than age-4 roach. This finding might partly be explained by the lower density of daphnids in the littoral zone, a consequence of higher predation pressure of age-0 perch on daphnids, compared to that in the pelagic zone of Bautzen Reservoir (HÜLSMANN et al. 1999). In this context it has to be noted that the majority (63%) of age-1 to age-2 roach included in the diet analysis had been caught in the littoral zone with the beach seine. The preference for structured habitats in the shallower part of the littoral zone is interpreted as a predator avoidance behaviour of juvenile roach (CHRISTENSEN & PERSSON 1993; BEAN & WINTFIELD 1995) and very likely accounts for the observed distribution pattern of young roach.

According to TOWSENM et al. (1986), roach switch to benthic food resources at a zooplankton density of fewer than 40 individuals per litre, or use other food resources such as macrophytes or detritus (HORPPILA & PELTONEN 1997). Such a predictable shift in the diet composition of the roach occurred in Bautzen Reservoir at the beginning of June 1998, when the population of daphnids collapsed. After this collapse roach fed mainly on chironomids and molluscs. Even ruffe up to 56 mm total length were frequently ingested by older roach, which has rarely been documented (MICHEL & OBERDORFF 1995) and might partly account for the good growth of roach in Bautzen Reservoir.

The estimation of fish abundance represents a greater source of error than calculation of consumption rates on an individual basis (HEWETT 1989). Our abundance estimates, though, show little variation (apart from value on 18 May) and no seasonal trend, making a systematic underestimation of the impact of the roach population on the *Daphnia* population unlikely. The low proportion (< 0.2% d⁻¹) of the standing stock biomass of the daphnid population consumed by the age-0 roach and the two dominant older age groups is clear evidence that predation by roach was not the reason for the collapse of the *D. galeata* population in 1998 in Bautzen Reservoir. Apart from roach, age-0 percids are the most important zooplanktivores (MEHNER et al. 1997, 1998a), while older percids are mainly benthivorous or piscivorous (DÖRNER et al. 1999 and in this volume). During early summer (1995 and 1996) consumption of *Daphnia* by age-0 percids never exceeded 1% d⁻¹ of the standing stock of *Daphnia* biomass and was in the same range as that of roach in 1998 (MEHNER et al. 1997, 1998a).
The aim of biomanipulation is a high density of large filtering fish. The stock of piscivorous fish is very high and has led to a strong reduction of the planktivorous fish stock and thus to a low impact of planktivores on the Daphnia galeata population. The existence of older roach, in a size refuge, with a reproductive capacity much higher than that of the younger individuals (Townsend & Perron 1989), may counteract the effects of biomanipulation. A solution to this problem is to enhance further the size refuge threshold by even higher stocks of piscivores such as pike and wels, which are less mouth gape limited than pikeperch of the same body size.

**Conclusions**

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