# PATTERN OF SPATIAL FISH DISTRIBUTION IN THE SULEJOW RESERVOIR MONITORED BY HORIZONTALLY BEAMING ECHOSOUNDER AND BY GILL NETTING. 

PIOTR FRANKIEWICZ ${ }^{1}$, ANDRZEJ ŚWIERZOWSKI ${ }^{2}$<br>${ }^{1}$ Department of Applied Ecology, University of Lodz, Banacha 12/16, 90-237 Lodz, Poland franek@biol.uni.lodz.pl<br>${ }^{2}$ Inland Fisheries Institute, Oczapowskiego 10, 10-719 Olsztyn, Poland a.swierzowski@infish.com.pl


#### Abstract

The Sulejów reservoir situated on the Pilica River in Central Poland serves as an important source of drinking water for the Lodz Agglomeration. Precise knowledge on fish abundance, community structure as well as spatial and temporal changeability is crucial for proper fishery management (biomanipulation) in order to slow down the reservoir eutrophication and prevent toxic algal blooms. As the reservoir is very shallow (average depth is 3.3 m ) it was necessary for fish distribution monitoring to apply, first time in Poland, horizontally looking split beam echosounder (Simrad EY-500 with elliptic transducer ES 120-4x10). Simultaneously, to collect fish for verification of acoustic data and determination of fish species composition, multimesh gill nets were used in representative parts of the reservoir. Prepared maps showing both spatial fish distribution and their density suggest that used methods were suitable for identification of specific areas characterized by different quality of environmental conditions.


## INTRODUCTION

Shallow, lowland reservoirs due to high nutrient load are especially exposed to the intensive cyanobacterial blooms, usually harmful for people and animals [16, 17]. Sulejów reservoir, is a typical example of such situation. One of the way to cope with symptoms of eutrophication is changing biotic structure of ecosystem in order to improve water quality, it means applying biomanipulation sensu Shapiro et al. [11]. The success of biomanipulation is frequently dependent on a proper estimation of fish community structure in the ecosystem, as well as their density and biomass. In the case of dammed reservoir high variability of abiotic and biotic conditions along longitudinal axis is observed. It may highly influence both
seasonal and daily pattern of spatial fish distribution and thus the effectiveness of biomanipulation. To improve our knowledge on the dynamics of fish distribution, apart the traditional "static" method as gill netting [1] the use of "dynamic" methods as hydroacoustic is necessary [ $9,7,15]$. However, in shallow ecosystem standard vertical beaming is not applicable due to extended hydroacoustic blind zone, and should be replaced by horizontal beaming. As there were only few attempts to use horizontally oriented transducer in shallow freshwater ecosystems [e.g. 6, 4] the main aim of this study was a further evaluation of methods based on mobile surveys with horizontally beaming transducer which would be effective in estimation of both fish density and biomass in such an environment.

## 1. STUDY AREA

Investigations were conducted at the Sulejów reservoir, which is situated in Central Poland on the Pilica River. Its average and maximum depths are 3.3 and 11 m , respectively. Due to high water level fluctuations the reservoir's area may vary from 630 to 2380 ha , and in consequence the littoral zone is almost devoid of macrophytes. In sparsely vegetated lacustrine parts of the reservoir following macrophytes are usually found: Potamogeton lucens, Potamogeton amphibium, Elodea canadensis, Galium palustre, Carex gracilis, Equizetum fluviatile, Eleocharis palustris, Gliceria fluitans and Iris pseudoacorus.

The reservoir is highly eutrophicated (mean concentration of total phosphorus at spring overturn is about $400 \mu \mathrm{~g} \mathrm{dm}^{-3}$ ), which results in a high mean summer concentration of chlorophyll $a$, about $30 \mu \mathrm{~g} \mathrm{dm}^{-3}$ (date from years 1990-2000). Under such conditions summer blooms of cyanobacteria (mainly Microcystis aeruginosa and Aphanizomenon flos-aque) have been frequently observed during resent years. The mean summer biomass of zooplankton in the reservoir has been ranged between 4 mg (1994) and $10.7 \mathrm{mg} \mathrm{dm}^{-3}$ (1996), consisting mostly of cladocerans: Bosmina coregoni, Daphnia cucullata and Leptodora kindtii (unpublished data). However, peaks of zooplankton biomass up to $60 \mathrm{mg} \mathrm{dm}{ }^{-3}$, caused exclusively by the high abundance of Bosmina coregoni, were noticed.

## 2. MATERIALS AND METHODS

Acoustic searching was conducted applying a "zigzag" method along selected transects, at nights in the last week of August 2003 (Figure 1). A research ECHO-type boat equipped with Simrad EY 500 split-beam echo sounder (with $120 \mathrm{kHz} 4 \times 10^{\circ}$ elliptic transducer) was used. To determine fish distribution and density in this shallow reservoir, horizontal beaming was, first time in Poland, carried out. A scheme of transducer fixing on the boat is shown at Figure 2. Additionally, the boat was equipped in navigation echo sounder, log and GPS. Acoustic data were registered by a computer in the real time. To calculate fish density, EP500 post-processing software was used. The method of counting echoes from the fish accepted by acoustic system of echo sounder was applied [12]. In order to prepare maps of fish spatial distribution and density, as well as to determine fish number, acquired data were interpolated by Kriging method applying computer system of data analyzing SURFER (Gold. Soft. Inc. 1989). Detailed description of this method may be found in following papers [8, 12, 13]. To collect fish for verification of acoustic data and determination of fish species composition, multimesh low selective gill nets were used. Four identical sets of nets, each 77 m long and 3 m high, consisting 11 different 7 m long panels, with the mesh size from 11 to 80 mm (knot to knot), were applied. Gill netting was conducted monthly from June to November in two selected regions (Karolinów and Bronisławów) of the reservoir (Figure 1). At each sampling station one set of nets was placed in the littoral zone and the second one in


Fig. 1. Sulejów reservoir - bathymetry and acoustic transects
the open water area of the reservoir. Collected fish were measured (total length, Lt ) and weighed to the nearest centimeter and gram, respectively. Knowledge of quantity, species structure, and specimens' weight allowed estimating the biomass of both individual species and whole fish community.


Fig. 2. Boat Echo equipments for hydroacoustic monitoring with horizontal beaming

## 3. RESULTS AND DISCUSSION

Research surveys with horizontally oriented split beam echo sounder conducted in the Sulejów reservoir allowed to estimate the mean fish density and biomass on 860 individ. $\mathrm{h}^{-1}$ and $114,1 \mathrm{~kg} \mathrm{~h}^{-1}$, respectively (Table 1). This fish density was 7 time lower comparing with mean estimation of this parameter by hydroacoustic method in other 28 Polish lakes and reservoirs [14], but was in the range of biomass and density estimated in reservoirs of comparable hydrological and hydrochemical characteristics and similar fish community structure $[5,10]$. There were no evident differences in fish density along the longitudinal axis

Tab. 1. Characteristics of fish resources estimated from acoustic - fishing data in the Sulejów Reservoir.

| Species | Numbers |  |  | Biomass |  |  | Mean individual weight (g) |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Total |  | N $\mathrm{ha}^{-1}$ | Total |  | kg $\mathrm{ha}^{-1}$ |  |
|  | N | \% |  | kg | \% |  |  |
| Roach | 527400 | 43.8 | 377 | 68351 | 42.7 | 48.8 | 129.6 |
| White bream | 220300 | 18.3 | 157 | 42099 | 26.3 | 30.1 | 191.1 |
| Pike perch | 180600 | 15.0 | 129 | 16128 | 10.1 | 11.5 | 89.3 |
| Perch | 83100 | 6.9 | 59 | 3964 | 2.5 | 2.8 | 47.7 |
| Ruffe | 73400 | 6.1 | 52 | 594 | 0.4 | 0.4 | 8.1 |
| Bleak | 54200 | 4.5 | 39 | 1068 | 0.7 | 0.8 | 19.7 |
| Bream | 53000 | 4.4 | 38 | 27613 | 17.3 | 19.7 | 521.0 |
| Others | 12000 | 1.0 | 9 | - | - | - | - |
| Total | 1204000 | 100.0 | 860 | 159817 | 100.0 | 114.1 | - |

Tab. 2. Characteristics of gill net catches in different seasons and regions in the Sulejów Reservoir ( N - fish number)

| Date of <br> fishing | Fishing regions |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  | Karolinow |  | Bronislawow |  | $\mathbf{N}$ |
|  | $\mathbf{N}$ | $\%$ | $\mathbf{N}$ | $\%$ |  |

Littoral zone

| 10.06 .03 | 116 | 40.7 | 169 | 59.3 | 285 |
| :---: | :---: | :---: | :---: | :---: | :---: |
| 16.07 .03 | 84 | 35.1 | 155 | 64.9 | 239 |
| 13.08 .03 | 9 | 3.8 | 229 | 96.2 | 238 |
| 4.09 .03 | 11 | 12.8 | 75 | 8.2 | 86 |
| 14.10 .03 | 51 | 31.9 | 109 | 68.1 | 160 |
| 13.11 .03 | 30 | 62.5 | 18 | 37.5 | 48 |
| Total | $\mathbf{3 0 1}$ | $\mathbf{2 8 . 5}$ | $\mathbf{7 5 5}$ | $\mathbf{7 1 . 5}$ | $\mathbf{1 0 5 6}$ |

Pelagic zone

| 10.06 .03 | 8 | 8.1 | 91 | 91.9 | 99 |
| :---: | :---: | :---: | :---: | :---: | :---: |
| 16.07 .03 | 50 | 24.0 | 158 | 76.0 | 208 |
| 13.08 .03 | 26 | 7.4 | 324 | 92.6 | 350 |
| 4.09 .03 | 7 | 9.7 | 65 | 90.3 | 72 |
| 14.10 .03 | 37 | 28.2 | 94 | 71.8 | 131 |
| 13.11 .03 | 40 | 65.6 | 21 | 34.4 | 61 |
| Total | $\mathbf{1 6 8}$ | $\mathbf{1 8 . 2}$ | $\mathbf{7 5 3}$ | $\mathbf{8 1 . 8}$ | $\mathbf{9 2 1}$ |

Total pelagic and littoral zone

| 10.06 .03 | 124 | 32.3 | 260 | 67.7 | 384 |
| :---: | :---: | :---: | :---: | :---: | :---: |
| 16.07 .03 | 134 | 30.0 | 313 | 70.0 | 447 |
| 13.08 .03 | 35 | 6.0 | 553 | 94.0 | 588 |
| 4.09 .03 | 18 | 11.4 | 140 | 88.6 | 158 |
| 14.10 .03 | 88 | 30.2 | 203 | 69.8 | 291 |
| 13.11 .03 | 70 | 64.2 | 39 | 35.8 | 109 |
| Total | $\mathbf{4 6 9}$ | $\mathbf{2 3 . 7}$ | $\mathbf{1 5 0 8}$ | $\mathbf{7 6 . 3}$ | $\mathbf{1 9 7 7}$ |

of the reservoir (Figure 3). High densities were observed close to the dam as well as in the central and most upper parts of the reservoir.To identify the species composition of the fish community, control gill net fishing was carried out in the reservoir. Taking into account summarized data from all gill netting occasions (Table 2) the distinct pattern of species dominance was found in both fishing regions (Table 3; Figure 4). Roach dominated evidently in the reservoir, and its total share to the community (by number as well as by weight) exceeded $40 \%$, in both the pelagic and littoral zones. Subdominants were white bream, bream and pikeperch. The $15 \%$ contribution of pikeperch is of particular significance, as its crucial role as a key predator in the reservoir was frequently emphasized [2]. More detailed analyses of fish distribution revealed that such species like roach, pikeperch, perch and ruffe tended to be more abundant in the littoral areas in both fishing regions (Figure 2), while in Karolinów region white bream and bream were more numerous in the pelagic zone. In the case of roach, the average length of fish caught in the littoral zone was, at each occasion, smaller than that of fish collected in the pelagic areas (Figure 5), which reflects the observed tendency of juvenile fish to gather in the near shore areas. High density of small prey fish in the littoral zone might also explain the tendency of pikeperch to stay there [3].

Tab. 3. Characteristics of fish collected by gill nets in littoral and pelagic zones of the Sulejów Reservoir in summer (June -September) 2003. SD - standard deviation.

|  | Littoral zone |  |  |  | Pelagic zone |  |  |  | Total |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Species | N | \% | $\begin{gathered} \mathrm{Lt} \\ \text { in cm } \\ \text { (SD) } \end{gathered}$ | $\begin{gathered} \text { W } \\ \text { in } \mathrm{g} \\ \text { (SD) } \end{gathered}$ | N | \% | $\begin{gathered} \mathrm{Lt} \\ \text { in cm } \\ \text { (SD) } \end{gathered}$ | $\begin{gathered} \text { W } \\ \text { in } \mathrm{g} \\ \text { (SD) } \end{gathered}$ | N | \% | $\begin{gathered} \mathrm{Lt} \\ \text { in cm } \\ \text { (SD) } \end{gathered}$ | $\begin{gathered} \text { W } \\ \text { in } \mathrm{g} \\ \text { (SD) } \end{gathered}$ |
| Roach | 394 | 44.9 | $\begin{array}{r} 17.1 \\ (7.4) \end{array}$ | $\begin{gathered} 111.8 \\ (161.0) \\ \hline \end{gathered}$ | 315 | 42.7 | $\begin{array}{r} 18.8 \\ (8.3) \\ \hline \end{array}$ | $\begin{array}{\|c\|} \hline 151.6 \\ (194.9) \\ \hline \end{array}$ | 716 | 43.9 | $\begin{array}{\|c\|} \hline 17.8 \\ (7.8) \\ \hline \end{array}$ | $\begin{gathered} 129.6 \\ (176.9) \\ \hline \end{gathered}$ |
| White bream | 124 | 14.1 | $\begin{gathered} 22.9 \\ (12.0) \end{gathered}$ | $\begin{gathered} 173.4 \\ (192.4) \end{gathered}$ | 174 | 23.6 | $\begin{aligned} & 23.6 \\ & (5.3) \\ & \hline \end{aligned}$ | $\begin{gathered} \hline 203.2 \\ (134.0) \\ \hline \end{gathered}$ | 299 | 18.3 | $\begin{array}{r} 23.3 \\ (8.7) \\ \hline \end{array}$ | $\begin{gathered} 191.1 \\ (161.1) \\ \hline \end{gathered}$ |
| Pike perch | 131 | 14.9 | $\begin{array}{r} 16.7 \\ (9.2) \\ \hline \end{array}$ | $\begin{array}{r} 91.7 \\ (228.1) \\ \hline \end{array}$ | 114 | 15.4 | $\begin{array}{r} 15.6 \\ (8.9) \\ \hline \end{array}$ | $\begin{gathered} 86.5 \\ (398.8) \\ \hline \end{gathered}$ | 245 | 15.0 | $\begin{array}{r} 16.2 \\ (9.1) \\ \hline \end{array}$ | $\begin{gathered} 89.3 \\ (318.8) \\ \hline \end{gathered}$ |
| Perch | 87 | 10.1 | $\begin{array}{r} 13.3 \\ (5.8) \\ \hline \end{array}$ | $\begin{gathered} 49.1 \\ (102.1) \\ \hline \end{gathered}$ | 25 | 3.4 | $\begin{aligned} & 12.9 \\ & (5.5) \end{aligned}$ | $\begin{gathered} 48.5 \\ (78.8) \end{gathered}$ | 112 | 6.9 | $\begin{array}{\|c} \hline 13.2 \\ (2.1) \\ \hline \end{array}$ | $\begin{gathered} 47.7 \\ (95.9) \\ \hline \end{gathered}$ |
| Ruffe | 65 | 7.4 | $\begin{gathered} 8.9 \\ (1.3) \end{gathered}$ | $\begin{gathered} \hline 7.9 \\ (3.1) \end{gathered}$ | 34 | 4.6 | $\begin{gathered} 9.2 \\ (1.4) \end{gathered}$ | $\begin{gathered} 8.4 \\ (2.7) \end{gathered}$ | 99 | 6.1 | $\begin{gathered} 9.0 \\ (1.3) \end{gathered}$ | $\begin{gathered} 8.1 \\ (3.0) \end{gathered}$ |
| Bleak | 44 | 5.0 | $\begin{array}{r} 13.3 \\ (2.0) \\ \hline \end{array}$ | $\begin{array}{r} 19.7 \\ (9.3) \end{array}$ | 28 | 3.8 | $\begin{array}{r} 13.2 \\ (2.2) \end{array}$ | $\begin{aligned} & 20.0 \\ & (9.9) \end{aligned}$ | 73 | 4.5 | $\begin{gathered} 13.2 \\ (2.1) \end{gathered}$ | $\begin{array}{r} 19.7 \\ (9.4) \end{array}$ |
| Bream | 22 | 2.5 | $\begin{gathered} 34.1 \\ (11.1) \end{gathered}$ | $\begin{gathered} 576.1 \\ (458.0) \\ \hline \end{gathered}$ | 45 | 6.1 | $\begin{gathered} 30.9 \\ (10.4) \end{gathered}$ | $\begin{array}{\|c\|} \hline 445.3 \\ (398.2) \\ \hline \end{array}$ | 72 | 4.4 | $\begin{gathered} 32.8 \\ (10.7) \end{gathered}$ | $\begin{gathered} 521.0 \\ (425.1) \\ \hline \end{gathered}$ |
| Others ${ }^{*}$ | 10 | 1.1 | - | - | 3 | 0.4 | - | - | 13 | 1.0 | - | - |
| Total | 877 | 100 | - | - | 738 | 100 | - | - | 1630 | 100 | - | - |

*/ wells, rapfen, carp, pike and sturgeon
Evident differences were noticed regarding quantity of fish in two compared fishing regions. There were much more fish caught in Bronisławów region during the summer than in Karolinów region. As the main hydro-chemical parameters did not differ significantly between these two areas (Table 4), the most likely explanation of this disparity are differences is food resources availability. As zooplankton density was extremely low during summer


Fig. 3. Distribution and density of pelagic fish in the Sulejów reservoir monitored by horizontal beaming


Fig. 4. Contribution of fish species (by biomass and by number) to the gill net catches in both littoral and pelagic zones of two fishing regions in the Sulejów reservoir.


Fig. 5. Changes of average length of roach from gill net catches in the Bronisławów fishing region in the Sulejów reservoir. L-littoral, P- pelagial

2003 (Wojtal, unpublished data), the factor responsible for observed pattern might be quantity of benthic food. However, to verify this hypothesis more data on availability of benthic prey are necessary. Described above differences in fish distribution disappeared later on during autumn (Figure 6), which might reflect fish migration to the deeper parts of the reservoir in the face of approaching winter.

## 4. CONCLUSIONS

1. Horizontally oriented echosounding was an effective method for determination fish distribution, density and biomass, in shallow eutrophic Sulejow reservoir.
2. Revealed pattern of fish distribution in the reservoir was not likely to reflect longitudinal changes in abiotic conditions but indicated rather food resources availability.
3. Data from gill net catches suggest fairly stable and heterogenous spatial fish distribution in the reservoir during the summer and more uniform one towards the winter.
4. Relatively high share of predatory fish (mainly of pike perch) to the fish community in the reservoir shows the potential for controlling juvenile fish density, and thus preventing filtering zooplankton ecosystem overexploitation.



Fig. 6. Comparison of fish number and biomass in control gill netting in the littoral and pelagic zones of the Sulejów reservoir. L- littoral, P- pelagial

Tab. 4. Hydrochemical characteristics of two selected fishing regions in the Sulejów Reservoir. Values are means of 8 measurements done weakly from August to September.
No significant differences were found between mean values of all parameters ( t -test, $\mathrm{p}>0.05$ ).

| Data | Karolinów |  | Bronisławów |  |
| :---: | :---: | :---: | :---: | :---: |
|  | Mean | SD | Mean | SD |
| $\mathrm{TP}^{\left[\mu \mathrm{g} \mathrm{dm}^{-3}\right]}$ | 166.9 | 59.9 | 210.0 | 46.8 |
| $\mathrm{PO}_{4}\left[\mu \mathrm{~g} \mathrm{dm}^{-3}\right]$ | 86.0 | 8.3 | 81.8 | 9.9 |
| ${\mathrm{TN}\left[\mathrm{mg} \mathrm{dm}^{-3}\right]}^{\mathrm{NO}_{3}\left[\mathrm{mg} \mathrm{dm}^{-3}\right]}$ | 1.6 | 0.5 | 1.6 | 0.6 |
| $\mathrm{NH}_{4}\left[\mathrm{mg} \mathrm{dm}^{-3}\right]$ | 0.7 | 0.4 | 0.8 | 0.4 |
| chlorofil $\left[\mu \mathrm{g} \mathrm{dm}^{-3}\right]$ | 0.07 | 0.05 | 0.07 | 0.04 |
| temperature | 25.0 | 14.9 | 21.6 | 8.1 |

## AKNOWLEDGEMENTS

We would like to thank Mr. L. Doroszczyk, Mr. B. Długoszewski, Mrs. E. Kanigowska and Msc S. Ratajski for their assistance in collecting and analyzing the data. This research was supported under Grant No. 3 PO4G 05023 Polish National Research Committee.

## REFERENCES

[1] A. Flesch, G. Masson, J-C. Moreteau, Temporal distribution of perch (Perca fluviatilis L.) in a lake-reservoir (Moselle, France): analysis of catches with vertical gill nets, Hydrobiologia Vol. 300/301, 335-343, 1995.
[2] P. Frankiewicz, Mechanizmy regulacyjne w obrębie zespołu ryb i ich wpływ, poprzez efekt kaskadowy, na jakość wody w nizinnym zbiorniku zaporowym, Folia limnologica, Uniwersytet Łódzki, 1-127, 1998.
[3] P. Frankiewicz, K. Dabrowski, M. Zalewski, Mechanism of establishing bimodality in a size distribution of age-0 pikeperch, Stizostedion lucioperca (L.) in the Sulejów Reservoir, Annalles Zoologici Fennici, Vol. 33, 321-327, 1996.
[4] F.R. Knudsen, H. Saegrov, Benefits from horizontal beaming during acoustic survey: application to three Norwegian lakes,Fisheries Research, Vol. 56, 205-211, 2002.
[5] J. Kubecka, A. Duncan, Acoustic size vs. real size relationships for common species of riverine fish, Fisheries Research, Vol. 35, 115-125, 1998.
[6] J. Kubecka, M. Wittingerova, Horizontal beaming as a crucial component of acoustic fish stock assessment in freshwater reservoirs, Fisheries Research, Vol. 35, 99-106, 1998.
[7] J. Kubecka, J. Seda, A. Duncan, J. Matena, H.A.M. Ketelaars, P. Visser, Composition and biomass of the fish stocks in various European reservoirs and ecological consequences, International Revue Gesamten Hydrobiology, Vol. 83, 559-568, 1998.
[8] D.N. MacLennan, E.J. Simmonds, Fisheries Acoustics, Chapman \& Hall, London, 1323, 1992.
[9] T. Malinen, H. Peltonen, Optimal sampling and traditional versus model-based data analysis in acoustic fish stock assessment in Lake Vesijarvi, Fisheries Research, Vol. 26, 295-308, 1996.
[10] J. Mastyński, Z. Wajdowicz, Fishery in reservoirs, Agricultural Academy Press, Poznań, 1-220 pp, 1994 (in polish).
[11] J. Shapiro, V. Lamarra, M. Lynch, Biomanipulation: an ecosystem approach to lake restoration [In:] Proceedings of a Symposium on Water Quality Management Through Biological Control. [Eds] P.L. Brezonik, J.L. Fox, University of Florida, 85-96, 1975.
[12] Simrad, EP 500 Echo Processing System. Subsea A/S Horten, Norway 1999.
[13] A. Stepnowski, Systems for the acoustic monitoring of the marine environment, Gdańskie Towarzystwo Naukowe, 1-283, 2001.
[14] A. Świerzowski, The variability of distribiution and density of pelagic fishes in the Rożnowski dam reservoir, Arch. Pol. Fish. Vol. 11, (2), 245-263, 2003.
[15] A. Świerzowski, M. Godlewska, T. Półtorak, The relationship between the spatial distribution of fish,zooplankton and other environmental parameters in the Solina reservoir, Poland - Aquat. Living Resour Vol. 13, 373-377, 2000.
[16] M. Tarczyńska, M. Zalewski, Toksyczność zakwitów sinicowych jako wynik eutrofizacji zbiorników wodnych, Gospodarka Wodna, Vol. 556, 83-87, 1995.
[17] M. Zalewski, Minimizing the risk and amplifying the opportunities for restoration of shallow reservoirs, Hydrobiologia Vol. 395/396, 107-114, 1999.

