Hydrobiologia **408/409:** 123–129, 1999.
N. Walz & B. Nixdorf (eds), Shallow Lakes '98: Trophic Interactions in Shallow Freshwater and Brackish Waterbodies
© 1999 *Kluwer Academic Publishers. Printed in the Netherlands.*

Feeding habits of two introduced fish species (*Lepomis gibbosus*, *Pseudorasbora parva*) in Neusiedler See (Austria), with special reference to chironomid larvae (Diptera: Chironomidae)

Anita Wolfram-Wais[1], Georg Wolfram[1], Brigitte Auer[2], Ernst Mikschi[3] & Arno Hain[4]
[1]*Donabaum & Wolfram OEG, Zentagasse 47/3, A–1050 Wien, Austria. E-mail: donabaum.wolfram@netway.at*
[2]*Universität Köln, Zoologisches Institut, Weyertal 119, D–50723 Köln, Germany*
[3]*Naturhistorisches Museum Wien, Burgring 7, A–1014 Wien, Austria*
[4]*Biologische Station Neusiedler See, A–7142 Illmitz, Austria*

Key words: benthivorous fishes, feeding habits, chironomid larvae, reed belt

Abstract

In Neusiedler See, a turbid shallow lake, *Lepomis gibbosus* (L.) and *Pseudorasbora parva* (Temminck & Schlegel) occur in large numbers within the reed belt. In April, June/July, August and September 1995, fishes were collected for gut analyses. The diet of both species consisted mainly of chironomid larvae. 0+ *L. gibbosus* whose total length exceeded 26 mm and 0+ *P. parva* larger than 32 mm preyed on chironomids almost exclusively. The food of >0+ *L. gibbosus*, in addition to chironomids, was made up of other aquatic insects (e.g. Zygoptera nymphs, Corixidae and Trichoptera larvae), gastropods and *Asellus aquaticus* L. The diet of >0+ *L. gibbosus* showed distinct seasonal variations. Detailed analyses of the chironomid larvae in the stomachs of the two fish species provided valuable information on their feeding grounds. Whereas *L. gibbosus* preyed mainly on sediment-dwelling chironomids, *P. parva* preferred epiphytic species. Diet overlaps between *L. gibbosus* and *P. parva* and other abundant fish species in the reed belt (*Anguilla anguilla* (L.), *Blicca bjoerkna* (L.), *Gymnocephalus cernuus* (L.)) are discussed.

Introduction

Neusiedler See is a turbid, shallow lake (mean depth 1 m, total area 321 km^2) with a large reed belt which is up to 5 km broad and covers more than half of the lake area. The typical fish association of the reed belt consists of *Anguilla anguilla*, *Esox lucius* L., *Blicca bjoerkna*, *Carassius auratus gibelio* (BLOCH), *Carassius carassius* (L.), *Pseudorasbora parva*, *Rutilus rutilus* (L.), *Scardinius erythrophthalmus* (L.), *Tinca tinca* (L.), *Lepomis gibbosus*, *Gymnocephalus cernuus* and *Perca fluviatilis* L.

In 1995, a fish-biological study was carried out to investigate the feeding ecology of fishes abundant within the reed belt. Different species or genera of chironomids consumed by the fishes were used to infer the location of feeding microhabitats. Earlier investigations of the feeding habits of four benthivorous fish species (*Abramis brama* (L.), *Blicca bjoerkna*, *Gymnocephalus cernuus* and *Anguilla anguilla*) in Neusiedler See already showed that the chironomid taxa in the intestines reflected foraging areas well (Wais, 1993; Herzig et al., 1994). Although chironomid larvae often play an important role as food items for benthivorous fishes, only little attention has been paid to the species composition of chironomids in fish diets (e.g. Kangur, 1989; Wais, 1993; A. Kangur & Kangur, 1994, 1995; Rieradevall et al., 1995; K. Kangur & Kangur, 1996a,b; Gysels et al., 1997). These studies underlined the significance of identifying chironomid larvae in gut contents for drawing conclusions on foraging areas, size selectivity and niche overlap between species. This paper provides results on two introduced species, *L. gibbosus* and *P. parva,* that have established reproducing populations within the reed belt. *L. gibbosus* was introduced by aquarists and has been known to exist in the lake since the early 1970s (Kritscher, 1973). The first occurrence of *P. parva* was recorded in 1994. It was probably introduced in the course of stocking with Asiatic fishes. As both species have become very abundant within the reed belt, an impact on indigenous fishes is likely and will be discussed here. Although *L. gibbosus* and *P. parva* are widely distributed in Europe, only little literature is available on their feeding habits in European water bodies and their impact on the indigenous fish fauna (Brabrand & Saltveit, 1989; Arnold, 1990; Guti et al., 1991; Zapata & Granado-Lorencio, 1993; Godinho et al., 1997; Rosecchi et al., 1997).

Material and methods

Fish were caught in the reed belt by electro-fishing at 24 different sampling sites during daytime (9:00–16:00) on 4 dates in 1995 (27–29 Apr, 29 Jun – 1 Jul, 2–4 Aug, 21–23 Sep). All sampling sites are located in the southeastern part of the lake. Sampling took place within or along the edge of reed stands. Submerged macrophytes were highly abundant in 67% of the sampling sites, the other sampling stations having less dense weed beds. Only one sampling site showed a complete absence of weeds. In addition to *Utricularia* sp., which was most abundant among submerged macrophytes, *Potamogeton pectinatus* L., *Chara* spp. and *Najas marina* L. were found.

The digestive systems of the fish were preserved in 4% formalin. Prior to gut analyses, the degree of fullness of the whole digestive system was estimated. Afterwards, the samples were analyzed microscopically to identify, count and measure food organisms. Chironomids, which dominated the samples, were determined on the species or genus level. The identifications are based on the species composition in Neusiedler See as described by Wolfram (1996). The width of head capsules was used to identify different instars of chironomid larvae, but also to estimate the total body length of chironomids, Trichoptera larvae and *Asellus aquaticus*. Biomass of food items was calculated by means of length-weight-regressions according to the following authors: Dumont et al. (1975), Bottrell et al. (1976), Mackey (1977), Meyer (1977), Adcock (1979), Smock (1980), Waringer & Humpesch (1984), Sephton & Paterson (1986) and Vuille (1991). For Ephemeroptera nymphs and Corixidae, a length-weight regression was calculated (Table 1). Mean biomass was estimated for some rare taxa, viz. Nematoda (1 μg), Hydracarina (40 μg), Ostracoda (4 μg), Cyclopoida (2.8 μg for small and 4.8 μg for large individuals), adult Nematocera (150 μg), *Chaoborus* larvae and pupae (300 μg), Diptera larvae except for chironomids and ceratopogonids (4100 μg), Coleoptera larvae (1000 μg) and adults (650 μg).

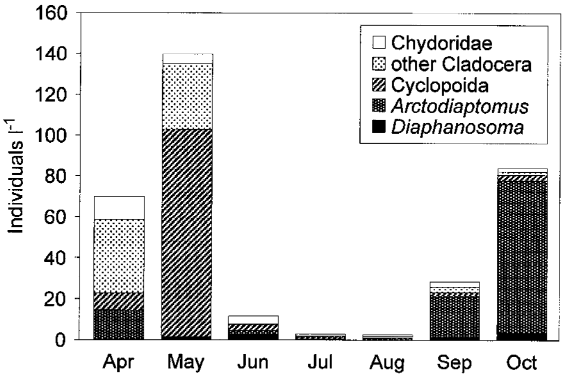

Figure 1. Densities and species composition of the zooplankton within the reed belt at one sampling site.

In the analysis of the data, 6 groups of food items were distinguished: microcrustaceans, chironomid larvae, chironomid pupae, *Asellus aquaticus*, gastropods and other invertebrates (mainly insects). Chironomids were separated further into sediment-dwelling species (e.g. *Chironomus* spp., *Procladius choreus* (Meigen), *Tanypus kraatzi* (Kieffer)), epiphytic species (e.g. *Cricotopus flavocinctus* (Kieffer), *Dicrotendipes nervosus* (Staeger), *Glyptotendipes* spp., *Paratanytarsus* cf. *intricatus* (Goetghebuer)) and species without clear habitat preferences (*Tanytarsus* spp.). The last group also includes individuals which could not be identified at the genus level.

At least 3 year classes of *L. gibbosus* could be distinguished. In the analysis, the data were divided into two pools. The small-sized group was formed by young of the year, which were present in the August and September samples. The large-sized group comprised the older fish, mainly 1+ representatives.

Zooplankton was collected on 8 dates at the same sites where fish were sampled. A volume of 20 l per sample was concentrated by filtering through a 150 μm mesh sieve. Individuals were counted; rotifers and copepod nauplii were not considered.

Information on the benthic community of Neusiedler See is given in Wolfram (1996), who primarily studied the open water zone of the lake. In 1995, several qualitative samples were taken within the reed belt in order to verify the distinction of the ecological groups of chironomid larvae as mentioned above.

Table 1. Length-weight regression of *Caenis* sp. (Ephemeroptera) and Corixidae (*Micronecta scholtzi, Cymatia coleoptrata, Hesperocorixa linnaei, Sigara lateralis, S. striata*) from Neusiedler See. $\ln W = \ln a + b * \ln L$, W ... dry weight in [μg], L ... length [mm], either total length (TL) or width of head capsule (HW), CL ... 95%-confidence limits

Taxon	ln *a*	*b*	r^2	*p*	*N*	Length	Range of length [mm]
Caenis sp.	−0.9810	4.5520±0.3200 CL	0.99	<0.01	10	HW	0.5–1.2
Corixidae	−1.5500	3.5750±0.4160 CL	0.94	<0.01	23	HW	0.71–3.31
Corixidae	−4.1190	2.7350±0.1900 CL	0.98	<0.01	23	TL	1.75–8.25

Results

Zooplankton

Figure 1 shows the densities and species composition of zooplankton for one sampling station in the reed belt. All other sampling stations showed similar patterns of seasonal variation. The zooplankton in the reed belt reached highest densities of up to 140 ind. l^{-1} in spring. At this time the species composition was dominated by cyclopoid copepods, *Ceriodaphnia reticulata* (Jurine), *Scapholeberis mucronata* (O. F. Müller) and chydorids. During summer, the abundances were very low, perhaps due to predation by 0+ fish. *Arctodiaptomus spinosus* (Daday) accounted for higher zooplankton densities in September and October. This species is typical of the open water zone of Neusiedler See. Within the reed belt, its abundance decreased with increasing distance from the open water zone. The represented sampling station is situated relatively close to the open water zone (550 m away).

Lepomis gibbosus, *pumpkinseed*

In April, June/July and August the digestive systems of 65% of both 0+ and >0+ pumpkinseeds were filled to more than half, while in September this was true for only 40% of the small-sized and large-sized group. Among all fishes investigated ($N_{0+} = 37$, $N_{>0+} = 151$) the stomachs and intestines of only two individuals were completely empty.

The diet of *L. gibbosus* was dominated by chironomid larvae, especially by species dwelling on the sediment like *Chironomus* spp., *Tanypus* spp. and *Procladius choreus* (Figures 2 & 3). While the food of the 0+ pumpkinseed was mainly restricted to chironomid larvae, other invertebrates were essential to the diet of >0+ fish. Important additional food resources were other insects (especially Zygoptera nymphs, Corixidae and Trichoptera larvae), chironomid pupae, gastropods (*Bithynia* sp. and *Planorbis* sp.), *Asellus aquaticus* and zooplankton (especially *Daphnia* sp., *Ceriodaphnia* sp., *Simocephalus* sp. and copepods) (Figure 2). All of these additional food items only rarely occurred in the diet of 0+ pumpkinseed. Gastropods, for example, were missing in this age class entirely.

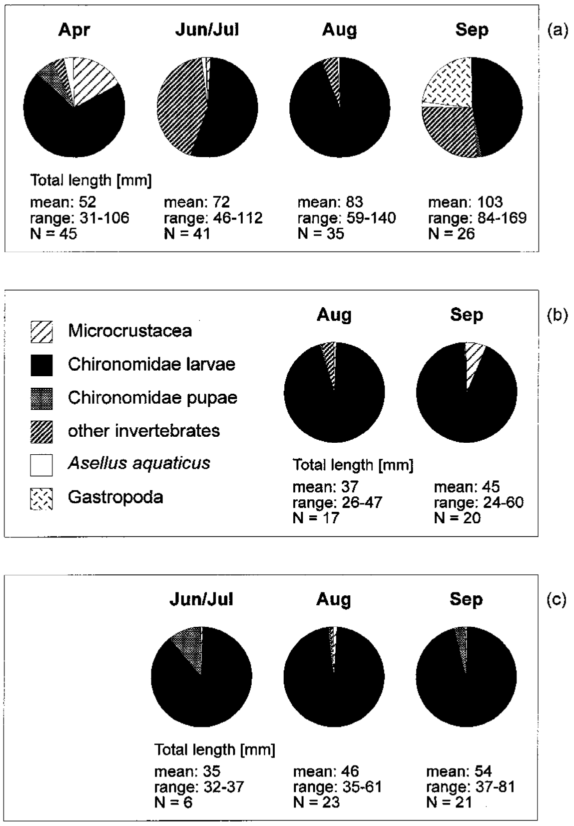

Figure 2. Food composition [% biomass] of >0+ *Lepomis gibbosus* (a), 0+ *L. gibbosus* (b) and 0+ *Pseudorasbora parva* (c) in April, June/July, August and September 1995.

The diet of the >0+ fish showed clear seasonal variations (Figures 2 & 3). Thus zooplankton contributed significantly to the mean biomass content of the diet only in April, while gastropods played an import-

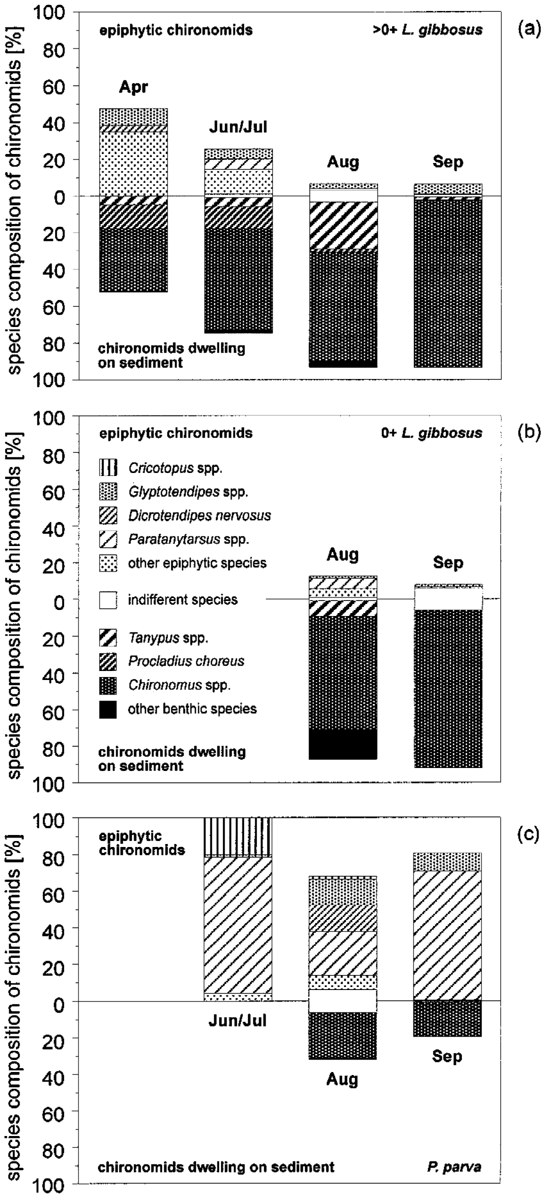

Figure 3. Species composition of chironomid larvae [% biomass] in the food of >0+ *Lepomis gibbosus* (a), 0+ *L. gibbosus* (b) and 0+ *Pseudorasbora parva* (c) in April, June/July, August and September 1995. Epiphytic chironomids are depicted above the x-axis, while the benthic species are given below the x-axis.

ant role only in September. Among the chironomid larvae the amount of epiphytic species decreased over the course of the year.

Pseudorasbora parva

All *P. parva* investigated were young of the year (N=52). 83% of them had their guts filled to more than 50%. *P. parva* fed almost exclusively on chironomids and showed practically no seasonal variation in food composition. Microcrustaceans, chironomid pupae and other insects (especially Trichoptera larvae) were found occasionally, but played a lesser role in the total biomass content of the diet (Figure 2).

The species composition of chironomids in the food of *P. parva* was dominated by epiphytic or mining species (Figure 3). *Paratanytarsus* spp., *Cricotopus* spp., *Glyptotendipes* spp. and *Dicrotendipes nervosus* showed the highest abundance. Among chironomids dwelling on the sediment, *Chironomus* spp. was found most frequently.

Discussion

The importance of chironomid larvae in the food of pumpkinseed is well documented in the literature (Keast, 1978a; Deacon & Keast, 1987; Fox & Keast, 1990; Guti et al., 1991; Zapata & Granado-Lorencio, 1993; Godinho et al., 1997). With increasing fish size, however, chironomids are replaced by gastropods if available (Keast, 1978a,b; Deacon & Keast, 1987; Fox & Keast, 1990). The pharyngeal teeth of pumpkinseed form efficient crushing plates, which preadapt them to feed on gastropods and other heavier-bodied prey (Keast, 1978a; Mittelbach et al., 1992; Osenberg et al., 1992). In Neusiedler See, gastropods did not play a major role in the pumpkinseed diet, except in the case of age-group >0+ in September (Figure 2). The *L. gibbosus* population in Neusiedler See is dominated by the first two year classes: fish might therefore be too small to prey extensively on gastropods. Another reason for the minor uptake of gastropods could be a limited availability of these prey items. Zooplankton, Isopoda, Ephemeroptera nymphs, Trichoptera larvae and other aquatic insects are described as regular food items of pumpkinseed (Keast, 1978a; Deacon & Keast, 1987; Arnold, 1990; Guti et al., 1991). In Neusiedler See, *Asellus aquaticus*, Zygoptera nymphs, Corixidae and Trichoptera larvae were frequently found in the diet of >0+ individuals. Zooplankton was abundant in the food of >0+ fish in April, when densities in the water were high (Figures 1 & 2). The autumn peak of zooplankton was utilized only by 0+ pumpkinseed, whereas >0+ representatives clearly preferred larger prey items. No data are available for very young fish, which heavily depend on zooplankton (Keast, 1978b; Lemly & Dimmick, 1982; Hart & Werner, 1987). In August and September, when the total lengths of 0+

fish in Neusiedler See had already exceeded 26 mm, they mainly preyed on chironomid larvae. Pumpkinseed is known as a flexible forager capable of taking advantage of seasonal and diurnal changes in food availability (Keast & Welsh, 1968; Werner & Hall, 1976; Keast, 1978a; Fox & Keast, 1990; Macchiusi & Baker, 1991; Collins & Hinch, 1993). Our results reflect the feeding habits only during daytime. In Neusiedler See the food of *L. gibbosus* showed obvious seasonal changes. The amount of zooplankton, chironomid larvae, other insects and gastropods in the diet differed from month to month. Within the chironomid larvae the portion of epiphytic species in the food was higher in April and June/July than in August and September. Seasonal changes in food availability, changes in food preference with increasing size of fish, and niche segregation due to competition for food with other fish species are possible reasons for this pattern.

Only little information is available on the diet of *P. parva*. Feeding on zooplankton and fish eggs as well as facultative parasitism on other fish species is reported in the literature (Trombitskiy & Kakhovskiy, 1987; Arnold, 1990; Jin et al., 1996; Rosecchi et al., 1997). In Neusiedler See, 0+ *P. parva* with a total length exceeding 32 mm fed extensively on chironomid larvae, especially epiphytic species (Figures 2 & 3). As for most very young fish, zooplankton might be important to the freshly hatched larvae. In 1995, the population of *P. parva* consisted mainly of young of the year. *P. parva* does not usually grow older than 1+ in Neusiedler See.

In Neusiedler See, chironomid larvae were the dominant food organisms in the diet of both *L. gibbosus* and *P. parva* (Figure 2). Furthermore, the detailed analyses of the chironomids in the food allowed the feeding grounds of the two species to be located on a finer scale. Whereas pumpkinseed preyed mainly on sediment-dwelling chironomids, *P. parva* preferred epiphytic species (Figure 3). Especially when considering dietary overlaps between benthivorous fishes, such information is crucial to prevent misinterpretations.

As *L. gibbosus* and *P. parva* are very abundant in the reed belt of Neusiedler See, interactions with other fish species are likely. Like pumpkinseed, white bream (*Blicca bjoerkna*) mainly inhabits the outer reed zone. Its diet is very diverse and consists of epipelic algae, benthic and planktonic microcrustaceans, aquatic insects (mainly Corixidae, Trichoptera and chironomid larvae) and terrestrial insects. Both epiphytic and sediment-dwelling chironomid species are present in the food (Wais, 1993; Herzig et al., 1994). There is a dietary overlap between white bream and pumpkinseed with respect to Corixidae, Trichoptera larvae and Chironomidae inhabiting the sediment. An even higher overlap can be assumed between pumpkinseed and ruffe (*Gymnocephalus cernuus*). Both species prefer sediment-dwelling chironomid larvae, although the diet of ruffe is dominated by such larvae to a much higher degree than that of pumpkinseed (Wais, 1993; Herzig et al., 1994).

Eel (*Anguilla anguilla*), which has been stocked in Neusiedler See since the 1950s, is another benthivorous species that shares at least segments of its food resource with pumpkinseed, specifically *Asellus aquaticus*, chironomid larvae and gastropods. Insects other than chironomids are also eaten by both species; however, eel clearly prefers larger prey items (Coleoptera larvae and imagines, Odonata nymphs and Stratiomyidae larvae).

Dietary overlap between pumpkinseed and crucian carp, *Carassius carassius*, was reported by Guti et al. (1991) from a Hungarian bog. Both species fed on chironomids, ceratopogonid larvae and gastropods. In Neusiedler See, no information on the feeding habits of crucian carp is available because its abundances are very low today (Mikschi et al., 1996).

Dietary overlaps are probably less frequent between *P. parva* and the species mentioned above. No other fish species investigated thus far feeds so extensively on epiphytic chironomids as *P. parva*. In addition, there are differences in the spatial distribution of benthivorous fish species within the reed belt. While white bream and ruffe are highly abundant in the outer zones, *P. parva* prefers the inner and intermediate zone of this belt. Eel inhabits the whole reed belt. Gut analyses of other fish species abundant within the reeds (e.g. roach, rudd and perch) will provide further information on dietary overlaps.

Conclusion

The results of this study comfirm the findings of other authors that detailed gut analyses provide valuable information on the feeding grounds of fish. In Neusiedler See it was the species composition of chironomids eaten by *Lepomis gibbosus* and *Pseudorasbora parva* that allowed to clearly differentiate between the feeding microhabitats of these two fish species. Additionally, the results suggest a dietary overlap between pumpkinseed and indigenous fish species such as *Gymnocephalus cernuus* and *Blicca bjoerkna*. The degree of overlap in the diet between these two species and *P. parva* appears to be much lower.

Acknowledgements

This study was financed by the National Park Neusiedler See/Seewinkel. We wish to thank Alois Herzig for providing working facilities at the Biologische Station Neusiedler See.

References

Adcock, L. A., 1979. Energetics of a population of isopod *Asellus aquaticus*: life history and production. Freshwat. Biol. 9: 343–355.

Arnold, A., 1990. Eingebürgerte Fischarten. Die Neue Brehm-Bücherei 602: 144 pp.

Bottrell, H. H., A. Duncan, Z. M. Gliwicz, E. Grygierek, A. Herzig, A. Hillbricht-Ilkowska, H. Kurasawa, P. Larsson & T. Weglenska, 1976. A review of some problems in zooplankton production studies. Norw. J. Zool. 24: 419–456.

Brabrand, A. & S. J. Saltveit, 1989. Ecological aspects of the fish fauna in three Portuguese reservoirs. Arch. Hydrobiol. 114: 575-589.

Collins, N. C. & S. G. Hinch, 1993. Diel and seasonal variation in foraging activities of pumpkinseed in an Ontario pond. Trans. am. Fish. Soc. 122: 357–365.

Deacon, L. I. & J. A. Keast, 1987. Patterns of reproduction in two populations of pumpkinseed sunfish, *Lepomis gibbosus*, with differing food resources. Envir. Biol. Fishes 19: 281–296.

Dumont, H. J., I. Van de Velde & S. Dumont, 1975. The dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from the plankton, periphyton and benthos of continental waters. Oecologia 19: 75–97.

Fox, M. G. & A. Keast, 1990. Effects of winterkill on population structure, body size and prey consumption patterns of pumpkinseed in isolated beaver ponds. Can. J. Zool. 68: 2489–2498.

Godinho, F. N., M. T. Ferreira & R. V. Cortes, 1997. The environmental basis of diet variation in pumpkinseed sunfish, *Lepomis gibbosus*, and largemouth bass, *Micropterus salmoides*, along an Iberian river basin. Envir. Biol. Fishes 50: 105–115.

Guti, G., S. Andrikowics & P. Biró, 1991. Nahrung von Hecht (*Esox lucius*), Hundsfisch (*Umbra krameri*), Karausche (*Carassius carassius*), Zwergwels (*Ictalurus nebulosus*) und Sonnenbarsch (*Lepomis gibbosus*) im Ócsa-Feuchtgebiet, Ungarn. Fischökologie 4: 45–66.

Gysels, E, L. Janssens de Bisthoven, L. De Vos & F. Ollevier, 1997. Food and habitat of four *Xenotilapia* species (Teleostei, Cichlidae) in a sandy bay of northern Lake Tanganyika (Burundi). J. Fish Biol. 50: 254-266.

Hart, T. F. Jr. & R. G. Werner, 1987. Effects of prey density on growth and survival of white sucker, *Catostomus commersoni* and pumpkinseed, *Lepomis gibbosus*, larvae. Envir. Biol. Fishes 18: 41–50.

Herzig, A., E. Mikschi, B. Auer, A. Wais & G. Wolfram, 1994. Fischbiologische Untersuchung des Neusiedler Sees. BFB-Bericht 81: 125 pp.

Jin, K., W. Shi, X. Yu, H. Hu & W. Li, 1996. The preliminary observation on eight small freshwater fishes eating adhesive fish eggs. J. dalian Fish. Coll. 11: 24–30.

Kangur, A., 1989. The significance of *Chironomus plumosus* L. on the feeding of eel in Lake Võrtsjärv (Estonian SSR, USSR). Acta Biologica Debrecina Suppl. Oecologia Hungarica 3: 177-187.

Kangur, A. & K. Kangur, 1994. The diet of bream (*Abramis brama* (L.)) and eel (*Anguilla anguilla* (L.)) in relation to the abundance of benthic organisms in lake Võrtsjärv (Estonia). Fishes and their environment, Oviedo: 35–36.

Kangur, A. & K. Kangur, 1995. The composition and seasonal changes in the diet of bream (*Abramis brama*) in relation to the abundance and biomass of its food items in Lake Võrtsjärv (Estonia). Proc. estonian Acad. Sci. Biol. 44: 11–22.

Kangur, K. & A. Kangur, 1996a. The composition and seasonal changes in the diet of ruffe (*Gymnocephalus cernuus*) in Lake Võrtsjärv, Estonia. Proc. estonian Acad. Sci. Biol. 45: 1–14.

Kangur, K. & A. Kangur, 1996b. Feeding of ruffe (*Gymnocephalus cernuus*) in relation to the abundance of benthic organisms in Lake Võrtsjärv (Estonia). Ann. Zool. Fenn. 33: 473–480.

Keast, A., 1978a. Feeding interrelations between age-groups of pumpkinseed (*Lepomis gibbosus*) and comparisons with bluegill (*L. macrochirus*). J. Fish Res. Bd Can. 35: 12–27.

Keast, A., 1978b. Trophic and spatial interrelationships in the fish species of an Ontario temperate lake. Envir. Biol. Fishes 3: 7–31.

Keast, A. & L. Welsh, 1968. Daily feeding periodicities, food uptake rates, and dietary changes with hour of day in some lake fishes. J. Fish Res. Bd Can. 25: 1133–1144.

Kritscher, E., 1973. Die Fische des Neusiedler Sees und ihre Parasiten. Ann. Nat. Mus. Wien 77: 289–297.

Lemly, A. D. & J. F. Dimmick, 1982. Growth of young-of-the-year centrarchids in relation to zooplankton in the littoral zone of lakes. Copeia 1982: 305–321.

Macchiusi, F. & R. L. Baker, 1991. Prey behaviour and size-selective predation by fish. Freshwat. Biol. 25: 533–538.

Mackey, A. P., 1977. Growth and development of larval Chironomidae. Oikos 28: 270–275.

Meyer, E., 1989. The relationship between body length parameters and dry mass in running water invertebrates. Arch. Hydrobiol. 117: 191-203.

Mikschi, E., G. Wolfram & A. Wais, 1996. Long-term changes in fish community of Neusiedler See (Burgenland, Austria). In A. Kirchhofer & D. Hefti (eds), Conservation of Endangered Freshwater Fish in Europe. Birkhäuser Verlag, Basel: 111–120.

Mittelbach, G. G., C. W. Osenberg & P. C. Wainwright, 1992. Variation in resource abundance affects diet and feeding morphology in the pumpkinseed sunfish (*Lepomis gibbosus*). Oecologia 90: 8–13.

Osenberg, C. W., G. G. Mittelbach & P. C. Wainwright, 1992. Two-stage life histories in fish: the interaction between juvenile competition and adult performance. Ecology 73: 255–267.

Rieradevall, M., E. García-Berthou & N. Prat, 1995. Chironomids in the diet of fish in Lake Banyoles (Catalonia, Spain). In P. Cranston (ed), Chironomids: From Genes to Ecosystems, CSIRO Australia: 335-340.

Rosecchi, E., G. Poizat & A. J. Crivelli, 1997. Introductions de poissons d'eau douce et d'écrevisses en Camargue: Historique, origines et modifications des peuplements. Bull. fr. Pêche Piscic. 344/345: 221–232.

Sephton, T. W. & C. G. Paterson, 1986. Production of the chironomid *Procladius bellus* in an annual drawdown reservoir. Freshwat. Biol. 16: 721–733.

Smock, L. A., 1980. Relationship between body size and biomass of aquatic insects. Freshwat. Biol. 10: 375–383.

Trombitskiy, I. D. & A. E. Kakhovskiy, 1987. On the facultative parasitism of the chebachok, *Pseudorasbora parva*, in fish ponds. J. Ichthyol. 27: 180–182.

Vuille, T., 1991. Abundance, standing crop and production of microcrustacean populations (Cladocera, Copepoda) in the littoral zone of Lake Biel, Switzerland. Arch. Hydrobiol. 123: 165–185.

Wais, A., 1993. Ernährungsbiologie des Brachsen, *Abramis brama* (L.), im Neusiedler See. Master thesis, University of Vienna: 69 pp.

Waringer, J. A. & U. H. Humpesch, 1984. Embryonic development, larval growth and life cycle of *Coenagrion puella* (Odonata: Zygoptera) from an Austrian pond. Freshwat. Biol. 14: 385–399.

Werner, E. E. & D. J. Hall, 1976. Niche shifts in sunfishes: experimental evidence and significance. Science 191: 404–406.

Wolfram, G., 1996. Distribution and production of chironomids (Diptera: Chironomidae) in a shallow, alkaline lake (Neusiedler See, Austria). Hydrobiologia 318: 103–115.

Zapata, S. C. & C. Granado-Lorencio, 1993. Age, growth and feeding of the exotic species *Lepomis gibbosus* in a Spanish cooling reservoir. Arch. Hydrobiol. Suppl. 90: 561–573.