

In situ* diel patterns of zooplankton consumption by subadult/adult roach *Rutilus rutilus*, bream *Abramis brama*, and bleak *Alburnus alburnus

Mojmír VAŠEK^{1,2} and Jan KUBEČKA¹

¹ Hydrobiological Institute, Academy of Sciences of the Czech Republic, Na sádkách 7, 370 05 České Budějovice, Czech Republic; e-mail: mojmir.vasek@seznam.cz

² Faculty of Biological Sciences, University of South Bohemia, Branišovská 31, 370 05 České Budějovice, Czech Republic

Received 26 May 2003; Accepted 4 June 2004

Abstract. Diel feeding patterns of subadult and adult cyprinids of three species (roach *Rutilus rutilus*, bream *Abramis brama*, bleak *Alburnus alburnus*), which foraged almost exclusively on microcrustacean plankton, were studied in the meso-eutrophic Římov Reservoir (Czech Republic). All cyprinids showed a daytime feeding periodicity, with a marked night-time decline in gut fullness. Diel variations in gut fullness were observed in roach 200–270 mm standard length (SL) and bream 220–330 mm SL during May and in bleak, roach and bream of 110–170 mm SL, respectively, during August. Our results corroborate other studies in which light intensity has been found to be an important factor affecting cyprinid foraging on zooplankton. Daily zooplankton consumption rates ranged from 1.5 % of wet body weight in bream (220–330 mm SL) to 9.9 % of wet body weight in bleak (110–170 mm SL).

Key words: cyprinids, feeding periodicity, gut fullness, daily food ration, zooplanktivorous fish

Introduction

Roach *Rutilus rutilus* (L.), bream *Abramis brama* (L.) and bleak *Alburnus alburnus* (L.) are amongst the most common European cyprinids, inhabiting both still and slow flowing fresh waters, particularly eutrophic ones. Juveniles of these three species are zooplanktivorous, as are most juvenile European cyprinids (Lammens & Hoogenboezem 1991). With increasing body size, roach and bream foraging gradually expands to encompass not only zooplankton (Lammens et al. 1985, Michelsen et al. 1994, García-Berthou 1999, Nauwerck 1999, Persson & Hansson 1999, Vašek et al. 2003) but also benthic macroinvertebrates (e.g. Martyniak et al. 1987, 1991, Lammens et al. 1987, Jamet 1994, Specziár et al. 1997, Persson & Hansson 1999), detritus (e.g. Niederholzer & Hofer 1980, Persson 1983, Michelsen et al. 1994), and in the case of roach filamentous algae and macrophytes (e.g. Hruška 1956, Prejs & Jackowska 1978, Niederholzer & Hofer 1980, Brabrand 1985). Bleak, however, is a more specialised open water feeder, foraging primarily on zooplankton throughout its entire life (Politou et al. 1993, Herzig 1994, Vinni et al. 2000).

Diel periodicity in fish activity is often closely connected with foraging (Helfman 1993). However, detailed *in situ* evaluations of diel feeding patterns of fish populations

are highly laborious due to the large samples of fish that have to be scrutinised frequently over 24 hours. Several authors studied diel variations in food consumption of adult roach foraging mostly on non-animal prey and reported diurnal or crepuscular feeding activity (Hruška 1956, Prejs 1978, Persson 1983, Jamet et al. 1990). Similarly, other authors (Kogan 1963, 1970, Nebolsina 1968, Zadorozhnaya 1977) observed mostly diurnal and/or crepuscular feeding pattern in large benthivorous bream. Nevertheless, detailed *in situ* descriptions of diel feeding on zooplankton by larger specimens and adults of these two cyprinids are still lacking and little has been reported about diel feeding periodicity even for planktivorous bleak (Politou et al. 1993). Thus, the objective of the present study was to *in situ* examine diel patterns of zooplankton consumption by subadult/adult roach, bream and bleak.

Study Site, Materials and Methods

The study was undertaken in the Římov Reservoir (area 210 ha, maximum depth 44 m, mean depth 16 m), a meso-eutrophic, dimictic water supply reservoir situated on the Malše River in Southern Bohemia (48°50'N, 14°30'E; 470 m a.s.l.), Czech Republic. The reservoir has a canyon-shaped character, it is approximately 12 km long with steep sides. Roach, bleak and bream are the three most abundant fish species in the reservoir (Vašek et al. 2003).

Cyprinids were collected in the open water area of three sites located along the longitudinal axis of the reservoir: near the dam, at the middle part and at the upper end close to the natural inflow of the major tributary (see Vašek et al. 2003 for a map). Hereafter these three sites are referred to as the dam, middle and tributary sites, their maximum depths were 40, 24 and 4 m, respectively. Fishing took place on 23–27 May and 14–19 August 1999 using gill nets. A set of eleven monofilament gill nets with different mesh sizes (8, 10, 12.5, 16, 19.5, 24, 29, 35, 43, 55 and 70 mm knot to knot; each net was 25 m long and 3 or 4.5 m high) was installed as surface nets throughout a 24-hour period, once at each site and month (samplings were always performed during calm weather conditions). Fish were removed from the nets at fixed 2 h intervals and killed immediately with an overdose of MS-222 (tricaine methane sulphonate). Their standard length (SL) and wet weight were measured to the nearest 5 mm and 1 g, respectively. Scales were taken for age determination, and then the fish were preserved in 10% formaldehyde. Individuals larger than 200 mm were dissected immediately and only their guts were preserved in 5% formaldehyde for later analyses.

Water temperature in the open water area was recorded at 0.5 m intervals from surface to 4 m depth twice a day (morning, evening) on each sampling date to obtain mean values for each reservoir site. Epilimnetic zooplankton was sampled simultaneously with fish, its assemblage structure and total abundance having been reported elsewhere (Vašek et al. 2003).

Despite extensive effort, not all fish species were captured in sufficient numbers in every 24-h sampling period. Therefore, data on diel feeding patterns were examined for cyprinids of five species/size classes: 110–170 mm SL bleak, roach and bream; >200 mm SL roach and bream. On the basis of reproductive status assessments of fish in the Římov Reservoir across seasons (unpubl. data), roach and bream >200 mm SL were assumed to represent adult individuals, whereas cyprinids of 110–170 mm SL represented adult specimens of bleak, subadult and adult specimens of roach and subadult specimens of bream. The present study deals only with microcrustacean prey – the dominant food component of the three cyprinids in the Římov Reservoir (Vašek et al. 2003).

Analysis of gut contents

In the laboratory, the content of the first two thirds of each intestine was examined under a binocular microscope using the numerical method (Hyslop 1980) for 187 roach (200–270 mm SL) and 117 bream (220–330 mm SL) collected in May and 298 bleak, 263 roach and 141 bream of 110–170 mm SL collected in August. Usually three subsamples from the contents of each gut were analyzed, and prey items were identified to the relevant taxonomic groups, counted (heads and entire prey specimens were enumerated; tailspines only were counted in cases of *Leptodora kindtii* (Focke) as prey) and measured. Whenever possible, the body lengths of 10–30 specimens of each prey type were measured in each gut. Zooplankton was measured from the top of the head to the base of either the tailspine (cladocerans) or the caudal setae (copepods). Body length of the large cladoceran *L. kindtii* was impossible to measure due to crushing by pharyngeal teeth, so we measured tailspine length and estimated body length from the relationship between tailspine length and body length (Branstrator & Holl 2000). Median body lengths of ingested prey types were converted to wet weights using the length – volume regressions of zooplankton listed in Hoehn et al. (1998), the volumes were converted to wet weights by assuming a specific gravity of 1.0.

Gut content weight of each fish was expressed as gut fullness, F_i (g wet weight per 100 g wet body weight):

$$F_i = 100G_i(W_i)^{-1}$$

where G_i is the reconstructed wet weight (g) of the gut content of fish i , and W_i is the net wet body weight (g) of fish i (total fish weight minus reconstructed gut content weight; g). In order to normalize percentage distributions, mean gut fullness for each 2-h interval was estimated from arcsine-transformed data ($\arcsin \sqrt{0.01F_i}$) and was used in further calculations in its backtransformed form.

Consumption estimates

In those sampling occasions during which fish were caught frequently over the 24-h period, we attempted to estimate the daily food consumption of individual fish by the method of Elliott & Persson (1978). The amount of food consumed was estimated for each 2-h interval using the equation:

$$C_t = (F_t - F_0 e^{-Rt}) Rt (1 - e^{-Rt})^{-1}$$

where C_t is the mean amount of food (g wet weight per 100 g wet weight of fish) consumed during a sample interval t (2 h), F_0 and F_t are, respectively, the mean gut fullness at the beginning and end of a sample interval t , and R (h^{-1}) is the instantaneous gastric evacuation rate. Gastric evacuation rate was estimated from the decrease in gut fullness observed for all cyprinids after the onset of darkness and during the night-time. It was assumed that the fish did not feed over this period and the decline in gut fullness therefore reflected only food evacuation. Since several studies have shown that the gut emptying of the three cyprinid species can be appropriately described by the exponential model (Persson 1982, Krasnoper 1989, Białokoz 1990, Specziár 2002), we determine the instantaneous gastric evacuation rate (R) as the slope of the relation between ln-transformed gut fullness and time.

Relative daily food intake, DI (g wet weight per 100 g wet weight of fish) was calculated as the sum of C_t over the 24-h period:

$$DI = \sum_{t=1}^{n=12} C_t$$

For DI estimates of bleak, roach and bream of 110–170 mm SL sampled at the tributary site in August, missing daytime values of gut fullness at few 2-h intervals were approximated by linear interpolation between the two nearby values of the gut fullness. For the same fish, missing night-time values of gut fullness for several 2-h intervals were estimated with the exponential model – i.e. assuming that no consumption has occurred during darkness, the missing values were approximated by linear interpolation of ln-transformed gut fullness night-time data and used in further computations in backtransformed form.

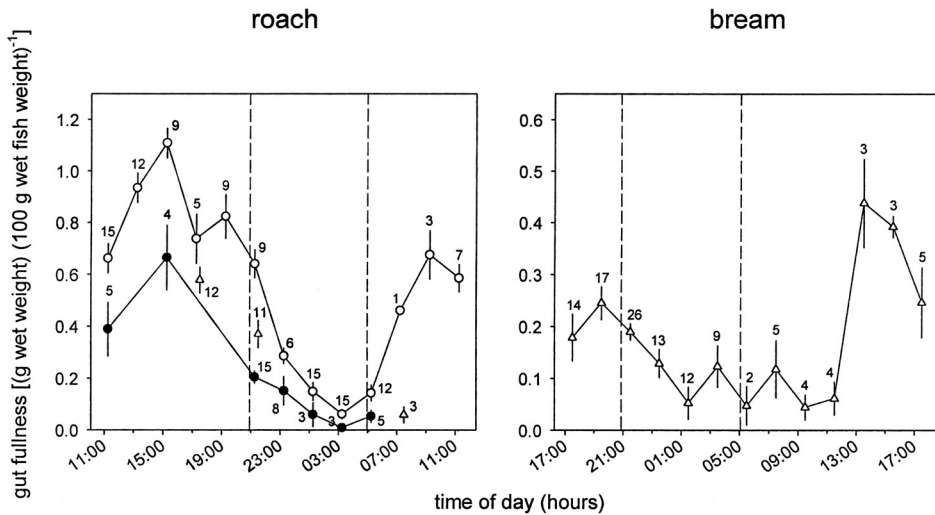


Fig. 1. Diel variation in the mean gut fullness of roach 200–270 mm SL and bream 220–330 mm SL in May 1999. Vertical bars represent ± 1 SE, numbers of analyzed fish are shown close to symbols or error bars. Fish sampled in the dam site (26–27 May, mean water temperature = 17.3°C) are indicated by open circles, in the middle site (23–24 May, °C = 16.8) by solid dots, and in the tributary site (24–25 May, °C = 14.4) by empty triangles. Times of sunset and sunrise are indicated by dashed vertical lines.

Results

In May, it was possible to determine diel feeding patterns of roach 200–270 mm SL and bream 220–330 mm SL. Both cyprinids showed daytime feeding activity (Fig. 1), with afternoon peaks and distinct night-time declines in gut fullness. Diel fluctuations in gut fullness of roach collected at the dam and middle sites seemed to have a synchronic pattern (Fig. 1), although the data from the latter site are incomplete. Furthermore, mean gut fullness of roach at the middle site remained below 60 % of those at the dam site at comparable times of a day. The diets of both roach and bream were strongly dominated by *Daphnia galeata* Sars (Fig. 2a).

In August, bleak, roach and bream of 110–170 mm SL showed daytime feeding activity (Fig. 3). Maximum gut fullness was observed around the noon for bleak and roach and shortly before the sunset for bream. In all cyprinids, a marked decrease in gut fullness over

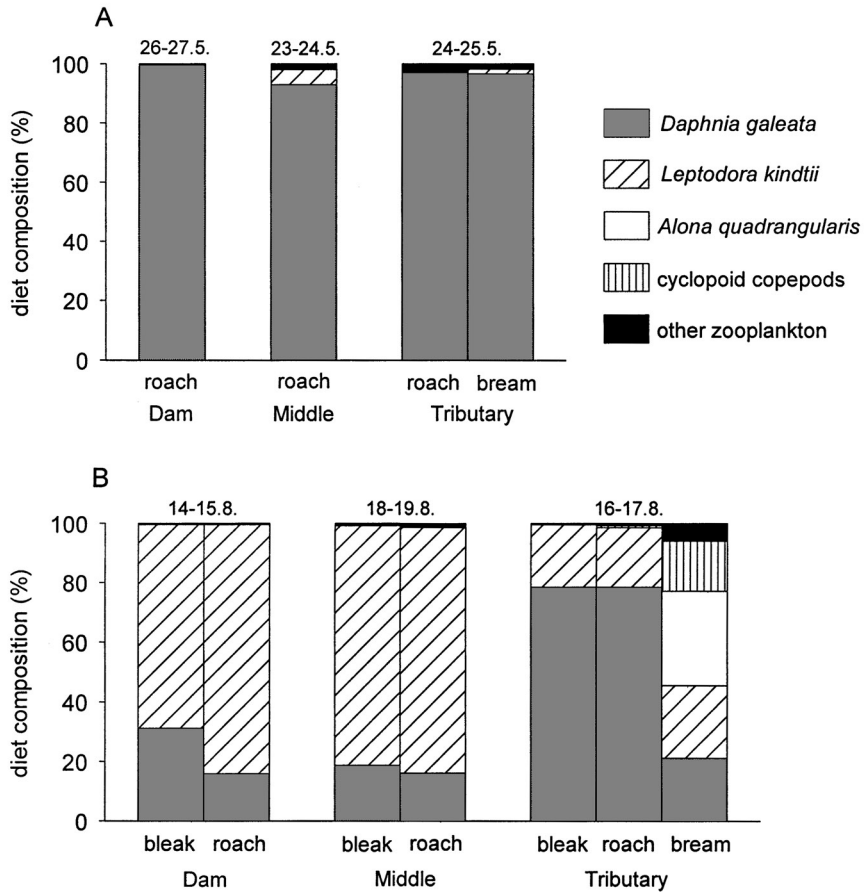


Fig. 2. Diet composition expressed as microcrustacean prey percentages by wet weight (weighted mean over the diel cycle) for roach and bream >200 mm SL sampled at different reservoir sites during May (A), and bleak, roach and bream 110–170 mm SL sampled at different reservoir sites during August 1999 (B). Exact sampling dates are shown above bars.

the hours of darkness was observed. Gut contents of bleak and roach were overwhelmingly dominated by *Leptodora kindtii* and *D. galeata* (Fig. 2b). Diet of bream at the tributary site consisted of cyclopoid copepods, *D. galeata*, *L. kindtii* and benthic cladoceran *Alona quadrangularis* (O. F. Müller) (Fig. 2b).

Daily food rations (Table 1) varied between species and sites, being lowest for bream (220–330 mm SL) at the tributary site in May, and highest for bleak (110–170 mm SL) at the tributary site in August.

Discussion

Gut fullness in three cyprinid species foraging on microcrustacean (mainly planktonic) prey in the Římov Reservoir peaked during the day and demonstrated decline at night in both May and August 1999. In one case (bream 110–170 mm SL), gut fullness was recorded

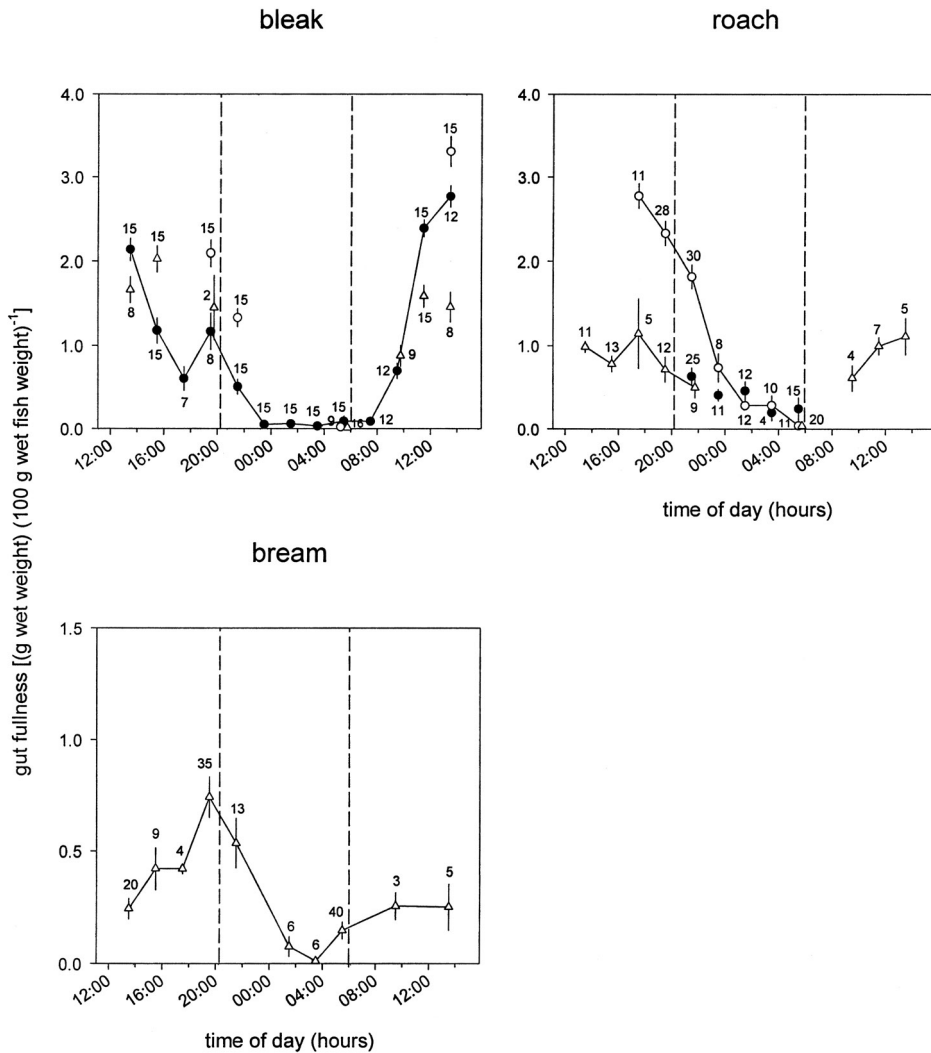


Fig. 3. Diel variation in the mean gut fullness of bleak, roach and bream 110–170 mm SL in August 1999. Vertical bars represent ± 1 SE, numbers of analyzed fish are shown close to symbols or error bars. Fish sampled in the dam site (14–15 August, mean water temperature = 19.6°C) are indicated by open circles, in the middle site (18–19 August, °C = 19.4) by solid dots, and in the tributary site (16–17 August, °C = 17.2) by empty triangles. Times of sunset and sunrise are indicated by dashed vertical lines.

at maximum just before dusk, but it dropped considerably throughout the night again. Apparently, cyprinids fed very little or not at all during darkness. This suggests that light intensity can be an important factor affecting feeding behaviour in zooplanktivorous fish.

Visual detection of prey is typical in particulate feeders, i.e. fish attacking individual planktonic prey item, which they visually select from the water column (Lazzaro 1987). On the contrary, visual detection is believed to be not necessary for filter feeders, i.e. fish foraging by engulfing a volume of water containing several prey items (Lazzaro 1987, Lammen & Hoogenboezem 1991). An intermediate feeding mode between

Table 1. Overview of daily consumption rates of cyprinids in the Římov Reservoir in 1999 (*SL* mean standard length of fish ± 1 SE, *W* mean weight of fish ± 1 SE, *temp.* mean water temperature, *R* gastric evacuation rate, *relative DI* daily food intake in g wet weight per 100 g wet fish weight and *absolute DI* daily food intake in g wet weight per fish). Fish were collected at three different sites located along the longitudinal axis of the reservoir: in the dam, middle (Mid) and tributary (Trib) sites, respectively.

Species	Month	Site	SL (mm)	W (g)	Temp. (°C)	R (h ⁻¹)	Relative DI	Absolute DI
roach	May	Dam	245 \pm 2	338 \pm 9	17.3	0.38	5.04	17.04
bream	May	Trib	284 \pm 3	522 \pm 14	14.4	0.32	1.46	7.60
bleak	August	Mid	151 \pm 1	45 \pm 1	19.4	0.46	9.55	4.30
roach	August	Trib	139 \pm 2	59 \pm 2	17.2	0.30	4.13	2.44
bream	August	Trib	147 \pm 1	74 \pm 2	17.2	0.52	3.70	2.76
bleak	August	Trib	135 \pm 2	30 \pm 2	17.2	0.48	9.94	2.96

particulate and filter feeding is gulping which is not directed to one prey, but it is visually orientated (Lazzaro 1987, Lammens & Hoogenboezem 1991). According to Lammens & Hoogenboezem (1991) most small zooplanktivorous cyprinids (body length <150 mm) are mainly particulate feeders. Direct laboratory observations with zooplankton densities similar to natural conditions showed that bream and roach at body length about 150 mm are able to forage by both particulate and filter feeding modes depending on prey size and density (Lammens 1985, Lammens et al. 1987). Particulate feeding occurs when prey size is relatively large, whereas filter feeding occurs when prey organisms are small and abundant. Lammens (1985) also observed that bream larger than 300 mm consumed *Daphnia* only by a sort of filter feeding. Laboratory experiments performed by Vandenberg et al. (1994) proved that bream and roach of c. 100–180 mm SL were able to filter-feed on zooplankton in complete darkness. However, when the light conditions were adequate, roach always used particulate feeding whereas bream preferred gulping. No evidence for filter feeding ability in bleak has been found in literature.

Considering the observations cited above, the daytime feeding pattern of cyprinids 110–170 mm SL described in this study was probably determined by visually aimed particulate foraging technique. It is clear that roach and bleak used particulate feeding, since their diets were dominated by largest available zooplankton – *Leptodora* and *Daphnia*, of which *Leptodora* was found at very low relative density in zooplankton collected simultaneously with fish samplings (Vašek et al. 2003). On the other hand, we assume that roach and bream >200 mm SL were so large in comparison to the size of their preferred prey (i.e. *Daphnia*) that they did not capture the prey one by one, but used rather filter feeding or gulping (Lammens & Hoogenboezem 1991, Hoogenboezem et al. 1992). A daytime feeding pattern was observed in both large roach and bream, as in the case of smaller cyprinids. However, this raises the question of why the large fish, which are able to filter feed, did not also forage during darkness. One presumable explanation of strictly daytime foraging is that large roach and bream used vision to locate patches with higher zooplankton densities and therefore fed only when there was enough light. Using echosounding, Čech & Kuběčka (2002) found that the majority of larger fish individuals (135–360 mm SL) in the Římov Reservoir stay in the epilimnion during warm period of the year and performed peculiar sinusoidal cyclic swimming in the vertical plane. They observed that fish start to swim sinusoidally after sunrise and continue doing so throughout daytime. Sinusoidal movement was replaced by direct swimming before sunset

Table 2. Overview of relative daily food intake rates (*DI*) of natural cyprinid populations in European waters (*SL* standard length, *TL* total length, *dw* dry body weight, *ww* wet body weight).

Species	Site (Country)	Time period	Fish length (mm) [Age classes]	Dominant prey	Water temperature (°C)	Relative DI (% dw)	Relative DI (% ww)	Reference
roach	Masurian lakes (Poland)	summer	110 - 240 SL	macrophytes	20.0	3.4-6.9	7.7-15.5	(Prejjs 1978)
roach	Lake Sövedborgsjön (Sweden)	August	112 - 130 TL	detritus	19.2	4.6	-	(Persson 1982)
roach	Lake Vesijärvi (Finland)	June - September	c. 120 - 200 TL* [3+ - 9+]	<i>Bosmina</i> sp.	11.0-21.0	max. 2.2-6.2	-	(Horppila & Peltonen 1997)
roach	Lake Vesijärvi (Finland)	July	c. 120 - 200 TL* [3+ - 9+]	zooplankton, zoobenthos, plant material	-	-	c. 4.8-7.7	(Horppila 1999)
roach	Lake Grosser Vätersee (Germany)	May - September	87 - 107 TL [3+]	zooplankton, zoobenthos, plant material	15.9-21.4	0.5-2.1	1.7-4.1	(Haertel & Eckmann 2002)
bleak	Lake Tajty (Poland)	July	56 - 96 SL [1+ - 4+]	insects, cladocerans	24.0	-	2.1-10.4	(Białokoz 1990)
bream	Tsimlyansk Reservoir (Russia)	May - September	- [4+ - 8+]	macrozoobenthos	14.0-27.6	-	0.3-3.0	(Kogan 1963)
bream	Volgograd Reservoir (Russia)	June - August	- [3+ - 7+]	macrozoobenthos, detritus	18.4-23.2	-	1.1-2.1	(Nebolsina 1968)
bream	Mozhaysk Reservoir (Russia)	May - September	c. 300-370 TL [6+ - 9+]	Chironomidae	c. 10.5-21.0	-	0.6-6.4	(Zadorozhnaya 1977)

* the lengths of fish according to Horppila (1994)

and was never observed during night. Since Thetmeyer & Kils (1995) showed that planktonic prey are more visible from above or below (i.e. against light sky or dark depths), the up-and-down cyclic movement described by Čech & Kubečka (2002) was probably used by fish to detect large-sized prey individuals (e.g. *Leptodora*, *Daphnia*) or patches of abundant zooplankton. Such a light-induced searching behaviour coincides well with the daytime feeding pattern of cyprinids observed in the present study. Moreover, it is important to note that the previously mentioned experimental observations of cyprinids feeding on zooplankton in darkness (Van den Berg et al. 1994) were performed at quite high prey densities and with fish that had been starved for 48 hours. Hence, we assume that the cyprinids observed in this study did not feed on zooplankton at night because foraging by random 'blind' snaps in darkness at relatively low prey density was not profitable (Hoggenboezem et al. 1992). It is also important to note here that *Daphnia* populations in the Římov Reservoir do not perform any pronounced diel vertical migration (Macháček & Seďa 2002), i.e. the densities of daphnids in the epilimnetic layer are similar in both day and night samples.

Daytime zooplankton foraging by cyprinids reported in the present study is in accordance with the field observations of a few other authors. Horppila (1999) revealed that the percentage of zooplankton in the diets of adult roach was higher and the percentage of zoobenthos, plants and detritus lower during daytime than during the night. Similarly, Schulz & Berg (1987) found benthic animals at night and zooplankton throughout daytime in the diet of bream. According to Jamet et al. (1990), young adult roach (age 2+ and 3+) feeding predominantly on zooplankton foraged from afternoon to dusk in summer. Politou et al. (1993) observed for bleak mainly crepuscular feeding activity in July and clearly diurnal feeding rhythm in August. They found the highest percentages of empty guts and the lowest of full ones during the night in both months. In contrast, Hertel & Eckmann (2002) observed in diet of 3-year-old roach littoral prey (benthos and plant material) during daytime and pelagic zooplankton at night. However, roach in that study had relatively small size at the given age (mean total length 87 mm in May and 107 mm in September) and therefore, apparently under the predation threat from piscivorous fish and birds, they performed diel habitat shifts, i.e. they stayed in the littoral zone during daytime and were found in the pelagic zone at night (Hertel & Eckmann 2002). Such an anti-predator behaviour is typical of juvenile fish (Bohl 1980, Gliwicz & Jachner 1992) and allows them to utilize profitable open water zooplankton only during night, i.e. under the low light conditions.

Differences in diet composition and gut fullness of cyprinids between different locations in the Římov Reservoir were observed. In our previously published study (Vašek et al. 2003), we reported that varying prey availability and competition within the fish community along the longitudinal axis of the Římov Reservoir can be the responsible factors for observed spatial differences in the diet composition. These biotic factors naturally affect also the intensity of food consumption, i.e. the gut fullness and daily intake rate of fish. However, it has been observed that the quantity of food consumed by fish in the wild varies significantly over consecutive days (Trudel & Boisclair 1993, Grant & Kott 1999) and since data on gut fullness of cyprinids in this study covers only a single 24-h period for each site and month, further investigation over an extended period is required to exclude possible effect of day-to-day variation in food intake on the estimates of food consumption at different reservoir sites. Before satisfying this condition, any conclusions

about mechanisms behind the spatial variation in the quantity of food consumed by fish in the Římov Reservoir remains rather speculative.

The daily consumption estimates for zooplanktivorous cyprinids in the Římov Reservoir are comparable with previously published estimates for other natural environments, including those with fish assemblages that are not as dominated by zooplanktivorous cyprinids as the assemblage in this study (Table 2). It should be noted that the food consumption intensity as well as the diel feeding pattern of large bream in the tributary site of the Římov Reservoir in May might have been affected by spawning. These bream were collected at the end of their spawning period within the given year (J. Kubečka, pers. observation) so part of their population was still reproductively active.

Acknowledgements

We would like to thank M. Čech, V. Draštík, D. Dušek, M. Hladík, J. Matěna, J. Peterka, M. Prchalová and P. Štafa, for their invaluable help during hard field work. Patrick Hill and Gordon Copp kindly checked the English. The study was financially supported by the Ministry of Education, Youth and Sports of the Czech Republic (FRVŠ, project No. 346/2000) and Grant Agency of the Academy of Sciences of the Czech Republic (projects Nos. A6017201 & S6017004).

LITERATURE

- BIAŁOKOZ W. 1990: Evaluation of the intensity and efficiency of bleak *Alburnus alburnus* (L.) feeding in Tajty Lake, Masurian Lakeland, Poland. Comparative analysis of methods. *Ekol. Pol.* 38: 163–183.
- BOHL E. 1980: Diel pattern of pelagic distribution and feeding in planktivorous fish. *Oecologia* 44: 368–375.
- BRABRAND A. 1985: Food of roach (*Rutilus rutilus*) and ide (*Leuciscus idus*): significance of diet shift for interspecific competition in omnivorous fishes. *Oecologia* 66: 461–467.
- BRANSTRATOR D.K. & HOLL C.M. 2000: Planktivory by bluegill (*Lepomis macrochirus*) on *Leptodora kindtii* in a small North American lake. *Hydrobiologia* 437: 101–106.
- ČECH M. & KUBEČKA J. 2002: Sinusoidal cycling swimming pattern of reservoir fishes. *J. Fish Biol.* 61: 456–471.
- ELLIOTT J.M. & PERSSON L. 1978: The estimation of daily rates of food consumption for fish. *J. Anim. Ecol.* 47: 977–991.
- GARCÍA-BERTHOUS E. 1999: Spatial heterogeneity in roach (*Rutilus rutilus*) diet among contrasting basins within a lake. *Arch. Hydrobiol.* 146: 239–256.
- GLIWICZ Z.M. & JACHNER A. 1992: Diel migrations of juvenile fish – a ghost of predation past or present. *Arch. Hydrobiol.* 124: 385–410.
- GRANT S.M. & KOTT E. 1999: Variation in field estimates of daily ration in young yellow perch. *J. Fish Biol.* 54: 396–403.
- HAERTEL S.S. & ECKMANN R. 2002: Diel diet shift of roach and its implications for the estimation of daily rations. *J. Fish Biol.* 60: 876–892.
- HELPMAN G.S. 1993: Fish behaviour by day, night and twilight. In: Pitcher T.J. (ed.), Behaviour of Teleost Fishes. Chapman & Hall, London: 479–512.
- HERZIG A. 1994: Predator-prey relationships within the pelagic community of Neusiedler See. *Hydrobiologia* 275/276: 81–96.
- HOEHN E., CLASEN J., SCHARF W., KETELAARS H.A.M., NIENHÜSER A.E., HORN H., KERSKEN H. & EWIG B. 1998: Erfassung und Bewertung von Planktonorganismen. R. Oldenbourg Verlag, München.
- HOOGENBOEZEM W., LAMMENS E.H.R.R., VAN VUGT Y. & OSSE J.W.M. 1992: A model for switching between particulate-feeding and filter-feeding in common bream, *Abramis brama*. *Environ. Biol. Fish.* 33: 13–21.
- HORPPILA J. 1994: The diet and growth of roach (*Rutilus rutilus* (L.)) in Lake Vesijärvi and possible changes in the course of biomanipulation. *Hydrobiologia* 294: 35–41.

- HORPPILA J. 1999: Diel changes in diet composition of an omnivorous cyprinid – a possible source of error in estimating food consumption. *Hydrobiologia* 400: 33–39.
- HORPPILA J. & PELTONEN H. 1997: A bioenergetic approach on food consumption of roach (*Rutilus rutilus* (L.)) in a eutrophic lake. *Arch. Hydrobiol.* 139: 207–222.
- HRUŠKA V. 1956: Příspěvek k potravní biologii plotice v tůni Poltrubě (Contribution to feeding habits of the roach in the pool Poltruba). *Acta Univ. Carol., Biol.* 2: 161–207 (in Czech with English summary).
- HYSLOP E.J. 1980: Stomach content analysis – a review of methods and their application. *J. Fish Biol.* 17: 411–429.
- JAMET J.L., GRES P., LAIR N. & LASSERRE G. 1990: Diel feeding cycle of roach (*Rutilus rutilus*, L.) in eutrophic Lake Aydat (Massif Central, France). *Arch. Hydrobiol.* 118: 371–382.
- JAMET J.L. 1994: Feeding activity of adult roach (*Rutilus rutilus* (L.)), perch (*Perca fluviatilis* L.) and ruffe (*Gymnocephalus cernuus* (L.)) in eutrophic Lake Aydat (France). *Aquat. Sci.* 56: 376–387.
- KOGAN A.V. 1963: [On daily ration and rhythm of feeding in *Abramis brama* (L.) in the Tsimlyansk Reservoir]. *Vopr. Ikhtiol.* 3: 319–325 (in Russian).
- KOGAN A.V. 1970: [Age-related and seasonal changes in the daily feeding rhythm of the Tsimlyansk Reservoir bream]. *Vopr. Ikhtiol.* 10: 747–751 (in Russian).
- KRASNOPER E.V. 1989: [The rate of evacuation of gut contents in bream, *Abramis brama*]. *Vopr. Ikhtiol.* 29: 624–633 (in Russian).
- LAMMENS E.H.R.R. 1985: A test of a model for planktivorous filter feeding by bream *Abramis brama*. *Environ. Biol. Fish.* 13: 288–296.
- LAMMENS E.H.R.R., DE NIE H.W., VIJVERBERG, J., & VAN DENSEN, W.L.T. 1985: Resource partitioning and niche shift of bream (*Abramis brama*) and eel (*Anguila anguila*) mediated by predation of smelt (*Osmerus eperlanus*) on *Daphnia hyalina*. *Can. J. Fish. Aquat. Sci.* 42: 1342–1351.
- LAMMENS E.H.R.R., GEURSEN J. & MCGILLAVRY P.J. 1987: Diet shifts, feeding efficiency and coexistence of bream (*Abramis brama*), roach (*Rutilus rutilus*) and white bream (*Blicca bjoerkna*) in hypertrophic lakes. *Proc. 5th Congr. Europ. Ichtyol., Stockholm: 153–162.*
- LAMMENS E.H.R.R. & HOOGENBOEZEM W. 1991: Diets and feeding behaviour. In: Winfield I.J. & Nelson J.S. (eds), Cyprinid fishes – systematic, biology and exploitation. *Chapman & Hall, London: 353–376.*
- LAZZARO X. 1987: A review of planktivorous fishes: their evolution, feeding behaviours, selectivities, and impacts. *Hydrobiologia* 146: 97–167.
- MACHÁČEK J. & SEĎA J. 2002: Diurnal aspect of vertical distribution of *Daphnia* species in the Římov Reservoir in the spring period. In: *Proceedings of 4th International Conference on Reservoir Limnology and Water Quality, Hydrobiological Institute, Academy of Sciences of the Czech Republic, České Budějovice: 204–206.*
- MARTYNIAK A., JERZYK M.S. & ADÁMEK Z. 1987: The food of bream (*Abramis brama*) in the Pierzchaly Reservoir (Poland). *Folia Zool.* 36: 273–280.
- MARTYNIAK A., GIRTLER K. & ADÁMEK Z. 1991: Food biology of roach (*Rutilus rutilus*) in the Pierzchaly Reservoir (Poland). *Folia Zool.* 40: 377–384.
- MICHELSSEN K., PEDERSEN J., CHRISTOFFERSEN K. & JENSEN F. 1994: Ecological consequences of food partitioning for the fish population structure in a eutrophic lake. *Hydrobiologia* 291: 35–45.
- NAUWERCK A. 1999: Facultativ planktivore Fische im Mondsee und ihre Nahrung, II. Das Rotaue (*Rutilus rutilus* [L.]). *Österr. Fischerei* 52: 17–29.
- NEBOLSINA T.K. 1968: [Daily ration and rhythm of feeding of bream (*Abramis brama* (L.)) in Volgograd Reservoir]. *Vopr. Ikhtiol.* 8: 131–138 (in Russian).
- NIEDERHOLZER R. & HOFER R. 1980: The feeding of roach (*Rutilus rutilus* L.) and rudd (*Scardinius erythrophthalmus* L.), I. Studies on natural populations. *Ekol. Pol.* 28: 45–59.
- PERSSON L. 1982: Rate of food evacuation in roach (*Rutilus rutilus*) in relation to temperature, and the application of evacuation rate estimates for studies on the rate of food consumption. *Freshwat. Biol.* 12: 203–210.
- PERSSON L. 1983: Food consumption and the significance of detritus and algae to intraspecific competition in roach *Rutilus rutilus* in a shallow eutrophic lake. *Oikos* 41: 118–125.
- PERSSON A. & HANSSON L.A. 1999: Diet shift in fish following competitive release. *Can. J. Fish. Aquat. Sci.* 56: 70–78.
- POLITOU C-Y., ECONOMIDIS P.S. & SINIS A.I. 1993: Feeding biology of bleak, *Alburnus alburnus*, in Lake Koronia, northern Greece. *J. Fish Biol.* 43: 33–43.
- PREJS A. 1978: Lake macrophytes as the food of roach (*Rutilus rutilus* L.) and rudd (*Scardinius erythrophthalmus* L.), II. Daily intake of macrophyte food in relation to body size of fish. *Ekol. Pol.* 26: 537–553.

- PREJS A. & JACKOWSKA H. 1978: Lake macrophytes as the food of roach (*Rutilus rutilus* L.) and rudd (*Scardinius erythrophthalmus* L.), I. Species composition and dominance relations in the lake and food. *Ekol. Pol.* 26: 429–438.
- SCHULZ U. & BERG R. 1987: The migration of ultrasonic-tagged bream, *Abramis brama* (L.), in Lake Constance (Bodensee-Untersee). *J. Fish Biol.* 31: 409–414.
- SPECZIÁR A., TÖLG L. & BÍRÓ P. 1997: Feeding strategy and growth of cyprinids in the littoral zone of Lake Balaton. *J. Fish Biol.* 51: 1109–1124.
- SPECZIÁR A. 2002: *In situ* estimates of gut evacuation and its dependence on temperature in five cyprinids. *J. Fish Biol.* 60: 1222–1236.
- THETMEYER H. & KILS U. 1995: To see and not to be seen: the visibility of predator and prey with respect to feeding behaviour. *Mar. Ecol. Prog. Ser.* 126: 1–8.
- TRUDEL M. & BOISCLAIR D. 1993: An *in situ* evaluation of day-to-day variation in the quantity of food consumed by fish. *Can. J. Fish. Aquat. Sci.* 50: 2157–2165.
- VAN DEN BERG C., VAN DEN BOGAART J.G.M., SIBBING F.A. & OSSE J.W.M. 1994: Zooplankton feeding in common bream (*Abramis brama*), white bream (*Blicca bjoerkna*) and roach (*Rutilus rutilus*): experiments, models and energy intake. *Neth. J. Zool.* 44: 15–42.
- VAŠEK M., KUBEČKA J. & SEĎA J. 2003: Cyprinid predation on zooplankton along the longitudinal profile of a canyon-shaped reservoir. *Arch. Hydrobiol.* 156: 535–550.
- VINNI M., HORPPILA J., OLIN M., RUUHIJÄRVI J. & NYBERG K. 2000: The food, growth and abundance of five co-existing cyprinids in lake basins of different morphometry and water quality. *Aquat. Ecol.* 34: 421–431.
- ZADOROZHNEYA E.A. 1977: [On the feeding biology of bream *Abramis brama* (L.) in reservoirs on small rivers (with reference to the Mozhaysk Reservoir)]. *Vopr. Ikhtiol.* 17: 890–899 (in Russian).