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Overwintering of farmed common carp (*Cyprinus carpio* L.) in the ponds of a central European aquaculture facility—measurement of activity by radio telemetry

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Abstract

In the aquaculture of farmed common carp (*Cyprinus carpio* L.) in Central Europe, it is believed that carp overwinter motionless and without feeding at the bottom of the ponds. However, only a few studies have investigated the behaviour of carp in winter, and data on the overwintering of carp in ponds are rare. This paper presents some new data on the activity of overwintering farmed common carp in Central European aquaculture. Altogether, 14 carp were equipped with surgically implanted radio telemetry transmitters and their activity was investigated by positional tracking in a pond (2.2 ha) during the winter seasons of 1999/2000, 2000/2001 and 2001/2002. Low weight loss, WL, and good condition factor, K, suggested that overwintering was successful (WL max.=3.8%, K=1.84–2.33). The carp were found to be relatively active in winter. The mean relative distances between the estimated fish positions on two consecutive tracking sessions ranged from 27.6 to 67.9 m. These activities correlated positively with water temperature in two winter seasons ($p<0.05$). The findings of the present study suggest that undisturbed overwintering carp restricted their activity to certain areas of the pond, but were clearly active throughout the winter. Moreover, evidence was found that foraging occurred at water temperatures of 3.1 °C. These findings indicate a need for further

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investigations not only on overwintering but also on feeding as well as on stocking densities of carp which overwinter in ponds. Refinement of overwintering methods and a reduced loss of fish should be the aim of these investigations.

Keywords: Activity; Aquaculture; Common carp; *Cyprinus carpio*; Overwintering; Winter

1. Introduction

According to Ultsch (1989), common carp belong to the class of northern hemisphere freshwater fish which restrict their activity in winter. This activity restriction is a physiological necessity, since the optimal temperature range for carp lies between 20 and 28 °C (Horváth et al., 1992; Schreckenbach, 2002a). Energy demands as well as the capacity for food processing in common carp are lower in winter (e.g., Schreckenbach, 2002b). Therefore, activity restriction is the best strategy to cope with the environmental conditions in winter, if undisturbed overwintering is possible. This field is of particular interest for the aquaculture of common carp in Central Europe, where carp are reared mostly in earthen ponds in an extensive and sustainable way. The winter is known to be a critical period in the production of common carp, with the risk of a heavy loss of valuable fish. Therefore, in order to optimise wintering, various guidelines exist which deal with the necessary features of a wintering pond and with the preparation of such a pond before stocking with carp (e.g., Kostomarov, 1961; Horváth et al., 1992; Lukowicz and Gerstner, 1998; Geldhauser and Gerstner, 2003). It has been noted that carp stop moving and feeding at low water temperatures in winter (e.g., Koch et al., 1982; Schmeller, 1988; Geldhauser, 1996; Reichle, 1998). The behaviour of carp in winter (overwintering) is often described as follows: The carp cluster together in large groups; they form a depression in the bottom of the pond and there pass the winter without movement or feeding (e.g., Heckel and Kner, 1858; Horák, 1869; Michaels, 1988; Schmeller, 1988; Reichle, 1998).

However, this generalised view has been put into perspective by others. Kostomarov (1961 after Sigow) observed that one-summer-old carp (C1) showed some activity even at water temperatures of 0.5 °C. Observations of actively feeding C1 at low water temperatures have been described by Steffens (1964) and Billard (1999). Even older carp are said occasionally to interrupt their overwintering inactivity, showing some movement (Kostomarov, 1961 after Sigow; Bohl, 1999). Moreover, studies of the overwintering of common carp carried out in the great reservoirs or lakes of North America and Russia (Johnsen and Hasler, 1977; Osipova, 1979; Otis and Weber, 1982) have further suggested activity in winter. As these water bodies are of a significantly greater size than wintering ponds, it is debateable whether the “typical” wintering behaviour of common carp—as described for aquaculture ponds—has been induced by the small and intensively stocked wintering ponds. The recommended sizes for wintering ponds differ from 500 m^2 to 1 ha (Kostomarov, 1961; Michaels, 1988; Horváth et al., 1992; Billard, 1999; Bohl 1999). Recommended stocking densities vary between 3500 and 12500 kg ha^{-1} (Michaels, 1988; Geldhauser and Gerstner, 2003).

Unfortunately, there have been only a few scientific attempts to investigate the behaviour of carp in wintering ponds (e.g., Kostomarov, 1961 after Sigow; Sebenzow; Gusar et al., 1989). Kostomarov stated in 1961 that, despite of the amount of literature dealing with carp overwintering, little is known about the behaviour of common carp during the winter. Little appears to have changed since then.

Therefore, the aim of this study was to investigate the overwintering of three-summer-old carp (C3) using radio telemetry. This technique has been widely used in fish (e.g., Baras, 1991) and was applied successfully in various studies on common carp, (e.g., Berry, 1982; Otis and Weber, 1982; Steinbach, 1986; Brown et al., 2001).

2. Materials and methods

2.1. Study area

To study the undisturbed wintering of farmed common carp, it is of importance to choose a pond which provides suitable water quality for the fish throughout the winter and where the carp will not face external disturbances (e.g., from winter sports). The influence of the otter (*Lutra lutra*) needs to be considered as well. The size of the pond has to be large enough to give the carp the opportunity to move around and choose their preferred wintering location within the pond, whilst being small enough to enable tracking of the fish using limited technical and personnel resources.

The Austrian carp breeding area of the Waldviertel, a region in the north of Austria near the Czech border, has a carp farming tradition reaching back more than 500 years, and various ponds in this area were found which matched the above requirements.

For this study, a pond was chosen (the *KB pond*) which has been used for the wintering of common carp for the last four decades by an established carp breeder. In the KB pond, the test carp were able to overwinter among other carp of a similar age and size (stocking density 1000 kg ha^{-1}).

The KB pond covers a total area of 2.2 ha. Ponds of this size are commonly used for the wintering of carp in northern Austria and southern Bohemia. The average depth is 2.0 m and the greatest depth reaches 3.5 m near the dam (Fig. 1). The bottom is covered mainly with mud, with sand near the shore. Tributary water for the pond comes from the drainage of coniferous forests. Archival data, recorded by the owner of the pond and in the course of various studies, show that physical and chemical parameters of the pond water, especially dissolved oxygen, has rarely reached a critical level for carp in winter (Scherzer, personal communication; Schlott et al., 2003 and unpublished data).

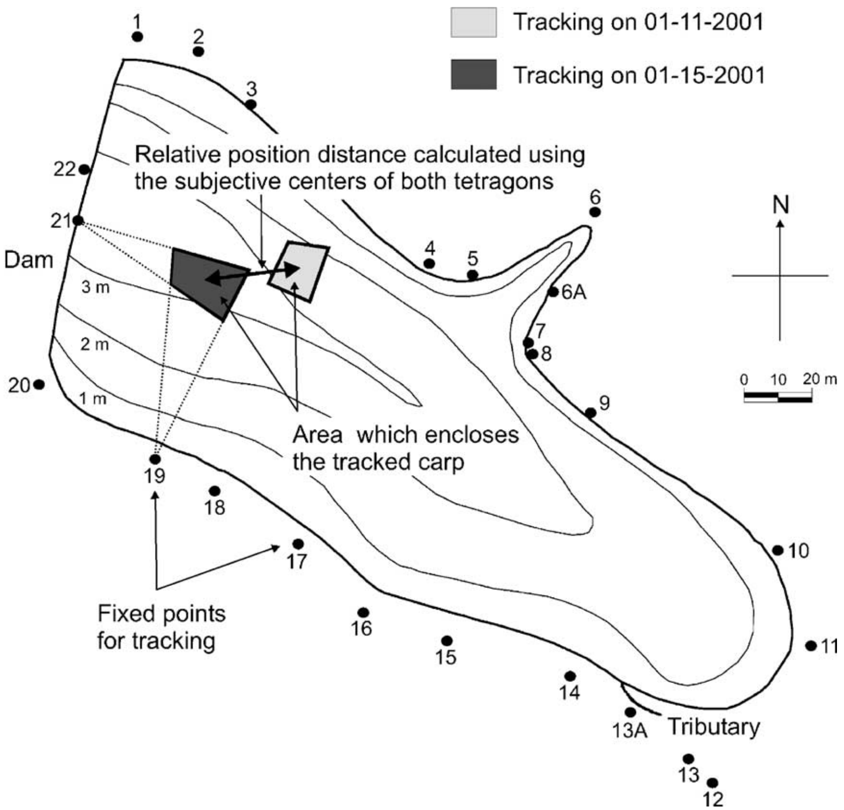

Fig. 1. The KB pond, size 2.2 ha, depth max. 3.5 m; tracking of the fish was carried out from a minimum of two out of 26 fixed points (3A and 3B are not visible). The direction of the transmitter's signal was estimated by using a compass and distinct landmarks, resulting in two defining bearing angles.

2.2. Test carp and surgical procedure

Altogether, 14 farmed common carp, all C3, were obtained from the owner of the KB pond. The carp were equipped with implanted radio telemetry transmitters in the winters of 1999/2000 (five carp), 2000/2001 (five carp) and 2001/2002 (four carp) and stocked in the KB pond for overwintering. Table 1 shows the total length, LT, weight, W, and condition factor, K=[weight (g)/length^3 (cm)]×100 (as described by Busacker et al, 1990), of the carp.

After recapture in the course of the annual draw down of wintering ponds in March, the carp were again weighed, measured and their K was calculated to evaluate changes in the course of overwintering (Table 1). Additionally, the carp were examined for ectoparasites.

The implantation of transmitters was conducted in late October. Lotek MBTF-5 radio telemetry transmitters with an external trailing antenna were used. These transmitters were 59 mm long, with a diameter of 11 mm. Transmitter weight of 4.6

Table 1
Weight, *W* (g), total length, TL (mm) and condition factor (*K*) of the carp before implantation of the transmitter and overwintering as well as W and K after overwintering and without the transmitter

Carp	Winter	Prior wintering			Post-wintering	
		W (g)	TL (mm)	*K*	W (g)	*K*
1	1999/2000	1382	420	1.86	1375 (−0.5%)	1.85 (−0.5%)
2	1999/2000	1600	425	2.08	1576 (−1.5%)	2.05 (−1.4%)
3	1999/2000	1850	425	2.40	1789 (−3.3%)	2.33 (−2.9%)
4	1999/2000	1800	455	1.91	1732 (−3.8%)	1.84 (−3.7%)
5	1999/2000	1520	425	1.98	1476 (−2.9%)	1.92 (−3.0%)
6	2000/2001	1192	370	2.35	1160 (−2.7%)	2.29 (−2.6%)
7	2000/2001	1446	400	2.26	1425 (−1.5%)	2.22 (−1.8%)
8	2000/2001	1383	395	2.24	1408 (+1.8%)	2.28 (+1.8%)
9	2000/2001	1608	395	2.61	1608 (±0%)	2.61 (±0%)
10	2000/2001	1669	415	2.38	–	–
11	2001/2002	1526	410	2.21	1522 (−0.3%)	2.21 (±0%)
12	2001/2002	2346	480	2.12	2281 (−2.8%)	2.06 (−2.8%)
13	2001/2002	1503	420	2.03	1466 (−2.5%)	1.98 (−2.5%)
14	2001/2002	1938	440	2.28	1901 (−1.9%)	2.23 (−2.2%)

TL has not changed during the winter.

g in water does not exceed 1.75% of the fish weight in air, as is recommended by Summerfelt and Mosier (1984). Fish were anaesthetized with MS222™ (100 mg l^{-1}) until anaesthesia stages 4–5 was reached (Summerfelt and Smith, 1990). The incision area as well as the transmitter were disinfected. The transmitters were rinsed with physiological saline and inserted into the body cavity through a 3-cm-long mid-ventral incision posterior of the pelvic girdle. The trailing antenna was led through the body wall dorso-lateral of the incision using a modification of the shielded needle technique described by Ross and Kleiner (1982). The incision was closed with three to four simple interrupted sutures using nonabsorbable material. After applying Baytril® (Bayer, 2.5%, 10 mg kg^{-1}) intraperitonealy, the carp were transferred to an outdoor pool and kept 6–7 days for recovery and observation. The carp were then transferred to the KB pond for overwintering.

The work was carried out with permission of the Government of Lower Austria according to the Austrian Law on Animal Welfare §6–8 TGV 1988 and under consideration of the Guidelines for the Use of Animals in Research (Animal Behaviour 1998).

2.3. Tracking

The carp were tracked on at least 2 days each week. During the winters of 2000/2001 and 2001/2002, tracking was carried out twice per day (in the morning and in the afternoon). A Lotek SRX-400 W4 receiver and a handheld three-element Yagi antenna were used. Tracking was carried out from a minimum of two points, selected variously from 26 fixed points on the shore, using a compass and distinct landmarks (Fig. 1). Since it is known that various factors can influence the accuracy of positional tracking (e.g., Minor and Crossman, 1978; MacDonald and Amlaner, 1980), the method was tested under various field conditions (e.g., ice-covered and pond free of ice, snow, rain, etc.) in ponds. The same tracking equipment was used and a transmitter was placed at precisely determined position and depth in the centre of the pond. These tests showed an accuracy of 81.4% (n=102) for the transmitter's being located within the estimated area (Bauer, unpublished data) which was considered sufficient.

Walking on the ice was avoided as this was found to disturb the carp, altering their behaviour and so leading to artefacts (Bauer, unpublished data).

The activity of the implanted carp was calculated as relative distances between the estimated fish positions [=position distance, PD (m)] on two consecutive tracking sessions, using the subjective centre of the estimated position area (Fig. 1). Higher PDs therefore indicated higher activity, but did not display the absolute distance covered by the carp.

To test if there were significant differences in the activity within a particular day and between two successive days of tracking, a Wilcoxon–Wilcox test was used on the position distances.

2.4. Physical/chemical data

In the course of the tracking sessions, water temperature, T_W (°C), and dissolved oxygen, O_2D (mg l^{-1}), were measured at the dam 50 cm below the water surface and at a depth of 200 cm using a WTW Oxi 315i digital measuring instrument.

Overall, weather conditions as well as ice and snow cover of the pond were also recorded.

Possible correlations between PD and T_W (at 50 cm, 200 cm and the mean of both these depths) as well as O_2D (at 50 cm, 200 cm and the mean of both these depths) were evaluated using linear regression.

3. Results

3.1. Implanting procedure, postwintering condition of carp

In this study, no post-operative mortality was recorded nor did any carp show signs of adverse effects (e.g., fungal infections) from the implantation procedure. Behaviour and swimming ability were normal within 24 h of the operations.

After 4 months of overwintering, the KB pond was drawn down in March 2000, 2001 and 2002 and the carp were recaptured. The carp showed signs of inflammation at the incision area and at the opening for the trailing antenna, but did not display any severe tissue necrosis or ulceration. In March 2001, one carp was missing and could not be recaptured. Attempts to recover the transmitter or remains of the missing carp were not successful, since they were covered with mud in the centre of the pond. The carp must have died shortly before the draw down, as it had shown no unusual behaviour (compared with other implanted carp) throughout the winter and had been successfully tracked near an established feeding point a few days before the draw down.

W and *K* of the carp before and after overwintering are described in Table 1.

After overwintering, none of the carp showed severe parasitosis although sporadic occurrences of *Argulus* sp., *Apiosoma* sp. and *Trichodina* sp. were noted.

3.2. Activity of the carp

In total, 682 positional fixes were recorded on the 14 radio-tagged carp in the KB pond (1999/2000 182 fixes on five carp; 2000/2001 277 fixes on five carp; 2001/2002 223 fixes on four carp). In the winter 1999/2000, because of a technical problem, tracking started rather late on November 22, 1999. Until November 13, 1999, shoals of carp as well as single specimens were observed near the water surface.

In the winter season of 2000/2001, tracking started on November 7, 2001. On November 23, 2000, large shoals of carp were observed at two feeding points near the dam, where commercial food was supplied. Until November 27, 2000, shoals of carp as well as single specimens were observed near the water surface. On this day, three carp were caught using a basking net at the feeding points near the dam (T_W=5.2 °C) where large shoals of fish were present. The intestines of the three captured carp contained chironomid larvae, copepods and commercial food. On the December 13, 2000, two carp were caught at a feeding point near the dam (T_W=3.1 °C). The intestines of both carp contained commercial food.

In the winter season of 2001/2002, tracking started on November 6, 2001. Single carp as well as shoals of carp were observed near the water surface until November 12, 2001.

Table 2 describes the mean monthly PD of all three winter seasons. The high mean PD in January of 2002 was caused mainly by the high activity of a single tracked carp. The reason for this behaviour remains unknown.

With the exception of November 2000, each winter season, the carp used similar areas of the KB pond. The carp concentrated in the centre or the western parts of the pond. They preferred deeper zones and avoided the shallow areas near the shore, especially the eastern part of the pond, near the tributary. Fig. 2 shows the area of the KB pond used by the carp during the three winter seasons.

No differences were found between PDs within one tracking day and PDs on two successive tracking days of the winter season of 2000/2001 and 2001/2002 (Wilcoxon–Wilcox, p>0.05).

In all three winter seasons, droppings of otter were detected several times prior to the freezing of the pond, but not later on.

Table 2
Mean position distance (m)±S.E. of the carp during the three winter seasons in the KB pond

	Winter season 1999/2000	Winter season 2000/2001	Winter season 2001/2002
November	47.8±3.9, *n*=21	67.9±5.3, *n*=72	43.1±3.5, *n*=53
December	35.8±2.8, *n*=48	31.3±2.6, *n*=67	27.6±2.1, *n*=60
January	44.8±4.0, *n*=70	27.8±1.5, *n*=76,	29.7±2.0, *n*=61
February	31.4±3.8, *n*=43	30.6±2.1, *n*=62	38.5±3.7, *n*=49

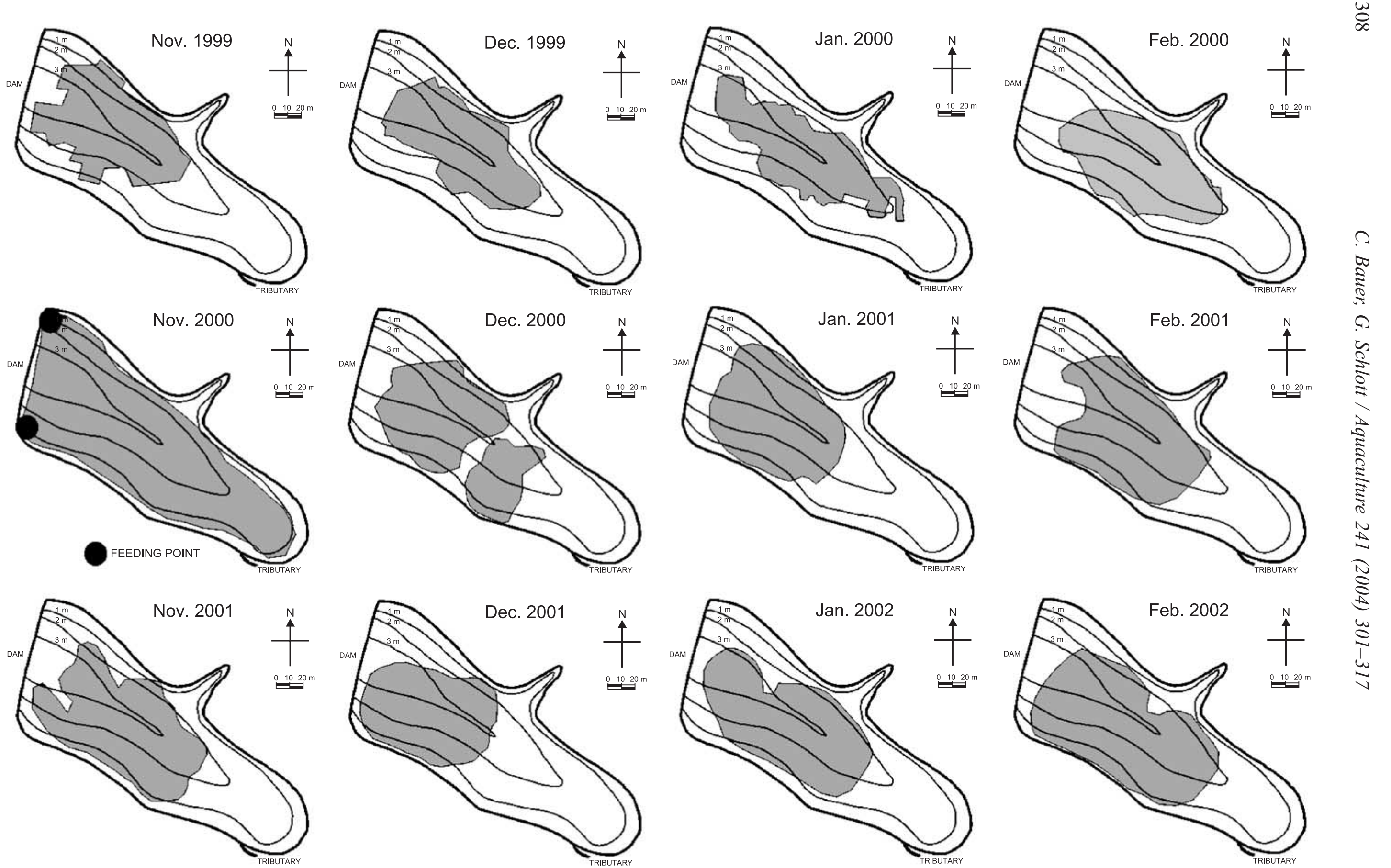

Fig. 2. Areas used by the carp in the KB pond in the winter seasons of 1999/2000, 2000/2001 and 2001/2002 as revealed by telemetry.

Table 3
Mean water temperature (°C)±S.E. at a depth of 50 and 200 cm in the three winter seasons in the KB pond

	1999/2000		2000/2001		2001/2002	
	50 cm	200 cm	50 cm	200 cm	50 cm	200 cm
November	5.4±1.5, *n*=3	5.7±1.2, *n*=3	6.5±1.3, *n*=4	6.5±1.3, *n*=4	4.4±0.4, *n*=4	4.7±0.4, *n*=4
December	3.7±0.3, *n*=4	4.2±0.4, *n*=4	3.3±0.8, *n*=4	3.5±0.6, *n*=4	1.7±0.1, *n*=5	2.8±0.2 ,*n*=5
January	3.0±0.2, *n*=4	4.0±0.2, *n*=4	2.5±0.1, *n*=5	3.8±0.1, *n*=5	1.8±0.2, *n*=4	3.5±0.1, *n*=4
February	3.9±0.2, *n*=4	4.4±0.3, *n*=4	3.0±0.8, *n*=4	3.9±0.4, *n*=4	3.5±0.4, *n*=4	3.0±0.5, *n*=4
Min/Max	2.5/8.2	3.7/8.1	2.2/7.7	2.9/7.7	1.0/7.4	0.7/7.4

3.3. Water temperature and dissolved oxygen

Table 3 shows the mean T_W at a depth of 50 and 200 cm for each month of the three winter seasons. Table 4 shows the mean O_2D at a depth of 50 and 200 cm for each month of the three winter seasons. The mean O_2D decreased in the months in which the pond was frozen.

In the winter season of 1999/2000, freezing of the pond was completed on Novervmber 25, 1999 and lasted until the beginning of March 2000. In the winter season of 2000/2001, due to the unusually mild November, freezing started on December 18, 2000 and lasted until the beginning of March 2001. In the winter season of 2001/2002, freezing of the ponds surface was completed on November 15, 2001, although it had melted again by the end of the month. The pond was free of ice on March 12, 2001. On December 6, 2001, the pond's surface was completely frozen again. This ice covering persisted until the middle of February 2002.

3.4. Environmental conditions and carp activity

In the winter season of 1999/2000, no statistically significant correlation between PD and T_W was found (50 cm: r^2=0.0002, p>0.05; 200 cm: r^2=0.0047, p>0.05; mean: r^2=0.0018, p>0.05). Neither was any statistically significant correlation found between PD and O_2D (50 cm: r^2=0.001, p>0.05; 200 cm: r^2=0.0053, p>0.05; mean: r^2=0.0028, p>0.05).

In the winter season of 2000/2001, PD and T_W correlated positively (50 cm: r^2=0.3107, p<0.05; 200 cm: r^2=0.2972, p<0.05; mean: r^2=0.3076, p<0.05) (Fig. 3).

Table 4
Mean dissolved oxygen (mg l^{-1})±S.E. at a depth of 50 and 200 cm in the three winter seasons in the KB pond

	1999/2000		2000/2001		2001/2002	
	50 cm	200 cm	50 cm	200 cm	50 cm	200 cm
November	10.7±0.4, *n*=3	10.7±0.1, *n*=3	10.4±0.6, *n*=4	10.4±0.4, *n*=4	10.6±0.2, *n*=4	10.4±0.2, *n*=4
December	13.0±0.1, *n*=4	12.2±0.4, *n*=4	11.2±0.7, *n*=4	11.4±0.4, *n*=4	11.2±0.4, *n*=5	9.0±0.7, *n*=5
January	6.5±0.6, *n*=4	5.4±0.7, *n*=4	9.6±0.8, *n*=5	8.6±1.2, *n*=5	7.7±0.3, *n*=4	5.5±0.4, *n*=4
February	8.0±0.7, *n*=4	7.6±0.8, *n*=4	8.1±1.2, *n*=4	6.6±1.1, *n*=4	9.9±0.9, *n*=4	9.6±1.0, *n*=4
Min/Max	4.8/13.0	3.8/12.6	6.9/11.9	5.5/11.8	6.3/12.4	4.6/11.8

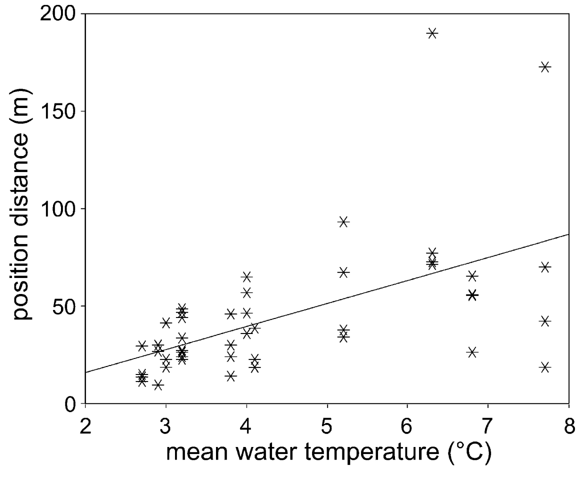

Fig. 3. Correlation between position distance (m) and water temperature (°C) in winter 2000/2001 (r^2=0.3076, p<0.005).

This was probably caused by the very mild November weather which induced the high activity of the carp. No statistically significant correlation was found between PD and O_2D at 50 cm (r^2=0.0618, p>0.05) and the mean O_2D (r^2=0.0806, p>0.05). At 200 cm, PD correlated positively with O_2D (r^2=0.1032, p<0.05) (Fig. 4). In the winter season of 2001/2002, T_W and PD correlated positively (50 cm: r^2=0.2805, p<0.001; 200 cm: r^2=0.2219, p<0.001; mean: r^2=0.2764, p<0.001) (Fig. 5). No statistically

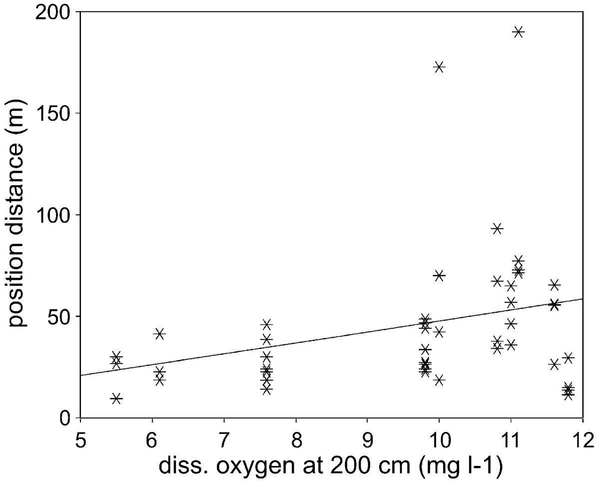

Fig. 4. Correlation between position distance (m) and dissolved oxygen (mg l^{-1}) in winter 2000/2001 (r^2=0.1032, p<0.05).

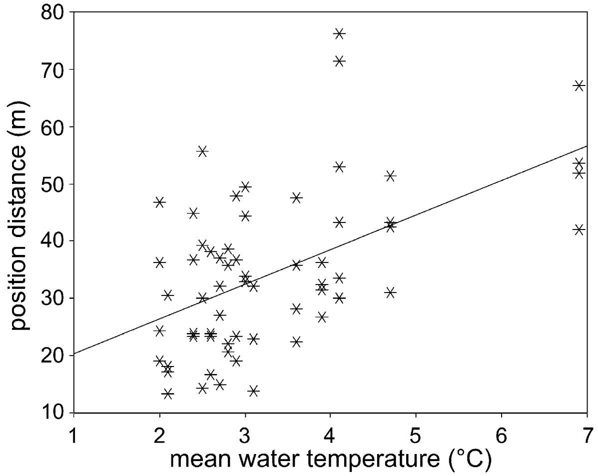

Fig. 5. Correlation between position distance (m) and water temperature (°C) in winter 2001/2002 (r^2=0.2764, p<0.005).

significant correlation was found between O_2D and PD (50 cm: r^2=0.0068, p>0.05; 200 cm: r^2=0.0022, p>0.05; mean: r^2=0.0001, p>0.05).

4. Discussion

4.1. Wintering success

Under the conditions of Central European aquaculture, common carp lose weight in winter. A weight loss, WL, of 5–10% is accepted for successful overwintering (Schäperclaus, 1961; Bohl, 1999; Geldhauser and Gerstner, 2003). Furthermore, the decrease in the condition factor, *K*, should not exceed 15–20% (Lukowicz and Gerstner, 1998). In general, for wintering successfully, an initial *K* between 1.6 and 2.0 (implanted carp 1.86–2.61) is deemed necessary (Steffens, 1964 after Sigow).

Despite the implanted transmitter, their general health condition, the low WL (0 to 3.8%) and the low decrease of *K* (0.4–4.5%) suggested that the carp had overwintered successfully. The increase of weight in one carp (+1.8%) is not easily to interpret. However, such findings have been described and are often believed to have resulted from good conditions, the late cessation of feeding in autumn and/or the early onset of feeding in spring (Włodek, 1959). As commercial food was supplied in autumn and early spring, this may have enabled the carp to limit their WL and allowed one carp even to gain some weight.

Overwintering carp are very susceptible to disturbance (e.g., Priegel, 1982; Huet, 1986; Verrill and Berry, 1995) and to stress caused by hunting otters, which could lead to WL, weakening of fish and increased susceptibility for infections and parasite invasions (Adámek et al., 2003). Considering the good overwintering performance of the carp, it can be assumed that the influence of otter was not significant. Other disturbances (e.g., skating) did not occur.

4.2. Activity in winter

The carp's overwintering inactivity (resulting in a near-motionless rest state on the bottom of the wintering pond), which has often been described in the literature (e.g., Koch et al., 1982; Michaels, 1988; Schmeller, 1988; Geldhauser, 1996; Reichle, 1998) could not be verified in this study. It has been stated that the movement of carp should stop below T_W of either 4 °C (Schmeller, 1988) or 6 °C (Reichle, 1998). In the present study, it was found that even in months which showed mean water temperatures below 4 °C, the carp showed restricted but explicit activity. However, activity could be influenced by other factors than T_W.

These findings correspond partly to the work of Gusar et al. (1989) who showed that overwintering C2 were active from November until the middle of January, when three of four transmitters stopped working. The last active transmitter indicated that the carp remained in the same place until the end of January and the beginning of February. Yet, this assumption was only based on three single tracking events. For other water bodies than ponds (lakes, reservoirs, rivers), it has also been reported that common carp showed some activity in winter (Johnsen and Hasler, 1977; Osipova, 1979; Otis and Weber 1982; Brown et al., 2001).

As no significant differences between the position distances (PD) on two successive tracking days and within the same day (p>0.05) were found, this could indicate that activity was relatively consistent within and between tracking days. However, as tracking was conducted on 2 days a week, twice a day and never at night, potential circadian and/or diel cycles could not be investigated.

4.3. Activity and environmental conditions

Activity of overwintering carp can be influenced by a combination of various factors (e.g., water quality, disturbances, etc.). For the overwintering of common carp, water temperature, T_W, and dissolved oxygen, O_2D, are considered to be the crucial parameters (e.g., Lukowicz and Gerstner, 1998) and linking these with PD might reveal a potential influence on changes in activity. However, the measurements of T_W and O_2D at a single point at depths of 50 and 200 cm did not cover the entire water body and the actual depth of the carp could not be measured in the course of tracking, thus leaving the ambient environmental conditions of the carp unknown. Although it is not likely that T_W and O_2D varied greatly in the relative homogenous KB pond, PD vs. T_W and O_2D can only be taken as gross changes in activity.

As mentioned earlier, O_2D, besides T_W, is considered to cause the most problems in wintering ponds. After Schäperclaus (1990), normally (e.g., in summer) carp require at least 4 mg l^{-1} O_2 for unrestricted life. Between 3.0 and 3.5 mg l^{-1}, the carp stop feeding and search for better-oxygenated water. Increased activity under hypoxic condition is also known from several other species of fish (Fry, 1971; Kutty, 1981). However, Haas and Menzel (2003) stated that even a level of 0.6–0.7 mg l^{-1} may not be harmful for carp if the decline occurs very slowly and at a low water temperature. In this study, O_2D fell only once, and for a short period, to 3.8 mg l^{-1} (in January 2000), and during the rest of the observed period was well within the optimal range for carp. Additionally, no correlation was found between PD and O_2D (p>0.05) in the winters of 1999/2000 and 2001/2002. Surprisingly, in the winter 2000/2001, a positive correlation between PD and O_2D at 200 cm (p<0.05), but not for mean O_2D and O_2D at 50 cm was found. If this correlation truly reflects a response of carp to oxygen, it should have been rather negative than positive, as carp tend to increase activity in their search for better-oxygenated water, as mentioned earlier. Nonetheless, Mohamed (1981) has reported decreased activity in *Oreochromis mossambicus* as a response to hypoxic conditions at T_W of 30 and 35 °C and suspected this to be a mechanism for energy saving. However, in the winter seasons of 1999/2000 and 2001/2002, the measured minimum O_2D was even lower than in the winter season of 2000/2001, although no correlation was found between PD and O_2D. The interpretation of the correlation in the winter season of 2000/2001, therefore, remains uncertain. In general, O_2D seemed to have contributed not perceptible to gross changes in activity of implanted carp in the KB pond.

The optimal range of T_W for common carp is between 23 and 28 °C (Schreckenbach, 2002a). Although carp are able to survive T_W even as low as 0.5 °C if proper acclimatisation is possible (Steffens, 1964, 1980), they will clearly try to avoid such low temperatures. After freezing of the pond is finished, T_W near the bottom is higher than near the surface and the temperature regime can be very stable throughout the winter until the thaw. Research has suggested that fish may be able to discriminate between changes in T_W as small as 0.03 °C (Bull, 1936) and that minor temperature changes (0.1 °C/h) are sufficient to alter activity (Cooke and Schreer, 2003). Therefore, carp might have preferred areas near the bottom because of higher T_W. In general, activity was positively correlated (p<0.05, p<0.001) with T_W in two winter seasons of this study. Gusar et al. (1989) also suggested the influence of T_W on the activity of carp. For the carp in the KB pond, the data suggest that T_W was one of the main factors influencing their activity. Yet, this conclusion seems not to be universally applicable. Brown et al. (2001) were unable to prove any correlation between T_W and the activity of carp, but did find a link between flood level and carp activity in a river in winter.

It was also suggested that reduced light caused by ice and snow has an influence on the carp's activity (Greenbank, 1956; Poddubny et al., 1970). Furthermore, parameters other than T_W can act as the greater stress factor, influencing activity of the carp: e.g., low levels of O_2D (Bauer, unpublished data). The potential influence of otter (Bodner, 1995; Adámek et al., 2003) or external disturbances on the ice (Priegel, 1982; Verrill and Berry, 1995) has been already mentioned. However, from only four tracking sessions a week, it was not possible to rule out any influence of otter.

4.4. Wintering site

In the present study, it was found that the carp restricted their activity to certain areas of the pond. Otis and Weber (1982) stated that carp in winter used only one-third of their summer home range. In the KB pond, the carp preferred deeper regions of the pond and avoided shallow areas near the shore. This is in accordance with descriptions in the literature on the aquaculture of common carp (e.g., Koch et al., 1982; Steffens, 1980). Also, the carp examined by Gusar et al. (1989) seemingly preferred deeper regions as they were found to use the centre of the pond. In water bodies other than ponds, carp have also been found in deeper regions in winter (Johnsen and Hasler, 1977; Osipova, 1979).

In all three winter seasons, the carp used nearly the same area for overwintering. Carp have also been reported to use the same overwintering sites over different years in larger water bodies (Johnsen and Hasler, 1977). Gusar et al. (1989) suggested that the carp actively select a suitable overwintering site. This was described also in a lake, where native as well as introduced carp selected the same wintering sites. The carp oriented themselves using environmental parameters to find suitable places for overwintering (Johnsen and Hasler, 1977; Johnson, 1980).

Foraging might also play a role in search of a suitable wintering site. Opinions differ about foraging of carp in winter; T_W at which carp will stop feeding range from 4 to 12 °C (e.g., Huet, 1986; Michaels, 1988; Schmeller, 1988; Reichle, 1998). However, various observations of feeding C1 at low T_W (0.5–3 °C) have been described (Bohl, 1999; Billard, 1999). Moreover, studies within the watershed of a great lake (Powles et al., 1983), in a reservoir (Schwartz, 1987) and a stream, and nearby lakes (Ziemiankowski and Cristea, 1961) have suggested that foraging of common carp is restricted but not completely suspended in winter. Consequently, some authors suggested to feed common carp in aquaculture at low T_W of 4 °C (e.g., Huet, 1986; Schreckenbach, 2002b). In this study, carp were caught at T_W between 3.1 and 6.5 °C, and their intestines contained copepods and chironomid larvae besides commercial food. Since it is known that the abundance of cladocerans in the open water body (an important food source for common carp) is low in winter (e.g., Christoffersen and Bosselmann, 1997; Jeppesen et al,. 1999, Schlott et al., 2003), carp might feed on copepods, whilst the bottom of the pond could provide another source of food [chironomid larvae, oligochaetes (*Tubifex* sp.)].

Predation by otter, which causes great problems in the European aquaculture of common carp (Bodner, 1995; Adámek et al., 2003), could also influence the choice of overwintering places. Since the otter is capable of hunting carp under an ice-covered pond, carp in shallow water near the shore might be more vulnerable to being discovered and attacked by an otter than carp in deeper parts of the pond and at greater distances from the shore. An otter was known to have visited the KB pond on only a few occasions; thus, avoidance of predation would seem to be a secondary, rather than primary, reason for any choice of overwintering site.

4.5. Conclusions and perspectives

It has been shown that, when undisturbed and under good environmental conditions, overwintering carp restrict their activity to certain areas in a wintering pond of 2.2 ha size, but remaining clearly active in winter. According to Ultsch (1989), the restriction of activity is a strategy to cope with unfavourable environmental conditions in winter. The selection of the overwintering habitat is influenced by various factors and it is obvious that only limited areas within any water body meet the requirements of the carp. This area decreases as the size of the overall water body decreases. Therefore, the widely described "motionless" wintering behaviour of carp has been based possibly on observations in the small ponds which are commonly recommended for overwintering of carp (e.g., Michaels, 1988; Horváth et al., 1992). In small ponds, the carp have simply no choice other than to congregate at the bottom, scarcely moving. Also, feeding is not possible throughout the winter in small ponds with very high stocking densities as the natural food supply is quickly depleted by the foraging carp. In addition, the observation of carp in larger ice- and snow-covered ponds without proper equipment is nearly impossible, whereas, in smaller ponds, this is easier to perform. At least one author has stated that the described observations were made in a small fish-storage pond (Steffens, 1980). During the preparations for this study, overwintering carp were observed in a fish-storage pond of about 100 m^2. The carp exhibited rather closely the behaviour described by authors since Heckel and Kner (1858). It seems that neither the overwintering activity of farmed common carp nor their foraging in ponds of aquaculture facilities can be generalised. Therefore, since overwintering is an important period in aquaculture of carp in Central Europe, more detailed investigations on this topic, especially on behaviour, foraging and stocking density, are necessary.

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