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Movement patterns, spatial distribution and depth preference by individual whitefish, *Coregonus lavaretus* in a small artificial lake

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Abstract. Using manual acoustic tracking our study quantified (1) the spatial distribution (2) the movement patterns and (3) the depth preference of adult whitefish, *Coregonus lavaretus* in a small artificial lake of eastern Belgium were the species was introduced in 1978 for recreational fishing. From June to October 2004, *n*=6 *C. lavaretus* (LF 285–519 mm) were tracked (pingers and depth sensor transmitters) from a small boat over periods ranging from 98 to 108 days in Robertville Lake (elevation: 490 m; area: 63 ha; max. depth: 47 m). Whitefish were consistently mobile but showed quite variable lake use patterns. Two individuals traveled the entire length and breadth of the lake, whereas others remained in movement in the deep zone in the middle part of the lake or near the retaining dam wall. Whitefish occupied positions in the water column ranging from 2.6 to 27.0 m (mean 12.7 m ± 5.6 m) that varied depending on individuals. This first study on individual whitefish behaviour provides a better understanding of the behavioural ecology of the species in small artificial lake.

Key words: mobility, individual behaviour, acoustic telemetry, lake, coregonids

Introduction

The whitefish, *C. lavaretus*, is an Eurasian cold-water fish species that has naturally remained confined at the end of the last glaciation in deep water lakes where the temperature of the bottom water is always less than 6°C, but it has been stocked into many other places outside of its native range. It is a pelagic fish living in schools, characterized by an important vulnerability (Bern convention 1979, Gerdeaux 2001). Currently, there is an increasing need to conserve and enhance whitefish populations as its natural biotope is increasingly altered by human activities. But, the interactions between fish and habitat in freshwater lakes is not always well understood because the spatial distribution of most aquatics habitats is poorly known and habitat use is difficult to quantify (Bégout Anras et al. 1999).

In *C. lavaretus*, scientific net fishing and echo-sounding have provided a good understanding of the spatial distribution of schools at different times of the year as well as the distribution of size categories in the water column (Lampert 1971, Skurdal et al. 1985, Eckmann 1991,1995, Naesje et al. 1991, Appenzeller 1995, Kahilainen et al. 2004). But, to date no studies have been conducted on mobility patterns and habitat use on the individual scale. Such observations would however bring complementary knowledges on different aspects of its behavioural ecology that may improve

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the management of whitefish populations. Acoustic biotelemetry is an effective technique for locating individual fish continuously and with high accuracy that has been used with *Coregonus clupeaformis* in a Canadian boreal lake (B é g o u t A n r a s et al. 1999).

Using manual acoustic tracking our study quantified (1) the spatial distribution (2) the movement patterns and (3) the depth preference of adult whitefish in a small artificial lake of eastern Belgium were the species was introduced in 1978 for recreational fishing.

Study Area

Robertville Lake (Fig. 1) is located in the East of Belgium on the Warche River at an altitude of 490 m. It was created in 1929 for hydroelectric production. It covers a surface area of 63 ha (length: 3.5 km; average width 150 m), its maximum volume is 7.7×10^6 m^3, maximum depth is 47 m, average depth is 12.2 m mean variation of water level is 3 m and its mean transparency is 2.5 m (M a r n e f f e 2002). It is classed as a mesotrophic to eutrophic lake. Between June 1999 and June 2000, the mean chlorophyll-a content was 9 $\mu g.l^{-1}$ (maximum: 46 $\mu g.l^{-1}$) (M a r n e f f e 2002).

Several scientific gillnet fishing campaigns (at the surface and at the bottom of the lake) were undertaken between 1996 and 2004 (T i g n y 2000, M e r g e n et al. 2003). The species most frequently encountered were the common bream (*Abramis brama*), roach (*Rutilus rutilus*), perch (*Perca fluviatilis*), zander (*Sander lucioperca*), ruffe (*Gymnocephalus cernua*), pike (*Esox lucius*), common carp (*Cyprinus carpio*), peled (*Coregonus peled*), whitefish and tench (*Tinca tinca*). Brown trout (*Salmo trutta*) were occasionally caught, as were chub (*Leuciscus cephalus*), rudd (*Scardinus erythrophthalmus*), ide (*Leuciscus idus*) and the common bleak (*Alburnus alburnus*).

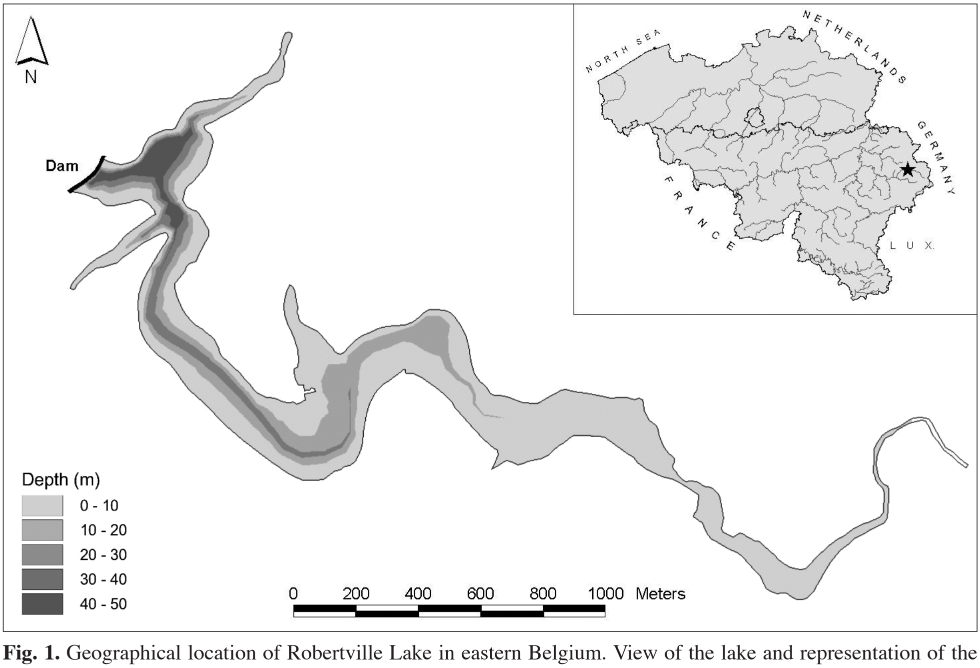

Fig. 1. Geographical location of Robertville Lake in eastern Belgium. View of the lake and representation of the water depth categories.

Material and Methods

As it was not possible to capture fish suitable for telemetric study from Robertville Lake using gillnet fishing (they died or were severely injured), six fish (Table 1) were more easily caught from the nearby Butgenbach Lake (7 km apart on the same river) in May/June 2004, during complete emptying required for maintenance work of the intake dam. These fish were than relocated to Robertville Lake (Table 1).

Three individuals were equipped with acoustic transmitters with pressure sensors weighing 30 g in the air (Vemco Ltd, model V16P-4l, 100PSI), with a battery life of 1 year. The relevance between the depth specified by the transmitter and its real position in the water column was successfully tested before fish tagging. The three other individuals were equipped with acoustic pingers weighing 4 g in the air (Vemco Ltd, model V8SC-2L), with a battery life of 3 months (Table 1).

Before tagging, the fish were anaesthetised using a 0.15 $ml.l^{-1}$ solution of 2-phenoxy-ethanol. When the fish were fully anaesthetised, showing no reaction to external stimuli, they were placed ventral side up in a V-shaped support adjusted to their morphology. The whole body except the ventral side stayed in the water, to avoid dehydration and to permit a continuous oxygenation of the gills. The transmitters were inserted into the peritoneal cavity of the fish through a 15- to 25-mm incision (depending on the transmitter model), 10–15 mm anterior to pelvic girdle. The incision was closed by three or four separate stitches made using sterile resorbable thread (polyglactin 910). The procedure took less than 15 minutes. For recovery, fish were placed in a tank with lake water. As soon as they had recovered spontaneous swimming (about 60 min after surgery), they were released in downstream Robertville Lake near the dam (Fig. 1) in order to avoid trauma due to long postoperative care.

Fish were located manually using a VR60 receiver and a V10 directional hydrophone (Vemco Ltd). In accordance with Holland et al. (1992), fish were located from a small boat to allow tracking by a single operator and rapid changes in direction, and to reduce the hydrodynamic and mechanical noise. Fish were located as follows (Jadot et al. 2002): (1) detection of the signal; (2) rotation of the directional hydrophone through an arc and determination of the signal direction; (3) movement in the direction of the signal until its intensity reached a maximum in every direction, indicating that the boat was above the fish; (4) location of the fish position with a mono-frequency GPS (Magellan®) and recording the depth on the dial of the receiver in the case of a V16P transmitter. Each fish was located every week or 10 days, except in August when only one tracking session was performed during the month. *Whitefish 3* and *Whitefish 1* were tracked for 24-Hr periods between 1 and

Table 1. Characteristics of the six tracked *Coregonus lavaretus* in the Robertville-lake.

Fish code	Fork length (mm)	Dry weight (g)	Date of capture	Date of tagging	End of tracking	Reason	Transmitter model
1	519	1641	26/05/2004	27/05/2004	15/10/2004	end of study	pressure
2	518	1450	26/05/2004	27/05/2004	02/09/2004	died?	pressure
3	486	1260	02/06/2004	02/06/2004	15/10/2004	end of study	pressure
4	470	1133	04/06/2004	07/06/2004	30/09/2004	battery life	position
5	285	220	04/06/2004	07/06/2004	16/09/2004	died?	position
6	482	1280	04/06/2004	16/06/2004	30/09/2004	battery life	position

2 July and 8 and 9 September 2004, respectively. Last locations of the study were performed from 2 September to 15 October depending on different reasons (Table 1).

GPS locations of each whitefish were mapped into Arcview ® software. The depths of the lake were estimated into Arcmap ® software by digitalisation and interpolation of height curves from a topographical map drawn before the Robertville dam wall construction (1929). The depth numerical model was then re-classed at 10-m depth interval. The percentage use of depth classes by the six whitefish and its equivalent area provided a normalised preference index of the water column.

Throughout the duration of the study, two temperature recorders were placed at depths of 1.5 m and 7 m in the centre of the lake (Fig. 2). Temperature recorders placed at deeper places were lost during the study. On 2 June 2005, a depth profile were established for water temperature, dissolved oxygen and pH in the deeper part of the lake (Fig. 3).

Results

Environmental records

During the study period (June to October 2004), the maximum daily temperature ranged form 14.5 to 23.8°C at depth of 1.5m, and from 12.9 to 20.3°C at depth of 7m (Fig. 2). The depth profile of June 2005 indicates that the temperature progressively decline with the depth and that the thermocline is located at 35-m depth (Fig. 3a). Oxygen concentration varied from 10.66 to 5.45 mg.l^{-1} from 0 to 30-m depth and than falls on an extremely low level (near zero) at 35-m depth (Fig. 3b). The pH varies from 8.83 to 6.35 from the surface to 35-m depth (Fig. 3c).

Movement patterns and spatial distribution

Whitefish 1 was very mobile and used nearly the entire surface area of the lake (Fig. 4). From one location session to another, it was almost always located in a different zone of the lake and a preferred resting place could not be distinguished. *Whitefish 2* was never located in the eastern part of the lake. It was often located in the deepest zones in the central part of the lake and just upstream of the water-supply dam. *Whitefish 3* was essentially located in the deepest zone of the lake, just upstream of the dam. This fish was located in only two locations outside

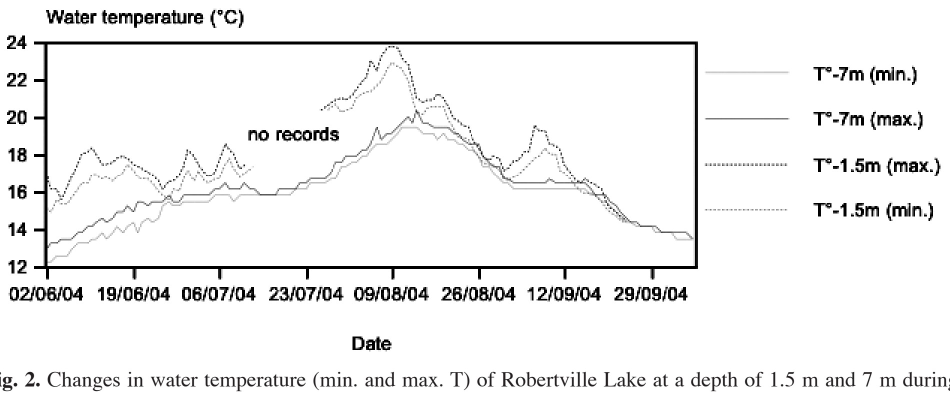

Fig. 2. Changes in water temperature (min. and max. T) of Robertville Lake at a depth of 1.5 m and 7 m during the period when the whitefish were tracked.

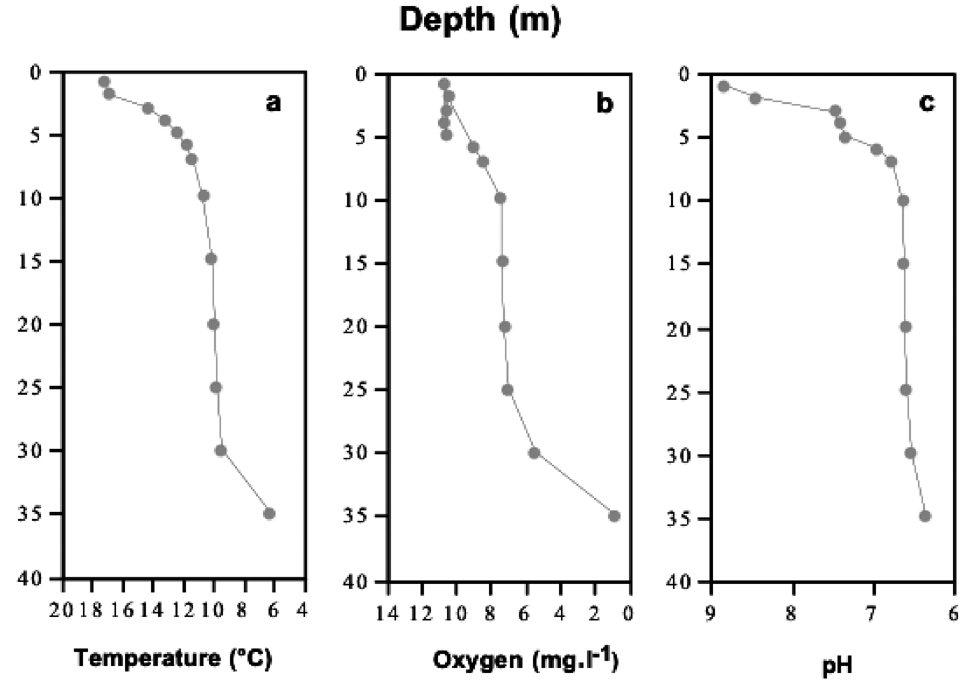

Fig. 3. Changes in temperature (A), oxygen saturation (B) and pH (C) of the water in Robertville Lake (zone upstream of the dam) according to depth on 2 June 2005.

of this zone. *Whitefish 4* mainly made use of the deepest zone of the lake, just upstream of the dam. However, the few recordings in the central and eastern zones of the lake indicate that this fish utilised a large part of the surface area of the lake. *Whitefish 5* (the smallest) was highly mobile and was located in the western and central part of the lake (deep zone) and did not seem to make preferential use of a precise zone. It was never located in the same place from one tracking session to another. *Whitefish 6* was also mobile and made preferential use of the central and western parts of the lake (deep zones) and was occasionally located between these two zones. Considering that *whitefish 1* used 100% of the lake length, the normalised utilisation of the lake length for the other individuals were 39% (*whitefish 3*), 50% (*whitefish 5*), 64% (*whitefish 6*), 78% (*whitefish 2*) and 98% (*whitefish 4*).

On some occasions (for example on 24 June and 22 July 2004) most of the tracked fish were located on the same site (near the dam) and, sometimes, they were isolated from each other's (for example on 9 September 2004). During a 24-h tracking session on 8 and 9 September 2004, the *whitefish 1* occupied a more than the half of the surface of the lake and covered 2.8 km. On the opposite a 24-h tracking session on 1 and 2 July 2004 demonstrated that *whitefish 3* remained in continuous movement in the deep zone situated upstream of the dam.

Depth preference

The three individuals equipped with acoustic transmitters with pressure sensors adopted a relatively variable depth utilisation (Fig. 5). *Whitefish 1* was for the most part located between 8 and 13 m water depth and occasionally moved towards the surface of the lake

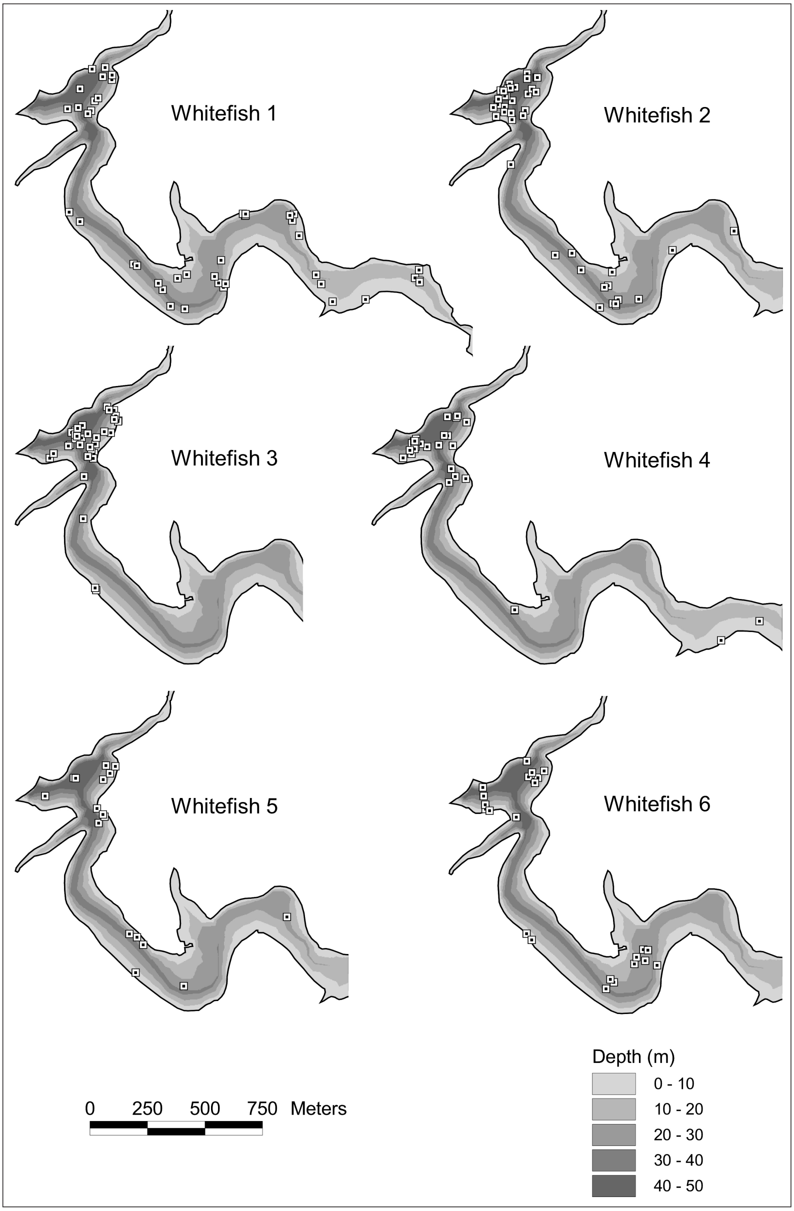

Fig. 4. Geographical representation of the locations (white spots) of the six whitefishes during the different tracking sessions carried out between 2 June and 30 September 2004 in Robertville Lake.

(min. depth, 2.6 m). Between the beginning of June and the beginning of August, *whitefish 2* was very stable in the water column and was consistently located between 14 and 17 m water depth. Then, from the beginning of September until the end of tracking, it was mainly located between 2.6 and 3.5 m deep. *Whitefish 3* was never recorded at a depth less than 13.9 m and was essentially located between 14.5 and 17 m, with incursions towards deeper waters during the autumn (max. depth, 26 m). The three individuals were regularly located at different depths during a single tracking session. Significant differences were found in the depth used by *whitefish 1* versus *whitefish 3* and by *whitefish 2* versus *whitefish 3* ($p<0.001$ Scheffe's test). Calculating normalised utilization index of the five depth-classes of the lake by the six tracked whitefish during the entire tracking period indicates individuals clearly prefer the deep-water zones of the lake that are intensively used despite there low availability (Table 2).

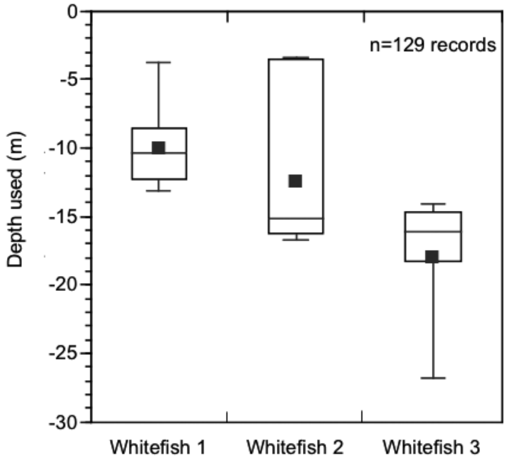

Fig. 5. Depth utilisation of the three whitefish equipped with a pressure transmitter. Values are median, percentiles 5, 25, 75 and 95.

Table 2. Available and utilise surface, depth-layers and normalised preference index of the six tracked *Coregonus lavaretus*.

Depth class (m)	Available surface (% of lake area)	Percentage of utilisation (%)	Preference of utilisation (utilisation/surface)	Normalised preference index
0< depth≤10	40.9	17.1	0.4	0.091
10< depth≤20	27.6	21.7	0.8	0.170
20< depth≤30	20.3	24.2	1.2	0.259
30< depth≤40	7.4	17.7	2.4	0.518
40< depth≤50	3.8	17.7	4.6	1.000

Discussion

Methodology

Due to the impossibility to capture alive individuals in Robertville lake, the whitefish tracked in this study were introduced from a neighbouring lake (7 km upstream in the same river) that was momentary emptied. The two lakes are very similar in terms of surface and depth availability and identical in terms of water quality. First locations of each fish were performed one week after their releasing, however, the adaptation time of the transferred fish in Robertville lake cannot be estimated. This investigation is the first contribution to the study of whitefish mobility patterns and depth preference using implanted acoustic biotelemetry transmitters with manual fish location. In the past, individual behavioural tracking has already been carried out to study the reaction of whitefish to leader nets and strobe lights using externally mounted acoustic transmitters and VRAP automatic radio positioning buoys (Köningson et al. 2002, Lunneryd et al. 2002). Intraperitoneal insertion of larger acoustic transmitters with pressure sensors meant we had to select individuals larger than the mean size in the lake. Despite the fragility of the species, no deaths were observed in the days immediately following tagging however two fish were considered dead at the end of tracking. A first whitefish was located several weeks after the experiment at more than 30 m deep. The second whitefish remained near the lake shore for 2 weeks at a depth of 4 m, where its transmitter was collected, but not the fish's body. It is unfortunately impossible to determine the precise cause of death of these two individuals, nearly 3 months after tagging.

Movement patterns and spatial distribution

Despite whitefish are gregarious fish, the individual tracking showed quite variable lake use patterns. Two individuals traveled the entire length and breadth of the lake, whereas others preferred deeper zones in the middle part of the lake or just near the retaining dam wall in the deepest zones of the lake. Different individual patterns of behaviour were also observed using acoustic biotelemetry in the *Coregonus clupeaformis* during the reproduction period (October–November) in a small boreal lake in Ontario, Canada (Bégout Anras et al. 1999). Individual tracking during 24-Hr periods attests the diversity of space over shorter time scale and suggests that whitefish are constantly mobile. Locations of fish taken a few minutes apart have always shown movement between observations. Certain movements clearly correspond to quasi-linear migrations from one part of the lake to another. Others are comparable to repetitive rotational movements in the same part of the lake. This high mobility of whitefish is probably related to the food intake of the species. In summer 2003 a single *C. peled* was followed using the same method as a preliminary feasibility study in Robertville and it was also highly mobile and traveled the entire lake surface (M. Ovidio, unpublished results). In Robertville Lake, analysing stomach contents of whitefish revealed an exclusively zooplankton diet (Malbrouck 2000). This essentially plankton diet of the Robertville whitefish could reflect the need for a nearly continuous search for low-energy-providing food and therefore high mobility. However, the literature indicates that *C. lavaretus* adults can adopt a diet mainly made up of zooplankton, benthos or a mixed diet, depending on the availability of prey encountered in the milieu (synthesis in Malbrouck 2000). Several authors have demonstrated that coregonids in general, and *C. lavaretus* in particular, engage in cannibalism on their eggs (Pomeroy 1991). Certain authors even describe situations where the young fish are consumed (Sandlund et al. 1987, Naesje et al. 1991). The precise tracking of individuals from one tracking session to another suggests that tracked whitefish were sometimes highly spaced out one day, then grouped another day. Unfortunately, the water in Robertville Lake is not sufficiently transparent for visual observation with underwater diving and it was impossible to determine if the whitefish were grouped in schools. In less turbid environment, combined studies using biotelemetry and visual observations while diving could improve our knowledge on schoal formation and break-up in whitefish.

Depth preference

Previous studies have suggested that the distribution in depth of *C. lavaretus* is highly variable from one site to another, and comparisons are difficult because of the variability of the lake's biological and physicochemical characteristics (volume, fish assemblage, oxygen concentration), the climate and the light intensity of the different study sites. In Tyrifjorden Lake (Norway), Hessen et al. (1986) showed that the whitefish present a bimodal distribution in the water column depending on the size of the individuals. Those that were less than 27 cm long were mainly captured in the littoral zone and the deepest layers in the pelagic zone. The whitefish longer than 27 cm were for the most part distributed in the upper layers of the pelagic zone. Using ultrasonic echosounding, Eckmann (1995) showed depth distribution variations of whitefish (all size categories) in Lake Constance. In November, few fish were detected at the surface (3–10 m) and most of them were found between 10 and 30 m. In December and January, the whitefish were essentially found between 10 and 60 m. In April, the greatest number of detections was between 3 and 10 m. In a subartic lake of Finland (Lake Muddusjärvi), the only planktivorous *C. lavaretus* used both epibenthic and pelagic habitats, but vertical habitat selection varied both over time of day and season. In June, when light intensity was continuously high, whitefish did not perform diel vertical migration. In August and September, when dark nights were distinguishable, whitefish ascended from the bottom to the pelagic zone at dusk to feed on zooplankton and descended at dawn. In our study, individuals presented quite variable patterns of use of the water column and were regularly located at different depths during a single tracking session. Two individuals were never located at more than 16 m deep and were sometimes recorded near the surface (0–5 m). The third individual never went into the upper layers of the water column (min. depth: 13.9 m) and was frequently recorded at depths greater than 20 m. The covering of the two dimensional locations of the six whitefish on the five lake-depth-classes clearly indicate a higher preference for the deepest classes, although the acoustic transmitters with pressure sensors indicated that they did not use the entire available water column, probably because the concentration in oxygen was very low below 30-m depth. A single *C. peled* tracked in Robertville in summer 2003 (M. Ovidio, unpublished results) revealed a depth utilization closer to the surface (mean 6.6 m) ranging from 0.8 m to 24.0 m. Marneffe (2002) showed that at Robertville Lake, the maximum concentration in zooplankton (cladocera, rotifers, copepods) during the summer were mainly encountered in the first 5 m of the water column. In September–October, plankton was distributed more homogeneously in the first 15 m of the water column, with lower concentrations than during the summer. During the summer, less than 20% of the daily recordings of whitefish with pressure sensors emerged in the first 5 m of the water column, and one individual was never recorded there. Habitat selection by the fish is a compromise that results from the interaction of abiotic factors (temperature, light intensity, season, etc.) and biotic factors such as predation risks and the abundance of food (Werner & Hall 1988, Becker & Eckmann 1992, Beauchamp et al. 1999). The fact that the whitefish in Robertville Lake do not necessarily inhabit areas where the plankton is the most plentiful during the summer period possibly results from a compromise between food availability and the presence of predatory species such as pike (*Esox lucius*) or fish-eating birds (heron, cormorant). Indeed, an important factor in habitat selection is the risk of predation, which can force fish to migrate to less profitable feeding areas (Werner & Hall 1988, L'Abée-Lund et al. 1993). In the particular case of Robertville Lake, the small number of locations of the whitefish in the 0–5 m depth-class could also probably be explained by temperature reached during the summer period (sometimes higher than 23.5 °C), as *C. lavaretus* is more thermo sensitive than *C. peled*.

Conclusion

Using an original methodology (manual acoustic telemetry), our study collected a great deal of original data on the behavioural ecology of the whitefish, particularly on the use of space and time on the individual scale. The results remain preliminary because of the small number of fish tracked during the spring and summer periods. Similar tracking studies on a larger number of resident individuals and over the entire annual cycle, in combination with more complete measures of the physiochemical variables as well as food abundance could be a particularly enriching perspective for future investigations.

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LITERATURE

Appenzeller A.R. 1995: Hydroacoustic measurement of spatial heterogeneity of European whitefish (*Coregonus lavaretus*) and perch (*Perca fluviatilis*) in lake Constance. *Arch. Hydrobiol. Issues Advanc. Limnol. 46: 261–266.*

Beauchamp D.A., Baldwin C.M., Vogel J.L. & Gubala C.P. 1999: Estimating diel, depth specific foraging opportunities with a visual encounter rate model for pelagic piscivores. *Can. J. Fish. Aquat. Sci. 56: 128–139.*

Bégout Anras M.-L., Cooley P.M., Bodaly R.A., Anras L.& Fudge R.J.P. 1999: Movement and habitat use by lake whitefish during spawning in a Boreal lake: integrating acoustic telemetry and geographic information systems. *Trans. Amer. Fish. Soc. 128: 939–952.*

Becker M. & Eckmann R. 1992: Plankton selection by pelagic European whitefish in Lake Constance: dependency of season and time of the day. *Polskie Archivum Hydrobiology 39: 393–402.*

Bern Convention 1979: Convention on the conservation of European wildlife and natural habitats. *Bern/Berne, Council of Europe, 19/09/1974.*

Eckmann R. 1991: A hydroacoustic study of the pelagic spawning behaviour of whitefish (*Coregonus lavaretus*) in lake Constance. *Can. J. Fish. Aquat. Sci. 48: 995–1002.*

Eckmann R. 1995: Abundance and horizontal distribution of Lake Constance pelagic whithefish (*Coregonus lavaretus* L.) during winter. *Arch. Hydrobiol. Issues Advanc. Limnol. 46: 249–259.*

Gerdeaux D. 2001: Les corégones *Coregonus lavaretus* (Linné, 1785). In: Keith P. & Allardi J. (eds), Atlas des poissons d'eau douce de France.Patrimoine naturel, n° 47, 2001. *Paris: Muséum National d'Histoire naturelle: 263–265 (744).*

Hessen D.O., Skurdal J., Vøllestad L.A. & Berge D. 1986: Habitat use among size groups of monomorphic whitefish *Coregonus lavaretus. Hydrobiologia 137:185–192.*

Holland K.N., Lowe C.G., Peterson J.D. & Gill A. 1992: Tracking coastal sharks with small boats: Hammerhead shark pups as a case of study. *Aust. J. Mar. Fresh. Res. 43: 61–66.*

Jadot C., Ovidio M. & Voss J. 2002: Diel activity of *Sarpa salpa* (Sparidae) by ultrasonic telemetry in a *Posidonia oceanica* meadow of Corsica (Mediterranean Sea). *Aquat. living Resour. 15: 343–350.*

Kahilainen K., Malinen T., Tuomaala A. & Lethonen H. 2004: Diel and seasonal habitat and food segregation of three sympatric *Coregonus lavaretus* forms in a subartic lake. *J. Fish Biol. 64: 418–434.*

Könignson S., Fjälling A. & Lunneryd S.G. 2002: Reactions in individual fish to strobe light. Field and aquarium experiments performed on whitefish (*Coregonus lavaretus*). *Hydrobiologia 483: 39–43*.

L'Abée Lund J.H., Langeland A., Jonsson B. & Ugedal O. 1993: Spatial segregation by age and size in Artic charr: a trade off between feeding possibility and risk of predation. *J. Anim. Ecol. 62: 160–168*.

Lampert W. 1971: Studies on the biology and the population dynamics of the Coregonids in Lake Schluchsee. *Arch. Hydrobiol. (Suppl.) 38: 237–314*.

Lunneryd S.G., Westerberg H. & Wahlberg M. 2002: Detection of leader net by whitefish *Coregonus lavaretus* during varying environmental conditions. *Fish. Res. 54: 355–362*.

Malbrouck C. 2000 : Etude des différentes espèces de corégones et de leur regime alimentaire en vue de leur valorisation halieutique dans les lacs barrage de Bütgenbach et de Robertville. *Rapport final pour le Ministère de la Région Wallonne, DGRNE., 66 pp*.

Marneffe Y. 2002. Etude d'un hydrosystème perturbé en Haute-Ardenne: impact des activités anthropiques et des retenues artificielle sur les flux de nutriments et sur les peuplements zoobenthiques et zooplanctoniques dans le bassin de la Warche. 2002. *PhD Thesis, University of Liège, 253 pp*.

Mergen P., Frank V., Gérard P. & Micha J.C. 2003 : Populations ichtyologiques dans les lacs barrages en Région wallonne. *Tribune de l'Eau 623: 22–51*.

Næsje T.F., Josson B. & Sandlund B. 1991 : Habitat switch and niche overlap in coregonid fish: effects of zooplankton abundance. *Can. J. Fish. Aquat. Sci. 48: 2307–2315*.

Pomeroy P.P. 1991: A comparative assessment of temporal variation in diet powan, *Coregonus lavaretus* (L.), from loch Lomond and Loch Eck, Scotland, U.K. *J. Fish Biol. 38: 457–478*.

Sandlund O.T., Naesje T.F. & Kjellberg G. 1987: The size selection of *Bosmina longispina* and *Daphnia geleata* by co-occurring cisco (*Coregonus albula*), whitefsh (*Coregonus lavaretus*) and smelt (*Osmerus eperlanus*). *Arch. Hydrobiol. 110: 357–363*.

Skrudal J., Hessen D.O. & Berge D. 1985: Food selection and vertical distribution of pelagic whitefish *Coregonus lavaretus* (L.) in Lake Tyrifjorden, Norway. *Fauna Norvegian series A6: 18–23*.

Tigny V. 2000: Contribution à l'étude du regime alimentaire des Corégones peled dans lacs de Robertville et Bütgenbach en vue de préciser leur position au sein du réseau trophique. *Ms Thesis, Catholic University of Louvain (Belgium), 78 pp*.

Werner E.E. & Hall D.J. 1988: Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. *Ecology 69: 1352–1366*.