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Annual and diel activity cycles of a northern population of the large migratory cyprinid fish asp (*Leuciscus aspius*)

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Abstract Little is known about the exact movement parameters of migratory cyprinids listed as conservation priorities. A northern population of predatory asp, listed on the Bern Convention Appendix III, was studied in a near natural lake–river ecosystem by tracking adult fish tagged with acoustic transmitters for 32 months. Activity levels in terms of swimming speed, swimming distance and movement range were four times higher during the warmer part of the year (water temperatures > 12–15 °C, April/ May–September), which coincides with their main feeding period, than other times of the year. All fish had an annual riverine movement range larger than 40 km (max 110 km). Asp activity was affected by light, habitat type and water discharge. For most of the year, activity levels, in terms of number of movements per time unit, were higher during dawn and dusk than during day and night. Under poor light conditions and low temperatures, activity was also relatively high during the day. Fish were more likely to swim upstream around sunrise or during the day than during other diel periods. Knowledge about high-activity periods, which may render the fish vulnerable to fishing and other impacts, can be used to develop and evaluate fishing regulations. Large annual movement ranges highlight the need for extensive continuous river systems open for migration between essential habitats. This study emphasises the need for region-specific research on the ecology and behaviour of fish populations in order to facilitate protection of the populations in the face of negative human impacts.

The second author, Dr. Odd Terje Sandlund, died unexpectedly prior to publication. This paper is dedicated to him with many fond memories of our joint work together. He will be greatly missed.

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Introduction

A major challenge for conservation managers in developing strategies for threatened and/or protected

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freshwater fishes is the lack of information on the threatened species' environmental biology (Miranda and Miqueleiz 2021). This applies to the European cyprinid, asp *Leuciscus aspius* (L.), a migratory lithophilous and piscivorous fish, which is listed for protection in Annex III of the Bern Convention (Council of Europe 1979). Like many migratory fishes, asp is threatened by various human-related impacts, although river regulation structures are a particular concern as barriers to migration (Freyhof and Kottelat 2018; Pfauserová et al. 2019). The need for better information is particularly acute on the migratory behaviour of native asp populations in the northerly parts of Europe, where the species remains poorly studied (Reebs 2002; Lehtola et al. 2006, but see, e.g. Kärgenberg et al. 2020a).

In most environments, fishes demonstrate both seasonal and diel cyclic behaviour. Many species are primarily diurnal/nocturnal and are active by day or night, some species move mainly during crepuscular periods of twilight (during dusk and/or dawn), whereas only a few species are cathemeral and show no periodicity (Arndt and Evans 2022; Reebs 2002; Helfman et al. 2009). Many circadian rhythms are under the control of endogenous molecular clocks (which persist even under constant light or darkness) and modulate most daily behavioural and physiological rhythms (Sánchez-Vázquez et al. 2019). Activity rhythms can also be caused by changes in the water oxygen content or some other external factor (Lucas and Baras 2001). Diel activity patterns may change during a year (Prchalová et al. 2006). In addition to diel periodicity, seasonal patterns in activity, feeding and distribution are found in most fish species. In temperate areas, these patterns are associated with seasonality in factors such as food and oxygen availability, vegetation cover, water flow and turbulence, and water clarity, which vary among habitats (Lucas and Baras 2001; Helfman et al. 2009). Consequently, human-generated habitat modifications can drastically alter both temporal (i.e. diel activity patterns, prey attack rates) and spatial (i.e. aggregation, foraging radius) components of behaviour in a mobile animal (Larranaga and Steingrímsson 2015). Four-season and diel telemetry data on activity patterns of free-living fish at high latitudes are scarce (Marsden et al. 2021; Reebs 2002).

A native species in Estonia, the asp has disappeared in several fragmented river systems (Tambets et al. 2018a). Earlier, the annual catch of asp was ca 1–5 t (Kirsipuu et al. 2003), but since 1992 commercial and recreational fishing for asp is prohibited (Riigi Teataja 2020). The asp population in River Emajõgi, which connects the two large lakes Peipsi and Võrtsjärv, was studied by means of acoustic telemetry. This lake–river water system is the top priority habitat for asp in Estonia. It is free of barriers to fish migration, it connects numerous Habitat Directive sites, and it provides valuable habitats for a variety of species listed in Annex II of the Directive, including asp, weatherfish (*Misgurnus fossilis* L.), spined loach (*Cobitis taenia* L.) and bullhead (*Cottus gobio* L.) (Council of the European Communities 1992). Recent conservation efforts, including restoration of habitats and stocking of juveniles, have improved the asp population status in this area (Wildlife Estonia 2018). Improved asp population status may indicate that there is an opportunity to develop and implement a management plan, which may include a limited catch (or catch and release) of asp in this lake–river system (Wildlife Estonia 2018; Tambets et al. 2018b). This opportunity raises a number of questions regarding issues such as closure seasons and areas, and the effects of various fishing methods and gear restrictions. Recent findings suggested that asp in the continuous Emajõgi lake–river system have broad-scale migration patterns that are different from populations in southern modified systems (Kärgenberg et al. 2020a). It may be assumed that the asp population in this system, adapted to the northern light and temperature regimes, also differs in other important behavioural features.

The aim of the present study is to improve our knowledge on asp migratory patterns in northerly latitudes. Using acoustic telemetry, the specific study objectives were to (1) assess the variability of movements, including intensity, speed, distance and direction; and (2) provide the first detailed information on seasonal and diel aspects of asp biology and behaviour in continuous (un-fragmented) lake–river systems.

Material and methods

Study design

The study was undertaken in River Emajõgi (100 km long, mean annual water discharge 70 m^3 s^{-1}), which

connects Lake Peipsi (3555 km^2) and Lake Võrtsjärv (269 km^2) (Fig. 1). The river has a low gradient (3.6 cm km^{-1}) and few rapids, and varies in water depth (mean 3.4 m, max 10.7 m, Maritime Administration of Estonia, unpublished data). The upper half of the river is highly meandering, with numerous oxbow lakes. Most rapids suitable for lithophilous spawners are located in the tributaries. The biggest tributary is the River Pedja (including the tributary Põltsamaa).

In total, 54 mature asp were captured using fyke and gill nets in the upper, middle and lower third of the study river between 10 October and 21 December 2011, and between 3 and 28 April 2012 (see details in Kärgenberg et al. 2020a). Fish were tagged on site the day of capture, or they were kept in keep net boxes

for 1 to 4 days before tagging. The fish were anaesthetised using 2-phenoxyethanol solution at a concentration 0.75 ml l^{-1} (Sigma-Aldrich, St. Louis, MO, USA). Coded acoustic transmitters were surgically implanted into the body cavity (Vemco, Nova Scotia, Canada, V13-1L-A69-1601 tags, 36×13 mm, 6.0 g in water, with a random pulse delay of 50–100 s, estimated battery life 755 days). After recovering for 2–6 min, all fish could hold position and swim normally, and were released into the river near the catch site. The large-scale migration patterns of these fish were described by Kärgenberg et al. (2020a). The data used in the present analyses have not been published before.

Tagged fish were monitored when within the range of stationary automatic receivers (Vemco VR2W) and

Fig. 1 Map of the study area. River Emajõgi flows from Lake Võrtsjärv to Lake Peipsi. Rivers where receivers were deployed to register fish tagged with acoustic receivers are in bold. Location of receivers deployed year-round (open circles) or for shorter periods (open triangles) as well as location of a hydrometric station (black arrow) in Tartu city are indicated. Base maps: Estonian Land Board and Natural Earth (Kelso and Patterson 2010)
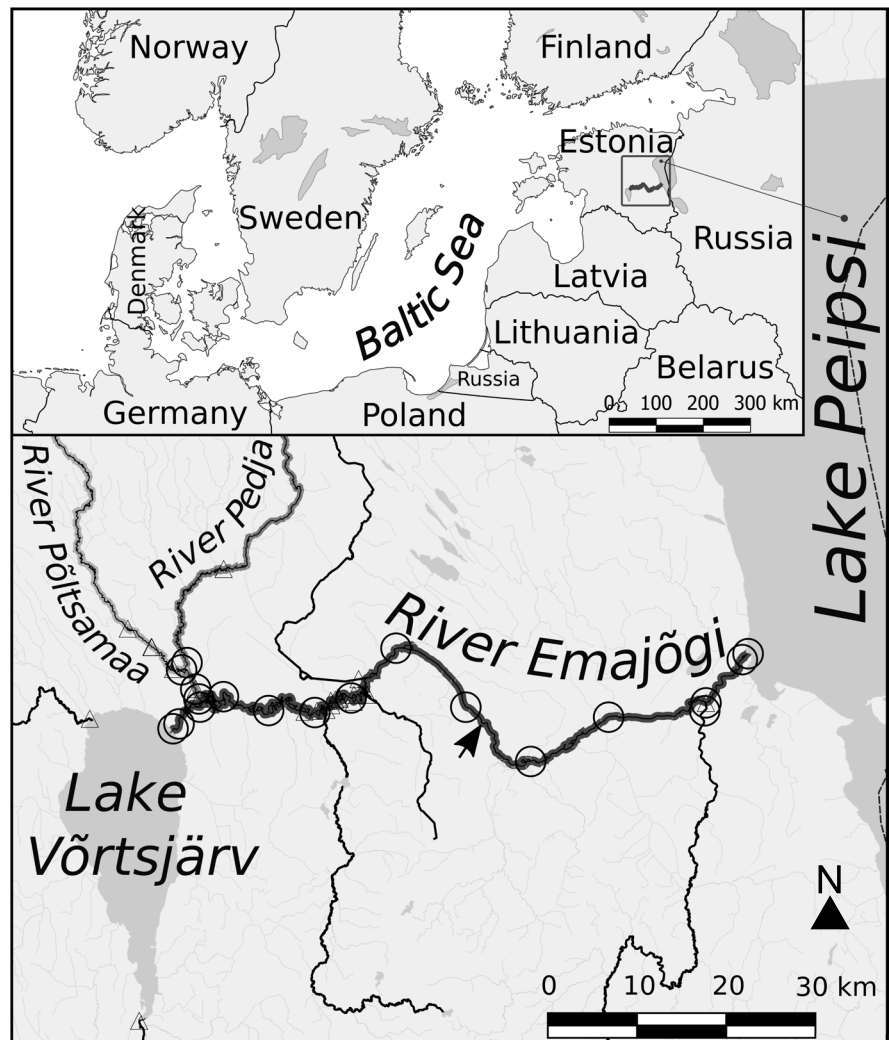
by manual tracking (Vemco VR100). Receivers were deployed in River Emajõgi and connected waterbodies (Fig. 1). Nineteen receivers were deployed year-round for 2.5 years. An additional 19 locations were temporarily deployed with receivers, depending on seasons and fish locations (mean duration about 2.5 months per site). When a tagged fish was within the detection range of a receiver, the date, time and individual fish code were automatically recorded and stored by the receiver, and periodically downloaded to a computer. Manual tracking to locate tagged fish was performed 71 times by boat from 17 November 2011 to 10 April 2014, covering River Emajõgi and tributaries, oxbow lakes and artificial waterbodies (gravel pits and boat channels). The river stretch covered by tracking was adjusted according to the data obtained from the automatic receivers. Individuals were recorded for up to 765 days (mean 325 days) until 23 May 2014 (see also Appendix 1).

Data analysis

To detect any diel or interannual variation in fish movement activity, the data were divided into four periods: dawn, day, dusk and night. Dawn and dusk periods were defined as ± 1 h (i.e. with a duration of 2 h) from the time when the sun's upper edge appeared or disappeared on the horizon according to local timetables. The duration of each day and night period was calculated by subtracting dawn and dusk periods. Data from 2012 to 2013 was used, because for these years there is data from the entire year facilitating tests of interannual variation in diel activity.

A 'movement activity' event of a fish was defined as arrival or departure in any receiver's detection range. These events were situations when a fish moved from one detection range to another, or returned to the detection range of the same receiver after an absence of at least 1 h. Since this study focused on movement, consecutive recordings at the same receiver within 1 h were excluded prior to data analysis, after which 12,435 activity events remained (53 individuals). The activity events of fish during each day period were counted and summed by month.

The null hypothesis for diel activity was that the fish did not differ in its number of activity events per unit of time between each of the individual diel periods (dawn, day, dusk or night). The deviation from the null hypothesis was tested by constructing

a zero-inflated Poisson rate model with correlated residuals using the glmmTMB function of the glmmTMB package in R (Brooks et al. 2017). The explanatory variables included in the model as fixed effects were month, year and the diel period (with full 3-way interaction). Distance between stations was used as a covariate and logarithm of the period length as model offset. To account for the within-fish autocorrelation, autoregressive structure (of order 1) of successive residuals was assumed. Estimated marginal means (EMMs) of diel activity were estimated using the emmeans package in R (Lenth 2021) and compared within months (between diel periods) using Bonferroni correction of multiple comparisons.

The direction of fish 'movement activities', derived from receiver detections, was categorised as 'upstream movements' or 'downstream movements' (51 individuals). The total number of upstream and downstream movements was counted for each diel period (dawn, day, dusk or night). There was no significant interannual variation in diel movement activity between 2012 and 2013 for upstream movements (tested with chi-square test, 2×4 table; $\chi^2 = 4.3462$, $n = 1400$, df $= 3$, $p = 0.23$; 31 individuals), or downstream movements (tested with chi-square test, 2×4 table; $\chi^2 = 3.2434$, $n = 1646$, df $= 3$, $p = 0.36$; 40 individuals), and monthly data were therefore not separated by year. Possible differences in activity in terms of upstream and downstream movements between each diel period were examined by constructing a binomial mixed model (GLMM) using the glmmTMB function of the glmmTMB package in R (Brooks et al. 2017). The explanatory variable included in the model as fixed effect was diel period. To account for the within-fish effects, fish ID code was used as a random effect. Marginal means of diel activity were estimated using the emmeans package in R (Lenth 2021) and compared within months (between diel periods) using Tukey correction of multiple comparisons.

The speed of seasonal riverine movements was measured from the time interval of detections between receivers, or based on positions recorded by manual tracking. The distances moved were calculated by using the Road Graph Plugin of QGIS (Hanson and Seeger 2017). The range area of stationary receivers along the rivers upstream and downstream (until the nearest river meander, max 500 m) was subtracted from the distance moved by fish. After subtracting, all distances shorter than

1 km were excluded to reduce possible inaccuracy in calculations of movement speed due to short distances.

Fish movement speeds were recorded 1550 times on distances between 1 and 43 km (mean distance ± SD: 7.0 ± 4.4 km) during the study period, which lasted 956 days in total. About 90% of the recordings were made in River Emajõgi, as this was the main habitat used by the tagged fish (Kärgenberg et al. 2020a). Nine per cent of recordings were made in the biggest tributary Pedja (a habitat for wintering and spawning) including its tributary Põltsamaa (a spawning habitat) and 1% in other tributaries and oxbow lakes. Asp movement speeds and activity were not measured when the fish were in the lakes Peipsi and Võrtsjärv (nearly 20% of the total study time).

Seasonal variations in fish riverine movement speed and possible relations with environmental and biological variables were assessed with a linear mixed-effects model (LMM) using the lmer function of the lme4 package in R (Bates et al. 2020). The dependent variable was transformed by taking the fourth root of movement speed in order to symmetrise residual distribution. The explanatory variables included in the initial model as fixed effects were water temperature, water temperature trend, discharge, discharge trend, river km (mean distance of movement route from Lake Peipsi), movement direction (upstream or downstream), final target of movement (binary coded as the same or different waterbody according to the location of the next change in movement direction), and fish total length. To account for the hierarchical structure of the data, fish ID code and the time of the movement were included as random effects. Trends in river water temperature and discharge were determined by comparing water characteristics during the 24-h period ending at the finish of the fish migration event. Model selection was then done by sequential removal of terms from the full model and comparison of Akaike information criterion (AIC) between the full model and these reduced models, leading to removal of water temperature trend, discharge trend and fish total length. Fixed-effect significances were derived using the mixed function of the afex package (Singmann et al. 2020). Water discharge and temperature data were obtained from the hydrometric station of River Emajõgi located in Tartu, 43 km from the river mouth (hourly measurements, Estonian Environment Agency).

The relationship between fish movement speed and environmental variables (water temperature and discharge) was explored by using segmented regression analysis to examine if the relationship between movement speed and environmental variables deviated from a linear relation. The R package 'segmented' (Muggeo 2020) partitions the independent variable into intervals and fits a separate line segment to each interval. The boundaries between the segments are breakpoints. The most relevant breakpoints for upstream and downstream movement were identified for both variables. The statistical significance of breakpoint values was examined by using Davies test for change in slope (Muggeo 2020).

'Movement range' (longitudinal range) was defined as riverine distance between the extreme upstream and downstream locations during month or year (the sum of riverine distances if several rivers were visited). To calculate fish yearly movement range, only fish tracked during the full calendar year were included, i.e. fish tagged during the same year, or lost before the end of the year were excluded. 'Movement distance' was the cumulative sum of movement routes during a month or year, which were calculated the same way as described above for movement speed, except that the range area of receivers was not subtracted. Some fish visited lakes, and in those cases distance travelled within the lakes was not measured.

Yearly variation of cumulative movement was analysed by feeding periods. Feeding periods were defined based on data in literature (Trzebiatowski and Leszczewicz 1976; Mikelsaar 1984; Kirsipuu et al. 2003; Lehtola et al. 2006; Mamcarz et al. 2008; Krpo-Ćetković et al. 2010) and our own unpublished data. According to this, asp substantially reduce feeding activity when water temperatures fall below 12 °C, whereas they feed actively at temperatures above 15 °C.

Results

Diel activity

In June, July and September, there were no differences in the activity level among diel periods (dawn, day, dusk and night). For the remaining 9 months of the year (August and the period from October to May),

asp movement activity levels differed among diel periods, in both study years. However, the diel variation in activity levels was not consistent, as it varied between months, and the pattern was not repeated in both years (year*month*period interaction: $\chi^2 = 57.9$, df $= 33$, $p = 0.005$). Thus, the diel patterns and the absolute values of activity varied between years in some of the months (Fig. 2). During 24 months, asp activity was generally highest during a crepuscular period; during dawn (16 times of 24) or dusk (6 times of 24). Asp activity was lowest during night (15 times of 24) or day (7 times of 24). During the period while it was cool and the nights were relatively long (October to March), fish activity at night was always lower than during twilight and day. In April and May, crepuscular activity dominated. Nocturnal activity in April and May was similar to daytime activity, or even higher. There were no circadian rhythms in asp activity in June, July and September. In August, there was an increase in activity during either the diurnal or nocturnal period, differing between years (Fig. 2).

There were differences in downstream and upstream movement ratios between dawn and dusk (GLMM, $t = 2.85$, $p = 0.023$), dawn and night (GLMM, $t = 5.01$, $p < 0.001$), day and dusk (GLMM, $t = 3.26$, $p = 0.006$), and between day and night (GLMM, $t = 6.84$, $p < 0.001$) (all months pooled; Fig. 3). No such differences were detected between dawn and day (GLMM, $t = 0.27$, $p = 0.99$), or between dusk and night (GLMM, $t = 1.41$, $p = 0.49$). Thus, during the entire study period, fish moved more actively upstream during dawn and day than during dusk and night. On a monthly basis, there were differences in downstream and upstream movement activity between diel periods in April, May, June, August and October (Appendix 2). In October, the probability of upstream swimming during dawn was higher than in all other periods of the day. A similar trend continued and finally changed at the beginning of the spawning season in March–April. From April to June, the probability of swimming upstream was higher during the day than at night or during dusk.

Seasonal activity and environmental variables

Asp movement speed was positively correlated with the absolute value of water temperature (LMM, $t = 13.37$, $p < 0.0001$; Fig. 4) and discharge (LMM, $t = 6.71$, $p < 0.0001$). Fish movement activity was low during the periods when the temperatures were near zero and the discharge was low (Fig. 4). Moreover, the number of activity events differed substantially during a year, being about ten times higher in midsummer than in mid-winter (Fig. 2).

Segmented regression analyses showed that for downstream movement speed, a breakpoint was detected at a temperature of 10.9 °C and discharge of 110 m^3 s^{-1}, with the highest mean speed near these values (Appendix 3, C and D). For upstream movement speed, a breakpoint was detected at a temperature of 11.3 °C and discharge of 35 m^3 s^{-1}. Mean speed was highest near this value for discharge and above this value for temperature (Appendix 3, A and B). All breakpoints were significant according to Davies test (temperature: both $p < 0.001$, discharge: both $p < 0.05$).

Downstream movements were performed at higher speeds than upstream movements (LMM, $t = -5.34$, $p < 0.0001$; Appendix 3 and 4). Moreover, fish movement speed differed between river segments (LMM, $t = -9.06$, $p < 0.0001$; Appendix 4).

About two thirds of fish movements (1010 of 1550) were performed without a change in movement direction before reaching a different waterbody (Table 1). For example, some fish were moving from lateral waterbodies directly to Lake Peipsi (Table 1). The remaining movements were performed inside the same waterbody (Table 1). Fish movement speed depended on the final target, as fish moved faster between waterbodies than inside the same waterbody (LMM, $t = 11.91$, $p < 0.0001$; Table 1).

Mean downstream movement speed reached its maximum in May (1.47 km h^{-1}), while mean upstream speed was highest in July (1.09 km h^{-1}). Minimum movement speeds were recorded in January and February (mean 0.35 and 0.07 km h^{-1} in downstream and upstream direction, respectively). The maximum speeds recorded for individual fish moving downstream were 5.4 and 4.4 km h^{-1} (over distances of 1.5 and 10.4 km, respectively), and for fish moving upstream 2.7 km h^{-1} (distance 10.4 km, Fig. 4 and Appendix 5).

Fish movement range and distance

Monthly cumulative fish movement distance was correlated with fish movement range ($R^2 = 0.87$; Fig. 5). On average, fish moved a mean distance that
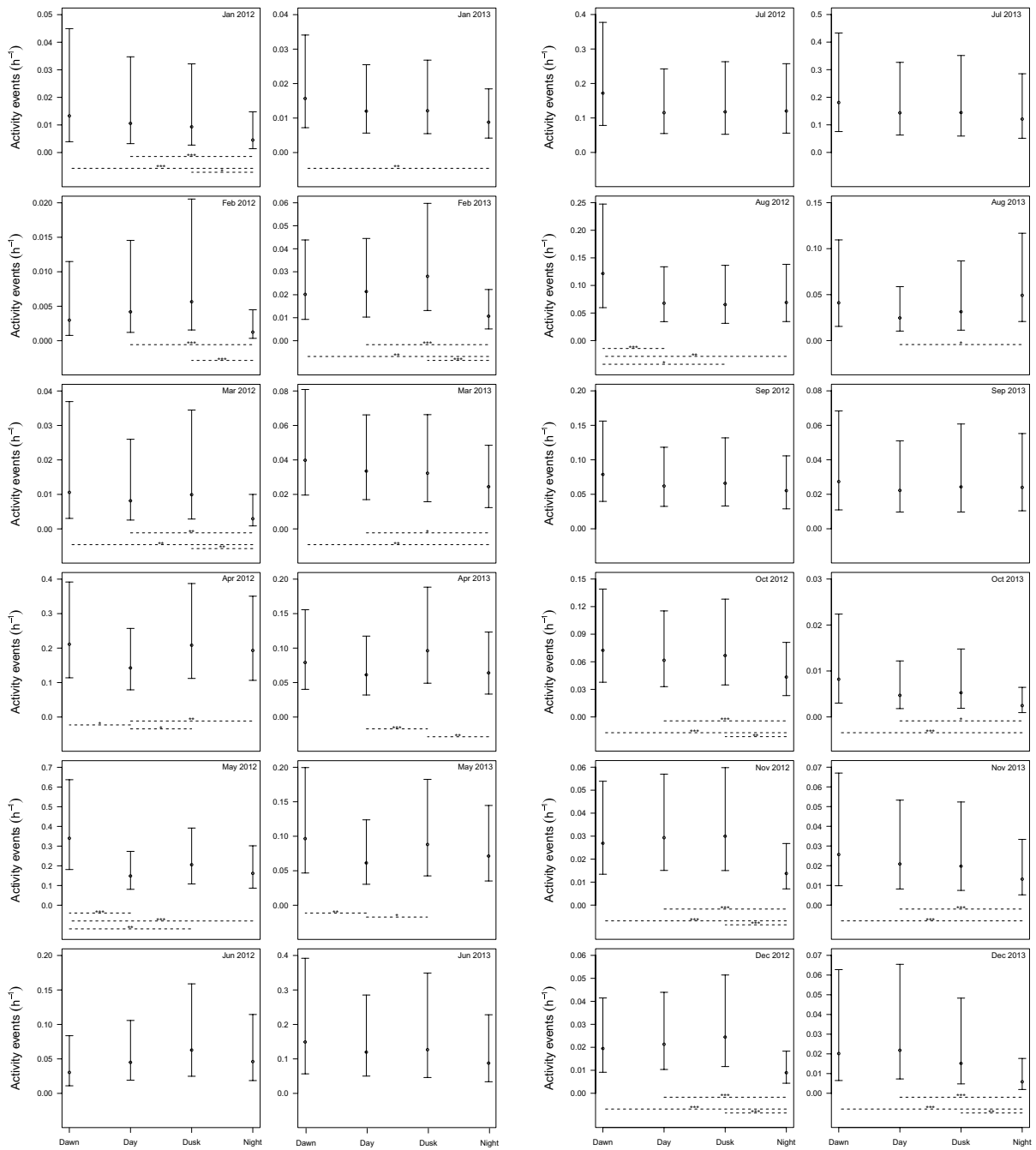
Fig. 2 Diel movement activity of asp in River Emajõgi and tributaries during 1 January 2012–31 December 2013. Each panel shows asp normalised activity (EMMs, mean and 95% confidence limits) per hour during four diel periods on the specific month and year. Statistical significance of differences of movement activity level between day phases has been shown on panels as *, $p \leq 0.05$; **, $p \leq 0.01$; ***, $p \leq 0.001$ using dashed horizontal lines for pairwise comparisons (non-significant differences have not been indicated on the panels). Please note the different scale
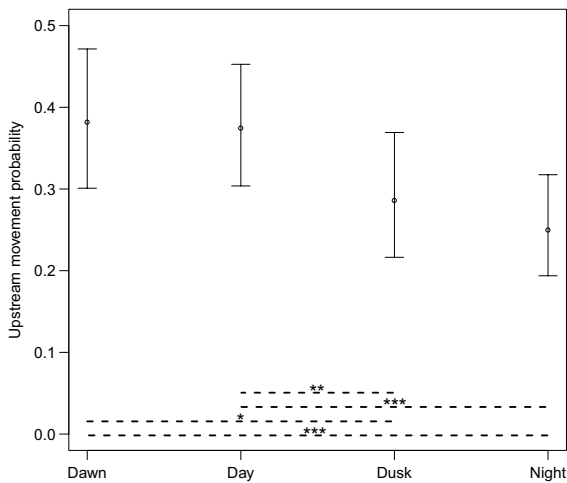
Fig. 3 Diel variation for asp upstream and downstream movement (from one receiver to the next) in River Emajõgi and tributaries during the entire study period. Normalised probabilities (EMMs) for upstream movements have been given (mean and 95% confidence limits). Statistical significance of differences of movement activity level between day phases has been shown on panels as *, $p \leq 0.05$; **, $p \leq 0.01$; ***, $p \leq 0.001$ (non-significant differences have not been indicated)

was $1.28 \times$ longer than its movement range within 1 month. In April and May, when fish performed long one-directional movements towards feeding areas (Table 1), the difference between movement range and distance travelled was small (Fig. 5). In June and July, the difference was relatively large, indicating high activity within the movement range. According to movement range size as well as distance travelled, fish were most active during April–September and least active during October–March (minimum and maximum of mean monthly movement range for all fish during all years 18.5–44.1 km and 2.4–11.2 km respectively, Fig. 5).

In 2012, total movement range was 77 ± 20 km, and in 2013 82 ± 20 km (mean $\pm$ SD, minimum and maximum for 2012 41–103 km, $n = 8$; minimum and maximum for 2013 44–104 km, $n = 14$). Daily movement range covered by an average asp (starting from midnight) was ≤ 10 km in 95% of the cases and > 25 km in only 0.8% of the cases (max 46.5 km). The largest monthly riverine movement range was 109 km (Fig. 5). The longest distance travelled during 1 month was 143 km (Fig. 5).
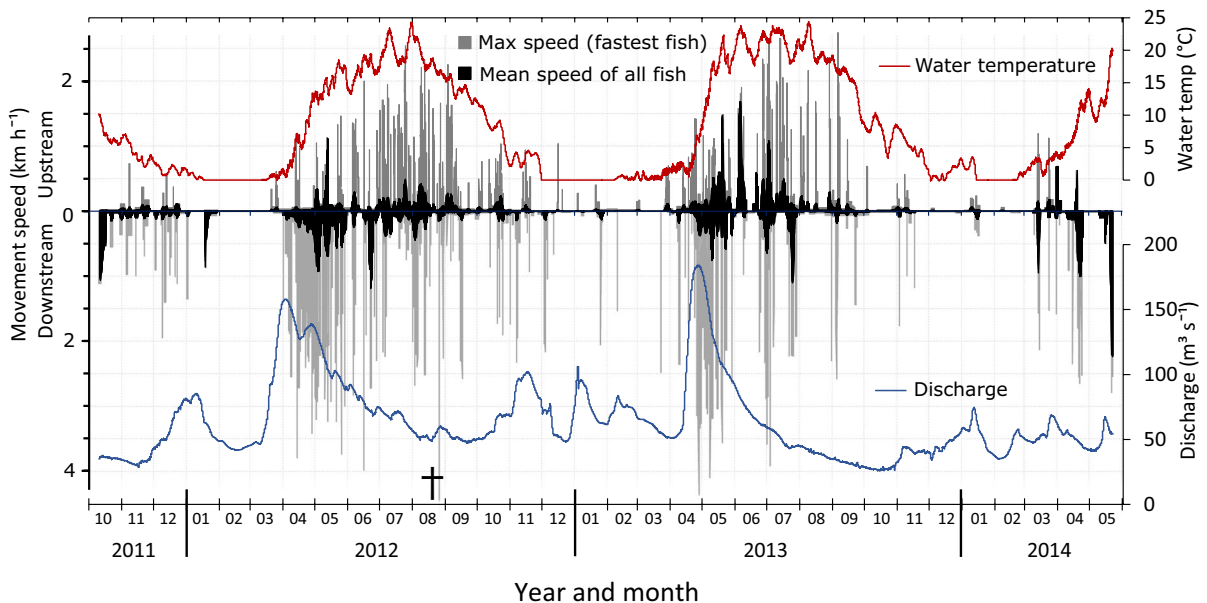

Fig. 4 Fish mean and maximum movement speed in upstream (upper panel) and downstream (lower panel) direction, with water temperature (red) and discharge (blue) in River Emajõgi during the study period. Mean speed is the group mean movement speed (48 h moving mean) and max speed is the speed of the fastest fish during every hour. † indicates maximum speed (5.4 km h.$^{-1}$, outside the figure scale range)

Table 1 Asp mean speed during upstream and downstream movement within or between waterbodies. Areas where fish changed its movement direction (upstream or downstream) were defined as endpoints of movement routes. Pe indicates Lake Peipsi, Võ Lake Võrtsjärv, Em River Emajõgi, and LatWB lateral waterbody (tributary to River Emajõgi). Standard error (SE) and sample size (n) of mean speeds are given. The right panel indicates the distribution of movements by months (all years pooled)

Movement direction and type	Movement route	Speed (mean, km h⁻¹)	SE	n	Movement timing
Downstream					
Lake ↔ River	LatWB → Pe	1.52	0.07	182	
	Võ → Pe	1.35	0.14	40	
	Em → Pe	1.23	0.07	223	
	Võ → Em	0.93	0.10	80	
River ↔ River	LatWB → Em	0.83	0.10	72	
	Em → Em	0.60	0.05	237	
	LatWB → LatWB	0.45	0.12	18	
Upstream					
Lake ↔ River	Pe → Em	1.12	0.06	179	
	Pe → LatWB	0.80	0.11	50	
	Em → Võ	0.56	0.05	82	
River ↔ River	LatWB → LatWB	0.46	0.09	35	
	Em → Em	0.35	0.03	250	
	Em → LatWB	0.31	0.03	95	

Distance travelled per 1-km movement range during 1 month varied up to seven times.

The mean annual cumulative movement distance covered by individual asp (average fish) was 351–356 km (years 2012 and 2013, including up- and downstream movements, Fig. 6). The maximum distance for one individual was 522 km. Most of the distance (77% for 2012 and 79% for 2013, Fig. 6) was passed during the relatively short period with river temperatures > 12 °C, which lasted 42% of the year in 2012 and 39% in 2013 (Fig. 6). The period with temperatures > 15 °C lasted 30% of the year in 2012 and 37% of the year in 2013 during which 57% and 75% of the distance was passed, respectively (Fig. 6).

Discussion

There was diel variation in the activity pattern of tagged asp during three-quarters of the year, but no diel variation during the rest of the year. During the long and cool period (October–March), when the amount of sunlight was limited, asp behavioural pattern was diurnal and crepuscular. This was unexpected, because previous studies of asp in its southern distribution area have shown that the diel activity does not vary in winter (Horký and Slavík 2017). At the time of spawning (April and May), the present study also shows a higher crepuscular activity, but the diurnal activity was somewhat replaced by nocturnal activity. The change to more nocturnal activity

Fig. 5 Correlation between direct measurement of monthly movement distance and estimated movement range length in River Emajõgi and its tributaries during 2011–2014. Blue circles indicate values for individual fish, black circles are mean values for all fish within each month, and bars show variation between years (min and max). The dashed line is the linear regression line
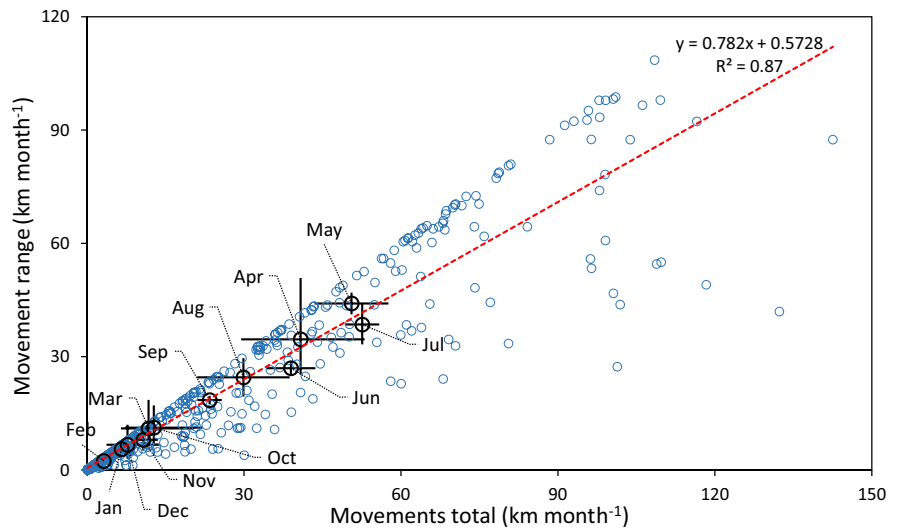

Fig. 6 Cumulative movement distance for average asp (the mean value for a group of fish) during the entire study period from October 2011 to May 2014, based on all tagged fish that were present in River Emajõgi and tributaries (sample size, *n*, is shown in the upper panel). The duration of the feeding periods based on water temperatures is indicated with yellow colour, and the beginning and termination of the main feeding period is indicated with a shaded pattern
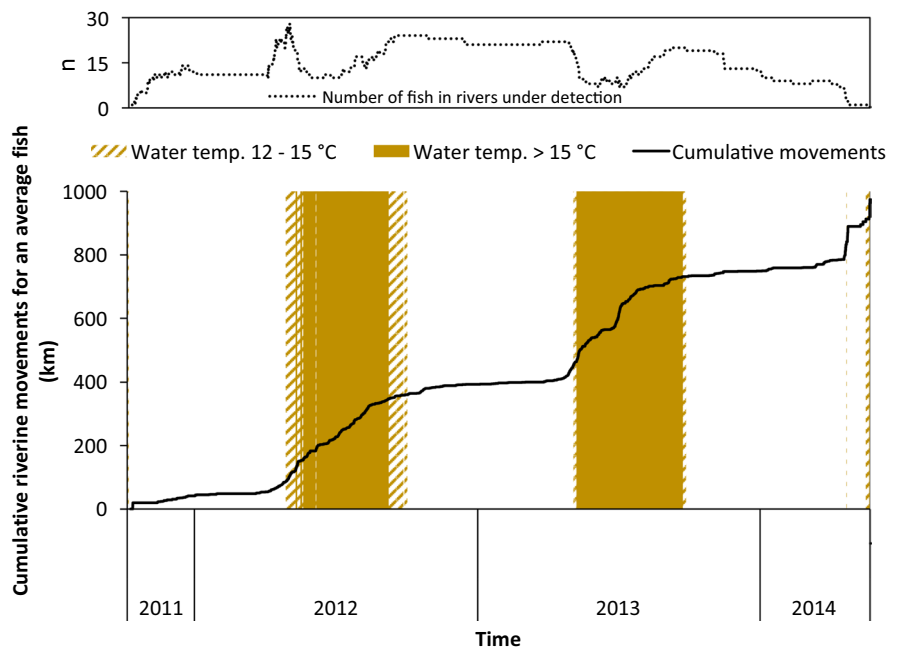
might have been due to spawning activity being nocturnal (see Šmejkal et al. 2018). In our study, during the bright June–July, when the sun did not disappear far below the horizon in our study area, there were no clear circadian rhythms in the activity of asp—the behaviour was rather cathemeral and the fish were active during all diel periods. In the darker summer nights further south, the nocturnal activity of asp decreased in summer (Horký and Slavík 2017). It is known that pelagic carnivores (like asp in the summer, Vašek et al. 2009) may have a cathemeral behavioural pattern (Arndt and Evans 2022). Clear diel rhythms were also not detected in September, although an increase in activity during either diurnal or nocturnal periods was observed in August. Thus, the behaviour of asp was plastic, similar to many other fish species that can change their rhythm during the year (Prchalová et al. 2006; Reebs 2002).

Asp in our study were more likely to swim upstream in the morning and during the day, and

more likely to move downstream in the evening and night. However, asp moved in both directions during all periods of the day, which seemed to contradict the assumption that they might interrupt movement during darkness (Fredrich 2003). In a previous study, cyclic behaviour documented during the spawning season has been attributed to periodic gathering in the spawning areas (Šmejkal et al. 2018). At other times of the year, cyclic behaviour is more difficult to explain. Downstream movement may be a result of increased passivity by the fish or increased river discharge. This would mean that the subsequent upstream movement during morning or day is a compensatory behaviour. Other cyprinids are known to display different movements at night, such as vimba (*Vimba vimba* L.), which moves in an upstream direction (Tambets et al. 2018b) and roach (*Rutilus rutilus* L.), which may seek areas with slower water current (Hammer et al. 1994). This may indicate that any diel cycle in the movement direction largely depends on the location of the most optimal habitats for feeding, spawning and resting (refuge). The optimal prey for asp are small fish (Trzebiatowski and Leszczewicz 1976; Vašek et al. 2018), which may display movements between the main river and floodplain water bodies that can be more intensive or restricted to the twilight period (Borcherding et al. 2002; Hohausová et al. 2003). Thus, the asp diel activity patterns could be explained by a combination of prey availability and sufficient light for efficient foraging. However, the presence of clear diel rhythms with higher activity during light hours also outside the feeding season may indicate the influence of other factors in addition to prey availability. Foraging success and predation risk are common driving forces to develop diel activity rhythms (Reebs 2002). This would seem to be less relevant for the big-bodied asp during the cold season, but it may indicate that the most optimal wintering refuge area in a natural river may differ during a diel cycle even for a big-bodied, non-feeding fish. In general, there is a lack of literature on the overwintering behaviour for the rare piscivore feeding guild of cyprinids (Allouche et al. 1999; Marsden et al. 2021; Reebs 2002; Vejřík et al. 2016).

The annual variation in asp behaviour in River Emajõgi, with a higher activity in the warmer part of the year (water temperatures > 12–15 °C), is generally in accordance with previous knowledge on asp biology. Asp is considered a warm-water species

(Mikelsaar 1984; Krpo-Ćetković et al. 2010). It has been shown to cease feeding when water temperatures fall below 12–15 °C (Trzebiatowski and Leszczewicz 1976; Mikelsaar 1984), with a declining condition factor during winter indicating a negative energy balance (Krpo-Ćetković et al. 2010). However, the annual variation in activity rates was greater than previously reported (e.g. Horký and Slavík 2017), which can be expected in cooler climates. In the present study, the number of activity events was approximately ten times higher in mid-summer than in mid-winter. About 60–80% of the cumulative movement distance of asp was covered during the relatively short feeding period, which, based on river temperatures, lasted about 30–40% of the year, starting in April/May and ending in September. Asp also lowered their activity, measured as mean movement speed, by 68–78% in 2012 and 80–82% in 2013 during the period of the year that appears not to be optimal for feeding. Our study area is located at latitude 58°N, which is near the northern edge of the distribution area of asp (35–66°N, Froese and Pauly 2019). In our northern study area, the short duration of periods with warm water temperatures and of daylight, resulting in a short feeding period, may be a limiting factor for a warm-water species like asp. On the other hand, predicted climate warming may contribute to increase the length of the optimal time for feeding in terms of temperature, and also in terms of light if ice cover periods are reduced (Lehtonen 1996; Ficke et al. 2007).

The mean annual riverine movement range was about 80 km for individual fish, connecting distinct protected areas (this study; European Environment Agency 2019; Kärgenberg et al. 2020a). In contrast, in the much larger River Elbe, 85% of asp tracked for 1 year or more had a yearly movement range length of < 40 km (Fredrich 2003). Neither Elbe nor Emajõgi had obstacles for fish migration. This seems to contradict the idea that fish home ranges increase with the size of the water body (Woolnough et al. 2009). The larger movement range in Emajõgi is in line with the larger home range predicted for terrestrial animals at higher latitudes (Harestad and Bunnel 1979). Large-scale habitat structures, such as the spatial distribution of spawning, feeding and wintering areas, are probably the main determinants for the annual movement range length formation of asp. According to monthly movement range, asp in River Emajõgi were

most active during the spring and summer months (April–September). This differs from studies on asp annual activity at lower latitudes (49–53°N). Based on movement range, Pfauserová et al. (2019) found that activity was low outside the spawning period in March–April. Horký and Slavík (2017) described low activity during spring and winter based on home range size and diel movements. These observations indicate that the design of conservation measures to protect migrating fish must be based on location-specific data.

Movement and home range estimates are used for decision-support in conservation biology (Fauvelle et al. 2017). These metrics are important, but provide insufficient information on the actual activity of fish inside its home range, which is crucial information for estimating fish vulnerability to various risk factors (e.g. various fishing gear, turbines/water intakes, migration obstacles, etc.). While some fish in this study moved a distance equal to the length of their longitudinal range, others moved up to seven times its longitudinal range length while still remaining inside the movement range. The methodology we used allowed only minimum estimates of the cumulative distance travelled, as the size of the study area set limits on the proportion of the area that can be covered by receivers recording tagged fish. There was certainly a lot of movement between the receiver stations that could not be mapped in this study. In addition, this methodology did not allow the monitoring of fish movements in the lakes, which were important feeding grounds for many asp individuals during the summer. More attention should be paid to the behaviour of asp in lakes.

Asp maximum swimming speed in this study was recorded at 5.4 km h^{-1} for downstream movements and 2.7 km h^{-1} for upstream movements (corresponding to 2.1 and 1.1 body lengths per second). These are higher speeds than recorded with similar methodology for other cyprinids (e.g. up to 1.8 km h^{-1} for downstream movements and 0.8 km h^{-1} for upstream movements for vimba bream, Tambets et al. 2018b). Maximum daily movement range was 47 km, implying that some fish might have been swimming for more than 10 h per day. This is similar to the results of Fredrich (2003), who calculated a swimming speed of asp at 3 km h^{-1}, and an estimated daily movement range up to about 50–60 km. These results confirm that asp have good and sustained swimming abilities,

even if they seem to avoid rapidly flowing waters, including both ordinary and modern fish passes (Fredrich 2003; Horký and Slavík 2017).

Asp annual and diel activity patterns were roughly similar between years. A previous study also showed high similarity in habitat use and migration patterns between the years (Kärgenberg et al. 2020a). Similar behaviour and habitat use between years have also been shown for asp elsewhere, such as strong spawning site fidelity (Pfauserová et al. 2019), repetitive seasonal protandry (Šmejkal et al. 2017) and diel spawning activity dynamics (Šmejkal et al. 2018). This indicates that for any asp population, conservation and management plans can be based on knowledge about the behaviour of the fish in relation to simple predictive factors like date and time of day. According to the linear mixed-effect model used in our study, these predictive factors can be supported with environmental variables like water temperature, discharge and waterbody segment inside the fish's movement range. Asp is vulnerable to multiple fishing techniques, especially to passive gears (gill nets, trammel nets, fyke nets) targeting active and big-bodied fish (Hubert et al. 2012), and the vulnerability to passive fishing gears increases with increasing water temperature. As fyke nets are usually directional, the vulnerability of the fish also depends on swimming direction (Hladík and Kubečka 2003; Hubert et al. 2012; Kärgenberg et al. 2020b). In the River Emajõgi, asp had a tendency to move towards the lake habitat during April and May, and towards the tributary (spawning) habitat between July and November (Kärgenberg et al. 2020a). These fast movements contributed to formation of temperature-dependent breakpoints for movement speed and direction close to a water temperature of 11 °C. Above this temperature, movement speed increased suddenly in an upstream direction and levelled off in a downstream direction. Habitat shifts near water temperatures of 10 °C have also been described for other asp populations (Fredrich 2003; Pfauserová et al. 2019), as fish moved towards wintering habitats when the temperatures in the river dropped below 10 °C.

In conclusion, the present knowledge about the behaviour by large predatory cyprinid fishes in near natural riverine habitats is limited, especially in northern parts of their distribution area. The complex study area and the use of telemetry methods in this study allowed new insights into the diverse movement

patterns of asp, which is a species under national and international conservation concern. A large diversity of activity patterns were found, which were new and somewhat unexpected based on previous studies. The results indicate that for any asp population, conservation and management plans can be based on region-specific knowledge about the behaviour of the fish in relation to simple predictive factors like date of the year and time of day. These predictive factors can be supported with environmental variables like water temperature, discharge and waterbody segment inside the fish's movement range.

Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval The authors have adhered to general guidelines for ethical use of animals in research. Research presented in this manuscript (fish capture and tagging) were approved by Environmental Board of Estonia (licenses 13/2011 and 14/2012). Estonian regulations pertaining to the use of animals adhere to the Directive 2010/63/EU.

Consent to participate and publication All authors participated in this study and consent to its publication.

Conflict of interest The authors declare no competing interests.

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