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Effects of a dispersal barrier on freshwater migration of the vimba bream (*Vimba vimba*)

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To study the effects of a dispersal barrier on migration of the semi-anadromous vimba bream in the Pärnu River, Estonia, we tagged thirty fish with acoustic transmitters and released above the barrier. Tagged fish showed variation in behaviour, and 16 different spawning movement patterns were identified. Several fish moved > 25 km upstream. Batch spawning was suggested by stops in up to four different spawning areas. The fish descended to the sea after spawning in spring; females earlier than males. After spending on average 137 days in the sea, they returned to the river during autumn and stayed in the river on average 174 days until the next spawning. The fish were most active during sunrise and sunset. In conclusion, the study shows that the dam prevents a diversification of migration behaviour and the associated expansion of spawning areas. A more efficient fishway could promote population growth and improve stock status.

Introduction

Semi-anadromous populations of the vimba bream have declined in most of its distribution area, and are now considered rare in the Baltic Sea and the Black Sea basins (Kottelat and Freyhof 2007). The vimba bream is a target species for commercial fisheries in several Baltic countries, and in Estonian waters, the mean annual catches have decreased from 250 tonnes in 1930–1934 to 55 tonnes in 2010–2014 (Erm *et al.* 2003, Eschbaum *et al.* 2013). As for many other migrating fishes, negative impacts during the riverine phase of the life cycle contribute significantly to the population decline. One major factor is hydropower dams and other constructions that create barriers and prevent upstream migration to reach spawning areas (Povž 1996, Penczak *et al.* 1998, Jurvelius and Auvinen 2001, Aleksejevs and Birzaks 2011). Other habitat modifications and altered water regimes, as well as pollution and overfishing, may also have negative effects. Any successful action to conserve and restore migratory fish populations depends on an understanding of the factors causing population decline. This includes species-specific knowledge on the timing, extent and dynamics of migrations.

The vimba bream is a riverine or semi-anadromous, batch-spawning cyprinid fish species,

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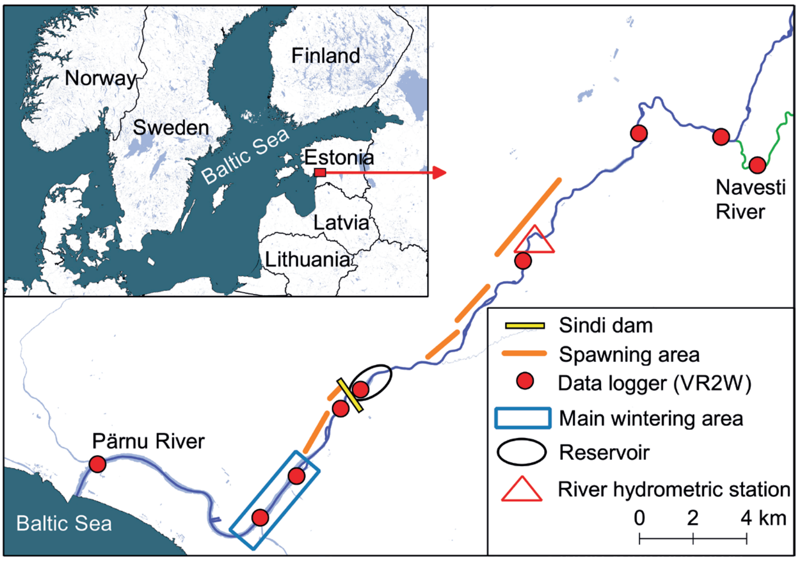

Fig. 1. The lower part of the Pärnu River with the Sindi dam and locations of the stationary VR2W receivers. Additional receivers positioned 35.7, 37.0, 52.7 and 53.9 km from the Pärnu/Navesti confluence are not shown on the map.

which occurs in coastal areas and rivers in the Baltic (Gasiūnaitė *et al.* 2008, Kotta *et al.* 2008, Telesh *et al.* 2008). Semi-anadromous populations inhabit coastal areas with low salinity and rivers and lakes connected to these areas. The vimba bream feed in brackish waters and move into rivers to spawn. They may also form freshwater resident populations in large lakes such as Ladoga, Ilmen, Peipsi, and in reservoirs in impounded rivers such as Daugava and Nemunas (Kesminas *et al.* 1999, Erm *et al.* 2003, Aleksejevs and Birzaks 2011). In Estonia, the most important spawning river for the semi-anadromous vimba bream is the Pärnu River.

Studies of the biology of anadromous and semi-anadromous fishes have to a large extent focused on salmonids, while there is less knowledge on anadromous cyprinids (Smith 1991, Lucas and Baras 2001, Marmulla 2001). Most studies of the vimba bream have focused on life history, morphometry, feeding and genetics (Hliwa and Martyniak 2002, Lusk *et al.* 2005, Ermolin and Shashulovskii 2006, Myszkowski *et al.* 2006, Hänfling *et al.* 2009, Czerniejewski *et al.* 2011, Okgerman *et al.* 2011, Popovic *et al.* 2013). Few studies were performed on the seasonal migration patterns (but cf. e.g. Erm *et al.* 1970, Calles and Greenberg 2007). Knowledge on the habitat use and behaviour during winter is scarce, although these are essential aspects in targeted management and conservation schemes.

By applying acoustic telemetry methods, migration patterns and seasonal habitat use can be recorded. In this study, we captured vimba bream below the Sindi dam, which is an obstacle for upstream migrants situated close to the river mouth, restricting the use of potential spawning sites in the upper parts of the Pärnu River. Thirty vimba bream were tagged with acoustic transmitters, and transported and released in the reservoir upstream of the dam in order to study their behaviour in areas that would be available if migration in the Pärnu River was not obstructed by the dam. The aims of this study were to (i) describe the movement patterns of semi-anadromous vimba bream during a year; including during spawning, descent to the sea, return to the river, and wintering, (ii) describe the individual variation of movement patterns, swimming speeds, the timing of habitat shifts and duration of periods spent at sea, in the river, and at spawning sites, and (iii) investigate the behaviour and utilization of spawning sites made available to the vimba bream if migration was not obstructed by the dam.

Material and methods

Study area

The Pärnu River (144 km; Fig. 1) is the second longest river in Estonia. The catchment area is

6920 km^2, and the mean annual discharge at the mouth is 50–65 m^3 s^{-1}. The 4.3 m high Sindi dam, created for industrial purposes, is situated 16 km upstream from the river mouth, creating a 1.5 km long impounded stretch with slow-flowing water. The impounded stretch above the dam is termed a reservoir, but it is not being used to regulate river discharge below the dam.

The dam functions as a weir, with water overflowing the concrete construction, but it is only passable for upstream migrating fish through the 70 m long vertical slot fish ladder. Monitoring fish ascent by fyke nets and electrofishing indicated low functionality (Erm 1978). This is supported by the absence of several anadromous and semi-anadromous fish species in catches upstream of the dam (i.e. river lamprey *Lampetra fluviatilis,* whitefish *Coregonus lavaretus*, smelt *Osmerus eperlanus*, and three-spined stickleback *Gasterosteus aculeatus*). Only a few Atlantic salmon *Salmo salar* and sea trout *S. trutta* have been caught (Anon. 2007, and Wildlife Estonia unpubl. data). Similarly, the vimba bream has rarely been caught, and only in low numbers. Thus, the dam constitutes an important obstacle, but is not a complete barrier to migration.

Spawning areas and spawning periods

The Pärnu River is mostly slow flowing with few rapids. Vimba bream spawning occurs only in rapids. Around 90% of the rapids potentially suitable for vimba bream spawning are located upstream of the Sindi dam (Anon. 2007), but at present the main spawning of the vimba bream occurs in two restricted rapid areas downstream of the dam.

In our main study area, which included the lowermost 29 km of the river, there were five spawning areas, each of them consisting of rapids and adjacent slow river segments. Three spawning areas were situated upstream and two downstream of the reservoir. Lowest spawning area covered partially earlier wintering area. The total length of the three upstream spawning areas was 9 km and of the two downstream areas 7 km (Fig. 1).

The spawning period of the vimba bream is defined as the time during the study when tagged fish remained in the spawning areas before descending to the sea. In 2013, the study started at the onset of the spawning period (some females with partly ovulated oocytes were present on the spawning areas). In 2014, the beginning of the spawning period was defined as the time when all tagged fish had left the wintering areas in the second half of April.

Fish and tagging

Thirty adult vimba bream (mean total length ± SD = 339 ± 24 mm, range 300–405 mm, approximate mass range 350–700 g) were captured for tagging on 14 and 15 May 2013, during the spawning migration. The fish were caught on a 100 m stretch in the Pärnu River below the Sindi dam and in the downstream end of the Sindi dam fish ladder using electrofishing. The fish were anaesthetized on site and coded acoustic transmitters were surgically implanted (Vemco, Nova Scotia, Canada, V-9 coded tag; length 24 mm; weight in air 3.6 g). Incisions were closed with two sutures. All the fish could hold position and swim normally after recovering for 3–6 minutes, and were then released into the Sindi reservoir, 50 m upstream of the dam.

Fish monitoring

The fish were monitored by using stationary Vemco VR2W automatic receivers and manual tracking (Vemco VR100). Twelve automatic receivers were deployed in the Pärnu River, up to 92 km upstream from the river mouth, and one in the tributary Navesti River, 1.5 km from the confluence with the Pärnu River (Fig. 1). When a tagged fish was within the detection range of a receiver, date, time and individual fish code were automatically recorded and stored by the receiver and later downloaded to a computer. Manual tracking was performed every fourth day by boat from 15 May to 11 June to locate tagged fish, covering the main spawning season of 2013. The tracking surveys covered the lowest 45 km of the river, and the length of the surveyed stretch was adjusted according to the data obtained from the automatic receivers.

To study fish movements in the wintering area, two receivers were deployed in the river where fish wintering was expected based on information from fisheries (9.5 km and 11.2 km from the river mouth). This is a slow flowing river section immediately below the lowermost rapids. The analyses of fish movements during winter were based on data from these two receivers during 9 October 2013–30 April 2014.

Statistical testing

Data were analysed using the statistical program R ver. 3.3.1. Non-parametric tests were used, due to low sample sizes and because the assumptions for parametric tests were not met.

A Wald-Wolfowitz runs test was used to test if the sequence of descent to the sea was associated with fish gender. Only the sequence of fish that descended to the sea in 2013 was analysed, because the number of females was too low during other periods and during upstream migration, to perform such tests.

To test if the fish movement activity had a diel or seasonal pattern, the data were divided into periods of the day (dawn, day, dusk and night) and into seasons. We considered the seasons defined by astronomical dates and times (UTC): vernal equinox, summer solstice, autumn equinox, winter solstice. The seasons were defined as follows: spring is 20 March–21 June, summer is 21 June–22 September, autumn is 22 September–21 December, and winter is 21 December–20 March. Dawn and dusk periods were defined as ±1 hour of the time when the sun's upper edge appeared or disappeared on the horizon according to local timetables. The length of the day and night was calculated for each day when fish activity was detected by subtracting dawn and dusk periods. An average length of day and night was calculated for each season. Average day/night length (hrs) was 15.7/4.3 for spring 2013, 15.9/4.1 for summer, 5.5/14.5 for autumn, 6.7/13.3 for winter and 12.1/7.9 for spring 2014. A fish movement activity event was defined as arrival or departure in the receiver detection range. Detections within one hour since last recording by the same receiver were excluded. All activity events during each day period were counted. The null hypothesis ("expected level") for diel activity was that the fish did not differ in number of activity events between dawn, day, dusk and night, adjusted for day and night lengths. The possible deviation from the null hypothesis was tested by using Pearson's χ^2 goodness-of-fit test for activity levels between night, dawn, day and dusk within each season. For seasonal variation in activity we used activity events per unit of time (two hours) to test the null hypotheses that there was no seasonal variation. This was tested by an independence test for possible seasonal differences.

To test the influence of diel period on movement direction (upstream or downstream) we studied movements between two receivers spaced 1.7 km apart downstream of the lowermost rapids, where there were enough data. The diel cycle was divided in two periods (00:00–12:00 and 12:00–24:00, UTC time), covering the sunrise and sunset periods when the fish were most active. Division in more than two periods was not done as this would reduce statistical power. The time for upstream/downstream movements was defined as the arrival time at the upstream receiver for upstream movements and at the downstream receiver for downstream movements. Analyses were done for two seasonal periods when the highest number of fish were present and moving (7 June–12 June, 2013 and 20 March–19 April, 2014). The number of movements was $n = 43$ and $n = 146$, respectively. Movements during these periods were counted and analyzed with a χ^2-test with "$n - 1$" correction as recommended for 2×2 tables by Campbell (2007).

Movement speeds between receivers were calculated based on the time between the last recording on one receiver and the first recording on the next receiver and the distance between these receivers. Movement speeds were only based on receivers spaced at least 3 km apart, because the size of the detection range of receivers may vary with environmental conditions. Hence, calculations based on receivers close to each other will be more uncertain because they will be more affected by uncertainties in the distance measure. Wilcoxon's signed-rank test was used to test if movement speeds differed between river stretches with or without rapids and between upstream and downstream movements. Average

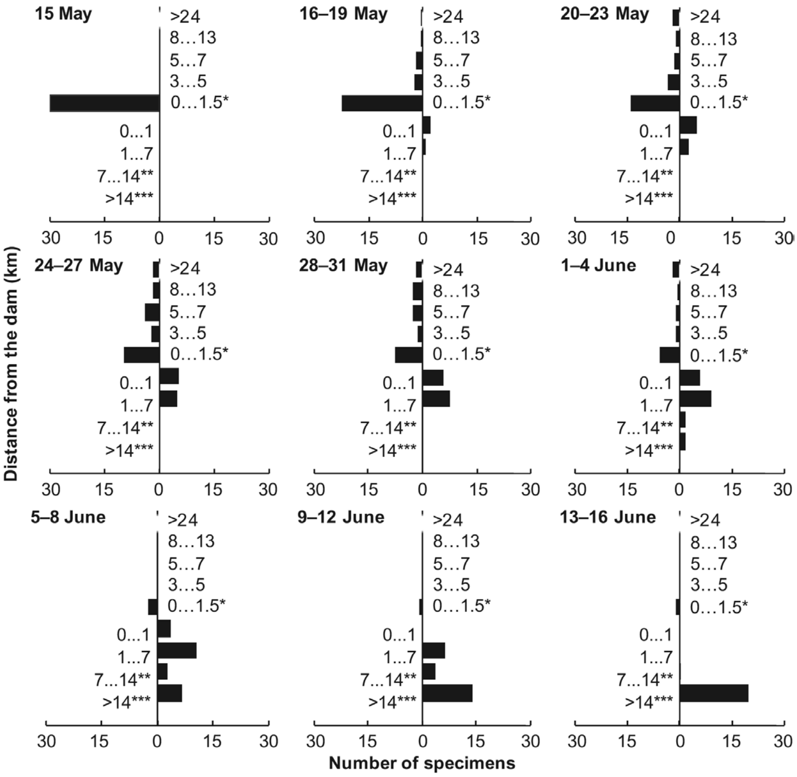

Fig. 2. Distribution of tagged vimba bream along the Pärnu River and Navesti River during the spawning period in 2013. Numbers on the vertical axis show the location of spawning areas (km from the Sindi dam), the reservoir (*), a slow running river segment (**), the sea (***) and the lower part of the river Navesti (> 24). Fish locations upstream of Sindi dam are shown as bars to the left of the vertical axis and downstream locations as bars to the right of the vertical axis. If an individual was recorded in several area in one period, it was divided equally between the periods.

speed for each individual on stretches with and without rapids during upstream and downstream movement, respectively, were used in the tests. Individuals with missing values were excluded (e.g., when only downstream, but not upstream swimming speed was known).

The data on river discharge and water temperature were obtained from Estonian Environment Agency and measured at river hydrometric station, 25.7 km from the river mouth (Fig. 1).

Results

Movements during the spawning and post-spawning period

Soon after release, the fish started moving, and the first fish left the reservoir during the first night (Fig. 2). Ten fish had left the reservoir by the third day, and by the seventh day, 20 fish (67%) had left the reservoir. The last fish left the reservoir on 8 June, 24 days after release. The fish moved to upstream ($n = 15$, movement pattern A–M in Fig. 3) and downstream ($n = 13$, movement pattern N–P in Fig. 3) areas from the reservoir. Two fish remained in the reservoir until signals from their transmitters were lost during the spawning period in 2013 (Appendix). Two individuals, which were the first to leave the reservoir, did the longest upstream migration, swimming at least 25 km upstream. Most of the fish ($n = 24$; all shown in Fig. 3) moved to spawning areas situated between 7 km downstream and 13 km upstream of the release site. Two fish descended to the sea from the reservoir without being detected pausing in any spawning area. The number of fish in the spawning areas reached its maximum by late May (Fig. 2).

The fish that had moved to the upstream areas returned and moved downstream through the reservoir and past the dam, starting from 21 May (Fig. 2). By the end of May, four fish had left the upstream spawning areas and passed the reservoir and dam. The last fish left the upstream spawning areas by 3 June (Fig. 2). At that time, the first fish had reached the sea. The females moved to sea earlier than the males (runs test:

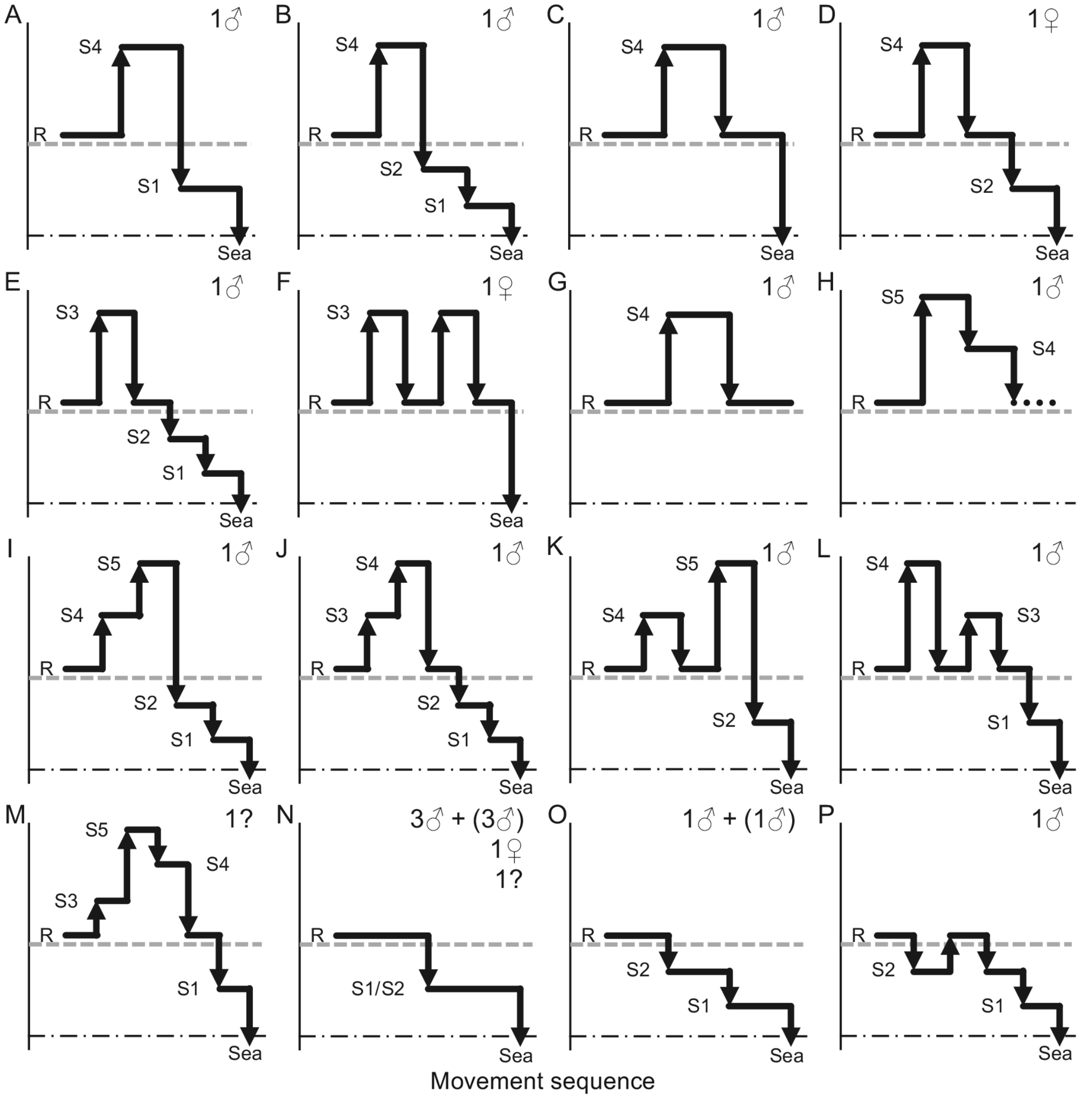

Fig. 3. Graphic illustration of movement directions of vimba bream individuals during the spawning period in the Pärnu River. — — indicates the Sindi dam, R the reservoir, S spawning areas (with sequence numbers), – · – the sea, ↑ upstream movement, ↓ downstream movement, — staying within a spawning area or the reservoir, · · · the fish was lost, + ( ) additional fish with unfinished pattern as fish were lost or dead before going to the sea. The gender (if known) and the number of fish are shown on the panels. Six fish were never detected staying within spawning areas, and these are not included in the figure. Vertical axes indicate sequences of movement direction and stops on the lowermost 29 km of the river, whereas horizontal axes indicate the movement sequence during the time period 15 May 2013–16 June 2013. Time and space are not to scale (e.g. the eight individuals in panel N moved downstream on different dates/spawning areas but illustrated with only one arrow/line).

$n1 = 4$, $n2 = 14$, $p < 0.0001$). By 8 June, eight fish remained in the lowermost spawning area, below the dam. The most intensive migration to the sea, with five fish migrating in one day, occurred on 11 June. The last fish reached the sea by 13 June, except one male that remained in the reservoir more than one year and descended to sea only after the spawning period in 2014.

The riverine movement patterns of the 24 individuals that moved to spawning areas during the spawning period in 2013 could be divided into 16 different types (Fig. 3). More than half of the fish (13 fish) were detected in more than one spawning area. Some (9 fish) remained for a while in the reservoir, both between movements to different spawning areas, and before moving to sea (Fig. 3). Fish that moved upstream from the reservoir, stayed in either one, two or three different spawning areas before moving downstream again. Some fish that moved upstream returned to the reservoir and then moved to upstream spawning areas a second time before moving downstream past the dam. When fish from upstream areas moved to sea, some moved directly from the dam to the sea, while some stopped in one or two downstream spawning areas before entering the sea. Eleven fish never moved upstream from the reservoir but moved to downstream spawning areas after release (Fig. 3). Among these fish, the most common movement pattern was a downstream movement from the reservoir to a spawning area, before moving to the sea. One individual that moved to a downstream spawning area later passed the dam and returned upstream into the reservoir (Fig. 3). This unique movement pattern was repeated by the same individual in 2014.

Re-entering the river

After the spawning period in 2013, almost all tagged fish that were presumably still alive and with operative transmitters (20 individuals; Appendix) entered the sea, except the one individual that remained in the reservoir and moved to sea only after the spawning period in 2014. Of these 20 fish, eight individuals returned to the Pärnu River for overwintering and two individuals appeared to remain in the river mouth area (Table 1), while ten fish were not detected again. The fish that returned to the river had stayed in the sea for 115–159 days. The first fish returned to the river in late September, while the main migration to the river occurred in October–November. The four fastest fish migrated to the wintering area (about 9–11 km from the river mouth, below the first rapid) in 8–26 hours, while the slowest fish spent two months to migrate this distance. When an ice cover formed in mid-January, all fish had reached the wintering area. The fish stayed in different parts of the wintering area, but the time spent moving from the lower to the upper section varied from two hours to almost ten weeks.

Movement in the wintering area

The fish that entered the wintering area (*n* = 7, the individual passing the receiver in river mouth

Table 1. Timing of vimba bream upstream migration from the sea to wintering habitats in the Pärnu River during 2013–2014. Re-entering is given as the date when the fish were detected by the lowermost receiver. Fish no. 59 re-entered the river without being detected by this receiver and was only recorded further upstream. In addition, fish no. 57 returned 13 November and no. 62 was registered in the river mouth both 9 August and in December but were not recorded to enter the river for wintering (Appendix).

Fish ID	Descending to the sea	Re-entering the river	Reaching 9.0 km upstream	Reaching 10.7 km upstream	Time spent at sea (days)	Time spent moving from mouth to 9.0 km upstream (hrs)	Time spent moving from 9.0 km to 10.7 km upstream (hrs)
39	3 June	26 Sept.	27 Sept.	10 Oct.	115	8	327
44	9 June	8 Oct.	9 Oct.	9 Oct.	121	16	7
43	7 June	5 Nov.	6 Nov.	7 Nov.	151	25	2
38	11 June	12 Nov.	15 Nov.	16 Nov.	154	67	21
45	7 June	12 Oct.	18 Nov.	21 Nov.	127	900	63
34	11 June	17 Nov.	18 Nov.	20 Nov.	159	26	49
42	4 June	15 Oct.	15 Dec.	26 Dec.	133	1473	267
59	11 June	?	7 Jan.	14 Mar.	?	?	1600
Average	7 June	25 Oct.	14 Nov.	26 Nov.	137	359	292
Median	8 June	15 Oct.	16 Nov.	18 Nov.	139	26	56

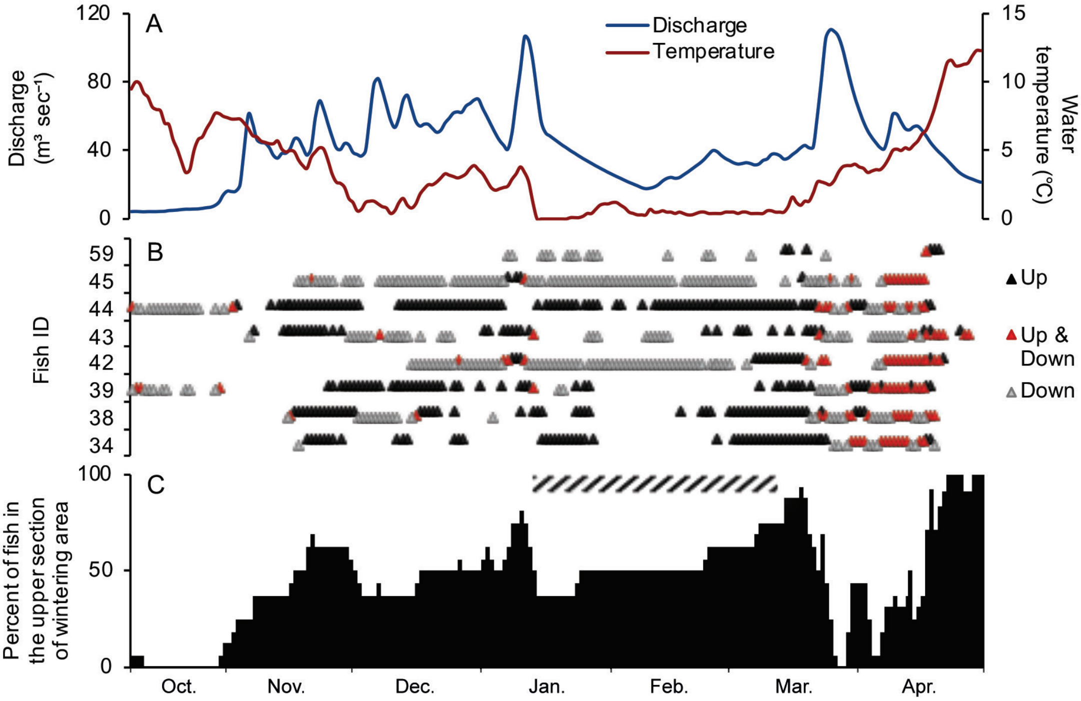

Fig. 4. (**A**) Water discharge and water temperature in the Pärnu River during 9 Oct. 2013–30 Apr. 2014. (**B**) Occurrence of vimba bream in the upper section (Up, river km 10.7) and the lower section (Down, river km 9.0) of the wintering area (Fig. 1) in Pärnu River until the spawning period in 2014. Symbols represent fish registrations on receivers. Up & Down indicates registrations on both receivers during the same day. (**C**) Occurrence of river-wintering vimba bream in the upper section of the wintering area of the Pärnu River until the spawning period. Diagonal lines indicate the ice-covered period. If an individual was recorded in both the upper and lower wintering area in one day, it was counted as half in one area and half in the other.

without being recorded is not included; Table 1) spent 152–203 days (mean ± SD = 174 ± 20 days) in the river between ascending from the sea and initiating the upstream movement during the spawning period. The fish also performed considerable movements while in the wintering area (Fig. 4). The fish were least active under the ice cover from early January until early March, although there was a tendency that they moved to the upper part of the wintering area (to within reception range of the receiver 11.2 km from the river mouth). Later fish changed resident area frequently and usually within one day. In the second half of March, after ice-break, the water temperature increased from 1.0 to 4.0 °C, the water discharge tripled over a period of 10 days, and all the eight fish moved downstream. As the water levels receded, and temperatures increased from 5.8 to 11.4 °C during a one-week period in mid-April, all the fish moved through the upper section of the wintering area and into the spawning areas situated below the dam. Two of the fish also passed the dam and moved further upstream.

Diel activity

There was diel variation in activity levels (between sunrise, day, sunset and night) both in spring (χ^2 = 21.319, n = 978, df = 3, p < 0.0001), autumn (χ^2 = 21.523, n = 1053, df = 3, p < 0.0001), winter (χ^2 = 108.58, n = 1513, df = 3, p < 0.0001) as well as in the next spring (χ^2 = 177.81, n = 1205, df = 3, p < 0.0001; Fig. 5). The diel activity pattern also differed among seasons (χ^2 = 46.925, n = 1924, df = 12, p < 0.0001; Fig. 5). There was no significant diel variation in activity in summer (χ^2 = 2.708, n = 143, df = 3, p = 0.44). The fish had the highest activity levels (per time unit) at sunrise or sunset

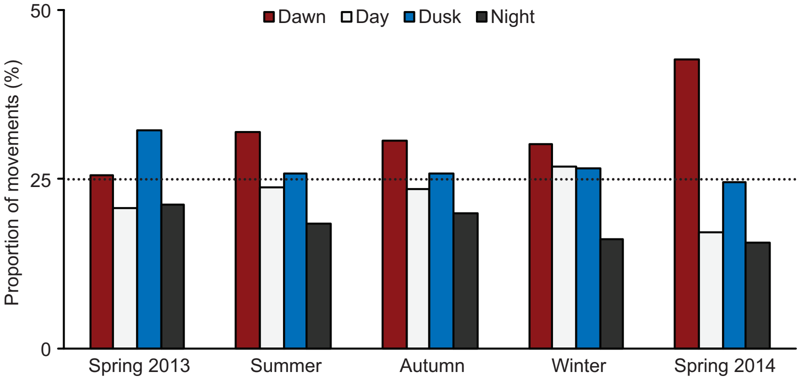

Fig. 5. Relative diel movement activity of vimba bream in Pärnu River in different seasons during 16 May 2013–12 June 2014. Bars shows proportion of activity events per hour relative the total activity events per hour for all periods of the day. Dotted line indicates expected activity value if there was no difference among the periods of the day (25%).

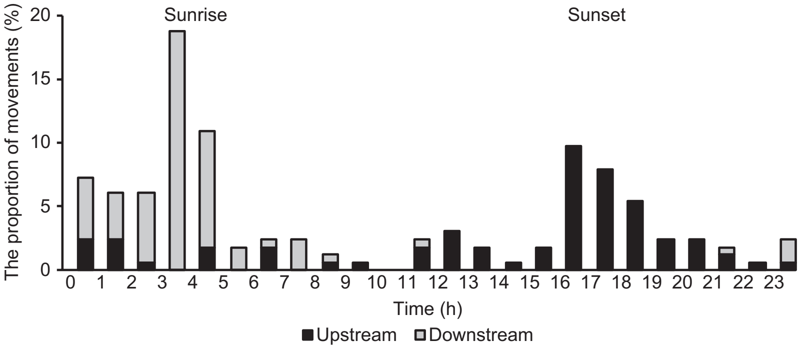

Fig. 6. Diel activity (UTC time) of upstream and downstream movements of the vimba bream before the spawning period (20 March–19 April) in 2014, based on receiver detections downstream of the lowermost rapids. All fish movements between automatic data receivers (arrivals into the detection area of a receiver) were counted as activity events. Approximate sunrise and sunset times are indicated in the figure.

during the entire study period (Fig. 5). The fish were generally least active during night, but the difference between day and night was smallest in spring (Fig. 5).

The largest variation in activity over the 24 h cycle was in spring 2014 (Figs. 5 and 6). Between ice break and the spawning period in 2014, the fish had the highest activity level during sunrise, but also a larger activity level during sunset than at day and night (Fig. 5 and 6). From 20 March to 19 April, upstream movement was mainly performed in the second half of the day (12:00–24:00, UTC), while most of the downstream movement occurred during the first half of the day ($\chi^2 = 83.88$, $n = 146$, df = 1, $p < 0.0001$; Fig. 6). More specifically, most of the upstream movement occurred at 16:00–17:00 hours (UTC) and most of the downstream movement at 03:00–04:00 hours. The sunrise during this period (20 March–19 April) was between 2:59 and 4:24, while sunset was between 16:36 and 17:44. A similar diel trend occurred at the end of the spawning period in 2013 (7–12 June), when upstream movement was also mainly performed in the second half of the day and most of the downstream movement occurred during the first half of the day ($\chi^2 = 9.29$, $n = 43$, df = 1, $p = 0.0023$).

Movement speeds

The movement speed over all river sections was on average 1.6 times greater when fish

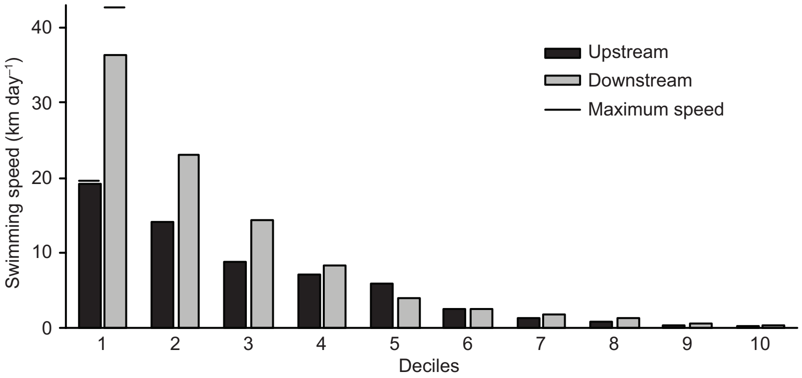

Fig. 7. Average swimming speed of vimba bream during upstream (black bars) and downstream (grey bars) movement. All the swimming velocities were sorted in order of decreasing value and divided into deciles.

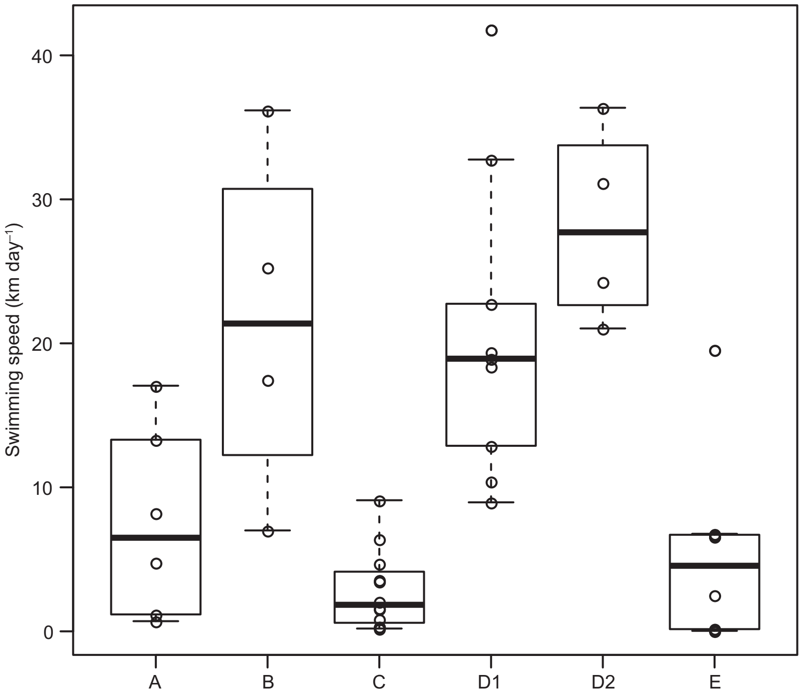

Fig. 8. Swimming speed of vimba bream in different river sections and time periods (average speed per fish are represented by circles). A: ascending upstream of the reservoir, B: descending upstream of the reservoir, C: descending over the lowermost spawning area, D1: descending to the sea in 2013, D2: descending to the sea in 2014, E: ascending to wintering. Quartiles 1 and 3: lower and upper box border, median: solid horizontal line, whiskers: smallest and greatest values excluding outliers.

were moving downstream than moving upstream (Fig. 7). The fastest 10% of the movements downstream had an average speed of 36.4 km day^{-1}, compared to 19.2 km day^{-1} during upstream movements. Average speeds were 8.0 km day^{-1} and 5.1 km day^{-1} during downstream and upstream migration, respectively.

During downstream movement, the fish moved faster through the slow-flowing parts of the river than through the rapids (Wilcoxon's signed-rank test: $n = 9$, $V = 0$, $p = 0.0039$; Fig. 8). The fastest speeds (42.7 km day^{-1} in 2013 and 40.1 km day^{-1} in 2014) were measured among fish that were migrating from spawning areas to the sea. The fastest upstream movement, 19.6 km day^{-1}, was achieved by the first fish that migrated from the sea to the wintering area in the autumn. The speed of the later arriving fish did not exceed 7.7 km day^{-1} in this river section. Comparing upstream and downstream swimming speeds (over the whole study period) at the individual level, indicated that fish, over any particular river section, moved significantly faster downstream than upstream (Wilcoxon's signed-rank test: $n = 17$, $V = 0$, $p < 0.0001$).

Discussion

In order to estimate the impact of migration barriers to a migratory fish population, it is essential to understand the potential role of blocked upstream habitats as reproduction areas (Benejam *et al.* 2016, Kruk *et al.* 2016, Silva *et al.* 2018). In this study, about half of the vimba bream that were caught under the dam and released in the reservoir upstream of the dam continued their upstream migration. The fish utilized all nearby upstream spawning grounds, and several fish performed longer migrations, more than 25 km. This demonstrates that there is a large potential for vimba bream reproduction upstream of the Sindi dam in Pärnu River and its tributaries, in areas that are presently not readily available to the fish due to low functionality of the fish ladder in the Sindi dam. Developing a functional fish passage at the dam could substantially expand the spawning area available for the vimba bream, thereby likely improve stock status. The same is valid for other anadromous and semi-anadromous fishes utilizing the Pärnu River, including river lamprey, Atlantic salmon, sea trout, whitefish, and smelt.

The drive for upstream migration varied among individual fish. The individuals with the longest upstream migration were the first ones to leave the reservoir. Some fish only moved downstream, which may indicate that fish could lose the stimulus for upstream migration after being stopped by the dam or in the reservoir.

Many fish stopped for a period in more than one spawning area. A similar behaviour is reported for other riverine batch spawning species, e.g. chub *Leuciscus cephalus* (Fredrich *et al.* 2003). In the upstream spawning sites, this behaviour may be attributed to a low abundance of fish and a need to search for a spawning partner. However, the same occurred in the downstream spawning sites where fish abundance was high. The movement pattern to and from a spawning site differed among individuals and was highly diverse. Some fish stopped at two, some at three, and some at four spawning sites. The vimba bream has been considered to have 2–3 spawning batches (Lelek 1987, Erm *et al.* 2003). However, our data suggest that the males could visit and possibly spawn at up to four different spawning sites. Females could visit and possibly spawn in two different spawning areas, or revisit and possibly spawn in one spawning area two times. Batch spawning, i.e. spawning at more than one site or several times in the same site may increase individual fitness through increasing the genetic diversity of the offspring, and possibly reduce mortality risks due to different conditions at different sites and time.

The fish made their upstream migration mostly in the beginning of the spawning season. The later movements between spawning sites occurred mainly in a downstream direction. Hence, the movement to different spawning sites was simultaneously a movement towards the sea. The strong motivation to reach the sea as soon as possible after spawning was demonstrated by the fact that the fish showed the highest moving speeds when leaving the last spawning area and heading for the sea. Females descended to the sea earlier than males. The difference in behaviour between the sexes may be associated with differences in reproductive biology as males may spend more time near to spawning grounds (Lucas and Batley 1996).

Fish showed higher maximum speeds than reported by Erm *et al.* (1970). This may be due to different methodologies (telemetry vs external tags). Telemetry tags and stationary receivers record the exact time when the fish leave one receiver and arrive at the next receiver. The time from release to recapture of externally tagged fish also include any time delay before and after the actual movement of the fish. In addition, in our study, movements were measured on a smaller scale (up to 23 km) than in the previous studies (up to 865 km). This may result in a higher maximum speed because swimming speed variation is not homogenized by long distances, which may also include e.g. resting periods.

In our study, movement speeds on the individual level depended on the swimming direction in the river as well as on the presence of rapids in the river section. Fish achieved higher speeds on downstream movement and on slow-flowing river sections. Although river flow can enhance fish migration during downstream movements, movement speed over some distance rather depends on the motivation to stop in various places. For example, river sections without rapids can be used for wintering during upstream movement, but apparently have no attraction during post-spawning migration towards the sea, as demonstrated by the high descending speeds.

Despite this, fish average speeds were lowest during downstream movement at the lowermost spawning area. This may be due to the high number of possible spawning partners present at this site, as all fish must visit this area on their way to the sea. One should also note that our results may be affected by a relatively high proportion of males, which may be motivated to stay longer at the spawning sites than females.

The tagged fish returned to the river mostly in autumn (September–November), although we cannot exclude the possibility that some fish remained in the brackish water areas. The literature reports return of vimba bream to freshwater both in autumn and spring (Erm *et al.* 1970, Volskis *et al.* 1970), indicating that the fish could stay over the winter in brackish water areas, perhaps due to poor wintering conditions in the river. For sea trout and anadromous Arctic char *Salvelinus alpinus*, it has been shown that most individuals in northern areas stay in freshwater during winter, but that individuals in watersheds without lakes, i.e., with poorer wintering conditions in freshwater, may to a larger extent stay at sea during the winter (Jensen and Rikardsen 2012). In our study, the fish that entered the river in autumn migrated to the sea in June and spent on average 62% of the year in the river.

In the Pärnu River, the vimba bream were concentrated in a short river section below the first rapid during the winter period. The fish became active and mobile in spring, performing regular movements both downstream and upstream. The high concentration and mobility make the fish potentially vulnerable to be caught by passive fishing gears, e.g. traps and gillnets. This should be taken into consideration when designing the vimba bream management and protection rules.

This study demonstrates that fish had the highest activity level during dusk and dawn prior to the spawning period as well as in the end of the spawning period, moving upstream in the evening and back downstream in the morning. We do not know the reasons for this pattern, but it might be associated with feeding, or even searching for suitable spawning sites. In general, the vimba bream were more active during dusk and dawn than at other times of the day. Higher mobility rate with location shifts during twilight has been described also among several other cyprinid species, e.g. dace, chub and roach (Clough and Ladle 1997, Baade and Fredrich 1998, Fredrich *et al.* 2003). Also many non-cyprinid fishes, e.g. Atlantic salmon and pikeperch *Sander lucioperca*, show clear diel variation in their behavioural patterns (e.g. Lilja *et al*. 2003, Davidsen *et al*. 2008, Horký *et al*. 2008). These patterns may be a compromise between predator avoidance (movements in daylight may be more dangerous because it increases the risk of being attacked by predators using vision), the advantage of using vision when moving and feeding instead of doing these activities during darkness, and feeding efficiency connected to the diel variation in the behaviour of the prey.

The complexity and individual variation of vimba bream behaviour were certainly larger than we were able to detect with our study design. Both a higher number of transmitters (i.e. tagged fish) and a higher density of receivers would enable studies of movement patterns on a finer scale and facilitate testing of more variables in relation to the behavioural responses of the fish. There is a big potential for describing vimba bream movement patterns on a finer scale (e.g. mobility inside and between several spawning areas). This is information that may be useful for a possible restoration of vimba bream populations in the Baltics.

During the manuscript stage of this study, demolishing works of Sindi dam started in October 2018. During the next three years, the Sindi dam will be partly removed, the water level of the reservoir will be lowered, and a nature-like rapid area will be constructed in the riverbed and act as a fish passage. Fish will gain renewed access to a large part of their original habitat. This will likely have a positive impact on the vimba bream as well as on other migrating species. It will soon be possible to study vimba bream migration in a river with restored connectivity.

Conclusions

This study provided basic information on the migration behaviour of the little studied vimba bream. This is important for management and to develop mitigation measures. The results indicate that semi-anadromous fishes can have complicated riverine movement patterns and would benefit from improved longitudinal connectivity in rivers impacted by migration obstacles. Anadromous species, such as the vimba bream, Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*), Atlantic salmon, brown trout, whitefish, smelt and river lamprey used to be important commercial fish in the Gulf of Finland area because they were abundant and had high commercial value (Lajus *et al*. 2013). Due to intensive exploitation and other human-induced factors, populations of most of these species had declined notably by the early 20th century and have now lost their commercial significance, although a salmon fishery has been maintained by extensive stocking (Lajus *et al.* 2013). The present study of the vimba bream in the Pärnu River demonstrated a large potential of increasing reproduction areas by improving the fish passage in the Sindi dam to allow unimpeded migration to upstream areas, which are now not readily available to anadromous fish.

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Appendix. The date and reason for individual fish being removed from the study.

Date	Reason	Fish ID
29 May 2013	Signal lost in the reservoir	40
3 June 2013	Signal lost in Navesti River	36; 51
3 June 2013	Signal lost in the reservoir	54
7 June 2013	Signal lost in the reservoir	55
11 June 2013	Signal lost on Pärnu River km 15	50
11 June 2013	Signal lost on Pärnu River km 13	52
11 June 2013	Signal lost on Pärnu River km 9	58
12 June 2013	Fish dead on Pärnu River km 13	61
16 June 2013	Fish descended to the sea, did not return to the river	35; 37; 41; 46; 47; 48; 49; 53; 56; 60
18 Dec. 2013	Signal lost in Pärnu River mouth	62
19 Jan. 2014	Signal lost in Pärnu River mouth	57
16 Apr. 2014	Signal lost on Pärnu River km 9	45
19 Apr. 2014	Signal lost on Pärnu River km 9	34
17 May 2014	Signal lost on Pärnu River km 9	39
23 May 2014	Signal lost in the reservoir	43
4 June 2014	Fish descended to the sea in the end of the study	33
5 June 2014	Fish descended to the sea in the end of the study	42
5 June 2014	Signal lost on Pärnu River km 10	59
10 June 2014	Fish descended to the sea in the end of the study	44
12 June 2014	Fish descended to the sea in the end of the study	38