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Home range and seasonal movement of taimen, *Hucho taimen*, in Mongolia

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Abstract – Taimen, *Hucho taimen*, is the world's largest salmonid and a prized sport fish. We used radio and acoustic telemetry to characterise movements of adult taimen in an extensive river system, the Eg–Uur, in north-central Mongolia. Forty-six taimen were tagged with transmitters (27 radio, 17 acoustic and 2 radio-acoustic combined) and tracked from 2004 to 2008 using mobile surveys and fixed receivers. The mean home range of individual taimen tracked for an average of 2.4 years was 23 km ($N = 41$, range = 0.5–93.2 km). Of the fish with over 10 relocations ($N = 16$), 90% remained within a range of 38 km. Four distinct movement patterns were observed: (i) restricted core home range, (ii) core range with seasonal departures, (iii) core range with separate seasonal range and (iv) home range transfer. Movement was greatest in May and June (spawning and postspawning period) with another peak period of movement in September and October (water temperature cooling).

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Key words: *Hucho taimen*; migration; movement; salmonidae; telemetry; trout

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Introduction

Taimen (*Hucho taimen*) is the largest species in the family Salmonidae, reaching up to 2 m in length and over 90 kg in weight (Levidanov 1959; Sigunov 1972). The distribution of taimen has been seriously diminished by dams, water diversion, pollution and overfishing (Holčík et al. 1988). As a result of its decline, the taimen is now listed as a threatened species throughout its native range, which includes Russia, China, Kazakhstan and Mongolia, and is being considered for listing in the International Union for Conservation of Nature's (IUCN) red list (Matveyev et al. 1998; Baasanjav & Tsend-Ayush 2001).

Although taimen are listed as 'endangered' on the Mongolian red list (Ocock et al. 2006), some of Mongolia's rivers still hold healthy taimen populations. Once persecuted as a nuisance predator of commercial fish species in Russia (Pirozhnikov 1955), the taimen is now highly prized by recreational fishermen who travel to Mongolia. Given the taimen's endangered status and growing fishing pressure, there is a need for better understanding of the ecology of taimen (Vander Zanden et al. 2007). A population model suggests that low intensity catch-release fishing is unlikely to pose a serious risk to taimen; however, even a relatively small recreational or subsistence harvest could lead to eventual extirpation (Jensen et al. 2009). Limited access recreational fishing concessions have been proposed as a means of conserving taimen (Vander Zanden et al. 2007). Knowledge of habitat use and movement is critical for the effective design of sustainable concessions, area closures and other spatial management strategies for taimen.

Taimen is one of four species in the genus *Hucho*, the second most archaic group of trout and salmon (*Salmoninae*) after the genus *Brachymystax* (Holčík 1982; Shed'ko et al. 1996). Taimen are restricted to freshwater, unlike the anadromous *Hucho perryi*. In

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contrast to semelparous salmonids, which expend all their energy in migration and reproduction and then die afterwards, all *Hucho* species are iteroparous (Holčík et al. 1988). Throughout their range, taimen are predominantly found in fluvial environments, with individuals occasionally being caught in the littoral zone of lakes and reservoirs (Holčík et al. 1988; Matveyev et al. 1998). In Mongolia, taimen are thought to have an upstream spawning migration in the spring and a downstream migration to wintering pools in the early to mid-fall (Dulmaa 1999). Although there have been some studies on their habitat use, quantitative evidence of distances travelled during any of their annual movements, essentially their home range, has not been available (Holčík et al. 1988).

The goal of this study was to identify the home range and movement patterns of mature taimen in a remote and relatively pristine watershed in north-western Mongolia. This was accomplished by tracking individual taimen using both radio and acoustic biotelemetry. Radio tracking allows determination of precise locations of fish, while acoustic tags provide continual year-round monitoring of fish movements using submerged, stationary receivers. Our specific objectives were to estimate: (i) home range size, (ii) the number and size of 'core areas' within the home range where individual fish are most commonly found and (iii) seasonal differences in taimen movement rates. The extended observation period of this study (>4 years of tracking for some individual fish) relative to other biotelemetry studies provides a unique perspective on how our perception of home range in fishes can depend on the observation period (Rodríguez 2002). In addition, this work was designed to provide movement and home range information to be used in designing a fisheries management strategy (including fishing concessions and protected areas) for the population.

Methods and study area

The Eg–Uur watershed (3.48 million ha) is located in a rural region of north-central Mongolia at the ecological boundary zone between the Mongolian steppe and the Siberian taiga forest. The Eg River (length = 277 km) originates from Lake Hovsgol and flows south and then east until it meets with the Uur River (length = 152 km), a river fed by groundwater and precipitation run-off from the eastern Sayan. The combined Eg–Uur, known as the Eg river after the confluence (length = 281 km), feeds into the Selenge River, the largest tributary of Lake Baikal, Russia. The Eg–Uur Rivers have an annual period of ice cover that usually spans from late November until early May. These rivers generally reach peak flow in July and August following summer thunderstorms.

The upper portion of the Eg River (hereafter referred to as the Upper Eg), above the Uur confluence, is characterised by a relatively high gradient, numerous braids and groundwater springs, and a dense, willow-larch riparian forest. The Uur is characterised by a lower gradient, a mixed riparian habitat with both steppe pasture-land and patches of larch-willow forest, and large meanders in a wide floodplain valley. The Eg below the Uur confluence (hereafter referred to as the Lower Eg), maintains a similar riparian habitat to the Uur River, but with increased width and reaches with large boulders. The core area of our research was conducted along 98 km of river centred around the confluence of the Eg and Uur. The Eg–Uur rivers are home to eight species of fish and one of Mongolia's largest populations of taimen (M. Erdenebat, personal communication). The rivers here are considered a trophy taimen fishery with individuals attaining lengths of over 150 cm and maximum ages of at least 28 years (Jensen et al. 2009).

Tagging

Between June and October of 2004, a total of 46 mature taimen, ranging in size from 48 cm (800 g) to 125 cm (14,900 g), were caught by angling using single-barbless hooks from the main channels of the Eg and Uur Rivers. Radio transmitters were implanted in 27 fish, acoustic transmitters in 17 fish and a combination of both a radio and acoustic transmitter in two fish. Surgical implantation of transmitters was based on standard fish surgery procedures (Harms 2005). Tagged fish were anaesthetised with Tricaine methanesulfonate (MS-222) prior to surgery and the incisions were closed with MAXON™ monofilament synthetic absorbable sutures (United States Surgical, a division of Tyco Healthcare Group LP, Norwalk, CT 06856, USA). Weight in air of implanted transmitters did not exceed 1.9% of an individual taimen's body weight (average tag to body weight ratio: 0.06). All but six of the tagged taimen were caught from the three river regions within 30 km of the Eg–Uur confluence, a region encompassed by Erdenebulgan soum (county). Six of the radio telemetry taimen were caught and tagged on the Lower Eg River approximately 80 km downstream from the Eg–Uur confluence, in Teshig soum (Fig. 1).

To maximise data collection possibilities, we used both acoustic and radio telemetry systems. The acoustic tracking system included Vemco V13-1L, V16-4L and V16-6L tags (expected transmission life 320, 1000 and 2000 days, respectively) and both a Vemco V100 manual tracking receiver and six Vemco VR2 monitoring receivers. The radio-tracking system comprised Lotek MCFT-3L and MCFT-3EM tags (expected transmission life of 598 and 2522 days,

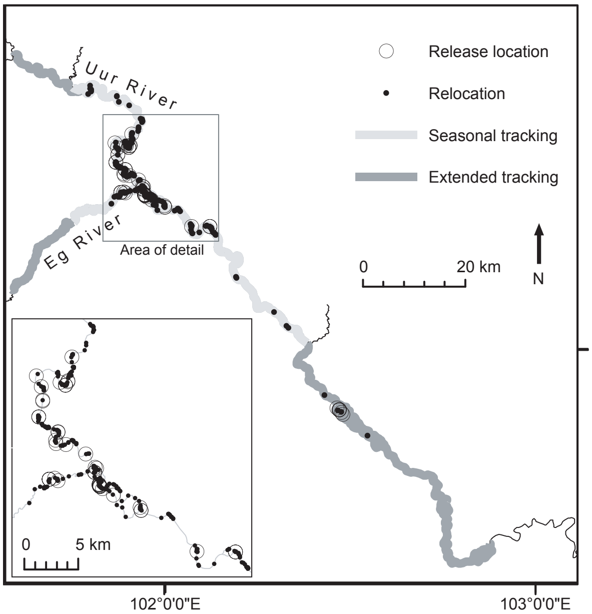

Fig. 1. Map of Eg–Uur study region illustrating manual tracking effort and fish tagging and relocations from manual tracking. The highlighted tracking regions represent broad-scale (210 km) and seasonal (98 km) tracking areas.

respectively) and Lotek SRX400A manual tracking receivers. Each transmitter emitted a unique pulse code that allowed us to identify individual fish while tracking. Field tests with dummy tags indicated that the range of reliable detection for the radio receiver varied between 600 m (transmitter depth = 1 m) to 100 m (transmitter depth = 3 m). For acoustic receivers, the range was approximately 200 m under normal flow conditions, but decreased dramatically at higher flow. Manual radio tracking allowed determination of precise locations of fish, while acoustic tags were manually located, as well as monitored year-round by automated, in-river receivers. The two complementary approaches allowed us to record coarse-scale movements throughout the year and identify fish locations at finer temporal and spatial scales during our field season.

Tracking

Tracking of tagged taimen began in July of 2004 and continued through October of 2008. Tracking surveys using Lotek SRX400 radio receivers to relocate radio tagged fish were conducted approximately once every 15–30 days (referred to here as seasonal tracking) from May through October (ice-free period), and from one to four times during each winter period (November through April). A Vemco VR100 acoustic receiver with hydrophone was simultaneously used to track acoustically tagged fish during tracking surveys during the ice-free period. During open water, fish tracking was conducted by drifting downstream with the radio antenna hoisted on a mast to a height of approximately 3 m and the acoustic hydrophone placed in the water just below the base of the raft. We observed only minor behavioural reactions by taimen to the presence of the boat, and in no instance did tagged fish appear to be pushed downstream further than the nearest pool (<100 m). Tracking during periods of ice cover was conducted either by foot or horseback, both maintaining a minimum antenna height of 4 m above the river level as angle of incidence to the water is critical in radio signal attenuation. Since the radio transmitters were programmed for 12-h on/off intervals to prolong battery life, all tracking surveys were performed between the hours of 08:00 and 20:00. Fish locations were collected using a geographic positioning system (GPS) and recorded in latitude and longitude coordinates.

The core tracking region spanned 98 river km of the Uur, Upper Eg and Lower Eg Rivers. This region included most of the tagged fish and was also logistically the most feasible region to conduct tracking surveys on a regular basis. Between March 2005 and October 2008, six extensive tracking surveys (in March 2005, August 2006, February & June 2007 and March & October 2008) were conducted over 210 river km to check for the presence of fish not found in the core survey region.

Continual monitoring of acoustic-tagged fish movements was conducted using six Vemco VR2 automated acoustic receivers for the 36-month period between August 2004 and July 2007. The VR2s are underwater units designed for 24-h remote monitoring and data logging of proximate passage of an acoustic-tagged fish. These receivers were placed approximately 10 km apart throughout the Eg–Uur confluence area in an array encompassing the 60 river km where the 19 taimen were tagged with acoustic transmitters (Fig. 2). Receivers were placed at the downstream end of a deep, slow pool with uniform cross-section, to maximise detection probability of fish swimming down-current. Acoustic tags were set to transmit at a random interval between 15 and 40 s. This interval represents a trade-off between detection probability and battery life.

Data analysis

All fish locations from seasonal-tracking data were plotted over a river layer in a Geographic Information System (GIS) to identify spatial distribution patterns of individuals along the river channels. Fish relocation coordinates were then affixed to the nearest point on the digitised river line (50-m accuracy) and river distance from each relocation to the Eg–Uur confluence, a reference point of 0 km, was calculated. The range of movement for each taimen, with at least one

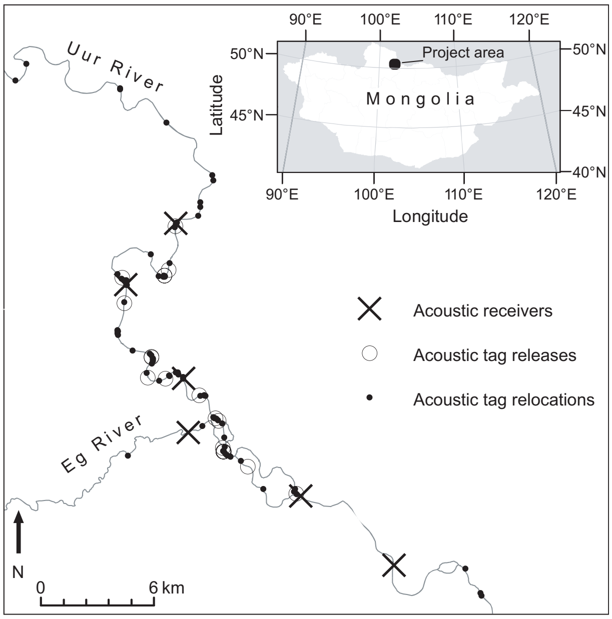

Fig. 2. The location of stationary acoustic receivers (Vemco© VR2s) and acoustic-tagged taimen release and relocation sites.

point of relocation, was calculated as the river distance between its most upstream point and most downstream point for all seasonal-tracking relocations during the period of the study. We defined three seasonal periods based on local observations of taimen spawning behaviour (Esteve et al. 2009) and river temperature regimes : a warming/spawning period (15 April–15 June), a postspawning summer period (16 June–15 September) and a winter period (16 September–14 April).

We use the term home range in this paper to mean the entire area within which an individual fish was observed during the period of the study. To do this, we used all taimen relocation data, radio and acoustic, to calculate linear home range estimates for each fish as per Logan (1963), the distance between an individual fish's most upstream and the most downstream relocation points. Fish location data during the first 30 days after a fish was tagged were not included in analysis to allow for a recovery period from being caught and implanted with a transmitter and to limit bias related to release location. To identify core areas of most frequent use for taimen within their linear home range, we employed kernel density estimates. Kernel density estimators smooth the relocation point data to create a continuous probabilistic distribution along the line of a river, thus providing a way to identify the number and size of core ranges (Worton 1989; Vokoun 2003; Vokoun & Rabeni 2005). We used a one-dimensional version of the kernel density estimator described by Worton (1989) with a smoothing parameter (h) value of 1 km, to analyse the relocation data of fish with >15 seasonal relocations ($N = 8$). For fish with <15 total relocations at the seasonal scale, we categorised their movement patterns qualitatively by plotting on a map. Fish tagged only with acoustic tags were also excluded from the kernel-based analysis since they were not tracked manually during ice cover. This threshold of 15 relocations is less than the minimum suggested by Vokoun (2003) of 30 relocations collected at a consistent time interval. However, in this case, using a minimum of 30 seasonal relocations would have required coarser seasonal aggregation (two, rather than three, seasonal periods) and/or reducing the number of tagged taimen whose movements we could characterise. We highlight regions of 95%, 90% and 50% habitat use for the selected taimen (Worton 1989). Similar to the linear home range estimate, the 95% and 90% estimates identify the greater region utilised by a fish over this period. We use Rodríguez-Robles (2003) definition of the 50% kernel range as the core home range of a fish.

To analyse logged data from the stationary acoustic receivers, we first determined the presence/absence of individual fish on a daily basis at each receiver. We considered fish with less than two consecutive days at any one receiver to be mobile. To determine how taimen movement varies over a year, receiver data for mobile acoustic-tagged fish were grouped by month and totalled over the 36 months of operating acoustic receivers. Maximum movement rates were quantified using logged data (1-min resolution) for all fish that moved between multiple receivers within 1 day. For individual fish that exhibited stationary behaviour at an acoustic receiver, we counted maximum days logged at that receiver over a year as well as consecutive days logged.

Results

Over >4 years and a combined 2460 km of manual tracking in the Eg–Uur, 41 of the 46 tagged taimen were relocated from 2 to 56 times (mean of 12 relocations per fish, see Table S1 in the Supporting Information for details of each individual). Eighteen of the 19 acoustic-tagged taimen, including the two dual tagged fish, were logged on between 1 and 363 separate days each on stationary acoustic receivers. Three of the logged codes (individual fish) did not match the code numbers labelled on any of the tags and we have been unable to positively identify those fish. Four fish (A28, A38, R3 and R16) were never relocated after their initial catch and tagging date and were excluded from further analysis. Although we could not recover the transmitter, we considered radio fish #11 to have died or expelled its tag due to lack of any movement over 24 relocations and also excluded it from analysis. Through both circumstantial and

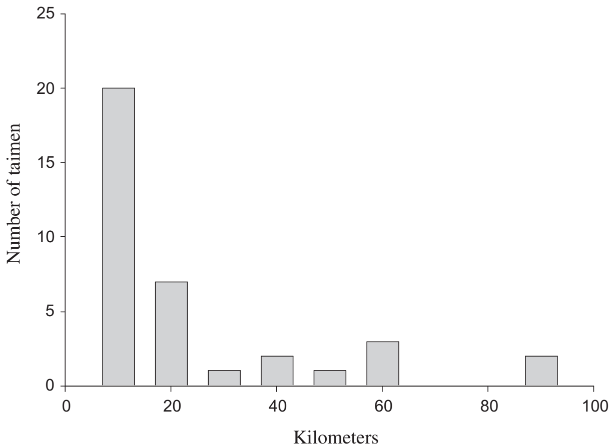

Fig. 3. The distribution of taimen home range estimates (total longitudinal displacement) for 41 tagged fish (individuals with >1 relocation) in the Eg–Uur over the period of July 2004–October 2008.

physical evidence we determined that six tagged taimen were killed by fishermen during the course of the study (A23, RA1, R1, R21, R28 and R25).

Home range

Of the 41 taimen included in data analysis, the mean river distance between the most upstream and most downstream relocations (i.e., the home range) was 23.0 km with a median of 13.8 km (Fig. 3, range: 0.5–93.2 km, SD: 25.7). Although there were movements of up to 93.2 km, 90% of the tagged fish were detected in linear home ranges of 64 km or less. There was no linear relationship ($r^2 = 0.001$, $P = 0.82$) between home range size and the number of relocations. There was a weakly positive, but not statistically significant, linear relationship between home range size and fish size ($r^2 = 0.069$, $P = 0.09$). Comparison of home ranges between rivers was not performed as both tracking effort and number of tagged fish were significantly less in the Upper Eg than the Uur and Lower Eg rivers.

Eight of the most frequently relocated taimen (≥15 seasonal-tracking relocations) were selected for further analysis of home range using a kernel density estimator (Figure S1). These eight individuals were slightly larger than the other tagged fish on average (90.6 cm compared to 79.8 cm), but this difference was not statistically significant (two-tailed *t*-test, $P = 0.09$). The mean 95% home range for these eight individuals was 10.6 km and mean core range (50%) was 2.8 km (Table 1). Three of the eight individuals exhibited both 95% and 90% kernel home range limits adjacent or very close to their core range (50%), essentially one core habitat where they were found at least 95% of the time. The other five individuals exhibited spatial separation between their 95% or 90% home range sections and their core range, illustrating periodic departures from the core range. Although relocation data were deemed insufficient for kernel density analysis on the remaining fish, the pattern of seasonal departures from a core area was commonly observed for these other taimen as well.

Movement patterns

We characterised movement patterns for the eight individuals with sufficient relocations for kernel density analysis (Table 1). Four relatively distinct patterns of movement were observed (Fig. 4). We then subjectively classified all taimen with sufficient relocations ($N = 22$) according to these four patterns. The simplest pattern was exhibited by six fish (27%) that stayed within a restricted range, with movements in a core home range within 3 km. Somewhat more common was the pattern of fish with a small core range (3 km or less) with seasonal departures to multiple other locations followed by a return to their core range. This pattern was exhibited by 10 fish (45%). It is interesting to note that individual R2 exhibited seasonal departures each year during the spawning period and annually alternated the direction that it swam from its core home range (downstream in

Table 1. Individual characteristics and movement patterns for eight individuals with 15 or more relocations.

Tag code	Length (cm)	Number of relocations	Mean time between relocations (days)	Mean distance between relocations (km)	Home range (km)			
					Linear	95% range	90% range	50% range
R1	76	25	45	1.81	11.6	9	7	3
R2	99	29	53	6.18	51.3	16	11	3
R4	97	21	77	1.51	8.8	8	6	3
R15	88	33	40	1.38	13.8	6	5	2
R20	79	29	49	1.43	27.5	8	6	2
R25	52	15	48	0.68	6.2	8	6	2
R26	110	27	57	3.32	14.1	13	11	3
RA1	125	17	85	5.38	67.6	17	12	4
Mean	90.6	24.5	56.8	2.7	25.1	10.6	8.0	2.8
Median	92	26	51	2	14	9	7	3
SD	22.3	6.3	15.9	2.0	22.5	4.1	2.8	0.7

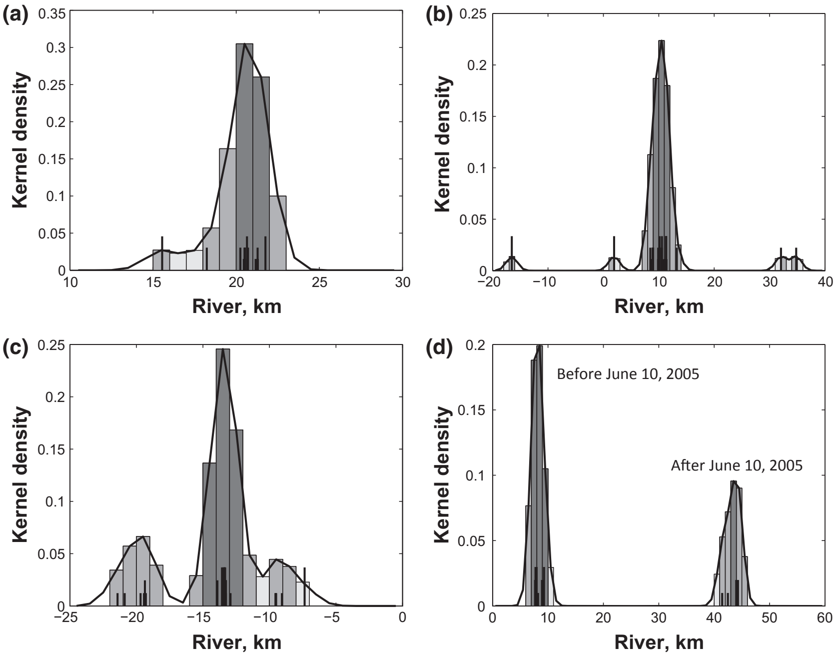

Fig. 4. Examples of the four distinct home range patterns exhibited by radio tagged taimen: restricted core home range (a), core range with seasonal departures (b), core range with separate seasonal range (c), and home range transfer (d). Bars represent kernel density home range estimates of 95% (light grey), 90% (medium grey) and 50% (dark grey). The small black bars on the *X*-axis represent relocation points for the spawning period (15 April–15 June, tall bar), summer (16 June–15 September, medium bar), and cooling and ice-cover period (16 September–14 April, short bar).

2005, 2007 and upstream in 2006 and 2008). A third pattern was exhibited by taimen with a core home range and seasonal movements to a single other location where they were observed multiple times, indicating some site fidelity. This pattern was observed for three (14%) of the tagged fish. The final pattern, also found in only three taimen, is one in which river fish appear to complete a home range shift. This is when a fish exists in one core range for a period and later is found to move to a new region where it persists for multiple seasons. This pattern is indicated by more than one nonoverlapping core range (e.g., individual R23).

We combined the stationary receiver data with the initial tag locations and manual tracking relocations to assess taimen movement between different river sections (Uur, Upper Eg and Lower Eg). Twenty-nine per cent (12 of 41) of taimen left the section that they were tagged in. Three fish (A26, A33 and RA1) were found to have moved between the Uur and the Lower Eg, and five (R7, R10, R12, R24 and A29) moved between the Upper Eg and Lower Eg. Four fish (A30, A36, R20 and RA2) were present in each of the three river sections, all of which were caught and tagged within 2 km of the Eg–Uur confluence. The linear kernel density approach was limited to characterising the movement of taimen within one river section or between two river sections.

Seasonal movement

From August 2004 until July 2007, the array of stationary acoustic receivers in the Eg–Uur logged 969,145 acoustic tag transmissions. The vast majority of these detections were repeated relocations of individual fish at the same receiver. Eight of the acoustic-tagged taimen were recorded on a single acoustic receiver for extended periods of time (>2 consecutive days). Only 85 signals from the receivers were from mobile fish that spent less than two consecutive days in a month in proximity to a single receiver. These data allowed us to measure movement differences over the course of a year. Movement peaked in May and June and then again in September and October (Fig. 5).

Acoustic fish A24 was logged as being present for 203 days in 2005 at receiver 2, 62 of them consecutive during 13 September–14 November. Likewise, fish

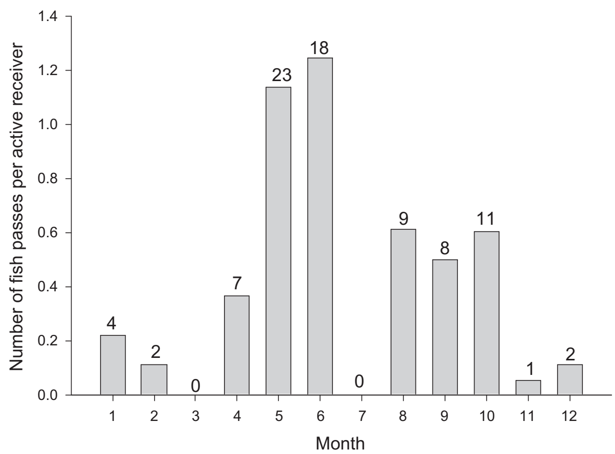

Fig. 5. Taimen seasonal movement in the Eg–Uur using stationary acoustic receivers. The bars indicate the mean monthly movement of individual taimen per operational acoustic station. Numbers on bars indicate the total number of acoustic-tagged taimen that passed a receiver for that month over the entire 36-month period.

A39 was recorded to be in proximity to receiver 3 for 132 days in 2005, 63 of them consecutive from 5 September to 7 November. A maximum upstream movement of 3.97 $km \cdot h^{-1}$ was recorded in the Uur River between receivers 3 and 2 (a distance of 8.4 km) when fish A39 (58 cm) passed on 5 January 2005. The maximum rate of downstream movement observed was 4.00 $km \cdot h^{-1}$ for fish A23 travelling between receivers 5 and 6 (a distance of 7 km) in late August of 2004.

Discussion

This is the first telemetry study of taimen and one of the longest telemetry studies of any lotic fish (Gowan et al. 1994; Minns 1995; Rodríguez 2002). Our results confirm some existing knowledge of taimen movements (e.g., high movement rates in spring and fall), and contradict others (there is greater individual variability than previously assumed and no mass migrations). Previous studies of taimen movement were based on short-term visual observations (Holčík et al. 1988). Sabaneev (1911) thought that taimen moved hundreds of kilometres during spawning migrations, although he lacked evidence of movement by specific individuals. Nieslanik visually followed pairs of the closely related huchen, *Hucho hucho*, in Danube basin rivers and found that spawning period movement does not exceed 10–25 km (reported by Holčík et al. 1988). Longer-term observations are critical for understanding seasonal and inter-annual patterns in movement.

The distance between a tagged individual's most upstream and most downstream relocation points is a common starting point to define a lotic fish's home range (Minns 1995). Using this metric, the maximum home range observed in this study was 93 km, four times greater than the mean home range of 23 km. Movements of this distance are the exception, however, as 90% of taimen had home ranges <65 km, and half had ranges <14 km. The leptokurtic distribution (Fig. 3) of home ranges is expected in univariate movement data because the chance of relocating a fish decreases as it gets further from the core tracking region (Fraser et al. 2001). Temporary departures may also be missed if the sampling interval is not fine enough to capture them. It is critical to understand that our observations, like most telemetry studies, provide a lower-bound estimate of actual fish movement (Gowan et al. 1994).

Analytical tools such as kernel density estimators are useful for characterising the spatial distribution of an individual within its home range (Worton 1989; Kernohan et al. 2001). Unfortunately, irregular relocation success, despite fairly regular effort, made it impossible to apply kernel density approaches to all fish. Still, we were able to generate kernel density utilisation distributions for eight individuals. With the exception of RA1, these fish spent 50% of their time over the study period in a single river reach of ≤3 km. However, these individuals also periodically undertook movements of up to 51 km during the year. Both the core range and the total linear home range are important for understanding taimen ecology. The size and location of a core range is important for understanding habitat use. Knowledge of occasional extreme movements away from the core range is necessary to understand population connectivity or identify potential barriers to natural movements.

Taimen do not fit the 'restricted movement paradigm' (Gerking 1959). We observed seasonal departures at distances of up to 10 times their core range. Similar occasional long-distance movements have been observed in other large-bodied river fish. For example, paddlefish (*Polyodon spathula*) in the Upper Mississippi moved up to 420 km (Zigler et al. 2003), muskellunge (*Esox masquinongy*) in the St. John River moved up to 100 km (Curry et al. 2007), and tigerfish (*Hydrocynus vittatus*) in the Upper Zambezi up to 71 km (Økland et al. 2005). Taimen home range appears to fit the log-linear home range versus body size relationship across species described by Minns (1995, data not shown). However, this pattern did not hold for individual taimen, as there was no significant relationship between an individual's home range and body size. The reasons for these occasional long-distance movements are unclear. If taimen are territorial as Pirozhnikov (1955) described, there may be some subordinate individuals that become displaced by social interactions potentially resulting in movements to find more hospitable habitat.

The large size of taimen allows a transmitter with long battery life (5–7 years) to be implanted without exceeding 2% of their body mass, a widely used rule of thumb for the upper limit of tag size in fish telemetry studies (Jepsen et al. 2002, 2005). The small size of the tags relative to body size helps limit the effects of tagging on behaviour, an important factor in telemetry studies (Garton et al. 2001; Bridger & Booth 2003). Although there are no previous telemetry studies on *Hucho* species, studies of other salmonids did not find any impact on fish feeding behaviour, growth, or general health from surgically implanted transmitters (Adams et al. 1998; Connors et al. 2002). We have recaptured, and re-released, four of our tagged fish (RA1, R06, R30 and A36) during angling for a population-survey. All appeared to have healed from the surgery with minimal, if any, noticeable scar tissue. Also, having caught the taimen by angling indicated they were actively feeding and their growth from the time they were tagged matched normal growth rates for taimen. Anecdotal reports from local residents indicated that tagging may have served as a deterrent to harvest. Nevertheless, six individuals are believed to have been taken by fishermen.

In animal tracking studies, the temporal scale of the sampling regime can affect estimates of home range size (Swihart & Slade 1985a; Vokoun 2003; Borger et al. 2006). One advantage of multi-year tracking is that it provides a picture of fish movement over multiple seasonal cycles. This longer-term view allowed us to classify individuals into four distinct movement patterns: (i) single core range, (ii) core range with seasonal departures to multiple locations, (iii) core range with a single alternate seasonal range and (iv) home range shift.

The several documented home range shifts in the population were multi-annual and often spanned long distances. If home range shifts are significant, it will be important to try to identify what initiates them as part of understanding the population stability in a region. Crook (2004) originally described such home range shifts for two riverine fishes, golden perch (*Macquaria ambigua*) and carp (*Cyprinus carpio*), in Australia. Movement patterns may vary among different habitats as well. The muskellunge tracked by Curry et al. (2007) is a good example of the differences in home ranges in different habitats. Muskellunge above a dam exhibited movements of up to 100 km whereas below a dam movements were restricted to 25 km. Vokoun (2003) noted that few fish telemetry studies have been conducted in rivers without impoundments or other anthropogenic alteration. Fish movement studies in unaltered rivers such as this provide an interesting contrast with fish movements in highly altered systems.

Seasonal movement

Taimen spawning activity generally begins in late spring after the ice melts and when river temperatures reach 6–8°C (Holčík et al. 1988; Dulmaa 1999). In Mongolia, this temperature threshold matched evidence of spawning activity in late May in the Eg–Uur (Vander Zanden et al. 2007; Esteve et al. 2009). It is also thought that taimen generally move downstream in the autumn to over-winter in deeper waters and avoid frozen upper reaches of rivers (M. Erdenebat, personal communication; Dulmaa 1999). We found that peak movement occurred in May and June, during and after the spawning season, with a second, slightly less pronounced, movement period in August through October when the water is cooling. The timing of these high movement periods matches with expectations from the literature, but there does not seem to be a consistent pattern between upstream and downstream movements in either the spring or fall. For example, fish R2 (99 cm) departed from its core range every May but did not move in the same direction. One odd contrast to the seasonal movement data is the fact that the fastest recorded upstream movement of 8 km in 2 h (A39) occurred under the ice in early January. Although winter is not a period of high movement for the population as a whole, it is important to note that there can be substantial individual movements at any time of year.

Spawning period movement for our tagged taimen has been difficult to understand since there has been no confirmation of any tagged fish paired-up at a redd. Finding taimen pairs spawning is difficult because of their short period of spawning activity and relatively inconspicuous spawning behaviour (Esteve et al. 2009). Similar to Sabaneev (1911), we noticed that not all taimen move during the spawning season. Earlier studies have suggested that mature taimen may spawn only once every 2–3 years (Misharin & Shutilo 1971; Sigunov 1972). We were unable to conclusively determine whether the high movement rates observed during the spawning season were in fact related to spawning or to other seasonal cues. In addition, the inability to accurately sex tagged individuals precluded any analysis of differences in movement patterns between males and females.

Ecological and management implications

There are five major conclusions with conservation and management implications that can be drawn from this study. First, taimen in the Eg–Uur watershed did not exhibit any coordinated migrations en mass over the course of the study. While seasonal differences in movement rates were observed, movements varied widely among individuals. Second, taimen have exhibited one-way movement of over 80 river km, travel extensive enough to cross soum (county) and even aimag (provincial) boundaries in the Eg–Uur watershed. Management of taimen will likewise need to occur at spatial/political scales larger than the aimag level. Third, all taimen with sufficient relocation data exhibited core areas of heavy use (>50%) <4 km in length, although for one individual (RA1), this core area occurred in two locations separated by nearly 30 km. These regions of intensive use are critical for identifying important habitat characteristics for taimen as well as investigating interactions among individuals. Fourth, observations of home range shift provide evidence of taimen's capacity not only for dispersal and recolonisation, but also for its susceptibility to threats outside its core range. Finally, movement peaked in May and June and to a lesser extent in August through October. During these periods of increased movement, taimen are likely to be more vulnerable to illegal passive fishing gears such as gill nets.

Knowledge of taimen movements will be useful for management of this endangered species. Nevertheless, the data and their analysis are not comprehensive. Variable relocation success, related to both logistical challenges of tracking surveys as well as adverse environmental conditions, make interpretation of the data more complicated (Kernohan et al. 2001; Gu & Swihart 2004). Movement of individuals outside the study area suggests that taimen movements can be more extensive than what was seen in the remaining individuals. As in most telemetry studies, individuals with extremely long movements were, in effect, censored from the data. The acoustic receivers most distant from the Eg–Uur confluence (for all three river sections) recorded the departure of 7 out of 19 (37%) acoustically tagged fish from the study area. Four of those fish appeared to have permanently exited the area without subsequently returning. The limited number of observations of any individual precluded more formal statistical analysis of movements (e.g., analysis of the scale of autocorrelation, Swihart & Slade 1985b). Given the practical difficulty of conducting frequent mobile telemetry surveys at the necessary spatial scale (100 s of km), we expect that future movement studies of taimen will make greater use of stationary receiver technology (including passive Radio Frequency Identification, RFID, tags and receivers) or aerial radio-tracking surveys. Population genetic studies to understand patterns of gene flow among tributaries and watersheds would provide a valuable broader context to these telemetry results.

Both the ecology and management of taimen involve inherently spatial processes. Measuring the links between 'source' and 'sink' populations, estimating the natural recolonisation potential of depleted river reaches, and understanding the frequency of movements outside protected areas are a few examples of the direct management implications of quantitative studies of fish movement (Kramer & Chapman 1999; Rodríguez 2002). To provide useful recommendations for protecting a taimen population with effective enforcement regions, it will be important to better understand both the frequency and key factors influencing periodic long-distance movements and home range shifts. Finally, this study of taimen movement in the Eg–Uur can serve as a model for large fish movement in pristine river systems and can be used as a valuable baseline for management of taimen and other comparable species in fragmented basins.

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References

Adams, N.S., Rondorf, D.W., Evans, S.D. & Kelly, J.E. 1998. Effects of surgically and gastrically implanted radio transmitters on growth and feeding behavior of juvenile chinook salmon. Transactions of the American Fisheries Society 127: 128–136.

Baasanjav, G. & Tsend-Ayush, A. 2001. Mongol Orny Zagas [Fish of Mongolia]. Ulaanbaatar: ADMON Publishing Company.

Borger, L., Franconi, N., De Michele, G., Gantz, A., Meschi, F., Manica, A., Lovari, S. & Coulson, T. 2006. Effects of sampling regime on the mean and variance of home range size estimates. Journal of Animal Ecology 75: 1393–1405.

Bridger, C.J. & Booth, R.K. 2003. The effects of biotelemetry transmitter presence and attachment procedures on fish physiology and behavior. Reviews in Fisheries Science 11: 13–34.

Connors, K.B., Scruton, D., Brown, J.A. & McKinley, R.S. 2002. The effects of surgically-implanted dummy radio transmitters on the behaviour of wild Atlantic salmon smolts. Hydrobiologia 483: 231–237.

Crook, D.A. 2004. Is the home range concept compatible with the movements of two species of lowland river fish? Journal of Animal Ecology 73: 353–366.

Curry, R.A., Doherty, C.A., Jardine, T.D. & Currie, S.L. 2007. Using movements and diet analyses to assess effects of introduced muskellunge (*Esox masquinongy*) on Atlantic salmon (*Salmo salar*) in the Saint John River, New Brunswick. Environmental Biology of Fishes 79: 49–60.

Dulmaa, A. 1999. Fish and fisheries in Mongolia. No. 385. Rome: FAO.

Esteve, M., Gilroy, D. & McLennan, D.A. 2009. Spawning behaviour of taimen (*Hucho taimen*) from the Uur River, Northern Mongolia. Environmental Biology of Fishes 84: 185–189.

Fraser, D.F., Gilliam, J.F., Daley, M.J., Le, A.N. & Skalski, G.T. 2001. Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. American Naturalist 158: 124–135.

Garton, E.O., Wisdom, M.J., Leban, F.A. & Johnson, B.K. 2001. Experimental design for radiotelemetry studies. In: Marzluff, J.M., ed. Radio Tracking and Animal Populations. New York: Academic Press, pp. 15–42.

Gerking, S.D. 1959. The restricted movement of fish populations. Biological Revue 34: 221–242.

Gowan, C., Young, M.K., Fausch, K.D. & Riley, S.C. 1994. Restricted movement in resident stream salmonids: a paradigm lost? Canadian Journal of Fisheries and Aquatic Sciences 51: 2626–2637.

Gu, W.D. & Swihart, R.K. 2004. Absent or undetected? Effects of non-detection of species occurrence on wildlife-habitat models. Biological Conservation 116: 195–203.

Harms, C.A. 2005. Surgery in fish research: common procedures and postoperative care. Lab Animal 34: 28–34.

Holčík, J. 1982. Towards the characteristics of the genera *Hucho* Günther, 1866 and *Brachymystax* Günther, 1866 (Pisces: Salmonidae). Folia Zoologica 31: 369–380.

Holčík, J., Hensel, K., Nieslanik, J. & Skácel, L. 1988. The Eurasian Huchen, *Hucho hucho*, largest salmon of the world. Boston, MA: Dr. W. Junk Publishers.

Jensen, O.P., Gilroy, D.J., Hogan, Z., Allen, B.C., Hrabik, T.R., Weidel, B.C., Chandra, S. & Vander Zanden, M.J. 2009. Evaluating recreational fisheries for taimen, *Hucho taimen*, in Mongolia. Canadian Journal of Fisheries and Aquatic Sciences 66: 1707–1718.

Jepsen, N., Koed, A., Thorstad, E.B. & Baras, E. 2002. Surgical implantation of telemetry transmitters in fish: how much have we learned? Hydrobiologia 483: 239–248.

Jepsen, N., Schreck, C., Clements, S. & Thorstad, E.B. 2005. A brief discussion on the 2% tag/bodymass rule of thumb. In: Spedicato, M.T., Lembo, G. & Marmulla, G., eds. Aquatic telemetry: advances and applications. Proceedings of the Fifth Conference on Fish Telemetry. Rome: FAO/COISPA, pp. 255–259.

Kernohan, B.J., Gitzen, R.A. & Millspaugh, J.J. 2001. Analysis of animal space use and movements. In: Marzluff, J.M., ed. Radio tracking and animal populations. New York: Academic Press, pp. 125–166.

Kramer, D.L. & Chapman, M.R. 1999. Implications of fish home range size and relocation for marine reserve function. Environmental Biology of Fishes 55: 65–79.

Levidanov, V.Y. 1959. Pitanie i pishchevye otnosheniya ryb v predgornykh pritokakh nizhnego techeniya Amura. Voprosi Ikhtiologi 13: 139–155 (in Russian).

Logan, S.M. 1963. Winter observations on bottom organisms and trout in Bridger Creek, Montana. Transactions of the American Fisheries Society 92: 140–145.

Matveyev, A.N., Pronin, N.M., Samusenok, V.P. & Bronte, C.R. 1998. Ecology of Siberian taimen *Hucho taimen* in the Lake Baikal Basin. Journal of Great Lakes Research 24: 905–916.

Minns, C.K. 1995. Allometry of home range size in lake and river fishes. Canadian Journal of Fisheries and Aquatic Sciences 52: 1499–1508.

Misharin, K.I. & Shutilo, N.V. 1971. Taimen', ego morfologiya, biologiya, i promysl [Taimen, its morphology, biology and commercial use.]. Izvestiya Biologicheskaya-Geografiya Nauchno-Issledovanie Institut [News of Biological-Geographic Scientific Research Institute] 24: 58–105 (in Russian).

Ocock, J., Baasanjav, G., Baillie, J.E.M., Erbenebat, M., Kottelat, M., Mendsaikhan, B. & Smith, K. (compilers and editors). 2006. Mongolian red list of fishes, Regional Red List Series Vol. 3. London: Zoological Society of London.

Økland, F., Thorstad, E.B., Hay, C.J., Naesje, T.F. & Chanda, B. 2005. Patterns of movement and habitat use by tigerfish (*Hydrocynus vittatus*) in the Upper Zambezi River (Namibia). Ecology of Freshwater Fish 14: 79–86.

Pirozhnikov, P.L. 1955. Materialy po biologii promyslovykh ryb reki Leny. Izvestiia VNIORKH 35: 97–178 (in Russian).

Rodríguez, M.A. 2002. Restricted movement in stream fish: the paradigm is incomplete, not lost. Ecology 83: 1–13.

Rodríguez-Robles, J.A. 2003. Home ranges of gopher snakes (*Pituophis catenifer*, Colubridae) in central California. Copeia 2003: 391–396.

Sabaneev, L.P. 1911. Ryby Rossii [Fish of Russia], 3rd edn. Moscow: Izdanie A. A. Kartseva. (in Russian).

Shed'ko, S.V., Ginatulina, L.K., Parpura, I.Z. & Ermolenko, A.V. 1996. Evolutionary and taxonomic relationships among Far-Eastern salmonid fishes inferred from mitochondrial DNA divergence. Journal of Fish Biology 49: 815–829.

Sigunov, P. 1972. Taimen'i istorii. In: Ozherelie Dzhekhkangira. Moscow: Izdatelstvo Nauka [Nauka Publishers], pp. 71–92 (in Russian).

Swihart, R.K. & Slade, N.A. 1985a. Influence of sampling interval on estimates of home-range size. Journal of Wildlife Management 49: 1019–1025.

Swihart, R.K. & Slade, N.A. 1985b. Testing for independence of observations in animal movements. Ecology 66: 1176–1184.

Vander Zanden, M.J., Joppa, L.N., Allen, B.C., Chandra, S., Gilroy, D., Hogan, Z., Maxted, J.T. & Zhu, J. 2007. Modeling spawning dates of *Hucho taimen* in Mongolia to establish fishery management zones. Ecological Applications 17: 2281–2289.

Vokoun, J.C. 2003. Kernel density estimates of linear home ranges for stream fishes: advantages and data requirements. North American Journal of Fisheries Management 23: 1020–1029.

Vokoun, J.C. & Rabeni, C.E. 2005. Home range and space use patterns of flathead catfish during the summer-fall period in two Missouri streams. Transactions of the American Fisheries Society 134: 509–517.

Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70: 164–168.

Zigler, S.J., Dewey, M.R., Knights, B.C., Runstrom, A.L. & Steingraeber, M.T. 2003. Movement and habitat use by radio-tagged paddlefish in the upper Mississippi River and tributaries. North American Journal of Fisheries Management 23: 189–205.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Kernel density home range estimates for individuals with 15 or more relocations.

Table S1. Individual characteristics and tracking data for all 46 tagged individuals.

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