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Body size scaling of space use in coastal pike (*Esox lucius*) in brackish lagoons of the southern

Baltic Sea

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Abstract

The northern pike (*Esox lucius*) has been intensively studied in terms of behaviour due to its relevance to fisheries and its importance for structuring fish communities in freshwater ecosystems. However, little is known about the behaviour of coastal pike living in brackish lagoons. Freshwater ecosystems, particularly lakes and small rivers, are usually finite in space, which can limit the expression of space use as a function of body size and other traits. Better understanding the spatial behaviour shown by coastal pike in extended brackish lagoons and its relationship to gear encounter and vulnerability to fishing allows examining fundamental size-based allometries and can inform management. Here, we present two years of acoustic telemetry data acquired on a large sample of coastal pike (n=216) with extended size range (480 to 1.210 mm total length) living in coastal lagoons bordered by the islands of Hiddensee, Rügen and Usedom in the Baltic sea. The extended home range (95% utilization distribution, UD) by pike scaled positively with body size, with larger fish using significantly more space overall, while the size-UD% relationship was not significant for core area (50% UD) after controlling for co-variates. However, the ratio of 50% UD on 95% UD scaled negatively with size, meaning that larger-sized pike used areas out of their core ranges more intensively. Space use also differed between seasons with activity spaces being elevated in spring likely due to spawning migrations and increased activity. Spatial behaviour of pike also varied by lagoon, but was independent of sex. All space-use proxies were found to be repeatable, suggesting the strong influence of pike personalities on their individual spatial behaviour. Fish that used less space were more likely to be captured by anglers and fishers, indicating fisheries can induce selection pressures on space use behaviour.

Keywords: Acoustic telemetry, Allometry, Angling, Catchability, Fishing, Personality

Introduction

The northern pike (*Esox lucius*) is large freshwater predatory fish, and an increasingly popular model organism in ecology and evolution (Forsman *et al.*, 2015). Broadly distributed in the northern hemisphere, pike is also an important species for recreational and commercial fisheries (Arlinghaus & Mehner, 2004; Arlinghaus *et al.*, 2021; Lehtonen *et al.*, 2009). Because of its relevance to fisheries and adequacy as a study model for (?), pike behaviour and population ecology has been extensively studied (Craig & Lucas, 1996; Raat, 1988; Skov & Nilsson, 2018). Detailed studies on the behaviour of pike have been conducted in aquaria and mesocosms (e.g., Nilsson *et al.*, 2006; Skov & Koed, 2004; Stålhammar *et al.*, 2012) as well as in lakes and rivers using radio telemetry, acoustic telemetry (Jepsen *et al.*, 2001; Koed *et al.*, 2006; Masters *et al.*, 2005; Ovidio & Philippart, 2005) and mark-recapture (Haugen *et al.*, 2006; Miller *et al.*, 2001). However, populations of pike are also present in brackish environments, most notably in the Baltic Sea (Forsman *et al.*, 2015; Wennerström *et al.*, 2017; Winkler, 1987), and there is limited knowledge on the behaviour of adult pike from such oligo- and mesohaline environments.

First insights on the spatial behaviour of coastal pike was generated through standard mark-recapture methods, which suggested that coastal pike rarely moved beyond 10 km in the Baltic across Finland and Sweden (Karas & Lehtonen, 1993). More recently, biotelemetry work in the Baltic has been completed using data storage tags to assess depth use of coastal pike in Sweden (Nordahl *et al.*, 2020) and passive integrated transponders to track anadromous behaviour of Swedish pike into streams and wetland (e.g., Tibblin *et al.*, 2016). As far as we are aware, only two acoustic telemetry-based studies have been completed on coastal pike, one of which documented that fish tagged in a tributary to a Danish lagoon did not use the brackish water (Birnie-Gauvin *et al.*, 2019) and the other revealing extensive movements from brackish lagoons to the open coast by a fraction of fish in Denmark (Jacobsen *et al.*, 2017). The lack of receiver networks in the open coastline outside the core lagoon where the study happened (Stege Nor), did not allow Jacobsen *et al.*, (2017)

to quantify the extent of the space used by the fish over the course of the year. Generally, adult pike have been reported to tolerate salinities up to 15 Practical Salinity Units (PSU; Raat, 1988) and may thus be found over a wide range of brackish conditions.

Understanding patterns of space-use is an important topic in species that are also fisheries targets. Vulnerability to capture by different fishing gears has been theorized to be higher in individuals that use more space as they have higher likelihood of encountering fishing gear, but whether selection on home range is positive, negative or not significant depends on the type of fishery and the movement behaviour of fishers (Alós *et al.*, 2012; Lennox *et al.*, 2017b; Villegas-Ríos *et al.*, 2017). Positive selection on larger home ranges was empirically documented in pearly razorfish (*Xyrichtys novacula*) fished by anglers near Mallorca, Spain (Alós *et al.*, 2016). This was also observed in a lake population of northern pike where individuals with larger home ranges were more likely captured by anglers (Monk *et al.*, 2021). In more complex fisheries with multiple gear types and a mixture of protected and open areas, support for the hypothesis that fish with larger home range are more likely to be captured remains mixed. For example, no selection on home range behaviour in a fjord was found in Atlantic cod (*Gadus morhua*; Olsen *et al.*, 2012), and the direction of harvest selection on home range size in anadromous trout (*Salmo trutta*) roaming along the coast depended on whether the fish were predominantly within protected area (positive) or outside protected areas (negative) (Thorbjørnsen *et al.*, 2021). Selection on space-use will be especially pronounced if individuals are consistent in their behaviour (i.e. exhibit personality; Thorbjørnsen *et al.*, 2021), for which there is evidence in freshwater pike (Kobler *et al.*, 2009; Laskowski *et al.*, 2016).

In pike, and in many other species, space-use has been shown to be related to the body length and in turn to the body mass of the fish (Rosten *et al.*, 2016). Moreover, larger and faster growing pike are systematically more vulnerable to harvest than smaller fish (Crane *et al.*, 2015; Monk *et al.*, 2021), and as pike show sex-dimorphic growth, the generally larger females are more likely captured by angling than males (Casselman, 1975). A positive relationship of body size with space-use (i.e.

allometric scaling of space use) can be expected because absolute metabolism is expected to scale with body mass (Darveau *et al.*, 2002), so that larger fish may require more space to fill their metabolic demand. Larger pike are also less likely to be cannibalized, which can increase their motivation to roam freely (Haugen *et al.*, 2006), while smaller conspecifics are often bound to littoral refuges with low relative movements (Chapman & Mackay, 1984; Eklöv, 1997; Grimm & Klinge, 1996). Although positive relationships between body-size and space-use have been reported in pike (Monk, 2019; Monk *et al.*, 2021; Rosten *et al.*, 2016), there is uncertainty regarding the rate of the scaling. In a meta-analysis across fish species, Woolnough *et al.* (2009) found the scaling of body size and space use to be shallower in rivers than in lakes, a phenomenon that the authors attributed to the differences in the water-body sizes. Relatedly, the allometric scaling of space use of freshwater fish was shallower than that of similar body-sized land mammals (Minns, 1995). But Rosten *et al.* (2016) found the allometric scaling of space use with the mass of pike to be higher (with an exponent of 1.08) than expected from mass-metabolism relationships (exponent of 0.75) in an English river pike population. Other work failed to relate the space use behavior to the size of pike (Jepsen *et al.*, 2001; Koed *et al.*, 2006). Possible explanation for the discrepancy in findings regarding the allometric scaling of space-use in the pike behavioural ecological literature may involve the ambush-like foraging behavior of pike, which is often confined to hunting from structures (Eklöv, 1997). Other local factors within a given ecosystem (e.g., underwater vegetation or turbidity) may also affect space use behavior and possibly override length effects (Andersen *et al.*, 2008; Říha *et al.*, 2021). Another reason could be that the space use of fish more generally is related to the size of the water-body in which the animals live, potentially confounding body size effects (Woolnough *et al.*, 2009). Methodologically, assessment of space-use depends on sampling methods that allow for regular position estimates (e.g. passive acoustic telemetry with broad receiver coverage), and irregular samplings, (e.g., in manual radio telemetry which was common in the past in lake studies; e.g., Jepsen *et al.* 2001), might substantially underestimate the space use of fish (Kobler *et al.*, 2008a, 2008b). A final issue is that the size gradient of the fish under investigation must be large

enough to be able to detect differences. Investigating body-size effects on space-use in the Baltic in fish with a large size gradient across an extensive network of lagoons alleviates some of these concerns, given that the area that the fish can explore is very large and thus the expression of extensive space use is not confined by the boundaries of for example small lakes (Rogers & White, 2007).

Sex effects may also explain discrepancies in the allometric scaling of space-use in pike. Pike are sexually dimorphic, with females achieving larger body sizes than males (Crane *et al.*, 2015; Haugen *et al.*, 2006; Tibblin *et al.*, 2016). After controlling for length, in some studies males have been found to use more space than females (in one of two study lakes, Jepsen *et al.*, 2001a). In this case, the presence of small-bodied males with high space-use in a sample may blur the expected allometric scaling of space-use if sex is not controlled for. Other work has shown that female pike might be more active than males during the spawning period, with no sex differences outside the spawning period (Koed *et al.*, 2006). If sex also affects behaviour of pike, the relationship between body size and space use is better studied when controlling for potential sex effects. This is further supported as a recent telemetry study from a Norwegian lake that reported complex interaction effects of sex and length on the behavioural response of pike to temperature variation across the year (Haugen, 2018). Sex effects on space use may be especially important to understand in brackish water pike, because in the Baltic, and notably in the lagoons surrounding the islands of Hiddensee, Rügen and Usedom in Germany, trophy pike (body-length > 100 cm) are a key target of recreational anglers (Koemle *et al.*, 2021). Such trophy pike are usually females, and harvest selection on body-size and/or space-use may disproportionately target these key individuals in the intensively fished lagoon of Rügen and similar exploited systems.

Spatial and temporal effects may also influence space-use, all adding potential confounding effect when investigating body size effects on space use. Pike have been shown to use more space in turbid conditions than in clear conditions (Jepsen *et al.*, 2001). The authors speculated that turbid waters

acted as a refuge, and therefore that pike space-use was less constrained by potential dangers than it would in a clear habitat. Similarly, shallow, and vegetated habitats have been found to be favoured by pike, serving as spawning habitat and refuge (Chapman & Mackay, 1990) and may have an effect on space use, with lower movement rates in more structured habitats (Řiha *et al.*, 2021). Further, temperature is known to affect pike activity, with spontaneous swimming activity being maximal around 19 – 20 °C, and pike being significantly less active at temperatures below 6 °C than at temperatures above 9 °C (Casselman, 1978). In this case, space use can be expected to be lowest in the winter months, but several studies have reported that summer and winter movements may be similar in pike (Baktoft *et al.*, 2012; Kobler *et al.*, 2008b), while home ranges might be elevated in the winter months as pike search for prey to build their gonads (Kobler *et al.*, 2008b). Elevated movements of pike have been repeatedly observed during spawning time in pike (Cook & Bergersen, 1988; Diana, 1980). But some studies did not report such increase in space use in spring (Baktoft *et al.*, 2012; Koed *et al.*, 2006). Because coastal Baltic pike are known to perform anadromous spawning migrations in spring from studies in Germany, Sweden, and Estonia (Engstedt, 2011; Tibblin *et al.*, 2015), we may expect space uses to be larger in spring.

Here, we present two years of acoustic telemetry data from 216 pike (n=120 females; n=134 males) with a large size range from roughly 50 to 120 cm total length tagged in the brackish lagoons surrounding the islands of Hiddensee, Rügen and Usedom in northern Germany (Figure 1). Pike were monitored using an array of 140 passive acoustic receivers deployed at fixed locations in an area spanning over more than 1.200 km² of interconnected brackish water lagoons and major freshwater tributaries (Figure 1). To test whether larger pike used more space, we computed utilization distributions (50% and 95%) as proxies for space use and expected to find a positive relationship of space use and pike body-size and an impact of sex on space use (after controlling for size effects), especially during spawning time. Because the lagoons around our study area differ in trophic state, salinity, underwater vegetation and turbidity and are differently exposed to hydrographic water inflows from the open Baltic (Selig *et al.*, 2009, and see Table 1.) we expected variation in space use

between lagoons. Finally, we expected pike to use different amounts of space across the season, with space use being highest in spring corresponding with the spawning period.

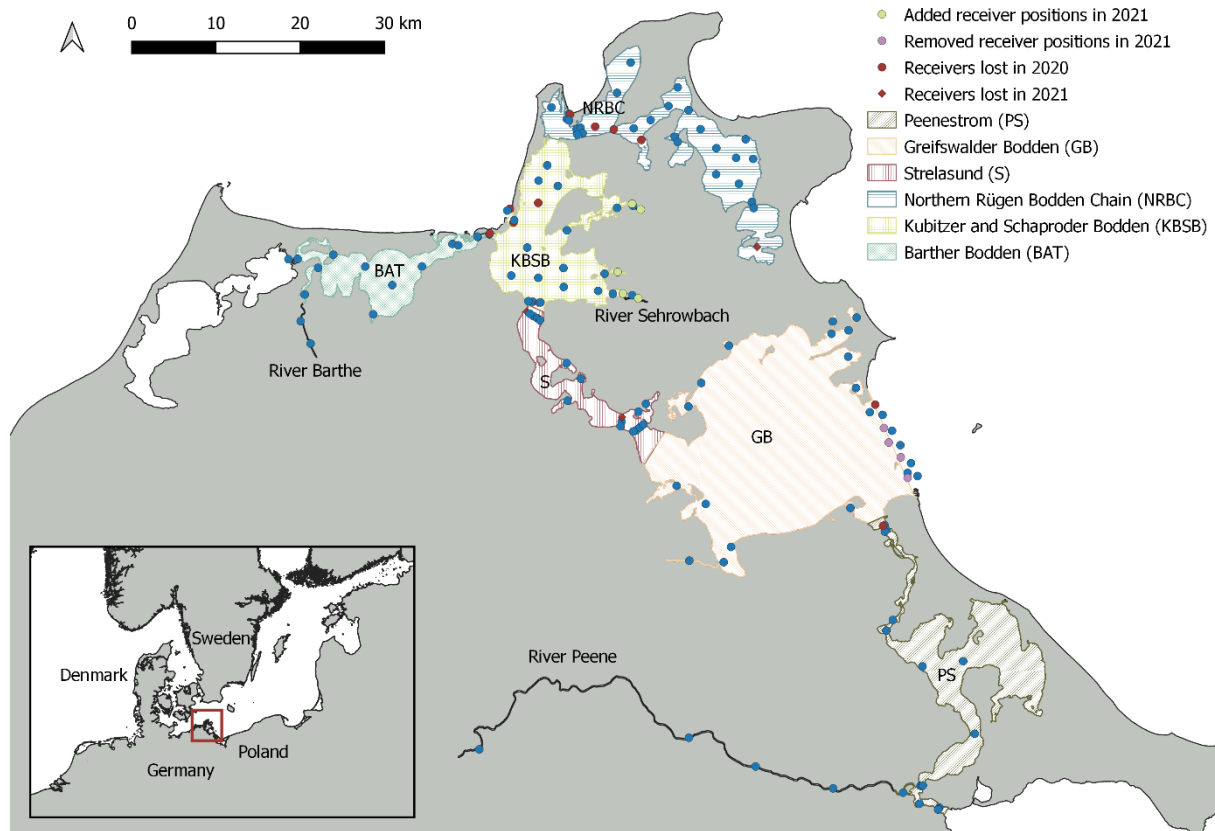


Figure 1. Map of the study area, featuring the positions of acoustic receivers and the main lagoons of interest. The study focuses on six different brackish water lagoons (Peenestrom = PS, Greifswalder Bodden = GB, North Rügen Bodden chain = NRBC, Kubitzer and Schaproder Bodden = KBSB, Barther Bodden = BAT and S = Strelasund). Inset shows, in a red square, the position of the study area in relation to Northern Europe.

*Table 1: Summary of environmental and geographic parameters of the lagoons within the study area of this work. Mean values were calculated for each area over the last 12 years (2010 – 2022) **BAT**: Barther Bodden; **KBSB**: Kubitzer and Schaproder Bodden; **NRBC**: Northern Rügen Bodden chain; **S**: Strelasund; **GB**: Greifswalder Bodden; **P**: Peenestrom. Values after \pm represent standard deviations.*

Parameter	BAT	KBSB	NRBC	S	GB	P
Chlorophyll a (mg/m ³)	27.7 \pm 19.6	7.9 \pm 6.9	16.8 \pm 12	15 \pm 9.1	14.6 \pm 13.6	63.6 \pm 48.1
Total phosphorus (μ mol/l)	1.8 \pm 0.7	1.3 \pm 0.6	1.8 \pm 1.1	1.6 \pm 0.6	1.5 \pm 0.7	3.2 \pm 1.9
Salinity (PSU)	8.3 \pm 1.6	8.7 \pm 1.1	8.3 \pm 1	7.8 \pm 1.1	7.2 \pm 0.9	3.2 \pm 2.1
Secchi depth (m)	1 \pm 0.8	1.9 \pm 0.8	1.4 \pm 0.7	1.4 \pm 0.6	1.7 \pm 0.8	0.7 \pm 0.5
Water temperature (°C)	11.5 \pm 6.6	11.6 \pm 6.7	12.5 \pm 6.5	11.9 \pm 7	11.7 \pm 6.8	11.9 \pm 6.7
Area (km ²)	59.8	231	132.9	47.6	540.1	181.9
Mean depth (m)	2	1.8	3.5	3.9	5.8	2.6
Max depth (m)	16.5	7.6	10.3	16	13.5	16
Catchment area (km ²)	1,578	NA	312	238	665	5,772

Methods

Study species and area

The study was conducted in lagoons bordered by the islands of Hiddensee, Rügen and Usedom in north-eastern Germany (Mecklenburg Vorpommern, 54.41N, 13.37E, Figure 1). The islands lie in the southern Baltic Sea and are surrounded by brackish water lagoons that are used by fauna of both freshwater and marine origin (Winkler, 1989). The lagoons are oligo- to mesohaline and show a pronounced salinity gradient from the more enclosed lagoons (oligohaline, e.g., Northern Rügen Bodden Chain) and lagoons in the estuary of large rivers (e.g., Peenestrom) to the mesohaline lagoons. Within the mesohaline lagoons salinity decreases from north (Kubitzer and Schraproder Bodden) to south (Greifswalder Bodden). The lagoons are typically shallow (with the more linear Strelasund linking Kubitzer and Schaproder Bodden and Greifswalder Bodden as an exception) and

vary in trophic state with the more enclosed lagoons being hypertrophic and turbid and the more exposed lagoons being eutrophic and having clearer water (see Secchi depth, Table. 1).

Northern pike have adapted to the waters of the Baltic and can be found in brackish waters up to 15 practical salinity units (PSU; Jacobsen & Engström-Öst, 2018; Jacobsen *et al.*, 2017), with some subpopulations known to use freshwater tributaries for spawning (Berggren *et al.*, 2016; Sunde *et al.*, 2019). Anadromy has also been documented at our study-site, but only 7% of 79 fish sampled in central Kubitzer Bodden and Strelasund right before spawning time were found to have freshwater origin (Möller *et al.*, 2019). Therefore, the current hypothesis is that most pike in the lagoons spawn in brackish waters, similar to what was reported by Jacobsen *et al.*, (2017) in southern Denmark where salinity goes up to of up to 10 PSU.

We captured pike (N = 316, see supplementary material section A for number of pike tagged per month) in our study area using rod and reel fishing, fyke nets, gill nets and electrofishing, mainly in the brackish water lagoons surrounding the island and their freshwater tributaries (Figure 1) between February 2020 and December 2020. Upon capture, pike were measured (total length, nearest mm; mean \pm standard deviation (SD) = 764 ± 123 , min = 480, max = 1.210), weighted (nearest g, mean \pm SD = $3,737 \pm 2,048$, min = 1,272, max = 15,000), externally sex determined (spilling of eggs or milt when gently pressing the body cavity or shape of the cloaca (Casselman, 1974); Females=176, males= 139, Unknown=1), externally tagged (Floy T-bar anchor, Floy Tag & Mfg. Inc., NE, U.S.A.) with a high reward of 100 € upon reporting, and implanted with an internal acoustic transmitter (MM-R-16-50 HP, random pulse rate: 60 to 180 s, Frequency = 69kHz, MAP-113, dry weight = 26.75 g, in-water weight = 17.2 g, Lotek Wireless Inc., ON, Canada). Tag in-water weight was always below 2% of the pike's body mass, with the lightest pike in our sample weighing 1.272g (2% of 1.272 = 25.44 > 17.2 g, Jepsen *et al.*, 2005). The tag implantation procedure followed previous work on pike (Hühn *et al.*, 2014). Once the tag implantation was completed, the pike were released, and we monitored their recovery until they swam off. Recovery of the pike usually took between 10

and 30 minutes. A full overview of the tagged pike is available as supplementary information (section A).

Recapture reporting

We used a participatory recapture database to record recaptures of the tagged pike by fishers and anglers. In addition to a unique ID, the Floy tags we used to externally mark the fish indicated the web address at which recaptures could be reported (www.boddenhecht-forschung.de). Using this website, anglers and commercial fishers could report the ID of the pike they recaptured as well as the capture location, the gear used and the body size. To motivate reports, a prize of 100 € was given to anyone who reported an individual pike with a transmitter for the first time. We added to this database the pike that we recaptured while scientific sampling for the project. Due to sample size issues, we only focused for this paper on whether a pike was recaptured or not, and disregarded potential gear effects (see supplementary material, section A).

Acoustic receiver network

Acoustic receivers (VR2Tx, Frequency: 69kHz, MAP-113, Innovasea Systems Inc. DE, U.S.A) were deployed in March 2020 at 140 locations in an area of approximately 1.000 km² of water, comprising brackish water lagoons and freshwater streams (Figure 1.). Having little a priori knowledge on the spatial behavior of northern pike in our lagoons, we created an array of non-overlapping receivers that covered all major lagoons with a focus on areas that are known to be key to pike fisheries (e.g. KBSB, BAT, NRBC, Figure 1.). Our array was not meant for fine scale movement analysis but rather as a tool to quantify broad movements and connectivity within the areas of interest. The receivers were mounted upright on the top of a fiberglass pole (approx. 50 cm) embedded into a concrete base (approx. 30 kg). The concrete base was attached with a 20 m polyester line (diameter = 1cm) to a 10 kg anchor. The anchor was deployed first, and its coordinates recorded (Global Positioning System, GPS), then the receiver on its concrete base was dropped in the water 15 to 20 m further,

and its coordinates recorded. Receivers were retrieved, cleaned, downloaded and their batteries changed in winter 2020 and winter 2021 in collaboration with the Institut für Fish und Umwelt (FIUM), Rostock. Thirteen receivers were lost during the study due to high currents and shifting substrate or equipment failure (i.e. mounting system damage; FIUM, personal communication). In the spring of 2021, five receivers were moved from brackish water areas to freshwater streams for a concurrent research project on anadromy behavior of pike (Figure 1).

Detection filtering

Upon download, the receiver logs (format .vrl) were processed in the FATHOM software (Innovasea Systems Inc. DE, U.S.A, <https://fathomcentral.com/>) to correct for clock drift, then saved as .csv. All further processing was done in R (R Core Team, 2017) version 4.0.5. We used the development version of ATfiltR (<https://github.com/FelicieDh/ATfiltR>) to filter the data. We first trimmed the detections and kept only data that belonged to our animals and that was within our deployment window (i.e. between the date and time of deployment and the date and time of retrieval). We then erased detections that were solitary on a given receiver in a 1 h window (similarly to Kessel *et al.*, 2014). If an individual was detected on two different receivers consecutively and the time span between detections was shorter than the time the fish would have needed to swim between the two receiver locations, the second detection was removed (similarly to Kessel *et al.*, 2014; Monk *et al.*, 2021). To achieve this, we calculated the in-water distance between receivers using *actel* (Flávio & Baktoft, 2021) and used the critical speed formula for freshwater fish provided by (Wolter & Arlinghaus, 2003) ($\text{critical speed (m/s)} = 0.019 * \text{Total Length}^{0.79}$) to estimate the time a pike would need to go from one receiver to another, taking into account the receiver range. Receiver range was estimated monthly at six different locations using the internal transmitters of the receiver units. These locations were selected because the receiver densities allowed for range estimations and receivers that were not part of the range testing were later assigned one of the six calculated ranges according to their environmental surroundings (see supplementary material section B). Detection

range was estimated as the maximum distance (in meters) at which at least 50% of emitted acoustic signals were detected.

Utilization distributions

Utilization distributions (UDs; probability distributions of individuals use of space; Van Winkle, 1975) were calculated monthly for each individual using a dynamic Brownian Bridge Movement Model (dBBMM) in the R package *move* (Kranstauber *et al.*, 2021). To avoid unrealistic movements over landmasses, we first processed the telemetry data in the package RSP (Niella *et al.*, 2020) to compute the shortest in-water paths for each individual. The obtained paths, which accounted for receiver ranges, were converted to a *move* object and used for utilization distribution calculations with the error computed by RSP used as dynamic error in the model. To avoid any error inflation of the model when pike were undetected, we constrained the variance anytime a pike had >24 h of absence from the receiver array. For the same reason, the dynBBMM was only applied if a minimum of 15 positions were available for a fish during a given month, and these positions were spanning over a minimum of 10 days. The landmasses were removed from the obtained rasters and their values redistributed to all in-water raster cells that contained positive values.

The size of the 50% and 95% UD were then calculated using the *fishtrack3d* package (Aspillaga *et al.*, 2019). The results are given in km² and represent the size of the core area used by the fish (50% UD), and the extended range (95%UD). We also computed the range-ratio, which represents the pattern of space use within the range, as the ratio between the size of the core area (50% UD) and the extended range (95% UD) (Börger *et al.*, 2008; Spiegel *et al.*, 2017; Webber *et al.*, 2020). Values closer to zero indicate bigger differences between the size of the core area and the extended range, and values closer to one indicate similarities in the sizes of the core and the range.

Maximum horizontal displacement

To describe pike spatial behavior in a way that is comparable to Karas & Lehtonen, (1993) we additionally computed the maximum horizontal displacement as the maximum distance between receivers visited per month for each fish. Because our study area is bound by many landmasses, calculating the distance between receiver locations “as the crow flies” using the haversine formula would not yield realistic results. Instead, we used the package *actel* (Flávio & Baktoft, 2021) to compute an in-water distance matrix between our receiver locations.

Statistical analysis

We built three linear mixed models using the *lme4* (Bates *et al.*, 2015, 4) library in R. One model had the logarithm (all logarithms calculated with base 10; log) of the size of the 50% UD as response variable, another had the log of the size of the 95% UD (hereafter logUD50 and logUD95), with the log transformations used to respect the normality assumptions and for examining allometric relationships that are expected to be non-linear (Rosten *et al.*, 2016). For the third model, range-ratio (UD50/UD95) was the response variable. In all models, we tested the hypothesis that body size predicted space use by including the log transformed total length (logTL) and the log transformed mass (logW) as fixed effects. Importantly, Rosten *et al.*, (2016) worked on the log of the mass, but we expect the body length on the log scale to behave similarly, as body size and mass can be expected to correlate. Importantly, Because some pike in the brackish waters of the Baltic are known to take seasonal spawning migrations (Tibblin *et al.*, 2015), we added season (categorical: Winter from December to February, Spring from March to May, Summer from June to August and Autumn from September to November) to the model. Pike being known to be sexually dimorphic, we expected size effects to depend on the pike’s sex (Haugen, 2018), we therefore added Sex (categorical: Male, Female, Unknown) as an interaction with total length and weight. We also tested whether the seasonality of movements depended on sex by exploratorily modelling an interaction between season and sex. To test whether pike that use a specific space are more likely to be captured, we added recaptured (by anglers or fishers; categorical: yes, no) to the models. Finally, we

estimated differences between fish coming from different lagoons, by adding lagoon (categorical: BAT, PS, S, GB, KBSB, NRBC, Fig. 1) to the model, and we estimated yearly effects by also adding year (categorical: 2020, 2021). Differences between individuals were accounted for by including fish ID as a random effect. We tested whether our fixed effects were correlated using Pearson correlation tests. In the event of correlated fixed effects, we kept in the model only the effect for which we had the most data (i.e., higher sample size).

The full models were backward simplified using consecutive chi-squared test until a most parsimonious model was found. Fit of each model was assessed by plotting the residuals on the fitted values and looking for any discernable patterns, if no patterns could be seen, fit was considered adequate (Martin *et al.*, 2017). The confidence intervals (CI) for each effect in the final model was computed using the `confint()` function in R, and fixed effects were considered significant if their 95% confidence interval excluded zero.

If the random term ID significantly improved the model, we calculated adjusted-repeatability ($R = \frac{\sigma_{\alpha}^2}{\sigma_{\alpha}^2 + \sigma_{\epsilon}^2}$ where σ_{α}^2 is the between-individual variance and σ_{ϵ}^2 is the within-individual variance, Nakagawa & Schielzeth, 2010) to assess how repeatable pike were in their space-use. High repeatability can be interpreted as evidence of the presence of spatial behavioural phenotypes (Stuber *et al.*, 2022).

Results

Sample description

Following data filtering and UD calculations, the dataset used for this analysis comprised a total of 210 individuals (88 males, 120 females and 2 individuals of unknown sex; see supplementary material, Section A for complete breakdown). Monthly sizes of the core area spanned from 0.17 to 8.66 km² at an average of 0.89 km² (figure 2.A.), and the monthly sizes of the extended range spanned from 0.57 to 71.16 km² for an average of 5.38 km² (figure 2.B.). Pike had a maximum

horizontal displacement ranging from 0 to 56.63 km, with the average being 3.36 km (Figure 2.C).

The distribution of core and extended home ranges were highly skewed with most individuals showing relatively small home ranges.

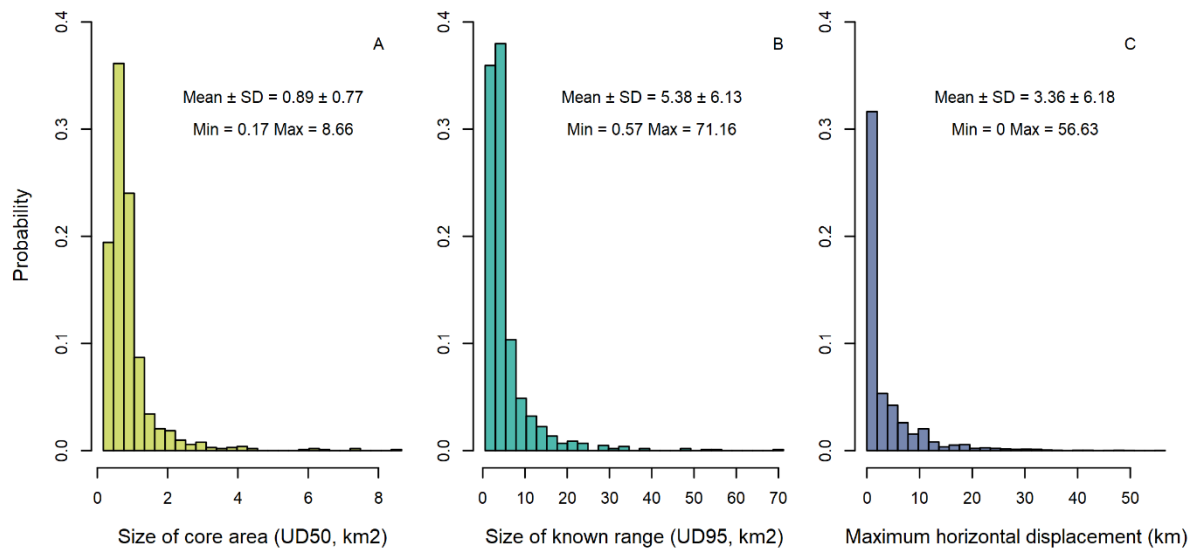


Figure 2. Probability distribution of A) the size of the core area (50% UD) b) the size of the extended range (95% UD) and C) the maximum horizontal displacement in Baltic pike.

As expected, length and weight were highly correlated ($R = 0.95$, $p < 0.0001$), and therefore we present in the main text only models that include length but not weight in the fixed effects, as we had the most data on length ($n=202$ vs. $n=189$). Models including weight instead of total length can be found in supplementary material, section C, and yielded similar results.

Monthly core area size

The most parsimonious model for size of the core area ($\log_{10}UD50$) included lagoon, recaptured by anglers/fishers and season as well as the random term ID (table 2). Sex, year and $\log_{10}TL$ were dropped from the model. Fish in Peenestrom (PS) had significantly smaller core areas than the intercept (taken as Barther Bodden, BAT), and fish in Strelasund (S) had significantly larger ones than the intercept (table 2, figure 3.A.). Core areas were largest in spring, with all other seasons not differing from one another (table 2, Figure 3.C.). Fish that were recaptured used significantly smaller

core areas than fish that were never recaptured by anglers or fishers (table 2, Figure 3.E.).

Repeatability for the size of the core area was high and estimated as 0.59 (see Table 2 for p-value).

*Table 2. Results of the consecutive chi-square tests performed on the full models. The full models were set up with the following formula $\text{Response} \sim \text{Season} * \text{Sex} + \text{logTL} * \text{Sex} + \text{Recaptured} + \text{Year} + \text{Lagoon} + (1|ID)$ and each row of this table indicates which effect was removed to perform the chi-square test. Effects that were not in an interaction were tested against a model that contained no interactions. Bold results indicate effects that improved model fit.*

Variable	logUD50		logUD95		UD50/UD95	
	Chi (DF)	P	Chi (DF)	P	Chi (DF)	P
Random ID	279.7 (1)	< 0.0001	237.6 (1)	< 0.0001	193.1 (1)	< 0.0001
<i>Season*Sex</i>	6.4 (5)	0.26	7.3 (5)	0.19	7.7 (5)	0.17
<i>logTL*Sex</i>	4.5 (2)	0.10	1.2 (2)	0.55	2.9 (2)	0.23
<i>no interaction</i>	10.3 (7)	0.17	8.1 (7)	0.32	11.4 (7)	0.12
<i>Year</i>	1.1 (1)	0.30	0.3	0.59	0.1 (1)	0.79
Lagoon	25.1 (5)	< 0.0001	36.1 (5)	< 0.0001	37.6 (5)	< 0.0001
Recaptured	7.1 (1)	0.007	4.3 (1)	0.03	1.1 (1)	0.29
Season	53.6 (3)	< 0.0001	67.7 (3)	< 0.0001	34.8 (3)	< 0.0001
<i>Sex</i>	2.3 (2)	0.31	1.2 (2)	0.55	0.1 (2)	0.92
logTL	2.5 (1)	0.11	4.7 (1)	0.03	11.3 (1)	< 0.001

Monthly extended range

For the extended range (logUD95), the most parsimonious model included lagoon, season, recaptured, and logTL (table 2). Sex and year were dropped from the model. Fish in Strelasund (S) and in the Northern Rügen Bodden Chain (NRBC) used the most space (with the intercept taken as

Barther Bodden, BAT, table 2., Figure 3.B.). Fish used the most space in spring, with no significant differences between the other seasons (table 2., Figure 3.D.). As before, fish that were recaptured used significantly less space than the others and the size of the extended range scaled positively with total length (with an exponent of 0.61 on total length Table 2., Figure 3.F and G.). There was also a significantly positive scaling of mass of pike and extended home range, where the estimate of the scaling was 0.24 [95% CI = 0.02, 0.47] (see supplementary material, Section C). Repeatability for the size of the extended range was estimated as 0.42 (see table 2. for p-value).

Monthly range-ratio

The range-ratio was also predicted by the lagoon, season and logTL, but did not vary according to whether a fish was recaptured and was independent of sex and year (Table 2.). Fish in Strelasund (S) and the Northern Rügen Bodden Chain (NRBC) had lower ratio indices, meaning that the size of their core area was more different from the size of their extended range than in other places (Table 2.). The ratio index was also lowest in Spring (Table 2.). Larger fish had significantly lower range-ratios, meaning that the differences between the size of the core area and the size of the extended range increased with the size of the fish (Table 2., Figure 4.).

Table 2. Estimates and 95% confidence intervals of the most parsimonious models for logUD50 (left) and logUD95 (right). The intercept is taken as Autumn in BAT and fish that were not recaptured (recaptures = "No"). Bold results indicate variables that are significantly different from the intercept, or slopes that differ significantly from zero (i.e. confidence intervals do not overlap zero).

	Log UD 50	Log UD 95	UD 50/UD 95
variable	Estimate [95%CI]	Estimate [95%CI]	Estimate [95%CI]
Intercept	-0.11 [-0.18, -0.03]	-1.19 [-2.78, 0.38]	0.60 [0.37, 0.84]

<i>Lagoon:GB</i>	-0.09 [-0.19, 0.01]	-0.07 [-0.20, 0.05]	-0.002 [-0.02, 0.02]
<i>Lagoon:KBSB</i>	0.02 [-0.06, 0.11]	0.10 [-0.01, 0.21]	-0.03 [-0.05, -0.01]
<i>Lagoon:NRBC</i>	0.08 [-0.03, 0.19]	0.15 [0.01, 0.28]	-0.03 [-0.05, -0.006]
<i>Lagoon:PS</i>	-0.11 [-0.21, -0.02]	-0.12 [-0.24, 0.001]	0.01 [-0.005, 0.03]
<i>Lagoon:S</i>	0.11 [0.01, 0.19]	0.18 [0.07, 0.29]	-0.03 [-0.04, -0.01]
<i>Spring</i>	0.08 [0.05, 0.11]	0.12 [0.08, 0.16]	-0.01 [-0.02, -0.008]
<i>Summer</i>	-0.01 [-0.04, 0.02]	-0.01 [-0.05, 0.04]	0.002 [-0.006, 0.01]
<i>Winter</i>	-0.03 [-0.06, 0.01]	-0.04 [-0.08, 0.01]	0.005 [-0.003, 0.01]
<i>Recaptured:Yes</i>	-0.10 [-0.18, -0.02]	-1.11 [-0.20, -0.01]	
<i>logTL</i>		0.61 [0.07, 1.15]	-0.13 [-0.22, -0.05]

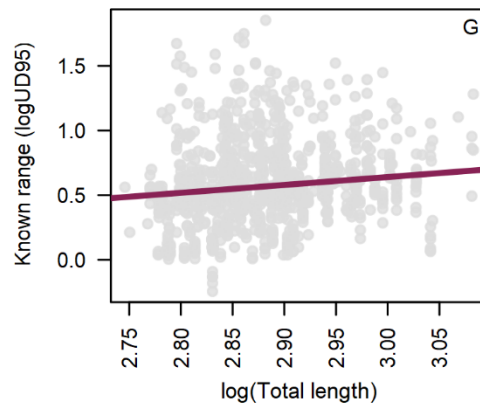
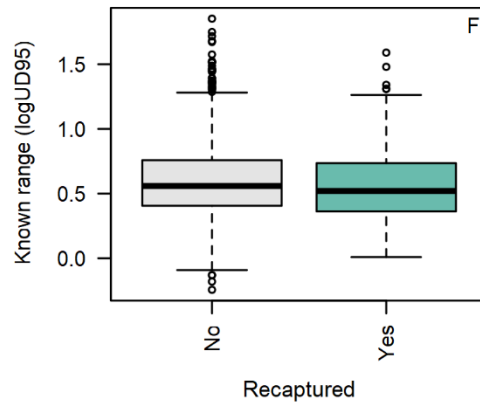
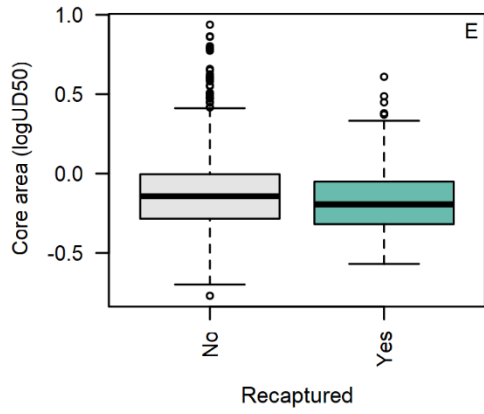
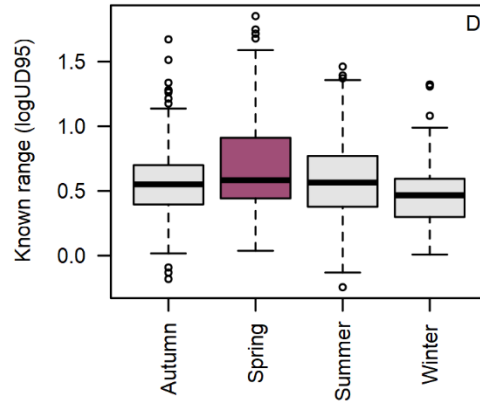
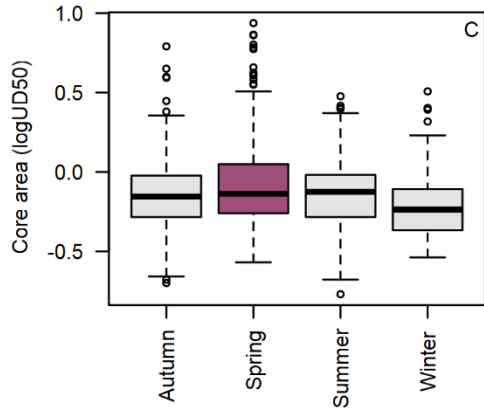
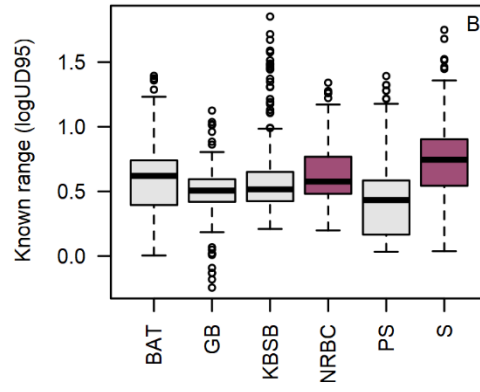
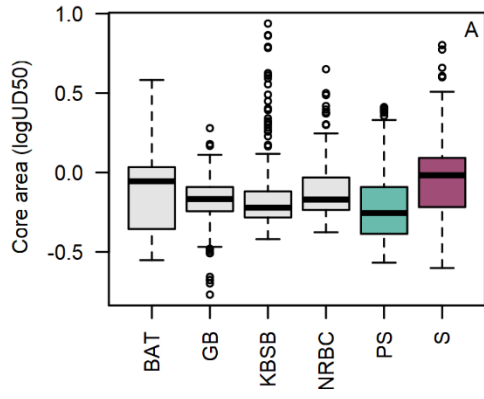


Figure 3. Effects of lagoon (see Figure 1. for legend of lagoons) (A, B), season (C, D), recaptures (E, F) and log (total length) on the size of the core area (logUD50, panels A, C, E) and the size of the extended range (logUD95, panels B, D, F, G). Significantly positive effects (For categorical effects, against the intercept taken as BAT, Autumn, non-recaptured, see table 2.) are shown in maroon, and the significantly negative ones are shown in teal.

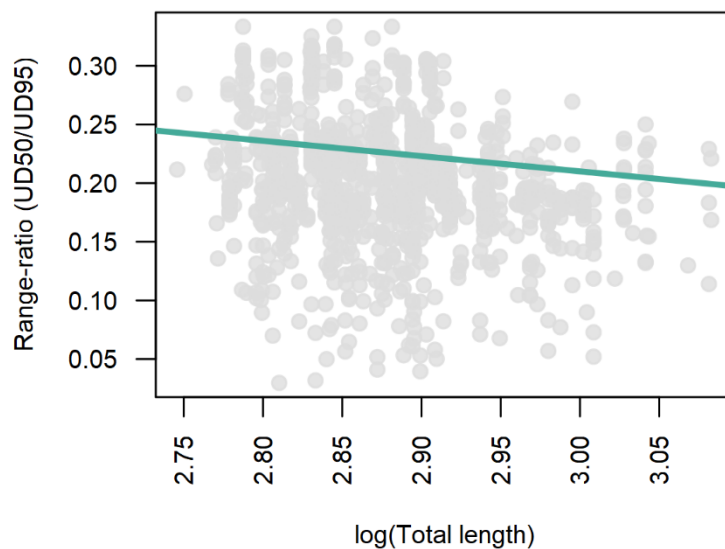


Figure 4. Effect of log(total length) on the range-ratio (50%UD/95%UD), the significant negative effect is represented in teal (see table 2.). Lower values of range-ratio indicate larger differences between the sizes of the core area and the extended range.

Discussion

In this paper, we present two years of acoustic telemetry data on 216 coastal pike with a large size range that roam in shallow brackish water lagoons of the southern Baltic Sea. We took advantage of our very large study system (> 1.200km²) and the broad size spectrum of our study animals (ranging from 480 to 1.210 mm total length) to firmly test the allometric scaling of space use in a virtually unbounded waterbody. We calculated the 50 and 95% Utilization Distribution (UD) of each individual pike on a monthly basis and found the size of the extended range (95% UD) to scale positively with pike size, according to our expectations, but not the size of the core area (50% UD). Further, we

found the range-ratio (ratio of core area size on extended range size) to scale negatively with body-size. We had males and females in our sample but found no sex effects on any of our space use proxies when controlling for body-size, contradicting our expectations. Space-use was also consistent among study years. The amount of space used by pike differed according to the lagoon of origin and according to the season with pike using the most space in spring. Fish that had smaller core areas and smaller ranges were more likely to be recaptured than their conspecifics, but there were no differences in range-ratio between the recaptured and non-recaptured fish. Finally, we found the size of the core area, the size of the extended range and the range-ratio to be highly repeatable, suggesting strong inter-individual variation in behaviour (i.e. personalities). The presence of personality is a precondition for potential impacts of behaviour-based selection (Arlinghaus *et al.*, 2017b; Olsen *et al.*, 2012).

This study is an important step to updating our knowledge on coastal pike behaviour in the Baltic Sea. Using mark-recapture of externally tagged pike, Karas & Lehtonen, (1993) suggested that Baltic pike across the adult stage do not move more than 10 km and often substantially less. We found pike to travel up to 56 km in a month, indicating either that the fish in the lagoons in Germany move more than reported from Sweden and Finland based on mark-recapture data or that mark-recapture data severely underestimate the movement rates of pike. However, similar to Karas and Lehtonen (1993) the distribution of the space use proxies we documented were right skewed with many fish showing localized behaviour and only a few individuals showing very high movements. Also, the monthly core areas were on average 0.89 km² or 89 ha, which is a rather localized movement given the extensive nature of the lagoon ecosystems. However, the small core areas may also be due to the non-overlapping nature of our telemetry array, which does not allow to capture spatial behaviour on a small scale. On average, the extended home range of the our fish was 5.38 km² (or 538 ha), which is substantially greater than the average home ranges reported from small lakes (e.g. mean extended range = 3.6 km² in winter and 1.4 km² in summer; Kobler *et al.*, 2008b). Jacobsen *et al.* (2017) is the only other study directly using telemetry in the Baltic, the authors did not quantify

space use but rather excursions out of their study areas. There, the number of spays spent outside of the lagoon correlated positively with pike size, which also suggests space-use allometry. In passive telemetry, where stationary acoustic receivers record the presence of animals that swim within their range from fixed locations, array design (i.e. positions of the receivers in the study area) is a particularly important consideration and will affect home range estimates. For example, we likely underestimated the extended ranges of fish in the Greifswalder Bodden given the poor coverage of receivers in that area. Array design of different studies depend on the study question, on the budget (i.e. number of receivers available) but also on prior knowledge on the spatial behaviour of the target species. Our results provide first estimates of the areal space use to expect in Baltic pike and can thus support future research effort that aim to use similar technologies on these pike populations.

Our finding that in the coastal pike of Rügen the size of extended range scales positively with body-size (with exponent 0.61), and with weight (with exponent 0.24) (see supplementary material section C for results of the weight models) is in agreement with many other studies that found proxies for space-use to be predicted by body-size (e.g. Andersen *et al.*, 2008; Jepsen *et al.*, 2001; Monk *et al.*, 2020; Rosten *et al.*, 2016). But both our scaling exponents for total length (0.61, see table 3.) and weight (0.24, see supplementary material section C) were lower than those calculated by Rosten *et al.*, in 2016 (1.08) and both were lower than those expected from body mass-metabolic rate scaling (roughly 0.75, Rosten *et al.* 2016). This is surprising because Woolnough *et al.* (2009) found the scaling of home range size to be higher for larger waterbody sizes (i.e. higher exponents in lakes than in rivers), so we expected to find higher scaling in our virtually unbounded study system than Rosten *et al.*, (2016) found in a river. One possible explanation is that the sample used by Rosten *et al.*, (2016) presented much more variability in body-masses than our study (range: 7 to 12,060 g) and allometric scaling on the arithmetic scale appeared to be much steeper for smaller individuals than for larger ones. The lack of fish < 1.200 g in our sample may then explain the shallower scaling exponent for extended range and may conceal waterbody size effects.

Alternatively, the lower scaling might represent ecosystem effects and be explained by the fact that pike as ambush predator can meet energetic demands and achieve growth rates that are similar to more active fish, who have higher prey encounter rates but also have higher energetic costs through swimming (Kobler *et al.*, 2009). Thus, metabolic rate-size scaling may not be expected to represent body size space-use scaling perfectly.

Importantly, the size of the core areas was not predicted by body size, which suggests that larger fish do not meet their energetic requirements by expanding their core areas but rather via an increase in excursions out of the core. This notion is further supported by the significant negative relationship between body-size and range-ratio we detected (Figure 4). Range-ratio can be linked to foraging, with higher indices being linked to more intense use of a small portion of their range (i.e. more intense use of a small portion of their 95% UD) by individuals, and smaller ones representing more rapid switches between different foraging spots within the extended range (95% UD) at longer distances from the core area (50% UD) by individuals (Spiegel *et al.*, 2017; Webber *et al.*, 2020). Such phenomenon can be explained in two ways. First, for a given resource patchiness, the intensification of foraging outside of the core area in large pike may be an effect of their higher energetic demand (Darveau *et al.*, 2002), with smaller fish being better able to sustain themselves within their core areas. Then, avoiding risk of predation is likely to play an important role in this pattern and affect the size-structure of pike and their spatial arrangements (Nilsson, 2006), with specifically the smaller individuals needing to balance the benefits of foraging with the risks of encountering predators (Pettersson & Brönmark, 1993). This is because larger pike are less vulnerable to natural predation (Nilsson & Brönmark, 2000, 1999), which can increase their motivation to roam freely (Haugen *et al.*, 2006; Skov & Koed, 2004). By contrast, smaller conspecifics are often bound to be hiding in littoral refuges (Chapman & Mackay, 1984; Grimm & Klinge, 1996), which can increase the overlap of the core and the extended home range (leading to higher home range ratios). These patterns are likely to hold only for the size range we tagged, which encompassed adult fish of 50 cm total length and larger. In larval and juvenile pike, the smaller conspecifics have been found to be displaced from

core vegetated refuge areas by superior, typically larger conspecifics, leading to largest movement distances found in the smallest pike individuals (Skov *et al.*, 2011). We suggest this pattern may reverse as the fish grow and the largest fish become freed from predation risk. The situation might change if larger predators, e.g. seals see their population increase in the study area.

We found the range-ratio (along with all other range metrics) to be highly repeatable, after controlling for body size and sex. This indicates that some individuals are consistently more likely to forage outside of their core areas (i.e. proactive phenotypes, Laskowski *et al.*, 2016; Monk *et al.*, 2021) and others less likely to do so (i.e. reactive phenotypes) (Spiegel *et al.*, 2017). The field of animal personality (i.e. consistent individual differences in behaviour) has long been guided by a framework recommending the study of five traits measured in standardized captive assays (Réale *et al.*, 2007). This common framework has allowed for the accumulation of knowledge on this phenomenon and the growth of the research field. More recently research has started advocating for a broader definition and the expansion to any behaviour (Dingemanse & Wright, 2020), normalizing research on “spatial-personalities” or “spatial-behaviour types” in free-ranging animals (Alós *et al.*, 2019; Stuber *et al.*, 2022). Our work suggests, unsurprisingly, that pike have spatial behavioural phenotypes, thereby extending previous knowledge on the presence of activity-based personalities in wild pike populations (Kobler *et al.*, 2009).

When spatial behaviour is repeatable, particular behavioural phenotypes may be more likely harvested than others, creating selection pressures and potentially influencing the evolution of behaviour towards the least harvested phenotypes (Alós *et al.*, 2019; Arlinghaus *et al.*, 2017b). We found the size of the core area and the size of the extended range to both be repeatable and to both be smaller in the portion of the fish we recaptured. This may seem surprising, because selection is predicted to happen on fish that use the most space, as higher space use coincide with higher probability of gear encounter (Alós *et al.*, 2012; Monk *et al.*, 2021). However, encounter is a necessary precondition, but not sufficient for capture in recreational fisheries (Lennox *et al.*, 2017a).

In angling for perch (*Perca fluviatilis*), for example, encounter was insufficient to explain vulnerability to the gear as the fish had to also attack the artificial lure once found by the angler (Monk & Arlinghaus, 2018). Alós et al. (2012) also showed in simulations that the direction of selection was determined by the movements of both the fish and the fisher, with limited potential for a directional hypothesis as to which direction of selection to expect on home range behaviour. Relatedly, Thorbjørnsen *et al.*, (2021) demonstrated that in anadromous brown trout, selection on home range depended on time spent in protected areas, with individuals that used more space being less vulnerable to harvest if they spent most time outside the protected zones. Our study area presents intricate area-based regulations, made of situational (e.g. that may apply only to anglers, but not fishers), temporal (e.g. that target only the spawning season) and spatial (i.e. two national parks, a biosphere reserve and multiple small conservation areas) limitations that can provide varying degrees of protection to pike (Arlinghaus *et al.*, 2021). This complexity of full and only partial protected areas that apply only to a selected subset of fishing gear renders it difficult to exactly estimate the overlap of the fish we tagged with level of protection. We found lower recaptures of pike with the larger ranges which may be due to an increased probability for these individual's ranges to overlap with protection zones. It is interesting to note that there were no differences in the range-ratio of recaptured and non-recaptured individuals, which indicates that the rate at which individuals explore out of their core-area does not predict their probabilities of being recaptured.

We found the space use of the pike to be driven by seasons, with pike using the most space in spring, which coincides with the spawning time of pike (Skov & Nilsson, 2018). Pike also had the lowest range-ratios in spring, which indicates an intensification of activity outside of their core area, possibly indicating the active use of spawning areas. Range-ratio is traditionally linked to foraging strategies (i.e. Genero *et al.*, 2020; Spiegel *et al.*, 2017; Webber *et al.*, 2020), but here the low ratios are most likely explained by individuals taking relatively large spawning migrations (Müller, 1986; Stott & Miner, 2022). Some coastal pike will have adapted to spawning in brackish lagoons as is documented in the similarly saline Danish populations (Jørgensen *et al.*, 2010) and for which there is

evidence in our study area (Möller *et al.*, 2021, 2019). Other fish will likely still depend on low salinities for successful egg development (Sunde *et al.*, 2018), encouraging the maintenance of anadromy in the sexually mature part of the population (Engstedt, 2011), which in turn might induce spawning migrations. Anadromy and brackish spawning might not be the only spawning strategies in our study system, as Birnie-Gauvin *et al.*, (2019) found pike that spend the whole year in a Danish freshwater tributary only rarely making use of the neighbouring brackish bay. The marked differences in space-use between the lagoons may in part be due to such distinct strategies or to the distance pike must travel to get to the next freshwater tributary. For instance, in the absence of tributaries in Strelasund (S) and the Northern Rügen Bodden Chain (NRBC), it may be reasonable to think that pike will have to travel a longer distance (expanding their ranges) to their spawning ground than pike in Barther Bodden (BAT) or in Kubitzer and Schaproder Bodden (KBSB), which are fed by rivers such as Barthe, Sehrowbach and Duwenbeek.

Differences in space-use between different lagoons may also be driven by environmental conditions and be additionally affected by the receiver network and where pike were tagged and released. Pike have been described to use more space in turbid waters (Jepsen *et al.*, 2001), which may be due to turbid water acting as a refuge for prey (encouraging their dispersal), thereby promoting higher space-use. Variation in behaviour can also emerge through variability in salinity (which is particularly high in lagoons that are opened to the Baltic Sea), variation in vegetation density or in lagoons serving as transitory spaces among other lagoons (e.g., Strelasund). This might explain why home ranges were larger in Strelasund relative to other areas. Interestingly, in the highly turbid lagoon (Peenestrom, PS) pike had the smallest core areas. The reason for this lower range might lie in the fact that many of the pike in this area were tagged in the River Peene (n=25) which may consist mainly of freshwater residents similarly to Birnie-Gauvin *et al.*, (2019). The ranges of fish in linear rivers are smaller than in lakes, and so, residents pikes in the Peene river could lower the range estimates for Peenestrom (Minns, 1995). Given the low receiver coverage in the Greifswalder Bodden we might have underestimated space use by pike there as well. Strelasund (S), where pike

had the largest space-uses is narrower than other areas and may be used as a corridor for pike to go from Greifswalder Bodden (GB) and Kubitzer and Schaproder Bodden (KBSB). This area is also deeper than other lagoons, possibly generating thermal refuges in summer. Fully explaining the environmental correlates of lagoon specific movements was however beyond the scope of our work.

Conclusions and implications

In conclusion, using a sample of pike tagged in coastal areas of the Baltic Sea we found space use of the extended home range to scale with pike's body sizes, but our scaling exponent was lower than one found in a river in England, suggesting that space-use is not bounded by the size of the waterbody alone. Larger pike used more space but also used the periphery of their ranges more intensively than smaller conspecifics, suggesting that the decline in predation risk and an increase in foraging needs drive these individuals away from their core areas. But this increase in range space did not result in these individuals being more likely to be recaptured despite a potential increase in their likelihood to encounter fishing gear. As the larger pike may have had more experiences with fishing gear, and lure avoidance behaviour is described in pike (Arlinghaus *et al.*, 2017a; Beukemaj, 1970), it is possible that the larger pike roam more, while being effective at avoiding being captured. The recaptured individuals in our sample had significantly smaller ranges, which might indicate that the more mobile fish are in fact more likely to encounter protected zones and decrease their recapture probabilities or are simply better at avoiding fishing gear. Because every space-use proxy used here was repeatable, our findings suggest that commercial and recreational fisheries in the Baltic Sea may induce selection pressures on space use behaviour and that full protection of the activity space used by specifically large pike might not be possible with protected areas alone, requiring other tools, such as implementation of harvest slots and maximum mesh sizes in gill nets (Ahrens *et al.*, 2020).

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