

Contrasting structural complexity differentiate hunting strategy in an ambush apex predator

Milan Říha (✉ milan.riha@hbu.cas.cz)

Biology Centre

Karl Ø. Gjelland

Norwegian Institute of Nature Research (NINA)

Vilém Děd

Biology Centre

Antti P. Eloranta

University of Jyväskylä

Ruben Rabaneda-Bueno

Biology Centre

Henrik Baktoft

Technical University of Denmark (DTU Aqua)

Lukáš Vejřík

Biology Centre

Ivana Vejříková

Biology Centre

Vladislav Draštík

Biology Centre

Marek Šmejkal

Biology Centre

Michaela Holubová

Biology Centre

Tomas Jůza

Biology Centre

Carolyn Rosten

Norwegian Institute of Nature Research (NINA)

Zuzana Sajdlová

Biology Centre

Finn Økland

Norwegian Institute of Nature Research (NINA)

Jiří Peterka

Biology Centre

Research Article

Keywords: environmental complexity, predator, behavioural plasticity, individual differences, pelagic habitat, telemetry, stable isotopes, *Esox lucius*

Posted Date: March 30th, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-290215/v1>

License:  This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Abstract

Structural complexity is known to influence prey behaviour, mortality and population structure, but the effects on predators has received less attention. We tested whether contrasting structural complexity in two newly colonised lakes (low structural complexity lake – LSC; high structural complexity - HSC) was associated with contrasting behaviour in an aquatic apex predator, Northern pike (*Esox lucius*; hereafter pike) present in the lakes. Behaviour of pike was studied with whole-lake acoustic telemetry tracking, supplemented by stable isotope analysis of pike prey utilization and survey fishing data on the prey fish community. Pike displayed increased activity, space use, individual growth as well as behavioural differentiation and spent more time in open waters in the LSC lake. Despite observed differences between lakes, stable isotopes analyses indicated a high dependency on littoral food sources in both lakes. We concluded that pike in the HSC lake displayed a behaviour consistent with a prevalent ambush predation behaviour, whereas the higher activity and larger space use in the LSC lake indicated a transition to more active search behaviour. It could lead to increased prey encounter and cause better growth in the LSC lake. Our study demonstrated how differences in structural complexity mediated prominent changes in the foraging behaviour of an apex predator, which in turn may have effects on the prey community.

Introduction

The composition of biotic assemblages is heavily influenced by habitat heterogeneity arising from both abiotic and biotic components. Much focus has been given to the role that habitat complexity plays in structuring and functioning at the population level, both in aquatic and terrestrial ecosystems¹⁻³. The presence of structures increases environmental heterogeneity and range of available potential habitats⁴, and by providing shelter for prey or cover for predators structures have a crucial role in predator-prey interactions⁵. Physical structures, either biotic or abiotic, may also provide suitable substrate for primary producers, filtering organisms etc. and thus increase the food availability for predators⁵.

Submerged macrophytes are among the main structuring components in freshwater ecosystems. Macrophytes can substantially alter the behaviour of both prey and predators (e.g.⁵⁻⁷) via affecting predator-prey detection, encounter and catchability⁸. Some predators can alter their foraging behaviour and activity by switching between ambush and active pursuit⁹⁻¹² depending on the presence/absence of macrophytes. This ability is considered to be species-specific and it has been documented in various groups of invertebrates^{6,12} and fish^{9,11}, where it has implications for hunting success. Predators able to shift their foraging strategies may be able to maintain the total number of prey captures as the yield of their favoured foraging strategy is reduced¹⁰⁻¹². However, switch in activity and foraging behaviour to maintain prey consumption do not necessarily imply maintained predator growth and fitness, as higher activity costs might not be balanced by the energy gain, and thus be less efficient⁶. The most beneficial strategy will obviously be influenced by the rewards of the alternative strategies.

Besides the inherent ability of some species to modify foraging mode, recent research has revealed that there might be large individual variation in how these behavioural traits are expressed^{13,14}. Such variability may be explained by sex-specific differences and individual variation in genetic and life-history traits^{13,14}, some individuals may be more risk-prone than others, individual behaviour may be modified by social hierarchies¹⁵, or individuals may get more skilled and effective at one foraging tactic at the expense of other tactics^{15,16}. Moreover, there might be physiological costs associated with prey switching¹⁷. Although many predators clearly may be able to change foraging mode, many of these mechanisms suggests individual foraging specialization to a certain foraging mode¹⁵.

Apex predators are able to modify ecosystem structure and this ability is tightly linked with structural complexity in freshwater ecosystems¹⁸. Intraspecific variation in predator behavioural types can determine prey abundance, community composition and trophic cascades¹⁹. Understanding apex predator behaviour and its variability in relation to structural complexity is therefore important to better understand their ability to cope with and/or elicit ecosystem changes, as well as the environmental drivers of phenotypic plasticity.

Research on behavioural responses of predators to changes in structural complexity has been carried out mainly at the species level in laboratory conditions or on small-scale experimental set-ups^{6,9-12}. Such conditions might be unsuitable for large predators or they could lead to important behavioural traits being ruled out²⁰. Data at natural scale is sparse and fragmented, and our understanding of aquatic apex predator behaviour in natural conditions is still highly insufficient. The development of high-resolution tracking techniques²¹ now gives the opportunity to explore behaviour with unprecedented spatiotemporal resolution that could bring new insights into predator behaviour and their interaction with environment²².

To test the effect of structural complexity on predator behaviour in natural conditions, we selected Northern pike (*Esox lucius*) as a model species. Pike is considered as an important model organism for identifying causes and consequences of phenotypic variation at the levels of individuals and populations as well as for investigating community processes²³. It is a freshwater apex predator typically associated with structurally complex habitats, often used as a classic example of a "sit-and-wait" ambush predator, and widely distributed in lakes and rivers across the Holarctic region^{24,25}. Pike is a voracious forager with a wide variety of fish and other prey types and its introduction can have large impacts on fish species composition^{24,26}. Recent research has revealed that pike can utilize a wider range of habitats, show active hunting in open water areas, and migrate many kilometres²⁷⁻²⁹. In some freshwater ecosystems, pike show behavioural types that differ in their level of activity and selection of habitat types³⁰. Most seem to be strongly associated with structurally complex habitats, but this may also vary with season and ontogeny³¹. These findings suggest that pike have the capability for phenotypic plasticity in habitat use and that differences in structural complexity might alter its foraging behaviour as a result of individual foraging specialization. On the other hand, some experimental studies indicate only minor

effects of macrophyte density on pike behaviour⁹, and there is so far no evidence for how habitat complexity might alter the species' behaviour in natural conditions.

We addressed the question of how pike behaviour change with contrasting structural complexity by tracking pike with very high spatiotemporal resolution in two newly created post-mining lakes. The lakes have similar morphological and environmental parameters, but highly different submerged macrophyte structural complexity (low and high structural complexity, respectively LSC and HSC). Pike behaviour was investigated by examining habitat use and activity (telemetry), food availability in different habitats (gillnet and acoustic sampling of fish community), long-term diet (stable isotope analysis, SIA) and individual growth in tracked pike (scale analysis). We hypothesised that (i) space use (horizontal and vertical) will be inversely related to habitat complexity; (ii) pike activity is inversely related to structural complexity; (iii) the pelagic habitat and food resources will be more important in the lake with lower habitat complexity; (iv) individual behaviour is consistent over time, but between-individual variation is higher in LSC lake; (v) growth is lower in the LSC lake, as activity costs are expected to be higher.

Materials And Methods

Study lakes

The study was conducted in two water bodies created after aquatic restorations of mining pits, Lakes Milada (2.5 km², high structural complexity; 50°39'N, 13°58'E) and Most (3.1 km², low structural complexity lake; 50°32'N, 13°38'E), in Czech Republic (Fig. 1). Aquatic restoration lasted from 2001 to 2010 in Milada and from 2008 to 2014 in Most. Both lakes are medium-sized (surface area = 252 and 311 hectares, respectively), relatively deep (Z_{mean} = 16 and 22 m, Z_{max} = 25 and 75 m), oligotrophic (mean summer total phosphorus <10 and <5 µg/L) and the Secchi depth varies between 4–9 m. The deeper Most has a well-oxygenated water column down to 50 m depth, whereas in Milada the profundal zone suffers from poor oxygen conditions below 20 m depth in summer³².

Macrophyte sampling was carried out prior to the study in September 2014 and May 2015³³. Macrophytes were dense only in the HSC lake where they covered 60-91% of 0-12 m deep inshore areas. In the LCS lake, there was only a sparse macrophyte coverage of 0.1-1.6% at 0–3 m depth. Dominant macrophyte species in both lakes were *Potamogeton pectinatus*, *Myriophyllum spicatum* and *Chara* sp.

Both lakes had similar fish community compositions. Roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*) were dominant in both lakes, while ruffe (*Gymnocephalus cernua*), tench (*Tinca tinca*), European catfish (*Silurus glanis*), Northern pike and pikeperch (*Sander lucioperca*) were less abundant³⁴. In addition, pelagic planktivorous maraena whitefish (*Coregnus maraena*) were present in the LSC lake. Stocking of predatory species including pike were performed in both lakes for biomanipulation purposes (stocking details are in the Supplementary material, herein referred as SM, sec. Stocking of pike). Stocked pike came from various breeding ponds in Central Bohemia region.

Telemetry system

Two separate MAP positioning systems (Lotek Wireless Inc., Canada) were deployed in the HSC and LSC lakes to track tagged fish (see below). The systems consisted of 91 receivers (Lotek Wireless Inc., WHS3250; 44 receivers in HSC lake, 47 receivers in LSC lake) deployed in arrays with distances between 3 nearest receivers ranging from 203 to 288 m (mean 251 ± 18 m) in HSC lake and 191 to 341 m (mean 264 ± 33 m) in LSC lake (Fig. 1). The exact position of deployed receivers was measured using a high-precision GNSS-unit (Trimble Geo7x with a cm-precision RTK-service). Depth of receivers varied between 4.5-5.5 m. According to range testing done prior to the study, in these lakes (September 2014), such setting of receiver arrays should provide full coverage of both lakes under appropriate environmental conditions. Monitoring of system accuracy was achieved by 20 stationary reference tags (10 tags in each lake; Lotek Wireless Inc., Canada, model MM-M-16-50-TP, burst rate 25 secs), located in 4 locations in each lake (2 open water locations at depths 1, 5 and 13 m, and 2 nearshore locations at depths 1 and 3 m). Further, testing of accuracy was performed by reference tags dragged below a boat after the deployment and before the final retrieval of the telemetry system. The systems were installed from April 2015 to March 2016 and data were manually downloaded every two months. The period targeted in this study lasted from 27 May 2015 to 10 October 2015 to cover the summer period with highest fish activity and development of macrophytes.

Fish tagging

A total of 30 pike individuals (15 in each lake) were captured by electrofishing (23 individuals), long-lines (6 individuals) and angling (1 individual). Mean total body length/mass was 79 cm/4.13 kg for HCS and 86 cm/4.15 kg for LSC lake, respectively (more details in Table 1). After capture, pike were anaesthetized by 2-phenoxy-ethanol (SIGMA Chemical Co., USA, 0.7 ml L^{-1} , mean time in anaesthetic bath was 3.75 min), measured, weighed and tagged. A 1-1.5 cm long incision was made on the ventral surface posterior to the pelvic girdle and the transmitter (Lotek Wireless Inc., MM-M-11-28-PM, 65x28 mm, mass in air of 13 g, including pressure and motion sensors, burst rate 25 s) was inserted through the incision and pushed forward into the body cavity. The incision was closed using two independent sutures. Mean surgery time was 2.8 min. Further, scales for age determination and stable isotope analysis (see below) were taken during anaesthesia. All pike were released immediately after recovery from anaesthesia on the same location in each lake regardless of their capture location. Fish were captured and tagged between 5 to 10 May 2015.

Macrophyte sampling

To obtain an assessment of macrophyte assemblage and coverage, two SCUBA divers visually assessed macrophyte occurrence along 25 (HSC lake) and 26 (LSC lake) transects at the end of June and the beginning of September 2015. Sampling considered both aquatic plants as well as submerged dead

terrestrial plants (only present in LSC lake). Transects were situated from the shore to a depth of 12 m or deeper when macrophytes were present there. The coverage of each macrophyte species, the uncovered bottom area, the percentage composition of each species and maximum and minimum height of each macrophyte species were measured at 1 m depth intervals. The height of macrophytes was measured using a measuring tape. Dead flooded terrestrial plants were mostly European elder *Sambucus nigra* and thus categorized as a single group. Structural Complexity Index (herein referred as SCI) in each lake was calculated to compare habitat complexity between lakes and its development during study period. Calculation of SCI was based on information from the 25 and 26 (HSC and LSC lake, respectively) scuba diver macrophyte assessment transects (see above). Species coverage and macrophyte height were both considered for calculation of the index. A detailed calculation procedure can be found in the SM (sec. Calculation of Structural Complexity Index).

Temperature and oxygen measurement

To obtain abiotic parameters which can drive pike spatial distribution^{35,36}, we monitored water temperature and oxygen concentration in both lakes. Water temperature was monitored using 60 data loggers (Onset, USA, HOBO Pendant temp/light 64K). Data loggers were placed at two sites in each lake in order to cover east/west (HSC) and south/north (LSC) gradients (Fig.1). At each site, data loggers were attached to a rope in 1 m intervals spanning from the surface to 13 meters (14 data loggers) with one extra data logger located at a depth of 20 m. The rope was tied to a floating buoy anchored at 22 m depth. This setup ensured both dense coverage in depths of rapid temperature change and, with a measurement interval of 5 minutes, high spatiotemporal resolution of the temperature profile. Oxygen concentration was measured in each lake (once a month in HSC, and once during observed period in LSC) by calibrated YSI 556 MPS probe (YSI Incorporated, USA). Measurements were performed close to the western (HSC lake) or northern (LSC lake) data logger station (Fig. 1).

Fish community sampling

To obtain data of pike prey distribution, we performed spatially stratified fish community sampling by gillnet and hydroacoustic surveys. Gillnet surveys were conducted in September 2014 and 2015 at two localities in each lake in benthic habitats and one central locality in each lake for pelagic habitats, using 30 m long standard European multi-mesh gillnets³⁷. At each locality in each lake, one series of three survey nets were set in the benthic and pelagic habitats at depths 0-3, 3-6, 6-9 and 9-18 m. In the deeper LSC lake, series of three survey nets were also set at depths 18-24, 24-30 and >30 m. Benthic and pelagic gillnets were 1.5 m and 3 m high, respectively. Gillnets were set overnight, i.e. installed 2 h before sunset and lifted 2 h after sunrise³⁸. Only catches of fish older than young-of-the-year were considered for this study. Catches were expressed as catch per unit of effort measured as number of fish caught per 1000 m² gillnet area per night (NPUE), and as kilogram fish 1000 m⁻² night⁻¹ (BPUE).

The acoustic surveys were performed both during day and night, using a calibrated Simrad EK 60 echosounder operating at frequency of 120 kHz and following a pre-set zig-zag cruise track. The transducer was mounted 0.2 m below water surface, beaming vertically downwards. Recorded data were analysed using Sonar5-Pro software version 6.0.3³⁹, using a Sv-threshold of -62 dB (thresholded at 40 logR) and a target strength (TS) threshold of -56 dB (corresponding to fish of an approximate total length of 4 cm,⁴⁰). Shoals were detected manually while fish tracking was used for individual fish. The following settings were used in the Sonar5-Pro auto-tracking tool to select fish tracks: minimum track length (MTL), maximum ping gap (MPG) and vertical range gating. MTL was set to 3 echoes, MPG was set to 1 and vertical gating to 0.15 m for whole water column. Only areas deeper than 10 m were included in further analysis. The relative fish density was calculated for shoals (shoals km⁻¹ cruise track) and individual fish (ind. km⁻¹ cruise track).

Data processing

Positions of individual fish were calculated using a proprietary post-processing software UMAP v.1.4.3, based on multilateration of time-difference-of-arrival (TDOA) of the acoustic signal received at different telemetry loggers (Lotek Wireless Inc., Newmarket, Ontario, Canada). Positions calculated using UMAP software can contain position duplicates and the use of TDOA for positioning implies large errors in a proportion of the position estimates⁴¹. Therefore, a position filter was applied in order to remove duplicate positions and positions with large errors. A detailed description of filtering procedure is given in the SM (sec. Filtering of positions estimated by the U-MAP software). The position estimates (unfiltered and filtered) and depth profiles of each individual fish was visually inspected. If both horizontal and vertical locations became constant without latter movement, this individual was considered dead or expelling the tag (2 ind. in LSC lake and 3 ind. in HSC lake) and removed from further analyses.

To obtain representative and balanced daily number of horizontal positions and depth locations for each fish, mean 15-minutes position (herein referred as q-position) and depth were calculated. Detailed description of the calculation is given in the SM (sec. Calculation of q-position and Calculation of depth location). Extent of horizontal area use was calculated using a 95 % kernel utilization distribution (herein referred as dH-KUD). dH-KUD was calculated for each day and individual separately and only for days with more than 12 daytime and 12 night-time q-positions. Night-time and daytime were defined as one hour after/prior to civil twilight periods³⁸. Exact time of sunset and sunrise in each day was calculated using R-package “maptools”⁴² and dH-KUD was calculated using R-package “adehabitatHR”⁴³. Parameters required for calculation of dH-KUD were set as follows: simplified lake shape polygon was used as a boundary, raster of a lake with dimension of cells 10x10 m was used as a grid and smoothing parameter h was set to value of 50. Extent of vertical movement was evaluated separately. Vertical space use (herein referred as dV-KS) was calculated as one-dimensional kernel estimate (95%) of Gaussian density function with smoothing bandwidth parameter set to 0.4 fitted on distribution of utilized depths.

Activity of fish was calculated as horizontal swimming speed (expressed in body lengths per second, $BL \cdot s^{-1}$) and vertical swimming speed (depth change per second, $m \cdot s^{-1}$) between two consecutive q-positions.

To test the importance of open water habitat for pike in both lakes, the proportion of time spent in open water was calculated (TOW). Each q-position was assigned to be either in the benthic (distance < 5m from the bottom) or in the open water habitat (≥ 5 m from the bottom).

Daily water temperature and day length were abiotic factors considered to potentially drive pike behaviour in lakes^{35,36,44}. Daily water temperature was calculated as mean temperature from measurement of all data loggers at depths 0-3 meters for each date during the study, separately for each lake. This parameter reflects both rapid daily and gradual seasonal temperature changes. Day length was calculated as time between sunrise and sunset.

Stable isotopes and growth

Stable isotopes are widely used in studies of food-web structure and function, as well as individual specialization among consumer populations^{45,46}. Here, we used stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes to estimate the relative reliance of individual pike on littoral carbon (food) resources (hereafter abbreviated as littoral reliance, *LR*). The *LR* estimates were calculated using the two-source isotopic mixing model described in Post⁴⁷, where the $\delta^{13}C$ value of a consumer (here measured from the outermost annual ring of pike scales) is compared to those of littoral and pelagic isotopic end-members. We used $\delta^{13}C$ values of littoral macrophytes and benthic algae, and pelagic particulate organic matter (POM) as the littoral and pelagic isotopic end-members, respectively, because some pike individuals and herbivorous prey fishes had considerably higher $\delta^{13}C$ values than littoral benthic invertebrates. For more details of sample collection and preparation for stable isotope analyses, see the previous studies of predatory⁴⁸ and generalist³² fishes in the two study lakes.

Age determination and growth calculation for each individual were conducted using scale reading. Three scales were read for each individual, results were then averaged and used for back-calculation of size-at-age of each individual using the Fraser-Lee equation⁴⁹. Only the body increment during the year prior to tagging was used to test for correlation of individual growth with the rates of horizontal and vertical movement, since this was the growth increment most relevant to the activity and body size during the study year.

Statistical analyses

Behavioural traits and use of pelagic zone

We tested whether individuals from both lakes exhibited consistent behavioural differences across time regarding horizontal area use (dH-KUD), vertical space use (dV-KS), daily mean depth, horizontal activity, vertical activity and time spent in open water (TOW), which could all be associated with either foraging or cover contexts. Before model building, we selected potentially important predictors influencing variables being modelled. Except for the analysis of TOW, which included dH-KUD, dV-KS and body length as predictors, the other variables were analysed using fish body length (i.e., total length) and environmental factors such as daily water temperature included as continuous covariates. Lake was considered used as a proxy of structural habitat complexity (SHC) and included as a categorical factor. Continuous predictors were normalized using z-score standardization (set to a mean of 0 and standard deviation of 2, ⁵⁰) to ease comparison between continuous predictors and with the untransformed factor Lake.

First, we investigated interactions between potential predictors by running a Random Forest (hereafter RF) regression analysis ⁵¹, which is suitable for the identification of relevant interactions between variables with low to negligible effects separately (further description in SM, sec. Identifying interactions with Random Forest). The RF analysis was conducted using the R package *randomForest* ⁵². After selection of important interaction terms, we fitted a generalized additive mixed model (GAMM) in order to test whether predictors had a linear or non-linear relationship with response and whether smooths terms (e.g., cubic splines) were necessary to be implemented for some covariates ⁵³. This model included relevant interaction terms from previous analysis as fixed factors and a simple random-intercept at the individual level as unique identifier (tag_ID) to account for individual repeated-measures. An analysis of variance (ANOVA) on the GAMM output allowed discerning of whether the relationship between response and predictors was linear ⁵⁴. To fit GAMM models, we used the *bam* function (R package *mgcv*, ⁵⁵), which is specifically designed for large datasets ⁵⁶.

If linearity was assumed, we ran separate linear mixed models (LMM) ^{57,58} including the time × Lake Interaction, with time (as a daily continuous variable) modelled both as a random slope effect and as a fixed factor along with a random intercept of tag ID (see SM for more details). This random effects structure was always selected in preliminary analyses using likelihood ratio tests ^{59,60} and models mean between-lake temporal trends rather than individual temporal trend lines which are more related to an individual by time interaction (i.e., reaction norms⁶¹). Time as a fixed effect represents the overall effect of time among individuals in the two lakes, which is a function of the grouping structure (i.e., the slope may vary over time but not necessarily between individuals), while time as a random intercept measures the variance of the temporal effects in response across individuals (i.e., repeatability) ⁶². For the analysis of continuous variables, we fitted linear random-intercept and random-slope mixed-effects models with Gaussian error distribution using the R package *nlme* ⁵⁷. TOW was analysed using zero-one beta inflated models ^{63,64} fitted with the function *gamlss* in R package *gamlss* ⁶⁵ specifying distribution BEINF. GAMLSS models are a particular type of GAM for Location, Scale and Shape which allow mixed distributions of continuous observations in the range (0, 1) and discrete values at zero and one often representing probabilities ruled by different processes ⁶⁶. We assumed that the inexistent use of the

pelagic habitat (i.e., stationarity) was associated with the probability at zero (p_0) while the complete use of it with the probability at one (p_1) (Equations 3, 4 in SM, sec. GAMLSS model of pelagic habitat use). On this basis, we modelled the four distribution parameters (μ , σ , v , τ) as a function of the between-lake temporal trends (time \times Lake interaction), behavioral and phenotypic predictors (dH-KUD, dV-KS and body length) and, where appropriate, smoothing functions. However, it should be noted that all distribution parameters were not necessarily modelled using additive terms and it depended on decisions made during the model selection procedure (see SM for further details on GAMLSS model parametrization, sec. GAMLSS model of pelagic habitat use). Since GAMLSS models already test the assumption of linearity between dependent and explanatory variables, we skipped the preliminary fitting and analysis of a GAMM model.

In addition to the random effects, models were fitted using an autocorrelation structure to account for past error residual correlations and prevent pseudoreplication⁵⁸. This would allow further unbiased evaluation of the differences in temporal trends by correctly partitioning inter- and within-individual sources of variance^{58,67} while accounting for slowly fluctuating trait values (i.e., behavioral lags) about those timelines. We compared models with different autocorrelation structures using Information theory^{54,68} and through preliminary inspection of their ACF and PACF residuals to determine the starting values (*rho* parameter)⁶⁹. Along with the individual identity (*tag_id*), time was included as a continuous variable to control for the correlation of residuals between any given days.

The base model was further used to determine the overall support to our hypotheses with respect to variation explained by the fixed effects. We added predictors one by one, thus creating sets of candidate models nested within the previously fitted model. We used maximum likelihood to obtain unbiased estimates of significance of the fixed effects. Next, we used information theory to rank models from best to worst average representation according to their AICc values (i.e., AIC with finite-size correction,⁷⁰) (lower is better) and AICc weights (higher is better). Lastly, we compared those models and weighed the importance of the interaction terms detected in the RF analysis using likelihood ratio tests (for more details see SM1). The selection and classification of models was conducted using the R package *AICcmodavg*⁷¹. For TOW, we used the different functions in the *gamlss* package to perform stepwise selection of appropriate terms for each distribution parameter (μ , σ , v , τ) (see SM for a detailed description of the GAMLSS selection procedure utilized, sec. GAMLSS model of pelagic habitat use).

Models were re-fitted with restricted maximum likelihood for the random-effects and autoregressive terms. We used the R package *MuMIn*⁷² for assessing variance components and to estimate marginal and conditional R^2 values. From the fitted models, we estimated inter- and within-individual variance components and calculated individual repeatability (R) both on data from both lakes and on subset data for each lake to evaluate qualitative differences of repeatability in temporal trend lines across lakes. Repeatability was calculated as the proportion of variance explained at the individual level relative to the

total variance following the expression $\frac{\tau_{00}^2}{(\tau_{00}^2 + \sigma_e^2)}$. A high R value either indicates high inter-individual

variation or low within-individual variability in the values of response, i.e., consistency in individual repeated-measures across time (see SM for further details on repeatability estimates). As a separate measure of repeatability, we compared the individual ranks in horizontal space use between June-July, June-August, and June-September using Spearman rank correlation test⁷³. The same procedure was done for swimming activity.

Stable isotopes

We ran linear models to test if the trophic niche of pike was related to individuals' behaviour (open-water use as a proxy), structural habitat complexity (SHC; lake factor as a proxy) or body length (i.e., total length). Prior to modelling, open-water use was logit-transformed and continuous explanatory variables were scaled (see above).

Growth

We used linear regression to find differences in individual growth in the previous season (log-transform of body increment in year 2014; dependent variable) between lakes and whether they were determined by the space use (mean daily dH-KUD and dV-KS), body length and age of fish (explanatory variables).

Results

Seasonal development of lakes environment

Both lakes were thermally stratified with the thermocline gradually declining from 6-7 to 9-10 m during the study period (Fig. 2 a, b). Oxygen concentration declined below the thermocline during the season in the HSC lake, to such an extent that the water was anoxic from 14 m depth and deeper in September (Fig. 2a), whereas oxygen concentrations were similar (around 10 mg/L) throughout the water column in LSC lake at end of September (Fig. 2b). As expected mean SCI was significantly higher in the HSC lake than in the LSC lake ($P < 0.001$; tested using permutation inference, SM sec. Testing of SCI differences between lakes), but this difference became much less in September as the SCI was relatively unchanged in the HSC lake, but greatly increased in the LSC lake ($P < 0.001$ for the lake by macrophyte period interaction; Fig.2 c, d).

Fish densities in terms of both number and biomass were higher in the benthic habitats than in the pelagic habitats in both lakes (Table 2; higher detail in SM sec. Fish community sampling). Pelagic fish densities were higher in the LSC lake as compared to the HSC lake, whereas the fish densities in benthic habitats were comparable in both lakes (Table 2; SM sec. Fish community sampling). Length distribution of suitable prey was similar in both lakes with higher proportion of larger prey in open water (SM sec. Fish community sampling). Hydroacoustic data showed almost no fish (school or single) in HSC in September during daytime and only low abundance of fish at night (Table 2). In the LSC lake, low densities of both schools and single fish were detected in open water during the daytime in June and September and the

number of single fish considerably increased at night in the habitat during both sampling months (Table 2).

Horizontal and vertical space use

The extent of explored horizontal area (dH-KUD) was significantly higher in the LSC lake ($t = -3.311$, $P < 0.01$), with temporal trends being positive and marginally varying between lakes (time \times pL, $t = -1.94$, $P = 0.052$) (Table 3). dH-KUD significantly increased with body length in both lakes (pBL, $t = 3.63$, $P < 0.01$) but with a steeper slope in LSC lake (Least-squares means on $BL_{\text{slope}} \pm SE$, HSC: 0.14 ± 0.04 ; LSC: 0.37 ± 0.05 ; $t = -3.552$, $P < 0.01$) (Fig. 3a). Water temperature was negatively related to horizontal range (pWT, $t = -2.42$, $P < 0.05$). Repeatability was the highest of all traits measured ($R \sim 0.43$) and in the LSC lake it was more than 1.6 times the amount observed in the HSC lake ($R \sim 0.49$ vs. 0.31) (Table 3; Fig. 3b). The Spearman rank correlation tests also revealed a consistent and strong individual repeatability in LSC, with Spearman's rank correlation coefficient 0.93, 0.75, and 0.78 in LSC for June-July, June-August, and June-September, respectively. Corresponding coefficients for HSC lake were 0.46, 0.20, 0.20. The lower coefficients for the HSC lake were associated with a much lower between-individual variation in activity (Fig. 3b).

In general, vertical utilization distribution (dV-KS) was not significantly different between lakes (pL, $t = -1.25$, $P > 0.1$), and neither were temporal trends (time \times pL, $t = -0.95$, $P = 0.34$; Table 3). The inter-individual variability over time was very marked between lakes, with pike in HSC lake showing stronger variability than conspecifics in LSC ($R \sim 0.3$ vs. 1.2^{-05} ; Fig. 4).

Mean daily depth of pike was not significantly different between lakes and neither were temporal trends of fish (both $P > 0.1$, Table 3, Fig. 5). Mean daily depth showed a positive relationship with increasing water temperature (pWT, $t = 2.61$, $P < 0.01$; Table A4 in SM). The inter-individual variation in mean depth was slightly higher in HSC than in LSC lake ($R \sim 0.18$ vs. 0.15 , Fig. 5 c, f). In the benthic habitats, pike were dispersed from the surface down to 12-15 m in HSC lake throughout the season, while in LSC lake pike utilized even deeper depths down to 35 m at the end of summer (likely even deeper but the depth sensor could not record depths below 35 m). In open water, pike were distributed primarily around the thermocline (Fig. 5).

Activity

Pike from the LSC lake were significantly more horizontally active than those from the HSC ($t = -3.03$, $P < 0.01$), and their temporal trends were in both cases negative and marginally different (time \times pL, $t = -1.79$, $P < 0.1$; Table 3; Fig. 6a). Water temperature negatively influenced the activity of fish in both lakes (pWT, $t = -4.43$, $P < 0.001$). The inter-individual variability was higher in the HSC lake compared to LSC lake ($R \sim 0.35$ vs. 0.23), but the Spearman rank correlation tests revealed a consistent and strong individual repeatability also in swimming activity in LSC, with Spearman's rank correlation coefficients 0.68, 0.73

and 0.50 in LSC for June-July, June-August, and June-September, respectively. Corresponding coefficients for HSC lake were 0.45, 0.05, 0.11. The lower coefficients for the HSC lake were associated with a much lower between-individual variation in activity (Fig. 6b).

Vertical activity were only marginal different between lakes (pL, $t = 2.07$, $P = 0.05$; Table 3) and apparently conditioned by the effects of time. Dropping the time \times Lake interaction from the model removed those initial differences (pL, $t = 1.37$, $P > 0.1$), suggesting that swimming speeds were on average different in both lakes at the end of the study (Fig. 6c). No other predictors were important for predicting vertical activity (all LRTs, $P > 0.1$) (Table A6 in SM). Differences between individuals were relatively low and consistent with the pattern of variability in vertical space use when HSC inter-individual differences were nearly four times higher than in LSC lake ($R \sim 0.26$ vs. 0.07 ; Fig. 6d).

Pelagic habitat use and food resources

Time spent in open water (TOW) differed between lakes and as a non-linear function of dH-KUD and dV-KS (Table 4). Overall, TOW (lake_(μ), $t = 7.99$, $P < 0.001$) and TOW variability (lake_(σ), $t = 7.70$, $P < 0.001$) was higher in the LSC lake and increased over time (time_(σ), $t = 4.05$, $P < 0.001$, Fig. 7a). Higher values of dH-KUD were correlated with increased likelihood of TOW in both lakes (dH-KUD_(μ), $t = 7.99$, $P < 0.001$, Fig. 6b), while increasing dV-KS was associated with a decreased likelihood (dV-KS_(μ), $t = -9.54$, $P < 0.001$, Fig. 7b) but increased variability (dV-KS_(σ), $t = -5.30$, $P < 0.001$), with both effects persisting over time.

A significant effect of lake and a negative effect of body length was found on pike littoral reliance (Fig. 8, Table 5, 6). The second best equally supported model ($\Delta AIC = 1.42$) also suggested a positive effect of open-water use on littoral reliance (Table 5). In both lakes, pike seemed to shift to a less littoral (i.e., more pelagic) diet with increasing body length (Fig. 8). Unexpectedly, pike tended to rely more on littoral resources in the LSC lake (Fig. 8), where the individual with the lowest littoral reliance estimate (excluded from modelling) also showed the lowest use of open-water areas. In fact, the stable isotope data indicates that only this single pike relied more on pelagic than on littoral food resources.

Growth

Pike growth varied between lakes (Least-squares means \pm SE, HSC: 90 ± 16.5 ; LSC: 142 ± 13.5 ; $t = -2.157$, $P = 0.045$), and with the age of individuals (pWT, $t = -3.90$, $P < 0.01$), while no significant correlation was found with body length. dH-KUD and dV-KS did not have significant main effects but their crossover interaction had a significant impact on growth (dH-KUD \times dV-KS, $t = 2.448$, $P = 0.025$). To further determine the relationship between the interaction term and the response variable, we ran a slope analysis showing that the effect of dH-KUD on growth was conditioned to specific dV-KS range. When dV-KS is high ($b > 1.32$), the slope of dH-KUD tends to be significant ($P < 0.1$) and in the same positive direction as in the fitted model. It means that the growth increased with increasing dH-KUD at high values of dV-KS (see SM for further details, sec. Analysis of growth rate using linear regression).

Discussion

Structural complexity was found to have a strong directional influence on multiple pike behavioural traits, with clear differences between LSC and HSC lakes. As hypothesized, pike exhibited higher horizontal space use and higher activity in the LSC lake as compared to the HSC lake. Moreover, the increased space use with increased activity also indicates that higher activity levels were associated with exploring new areas rather than revisiting already visited areas. Exploration of more extended areas were positively related with pike size and linked with higher use of open water, also reflected in lower littoral reliance in the diet. There was a high degree of consistency in individual behaviour, individuals having high space use, activity and/or open water use in one month, also had so in the next month (high repeatability) when there was a high degree of between-individual variation. Inter-individual differences varied between lakes, with activity and exploration of horizontal space showing higher individual rank correlation between months in the LSC lake where the between-individual variation was high. With low-between-individual variability, rank correlation between months also tended to be low. Although rank correlation decreased over time in both lakes, the correlation was consistently much higher in the LSC lake. Contrary to what expected, individual growth was overall higher in the LSC lake, indicating that pike in the LSC lake was able to more than compensate for increased activity costs by increased foraging success. Despite observed differences in pike behaviour and growth, stable isotopes showed a low degree of specialization and a high dependence on littoral food sources in both lakes.

Horizontal space use and activity

We found that activity and horizontal space use and activity were higher with lower structural complexity. Predator space use is largely driven by prey abundance and predator body size⁷⁴⁻⁷⁶, and a positive relationship between pike body size and horizontal space use has been documented in numerous studies^{22,30,77-80}. Previous research on predators capable of performing both active pursuit and ambush strategies indicated that a switch between these modes was primarily linked to prey density or prey type⁸¹⁻⁸⁴. However, contrary to general expectations, prey abundance alone cannot explain the larger space use and active foraging of pike in the LSC lake. Comparison of prey density and type in pike-preferred littoral habitat showed large similarities between lakes (we detected even higher prey abundance in LSC lake in 2015). Moreover, similar alteration of activity, forage mode or space use with habitat complexity has been observed in several fish species^{7,85-87}. As in our study, Ahrenstorff et al. [85] found that largemouth bass (*Micropterus salmoides*) home range increased and that the bass switched from ambush predation to active searching behaviour when structural complexity decreased. Pike body morphology is clearly adapted to ambush and attack foraging, which is also regarded as the preferred foraging strategy of pike⁸⁸. But structurally complex macrophytes also serves as cover/camouflage for ambush pike as well as attraction for prey fish, and in the lack of macrophytes pike cannot rely on camouflage, as they will much more easily be spotted and avoided. This may force pike into a more active search to find local distributions of prey. The higher availability of pelagic prey may increase the

potential profitability of pelagic foraging, but this is not a necessary condition to explain altered behaviour from ambush predation to active search. Therefore, we propose differences in habitat complexity between lakes as a crucial driver for observed behavioural differences among pike. Ambush individuals (prevalent behaviour in the HSC lake) have camouflage, use a small area of the macrophyte bed and limited vertical movement as they wait to ambush their prey. On the contrary, pike in the LSC lake cannot rely on camouflage as they will much more easily be spotted and avoided in the lack of macrophytes, and are forced into a more active search to find local distributions of prey. The pattern of inter-individual differences and repeatability also suggest that while in their preferred macrophyte habitat, pike behaviour has low variability. In contrast, when pike is forced away from the ambush-strategy, inter-individual differences get larger, indicating a wider range of hunting strategies with individual specialization into pattern repeated over time.

Vertical space use and activity

Our results showed that, despite similarity in vertical space use and depth preference in both lakes, vertical activity was significantly higher and several individuals performed very deep dives in the LSC lake. Temperature conditions within the water column were similar between our study lakes, and pike mostly preferred the area from the surface down to the upper hypolimnion in benthic habitats and around the thermocline in open water. Recent behavioural studies have highlighted that exploration of movement in the vertical dimension is important for understanding animal habitat use⁸⁹. The limited available information suggests that water temperature is an important driver of pike vertical distribution⁴⁴, with pike normally preferring relatively cold parts of the water column³⁵. This would force pike deeper as the surface waters get very warm, as we indeed observed in our study. Bioenergetic advantages of heat gain from “sun basking” in surface waters has been suggested for some circumstances⁴⁴, however this may likely occur only at lower water temperatures than observed in surface waters in our study in July and August. Too warm surface waters may also explain why the development of higher structural complexity at depths shallower than 5 m in the LSC lake towards the end of the season was not accompanied by increased pike association to this. Higher vertical activity in the LSC lake meant individuals were more active within the vertical space, which is in concordance with higher activity in horizontal space and reflects the active hunting strategy in both spatial dimensions.

Open Water and prey distribution

We proposed macrophytes to act as a crucial driver of pike activity and space use in both lakes, without differences in prey distribution being a prerequisite. But prey distribution may clearly play an important role for pike habitat use⁹⁰, since there would be no benefit of pelagic prey search without pelagic prey present. In the LSC lake, use of extensive horizontal areas was tightly linked with frequent use of open water, contrary to the HSC lake where open water areas were rarely explored. This corresponded with much higher abundance of pelagic prey fish in the LSC lake as compared to the HSC lake. When foraging

in the pelagic areas, there is no structural complexity to aid cover or camouflage for ambush predation, and a search-based foraging mode is likely more effective. Low environmental complexity may induce individual differentiation in food source and higher inter-individual trophic niche^{33,48,91}, which are in line with our observations in this study.

Potential dietary specialization

Our results showed higher inter-individual differences in horizontal space use among pike in LSC lake, suggesting a link between behaviour and prey specialization. However, our results showed minor, if any, individual dietary specialization. Even the pike individual with the highest open water use depended strongly on littoral food resources, and only one individual had higher pelagic than littoral reliance. These findings suggest that, even though pike in the LSC lake had a wider spatial niche, the littoral prey fishes like tench, perch, rudd, roach and ruffe were still the most important prey^{32,34,48}. The results from telemetry and stable isotope analyses are not directly comparable, since the stable isotopes reflected the time before the telemetry study. However, we do not expect substantial changes in pike diet and behaviour because the environmental conditions in both study lakes had been similar the year before our study. Vejřík et al. [48] studied the diet and trophic position of pike in our study lakes, and also found that pike in the LSC lake had a wider trophic niche as well as a lower trophic position than pike in HSC lake. Together with our findings, this indicates an existence of open water and littoral prey specialists in pike in the LSC lake, but also that altered foraging mode from ambush behaviour to search behaviour is not necessarily accompanied by a switch from littoral to pelagic prey reliance. Rather, the structural complexity in the littoral zone seems to be the main key for altered behaviour in pike.

Pike activity, energy gains and growth

The growth rate of pike was higher in the LSC lake, contrary to our expectations based on higher metabolic costs associated with higher activity. Moreover, growth was positively correlated with increased activity and space use in both horizontal and vertical dimensions. Such findings suggest that increased activity was more than compensated by increased energy intake. As with the stable isotopes, our growth analyses reflected the time before the telemetry analyses. But as the effects of individual and size on behaviour were consistent, we assume there was a good correspondence between growth in the previous year and activity in the present year. Switch between ambush and active mode does not imply large increase in expended energy in ectotherms^{82,83}, and Lucas et al. [92] calculated that the cost of activity comprised only up to 15% of standard metabolism for even relatively active pike. Given that the prey density was similar in both study lakes, the higher pike activity in the LSC lake would imply an increased prey encounter rate⁹³, potentially leading to higher ingestion rate if capture rate was not severely reduced. Recent studies have shown contrasting evidence for the relationship between pike growth and activity. Laskowski et al. [20] found no correlation between pike behaviour and growth rate in a standardized assay. In contrast, Nyqvist et al. [29,94] found higher activity to support increased growth rate

of riverine pike juveniles, whereas Kobler et al. [30] found active and opportunistic adult pike to grow faster than the less explorative individuals in a small lake. Savino and Stein [9] found that pike had higher attack rates and hunt success in a homogeneous environment. Our results support the latter findings, supporting altered behaviour as the mechanism underlying our observation of higher growth in the LSC lake even under similar prey availability.

Contribution of pike origin

We were not able to distinguish between autochthonous (born in lakes) and allochthones (stocked) pike, and some large pike tagged in the LSC lake might have a stocking origin. Recent research showed that translocation to a novel environment might influence space use for up to several months²². Pike stocking ceased 2 and 10 years before our study in the LSC and HSC lake, respectively, there would be a large proportion of in-lake recruited pike in both lakes, and translocated pike would have had years to adapt their behavior to local conditions. Moreover, pike in our recently created study lakes had a similar origin and thus no time for genetic adaptation to the new local conditions. Since the allometric influence on activity and space use were similar in both lakes, we do not believe that potentially stocked fish had any influence on our results and conclusions.

General Conclusions

Our study showed that structural complexity can have large impacts on behaviour of apex predators in natural conditions. The observed behavioural differences of the apex predator may have contrasting, potentially cascading impacts on lower trophic levels. Different predator behaviour may favour different prey behaviour or species and per capita consumptive effects of pike on lower trophic levels must differ in our study lakes. Our results suggest that higher activity levels and thus and energy expenditure can be associated with higher growth, which must be balanced by increased consumption. On the other hand, piscivorous fish in habitats with low structural complexity may be more vulnerable to fishing mortality, since the increased activity implies increased encounter probabilities with anglers and/or fishing nets. Ecosystem effects of observed behavioural differences are beyond scope of this paper and further research is highly needed in this respect, but we argue that the design of concurrently comparing lakes with contrasting structural complexity has a large potential for such research.

Declarations

Acknowledgements

Authors would like to acknowledge all FishEcU members for their help during fieldwork and data processing. The work was supported from ERDF/ESF project Biomanipulation as a tool for improving water quality of dam reservoirs (No. CZ.02.1.01/0.0/0.0/16_025/0007417) and the project QK1920011

“Methodology of predatory fish quantification in drinking-water reservoirs to optimize the management of aquatic ecosystems”.

Availability of supporting data and materials

The datasets used and analysed during the current study are available from the corresponding author on reasonable request.

Ethics approval and consent to participate

This study complied with and was approved by the Animal Welfare Committee of the Biology Centre CAS (45/2014) according to § 16a of the Act No. 246/1992 Coll., on the protection of animals against cruelty, as amended.

Consent for publication

This manuscript presents work that has not been published and is not under consideration for publication elsewhere. All authors involved in the manuscript have agreed to be listed and contributed to the research reported.

Availability of supporting data and materials

The datasets used and analysed during the current study are available from the corresponding author on reasonable request.

Competing interests

The authors declare that they have no competing interests.

Author's contributions

All authors contributed substantial comments during manuscript preparation:

Conceptualization: JP, KØG, MŘ

Data curation: VDěd, KØG, MŘ

Formal analysis: VDěd, APE, VDraštíř, CR, APE, MŘ

Statistical analysis: APE, RRB

Funding acquisition: JP, KØG

Investigation: MŘ, KØG, HB, LV, IV, VDrašík, MŠ, MH, TJ, ZSá, FØ, JP

Methodology: MŘ, KØG, HB, JP, CR, APE

Project administration: JP

Visualization: VDěd, MŘ, KØG, APE

Writing – original draft: MŘ, V.Děd, KØG, APE, VDrašík, CR, RRB

Writing – review & editing: all authors

References

1. Kerr, J. T. & Packer, L. Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. *Nature* **385**, 252–254 (1997).
2. Kovalenko, K. E., Thomaz, S. M. & Warfe, D. M. Habitat complexity: Approaches and future directions. *Hydrobiologia* **685**, 1–17 (2012).
3. Stein, A., Gerstner, K. & Kreft, H. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecol. Lett.* **17**, 866–880 (2014).
4. Willis, S. C., Winemiller, K. O. & Lopez-Fernandez, H. Habitat structural complexity and morphological diversity of fish assemblages in a Neotropical floodplain river. *Oecologia* **142**, 284–295 (2005).
5. Denno, R. F., Finke, D. & Langellotto, G. A. Direct and indirect effects of vegetation structure and habitat complexity on predator-prey and predator-predator interactions. in *Ecology of predator-prey interactions* (eds. Barbosa, P. & Castellanos, I.) 211–239 (Oxford University Press, 2005).
6. Olsson, K. & Nyström, P. Non-interactive effects of habitat complexity and adult crayfish on survival and growth of juvenile crayfish (*Pacifastacus leniusculus*). *Freshw. Biol.* **54**, 35–46 (2009).
7. DeBoom, C. S. & Wahl, D. H. Effects of Coarse Woody Habitat Complexity on Predator-Prey Interactions of Four Freshwater Fish Species. *Trans. Am. Fish. Soc.* **142**, 1602–1614 (2013).
8. Schmitz, O. J. Behaviour of predators and prey and links with population-level processes. in *Ecology of predator-prey interactions* (eds. Barbosa, P. & Castellanos, I.) 256–279 (Oxford University Press, 2005).
9. Savino, J. F. & Stein, R. A. Behavioural interactions between fish predators and their prey: effects of plant density. *Anim. Behav.* **37**, 311–321 (1989).
10. Laurel, B. J. & Brown, J. A. Influence of cruising and ambush predators on 3-dimensional habitat use in age 0 juvenile Atlantic cod *Gadus morhua*. *J. Exp. Mar. Bio. Ecol.* **329**, 34–46 (2006).

11. Pamala, J. L. & Heck, K. L. The effects of habitat complexity and light intensity on ambush predation within a simulated seagrass habitat. *J. Exp. Mar. Bio. Ecol.* **176**, 187–200 (1994).
12. Michel, M. J. & Adams, M. M. Differential effects of structural complexity on predator foraging behavior. *Behav. Ecol.* **20**, 313–317 (2009).
13. Towner, A. V. *et al.* Sex-specific and individual preferences for hunting strategies in white sharks. *Funct. Ecol.* **30**, 1397–1407 (2016).
14. Nakayama, S., Laskowski, K. L., Klefoth, T. & Arlinghaus, R. Between- and within-individual variation in activity increases with water temperature in wild perch. *Behav. Ecol.* **00**, arw090 (2016).
15. Araújo, M. S., Bolnick, D. I. & Layman, C. A. The ecological causes of individual specialisation. *Ecology Letters* vol. 14 948–958 (2011).
16. Ryer, C. H. & Olla, B. L. The influence of food distribution upon the development of aggressive and competitive behaviour in juvenile chum salmon, *Oncorhynchus keta*. *J. Fish Biol.* **46**, 264–272 (1995).
17. Hooker, O. E., Van Leeuwen, T. E. & Adams, C. E. The physiological costs of prey switching reinforce foraging specialization. *J. Anim. Ecol.* **86**, 605–614 (2017).
18. Carpenter, S. R., Kitchell, J. F. & Hodgson, J. R. Cascading Trophic Interactions and Lake Productivity. *Bioscience* **35**, 634–639 (1985).
19. Start, D. & Gilbert, B. Predator personality structures prey communities and trophic cascades. *Ecol. Lett.* **20**, 366–374 (2017).
20. Laskowski, K. L. *et al.* Behaviour in a standardized assay, but not metabolic or growth rate, predicts behavioural variation in an adult aquatic top predator *Esox lucius* in the wild. *J. Fish Biol.* **88**, 1544–1563 (2016).
21. Hussey, N. E. *et al.* Aquatic animal telemetry: A panoramic window into the underwater world. *Science* (80-). **348**, 1255642 (2015).
22. Monk, C. T. *et al.* Behavioural and fitness effects of translocation to a novel environment: whole-lake experiments in two aquatic top predators. *J. Anim. Ecol.* 1365-2656.13298 (2020) doi:10.1111/1365-2656.13298.
23. Forsman, A. *et al.* Pike *Esox lucius* as an emerging model organism for studies in ecology and evolutionary biology: a review. *J. Fish Biol.* **87**, 472–479 (2015).
24. Skov, C., Lucas, M. C. & Jacobsen, L. Spatial ecology. in *Biology and Ecology of Pike* (eds. Skov, C. & Nilsson, P. A.) 91–128 (2018).
25. Craig, J. F. A short review of pike ecology. *Hydrobiologia* **601**, 5–16 (2008).
26. Byström, P. *et al.* Substitution of top predators: effects of pike invasion in a subarctic lake. *Freshw. Biol.* **52**, 1271–1280 (2007).
27. Sandlund, O. T., Museth, J. & Øistad, S. Migration, growth patterns, and diet of pike (*Esox lucius*) in a river reservoir and its inflowing river. *Fish. Res.* **173**, 53–60 (2016).

28. Jacobsen, L. *et al.* Pike (*Esox lucius* L.) on the edge: consistent individual movement patterns in transitional waters of the western Baltic. *Hydrobiologia* **784**, 143–154 (2017).
29. Nyqvist, M. J., Cucherousset, J., Gozlan, R. E., Beaumont, W. R. C. & Britton, J. R. Dispersal strategies of juvenile pike (*Esox lucius* L.): Influences and consequences for body size, somatic growth and trophic position. *Ecol. Freshw. Fish* **29**, 377–383 (2020).
30. Kobler, A., Klefoth, T., Mehner, T. & Arlinghaus, R. Coexistence of behavioural types in an aquatic top predator: A response to resource limitation? *Oecologia* **161**, 837–847 (2009).
31. Eklöv, P. Effects of habitat complexity and prey abundance on the spatial and temporal distributions of perch (*Perca fluviatilis*) and pike (*Esox lucius*). *Can. J. Fish. Aquat. Sci.* **54**, 1520–1531 (1997).
32. Vejříková, I. *et al.* Macrophytes shape trophic niche variation among generalist fishes. *PLoS One* **12**, 1–13 (2017).
33. Vejříková, I. *et al.* Distribution of Herbivorous Fish Is Frozen by Low Temperature. *Sci. Rep.* **6**, 1–11 (2016).
34. Eloranta, A. P. *et al.* Some like it deep: Intraspecific niche segregation in ruffe (*Gymnocephalus cernua*). *Freshw. Biol.* **62**, 1401–1409 (2017).
35. Pierce, R. B., Carlson, A. J., Carlson, B. M., Hudson, D. & Staples, D. F. Depths and thermal habitat used by large versus small Northern pike in three Minnesota lakes. *Trans. Am. Fish. Soc.* **142**, 1629–1639 (2013).
36. Baktoft, H. *et al.* Seasonal and diel effects on the activity of northern pike studied by high-resolution positional telemetry. *Ecol. Freshw. Fish* **21**, 386–394 (2012).
37. CEN. EN 14 757, CEN TC 230, Water quality – Sampling fish with Multimesh gillnets. (2005).
38. Prchalová, M. *et al.* Fish activity as determined by gillnet catch: A comparison of two reservoirs of different turbidity. *Fish. Res.* **102**, 291–296 (2010).
39. Balk, H. & Lindem, T. Sonar 4 and Sonar 5-Pro post processing systems. Operator manual 6.0.3. 464 (2014).
40. Frouzova, J., Kubecka, J., Balk, H. & Frouz, J. Target strength of some European fish species and its dependence on fish body parameters. *Fish. Res.* **75**, 86–96 (2005).
41. Baktoft, H., Gjelland, K. Ø., Økland, F. & Thygesen, U. H. Positioning of aquatic animals based on time-of-arrival and random walk models using YAPS (Yet Another Positioning Solver). *Sci. Rep.* **7**, 1–10 (2017).
42. Bivand, R. S. & Lewin-Koh, N. "maptools: Tools for reading and handling spatial objects. (2015).
43. Calenge, C. & Fortmann-Roe, S. Home range estimation in R: the adehabitatHR package. (2019).
44. Nordahl, O., Koch-Schmidt, P., Tibblin, P., Forsman, A. & Larsson, P. Vertical movements of coastal pike (*Esox lucius*)—On the role of sun basking. *Ecol. Freshw. Fish* **29**, 18–30 (2020).
45. Boecklen, W. J., Yarnes, C. T., Cook, B. A. & James, A. C. On the Use of Stable Isotopes in Trophic Ecology. *Annu. Rev. Ecol. Evol. Syst.* **42**, 411–440 (2011).

46. Layman, C. A. *et al.* Applying stable isotopes to examine food-web structure: an overview of analytical tools. *Biol. Rev.* **87**, 545–562 (2012).
47. Post, D. M. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* **83**, 703–718 (2002).
48. Vejřík, L. *et al.* European catfish (*Silurus glanis*) as a freshwater apex predator drives ecosystem via its diet adaptability. *Sci. Rep.* **7**, 1–15 (2017).
49. Francis, R. I. C. C. Back-calculation of fish length: a critical review. *J. Fish Biol.* **36**, 883–902 (1990).
50. Gelman, A. Scaling regression inputs by dividing by two standard deviations. *Stat. Med.* **27**, 2865–2873 (2008).
51. Breiman, L. Random forests. *Mach. Learn.* **45**, 5–32 (2001).
52. Liaw, A. & Wiener, M. *Classification and Regression by RandomForest*. <https://www.researchgate.net/publication/228451484> (2001).
53. Jones, K. & Almond, S. Moving out of the Linear Rut: The Possibilities of Generalized Additive Models. *Trans. Inst. Br. Geogr.* **17**, 434 (1992).
54. Kinney, M. J., Kacev, D., Kohin, S. & Eguchi, T. An analytical approach to sparse telemetry data. *PLoS One* **12**, e0188660 (2017).
55. Wood, S. mgcv: GAMs and generalized ridge regression for R. *R news* **1/2**, 20–25 (2001).
56. Wood, S. N., Goude, Y. & Shaw, S. Generalized additive models for large datasets. *J. R. Stat. Soc. Ser. C (Applied Stat.)* **64**, 139–155 (2015).
57. Pinheiro, J., Bates, D., DebRoy, S. & Sarkar, D. *nlme: Linear and Nonlinear Mixed Effects Models*. (2020).
58. Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. & Smith, G. M. *Mixed effects models and extensions in ecology with R*. (Springer Science & Business Media, 2009).
59. Ripley, B. D. Selecting amongst large classes of models. in *Methods and Models in Statistics: In Honour of Professor John Nelder* 155–170 (FRS, 2004). doi:10.1142/9781860945410_0007.
60. Bolker, B. M. *et al.* Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.* **24**, 127–135 (2009).
61. Biro, P. A. & Stamps, J. A. Using repeatability to study physiological and behavioural traits: Ignore time-related change at your peril. *Anim. Behav.* **105**, 223–230 (2015).
62. Nakagawa, S. & Schielzeth, H. Repeatability for Gaussian and non-Gaussian data: A practical guide for biologists. *Biol. Rev.* **85**, 935–956 (2010).
63. Ospina, R. & Ferrari, S. L. P. Inflated beta distributions. *Stat Pap.* **51**, 111–126 (2010).
64. Ospina, R. & Ferrari, S. L. P. A general class of zero-or-one inflated beta regression models. *Comput. Stat. Data Anal.* **56**, 1609–1623 (2012).
65. Rigby, R. A. & Stasinopoulos, D. M. Generalized additive models for location, scale and shape. *J. R. Stat. Soc. Ser. C (Applied Stat.)* **54**, 507–554 (2005).

66. Stasinopoulos, D. M. & Rigby, R. A. Generalized additive models for Location Scale and Shape (GAMLSS) in R. (2007) doi:10.18637/jss.v023.i07.
67. Mitchell, D. J., Dujon, A. M., Beckmann, C. & Biro, P. A. Temporal autocorrelation: A neglected factor in the study of behavioral repeatability and plasticity. *Behav. Ecol.* **31**, 222–231 (2020).
68. Burnham, K. P. & Anderson, D. R. *Model selection and multimodel inference: A practical information-theoretic approach*. (Springer-Verlag, 2002).
69. Box, G. E., Jenkins, G. M. & Reinsel, G. C. *Time series analysis: Forecasting and control*. (Prentice Hall, 1994).
70. Burnham, K. P. & Anderson, D. R. Multimodel Inference. *Sociol. Methods Res.* **33**, 261–304 (2004).
71. Mazerolle, M. J. AICcmodavg: Model selection and multimodel inference based on (Q) AIC (c). (2016).
72. Barton, K. MuMIn: multi-model inference. *ci.nii.ac.jp* (2018).
73. Davy, C. M., Paterson, J. E. & Leifso, A. E. When righting is wrong: Performance measures require rank repeatability for estimates of individual fitness. *Anim. Behav.* **93**, 15–23 (2014).
74. Hansen, E. A. & Closs, G. P. Diel activity and home range size in relation to food supply in a drift-feeding stream fish. *Behav. Ecol.* **16**, 640–648 (2005).
75. Steingrímsson, S. Ó. & Grant, J. W. A. Determinants of multiple central-place territory use in wild young-of-the-year Atlantic salmon (*Salmo salar*). *Behav. Ecol. Sociobiol.* **65**, 275–286 (2011).
76. McIntosh, A. R. *et al.* Capacity to support predators scales with habitat size. *Sci. Adv.* **4**, eaap7523 (2018).
77. Diana, J. S., Mackay, W. C. & Ehrman, M. Movements and Habitat Preference of Northern Pike (*Esox lucius*) in Lac Ste. Anne, Alberta. *Trans. Am. Fish. Soc.* **106**, 560–565 (1977).
78. Nilsson, P. A. *et al.* Visibility conditions and diel period affect small-scale spatio-temporal behaviour of pike *Esox lucius* in the absence of prey and conspecifics. *J. Fish Biol.* **80**, 2384–2389 (2012).
79. Rosten, C. M., Gozlan, R. E. & Lucas, M. C. Allometric scaling of intraspecific space use. *Biol. Lett.* **12**, 20150673 (2016).
80. Eklöv, P. Group foraging versus solitary foraging efficiency in piscivorous predators: the perch, *Perca fluviatilis*, and pike, *Esox lucius*, patterns. *Anim. Behav.* **44**, 313–326 (1992).
81. Norberg, R. A. An Ecological Theory on Foraging Time and Energetics and Choice of Optimal Food-Searching Method. *J. Anim. Ecol.* **46**, 511 (1977).
82. Helfman, G. S. Mode Selection and Mode Switching in Foraging Animals. *Adv. Study Behav.* **19**, 249–298 (1990).
83. Killen, S. S., Brown, J. A. & Gamperl, K. A. The effect of prey density on foraging mode selection in juvenile lumpfish: balancing food intake with the metabolic cost of foraging. *J. Anim. Ecol.* **76**, 814–825 (2007).
84. Fausch, K. D., Nakano, S. & Kitano, S. Experimentally induced foraging mode shift by sympatric charrs in a Japanese mountain stream. *Behav. Ecol.* **8**, 414–420 (1997).

85. Ahrenstorff, T. D., Sass, G. G. & Helmus, M. R. The influence of littoral zone coarse woody habitat on home range size, spatial distribution, and feeding ecology of largemouth bass (*Micropterus salmoides*). *Hydrobiologia* **623**, 223–233 (2009).
86. Enefalk, Å. & Bergman, E. Effect of fine wood on juvenile brown trout behaviour in experimental stream channels. *Ecol. Freshw. Fish* **25**, 664–673 (2016).
87. Church, K. D. W. & Grant, J. W. A. Does increasing habitat complexity favour particular personality types of juvenile Atlantic salmon, *Salmo salar*? *Anim. Behav.* **135**, 139–146 (2018).
88. Webb, P. W. Body Form, Locomotion and Foraging in Aquatic Vertebrates. *Am. Zool.* **24**, 107–120 (1984).
89. Tracey, J. A. *et al.* Movement-Based Estimation and Visualization of Space Use in 3D for Wildlife Ecology and Conservation. *PLoS One* **9**, e101205 (2014).
90. Brodersen, J., Howeth, J. G. & Post, D. M. Emergence of a novel prey life history promotes contemporary sympatric diversification in a top predator. *Nat. Commun.* **6**, 1–9 (2015).
91. Paz Cardozo, A. L., Quirino, B. A., Yofukuji, K. Y., Ferreira Aleixo, M. H. & Fugli, R. Habitat complexity and individual variation in diet and morphology of a fish species associated with macrophytes. *Ecol. Freshw. Fish* eff.12574 (2020) doi:10.1111/eff.12574.
92. Lucas, M. C., Priede, I. G., Armstrong, J. D., Gindy, A. N. Z. & Vera, L. Direct measurements of metabolism, activity and feeding behaviour of pike, *Esox Zucius* L., in the wild, by the use of heart rate telemetry. *J. Fish Biol.* **39**, 325–345 (1991).
93. Ioannou, C. C., Ruxton, G. D. & Krause, J. Search rate, attack probability, and the relationship between prey density and prey encounter rate. *Behav. Ecol.* **19**, 842–846 (2008).
94. Nyqvist, M. J., Cucherousset, J., Gozlan, R. E. & Britton, J. R. Relationships between individual movement, trophic position and growth of juvenile pike (*Esox lucius*). *Ecol. Freshw. Fish* **27**, 398–407 (2018).

Tables

Please see the supplementary files section to view the tables.

Figures

System

- ★ Dataloggers
- Receivers

Depth (m)

- 0
- 10
- 20
- 30
- 40
- 50
- 60
- 70

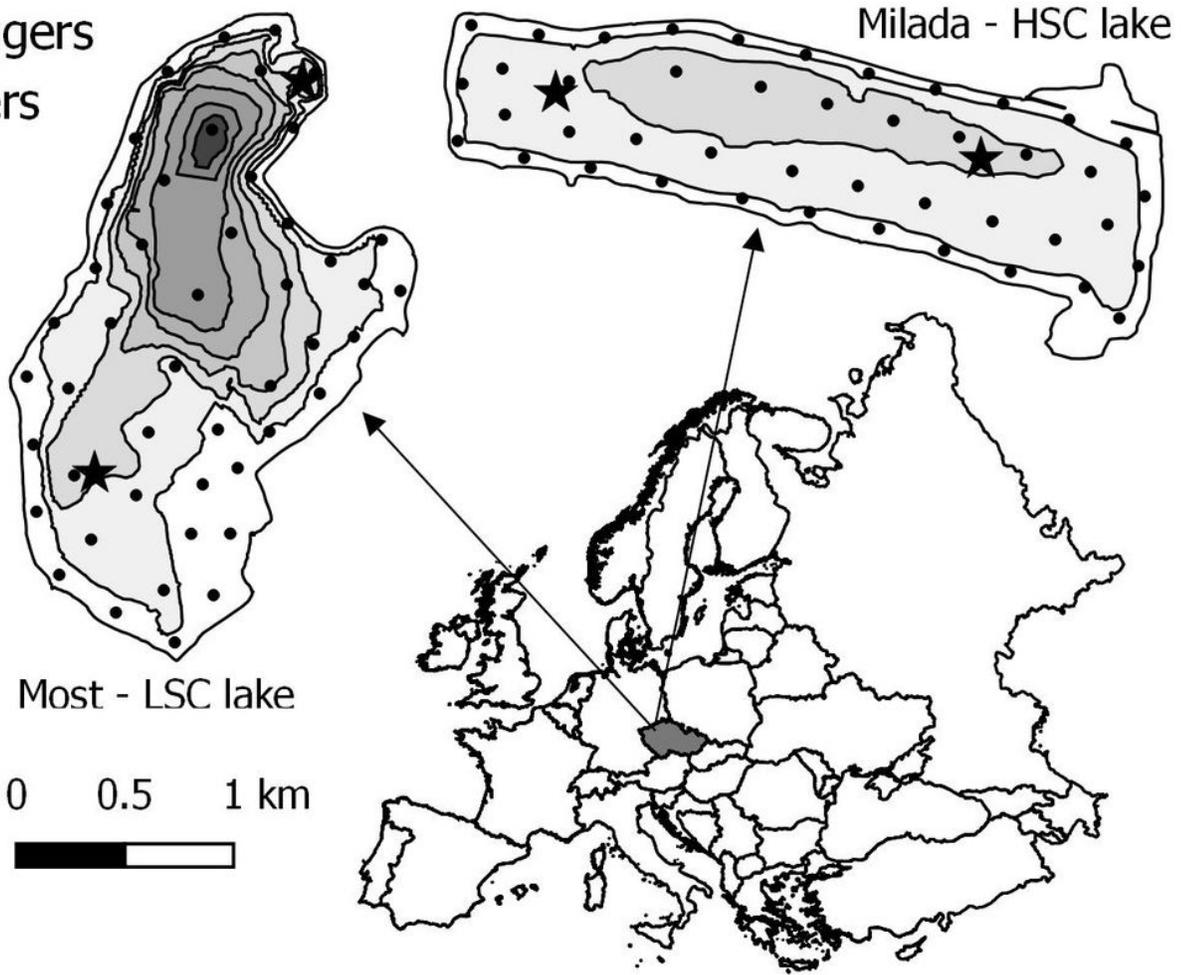


Figure 1

Locations and bathymetric maps of investigated lakes and positions of telemetry systems. Dots represent positions of each telemetry receiver and stars positions of temperature loggers. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

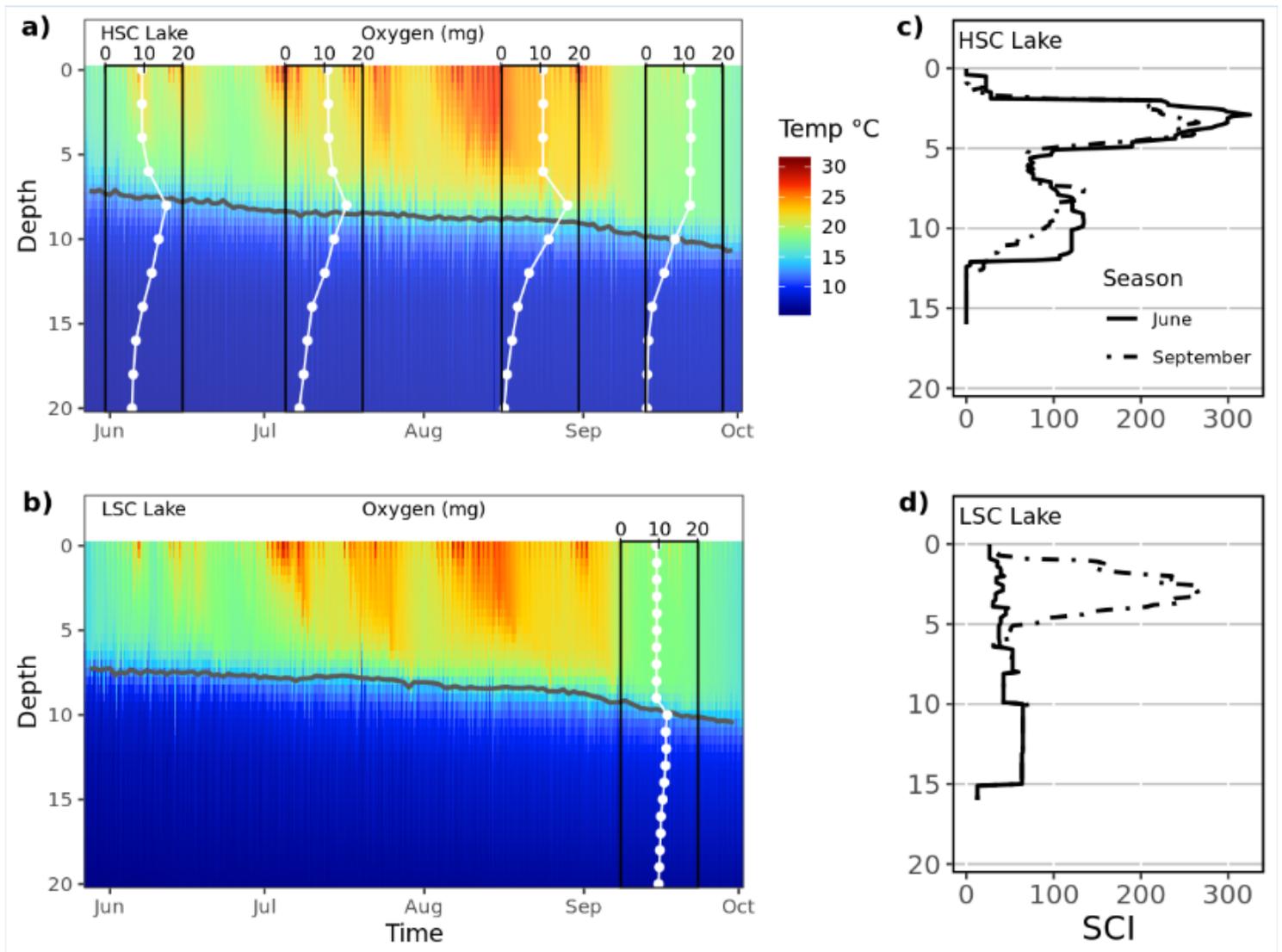


Figure 2

Temperature and oxygen stratification of water column at HSC a) and LSC lakes b) and the Structural Complexity Index (SCI) at HSC lake c) and LSC lake d).

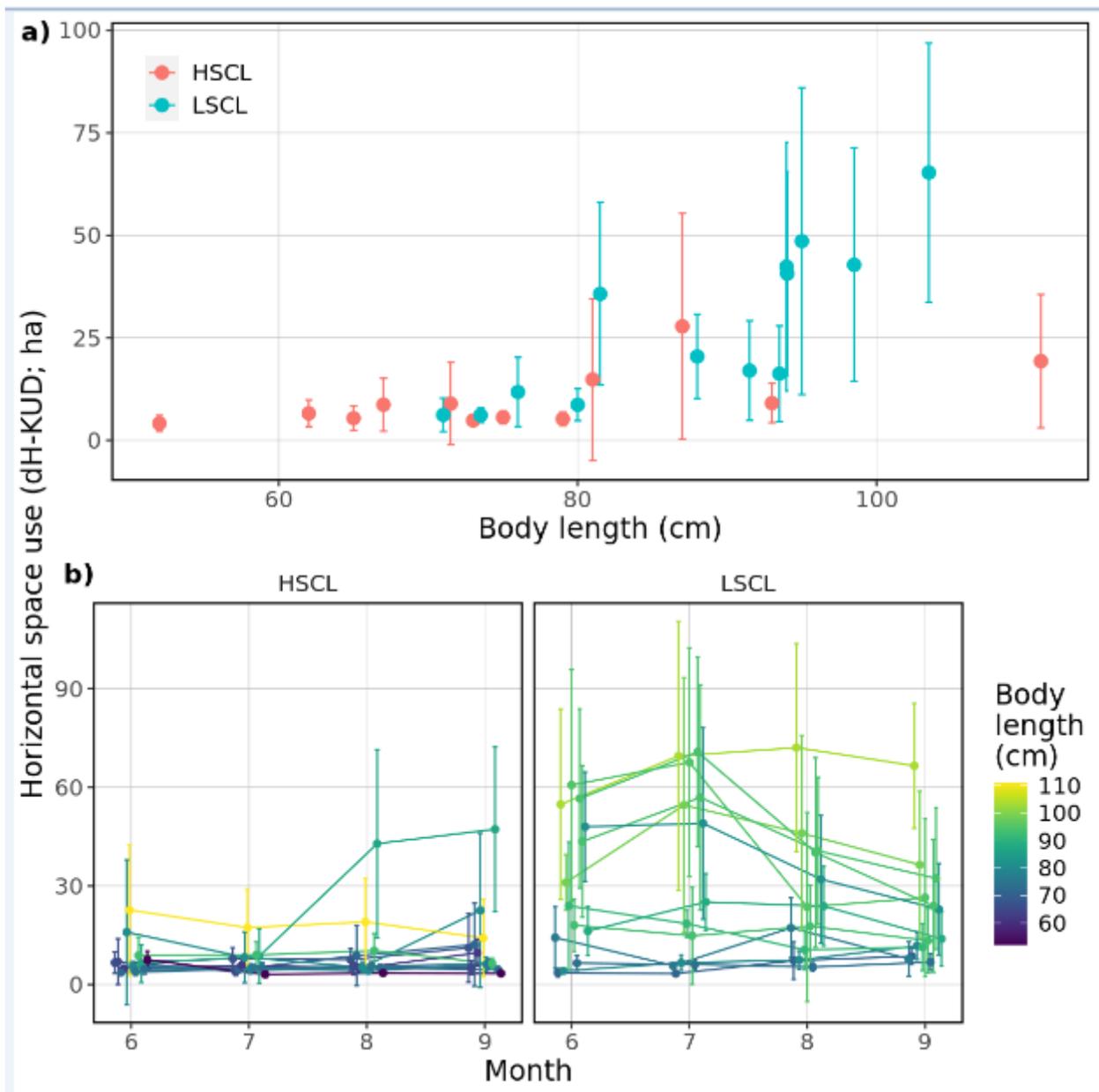


Figure 3

a) Dependence of daily extent of horizontal area (dH-KUD) and body length of observed pike, b) dH-KUD of each individual in each month. Dots represent mean values for the whole observed season/month, error bars denote standard deviation. Colours in b) were set according to body length of tracked individuals.

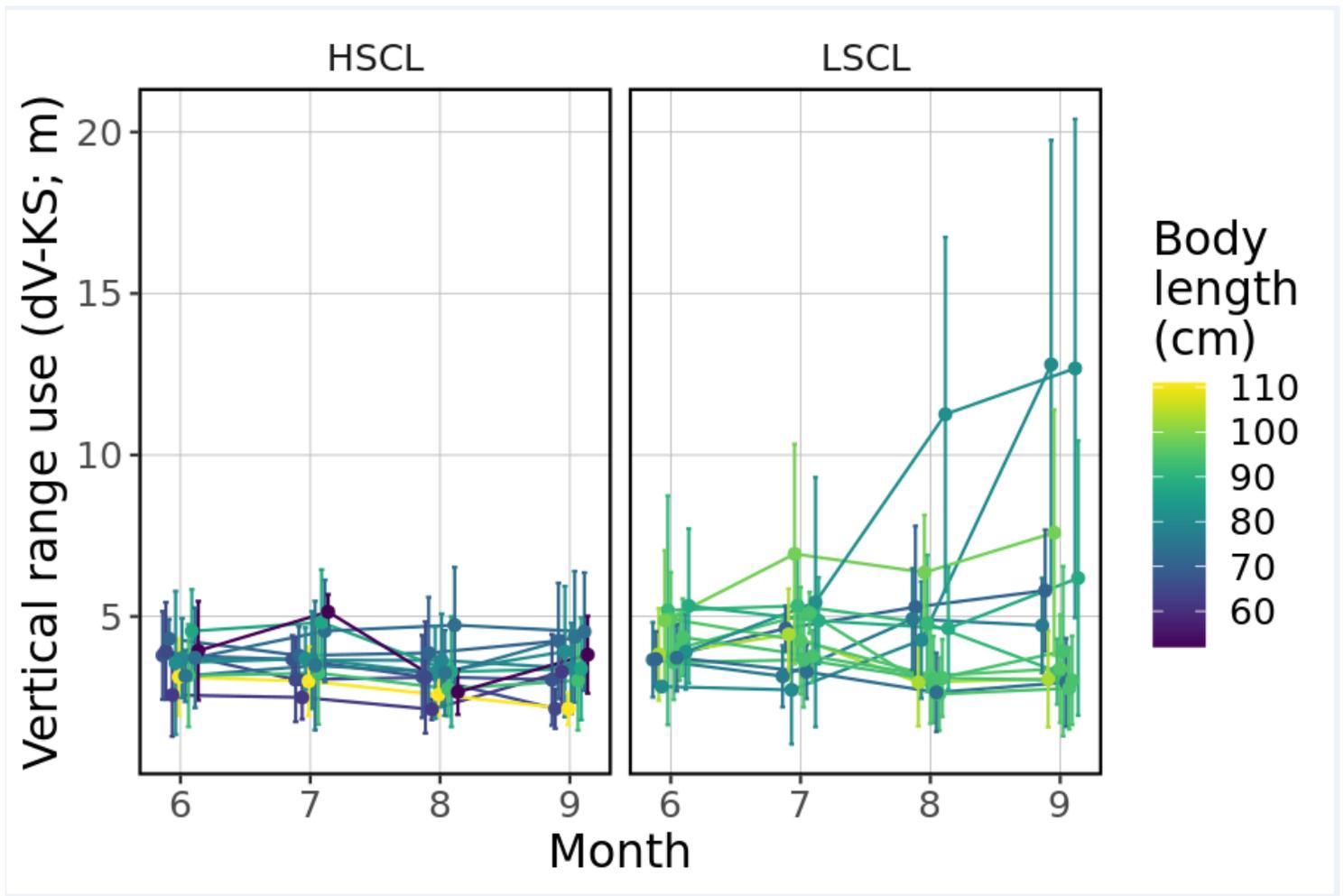


Figure 4

Daily extent of vertical space use for each individual in each month. Dots represent mean values for the whole observed month and error bars denote standard deviation. Colours are set according to body length of tracked individuals.

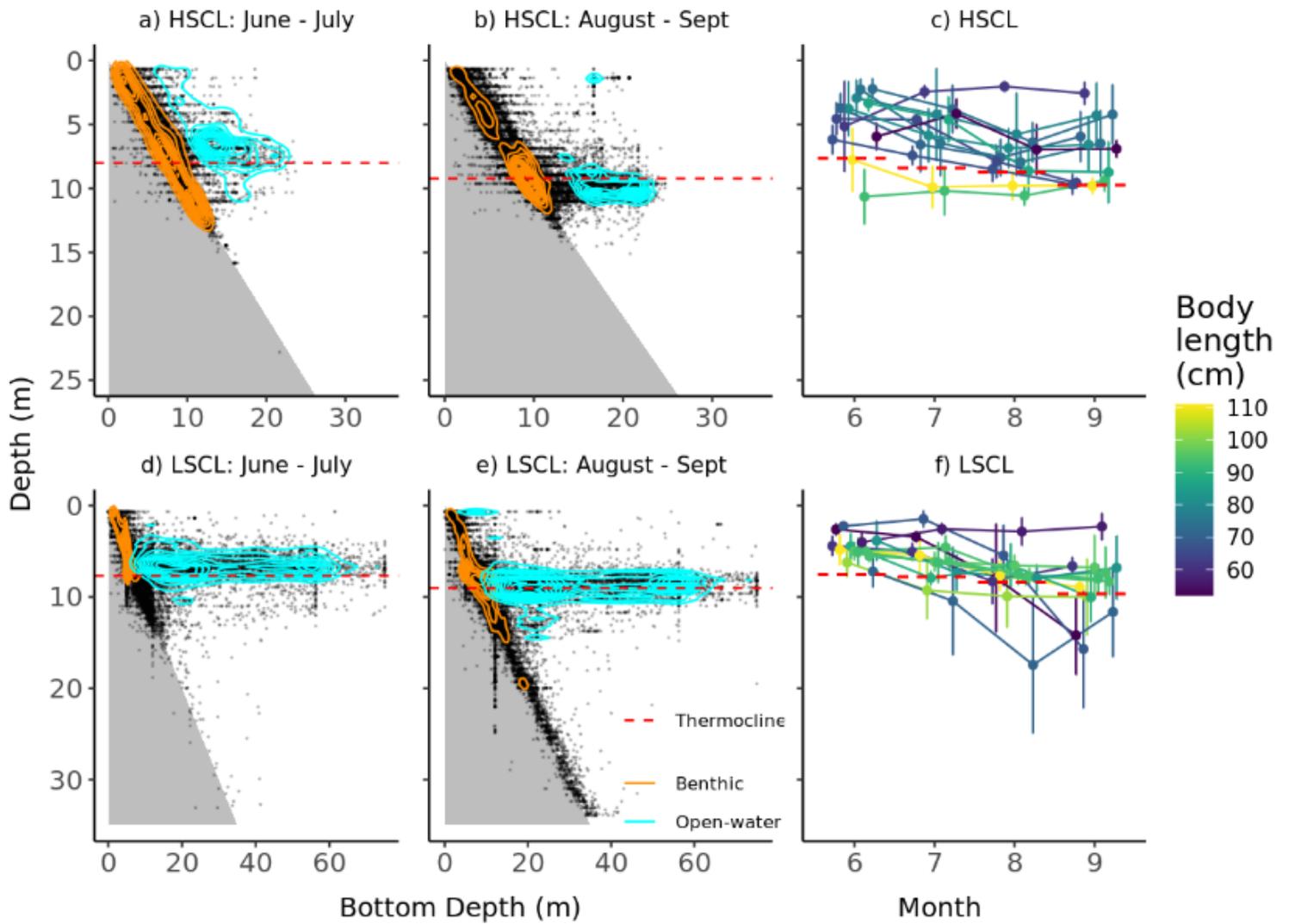


Figure 5

Two-dimensional distribution of all pike positions (dots) in relation to bottom depth for HSC lake (a-b) and LSC lake (d-e) and depth use for each individual in each month (c, f). Isoclines depict the highest concentration of positions in the benthic (orange) and open water (light blue) habitats. Mean thermocline depth within each period is indicated by a dashed line.

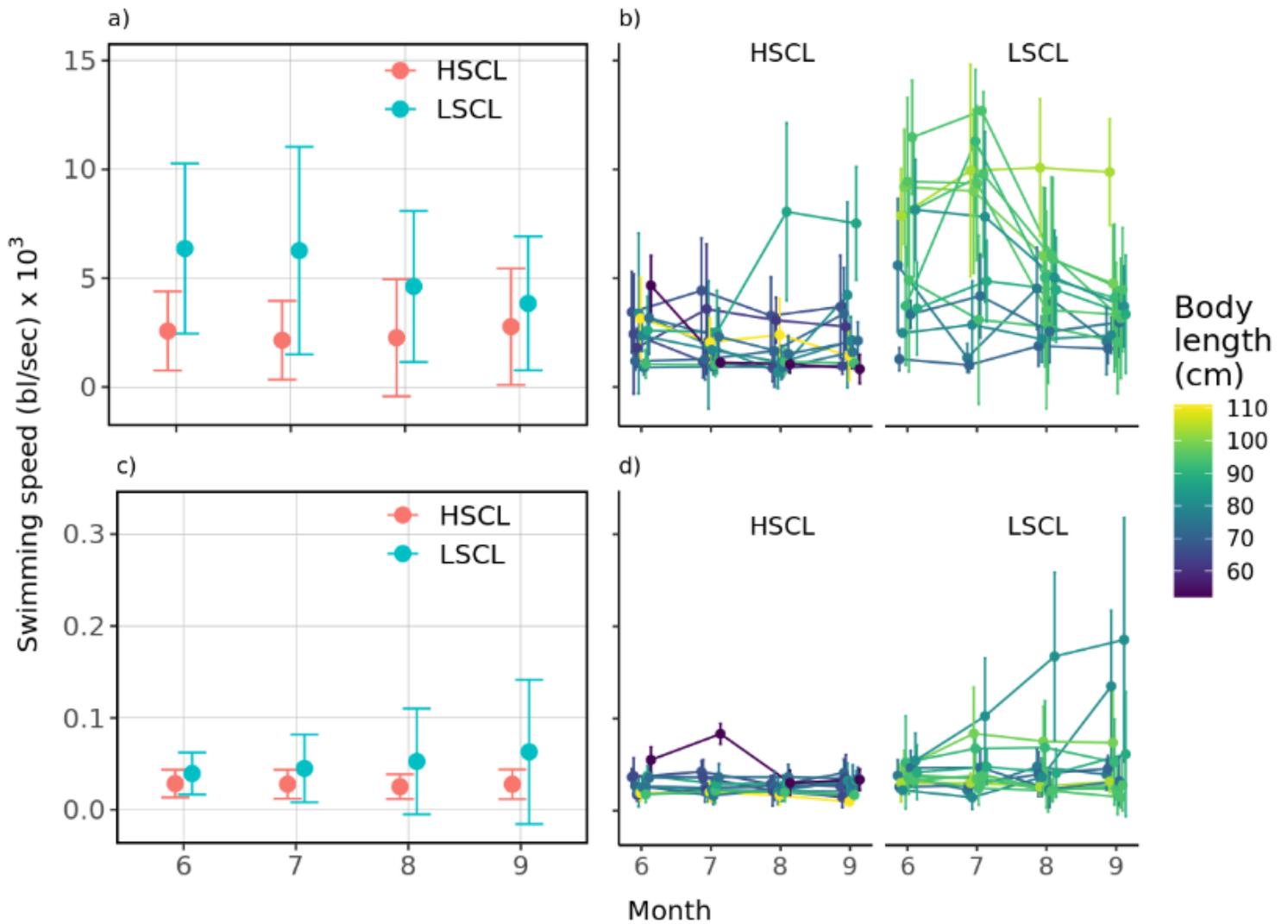


Figure 6

Development of mean horizontal and vertical activity during tracking period. Pooled (a) and individual (b) horizontal activity; pooled (c) and individual (d) vertical activity in each month of tracking. Dots represent mean values for the whole observed season/month and error bars indicate standard deviations. Colours in b) and d) were set according to body length of tracked individuals.

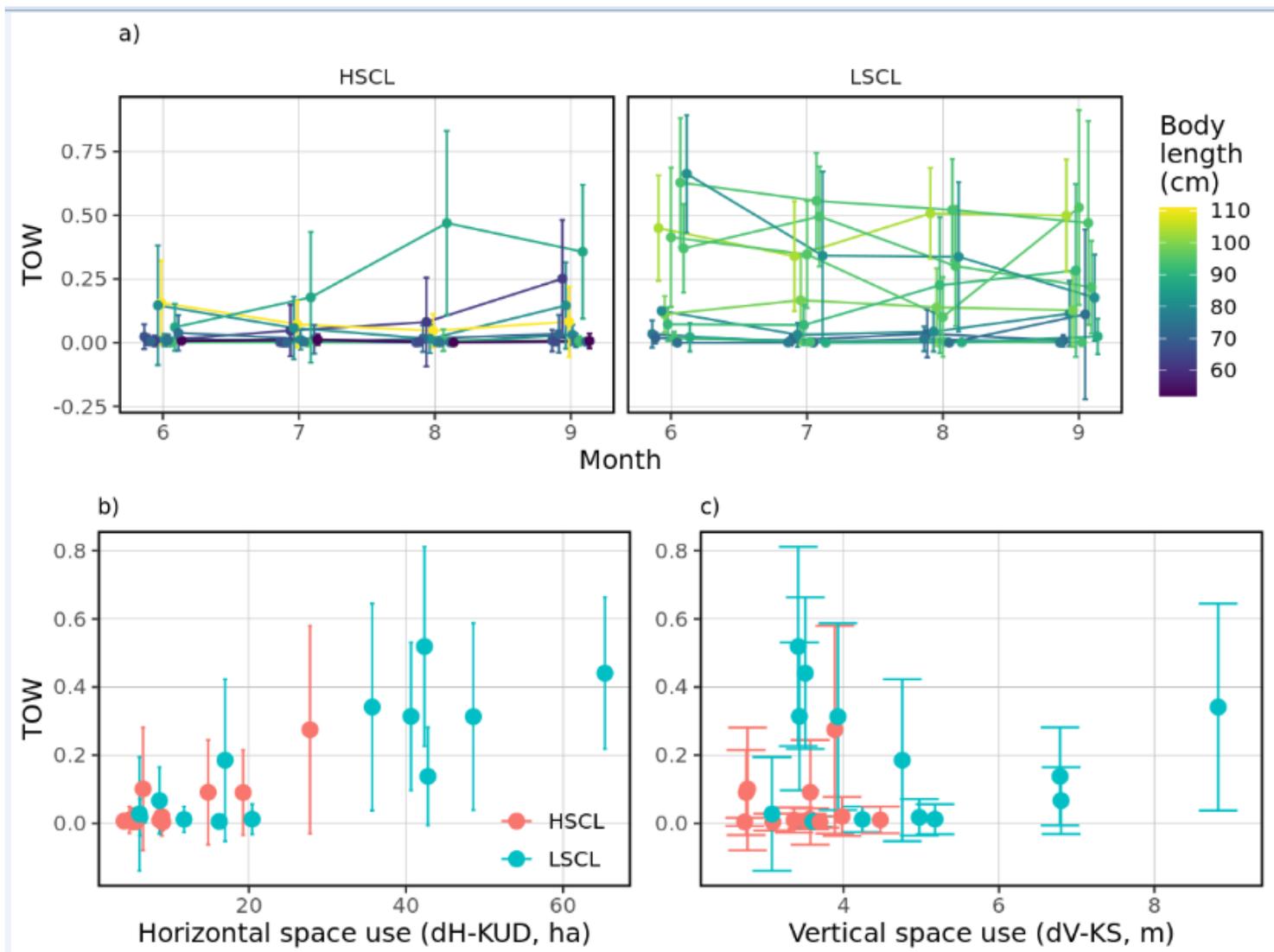


Figure 7

(a) Individual development of TOW during tracking period; relation between mean dH-KUD (b) or dV-KS (c) and mean TOW. Dots represent mean values for the whole observed season/month and error bars indicate standard deviations. Colours in a) were set according to body length of tracked individuals.

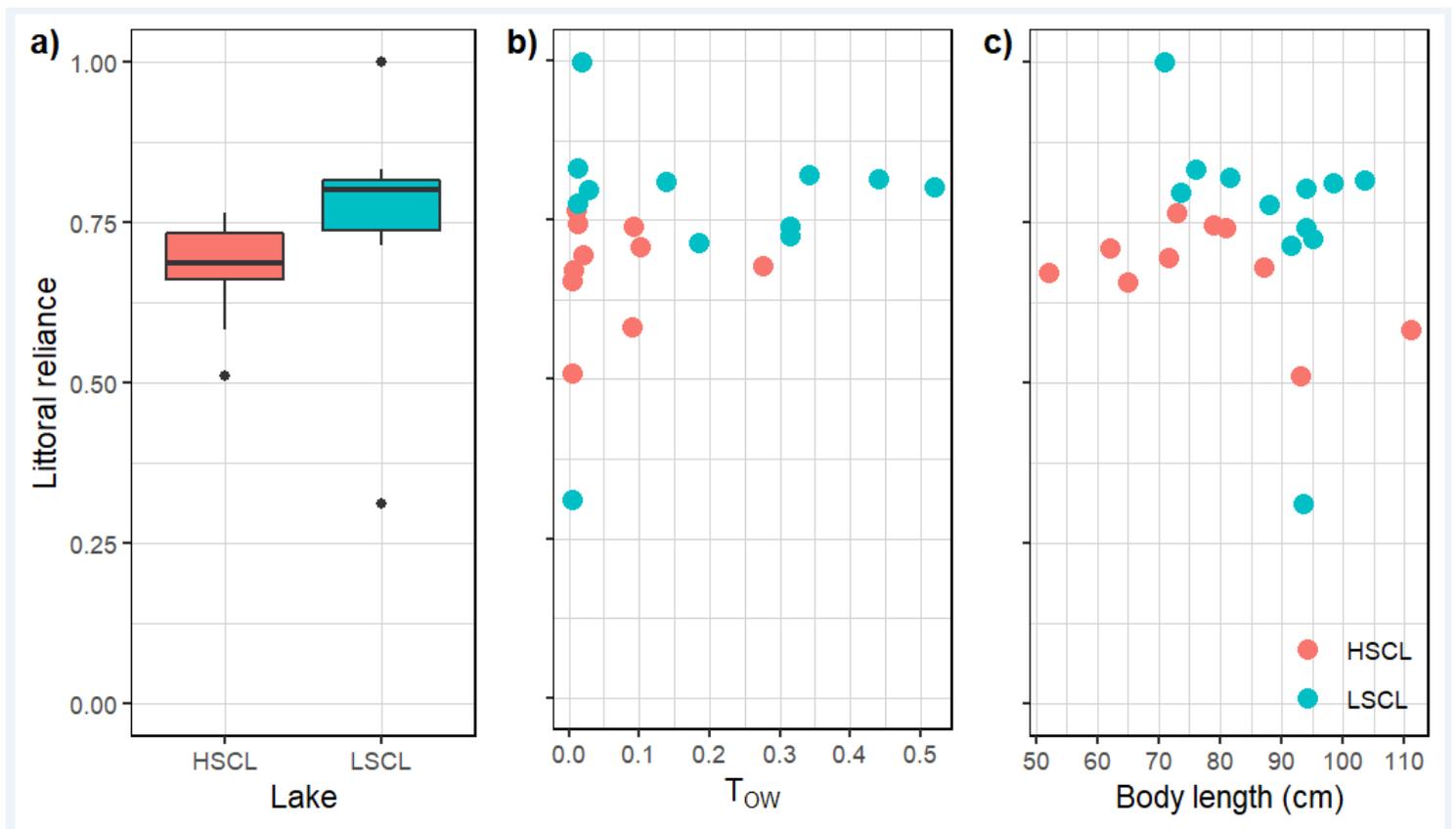


Figure 8

Pike littoral reliance [52] as a function of structural habitat complexity (Lake as a factor), open-water use (based on telemetry data) and total length in HSC and LSC lakes. The individual with the lowest littoral reliance estimate was excluded from the modelling due to its high influence on final results.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [Table1.docx](#)
- [Table2.docx](#)
- [Table3.docx](#)
- [Table4.docx](#)
- [Table5.docx](#)
- [Table6.docx](#)
- [PikehabitatSupMatSR.docx](#)