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Abstract

The diversity of predatory species plays a key role in ecosystem functioning but our understanding of the mechanisms underlying their coexistence is limited, particularly in freshwater ecosystems. Northern pike *Esox lucius*, European perch *Perca fluviatilis* and pikeperch *Sander lucioperca* are three widespread predatory species

in European lakes, where they often coexist. As potential competitors, we hypothesized that partitioning habitat is a determinant of species coexistence. This was tested by quantifying the variability of their habitat use in tracking adult individuals in the Bariousses reservoir (France, 86.6 ha, mean depth 7.1 m). Specifically, we investigated their distribution along the littoral - pelagic and depth axes along the daily cycle and across seasons. From littoral to pelagic waters were first found pike, then perch and finally pikeperch. Pike was the closest to the surface while pikeperch was the deepest. This general pattern was, however, variable across seasons with the three species located in the upper layer in summer during reservoir stratification. Individuals were more evenly distributed along the littoral-pelagic axis and closer to the bottom when water was mixing (autumn, winter). In summer, perch used more intensively the pelagic zone during daytime. Other species did not show any diel change of habitats. Our results highlighted that species coexistence is associated with habitat partitioning among these three predators, with perch showing a more variable behavior regarding habitat characteristics. Now more than ever, in the context of global change which modifies habitats, it is of crucial importance to understand coexistence mechanisms of species that shape ecosystems.

Keywords: *Esox lucius*; *Perca fluviatilis*; *Sander lucioperca*; littoral - pelagic habitat use; vertical habitat use; diel and seasonal habitat use

1 Introduction

Top predators play a key role in ecosystem functioning (Hairston et al., 1960; Fretwell, 1987) and more specifically their diversity is of the utmost importance (Sinclair et al., 2003). Understanding how these competing species can coexist (Sommer, 1999) is a crucial question in ecology (Schmitz, 2007). The differential use of resources among species (i.e. resource partitioning) is a key mechanism allowing species coexistence (Schoener, 1986; Chesson, 2000). In fish, niche segregation was shown to be primarily driven by partitioning of food resources and habitat (Ross, 1986). The coexistence of fish can also occur through more complex mechanisms such as spatial segregation with diet overlap linked to different feeding strategies or foraging sites (e.g. Sala & Ballesteros, 1997; Liedke et al., 2017; Pothoven, 2018; Raby et al., 2019). Competition can lead to shift of habitat use and diet (e.g. Brodersen et al., 2012). To date, however, our understanding of the coexistence of top predators in lakes is overall limited (but see Guzzo et al., 2016).

Northern pike (*Esox lucius*, hereafter pike), European perch (*Perca fluviatilis*, hereafter perch) and pikeperch (*Sander lucioperca*) are three common predatory species in European lakes (Kottelat & Freyhof, 2007) that are primarily piscivorous when adults, although variability in their diet has commonly been reported (Campbell, 1992; Craig, 2008). Pike is a diurnal predator that ambushes prey (Raat, 1988; Eklöv, 1997); perch can hunt in schools during daytime in pelagic zone (Eklöv, 1992; Craig, 2000) and pikeperch hunts in the twilight in open waters (Craig, 2000). These different feeding strategies could favor a trophic segregation, with competition affecting the trophic niche of perch (Schulze et al., 2012). In ectotherms, environment may influence resource partitioning to fulfill physiological requirements as optimal temperature and oxygen conditions vary among species, especially in the case of stratified lakes where vertical gradients of temperature and oxygen segregate the physical habitat, depending on the season. This affects the spatial distribution of fish (Magnuson et al., 1979) and habitat partitioning could then be more pronounced in stratified lakes (Guzzo et al., 2016). These three species have different physiological requirements for temperature and oxygen that could contribute to their coexistence (Helland et al., 2008; Verberk et al., 2012) along environmental gradients. The optimum temperatures increase from pike to perch and pikeperch, 10-24°C, 16-27°C and 27-30°C, respectively (Souchon & Tissot, 2012). Perch is able to cope with hypoxic conditions down to 1.1-2 mg/L (Jones, 1964) while pike avoids zones with less than 3-4 mg/L of dissolved oxygen (Casselman & Lewis, 1996) and pikeperch appears as the most demanding in oxygen (> 4mg/L at 5°C and > 7 mg/L at 20°C, Dolinin, 1974). Pike is mainly littoral and present in shallow waters (Chapman & Mackay, 1984a; Craig, 1996). In summer, piscivorous perch frequents the pelagic zone during daytime and moves to the littoral, laying on the bottom, during the night (Imbrock et al., 1996; Pekcan-Hekim et al., 2005), while it migrates to deeper waters in winter (Thorpe, 1977). Pikeperch prefers open waters and occupies deeper waters in winter compared to summer (Vehanen & Lahti, 2003). In a manipulative experiment, Schulze et al. (2006) showed that the introduction of pikeperch in a lake where pike and perch were residential led to a shift of perch habitat use towards the littoral over spring and summer. While these studies suggest that habitat segregation might occur among the three species when they coexist, quantification of their habitat use, including the vertical dimension and daily cycle, is lacking.

In the present study, we quantified the habitat use of coexisting pike, perch and pikeperch in a deep reservoir in France. Adults of each species were tracked over two years and their spatial distribution (littoral - pelagic and vertical) analyzed over the different stratification periods and over the daily cycle. We predicted that species coexistence was associated with habitat partitioning, pike mainly using the littoral zone, pikeperch

deeper waters and perch the pelagic zone. We expected these main patterns to vary across seasons, when the lake was stratified and the physical habitat became very constraining. We also expected some diel variation associated with the circadian rhythm of each species.

2 Materials and methods

2.1 Study site

The study was conducted in the Bariousses reservoir (45.33°N, 1.49°E) in the western central part of France (Figure 1). At the mean water level, which was hourly measured by Electricité de France (EDF), its area covered 86.6 ha, mean depth was 7.1 m and maximum depth was 19.4 m. Main annual features emerge in the water regulation scheme of this reservoir whose levels varied between 507.1 m and 513.5 m above sea level over the study period (March 2012 – March 2014). High water levels (> 511.9 m, quantile 66%) are from far the most frequent in spring whereas the low ones (< 511.3 m, quantile 33%) are the most frequent in autumn because, at the beginning of this season, the water level is lowered in order to collect rainwater. In winter, water levels are more evenly distributed over their whole range. In summer, the water level is kept stable around its mean value ([511.3; 511.9 m]) to sustain recreational activities concentrated between the shore and the island (Figure 1). The thermal regime of this reservoir was monomictic with four distinct temperature regimes. In spring (April to June), the water temperature rapidly increased and stratification occurred. In summer (July to September), water was warmer and a thermocline at about 4.5 m depth was observed. In autumn (October to December), water temperatures decreased rapidly when water mixing occurred and, in winter (January to March), water was mixed and homogeneously cold (Figure 2). The summer thermocline was associated with an oxycline that separated saturated surface waters from unsaturated deep waters; the hypolimnion had an oxygen saturation rate ranging from approximately 40% (4 mg/L) at its top to 15% (1.5 mg/L) at its basis. During the other seasons and over all depths, the dissolved oxygen concentration was 6 mg/L at the lowest. Representative oxygen profiles based on measurements made in 2011 are given in Online Resource 1. The Secchi transparency depth varied between 1.3 and 2.5 m. In 2010, measurements made for the European Water Framework Directive monitoring program (EC, 2000) gave concentrations of 0.73 mg/L and <0.01 mg/L for total nitrogen and total phosphorus in the euphotic zone, respectively. This corresponds to an oligotrophic reservoir. The fish assemblage of the reservoir was determined with a standardized procedure using a multi-mesh gillnet fishing protocol in 2010 (CEN, 2005) and included 11 species. It was dominated by Cyprinidae and Percidae, as commonly observed in lowland reservoirs (Irz et al., 2002). In terms of catch per unit effort (cpue, number per net in 12 hours), the dominant species were roach (*Rutilus rutilus*, cpue 0.37, biomass per unit effort -bpue in g per net in 12 hours, 15.3), ruffe (*Gymnocephalus cernua*, cpue 0.14, bpue 2.1), perch (cpue 0.06, bpue 3.6), pikeperch (cpue 0.02, bpue 4.0) and common bream (*Abramis brama*, cpue 0.01, bpue 3.7). In terms of bpue, the dominant species were roach, carp (*Cyprinus carpio*, bpue 10.7, cpue <0.01), tench (*Tinca tinca*, bpue 8.3, cpue <0.01), chub (*Squalius cephalus*, bpue 4.8, cpue <0.01), pikeperch and common bream.

2.2 Fish tagging

The surgical procedure is detailed in Westrelin et al. (2018) as advocated by Thiem et al. (2011). Specifically, a total of 17 pike, 29 perch and 25 pikeperch, all adults, were caught by fishing in the whole reservoir or with nets set up at dawn, during daytime and at dusk for a maximum of 2 hours over four sampling campaigns (winter, summer and autumn 2012 and spring 2013). Fyke nets were used in shallow areas (< 3 m depth), whereas in deeper areas, pelagic gillnets fishing from 2 m above the bottom and benthic gillnets fishing up to 2m above the bottom were set. Twelve pikeperch originating from a fish farm completed this sample. Fish mean total length was 498 mm, 395 mm and 485 mm, and mean weight 788 g, 958 g and 1059 g for pike, perch and pikeperch, respectively. Vemco V9P-2L (47 mm long, 6.3 g in the air, 90 s mean burst interval, mean battery life 385 days, pressure sensor that gave the fish depth) and V8-4L (20.5 mm long, 2 g in the air, 90 s mean burst interval, mean battery life 163 days, no pressure sensor) acoustic transmitters were used. Twelve pike, 22 perch and the 37 pikeperch had a tag with a pressure sensor. The transmitter weight in the air did not exceed 2% of the fish body weight in accordance with literature recommendations (Winter, 1996; Snobl et al., 2015). Great attention was paid to fish welfare during fish handling and surgery, and all protocols were accepted by the veterinary authority.

2.3 Fish tracking

An array of 40 underwater VR2W 69kHz omnidirectional acoustic receivers (Vemco) with their associated synchronization tag (V13-1L) plus eight reference tags were anchored at the bottom (between 0.65 and 1.5 m above the bottom), and throughout the reservoir between January 2012 and March 2014 (Figure 1, for details see Roy et al., 2014; Westrelin et al., 2018). The synchronization tags, deployed at known locations, allowed for the correction of the receiver internal clock drift and thus indicated the exact time of each detection (Smith, 2013). The reference tags, also deployed at known locations but different from those of the receivers, were spread all over the reservoir to detect potential anomalies in the network. Vemco Positioning System was used to calculate 2D fish positions that were filtered according to Roy et al. (2014) recommendations; the mean position error was 3.3 m throughout the reservoir. Fish depth was assessed using pressure sensors (accuracy of 0.5 m and resolution of 0.075m in our environmental conditions). Only the positions recorded after a minimum of 2 days after release were included in the analyses to limit potential effects of surgery (Bridger & Booth, 2003; Vehanen & Lahti, 2003). At the end of the study, 16 stationary individuals (3 pike, 3 perch, 8 pikeperch) were considered to be dead or to have lost their tag rapidly after release and 18 individuals (5 pike, 4 perch, 3 pikeperch) were rarely located (less than 5 days in a season). These 34 individuals were removed from the analyses. Hence, 9 pike, 22 perch and 26 pikeperch (8 from farm), corresponding to 5-8 pike, 12-20 perch, 14-23 pikeperch individuals depending on the season, were subsequently used in the analyses (Table 1). The time series of their positions used in this study are represented on Online Resources 2, 3 and 4 for pike, perch and pikeperch, respectively.

2.4 Data analysis

2.4.1 Timescales

Analyses were conducted according to season and daily cycle. The four seasons (Table 1) corresponded to the thermal regimes (Figure 2). As water temperature regimes were very similar over the 2-year study period (Figure 2, Online Resource 5), data from the same seasons were pooled as in Westrelin et al. (2018). The daily cycle was defined at an hourly resolution. Dawn was defined as the period including the hour preceding the sunrise hour,

the sunrise hour itself and the following hour. Dusk was defined as the period including the hour preceding the sunset hour, the sunset hour itself and the following hour. These two periods of the day lasted three hours each. Daytime was the period following dawn and preceding dusk; night was the period following dusk and preceding dawn.

2.4.2 Water depth

The lake was discretized in a 10 m × 10 m grid. In each grid cell, the mean water depth, deduced from bathymetry and hourly water level, was computed (5 classes: [0; 2.5[- littoral zone, [2.5; 5[- sublittoral zone, [5; 7.5[, [7.5; 10[and [10; 22[m). The deepest class had a broader range to avoid very small numbers of positions. Each fish position was associated to a grid cell. For each individual, the use of a water depth was calculated as the proportion of positions observed in the corresponding class (see Westrelin et al., 2018 for methodological details). It was then averaged across individuals and by species. The selection is the process by which an animal chooses a habitat (Johnson, 1980), in our case the water depth, and the species mean selection ratios quantify it by estimating the use of a water depth regarding its availability (Manly et al., 2002). They were calculated for each combination of season and day periods, and also for each season. The mean selection ratio pools observations from all fish of the same species in the sample, but the confidence interval accounts for the variation in water depth selection across individuals (Manly et al., 2002). When a selection ratio and confidence interval are higher or lower than 1.0 for a water depth, respectively, the preference or avoidance for this water depth is significant (Manly et al., 2002; Rogers & White, 2007).

2.4.3 Fish depth and bottom ratio

The fish depth in the water column was used to calculate the bottom ratio, defined as the ratio of the distance of the fish to the bottom over the water depth, varying between 0 (close to the bottom) and 1 (close to the surface). Mean individual bottom ratios were calculated over seasons and periods of the day. These individual ratios were averaged by species and their standard deviations were calculated. The effects of species, season, period of the day and water depth on individual bottom ratios were tested using beta regressions (Ferrari & Cribari-Neto, 2004). Fish identity was considered as a random effect to explicitly account for individual variability and repeated measurements on the same individual. The full model could be written as follows:

$$\text{logit}(\overline{\text{BR}}_{\text{ind}}) = \alpha + \text{SPECIES} * \text{WATER DEPTH} * \text{SEASON} * \text{DAY PERIOD} + s(\text{ind}) + \varepsilon$$

where $\overline{\text{BR}}_{\text{ind}}$ is the expected mean individual bottom ratio in]0,1[, α is the overall intercept, day period is the period of the day, $s(\text{ind})$ is a smoothing function modelling the individual effects (Wood, 2008) having the advantage of getting a significance test of these effects and an evaluation of the explained variance of the model, and ε is the error term following a normal distribution with zero mean. The most parsimonious simple model was selected by running a forward stepwise-based procedure (Venables & Ripley, 2002). Following the recommendations of Richards (2008), all models having an AIC value within a range of 6 from the lowest AIC value were initially selected and, among them, the more complex models that did not have an AIC value lower than all the simpler models within which they were nested were removed. The model fitting was assessed with regards to the homogeneity and normality of the residuals (Zuur et al., 2009) and to the percentage of explained variance (Hastie & Tibshirani, 1990). Significant interactions involving species were further analyzed by Tukey

comparisons of pairwise estimated marginal means of the different factor levels of predictors (Lenth, 2016). The thermocline depth was calculated from vertical temperature profiles with R 3.0.1 (R Core Team, 2013) and rLakeAnalyzer package (Winslow et al., 2018). Selection ratios were generated by using adehabitatHS package (Calenge, 2006). The selection is the process by which an animal chooses a habitat (Johnson, 1980) and selection ratios quantify it by estimating the use of a habitat regarding its availability (Manly et al., 2002). Beta regressions were performed in the mgcv package (Wood, 2006) and pairwise comparisons of estimated marginal means in the emmeans package (Lenth, 2016).

Importantly, as there were no significant differences in habitat use (selection and bottom ratios) between farmed and wild pikeperch (Online Resources 6 - 9), individuals from both origins were pooled in the analyses.

3 Results

No significant diel pattern was observed in the selection ratio of water depth between species, seasons, and day periods (Online Resource 10), except in one case. Specifically, perch in summer preferred the littoral and sublittoral zones during dawn, dusk and night but shifted to the sublittoral and [5;7.5[m water depths during daytime (Figure 3). The bottom ratio was significantly impacted by the combination of species, season and water depth but the period of the day was not involved in any significant interaction with species (Table 2). This means that the season and water depth impacted the vertical distribution of species whereas the period of the day did not (Online Resource 11). In the following, only seasonal scale is considered.

Regarding littoral - pelagic seasonal partitioning, during all seasons, pike was the species that used the littoral zone the most. This corresponded to 65.5 % of the time in spring and 58.4 % in summer when this zone was preferred (Figures 4a and 4b). In autumn and in winter, it lowered to 31.2 % and 32.1 %, respectively (Figures 4c and 4d). The sublittoral zone was the second most used zone by pike all year long (range 17.9 % - 31.2 %), preferred in summer and autumn (Figures 4b and 4c). Its intense use of the littoral zone in spring and summer was associated with an avoidance of zones deeper than 5 m. These deeper zones became more frequented by this species in autumn and winter. Perch was the species that used the sublittoral zone the most, range 40.0 % - 42.4 % over all seasons, and also preferred it except in winter (Figures 4a to 4d). In spring and summer, perch also preferred the littoral zone which was its second most used zone (Figures 4a and 4b). In summer, perch also used the [5; 7.5[m zone (20.9 %), zone that progressively became its second most used in autumn (Figure 4c), and evenly frequented the [7.5; 10[m zone in winter (Figures 4d). Pikeperch did not show any strong consistent pattern across the seasons. In spring, it preferred the [5; 7.5[m zone which was its most used (41.8 %) and also used [2.5; 5[and [7.5; 10[m zones (20.1 % and 17.2 %, respectively) (Figure 4a). In summer, its littoral use raised up to 29.1 % while it used all other zones relatively homogeneously without any preference (Figure 4b). In autumn, it left the littoral (Figure 4c) and, in winter, used the deepest parts (40.5 %) followed by the [7.5; 10[(29.9 %) and [5; 7.5[m (16.8 %) ones (Figure 4d).

Regarding vertical seasonal partitioning, in spring, perch and pikeperch were very close to the bottom down to 10 m depths (Figure 5a). On the other hand, pike was very close to the bottom in the littoral zone but in the third

quarter above perch and pikeperch in the sublittoral zone (Figure 5a). When it visited zones deeper than 5 m, pike was much above the thermocline albeit with a very high variability (Figures 5a and 6a), again less deep than perch and pikeperch. Generally all species were closer to the surface in summer compared to spring; the between-individual variability appeared quite high though (Figures 5b and 6b). Pike was found around the third deepest quarter of the water column when in its preferred littoral and sublittoral zones, above perch and pikeperch (Figure 5b). In autumn, while migrating towards deeper waters, species were getting much closer to the bottom (Figures 5c and 6c), this being pronounced in the deepest zone in winter (Figures 5d and 6d). Statistical background of these analyses is provided in Online Resource 12.

Littoral - pelagic and vertical seasonal partitionings of species are synthesized in Figure 6. The general pattern of the species distribution along the littoral - pelagic axis was the following: pike, perch and pikeperch. Pike was closer to the surface than both other species. Pikeperch was often found deeper than the other two species. This general pattern was modulated by the season, species becoming more evenly distributed from littoral to pelagic, but closer to the bottom when the lake water was mixed in autumn and winter. All species appeared more concentrated in the 0-7.5 m zone in spring and summer, and closer to the surface in summer, following the thermocline and avoiding the deoxygenated hypolimnion.

4 Discussion

The present study demonstrated that habitat partitioning occurred along both the littoral - pelagic axis and the depth axis when the three species coexisted. The main driver was seasonal and contrary to our expectation, no diel vertical migration was observed. The only significant diel pattern was the more intensive use of the pelagic zone by perch during daytime in summer.

4.1 Seasonal movement patterns

As expected, fish movement patterns were influenced by the season, in all likelihood, to avoid unfavorable physical conditions and to satisfy different physiological and biological requirements. We could observe that more than half of the fish, including some of the smallest ones, were mature. By considering the size of the remaining ones, we could reasonably suppose most of them as also being mature. Spring corresponds to the reproduction period of pike, perch and pikeperch (Kottelat & Freyhof, 2007), when perch and pikeperch also move closer to the littoral to find spawning habitats (Craig, 2000). In summer, the deoxygenated and colder deep hypolimnetic waters could explain the concentration of the three species closer to the surface to reach satisfying oxygenation conditions and/or to remain the closest to their optimum temperature range (Kubečka & Wittingerova, 1998; Čech & Kubečka, 2002; Nordahl et al., 2020), following the rising of the thermocline which was very closely linked to the reservoir's hydrological management.

4.1.1 Pike

Pike was mainly in the littoral zone with rare incursions into the pelagic zone. Its littoral position and migrations between the littoral and central parts of the lake confirmed results of some previous studies (Chapman & Mackay, 1984a; Chapman & Mackay, 1984b; Cook & Bergersen, 1988). The deepest movements of pike were observed in autumn and winter, when temperature was lower and when dissolved oxygen concentration in the

deeper zones was not limiting. Pierce et al. (2013) also observed that depth selection by pike was constrained by low dissolved oxygen concentration in some seasons. In the present study, the limited number of pike should make us cautious about findings even if these individuals were tracked over long periods.

4.1.2 Pikeperch

Pikeperch used different parts of the reservoir according to the season and spent a lot of time in shallow areas in summer, which is similar to what was found in Jepsen et al. (1999), Vehanen & Lahti (2003) and Huuskonen et al. (2019). With the exception of summer when the lake was well stratified and the deepest areas less favorable in terms of oxygen, pikeperch was generally located in the deepest decile of the water column, probably seeking darkness (Craig, 1987) or prey (Huuskonen et al., 2019). This was in complete agreement with what Gorman et al. (2019) found on the walleye (*Sander vitreus*), a Northern American fish close relative of the European pikeperch (Craig, 2000).

4.1.3 Perch

Perch frequented deep waters in winter and moved inshore in spring. This was likely associated with spawning, as observed elsewhere (Eckmann & Imbrock, 1996). Perch remained in the littoral or epilimnetic waters until the autumn and then returned to deep waters for overwintering. Our results confirmed previous results showing that this species was more homogeneously distributed in winter than in summer (Eckmann & Imbrock, 1996; Imbrock et al., 1996).

The seasonal variations of habitat partitioning seemed to be mainly linked to the life history traits of species. Even if water level was shown not to influence the habitat use of perch in this reservoir, the highest diversity of littoral habitats in spring and intermediate in summer, due to the water regulation scheme (Westrelin et al., 2018), could make this littoral zone even more attractive for these predatory species in these seasons. On the other hand, the lower structural complexity of littoral habitat in autumn and to a lesser extent in winter could contribute to its lower use.

4.2 Diel movement patterns

Whereas seasonal patterns of habitat use seem to be essentially associated with avoiding unfavorable physical conditions (Lucas & Baras, 2001) and with finding favorable spawning sites (Eckmann & Imbrock, 1996) or prey (Huuskonen et al., 2019), diel movements are generally interpreted as a trade-off between foraging and predator avoidance behavior (Lucas & Baras, 2001). In general, small prey fishes in lakes escape predators by finding refuge in littoral shelters during daytime and moving offshore at night (Kubečka, 1993; Riha et al., 2015), which also seemed to be the case in the Bariousses reservoir (Goulon et al., 2018). We could have expected that these prey migrations would drive movements of piscivorous pike and perch. They are visual predators (Jepsen et al., 2001; Zamora & Moreno-Amich, 2002) and could then be particularly attracted by the littoral zone during daytime and less at night. Pikeperch, active in twilight (Jepsen et al., 1999; Poulet et al., 2005), could have performed diel vertical migrations from the bottom to forage pelagic prey during dawn and dusk as it has been reported to forage in the pelagic zone (Craig, 1987; Huuskonen et al., 2019).

4.2.1 Pike

Although pike shows a diel activity pattern, being active during daytime and at rest during the night (Craig, 1996; Baktoft et al., 2012), no corresponding diel pattern emerged in habitat use in our study, as pike was in the

littoral zone all day long. Cook & Bergersen (1988) described pike that were positioned deeper, and in deeper waters at night, whereas Riha et al. (2015) found higher littoral densities at night.

4.2.2 Pikeperch

No diel vertical migration was observed for pikeperch in our study. Horký et al. (2008) found a predominant nocturnal or crepuscular activity of pikeperch which they linked to foraging and which was associated with diel migrations: resting in shallow areas at night and in deeper zones during the daytime. Jepsen et al. (1999) did not find clear diel activity rhythm, with the exception of certain periods in the late summer, when activity was predominantly nocturnal. Gorman et al. (2019) found weak evidence of diel vertical migration for walleye.

4.2.3 Perch

Perch movement from littoral to pelagic waters during daytime in summer was the only diel pattern highlighted by our study, which was the opposite way to the diel migration of prey. This diel pattern has already been described but seemed dependent on the trophic status of the lake (Imbrock et al., 1996; Jarvalt et al., 2005; Jacobsen et al., 2015; Nakayama et al., 2018). Imbrock et al. (1996) reported that, in summer and at night, perch rested on the littoral bottom. In our case, perch was close to the bottom all day long, in its preferred zones, except in summer when it was constrained by the physical habitat partitioning to stay close to the thermocline.

4.3 Farmed versus wild pikeperch

Interestingly farmed and wild pikeperch used the littoral-pelagic and vertical habitats similarly. The stress of establishing themselves in a novel environment could however lead to behavioral changes. Farmed fish are capable of adopting dispersion behavior similar to wild individuals (e.g. Solem et al., 2013; Zimmermann et al., 2013) but they need to explore more their new environment (e.g. Uglem et al., 2008; Dempster et al., 2010). This could lead to a habitat use different from wild conspecifics. Eel-tailed catfish *Tandanus tandanus* translocated from a reservoir to a river selected habitats that were more common in their original environment and different from the riverine individuals (Carpenter-Bundhoo et al., 2020). In a translocation experiment of wild large-bodied pike and European catfish *Silurus glanis*, translocated individuals showed persistent larger activity space-sizes than residents but no difference in activity (Monk et al., 2020). In our case, farmed fish exploited the most favorable habitats as wild residents did which could mean that the carrying capacity of the reservoir was not reached. This could prevent stocked fish from being displaced from favorable habitats through prior-residence effects (Deverill et al., 1999). Moreover, our farmed pikeperch came from an extensive pond farm which had possibly got them used to conditions close to wild ones and could have helped them to well establish in the reservoir.

4.4 Habitat partitioning

The main movements of potential preys did not seem to strongly drive the habitat use of the adults of the studied piscivorous species. Our results suggest that other factors played a role, such as temperature (Nakayama et al. 2018), competition and/or intraguild predation. All tagged fishes had not reached a refuge size and the smallest could be preyed upon by the biggest piscivorous individuals present in the reservoir. It has been shown that cannibalism and intraguild predation were enhanced in low productive systems in which other prey fishes are

lacking (Mehner et al., 1996). Typically, the smallest perch could avoid the littoral zone during daytime to escape large pike.

Although the three species have marked circadian rhythms of activity, very little evidence of diel variations of habitat partitioning existed. Pike and pikeperch stayed in their preferred habitats, littoral and deep waters, respectively. Only perch performed diel movements between the littoral and pelagic zones. The plastic nature of perch regarding the environment (Craig, 2000) probably played a role in the habitat partitioning between the three species. In a manipulative experiment that consisted of introducing pikeperch in a lake already inhabited by perch and pike, perch shifted its habitat use towards the littoral while pike was hardly affected (Schulze et al., 2006). In this case, large perch were exclusively pelagic during daytime before pikeperch introduction, and became half pelagic half littoral after (Hölker et al., 2007). Perch would then modify its habitat niche to minimize interaction with pike and pikeperch. The plasticity in habitat use of perch is associated with a generalist diet (Craig, 1978; Craig, 2000) that enables the species to coexist with more specialist species like pike and pikeperch (Schulze et al., 2012), mainly piscivorous (Kangur & Kangur, 1998). This resource partitioning was probably enhanced by the oligotrophic nature of the Bariousses reservoir (Kobler et al., 2009; Guzzo et al., 2016) which did not offer abundant preys, forcing species to specialize in order to reduce interspecific competition (Araújo et al., 2011). Large variations of selection ratios and bottom ratios in some cases stressed that a high within-species individual variability could also be important and could correspond to the coexistence of different behavioral types using separated habitats, as already observed with pike (Kobler et al., 2009) and perch (Marklund et al., 2019). This could aim at reducing the intraspecific competition (Kobler et al., 2009).

4.5 Conclusions

More knowledge is needed to fully understand how predatory species coexist. Leading a similar study with different assemblages of predators (e.g. any combination from one species alone to all three together, as in our case), along with a trophic component, would allow us to validate our hypotheses regarding the underlying mechanisms of habitat partitioning. In conclusion, this study revealed the existence of seasonal habitat partitioning among these three predatory species both in the littoral - pelagic and vertical dimensions. Our results highlighted that habitat partitioning is associated with the coexistence of predatory fish species in a reservoir. This mechanism, supported by the plasticity of perch in its habitat use, could explain how pike, perch and pikeperch coexist in numerous European lakes. In the context of global change that modifies habitats and their availability, understanding coexistence mechanisms of predatory species that shape ecosystems is more than ever of crucial importance.

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Authors' contribution

SW: Participated to field surveys, performed data analyses, designed and wrote the paper. JC: Contributed to design the paper, made several careful readings and substantial improvements. RR: Designed the field surveys, collected the data, made exploratory analyses, carefully read and commented the paper. LT: Contributed to design the field surveys, participated to data collection, carefully read and corrected the paper. FS: Contributed to design the paper, made several careful readings and substantial improvements. CA: Contributed to design the field surveys, participated to data collection, carefully read and corrected the paper.

Data Availability Statement

Data used in this manuscript are the sole property of INRAE and EDF. They can be made available from the corresponding author upon reasonable request.

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Tables

Table 1 Number of individuals (n) tracked by season for each species with the total number of positions (Npos). The total length (TL, mm, mean and range) and weight (W, g, mean and range) are given at the time of tagging.

		Spring	Summer	Autumn	Winter
Pike	n	5	8	5	5
	Npos	22,244	32,996	44,729	54,359
	TL	553 425-629	535 425-629	515 425-596	553 425-629
	W	1072 398-1513	978 398-1513	861 398-1221	1072 398-1513
Perch	n	13	20	16	12
	Npos	170,032	214,035	194,037	263,292
	TL	412 320-486	404 320-486	415 320-486	409 320-486
	W	1033 383-1800	964 383-1800	1071 383-1800	990 383-1800
Pikeperch	n	14	23	17	18
	Npos	70,650	185,519	282,974	269,500
	TL	464 360-596	507 360-695	502 360-695	477 360-695
	W	931 354-1914	1223 354-3000	1221 354-3000	1038 354-3000

Table 2 Numeric results from the Beta regression that tested the fixed effects of season, water depth, species, period of the day and their interactions, on individual bottom ratios. Fish identity was used as a random effect.

ALL SPECIES	Bottom ratio		
	d.f.	Chi-sq	p-value
Season	3	87.953	< 0.001
Water depth	4	84.081	< 0.001
Species	2	4.794	0.091
Day period	3	6.732	0.081
Season: Water depth	12	42.866	< 0.001
Season: Species	6	32.393	< 0.001
Water depth: Species	8	52.708	< 0.001
Water depth: Day period	12	48.498	< 0.001
Season: Water depth: Species	24	133.768	< 0.001
Individual	51	1220	< 0.001
	Fixed effects	Fixed and random effects	
Explained variance (%)	42.7	57.7	

Figures

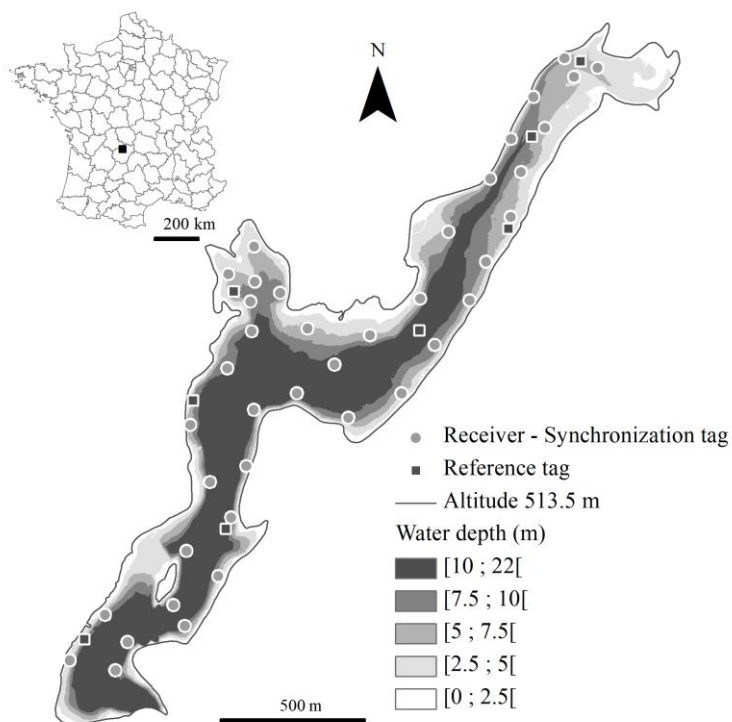


Fig. 1 Location of the study site (black square over France map with department boundaries) and bathymetric map of the Barriousses reservoir at the high water level with the location of the receivers and synchronizing tags (adapted from Westrelin et al., 2018).

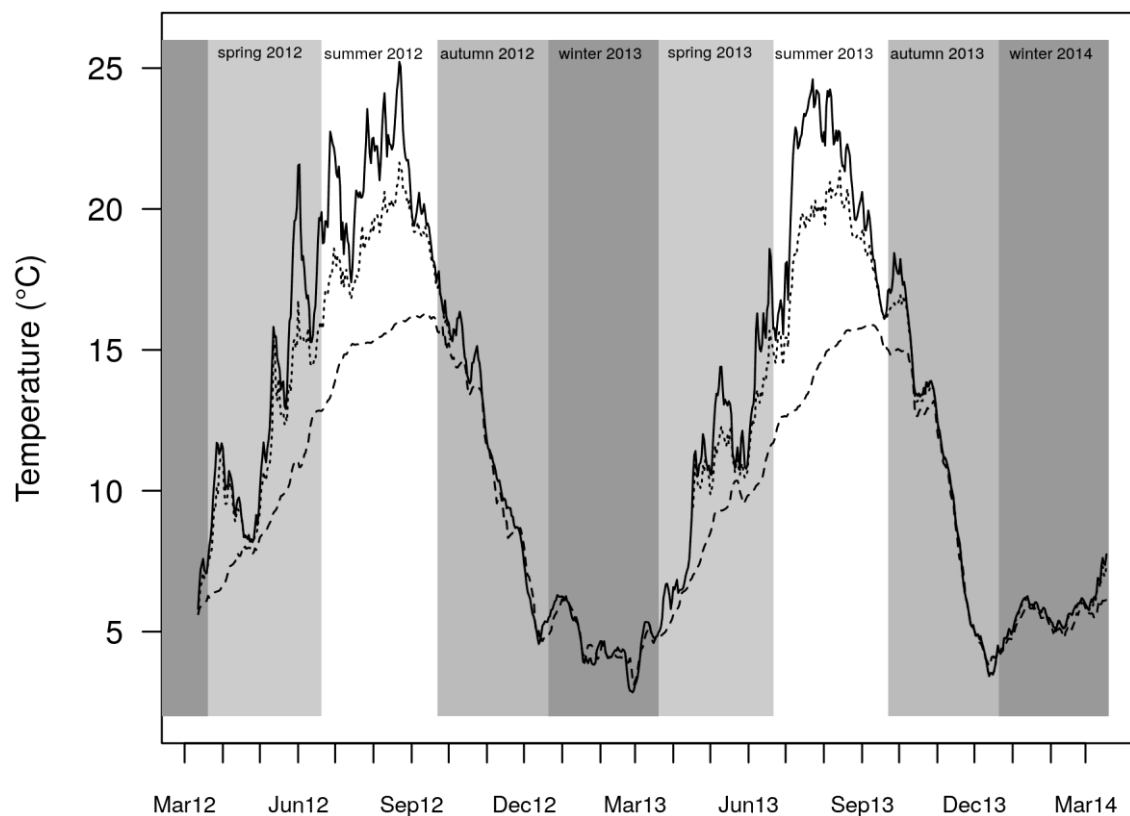


Fig. 2 Mean daily temperature (°C) measured at three different depths (solid, dotted and dashed lines for 0.5, 3.5 and 18.5 m, respectively) at the deepest point of the lake. The shading of periods in deep dark grey, dark grey, light grey and white represents winter (mixed water), autumn (mixing occurring), spring (stratified water) and summer (stratified water), respectively.

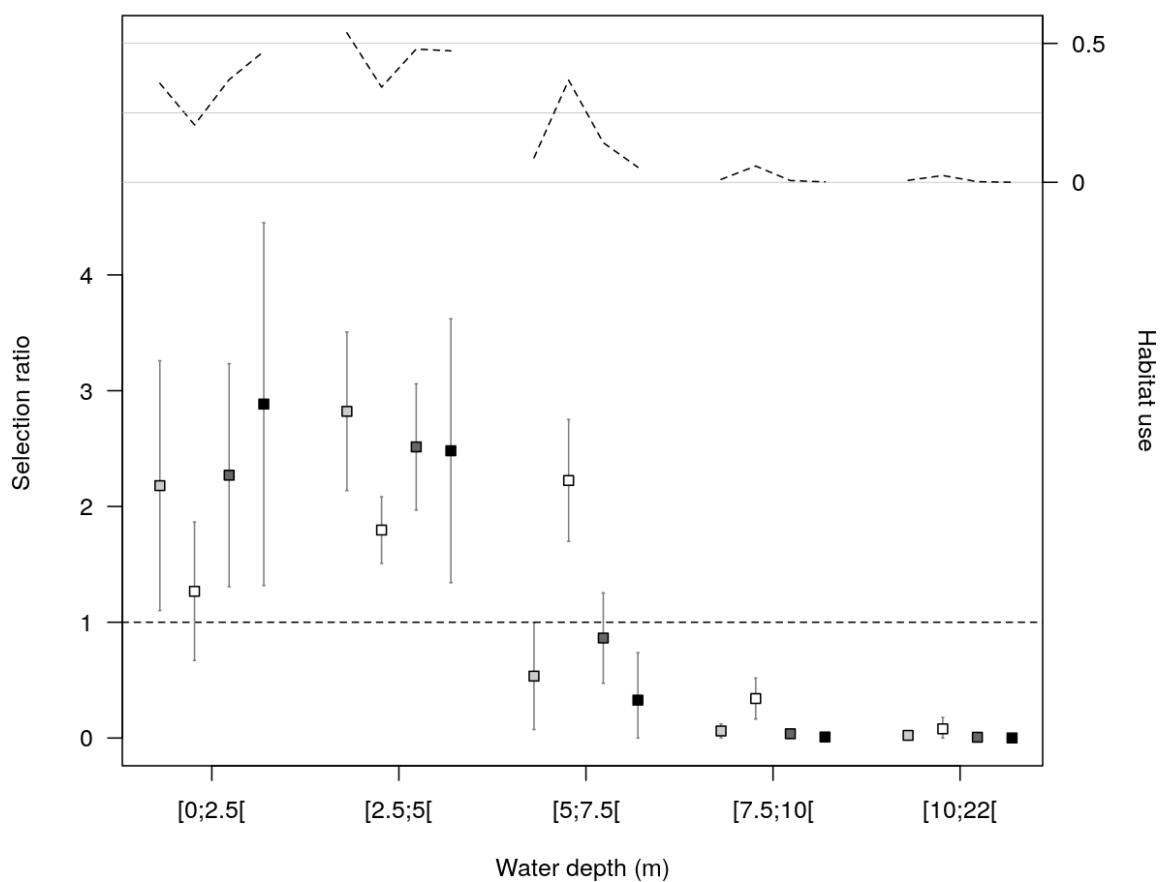


Fig. 3 Selection ratio of water depth (Mean \pm 95% Bonferroni confidence interval) for perch ($n = 20$) in summer for each period of the day (light grey, white, dark grey and black squares for dawn, daytime, dusk and night, respectively) on the left axis. A selection ratio of 1 indicates “no preference” and is represented by a horizontal dashed line. Habitat use (used proportion of each water depth) is represented on the right axis with a dashed line.

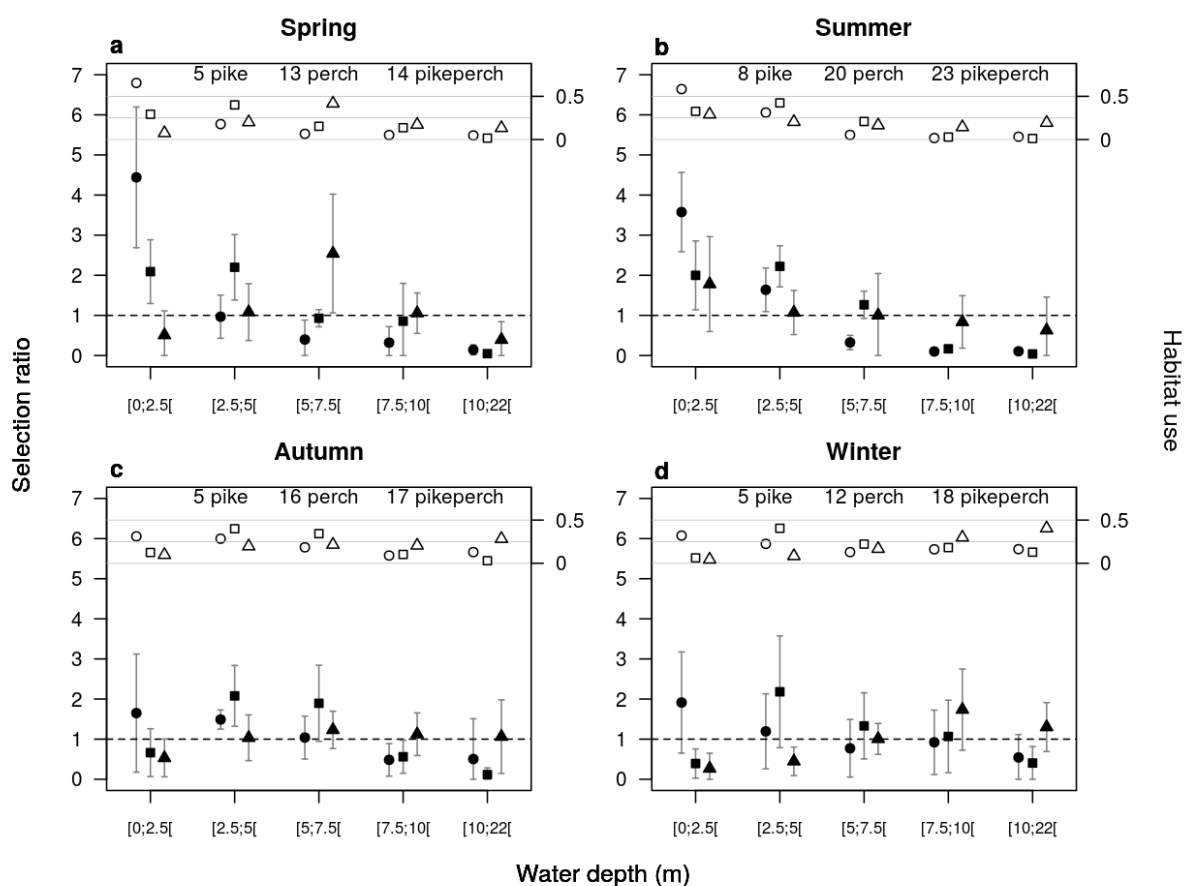


Fig. 4 Selection ratio of water depth (Mean \pm 95% Bonferroni confidence interval) in each season (spring, summer, autumn and winter in panels a, b, c and d, respectively) and for each species (black dots, black squares and black triangles for pike, perch and pikeperch, respectively) on the left axis. A selection ratio of 1 indicates “no preference” and is represented by a horizontal dashed line. Habitat use (used proportion of each water depth) is represented on the right axis (circles, white squares and white triangles for pike, perch and pikeperch, respectively). In each season, the number of pike, perch and pikeperch taken into account is provided.

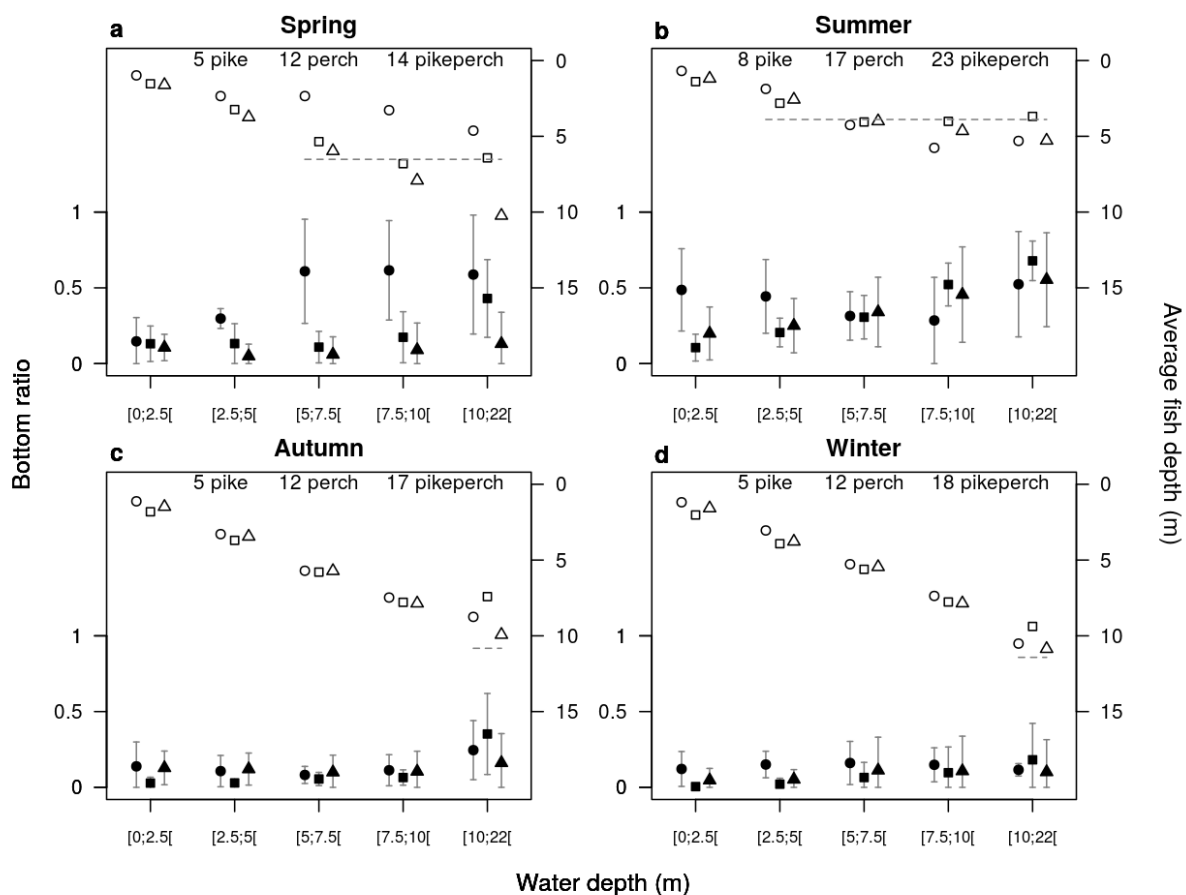


Fig. 5 Bottom ratio (Mean \pm SD) in each season (a) spring, b) summer, c) autumn and d) winter) for each species (black dots, black squares and black triangles for pike, perch and pikeperch, respectively) on the left axis. The average depth of species (circles, white squares and white triangles for pike, perch and pikeperch, respectively) and of the thermocline (grey dashed line) are represented on the right axis. In each season, the number of pike, perch and pikeperch taken into account is provided.

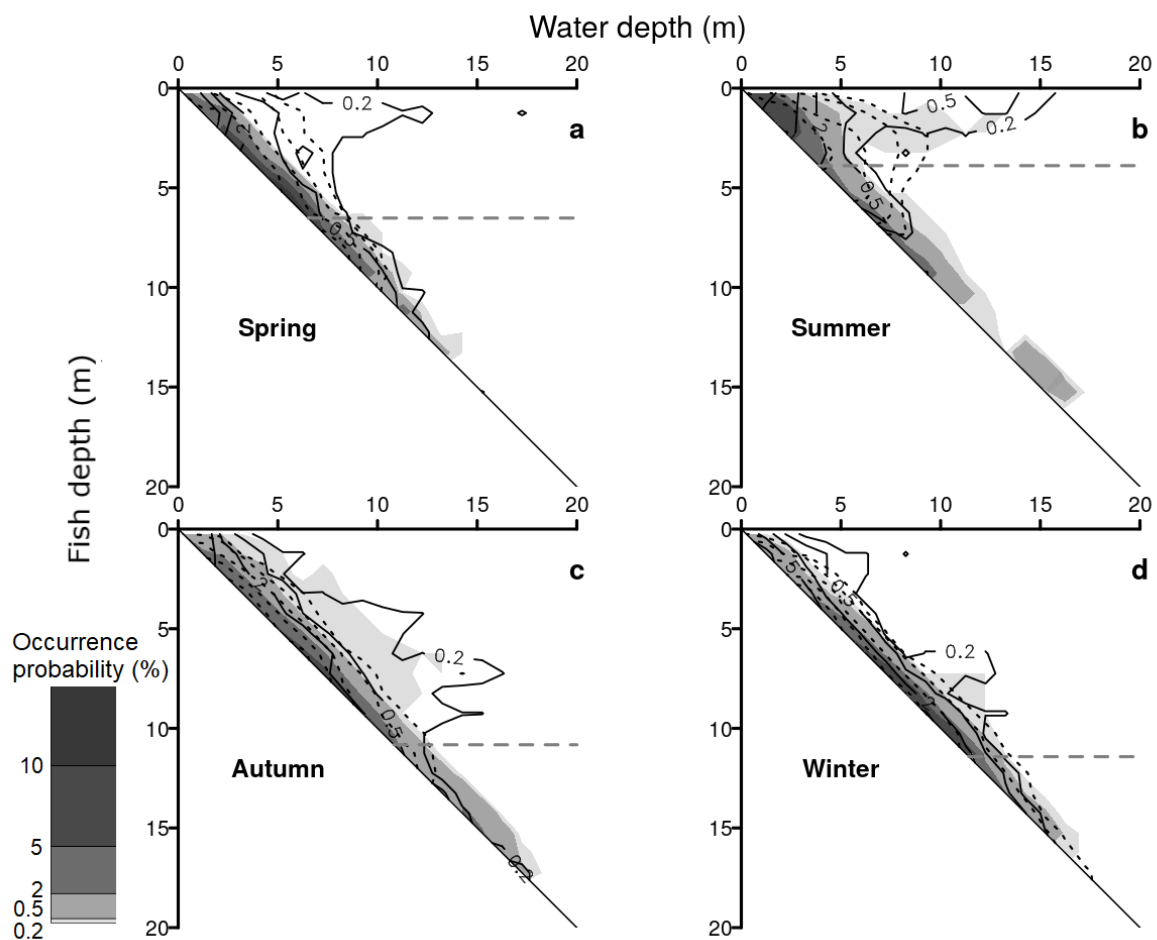


Fig. 6 Occurrence probability (%) of each species (black solid, black dashed and grey-filled contours for pike, perch and pikeperch, respectively) along the littoral-pelagic and depth axes in each season (a) spring, b) summer, c) autumn and d) winter). The occurrence probability at one point of the space defined by the water depth and the fish depth is the proportion of positions (%) at this point. It has been calculated over 1 m-sided cells. The thermocline mean depth is represented by the horizontal grey dashed line.

Supplementary materials for: Habitat partitioning among three predatory fish in a temperate reservoir

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Online Resource 1: Seasonal oxygen and temperature vertical profiles in 2011.

Online resources 2, 3 and 4: Time series of the positions of pike, perch and pikeperch respectively

Online Resource 5: Comparison of seasonal mean daily temperature profiles between the different years (from spring 2012 to winter 2014).

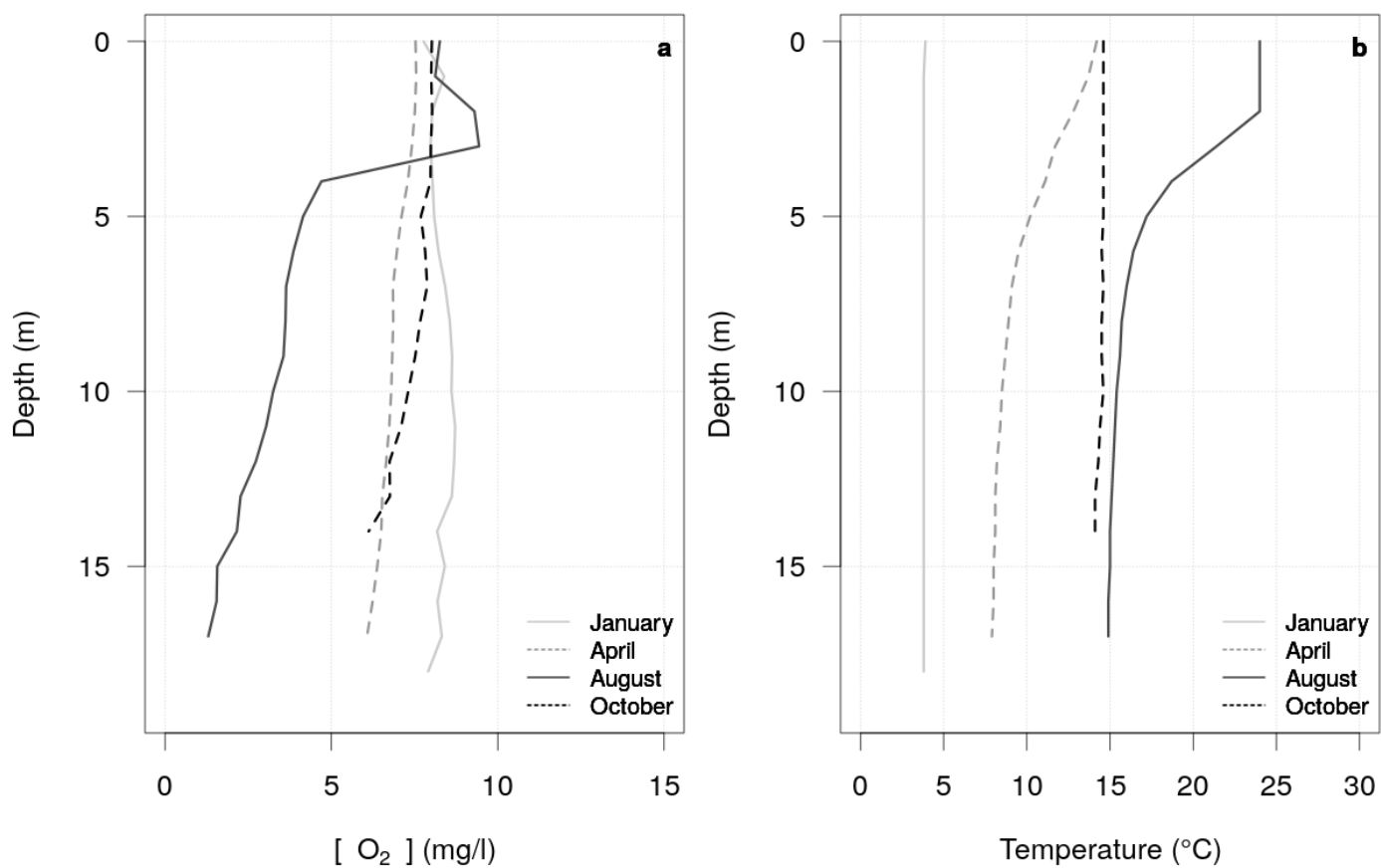
Online resources 6 and 7: Mean individual seasonal selection ratio of water depth class for pikeperch according to their origin (farmed or wild) and the results of the generalized additive mixed-effects model testing the origin effect

Online resources 8 and 9: Mean individual seasonal bottom ratio for pikeperch according to their origin (farmed or wild) and the results of the beta regression testing the origin effect

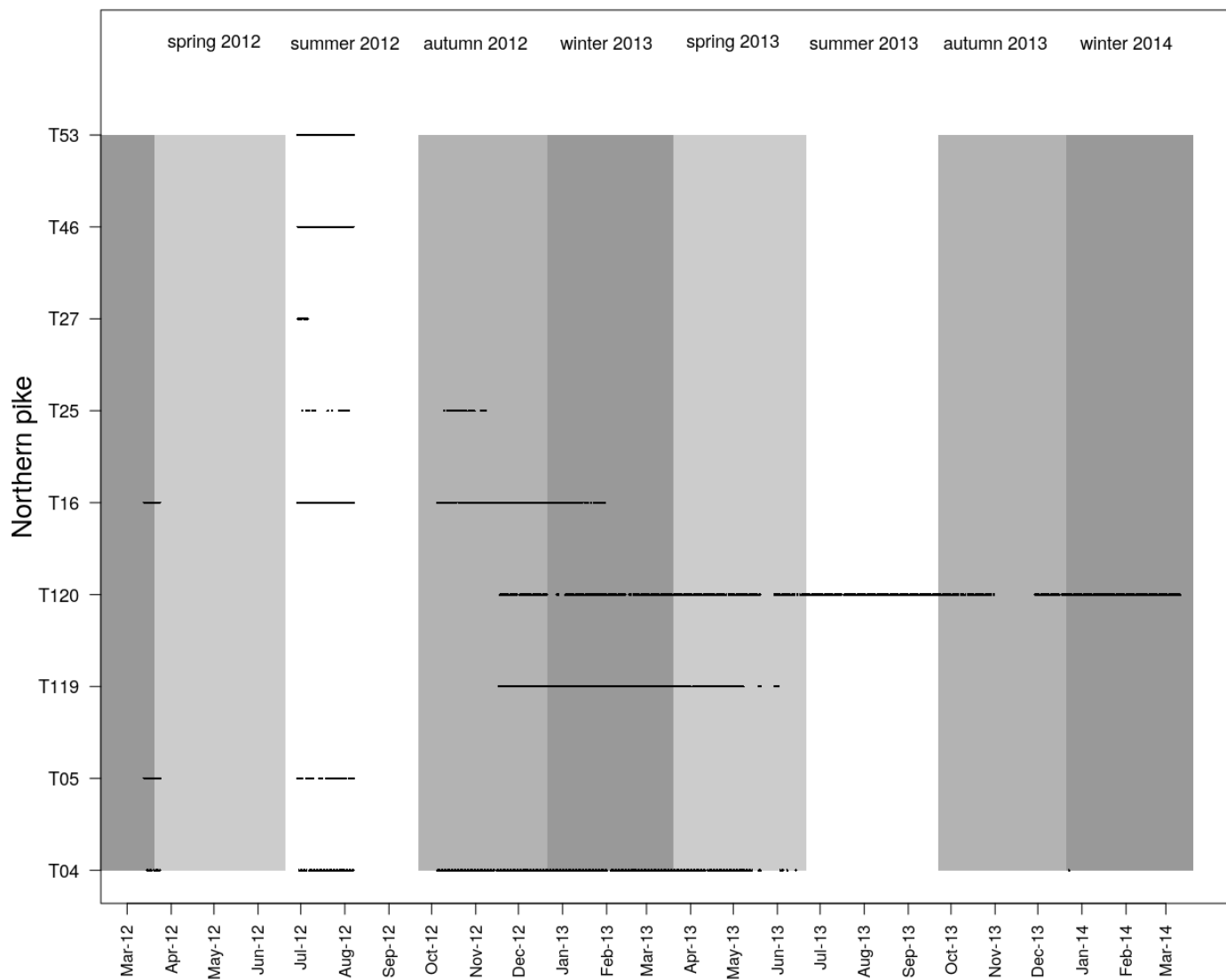
Online resource 10: Mean selection ratio of water depth class for pike, perch and pikeperch according to season and period of the day

Online resource 11: Mean bottom ratio for pike, perch and pikeperch according to season and period of the day

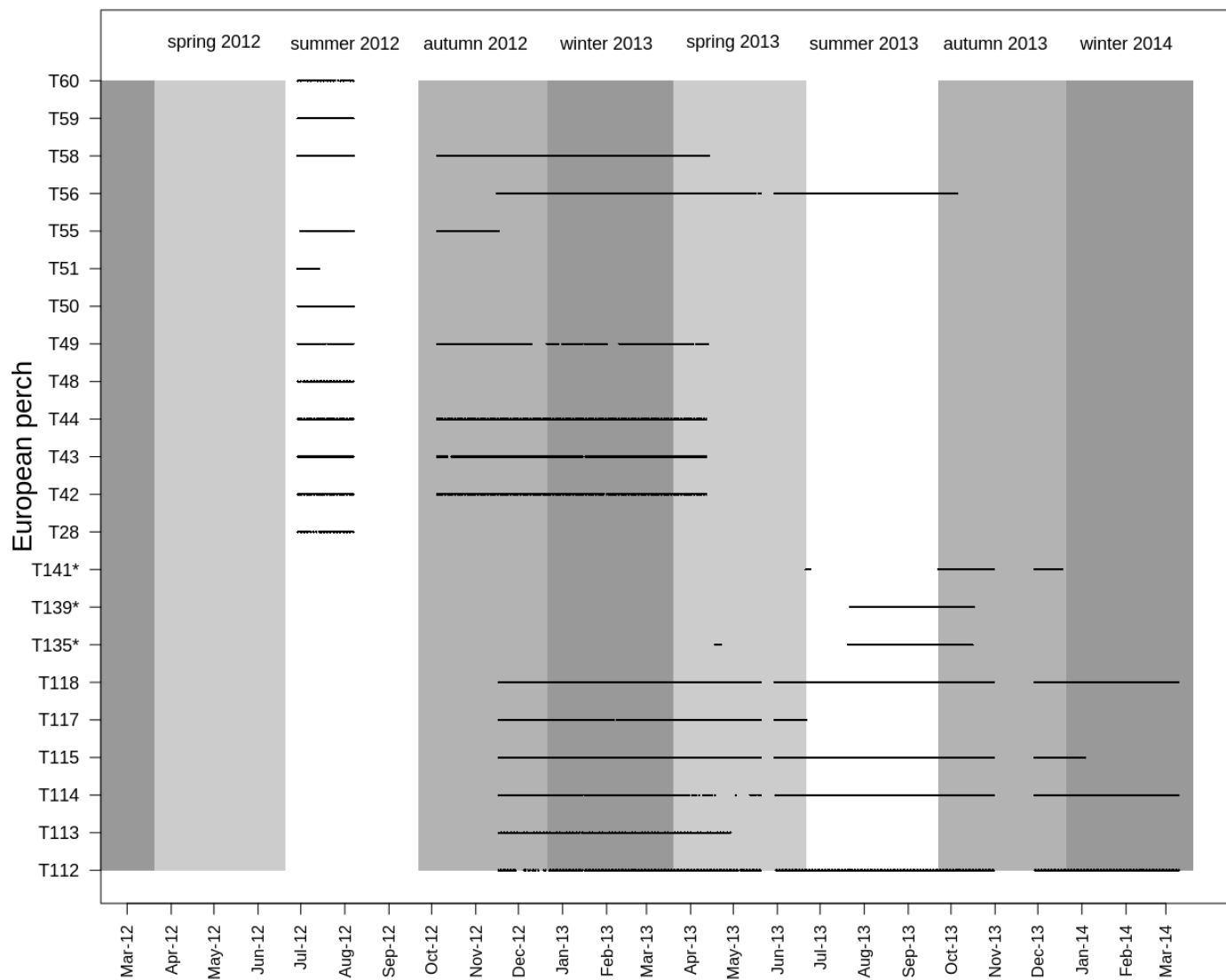
Online resource 12: Estimated marginal means of bottom ratio for the different species, season and depth combinations



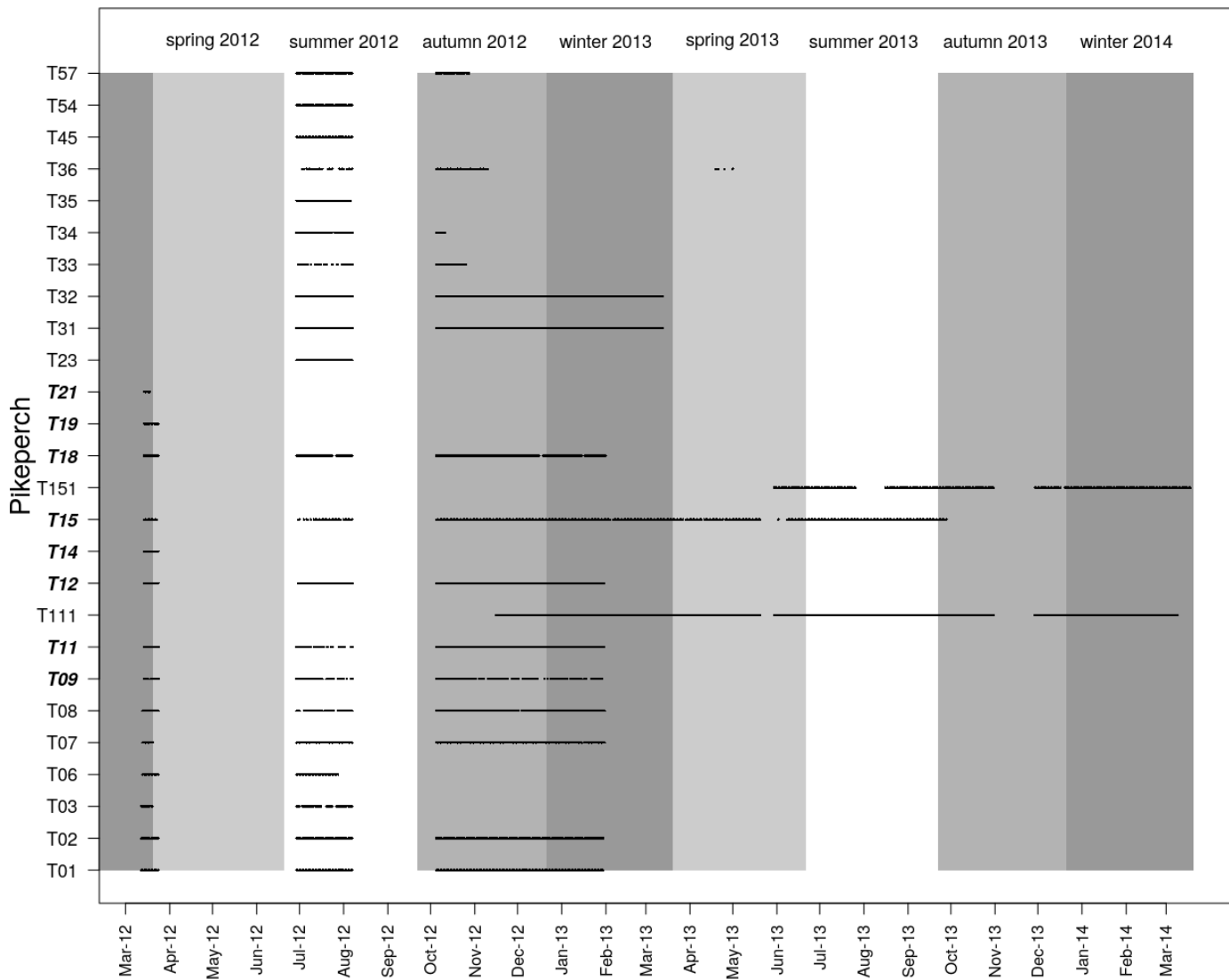
Online Resource 1 Seasonal oxygen and temperature vertical profiles in 2011 (panels a and b, respectively). The profiles in solid grey, dashed grey, solid black and dashed black lines were measured on 20th January, 21st April, 23rd August and 19th October 2011, respectively, close to the dam in the southern part of the Bariousses reservoir.



Online Resource 2 Time series of the positions of pike, *Esox lucius* (black dots). The shading of periods in dark grey, grey, light grey and no shading are representative of winter, autumn, spring and summer, respectively.



Online Resource 3 Time series of the positions of perch, *Perca fluviatilis* (black dots). * indicates tags without pressure sensor. The shading of periods in dark grey, grey, light grey and no shading are representative of winter, autumn, spring and summer, respectively.

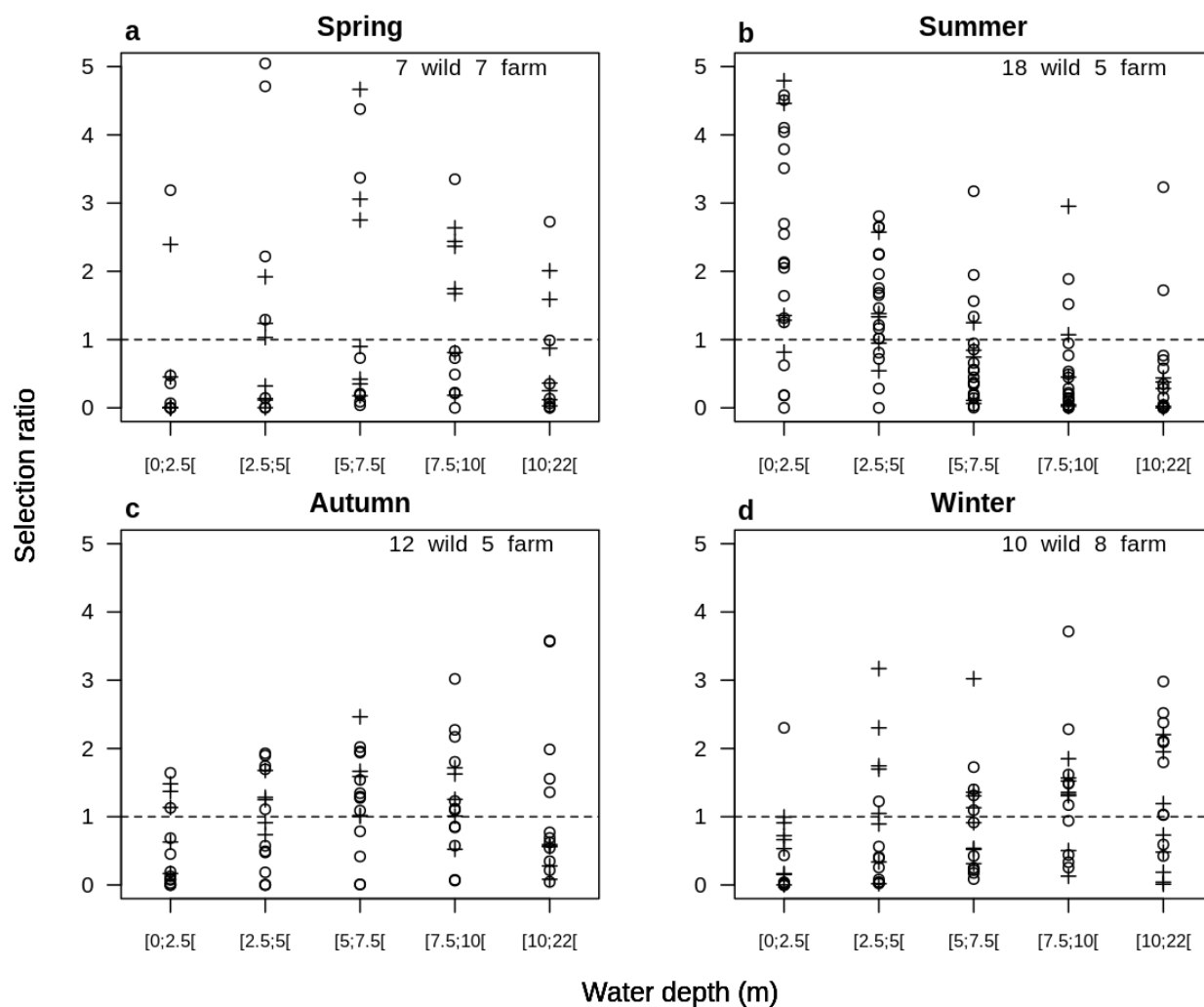


Online Resource 4 Time series of the positions of pikeperch, *Sander lucioperca* (black dots). ***ID*** indicates farmed pikeperch. The shading of periods in dark grey, grey, light grey and no shading are representative of winter, autumn, spring and summer, respectively.

Online Resource 5 Comparison of seasonal mean daily temperature profiles between the different years (from spring 2012 to winter 2014). The distributions of mean daily temperatures at three depths (0.5, 3.5 and 18.5 m corresponding to Figure 2) were compared between the same seasons of the different years with a Kruskal-Wallis test. When temperatures are different, both means are given; when they are not different, the global mean is given. P-values are given in italics. In spring, temperatures between 2012 and 2013 were not different at 3.5 and 18.5 m but at 0.5 m, the mean temperature was warmer in 2012 than in 2013 (13.0 °C and 11.1 °C, respectively). In summer, temperatures between 2012 and 2013 were not different at 0.5 and 3.5 m; at 18.5 m, the mean temperature was warmer in 2012 than in 2013 by 0.8 °C. In autumn, temperatures between 2012 and 2013 were not different at 0.5 and 18.5 m. The comparison was not made at 3.5 m but, except in early fall, temperature was very homogeneous all along the vertical profile in autumn (see Figure 2). The winter was colder in 2013 compared to 2014 by about 1 °C in average. Yet temperatures during both winters were much cooler than in any other season and characteristic of this season. In general, temperature differences between years ranged between a 1 °C interval, the biggest difference appearing in spring when the surface layer was warmer in 2012 compared to 2013 by about 2 °C. Aside these values, each season clearly kept its main features whatever the year with rapidly increasing temperatures in spring, water stratification all along the summer when the temperatures were the highest, fast decreasing temperatures in autumn and cool and relatively stable temperatures in winter (see Figure 2). This led us to pool data from the same seasons over the two-year study.

	Spring	Summer	Autumn	Winter
0.5 m depth	$\overline{T}_{2012} = 13.0$	$\overline{T} = 20.7$	$\overline{T} = 10.9$	$\overline{T}_{2013} = 4.7$
	$\overline{T}_{2013} = 11.1$			$\overline{T}_{2014} = 5.8$
	<i>0.009</i>	<i>0.99</i>	<i>0.29</i>	<i>< 0.001</i>
3.5 m depth	$\overline{T} = 11.7$	$\overline{T} = 18.7$	(1)	No data in 2013
	<i>0.31</i>	<i>0.83</i>		
18.5 m depth	$\overline{T} = 8.7$	$\overline{T}_{2012} = 15.3$	$\overline{T} = 10.3$	$\overline{T}_{2013} = 4.1$
		$\overline{T}_{2013} = 14.5$		$\overline{T}_{2014} = 5.1$
	<i>0.11</i>	<i>< 0.001</i>	<i>0.15</i>	<i>< 0.001</i>

⁽¹⁾ As only the first 10 days of autumn are available in 2012 at 3.5 m depth, the comparison was not made with the full time series in 2013 (90 days).



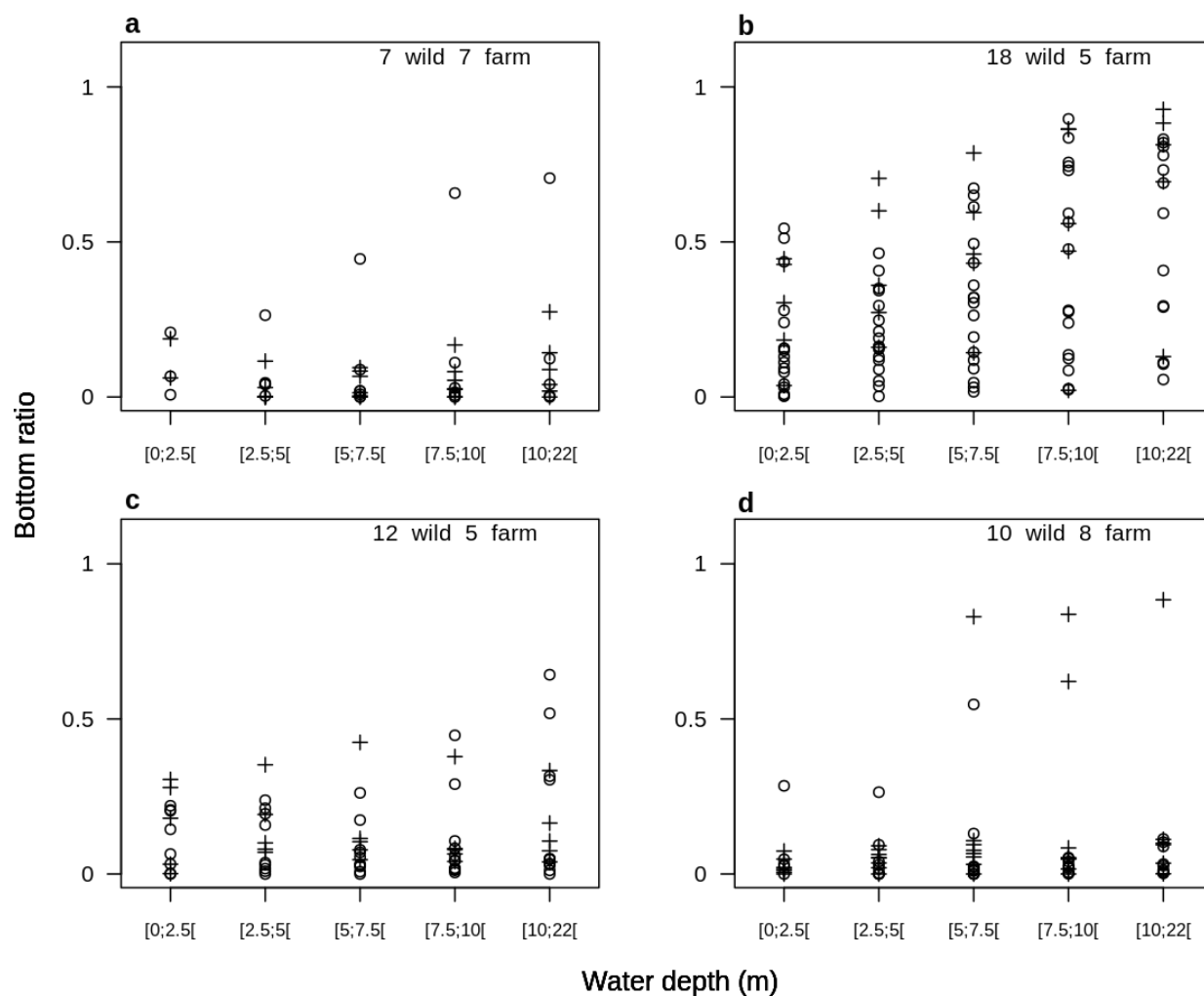
Online Resource 6 Mean individual selection ratio of water depth in each season (spring, summer, autumn and winter in panels a, b, c and d, respectively) for pikeperch (crosses for farmed individuals and white dots for wild individuals). In each season, the numbers of farmed and wild pikeperch are provided.

Online Resource 7 Results of the following generalized additive mixed-effects model

$$\log(\overline{SR_{ind}}) = \alpha + \text{WATER DEPTH} * \text{SEASON} + \text{WATER DEPTH} * \text{ORIGIN} + s(\text{ind}) + \varepsilon$$

where $\overline{SR_{ind}}$ is the expected mean individual selection ratio of pikeperch, strictly positive; α is the overall intercept; origin discriminates wild from farmed pikeperch, $s(\text{ind})$ is a smoothing function modelling the individual effects (Wood, 2008) and ε is the error term following a normal distribution with zero mean. To take into account the skewed distribution of individual selection ratios towards zero, a Tweedie family function with a log-link was used (Gilman et al., 2012). This model tested the fixed effects of water depth, season, pikeperch origin and some of their interactions, as well as the individual effects, on selection ratios. The percentage of explained variance quantified the data variability represented by this model. Results demonstrated that there was no effect of pikeperch origin.

Pikeperch	Selection ratio		
	d.f.	F	p-value
Water depth	4	3.008	0.018
Season	3	14.297	<0.001
Origin	1	1.396	0.238
Water depth: Season	12	6.327	<0.001
Water depth: Origin	4	1.786	0.131
Individual	24	0	1
All effects			
Explained variance (%)	17.1		



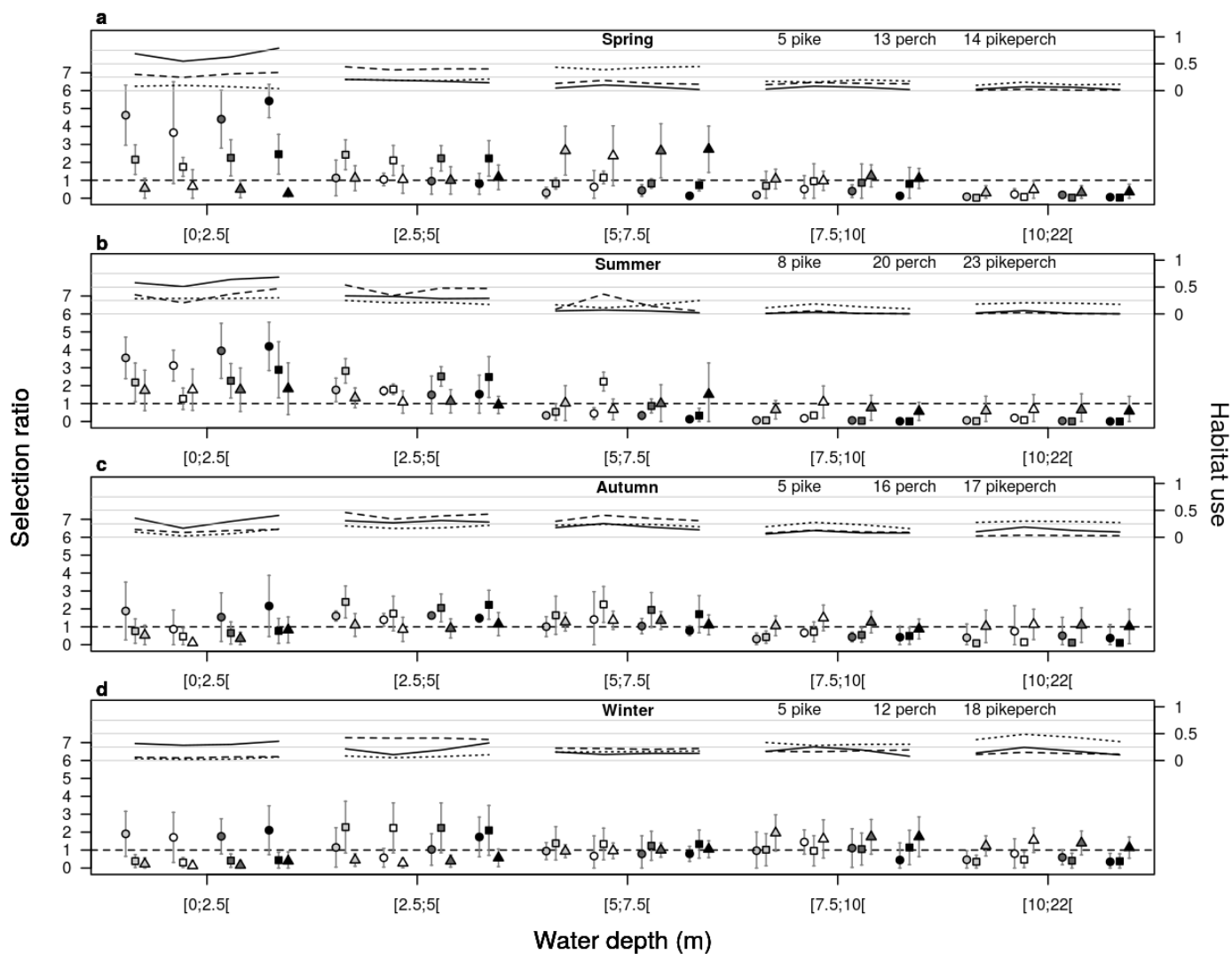
Online Resource 8 Mean individual bottom ratio in each season (spring, summer, autumn and winter in panels a, b, c and d, respectively) for pikeperch (crosses for farmed pikeperch and white dots for wild ones). In each season, the numbers of farmed and wild pikeperch are provided.

Online Resource 9 Results of the following Beta regression

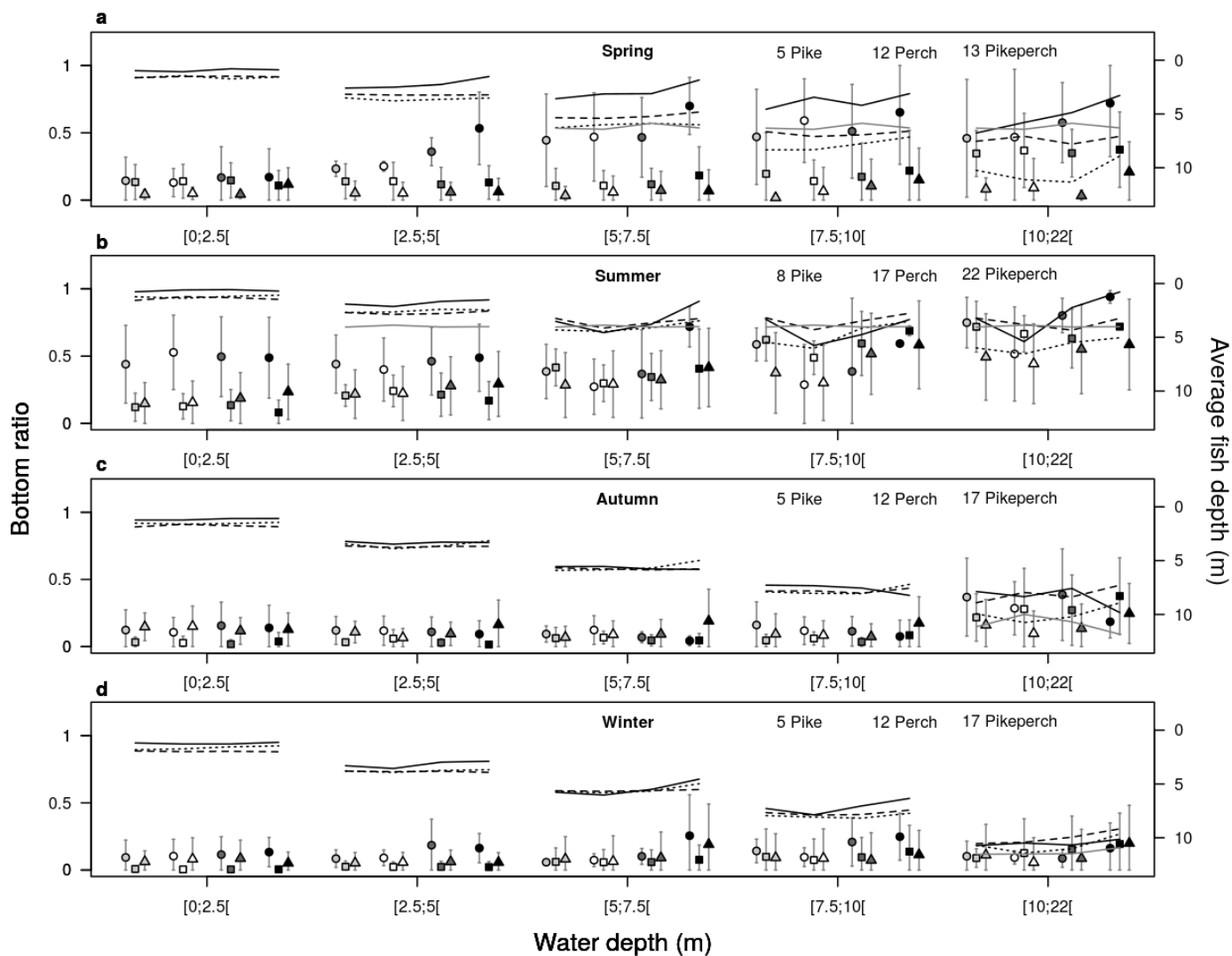
$$\text{logit}(\overline{\text{BR}}_{\text{ind}}) = \alpha + \text{WATER DEPTH} * \text{SEASON} + \text{WATER DEPTH} * \text{ORIGIN} + s(\text{ind}) + \varepsilon$$

where $\overline{\text{BR}}_{\text{ind}}$ is the expected mean individual bottom ratio in]0,1[, α is the overall intercept, origin discriminates wild from farmed pikeperch, $s(\text{ind})$ is a smoothing function modelling the individual effects (Wood, 2008) and ε is the error term following a normal distribution with zero mean. This model tested the fixed effects of water depth, season, pikeperch origin and some of their interactions, as well as the individual effects, on bottom ratios. The percentage of explained variance quantified the data variability represented by this model. Results demonstrated that there was no effect of pikeperch origin.

Pikeperch	Bottom ratio		
	d.f.	Chi-sq	p-value
Water depth	4	21.820	<0.001
Season	3	53.694	<0.001
Origin	1	3.527	0.060
Water depth: Season	12	43.790	<0.001
Water depth: Origin	4	0.737	0.947
Individual	24	177.6	<0.001
	All effects		
Explained variance (%)	50.7		



Online Resource 10 Selection ratio of water depth (mean \pm 95% Bonferroni Confidence Interval) for each species (dots, squares and triangles for pike, perch and pikeperch, respectively) and each period of the day (dawn, daytime, dusk and night displayed in light grey, white, dark grey and black symbols, respectively) in each season (spring, summer, autumn and winter in panels a, b, c and d, respectively) on the left axis. A selection ratio of 1 indicates “no preference” and is represented by a horizontal dashed line. Habitat use (used proportion of each water depth) is represented on the right axis (solid, dashed and dotted line for pike, perch and pikeperch, respectively). In each season, the number of pike, perch and pikeperch is provided.



Online Resource 11 Bottom ratio (mean \pm SD) for each species (dots, squares and triangles for pike, perch and pikeperch, respectively) and each period of the day (dawn, daytime, dusk and night displayed in light grey, white, dark grey and black symbols, respectively) in each season (spring, summer, autumn and winter in panels a, b, c and d, respectively) on the left axis. The average depth of species (solid, dashed and dotted line for pike, perch and pikeperch, respectively) and of the thermocline (grey solid line) are represented on the right axis. In each season, the number of pike, perch and pikeperch is provided.

Online Resource 12 Estimated marginal means of bottom ratio for the different species, season and water depth combinations. In each season/water depth category, estimated bottom ratios that are significantly different between species (based on Tukey comparisons of pairwise estimated marginal means at the 95% level of the beta regression) are labelled with different letters (a, b, c).

	Spring				
	[0;2.5[[2.5;5[[5;7.5[[7.5;10[[10;22[
Pike	0.09 ^a	0.18 ^a	0.37 ^a	0.44 ^a	0.60 ^a
Perch	0.04 ^b	0.08 ^b	0.11 ^b	0.13 ^b	0.30 ^b
Pikeperch	0.04 ^b	0.02 ^c	0.04 ^c	0.07 ^c	0.07 ^c
	Summer				
	[0;2.5[[2.5;5[[5;7.5[[7.5;10[[10;22[
Pike	0.37 ^a	0.40 ^a	0.40 ^a	0.67 ^a	0.60 ^{a,b}
Perch	0.11 ^b	0.23 ^b	0.41 ^b	0.60 ^a	0.72 ^a
Pikeperch	0.09 ^b	0.25 ^b	0.31 ^a	0.37 ^b	0.51 ^b
	Autumn				
	[0;2.5[[2.5;5[[5;7.5[[7.5;10[[10;22[
Pike	0.05 ^a	0.08 ^a	0.09 ^a	0.13 ^a	0.22 ^a
Perch	0.02 ^b	0.06 ^a	0.10 ^a	0.10 ^a	0.31 ^a
Pikeperch	0.02 ^b	0.07 ^a	0.07 ^a	0.10 ^a	0.11 ^b
	Winter				
	[0;2.5[[2.5;5[[5;7.5[[7.5;10[[10;22[
Pike	0.10 ^a	0.09 ^a	0.08 ^a	0.14 ^a	0.13 ^{a,b}
Perch	0.01 ^b	0.03 ^b	0.08 ^a	0.12 ^a	0.15 ^a
Pikeperch	0.01 ^b	0.03 ^b	0.06 ^a	0.07 ^b	0.09 ^b

References

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doi:10.1002/aqc.2237.
- Wood, S. N., 2008. Fast stable direct fitting and smoothness selection for generalized additive models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* 70:495-518.