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The effect of water temperature, prey availability and presence of conspecifics on prey consumption of pikeperch (*Sander lucioperca*)

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Abstract: In this study, the effect of water temperature, predator's sex, prey density, and the presence of conspecifics on prey consumption of pikeperch (*Sander lucioperca*) was experimentally tested. In Experiment 1, predators of both sexes [males: total length (TL) = 473 ± 22 mm and body weight (BW) = 1 070 ± 100 g and females: TL = 464 ± 12 mm and BW = 1 060 ± 100 g] were kept in separate tanks and exposed to different densities of prey (*Pseudorasbora parva*; 3, 6, 12, 24 and 48 prey fishes per tank) under fixed water temperatures of 4.5 °C, 8.5 °C, and 12.5 °C. After 63 days of this experiment, it was found that pikeperch predation was significantly affected by increasing water temperature. The effect of prey density was significant at all tested temperatures. Pikeperch females tended to have the higher prey consumption than males, although that trend was statistically insignificant. Results suggest that increased feeding demands at temperatures above 4.5 °C can lead to predator starvation in conditions of low prey availability. Due to the higher prey consumption, pikeperch females could be more vulnerable to low prey availability during their culture. In Experiment 2, pikeperch were kept at different densities of 1, 2, 4, and 8 individuals per tank supplied with a prey rate of 50 individuals per predator, ensuring *ad libitum* feeding rate. The average daily prey consumption was significantly higher in the tanks with multiple predators, accounting for 17.6 ± 3.57 prey fishes/day compared to 11.6 ± 2.33 prey fishes/day in the tank with a single predator. These results indicate that pikeperch predation activity and prey consumption can be significantly affected by the water temperature, prey availability, and the presence of conspecifics. The findings contribute to understanding the predatory function, natural feeding request of pikeperch and its potential importance for broodstock culture and broodstock final maturation for a successful spawning season. Also, this information can be used for better management of pikeperch pond aquaculture or bio-melioration process in open water bodies and ecosystems.

Keywords: feeding behaviour; predation; competition; pond aquaculture; water bodies

Temperature is one of the most critical drivers of biological processes (Brown et al. 2004). It directly influences biological rates of ectotherms – animals depending on the environmental sources of heat, significantly affecting their migration, growth, reproduction, and foraging activity (Kokkonen et al.

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2019). Temperature affects primary production in freshwater ecosystems – the basement of the food web structure (Kratina et al. 2012). Therefore, its fluctuation can cause low production of predatory fish species and higher proportion of the species of low trophic levels, for example small cyprinid species (Rall et al. 2008). In this regard, natural production in open waters or pond aquaculture of predatory fish species is disproportionately influenced by environmental changes compared to lower trophic levels (de Ruiter et al. 1995).

Depending on latitude, the winter season poses one of the biggest challenges for predatory fish triggering substantial changes of physiological functions, as a temperature decline forces them to rely more on internal energy storage to meet metabolic requirements (Ostrand et al. 2005). Coldwater piscivores are well adapted to winter, however, they are rather sensitive to low prey availability in the following spring (Kallis and Marschall 2014), when their metabolic demand increases faster than their feeding rate, creating a risk of starvation (Rall et al. 2010; Fussmann et al. 2014).

An artificially built community – polyculture stocks of pond aquaculture rarely comprise several species of predators (Aubin et al. 2019). Therefore, their functioning is particularly sensitive to oscillations of abiotic and biotic parameters. Pikeperch (*Sander lucioperca*) is the top predator of European aquatic ecosystems and serves top-down control for both commercial and ecological purposes (Adamek and Opacak 2005). It is often a complementary species of polyculture stock as the main tool for the control of less valued fish in pond aquaculture (Keskinen and Marjomaki 2004; Specziar 2011). Serving as a main tool of bio-melioration, pikeperch, however, is a gape-limited predator, favouring smaller, rather than larger, available prey (Keskinen and Marjomaki 2004; Turesson and Bronmark 2004), which makes them particularly sensitive to a change of prey availability suitable for consumption.

Identification of species vulnerabilities to the specific environmental conditions is important for pond aquaculture practices and can largely determine species success and following production output. Classic pond aquaculture is operating within a 3–4 years long culture cycle, meaning the fish are going through several seasons with drastic temperature fluctuations and certain risk of starvation for the species at higher trophic levels (Farmer et al. 2015). Despite the importance of photothermal variations for the biology of freshwater piscivores, there is a paucity of literature about the effect of temperatures on their feeding activity and behaviour, creating a significant gap in the understanding of potential threats to the species success. Therefore, this study pursues the determination of the factors modulating the prey consumption of pikeperch. Two experiments of this study aimed at the determination of (1) the temperature threshold when pikeperch begin to exhibit trophic interactions, (2) how prey availability, and (3) presence of conspecifics influence them.

MATERIAL AND METHODS

Fish origin

In late October, pikeperch individuals were collected from the polyculture ponds of the fish farm Nove Hrady Ltd (Czech Republic) and transferred to a small drainable earthen pond (0.1 ha) to overwinter; the pond belongs to the Faculty of Fisheries and Protection of Waters, University of South Bohemia. Throughout winter, fish were continuously supplied with prey fish (Malinovskyi et al. 2019). On demand, the water level in the pond was reduced, allowing easy extraction and transporting of fish to the experimental facilities. On the day of manipulation, pikeperch were treated with a salt bath in the concentration of 5 g/l for 3 h to reduce stress and the risk of an emerging fungal infection of the body skin (Policar et al. 2019).

Experimental facility

The experiments were performed in a recirculating aquaculture system (RAS) comprising a set of 380 l tanks, an oxygen reactor, and mechanical and biological filters. The system allowed gradual adjustment of photothermal conditions, water flow rate, and oxygen saturation in the tanks. The water quality was monitored daily, by measuring dissolved oxygen (94 ± 3%; measured with OxyGuard International A/S probe, Farum, Denmark), pH (6.91 ± 0.09; measured with HI98129 meter, Hanna Combo; Hanna Instruments, Prague, Czech Republic), total ammonia nitrogen (0.13 ± 0.11 mg/l; measured with HI83300 photometer; Hanna Instruments, Prague, Czech Republic), and

https://doi.org/10.17221/162/2022-CJAS

nitrite (0.16 ± 0.07 mg/l; measured with HI83300 photometer; Hanna Instruments, Prague, Czech Republic) concentrations in the water. Service and maintenance of RAS were done daily during the first hour of the light phase.

Experiment 1 – The effect of water temperature and prey density on prey consumption

In January (water temperature 2.5 °C), pond-cultured pikeperch were transferred to the controlled conditions of a recirculating aquaculture system (RAS) and were kept with a continuous supply of prey fish for two weeks before the beginning of experimental trials. Following the adaptation, the sex was determined using a catheter (Zarski et al. 2012), and five males (total length TL = 473 ± 22 mm and body weight BW = 1 070 ± 100 g) and five females (TL = 464 ± 12 mm and BW = 1 060 ± 100 g) were selected for the experiment.

The experiment lasted 64 days from late January to March and included 14 days of initial adaptation followed by a gradual increase of water temperature from 4.5 to 8.5, and 12.5 °C, therefore creating three thermal trials of 12 days each. Each fish was kept in a separate 380 l tank (10 tanks connected to a RAS) starting from initial adaptation at 2.6 °C before the first thermal trial. The photoperiod was simulated to keep photothermal conditions without changes during the experimental trials. Artificial light (50 lux on the water surface of the tank; Tommi LFL−CL 600; Tommi CZ s.r.o., Pisek, Czech Republic) was applied with a duration following the latitude of Central Europe. Photothermal regime changes were gradually performed (0.5 °C and 15 min of light duration per day) during the 7-day adaptation and rest period following each experimental trial.

Both males and females were supplied daily with the prey fish *Pseudorasbora parva* at densities of 3, 6, 12, 24, and 48 individuals per tank (one predator), therefore each density was replicated for both sexes. The predator-prey size ratio (PPR) was selected according to the prey size commonly accepted by pikeperch in natural water bodies (Specziar 2011; TL = 63.1 ± 3.5 mm; BW = 2.06 ± 0.4 g; PPR = 0.13). No shelter was provided for prey fish. During the adaptation and rest periods between the experimental trials, all pikeperch were fed *ad libitum* on the same prey species and size to ensure satiation before the beginning of the next trial. After the beginning of the new trial, prey fish were stocked in the same arrangement, therefore each predator was exposed to the same prey density during the experiment. The predator was not exposed to direct handling during the experiment to avoid the effect of handling on prey consumption. Therefore, once stocked, pikeperch stayed in a particular tank till the end of the last trial at 12.5 °C.

Experiment 2 – The presence of conspecifics and its effect on prey consumption

In late March, a total of fifteen pond-cultured pikeperches (total length TL = 346 ± 11 mm and body weight BW = 560 ± 61 g) were selected for the second experiment. Fish were transferred from the outdoor pond (water temperature 11.7 °C) to the RAS without sex determination and were continuously supplied with prey fish (50 prey fishes per pikeperch; Malinovskyi et al. 2019) for two weeks of adaptation before the beginning of the experimental trials. The photothermal regime was artificially simulated providing 50 lux light intensity on the water surface, and light duration following the latitude of Central Europe. Water temperature was increased gradually, targeting 20 °C by the end of adaptation period. After achieving stable temperature conditions (19.8 ± 0.3 °C), pikeperch were randomly divided among four tanks of 380 l volume, forming four experimental tanks with a stocking density of 1, 2, 4, and 8 pikeperch per tank. After the division, predators were not exposed to direct handling till the end of the experimental trial. Each tank was supplied with prey fish providing 50 prey fish individuals per predator, with no shelter for the prey. The prey consumption of the experimental pikeperch was monitored daily for the next 10 days.

Evidence of prey consumption

The predator was not exposed to direct handling during the experiment to reduce the effect of handling stress on prey consumption. In both experiments, once stocked, pikeperch remained in a dedicated tank till the end of experimental trials. The prey consumption was checked daily during the

https://doi.org/10.17221/162/2022-CJAS

first light hour in the morning. To avoid a learning effect, all prey fish were replaced daily with individuals that had no prior contact with the predators. The number of consumed preys was determined by counting the survived prey fish in each tank. While counting, all the predators were exposed to an equal amount of disturbance, e. g., the same number of scooping actions needed for prey counting and replacement. Therefore, predators with the least number of preys in the tank were disturbed equally to those with the maximum number of unconsumed fish.

Statistical analyses

Data were analysed by Statistica v13 (StatSoft CR s.r.o., Prague, Czech Republic). The effect of prey density and predator's sex within each of the temperature trials on prey consumption per pikeperch was analysed by repeated measures ANOVA. For analysis, the density of prey and the sex of the predators were set as categorical variables, and the number of consumed prey fish at each tested temperature was set as a dependent variable. In Experiment 2, data were analysed using one-way ANOVA, where the average prey consumption per predator was set as a dependent variable, and predator density as a categorical one. Tukey's test followed both analyses to identify differences between treatments. Statistical significance was set at $P < 0.05$. All data are presented as mean ± SD.

RESULTS

Experiment 1

The temperature and prey density had a significant influence on predator activity and prey consumption (Figure 1). The effect of prey density on prey consumption per pikeperch was significant at all tested temperatures (Table 1). The general tendency of higher prey consumption in pikeperch females was evident, although the general effect of the sex on the prey consumption was not statistically significant (Table 1). Despite the general insignificance of the sex on prey consumption, females exhibited remarkably higher consumption in 8.5 °C trial at the density of 24 prey fishes compared to males (Figure 1). At 4.5 °C and 12.5 °C temperature trials there was no significant difference in consumption between the sexes (Figure 1).

Experiment 2

The consumed average was significantly affected by pikeperch density (Figure 2). The consumption

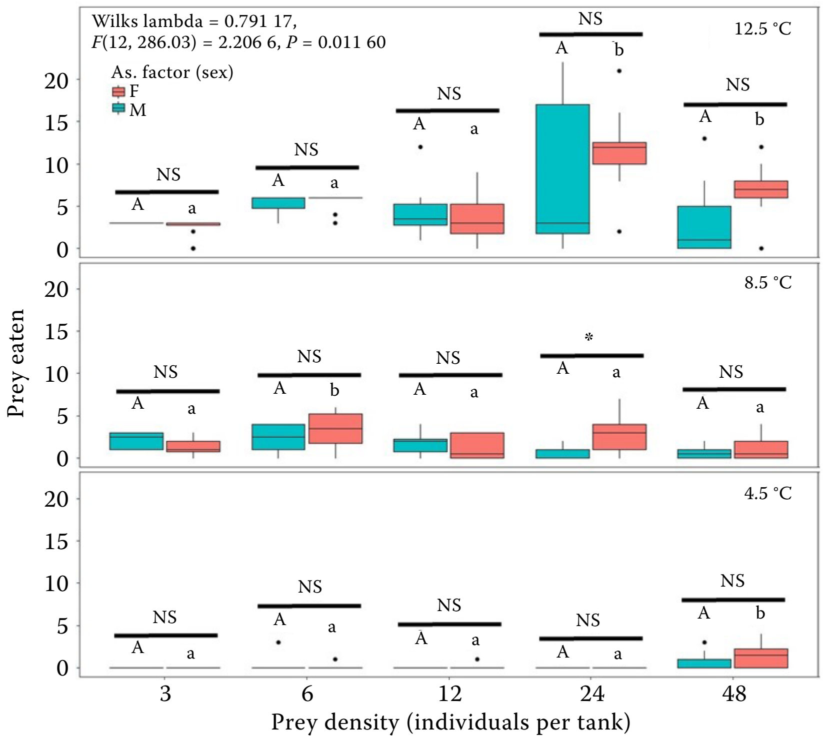

Figure 1. The number of consumed preys by pikeperch (*Sander lucioperca*) for all prey densities in three temperature trials

NS = non-significant differences between the sexes at each prey density (horizontal bars)

*Significant differences between the sexes at each prey density (horizontal bars)

[A,a,b]Different letters denote significant ($P < 0.05$) differences between prey densities at a given temperature (males = capital, females = small) and prey density

Box limits correspond to upper and lower quartiles, horizontal bar to the median, and points show outliers outside 1.5 times the interquartile range

https://doi.org/10.17221/162/2022-CJAS

Table 1. The effect of water temperature, prey density and pikeperch (*Sander lucioperca*) sex on its predatory activity and prey consumption

	Water temperature (°C)		
	4.5	8.5	12.5
Predator's sex (pcs)			
Female	0.32 ± 0.85	1.93 ± 1.90	6.03 ± 4.20
Male	0.22 ± 0.64	1.50 ± 1.31	4.83 ± 4.81
Prey density (pcs)			
3	n/a	1.71 ± 1.08	2.71 ± 0.86
6	0.17 ± 0.64	2.83 ± 2.04	5.46 ± 1.02
12	0.04 ± 0.20	1.42 ± 1.35	3.88 ± 2.79
24	n/a	1.75 ± 1.85	10.1 ± 6.93
48	1.13 ± 1.23	0.88 ± 1.11	5.04 ± 3.98
Main effects ANOVA, *P*-value			
Predator's sex	$P = 0.381$	$P = 0.106$	$P = 0.082$
Prey density	$P > 0.005$	$P > 0.005$	$P > 0.005$
Predator's sex × prey density	$P = 0.291$	$P = 0.005$	$P = 0.118$

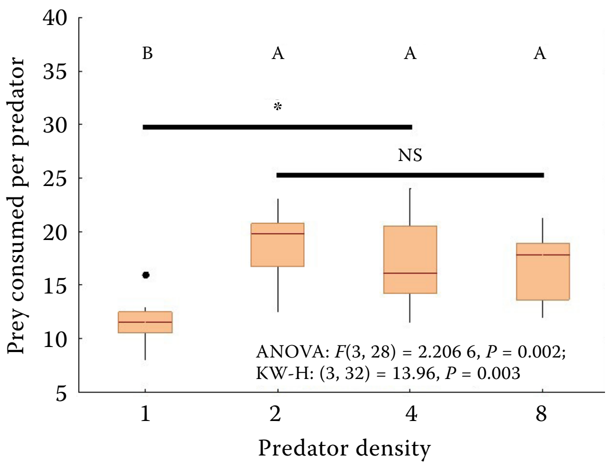

Figure 2. The average number of consumed preys by pikeperch (*Sander lucioperca*) related to the density of the predators

NS = non-significant differences between predator densities

*Significant differences between predator densities

[A,B]Different letters denote significant ($P < 0.05$) differences in consumption between predator densities

Box limits correspond to upper and lower quartiles, horizontal bar to the median, and points show outliers outside 1.5 times the interquartile range

in the tanks with multiple predators (the densities of 2, 4, and 8) averaged 17.6 ± 3.57 prey fishes per predator without significant differences between them. A single predator had consistently low average prey consumption of 11.6 ± 2.33 prey fishes per day.

DISCUSSION

Despite the large progress in pikeperch aquaculture, vast majority of its production comes either from the catches in the open waters or extensive aquaculture practices. Therefore, investigation on its biology and behaviour gains its importance in predicting and modulation of species success. This study reports the results from two experiments aimed to investigate the effect of water temperature and factors of the predator's sex (1), the density of prey (2), and the presence of conspecifics (3) on pikeperch prey consumption. These results are in line with the metabolic theory of ecology predicting the significant relationship of temperature and prey consumption (Brown et al. 2004; Rall et al. 2010). It was found that the effect of the prey density was significant at all tested water temperatures (Table 1). It can suggest the vulnerability to the winter conditions, where pikeperch could be unable to satisfy feeding and energy demands due to the density of the prey being insufficient for successful predation.

Although in general behavioural patterns of pikeperch are well understood, the various observations of its ethology are based on indirect evidence such as tagging and telemetry data and, therefore, they lack details. The controlled experiments are rare and often performed on larval or juvenile fish, as they are easier to handle in the conditions of the

https://doi.org/10.17221/162/2022-CJAS

laboratory, therefore creating a gap in understanding the behaviour of the adult fish (Peterka et al. 2003; Adamek and Opacak 2005). At the same time the limitation for the behaviour of the adult fish that come from the controlled environment of the laboratory can significantly affect the obtained results. Nevertheless, some aspects of the behaviour such as feed request can be studied in controlled conditions and provide valuable knowledge and perspective for the future investigations (Adamek and Opacak 2005). Identification of species vulnerabilities to certain conditions is particularly important for the extensive aquaculture where direct observation and control are complicated, and problems are identified based on the already experienced mortality of the fish.

Most of the reports concerning the relation of water temperature and predation refer to 4–5 °C as a borderline temperature and values above this range are identified as growing degree-days (GDD). In a sibling to pikeperch species – walleye (*Sander vitreus*), a higher number of GDD was associated with the increased biomass of the species in the ecosystem, suggesting the similarities in the response to the water temperature within the genus *Sander* (Shuter et al. 2002). Similarly, previous laboratory observations of pikeperch feeding activity reported almost no prey consumption at the temperature below 5 °C, although the factor of the prey availability was not considered (Malinovskyi et al. 2019). These reports indicate potential threats of starvation to the pikeperch that are exposed to the temperature higher than 5 °C throughout the winter season, when there is a limited availability of the prey. If such conditions occur, fish belonging to the order Perciformes seem to adjust their prey consumption in the following temperature increase e.g. in spring. In largemouth bass (*Micropterus salmoides*), swimming during the spring was affected by the winter food supply (Ostrand et al. 2005). According to Kallis and Marschall (2014), starvation of age-0 saugeyes (female walleye × male sauger *Sander canadensis*) before entering the winter season resulted in a higher prey consumption rate following the temperature increase. The overall trends of these reports presume the importance of the prey availability to the temperate predators, including pikeperch, during and after wintering. A deeper analysis of these effects in yellow perch (*Perca flavescens*) showed that the warm and short winters affected lipid content and eggs size, and embryo survival, suggesting disturbances in energy allocation due to low prey availability when the metabolic rate increased (Farmer et al. 2015). Such a trend likely applies to pikeperch, and threat-posing conditions can emerge when consumer demand cannot be compensated with increased energy intake. In this study, prey consumption of pikeperch was significantly affected by the water temperature. At 4.5 °C consumption was almost absent, and a significant shift occurred after the temperature increased to 8.5 °C (Figure 1). Nevertheless, both males and females of pikeperch showed a request for prey consumption at 4.5 °C in the highest tested densities of prey. It can be suggested that pikeperch have a metabolic demand for prey consumption, however, it cannot be satisfied at low temperatures, if only the density of the prey was high enough to ensure a mild success in predation.

In pikeperch aquaculture, the differences in behaviour between the sexes usually gain the attention only during controlled reproduction (Jepsen et al. 1999; Koed et al. 2000). Therefore a linkage between the sex of the fish and its predatory activity is vague, as there are very few studies concerning the direct evidence of its predatory behaviour (Adamek and Opacak 2005). Nevertheless, one of the most reliable indicators of consistently higher prey consumption in one of the sexes is size dimorphism, and for percids it is commonly expressed as higher body weight of females (Feiner and Hook 2015). For pikeperch, however, size dimorphism is not significant and most data from catches report no differences in length between the sexes (Lappalainen et al. 2005). Despite that, the analysis of pikeperch growth dynamics using a biphasic growth model (BGM) showed higher energy investments in reproduction for males, explained by significant energy investments in paternal care (Rennie and Venturelli 2015). Disproportion of the sex ratio in wild pikeperch populations supports that assumption, as females dominate in a size group > 55 cm total length suggesting the lower life expectancy of pikeperch males (Raikova-Petrova and Zivkov 1998; M'Hetli et al. 2011). The annual observation of pikeperch movement activity indicated significant differences in movement distance between males and females after reproduction, which could further support that suggestion, as, apart from the reproduction

https://doi.org/10.17221/162/2022-CJAS

season, migrations in pikeperch are prey-driven (Koed et al. 2000). Previous reports on pikeperch declare a 30% higher prey consumption in females during the winter-spring period, suggesting higher metabolic requirements during late phases of gametogenesis (Malinovskyi et al. 2019). Similarly, in this study females showed higher requests for the prey, particularly at a lower temperature. The BGM analysis suggests that for the males the energy demanding period would occur later in the spring and early summer, after completion of the paternal care (Rennie and Venturelli 2015). After all, the annual prey consumption could be similar for both males and females, explaining the absence of size dimorphism in pikeperch of the same age, however knowing differences in peak consumption could be potentially implemented in fisheries management (Lappalainen et al. 2005; Feiner and Hook 2015). Indication of the periods when the predator exhibits higher prey consumption would be beneficial to extensive aquaculture. It would indicate crucial periods within the production cycle when the predator could be particularly vulnerable to the low prey availability and contribute to the understanding of species success. Moreover, consideration of the species- and sex-specific predation patterns can be useful for modulation of the top-down control in pond aquaculture.

The reports on intraspecific interactions of pikeperch commonly refer to closed systems and their effect on management strategies during pikeperch aquaculture. In the controlled conditions of aquaculture the behaviour of the fish can alter significantly, therefore those reports are not usually considered as serious in the context of the species biology (Liu et al. 2021). One of the most frequently reported issues in percids is juvenile cannibalism during intensive culture (Molnar et al. 2018; Policar et al. 2019). Barry et al. (2017) reported an increased growth of yellow perch (*Perca flavescens*) exposed to the odour of the hunting predator, suggesting that fast growth is aimed at reaching the body size unacceptable to the predator. Similar findings were reported in crucian carp (*Carassius carassius*) and *C. auratus*, increasing their body height in response to the presence of predators (Stabell et al. 2010). The exchange of pheromones that can occur within one aquaculture unit has been reported to alter final oocyte maturation in pikeperch and walleye (*Sander vitreus*; Barry et al. 1995; Zarski et al. 2012), suggesting the importance of pheromonal and alarm cue systems for pikeperch intraspecific interactions. This suggestion is in line with the biology of the pikeperch, as they tend to form cohorts in nature (Lappalainen et al. 2003; Saulamo et al. 2005) and are likely to utilize such communication mechanism. Pikeperch are also known to express an age-driven hierarchy during reproduction, when older and bigger individuals spawn first and younger fish are following them (Lappalainen et al. 2003). Nevertheless, the was no direct evidence on how the presence of conspecifics affects prey consumption in adult pikeperch, although based on the migration patterns it could be suggested that pikeperch may express intraspecific interactions as they tend to stay in a cohort throughout the year (Koed et al. 2000). In this study, the experimental trial showed that the presence of conspecifics in proximity leads to a significant increase in per capita prey consumption of adult pikeperch. It may be suggested that the nature of such effect is related to alarm cues released by predator or prey, inducing prey consumption. These findings suggest a further investigation of alarm cues in pikeperch can complete the understanding of communication between the specimens.

This study investigated the effect of water temperature, prey density, and the presence of conspecifics on the prey consumption rate of pikeperch. The results indicate the significant effect of water temperature on pikeperch predation and the potential threat of low prey availability during winter and spring. The experiments have shown that the prey consumption of pikeperch is also influenced by the presence of conspecifics, suggesting an emergence of intraspecific competition towards the specimens in proximity. These data significantly contribute to the understanding of the details of pikeperch biology and have a particular importance for the extensive aquaculture where fish are exposed to several seasons at higher stocking density. Further research on pikeperch biology could be used for the modulation of production outputs within extensive or pond-based aquaculture.

Conflict of interest

The authors declare no conflict of interest.

https://doi.org/10.17221/162/2022-CJAS

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