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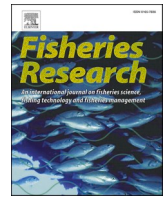
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Hydroacoustics and concurrent experimental trawling reveal extreme annual variation in the density of 0+ pikeperch in late summer

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ABSTRACT

The density and mean size of 0 + pikeperch (*Sander lucioperca*) were studied in late summer in 2004–2017 in clay-turbid and eutrophic Lake Tuusulanjärvi in southern Finland. Hydroacoustics and simultaneous experimental trawling were used to estimate the density of 0 + pikeperch. In some autumns, 0 + pikeperch was the most abundant species in the pelagic fish assemblage. However, the annual amplitude of pikeperch density was extremely high (1,300 - 19,900 individuals ha⁻¹). The density and size variations of 0 + pikeperch were analysed in relation to air temperature sums and degree days. Unexpectedly, the density of 0 + pikeperch showed no correlation with the air temperature sums or degree days, but both the mean length and weight of 0 + pikeperch correlated positively with these temperature variables. The highest correlation coefficients between mean size and temperature were found with temperature sums over 10 °C and degree days over 5 °C. The correlation between density and condition of 0 + pikeperch was negative but non-significant. The high density of 0 + pikeperch in some autumns suggests that pikeperch may play a central role in the pelagic food web in eutrophic lakes – not only as a predator of planktivores but also by its own planktivory.

1. Introduction

The first growing season is the most critical period in fish life. During the first summer, mortality is extremely high and changes in mortality induce large differences in abundance in autumn. Abundance is highest at the time of hatching but begins to drastically reduce immediately after. A higher growth rate is generally seen in lower mortality and higher abundance after the first growth season than in years with a slower growth rate (Sogard, 1997). Further, higher abundance at the end of the first growing season correlates with stronger year classes and higher catches in the following years. This is most apparent in fish species which have a short lifespan or show large variations in year-class strength or have both characteristics (Krause and Palm, 2008; Kangur et al., 2007; Pekcan-Hekim et al., 2011).

Pikeperch (*Sander lucioperca*) is a common pelagic predatory fish species that is found in many large lakes in Europe (Lammens et al., 1992; Wysujack et al., 2002; Argillier et al., 2003; Kopp et al., 2009; Nöges et al., 2016). It is also highly valued in the recreational and commercial fishery (Johnston et al., 2013; Heikinheimo et al., 2014;

Mustamäki et al., 2014; Ginter et al., 2015). It prefers warm waters up to 30 °C or even more (Hokanson, 1977; Souchon and Tissot, 2012). In the northern latitudes, water temperature seldom or never attains such high levels and, consequently, positive effects of summer temperature on juvenile and adult growth, abundance and future yields have been found in many studies (Buijse and Houthuijzen, 1992; Mooij et al., 1994; Lappalainen et al., 2000; Kjellman et al., 2001; Heikinheimo et al., 2014; Specziár and Turcsányi, 2018).

Continuous water temperature measurements are not always available, and hence daily air temperature has often been used as a proxy for water temperature (e.g. Lappalainen et al., 2005a; Chezik et al., 2014). Degree days or different temperature sums have been widely used to analyse differences in growth among fish populations in larger geographical areas but also in smaller areas or within only one population (Lappalainen et al., 2005a; Uphoff et al., 2013; Chezik et al., 2014). In a meta-analysis of pikeperch growth based on the von Bertalanffy growth equation in different populations, Nolan and Britton (2019) found that the growth coefficient K had a unimodal maximum at latitudes 45–55° N and then decreased towards both the north and

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south. Similarly, pikeperch lengths at ages 2 and 4 years decreased northward from 58° to 66° N in lakes (Lappalainen and Malinen, 2002). Nolan and Britton (2019) suggested that the maximum growth rate was due to more optimal temperatures in the central parts of the distribution range of pikeperch, and probably factors other than temperature caused a decreased growth rate south of 45° N. However, there were large differences in the growth rate between populations even at the same latitudes (Nolan and Britton, 2019). Nolan and Britton (2019) further discussed the possible effects of density-dependent factors on growth, but such studies are few for pikeperch (Mooij et al., 1994; Lappalainen et al., 2009; Saulamo et al., 2020).

Evaluation of the density of 0 + pikeperch is needed to estimate whether the stock suffers recruitment overfishing, i.e. when intensive fishing depletes spawning stock to such a low level that it reduces the number of juveniles. This is a matter of concern especially in Finland, because intensive gill-net fishing also targets immature and small pikeperch (Ruuhijärvi et al., 2005; Milardi et al., 2011; Vainikka and Hyvärinen, 2012). The low density of juveniles from year to year would strongly support an increase in the minimum mesh size for the gill-net fishery. In addition, information on the density and size of 0 + pikeperch enables forecasting of the strength of future recruiting year classes (Lappalainen et al., 1995, 2000; Pekcan-Hekim et al., 2011; Heikinheimo et al., 2014). If there are two or more successive weak year classes, the future spawning stock and catches can be secured with juvenile stocking. Studying the effect of air temperature may yield a shortcut for planning the stocking – if the relationship between the temperature and the year-class strength is strong and positive, then the time-consuming estimation of juvenile densities may be replaced with analysis of appropriate temperature statistics alone.

The reliable estimation of juvenile density is difficult because the occurrence of juveniles may be patchy both vertically and horizontally, which makes heavy demands on sampling. Patchiness can also change during the day or growing season (Urho, 1997; Malinen et al., 2005a). Therefore, the estimation of juvenile density requires high sampling effort and good knowledge of the studied species (Urho, 1997; Buijse et al., 1992; Olin and Malinen, 2003). In research, 0 + pikeperch have usually been sampled with gear like a seine or trawl (Sutela and Hyvärinen, 2002; Kjellman et al., 2003; Lappalainen et al., 2005b; Ginter et al., 2012; Blabolil et al., 2016). The use of this gear can be problematic because it cannot be used efficiently in all habitats, and comparison of the catches and obtained abundance between gear types is difficult (Blabolil et al., 2016). One possible way to overcome these problems is to use hydroacoustics. In relatively small lakes, hydroacoustics enables high areal coverage even with a one-day survey. To our knowledge, however, hydroacoustics has not been applied in the estimation of 0 + pikeperch in late summer, but there are studies that focused on both perch (*Perca fluviatilis*) and pikeperch larvae and juveniles in early summer (Čech et al., 2005, 2007; Kratochvíl et al., 2010; Sajdlová et al., 2017). Hydroacoustics should always be supported by experimental fishing to determine the species distribution, preferably with active gear such as a trawl (Simmonds and MacLennan, 2005). In addition, during the survey, pikeperch juveniles should be pelagic, i.e. avoid the bottom dead zone of echo sounder and littoral areas outside the acoustic sampling area.

Here, the density and size of 0 + pikeperch and other fish species were studied in early autumn in 2004–2017 in the pelagic areas of Lake Tuusulanjärvi, a clay-turbid and eutrophic lake located in southern Finland. The density of 0 + pikeperch was estimated as ind. ha⁻¹ based on hydroacoustics and simultaneous experimental trawling. The mean lengths, weights and length distributions of 0 + pikeperch were determined in each year from the experimental trawl catches. The skewness of the length distribution was estimated, partly to add a variable that describes the shape of the length distribution and partly because the positive skewness indicates the onset of piscivory (van Densen, 1985; Buijse and Houthuijzen, 1992). When the shift from zooplanktivory to piscivory has passed, the skewness of the length distribution of 0 +

pikeperch turns from positive (mean lengths in autumn between 6 and 11 cm; Lappalainen et al., 2000) to negative (mean lengths in autumn between 11 and 17 cm; Buijse and Houthuijzen, 1992).

The main aim of the present study was to study the possible effects of summer temperature on the variation of pikeperch density and size at the end of the first growing season. Because these variables largely determine the year-class strength and are connected with future catches (Lappalainen et al., 1995, 2009), knowledge of their possible relationship with temperature would be useful for management purposes. In addition, the aim was to evaluate whether recruitment overfishing takes place in Lake Tuusulanjärvi, which would be indicated by a continuously low density of 0 + pikeperch. The corresponding hypotheses of the study were that temperature correlates positively with density (i) and with mean size of 0 + pikeperch (ii) at the end of the first growing season (Buijse and Houthuijzen, 1992; Lappalainen et al., 1995). The intra-specific competition at high 0 + densities should reduce the condition of juveniles, seen as a negative correlation between density and condition (iii). Similarly, interspecific competition between 0 + pikeperch and other pelagic species should be seen as a negative correlation between size of 0 + pikeperch and the density of other species (iv). Furthermore, we hypothesized that the skewness of the length distribution is correlated negatively with the mean length (v).

2. Materials and methods

2.1. Study lake

The present study was carried out in eutrophic Lake Tuusulanjärvi, southern Finland (60° 25' N, 25° 04' E). The total area of the lake is 595 ha, the mean depth 3.2 m and the maximum depth 10 m. The bottom consists mainly of clay and mud. The water is clay-turbid (Secchi depth ca 0.6 m, Herta database), and a high phosphorus concentration (ca 90 µg l⁻¹, Horppila et al., 2017) supports frequent cyanobacterial blooms. Since the end of the 1990 s, the lake has been managed with intensive fishing of planktivorous and benthivorous fish as well as oxygenation by pumping of epilimnetic water into the hypolimnion, which has frequently broken down the temperature stratification (Saarijärvi and Lappalainen, 2004; Rask et al., 2020). The management fishing catch consists mainly of common bream (*Abramis brama*), roach (*Rutilus rutilus*), white bream (*Abramis bjoerkna*) and smelt (*Osmerus eperlanus*), while pikeperch is the most abundant predatory fish species (Rask et al., 2020). Pikeperch is the most important species for local fishermen facing the very effective gill-net fishery, which has initiated a fear of recruitment overfishing. The spawning areas of pikeperch are located at 1–4 m depth in the northern and southern banks of the deep area (Lehtonen et al., 2006). The density of 0 + pikeperch was estimated using various seine nets and trawls during the years 1998–2003 (Kervinen et al., 2004) but these estimates were not applicable due to high variation between the hauls and difficulties obtaining satisfactory horizontal and vertical coverage. Estimation of the strength of the present year class is considered to be important to avoid recruitment overfishing and for evaluating the possible need for juvenile stocking.

2.2. Hydroacoustics and trawling

The hydroacoustic fish density was estimated by echo surveys during late August to early September in 2004–2017. To estimate the proportion, length distribution, and density of each species in the surface blind zone of the echo sounder, a simultaneous trawl was accomplished. Surveys were done during the daytime, which has proved to be a suitable time in clay-turbid Finnish lakes (Malinen and Tuomaala, 2005; Malinen, 2018), along seven constant and equidistant transects (0.5–1.5 km in length) at intervals of 200 m covering areas > 5 m deep (Malinen, 2018). The location of the first transect was randomized before the first survey. The acoustic equipment consisted of a Simrad EY500 echo sounder equipped with a split-beam transducer ES120-7 C (with

operating frequency 120 kHz and beam opening angle 7° at –3 dB level). The speed of the boat was ca. 7 km/h and the depth of the transducer ca. 0.6 m. Pulse duration was set to 0.3 ms, ping rate to ‘maximum value’ and the minimum target strength to –65 dB. The transducer was calibrated using a standard copper sphere with Simrad’s LOBE program.

The trawling was conducted in high-density areas and layers because the species and length distributions within these aggregations have the greatest effect on the acoustic density estimate. In addition, to estimate the fish density in the surface blind zone of the echo sounder, 1–2 hauls per survey were taken from 0 to 2 m depth at randomized locations. During most surveys, the trawl was hauled from four depth layers covering almost the whole water column. The trawl had a height of 2–4 m and width of 5–8 m, and the cod-end mesh size was 3 mm. In surface trawling (0–2 m), the height of the trawl was always 2 m. The length of the trawl hauls varied between 0.5 and 2 km and the average towing speed was ca 3 km/h. From each haul, either the whole catch or a random sample was taken for analyses.

The fish density of each transect was computed by echo integration, because the very low proportion of single echoes in most surveys hampered the use of echo counting. The integrator threshold was set to –60 dB based on a detailed study conducted in nearby Lake Hiidenvesi (Malinen et al., 2005b). The total backscattering coefficient (s_a , MacLennan et al., 2002) was calculated by the EP500 software and the mean cross section (σ) was determined by using the length distribution of trawl catches and the relationship between fish length and target strength:

$$\text{smelt (Peltonen et al., 2006): } TS = 23.4 \log_{10} TL - 68.7 \quad (1)$$

$$\text{other fish species (Malinen, 2018): } TS = 17.3 \log_{10} TL - 64.5 \quad (2)$$

$$\sigma_{sp} = 4\pi 10^{(TS/10)} \text{ (m}^2\text{)} \quad (3)$$

where

TS = target strength (dB).

TL = fish total length in cm.

σ_{sp} = spherical cross section (should be used instead of a backscattering cross section when calculating fish density from s_a value computed by the EP500 program; Simrad, 1995).

The fish density of each depth layer of the transect was computed as s_a/σ (Simmonds and MacLennan, 2005), and it was divided into species-specific estimates based on species distribution in the trawl catch from that layer. The density in the whole transect was computed by summing the densities in all depth layers. Finally, the mean fish density in the whole study area was computed using the transect lengths as weights (Shotton and Bazigos, 1984) and the 95% confidence limits were estimated based on the Poisson distribution (Jolly and Hampton, 1990). Small common bream and white bream (< 75 mm in total length (TL)) were treated as one group (small *Abramis*), because exact species determination would have been very time-consuming. Due to the lack of an unbiased method for combining the variances of trawling and acoustic estimates, the confidence intervals were computed only for those surveys in which the fish biomass in the surface blind zone was negligible. If the 95% confidence limits between successive years were non-overlapping, the change was considered to be statistically significant ($p < 0.01$) (Austin and Hux, 2002).

The TL and weight of pikeperch were measured at an accuracy of 1 mm and 0.01 g. Pikeperch age was checked frequently from the scales of juveniles longer than 80 mm TL to exclude the possibility that they would have been 1 + juveniles. However, the length distributions of 0 + and older pikeperch were non-overlapping and age determinations were actually not relevant. The possible effect of density on the condition of 0 + pikeperch was analysed using weight residuals (Lappalainen et al., 2005b) from the linear log-transformed length–weight relationship including all years ($N = 5812$). After obtaining individual weight residuals, annual mean residuals were calculated. The relationship

between annual residuals and the density of pikeperch was studied with non-parametric Spearman correlation. The number of degrees of freedom (df) was reduced by one as suggested by García-Berthou (2001) because of the use of residuals from the length–weight relationship.

2.3. Temperature thresholds and statistical methods

The temperature estimates were calculated using mean daily air temperatures from Helsinki-Vantaa Airport (60° 19' N, 24° 58' E). The distance between the airport (51 m above sea level (asl)) and the lake (38 m asl) is about 11 km. Two different temperature sums were calculated from 1 June, which matches the typical spawning date of pikeperch in the lake (Lehtonen et al., 2006). In each year, temperature estimates were calculated until one day before capture:

$$TS = \sum_{i=1}^d AT, AT \geq TH, \text{ or,} \quad (4)$$

$$DD = \sum_{i=1}^d AT - TH, AT \geq TH \quad (5)$$

where TS is temperature sum, DD is degree-day sum, d is one day before juveniles were caught, i is 1 June if air temperature (AT) \geq TH – the threshold value of 5, 10, 15 or 20 °C. The use of 0, 5, 10 and 15 °C thresholds was suggested by Chezick et al. (2014), but instead of using 0 °C here, the threshold of 20 °C was selected. The reason for dropping the 0 °C threshold was that the temperature was always over 5 °C, so the temperature sums over the 0 and 5 °C thresholds were the same. The possible effects of the temperature sums and degree days on the density, length and weight of 0 + pikeperch were evaluated with Spearman correlation analysis. Skewness was estimated from length distributions divided into 5 mm bins (Fig. 1), and the number of juveniles in each 5 mm bin was divided by the total number of juveniles in each year. The skewness was estimated with R package e1071 (Meyer et al., 2019). The R program was applied in all statistical analyses (R Core Team, 2015).

3. Results

3.1. Pelagic fish assemblage in Lake Tuusulanjärvi

In Lake Tuusulanjärvi, the pelagic fish density and species distribution showed high annual variation. The non-overlapping confidence intervals (95%) of many successive years (2006 vs 2007, 2012 vs 2013, 2013 vs 2014, and 2016 vs 2017) revealed that the fish density changed repeatedly between two successive summers ($p < 0.01$) (Fig. 2). The

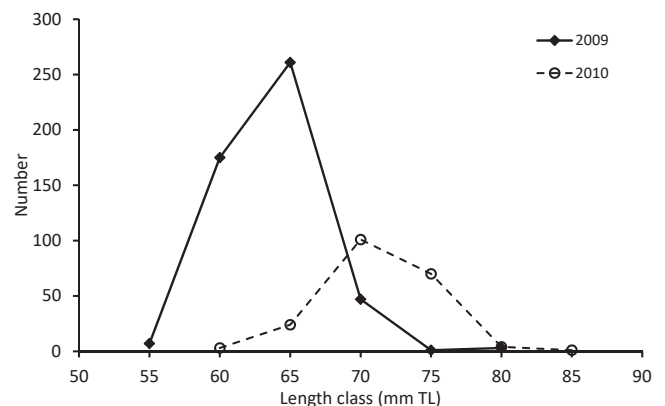


Fig. 1. Two examples of length distribution in late summer in 2009 (skewness = 2.69, total number of 0 + pikeperch, $N = 494$) and in 2010 (skewness = 0.68, total $N = 203$). The y-axis is the number of 0 + pikeperch in each length class (55, 60, 65 up to 85 mm).

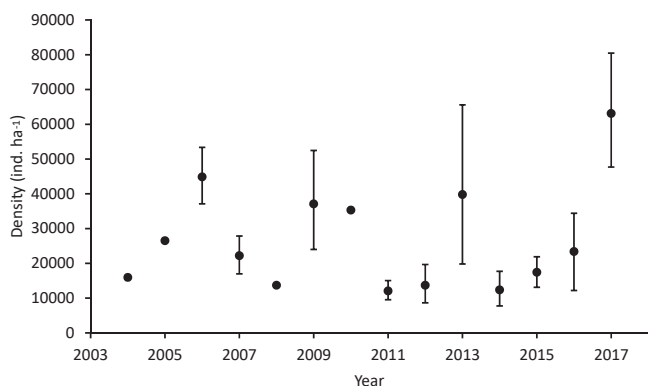


Fig. 2. Total fish density in pelagic areas (depth > 5 m) with 95% confidence intervals based on hydroacoustics and experimental trawling during years 2004–2017 in Lake Tuusulanjärvi. Due to the lack of an unbiased method for combining the variances of trawling and acoustic estimates, the confidence intervals were computed only for those surveys in which the fish biomass in the surface blind zone was negligible.

pelagic fish assemblage was generally dominated by small-sized fish (< 100 mm TL), which accounted for over 95% of the total fish density. The majority of these small fish were 0 + juveniles (0 + pikeperch, 0 + smelt and small *Abramis*).

0 + pikeperch was the most abundant species in the pelagic fish assemblage in autumns 2005, 2006 and 2013, whereas in 2008 and 2017, the 0 + pikeperch density was low (Table 1). The average 0 + pikeperch density was 7674 ind. ha⁻¹, varying from ca 1000 to almost 20,000 ind. ha⁻¹ (Table 1). The coefficient of variation of 0 + pikeperch density was 86.0%. The other abundant species in the pelagic area were smelt, small *Abramis* and perch.

In the same way as density, the mean length and weight of 0 + pikeperch showed large annual variations in different autumns (Table 2). Annual mean lengths varied from 49.5 to 77.7 mm TL and mean weights from 0.77 to 2.69 g. Autumnal length distributions of 0 + pikeperch were all positively skewed, and skewness varied from 0.68 to 2.50 (Table 2).

3.2. Effects of temperature

The temperature estimates over the four thresholds used showed no correlation with the density of 0 + pikeperch (Table 3), and therefore hypothesis (i) was not supported (Fig. 3). On the other hand, most of the analysed temperature estimates were positively correlated with the mean length and weight of 0 + pikeperch (hypothesis ii) (Table 3). In general, the temperature sums showed stronger correlations with size of 0 + pikeperch than degree days. The strongest correlation was found with temperature sums over the 10 °C threshold in both weight and length (Fig. 4), while temperature sums over the 20 °C threshold were not correlated with either the mean length or weight (Table 3). All correlations between temperature estimates and skewness were negative but non-significant (Table 3).

3.3. Correlations between biotic factors

The log-transformed lengths described 97.0% of the log-transformed weights in the pooled data of 0 + pikeperch (N = 5812). The parameters for the length–weight relationship for the whole study period was log (estimated weight (g)) = -5.27 + 3.04 * log(length (mm TL)). The annual mean residuals from the length–weight relationship were negatively correlated with the density of 0 + pikeperch, but the correlation or heteroscedasticity between these variables was non-significant (Spearman correlation: $r_s = -0.341$, $p = ns$, $df = 13$; heteroscedasticity, Breusch–Pagan test: $BP = 2.40$, $p = ns$, $df = 1$) (Fig. 5).

Table 1 Density estimates (individuals ha⁻¹) of 0 + pikeperch in > 5 m deep areas based on hydroacoustics and trawling, and the proportion of each fish species relative to the total fish density. Density was estimated in late August – early September. Small *Abramis* includes common bream and white bream, and other species include mainly bleak (*Alburnus alburnus*) and rudd (*Scardinius erythrophthalmus*). Air temperature is summed from 1 June to the day before sampling. TS is temperature sum and DD degree days over used temperature thresholds (5, 10, 15 and 20 °C).

Year	Fish species										Air temperature sums						
	0 + pikeperch	0 + pikeperch (%)	Smelt (%)	Small <i>Abramis</i> (%)	Roach (%)	Common bream (%)	White bream (%)	Perch (%)	Other species (%)	TS > 5	TS > 10	TS > 15	TS > 20	DD > 5	DD > 10	DD > 15	DD > 20
2004	3701	23.3	34.1	8.6	0.1	1.6	4.0	27.7	0.7	1316	1316	828	151	891	466	123	11
2005	14992	44.6	41.4	2.9	0.5	0.6	0.8	7.3	1.8	1367	1360	1086	280	957	550	186	20
2006	19934	44.1	9.6	29.8	0.8	0.2	2.4	12.8	0.4	1459	1449	1308	392	1054	649	273	32
2007	3606	16.0	26.9	19.4	2.6	18.5	9.1	0.7	6.8	1537	1517	1289	361	1087	637	224	21
2008	1251	9.0	33.1	4.1	1.6	23.1	12.4	0.0	16.7	1376	1376	889	85	941	506	124	5
2009	12277	33.3	52.1	1.6	3.7	0.2	0.6	1.3	7.3	1338	1299	1017	127	918	509	162	7
2010	7899	22.5	0.7	43.2	5.0	0.5	0.4	22.7	5.0	1599	1599	1356	824	1179	759	366	104
2011	2525	20.8	34.3	17.8	0.3	14.9	0.6	0.0	11.4	1526	1526	1375	648	1116	706	310	68
2012	3646	26.2	47.3	7.5	1.3	9.4	3.0	0.4	4.9	1542	1523	1049	147	1052	563	149	7
2013	19643	49.6	4.0	44.7	0.8	0.3	0.2	0.5	0.1	1550	1550	1353	491	1120	690	273	31
2014	3497	28.4	25.7	30.8	0.0	8.1	0.4	6.1	0.6	1528	1503	1110	694	1088	653	285	74
2015	9837	57.0	27.1	0.2	3.0	1.3	0.0	11.4	0.0	1340	1340	910	66	915	490	115	6
2016	3209	13.8	50.8	0.8	0.1	1.8	0.1	31.7	1.0	1498	1480	1126	146	1043	590	181	6
2017	1426	2.2	97.4	0.1	0.0	0.1	0.1	0.1	0.0	1349	1317	897	0	909	477	117	0

Table 2

Mean size of 0 + pikeperch in length (mm total length) and weight (g) in late August or early September in Lake Tuusulanjärvi. Skewness is based on length distribution in each year. Annually more than 200 specimens of pikeperch were measured.

Year	Length	Weight	Skewness	Sampling date
2004	61.3	1.47	1.31	25 Aug
2005	60.2	1.64	2.31	22 Aug
2006	63.6	1.58	2.01	21 Aug
2007	77.7	2.97	1.89	30 Aug
2008	50.0	0.84	1.28	27 Aug
2009	61.5	1.36	2.69	24 Aug
2010	69.2	2.23	0.68	24 Aug
2011	75.9	3.37	1.42	22 Aug
2012	70.7	2.09	2.24	7 Sep
2013	64.5	1.59	1.80	26 Aug
2014	64.2	1.68	2.23	28 Aug
2015	67.1	1.94	2.37	25 Aug
2016	66.9	1.80	1.43	31 Aug
2017	49.5	0.77	2.50	28 Aug

Table 3

Spearman correlation coefficients (r_s) between air temperature (At) sums with density, size and skewness. Air temperature sums (TS) and degree days (DD) were calculated over four thresholds (5, 10, 15 and 20 °C) from 1 June until the day before survey (ns = not significant, ** = 0.001 < p < 0.01, * = 0.01 < p < 0.05, N = 14).

Threshold (°C)	Density r_s	Length r_s	Weight r_s	Skewness r_s
TS At > 5	-0.007 ^{ns}	0.635*	0.604*	-0.398 ^{ns}
TS At > 10	-0.024 ^{ns}	0.697**	0.692**	-0.512 ^{ns}
TS At > 15	0.240 ^{ns}	0.640*	0.648*	-0.310 ^{ns}
TS At > 20	0.088 ^{ns}	0.319 ^{ns}	0.407 ^{ns}	-0.352 ^{ns}
DD At > At- 5	0.138 ^{ns}	0.618*	0.618*	-0.415 ^{ns}
DD At > At- 10	0.160 ^{ns}	0.604*	0.613*	-0.389 ^{ns}
DD At > At- 15	0.182 ^{ns}	0.451 ^{ns}	0.508 ^{ns}	-0.407 ^{ns}
DD At > At- 20	0.198 ^{ns}	0.291 ^{ns}	0.368 ^{ns}	-0.225 ^{ns}

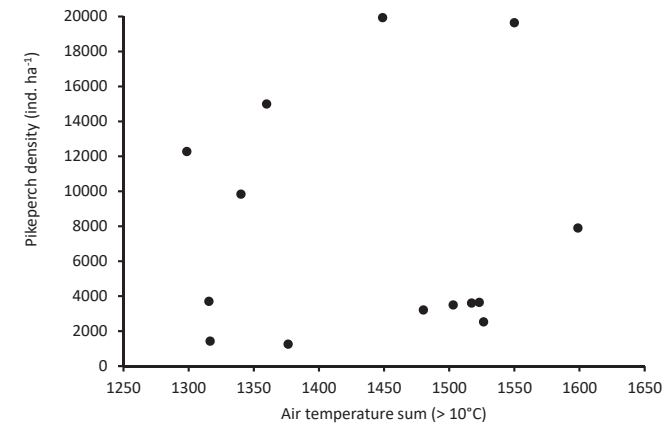


Fig. 3. Relationship between air temperature sum (threshold > 10 °C) and density of 0 + pikeperch.

Thus, hypothesis (iii) was not supported.

The density of 0 + pikeperch was not correlated either with the mean size (length: $r_s = 0.020$, $p = ns$, $N = 14$; weight: $r_s = -0.024$, $p = ns$, $N = 14$) (Fig. 6) or the skewness of the length distribution, even though the latter relationship was positive ($r_s = 0.271$, $p = ns$, $N = 14$). Both the length and weight of 0 + pikeperch were negatively correlated with the summed densities of the other fish species (iv), albeit not significantly (length: $r_s = -0.367$, $p = ns$, $N = 14$; weight: $r_s = -0.288$, $p = ns$, $N = 14$). As hypothesized (v), the correlation between the skewness and mean lengths was negative, but it was also non-significant ($r_s = -0.222$, $p = ns$, $N = 14$).

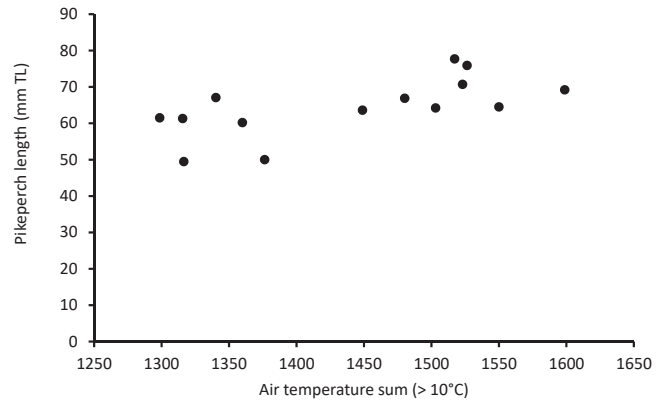


Fig. 4. Relationship between air temperature sum (threshold > 10 °C) and mean total length (TL) of 0 + pikeperch.

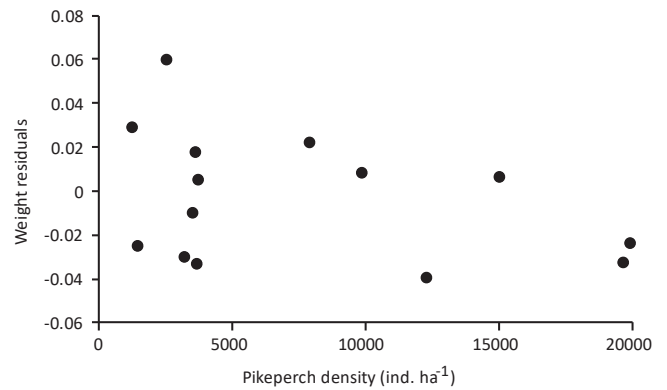


Fig. 5. Pikeperch density in relation to mean annual weight residuals.

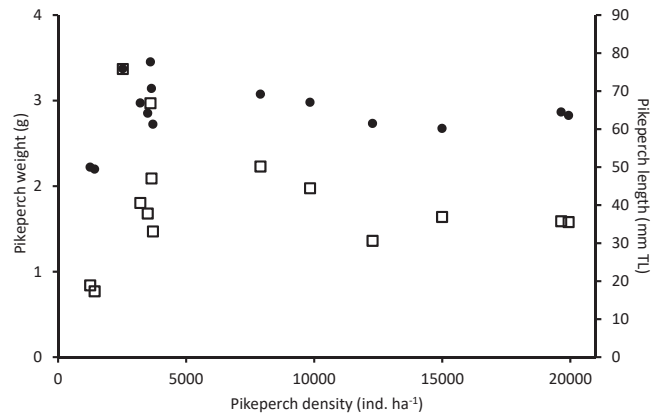


Fig. 6. Density of 0 + pikeperch in relation to mean weight (g) (open rectangles □) and mean total length (mm) (black dots ●) (TL is total length).

4. Discussion

As hypothesized, both temperature estimates (temperature sums and degree days) correlated positively with size of 0 + pikeperch. Opposite to our hypothesis, the correlation between temperature and 0 + density was negligibly low and non-significant. The annual density of 0 + pikeperch was, however, very high in several years, but despite this, there were no significant correlations between juvenile density and size, either with the mean length or weight. In years when the 0 + density of pikeperch was high, the condition of 0 + pikeperch was lower, but the correlation between density and condition was non-significant. Thus, it

appears that in Lake Tuusulanjärvi, the summer temperature plays only a minor role in the density variations of 0 + pikeperch, and the strength of year class is mainly determined by other, unstudied factors.

The negligible effect of temperature on density, as well as surprisingly high densities of 0 + pikeperch in some years, suggest that 0 + pikeperch face low predation pressure. This is probably also seen in a relatively weak positive correlation between the temperature and mean size. The low predation pressure could be expected, because the pelagic fish assemblage of Lake Tuusulanjärvi is strongly dominated by non-predatory fish species. The dense smelt population might be a potential threat for pikeperch juveniles because smelt may turn piscivorous at a length of 8 cm (Vinni et al., 2004). However, the smelt population in Lake Tuusulanjärvi consists largely of 0 + smelt, which do not reach this size by late August (Hietala, 2017). In addition, turbid water may considerably reduce the predation efficiency of the scarce piscivorous fish present (Abrahams and Kattenfeld, 1997; Radke and Gaupisch, 2005). High turbidity may also diminish the positive relationship between the growth rate and survival and hence increase the survival of smaller juveniles (Abrahams and Kattenfeld, 1997; Pekcan-Hekim and Lappalainen, 2006). According to experiments by Abrahams and Kattenfeld (1997), in clear water the predator more often selected small prey, whereas in turbid water, the size selection of prey was random. Because such size-selective predation should increase mean size more in clear water lakes than in turbid ones, the low correlation coefficients (although significant) between temperature and juvenile size may be at least partly explained by clay turbidity and phytoplankton-induced turbidity.

Another possible mechanism behind the low correlations between temperature and size may be the interannual variation in the timing and opportunities to shift piscivory. The shift is important for juvenile pikeperch because increased growth rate decreases mortality (Buijse and Houthuijzen, 1992). The increased growth of piscivorous pikeperch juveniles is reflected in the positive skewness of the length distributions (van Densen, 1985; Buijse and Houthuijzen, 1992), which was also observed in Lake Tuusulanjärvi. This indicates that at least some 0 + pikeperch turned piscivorous by late summer. As an abundant small-sized pelagic fish, smelt is the most obvious first prey species for piscivorous pikeperch juveniles (Sutela and Hyvärinen, 2002; Lappalainen et al., 2005b). However, in Lake Tuusulanjärvi, the smelt stock has extreme year-to-year variation (Rask et al., 2020), which may partly explain the high variations in mean size and density of 0 + pikeperch and low correlations with temperature.

In addition to the shift to piscivory, the discontinuous supply of zooplanktonic food may increase mortality and reduce the growth rate of 0 + pikeperch (van Densen et al., 1996). Especially during the first week of exogenous feeding, a shortage of suitable prey may be very important (Ljunggren, 2002). Later, cannibalism can also increase the mortality of 0 + pikeperch, especially in warmer summers when the density of 0 + pikeperch is higher than normal (Frankiewicz et al., 1999; Argillier et al., 2003; Lappalainen et al., 2006). In a riverine reservoir, the recruitment of 0 + pikeperch was negatively affected by perch predation (Blabolil et al., 2016). Blabolil et al. (2016) also found that when the recruitment estimates for 0 + pikeperch were based on gill-net catches, the effects of temperature in April were negative and those of water level changes in April and May positive. However, Blabolil et al. (2016) warranted that the recruitment estimated with gill nets could be biased because small pikeperch are not effectively caught with gill nets.

At first glance, the negligible relationship between temperature and density contradicts the present consensus on the positive effect of first summer temperature on the strength of future recruiting year class (Buijse and Houthuijzen, 1992; Pekcan-Hekim et al., 2011; Heikinheimo et al., 2014). However, the density of juveniles at the end of the first growing season does not necessarily correlate with the strength of future year class. In northern latitudes, the mortality during the first winter decreases as the body size increases (Lappalainen et al., 2000, 2005b). Thus, it is possible that the positive effect of temperature in Lake

Tuusulanjärvi on the strength of the future year class is mediated mainly via the increased size of juveniles improving survival during the first winter and not directly via increased density at the end of the first growing season.

The temperature estimates were calculated both by summing up the daily mean air temperatures over each threshold and by subtracting the threshold value from the daily air temperature (Neuheimer and Taggart, 2007; Chezik et al., 2014). Interestingly, air temperatures summed up directly over the used thresholds better captured the differences between different summers than degree days. Notably, both temperature estimates correlated positively with the size of 0 + pikeperch. Kjellman et al. (2001) found that degree days based on water temperature better explained the growth of 0 + pikeperch than those based on air temperature. However, in their study, both models of regression between growth and degree days based on air or water temperature were highly significant. Therefore, we could expect higher correlation coefficients if daily water temperatures were used, and this could change these correlation patterns to favor the degree days.

Although the data did not support the hypothesis about the density-dependent condition or growth of 0 + pikeperch, it appears that density and growth may be connected – not density and mean weight but density and variation in mean weight. The data show heteroscedasticity, which was not significant, but the variations in mean weight were much higher in low than in high 0 + juvenile densities. It seems possible that only very high density can have notable negative effects on condition or growth, and at low to moderate density the mean weight may be determined by other factors, particularly temperature. In other words, it appears that in relatively low densities, cool summers produce small juveniles and warm summers large juveniles, whereas when density is high, juveniles remain small, irrespective of the temperature.

The observed high 0 + pikeperch densities showed that there was not serious recruitment overfishing during the studied years in Lake Tuusulanjärvi. By contrast, very high densities in some years may have contributed to the small size of juveniles at the end of the first growing season, inducing high mortality during the first winter (Lappalainen et al., 2000, 2005b) and hence a possible negative effect on the year-class strength. The negligible correlation between temperature and density, as well as only a weak correlation between temperature and mean size of 0 + pikeperch, suggest that temperature may not be a useful tool in planning juvenile stockings, at least in Lake Tuusulanjärvi.

The method applied – daytime vertical hydroacoustics and simultaneous fishing with a small trawl – is vulnerable to various sources of bias. One of the most obvious is the bottom dead zone of the echosounder, because perch and pikeperch juveniles may stay close to the bottom during the day (Kratohvil et al., 2010; Vejřík et al., 2016). However, in August–September in Lake Tuusulanjärvi, pikeperch juveniles prefer the mid-water layer also during the daytime. This actually appears to be typical behavior also for other pelagic fish in clay-turbid and eutrophic lakes in Finland, and the daytime has proven to be as suitable a survey time as the night-time (Malinen and Tuomaala, 2005; Malinen, 2018). The ultimate cause of the preference for mid-water is most likely low visibility, which reduces the predation threat and probably also hypolimnetic oxygen depletion, which is usual in these lakes during late summer stagnation. It is still possible that we have slightly underestimated the density of pikeperch juveniles due to the bottom dead zone. Another obvious source of bias is the variation in catchability with the size of fish. Large fish may more likely avoid an incoming trawl than small fish (Sajdlová et al., 2015), which induces bias in the estimated size and species distributions and hence biases the density estimates when echo integration is applied. Unfortunately, in Lake Tuusulanjärvi, the target strength distributions, which would have given independent information on the presence of large fish, were not applicable due to a very low proportion of single-fish echoes (typically < 10% of backscatter). Although high turbidity should reduce the escapement, estimates may still contain some bias due to this factor. To conclude, our density values should be considered only approximate

estimates but because the methods have been similar from year to year, serious biases in the conclusions concerning our hypotheses are unlikely.

The present study revealed a very surprising finding: the density of 0+ pikeperch was so high in some years that pikeperch, which is traditionally considered a predatory fish species, may occasionally even be a key planktivore of the pelagic food web in Lake Tuusulanjärvi. Juvenile 0+ pikeperch feed on zooplankton, and their consumption of cladoceran zooplankton (Ginter et al., 2011) may be of great importance in controlling the biomass of phytoplankton and hence also cyanobacterial blooms. Perhaps the effect of pikeperch is in some circumstances even more important than that of cyprinid fish and smelt, whose dense stocks are usually considered to be responsible for the lowered filtering capacity of zooplankton in eutrophic lakes (Meijer and Hosper, 1997; Sarvala et al., 1998; Ruuhijärvi et al., 2020). The results from Lake Tuusulanjärvi underline that more information is needed on the abundance of 0+ pikeperch and their role in the pelagic food web.

Credit author statement

Jyrki Lappalainen: Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing, Visualization. **Tommi Malinen:** Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization..

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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