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Research Article

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Comparisons of day-time and night-time hydroacoustic surveys in temperate lakes

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Abstract – In recent years, due to an increased need for non-intrusive sampling techniques, hydroacoustics has attracted attention in fishery science and management. Efforts to promote standardisation are increasing the accuracy, efficiency, and comparability of this method. The European Water Framework Directive and the Standard Operating Procedures for Fisheries Hydroacoustic Surveys in North American Great Lakes has recommended that surveys be conducted at night. At night, fish usually disperse in the water column, thus allowing for single echo detection and subsequent accurate fish size estimation, while day-time schooling behaviour hampers the estimation of fish size. However, sampling during the day would often be safer and cheaper. This study analyses how fisheries hydroacoustic results differ between day-time and night-time surveys, using data from 14 natural temperate lakes of various size. Data collected during the day and night at two depth layers linked to thermal stratification were compared in terms of acoustic scattering strength, target strength, and biomass estimates. The results showed a significant correlation between day-time and night-time estimates, though biomass in the upper layer was biased for day-time surveys, mainly due to incorrect fish size estimates resulting from rare single echo detections and schooling behaviour. Biomass estimates for the lower depth layer did not significantly differ between the two diel periods. Thus, this study confirms that hydroacoustic sampling in temperate lakes should be performed at night for accurate fish stock biomass estimates.

Keywords: Fish stock / diel migration / lake / standardisation / behaviour

1 Introduction

Hydroacoustics is now a recognised method (Draštík et al., 2017) for estimating the abundance and biomass of freshwater fish populations (Pollom and Rose, 2016), especially in lakes. Recent studies have shown a good relationship between biomass estimates obtained by hydroacoustics (see description in Simmonds and MacLennan, 2005) and common standard benthic gillnets described in CEN (2005) (Emmrich et al., 2012; Yule et al., 2013). Hydroacoustics must be complemented with additional sampling (e.g., gillnetting or trawling) (Kubečka et al., 2009; DuFour et al., 2019) to obtain species composition, individual fish characteristics (e.g., length and weight), and biological samples (scales, flesh, and stomachs). Hydroacoustics has been standardised in Europe (CEN, 2009) and in North America (Parker-Stetter et al., 2009). Compared to other fishery-independent methods, such as gillnetting and trawling, its main advantage is non-intrusive sampling of fish populations (Simmonds and MacLennan, 2005) and the capability of stock estimation at large scales in natural lakes (Wheeland and Rose, 2014; Morrissey-McCaffrey et al., 2018), and in reservoirs (Godlewska et al., 2016; Guo et al., 2019; Tessier et al., 2020).

Like other sampling methods, hydroacoustics has inherent biases and limitations regarding fish species discrimination, blind zones (areas close to the surface or near the lake bottom), individual variability (individual size measurements are highly variable), and varying accessibility due to fish behaviour (e.g., very shallow waters, dense macrophyte areas) (Rudstam et al., 2012). Thus, fish behaviour must be considered when defining the best survey period, with species-specific behaviour and

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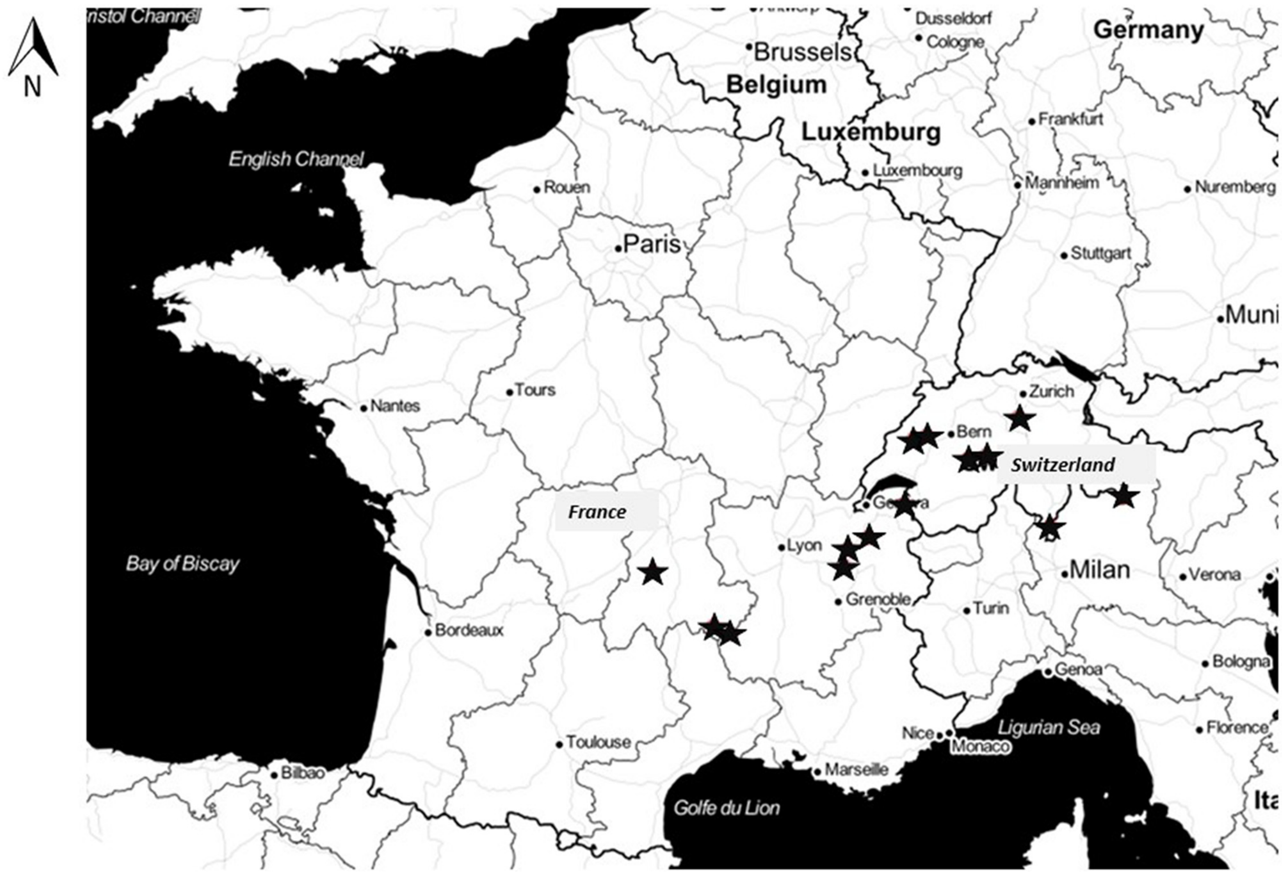

Fig. 1. Geographical location (stars) of the 14 studied lakes distributed in France and Switzerland.

spatial distributions adding uncertainty to hydroacoustic estimates. Furthermore, fish species diversity implies a high variability of behaviours and movements, according to biotic and abiotic factors (Matthews, 2012). Fish perform vertical and horizontal migrations depending on abiotic factors, such as temperature, luminosity (day, night, and lunar cycle), and turbidity, and on biotic factors such as life stage (adults, juveniles, and larvae), species interactions (e.g., prey-predator and competition), and resources (Bohl, 1979; Mehner, 2012; Sajdlová et al., 2018). Therefore, the choice of the sampling period (e.g., season and time of day) is important as it can greatly affect hydroacoustic results.

In temperate freshwater ecosystems, standard procedures (CEN, 2009; Parker-Stetter et al., 2009) recommend sampling during the night at the end of the summer, when thermal stratification separates fish species (Brandt et al., 1980; Mehner, 2012; Anderson et al., 2019). During the day-time, many species form schools, stay in littoral zones, or remain near the lake bottom (Bohl, 1979; Gliwicz et al., 2006; Říha et al., 2014). As a result, during day-time surveys, the estimation of fish size is usually difficult, leading to biased estimates (Appenzeller and Leggett, 1992). At dusk, schools disperse to locate food or optimal temperatures in the pelagic zone (Bohl, 1979; Mehner et al., 2010), facilitating night-time detection of single echoes, accurate target strength (TS) measurements, and thus representative fish size distributions (Rudstam et al., 2012).

However, night-time sampling is often more expensive, especially due to increased staff costs linked to labour-related legislation. Furthermore, it is also less safe on the small boats usually used during freshwater surveys (risk of falling asleep, risk of collision with obstacles), and especially in reservoirs, where submerged trees are frequently encountered (Coll et al., 2007; Tessier et al., 2020). While many studies have already described day-time to night-time hydroacoustic survey results (Vondracek and Degan, 1995; Guillard and Vergés, 2007; Ye et al., 2013), this study is the first, to the best of our knowledge, to compare hydroacoustic day-time and night-time data from 14 different temperate natural lakes. In this study, we compared a proxy of fish density, mean acoustic scattering strength (sA with units m^2 ha^{-1}) (MacLennan et al., 2002; Yule et al., 2013), and a proxy of fish size, mean target strength (TS with units dB) (MacLennan et al., 2002), between day and night samplings. Biomass estimates computed from these two metrics were analysed to identify differences and verify if night-time is the most appropriate sampling period, as described in the literature and standards.

2 Materials and methods

2.1 Study sites

We sampled 14 natural temperate lakes in France and Switzerland (Fig. 1). The lakes have different trophic statuses,

Table 1. Characteristics of the 14 studied lakes. DoC: degree of coverage of acoustics surveys at day-time and night-time.

Lake	Survey date	Thermocline depth (m)	Maximum depth (m)	Altitude (m)	Surface (km^2)	Trophic status	DoC day	DoC night
France								
Aiguebelette	25/10/2005	12	71	373	5.45	Mesotrophic	7.2	7.1
Annecy	17/09/2012	13	65	447	27.59	Oligotrophic	8.7	8.9
Bouchet	15/09/2005	11	27	1200	0.44	Oligotrophic	5.4	6.2
Bourget	01-02/10/2012	15	147	231	44.5	Oligo-mesotrophic	13.9	13.7
Issarlès	13/09/2005	12	110	1003	0.97	Ultra-oligotrophic	11.1	9.0
Montriond	28/09/2006	6	15	1055	0.32	Mesotrophic	7.7	5.8
Pavin	22/09/2005	10	93	1197	0.44	Oligo-mesotrophic	9.4	9.0
Switzerland								
Brienz	13-14/09/2011	20	260	564	29.8	Ultra-oligotrophic	9.3	13.3
Lugano	18-19/10/2011	10	288	271	48.7	Eutrophic	8.0	10.4
Morat	11/10/2010	15	45	429	22.8	Meso-eutrophic	8.0	10.2
Neufchâtel	03-04-05/10/2011	20	152	429	218.3	Oligotrophic	4.9	5.1
Poschiavo	13/08/2012	15	85	962	1.98	Mesotrophic	6.0	6.3
Thoune	15-16/10/2013	18	217	588	48.3	Ultra-oligotrophic	5.6	5.6
Zoug	20-21/08/2013	10	198	413	38.3	Eutrophic	11.9	11.6

ranging from ultra-oligotrophic to eutrophic, are of various shape and size (0.32 to 218.3 km^2), and include shallow and deeper lakes (maximum depth 15 to 288 m) (Tab. 1).

Temperature profiles were determined at the maximum depth of each lake using a multi-parameter probe the same week the hydroacoustic surveys were carried out. All lakes were thermally stratified at the sampling time (Deceliere-Vergès, 2010; Périat, 2012; Périat and Vonlanthen, 2013; Vonlanthen and Périat, 2013). Fish communities, which were sampled by gillnetting according to the European standard procedure (CEN, 2005), were mainly dominated by Cyprinidae, Percidae, and Salmonidae (Deceliere-Vergès, 2010; Périat, 2012; Périat and Vonlanthen, 2013; Vonlanthen and Périat, 2013).

2.2 Surveys

Hydroacoustic surveys were carried out using a Simrad EK60 echosounder (Simrad Kongsberg Maritime AS, Horten, Norway) operating at a frequency of 70 kHz, with a pulse length of 0.256 ms (Godlewska et al., 2011). The power was fixed at 100 W, and the sampling intervals were set at 5 pulses s^{-1}. The split-beam transducer has a half-power beam angle of 11° at −3 dB, transmitted vertically, and was positioned at a depth of 0.5 m below the water surface. Calibrations were performed before the surveys according to the procedure reported by Foote et al. (1987) and recommended by the manufacturer. Data were collected according to the standard protocol for hydroacoustics in Europe (CEN, 2009), during calm to moderate wind conditions, 1 h after sunset for the night survey at a mean speed of 8 km h^{-1}. Data were georeferenced using a global positioning system (GPS). The survey design, a series of equally spaced parallel transects, covering areas with depths >5 m, was similar between day-time and night-time, but due to logistic reasons, the tracks were not strictly identical between the two periods. The sampling effort was computed by calculating the degree of coverage, which is defined as the ratio between the sampling distance travelled (km) and the square root of the lake surface area (km^2) (Aglen et al., 1983). As a general recommendation, the degree of coverage should be at least 3.0 and preferably near or above 6.0. (Emmrich et al., 2012). All studied lakes had a minimum degree of coverage greater than 4.9, being mainly above 6 (Tab. 1). The acoustic data recording was limited to the first 100 m because fish are scarce at greater depths in these type of lakes (Yule et al., 2013).

For analysis, the water column was split into two layers according to the separation of fish assemblages by temperature (Mehner et al., 2010). The upper layer extended from 3 m below the lake surface to avoid the acoustic near field, where backscattering measurements are unreliable, to the thermocline depth. The lower layer started at the thermocline and extended to 0.3 m above the lake bottom.

2.3 Hydroacoustic data

For each lake, all hydroacoustic transects were merged into a single file and analysed using a whole-lake approach following Emmrich et al. (2012). This approach overcame the issue of the non-matching day- and night-time transects. Mean acoustic scattering strength (sA in m^2 ha^{-1}) and mean target strength (TS in dB), calculated in the linear domain, were computed for both depth layers. TS was converted into the fish length in centimetres (total length = TL) by inversing Love's (1971) equation:

$$\mathrm{TS} = 19.1 \log_{10}(TL) - 0.9 \log_{10}(70) - 62. \quad (1)$$

This equation was used because it was derived from several species assemblages with a large range of species and sizes, and is still commonly used and relevant (MacNamara et al., 2016; DuFour et al., 2017; Zenone et al., 2017), especially for freshwater ecosystems (Emmrich et al., 2012; Draštík et al., 2017; Morrissey-McCaffrey et al., 2018).

Table 2. Hydroacoustic survey results. Estimated mean *SA*, mean TS, and biomass from day-time and night-time surveys by lake and depth layer.

Lake	Mean TS (dB)				*SA* (m^2 ha^{-1})				Biomass (kg ha^{-1})			
	Upper layer		Lower layer		Upper layer		Lower layer		Upper layer		Lower layer	
	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
Aiguebelette	–36.95	–40.31	–36.58	–37.79	0.20	0.59	0.33	0.56	7.35	13.59	12.29	18.12
Annecy	–37.75	–47.18	–35.75	–36.03	0.56	0.73	0.65	1.17	18.15	6.81	27.24	47.55
Bouchet	–40.00	–40.43	–35.04	–33.91	0.38	0.20	0.01	0.01	9.14	4.65	0.23	0.75
Bourget	–40.23	–45.35	–37.49	–37.29	1.09	2.73	1.07	0.84	25.48	32.65	35.89	28.93
Issarles	–38.87	–35.87	–38.47	–38.22	0.04	0.02	0.02	0.01	1.20	0.79	0.44	0.37
Montriond	–57.44	–53.36	–42.7	–43.99	0.01	0.00	0.01	0.05	0.03	0.02	0.19	0.66
Pavin	–37.69	–46.85	–37.77	–38.74	0.25	0.00	0.38	0.74	8.01	0.04	12.29	21.15
Brienz	–48.24	–42.4	–43.51	–43.11	0.28	0.22	0.03	0.03	2.29	3.89	0.52	0.51
Lugano	–39.28	–45.89	–44.61	–42.77	0.11	0.11	0.08	0.03	2.84	1.23	1.05	0.47
Morat	–45.03	–43.39	–48.31	–45.03	0.39	0.23	0.02	0.01	4.91	3.57	0.12	0.17
Neufchatel	–36.15	–46.29	–35.2	–37.58	1.56	2.25	0.35	0.54	62.28	23.76	15.82	17.73
Poschiavo	–37.83	–39.79	–35.99	–40.51	0.28	0.04	0.11	0.12	8.85	0.89	4.62	2.80
Thoune	–34.76	–40.51	–37.74	–37.75	0.12	0.09	0.19	0.34	5.71	2.03	6.26	11.09
Zoug	–39.78	–47.09	–39.69	–38.81	0.84	1.14	0.08	0.15	20.95	10.85	1.98	4.20

Fish density (ρ_a) per ha was estimated using Forbes and Nakken's (1972) equation:

$$\rho_a = \frac{\boldsymbol{sA}}{4\pi^{*}10^{\mathrm{TS}/10}}. \quad (2)$$

Average individual fish weight $\overline{w}$ (kg) was calculated from individual sizes based on Carlander's (1969) equation ($w = \mathrm{TL}^3$). Then, fish biomass B (kg ha^{-1}) was calculated by multiplying mean fish density by average fish weight:

$$B = \overline{\rho}\,\overline{w}. \quad (3)$$

2.4 Data analysis

Data were analysed using the Sonar 5-Pro software (version 6.0.4) (Balk and Lindem, 2011). Lake bottoms were automatically detected by the software and then manually corrected. An exclusion zone of 0.3 m above the bottom was used to avoid false echoes from the bottom. Non-fish echoes from air bubbles, macrophytes, secondary bottom echo detections, and similar were manually removed. Furthermore, data from the surface to 3 m were removed to avoid surface noise and data from the near-field (Draštík et al., 2017). TS thresholds were set to −60 dB to include juvenile fish [i.e., greater than ~2 cm in total length, based on equation (1)] and the threshold of area backscattering strength was set 6 dB lower, at −66 dB, according to Parker-Stetter et al. (2009). Single echoes were detected using the following settings: a pulse length ratio between 0.8 and 1.3, a maximum gain compensation of 3 dB (one way), and a sample angle standard deviation of 0.3 degrees (Godlewska et al., 2011; Guillard et al., 2004). In previous analyses (Girard, 2018), the number of single echo detections was checked for elementary sampling units of 250 m in accordance with the Sawada index *Nv* (the number of fish per hydroacoustic volume sampled) (Sawada et al., 1993), as recommended in the hydroacoustic standards (CEN, 2009). When the index is greater than 0.1, the results should be analysed with caution (CEN, 2009), but no result exceeded this threshold in the surveys (Girard, 2018).

2.5 Statistical analysis

We analysed differences between mean ***sA***, mean TS, and biomass estimated during day-time and night-time hydroacoustic surveys using paired Student's t-tests or non-parametric Wilcoxon tests. Parametric Pearson or non-parametric Spearman correlation tests were used to test the correlation between the estimates from the two periods. Non-parametric tests were used when the homogeneity or normality of the data was not achieved. Furthermore, a standardised main axis (SMA) test was performed according to Warton et al. (2006). This test has previously been used to compare hydroacoustics data from two different situations (Godlewska et al., 2011; Mouget et al., 2019). This procedure is appropriate to enhance and complete linear regression, and when measurement error is unknown (Warton et al., 2006), which is the case for acoustic metrics. The SMA evaluates whether the major-axis regression results for the comparison of day-time and night-time periods follow a 1:1 line, which would indicate no difference. In other words, it tests the null hypothesis of intercept zero and slope 1 of a linear relationship. All analyses were carried out using software R, version 3.4.3 (R Core Team, 2014) and the *Smatr* package (version 3.4-8; Warton et al., 2012) for the SMA test.

3 Results

Results for the three metrics, *sA*, TS, and biomass are shown by lake in Table 2. Acoustic scattering strength *sA* in the upper depth layer did not significantly differ between day-time and night-time surveys for the 14 lakes (Wilcoxon test,

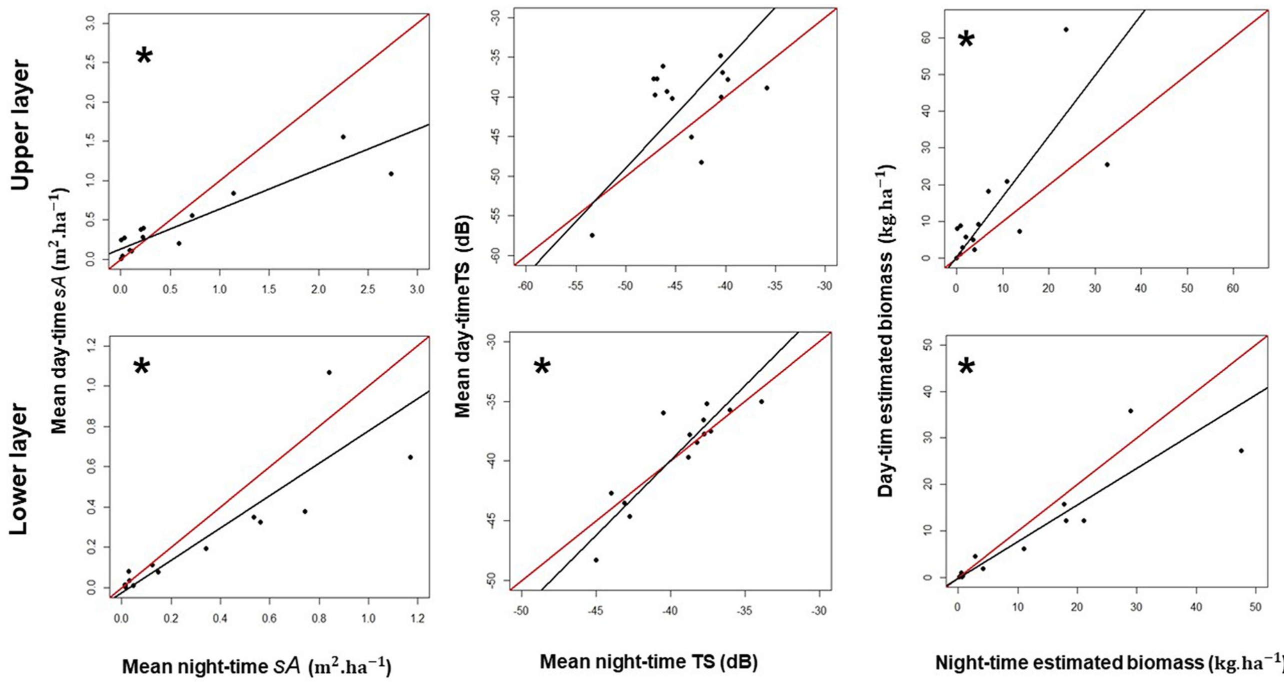

Fig. 2. Linear relationship between day and night results for upper (A) and lower (B) depth layers in 14 temperate lakes. A star indicates significant correlations ($p < 0.05$). The red line represents the 1:1 line, and the black line the relationship estimated by the SMA ($N = 14$).

Table 3. Summary of statistical tests ($p < 0.05$) comparing results for day-time and night-time surveys. Wilcoxon or Student tests were used to test for differences in means. Pearson or Spearman tests for testing correlations and standardised mean axis (SMA) tests for testing linear relationships (null hypothesis: intercept 0 and slope 1).

Variable		Upper layer	Lower layer
	Mean values	No difference	No difference
sA ($m^2\,ha^{-1}$)	*Correlation*	Yes	Yes
	SMA	Yes	No
	Mean values	Difference	No difference
TS (dB)	*Correlation*	No	Yes
	SMA	No	No
	Mean values	Difference	No difference
Biomass ($kg\,ha^{-1}$)	*Correlation*	Yes	Yes
	SMA	Yes	No

$p = 0.76$) and mean values from the two periods were significantly correlated (Spearman's $r = 0.84$; $p < 0.001$). However, the slope of the linear relationship was significantly lower than 1 (SMA $r = -0.87$, $p < 0.0001$), while the intercept was not significantly different from 0 (SMA intercept = 2.13, $p = 0.055$) (Tab. 3 and Fig. 2). This means lakes with larger mean *sA* had lower day-night differences in absolute terms. Similar results were found for the lower depth layer except that the slope in the SMA was not significantly different from 1 (Student $t = -1.84$. $p = 0.089$; Pearson's $r = 0.87$. $p < 0.0001$; SMA $r = -0.40$. $p = 0.15$; SMA intercept = −0.50. $p = 0.63$) (Tab. 3 and Fig. 2).

The mean number of single echoes detected in the upper depth layer was lower during the day than at night, though this did not reach statistical significance (Wilcoxon test, $p = 0.119$), while for the lower depth layer, the mean number of single echoes was significantly lower during day-time in most lakes (Wilcoxon test, $p = 0.0067$) (Fig. 3).

Regarding mean TS, for the upper depth layer, a significant difference between day and night values was observed (Student $t = 2.25$, $p = 0.04$), with higher values during day-time in most lakes (Tab. 3 and Fig. 2). No significant correlation was found (Pearson's $r = 0.50$, $p = 0.07$), though the SMA slope was not significantly different from 1 (SMA $r = 0.33$, $p = 0.24$) and the intercept was not significantly different from 0 (SMA intercept = 1.25, $p = 0.23$). In contrast, for the lower depth layer, no significant difference was found between day-time and night-time mean TS values (Student $t = 0.38$, $p = 0.71$), and the correlation between the results from the two periods was significant (Pearson's $r = 0.89$, $p < 0.0001$). Similarly, neither the observed SMA slope nor the intercept was significantly different from the null hypothesis (SMA $r = 0.45$, $p = 0.11$; SMA intercept = 1.56, $p = 0.15$). The mean value across lakes of the absolute difference between day-time and night-time TS values was more than 5 dB for the upper depth layer and close to 1 dB for the lower depth layer.

The biomass in the upper depth layer differed significantly between day and night-time (Wilcoxon, $p = 0.049$). Despite this, mean values were significantly correlated (Spearman's $r = 0.73$, $p = 0.004$) (Tab. 3 and Fig. 2). Biomass were higher at in the day in 78% of the lakes. A significant difference was detected between the observed slope and 1 (SMA $r = 0.61$, $p = 0.02$), but no difference in intercept was found (SMA intercept = 0.08, $p = 0.94$). Again, for the lower depth layer,

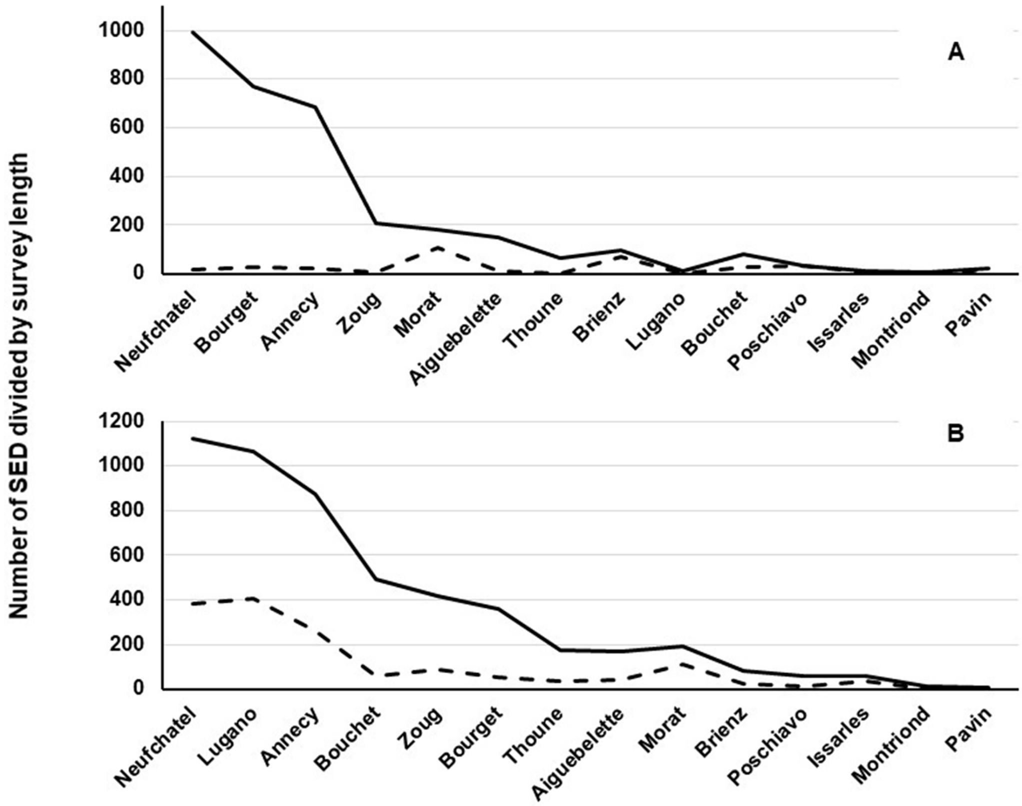

Fig. 3. Number of single echo detections (SED) by survey, weighted by survey length in km. Lakes are sorted by decreasing night-time SED: (A) upper depth layer; (B) lower depth layer. Solid line night-time results; dashed line day-time results.

there was no significant difference between day-time and night-time estimated biomass (Wilcoxon, $p = 0.15$). Values were significantly correlated (Spearman's $r = 0.90$, $p < 0.0001$) and neither the slope nor the intercept differed from the expected value (SMA intercept $= -0.49$, $p = 0.08$; SMA $r = -0.12$, $p = 0.91$).

4 Discussion

Hydroacoustics provide accurate estimates of fish stock biomass in lakes, but the results depend on fish behaviours which must be considered when defining the best survey period (Rudstam et al., 2012). In temperate lakes, fish assemblages are mainly dominated by Percidae and Cyprinidae and, to a lesser extent, by Salmonidae. These assemblages are not evenly distributed in the water column due to thermal stratification during the survey season in late summer/early autumn. In the upper depth layers perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) are usually dominant, with frequently high densities of juveniles (Masson et al., 2001; Guillard et al., 2006a). At this time of the year in natural lakes, these species are far enough from the surface to avoid underestimation using hydroacoustics (Guillard et al., 2006b; Emmrich et al., 2012). In the deeper and colder depth layers, Salmonidae (*Coregonus* spp. and *Salvelinus* spp.) are the dominant species (Dembiński, 1971; Probst et al., 2009; Mehner et al., 2010), while density depends on the lake's trophic status (Gerdeaux et al., 2006). Similar to previous studies (Appenzeller and Leggett, 1992; Draštík et al., 2009; Ye et al., 2013), we found that the diel survey period affected hydroacoustic measurements in 14 temperate natural lakes.

In the upper depth layer, day-time and night-time estimates were significantly correlated across lakes, except for mean TS values. For *sA*, the differences between day and night values were not significant, but correlation and SMA tests highlighted that differences occurred between the two periods. Not surprisingly, significant diel differences were found for biomass estimates. These differences were due to differences in TS estimates linked to fish aggregation behaviour and a smaller number of single echoes detected during the day-time. Day-time biomass were higher than night-time results for most lakes. Juvenile fish in warmer water layers form schools (Appenzeller and Leggett, 1992; Probst et al., 2009; Ye et al., 2013) and this behaviour impacts hydroacoustic results during the day-time. Schooling creates hydroacoustic shadowing and prevents the reliable detection of individuals, thus hampering accurate size estimation (Probst et al., 2009; Rudstam et al., 2012). Furthermore, there is a higher probability of obtaining TS from non-individual fish (two or more fish in the same volume considered as one fish). As a result, the mean TS is overestimated, leading to overestimated average individual fish size (Bohl, 1979; Fréon and Misund, 1998; Axenrot et al., 2004). Furthermore, as the number of single echo detections is limited, the estimated size distribution is imprecise. As a consequence, sampling during the day-time in the upper depth layer of temperate lakes led to biased size metrics and overestimated biomass, which was confirmed by this study.

Considering the lower depth layer, data for day-time and night-time were significantly correlated, and no significant differences were observed for any metrics. In contrast to the upper depth layer, no fish aggregations were observed in our study below the thermocline, although whitefish (*Coregonus sp.*), the main Salmonidae species in the sampled lakes, sometimes aggregate (Kahilainen et al., 2004) or form shoals (Shaw, 1962; Mehner, 2012). Coregonids usually migrate to the upper part of this depth layer at night and return to deeper water during the day-time (Swales, 2006), but such behaviours do not impact the results.

Draštík et al. (2009) have also discussed detection differences between day and night, but only for European reservoirs. These authors highlighted the issues related to the formation of fish schools and the horizontal and vertical movements between day and night. However, other explanations cannot be totally excluded, such as boat avoidance, which also biases TS estimates (Fréon et al., 1993) and, therefore, affects biomass estimates. Vessel noise can affect abundance and biomass estimates (Wheeland and Rose, 2015; DuFour et al., 2018), but should not lead to differences between day and night. However, as higher traffic usually occurs in the day-time, this could nevertheless increase the difference between the two sampling periods (Godlewska, 2002). Lake specific parameters (refuge sites, predators) could also influence abundance and biomass (Bohl, 1979; Gliwicz et al., 2006). The presence of predators could modify schooling behaviour (Eklöv and VanKooten, 2001; Jacobsen et al., 2004; Hölker et al., 2007), thus affecting estimates. In the presence of a predator, the prey will hide among the vegetation, where acoustic detection is not possible (Christensen and Persson, 1993; Persson and Eklöv, 1995). Acoustic detection problems for day-time sampling could be mainly due to the need to feed and seek protection from predation (Godlewska, 2002; Snickars et al., 2004). In the same way, light conditions (moon phase and artificial lights) can affect population estimates of pelagic fish in lakes (Luecke and Wurtsbaugh, 1993). Fish behaviour involves complex mechanisms due to multiple parameters, and it is difficult to identify the most important ones (Brehmer et al., 2019).

In summary, fish behaviour biases hydroacoustic estimates, and this study – using data from 14 natural temperate lakes – confirms that hydroacoustic sampling should be performed at night-time to obtain accurate estimates, as recommended by standards and the literature. Nevertheless, in the lower depth layer of temperate lakes, where Salmonidae are dominant, behaviours such as schooling and migration are less pronounced. Hence, the lower depth layer can be sampled during day-time without affecting acoustic biomass estimates.

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