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Acoustic fish biomass assessment in a deep Tunisian reservoir: effects of season and diel rhythm on survey results

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Abstract

To determine the best acoustic sampling period for obtaining fish biomass estimates of a Mediterranean deep reservoir in Tunisia, we carried out day and night surveys in each of four seasons [spring (April), summer (September), autumn (December) and winter (March)]. A Simrad EK60 echosounder, equipped with two 120 kHz split-beam transducers for simultaneous horizontal and vertical beaming, was used to sample the entire water column. Data collected in December were not usable because fish merged with methane gas bubbles. However, fish abundance varied across the other seasons with a peak in acoustic biomass observed during summer nighttime hours that was associated with high water temperatures. Across seasons, the fish occupied the entire water column, and fish schools were rarely observed. The preferential timeframe (i.e. maximum fish detectability and low gas flux) for acoustic sampling was nighttime hours in summer and daytime hours during spring and winter. Our findings highlight the importance of collecting data across seasons and photoperiods when determining an acoustic sampling strategy.

Keywords: target strength, fisheries, North Africa, photoperiod, man-made lake, gas bubbles

Introduction

Surface water reservoirs have been increasingly developed in Tunisia since the 1980s to regulate the seasonal stream flows and to provide the necessary water for meeting expanding demands for agriculture and domestic needs (Zouabi et al. 2009). Large scale introduction of freshwater fish species into reservoirs the early 1990s created fisheries to compensate for the lack of marine fish landings and to help reduce rural exodus in areas where unemployment is high; these now must be managed to ensure sustainable output (Djemali et al. 2009). The main species exploited in the reservoirs are carp (*Cyprinus carpio*), barbel (*Barbus callensis*), roach (*Rutilus rubilio*), and rudd (*Scardinius erythrophthalmus*), as well as species with higher commercial value, such as mullet (*Mugil cephalus* and *Liza ramada*) and pikeperch (*Sander lucioperca*) (Losse et al. 1991). Populations of economically important fishes in the reservoirs remain poorly studied, and there is a critical need for reliable information on the distribution and biomass of these stocks to ensure their effective management (Methot and Wetzel 2013; Cardoso and Haimovici 2015). Hydroacoustic methods provide one potentially important tool for meeting these data requirements.

Acoustic methods have been applied in many inland and marine systems to estimate abundance and size of fish (Simmonds and MacLennan, 2005; Kubecka et al. 2012; Loures and Pompeu 2015; Tupper et al. 2016). Acoustic sampling is an accepted sampling technique and a reliable tool for aquatic ecosystem study particularly in deep lakes (Yule et al. 2009; Rudstam et al. 2013; Rechencq et al. 2014). In shallow waters acoustic techniques are less used due to methodological issues (Balk, 2001). In addition to fish biomass estimates and comparison to fixed gillnets, the advantage of active acoustic sampling is the ability to simultaneously sample across several trophic levels including large carnivorous fish, smaller forage fish, and zooplankton (Trenkel et al. 2011). Relative to capture netting acoustic

sampling can also include greater coverage of the water column, especially pelagic regions; it is also less size selective and non-invasive (Simmonds and MacLennan 2005). However, there are some limitations of acoustic methods because (1) fish are difficult to detect close to the bottom and (2) they merge with gas bubbles. Night and day acoustic sampling have been performed in order to compensate for low detectability near the bottom given that fish behavior can change on a diel basis (Knudsen et al. 2009; Winfield et al. 2007); however, acoustic software is still unable to discriminate between fish and bubbles (Ostrovsky 2009a; Anderson and Martinez 2015). The amount of methane bubbles in the water column depends on the type of sediment, bottom depth, and the history of sediment degassing; and the outcome of the methane production can be an overestimation of fish biomass estimates (Ostrovsky, 2009b). Thus, to apply acoustic tools for fish biomass estimates, an important first step is considering potential limitations that may be general or system specific.

The goal of this study was to contribute to the development of an acoustic sampling strategy for Tunisian reservoirs and more generally for North African inland waters by evaluating seasonal and diel variation.

Materials and methods

Study area

The Joumine Reservoir, located in the northern region of Tunisia (36°58'48''N, 9°35'32''E) in the Bizerte province, was filled in 1983 (Figure 1). It provides irrigation waters for 1500 ha of farm land in the Mateur area, which is characterized by a Mediterranean climate (Peel et al. 2007). The reservoir has an area of 660 ha and a maximum depth of 41.1 m in the winter (Table 1). The fish community in this reservoir consists mainly of the indigenous barbel (*Barbus callensis*, Cyprinidae), as well as introduced mullets (Mugilidae) and pikeperch (*Sander lucioperca*, Percidae) (DGPA 2012). Catches from fishers' gillnets were sampled during July 2012 and showed that the fish community consisted of 35% mullets by weight (two species: *Mugil cephalus* and *Liza ramada*), 50% barbel and 15% pikeperch. These fish are mainly pelagic (Losse et al. 1991), so they can be detected easily by an echosounder, though distinguishing among the two species is not possible.

Previous hydrobiological sampling of Joumine Reservoir indicated temperature and dissolved oxygen homogeneity in the water column except in summer where a difference of 8 C° was observed between the top and the bottom, with a thermocline at 12 m of depth in the deepest area of the reservoir (Jenhani A., *Institut National Agronomique de Tunisie*, unpublished data). Based on these earlier observations, we collected water temperature and dissolved oxygen concentration 0.2 m under the surface water and 0.2 m above the bottom near the vantage tower (Figure 1) to detect stratification using a Wissenschaftlich Technische Werkstätten (WTW) depth probe, model oxi 197i (Nova Analytics Company, Weilheim, Germany). Our sampling was limited to one station in the deepest part of the reservoir, because the thermocline and oxycline are detected only in areas > 30 m of depth (Mouelhi, 2000).

Acoustic surveys

Four surveys were carried out, including day and night sampling during four seasons: spring (25 April 2012), summer (06 September 2012), autumn (10 December 2012) and winter (17 March 2013). During these surveys we did not differentiate among the three species.

Because zig-zag acoustic transects give statistically equivalent biomass estimates and size distributions as parallel transects (Guillard and Verges 2007), we decided to use 28 zig-zag transects for safety reasons notably during nighttime sampling. The degree of coverage indices at a constant boat speed of 3 knots, estimated using the formula of Aglen (1983), exceeded the recommended level of 2 for all surveys (Godlewska et al. 2009a) (Table 1). Day surveys and night surveys were completed, on average, in 3 hr and 38 min. To account for fish density gradients that may exist in reservoirs (Kubecka and Wittingerova 1998), the lake was divided into three zones (upstream, middle and downstream) with similar surface areas but different depths (Figure 1).

A portable echosounder (SIMRAD EK60, Kongsberg Maritime AS *Horten*, Norway) was used. It was equipped with two 120 kHz split-beam transducers connected by a multiplexer to a "General Purpose Transceiver" (GPT). One transducer was circular with a half-power beam width of 7° and was used for down-looking. The other transducer had an elliptic beam of 4°x10° and was used for side-looking. Both transducers were mounted on a stainless steel stand, so that they could be fixed 0.5 m beneath the surface with the horizontal transducer aimed 2° below the surface. With a maximum range of 36 m, the bottom of the elliptical beam was at 3 m of depth. In this way, the 0-3 m layer was sampled by side-looking (Kubecka and Wittingerova 1998) and the deeper layer (> 3 m) by down-looking. Night surveys began 1 hr after effective sunset. The echosounder was connected to a portable computer, which provided a real-time display and data storage. A global positioning system (GPS) was used to

record position during the surveys. The pulse length was fixed at 0.256 ms, and the repetition rate was set at 10 pings per second with transducers pinging alternately. The equipment was field calibrated before each pair of surveys using a 23-mm diameter copper sphere, following the protocol of Foote et al. (1987).

Hydroacoustics data were analyzed using Sonar5-pro software (Balk and Lindem 2006, version 6.0.1), using image analysis that greatly improves fish detection in noisy environments (Balk 2001) such as the surface-water interface. We used the default image analysis settings (Foreground filter = height 5 and width 1, Background filter = height 55 and width 1, Offset +6 dB) because they were developed for data with a similar ping rate and range resolution. The SEDs were combined into fish traces using a fish tracking algorithm (Balk and Lindem 2006). To be considered as a fish, the traces needed to have a minimum of 2 echoes, could contain no more than 2 lost echoes, and the maximum depth change between consecutive echoes could not exceed 0.3 m. During data collection, the threshold was set at -70 dB for the 40 log R time varied gain (TVG).

During a survey a large number of indeterminate rising traces were observed by down-looking. Therefore, we separated fish from rising targets (bubbles) using the Sonar-5 cross filter tracker (CFT) followed by the track classification system that set up one “fish basket” accepting rising targets assumed to be bubbles and one accepting only non-rising targets assumed to be fish (H. Balk personal communication).

To estimate fish lengths of tracked fish detected by down-looking, we used the all mean pooled fish length-TS relationship of Frouzova et al. (2005) because it was developed for Cyprinidae and Percidae that inhabit Joumine Reservoir.

Down-looking: $TS_{(dB)} = 20.45 \log (L_{t(mm)}) - 96.13$,
where dB is in decibel and L_t is fish total length in millimeters.

For side-looking, we also used the mean pooled fish length-TS relationship of Frouzova et al. (2005).

$$\text{Side looking: } TS_{\text{(dB)}} = 24.73 \log (L_{\text{(mm)}}) - 103.61,$$

The equations of Frouzova et al. (2005) were developed using the same echo sounder (split beam with a 120 kHz frequency) used in this study.

Each zig and zag was used as the elementary sampling distance unit (ESDU) in order to minimize the effect of area close to the bank. For each transducer and ESDU, we obtained from tracked fish the acoustic size distribution in decibels (dB), the mean TS calculated in the linear domain, and the fish density estimates (fish ha⁻¹) calculated by dividing the number of tracked fish by the area of the reservoir surface sampled by the beams. Because biological sampling was impossible, we did not have information on individual fish length and weight. Hence we estimated mean weight of fish detected by down-looking from the predicted mean length using the cube law (Minns 1995) whereby the weight of a fish is proportional to the cube of its length ($W_{\text{(g)}} = 0.001 L^3_{\text{(cm)}}$). Fish biomass was estimated by multiplying fish density by the average fish weight along each ESDU. The biomass per unit area of the entire water column was the sum of the two (side-looking and down-looking) layers (Kubecka and Wittingerova 1998).

The average density and biomass obtained for each zone of the reservoir corresponded to the weighted average of the ESDU estimates (Sokal and Rohlf 1981; Djemali et al. 2010).

$$\bar{x}_p = \frac{\sum_{i=1}^{i=n} (B_i * A_{s_i})}{\sum_{i=1}^{i=n} A_{s_i}}$$

where $\bar{x}_p$ is weighted average biomass (or density), n is the number of ESDUs per zone, B_i is the biomass (or density) along ESDU i and A_{s_i} is the sampled area of transect i .

Statistical analysis

As the number of detected fish per strata was sometimes low, data were combined across strata to compare TS distributions of fish between day and night sampling. In addition, as data normality could not be assumed, the Mann-Whitney (U) nonparametric test was used to detect differences between the distributions (%) of TS frequencies (Zar 1999).

Multi-way ANOVAs were used to test the influence of season, photoperiod, strata, and depth (independent variables) on fish density (fish ha⁻¹) and biomass (kg ha⁻¹) (dependent variables) with the ESDUs serving as sample units. As it was not possible to discriminate between fish and bubbles within echograms obtained in December, the corresponding data were not considered reliable and thus they were not used in this statistical analysis. Just two-way interaction terms in the final model were included; however, inclusion of three- and four-way interactions did not change the significance of the main factors. In order to compare the biomass between strata and seasons, the multi-way ANOVA was followed by a Tukey HSD post hoc test when significant differences were detected. Dependent data were log₁₀ transformed to stabilize the variance. Statistical tests were performed with ‘‘Statistica’’ Software (version 5.5) with α set at 0.05.

Results

Fish behavior and presence of gas bubbles

Water temperature during spring, autumn, and winter was homogeneous throughout the water column; while in summer, the deep water was colder (< 7 °C) than the surface layer. The entire water column was well oxygenated during all sampling periods (Table 1).

The seasonal echograms showed that fish were largely scattered (Figure 2) during daytime and nighttime, except two small schools that were detected in a single echogram downstream in the summer (Figures 3). Thus, we opted to measure fish biomass through fish counting instead of echo-integration. Fish occupied the entire water column during both photoperiods across seasons, and some individual fish were observed diving as the vessel passed overhead. High proportions ($> 80\%$) of fish traces were inclined upward in the late autumn acoustic sampling on a diel basis. These targets were likely methane gas bubbles (Anderson and Martinez 2015); and, we therefore opted not to estimate fish densities and biomass for this sampling period. During both night and day surveys in the other seasons, rising targets were uncommon and easily discriminated from fish (Figure 2).

Target strengths, fish density and biomass

TS distributions gathered by the downward-aimed transducer during the two photoperiods did not differ during spring ($U = 99$, $P = 0.58$), summer ($U = 93.5$, $P = 0.85$) and winter ($U = 71$, $P = 0.22$). The greatest difference in modal values between night and day was observed in winter with a difference of -15 dB (Figure 4). During this season, both day and night TS distributions were bimodal. This could represent two size classes of fish in the reservoir; however, given the size difference in modal lengths it is likely these modes do not represent consecutive year classes.

In layer deeper than 3 m, the mode values of the predicted length frequency were consistently greater during daytime than during the nighttime in winter and spring (Figure 4). Acoustic mean target strengths during summer were similar during nighttime and daytime with a high modal value of -37 dB corresponding to a total fish length of 78 cm. In the side-looking aspect, differences in the TS distributions between night and day collections differed among seasons. A higher proportion of large targets (between -40 and -31 dB) were detected

in the surface layer during each season, the highest proportion being observed during night surveys of winter.

Average fish density differed between day and night when estimation was possible (i.e. spring, summer, and winter, Table 2). In spring, with vertical beaming, average values showed clear trends according to area (Figure 5). During the summer, daytime values measured by vertical beaming were always lower than nighttime regardless of strata; however, during winter it was the opposite. The number of fish per hectare measured in the upper layer was lower than in the deep layer (Table 2) during spring, summer and winter, evidence that the majority of the fish occupied the deep layer. In addition, fish density differed among strata (Table 2) with a gradient from downstream to upstream at water column depths > 3 m during daytime (Figure 5). Inversely, during nighttime, no clear trends could be detected among fish densities between strata.

Biomass also differed between night- and day-sampling (Table 2). During spring and winter, daytime values were higher than nighttime (Figure 5). In spring, this result corresponded with higher densities in downstream and middle areas. In summer, higher biomass was measured at nighttime than daytime and was correlated with higher densities. During summer and winter biomass was lower in the upper 3 m suggesting that most of the fish biomass was found at water column depths > 3 m. In spring it was the opposite with fish biomass greater near the surface. There were also significant interactive effects between layers and seasons (Table 2). Overall results indicate that biomass distributions in the water column are dependent on season.

Biomass estimates differed among the three seasons for which acoustic estimation was possible (Table 2). Biomass increased from spring to summer and decreased from summer to winter (Tukey post-hoc test, $P < 0.01$). Average acoustic biomass peaked in summer nighttime

with $140 \pm 37 \text{ kg ha}^{-1}$ related to a high proportion of large fish in the deepest area of the reservoir (Figure 6) and corresponded to a biomass of 19 metric tons (MT).

Discussion

This study quantified seasonal and diel acoustic data in order to estimate the biomass of fish in a deep Tunisian reservoir. We highlighted some technical limitations using acoustic methods because of high methane gas ebullition on a diel basis during autumn, which prevented fish discrimination from bubbles and therefore biomass estimation. Our findings demonstrate, for this system, that quantifying variation across seasons and between photoperiods is important in improving the rigor of acoustic sampling; that gas bubble emissions can affect the accuracy of estimates during the colder season; and that the preferential timeframe for acoustic sampling is nighttime (i.e. higher detectability than daytime) in summer while during spring and winter it is daytime, highlighting changes in the diel pattern of fish behavior among seasons.

Results of this study showed higher biomass estimates in the summer, which may reflect a concentration of large fish at nighttime in the deepest area of the reservoir. Overall, reservoir biomass was obtained by weighting strata biomass, so more importance was given to the deepest area rich in fish. Fishers avoid this area because its access is forbidden by authorities, in particular near the vantage tower. Based on our summer nighttime survey, biomass in Joumine Reservoir was estimated to be 19 MT, but annual exploitation of the fishery does not exceed a yield of 4-6 metric tons (DGPA, 2012). Despite the problem of gas bubbles in December that precluded good biomass estimates, biomass-based acoustic survey methods showed the potential to assess between-season changes in fish abundance in this system. It will be useful in long-term monitoring of productivity and therefore management in deep

Tunisian’s reservoirs similar to what Pollom and Rose (2015) and Loures and Pompeu, (2015) showed for a boreal lake and a Brazilian reservoir, respectively.

Mobile acoustic sampling

The present study provided evidence of fish diving towards the reservoir bottom when disturbed by the passing boat. Avoidance is a phenomenon of fish behavior that can introduce uncertainties in mobile acoustic sampling results (De Robertis and Handegard 2013). Depth from the boat (Guillard et al. 2010) and differences in the sizes of fish present (Godlewska et al. 2009b) can also affect how fish in lakes respond to an acoustic survey vessel. The ideal situation is that fish are undisturbed. The reaction of fish to the passage of a boat can result in lateral or vertical movements. Lateral avoidance may cause fewer fish to be ensonified, and may or may not effect TS estimation. Diving responses may alter both the measured depth distribution, and the angle of a fish’s body relative to the acoustic beam, potentially impacting both TS measurements and coincident integrated backscatter (Wheeland and Rose, 2015). We were able to minimize our underestimation in the surface blind zone by incorporating side-looking, but we still lack standard approaches to quantify or limit bias from boat avoidance. Joumine is a deep reservoir, but maximum depth does not exceed 40 m downstream, so avoidance may be a significant issue (Drastik and Kubescka 2005) especially upstream. Mullet and barbel are benthophages (Glamuzina et al. 2007; Pegg and Britton, 2011) resulting in a higher individual tilt, and therefore a lower TS when feeding. Differences in TS distribution in winter with higher modal values daytime with vertical beaming, suggest that fish in Joumine mainly feed at night. The risk of mortality during the feeding process can influence behavior of prey fish on a diel basis as they try to balance their own energy needs while reducing their vulnerability to predators (Schneider et al. 2014).

Local freshwater fishing

In Tunisia, freshwater fishing is a secondary activity for populations. In fact, these fishers are mainly farmers who **livelihoods are based** on sheep or chicken-farming and fishing activities allow them to improve their revenue in poor areas (Hadj salah 2002). Low fish exploitation is mainly due to the use of unsuitable artisanal fishing gears. Indeed, local fishers generally use gillnets with a height < 7 m, which are fixed near the banks. In deep waters, these fishing gears are ineffective. Given that the largest mullet's catches occur in the spawning months (i.e. September) of the species (Mendonça and Bonfante 2011), it would be interesting to increase fishing effort during this time because the fish will be closer to the bank. In its repartition area, Mugilidae are high in abundance and accessibility meaning that they are targeted by commercial and artisanal seiners and gillnetters throughout their range, and by recreational fishers in developed countries (Broadhurst et al. 2011). Because outboard motors are forbidden in Tunisian's reservoirs, and the use of seines is excluded, deep-water angling in the context of recreational activity might be an important way to utilize the fishery in the deeper area of the lake.

Thermal and trophic conditions from spring to late summer in Tunisian reservoirs are considered favorable for active feeding and growth of fish (Mhetli et al. 2011). Therefore, new production both from successful reproduction (Cejko et al. 2014) and significant growth, likely leads to an increase in the standing biomass of fish. The local fishers unanimously say that catchability of fish increases in September, and this has been confirmed by yield statistics (DGPA 2012). Fishers have attributed this phenomenon to increased water turbidity with the first rains of August-September making their nets less visible to fish. In this study we showed increasing fish biomass from April to September, which suggests that the reputed explanation for higher catch rates is, in fact, probably linked to a response of fish growth during warm months. Indeed, during the spring bloom the turbidity increases significantly (Jenhani A.,

Institut National Agronomique de Tunisie, unpublished data), but catches are unaffected (DGPA 2012).

We conclude that the preferential period for acoustic sampling in the Joumine Reservoir is nighttime hours in summer and daytime hours in spring and winter. It was impossible to estimate fish acoustic biomass during the colder season of autumn because of the disturbing biogeochemical phenomenon of gas bubble emissions. This study showed that fish distribution within the water column may stay unchanged across seasons but fish behavior can change on a diel basis influencing biomass estimation. Moreover, our surveys showed that fish biomass can changed significantly over seasons and reach a maximum in summer nighttime. Considering total fish standing biomass in present study (19 MT) versus official yields (4-6 MT), further acoustic surveys within season will be necessary in order to confirm that the fish stocks are underexploited.

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Figures

Figure 1: Map of the Joumine Reservoir and its location within Tunisia and Africa, showing the three geographic strata (U = upstream; M = middle; and D = downstream) and the numbers of zig-zag transects (between brackets). $Z_{\max}$ represent the maximum depth per strata.

Figure 2: Example of a downward-looking echogram (40 log R with a -70 dB as threshold) showing how fish were distributed in the water column of the Joumine Reservoir during day and night surveys over four seasons: spring (S), summer (SU), autumn (A) and winter (W)

Figure 3: Downward-looking echogram (20 log R with -70 dB as threshold) showing schools of fish, which were only observed, fish in the water column, and fish diving during the summer daytime period.

Figure 4: Target strength (TS in decibel, dB) frequency distributions of target sampled in Joumine Reservoir by down-looking (D) and side-looking (S) sampling in three seasons. The n and n' represent the number of tracked targets detected during day and night surveys, respectively. Dotted lines and black lines represent day and night data, respectively. Predicted total fish length (L_t) was obtained with the formula of Frouzova et al. (2005) in vertical and horizontal beaming.

Figure 5: Mean fish biomass and density measured by down-looking (D) and side-looking (S) sampling in three zones (u = upstream; m = middle; and d = downstream) of the Joumine Reservoir sampled in four seasons. The white bars correspond to day surveys and black bars correspond to night surveys. Error bars show standard deviations. Seasons are shown in each panel, abbreviated as follows: spring = S, summer = SU and winter = W.

Figure 6: Fish biomass of the entire water column for each 250 m ESDU of Joumine Reservoir during summer nighttime survey.

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List of tables

Table 1: Hydraulic characteristics of the Joumine Reservoir when surveyed, and the degree of coverage of the four seasonal acoustic surveys. Water temperature and dissolved oxygen concentration were measured downstream near the vantage tower (see Figure 1 for location).

Table 2: Multi-way analysis of variance (ANOVA) of fish density (fish ha⁻¹) and biomass (kg ha⁻¹). The independent variables included photoperiod, layer, season and strata.

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Figure 1: Map of the Joumine Reservoir and its location within Tunisia and Africa, showing the three geographic strata (U = upstream; M = middle; and D = downstream) and the numbers of zig-zag transects (between brackets). Zmax represent the maximum depth per strata.

222x125mm (150 x 150 DPI)

Figure 2: Example of a downward-looking echogram (40 log R with a -70 dB as threshold) showing how fish were distributed in the water column of the Joumine Reservoir during day and night surveys over four seasons: spring (S), summer (SU), autumn (A) and winter (W)

318x220mm (150 x 150 DPI)

Figure 3: Downward-looking echogram (20 log R with -70 dB as threshold) showing schools of fish, which were only observed, fish in the water column, and fish diving during the summer daytime period.

209x84mm (150 x 150 DPI)

Figure 4: Target strength (TS in decibel, dB) frequency distributions of target sampled in Joumine Reservoir by down-looking (D) and side-looking (S) sampling in three seasons. The n and n' represent the number of tracked targets detected during day and night surveys, respectively. Dotted lines and black lines represent day and night data, respectively. Predicted total fish length (Lt) was obtained with the formula of Frouzova et al. (2005) in vertical and horizontal beaming.

303x266mm (150 x 150 DPI)

Figure 5: Mean fish biomass and density measured by down-looking (D) and side-looking (S) sampling in three zones (u = upstream; m = middle; and d = downstream) of the Joumine Reservoir sampled in four seasons. The white bars correspond to day surveys and black bars correspond to night surveys. Error bars show standard deviations. Seasons are shown in each panel, abbreviated as follows: spring = S, summer = SU and winter =W.

410x220mm (150 x 150 DPI)

Figure 6: Fish biomass of the entire water column for each 250 m ESDU of Joumine Reservoir during summer nighttime survey.

208x89mm (150 x 150 DPI)

Season	Sampling period	Volume	Area	Maximum depth	Vertical average temperature surface/bottom °C	Vertical average oxygen concentration surface/bottom mg L ⁻¹	Coverage degree day/night
		million m ³	ha	m			
Spring	25/04/2012	130.0	626	38.5	16.1/15.8	7.3/7.2	6.1/6.8
Summer	06/09/2012	130.0	622	36.3	25.8/17.6	6.4/6.1	6.3/6.2
Autumn	10/12/2012	163.0	659	39.8	13.0/12.8	8.9/8.4	6.3/6.1
Winter	19/03/2013	188.0	692	41.1	14.8/14.7	8.6/8.0	6.8/6.0

Effect	Sum of square	df	F	P
Density				
Photoperiod (P)	4.11	1	554.61	< 0.0001
Layer (L)	1.20	1	17.90	< 0.0001
Season (S)	0.60	2	53.15	< 0.0001
Strata (ST)	0.12	2	355.42	< 0.001
P x L	0.45	1	7.60	< 0.001
P x S	3.22	2	15.91	< 0.01
L x S	1.71	2	5.64	< 0.01
P x ST	1.66	2	5.85	< 0.001
L x ST	2.35	2	13.20	< 0.01
S x ST	3.50	2	7.82	< 0.01
Biomass				
Photoperiod (P)	21.40	1	334.82	< 0.0001
Layer (L)	3.21	1	155.30	< 0.0001
Season (S)	9.30	2	277.72	< 0.0001
Strata (ST)	3.12	2	56.45	< 0.001
P x L	8.75	1	75.41	< 0.01
P x S	1.25	2	14.69	0.03
L x S	2.62	2	2.48	< 0.01
P x ST	1.54	2	15.70	< 0.001
L x ST	3.25	2	32.65	< 0.01
S x ST	4.56	2	28.23	< 0.01

df, degree of freedom; F, computed statistic for test of significance and P, probability