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„*Hydroacoustic estimation of fish activity at the confluence of a reconnected side arm ("Johler Arm") of the River Danube east of Vienna*"

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For my grandmother *Gisela*

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CONTENTS

ABSTRACT

Lateral interconnection of inland water has been proven to enhance habitat quality for fishes and other aquatic organisms, yet is rare over major portions of large river systems due to anthropogenic impacts. During the course of the Integrated River Engineering Project, conducted in one of the last free-flowing stretches of the Danube River in Austria, a formerly disconnected sidearm (Johler Arm) was reconnected in 2014 to allow permanent flooding. The lateral migration, movements and distribution patterns of fish in this backwater were subsequently monitored. In addition to using methods (e.g. electro-fishing and long-lines) to examine species diversity and abundance, the activity of fish and size and direction of movement were investigated using a hydroacoustic technique. Specifically, four fixed-location imaging sonar hydroacoustic surveys were performed for 24 hours every season to detect diurnal patterns of fish activity and different seasonal utilization of the sidearm. An Aris Explorer 1800 (SoundMetrics®, Washington) operating at 1.1 MHz while submerged approximately 30 cm below the water surface, tilted -75° to -81° and aimed across the Johler sidearm to create a horizontal array was used. The recorded files were analysed in 5-minute subsamples every hour using *ARISFish®* software with background subtraction and transmission loss filters. Individual fish were marked, measured (if possible), counted and returned to the respective direction and position in which the individual was moving.

In general, seasonal variation of parameters was observed. Fish abundance was highest in winter (12 ± 17 ind. min^{-1}) and lowest in summer (10 ± 5 ind. min^{-1}). The extrapolated abundance of estimated individuals per day was 14 000 in spring, 14 424 in summer, 15 552 in autumn and 17 868 in winter; seasonal differences were not significant. Diurnal investigation revealed 61% of all recorded fish to be active in daylight and seasonal variation was significant ($p < 0.01$). Fish size differed significantly between the seasons ($p < 0.001$), with fish the largest in spring (20.4 ± 10.5 cm) and smallest in winter (11.0 ± 2.6 cm), ranging from 5.3 cm to 75.9 cm with an average of 15.5 ± 8.5 cm. On average, 5 ± 8 ind. min^{-1} moved upstream while 4 ± 7 ind. min^{-1} moved downstream. The 24-hour extrapolation was 7294 upstream swimming and 5977 downstream. Over the course of four seasons, no significant differences were found. However, within some seasons, emigration and immigration varied significantly ($p < 0.001$). On average, upstream moving individuals were larger (16.2 ± 9.1 cm) than downstream (14.4 ± 7.5 cm). In three seasons this difference was significant ($p < 0.05$). High mobility of fish was shown: the minimal distance from the device was 1.0 m, the maximal distance 24.3 m (average 9.3 ± 5.4 m). Largest fish were closest to the opposing shore. In winter, large fish schools were

observed with 78 ± 95 (avg.) fish in one aggregation and each school ranged from 7 to 290 individuals. Body length varied significantly in these schools ($p < 0.001$), indicating the presence of more than one school. The first hydroacoustic monitoring of the Johler Arm after its reconnection revealed a high degree of fish activity, provided new information about diurnal patterns and different positions of fish within the waterbody and indicated an active utilization of the reconnected sidearm by various fish species in different life stages. This study underlines the importance of lateral connectivity for fishes in rivers.

ZUSAMMENFASSUNG

Die laterale Vernetzung von Binnengewässer erhöht erwiesenermaßen die Habitatqualität für Fische und andere aquatische Organismen. Aufgrund menschlicher Einflüsse ist ein Gewässernetzwerk heutzutage im Großteil der großen Flusssysteme nicht mehr vorhanden. Im Zuge des "Integrated River Engineering Project", das in einem der letzten freifließenden Abschnitte der Donau in Österreich durchgeführt wurde, wurde ein zuvor vom Hauptstrom abgeschnittener Seitenarm (Johler Arm) 2014 wieder angebunden. Diese Maßnahme führte zur permanenten Wasserführung und damit zur ganzjährigen Verbindung des Johler Armes mit dem Hauptstrom. Diese Anbindung bedingt eine ressourcenreiche Umwelt für viele Organismen. Innerhalb des Projektmonitorings wurden die laterale Migration sowie die räumlichen Verteilungsmuster von Fischen in einem Gewässerquerschnitt eingehend untersucht.

Neben anderen Methoden (Elektrobefischungen, Langleinen) zur Erhebung der Diversität und Abundanz von Fischen wurden die Aktivität von Fischen, ihre Größe und die Richtung ihrer Bewegungen mittels einer hydroakustischen Kamera untersucht. Ein bildgebendes Sonar wurde im Zuge von vier (äquivalent zu den Jahreszeiten), jeweils 24 Stunden währenden hydroakustischen Untersuchungsserien eingesetzt, um tageszeitlich abhängige Muster der Fischaktivät sowie die saisonale Nutzung des Seitenarmes darzustellen. Verwendet wurde dazu ein Aris Explorer 1800 (SoundMetrics®, Washington). Die Ausrichung der Kamera war horizontal, um einen Querschnitt des Gewässers zu erfassen. Die Aufnahmen erfolgten mit einer Frequenz von 1.1 MHz, das Gerät war ca. 30 cm unter der Wasseroberfläche untergetaucht, der Neigungswinkel variierte zwischen 75° bis 81°. Die Analyse der aufgezeichneten Videos erfolgte mit der Software *ARISFish*® und umfasste jeweils zufällig ausgewählte fünf Minuten Sequenzen pro aufgenommener Stunde. Die Filter „background substraction" und „transmission loss" wurden verwendet, um die Erkennung von Fischindividuen zu verbessern. Individuen wurden mittels der Software markiert, bei entsprechender Bildqualität und Position in der akustischen Achse gemessen, gezählt und ihre Bewegungsrichtung gekennzeichnet.

Die meisten Fische wurden im Winter gezählt (13 ± 18 Ind. Min^{-1}), während die wenigsten im Sommer beobachtet wurden (10 ± 5 Ind. Min^{-1}). Nach Extrapolation umfasste die Abundanz der geschätzten Individuen pro Tag 14 000 im Frühling, 14 424 im Sommer, 15 552 im Herbst und 17 868 im Winter, die saisonalen Unterschiede waren nicht signifikant unterschiedlich (p = 0.08). Untersuchungen der diurnalen Aktivität zeigte einen tagaktiven Anteil von 61%, wobei

signifikante Unterschiede zwischen den Jahreszeiten zu beobachten waren. Auch die Größe der Fische zwischen den saisonalen Untersuchungen variierte signifikant ($p < 0.01$), die größten Fische wurden im Frühling (20.4 ± 10.5 cm), die kleinsten im Winter (11.0 ± 2.6 cm) gefunden. Es wurden insgesamt Größen zwischen 5.3 und 75.9 cm beobachtet, durchschnittlich maßen die Fische 15.5 ± 8.5 cm. Im Mittel bewegten sich 5 ± 8 Ind. Min $^{-1}$ stromaufwärts, während 4 ± 7 Ind. Min $^{-1}$ stromabwärts schwammen. Nach Extrapolation schwammen in Summe in 24 Stunden 7 294 stromauf- und 5 977 stromabwärts. In diesem Zusammenhang wurden keine signifikanten Unterschiede zwischen den verschiedenen Saisonen festgestellt. Allerdings variierten die Bewegungsrichtungen innerhalb einiger Jahreszeiten signifikant ($p < 0.001$). Im Durchschnitt waren stromaufwärts schwimmende Individuen größer (16.2 ± 9.1 cm) als stromabwärts schwimmende (14.4 ± 7.5 cm), mit signifikanten Unterschieden in drei Saisonen ($p < 0.05$).

Die hohe Mobilität der Fische bzw. die räumliche Nutzung des Seitenarmes zeigte sich in den festgestellten unterschiedlichen Positionen in verschiedener Distanzen vom Gerät, der minimale Abstand betrug 1.0 m und der maximale Abstand 24.3 m. Durchschnittlich positionierten sich die Fische bei 9.3 ± 5.4 m Distanz vom Ufer. Die größten Individuen wurden nahe des gegenüberliegenden Ufers beobachtet.

Im Winter wurden große Fischschwärme beobachtet, wobei eine Aggregation 7 bis 290 Individuen umfasste und im Mittel 78 ± 95 Fische in einer Aggregation vorhanden waren. Die gemessene Körperlänge in diesen Schwärmen zeigte signifikante Unterschiede ($p < 0.001$), was auf unterschiedliche Schwärme hindeutet.

Die erstmalig durchgeführten hydroakustischen Untersuchungen des Johler Armes nach seiner Wiederanbindung an den Hauptstrom der Donau zeigte eine generell hohe Aktivität von Fischen, diurnale Aktivitätsmuster und Unterschiede bezüglich der räumlichen Nutzung der Wassersäule. Zusammenfassend konnte die aktive Nutzung des Johler Armes durch verschiedene Fischarten sowie unterschiedliche Altersklassen beobachtet werden. Diese Studie unterstreicht die Bedeutung von lateralen Gewässervernetzungen und stellt erstmalig die zeitlich- räumlichen Aktivitätsmuster von Fischen in einem Seitenarm der Donau quantitativ dar.

INTRODUCTION

The importance of lateral interconnection of inland waters with respect to ecological habitat quality for fishes as well as other organisms has long been realized (Schiemer, 1994; Rakowitz and Zweimüller, 2000; Keckeis and Schiemer, 2002; Rakowitz and Berger 2010). A dendritic river system has been shown to provide great spatial and temporal variation of physical and chemical characteristics (Northcote, 1984) for different species of fish (Schiemer, 1994). However, due to anthropogenic impacts (e.g. Hoffmann, 1996), few sidearms of the free-flowing section of the Danube River remain (Nanson and Knighton,1996; Hohensinner *et al.*, 2011; Hohensinner *et al.*, 2013), and the availability of backwaters as important spawning and feeding areas for fish, as refuge and nurseries for young stages, is limited (Schiemer, 1985; Schiemer and Spindler, 1989).

Various restoration measures were conducted in the Danube within the framework of the Integrated River Engineering Project ("Pilotprojekt Bad Deutsch – Altenburg"; Reckendorfer *et al.*, 2005) in order to simultaneously improve general ecological conditions and habitat quality, navigational conditions, and to inhibit the ongoing deepening of the river bed. These measures aim to prevent one of the last remaining free-flowing stretches of the river in Austria and one of the largest riverine floodplains of its kind in Central Europe (Schiemer & Spindler 1989) from further destruction. This extensive, interdisciplinary approach includes restoration of shorelines, optimization of low water regulation, granulometric riverbed improvement, and reconnection of a sidearm (Reckendorfer *et al.*, 2005; Tögel 2015) — all applied on a test reach three km long (Tögel 2015) and complemented by an abiotic and biotic monitoring scheme performed over a period of 20 years (Scheiblechner 2015).

Within this project, the Johler Arm, a 1.35 km long sidearm of the River Danube in Hainburg an der Donau, Austria, was reconnected at its upstream end to the main stem of the river, along with subsiding the influx mouth and riverbed. These measures result in a now permanently-(nearly perennial) flooded sidearm (Tögel 2015), providing a resource-rich environment for many species (Schiemer, 1985; Schiemer and Spindler, 1989), including organisms endemic to or even endangered in this area of the river (Schiemer, 1985; Lelek, 1987; Schiemer and Spindler, 1989).

As temporal and spatial lateral migration and distribution patterns of fish into backwaters and sidearms provide crucial information about ontogenetic requirements (such as need of nurseries, refuges and spawning sites) of the assemblages (Spindler, 1988; Schiemer and Spindler, 1989; Schiemer, 2000), quantitative information of these migration and movement patterns is of high concern. Furthermore, fish demonstrate high ecological value, being the most important

indicator group for assessing ecological connectivity and integrity of rivers (Schiemer and Spindler, 1989; Karr, 1991; Schiemer, 2000) as they are dependent on specific spawning sites and show species-specific changes in habitat requirements in the course of their life cycle (Schiemer, 1985; Schiemer and Spindler, 1989; Schiemer, 1994).

Various fishing methods (boat electrofishing, wading electrofishing and longline fishing) have been used in the Johler Arm to collect abundant information regarding, for example, abundance and biodiversity (Loisl *et al.*, 2014). Additionally, horizontal hydroacoustic measurements have been undertaken due to their unique ability to provide quantitative data on fish movements, migration patterns, and individual size (Keckeis and Rakowitz, 2005; Rakowitz and Kubečka, 2006; Rakowitz *et al.*, 2008) over longer time periods

Hydroacoustic techniques offer a wide range of application for shallow waters such as the Johler Arm where horizontal beaming is recommended (Gerlotto *et al.,* 1998; Kubecka and Wittingerova, 1998; Thorne, 1998; Gerlotto *et al.,* 2000; Godlewska *et al.*, 2012), but also in the ocean and estuaries (for example Guillard *et al.*, 2012; O'Connell *et al.*, 2014), lagoons (Gonzalez and Gerlotto, 1998), lakes (Arrhenius *et al.*, 2000; Cech and Kubečka, 2002; Rakowitz *et al*., 2012) or deep riverine pools (Rakowitz et al., 2014). Sonar imaging offers the possibility of fish abundance estimation where visual (and therefore light-dependent) observations fail due to high turbidity (Singer, 2011) or low light conditions (Simmonds and MacLennan, 2005; Tušer, 2013). Additionally, individual fish can be observed in their natural and undisturbed environments (Axenrot et al., 2004; Foote, 2009) without the flight behaviour or injuries caused by all other sampling techniques (e.g. Carline, 2004). Although it is not possible to identify individuals of specific species with this method (Frouzova *et al.*, 2005), the advantages of the method are indisputable, especially in habitats such as the Johler Arm.

In summary, using this unique technique, the goals of this work are to quantify the abundance and body size of fish as well as determine the direction of migration or movements (either into or out of the backwater). Additionally, the size distribution within a transect was studied, and we wanted to know if the size-distribution within the transect is related to a specific gradient of flow-velocity. Finally, the differences in fish activity and fish sizes between seasons and times of day were examined.

In more detail, it is intended to investigate whether the reconnection affects the abundance of fish, as it leads to changes in environmental conditions and habitat heterogeneity which should provide suitable conditions for fishes belonging to different ecological guilds (i.e. for rheophilic as well as limnophilic species, Schiemer and Waidbacher, 1992). Studies covering diel periods indicated longitudinal, lateral and sometimes also vertical elements in the movement patterns

(Kubecka and Duncan, 1998; Lucas and Baras, 2001). Since diurnal, as well as seasonal changes of fish activity and migration, were frequently observed (resumed in Lucas and Baras, 2001) this study will examine these variations of the aforementioned factors. It is expected the results will, therefore, vary over the course of the year. This will potentially inform future projects seeking to reconnect other truncated backwaters.

MATERIAL & METHODS

Study site

This study was conducted at the Johler Arm (48.146350 N, 16.934035 E), a restored and permanently connected sidearm of the Danube River east of Vienna, Austria, located at river kilometre 1884.40 (Fig. 1). In 2014 the sidearm was reconnected at its upstream end to the main stem, significantly changing its hydraulic and morphologic features due to permanent

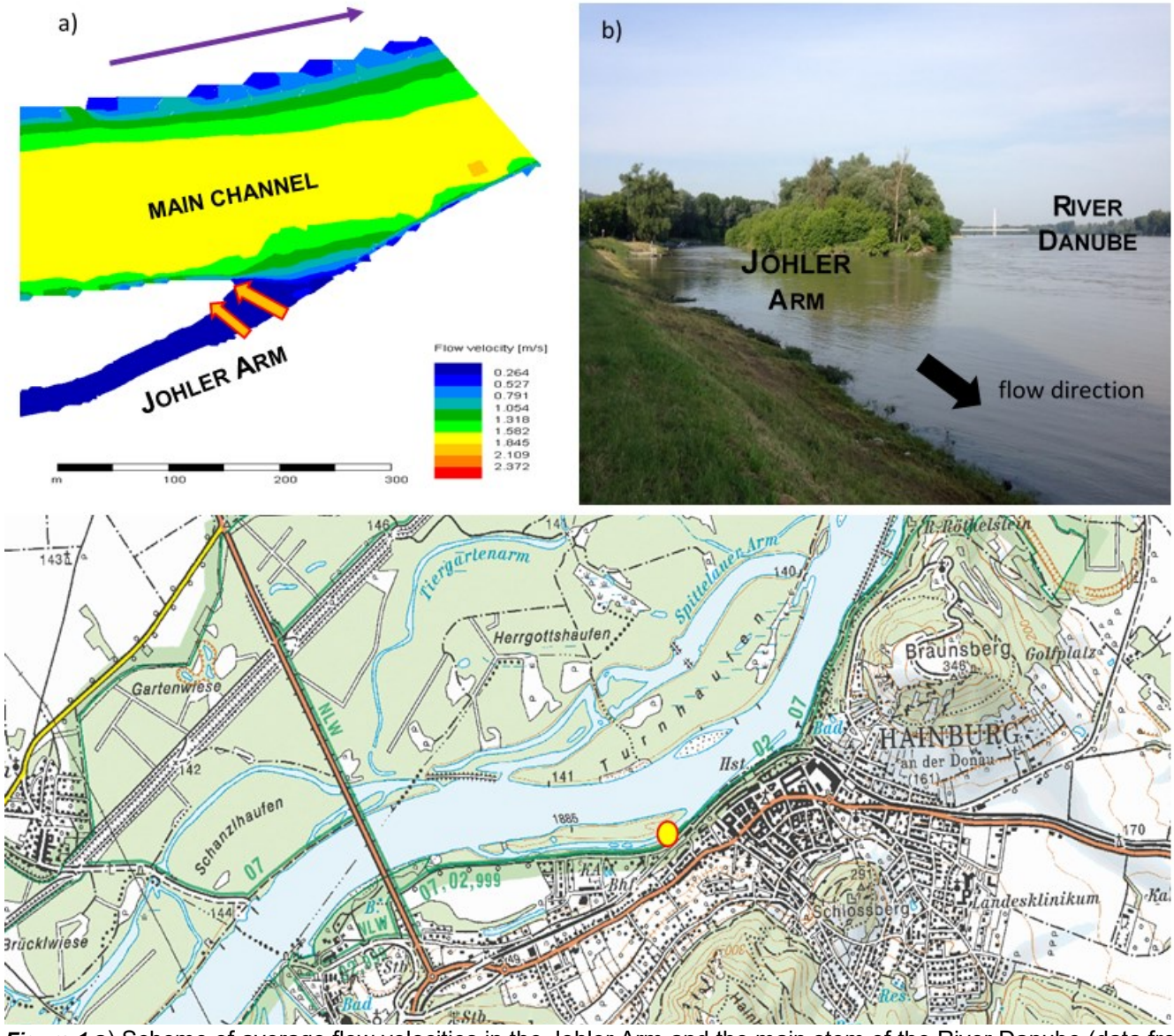

Figure 1 a) Scheme of average flow velocities in the Johler Arm and the main stem of the River Danube (data from hydrodynamic model, Tritthart and Gutknecht, 2007). a) The violet arrow marks the direction of flow, the red marks indicate the sampled transects. b) Picture from the confluence of the Johler arm with the main stem. ©*Hubert Keckeis* c) Map section of Bad Deutsch – Altenburg and Hainburg an der Donau. The symbol indicates the sampling site. ©*BEV 2019, reproduced with friendly permission of BEV – Bundesamt für Eich- und Vermissungswesen in Wien, N2019/64170*

water flow even at low discharge. The upstream reconnection resulted in generally increased discharge-specific flow velocities.

Due to a naturally fluctuating water level, the surface width of the arm at the sampling station varied between 30 and 35 meters, while the water level at the water gauge Wildungsmauer, Austria, ranged from 1.7 m (min.) to 4.3 m (max.) in different seasons, according to data obtained from ViaDonau (minimum in December 2014; ViaDonau *online*, 2015). The discharge in the river ranged from 1040 m^3 s^{-1} to 3217 m^3 s^{-1} during the different surveys. Based on the water level at the reference point Wildungsmauer, flow velocities in the sidearm were calculated by our research group using the 3D hydrodynamic model RSIM (Tritthart and Gutknecht, 2007), showing an increasing tendency from the shores towards the centre as well as ascending from the river bottom to the top of the channel (Fig. 2 and 5; data from DoRIS, ViaDonau *online*, 2015).

Table 1 Overview of discharge of the River Danube at reference point Wildungsmauer in the sampling seasons and associated discharges for RSim-Software in order to create adequate schemes.

Season	Date	$Q_{measured}$	$Q_{associated\ for\ RSim}$
winter	15. - 16.12.2014	1040 m^3 s^{-1}	1200 m^3 s^{-1}
spring	28. - 29.05.2015	3217 m^3 s^{-1}	4000 m^3 s^{-1}
summer	27. - 28.08.2015	1163 m^3 s^{-1}	1200 m^3 s^{-1}
autumn	20. - 21.10.2015	1458 m^3 s^{-1}	1500 m^3 s^{-1}

A sampling station with steep shores was selected to observe migrating fish using fixed-location hydroacoustics. The river bottom on both sides of the sidearm at the sampling site was rather uniform, consisting of gravel and silt.

In order to analyse the spatial distribution of fish sizes within the channel transects, and to relate them with the flow velocity patterns, fish position was projected into 3D transects derived from the software RSim 3D (Tritthart and Gutknecht, 2007). As the software works with categorized discharge values, the most appropriate values ($Q_{associated}$; with the least variation from the original data) for the observed discharges ($Q_{measured}$, Tab. 1) were chosen to model the calculation, resulting in transects of the sidearm with calculated flow velocities of the water column at the different sampling dates (i.e. seasons; Fig. 5).

ARIS Sonar

In order to investigate in-stream fish activity, sampling was performed with an imaging sonar ARIS EXPLORER 1800 (SOUND METRICS®, Washington, USA) operating at two frequencies (1.1 MHz and 1.8 MHz) and mounted on an adjustable pan and tilt rotator. The standard angle of the integrated lens was 12°, at the spring sampling date a 3° lens (attached to the device) was used to increase the contrast, narrowing the beamed area/volume. Therefore, a multiplication factor of four was applied for this observation. The sonar unit was submerged approx. 30 cm below the surface and tilted downwards (-75 to -81°) to maximize the beam volume without disturbing reflections from the water surface or the river bottom (Table 2). To achieve optimal fish detection up to the range limit of approximately 30 m, the low-frequency operation mode (1.1 MHz, technical range limit of 35 m, Sound Metrics 2016) was applied, using 96 single beams to create a horizontal array. The transmission power was fixed at 48.2 V and the receiver gain was set to 20 dB.

Table 2 Overview of the main settings used during four sampling trips. Tilt angle and beam range varied due to water level and exact position of the set-up.

	Winter	**Spring**	**Summer**	**Autumn**
Sampling date	15. – 16. 12. 2014	28. – 29. 05. 2015	27. – 28. 08. 2015	20. – 21. 10. 2015
Frequency mode (MHz)	1.1	1.1	1.1	1.1
No. of beams	96	96	96	96
Frames s^{-1}	7.2	4.8 – 5.3	5.3	5.3
Receiver Gain (dB)	20	20	20	20
Tilt angle (°)	-80°	-75° – -78°	-81°	-81°
Beam range (m)	15.09	21.31	21.34	21.34
Resolution (mm)	14.5	14.5	14.5	14.5

The hydroacoustic equipment was mounted on the stern of the research vessel which was fixed with two ropes at the right shore, parallel to the current and close to the mouth of the sidearm (Fig.3).

To detect diurnal patterns of fish activity as well as differences in seasonal utilization of the arm, fixed-location hydroacoustic studies were performed in winter, spring, summer and autumn (Table 3) over 24 hours. In winter, the data was collected close at the confluence of the

arm, while further investigations were carried out 70 m upstream, due to safer fastening conditions. The beam range during data collection ranged from approximately15 to 21m (Figs. 1 and 2).

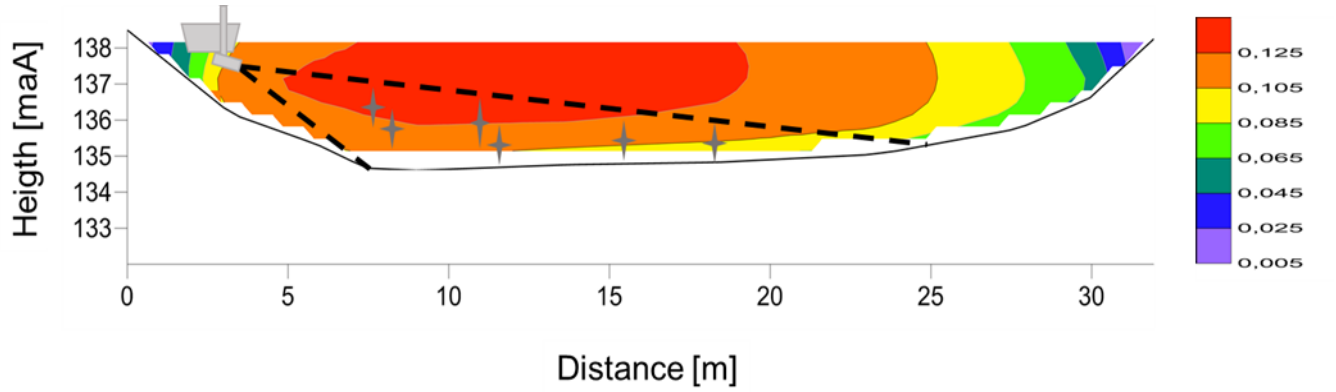

Figure 2 Scheme of the profile of the investigated transect, showing the position of the boat with the sonar, the beam of the sonar together with the flow-velocity pattern in the side arm. The survey vessel containing the sonar (grey) was fixed to the right shore of the Johler Arm. The black line indicates the river bottom, the dashed lines indicate the beam of the sonar. The coloured areas indicate the flow velocities, derived from a 3D hydrodynamic model (Tritthart and Gutknecht, 2007). maA = meters above sea level, stars reflect possible fish lingering in or passing the beam.

Beam mapping

Beam mapping was performed in summer (August 2015) to evaluate the beam produced by the ARIS 1800. A rope with one-meter marks was fixed across the channel to enable the measurements. An iron sphere (Ø approx. 10.5 cm) was manually submerged from the boat and at every mark, the position and appearance or disappearance from the beam was observed, resulting in theoretical and actual beam positions across the transect.

Figure 3 Pictures from the sampling site at Johler Arm in Hainburg /Donau, Lower Austria, Austria illustrating the sampling site, the fixation of the camera as well as the beam mapping procedure. In the winter study, the pier was used in order to secure the research vessel (a), while in spring, summer and autumn the set up was located approximately 70 m upstream (b). The ARIS Explorer 1800 was fixed at the rear of the boat and submerged between -0.27 m and -0.30 m below the water surface (c), beam mapping measurements across the sidearm (d). All pictures ©*Hubert Keckeis*

Data analysis

The recorded hydroacoustic data were analysed with the *ARISFish*® post-processing software Version 2.2 (Sound Metrics®, Washington, 2014). Background subtraction and transmission loss filters were used during the analysis of the files to increase recognition of individual fish Identified individuals were marked and total length from snout to tail was measured when the fish passed the centre of the beam; clear and well-shaped fish images were preferred. Individual fish considered too small or malpositioned for reliable measurement were counted. Swimming directions were divided into three categories: upstream (right to left), downstream (left to right) or undefined (no direction of movement was recognized, e.g. dwelling fish). Measured fish

were automatically categorized, whereas the swimming direction of marked fish had to be manually adjusted. Different positions of fish in the horizontal beam were also noted. In the case of large fish schools, the first 50 individuals passing the centre of the beam were measured, while the remaining fish were marked for recording abundance.

To evaluate the diurnal activity and movement patterns, randomly selected subsamples five minutes in length were analysed every recorded hour. The reliability of these short intervals (5 minutes and an alternative of 15 minutes per hour) was tested by comparison with the analysis of three separate full hours (60 minutes = e.g. 12 intervals of 5 minutes) with various fish abundance and was thus proved to be representative. In comparison, fish abundance expressed as the number of fish per minute in the 5 min observation periods and three one-hour periods showed similar results (e.g. 9 individuals min^{-1} in a 5 min subsample versus 10 ± 0.2 ind. min^{-1} in 5 minutes based on the analysis of an hour with an average abundance of 3 ind. min^{-1} versus 4 ± 0.5 ind. min^{-1} in an hour of low abundance and 45 ind. min^{-1} vs. 43 ± 12 ind. min^{-1} in an hour of high abundance). On average, the two estimates varied by a difference of ± 1 fish per minute, irrespective of an overall low, average or high abundance (Fig. 4). The values for individuals per minute found in intervals of 15 minutes and 60 minutes (one hour) were the same. Because of the very small difference, 5 min subsamples were assumed to be representative for a full-hour cycle. In total, 480 minutes over 96 recording hours were analysed in these subsamples. Lilja *et al.*, 2008, recommended a minimum sample effort of 10 min h^{-1}, however, the 5 min h^{-1} effort, in this case, has been approved to be sufficient by an additional, more in-depth analysis by Neuhold (2016).

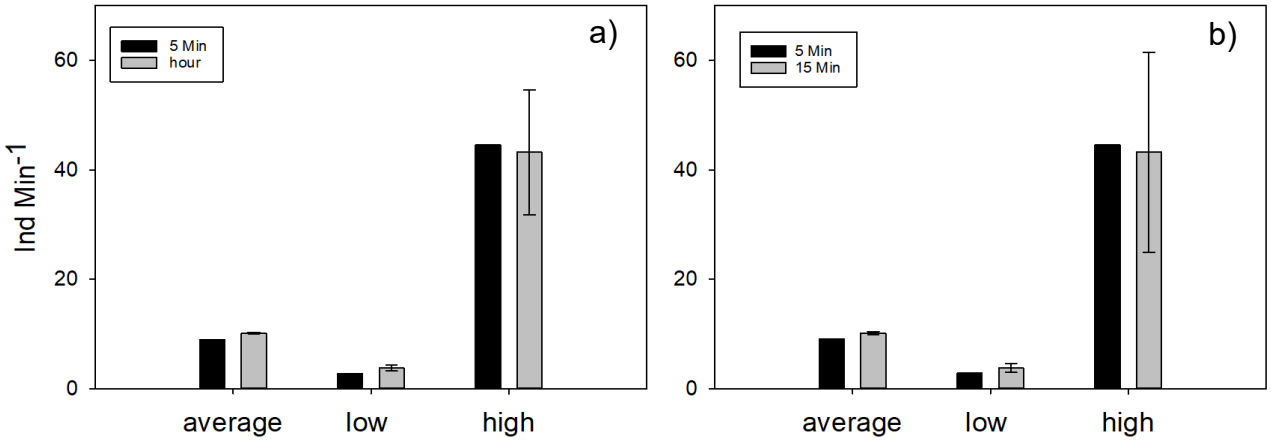

***Figure* 4** Comparison of Individuals min^{-1} in 5-min intervals and an hour (a) as well as per-minute values of 5-min intervals and 15-min intervals (b) with 95 % confidence intervals, respectively. Fish counts differed ± 1 fish per minute.

Diurnal changes

To detect diurnal changes, different times of day (dawn, day, dusk and night) were considered, allowing a comparison of changes in fish activity, size and position in the waterbody during a 24-hour cycle. Different light conditions were categorized by time of day based on the civil twilight for the respective sampling date (Tab. 3).

Table 3 Times of civil twilight in the different seasons (Online 2015).

	Date	Dawn (start)	Dawn (end)	Dusk (start)	Dusk (end)
Spring	29.05.2015	04:18	04:58		
	28.05.2015			20:40	21:19
Summer	28.08.2015	05:32	06:04		
	27.08.2015			19:43	20:16
Autumn	21.10.2015	06:50	07:22		
	20.10.2015			17:52	18:24
Winter	16.12.2014	07:00	07:36		
	15.12.2014			15:58	16:35

Statistical analysis

Data were tested for divergence from normal distribution using the Shapiro-Wilk normality test and homogeneity of variances using the Bartlett test of homogeneity of variances, both conducted in RStudio. Due to the divergent distribution of the abundance data (observed individuals per minute) from normal distribution and inhomogeneity of variances, non-parametric tests were chosen to test differences between seasons, distances and diurnal changes. The main test was the Kruskal-Wallis H-ANOVA and the Mann-Whitney U-test was used post hoc. To compare the two different directions (upstream, downstream), Mann-Whitney U-tests were applied. Statistical analyses were evaluated with RStudio (R-3.2.5). Changes in fish size along the vertical transect were analysed by polynomial regression with distance from the transducer as the independent and length as the dependent variable in IBM SPSS Statistics® (Ver. 23.0). SigmaPlot® (Systat Software Inc. 2016, Ver.12.5) was used to graphically illustrate the results.

RESULTS

Abiotic conditions

Discharge, water level, and water temperature varied according to season. Discharge was highest in spring (variations between 3217 m^3 sec^{-1} on day 1 and 2850 m^3 sec^{-1} on day 2) and lowest in winter (1040 m^3 sec^{-1} and 1052 m^3 sec^{-1} on days 1 and 2, respectively). The water level was in spring (434 cm above ground level) and lowest in winter (135 cm above ground level). Water temperature was highest in summer (20°C) and lowest in winter (6.1°C). Data are shown in Table 4.

Table 4 Date and duration of the investigation series in the Johler Arm. The daily means of discharge, water level and water temperature of the Danube River (measurement site Hainburg, reference point Wildungsmauer, data ViaDonau) are given for the days of investigation.

season	date / time from		date / time to		discharge (m^3 $sec.^{-1}$)	water level (maA)	water temperatur (°C)
winter	15.12.2014	13:00:00	16.12.2014	13:00:00	1040 - 1052	135 - 137	6.1 - 6.2
spring	28.05.2015	13:00:00	29.05.2015	13:00:00	3217 - 2850	434 - 394	12.2 - 12.9
summer	27.08.2015	10:00:00	28.08.2015	10:00:00	1163 - 1079	157 - 142	19.8 - 20.0
autumn	21.10.2015	10:00:00	22.10.2015	10:00:00	1458 - 1365	207 - 191	11.0

Slightly different patterns of flow velocity were observed during the different seasons (Fig. 5) but did not directly impact the measurements. In every season flow velocity increased from the shores towards the middle of the stream, with highest values in the open-water area of the sidearm. It can be stated that fish found in this area have to withstand or use these higher current velocities. A more detailed analysis of flow velocity can be found with the subheading "position along the transect" later in this document.

Data overview

A total of 4287 individual fish (total N = 4287) were counted with *ArisFish*® Software in 5-minute subsamples, of which 1809 (42.0 %) were used for size measurements.

Regarding the seasonal changes of the census, most fish were reported in winter (1489 individuals counted, 39.0% measured), followed by autumn (1296 individuals counted, 49.0% measured) and summer (1202 individuals counted, 41.0% measured). Concerning these seasons, few individuals were observed in spring (300 individuals counted, 37.0% measured; extrapolation *4 because of difference in measurement). For further analysis, especially regarding abundance (fish activity min^{-1}), a census of 1200 individuals in spring data was estimated. It has to be highlighted, that this census was found within subsamples of five

minutes. Estimation of total fish activity within a 24-hour interval can be found in the result section. For a detailed data overview with total numbers measured see Table 5.

Table 5 Overview of individuals counted and measured in 5-minute-subsamples in different seasons and daytimes, as well as in all investigations together. Please note that in spring, data were multiplied by four due to the application of a lense narrowing the area insonified by the device to one quarter of the possible examination area (12°).

Season	dawn	day	dusk	night	measured	mean ± S.D.
autumn	47	735	85	429	629	324 ± 323
spring	12	760	124	304	112	300 ± 329
summer	97	466	89	550	488	300 ± 242
winter	34	1237	24	194	580	372 ± 582
all seasons	190	3198	322	1477	1809	1297 ± 136

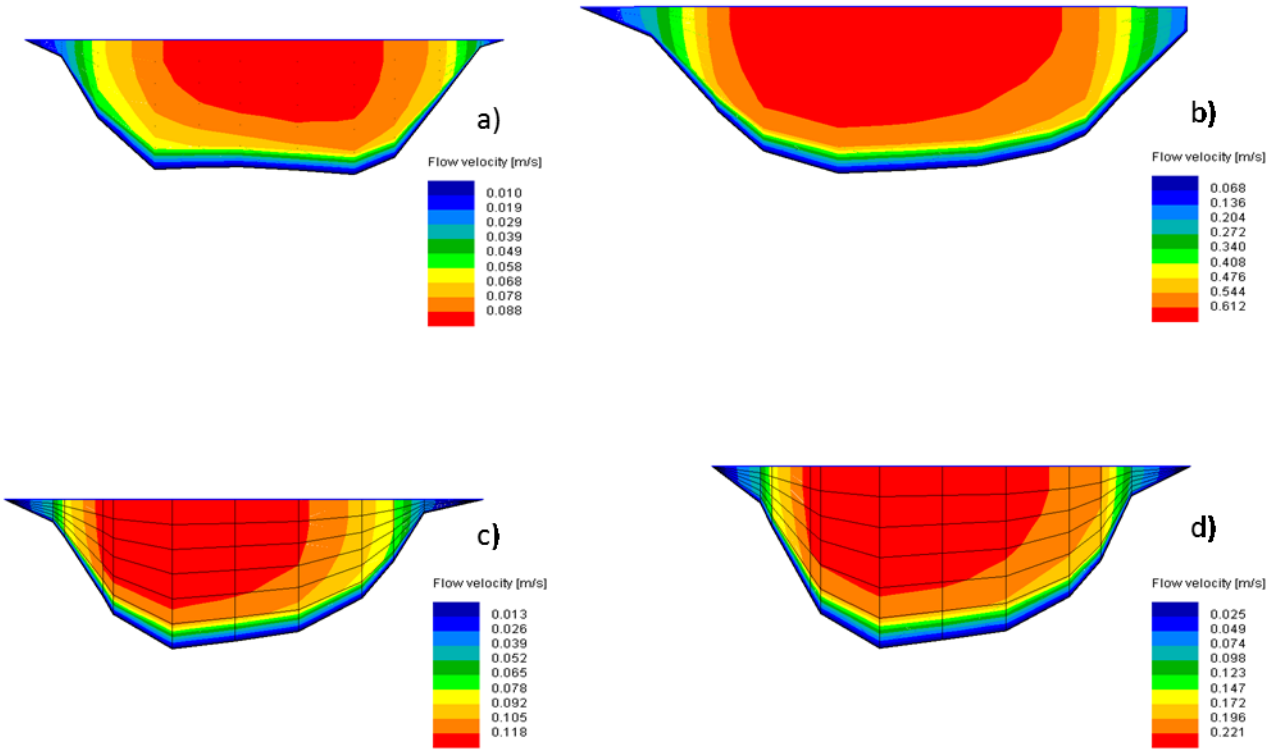

Figure 5 Flow velocities in the Johler Arm at different seasons and discharges, increasing from shores towards middle of the stream. a) winter b) spring c) summer and d) autumn. Please note that the sampling site chosen for the winter recording (a) was most downstream and very close to the mouth of the arm, while another site about 70 m upstream was investigated during the remaining seasonal settings (b to d) (RSim: Tritthart and Gutknecht, 2007)

Seasonal abundance estimation and diurnal changes

Abundance of fish was measured and individuals were counted according to their time of occurrence within the 24-hour interval. Fish abundance expressed in individuals min^{-1} ranged from 0 ind. min^{-1} in spring to 58 ind. min^{-1} in winter, with an average of 9 ±10 individuals per minute. For a detailed data overview with total numbers measured see Table 6. The highest abundance was observed in winter (N = 298 ind. min^{-1}), lowest values were found in spring and summer (240 ind. min^{-1}). The extrapolated abundance of estimated individuals per day was found to be 14 000 in spring, 14 424 in summer, 15 552 in autumn and 17 868 in winter.

Table 6 Overview of fish abundance from 4 x 24 h surveys expressed in individuals per minute (ind. min^{-1}) in different seasons. Minimum (min), maximum (max), average (avg) as well as standard deviation (S.D.) of indivuduals per minute are shown.

Season	Ind. min^{-1}_{min}	Ind. min^{-1}_{max}	Ind. min^{-1}_{avg}	Ind. $min^{-1}_{S.D.}$
spring	1	26	10	8
summer	3	21	10	5
autumn	4	25	11	5
winter	0	58	12	17
all seasons	0	58	11	10

Seasonal changes in fish abundance (ind. min^{-1}) were not significantly different (Kruskal-Wallis test, df = 3, p =0.08; Fig. 6). Fish activity, as well as estimated 24h-abundance (extrapolation from our data to 24 hours), was highest in winter. Also, among single fish observations, fish also aggregated to fish schools of more than 7 individuals in the winter, providing several occurrences of extremely high abundance. Data used in hourly estimation (as can be seen in Fig. 7) was pooled to longer time units, (e.g. dawn, day, dusk and night) to enable statistical analysis. Therefore, fish in certain time frames (e.g. "day", see Table 3 for an overview of the time frames used) were compared to individuals of another time frame instead of another hour. This also assisted in the analysis of diurnal changes.

A diurnal pattern of fish activity with a unimodal peak during daytime in autumn and winter and a multimodal distribution in spring and summer was observed. In autumn and winter, the highest abundance was reached in the hours from late morning to early afternoon, while the two peaks in spring resulted from higher abundance in the late morning and late evening hours. In summer, fish were observed most frequently in the early morning as well as the late evening hours (Fig. 7 and 8).

The comparison of fish activity during different times of day showed a percentage of 4.0% of all individuals being active at dawn, 5.0% in dusk, 29.0% in night and the major part of 61.0% during day (Table 7). Statistical analysis revealed significant differences between dawn, day, dusk and night (Kruskal-Wallis test, df = 3, $p < 0.01$, multiple Mann-Whitney U, $p < 0.01$) between the seasons. Within the seasons, differences were found in autumn and winter between day and night, respectively (Kruskal-Wallis test, df = 3, $p < 0.01$, multiple Mann-Whitney U,

$p < 0.01$; Fig. 9). Because of the short duration of dusk and dawn and the pooling of data for the different categories, distinctly lower numbers of fish were observed for dawn and dusk.

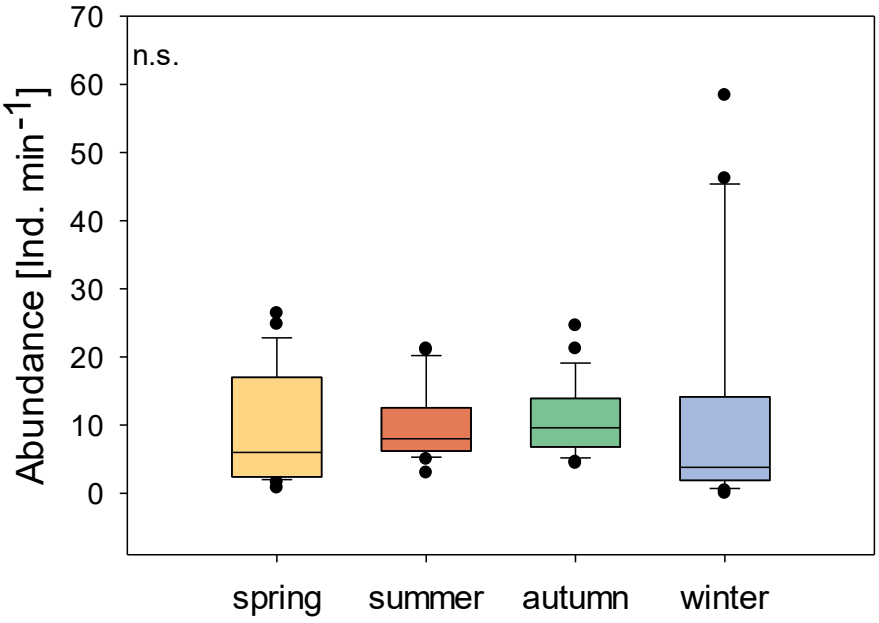

Figure 6 Comparison of fish abundance between different seasons

Table 7 Overview of individuals per minute and their proportion of the sampled fish observed in different seasons and daytimes

		dawn	day	dusk	night
spring	**Ind. min^{-1}**	2	152	25	61
	%	0.8	63.3	10.4	25.4
summer	**Ind. min^{-1}**	19	93	18	110
	%	7.9	38.8	7.5	45.8
autumn	**Ind. min^{-1}**	9	147	17	86
	%	3.5	56.8	6.6	33.2
winter	**Ind. min^{-1}**	7	247	5	39
	%	2.3	82.9	1.7	13.1
all seasons	**Ind. min^{-1}**	9 ± 7	160 ± 64	16 ± 8	74 ± 31
	%	3.6 ± 2.8	61.6 ± 24.7	6.3 ± 3.2	28.5 ± 11.9

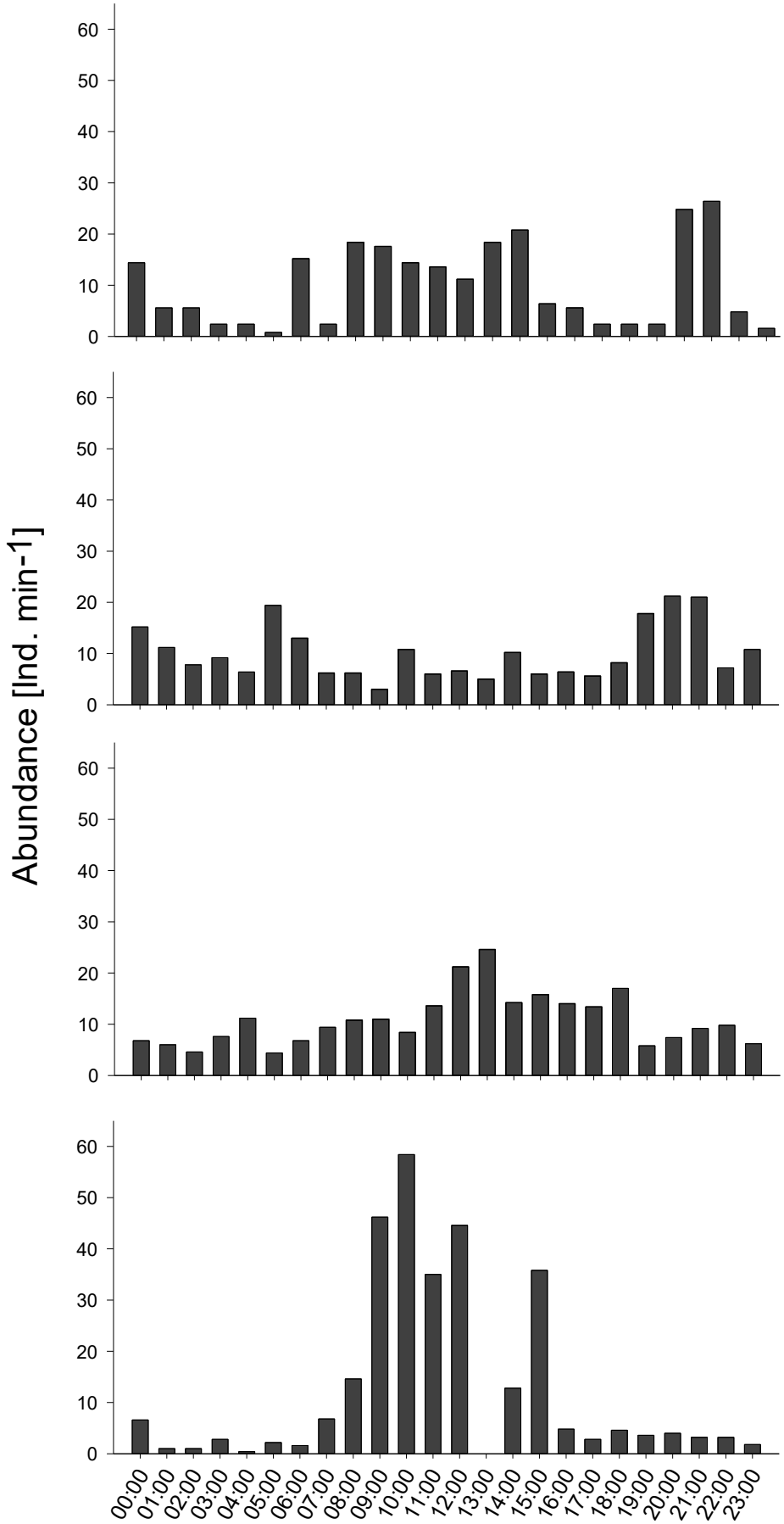

Figure 7
Diurnal variation of fish abundance as a proxy for activity in spring (a), summer (b), autumn (c) and winter (d). Different daytimes are indicated by color-coding: night (grey), day (white), dawn and dusk (light grey). Abundance in autumn and winter shows one peak from late morning to early afternoon while spring and summer show a trend towards a multi-modal distribution.

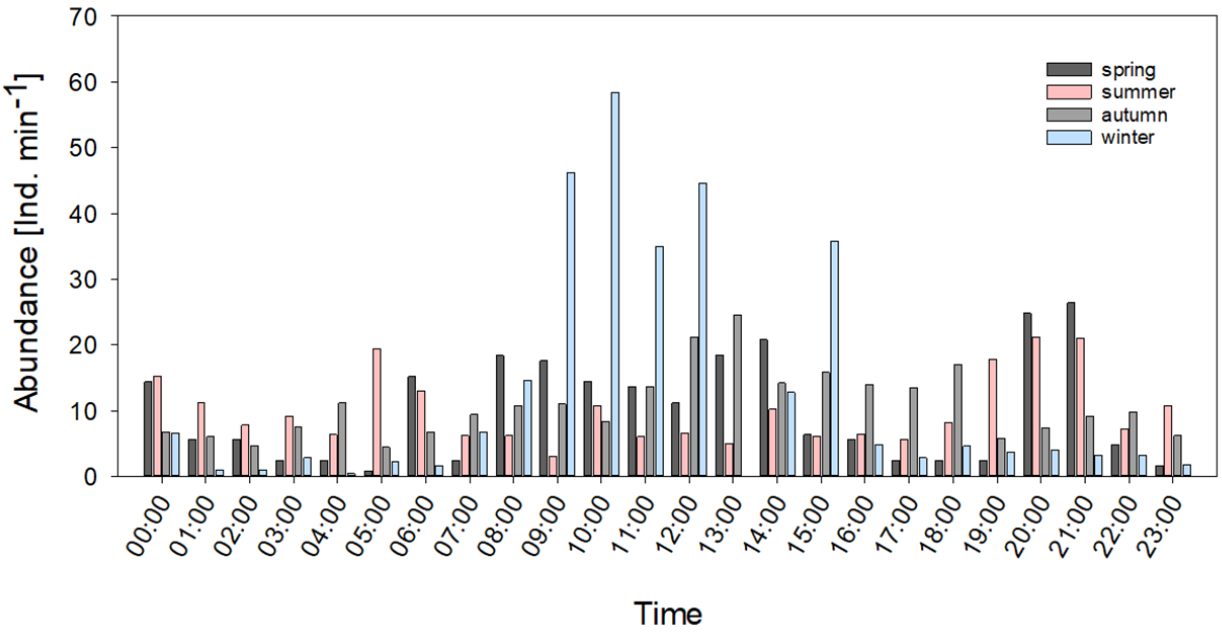

Figure 8 Overview of number of fish activity (Individuals min^{-1}) found in different seasons in every hour of the survey (24 h).

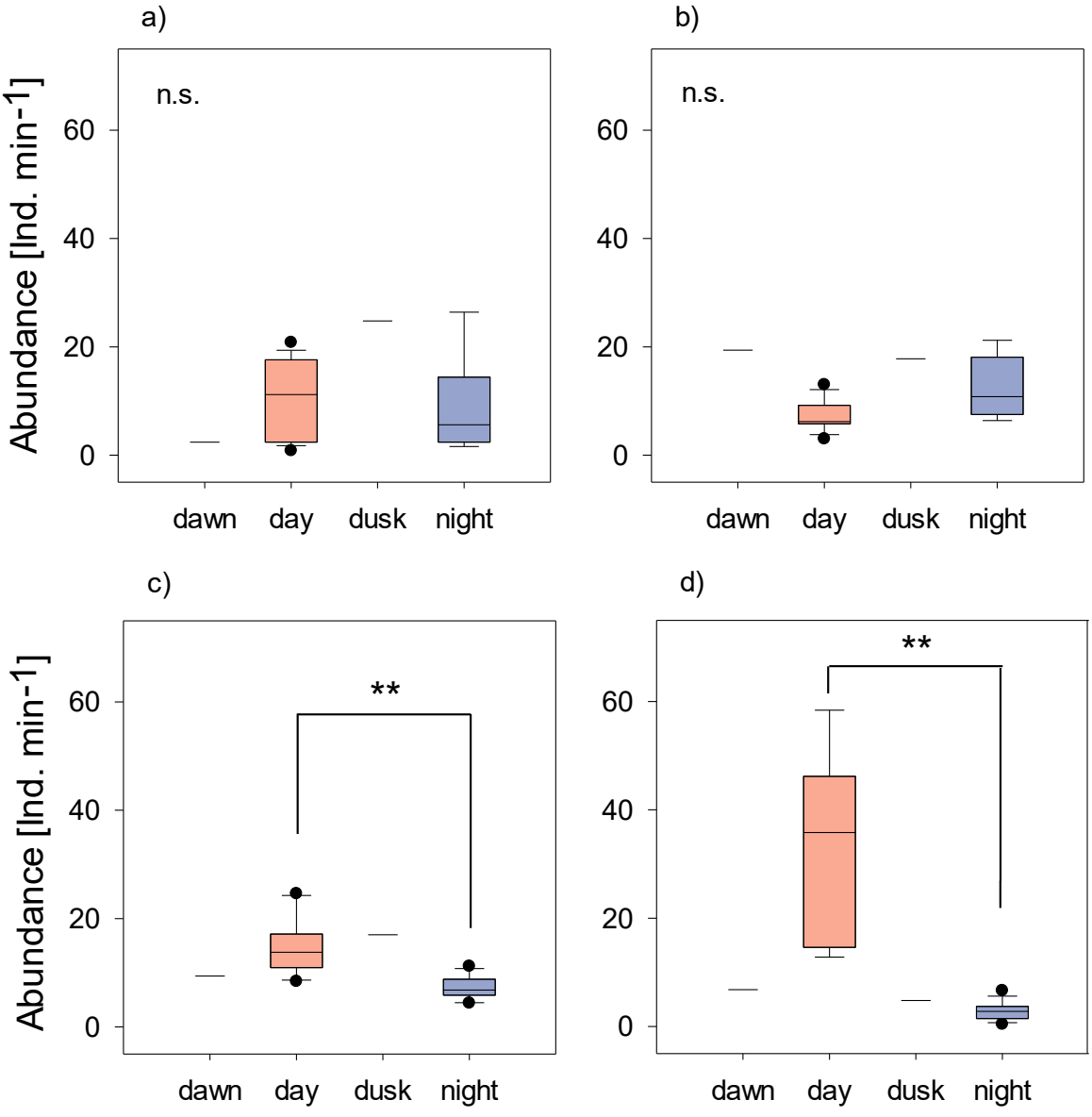

Figure 9 Individuals min^{-1} pooled for different solar episodes in spring (a), summer (b), autumn (c) and winter (d). Single values for dawn and dusk appear because of the limited values available. Significant differences are pointed out by stars: ** = p < 0.01).

Size structure of fish in the Johler Arm

Seasonal and diurnal differences were observed in the size of individual fish. On average, fish were found to be largest in spring (20.4 cm ± 10.5 cm, mean ± SD) and smallest in winter (11.0 cm ± 2.6 cm). Overall minimum length (TL_{min}) was 5.3 cm, maximum length (TL_{max}) was 75.9

Table 8 Minimum, maximum, average and standard deviation of the total length of fish observed in different seasons.

	[cm] TL_{min}	[cm] TL_{max}	[cm] mean of TL	[cm] SD of TL
autumn	5.7	75.9	16.1	8.5
spring	8.3	63.3	20.4	10.5
summer	7.5	62.6	19.0	10.1
winter	5.3	36.1	11.0	2.6
all seasons	5.3	75.9	15.5	8.5

cm and average (mean of TL) 15.5 cm ± 8.5 cm (Tab. 8). Fish size differed significantly between seasons, except summer and spring ($p = 0.36$) (Fig. 10, Tab. 9; Kruskal-Wallis, df = 3, $p < 0.001$; multiple Mann-Whitney U, $p < 0.001$). Comparative analysis of total fish length between different times (hours) of day revealed significant differences within each sampling collection event (Kruskal-Wallis test, df = 23, $p < 0.001$; Fig. 11). This indicates that sizes varied within a 24-hour cycle in every season.

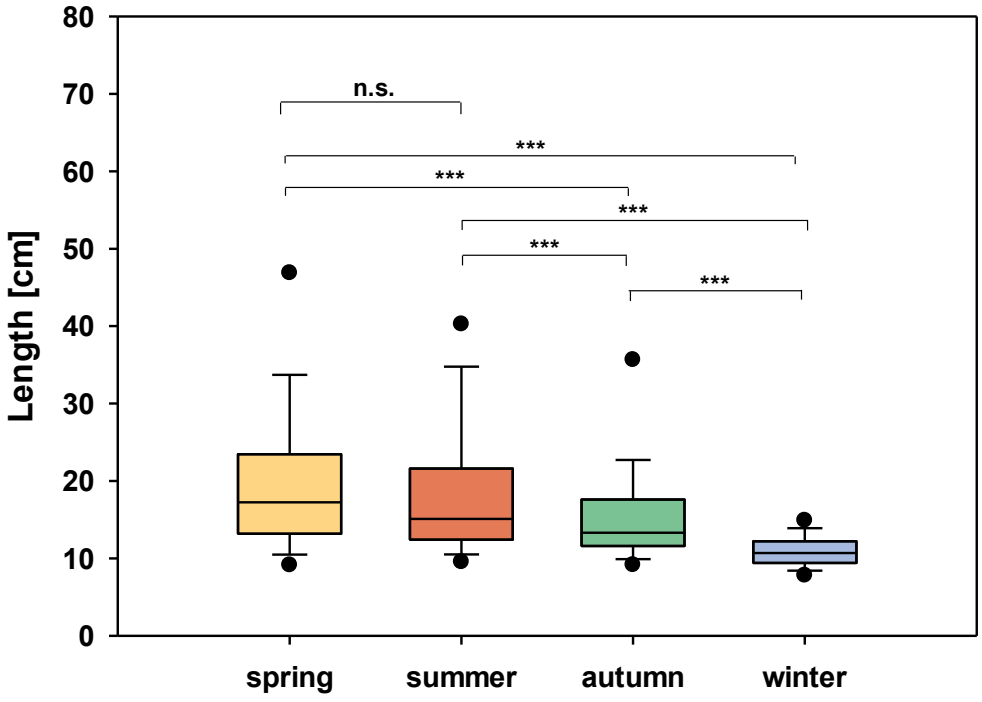

Figure 10 Comparison of fish size expressed as total length between the seasons. The values of spring and summer showed no significant differences while autumn and winter differed significantly from all other seasons, respectively ($p < 0.001$).

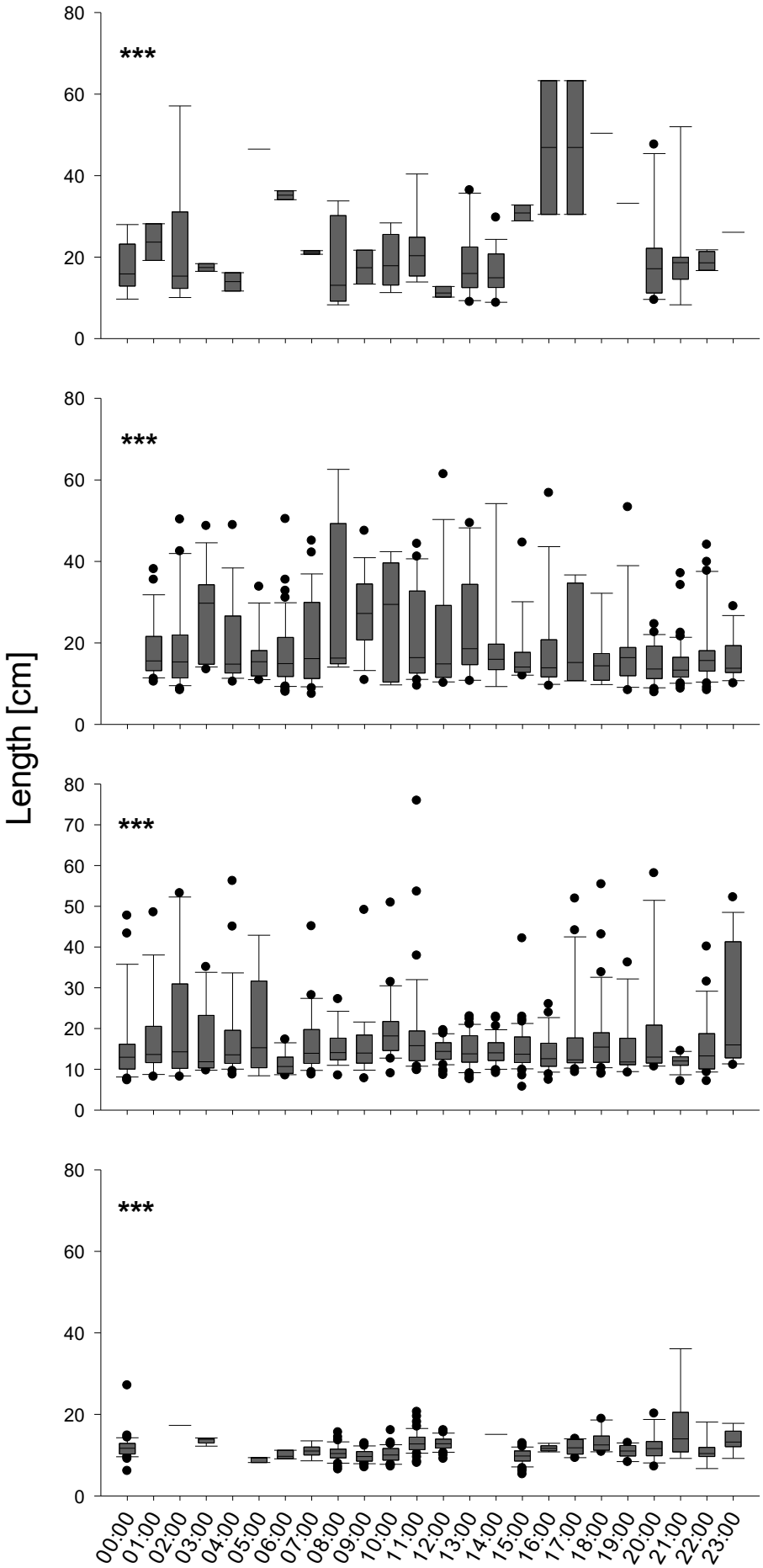

Figure 11
Diurnal variation of total fish length (cm) in spring (a), summer (b), autumn (c) and winter (d). Different daytimes are indicated by color-coding: night (grey), day (white), dawn and dusk (light grey). Box-Whisker Plots are given with median, quartiles (25 %, 75%) and percentiles (5%, 95%). Significance is indicated by ***. Explicit differences between the individual hours is not shown in order to prevent confusion.

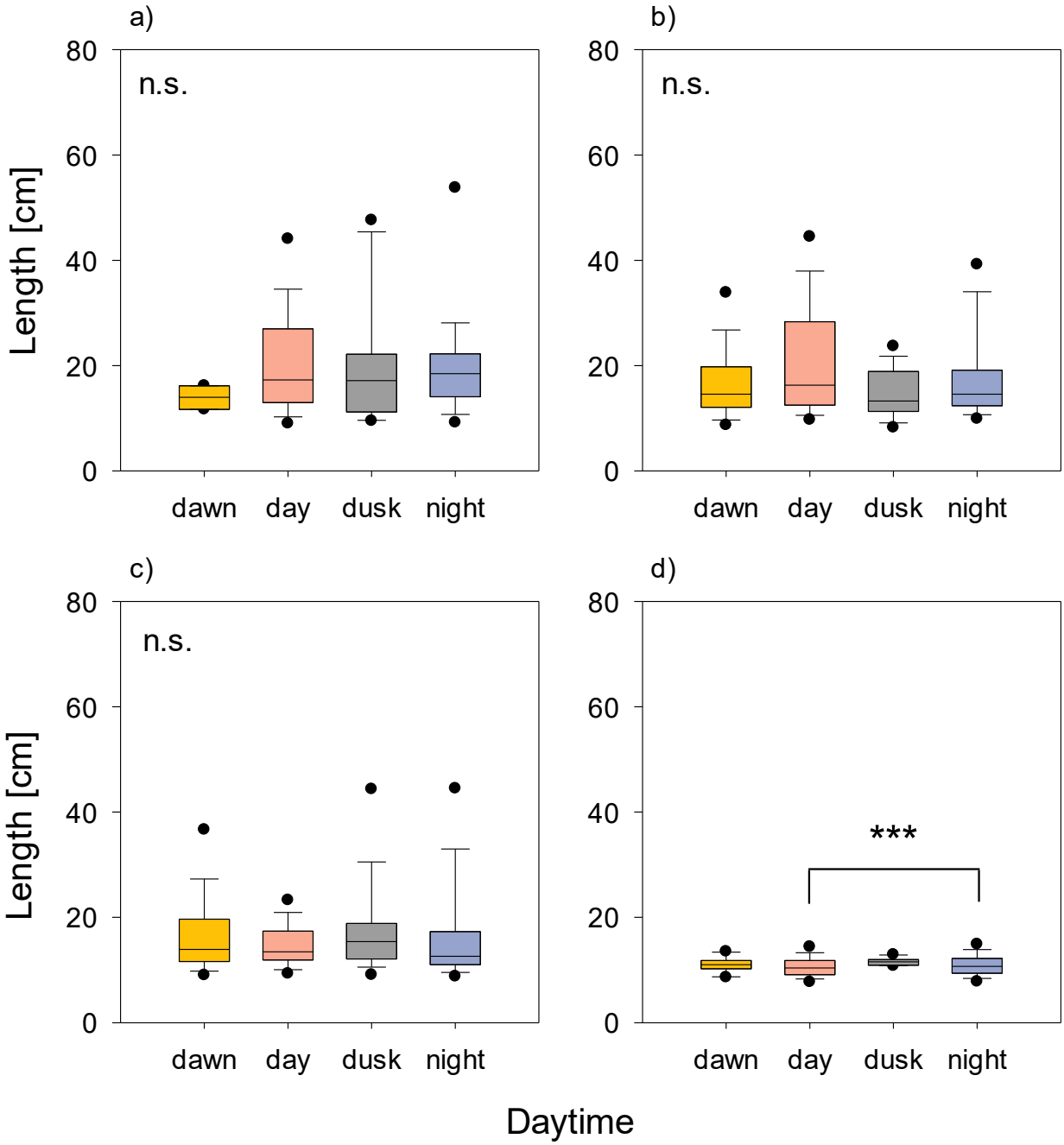

Figure 12 Changes in fish size at different daytimes in different seasons, spring (a), summer (b), autumn (c) and winter (d). In winter, size was found to differ significantly in day and night ($p < 0.001$).

Table 9 Comparison of body size in different seasons. The statistical test as well as the following multiple comparisons showed significant results.

Test	df	P
Kruskal-Wallis H	3	< 0.001
Multiple Comparisons	3	see below

	spring	summer	autumn	winter
spring		0.360	< 0.001	< 0.001
summer	0.360		< 0.001	< 0.001
autumn	< 0.001	< 0.001		< 0.001
winter	< 0.001	< 0.001	< 0.001	

No cross-seasonal pattern for body size (Fig. 11) by specific hour of the day was found.

Body size of fish observed at different times of day proved to be significantly different when including all seasons (Kruskal-Wallis test, df = 3, $p < 0.001$; Fig. 13). Variations were observed between night and day, dusk and day as well as dawn and day. A comparison of daytimes within the seasons (Fig. 12) resulted in significant differences between day and night in winter. The significant result of the Kruskal-Wallis test ($p < 0.05$) for the summer season showed to be not significant in the post hoc procedure (multiple Mann-Whitney U – test, $p > 0.05$; Table 10).

Table 10 Comparison of daytime (dawn, day, dusk, night) within the seasons. * = the statistical test chosen for this data originally showed a significant divergence to some extent; this was disproved by multiple comparisons (all event $p > 0.1$).

Test	Season	df	variation between	P
Kruskal Wallis H & multiple U	spring	3		0.55
	summer	3		0.04*
	autumn	3		0.06
	winter	3	day night	< 0.001

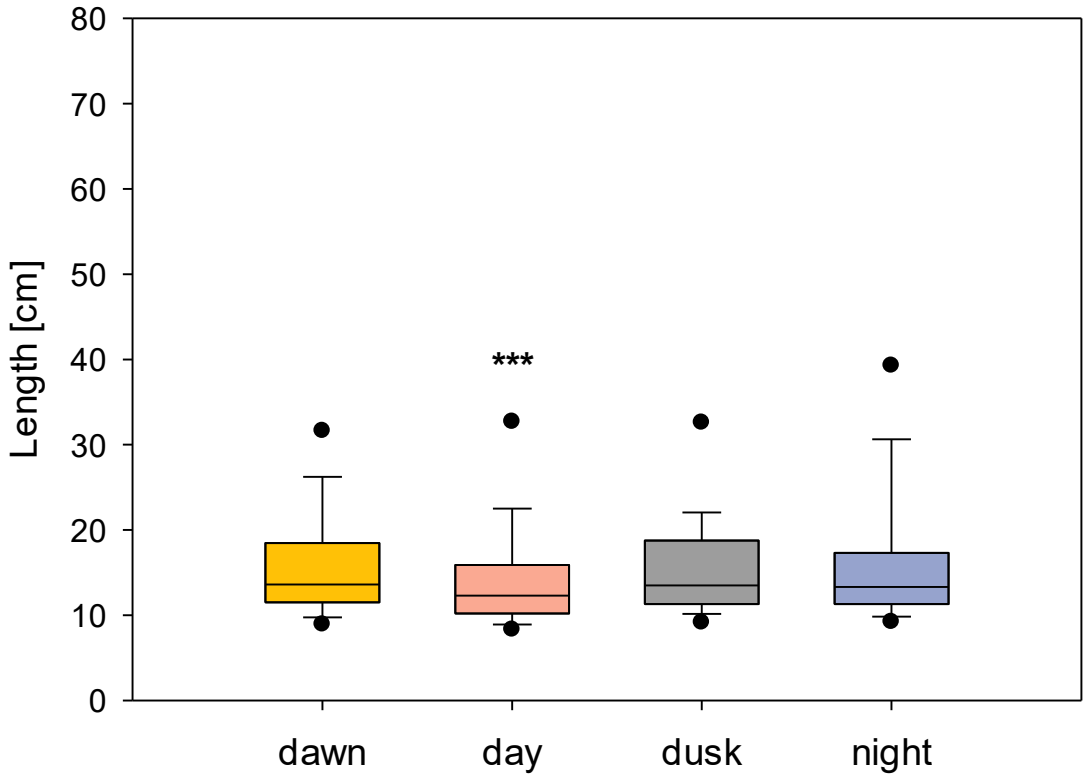

Figure 13 Differences between the daytimes when data of all seasons are considered. Kruskal-Wallis test, $p < 0.001$, medians, quartiles and percentiles are given.

Swimming direction, immigration, and emigration

Considering all sample collection events (4 x 24 hours, segmented into 5-minute subsamples), a total of 1847 individuals were counted emigrating from the sidearm, while 2406 fish immigrated into the sidearm. Immigration, therefore, resulted, on average, in 5 ± 8 ind. min^{-1} moving upstream, while emigration averaged 4 ± 7 ind. min^{-1} swimming downstream. Extrapolation for 24-hour runs resulted in 7294 fish swimming upstream and 5977 individuals migrating upstream in one 24-hour period. No significant differences were found between immigration and emigration in one year (all seasons pooled, Kruskal-Wallis test, df = 1, p = 0.91). Within different seasons significant variations were observed: in spring, summer and winter up- and downstream movement was found to differ significantly (Mann-Whitney U tests, see Table 11, Fig. 14 and 15), with an average of 2 ± 2 ind. min^{-1} emigrating and 1± 0 ind. min^{-1} immigrating in spring, 4 ± 2 ind. min^{-1} emigrating and 6 ± 4 ind. min^{-1} immigrating in summer, 6 ± 3 ind. min^{-1} emigrating and 5 ± 3 ind. min^{-1} immigrating in autumn and 5 ± 13 ind. min^{-1} emigrating and 9 ± 15 ind. min^{-1} immigrating in winter (Fig. 15). Within the abundance distributions observed in different seasons, migration patterns showed high downstream movement of individuals during daytime in spring and balanced migration (without any clear differences of immigration and emigration) in summer and autumn. In winter, movement was found to be alternating in different intervals, with individuals migrating either one way or another in single hours. Furthermore, immigration in winter predominated, especially in the late morning and afternoon hours. The activity of fish movement shifted from very early morning and evening in summer to a unimodal distribution peaking at midday and early afternoon in autumn. Nevertheless, no clear differences between swimming directions can be found in autumn (Fig. 14).

Table 11 Overview of results in migration direction analysis for abundnace in different seasons. Possible migration directions are up and down, significance levels are shown.

Test	Season	P	Significance
Mann-Whitney U	spring	< 0.05	*
	summer	< 0.05	*
	autumn	0.3	n.s.
	winter	< 0.05	*

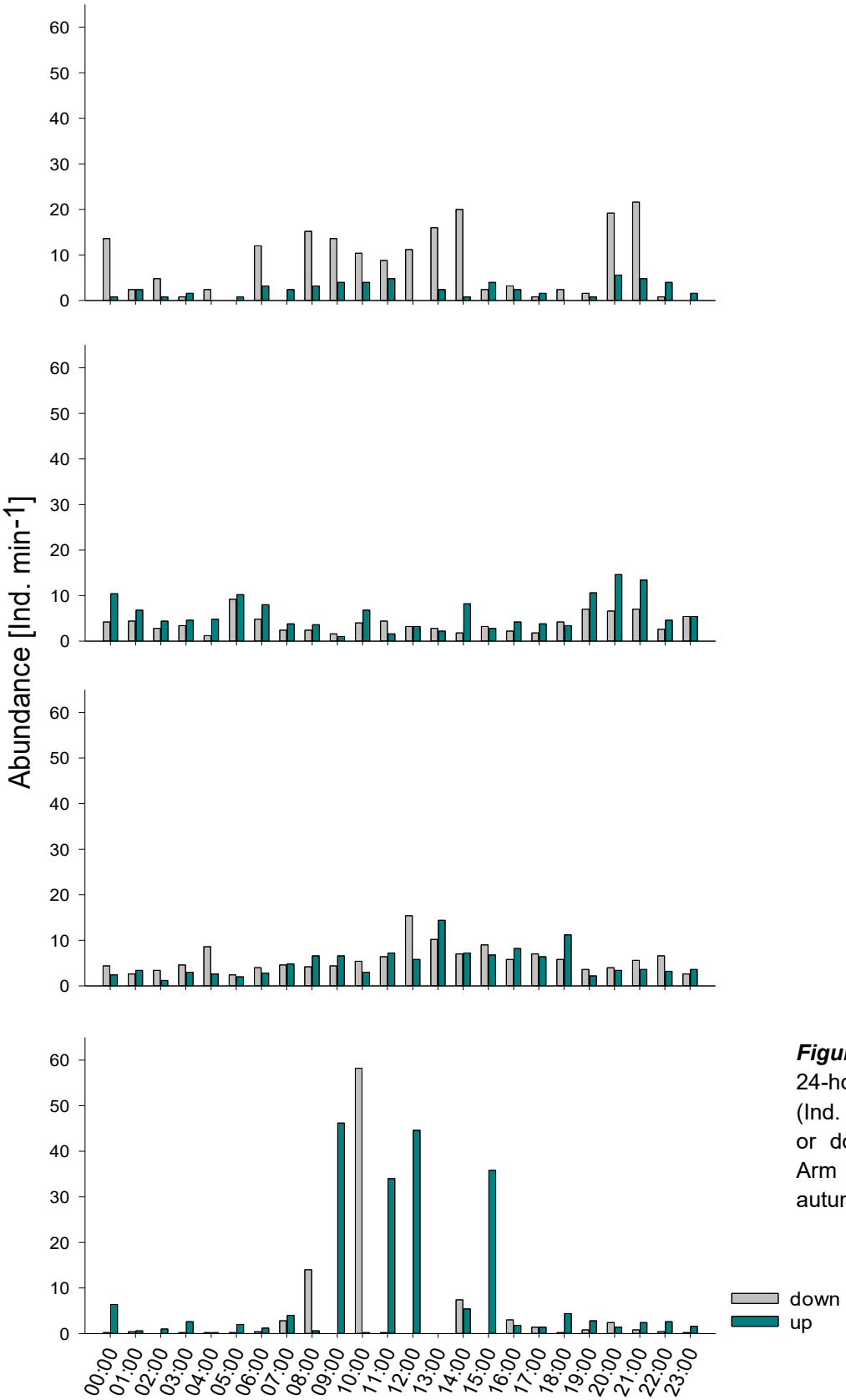

Figure 14
24-hour investigation of fish (Ind. min^{-1}) travelling upstream or downstream in the Johler Arm in spring (a), summer (b), autumn (c) and winter (d).

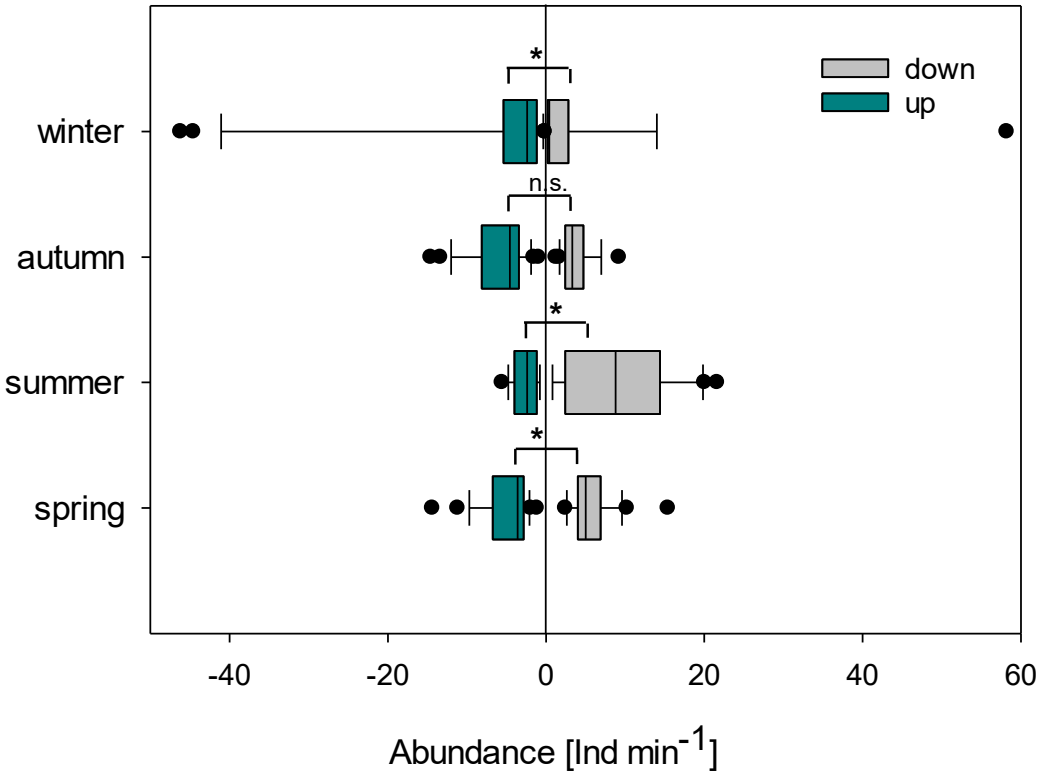

Figure 15 Upstream and downstream movements of fish activity (Ind. min^{-1}) in all seasons investigated in different seasons, distinguished for direction of movement (downstream, upstream migration). n.s. = not significant, * = $p < 0.05$.

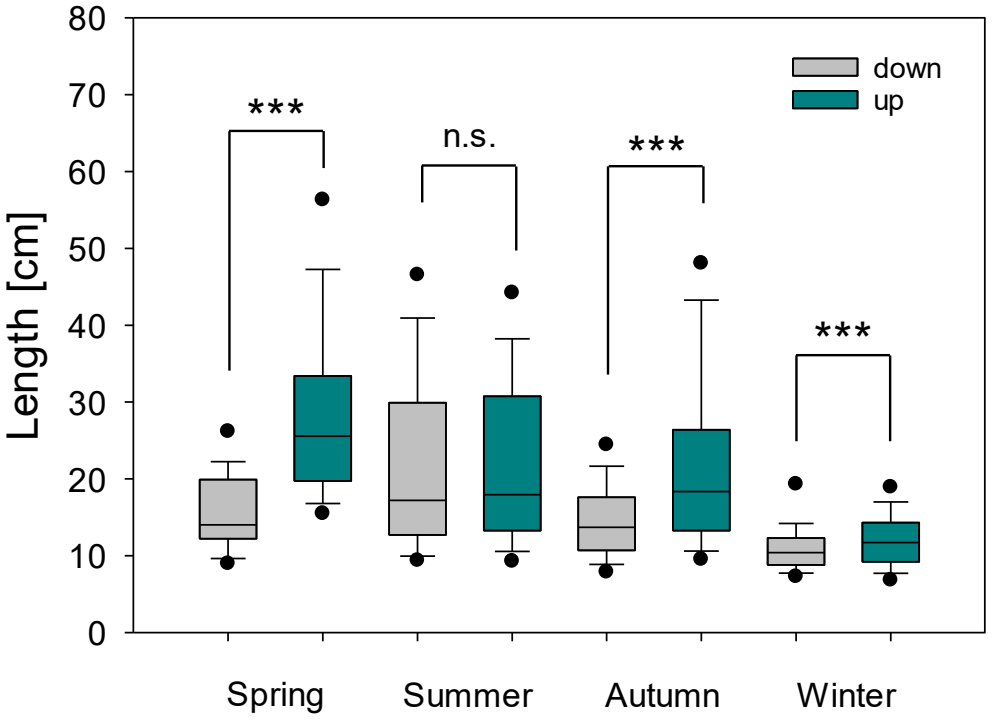

Figure 16 Size differences of individuals migrating upstream or downstream in the different seasons. n.s. = not significantly different, *** = $p < 0.001$. Medians, quartiles and 5% and 95% percentils are given.

Table 12 Summary of total body length of all individuals measured with regard to season and direction of migration (upstream, downstream).

		DOWN			
		[cm] TL_{min}	[cm] TL_{max}	[cm] mean of TL	[cm] SD of TL
Total length	autumn	5.7	58.1	13.5	5.4
	spring	8.3	50.4	15.6	6.1
	summer	8	61.4	20.2	11.3
	winter	6.5	20.9	10.4	2.2
	all seasons	5.7	61.4	14.4	7.5
		UP			
		[cm] TL_{min}	[cm] TL_{max}	[cm] mean of TL	[cm] SD of TL
Total length	autumn	7.3	75.9	18.6	10.2
	spring	12.4	63.3	28.3	11.6
	summer	7.5	62.6	18.5	9.5
	winter	5.3	36.1	11.2	2.7
	all seasons	5.3	75.9	16.2	9.1

The size of upstream and downstream migrating fish va–ried between the seasons. The smallest (TL_{min} = 5.3 cm, found in a winter sample), as well as largest (TL_{max} = 75.9 cm, autumn sample) individuals were found to move upstream in the sidearm. On average, upstream migrating fish were larger (16.2 cm ± 9.1 cm; mean ± SD) than downstream swimming (14.4 cm ± 7.5 cm). Data on the minimum and maximum length as well as an average total length is given in Table 12 for all seasons, as well as pooled for the whole sampling year. In summer, fish migrating upstream were equal in size as fish swimming downstream, while in the remaining seasons, upstream migrating individuals were significantly larger (Fig. 16, Mann-Whitney U test, $p < 0.001$).

Aside from directed up- or downstream movement, various patterns were observed during analysis:

- lingering (remaining in the same position for a certain amount of time)
- passive drift (snout against the current while moving downstream)
- circling (e.g. around objects)

- active hunting (sudden change of direction with enhanced speed towards another individual, very rare)

No further analyses of these movements were performed.

Position along the transect

Distance from the right shore of the Johler Arm (given as distance from device) varied for individuals and showed significant differences between seasons. Fish were observed at a minimal distance ($Dist_{min}$) of 1.0 m from the device, while individuals farthest away were found to swim or linger at a distance ($Dist_{max}$) of 24.3 m. The average distance was 9.3 m ± 5.4 m (mean ± S.D.), with variations found by season (Table 13).

Table 13 Minimal, maximal and average (± S.D) distance of fish that occurred in different seasons and as a total. $Dist_{max}$ was lowest in winter due to the slightly different set-up of the experiment (the research vessel was mounted on a platform instead of directly at the shore). Distance from shore equals Distance from device + 3 m.

		[m] **$Dist_{min}$**	[m] **$Dist_{max}$**	[m] **mean of Dist**	[m] **SD of Dist**
Distance from device [m]	**autumn**	1.2	22	12.0	5.2
	spring	1.2	21.7	9.9	5.5
	summer	1.0	24.3	10.9	5.8
	winter	1.6	15.2	5.6	2.5
	all seasons	1.0	24.3	9.3	5.4

Comparing all seasons, significant differences were observed in the position of individuals along the investigated transect (Kruskal-Wallis test, df = 3, $p < 0.001$). Additionally, multiple comparisons (Mann-Whitney U tests) showed significant differences between spring and summer ($p < 0.05$) as well as between all other seasons when compared pairwise ($p < 0.001$, Fig. 17). This indicates the degree of mobility of fish in the waterbody. Furthermore, hourly recordings of distance from device varied in every season. In order to investigate the distances of positions taken at different daytimes, values were pooled (all seasons) into intervals of 5 meters (0 – 5 m, 5 – 10 m, 10 – 15 m, 15 – 20 m, 20 – 25 m and > 25 m) and shown with length for graphical illustration.

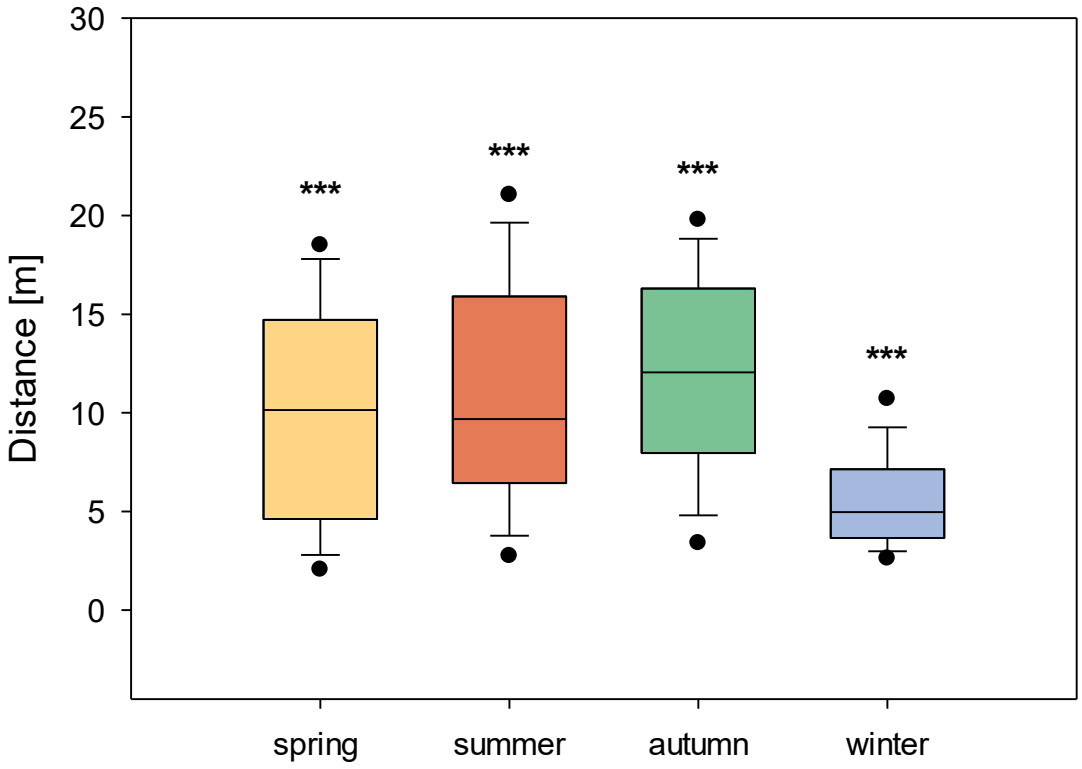

Figure 17 Position of fish along the transect, given as distance in meters, in the different seasons. Kruskal-Wallis test and multiple comparisons, $p < 0.001$, medians, quartiles and percentiles are given.

Table 14 Observation distance of fish at different seasons and daytimes. (dawn, day, dusk, night

Test	Season	df	variation between	P
Kruskal Wallis H & multiple Mann Whitney U	spring	3	dawn - dusk	< 0.05
	summer	3	dawn - night	< 0.01
			day - night	< 0.001
			dusk - night	< 0.001
	autumn	3	dusk - night	< 0.05
	winter	3	dawn - day	< 0.001
			dawn - night	< 0.01

Differences in body length and distance from the device were significant between dawn, day, dusk and night (Kruskal-Wallis test, df = 3, $p < 0.001$), with the significance between dawn and dusk being refuted by post hoc analysis ($p = 1.00$ in multiple comparison via Mann-Whitney U test). By comparison within the seasons, the position of fish along the transect was found to be associated with daytime (Tables 14 and 16) and total length (Fig. 18). In this context, body length varied significantly for the different distance intervals, especially the nearest (0-5 m) and one of the farthest (20-25 m) intervals. The interval from 20 to 25 m is an exception as body length did not differ from 5 – 10 m, 10 – 15 m and 15 – 20 m intervals. Additionally, times of day are given in Table 14 in order to investigate the question of whether individuals of different sizes were observed at different times of the day, e.g. because of differences in foraging. Although the connection between body size and distance was statistically analysed, no indicators are given in the graph to prevent confusion.

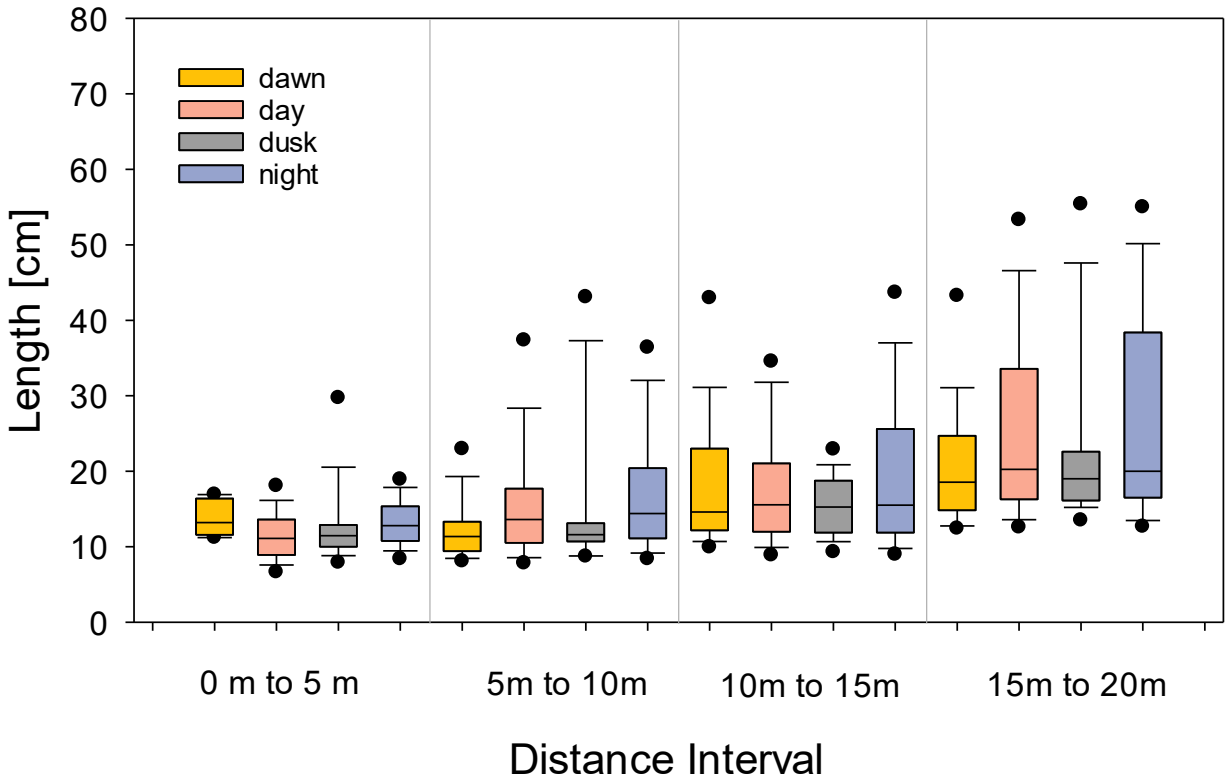

Figure 18 Significant differences were observed regarding size of individuals with increasing distance from the device (i.e. from the shore) at different daytimes. No indicators for statistical analyzes are given to prevent confusion. See Tab. 12 as well as Tab. 13.

Regression analysis of distance from device (independent variable) vs. total body length (dependent variable) indicated a significant increase in body size with increasing distance from the device ($p < 0.001$). Although significant, the explained variation of the different regressions

ranged between 6 and 36% (spring $R^2 = 0.36$, summer $R^2 = 0.18$, autumn $R^2 = 0.14$, winter $R^2 = 0.06$; Table 15) indicating factors other than distance from the shore influenced this distribution pattern. For further analyses, the regressions were combined with average current velocity values of the water column for visualization of flow conditions at the positions taken by different sized individuals (Fig. 19). In spring, the average current velocity was relatively high with a decrease towards the left shore (right in the figure). In summer, the current velocity was comparably low, with a strong decrease towards the left shore. In autumn, however, the flow was low, with a slight increase in the central area and a decrease towards the left shore while in winter, low current velocity with a decrease towards the left shore was observed due to a different transect position. In this context, the same approach was performed to examine variations in body size and position for up- and downstream swimming fish in the different given seasons. These regression analyses resulted in significant effects ($p < 0.05$, $p < 0.01$ and $p < 0.001$; see Figs. 20 and 21). The R^2 ranged from a minimum of $R^2 = 0.02$ for emigration in winter and a maximum of $R^2 = 0.19$ for emigration in summer (see figures legends for equation and exact results).

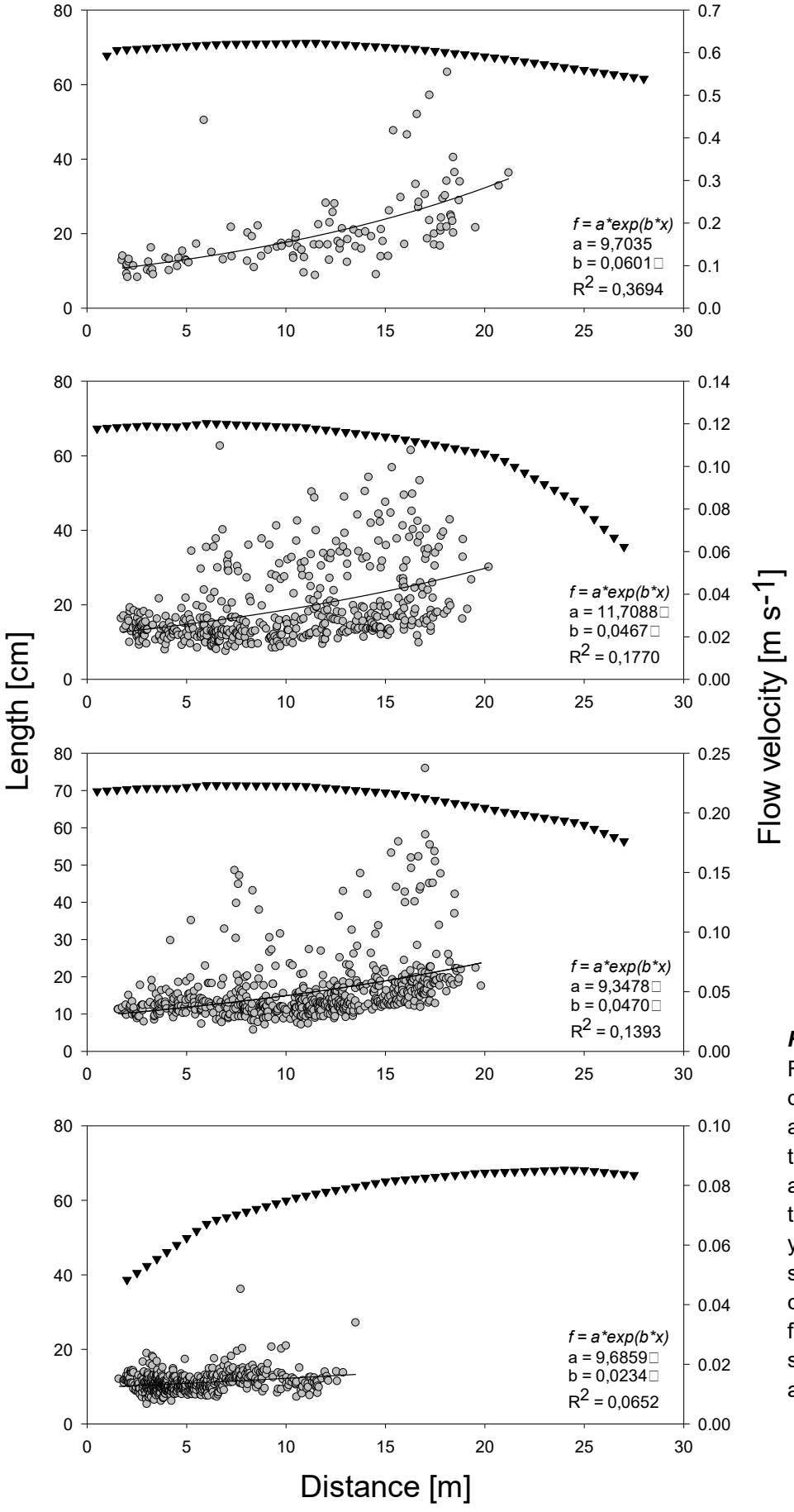

Figure 19
Relationship between distance from the shore and fish size. The triangles indicate the average flow velocity in the water column (right y- axis, note different scaling of this axis), circles represent size of fish individuals in a) spring, b) summer, c) autumn and d) winter.

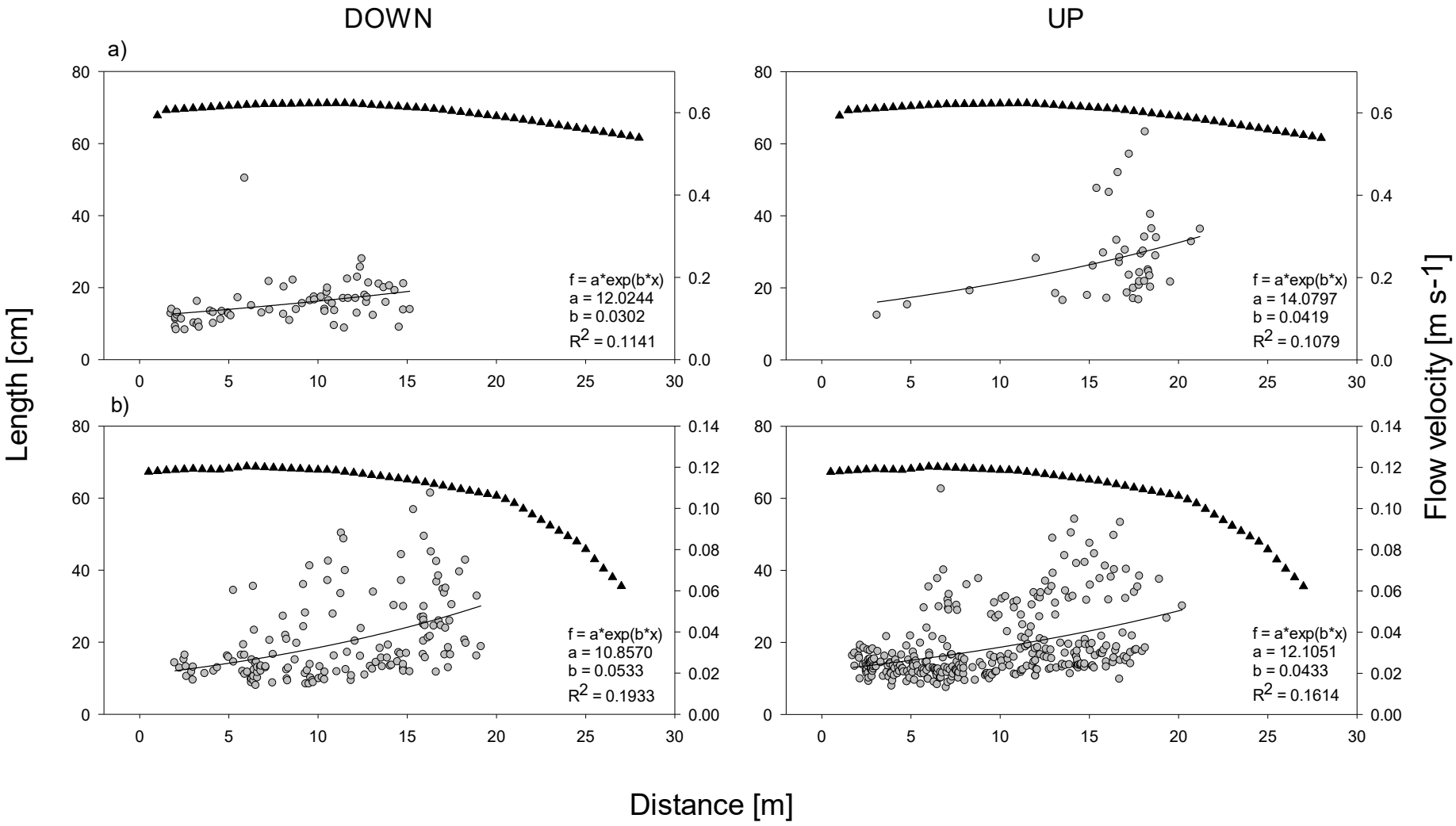

Figure 20 Relationship between distance from the shore and fish size. The triangles indicate the average flow velocity in the water column (right y- axis, note different scaling of this axis), circles represent fish migrating down (left) and up (right) in a) spring and b) summer.

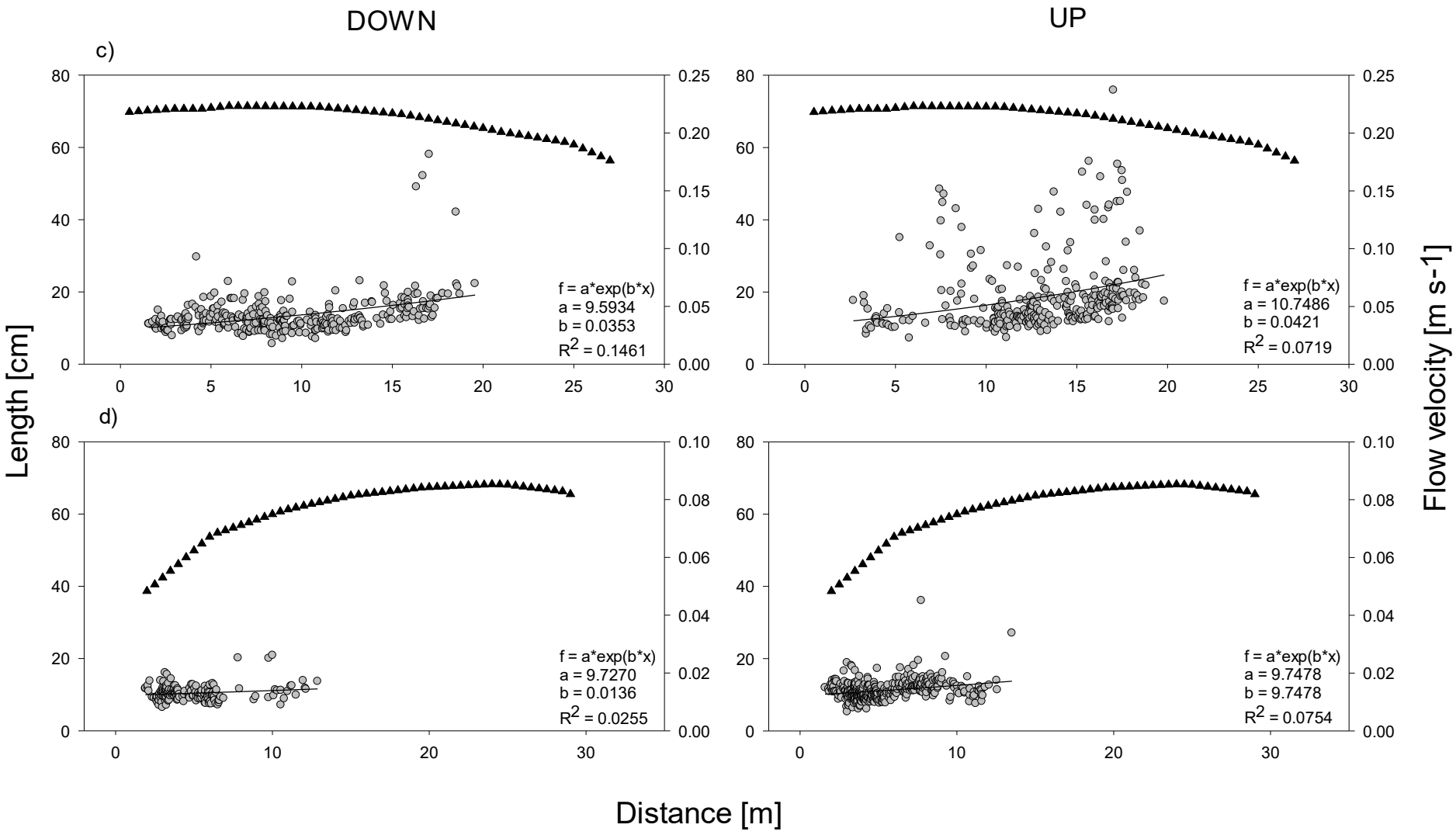

Figure 21 Relationship between distance from the shore and fish size in c) autumn and d) winter.

Table 15 Results of regression analysis of length and distance. The relationship between total length of fish and dwelling distance from device in all seasons was highly significant.

Season	Equation	a	b	F	R^2	P
spring		9.70	0.06	64.41	0.36	<0.001
summer	f = a*exp(b*x)	11.7088	0.05	104.49	0.18	<0.001
autumn		9.35	0.05	101.52	0.14	<0.001
winter		9.69	0.02	40.31	0.06	<0.001

Table 16 Overview of total body length (cm) and distance of occurrence measured from device (m) for the different daytimes (dawn, day, dusk, night) in every season.

		DAWN				DAY			
		[cm] TL_{min}	[cm] TL_{max}	[cm] mean of TL	[cm] SD of TL	[cm] TL_{min}	[cm] TL_{max}	[cm] mean of TL	[cm] SD of TL
Total length [cm]	autumn	8.7	45.1	16.9	7.9	5.7	75.9	15.4	7.1
	spring	11.7	16.2	14.0	2.3	8.3	63.3	20.9	10.8
	summer	8.0	50.4	17.2	7.8	7.5	62.6	21.0	11.7
	winter	8.6	13.5	11.0	1.4	5.3	20.6	10.6	2.1
	all seasons	8.0	50.4	16.3	7.5	5.3	75.9	14.7	8.2

		DAWN				DAY			
		[m] $Dist_{min}$	[m] $Dist_{max}$	[m] mean of Dist	[m] SD of Dist	[m] $Dist_{min}$	[m] $Dist_{max}$	[m] mean of Dist	[m] SD of Dist
Distance fron device [m]	autumn	2.0	20.9	12.1	4.8	1.2	22.0	12.1	5.1
	spring	1.8	3.2	2.4	0.8	1.2	21.7	10.4	5.7
	summer	2.9	21.9	12.0	5.3	1.8	24.3	11.5	5.2
	winter	7.1	15.2	9.4	2.1	2.1	11.4	5.3	1.9
	all seasons	1.8	21.9	11.4	4.9	1.2	24.3	8.7	5.2

		DUSK				NIGHT			
		[cm] TL_{min}	[cm] TL_{max}	[cm] mean of TL	[cm] SD of TL	[cm] TL_{min}	[cm] TL_{max}	[cm] mean of TL	[cm] SD of TL
Total length [cm]	autumn	8.9	55.4	17.6	9.3	7.1	58.1	16.7	10.5
	spring	9.5	47.6	19.3	11.2	8.3	57.1	20.2	10.3
	summer	7.9	24.6	14.8	4.6	8.4	50.3	18.3	9.4
	winter	10.8	12.9	11.6	0.7	6.1	36.1	12.4	3.7
	all seasons	7.9	55.4	16.2	7.9	6.1	58.1	16.6	9.3

		DUSK				NIGHT			
		[m] $Dist_{min}$	[m] $Dist_{max}$	[m] mean of Dist	[m] SD of Dist	[m] $Dist_{min}$	[m] $Dist_{max}$	[m] mean of Dist	[m] SD of Dist
Distance fron device [m]	autumn	1.5	22.0	13.3	5.2	1.6	21.9	11.5	5.2
	spring	1.9	18.5	9.5	4.4	2.0	20.2	9.0	5.3
	summer	1.7	21.9	12.7	6.6	1.0	22.0	10.0	6.0
	winter	1.8	13.6	7.9	5.1	1.6	14.0	6.4	4.0
	all seasons	1.5	22.0	12.0	5.9	1.0	22.0	9.9	5.7

Aggregation of individuals

Accumulation of individual fish in larger fish shoals was observed in winter. This leads to the question of whether various schools were passing the transect or one circling school was present. Therefore, schools were labelled in the data (school 1, school 2, etc.) to allow for analysis of differences regarding body length and size of the school.

On average, 77.7 ± 94.9 fish were counted in a school, with accumulations sized from a minimum of 7 to a maximum of 290 individuals. There were distinct variations in the number of individuals per shoal. Furthermore, the body length of fish in different accumulations was significantly different, which may be evidence for fish shoals alternating over a 24-hour period (Kruskal-Wallis test, df = 12, $p < 0.001$, Fig. 22). Other than in winter, where 1339 individuals were observed to accumulate into shoals, in the remaining seasons, no aggregations of this size (more than 7 individuals) were observed, although fish were recorded swimming in pairs and triplets.

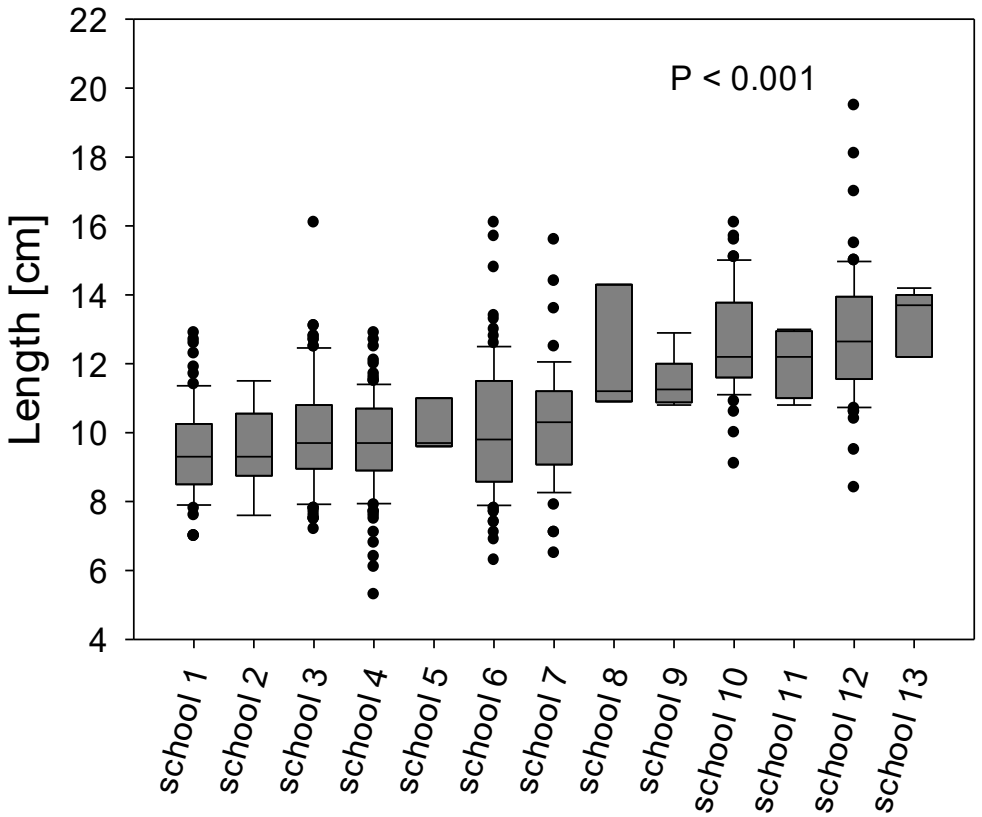

Figure 22 Body length shown for different groupings, underpinning the assumption of more than one fish school appearing in the Johler Arm in winter. Kruskal-Wallis test, $p < 0.001$, medians, quartiles, percentiles and outliers are given.

DISCUSSION

The newly connected sidearm was used intensively throughout the whole year, indicating a positive effect of its presence as well as its reconnection. As well, in this work for the first time, fish activity in a reconnected sidearm of a large temperate river was investigated with hydroacoustic techniques, with overall satisfying results. The same sidearm has been examined in the same way (with another device) in 2007 and 2008 before the reconnection. For the present study, which covers part of the project's post-monitoring, various factors have been taken into consideration. For example, abiotic conditions, seasonal and diurnal changes and other details which had also been considered in investigations conducted before the reconnection. Therefore, before and after reconnection data can be compared and the importance of lateral reconnection of backwaters can be evaluated.

Abiotic conditions

Lucas and Baras (2001) list environmental conditions such as light, temperature, discharge, water quality, food availability and the interaction between them as important external factors for either migration or homing. In this study, water quality, food availability and water temperature were not considered due to the study design. However, differences in light, discharge and water level were observed and therefore, seasonal changes in the habitat can be assumed. As fish activity and migration are critically impacted by these parameters (Lucas and Baras, 2001), they deserve abundant consideration. Light conditions and discharge as a driving factor of fish movement will be discussed later.

Fish are ectothermic creatures and temperature is highly important for their activity level and ability to move, forage, mate and spawn. Additionally, increased temperature decreases dissolved oxygen concentrations, affecting the fish's ability to breathe. Generally, most fish species show higher activity at higher temperatures within their normal range of tolerance (Lucas and Baras, 2001), even influencing diel patterns in different seasons. Even though this study cannot provide information on individual species, the species inventory found in the river, as well as its backwaters and sidearms, has been investigated by Schiemer and Spindler (1989). Based on this earlier work and the Integrated River Engineering Project's monitoring of biota, which included electrofishing in addition to hydroacoustic measurements, many fish species have been found in the Johler Arm. One of those, the common barbel *Barbus barbus*, tends to feed in morning and evening hours at water temperatures greater than 12 °C while

demonstrating a more diurnal pattern at lower temperatures (Baras 1995; Lucas and Baras, 2001); mature fish generally do not feed during hibernation (Gyurko *et al.,* 1964 in Banarescu *et al.* 2003). In this study, this would lead to barbel foraging at dawn and dusk in spring and summer, while being more diurnal in autumn and winter. This species alone, therefore, could influence the results of diurnal activity solely because of their specific temperature optimum, emphasising the importance of species-specific life cycle optima and abiotic conditions. Another phenomenon explained by temperature is shoaling behaviour in winter (Pavlov and Kasumyan, 2000), as found in young of the year (YOY) cyprinids (Brown 1979 *in* Lucas and Baras 2001). Although not observed in this study, long upstream spawning migrations are also dependent on temperature (Lam 1983, Rodriguez-Ruiz and Granado-Lorencio 1992; Trebitz 1992).

Discharge-related events can also work as driving forces for migration in many fish species, for example some cyprinids like *Chondrostoma nasus*,, who are stimulated to move upstream on spawning migrations following high water flow (Rakowitz *et al.*, 2008b).Within the sampling time considered in this work, higher flow caused by rainfall and maybe snowmelt (as described in Lucas & Baras, 2001) was only observed in spring when high downstream migration was observed while enhanced upstream migration would be expected. Hence, in this work it is not known if the time frame of observation was sufficient to assess this question and we cannot speculate on whether this kind of high flow is enough to cause spawning migrations, however, other authors (Rakowitz and Zweimüller, 2000; Rakowitz *et al.*, 2008b) provide further information on this topic.

Although barbels, as described above, are strongly influenced by temperature, they do not show discharge dependent movement (Baras and Cherry, 1990). As both, discharge and temperature, although measured, were not implicated in any statistical analyses, actual correlations of either could not be proved in this study. They still are an important part of seasonal investigations and therefore need to be considered at least theoretically as possible influences.

Seasonal abundance estimation and diurnal changes

Observed differences in abundance of fish throughout a year were statistically not significant, indicating small impact of discharge and temperature in this setup. However, winter – with a high number of fish, low median and large outliers – was the most variable season in this study. This result highlights the occurrence of fish schools in this season, leading to highly variable abundance in single hours. Various reasons for this high abundance in winter may include: aggregation of juveniles in the sidearm feeding migration due to spatiotemporal productivity

variations between seasons, refuge-seeking movement or undirected movements such as performed during foraging within a wintering area (Lucas & Baras, 2001). Alternatively, due to the position of winter sampling in this study, an influence from the main stem is possible (Dettmers *et al.*, 2014). Unfortunately, winter was not included in the pre-monitoring. Therefore, no direct comparison can be drawn.

Overall, abundance distribution was different than expected. Namely, Lucas and Baras (2001) reported an activity peak in spring and early summer due to the spawning migration of many riverine cyprinid species, yet no significant differences were found in fish activity in the present study in spring and summer. However, this does not necessarily indicate a lack of spring-associated spawning migrations into the Johler Arm. By the time the recordings were performed, the migration might already have taken place or not started. The high water level at that time may have triggered a later spawning migration as can be observed in many salmonid (Banks, 1969; Jonnson, 1991) but also various cyprinid species (for example Rakowitz *et al.*, 2008b).

High numbers of individuals in the late seasons (autumn and winter) indicate the utilization of the Johler Arm as a seasonal refuge, used in low water temperatures (Lorensen, 2005) and changed light regime (Lucas and Baras, 2001). In spring and summer, on the other hand, individuals were also observed earlier and later in the day, resulting in various peaks within a 24 h interval. As it is known that fish are influenced by dusk conditions (Lucas & Baras, 2001), dawn and dusk were analysed separately but no significant difference in movement activity and abundance were observed, while day and night were significantly different. Reasons for this pattern are found in the behaviour of different species. For example, common barbel as typical dusk and dawn feeders shift their foraging activity to daytime in cold seasons to meet their thermal optimum (Baras 1995; Lucas & Baras, 2001). Certain species of salmonids also change their behaviour in a spatiotemporal context (Heggenes *et al.*, 1993; Fraser *et al.*, 1993). Therefore, along with other indicators, the shift from crepuscular activity in spring and summer to a more diurnal pattern is logical. Between day and night, however, significant differences were observed in autumn and winter, both pointing out the possibility of the presence of numerous visual predators or diurnal species, while nocturnal or crepuscular species were a minority. Especially in winter, where primarily large fish shoals were observed during the day but not at night, dormancy and therefore undetectability of different species should be considered a factor leading to the relative absence of large individuals at all day times investigated (Lucas and Baras, 2001). Furthermore, Fréon *et al.*, (1996), Pavlov and Kasumyan (2000) and Axenrot *et al.* (2004) found schools to be absent at night, with a rapid decrease from

presence to absence in about 30 minutes, during hydroacoustic investigations in the Catalan and Baltic Sea.

Swimming direction, immigration, and emigration

Migration of fish is influenced by various factors, including resource utilization, climatic conditions (e.g. winter migrations), spawning, refuges, predator avoidance, lifecycle processes and developmental stage and is described by a wide range of definitions. Generally, migrations occur at certain lifecycle stages and are synchronized movements of parts or whole populations of species, travelling large distances relative to their home range (Lucas and Baras, 2001). According to this definition, this study did not measure migration, but rather examined home range movements as the study design did not allow for differentiation of the two aspects. Therefore, the activity of individuals is seen as upstream or downstream movement and referred to as emigration and immigration, although the traditional definition of migration is likely not fully met.

Upstream movement within the created transect prevailed in winter and summer, while in spring and autumn, fish moved primarily downstream. Although these movements might generally be interpreted as immigration into the sidearm, as mentioned, the limits of the technique used need to be considered. As fish have been observed to turn around and head in the other direction during sampling as well as analysis (no further investigation was performed, however), the seemingly simple question of migration direction becomes more complex. Due to the lack of physical limitation at the transect edges, as well as the loss of a tethering configuration (such as performed in Burwen *et al.*, 2010), fish can move freely, turn around within or outside the transect and move through it multiple times. While turns within the transect can potentially — but not necessarily — be displayed, this is not true for turns being performed beyond the boundaries of sonification. This does not only affect the interpretation of movement direction, but also the number of active fish. Therefore, all results need to be interpreted with care.

High numbers of fish moved upstream in winter. This indicates the Johler Arm is a winter refuge for small individuals, which could be members of smaller-sized species or juveniles of larger growing ones, supported by the observed small body length and schooling behaviour of the recorded individuals. Dettmers *et al.*, 2014 stated that fish schools from the main channel stay in the stream for > 50 min/h at the confluence of Mississippi and Illinois River. Based on these findings, I tend to interpret the upstream movements of fish in winter as refuge and resource utilization (as in Schiemer and Waidbacher, 1992). Still, the potential for analytical

bias exists because of the aforementioned reasons, also noted in Maxwell (2007) and Martignac *et al.* (2015). Generally, fish were recorded when they first entered the field of view and counted in the centre of the beam. Often, schools entered the beam and circled before exiting, which makes it possible that fish shoals especially were counted only as upstream migrating despite leaving the sidearm almost immediately. In summer, however, the prevailing upstream movement can be a result of factors such as food availability (Lucas and Baras, 2001), possibly caused by sidearm size and abiotic conditions as well as those in the associated floodplain. These factors may establish, depending on discharge, a food web different from the main channel (Vannote *et al.*, 1980; Junk *et al.*, 1989; Hein *et al.*, 1999; Dettmers *et al.,* 2014). The autumnal change in migration direction has been observed previously in many temperate rivers. Lucas and Baras (2001) point out the possibility of movement from warm and productive shallow areas in summer to deeper pools further downstream in autumn, where current velocity is slower. They do not necessarily put side channels in the same context; therefore, no comparison is possible. It remains uncertain if late spawning movements were observed or if fish do search for deeper slower pools in autumn. Since many species of the cyprinid family are found in Johler Arm and the measured current velocity in autumn was higher than in summer, the first interpretation seems reasonable.

The prevailing upstream migration in spring that would have been expected due to spawning events (Hladík and Kubečka, 2003) did not occur, although the enhanced emigration from the sidearm potentially could indicate the end of such events. However, the high current velocity in combination with the high water level might have induced downstream movement.

Size structure

Other than abundance, body size of fish did vary significantly in different seasons, showing the use of the sidearm by different fish. Not only was it obvious that the significantly smaller size fraction of fish, which additionally aggregated in schools, predominated in winter (Pavlov and Kasumyan, 2000), but also largest fish were observed in spring when life cycle stage makes a spawning migration to a backwater of the home river likely (Schiemer and Waidbacher, 1992; Lucas and Baras, 2001; Schiemer *et al.* 2004). Generally, the recorded size distribution underpins the utilization of this specific backwater by different developmental stages, although not all of these can be specifically investigated with hydroacoustic techniques (Mueller *et al.*, 2006; Martignac *et al.*, 2015). Based on our data, the occurrence of young fish of large-sized species as well as adults of small-sized species is very likely. For example, the common bleak, *Alburnus alburnus*, a schooling fish shown to be common in this section of the Danube

(Schiemer and Spindler, 1989) as well as in the Johler Arm (Keckeis, *pers. comm*.) and reaches a maximum body length of approximately 25 cm; juvenile individuals are approximately 5 cm long (Grenouillet, 2001). The length recordings from our winter data potentially match these characteristics. In contrast, many fish species tend to form schools as a part of their ontogeny and are likely to aggregate as a protective behaviour (Pavlov and Kasumyan, 2000).

The large individuals in spring and summer, however, indicate the utilization of the arm by adult fishes, either as a feeding or spawning ground. A spawning migration, as already described, is not necessarily assumed based on these data. Therefore, the sidearm serving as foraging ground or general habitat is more probable in this case and supported by Schiemer and Waidbacher (1992). Nevertheless, the potential and importance of the Johler Arm for spawning migration and as a nursery still exist. Single individuals found to show characteristic body movements may support identification of the species monitored (Burwen *et al.*, 2010; Martignac *et al.*, 2015). For example, an individual approximately 60 cm in length displayed movements typical for wels catfish, *Silurus glanis*. Data recordings gained by other methods (Keckeis, *pers. comm*.) show that this species could be observed in the hydroacoustic data of this sidearm as well as the Danube River (Schiemer and Spindler, 1989). Furthermore, large fish (> 20 cm) with different body movements were observed.

Based on the data as well as the study design chosen, individual movement was not quantified beyond the direction of movement already discussed. Motion analysis would be a promising interesting addition to future investigations, although more as a behavioural assessment rather than part of project monitoring.

Significant differences were found regarding the diurnal distribution of body length, specifically with day and night sampling times, most likely because of the varying lifestyles as well as life cycle stages of particular species observed (Schiemer and Spindler, 1989; Schiemer and Waidbacher, 1992). This leads to different behavioural activities, such as hunting in adult asp *Aspius aspius* and foraging characteristics of young individuals of the same species (Lelek, 1987; Gerstmeier and Romig, 1998). This species is common in the river run of the Danube and has been found in the Johler Arm as well, most probably showing different length patterns as individuals of different age can be assumed. Of course, this is likely not limited to one species.

Interestingly, fish moving upstream into the sidearm were found to be significantly larger (except in summer) than fish moving downstream. Insight into this may be found in the active or active-passive downstream movement of young (smaller) fish as well as their species and stage of life cycle (Pavlov and Mikheev, 2017). Large fish were often observed lingering close

to the left shore, nose pointing against the current. It is possible that individuals of species such as the common barbel were observed during foraging or sleeping (Lucas and Baras, 2001). Movement behaviour such as lingering and passive drift was observed and would be worthy of future study.

Position along the transect

As was shown, differences associated with position along the transect were found, especially in body size and time of day. At all times of day, large fish (> 20 cm) were observed in positions close to the left shore of the sidearm, where current velocity was slower than in areas used by smaller fish in all seasons except winter. Potential explanations for this phenomenon could be found in different mechanisms of foraging and habitat use by different species. While the common barbel and the nase (*Chondrostoma nasus*), are species with potentially large body size (> 20 cm) that feed close to the ground because of their consumption of benthic organisms (Banarescu *et al.* 2003, Gerstmeier and Romig, 1998), smaller species as well as juveniles of many others often use the pelagic area of the stream due to their planktivory (Lelek, 1987, Banarescu *et al.* 2003). Although no correlation of the current velocity to total length and position was performed other than for illustration, in this data it seems that large fish use areas of slightly lower or transient flow velocities. Based on the example of common barbel, no such correlation was stated in the literature (aside from a decrease of abundance along with decreased water velocity and oxygen (Baras 1995; Lucas and Baras, 2001), however, a correlation with water depth could be possible (Banarescu *et al.* 2003) but was not investigated here. In the case of the Johler Arm, differences in flow velocity are extremely small but nevertheless could result in enhanced growth of algae (Gosh and Gaur, 1998; Biggs *et al.*, 2002) or biofilm on the ground in areas with slow flow (Battin *et al.*, 2003). This would favour stationary and / or territorial fish such as the aforementioned common barbel (Banarescu *et al.* 2003) indirectly by favouring zoobenthic organisms and the nase (Lelek, 1987) by favouring benthic algae. Furthermore, mixed foraging patterns have been observed in other species such as the common bream, *Abramis brama*, demonstrated to show rhythmic diel migrations between the littoral and pelagic zones in a lentic ecosystem, feeding on benthic organisms in the littoral area and on zooplankton in the pelagic area (Schulz and Berg, 1987). However, this has been shown for a lentic ecosystem and does not necessarily characterise a lotic one. Another lotic ecosystem investigated by Kubecka and Duncan (1998b) showed that nightly vertical migration in the River Thames moves fish into shallower and more oxygenated layers, a phenomenon potentially only partly possible in the Johler Arm due to its absence of layers

(Keckeis, *pers. comm*.). Another observation regarding position in the water current was made by Fausch (1984), who found that dominant salmonids held positions that were most favourable regarding their potential profit, a behaviour that might influence fish location in a stream.

Considering the area beamed with the hydroacoustic instrument, with which a conical area can be investigated, tilted from the device at one shore to the ground at the other shore, it becomes obvious that the middle of the stream is viewed differently than the area farther from the device. In the middle, a certain volume in the central water column is shown, while a different volume closer to the ground is investigated at the distant shore. Therefore, we need to consider this technical constriction in the holistic view of our data. Although the experimental setup was determined to be sufficient in observation of fish activity, it cannot be prevented from "blind spots" beneath and above the beam. At these spots, a lack of information on the presence and size of fish is provided (Kubecka and Duncan, 1998). However, this can also be considered a major advantage of the technique as it offers an overview of all potential habitats (from top to bottom) and is not restricted to one layer of the water column. Of course, another setup in future analyses could focus on the exact position of individuals in the stream, for which a more even angle would be used for the tilt of the instrument along with episodic recordings in different layers of the water column. Unfortunately, this kind of setup potentially increases the time needed for recording and analysis and therefore also increases costs of the investigation.

Aggregation of individuals

Since analysis of various aggregations showed the fish to be of different sizes and therefore most probably indicating different fish schools in winter, the question of how these aggregations occur remains. On the one hand, the sidearm investigated is inhabited by species that show natural gregarious behaviour in adult stages, such as the common bleak (Lelek, 1987; Gerstmeier and Romig, 1998). On the other hand, larval as well as juvenile stages of many species show aggregations to a certain extent and often retain this collective behaviour as adult fish (Keenleyside, 1955, Pitcher and Parrish, 1993; Pavlov and Kasumyan, 2000). Often these assemblages of young fish serve to protect and provide effective foraging (Pavlov and Kasumyan, 2000; Pavlov and Mikheev, 2017). Although the individuals observed in these investigations were larger in size than larval fish, juvenile fish grouping in a refuge habitat like the Johler Arm is likely and does not exclude the use of adult fish. The analysis of body length in the various aggregations primarily showed the simultaneous presence of more than two different schools. This could indicate a difference in species or a variation in age since fish were found to "aggregate in a far from random fashion" (Krause, 1994; Krause *et al.* 1996, etc.

as reviewed by Pavlov and Kasumyan, 2000). Although no identification of different species and age in aggregations exist in this data, both possibilities show a positive outcome in the reconnection of the Johler Arm to the main stem of the Danube River. For further investigation of fish schools occurring in this habitat, additional parameters such as swimming speed, stability of grouping or space between individual fish could be considered (like e.g. Bonabeau *et al.,* 1998).

CONCLUSION

The analysis of fish of the Johler Arm by means of hydroacoustic surveys after its reconnection to the main stem of the Danube River in early 2014 revealed high numbers of fish being active in a 24-hour period in every season. Along with the high activity and abundance of fish, differences in diurnal patterns (varying from season to season as well assize-dependent), direction of migration as well as position along the investigated transect were observed. Noteworthy differences were found regarding migration movements (up- or downstream direction) in all seasons.

Altogether, the results show an active utilization of the Johler Arm by various fish species and fish at different life cycle stages, which is especially encouraging from an ecological point of view. Although I could not observe the reasons of habitat use per se, the results obtained in this study, such as abundance of active individuals, indicate an intense utilization of this sidearm, a substantial improvement over the pre-monitoring conducted 2007–2008 (Rakowitz and Berger, 2010), when less individuals were found in every season. This highlights the importance of lateral interconnection of inland waters and the efficiency of sidearm reconnection. Hence, I would like to encourage future reconnection attempts to further sidearms. This study further shows that hydroacoustic estimation is one of the most useful tools to examine seasonal and diurnal migrations in a large river sidearm, although four recording cycles seem to be insufficient to utterly answer the research questions, but offer a profound basis of knowledge. More post-monitoring measurements will contribute to understanding the importance of the present and future of this lateral interconnection between the Danube River and the Johler Arm.

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