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Fish orientation along the longitudinal profile of the Rimov reservoir

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Anotace:

Cílem této práce bylo ověřit předpoklad náhodné orientace ryb v „jezerní“ části kaňonovité Římovské nádrže a porovnat distribuce orientace ryb v této jezerní a v přítokové oblasti. Tato studie potvrdila, že většina ryb byla orientována náhodně v jezerní oblasti nádrže, zatímco v přítoku se ryby pohybovaly převážně souběžně s podélnou osou nádrže.

Annotation:

The aim of this work was to verify the assumption of random fish orientation in the lacustrine zone of the “canyon-shaped” Rimov reservoir and to compare distributions of fish orientation in the lacustrine and tributary zone. The study confirmed that most fish were oriented randomly in the lacustrine zone of the reservoir, whereas in the tributary fish moved predominantly in parallel with the longitudinal axis of reservoir.

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Michal Tušer

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Úvodní komentář

Tato práce se zabývá orientací ryb při horizontálním akustickém snímkování v podélném profilu nádrže Římov. Důležitost orientace ryb ve vztahu k akustickému kuželu je velmi dobře známá. Postavení těla ryby ve vodním sloupci silně ovlivňuje akustickou sílu odrazu tohoto objektu, tzv. target strength (TS; např. Foote 1980, Midttun 1984, Horne & Clay 1998, MacLennan *et al.* 1990, Frouzová *et al.* 2005). Horizontální nastavení akustického kuželu vede k pozorování ryb z bočního pohledu (tzv. side aspect) a natáčením ryby v horizontální rovině výrazně roste variabilita TS (Love 1977). Přesné změření TS u jednotlivých ryb závisí na jejich orientaci a je rozhodující pro získání přesnějších odhadů rybí biomasy (Midttun 1984, MacLennan 1990, Simmonds & MacLennan 2005). Data o orientaci ryb jsou velmi řídká, pouze několik skupin rozvíjí metody pro tyto „side-aspect“ průzkumy, např. Kubečka *et al.* (1992), Tarbox & Thorne (1996), Kubečka & Wittingerová (1998), Trevorrow (1998), Knudsen & Saegrove (2002), Lilja (2004) a Frouzová *et al.* (2005). Při průzkumech na jezerech a nádržích se běžně předpokládá náhodná orientace ryb (Kubečka *et al.* 1994, Draštík and Kubečka 2005). Avšak pokud by předpoklad náhodného směru plavání ryb v dlouhých kaňonovitých nádržích neplatil, mohlo by dojít k nadhodnocení TS především v přítokové oblasti a tím i k nadhodnocení celkové biomasy v nádrži.

Hlavním cílem této práce bylo ověřit platnost předpokladu o náhodné orientaci ryb v jezerní části Římovské nádrže a dále porovnat distribuce rybí orientace mezi jezerní a přítokovou oblastí. Pro popis orientace ryb z akustických záznamů byl použit tzv. „echogramový sklon“ (echogram slope) a „horizontální aspekt ryb“ (fish horizontal aspect).

V roce 2005 bylo provedeno akustické snímkování z pevných stanovišť (tzv. fixed locations) na čtyřech lokalitách podél nádrže. Vysílač echolotu vždy směřoval kolmo na podélnou osu nádrže. Na všech stanovištích se většina zaznamenaných ryb pohybovala převážně ve více méně kolmých směrech vůči hlavní ose akustického kužele (echogramový sklon = 0 - 0.04 m/s, boční aspekty 81° - 90°), na podélném profilu nádrže tedy nebyly zaznamenány žádné odlišnosti v orientaci ryb.

Během zpracovávání akustických dat bylo však zjištěno, že standardní nastavení detektoru pro jednotlivé ozvy ryb (single echo detector v programu SONAR 5, Balk & Lindem 2006) diskriminovalo ryby plavající prakticky rovnoběžně s podélnou osou kužele (head- a tail-aspects). Pro další zpracování akustických dat byl použit tzv. „cross-filter“ detektor (Balk & Lindem 2000), který umožnil několikanásobně zlepšit detekci ryb v akustických záznamech.

V roce 2006 v jezerní části Římovské nádrže byl proveden křížový snímkovací experiment („crisscross-beaming acoustic experiment“). Akustický vysílač byl nejdříve nasměrován kolmo na podélnou osu nádrže, a následně souběžně s touto osou. Tato akustická data byla zpracována použitím „cross-filter“ detektoru. Aby bylo možné jejich porovnání s přítokovou oblastí, byla znovu zpracována část předchozích dat z přítoku (2005).

Z obou pozorování (kolmého a rovnoběžného s podélnou osou nádrže) v křížovém snímkovacím experimentu vyplynulo, že ryby se v jezerní části nádrže pohybují zcela náhodně a žádný směr nepřevládá, protože frekvenční distribuce orientace ryb vyšla velmi podobná. Naopak v přítokové oblasti většina ryb plavala souběžně s podélnou osou nádrže. Z toho vyplývá, že předpoklad náhodné distribuce neplatí v přítokové oblasti kaňonovité nádrže, a proto by při dalších výzkumech rybí obsádky měl být zohledněn výrazný longitudinální gradient v morfometrii při způsobu zpracování akustických záznamů ryb.

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Manuscript

Fish orientation along the longitudinal profile of the Rimov reservoir

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Abstract

The aim of this work was to verify the assumption of random fish orientation in the lacustrine zone of the “canyon-shaped” Rimov reservoir and to compare distributions of fish orientation in the lacustrine and tributary (riverine) zones. Fish orientation was acoustically surveyed by the SIMRAD EK 60 split-beam echo sounder (elliptical beam, 120 kHz, pulse duration 0.1 ms) with a horizontally aligned transducer at fixed locations. The SONAR 5 post processing software was used for acoustic-data collection and processing. The echogram slope and fish horizontal aspect was used for description of fish orientation. The conventional single-echo detector (SED) and cross-filter detector (CFD) were applied.

No trend was found along the reservoir when comparing records from four sites processed with the conventional SED. On all sites, most fish move predominantly in more perpendicular directions (slope = 0 – 0.04 m/s) and side-aspects (90°) of fish prevail over other aspects. CFD gained several times more tracked fish than SED. Fish aspect frequency distribution appears very similar when recorded by the sonar beam oriented in parallel with and across the longitudinal axis of the reservoir (crisscross-beaming acoustic experiment). Beaming perpendicularly to the longitudinal axis of the reservoir revealed significantly higher proportion of fish moving along this axis in the tributary zone of the reservoir. Therefore, the assumption of random fish orientation will not be applicable in tributary zones of the canyon-shaped reservoirs and more studies are needed for obtaining reliable estimates in tributary zone.

1 INTRODUCTION

For several decades, echo sounders have been employed as the most important devices for estimating sizes of fish stock and visualizing their spatiotemporal distributions and behaviour (Simmonds & MacLennan 2005). Their ability to actively sample fish populations in large volumes of open water is a major advantage of hydroacoustic surveys. Hydroacoustics is commonly used on “canyon-shaped” reservoirs, namely artificial lakes formed by damming of rivers, where open water represents the largest volume and area of reservoir. In general, sampling of the open waters is difficult and fish assemblage of this part of reservoirs is least known (Kubecka *et al.* 2003). In many stratified meso- and eutrophic reservoirs, echo sounders and other sampling gears revealed that most of fish community live predominantly within uppermost layer of the surface (4 m, Kubecka & Wittingerova 1998, Cech & Kubecka 2002, Vasek *et al.* 2004, Prchalova *et al.* 2006) which is available for horizontal rather than for vertical beaming (Kubecka & Wittingerova 1998).

Horizontal beaming leads to observing fish targets in side aspect. Variability in target strength (TS) is strongly influenced by the aspect or orientation of fish relative to the incident sound wave (e.g. Foote 1980, Midttun 1984, Horne & Clay 1998, MacLennan 1990, Frouzova *et al.* 2005). Many *ex-situ* experiments have attempted to relate TS to fish length or weight, respectively. The TS-length regressions derived from these studies are often used in estimations of fish abundance and size (Simmonds & MacLennan 2005). Consequently, some assumption of fish aspect distribution in the observed population of targets is always needed for converting between TS and fish length (e.g. Kubecka *et al.* 1994). In lakes and reservoirs, random fish orientation is usually assumed (Kubecka *et al.* 1994, Drastik & Kubecka 2005), however, without proper verification. The situation could be more complicated in “canyon-shaped” reservoirs, which are longer than wider and longitudinal fish swimming may prevail. If the aspect of fish to the transducer is unknown, the conversion of TS data to fish lengths is complicated. Area of tributary such reservoirs could be of special interest as the reservoir gradually changing into the river here.

The aim of this work was to verify the assumption of random fish orientation in the lacustrine zone of the Rimov reservoir and to compare orientation of fish in the lacustrine and tributary zones.

2 MATERIALS AND METHODS

2.1 Study sites

All acoustic measurement was carried out in the canyon-shaped Rimov reservoir (48°50’ N, 14°30’ E; 170 km south of Prague), Czech Republic. During 7th – 12th September 2005, four sites in the longitudinal profile of the Rimov reservoir, approximately corresponding to sampling areas of Vasek *et al.* 2004, were acoustically surveyed (Fig. 1). Surveyed ranges from the tributary to the dam were 10, 20, 40, and 80 meters of open water depending on the width of the reservoir. On September 1st 2006, a crisscross-beaming acoustic experiment was performed in open water in the lacustrine part of the reservoir (Fig. 1), in order to prove random distribution of fish.

2.2 Hydroacoustic equipment

All field measurements were carried out with a scientific split-beam echo sounder SIMRAD EK 60. The echo-sounder system worked on a 120-kHz frequency with 0.1 ms pulse duration, and with a ping rate of 2.9 – 10 pulses per second (Fig. 1). An elliptical transducer ES120_4 (4.3° and 9.2° nominal beam angles) was deployed and calibrated using a 33.2 mm tungsten-carbide sphere (-41.0 dB, Foote *et al.* 1991). The sonar equipment was installed at fixed locations along the reservoir. The transducer was boat-mounted and the boat was moored to shore. The sonar beam was oriented horizontally across the reservoir perpendicularly to the longitudinal axis of the reservoir.

In the crisscross-beaming acoustic experiment, the boat-mounted transducer was based for half-a-day in the middle of the reservoir and its beam was aimed perpendicularly and then for the second half of day also in parallel to the longitudinal axis of the reservoir (Fig. 1: C_{TRANS}, C_{PARA}).

All acoustic data was continuously stored on a hard-drive of a portable laptop for later evaluation.

2.3 Data analysis

All acoustic data were evaluated from echograms using post-processing software Sonar5-Pro (version 5.9.6, Balk & Lindem 2006). For basic detection of single echoes, the conventional single-echo detector (SED) was deployed. Parameters applied for SED were as follows:

Min. value TS = -70 dB

Echo length min = 0.3, max = 1.8 relative to the transmitted pulses

Max beam comp. = 3 dB

Max phase dev. = 10 monitored degrees

In addition, the ‘cross-filter detector’ (CFD, alternative method to the conventional SED) was used for the data from the crisscross-beaming acoustic experiment and consequently for a part of data set from the site Tributary (T_{CF}). The CFD was set up with the following parameters:

Step 1 Detector:

Foreground Filter = Height 5 and Width 1

Background Filter = Height 55 and Width 1

Offset +8 dB

Step 2 Refinements (at every echogram, there were used different combination of these three parameters to remove unwanted targets as many as possible):

Perimeter length min = 10, max = 10000 samples around a detected region

Ratio (Track length/Mean Echo length) min = 1.00, max = 270.00

Max TS min = -60 dB, max = -10 dB

Further information about the meaning of CFD and its parameters is provided in Balk & Lindem (2006).

2.3.1 Principle of the method – Echogram slope and fish aspect

After detecting single echoes, all fish were manually tracked (i.e. target tracking, Brede *et al.* 1990, Ehrenberg & Torkelson 1996) such a way that one fish track meant a series of contiguous single echoes with the same direction of movement in a horizontal plane. When the fish changed a direction of movement during passing through the beam, its track was divided into parts with the same direction. Each direction of fish track on a SED-echogram, so called “echogram slope” (ESL), was defined by the ratio of the change in range and duration between the last and first echo of the fish track:

$$\mathrm{ESL} = \Delta \mathrm{R} / (\Delta \mathrm{n} \times \mathrm{PR}) \qquad (1)$$

Thus, ESL is expressed in meters per second (i.e., the change in range per second) where ΔR is the change in range expressed in meters, and duration is calculated from the total count of pings (Δn, #) and a ping rate (PR, pulses per second). A resulting value of this equation is either positive one when fish moves outwards from the transducer or negative one when fish moves towards the transducer or zero one when there’s no change in range and fish moves perpendicularly to main beam axis of the transducer.

Fish horizontal aspect (α) of a given fish track was simply calculated as:

$$\alpha = \sin\left[\frac{\Delta R}{\sqrt{\Delta X^2 + \Delta R^2}}\right] \qquad (2)$$

where ΔR is the change in range expressed in meters, and ΔX is the distance in meters along the X axis between the last and first echo (Fig. 2).

2.3.2 Statistical evaluation

Absolute values of slopes and aspects were used and weighted by total count of pings from individual tracks. For comparison of their frequency distributions, the one-way ANOVA with the Poisson distribution and identity link function was used (program Statistica 6.0, mode of Generalized Linear/Nonlinear Models). Likelihood Type 3 test was chosen. In addition, Bonferroni’s correction was used for adjusting the significance levels for the individual comparisons. Comparisons of proportional distributions of fish aspects were performed in a 2 x 2 contingency table by Chi-square test.

3 RESULTS

In 2005, we performed acoustic observations on fish orientation in fixed locations along the longitudinal axis of the Rimov reservoir. The total number of obtained records was 1,713 fish tracks (Tributary 901, Upper 285, Middle 228, Dam 299) detected by SED only and after weighting in total 37,965 observations (see Tab. 1). For description of fish orientation, we first calculated the echogram slope according to Equation (1). No apparent trend of fish orientation from the tributary to the dam of the reservoir is found from the frequency distributions of slope (Fig. 1-4). On all sites, most fish move predominantly in more perpendicular directions (slope = 0 – 0.04 m/s). Distribution comparison between each site is compiled in Tab. 2. In fact, no difference is found between sites expect the site Upper. The site Upper is significantly different due to far higher mean slope and standard deviation 0.047 ± 0.062 m/s by comparison with others (0.033 – 0.039 ± 0.028 – 0.055 m/s, see Tab. 1). These results didn't confirm clearly different fish orientation between the lacustrine and riverine part of the reservoir. As a result, due to dependence of echogram slope upon the aspect and speed of fish, we decided to look at fish aspects directly.

Random fish distribution would be immediately apparent from the aspect distributions of the lacustrine zone. The means and medians of these distributions would be ideally approximately 45 degrees with certain deviations. Our measured values of means are at range 63.2 – 73.7 degrees (for details of descriptive statistics of fish aspects see Tab. 3). Fig. 8-11 depict frequency distributions of fish aspects along the Rimov reservoir. Side aspects (90°) of fish prevail over other angles and only tiny proportion is presented by head- and tail-aspects. Though comparisons between the sites are significantly different from each other (Tab. 4), no obvious trend is seen in longitudinal profile again. These results indicate that most fish would also move side-on to the transducer in the lacustrine zone as well as in the riverine one.

Data processing from year 2005 revealed that in amplitude echograms many fish tracks with steeper echogram slopes were not displayed in the conventional SED-echograms; especially the slopy tracks were obviously rejected by the conventional SED. The conventional SED settings were too strict for these fish tracks. In order to gain all fish in our “target population”, we decided to apply the cross-filter detector (CFD) to next acoustic data. Applying of the CFD for improving processed targets enhanced extensively our possibilities in detecting fish numbers. This enabled us to obtain even fish in steeper slopes and their less reflective aspects (i.e. head- and tail-aspects), thereby approximate to better insight on fish orientation in open water.

In 2006, we performed the crisscross-beaming acoustic experiment in order to prove random orientation of fish in the lacustrine zone of the Rimov reservoir. Moreover, for comparison with riverine zone, we decided to reprocess a part of data set from the site Tributary (T_{CF}) with the applying CFD.

The total number of 4,259 fish tracks was obtained from the sites C_{TRANS} (2318), C_{PARA} (1031), and T_{CF} (910). After weighting by number of pings, we gained 89,261 observations. Descriptive statistics of echogram slopes from these data is displayed in Tab. 1. By comparison with previous data, almost double values of the means (0.051 – 0.069 m/s) and medians (0.044 – 0.048 m/s) are found out. The echogram-slope frequency histograms are showed in Fig. 5-7 and their comparison is illustrated in Tab. 2. The site C_{TRANS} is significantly different from the site C_{PARA} (Log-Likelihood = -15, 962.5; $p<10^{-6}$) and the site T_{CF} (Log-Likelihood = -14,039.4; $p<10^{-6}$). No difference is found between the sites C_{PARA} and T_{CF} (Log-Likelihood = -10, 851.1; p = 0.831). The result of this analysis is given by greater proportion of slopes from 0.14 up to 0.4 m/s at C_{PARA} and T_{CF} than C_{TRANS}, causing that C_{PARA} is statistically more similar to T_{CF} than C_{TRANS}. In spite of this result, the proportional distributions of C_{TRANS} and C_{PARA}, mainly at range from 0 up to 0.14 m/s, are evidently more similar in a gradual decline of slope (Fig. 5-6). Conversely, the proportional distribution of T_{CF} has high proportion of perpendicular slopes (0 - 0.02 m/s, 33%) and then has sharply descending trend. This indicates that most fish moves more perpendicular directions in the riverine zones, whereas most fish in the lacustrine zone utilizes greater range of movements.

Provided that randomness of fish orientation in the lacustrine zone is valid, the aspect distributions of C_{TRANS} and C_{PARA} would be same and their means and medians would be ideally about 45°. At aspect's statistics of cross-filtered data (Tab. 3), the difference between the lacustrine and riverine zone is better apparent than in previous data. The means and medians differ markedly between the lacustrine part (C_{TRANS} and C_{PARA}) and the tributary (T_{CF}). The means of C_{TRANS} (55.3°) and C_{PARA} (52.5°) are greatly close to the ideal value of 45° against T_{CF} (63.4°). The medians of C_{TRANS} and C_{PARA} are 60.1° and 57.4°, respectively, whereas the median of T_{CF} is 71.6°. The aspect-frequency histograms for each site are illustrated in Fig. 12-14 and their comparison in Tab. 4. Significant difference is found between all sites (C_{TRANS}, C_{PARA}, and T_{CF}) due to high number of the observations, which make the analysis liable to be significantly different already with small deviations in distribution. In spite of this, we can see that the proportional distributions of C_{TRANS} and C_{PARA} are evidently more similar (Fig. 12-13) than that of T_{CF} (Fig. 14). T_{CF} is characterized by high proportion of side-aspects (32%, 81° – 90°) with sharply descending trend to head- and tail-aspects. It shows that most fish in the riverine zone is present predominantly side-aspects to acoustic beam. On the other hand, C_{TRANS} and C_{PARA} show similar shape with slightly higher proportion of side-aspects (20 - 21% in the category 81° – 90°, and 14 - 16% in the category 72° –

80°) but with the approximately same level of representation between angles 0°-72°. Both parts of this proportional distribution were compared by Chi-square test in a 2 x 2 table. No significant difference is found between the sites C_{TRANS} and C_{PARA} ($df = 1$, $p = 0.6575$). It confirms random fish orientation in the lacustrine zone of the reservoir.

4 DISCUSSION

With the using of the conventional single-echo detector (SED), scarcely any difference between slope-frequency distributions in longitudinal profile of the Rimov reservoir was found. According to distributions of fish aspects, side-aspects would be strongly dominant in all parts of the reservoir. The conventional used setting of SED obstructed strongly receiving acoustic information, so that “weaker” echoes of fish were ignored. On the other hand, the applying of the cross-filter detector (CFD) improved detecting fish with respect to less reflective aspects (i.e. head- and tail-aspects), especially in environments with low signal-to-noise ratio (Balk & Lindem 2000).

According to our results, fish orientation in the canyon-shaped reservoirs is different between the lacustrine and riverine zones (see Fig. 5-7). The fish assemblage of the riverine zone is represented predominantly side-aspects to acoustic beam (Fig. 14) and moves parallel to the main flow (Kubecka 1996, Kubecka & Duncan 1998). In lacustrine environments of the reservoir, fish appear to move in random directions (Fig. 5-6, Fig. 12-13). The assumption of randomness of fish orientation used in acoustic survey for biomass estimation may not be valid in the tributary area of canyon-shaped reservoirs and may lead to TS-overestimated size and biomass in these zones. With the “deconvolution” approach of Kubecka *et al.* 1994, some side aspects would be inevitably interpreted as “weaker” aspects and their length would be “over-corrected”. Consequently, fish sizing and biomass assessment in the tributary area would probably need a special handling. Comparison of CPUE of different gear in riverine/lacustrine zone could be useful. Also the use of acoustic cameras (DIDSON, Moursund *et al.* 2003, Hateley *et al.* 2006) for fish sizing could be used. Acoustic cameras could also be used to determine the breaking point between the random and nonrandom distribution of fish along the reservoir.

Further, the study confirmed that echogram slope could be useful as the indicator of changes in horizontal movement of fish swimming and its frequency distribution may inform on fish orientation in any environment. However, interpretation of the echogram slopes is difficult due to their dependence on the aspect and speed of fish. On this account, knowing fish aspect is far reliable than the echogram slope. Even with the use of a horizontal aspect as an indicator of fish orientation, we encountered some difficulties. Both in parallel and transversal beaming, the most frequent recorded groups of fish were recorded from the side or nearside aspect. If all fish were recorded, such result of crisscross experiment is impossible by definition. The most obvious explanation of the observed results is the possibility of not-detecting some targets in less reflective aspects. This could happen with smaller fish (Kubecka 1996, Kieser 2000). Another possible explanation may be stops in fish swimming, which may be interpreted as side aspects due to much higher precision of estimation of ΔR compared to ΔX (Equation 2, Balk pers. commun.). Stops frequently happen with change of swimming direction during “sinusoidal swimming” (Cech & Kubecka 2002). However, very small differences between fish aspects in C_{TRANS} and C_{PARA} observations indicate that there is no prevailing direction of fish orientation in the lacustrine zone and that the assumption of random orientation can be used in further studies.

5 ACKNOWLEDGEMENTS

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Table 1: Descriptive statistics of echogram slope (expressed in m/s) from the longitudinal acoustic survey in 2005, the crisscross-beaming acoustic experiment in 2006 and the Tributary (cross-filtered).

Year	Site	Valid N	Mean	Median	Variance	Standard deviation	Standard error of mean
2005	Tributary	24843	0.039	0.027	0.0018	0.043	0.0003
	Upper	4312	0.047	0.025	0.0038	0.062	0.0009
	Middle	4539	0.037	0.020	0.0031	0.056	0.0008
	Dam	4271	0.033	0.029	0.0008	0.029	0.0004
2006	C_{TRANS}	46739	0.051	0.044	0.0019	0.044	0.0002
	C_{PARA}	25074	0.069	0.048	0.0061	0.078	0.0005
	T_{CF}	17448	0.070	0.044	0.0061	0.078	0.0006

Table 2: Comparisons of slope-frequency distributions of fish between individual sites from the longitudinal survey (2005), and between the sites of the crisscross-beaming acoustic experiment (2006) with the Tributary (cross-filtered). Significant results according to Bonferroni's correction are in bold.

Year	Comparison between two sites	Degrees of freedom	Log-likelihood	Bonferroni's correction of significance level	p
2005	Tributary x Upper	1	-4915.87	0.017	**0.011**
	Tributary x Middle	1	-4803.25	0.017	0.509
	Tributary x Dam	1	-4716.69	0.017	0.098
	Upper x Middle	1	-1544.35	0.017	**0.015**
	Upper x Dam	1	-1458.74	0.017	**0.001**
	Middle x Dam	1	-1344.34	0.017	0.426
2006	C_{TRANS} x C_{PARA}	1	-15962.5	0.025	**0.000**
	C_{TRANS} x T_{CF}	1	-14039.4	0.025	**0.000**
	C_{PARA} x T_{CF}	1	-10851.1	0.025	0.831

Table 3: Descriptive statistics of fish horizontal aspect (expressed in degrees) from the longitudinal acoustic survey in 2005, the crisscross-beaming acoustic experiment in 2006 and the Tributary (cross-filtered).

Year	Site	Valid N	Mean	Median	Variance	Standard deviation	Standard error of mean
2005	Tributary	24843	63.2	69.9	511.8	22.6	0.14
	Upper	4312	73.7	79.3	290.5	17.0	0.26
	Middle	4539	63.7	75.1	699.2	26.4	0.39
	Dam	4271	67.0	75.8	543.9	23.3	0.36
2006	C_{TRANS}	46739	55.3	60.1	693.1	26.3	0.12
	C_{PARA}	25074	52.5	57.4	777.9	27.9	0.18
	T_{CF}	17448	63.4	71.6	583.7	24.2	0.18

Table 4: Comparisons of aspect-frequency distributions of fish between individual sites from the longitudinal survey (2005), and between the sites of the crisscross-beaming acoustic experiment (2006) with the Tributary (cross-filtered). Significant results according to Bonferroni's correction are in bold.

Year	Comparison between two sites	Degrees of freedom	Log-likelihood	Bonferroni's correction of significance level	p
2005	Tributary x Upper	1	5734410	0.017	**0.00000**
	Tributary x Middle	1	5617501	0.017	**0.00022**
	Tributary x Dam	1	5602736	0.017	**0.00000**
	Upper x Middle	1	1837655	0.017	**0.00000**
	Upper x Dam	1	1824214	0.017	**0.00000**
	Middle x Dam	1	1704814	0.017	**0.00000**
2006	C_{TRANS} x C_{PARA}	1	11040008	0.025	**0.00000**
	C_{TRANS} x T_{CF}	1	10630170	0.025	**0.00000**
	C_{PARA} x T_{CF}	1	6982133	0.025	**0.00000**

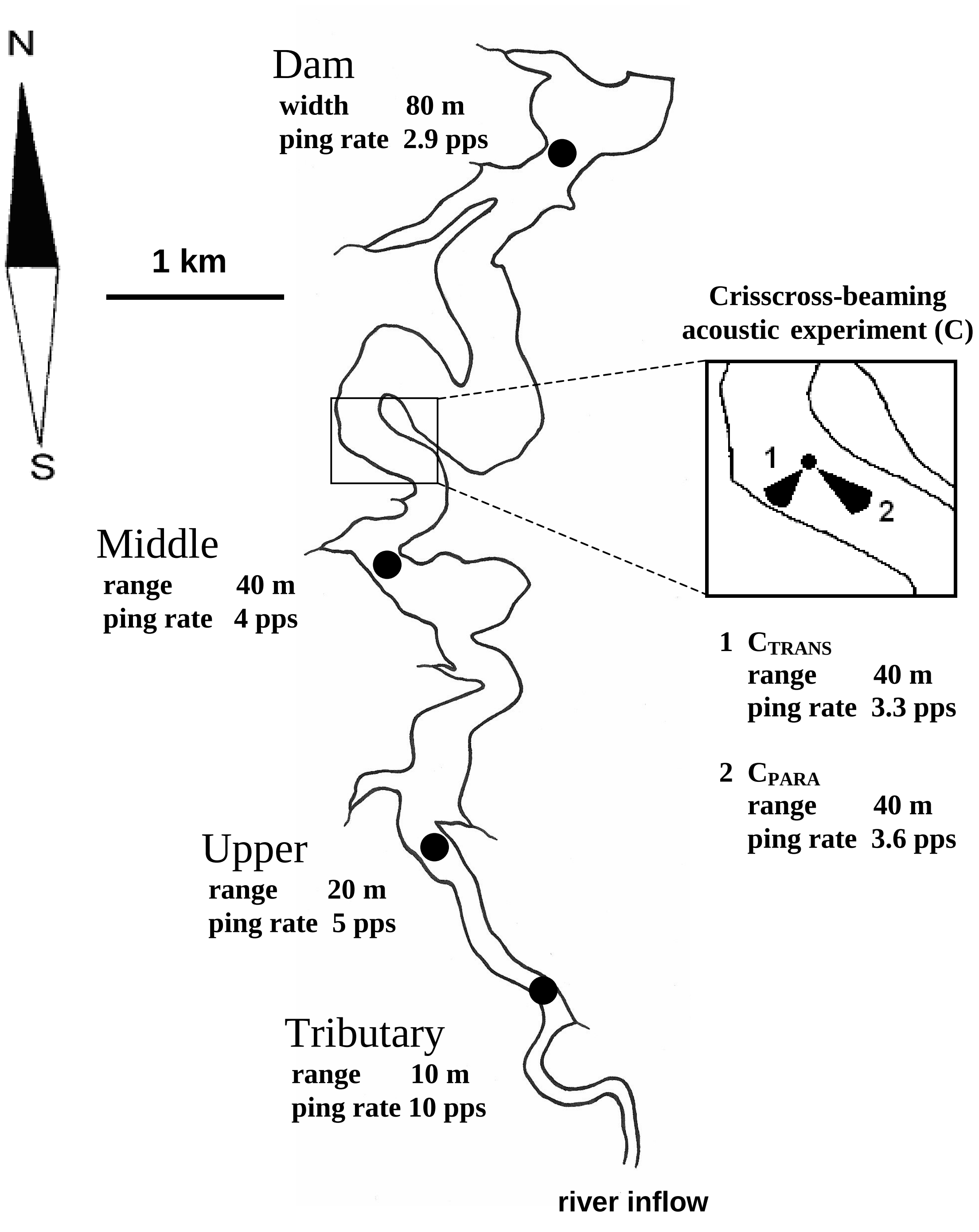


Figure 1: Map of the Rimov reservoir. Four sites along the longitudinal axis of the reservoir (carried out in 2005) and the crisscross-beaming acoustic experiment (2006) are shown with surveyed ranges of open water (expressed in meters) and ping rates (expressed in pulses per second).

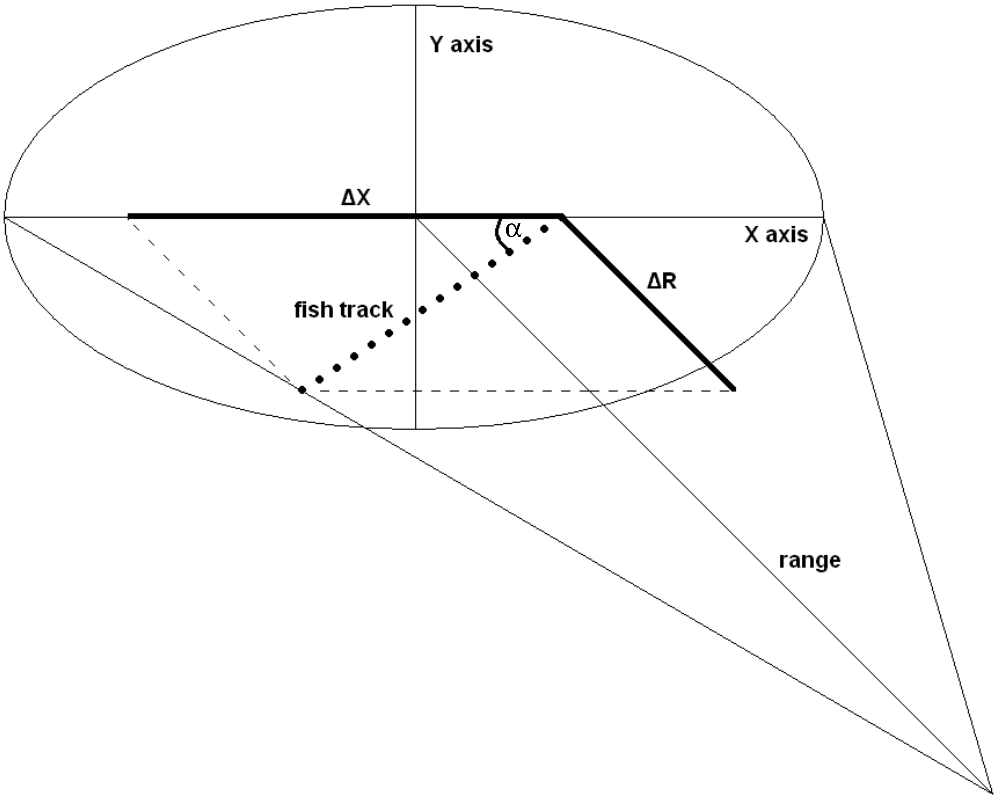
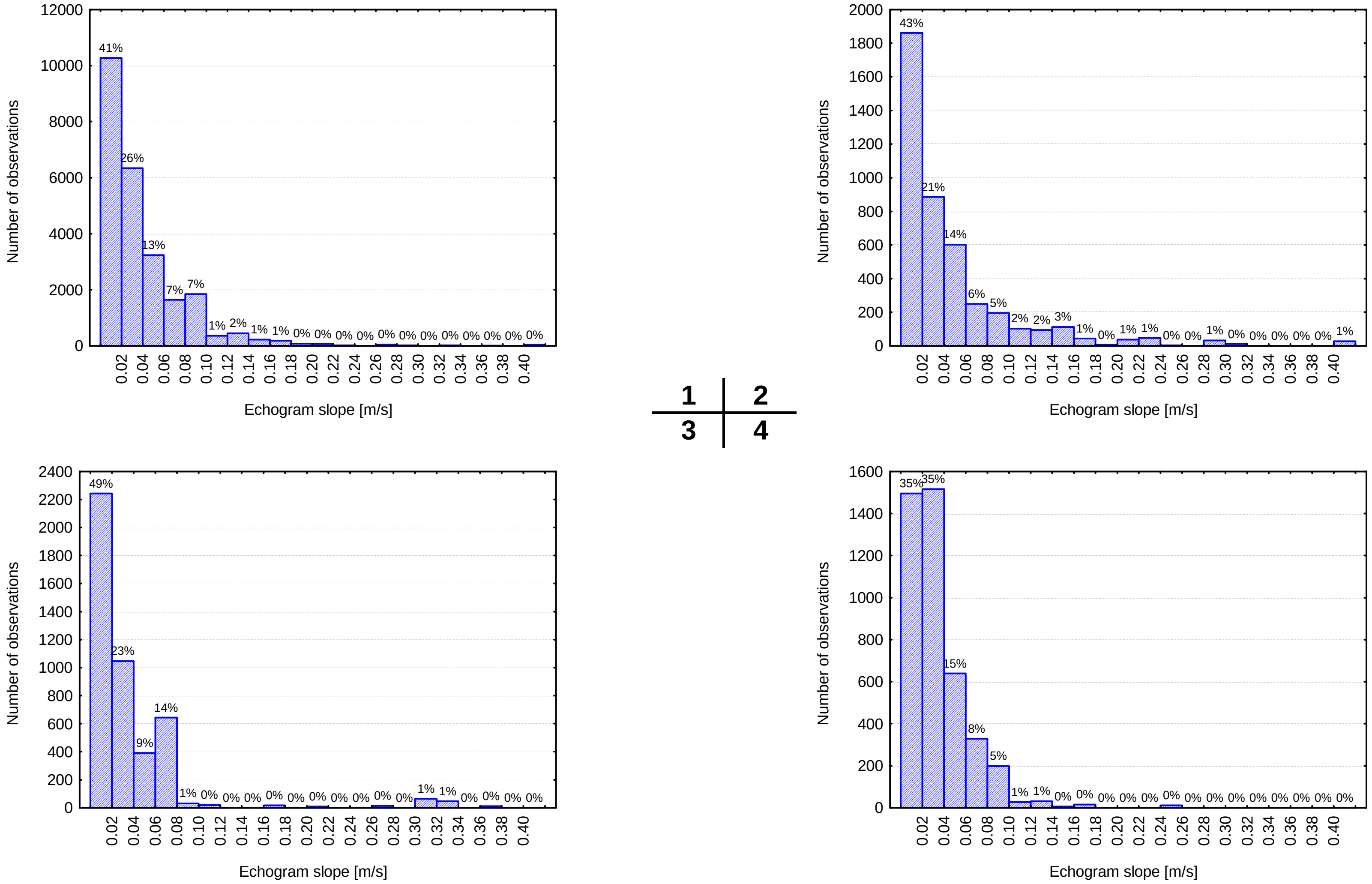


Figure 2: Sonar projection of a given fish track (•••) with parameters used in Equation 1. Fish horizontal aspect (α), the change in range (ΔR), and the distance in meters along the X axis between the first and last echo (ΔX) are shown.



Figures 1 - 4: Slope-frequency histograms with proportional representation of individual categories from the longitudinal survey of the Rimov reservoir: (1) Tributary, (2) Upper, (3) Middle, and (4) Dam.

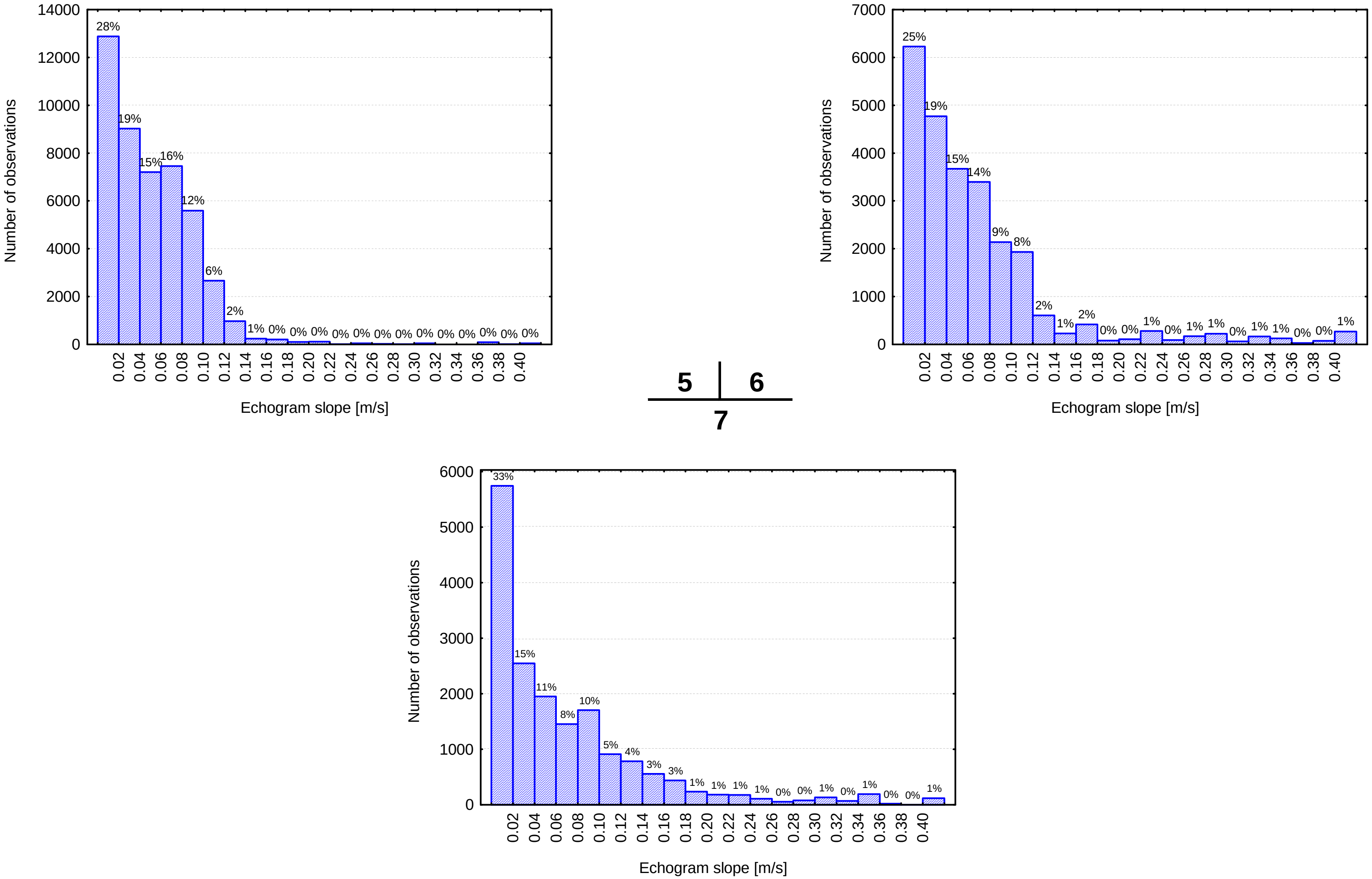
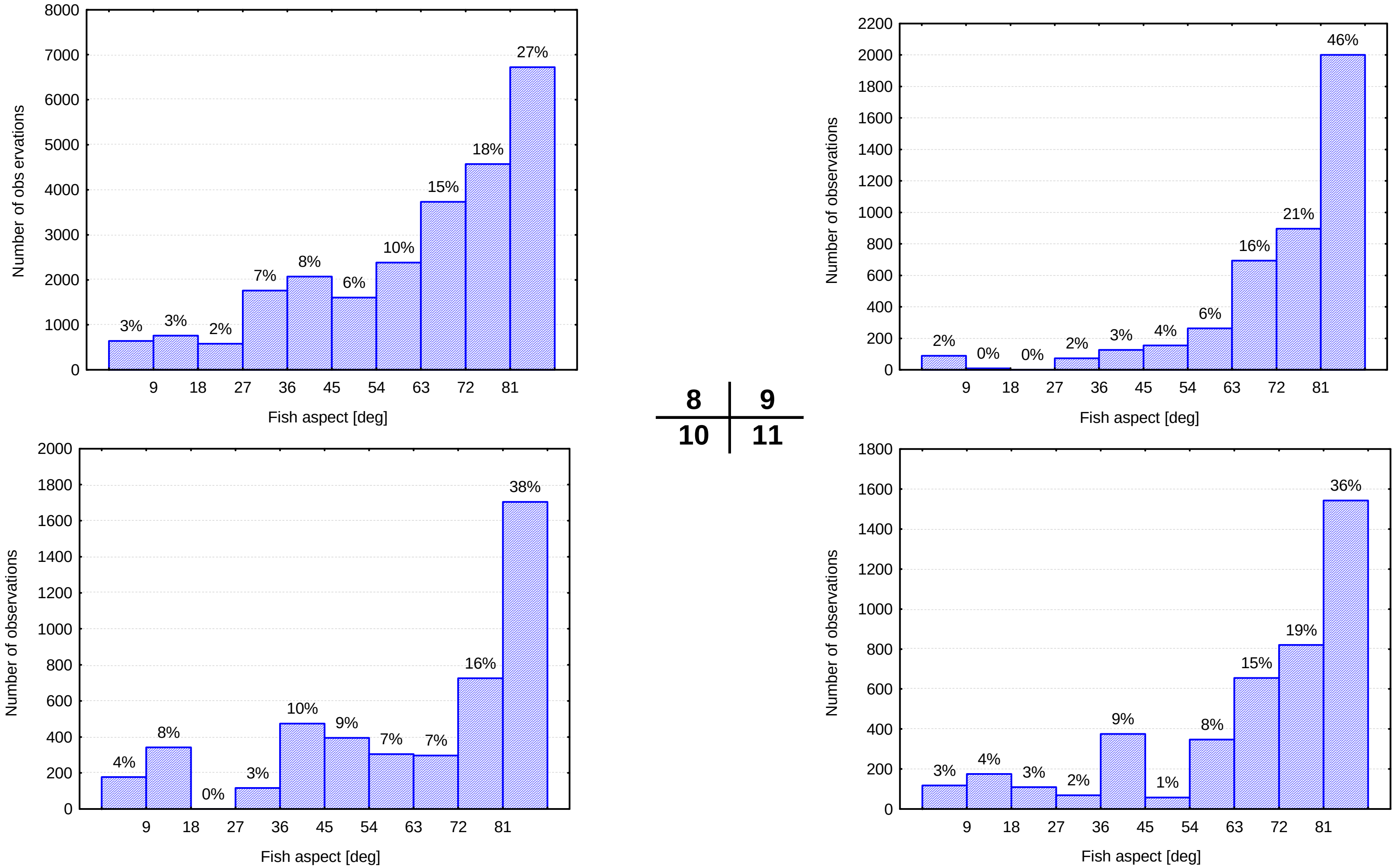


Figure 5-7: Slope-frequency histograms with proportional representation of individual categories from the crisscross-beaming acoustic experiment and the Tributary (cross-filtered): (5) C_{TRANS} (6) C_{PARA}, and (7) T_{CF}.



Figures 8 - 11: Aspect-frequency histograms with proportional representation of individual categories from the longitudinal survey of the Rimov reservoir: (8) Tributary, (9) Upper, (10) Middle, and (11) Dam.

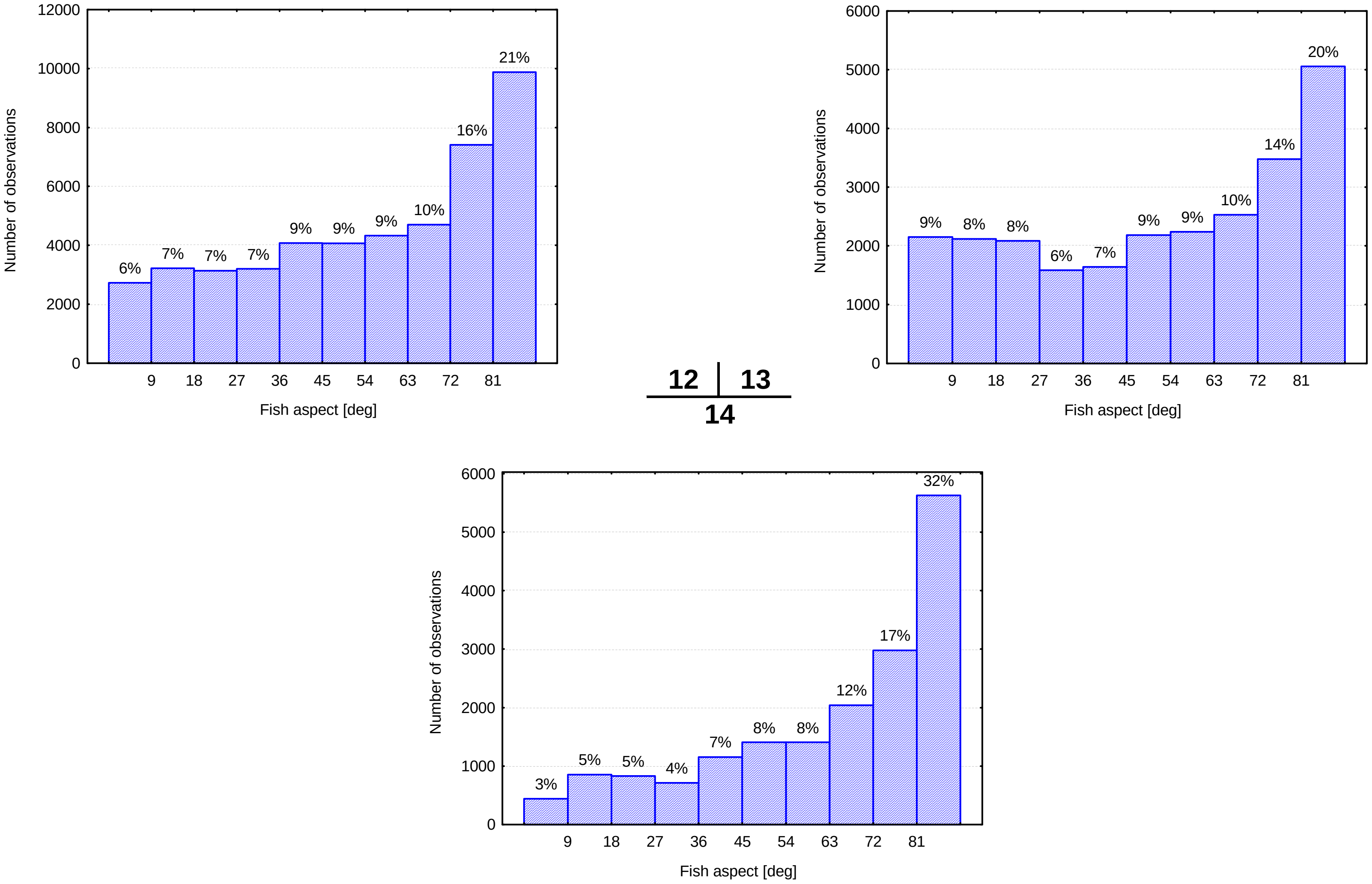


Figure 12 - 14: Aspect-frequency histograms with proportional representation of individual categories from the crisscross-beaming acoustic experiment and the Tributary (cross-filtered): (12) C_{TRANS} (13) C_{PARA}, and (14) T_{CF}.