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GEOGRAPHIC AND ECOLOGIC ASPECTS OF THE COMMUNITY STRUCTURE OF TREMATODES OF MALLARDS (*ANAS PLATYRHYNCHOS*) IN NORTHERN POLAND AND THE CZECH REPUBLIC

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ABSTRACT: Trematode infestation of Mallards (*Anas platyrhynchos*) varies between northern Poland and the Czech Republic. We determined the trematode fauna of juvenile and adult Mallards from Poland in 2010–16 (n=79 Mallards) and from the Czech Republic in 1964–2001 (n=296). Infracommunity diversity of trematodes from juvenile Mallards, defined by the Brillouin index and mean number of species, was significantly greater in Poland than it was in the Czech Republic. There were more species and greater biodiversity in the trematode communities of Mallards from Poland, where the environment is more natural and less altered by human activity than it is in the Czech Republic. In the trematode community of juvenile Mallards, the Simpson's index of biodiversity was higher in the Czech Republic than it was in Poland. The Berger-Parker dominance index was comparable in both countries. In terms of prevalence, the structure of the trematode fauna was hierarchic, and trematode species had different positions in this hierarchy in the two countries. Statistically significant differences in the epidemiologic indices between infection of juvenile Mallards from Poland and the Czech Republic were noted for *Bilharziella polonica*, *Echinostoma miyagawai*, *Echinostoma revolutum*, *Prosthogonimus cuneatus*, *Prosthogonimus ovatus*, *Notocotylus attenuatus*, *Echinoparyphium recurvatum*, *Australapatemon minor*, *Apatemon gracilis*, *Cyathocotyle prussica*, *Hypoderaeum conoideum*, *Metorchis xanthosomus*, *Psilochasmus oxyurus*, and *Cotylurus cornutus*.

Key words: Biodiversity, community structure, Digenea, mainland, Mallard, seacoast.

INTRODUCTION

Mallards (*Anas platyrhynchos*) lead a migratory life and transfer parasites between ecosystems during migration. In Central Europe, trematodes occurring in the Mallard are particularly well documented in the Czech Republic (Sitko et al. 2006) and in Poland (Sulgostowska and Czaplińska 1987; Betlejewska and Korol 2002; Kavetska et al. 2008a, b).

Our aim was to develop knowledge of the community structure of the trematodes of the Mallard populations based on data acquired in Poland and in the Czech Republic. We tested the hypothesis that there should be no geographic variation in infection of Mallards in Poland and the Czech Republic because of the wide geographic range and common occurrence of the Mallard and its trematodes.

MATERIALS AND METHODS

Poland is located in the northern zone of the temperate waters of the Baltic Sea catchment. Most of the country—its northern and central parts—is occupied by the lowland areas of the eastern part of the North European Plain. The Czech Republic is predominantly an upland country, with lowlands covering a smaller area, forming a series of depressions associated with the Morava River in the south. The Czech Republic lacks direct access to the sea. Our research on Mallards in Poland (2010–16; n=79 Mallards) was performed on ducks collected in the northwest of the country (*n*=65), in the Szczecin region (53°26′N, 14°32′E), where the Oder River empties into the Szczecin Lagoon (53°38′N, 14°34′E) and Lake Dąbie (53°27′N, 14°40′E), and in the northeast (*n*=14), in the Olsztyn region (53°46′N, 20°28′E), an area containing commercial carp (*Cyprinus carpio*) fish ponds several kilometers apart, with shores overgrown by reeds and natural marshes. Mallards (*n*=296) were collected in the Czech Republic (1964–2001) in southern Bohemia (*n*=81) in the vicinity of Lomnice (49°05′N, 14°43′E), where the study area was a system of fish ponds; in southern Moravia (*n*=46) in the vicinity of Strachotín (48°54′N, 16°40′E), where the study area was a natural marsh environment; and in Central Moravia (*n*=169) in the vicinity of Tovačov (49°25′N, 17°17′E) and Záhlinice (49°17′N, 17°29′E), where the study area was a system of fish ponds. The individual sites were combined to obtain baseline data because the distances between sites within each country were much smaller than between Polish and Czech sites. Estimation of the age of the Mallards was based on the presence of the bursa of Fabricius; its presence was assumed to indicate young birds in their first year of life, and its absence indicated adult ducks. The data for juvenile Mallards belonging to cohorts in the Czech Republic were tested for the time effect on the data. The Mallards were hunted in compliance with Polish and Czech laws regarding hunting of game birds, established by the respective Ministries of the Environment in Poland and in the Czech Republic or collected dead from the environment.

Mallards classified as local or summer birds were mainly hunted immediately after the end of the nesting season, from 15 August to 5 September, or earlier in some years (1967–69). Local juvenile Mallards were birds that had not begun seasonal migration. Their trematode infections must have been acquired locally because juvenile migration begins around mid-September (Dement'yev and Gladkov 1952). Adult Mallards were ducks for which the current breeding season was occurring in at least the second summer of their lives. Thus, the status of the Mallards was certain, as during this period there was little risk that the cohorts included juvenile ducks that had arrived from other geographic regions during autumn migration. Data obtained after 5 September were not included in the analyses because of the greater likelihood of mixing local ducks with migrants carrying flukes from other ecosystems.

Trematodes were fixed in 70–75% ethanol, and permanent slides were prepared. Alum carmine and borax carmine were used for staining, and clove oil and creosol were used for clearing. The slides were mounted with Canada balsam. To determine similarities and differences in the trematode fauna of Mallards from Poland and the Czech Republic, we compared indices of the component community and infracommunity of trematodes and their epidemiologic parameters: prevalence, abundance, and intensity of infection. The component community in this study was the community of all infrapopulations of trematodes associated with a subset of Mallards in Poland and the Czech Republic. An infrapopulation of parasites was composed of all individuals of a given trematode species in an individual Mallard. An infracommunity is understood as the community of trematode infrapopulations in a single Mallard. The terminology describing parasite communities follows that of Bush et al. (1997). The ecologic indices used included Simpson's index of diversity, the Berger-Parker dominance index, and the Brillouin index and followed Magurran (2004). Faunistic similarity of trematode fauna in groups of Mallards was defined using the Jaccard (1908) index (Real and Vargas 1996).

Trematode prevalence in the ducks was determined by comparison of frequencies. Abundance and intensity of trematode infection were compared with a *t*-test after log transformation of values because the variables were not normally distributed (Dytham 2011). The statistical significance levels in the data calculated with and without log transformation of the source data only occasionally differed. This was also the case when differences were tested by *t*-test bootstrap *P* values (Rózsa et al. 2000). We used a more conservative presentation style, and the tables show the results after log transformation. Values that are at the level of at least $P \leq 0.05$ were considered to differ significantly. Intensity was compared in groups of Mallards in which more than five individuals were infected. To compare dominance patterns in parasite communities of individual groups of Mallards, we graphed the dependence of species prevalence on the position of the trematode in the rank order of prevalences (from the position with the highest prevalence to the one with the lowest prevalence), called a *dominance profile*. Spearman's rank correlation coefficient (r_s) was calculated for an overall evaluation of the degree of their variation. Significance of differences between mean numbers of trematode species and between means for Brillouin's index were determined by the Mann-Whitney *U*-test in PAST (version 2.11) software (Hammer et al. 2001).

RESULTS

In both countries, trematode fauna of juvenile Mallards was richer in species than

TABLE 1. Characterization of trematode communities of Mallards (*Anas platyrhynchos*) from Poland (2010–16) and the Czech Republic (1964–2001) in the summer.

Age	Country	Location	No.		Component community			Infracommunity		
			Birds	Trematode species	Simpson index	Berger-Parker index	Dominant species	Mean Brillouin index (SD)	No. species/bird Mean (SD)	No. species/bird Maximum
Juvenile										
	Poland	Szczecin	50	18	0.67	0.54	*Bilharziella polonica*	0.59 (0.35)	3.56 (1.76)	9
	Czech Republic	Lomnice	55	12	0.80	0.31	*Australapatemon minor*	0.56 (0.38)	2.83 (1.38)	7
		Strachotín	27	22	0.86	0.28	*Notocotylus attenuatus*	0.82 (0.42)	4.64 (2.25)	10
		Tovačov	102	19	0.71	0.49	*Australapatemon minor*	0.39 (0.35)	2.40 (1.25)	5
		Záhlinice	56	14	0.74	0.44	*Australapatemon minor*	0.70 (0.24)	3.13 (1.21)	6
		Total	240	28	0.81	0.37	*Australapatemon minor*	0.47 (0.39)	2.72 (1.61)	10
Adult										
	Poland		29	13	0.80	0.37	*Bilharziella polonica*	0.45 (0.41)	2.56 (1.55)	6
	Czech Republic		56	13	0.79	0.30	*Australapatemon minor*	0.31 (0.31)	2.13 (1.20)	5

in it was in adults (Table 1). Faunistic similarity of trematode fauna, expressed by the Jaccard (1908) index, between Mallards from Poland and the Czech Republic was 0.44 for juveniles and 0.53 for adults. Faunistic similarity between juvenile and adult Mallards was 0.63 for birds from Poland and 0.41 for those from the Czech Republic.

The data for epidemiologic parameters for juvenile Mallards belonging to cohorts in the Czech Republic were tested for the time effect on the data, and no significant time-dependent differences were found: for Czech data from the entire period of 1964–2001, the regression coefficient b of intensity of infection against years was –0.0098 (=0.088, SE_b=0.0072, F_{205}=1.84, R^2=0.01). The same held for the locations (Zahlinice and Tovacov) that were closest to one another and the most similar in 1976–2001: regression coefficient was +0.022 (P=0.050, SE_b=0.013, F_{126}=2.79, R^2=0.02). Thus, the time dependence was highly unlikely to have affected the results.

Comparison of the trematode communities of different cohorts of juvenile Mallards showed geographic variation between Poland and the Czech Republic, as well as between the types of ecosystems the birds were from. Component community diversity was greater in the Czech Republic than it was in Poland, but infracommunity diversity and the mean number of trematode species were greater in Poland, and the differences were statistically significant (P=0.041 and P=0.001, respectively; Table 1). Differences between values for the Brillouin index and the average number of species in the infracommunity in ducks from different locations were mostly statistically significant: between Lomnice and Strachotin (P=0.016), Lomnice and Tovacov (P=0.012), Strachotin and Szczecin (P=0.022), Strachotin and Tovacov (P=0.000), Tovacov and Szczecin (P=0.002), and Tovacov and Zahlinice (P=0.000) (for the Brillouin index) and between Lomnice and Szczecin (P=0.033), Lomnice and Strachotin (P=0.000), Strachotin and Szczecin (P=0.045), Strachotin and Tovacov (P=0.000), Strachotin and Zahlinice (P=0.002), Tovacov and Szczecin (P=0.000),

TABLE 2. General characterization as to prevalence of infection of trematode communities of juvenile Mallards (*Anas platyrhynchos*) from Poland (PL; 2010–16) and the Czech Republic (CZ; 1964–2001) localities in the summer. *P*-values for comparisons between localities ($P<0.05$ in bold).

			P values[a]				
Locality	No.	% Prevalence	Lomnice CZ	Strachotin CZ	Zahlinice CZ	Tovacov CZ	Total CZ
Szczecin PL	50	96.0	0.510	0.573	**0.031**	**0.001**	**0.001**
Lomnice CZ	55	98.2	—	0.304	**0.007**	**0.001**	**0.001**
Strachotin CZ	27	92.6	—	—	0.216	**0.044**	0.252
Zahlinice CZ	56	83.9	—	—	—	0.485	0.661
Tovacov CZ	102	79.4	—	—	—	—	0.130
Total CZ	240	86.3	—	—	—	—	—

[a] — = not applicable.

and Tovacov and Zahlinice (P=0.001) (for average number of species).

The faunistic similarity of trematode communities was greatest between Strachotin and Zahlinice (Jaccard index: 0.56) and was least similar between Szczecin and Tovacov (Jaccard index: 0.37). The Berger-Parker index was higher in Szczecin (with dominance of *Bilharziella polonica* than it was in individual locations in the Czech Republic (with dominance of *Australapatemon minor* and *Notocotylus attenuatus*).

Analysis of epidemiologic parameters of trematode fauna from juvenile birds revealed statistically significant differences in total prevalence (Table 2 and Supplementary Material Table 1). There was some variation between Czech locations (Table 2). The value for Lomnice was close (*t*-test, $P>0.05$) to the value for Szczecin. Values for locations in Central Moravia (Zahlinice and Tovacov) were similar and markedly lower than those for sites located in South Bohemia and South Moravia. The total intensity of infection in Strachotin (South Moravia) was significantly greater than in it was in other Czech locations (*t*-test, $P<0.01$) and was even greater than in Poland (Table 3).

In terms of prevalence, the structure of trematode fauna was hierarchic, and trematode species had different positions in this hierarchy in Poland and in the Czech Republic (Fig. 1). However, the order of more important species (prevalence >5%) in the profile was significantly correlated (r_s=0.48, $P<0.05$). Prevalence, abundance, and intensity defining the infection of juvenile Mallards by *B. polonica* and some other trematode species differed significantly (Figs. 2–4 and Supplementary Material Table 1).

TABLE 3. General characterization as to intensity of infection of trematode communities of juvenile Mallards (*Anas platyrhynchos*) from Poland (PL; 2010–16) and the Czech Republic (CZ; 1964–2001) localities in the summer. *P*-values for comparisons between localities ($P<0.05$ in bold).

			P value[a]				
Locality	No. infected	Intensity	Lomnice CZ	Strachotin CZ	Zahlinice CZ	Tovacov CZ	Total CZ
Szczecin PL	48	43.6	**0.001**	**0.001**	**0.006**	**0.001**	**0.009**
Lomnice CZ	54	21.0	—	**0.007**	**0.038**	0.530	0.697
Strachotin CZ	25	49.7	—	—	**0.000**	**0.001**	**0.001**
Zahlinice CZ	47	17.6	—	—	—	0.094	**0.033**
Tovacov CZ	81	23.7	—	—	—	—	**0.000**
Total CZ	207	24.7	—	—	—	—	—

[a] — = not applicable.

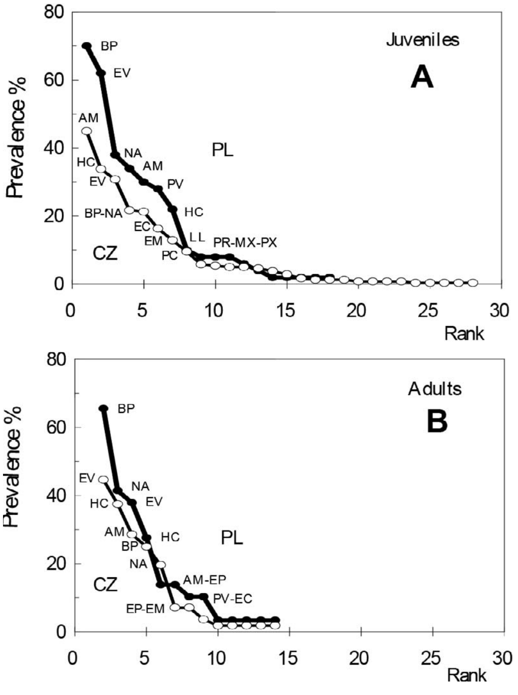

FIGURE 1. Comparison of dominance profiles of trematodes in Poland (PL, thick line, black dots) and the Czech Republic (CZ, thin line, white dots) and dependence of prevalence value on the trematode's position in the rank order of these values. (A) Trematodes in juvenile Mallards (*Anas platyrhynchos*). (B) Trematodes in adults. Species codes: AG=*Apatemon gracilis*; AM=*Australapatemon minor*; BP=*Bilharziella polonica*; CB=*Cotylurus brevis*; CC=*Cotylurus cornutus*; CR=*Cotylurus raabei*; CS=*Cotylurus strigeoides*; CO=*Cyathocotyle opaca*; CP=*Cyathocotyle prussica*; EM=*Echinostoma miyagawai*; EP=*Echinostoma paraulum*; EV=*Echinostoma revolutum*; EC=*Echinoparyphium recurvatum*; HC=*Hypoderaeum conoideum*; LC=*Leucochloridiomorpha constantiae*; LL=*Leucochloridiomorpha lutea*; LP=*Leucochloridium perturbatum*; MX=*Metorchis xanthosomus*; NA=*Notocotylus attenuatus*; NE=*Notocotylus ephemera*; PA=*Parorchis acanthus*; PC=*Prosthogonimus cuneatus*; PV=*Prosthogonimus ovatus*; PP=*Prosthogonimus pellucidus*; PU=*Prosthogonimus rarus*; PE=*Plagiorchis elegans*; PX=*Psilochasmus oxyurus*; PB=*Parastrigea robusta*; PS=*Psilotrema simillimum*; PM=*Psilotrema spiculigerum*; SG=*Sphaeridiotrema globulus*; TS=*Typhlocoelum sisowi*. Species codes are not given for values below 5%.

The differences in ecologic parameters between adult Mallards from Poland and those from the Czech Republic were not significant (Table 1). The profiles of the distribution of prevalence values for the most frequently occurring species were less strongly correlated (r_s=0.35, P>0.05; Fig. 1).

The community structure profiles of trematodes in adult birds strongly varied between the two countries, despite the apparent similarity of the curves illustrating the structure: in Poland, the correlation coefficient r_s was 0.27 (P>0.05) and, in the Czech Republic, only 0.13 (P>0.05). Total prevalence, intensity, and abundance were not statistically significant, but all parameters differed significantly for *B. polonica* and *N. attenuatus* (Figs. 2–4 and Supplementary Material Table 2).

The position of trematode species in the hierarchy was similar in juvenile and adult Mallards (Fig. 5). Juveniles and adults in Poland did not differ significantly in total prevalence, intensity, or abundance, but differences in parameters of some trematode species were statistically significant (Fig. 6 and Supplementary Material Table 3). In the Czech Republic, differences between juvenile and adult Mallards in total prevalence, abundance, and intensity of infection were not statistically significant (Supplementary Material Table 4). The results indicated that juvenile and adult Mallards in the Czech Republic had quantitatively more-varied trematode fauna than that in Poland (Fig. 6 and Supplementary Material Table 4).

DISCUSSION

Numerous studies in the world literature indicate that the diversity and richness of parasites of animals colonizing a given area depend on the characteristics of the environment (Combes 1995; Poulin 2007). Our research demonstrated that, despite the wide geographic range and common occurrence of the Mallard and its trematodes, there is geographic variation in the infestation of Mallards between northern Poland and the Czech Republic. Zoogeographically, the northern part of Poland is in the European–West Siberian Province of the Palearctic. The fauna of this region is associated with the marine environment and the Baltic Sea coast.

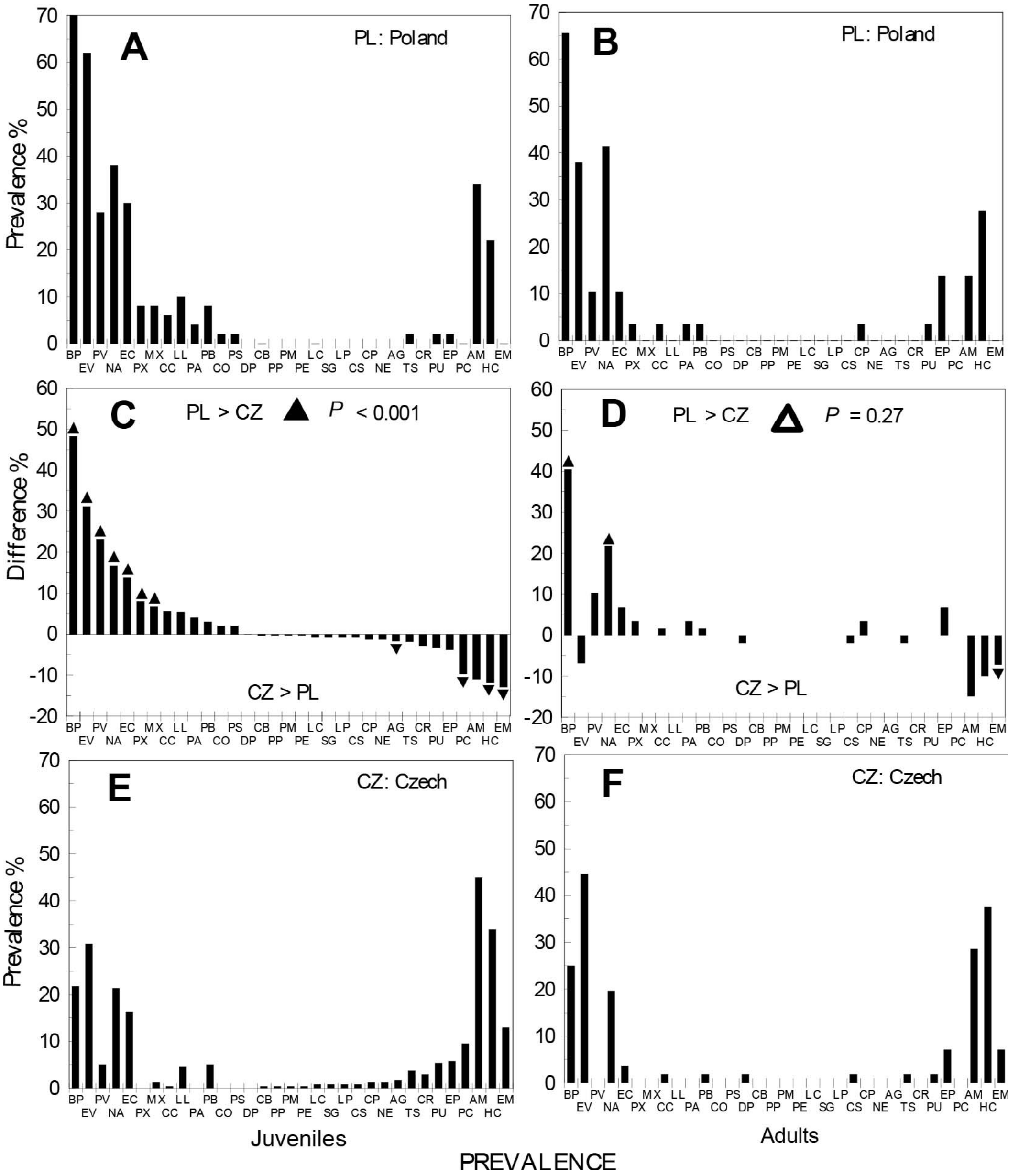

FIGURE 2. Prevalence of infection of Mallards (*Anas platyrhynchos*) by trematodes in Poland (PL; A and B) and the Czech Republic (CZ; E and F). X-axis=codes of parasite species (in the same order in every panel; species codes are the same as those in Figure 1); y-axis=prevalence (%). Species differences in prevalence are shown in the middle panels: positive values=value for Poland is greater than that for the Czech Republic; negative values=value for Czech Republic is greater than for Poland. Black triangles=statistically significant difference at the level specified in Supplementary Material Tables 1 (juveniles) and 2 (adults). (C and D) The total relation for all trematodes is given at the top: e.g., PL>CZ, black triangle, $P<0.001$ means that the total value for PL is greater than that for CZ, and the difference is significant at the level 0.001; white triangle indicates that the difference is not statistically significant at the 0.05 level.

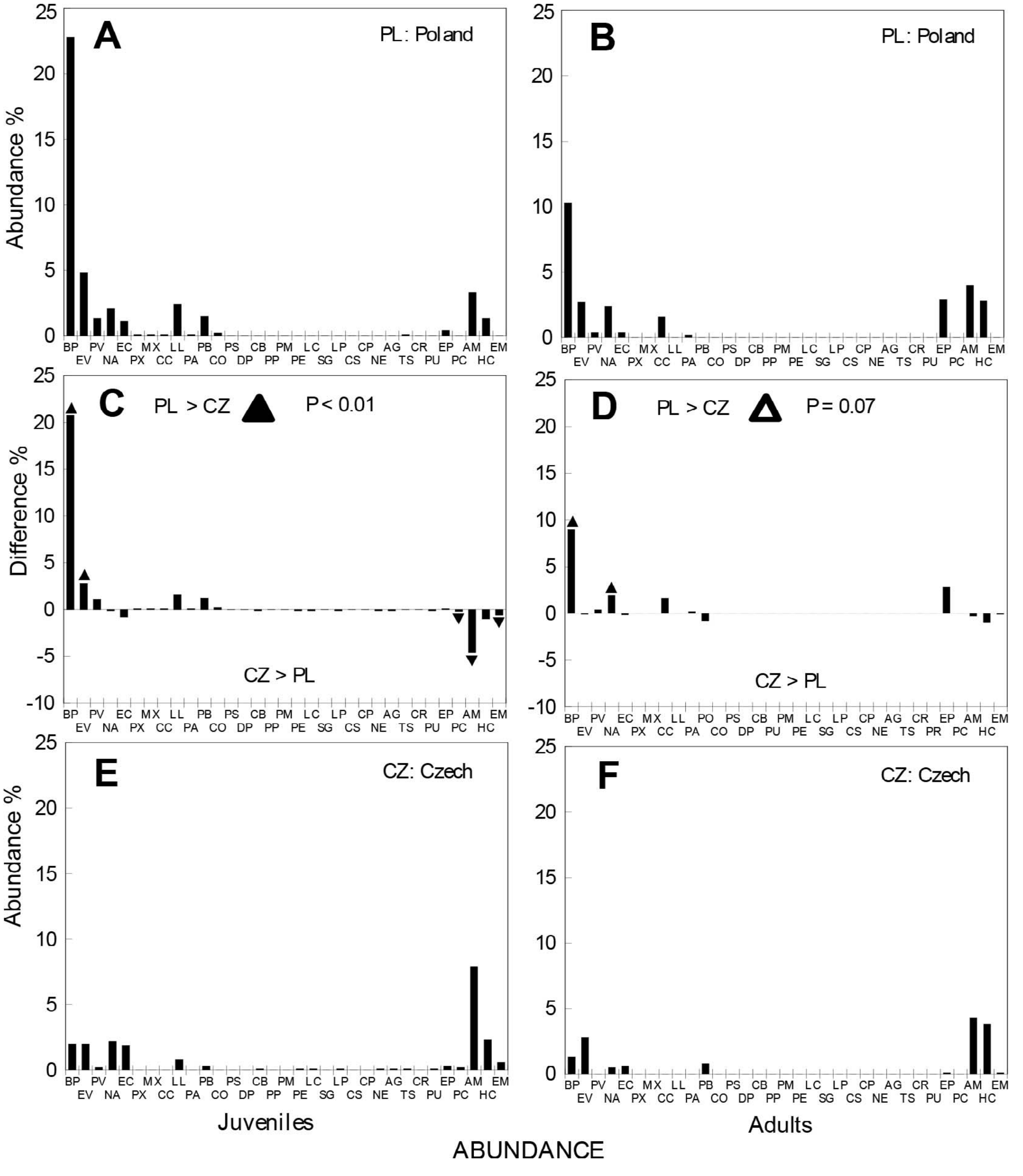

FIGURE 3. Abundance of trematodes in Mallards (*Anas platyrhynchos*) in Poland (PL; A and B) and the Czech Republic (CZ; E and F). Explanations are the same as those for Figure 2, but on the y-axis, abundance values are presented from the same tables.

The region has abundant water bodies and wetlands, and birds have close access to marine waters. Our research indicates that the encounter screen (Euzet and Combes 1980; Holmes 1987; Combes 1995) with the Mallard is open in Poland for some trematodes: *Cyathocotyle opaca*, *Psilochasmus oxyurus*, and *Psilotrema simillimum* in freshwater ecosystems and *Parorchis acanthus* in brackish and marine water ecosystems. The occurrence of these trematodes in juvenile Mallards in Poland is favored by the broad species spectrum and high abundance of definitive hosts. Gathering of large numbers

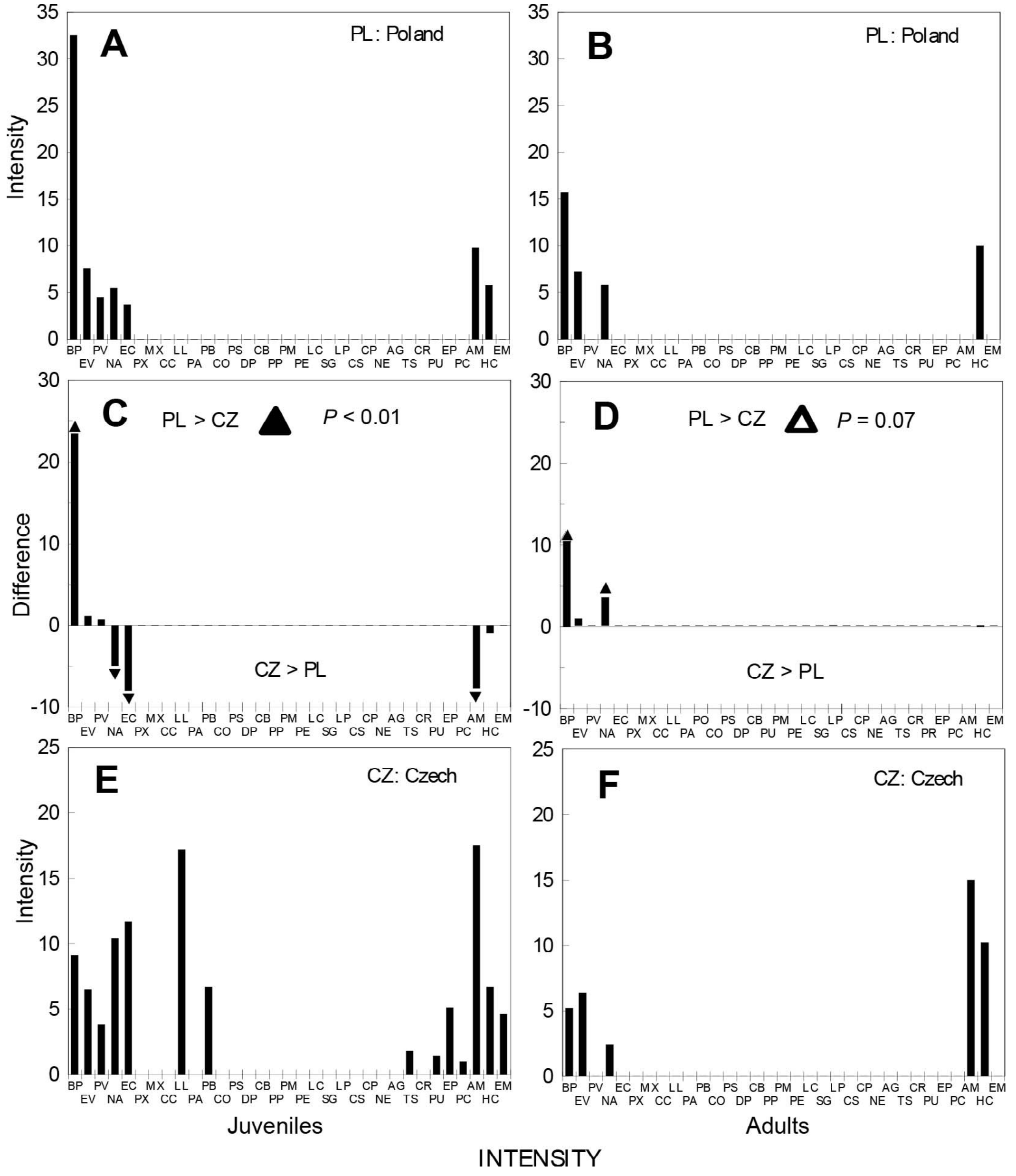

FIGURE 4. Intensity of trematode infection of Mallards (*Anas platyrhynchos*) in Poland (PL; A and B) and the Czech Republic (CZ; E and F). Explanations are the same as those for Figure 2, but on the y-axis, intensity values are presented from the same tables.

of waterfowl in the autumn and winter is conducive to high parameters of Mallard infection by those trematodes in Poland; from 172,000 to 515,000 Mallards during winter in Poland, mostly in the west (Tomiałojć and Stawarczyk 2003).

Some trematodes are rare in the ecosystems studied here, but their distribution should be monitored because of their role in the environment. An example is *Sphaeriodiotrema globulus* in the Czech Republic because trematodes of the genus *Sphaeriodiotrema* may pose a threat to ducks. In the midwestern

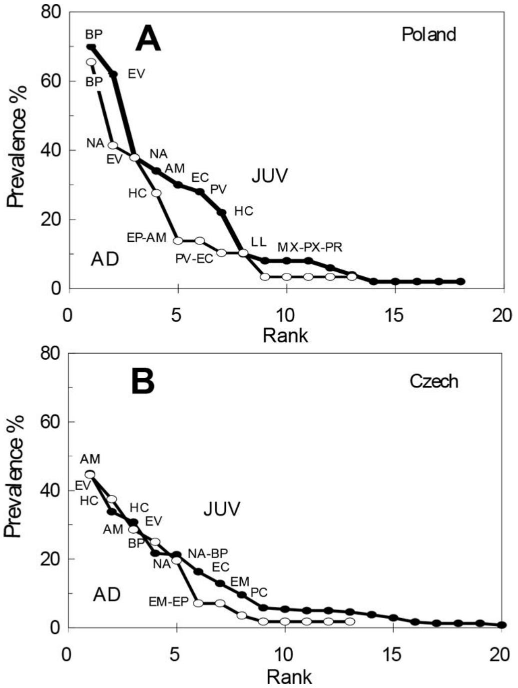

FIGURE 5. Comparison of dominance profiles of trematodes in juvenile Mallards (*Anas platyrhynchos*) (JUV, thick line, black dots) and adults (AD, thin line, white dots); dependence of prevalence value is on the trematode's position in the rank order of those values. (A) Poland. (B) Czech Republic. Species codes are the same as those in Figure 1.

US and Canada, nonnative trematodes (*Cyathocotyle bushiensis* and *Sphaeriodiotrema* spp.), whose host is the invasive Eurasian faucet snail (*Bithynia tentaculata*), have been the cause of die-offs of waterfowl for several decades (Roy and St-Louis 2017). In view of the severe consequences of infection for waterfowl, Roy and St-Louis (2017), based on their study of spatiotemporal variation in the prevalence and intensity of these trematodes in the faucet snail, emphasize the need for a better understanding of trematodes causing die-offs of waterfowl.

The hierarchic structure of the community of trematodes, based on their frequencies, is different in Poland than it is in the Czech Republic, but in both countries, the trematodes with the highest prevalence co-occur because they require similar environmental conditions in their life cycles (Fig. 1). Based on knowledge of the development cycles of these trematodes, the main factors determining the composition of these communities can be determined. In Poland, these factors are the presence of juvenile Mallards in breeding habitats with shallow water, with potentially large numbers of *B. polonica* cercariae; the presence of juvenile Mallards in water bodies with abundant aquatic vegetation, with metacercariae of *N. attenuatus*; and a Mallard diet of mollusks, bivalves, leeches (Hirudinea), and Turbellaria, potentially containing metacercariae of *Echinostoma revolutum*. *Bilharziella polonica* is a common parasite with broad definitive host specificity (Pojmańska et al. 2007). Furcocercariae in *Planorbarius corneus* have been recorded in many regions of Poland (Żbikowska 2007; Żbikowska and Nowak 2009; Cichy et al. 2011). In the Czech Republic, water areas for intermediate hosts (i.e., gastropods), are significantly smaller because of the fragmentation of the aquatic environment into ponds and the periodic drying out of natural marshlands in the area. Furthermore, in the Czech Republic, unlike in Poland, there is no phenomenon of flocks numbering thousands of birds gathering during migration and wintering. In the Czech Republic, the main factors determining the community of trematodes with the highest prevalence are consumption by Mallards of leeches containing metacercariae of *A. minor* and consumption of mollusks and other intermediate hosts containing metacercariae of *Hypoderaeum conoideum* and *E. revolutum*. Prevalence of *H. conoideum* varies not only between Poland and the Czech Republic but also between ecosystems in the Czech Republic, which indicates that the determinants of infection are the features of the ecosystem with which the Mallards are associated.

The differences are undoubtedly influenced significantly by the different degrees of naturalness of the environment between the two countries. In particular, because of the degradation of certain water bodies in the Czech Republic by transformation into fishponds, some cohorts may include Mallards that have been artificially fed by fishpond owners or hunters. Such birds are known to

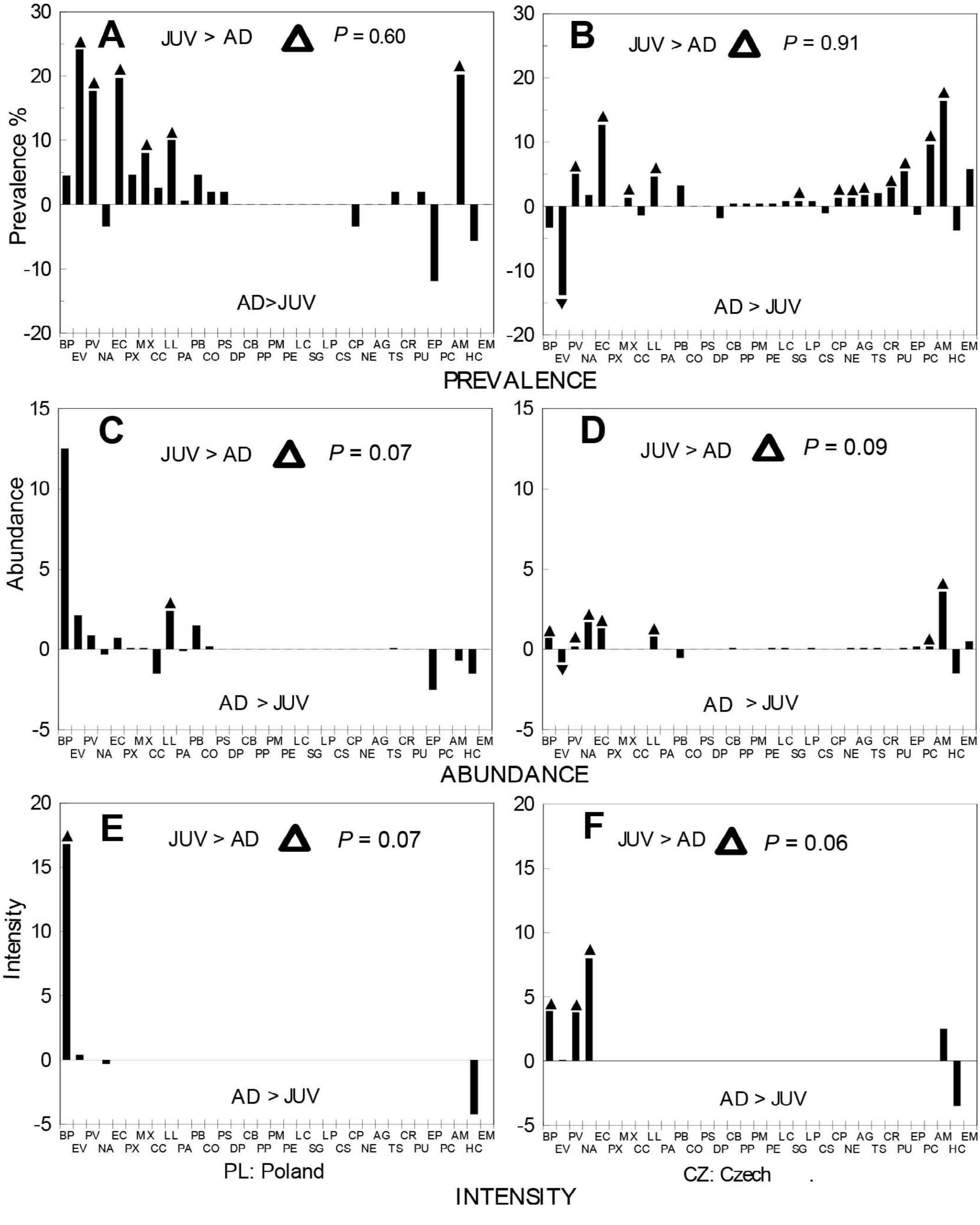

FIGURE 6. Differences in prevalence, abundance, and intensity of trematode infection in juvenile (JUV) and adult (AD) Mallards (*Anas platyrhynchos*) in PL and in the CZ. Legend is the same as it is in Figure 2.

host fewer helminths, which may explain the seemingly lower abundance of individual helminth species in the Czech cohorts.

Faunistic variation associated with the biogeographic regions of research in Poland and the Czech Republic is also indicated by the higher faunistic similarity in adult Mallards than in juveniles in Poland and the Czech Republic. These differences may be related to the age of the birds and may indicate links between the occurrence of trematodes and seasonal migration of ducks. Mallards of Central Europe are genetically similar because of the high potential for crossing of their populations, facilitating the exchange of parasites between Mallard populations. Both countries are located in the Palearctic realm, which is highly varied and has very distinct fauna in its individual parts. In terms of habitat, the same host population is present in southern Poland and the Czech Republic and differs from that found in northern Poland on the Baltic coast. If we were to compare the trematode fauna of Mallards from the Czech Republic and southern Poland, the results would very likely be the same. Various Mallard populations nest and winter in Europe. In principle, they can become mixed all over Europe, but mixed breeding on a smaller scale unquestionably takes place at the edges of the Mallard distribution area (northern Europe) and at the edges of the range of individual populations. A schematic pattern based on bird ringing atlases (Fransson and Pettersson 2001; Wernham et al. 2002; Cepak et al. 2008; Spina and Volponi 2008; Bairlein et al. 2014) is shown in Figure 7. The zone in which populations mix along migration routes through Poland and the Czech Republic runs largely through both countries, although the proportions of birds from different populations may vary (Fig. 7). The boundaries of the ranges of individual populations cannot be precisely described, but an overall analysis of available Mallard ringing recovery data has shown that they migrate in defined lanes, within which, they become partially mixed (Busse 1969; Busse and Maksalon 1986). Mallard migration, however, is not yet fully known, and the degree of population mixing has not been precisely determined. Moreover, recovery patterns (e.g., Syrota et al. 2018) may not be fully representative if the effect of wintering area change by birds originating in mixed population zones is not considered (Busse 1969). The main elements of the parasite communities in the study areas can be referred to as local (i.e., specific to the study sites) or introduced. Among adult birds, summer parasites originating in the winter quarters of northern and southern Mallard populations exert stronger, direct influences. Later, in autumn, there may be direct influences of trematode fauna from Mallards originating in northern and southern breeding areas.

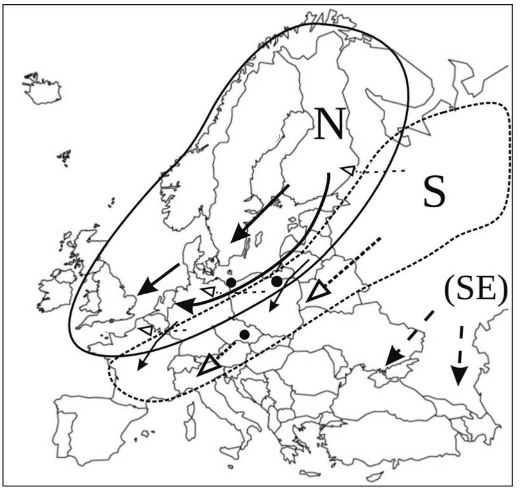

FIGURE 7. Simplified pattern of migrating populations of Mallards (*Anas platyrhynchos*) in Europe: black dots=study sites; northern population (N, continuous line; black-headed arrows=autumn migration routes); southern population (S, short broken line; white-headed arrows=autumn migration routes); unspecified southeastern populations (SE=broken black-headed arrow). Thin arrows indicate wide mixing zones of N and S (and probably other) population groups. Estimation based on a few bird ringing atlases: Fransson and Pettersson 2001; Wernham et al. 2002; Cepak et al. 2008; Spina and Volponi 2008; Bairlein et al. 2014.

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SUPPLEMENTARY MATERIAL

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