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THE SPATIAL DISTRIBUTION OF PERCH (*PERCA FLUVIATILIS*) ECTOPARASITES AND THE EFFECT OF CHEMICAL WATER QUALITY PARAMETERS ON ECTOPARASITE SPATIAL NICHE SIZE

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*Seasonal changes of abiotic factors and their influence on parasite occurrence have repeatedly been studied. Most of the studies have been conducted to evaluate the effect of water physicochemical parameters on changes in the intensity of infection, prevalence and component community of a number of parasite species. However, insufficient attention has been paid to the link between water quality parameters and spatial niche size of ectoparasites. The distribution of ectoparasite species on perch (*Perca fluviatilis *L.) was studied to establish whether seasonal changes of water quality parameters are associated with ectoparasite spatial niche size. The concentration of phosphates (PO_4^{3-}), nitrates (NO_3^-), sulphates (SO_4^{2-}) and dissolved oxygen (DO) in the water of Lake Sila (Latvia) was measured every month throughout the year and recorded all ectoparasites on perch. Zero-inflated mixed models were used to evaluate which of the water parameters influence the spatial niche size of ectoparasites. Our findings showed that spatial niche size of some ectoparasite species is affected by a set of water quality parameters and that this effect is negative. The spatial niche size of *Anodonta cygnea* *was negatively associated with phosphate, nitrate, sulphate and dissolved oxygen concentration. The spatial niche size of *Ancyrocephalus percae* *was negatively associated with sulphate, and the spatial niche size of *Ergasilus sieboldi* *was negatively associated with nitrate concentration.*

Key words: *perch, ectoparasites, niche size model, boreal lake, water parameters, Latvia.*

INTRODUCTION

Host and water environments influence the presence and abundance of fish parasites. However, the strength of this influence may vary between ectoparasites and endoparasites. Higher susceptibility to changes in the aquatic environment is expected for ectoparasites because they require physiological adaptation and tolerance similar to that of their host, whereas endoparasites are more susceptible to changes in homeostasis of the host and changes associated with the life cycle of this host (maturation, migration, breeding, etc.) (Willmer *et al*., 2004).

A parasite's habitat is made up of a variety of biotic and abiotic factors. Abiotic factors are physicochemical components (temperature, pH, light intensity, salinity), whereas biotic factors are usually associated with the host (age, sex, length, immune response) (Dogel, 1962; Poulin, 2004; 2008; Morand and Krasnov, 2010). Seasonal changes of abiotic factors and their influence on parasite occurrence have been the focus of many ecological studies (Öztürk and Altunel, 2006; Lamková *et al*., 2007; Khidr *et al*., 2012; Majumder *et al*., 2013; Wali *et al*., 2016). For example, prevalence and intensity of parasitic infection have been evaluated considering several parameters of water quality (temperature, dissolved oxygen, free CO_2, alkalinity, hardness, clarity) and water pollutants (heavy metals, petrochemicals, effluents, organic pollutants) (Siddall *et al*., 1997; Yeomans *et al*., 1997; Faulkner and Lochmiller, 2000; Lefcort *et al.,* 2002; Billiard and Khan, 2003). An increase in the prevalence and abundance for some parasite species, and decrease for the other species to these factors have been observed (Sures, 2004). Meta-analysis of the 52 studies showed that responses of parasites to stressors are not equal (Vidal-Martínez *et al*., 2010).

While the effect of stressors on parasite's prevalence, intensity of infection, abundance and component community has repeatedly been studied (see reviews of Gilbert and Avenant-Oldewage (2017) and Sures *et al.* (2017), insufficient attention has been paid to the link between water quality parameters and spatial niche size of ectoparasites.

Several natural and/or anthropogenic sources may increase concentration of phosphates (PO_4^{3-}), nitrates (NO_3^-), sulphates (SO_4^{2-}) to a level toxic for some aquatic organisms (Kutty, 1987; Shen *et al.*, 2013). The association between the abundance of parasites and phosphate, nitrate, and sulphate ion concentration has rarely been studied or evaluated indirectly since most of the ion concentrations are related to the trophic state of a lake. Although eutrophication of a lake is a slow natural process, the concentration of those parameters depends on many factors, which markedly fluctuate throughout the year (Shen *et al.*, 2013). Also, parasite abundance fluctuates throughout the year and is associated with some water quality parameters (Vidal-Martínez *et al.*, 2010).

The aim of this study was to evaluate spatial distribution of perch ectoparasites, measure chemical water quality parameters in each month throughout the year, and to test whether seasonal changes of water quality parameters are associated with ectoparasite spatial niche size. To answer this question we measured the concentration of phosphates, nitrates, sulphates and dissolved oxygen in the water of Lake Sila (Latvia) every month throughout the year and recorded the distribution of ectoparasites on perch (*Perca fluviatilis* L.). We expected that ectoparasites will show specific response to the set of water quality parameters. Our expectations were mainly based on the findings of Vidal-Martínez *et al.* (2010) that the concentration of water quality parameters were positively associated with spatial niche size of protists, negatively with crustaceans and glochidians, and were not associated with monogeneans. The relationship between physical water quality variables (for example, temperature) and parasite infection parameters has been addressed in a number of studies (Harvell, 1999; 2002; Marcogliese, 2001; Retief *et al.*, 2007; Blažek *et al.*, 2008). Therefore, the present investigation focuses only on relationships between ion concentrations and niche breadth of ectoparasites.

MATERIALS AND METHODS

Investigated waterbody. Lake Sila (55°44'07.0"N 26°47'34.0"E) is a small lake with surface area 262.0 ha and mean depth 4.1 m. It lies within the nature park "Silene" in Latvia (Fig. 1). It has a flow-through hydrological regime: two rivers and streams enter the lake and one river flows out (Tidriķis, 1998).

Collecting of water samples and quality analysis. Water samples were collected every month from June 2015 to May 2016. Overall, a total of 60 (5 per month) surface grab water samples were collected using 2 l polythelene bottles. All samples were stored and stabilised according to ISO (International Organization for Standardization), delivered to the laboratory and examined on the same day of collection. Phosphate, nitrate and sulphate ions were measured with the spectrophotometry according to ISO standards: ISO 6878:2005; ISO 7890-3:2002 and ISO 9280:1990. Dissolved oxygen concentration of water was measured by titration according to ISO 8467:1995.

Collecting and examination of perch and ectoparasites. The necessary fish individuals needed to estimate association between seasonal changes of water quality parameters and ectoparasite spatial niche size were calculated with G*Power 3 (Faul *et al.*, 2007; 2009). The following parameters were used: number of predictors = 5, power (1-β error probability) = 0.95, α error probability = 0.05 and effect size f2 = 0.15 (correspond to medium effect size). Output parameters showed that for this study the necessary minimum total sample size was 138 fish individuals.

Perch were collected from Lake Sila every month (~12 individuals) throughout the year. In total, 149 fish were captured by fishing rod and gill nets (total length of fish 16.8 ± 5.0, mean ± SD) and examined on the same day of collection. Before examination fish were euthanised according to Algers *et al.* (2009). Gill apparatus, fins, surface, and the nasal and oral cavities were examined of each side of each fish. Gill arches were numbered from the anterior to the posterior as 1-4. Each arch was divided into three sectors from the dorsal to the ventral end as I-III (Simková *et al.*, 2000; Zolovs *et al.*, 2016). Fins were examined as follow: D – dorsal fin, C – caudal fin, A – anal fin, Pc – pectoral fins and Pl – pelvic fins and scraped mucus from the entire surface, and the nasal and oral cavities. All ectoparasites were counted and identified to species level using microscopy and identification keys (Sulman, 1984; Gussev, 1985; Bauer, 1987).

There are a number of niche concepts. We used the Hutchinsonian niche concept that is defined as an "n-dimensional hypervolume", where the dimensions are environmental conditions and resources (Hutchinson, 1957). However, in the present study, we examine only one dimension and use the term 'niche' as a synonym of space occupied (spatial unit on host occupied by ectoparasites).

Statistical data analysis. The Kruskal–Wallis test was conducted to determine if there were differences between months for concentration of water quality parameters and niche breadth of parasites. The chi-square test was used to test whether a parasite prefers certain a localisation over others. Those tests were carried out using SPSS Statistics version 22 (IBM Corporation, Chicago, Illinois). Parasite counts often have highly skewed distribution with an excessive number of zeroes. To cope with this, zero-inflated mixed modelling was applied (Pilosof *et al.*, 2012; Barnard *et al.*, 2015). To account for a large number of zeroes in our data, we applied zero-inflated Poisson (ZIP) or zero-inflated negative binomial (ZINB) mixed models to test for the effects of phosphate, nitrate, sulphate and dissolved oxygen concentration on the count and niche breadth of ecto-

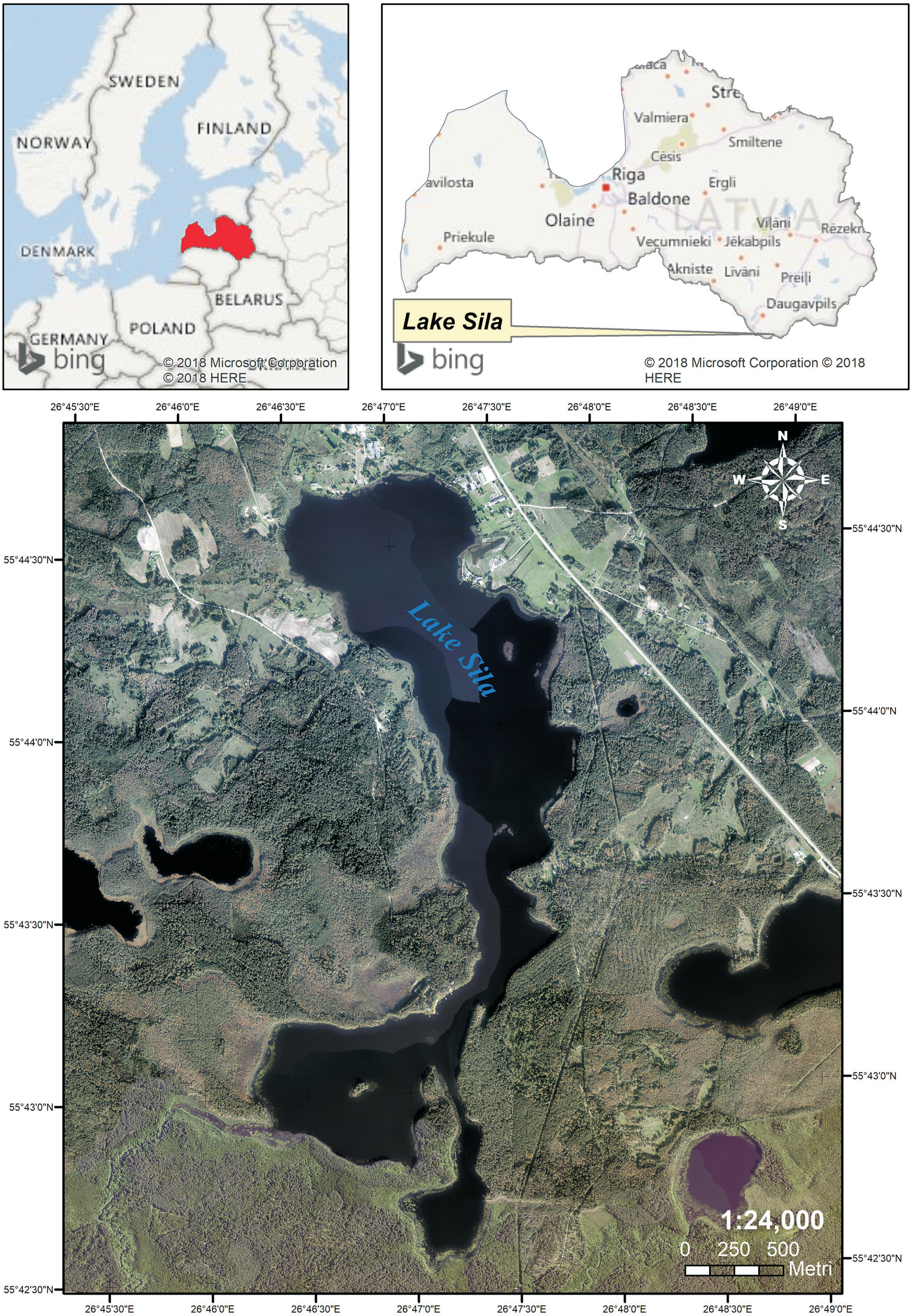

Fig. 1. Location of Lake Sila.

parasites. Fish total length was added in the analysis due to the influence of this parameter on parasite counts (Cardon *et al.*, 2011). For each species, we ran two models (negative binomial and Poisson distribution) using a "psc_1" package (Jackman, 2015) implemented in R (R Development Core Team, 2016). Akaike Information Criterion (AIC) was used to select the best model for each data set. The significance of the estimated coefficients was tested against a reference level that was chosen arbitrarily among five-factor levels (phosphate, nitrate, sulphate, and dissolved oxygen concentration and fish length). To have all explanatory variables (predictors) in comparable scales, data were scaled by the standard deviation method. Only weakly inter-correlated water quality parameters were included in the models.

Standardised Levin's niche breadth was calculated according to Krebs (1998), where p_i is a proportion of individuals found in the localisation *i*, and *n* is the number of possible localisations. Overall, a total of 34 localisations were used to calculate Levin's niche breadth. The standardised Levin's index ranges from 0 to 1, where 0 indicates the absence of a species and 1 indicates that a species occupies all available localisations.

RESULTS

Data on parasite count and water quality parameters at each month are presented in Table 1. In total, we recorded 2822 parasite individuals belonging to one protist species (*Trichodina* sp.) and six metazoan species (*Ancyrocephalus percae, Anodonta cygnea, Unio* sp., *Achtheres percarum, Argulus foliaceus* and *Ergasilus sieboldi*). The mean niche breadths of metazoan ectoparasites on perch in each month are presented in Table 2. The Kruskal–Wallis test showed that niche breadths differed between sampling months only for *A. cygnea* $X^2(5) = 16.846$, $p = 0.005$. Data on parasite count within gill apparatus, fins, body surface, nasal and oral cavities are presented in Tables 3 and 4. The chi-square test showed that *A. cygnea*, *Unio* sp., *A. percarum* and *E. sieboldi* ($p < 0.05$) preferred a specific localisation, whereas *A. percae* and *A. foliaceus* ($p > 0.05$) were randomly distributed.

The concentration of phosphates, nitrates, sulphates and dissolved oxygen differed between sampling months ($p < 0.05$). The monthly variation in the concentration of phosphate (CV (coefficient of variation) = 94.3%) and nitrate (CV = 139.3%) in the lake was at least two times higher than the concentration of sulphate ions (CV = 36.9%) and dissolved oxygen (CV = 11.2%) ($p < 0.05$).

Zero-inflated models showed that niche breadth of three ectoparasite species was negatively associated with water quality parameters and positively associated with fish length (Table 5). We observed that only fish length might generate false zeros for niche breadth. Our findings showed that the spatial niche size of *A. cygnea* was negatively associated with phosphate, nitrate, sulphate and dissolved oxygen concentration. The spatial niche size of *A. percae* was negatively associated with sulphate concentration, and the spatial niche size of *E. sieboldi* was negatively associated with nitrate concentration.

DISCUSSION

Our main expectations were supported only partly because data showed that not all ectoparasite species responded to the phosphate, nitrate, sulphate and dissolved oxygen con-

Table 1

MEAN VALUES OF WATER QUALITY PARAMETERS AND MEAN PARASITE COUNTS ON PERCH (*PERCA FLUVIATILIS*) FROM LAKE SILA IN EACH MONTH (LATVIA)

	SO_4^{2-} mg l^{-1}	PO_4^{3-} mg l^{-1}	NO_3^- mg l^{-1}	DO mg l^{-1}	*Ancyrocephalus percae*	*Anodonta cygnea*	*Unio* sp.	*Achtheres percarum*	*Argulus foliaceus*	*Ergasilus sieboldi*
June	6.0901	0.0099	0.0253	6.68	2		65		1	2
July	8.8889	0.0043	0.0008	7.64			35			2
August	10.8890	0.0084	0.0099	6.76	1		13	1		3
September	8.8943	0.0214	0.1537	5.95	2.5			1	1	3
October	7.9024	0.0354	0.0167	6.73	1.5	1		1	1	7
November	4.2469	0.0062	0.0026	6.03	3	5		1		7
December	5.3097	0.0167	0.0154	5.07	2	6				1.5
January	7.9370	0.0281	0.0537	6.80	2	2			1	
February	5.2759	0.0317	0.0205	6.23		8				1.5
March	8.9091	0.0234	0.0758	6.51	1.5	4				
April	10.8870	0.0053	0.0341	7.01		6				
May	9.9459	0.0279	0.0002	6.57		14	92			1
Range	13.945	0.085	0.245	3.150	2	13	79	1	1	6
Mean	7.931	0.018	0.034	6.502	2	5.8	51.3	1	1	3
SD	2.929	0.017	0.048	0.728	0.6	4	34.5	1	1	2
Prevalence, %					23	42	21	9	7	33

DO, dissolved oxygen; SD, standard deviation

Table 2

MEAN NICHE BREADTH OF ECTOPARASITES ON PERCH (*PERCA FLUVIATILIS*) FROM LAKE SILA IN EACH MONTH (LATVIA)

	Ancyrocephalus percae	*Anodonta cygnea*	*Unio* sp.	*Achtheres percarum*	*Argulus foliaceus*	*Ergasilus sie boldi*
June	0.03		0.37		0.03	0.11
July			0.22			0.09
August			0.12			0.08
September	0.06					0.09
October	0.03			0.03		0.14
November	0.07	0.10				0.13
December	0.03	0.04				0.03
January	0.04	0.04		0.01	0.01	
February		0.11				0.02
March		0.12				
April		0.17				
May		0.24	0.37			

Table 3

DISTRIBUTION OF PARASITE SPECIES WITHIN GILL APPARATUS OF PERCH *(PERCA FLUVIATILIS)* FROM LAKE SILA (LATVIA)

Species	Arch	Side	Sectors of arch			Total
			I	II	III	
Ancyrocephalus percae	1	R	3	5	4	12
		L	2	3	7	12
	2	R	1	3	8	12
		L	2	5	5	12
	3	R	1	3	2	6
		L	4	0	3	7
	4	R	0	1	3	4
		L	1	0	3	4
Anodonta cygnea	1	R	18	16	12	46
		L	15	23	13	51
	2	R	11	29	19	59
		L	12	27	24	63
	3	R	11	22	18	51
		L	16	28	9	53
	4	R	3	9	2	14
		L	0	16	2	18
Unio sp.	1	R	43	96	65	204
		L	44	76	40	160
	2	R	84	135	90	309
		L	79	125	61	265
	3	R	58	96	79	233
		L	80	103	60	243
	4	R	34	58	35	127
		L	35	54	43	132
Achtheres percarum	1	R	7	0	0	7
		L	6	1	0	6
	2	R	0	0	1	1
		L	0	1	0	1
	3	R	0	0	0	1
		L	0	0	0	0
	4	R	0	0	0	0
		L	0	0	0	0
Argulus foliaceus	1	R	0	0	0	0
		L	1	0	0	1
	2	R	0	1	0	1
		L	0	1	1	2
	3	R	0	1	0	1
		L	0	0	0	0
	4	R	0	0	1	1
		L	0	0	0	0
Ergasilus sieboldi	1	R	7	4	7	18
		L	6	7	9	22
	2	R	11	9	8	28
		L	10	16	15	42
	3	R	15	9	6	30
		L	16	3	12	31
	4	R	9	12	3	24
		L	13	10	7	30

The number of specimens found in given sector in all fish examined throughout the year.

centration. We recorded only negative association between niche breadth and water parameters for some species. However, our additional expectation according to Cardon *et al.* (2011) was supported because we found a positive association between niche breadth and fish length.

Usually, the spatial niches of ectoparasites are restricted and the parasite niches are segregated between species (Morand *et al.*, 2015). However, Rohde (1991) showed that it is not influenced by the presence of competing species. The low density of parasite individuals and resource richness in the host prevent parasite interaction.

The association between parasite niche breadth and water parameters might be not strongly linear. For example, nitrates and phosphates are two nutrients of primary concern

Table 4

DISTRIBUTION OF PARASITE SPECIES ON FINS, BODY SURFACE, NASAL AND ORAL CAVITIES OF PERCH *(PERCA FLUVIATILIS)* FROM LAKE SILA (LATVIA)

Parasite species	Perch fins							BS	NC	OC	Total
	D	C	A	PcR	PcL	PlR	PlL				
Anodonta cygnea	191	30	48	51	47	30	36	10	1	0	444
Unio sp.	8	5	1	2	0	0	0	0	0	0	16
Argulus foliaceus	4	4	0	0	0	0	0	1	0	0	9
Ergasilus sieboldi larva	0	0	0	0	0	0	0	0	3	0	3

D, dorsal fin; C, caudal fin; A, anal fin; PcR, pectoral fin right side; PcL, pectoral fin left side; PlR, pelvic fin rigth side; PlL, pelvic fin left side; BS, body surface; NC, nasal cavity; OC, oral cavity. Number of specimens found in given sector in all fish examined throughout the year.

Table 5

SUMMARY OF ZERO-INFLATED MODELS OF FACTORS SIGNIFICANTLY AFFECTING NICHE BREADTH OF ECTOPARASITES ON PERCH (*PERCA FLUVIATILIS*)

Parasite species	Model	Mean niche breadth	Factors	Estimated coefficient ± SE	Z value	p
A. cygnea count model	ZINB	0.04	phosphates	–0.70 ± 0.25	2.76	0.005
			sulphates	–2.99 ± 0.44	6.76	< 0.001
			nitrates	–2.97 ± 0.41	–7.09	< 0.001
			oxygen	–2.78 ± 0.51	–5.44	< 0.001
A. cygnea zero inflation						
A. percae count model	ZINB	0.01	sulphates	–1.18 ± 0.42	–2.83	0.004
A. percae zero inflation			fish length	–7.54 ± 3.61	–2.08	0.03
E. sieboldi count model	ZINB	0.02	nitrates	–0.47 ± 0.22	–2.08	0.03
			fish length	1.30 ± 0.19	6.54	< 0.001
E. sieboldi zero inflation						

ZIP, zero-inflated Poisson mixed model; ZINB, zero-inflated negative binomial mixed model. Results are shown only for models with significant coefficients.

in lakes. They may benefit some organisms up to a specific concentration, above which toxicity might occur. For example, Johnson *et al*. (2007) provided experimental evidence that eutrophication promotes parasite infection in amphibians. However, the enrichment of nitrate concentration was shown to reduce ectoparasite *Gyrodactylus turnbulli* infection intensity in Trinidadian guppies (*Poecilia reticulate*) (Smallbone *et al*., 2016). Sulphate ions are an essential plant nutrient and are not considered toxic to animals (Zhou, 1989). However, our findings showed that sulphate concentration was negatively associated with ectoparasite niche breadth.

Oxygen plays a crucial role in various biochemical and physiological processes of many organisms. For example, parasites use oxygen for energy production and oxidative catabolism and anabolism (Moulder, 1950). However, the oxygen concentration in water at a high or low level may harm aquatic organisms. Organic decomposition and respiration of aquatic organisms decrease oxygen concentrations, whereas photosynthesis and aeration contribute to supersaturation of water (Shen *et al.*, 2013). Eutrophication-induced reduction in dissolved oxygen may cause hypoxic stress in many aquatic organisms (Vaquer-Sunyer and Duarte, 2008). For example, hypoxic stress may promote release of the parasitic glochidia from *Unio* mussels (Aldridge and McIvor, 2003). The minimal requirements of oxygen concentration have been studied for many fish species. For example, the lower optimum limit of dissolved oxygen concentration for perch is 5 $mg \cdot l^{-1}$ (Krieger *et al.*, 1983). Our data show that oxygen concentration in Lake Sila may drop to the lower optimal limit for perch (min DO = 5.01 $mg \cdot l^{-1}$). However, the minimal requirements of oxygen concentration for parasites are unknown. Oxygen concentration on the bottom of lake drops even lower, which may influence development of parasite eggs. Saunders *et al*. (2000) found that availability of oxygen plays a significant role in the embryonation of parasite eggs. Some studies have recorded an association between oxygen concentration in water and ectoparasite spatial preferences. For example, Chapman *et al*. (2000) studied the prevalence and intensity of the gill monogenean *Neodiplozoon polycotyleus* Paperna in cyprinid fish from oxygen-poor waters (mean 2.5 $mg \cdot l^{-1}$) and noted that site specificity of parasites on gills may be related to oxygen availability.

In conclusion, the relationship between water quality and spatial niche breadth of ectoparasites is likely to be variable and more complex than reported here. We suggest that changes in spatial niche breadth of ectoparasites are not solely due to changes in water chemical variables. A number of several physical parameters (such as temperature, pH and salinity) and biotic factors (such as parasite intensity of infection, host sex and age) may operate in synergy with water chemical variables. However, the analysis of all mentioned variables requires a significantly larger sample size (number of examined fish individuals) and perhaps should be analysed as a meta-analysis. Nevertheless, our study shows that seasonal changes of water chemical parameters in the lake are enough to affect the spatial niche of some ectoparasites species on the host.

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ASARU (*PERCA FLUVIATILIS*) EKTOPARAZĪTU TELPISKAIS SADALĪJUMS UN ŪDENS ĶĪMISKO KVALITĀTES PARAMETRU IETEKME UZ EKTOPARAZĪTU TELPISKO NIŠAS LIELUMU

Abiotisko faktoru sezonālās izmaiņas un to ietekme uz parazītu sastopamību ir plaši pētīta. Lielākā daļa pētījumu ir veikti, lai novērtētu ūdens fizikāli ķīmisko parametru ietekmi uz dažu parazītu sugu intensitātes, ekstensitātes un komponentu sabiedrības izmaiņām. Tomēr nepietiekama uzmanība tika veltīta saiknei starp ūdens kvalitātes parametriem un ektoparazītu telpisko nišu. Šajā darbā tika pētītas ektoparazītu lokalizācijas vietas uz asara (*Perca fluviatilis* L.), lai noskaidrotu, vai ūdens kvalitātes parametru sezonālas izmaiņas ir saistītas ar ektoparazītu telpiskās nišas lielumu. Tika mērīta fosfātu PO_4^{3-}, nitrātu NO_3^-, sulfātu SO_4^{2-} un izšķīdušā skābekļa (DO) koncentrācija Sila ezerā (Latvija) katru mēnesi visa gada garumā, un no asariem tika ievākti ektoparazīti. Statistiskajai analīzei izmantoti *zero-inflated* jauktie modeļi, lai novērtētu, kuri ūdens parametri ietekmē ektoparazītu telpiskās nišas lielumu. Mūsu rezultāti parādīja, ka dažu ektoparazītu sugu telpiskās nišas lielumus ietekmē ūdens kvalitātes parametru kopums, un šis efekts ir negatīvs. Dižās bezzobes *Anodonta cygnea* glohīdiju telpiskās nišas lielums ir negatīvi saistīts ar fosfātu, nitrātu, sulfātu un izšķīdušā skābekļa koncentrāciju. Trematodes *Ancyrocephalus percae* telpiskās nišas lielums ir negatīvi saistīts ar sulfātu koncentrāciju, un airkājvēža *Ergasilus sieboldi* telpiskās nišas lielums ir negatīvi saistīts ar nitrātu koncentrāciju.