

Do abundance and percentage of dipteran larvae and Oligochaeta indicate low water quality in streams and lake littoral?

by

Henn Timm*, Marina Haldna

DOI: [10.2478/ohs-2019-0036](https://doi.org/10.2478/ohs-2019-0036)

Category: **Original research paper**

Received: **February 26, 2019**

Accepted: **April 09, 2019**

Centre for Limnology, Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, 61101 Rannu, Tartumaa, Estonia

Abstract

The presence of chironomids and/or oligochaetes is generally considered to be an indication of poor status of freshwater. Non-chironomid dipterans show unclear trends. The abundance and percentage of these groups are rarely used as potential indicators. We attempted to determine whether these metrics reveal freshwater quality in lowland streams and lake littoral (Northern Europe, Baltic ecoregion, Estonia). The water quality was assessed based either on the water itself or on macroinvertebrates, fish, macrophytes, phytobenthos (in streams only) and/or phytoplankton (in lakes only). As expected, the high abundance and high percentage of chironomids and ceratopogonids indicated low quality of water in lakes. The high percentage of chironomids indicated low water quality also in streams. The high percentage of oligochaetes indicated low water quality in lakes. However, their high abundance (but not the percentage) was unexpectedly a symptom of high water quality in streams and to a lesser extent in lakes. In these cases, oligochaetes were represented by rheophilic, rather than saprophilic species. The abundance of simuliids (but not the percentage) and the richness of dipteran families indicated high water quality in streams. We suggest that the obtained results will allow better use of the indicative potential of freshwater macroinvertebrates.

Key words: Diptera, Chironomidae, Ceratopogonidae, Oligochaeta, water quality, streams, lake littoral, biotic index

* Corresponding author: henn.timm@emu.ee

Introduction

The taxonomic composition of macroinvertebrates is a standard indicator of human impact on freshwater. For example, stoneflies are sensitive to organic pollution and mollusks are sensitive to acidification. Dipteran larvae and oligochaetes are generally considered tolerant or moderately tolerant of disturbances in streams, particularly organic pollution (Armitage et al. 1983; Rolauuffs et al. 2003). In the profundal zone of lakes, which is a naturally deficient biotope compared to shallow waters, macrozoobenthos often consists of only a few dipteran families (Chironomidae, Chaoboridae, and Ceratopogonidae) and oligochaete species (Saether 1979; Lang 2000). Similarly, in shallow waters with naturally harsh conditions (e.g. arctic or alpine), taxa other than chironomids may also be rare or absent (Medeiros & Quinlan 2011; Parker & Huryn 2011). Some species of Chironomidae and Simuliidae can easily withstand desiccation, thus being the primary colonizers of temporary or restored waters. They can therefore be used as indicators of hydrological variability and the impact of drought (Ruse 2002; Suemoto et al. 2005; Canedo-Arguelles et al. 2016). In streams, chironomids may also dominate after natural disasters such as wildfires (Mellon et al. 2008).

There are 4147 chironomid species worldwide – 5.5% of all freshwater insects (Balian et al. 2008; Ferrington 2008), including 788 species inhabiting northern European freshwater (Nilsson 1997). A total of 1119 species of freshwater oligochaetes (here referred to as a subclass of Clitellata) occur worldwide (Martin et al. 2008), including 242 species in Northern and Central Europe (Timm 2009). Both water-dwelling dipteran larvae and oligochaetes have slender bodies without true legs or any other distinctive features. Therefore, preparation of specimens before their identification at the species level as well as high magnification (> 100x) are usually necessary. To save resources, chironomids are often identified to the family level and oligochaetes to the subclass level only. However, the identification of chironomids and oligochaetes to the species level provides indispensable information on their role as indicator organisms, while higher taxonomic levels (usually family or subfamily) mask the actual sensitivity (Adriaenssens et al. 2004; Verdonschot 2006; Marziali et al. 2009; Serra et al. 2017). At the same time, the diversity of chironomids also significantly depends on stream discharge and current velocity rather than on the level of pollution. Diverse communities may inhabit moderately polluted streams, such as near natural areas (Lenat 1983; Rabeni & Wang 2001).

Abundance and percentage of chironomids and oligochaetes as potential indicators of freshwater quality

In order to provide a relevant assessment of freshwater quality based on macroinvertebrates, the Water Framework Directive (2000) requires the use of metrics that express abundance, in addition to the taxonomic composition, the number of disturbance-sensitive taxa and diversity. Qualitative data are still preferred to quantitative data in many shallow-water quality assessment systems, especially in terms of time efficiency. A high abundance of a taxon may not always indicate a high percentage, because several abundant species may co-occur. However, a high percentage undoubtedly indicates that there are few or no other species.

The total abundance of macroinvertebrates equally decreases or increases in the case of disturbance (Fore et al. 1996; Morais et al. 2004), or varies too much to serve as a reliable indicator (Sandin & Johnson 2000; Ofenböck et al. 2004). However, there are sufficient grounds to believe that the abundance of potentially tolerant taxa (e.g. some dipterans and oligochaetes) increases in a deteriorating environment, while the abundance of mostly intolerant taxa (e.g. Ephemeroptera) decreases. Although the percentage of sensitive taxa is often included in quality assessment systems (Davis et al. 2003; Dahl & Johnson 2004; Milner et al. 2006; Böhmer et al. 2014), quite a few authors have considered the corresponding contribution of dipterans or oligochaetes as reliable measures, despite their high abundance.

The percentage of chironomid larvae (Chir%) was determined to be sensitive to general degradation of streams in Germany and included in a local multimetric index for stream quality assessment (Böhmer et al. 2004). Chir% also increased in the case of disturbance in North American streams (Rapid Bioassessment Protocols 1999). However, unlike oligochaetes and leeches, Chir% and taxon richness of all dipterans decreased in the case of siltation of offshore areas of lakes (New Jersey, USA). As a result, these metrics were included in the corresponding North American Lake Macroinvertebrate Integrity Index as positive indicators (Blocksom et al. 2002). Klemm et al. (2002) observed a weak discriminatory potential of the EPT/Chironomidae ratio for reference and disturbed stream sites in the eastern USA. However, it varied too much across the reference sites to be effective in detecting disturbances. The percentage of chironomids, oligochaetes and leeches was also expected to increase under conditions of disturbance, but turned out to be insensitive.

The percentage of oligochaetes (Olig%) was considered a significant indicator of water pollution in streams (Goodnight & Whitley 1961). Wiederholm (1984) recorded an increase in the abundance of depth-adjusted oligochaetes and the oligochaete/chironomid ratio with an increasing trophic level in the profundal of large Swedish lakes. The ratio of EPT (Ephemeroptera, Plecoptera and Trichoptera – orders of intolerant insects) species richness to Olig% was considered a positive water quality indicator in a Dutch multimetric system (Nijboer & Schmidt-Kloiber 2006). In Lake Geneva, an increase in the relative abundance of oligotrophic oligochaete species in offshore areas was in good concordance with a decrease in dissolved phosphorus content in water (Lang 1998). The percentage of Oligochaeta and Psychodidae (Diptera) in Central Amazon streams increased with urbanization (Martins et al. 2017).

Representation of Diptera and Oligochaeta in European intercalibration indices and in the Estonian macroinvertebrate-based quality system

The Water Framework Directive requires harmonization of national ecological assessment systems and classifications through an intercalibration exercise to ensure uniform interpretation of the “good ecological quality” of surface waters across Europe. However, in the corresponding multimetric index for macroinvertebrate community-related intercalibration in lotic waters (STAR_ICMi in Buffagni et al. 2005), the indicative meaning of dipterans and oligochaetes is quite controversial. STAR_ICMi includes the following metrics:

- 1) The total number of families, which implies that the presence of all groups (Diptera families as well as Oligochaeta) is a positive indication;
- 2) The Shannon–Wiener diversity index, which recognizes a high diversity as a positive indication and cases where any of the groups is highly dominant – as a negative indication;
- 3) The Average Score Per Taxon (ASPT), which considers Chironomidae and Oligochaeta as highly tolerant and Simuliidae and Tipulidae as moderately tolerant;
- 4) The $\log_{10}(\text{sel_EPTD})$ index, which considers some dipteran families (Dolichopodidae, Stratiomyidae, Dixidae, Empididae, and Athericidae), even intolerant ones as some sensitive EPT families;
- 5) The 1-GOLD index (relative abundance of Gastropoda, Oligochaeta, and Diptera), which considers all Diptera and Oligochaeta as tolerant;
- 6) The number of EPT families, ignoring all other groups.

The corresponding multimetric index for lakes of the European Central-Baltic region (Böhmer et al. 2014) includes four metrics: 1) the number of Ephemeroptera, Plecoptera, Trichoptera, Coleoptera, Bivalvia and Odonata taxa; 2) the ASPT index; 3) % abundance classes of Ephemeroptera, Trichoptera and Odonata taxa; and 4) % abundance classes with preference for lithal microhabitats (% HL). In this study, the ASPT index considers the sensitivity of Diptera and Oligochaeta, the same way as in the case of lotic waters. % HL considers Psychodidae as a strong indicator, while *Atherix ibis*, Dixidae and Simuliidae as moderate indicators of a rocky bottom. The other indices do not include Diptera or Oligochaeta.

The monitoring program, which takes into account shallow freshwater macroinvertebrates occurring in the study area (Estonia, Baltic ecoregion of Europe), applies two multimetric indices, each with five metrics for lotic waters and lakes. Both indices include the total taxon richness (Diptera at the family level, Oligochaeta at the whole-group level), the EPT taxon richness (Lenat 1988), the ASPT index, and the Shannon diversity index. In addition, the Danish Stream Fauna Index (DSFI, Skriver et al. 2000) is used for lotic waters and the Swedish Acidity Index (Johnson 1999) is used for lakes. DSFI considers Diptera (*Chironomus*, Psychodidae, Chironomidae and Eristalinae) and Oligochaeta (Tubificidae) as indicators of organic pollution. According to the Acidity Index, Diptera and Oligochaeta have no indicative value, except that they contribute to biodiversity, which indicates lower acidity of water. In conclusion, the same abundant groups that are poorly or disproportionately represented in the European intercalibration indices are also inadequately included in the local freshwater quality assessment system.

Diversity of Diptera as a potential indicator of freshwater quality

Despite the high diversity of other shallow-water dipterans (except for chironomids, simuliids and ceratopogonids), their indicative value is quite poorly documented or is based on relatively old data. Doubts as to whether they could be considered as indicators may result from the ability of some groups to inhabit even septic conditions (Culicidae, Stratiomyidae,

Syrphidae), or to move to surface or to temporarily leave a waterbody (Tabanidae, Ceratopogonidae; Paine & Gaufin 1956). Nevertheless, DeShon (1995) suggested that the number of dipteran taxa (including chironomids) decreases in deteriorating conditions. Many of these taxa inhabit sites with a dense vegetation cover and moderate current velocity (Gallardo & Prenda 1994).

Objectives

We believe that the indicative value of Diptera and Oligochaeta in shallow waters requires specification, even if only larger groups are taken into account. We assumed the following:

- i) the high percentage and/or high abundance of potentially tolerant and often very abundant taxa (Chironomidae, Oligochaeta, Simuliidae and Ceratopogonidae) are negatively related to freshwater quality,
- ii) the total taxa richness of Diptera is positively related to freshwater quality.

Study area

Estonia is a small country (45 200 km²) with a flat landscape, located on the eastern coast of the Baltic Sea (Fig. 1). Together with Latvia and Lithuania, it forms the Baltic ecoregion within the meaning of the Water Framework Directive. The altitude is mostly below 200 m, water hardness and content of humic substances are often high at the same time. Estonia is located in the area of mixed forests of the temperate zone, bordering on taiga. Compared to other European areas, it is distinguished by a large proportion of raised bogs and forests (Raukas 1995). As a rule, local species assemblages are mostly composed of widespread postglacial colonists.

Materials and methods

Sampling and identification

Macroinvertebrates were collected in 126 different lotic water bodies (210 sites, 242 samples; hereinafter referred to as streams) and in the littoral of 67 lakes (67 sites, 103 samples) in 2012–2015. In total, 345 samples were analyzed (Table 1, Fig. 1). The offshore areas of the lakes were not included, as their natural conditions were considered incomparable to those in shallow

waters. A total of 93 sites were hydromorphologically affected (mainly by channelization of streams) and 12 sites were likely to be organically polluted. Most samples represented near-natural or insignificantly affected conditions.

Samples were collected in April–May or September–October. Some areas were visited repeatedly, but never sampled more than once in the same year. The distance from a stream source varied and ranged from 3 to 638 (median 29) km and the lake surface area ranged from 1 to 960 (median 84) ha. Seven natural types of streams and six types of lakes were studied (Table 1).

The sampling device was a standard hand net with a mesh size of 500 µm (Water quality 2012). Each sample consisted of five 0.25 m² replicates collected from a 10 m section of the most typical bottom and of a qualitative sample representing all adjacent (50 m) accessible bottom substrates. As a rule, the sample size comprised at least 300 individuals (Lorenz et al. 2004). Taxa found in the qualitative samples were assigned an abundance value of 1. The collected animals were fixed together with sieving residue (debris, sand and gravel) in 96% ethanol and transported to the laboratory for further analysis. The material was mostly identified to the species or genus level. Chironomids, oligochaetes and other groups requiring high magnification were not further identified.

Water quality

To assess biotic quality based on macroinvertebrates, high, good, moderate, poor or bad quality levels were assigned to each index in all waterbody types and subtypes in accordance with the Water Framework Directive (2000) and Status classes (2010). The ratios of the observed values to the expected (reference) values for multimetric macroinvertebrate quality (EQRMMQ) ranged as follows: > 0.9 (high for streams), > 0.85 (high for lakes), > 0.7–0.9 (good for streams), > 0.7–0.85 (good for lakes), > 0.4–0.7 (moderate), > 0.25–0.4 (poor) and ≤ 0.25 (bad). Among the streams, 128 sites were of high, 69 of good, 38 of moderate, five of poor and two of bad macroinvertebrate-based quality. Among the lakes, 36 sites were of high, 31 of good, 33 of moderate, and three of poor quality.

The following hydrophysical and hydrochemical factors were available with regard to the macroinvertebrate data: the distance from a stream source, lake surface area, water pH, water conductivity, water oxygen content, water oxygen saturation (Estonian National Environment Monitoring Program 2017). Coordinated assessments of hydrochemical

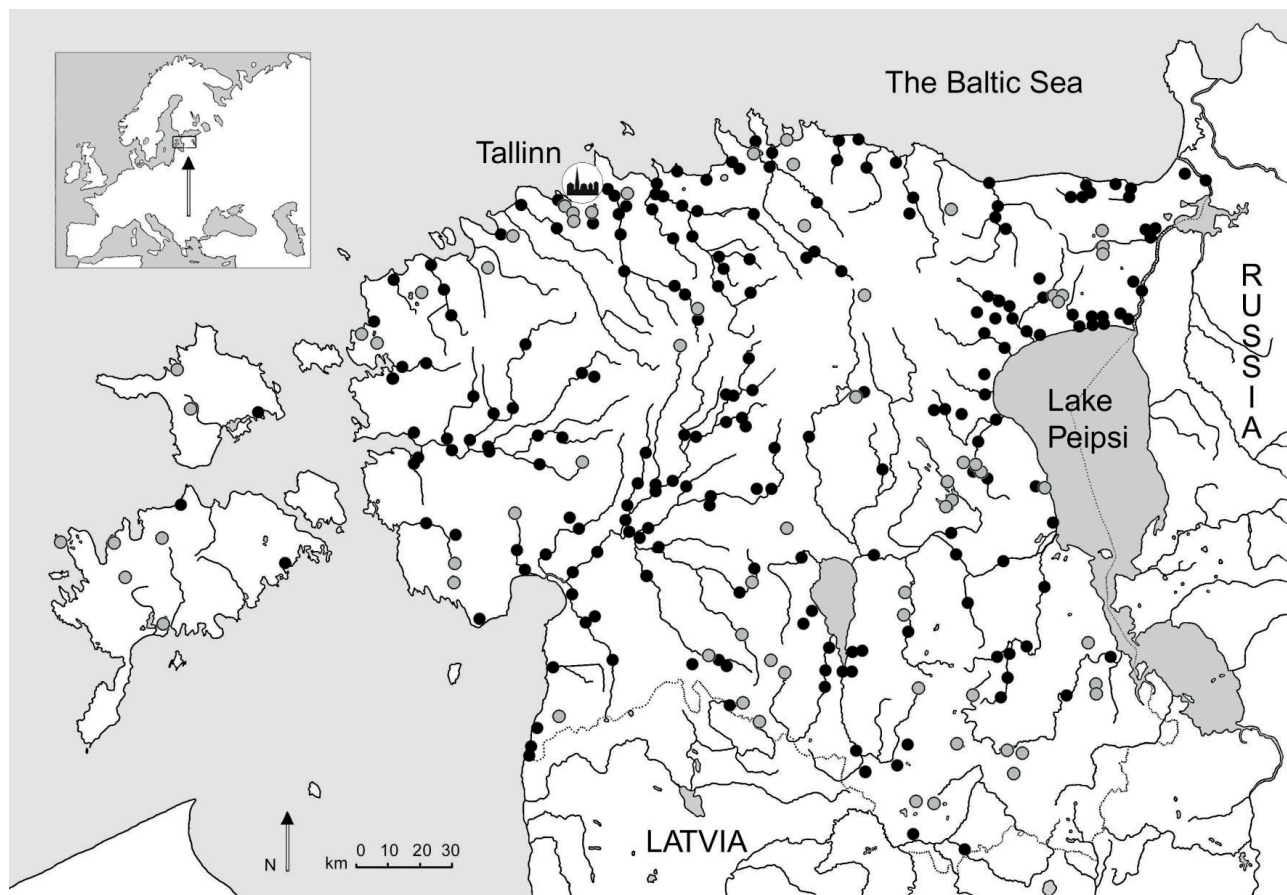


Figure 1

Study area. Black dots – stream sites, grey dots – lake sites

Table 1

The number of macroinvertebrate samples (n) in relation to hydrochemical and hydrophysical stream and lake types (Status classes 2010)

Type	Water properties	Catchment area (km ²)	Alkalinity (mg l ⁻¹ HCO ₃ ⁻)	Cond (μS cm ⁻¹)	Salinity (mg l ⁻¹ Cl ⁻)	Strat	n
Streams							
I A	Dark water (> 25)	10–100					44
I B	Light water (< 25)	10–100					70
II A	Dark water (> 25)	100–1000					31
II B	Light water (< 25)	100–1000					75
III A	Dark water (> 25)	1000–10 000					1
III B	Light water (< 25)	1000–10 000					19
IV		> 10 000					2
Lakes							
I	Calcareous		> 240	> 400	< 25	no	1
II	Medium water hardness		80–240	165–400	< 25	no	49
III	Medium water hardness		80–240	165–400	< 25	yes	13
IV	Soft water, dark (≥ 4)		< 80	< 165	< 25	no	9
V	Soft water, light (≤ 4)		< 80	< 165	< 25	no	19
VIII	Former lagoons (distance from the sea < 5 km)				> 25	no	12

Water color: streams – COD_{Mn} as mg l⁻¹ O (90% of values); lakes – absorption coefficient per m at 400 nm (in IV and V). Cond – conductivity, Strat – stratification

and hydrobiological quality included water (238 samples from streams and 103 samples from lakes), phytobenthos (242 samples from streams and 23 samples from lakes), phytoplankton (56 samples from lakes), macrophytes (223 samples from streams and 53 samples from lakes) and fish (206 samples from streams and 22 samples from lakes). The hydromorphological habitat types, based on the macroinvertebrate indicator taxa, were established according to the MESH score (Timm et al. 2011). Higher score values indicated a faster flow and/or harder bottom.

Water and phytoplankton data from the lakes were collected in offshore areas in spring. Data for lotic waters (except for macroinvertebrates) were collected in summer or in autumn of the same year.

We are aware that the occurrence of chironomids, oligochaetes and simuliids in samples could have some impact on the values of several quality metrics (total taxon richness, Average Score Per Taxon, Danish Stream Fauna Index, Shannon diversity index) that were used as factors in statistical analyses. However, all these taxa were either fairly common or completely absent, such as simuliids in lakes (Table 2). Moreover, as most of the samples represented conditions that were not significantly affected, most of them contained many species, thus reducing the potential impact of the above-mentioned groups. The number of other shallow-water dipterans could affect only taxon richness. Therefore, the impact of the presence or absence of Diptera and Oligochaeta on water quality was considered irrelevant in this context.

Statistical analyses

The analysis was conducted using SAS/STAT® software Version 9.2 of the SAS System for Windows (SAS Institute Inc. 2009). The effects of different factors on the following biotic metrics were studied: abundance of chironomids (Chir), percentage of chironomids (Chir%), abundance of simuliids (Sim), percentage of simuliids (Sim%), abundance of ceratopogonids (Cer), percentage of ceratopogonids (Cer%), abundance of oligochaetes (Olig), percentage of oligochaetes (Olig%), and richness of dipteran families (DiptR). All water quality data were transformed as follows: high quality – 5 points, good quality – 4 points, moderate quality – 3 points, poor quality – 2 points, bad quality – 1 point.

Mean values of macroinvertebrate metrics for different types of waterbodies were tested by the t-test or the Wilcoxon test, depending on the distribution of the variables. To establish possible relationships, plots of the macroinvertebrate metrics

vs factors were examined, using the smooth spline method (GPLOT procedure). The metrics were transformed as follows: square root for Chir and Olig (Poisson distribution with logarithm), arcsin for percentages, binomial for “almost zero” data (Sim, Cer). DiptR was originally normally distributed. The effects of factors were assessed by the GLM procedure with stepwise selection (direction = “both”), using Akaike's information criteria. Factors were included in the model if they had a significant effect on the biotic metrics.

Results

Chironomidae were the most frequent (accounting for almost 100%) and the most abundant (> 24% of all macroinvertebrates) taxon, followed by Oligochaeta (> 80% and > 3.6%, respectively). Simuliidae were present in more than 60% of the stream samples (> 11%), but they were missing in the lakes. The frequency of *Atherix*, *Dicranota* and *Eloeophila* was quite high in the streams, but their abundance was relatively low (Tables 2 and 3). In the streams, the most abundant groups were chironomids and simuliids,

Table 2

Frequency of different dipteran groups and oligochaetes in streams and lakes

	Streams		Lakes	
	n	%	n	%
Chironomidae	241	99.6	103	100
Oligochaeta	210	86.8	86	83.5
Ceratopogonidae	108	44.6	63	61.2
Simuliidae	161	66.5	0	0
Athericidae: <i>Atherix</i>	92	38.0	0	0
Chaoboridae: <i>Chaoborus</i>	3	1.2	14	13.6
Culicidae	8	3.3	3	2.9
Cylindrotomidae: <i>Phalacrocera replicata</i>	1	0.4	2	1.9
Dixidae	6	2.5	6	5.8
Dolichopodidae	4	1.7	1	1.0
Limoniidae: <i>Antocha</i>	22	9.1	0	0
Limoniidae: <i>Eloeophila</i>	97	40.1	1	1.0
Limoniidae: <i>Gnophomyia</i>	1	0.4	1	1.0
Muscidae: <i>Limnophora</i>	17	7.0	0	0
Pediciidae: <i>Dicranota</i>	105	43.4	1	1.0
Psychodidae: <i>Pericoma</i>	21	8.7	0	0
Ptychopteridae: <i>Ptychoptera</i>	9	3.7	1	1.0
Sciomyzidae	1	0.4	0	0
Stratiomyiidae	3	1.2	1	1.0
Syrphidae	0	0	1	1.0
Tabanidae: <i>Chrysops</i>	41	16.9	6	5.8
Tipulidae	29	12.0	2	1.9
Diptera indet.	106	43.8	9	8.7

Table 3

Mean abundance (individuals m⁻² ± SE) and contribution of the most abundant dipteran groups and oligochaetes in streams and lakes

	Streams		Lakes	
	mean ± SE	%	mean ± SE	%
Chironomidae	142 ± 35	24.2	93 ± 11	32.6
Oligochaeta	21 ± 3	3.6	23 ± 5	8.1
Ceratopogonidae	1.7 ± 0.5	< 0.1	5.3 ± 1.0	1.9
Simuliidae	68 ± 30	11.6	0	0
Atherix	4.1 ± 1.0	0.7	0	0
Eloeophila	1.3 ± 0.2	< 0.1	< 0.1	< 0.1
Dicranota	2.9 ± 0.4	< 0.1	< 0.1	< 0.1

and in the lakes – chironomids and oligochaetes. Chironomids were represented in all lake samples and in almost all stream samples. The dipteran groups with low frequency and abundance were not analyzed further, except for the richness of dipteran families (Tables 4 and 5).

The lakes showed significantly higher Chir%, higher Cer and Cer%, and lower DiptR than the streams (Table 4). There were only a few small differences between dark-water and light-water streams, and between hard-water (types I, II, III, VIII) and soft-water lakes (types IV and V). The distance from a stream source and water pH had a positive effect on the abundance and percentage of oligochaetes, and a negative effect on the abundance of simuliids and the richness of the dipteran groups. At the same time, an unexpected negative relationship was observed between Olig% and water conductivity. The oxygen content in the water had a small positive effect on Olig and DiptR, but

no significant relationships were observed between any of the biotic metrics and O₂%. However, O₂% was significantly higher in the lakes than in the streams.

Relationships with macroinvertebrate-based water quality

Significant relationships were observed between the examined metrics and almost all macroinvertebrate-based quality indices (except EQRDSFI). As expected, Chir% indicated low multimetric quality (EQRMMQ) both in the streams and in the lakes. Chir, Olig% and Cer% indicated low EQRMMQ in the lakes but were indifferent in the streams. Olig, Sim and DiptR indicated high EQRMMQ in the streams but almost no significant relationships in the lakes (Olig weak, Sim absent, DiptR indifferent).

Chir was significantly related to EQREPT (polynomial relationship, both in streams and in lakes) and significantly negatively related to EQRH'. Chir% indicated low EQRH' (both in streams and lakes) and low EQRT and EQREPT (only in lakes).

According to EQRT and EQREPT, Olig indicated high quality in the streams and low quality in the lakes. In addition, it indicated low EQRH' in the streams and low EQRASPT both in the streams and in the lakes. Olig% indicated low quality in the lakes according to EQREPT and EQRASPT and high quality in the streams according to EQRH'.

Cer and Cer% were surprisingly highly positively related to EQRT in the streams. Cer% was negatively related to EQRT and EQREPT in the lakes. Sim showed only a single positive relationship with EQRH' in the streams, while Sim% was indifferent in all cases.

Table 4

Significant differences between the abiotic characteristics (> and <, columns 2–4); positive (+) and negative (–) directions of significant relationships between biotic metrics and abiotic factors (columns 5–8)

Variable	S vs L	S: dark water vs light water	L: hard water vs soft water	S: DistS	All: pH	All: O ₂	All: Cond
1	2	3	4	5	6	7	8
Chir		<*					
Chir%	<***						
Olig		>*		+***	+**	+*	
Olig%				+***	+**		–**
Cer	<***						
Cer%	<***						
Sim	---		---	–**			
Sim%	---		---				
DiptR	>***		<*	–*		+**	

*** – p-value < 0.0001, ** – p-value < 0.01, * – p-value < 0.05. S – streams, L – lakes, All – streams and lakes. Chir – abundance of chironomids, Chir% – percentage of chironomids, Olig – abundance of oligochaetes, Olig% – percentage of oligochaetes, Cer – abundance of ceratopogonids, Cer% – percentage of ceratopogonids, Sim – abundance of simuliids, Sim% – percentage of simuliids, DiptR – richness of dipteran families. DistS – distance from a stream source, O₂ – water oxygen content, Cond – water conductivity

Table 5

Significant relationships with model parameter estimates between biotic metrics and water quality factors (where relevant)

	Comparison	Streams	Lakes
EQRMMQ	Chir		-0.5**
	Olig	0.8***	-0.7*
	Cer		-2.2***
	Sim	2.5***	
	Chir%	-0.2**	-0.5***
	Olig%		-0.3**
	Cer%		-0.1*
	DiptR	3.8***	
MESH	Olig	0.18*	0.6**
	Cer	-1.1*	
	Sim	2.3*	
	Chir%	-0.1*	
	Cer%	-0.04***	
	DiptR	3.8***	
QWat	Olig		-1.2**
	Olig%		-0.1**
QFish	Olig	0.2*	
	Olig%	0.03**	
QPhybe	DiptR	0.4*	
	Olig		-0.3**
EQRT	Olig%		-0.06**
	Olig	0.2*	-0.5*
	Cer	1.4***	
	Chir%		-0.4***
	Cer%	0.03**	-0.1**
EQREPT	DiptR	1.6***	
	Chir	6.1***	**
	Olig	0.5***	-0.4**
	Chir%		-0.1*
	Olig%		-0.1*
	Cer%		-0.05**
EQRH'	DiptR	1.7***	
	Chir	-0.9***	-0.7***
	Olig	1.3***	
	Sim	1.5**	
	Chir%	-0.3***	-0.1*
	Olig%	0.07**	
EQRASPT	DiptR	1.6**	
	Olig	-0.8*	-1.8**
	Olig%		-0.7**
	DiptR	4.5***	

*** - p -value < 0.001, ** - p -value < 0.01, * - p -value < 0.05. Metrics: Chir - abundance of chironomids, Chir% - percentage of chironomids, Olig - abundance of oligochaetes, Olig% - percentage of oligochaetes, Cer - abundance of ceratopogonids, Cer% - percentage of ceratopogonids, Sim - abundance of simuliids, percentage of simuliids Sim%, DiptR - richness of dipteran families. Quality factors: EQR - ecological quality ratio, MMQ - macroinvertebrate-based multimetric quality, T - total taxon richness, H' - Shannon diversity index, ASPT - Average Score Per Taxon, EPT - Ephemeroptera, Plecoptera and Trichoptera taxon richness; MESH - hydromorphological score, QWat - water quality, QFish - fish quality, QPhybe - phytobenthos quality, QPhypl - phytoplankton quality

DiptR showed positive relationships in the streams with EQRT, EQREPT, EQRH' and EQRASPT, but was indifferent in the lakes. DiptR was much higher in the streams (4.4 ± 0.5) compared to the lakes (2.1 ± 0.2), where it was largely formed only by chironomids and ceratopogonids.

Relationships with other indicators of freshwater quality

In the streams, several metrics (Olig, Sim, DiptR) indicated a positive relationship and several metrics (Chir%, Cer, Cer%) indicated a negative relationship with the hydromorphological score (MESH). In the lakes, the only significant relationship was found between Olig and MESH, indicating higher oligochaete abundance on the harder bottom.

Among the relationships with the non-macroinvertebrate-based freshwater quality indicators, oligochaetes (both Olig and Olig%) showed high fish quality in the streams, as well as low water quality and low phytoplankton quality in the lakes. The other metrics were mostly indifferent. No significant relationships were found between the biotic metrics and macrophyte quality (neither in streams nor in lakes).

Table 5 shows important relationships between biotic metrics and water quality indices. The most important results are shown in Figures 2–3.

Discussion

Chironomids

As the most species-rich group in freshwater, chironomids include many species with varying tolerance to pollution and trophic guilds, which may lead to dispersal of effects at the group level. For example, only 26 out of 184 chironomid species or species groups were significantly related to biological oxygen demand (BOD) of water in Estonian streams (Seire & Pall 2000). This could account for the relatively small number of significant relationships between chironomid abundance (Chir) and both abiotic and biotic factors. The negative relationship between Chir and the Shannon diversity index, both in the streams and in the lakes, probably indicated that chironomid larvae were often strikingly abundant. In the lakes, Chir had also a negative impact on multimetric quality. The positive relationships with the EPT taxa, both in the streams and in the lakes, were polynomial, indicating the highest chironomid abundance at moderate values of EPT.

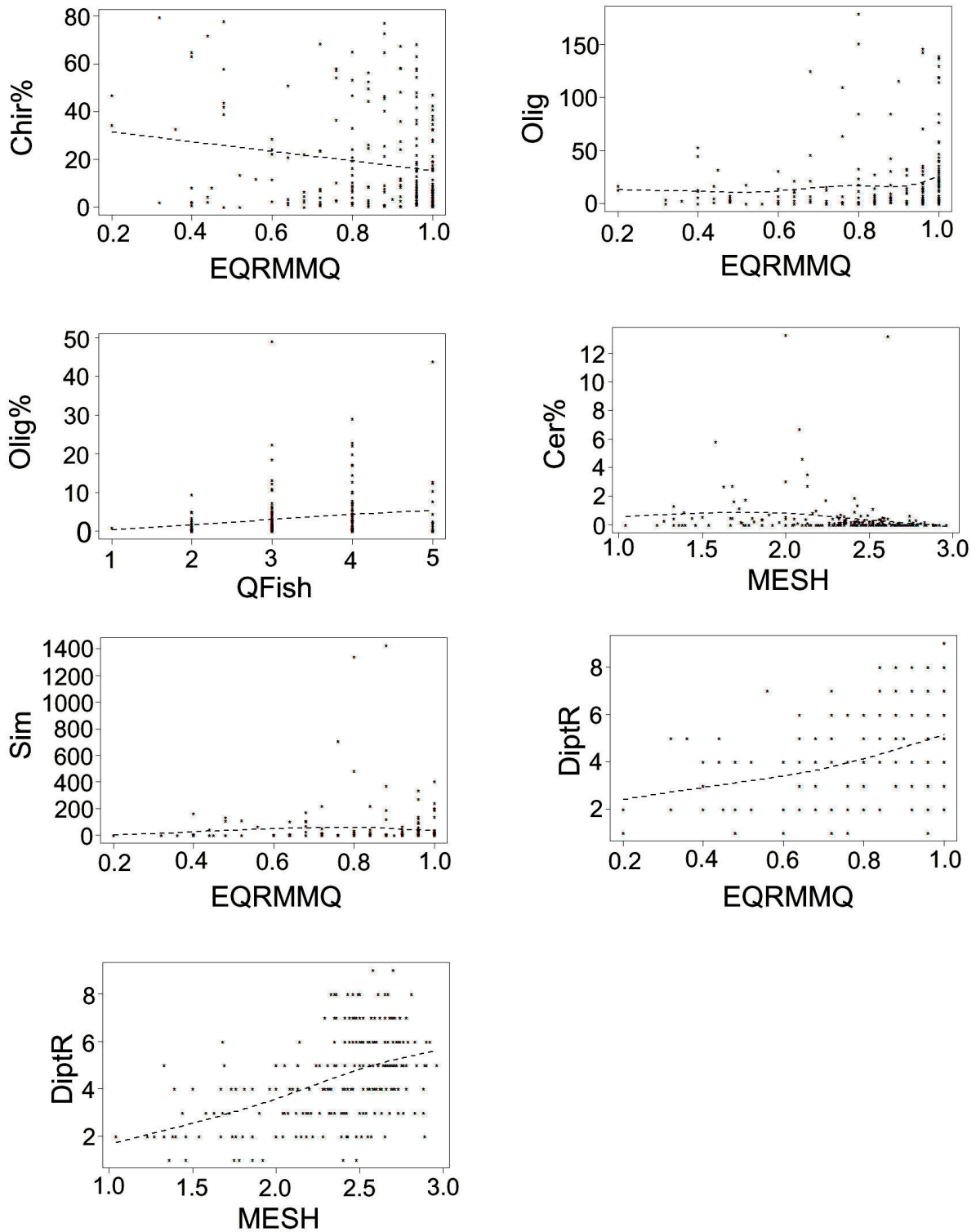


Figure 2

Plots with the most significant relationships between the studied factors and metrics in streams. Chir% – percentage of chironomids, Olig – abundance of oligochaetes, Olig% – percentage of oligochaetes, Cer% – percentage of ceratopogonids, Sim – abundance of simuliids, DiptR – richness of dipteran families. EQRMMQ – ecological quality ratio of macroinvertebrate-based multimetric quality, QFish – fish quality, MESH – hydromorphological score

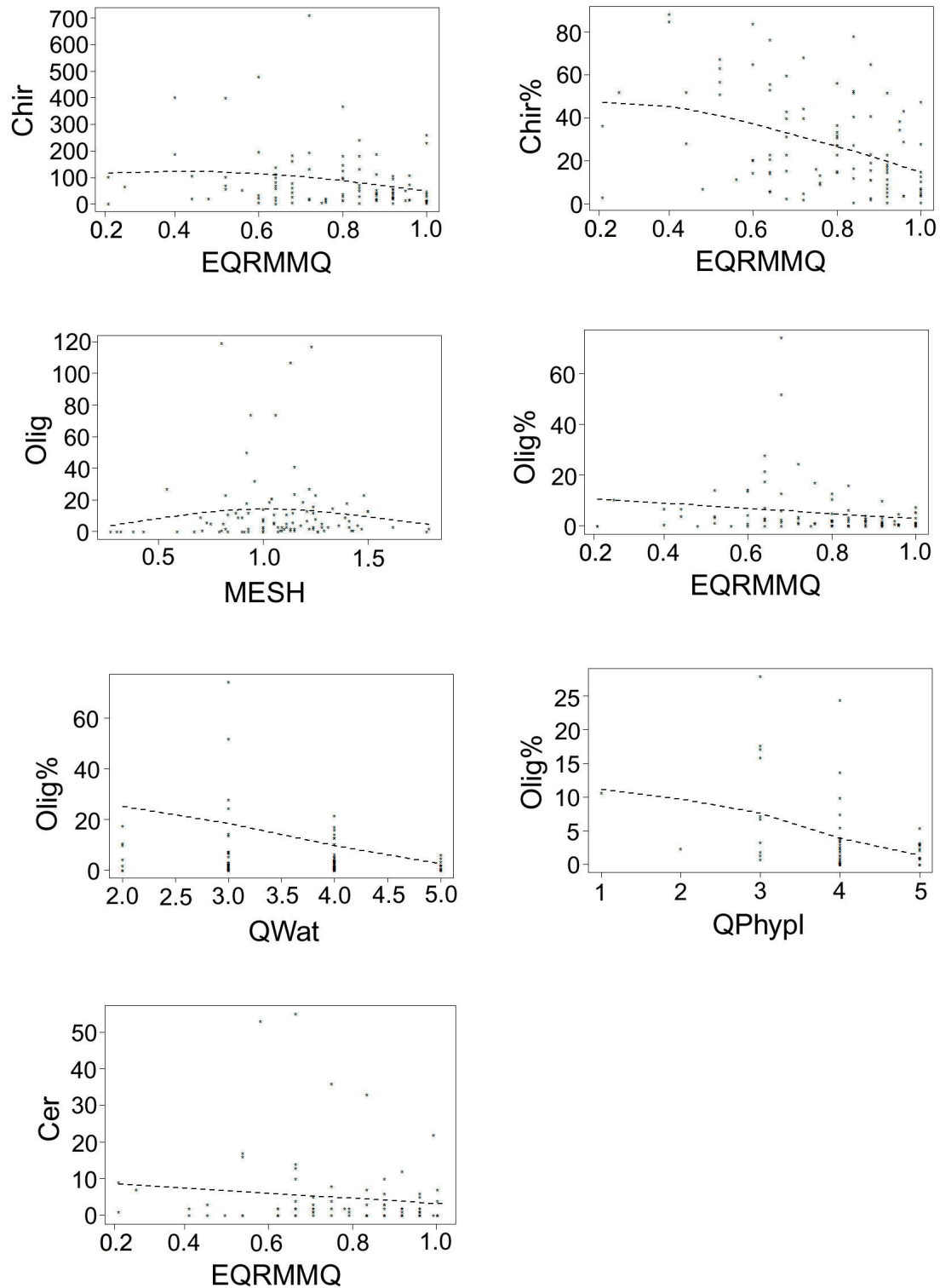


Figure 3

Plots with the most significant relationships between the studied factors and metrics in lakes. Chir – abundance of chironomids, Chir% – percentage of chironomids, Olig – abundance of oligochaetes, Olig% – percentage of oligochaetes, Cer – abundance of ceratopogonids. EQRMMQ – ecological quality ratio of macroinvertebrate-based multimetric quality, QWat – water quality, QPhypl – phytoplankton quality, MESH – hydromorphological score

The percentage of chironomid larvae (Chir%) had more significant relationships with environmental factors compared to Chir. Compared to Chir, high Chir% is more likely caused by the presence of few or single tolerant species. The probability of encountering high Chir% was much higher in the lakes than in the streams.

Both in the streams and in the lakes, Chir% served as a significant macroinvertebrate-based indicator of low multimetric quality. This particularly reduced the Shannon diversity index in the streams and total taxon richness in the lakes. Therefore, if the current multimetric indication system in Estonia should be supplemented with new elements, Chir% would be a new universal metric characterizing the disturbance conditions.

The total abundance of both oligochaetes and chironomids was not related to hydraulic conditions in a Czech rocky-bottom stream (Szyrovátka et al. 2009).

Oligochaetes

As far as the abiotic factors are concerned, the abundance of oligochaetes (Olig) responded positively to the stream size and water pH. This most likely indicates that the majority of stream-dwelling oligochaetes are sediment-feeders, as the amount of fine sediments increases in the downstream sections of rivers. The stream size will also contribute to an increase in water pH, which is less affected by acid bogs in downstream areas than those located near stream sources.

The number of significant relationships between Olig and Olig% and the biotic factors was the highest among the compared metrics. The most surprising result was the significant positive relationship between Olig (but not Olig%) and EQRMMQ (model parameter estimate 0.3) in the streams. This was fundamentally different in the case of chironomids that were either indifferent (abundance) or strongly negatively related (percentage) to EQRMMQ. We believe that this relationship may have resulted from the natural status of the streams in the study area, as most sampling sites were not affected by pollution or hydromorphological degradation. Among the common oligochaete species in Estonian streams, *Psammoryctides barbatus*, *Rhyacodrilus coccineus* and *Spirosperma ferox* often inhabit areas with riffles, while *Limnodrilus hoffmeisteri* and *Tubifex tubifex* prefer a soft bottom. Species dwelling on a hard bottom are also more common at lower BOD values (Timm et al. 2001). In a SE Brazil stream, Rosa et al. (2014) also found no correlation between the response of Chironomidae and Oligochaeta assemblages and environmental

variables.

On the other hand, a strong negative relationship between both Olig and Olig% and EQRMMQ (model parameter estimates -0.7 and -0.3) was observed in the lakes. In this case, the pattern displayed by oligochaetes was similar to that displayed by chironomids.

The positive relationship between Olig and EQRMMQ in the streams was first based on EQREPT and EQRH'. The negative relationships between Olig and Olig% and EQRMMQ in the lakes can be primarily attributed to EQREPT and EQRASPT. The latter result was probably affected by the very low tolerance value of oligochaetes on the ASPT scale.

Oligochaetes were the only studied group that revealed significant relationships also with the water quality assessments, when factors other than macroinvertebrates were considered. Particularly noteworthy is their negative response to high water quality and high phytoplankton quality in the lakes. These relationships occurred despite the fact that oligochaetes were sampled in the littoral, while water and plankton were collected in the offshore area. In the streams, both of these oligochaete metrics were positively related to fish quality. This may reflect a corresponding positive relationship between Olig and EQRMMQ.

In conclusion, oligochaetes showed a large number of significant relationships with the studied factors, but at the same time showed parallel opposite responses to water quality in the streams and lakes. High abundance of oligochaetes as an expected indicator of low quality in lotic waters and in the lake littoral was not confirmed. At the same time, the results were probably affected by the small proportion of low-quality samples in our study. The populations consisted presumably of natural inhabitants of a sand-gravel bottom and not of common indicators of pollution. The results do not in any way exclude the possibility that oligochaetes could indicate low water quality, particularly when they form the only or almost the only group in a sample. However, we stress the need to restore the reputation of oligochaetes as relevant members of species-rich communities.

Ceratopogonids

In the lakes, the abundance of ceratopogonids (Cer) had a strong negative relationship with EQRMMQ. Their percentage (Cer%) was strongly negatively related to EQRT and EQREPT but relatively weakly related to EQRMMQ. Both Cer and Cer% were significantly higher in the lakes than in the streams. Ceratopogonidae are a family characterized by high

tolerance to extreme conditions in lentic waters (Wazbinski & Quinlan 2013; Romero et al. 2017). The increase in Cer in offshore areas also indicated long-term eutrophication in Estonian small lakes (Timm et al. 2006).

In the streams, Cer% was also negatively related to the hydromorphological score, thus indicating a slower flow and/or soft bottom. The positive relationship between Cer and Cer% and the total taxon richness in the streams can be explained by high taxon richness in large slow-flowing streams.

Simuliids

Contrary to the hypothesis, both high abundance (Sim) and high percentage of simuliids (Sim%) indicated high multimetric quality of macroinvertebrates in the streams, similarly to Olig. The highest abundance occurred in small streams. Although their very large number should reduce species diversity, Sim showed a significant positive relationship with the Shannon diversity index in our study. In German streams, significantly larger numbers of simuliid taxa were recorded from unstressed sites (high or good morphological quality) compared to stressed sites (Feld et al. 2002). Lock et al. (2014) predicted a gradual increase in the simuliid abundance in Flandrian streams in parallel with increasing water quality, which is also confirmed by our result.

Diversity of dipteran families

As expected, DiptR had a significantly positive relationship with macroinvertebrate-based freshwater quality and with most of its components in the streams. The number of groups was higher in the case of a faster flow and harder bottom. DiptR was significantly higher in the streams than in the lakes and preferred high oxygen content. Consequently, it could be a simple and good indicator of stream quality but remains indifferent in terms of lake quality.

Concluding remarks

We confirmed that the studied simple metrics of dipteran larvae and oligochaetes reflected significant relationships with different abiotic factors as well as with freshwater quality. However, some of the expected relationships were not found and some others showed even opposite directions. We believe that the local quality assessment system, based on the Water Framework Directive requirements, can be effectively improved using the obtained results. We also hope that the relationships established in our

study will encourage: 1) environmental managers to initiate discussions, 2) specialists from neighboring areas to check the suggested measures.

Acknowledgements

The data were collected within the framework of national hydrobiological monitoring programs for streams and small lakes (Chair of Hydrobiology and Fisheries, Estonian University of Life Sciences) and within the framework of hydrochemical monitoring of streams (Estonian Environmental Research Centre). The work was supported by IUT 21-2 of the Estonian Ministry of Education and Research and by the Estonian national program "Humanitarian and natural science collections". We thank Dr. Tarmo Timm (Chair of Hydrobiology and Fisheries) and two anonymous reviewers for helpful critical remarks. Mrs. Ester Jaigma (Estonian University of Life Sciences) kindly revised the English text of the manuscript.

References

- Adriaenssens, V., Simons, F., Nguyen, L.T.H., Goddeeris, B., Goethals, P.L.M. et al. (2004). Potential of bio-indication of chironomid communities for assessment of running water quality in Flanders (Belgium). *Belgian Journal of Zoology* 134: 31–40.
- Armitage, P.D., Moss, D., Wright, J.F. & Furse, M.T. (1983). The performance of a new biological water quality score system based on a wide range of unpolluted running-water sites. *Water Research* 17: 333–347.
- Balian, E.V., Segers, H., Lévêque, C. & Martens, K. (2008). The freshwater animal diversity assessment: an overview of the results. *Hydrobiologia* 595: 627–637.
- Blocksom, K.A., Kurtenbach, J.P., Klemm, D.J., Fulk, F.A. & Cormier, S.M. (2002). Development and evaluation of the Lake Macroinvertebrate Integrity Index (LMII) for New Jersey lakes and reservoirs. *Environmental Monitoring and Assessment* 77: 311–333.
- Böhmer, J., Arbačiauskas, K., Benstead, R., Gabriels, W., Porst, G. et al. (2014). *Central Baltic Lake Benthic invertebrate ecological assessment methods. Water Framework Directive Intercalibration Technical Report, Report EUR 26504 EN*. Ed. by S. Poikane. European Commission Joint Research Centre, Institute for Environment and Sustainability.
- Böhmer, J., Rawer-Jost, C., Zenker, A., Meier, C., Feld, C.K. et al. (2004). Assessing streams in Germany with benthic invertebrates: Development of a multimetric invertebrate based assessment system. *Limnologia* 34: 416–432.
- Buffagni, A., Erba, S., Birk, S., Cazzola, M., Feld, C. et al. (2005). *Towards European inter-calibration for the Water Framework*

- Directive: Procedures and examples for different river types from the E.C. project STAR.* Rome, March 1005, Quaderni 123.
- Canedo-Arguelles, M., Bogan, M.T., Lytle, D.A. & Prat, N. (2016). Are Chironomidae (Diptera) good indicators of water scarcity? Dryland streams as a case study. *Ecological Indicators* 71: 155–162.
- Dahl, J. & Johnson, R.K. (2004). A multimetric macroinvertebrate index for detecting organic pollution of streams in southern Sweden. *Archiv für Hydrobiologie* 160: 487–513.
- Davis, S., Golladay, S.W., Vellidis, G. & Pringle, C.M. (2003). Macroinvertebrate biomonitoring in intermittent coastal plain streams impacted by animal agriculture. *Journal of Environmental Quality* 32: 1036–1043.
- DeShon, J.E. 1995. Development and application of the invertebrate community index (ICI). In W.S. Davis & T.P. Simon (Eds.), *Biological assessment and criteria: Tools for water resource planning and decision making* (pp. 217–243). Boca Raton, Florida: Lewis Publishers.
- Feld, C.K., Kiel, E. & Lautenschläger, M. (2002). The indication of morphological degradation of streams and rivers using Simuliidae. *Limnologia* 32: 273–288.
- Ferrington, L.C. (2008). Global diversity of non-biting midges (Chironomidae; Insecta-Diptera) in freshwater. *Hydrobiologia* 595: 447–455.
- Fore, L.S., Karr, J.R. & Wiseman, R.W. (1996). Assessing invertebrate responses to human activities: Evaluating alternative approaches. *Journal of the North American Benthological Society* 15: 212–231.
- Gallardo, A. & Prenda, J. (1994). Influence of some environmental factors on the freshwater macroinvertebrates distribution in 2 adjacent river basins under Mediterranean climate. 1. Dipteran larvae (excepting Chironomids and Simuliids) as ecological indicators. *Archiv Für Hydrobiologie* 131: 435–447.
- Goodnight, C.J. & Whitley, L. S. (1961). Oligochaetes as indicators of pollution. Proceedings of 15th Industrial Water Conference. Purdue University. *Eng. Ext. Ser.* 106: 139–142.
- Estonian National Environment Monitoring Program. Retrieved February 22, 2019, from <http://seire.keskkonnainfo.ee/> (In Estonian).
- Johnson, R.K. (1999). Benthic macroinvertebrates. In T. Wiederholm (Ed.), *Bedömningsgrunder för miljö kvalitet. Sjöar och vattendrag. Bakgrundsrapport 2. Biologiska parametrar* (pp. 85–166). Naturvårdsverket Förlag.
- Klemm, D.J., Blocksom, K.A., Thoeny, W.T., Fulk, F.A., Herlihy, A.T. et al. (2002). Methods development and use of macroinvertebrates as indicators of ecological conditions for streams in the Mid-Atlantic Highlands Region. *Environmental Monitoring and Assessment* 78: 169–212.
- Lang, C. (1998). Using oligochaetes to monitor the decrease of eutrophication: the 1982–1996 trend in Lake Geneva. *Archiv für Hydrobiologie* 141: 447–458.
- Lang, C. (2000). Response of oligochaete (Tubificidae and Lumbriculidae) and Diptera (Chironomidae) communities to the decrease of phosphorus concentrations in Lake Geneva (Little Lake). *Annales de Limnologie – International Journal of Limnology* 36: 13–20.
- Lenat, D.R. (1983). Chironomid taxa richness: natural variation and use in pollution assessment. *Freshwater Invertebrate Biology* 2: 192–198.
- Lenat, D.R. (1988). Water quality assessment of streams using a qualitative collection method for benthic macroinvertebrates. *Journal of North American Benthological Society* 7: 222–233.
- Lock, K., Adriaens, T. & Goethals, P. (2014). Effect of water quality on blackflies (Diptera: Simuliidae) in Flanders (Belgium). *Limnologia* 44: 58–65.
- Lorenz, A., Kirchner, L. & Hering, D. (2004). 'Electronic subsampling' of macrobenthic samples: how many individuals are needed for a valid assessment result? *Hydrobiologia* 516: 299–312.
- Martin, P., Martinez-Ansemil, E., Pinder, A., Timm, T. & Wetzel, M.J. (2008). Global diversity of oligochaetous clitellates ("Oligochaeta"; Clitellata) in freshwater. *Hydrobiologia* 595: 117–127.
- Martins, R.T., Couceiro, S.R.M., Melo, A.S., Moreira, M.P. & Hamada, N. (2017). Effects of urbanization on stream benthic invertebrate communities in Central Amazon. *Ecological Indicators* 73: 480–491.
- Marziali, L., Armanini, D.G., Cazzola, M., Erba, S., Toppi, E. et al. (2009). Responses of chironomid larvae (Insecta, Diptera) to ecological quality in Mediterranean river mesohabitats (South Italy). *River Research and Applications* 26: 1036–1051.
- Medeiros, A.S. & Quinlan, R. (2011). The distribution of the Chironomidae (Insecta: Diptera) along multiple environmental gradients in lakes and ponds of the eastern Canadian Arctic. *Canadian Journal of Fisheries and Aquatic Sciences* 68: 1511–1527.
- Mellon, C.D., Wipfli, M.S. & Li, J.L. (2008). Effects of forest fire on headwater stream macroinvertebrate communities in eastern Washington, U.S.A. *Freshwater Biology* 53: 2331–2343.
- Parker, S.M. & Huryn, A.D. (2011). Effects of natural disturbance on stream communities: a habitat template analysis on arctic headwater streams. *Freshwater Biology* 56: 1342–1357.
- Milner, A.M., Conn, S.C. & Brown, L.E. (2006). Persistence and stability of macroinvertebrate communities in streams of Denali National Park, Alaska: implications for biological monitoring. *Freshwater Biology* 51: 373–387.
- Morais, M., Pinto, P., Guilherme, P., Rosado, J. & Antunes, I. (2004). Assessment of temporary streams: the robustness of metric and multimetric indices under different hydrological conditions. *Hydrobiologia* 516: 229–249.
- Nijboer, R.C. & Schmidt-Kloiber, A. (2006). The effect of

- excluding taxa with low abundances of taxa with small distribution ranges on ecological assessment. In: R.C. Nijboer (Ed.), *The myth of communities: determining ecological quality of surface waters using macroinvertebrate community patterns*. Alterra Scientific Contributions 117: 57–84.
- Nilsson, A.N. (1997). *Aquatic insects of North Europe: A taxonomic handbook. Vol. 2. Diptera, Odonata*. Apollo (Denmark).
- Ofenböck, T., Moog, O., Gerritsen, J. & Barbour, M. (2004). A stressor specific multimetric approach for monitoring running waters in Austria using benthic macroinvertebrates. *Hydrobiologia* 516: 251–268.
- Paine, G.H. & Gaufin, A.R. (1956). Aquatic Diptera as indicators of pollution in a midwestern stream. *Ohio Journal of Science* 56: 291–304.
- Rabeni, C.F. & Wang, N. (2001). Bioassessment of streams using macroinvertebrates: Are the chironomidae necessary? *Environmental Monitoring and Assessment* 71: 177–185.
- Rapid Bioassessment Protocols For Use in Streams and Rivers: Periphyton, Benthic, Macroinvertebrates, and Fish, 2nd Edition. EPA 841-B-99-002. Retrieved February 22, 2019, from <http://www.water-research.net/index.php/macroinvertebrates>.
- Raukas, A. (1995). *Estonian Nature*. Tallinn, Valgus/Eesti Entsüklopeediakirjastus (In Estonian).
- Rolauffs, P., Hering, D., Sommerhäuser, M., Rödiger, S. & Jähnig, S. (2003). Entwicklung eines leitbildorientierten Saprobienindex für die biologische Fließgewässerbewertung. *Umweltbundesamt Texte* 11/03: 1–137.
- Romero, K.C., Del Rio, J.P., Villarreal, K.C., Anillo, J.C.C., Zarate, Z.P. et al. (2017). Lentic water quality characterization using macroinvertebrates as bioindicators: An adapted BMWP index. *Ecological Indicators* 72: 53–66.
- Rosa, B., Jabour, F.V., Rodrigues, L.F.T., de Oliveira, G.S. & da Gama Alves, R. (2014). Chironomidae and Oligochaeta for water quality evaluation in an urban river in southeastern Brazil. *Environmental Monitoring and Assessment* 186: 7771–7779.
- Ruse, L. (2002). Colonisation of gravel lakes by Chironomidae. *Archiv für Hydrobiologie* 153: 391–407.
- Saether, O.A. (1979). Chironomid communities as water quality indicators. *Holarctic Ecology* 2: 65–74.
- Sandin, L. & Johnson, R.K. (2000). The statistical power of selected indicator metrics using macroinvertebrates for assessing acidification and eutrophication of running waters. *Hydrobiologia* 422: 233–243.
- SAS Institute Inc. (2009). *SAS Online Doc, version 9.2 SAS Institute Inc., Cary, NC, USA*.
- Seire, A. & Pall, P. (2000). Chironomid larvae (Diptera, Chironomidae) as indicators of water quality in Estonian streams. *Proceedings of Estonian Academy of Sciences. Biology and Ecology* 49: 307–316.
- Serra, S.R.Q., Graca, M.A.S., Doledec, S. & Feio, M.J. (2017). Chironomidae traits and life history strategies as indicators of anthropogenic disturbance. *Environmental Monitoring and Assessment* 189: 326.
- Skriver, J., Friberg, N. & Kirkegaard, J. (2000). Biological assessment of watercourse quality in Denmark: Introduction of the Danish Stream Fauna Index (DSFI) as the official biomonitoring method. *Verhandlungen des Internationalen Verein Limnologie* 27: 1822–1830.
- Rapid Bioassessment Protocols For Use in Streams and Rivers: Periphyton, Benthic, Macroinvertebrates, and Fish, 2nd Edition. EPA 841-B-99-002. Retrieved February 22, 2019, from <http://www.water-research.net/index.php/macroinvertebrates>.
- Status classes and class boundaries for surface water bodies and the procedure of classification (2010). Retrieved February 22, 2019, from <https://www.riigiteataja.ee/akt/125112010015> (In Estonian).
- Suemoto, T., Kawai, K. & Imabayashi, H. (2005). Dried-up zone as a temporal stock of chironomid larvae: survival periods and density in a reservoir bank. *Hydrobiologia* 545: 145–152.
- Syrovátka, V., Schenková, J. & Brabec, K. (2009). The distribution of chironomid larvae and oligochaetes within a stony-bottomed river stretch: the role of substrate and hydraulic characteristics. *Fundamental and Applied Limnology* 174/1: 43–62.
- Timm, H., Käiro, K., Möls, T. & Virro, T. (2011). An index to assess hydromorphological quality of Estonian surface waters based on macroinvertebrate taxonomic composition. *Limnologica* 41: 398–410.
- Timm, H., Möls, T. & Timm, T. (2006). Effects of long-term non-point eutrophication on the abundance and biomass of macrozoobenthos in small lakes of Estonia. *Proceedings of Estonian Academy of Sciences. Biology and Ecology* 55: 187–198.
- Timm, T. (2009). A guide to the freshwater Oligochaeta and Polychaeta of Northern and Central Europe. *Lauterbornia* (International Journal of Faunistics and Floristics of European Inland Waters) 66: 235 pp.
- Timm, T., Seire, A. & Pall, P. (2001). Half a century of oligochaete research in Estonian running waters. *Hydrobiologia* 463: 223–234.
- Verdonschot, P.F.M. (2006). Beyond masses and blooms: the indicative value of oligochaetes. *Hydrobiologia* 564: 127–142.
- Water Framework Directive (2000). The European Parliament and the Council of the European Union. Directive 2000/60/EC.
- Water quality – Guidelines for the selection of sampling methods and devices for benthic macroinvertebrates in fresh waters (ISO 10870:2012).
- Wazbinski, K.E. & Quinlan, R. (2013). Midge (Chironomidae, Chaoboridae, Ceratopogonidae) assemblages and

their relationship with biological and physicochemical variables in shallow, polymictic lakes. *Freshwater Biology* 58: 2464–2480.

Wiederholm T. (1984). Responses of aquatic insects to environmental pollution. In: V.H. Resh & D.M. Rosenberg (Eds.), *The ecology of aquatic insects* (508–557). Chapman & Hall.