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Lokalna i regionalna różnorodność gatunkowa Chironomidae (Diptera) w rzekach centralnej Polski

Local and regional species diversity of
Chironomidae (Diptera) in rivers of central Poland

Praca doktorska

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1. LISTA PUBLIKACJI WCHODZĄCYCH W SKŁAD ROZPRAWY DOKTORSKIEJ

Niniejsza rozprawa doktorska składa się z trzech artykułów o zróżnicowaniu zgrupowań Chironomidae w wybranych odcinkach rzek o odmiennej rzędowości oraz o czynnikach determinujących ich bogactwo gatunkowe. Dwa spośród trzech artykułów opublikowano w czasopismach z listy JCR (Journal Citation Reports): *Community Ecology* i *Environmental Entomology*. Trzeci artykuł został odesłany do redakcji *The European Zoological Journal* po recenzjach i aktualnie jest procedowany. Przy każdym z artykułów podano wartość współczynnika Impact Factor (IF) aktualną dla roku publikacji (albo najnowszą dostępną) oraz liczbę punktów Ministerstwa Nauki i Szkolnictwa Wyższego według najnowszej listy (z dn. 9 lutego 2021 r.).

W skład dysertacji wchodzą następujące artykuły:

1. Leszczyńska J., Głowacki Ł., Grzybkowska M., Przybylski M. 2021. Chironomid riverine assemblages at the regional temperate scale – compositional distance and species diversity. *The European Zoological Journal* 00(0): 000-000 (*po recenzji*).

punkty MNiSW = 140, IF_{2019} = 1,656

Mój udział w pracy oceniam na 40%. Polegał on na wykonaniu części prac terenowych i laboratoryjnych, uczestnictwie w zaproponowaniu koncepcji artykułu, wstępnym opracowaniu danych oraz przygotowaniu treści manuskryptu (autor korespondencyjny).

2. Leszczyńska J., Głowacki Ł., Grzybkowska M. 2017. Factors shaping species richness and biodiversity of riverine macroinvertebrate assemblages at the local and regional scale. *Community Ecology* 18(3): 227-236.

punkty MNiSW = 40, IF_{2017} = 0,981

Mój udział w pracy oceniam na 60%. Polegał on na zaproponowaniu koncepcji artykułu, przeglądzie literatury, wykonaniu szaty graficznej oraz przygotowaniu treści manuskryptu (autor korespondencyjny).

3. Leszczyńska J., Grzybkowska M., Głowacki Ł., Dukowska M. 2019. Environmental Variables Influencing Chironomid Assemblages (Diptera: Chironomidae) in Lowland Rivers of Central Poland. *Environmental Entomology* 48(4): 988-997.

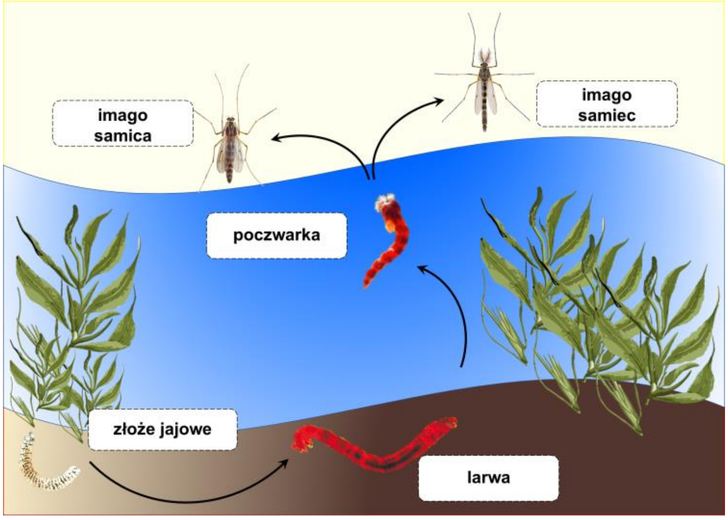
punkty MNiSW = 100, IF_{2019} = 1,584

Mój udział w pracy oceniam na 50%. Polegał on na wykonaniu części prac terenowych i laboratoryjnych, uczestnictwie w zaproponowaniu koncepcji artykułu, opracowaniu danych (środowisko R, modelowanie bayesowskie), wykonaniu szaty graficznej oraz przygotowaniu treści manuskryptu (autor korespondencyjny).

Sumaryczna wartość współczynnika Impact Factor publikacji wchodzących w skład cyklu – 4.221, a suma punktów MNiSW – 280 (bez publikacji *TEZJ*, IF = 2,565, 140 pkt).

2. WSTĘP

Ochotki (Chironomidae) są rodziną niewielkich długoczułkich muchówek (Diptera, Nematocera), których cykl życiowy, w zależności od warunków środowiskowych, może trwać od kilku dni w gorących strefach klimatycznych (Nolte 1995) do nawet kilku lat w ekstremalnych górskich i arktycznych ekosystemach (Butler 1982). Składa się on z czterech stadiów (jajo, larwa, poczwarka, imago; Rys. 1).



Rys. 1. Cykl rozwojowy Chironomidae.

Samica po zapłodnieniu składa do wody pojedyncze jaja lub złoża jajowe w galaretowatej osłonie, które po dryfowaniu w toni wodnej osiadają na dnie, makrofitach lub innych zanurzonych elementach podłoża. Z jaj wykluwają się larwy (Armitage i in. 1995). Czwarte (ostatnie) stadium larwalne trwa najdłużej w cyklu życiowym. Larwy charakteryzują się niezwykłą różnorodnością preferencji siedliskowych i pokarmowych (Franquet 1999), mając swych przedstawicieli w każdej gildii troficznej, z wyjątkiem rozdrabniaczy. Dla przykładu larwy plemienia Tanytarsini to głównie filtratory, wiele gatunków z plemienia Chironomini również zbiera cząstki materii organicznej, ale przy dnie. Przedstawiciele Orthocladiinae związani często z roślinami zanurzonymi reprezentują grupę funkcjonalną zdrapywaczy, żywiąc się pokrywającym liście i łodygi biofilmem. Z kolei larwy Tanypodinae to najczęściej drapieżniki lub gatunki wszystkożerne (Dukowska i in. 1999, Grzybowska i in. 2009). W zależności od ilości i jakości zasobów pokarmowych dostępnych w środowisku, osobniki niektórych gatunków jak np. *Chironomus riparius* mogą modyfikować sposób pobierania pokarmu: filtrator – zbieracz (Ali 1990, Berg 1995). Kolejne stadium w cyklu rozwojowym Chironomidae to poczwarka, która przebudowuje formę wodną w lądową. Dojrzała, najczęściej kilkudniowa poczwarka migruje ku powierzchni wody, gdzie przepoczwarza się (przeobrażenie zupełne), a następnie wylatuje. Masowe wyloty samców Chironomidae, przypominające smugi dymu nad powierzchnią wody, zwane są rójkami. Po rójce samce odnajdują samice wśród okolicznej roślinności i kopulują z nimi. W niedługim czasie po kopulacji samce, a po złożeniu jaj także samice, giną (Armitage i in. 1995).

Chironomidae uważane są za jedne z najbardziej plastycznych owadów świata (Pinder 1995); powszechnie występują w gradiencie szerokości geograficznej od 81^{o}N do 68^{o}S (Ferrington 2008). Większość gatunków związana jest z ekosystemami słodkowodnymi zarówno lotycznymi (strugi, strumienie, rzeki), jak i lenitycznymi (zbiorniki efemeryczne, stawy, jeziora). Znane są również nieliczne taksony charakterystyczne dla ekosystemów słono- i słonawowodnych oraz kilka gatunków obligatoryjnie lądowych (Armitage i in. 1995).

Ochotki często dominują w zgrupowaniu bezkręgowców bentosowych, szczególnie pod względem zagęszczenia i bogactwa gatunkowego (rzadziej biomasy). Ze względu na swoje liczne występowanie stanowią ważny składnik diety wielu organizmów wodnych (makrobezkręgowców, ryb), lądowych (gadów, ptaków i ssaków), a także dwuśrodowiskowych (płazów). Stąd też pełnią niezwykle istotną rolę w obiegu materii oraz przepływie energii w ekosystemach wodnych i lądowych (Benke 1995).

Zróżnicowanie zgrupowań, także Chironomidae, może być wyrażone wieloma miarami (Magurran 1988, 2004). W analizowaniu różnorodności względem skali przestrzennej, dominującą koncepcją jest jej partycjonowanie na komponent alfa (α) stanowiący liczbę gatunków występujących lokalnie w jednym z siedlisk i beta (β) będący z kolei względną miarą zróżnicowania siedlisk wewnątrz większego obszaru. Obie te składowe, bez względu na zastosowany paradygmat: addytywny (α + β) lub multiplikatywny (α × β), dają różnorodność regionalną (różnorodność gamma γ; Whittaker 1972, Whittaker i in. 2001). Pomiar różnorodności α i γ opiera się na liczbie gatunków, natomiast różnorodność β stanowi liczbę niemianowaną.

Spośród miar różnorodności odnoszących się jedynie do badanego zgrupowania (lokalnie, wewnątrz pojedynczej próby), jedną z najczęściej stosowanych jest indeks bogactwa gatunkowego, który nie uwzględnia jednak proporcji ilościowych pomiędzy poszczególnymi gatunkami zgrupowania. Uzupełnienie danych bogactwa gatunkowego o liczebność, bądź biomasę poszczególnych gatunków, daje możliwość zastosowania innych miar struktury zgrupowania, m. in. indeksów Shannona (Shannon and Weaver 1949), Simpsona czy Pielou (Jost 2006, 2007, 2010, Głowacki 2009). Najbardziej spójny system miar różnorodności obejmujący zarówno bogactwo gatunkowe, jak i proporcje liczebności gatunków w zgrupowaniu, stworzył Hill, a miary te nazwano różnorodnością rzędu zerowego N_0, pierwszego N_1, drugiego N_2 i dalej właściwie każdego dodatniego indeksu N (Hill 1973).

Mimo, iż pierwotnie zakładaną składową powyższych miar był poziom gatunku, w wyniku wielu badań eksperymentalnych okazało się, iż dla niektórych grup makrobezkręgowców bentosowych do określania różnorodności z powodzeniem można stosować także poziom rodzaju (Raunio i in. 2011). Biorąc jednak pod uwagę szacowaną liczbę gatunków Chironomidae na ok. 15 000 (Ferrington 2008) to właśnie poziom gatunku wydaje się być bardziej odpowiedni, mimo trudności w identyfikacji taksonomicznej tych owadów (szczególnie larw).

W rzekach, gdzie zgrupowania organizmów zmieniają się wzdłuż ich biegu (Vannote i in. 1980), bogactwo gatunkowe Chironomidae wzrasta osiągając maksimum w odcinkach trzeciorzędowych (Coffman 1989). Niezwykle trudna jest jednak ocena, czy zmienne środowiskowe czy też przestrzenne pełnią kluczową rolę w kształtowaniu gradientów bioróżnorodności w ciekach (Heino i in. 2003, Mykra i in. 2007, Heino 2013, Rezende i in. 2014). Rozstrzygnięcie tej ważnej z punktu widzenia ochrony bioróżnorodności kwestii staje się tym trudniejsze, iż bardzo często te dwa rodzaje czynników mogą być ze sobą skorelowane, a tym samym ocena wpływu poszczególnych składowych staje się bardzo trudna, a często praktycznie niemożliwa. Uzyskanie jednoznacznych wyników może być także komplikowane poprzez inne, niezależnie występujące zjawiska, takie jak m.in. ekstremalne stany pogodowe, zmiany w sposobie użytkowania ekosystemów oraz ingerencja antropogeniczna, prowadząca do pogorszenia jakości wody (Azrina i in. 2006, Mykra i in. 2007, Costa i Melo 2008, Koperski 2009, Flores i Zafaralla 2012).

Część hydrobiologów postuluje, iż czynniki środowiskowe wyjaśniają relatywnie niewiele zróżnicowania w zgrupowaniach ochotek (Heino i in. 2003, Punti i in. 2009). Z drugiej strony, wnioski sformułowane na podstawie wielu badań terenowych prowadzonych w ostatnich dekadach na całym świecie wskazują, iż zagęszczenie i różnorodność bezkręgowców (w tym ochotek) w poszczególnych siedliskach stanowi odzwierciedlenie panujących lokalnie warunków abiotycznych (Malmqvist 2002). Do głównych parametrów determinujących obfitość i różnorodność fauny dennej zalicza się wyodrębnione jeszcze w XX wieku czynniki takie jak: temperatura wody, zawartość rozpuszczonego tlenu, szybkość prądu, typ nieorganicznego substratu budującego dno, ilość i jakość cząsteczkowej materii organicznej oraz parametry fizyko-chemiczne tj. pH i konduktywność (Thieneman 1954, Hynes 1970).

W obliczu niewystarczającej wiedzy na temat zgrupowań Chironomidae w rzekach położonych w stosunkowo jednorodnym zoogeograficznie regionie centralnej Polski, celami rozprawy doktorskiej były:

- analiza zróżnicowania/podobieństwa zagęszczenia zgrupowań Chironomidae (Leszczyńska i in. 2019, Leszczyńska i in. 2021),
- analiza struktury zgrupowań Chironomidae wyrażona powszechnie stosowanymi miarami: liczby Hilla N_0, N_1, N_2, indeks różnorodności Shannona, dominacji Simpsona, równomierności Pielou i równomierności Buzas-Gibsona/Sheldona (tu: BGS) oraz partycjonowaniem różnorodności w skali przestrzennej (różnorodność α, β, γ) (Leszczyńska i in. 2021),
- przegląd czynników abiotycznych determinujących różnorodność makrobezkręgowców bentosowych (Leszczyńska i in. 2017) oraz wskazanie, które z nich są kluczowe dla bogactwa gatunkowego Chironomidae badanych cieków (Leszczyńska i in. 2019).

Aby zrealizować powyższe zadania, materiał biologiczny pobierano w cyklu rocznym (raz w miesiącu) z siedmiu stanowisk wyznaczonych w odcinkach nizinnych rzek o różnej rzędowości (Strahler 1957): Bzura (I), Mroga (II), Mrożyca (II), Moszczenica (III), Grabia (III), Widawka (IV), Warta (V). Materiał stanowiły dane zebrane w ciągu ostatnich 30 lat, uzupełnione o materiał zebrany w Moszczenicy.

W toku badań pozyskano 840 prób, z których wyselekcjonowano i oznaczono łącznie 61 gatunków Chironomidae. W czasie poboru prób mierzono również podstawowe parametry środowiskowe rzek.

3. STRESZCZENIA PUBLIKACJI WCHODZĄCYCH W SKŁAD ROZPRAWY DOKTORSKIEJ

Leszczyńska J., Głowacki Ł., Grzybkowska M., Przybylski M. 2021. Chironomid riverine assemblages at the regional temperate scale – compositional distance and species diversity. *The European Zoological Journal* 00(0): 000-000 (*po recenzji*).

W badaniach nad strukturą zgrupowań makrobezkręgowców bentosowych wyniki dotyczące muchówek Chironomidae często ograniczone są do wyższych jednostek taksonomicznych (trudności w identyfikacji do gatunku) lub zawierają jedynie odniesienie do liczby gatunków (bez proporcji ilościowych pomiędzy nimi). Niniejszy artykuł, poza danymi typu ‘obecny/nieobecny’, uwzględnia również zagęszczenia poszczególnych gatunków, tworząc podstawę dla kompleksowej analizy cech zgrupowań ochotek (różnorodność, równomierność, dominacja) w skali regionalnej (tu: Polska centralna).

Na podstawie analizy głównych składowych (PCA – Principal Component Analysis) z wykorzystaniem jednoczynnikowej analizy wariancji (ANOVA I) stwierdzono, iż badane odcinki rzek istotnie różniły się pod względem profili siedliskowych. Pierwsza oś, PC 1, odzwierciedlała gradient od malejącej szybkości prądu i granulacji nieorganicznego podłoża wyrażonego wskaźnikiem SI (Inorganic Substrate Index) do wzrastającej biomasy bentonicznej cząsteczkowej materii organicznej (BPOM). Z kolei druga oś, PC 2, przedstawiała gradient od malejącej zawartości rozpuszczonego w wodzie tlenu do wzrastającej biomasy transportowanej cząsteczkowej materii organicznej (TPOM).

Wzorce podobieństw i różnic profili siedliskowych badanych rzek miały swoje odzwierciedlenie w zgrupowaniach ochotek, co wykazała analiza klasterowa i ANOSIM, a także niektóre wartości jednowymiarowych miar struktury zgrupowań (N_0, N_1, N_2, indeks Shannona – odrębne grupy dla Grabi i Moszczenicy; N_1, N_2, indeks Shannona – ta sama grupa dla Mrogi i Mrożycy; wszystkie miary za wyjątkiem indeksu Pielou – odrębna grupa dla Bzury; wszystkie miary za wyjątkiem indeksów równomierności – odrębna grupa dla Warty, podczas gdy w BGS – Warta w jednej grupie z Grabią i Widawką).

Analiza SIMPER wyodrębniła grupę 14 gatunków: *Chironomus riparius, Polypedilum convictum, Prodiamesa olivacea, Polypedilum scalaenum, Micropsectra notescens*, *Stictochironomus sticticus*, *Cladotanytarsus mancus*, *Cryptochironomus defectus*, *Paratendipes albimanus*, *Cricotopus sylvestris*, *Microtendipes chloris, Macropelopia* *nebulosa, Paratanytarsus dissimilis, Robackia demeijerei,* które wyjaśniały prawie 60% różnic między zgrupowaniami. Wśród nich większość stanowiły gatunki pospolite w zbiorze danych.

Jednowymiarowe wartości zróżnicowania różniły się zarówno w zależności od zastosowanej miary, jak i pomiędzy badanymi rzekami. Zróżnicowanie gamma N_1 całego regionu wyniosło 18,31 gatunków, co zostało rozłożone na średni składnik alfa o wartości 4,04 gatunków i składnik beta o wartości 4,53 zgrupowań.

Leszczyńska J., Głowacki Ł., Grzybkowska M. 2017. Factors shaping species richness and biodiversity of riverine macroinvertebrate assemblages at the local and regional scale. *Community Ecology* 18(3): 227-236.

Od końca XX wieku różnorodność biologiczna zgrupowań/ekosystemów oraz czynniki ją determinujące stanowią jedno z najczęściej dyskutowanych zagadnień ekologicznych. Zarówno samo pojęcie, jak i mnogość wskaźników stworzonych do jej szacowania ewoluowało znacznie w toku prowadzonych prac naukowych. Celem niniejszej przeglądowej publikacji była krótka charakterystyka pojęcia i koncepcji mających na celu jej odzwierciedlenie liczbowe, a także analiza wpływu wybranych, najczęściej podkreślanych w literaturze, czynników determinujących bogactwo gatunkowe i różnorodność makrobezkręgowców rzecznych w różnych skalach przestrzennych i czasowych. Przegląd opiera się głównie na publikacjach z ostatnich 20 lat. W artykule przedstawiono związek między dobrze udokumentowaną wiedzą z Europy i Ameryki Północnej a rzadziej cytowanymi doniesieniami z Azji, Ameryki Południowej i Afryki.

Na podstawie analizy literatury stwierdzono, iż lokalnie liczba gatunków oraz struktura ich zgrupowania znajduje się pod wpływem zmiennych środowiskowych, a także zjawisk geograficznych i historycznych, zarówno tych zachodzących naturalnie, jak i wywołanych przez człowieka. W poszczególnych siedliskach mogą utrzymać się tylko te gatunki, których preferencje mieszczą się w ich zakresie tolerancji. Strukturę biocenozy makrobezkręgowców bentosowych w skali lokalnej determinują więc zmienne abiotyczne takie jak: szybkość prądu, granulacja nieorganicznego podłoża, ilość i jakość materii organicznej stanowiącej podstawowe zasoby pokarmowe oraz parametry fizyko-chemiczne odzwierciedlające jakość wody.

Z kolei zdolność do dyspersji odgrywa kluczową rolę w kształtowaniu regionalnych gradientów różnorodności, co sprzyja ciągłemu napływowi osobników i ich wymianie między dorzeczami. Ponadto dyspersja stanowi również jeden z podstawowych aspektów nasycenia/nienasycenia zgrupowań lokalnych gatunkami z regionalnej puli gatunków, co daje podstawy do odpowiedzi na pytania jak, dlaczego i w jakim stopniu, lokalne bogactwo gatunkowe zależy od bogactwa gatunkowego regionów.

Leszczyńska J., Grzybkowska M., Głowacki Ł., Dukowska M. 2019. Environmental Variables Influencing Chironomid Assemblages (Diptera: Chironomidae) in Lowland Rivers of Central Poland. *Environmental Entomology* 48(4): 988-997.

Celem niniejszej pracy była analiza bogactwa gatunkowego ochotek oraz zidentyfikowanie parametrów środowiskowych o kluczowym znaczeniu dla kształtowania się struktury zgrupowań.

Na podstawie przeglądu literatury oraz doświadczenia w badaniu nizinnych rzek, (podejście teoretyczne Information Theoretic Approach), zaproponowano dwanaście alternatywnych modeli, z których każdy zawierał odmienny zestaw parametrów środowiskowych o potencjalnie istotnym wpływie na zgrupowania Chironomidae. Analizę danych – wnioskowanie bayesowskie przeprowadzono w ‘środowisku R’ z wykorzystaniem pakietu *INLA* (*Integrated Nested Laplace Approximation*).

Ogólna analiza bogactwa gatunkowego muchówek Chironomidae wykazała, iż wzrastało ono wraz z rzędowością rzeki, osiągając wartości maksymalne w ciekach trzeciego i czwartego rzędu. W wyższych rzędowościach następował gwałtowny spadek liczby gatunków. Pod względem struktury zgrupowań ochotek (podrodzin i plemion), rzeki Bzura i Mroga charakteryzowały się wysokim udziałem procentowym Prodiamesinae, podczas gdy dominującymi grupami w Moszczenicy, Warcie i Widawce były Chironomini (Chironominae). Grabia wyróżniała się spośród pozostałych rzek wysoką liczebnością zarówno Orthocladiinae, jak i Tanytarsini (Chironominae), podczas gdy Mrożycę charakteryzował najwyższy udział Tanytarsini.

Model (M08) najlepiej dopasowany do danych, wskazał na istnienie pozytywnej zależności pomiędzy liczbą gatunków muchówek Chironomidae a granulacją nieorganicznego podłoża (SI) oraz zawartością rozpuszczonego w wodzie tlenu. Bardziej gruboziarnisty substrat oraz większa koncentracja tlenu w wodzie umożliwia kolonizację siedlisk, poza gatunkami oportunistycznymi także gatunkom bardziej wyspecjalizowanym i rzadkim.

4. PODSUMOWANIE I WNIOSKI

1. W badanych zgrupowaniach Chironomidae zidentyfikowano gatunki typowe dla potamalu rzek nizinnych regionu palearktycznego z dominacją szeroko rozpowszechnionych w obrębie wszystkich kontynentów rodzajów *Chironomus* i *Polypedilum*. Zdolności adaptacyjne tych ochotek są kluczowe dla utrzymania się w zmiennych warunkach siedliskowych.
2. Struktura zgrupowań Chironomidae w poszczególnych rzekach istotnie różniła się i odzwierciedlała zróżnicowanie profili siedliskowych względem szybkości prądu, granulacji nieorganicznego podłoża, biomasy bentonicznej i transportowanej cząsteczkowej materii organicznej oraz zawartości rozpuszczonego w wodzie tlenu. Ponadto profile siedliskowe były zależne również od wielkości cieków oraz systemu rzecznego (Wisły i Odry).
3. Na bogactwo gatunkowe Chironomidae istotny wpływ miały przede wszystkim granulacja nieorganicznego podłoża (SI) oraz zawartość rozpuszczonego w wodzie tlenu, które stwarzały optymalne warunki w skali mikro (jako refugium) i makro (homeostaza procesów życiowych). Te czynniki należą do determinantów najczęściej wskazywanych w literaturze światowej.
4. Struktura funkcjonalna zgrupowań Chironomidae w poszczególnych rzekach nie odbiegała od teorii ciągłości rzeki z dominacją zbieraczy w rzekach o niższej i średniej rzędowości (Prodiamesinae i wiele gatunków Chironomini) oraz wysokim udziałem zdrapywaczy (wiele gatunków Orthocladiinae) i filtratorów (Tanytarsini) w rzekach o wyższej rzędowości.
5. Wartości zastosowanych miar różnorodności znacznie różniły się zarówno pomiędzy miarami, jak i pomiędzy rzekami. Wskazuje to, iż jedynie szeroki wybór miar i ich analiza dają relatywnie wiarygodne wyniki w badaniach struktury zgrupowań makrobezkręgowców bentosowych.

5. LIST OF PUBLICATIONS INCLUDED IN THE PH.D. THESIS

The presented Ph.D. thesis consists of three papers about the variation in chironomid assemblages inhabiting chosen sections of rivers of different orders, and about factors determining their species richness. Two of the three studies were published in journals of the JCR (Journal Citation Reports) list: *Community Ecology* and *Environmental Entomology*. The third paper has been sent to the Editor of *The European Zoological Journal* after obtaining reviews and it is now reconsidered for publication. For each of the three articles the following information is given: the Impact Factor values from the year of publication or the latest available) and Polish Ministry of Science and Higher Education score according to the latest list of journals (from the 9th February 2021).

The Ph.D. thesis includes the following scientific papers:

1. Leszczyńska J., Głowacki Ł., Grzybkowska M., Przybylski M. 2021. Chironomid riverine assemblages at the regional temperate scale – compositional distance and species diversity. *The European Zoological Journal* 00(0): 000-000 (*after review*).

PMS&HE score = 140, IF_{2019} = 1.656

I declare that my contribution to the study is 40%. My contribution to the publication consisted in: the realization of a part of the field and lab work; the participation in the formulating the concept of the study; the preliminary analysis of data; and the preparation of the manuscript (corresponding author).

2. Leszczyńska J., Głowacki Ł., Grzybkowska M. 2017. Factors shaping species richness and biodiversity of riverine macroinvertebrate assemblages at the local and regional scale. *Community Ecology* 18(3): 227-236.

PMS&HE score = 40, IF_{2017} = 0.981

I declare that my contribution to the study is 60%. My contribution to the publication consisted in: the formulating of the concept of the study; the review of the literature; the preparation of the graphical layout and of the manuscript (corresponding author).

3. Leszczyńska J., Grzybkowska M., Głowacki Ł., Dukowska M. 2019. Environmental Variables Influencing Chironomid Assemblages (Diptera: Chironomidae) in Lowland Rivers of Central Poland. *Environmental Entomology* 48(4): 988-997.

PMS&HE score = 100, IF_{2019} = 1.584.

I declare that my contribution to the study is 50%. My contribution to the publication consisted in: the realization of a part of the field and lab work; the participation in the formulating the concept of the study; the analysis of data ('R' environment, Bayesian modeling); and the preparation of the graphical layout and of the manuscript (corresponding author).

The total Impact Factor of publications included in the Ph.D. thesis – 4.221 and the sum of the Ministry of Science and Higher Education score is 280 points (without *TEZJ*, IF = 2.565, PMS&HE score = 140).

6. INTRODUCTION

Non-biting midges (Chironomidae) are a family of small flies with long antennas (Diptera: Nematocera); their life cycle, depending on environmental conditions, can last from several days in hot climatic zones (Nolte 1995) to even several years in extremely harsh mountain and arctic ecosystems (Butler 1982). The life cycle consists of four stages (egg, larvae, pupa, adult; Fig. 1).

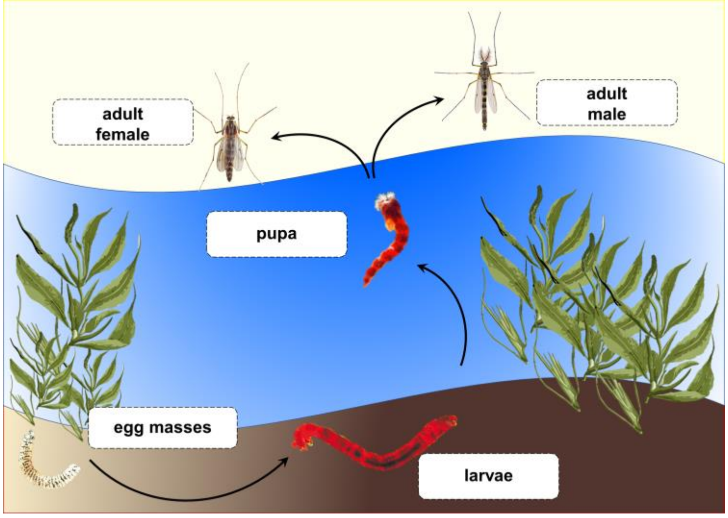


Fig. 1. Life cycle of Chironomidae.

Females lay fertilized single eggs or egg masses in a jelly cover onto water surface. The eggs first drift in the water column and then fall to the surface of the river bottom, onto macrophytes or other submersed bottom elements. From the eggs larvae develop (Armitage et al. 1995). Fourth and the last larval stage (instar) is the longest of the whole life cycle. These larvae are characterized by a great variety of habitat and feeding preferences (Franquet 1999), having their representatives in each trophic guild, except the shredders. For example, larvae of the Tanytarsini tribe are mostly filtrators. Many species from the Chironomini tribe are also collecting particles of organic matter, but only from the bottom. Individuals of Orthocladiinae are often connected to submersed aquatic macrophytes, representing the functional group of scrapers feeding on the biofilm covered leaves and stems of aquatic vegetation. In turn, Tanypodinae larvae are mostly predators or omnivorous species (Dukowska et al. 1999, Grzybkowska et al. 2009). In relation to the quantity and quality of feeding resources available in the environment, individuals of some species, such as *Chironomus riparius* Meigen, can modify the type of food collecting: filtering collector – gathering collector (Ali 1990, Berg 1995). The next stage of the life cycle of Chironomidae is the pupa. During this stage, a transformation from an aquatic form into the terrestrial one occurs. Mature, mostly several days old pupa migrate to the water surface, where they emerge (after complete metamorphosis) and fly out. Massive swarms of chironomid males remind smoke streaks above water surface. After swarming, males find females among the nearest vegetation and copulate with them. Shortly after the copulation, males, and after laying eggs also females, die (Armitage et al. 1995).

Chironomids are considered as one of the most flexible insect families in the world (Pinder 1995); they occur commonly from 81^{o}N to 68^{o}S (Ferrington 2008). The majority of species are connected to freshwater ecosystems, both lotic (streams, rivers) and lentic (ephemeral waterbodies, ponds, lakes). Some species are also known as the taxa characteristic for marine waters, several are obligatorily terrestrial (Armitage et al. 1995).

Chironomids usually dominate in benthic macorinvertebrate assemblages, especially in terms of density and species richness (less frequently in biomass). In view of their abundant presence they are an important food resource for many different types of organisms: aquatic (macroinvertebrates, fish), terrestrial (reptiles, birds and mammals), and bi-environmental ones (amphibians). Because of that, they play an essential role in the organic matter circulation and the flow of the energy within both aquatic and land ecosystems (Benke 1995).

The variability of assemblages, including chironomids, can be expressed in many types of measurement (Magurran 1988, 2004). If we restrict our attention to species ignoring their abundances, then in the analysis of diversity according to the spatial scale, the dominant concept seems to be its partitioning into the average component alpha (α), the average number of species occurring in one particular habitat, and the component beta (β), describing the relative differentiation of habitats within a greater area (region). Both above mentioned components occur in both used diversity partitioning/decomposition paradigms: additive (α + β) and multiplicative (α x β), producing the regional diversity (gamma, γ; Whittaker 1972, Whittaker et al. 2001).

Species richness is among the most popular diversity measures applicable to individual assemblages (locally, inside the single sample). However, it does not take into account the quantity proportions between particular species. The supplementation of species richness with the number (density) or biomass of particular species gives the opportunity of using other measures that take quantitative assemblage structure into account, e. g. Shannon (Shannon and Weaver 1949), Simpson or Pielou indices (Jost 2006, 2007, 2010, Głowacki 2009). The most coherent system of diversity measures consisting of both species richness and measures based on proportions of species' abundances in an assemblage was created by Hill, and the measures are named diversity of order 0, 1, 2 (N_0, N_1, N_2) (Hill 1973), and in fact of any positive subscript to N.

Many experimental studies showed that for some benthic macroinvertebrate taxa also the genus level could be sufficient instead of the species level to draw valuable assemblage structure conclusion (Raunio et al. 2011), which may be advantageous in view of the fact that identification of chironomids to the species level is usually difficult. However, taking into consideration the estimated number of chironomid species – 15,000 (Ferrington 2008), which much exceeds the determined number, the species level seems to be more proper for such conclusions, despite some difficulties in the taxonomic identification (especially larvae).

In rivers, where the assemblages change along their course (Vannote et al. 1980), the chironomid species richness increases achieving the maximum in the third order sections (Coffman 1989). Extraordinarily difficult is the determination of which variables: environmental or spatial play a key role in shaping the biodiversity gradient in riverine ecosystems (Heino et al. 2003, Mykra et al. 2007, Heino 2013, Rezende et al. 2014). The conclusion of this from the diversity protection's point of view is getting more complicated, because those two types of factors are often correlated and the final decision about the influence of particular components becomes practically impossible. The obtaining of clear results can be also complicated by other, independently occurring phenomena, such as extreme weather conditions, changes in the ecosystem using and anthropogenic impact leading to the deterioration of water quality (Azrina et al. 2006, Mykra et al. 2007, Costa and Melo 2008, Koperski 2009, Flores and Zafaralla 2012).

Some hydrobiologists postulate that environmental factors explain relatively few differences in the variability of chironomid assemblages (Heino et al. 2003, Punti et al. 2009). On the other hand, conclusions formulated on the basis of many field experiments conducted during the latest decades worldwide, pointed out that the density and the diversity of macroinvertebrates (including chironomids) constitutes the reflection of locally prevailing abiotic conditions (Malmqvist 2002). The main determinants of the abundance and diversity of benthic fauna, defined back in the 20th century, are: water temperature, dissolved oxygen content, current velocity, type of inorganic bottom substrate, quantity and quality of particulate organic matter and physico-chemical parameters such as, pH and conductivity (Thienemann 1954, Hynes 1970).

In view of the insufficient knowledge of the chironomid assemblages from rivers located in a relatively zoographically homogeneous region of central Poland, the objectives of the Ph.D. were:

- analysis of the diversity/similarity of the density of chironomid assemblages (Leszczyńska et al. 2019, Leszczyńska et al. 2021),
- analysis of the structure of chironomid assemblages expressed by commonly used univariate measures: Hill numbers N_0, N_1, N_2, Shannon diversity index, Simpson dominance index, Pielou and Buzas-Gibson/Sheldon (here: BGS) evenness indices and partitioning of the diversity at a given spatial scale (α, β, γ diversity) (Leszczyńska et al. 2021),
- a review of abiotic factors determining the diversity of benthic macroinvertebrates (Leszczyńska et al. 2017) and an indication of which of them are crucial for the species richness for the chironomids of the studied watercourses (Leszczyńska et al. 2019).

In order to accomplish the above tasks, biological material was collected over annual cycles (once a month) from seven sites in the sections of lowland rivers of various orders (Strahler 1957): Bzura (I), Mroga (II), Mrożyca (II), Moszczenica (III), Grabia (III), Widawka (IV), Warta (V). The material consisted of data collected over the latest 30 years, which were additionally supplemented with materials collected in the Moszczenica.

In the whole study cycle, 840 samples were obtained, from which a total of 61 chironomid species were selected and identified. During the sampling, the basic environmental parameters of the rivers were also measured.

7. ARTICLES' SUMMARIES INCLUDED IN THE PH.D. THESIS

Leszczyńska J., Głowacki Ł., Grzybkowska M., Przybylski M. 2021. Chironomid riverine assemblages at the regional temperate scale – compositional distance and species diversity. *The European Zoological Journal* 00(0): 000-000 (*after review*).

In the studies on the structure of benthic macroinvertebrate assemblages, the results concerning chironomids are often limited to higher taxonomic levels (due to difficulties in identifying organisms to species level) or refer only to the number of species (without quantitative proportions between them). This article, in addition to the 'present/absent' data, also takes into account the densities of particular species, presenting the basis for a comprehensive analysis of the characteristics of chironomid assemblages (diversity, dominance, evenness) at a regional scale (here: central Poland).

Based on the PCA (Principal Component Analysis) with the use of one-way analysis of variance (ANOVA I), it was found that the studied river sections differed significantly in terms of their habitat profiles. The first axis of PCA, PC 1, reflected the gradient from decreasing current velocity and granulation of the inorganic substrate expressed by the SI (Inorganic Substrate Index) to increasing benthic particulate organic matter (BPOM) biomass. The second axis of PCA, PC 2, showed a gradient from a decreasing content of dissolved oxygen in water to an increasing biomass of transported particulate organic matter (TPOM).

The patterns of similarities and differences in the habitat profiles of the studied rivers reflected these of the chironomid assemblages (grouped by river) demonstrated by the cluster and ANOSIM analyses, as well as some patterns of the values of univariate measures (N_0, N_1, N_2, Shannon index – a separate groups for Grabia and Moszczenica; N_1, N_2, Shannon index – the same group for Mroga and Mrożyca; all measures except the Pielou index – a separate group for the Bzura; all measures except for evenness indices – a separate group for the Warta, while in the BGS measure – Warta in the same group as Grabia and Widawka).

The SIMPER analysis identified a group of 14 species: *Chironomus riparius*, *Polypedilum convictum*, *Prodiamesa olivacea*, *Polypedilum scalaenum, Micropsectra notescens, Stictochironomus sticticus, Cladotanytarsus mancus, Cryptochironomus defectus, Paratendipes albimanus, Cricotopus sylvestris, Microtendipes chloris, Macropelopia nebulosa, Paratanytarsus dissimilis, Robackia demeijerei*, which explained almost 60% of the differences between the assemblages. The majority of the above mentioned species were the most common ones in the whole dataset.

Values of the univariate diversity measures differed both from measure to measure and from river to river. The gamma (N_1) diversity of the entire region was 18.31 species, which was decomposed into the mean alpha component of 4.04 species and the beta component of 4.53 assemblages.

Leszczyńska J., Głowacki Ł., Grzybkowska M. 2017. Factors shaping species richness and biodiversity of riverine macroinvertebrate assemblages at the local and regional scale. *Community Ecology* 18(3): 227-236.

Since the end of the 20th century, the biodiversity of assemblages/ecosystems and the factors that determine it have been one of the most frequently discussed ecological issues. Both the concept itself and the multitude of indices used to estimate it have significantly evolved in the course of the recent decades. The aim of this overview publication was a brief characterisation of the terms and concepts and their numerical representations, as well as the analysis of the influence of selected, most often emphasized in the literature, factors determining species richness and diversity of river macroinvertebrates at various spatial and temporal scales. The review is mainly based on publications from the latest 20 years. The article presents the relationship between well-documented knowledge from Europe and North America, and less cited reports from Asia, South America and Africa.

Based on the above review, it was found that the local number of species and the structure of their assemblages are influenced by environmental variables as well as geographical and historical phenomena, both naturally occurring and man-made. Only species whose preferences are within their tolerance range can survive in a particular habitats. The structure of the biocenosis of benthic macroinvertebrates at a local scale is therefore determined by abiotic variables, such as: current velocity, granulation of inorganic bottom substrate, quantity and quality of particulate organic matter constituting the basic food resources, and physico-chemical parameters reflecting water quality.

In turn, the ability to disperse plays a key role in shaping regional diversity gradients, which favors the permanent inflow of individuals and their exchange between river basins. Moreover, dispersal is also one of the basic aspects of saturation/unsaturation with local species from the regional species pool, which gives rise to an answer to the question of how, why and to what extent local species richness depends on the species richness of the region.

Leszczyńska J., Grzybkowska M., Głowacki Ł., Dukowska M. 2019. Environmental Variables Influencing Chironomid Assemblages (Diptera: Chironomidae) in Lowland Rivers of Central Poland. *Environmental Entomology* 48(4): 988-997.

The aim of this study was to analyze the species richness of chironomid assemblages and to identify environmental parameters of key importance for the shaping of assemblage structure.

On the basis of the literature review and the experience in the investigation of lowland rivers (the Information Theoretic Approach), twelve alternative models were proposed, each with a set of different environmental parameters with a possible significant impact on the assemblages of chironomids. Data analysis – Bayesian inference was carried out in the 'R environment' using the INLA package (*Integrated Nested Laplace Approximation*).

A general analysis of the species richness of chironomids showed that it increased along the river's course, with the river's order, reaching its maximum values in the third and fourth order streams. In the higher order sections there was a rapid decline in the number of species. In terms of the structure of chironomid groups (subfamilies and tribes), the Bzura and Mroga rivers were characterized by a high percentage of Prodiamesinae, while the dominant groups in the Moszczenica, Warta and Widawka rivers were Chironomini (Chironominae). The Grabia was distinguished from other rivers with a high abundance of both Orthocladiinae and Tanytarsini (Chironominae), while Mrożyca was characterized by the highest share of Tanytarsini.

The model (M08) best suited the data, showed a positive relationship between the number of chironomid species and the granulation of the inorganic bottom substrate (SI) and the content of oxygen dissolved in water. Coarser substrate and higher oxygen concentration in water enable the colonization of habitats by, besides opportunistic species, also more specialized and rare species.

8. SUMMARY AND CONCLUSIONS

1. In the investigated chironomid assemblages, species typical of the potamal of lowland rivers of the Palearctic region were identified. These species included those of the *Chironomus* and *Polypedilum* genera that are dominant and widely distributed in all continents. Their flexibility may be crucial for the maintenance of chironomid species in changeable habitat conditions.

2. The structure of chironomid assemblages in particular rivers differed significantly and reflected the diversity of the habitat profiles in terms of current velocity, granulation of inorganic bottom substrate, biomass of benthic and transported particulate organic matter, and dissolved oxygen contents. Moreover, the habitat profiles depended on the size of the watercourses and the river system (Vistula and Oder).

3. The species richness of Chironomidae was mainly influenced by the granulation of inorganic bottom substrate (SI) and the content of dissolved oxygen in water, creating optimal conditions at the micro (as refugium) and macro (homeostasis of life processes) scale. These factors are among the determinants most frequently indicated in the world literature.

4. The functional structure of Chironomidae assemblages, in particular rivers, was similar to this from the river continuum concept, with the predominance of collectors in rivers of lower and medium orders (Prodiamesinae and many Chironomini species) and a high share of scrapers (many species of Orthocladiinae) and filterers (Tanytarsini) in rivers of higher orders.

5. The values of used univariate diversity measures differed from measure to measure and from river to river. These values show that only a comprehensive choice of diversity measures may supply relatively reliable results in the study of the structure of benthic macroinvertebrate assemblages.

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ZAŁĄCZNIK I/ APPENDIX I

PUBLIKACJE WCHODZĄCE W SKŁAD ROZPRAWY DOKTORSKIEJ/

PUBLICATIONS INCLUDED IN THE PHD THESIS

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Chironomid riverine assemblages at the regional temperate scale – compositional distance and species diversity

Running title: Chironomid riverine assemblages

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Abstract

Chironomids are the most common and abundant benthic invertebrate family in freshwater environments worldwide, but their widespread occurrence is known mostly as species richness. This makes the assessment of chironomid assemblage composition and diversity limited in any physiographic zone and at any scale. This study enhances knowledge of chironomid abundance in rivers in central Europe, which is typical part of the temperate climatic zone, and investigates chironomid (inter-)assemblage characteristics. Benthic assemblages of seven lowland rivers were sampled monthly over annual cycles with a total of 61 chironomid species detected. PCA was used to determine the environmental profile of the rivers at study sites, while cluster and ANOSIM analysis and univariate diversity measures were applied to the chironomid samples of the assemblages grouped at the river level to identify their similarities and differences. The environmental profile explained much of the cluster and ANOSIM-based patterns of the rivers' compositional distances, and also some values of given univariate diversity measures. SIMPER analysis distinguished a group of 14 species that explained almost 60% of differences between the assemblages. The contribution of each species of the group was similar, ranging between 6.13 and 2.87%, yet on average several times greater than that of each of the remaining 47 species. Univariate diversity values differed from measure to measure and from river to river, and indicated that the application of few such measures, particularly one, may be misleading. The N_1 gamma diversity of the whole region (calculated from 82 samples) was 18.31 species, which was multiplicatively decomposed into the average alpha component of 4.04 species, and beta component of 4.53 assemblages.

Keywords: *benthic macroinvertebrates, stream order section, assemblage structure, alpha (*α*), beta (*β*), gamma (*γ*) diversity*

1. Introduction

Owing to their tolerance of extremely high and low air and water temperatures (Rossaro 1991; Hayford et al. 1995; Bouchard et al. 2006), and thanks to specific ontogenetic strategies, such as immature aquatic and adult aerial stages, or highly variable duration of life cycles and diverse voltinism (Nolte 1996; Tokeshi 1995), chironomids have colonized freshwater bodies from arctic zones to the tropics (Edwards & Usher 1985; Oliver & Corbet 1966), between high mountains (Koshima 1984) and deep lakes (Linevich 1971). This distribution makes them the most globally widespread aquatic insect family (Ribera 2008), whose species provide essential roles in nutrient cycling and energy flow in almost all freshwater ecosystem processes (Ferrington 2008). They are important consumers, recycling allochthonous and autochthonous organic matter (Jones & Grey 2004), and thus essential secondary producers as well as prey of other animals (Dukowska & Grzybkowska 2014).

Despite their ubiquity, descriptions of chironomid occurrence are mostly in terms of species (or higher taxa) richness (Raunio et al. 2011), which, at the global scale, amounts to 4,000 determined (Ferrington 2008) and 20,000 predicted species (Giller & Malmqvist 1998). The limitation to richness is not surprising considering the difficult and time-consuming identification of chironomids (Cranston 1995). While the identity of a single individual is enough to assess the presence of a given taxon, the identities of all individuals of all taxa are necessary to assess other (inter-)assemblage parameters, such as compositional structure, compositional distance or diversity *per se* (i.e. diversity measurement taking abundance or density into account), as well as assemblage dependence on environmental factors. Due to these difficulties, macroinvertebrate studies usually distinguish only chironomid genera, consider all chironomids as a single taxon (Mykrä et al 2008; Jones 2008), or ignore chironomids altogether, with rare exceptions (Puntí et al. 2007, 2009; Chaib et al. 2013), particularly in temperate Europe (Grzybkowska 1989, 1995; Ruse 1995; Koperski 2009; 2010; Árva et al. 2017; Leszczyńska et al. 2019).

These limited approaches have consequences for our understanding of freshwater systems. One of them is a disparity between the determined and predicted species (and higher taxa) richness, not only at the global, but at all other scales. The cause of the disparity seems obvious: when most individuals remain unidentified it is impossible to be certain how many taxa may actually be in a site or region. Another and more serious consequence is the fact that assemblages are compared (also with environmental factors) only in terms of species richness while unbiased assessments of other (inter-)assemblage parameters at both local and larger spatial scales are impossible because the abundance, density or biomass of species are unknown.

In this study, we attempted to address this gap in the knowledge of chironomid abundance and its meaning in the study of chironomid assemblages and their comparisons at a greater than local scale. Therefore, chironomid assemblage structure/composition and diversity were investigated in several rivers of a physiographically typical central European region, which is representative of a substantial part of the temperate climatic zone. We addressed the following questions:

1) What are the general characteristics of chironomid species occurrence and abundance in rivers of central Poland?
2) What are the patterns of compositional distances between chironomid assemblages and to what extent are they explained by the environmental profile of the rivers at the study sites?
3) What group of species explain the differences in structure of chironomid assemblages?
4) How are the differences in structure of chironomid assemblages reflected by diversity measures?

2. Material and methods

2.1. Study area

The study was performed in seven lowland rivers, i.e. the Bzura, Morga, Mrożyca, Moszczenica, Grabia, Widawka and Warta rivers, located in central Poland (part of the Łódź Voivodeship, Poland). The region is several thousand square kilometers in area (the most distant study sites are 88 km apart), and in many respects homogenous (Figure 1). It is of geologically uniform post-glacial (Pleistocene and Holocene) origin (Przybylski et al. 2020), with several dozen to over a hundred meter thick layer of sand, gravel or clay, and distant from mountain, marine, or large lake influences. The surroundings of the rivers are not urbanized and mostly agricultural (Grzybkowska & Głowacki 2011). However, the region is heterogeneous in certain other respects. Its rivers are of different sizes (and their studied sections are of different stream orders), and differ in water, streambed and other environmental parameters' values. The first four rivers belong to the Vistula catchment, and the last three to the Oder catchment. The sampling sites, one in each river, were established in potamon river sections whose stream order (Strahler 1957) ranged from the first (the Bzura) to the fifth (the Warta) (Figure 1). Dependent on context, the name of a river is usually used as meaning “the set of assemblages sampled in the river”, or “the value of a measure obtained in the river”. A detailed description of all investigated study sites is presented in Table I.

2.2. Field sampling

Benthic chironomid larvae with particulate organic and inorganic substrate were collected from each river once a month in an annual cycle, which produced 12 samples from each river. A monthly sample from a river/site consisted of 10 sub-samples collected at sampling points established at regular distances from one another along a transect extending from the bank to the mid-channel. Each sub-sample was composed of 10 cores of benthos obtained by driving a tubular sampler 10 cm^2 in cross-section area 10 times into the streambed randomly around each sampling point. This was done to capture greater species diversity, and individuals were identified to the species level, if possible.

The sampler was pushed to a depth of about 150 mm, and after pulling it out each obtained core was extracted from the sampler and preserved in plastic containers with riverine water. As a result, the material of each whole monthly sample from each river consisted of 100 cores (Leszczyńska et al. 2019). Values for several environmental parameters, including water velocity [$m\ s^{-1}$], river width [m], river depth [m], surface of bottom covered by submersed aquatic macrophytes [%], water temperature [^oC] and oxygen content [$mg\ dm^{-1}$] were measured or assessed in the fields (three times per each transect).

2.3. Laboratory analysis

The samples were transported to the laboratory where they were carefully examined and invertebrates were manually sorted from benthic sediment. Chironomids were separated, preserved in 70% ethanol and identified to species level using a microscope (Nikon Eclipse 50i).

As an exact identification on the basis of larvae was impossible in some species, immature chironomid stages of certain species were reared in the laboratory from additional qualitative samples to obtain larval and pupal skins, and imagines. Keys written by several taxonomists and edited by Wiederholm (in three parts: for larvae (1983), pupae (1986) and imagines (1989)), as well as a key by Nilsson (1997) were used to determine taxonomic membership. After identification, all chironomids were counted, and their density was estimated [ind. m^{-2}]. Chironomids that were identified only to genus or higher taxonomic level were excluded from the statistical analysis.

The granularity of inorganic particles, using sieves of various mesh size, and inorganic substrate index, SI [mm] (Cummins 1962; Quinn & Hickey 1990), were calculated on the basis of collected samples. In addition, the amounts of benthic particulate organic matter, thereafter BPOM [g m^{-2}]; (Petersen et al. 1989) and transported particulate organic matter, therefore TPOM [g m^{-3}] were assessed (Grzybkowska and Witczak 1990).

2.4. *Statistical methods*

To produce the environmental profile of the examined rivers at the sampling sites, principal component analysis (PCA) was performed on a matrix consisting of the values of five environmental variables (water velocity, SI, BPOM, TPOM, oxygen content) × 82 monthly measurements of these variables in the seven rivers. Prior to analysis, habitat variables were tested for normality, and checked for the presence of outliers. Diagnostic plots of residuals against fitted values and normal QQ plots of residuals were used to assess assumptions of normality. The environmental profile was obtained by a reduction of the five entry variables to a limited set of uncorrelated components (PC axes). However, only PC axes with eigenvalues >1 (the Kaiser criterion) were used in further analysis. The interpretation of each selected component (PC axis) was made on the basis of correlations (loads) between the component and original variables. One way analysis of variance (ANOVA I) was performed, separately for each PC component, to find differences among rivers in the environmental profile. If ANOVA I showed significant differences among rivers, Fisher's Least Significant Difference (LSD) *post-hoc* test was implemented. All statistical analyses were performed in Statistica 13 software (Dell Inc., 2016). Probability values $P < 0.05$ were considered significant. Data are reported as mean ± standard error (SE).

Cluster analysis with Pearson correlation as a criterion of similarity and UPGM as a method of clustering were used to detect the resemblance between particular rivers. The measure was applied to the density matrix of averaged chironomid species' densities in given rivers.

One-way permutational analysis of similarity, i.e. ANOSIM, a test of significant difference between groups of sites/samples, was adopted as a method of assessing river similarities. Bray-Curtis was the applied measure of similarity between assemblages (Clarke 1993). ANOSIM is analogous to an ANOVA procedure, with a non-parametric permutation (10,000 permutations were used) applied to a rank similarity matrix of samples (Clarke 1993). In this procedure, the R statistic provides an absolute measure of how groups are separated. Generally, R values lie between 0, when groups are indistinguishable, and +1, when all similarities within groups are less than the similarity between groups (Clarke & Warwick 1994). When the overall difference was significant, indicating which riverine sets of assemblages were different from others, the pairwise ANOSIM comparisons were performed and p-values were determined based on a step-down sequential Bonferroni procedure.

SIMPER, a percentage similarity analysis, was used to identify which taxa were primarily responsible for the observed differences between assemblages (Clarke 1993). Similarly to ANOSIM, the Bray-Curtis assemblage similarity measure was used for SIMPER analysis. Only species whose cumulative contribution to overall dissimilarity was equal to or higher than 60% were considered. ANOSIM and SIMPER analyses were conducted using the PAST v3.26 software (Hammer et al. 2001; Hammer 2019).

A number of univariate alpha diversity measures were applied to assess the within river characteristics. To avoid spurious conclusions that may result from a narrow choice of such measures (Magurran & McGill 2011) the present selection was comprehensive, because it included species richness, entropy used as a diversity index, dominance index, and two evenness measures. The measures were:

Hill numbers $N_0, N_1, N_2,$ i.e.

$N_0=\sum p_i^0=S$, $N_1=\exp(-\sum p_i \ln p_i)=e^{H'}$, $N_2=1/\sum p_i^2$ (Hill 1973),

Shannon $H'=-\sum p_i \ln p_i$ (Shannon & Weaver 1949),

Pielou $J'=H'/\ln S$ (Pielou 1966),

Simpson $\lambda=\sum p_i^2$ (Simpson 1949),

$BGS=e^{H'}/S$ (Buzas & Gibson 1969, Sheldon 1969),

where: p_i – the proportion of individuals belonging to the ith species in the dataset, S – species richness.

The univariate alpha diversity measures were calculated for each monthly sample obtained in each river over the annual cycle. As a result, in the case of each diversity measure, we obtained a set of 10 values for the Warta River, and sets of 12 values for each other river. Because the distributions of the values of each measure were unknown we could not average the values for each river to compare them. Instead, we bootstrapped each set of monthly values. 100 pseudo samples were produced for each measure and each river to obtain normal distributions of data sets. This number of pseudo samples was selected to avoid spurious small or large sample effects on the significance of the comparison of the means of bootstrap pseudo-samples using the ANOVA test: i.e. Type I and Type II errors (Fritz et al. 2012; Khalizadeh & Tasci 2017). The bootstrap sets for each measure were then compared using ANOVA. A *post-hoc* Tukey test was used to distinguish homogenous groups of assemblages/rivers of each measure.

However, beside the above stand-alone alpha diversity assessment of given rivers, diversity was also calculated as a multiplicative partitioning/decomposition paradigm. In this paradigm, the average alpha and beta components are calculated for neither a specific assemblage or river, but for the whole region. When multiplied by each other these average alpha and beta components create gamma, total regional diversity (Whittaker 1960). The alpha and gamma are in number of species, while the beta in number of assemblages. The possible range of the beta component is between unity, when all assemblages are identical, and the total number of assemblages, when each and every assemblage contains all different species. In this study, we calculated the average alpha and beta components for all 82 assemblages. This was done in the case of only these measures, in which meaningful decomposition might be carried out, i.e. N_0 and N_1.

3. Results

In total, 61 chironomid species from 5 subfamilies (Tanypodinae, Diamesinae, Prodiamesinae, Orthocladiinae, Chironominae) were identified in the studied streams. An additional 12 genera were also recorded, though it was impossible to identify these taxa to the species level (Table II).

The most frequent species in macroinvertebrate assemblages were: *Prodiamesa olivacea*, *Polypedilum convictum*, *Polypedilum scalaenum*, *Micropsectra notescens*, *Chironomus riparius* and *Robackia demeijerei*. Subdominants, which were present in more than one stream, but in different densities, were *Paratendipes albimanus* (Mrożyca, Moszczenica, Warta), *Stictochironomus sticticus* (Mroga, Mrożyca), and *Cladotanytarsus mancus* (Grabia, Widawka).

The environmental profile of the rivers is presented in Figure 2. Each point of the figure represents a multidimensional environmental condition in which a respective chironomid sample was collected. The PCA allowed a reduction of the five environmental variables to two orthogonal axes/components (PC 1 and PC 2) with eigenvalues higher than unity. These two axes/components explained 64.75% of the total variance (Table III). The correlation between the abundance of particular environmental variables and the new components revealed that the first axis (PC 1) represents a gradient extending from decreasing water velocity and SI to increasing amount of BPOM. The second axis (PC 2) represents a gradient extending from declining oxygen concentration to growing amount of TPOM.

Analysis of variance showed that the examined rivers differ significantly ($F_{6,73}$ = 95.58, $p<0.001$) in PC 1 scores, and the multiple comparison LSD *post-hoc* test identified five homogenous groups, i.e. Grabia, Warta=Widawka=Bzura, Mroga, Mrożyca, Moszczenica. Similar differences in the environmental profile were also noted for the PC 2 scores ($F_{6,73}$ = 12.76, $p<0.001$), where four homogenous groups: Grabia, Moszczenica=Widawka, Widawka=Mroga=Mrożyca=Warta, Bzura, were distinguished. The Widawka River cannot be precisely situated (and thus should be considered belonging to no group), because it belongs to two homogenous groups simultaneously.

The chironomid assemblages differed significantly using the ANOSIM measure (R-statistic = 0.8817, $p<0.001$), and pairwise comparisons revealed that each river differed significantly from all the others (Table IV).

Three main clusters were identified based on cluster analysis (Figure 3). Streams of lower orders (the Bzura, Mroga, Mrożyca and Moszczenica) formed the first cluster (separated at a distance of 0.53). The second cluster comprised two larger rivers: the Grabia and Widawka (separated at a distance of 0.67). The chironomid assemblage of the Warta River, the largest river in Central Poland, was the most different from the other assemblages (at a distance of 0.79), constituting a separated branch (and the third cluster) in the dendrogram.

SIMPER analysis indicated that overall dissimilarity among the rivers was 76.9%, and 14 of the total of 61 species produced over 57.3% of cumulative dissimilarity (Table V). Seven of the 14 species (*C. riparius* and *P. olivacea* in the River Bzura, *P. scalaenum* and *P. convictum* in the Mrożyca, *M. notescens* in the Moszczenica, and *P. albimanus*, and *C. mancus* in the Grabia) were the most abundant ones (usually over 4500 ind. m^{-2} in one water body). Moreover, these species were the most frequent chironomids in the whole dataset. The seven species produced over 33.7% of cumulative dissimilarity and could be related to significant differences in the chironomid assemblages (Table V).

Univariate alpha species diversity measures (species richness, diversity *per se*, Shannon entropy, Simpson domination and evenness measures) (Figure 4) showed that variation occurred both from measure to measure and from river to river. Besides, there were only five two-river homogeneous groups in all the seven measures, one three-river group, and two two-river groups that overlapped. In two measures, all rivers were completely heterogeneous (i.e. each river constituted a different group).

In N_0 of the multiplicative partitioning/decomposition paradigm, the gamma diversity of the region amounted to 61 species, the beta component to 5.50 assemblages, and the average alpha component to 11.00 species. In N_1 of the paradigm, the gamma diversity of the region amounted to 18.31 species, the beta component to 4.53 assemblages, and the average alpha component to 4.04 species.

4. Discussion

4.1. General chironomid abundance and assemblage structure as regards subfamily, tribe and genus levels

The composition of chironomid assemblages inhabiting all the study rivers was typical for lowland water bodies from the Palaearctic zone (Pinder 1995; Ferrington 2008). In such rivers, the chironomid fauna of a rhithral section (Armitage et al. 1995; Andersen et al. 2013) is usually dominated by the subfamily Orthocladiinae and other taxa preferring cool, well-oxygenated environments. Meanwhile, the dominant chironomid fauna in potamal river sections are representatives of the Chironomini (subfamily Chironominae). Generally, species of the latter subfamily live in soft sediment and present a wide range of tolerance, especially in terms of higher water temperature and lower oxygen concentrations (Armitage et al. 1995).

The highest abundance or species richness of the genera *Chironomus* and *Polypedilum*, which were also the most abundant in our investigation, was observed in chironomid assemblages from lowland rivers both in Europe (Popović et al. 2016; Árva et al. 2017) and in other continents (Ashe et al. 1987; Armitage et al. 1995; Chaib et al. 2013). In the study of the Arkansas River basin (USA) conducted by Hermann et al. (2016), for example, 12 species of *Polypedilum* and 11 species of *Chironomus* were recorded. Moreover, *Chironomus decorus* was the most common species that appeared at all their study sites, excluding one. In turn, in the floodplain of the Paraná River (Brazil), larvae of *Polypedilum* were the subdominant component of chironomid assemblages (*Tanytarsus* dominated). Two species of *Chironomus* were also mentioned as those with high density (Júnior et al. 2016). In the Phong River in Thailand, *Polypedilum nubifer* constituted more than one fourth of the assemblage (Sriariyanuwath et al. 2015). In the African Swartkops River, Odume et al. (2016) also indicated *Chironomus* and *Polypedilum* (tribe Chironomini) as two of the five most abundant taxa.

In general, in the temperate regions, the species richness of Chironominae and Orthocladiinae subfamilies amounts to 30% each of the total number of species (Thienemann 1954; Cummins and Lauff 1969; Tolkamp 1982; Armitage et al. 1995; Pinder 1995; Bournaud et al. 1998; Andersen et al. 2013). In our study, the percentage of Chironomini species was even higher and constituted about 47% of the total number of species, while that of Orthocladiinae about 33%. However, in the case of density, Orthocladiinae larvae were not numerous and can be treated here as rare species, in contrast to ecosystems rich in submersed aquatic macrophytes where they are present at high densities, mostly because many of them are grazers or scrapers (Grzybkowska et al. 2017, 2020).

The remaining chironomid subfamilies, Tanypodinae, Prodiamesinae and Diamesinae, assumed the values of 10%, 7%, 3%, respectively. The density of Tanypodinae usually displays high fluctuations between study sites, and this is typical for most non-disturbed rivers (Rossaro 1991). Prodiamesinae were represented mainly by *P. olivacea,* which rarely is the dominant component of chironomid assemblages, except the Bzura River in central Poland (Grzybkowska 1995). In the Zwalm River in Belgium, for instance, it was the most common larvae present at all examined sites (Adriaenssens et al. 2004), whereas the sub-family Diamesinae was represented by only two species, *Potthastia longimanus* and *Potthastia gaedii*, which are two of the most flexible taxa of this subfamily (in both rhithral and potamal sections of streams and rivers; Moubayed-Breil & Orsini 2016). In general, this occurrence of the two *Potthastia* species is in contrast to other geographical areas or altitudes, because Diamesinae, and especially the genus *Diamesa*, are the first taxa that colonize streams immediately downstream of source glaciers (Lencioni & Rossaro 2005). They are cold-stenobionts that prefer low water temperature and fast flowing streams, where they are usually the dominant component of assemblages (Rossaro 1991; Lods-Crozet et al. 2001).

4.2. Environmental profile of the rivers at the sampling sites

Each point of Figure 2 represents a 5-dimensional environmental location (reduced to two orthogonal dimensions, Table III), in the conditions of which a monthly sample was collected in a river. Each of the ellipses is a 95% prediction area where the points of each river would occur. The general arrangement of the ellipses is ecologically informative because each of them either overlap or adjoin, and thus they all form a single connected group. Consequently, the regional environmental conditions of the sampled chironomid assemblages were relatively homogeneous. If any of the ellipses had been disconnected from others, this would have indicated that the conditions of the region were more heterogeneous. Technically, the ellipses differ from one another in terms of characteristics such as: location along PC axes, size of area, elongation, orientation, and overlap. Each of the characteristics has its own (or combined with others) ecological interpretation.

As regards location along PC axes, the ellipses of the Widawka, Warta, Mroga and Mrożyca are situated almost horizontally, i.e. along axis PC 1, and their centers (i.e. crossings of the shorter and longer axes) lie at PC 2 values close to zero. The ellipses of the Grabia and Moszczenica are situated peripherally at the opposite ends of the group of ellipses as regards axis PC 1, and they do not overlap any other ellipsis each. They both extend slightly more along axis PC 2 than along axis PC 1, and both along negative values of PC 2, although the former river to a much lower value (-3) of the axis than the latter (-2). The greatest difference between the two rivers is that the Grabia is located at the most negative values of axis PC 1 (down to -3), whereas the Moszczenica at the most positive values of axis PC 1 (up to 3). The ellipsis of the Bzura extends along both axes (owing to its slanting orientation), from the crossing of their point zero gridlines to positive values of axis PC 2 and negative values of axis PC 1.

These findings indicate that the assemblages of the first four rivers (Widawka, Warta, Mroga, Mrożyca) were sampled under conditions of water velocity, SI and BPOM (Table III) that assumed values typical for the whole studied region. Meanwhile, the sampling conditions of the Grabia, Bzura and Moszczenica greatly differed in terms of these three variables, because their ellipses were more distant from one another. SI and water velocity was highest in the Grabia, close to regionally average values in the Bzura, and lowest in the Moszczenica, while BPOM was lowest in the Grabia, close to regionally average values in the Bzura and highest in the Moszczenica. However, the three rivers also differed in terms of TPOM and dissolved oxygen. TPOM was below regionally average values in the Grabia and Moszczenica, and above the average values in the Bzura, whereas dissolved oxygen was above average values in the Grabia and Moszczenica, and below average values in the Bzura.

As regards size of area, the ellipses of the Grabia, Widawka, Bzura, Mroga and Mrożyca are greatly similar, that of the Moszczenica is a little smaller, and the ellipsis of the Warta is the smallest. Ecologically, this indicates that the dispersal of monthly values over the annual sampling cycle was smallest in the Warta, substantially larger in the

Moszczenica, and greatest in the rest of the rivers. Note, however, that we ignore elongation, which will to a certain extent alter this pattern of dispersal.

As regards elongation, it is similarly moderate in all rivers except the Bzura, in which it is greatest; the longer axis of the ellipsis being almost three times longer than the shorter axis. Ecologically, this indicates temporal dispersal (over the sampling year) and variability of environmental conditions, which frequently assumed extreme values in the Bzura, particularly high values of TPOM and low values of dissolved oxygen (Table III; Figure 2). The slanting orientation of the Bzura ellipsis indicated this variability concerned all five environmental variables.

As regards orientation, the longer axes of the ellipses of the Grabia and Moszczenica are parallel to axis PC 2, that of the Mroga is parallel to axis PC 1, those of Widawka, Warta, and Bzura extend from the left upper to right lower corner, and only that of the Mrożyca from the lower left to upper right corner. Ecologically, the right and left skewed orientations have similar meaning, because they both indicate that environmental conditions varied along both PC axes, and thus in all five variables, in the case of the Widawka, Warta, Bzura and Mrożyca. However, the vertical orientation of the Grabia and Moszczenica indicates that their environmental conditions varied slightly more in terms of TPOM and dissolved oxygen than in terms of water velocity, SI and BPOM, whereas the horizontal orientation of the Mroga indicates that its conditions varied slightly more in water velocity, SI and BPOM than in TPOM and dissolved oxygen.

As regards overlap, only the ellipses of the Grabia and Moszczenica do not overlap any other ellipsis each, although the former adjoins this of the Widawka, and the latter that of the Mrożyca. In contrast, the ellipsis of the Warta is almost completely ‘nested’ within that of the Widawka, and the second considerable overlap, by about half of area, is that of the Mroga and Mrożyca ellipses. Ecologically, this means that the conditions of the Grabia and Moszczenica were, on average, most different from those of the other rivers and that the conditions of the Mroga and Mrożyca were to a great extent similar, while those of the Warta were a ‘subset’ of those of the Widawka. Note, however, that this is only the spatial perspective. If we take the size of ellipsis area into consideration, we add the aspect of temporal dispersal, which has the ecological dimension of stability of environmental conditions. This temporal dimension may be ecologically more important than the spatial one (see later sections for details).

Each of the above five characteristics of the environmental profile supplies also some ecological information in view of the geo- and fluvio-statistical knowledge that we possess. Firstly, the excessive elongation of the ellipsis of the Bzura is quite understandable because the investigated section of the river was a first stream order section (although already in the potamon), while such sections are more environmentally unstable than others. Secondly, the small and little elongated ellipsis of the Warta is also explainable by the large size of the river, (and resulting stable environmental conditions over the year) because the investigated river section was a fifth stream order section. Thirdly, the peripheral location of the ellipses of the Grabia and Moszczenica, at the opposite extremes of PC 1, might suggest that their location is catchment-specific (i.e. greatly affected by environmental properties of a given catchment) as each of the two rivers belongs to a different catchment. However, the locations are probably not catchment-specific, because the rivers do not flow at the edges of the study area.

4.3. ANOSIM-based pattern of the rivers and its relation to the environmental profile and clustering pattern

ANOSIM-based Table IV presents similarities among rivers. The congruence of the similarities with the environmental profile varies. It is the Widawka and Grabia Rivers that are most similar to each other in the ANOSIM-based pattern (distance 47.64; range 0-100). The ellipses of these rivers only adjoin in the environmental profile. The Mrożyca and Mroga are the second most similar pair of rivers (distance 57.72) in the ANOSIM-based pattern, which also agrees with the environmental profile, where the ellipses of the two rivers overlap by more than half of their area. The third greatest ANOSIM-based similarity (67.76), that of the Moszczenica and Mrożyca, is also congruent with the profile, in which the ellipses of the two rivers adjoin. But there is also some divergence. The Grabia and Mrożyca are the fourth most similar pair of the ANOSIM-based pattern, while they are distant in the environmental profile. In contrast to the environmental profile, the ANOSIM-based Warta differs from all the other rivers (14th, 15th, 17th, 18th, 19th and 21st similarity values among 21 comparisons, Table IV). Consequently, the Warta is least explained by the environmental profile, unless it is assumed that the great stability and average values of environmental parameters are factors that decided about the river's separateness, which is of course possible.

The differentiation of chironomid assemblages among the investigated rivers indicated by the ANOSIM-based analysis seems to be connected to rather common than rare species, i.e. *P. olivacea* (Prodiamesinae), *C. riparius, P. scalaenum, P. convictum, S. sticticus* (Chironominae: Chironomini), *M. notescens* and *C. mancus* (Chironominae:

Tanytarsini). The above mentioned species are classified as eurytopic and opportunistic (Wiederholm 1983).

4.4. Clustering pattern of the rivers and its relation to the environmental profile and the ANOSIM-based pattern

Clusters of Figure 3 show the distances among the rivers. There is a considerable degree of congruence between the clustering pattern and the environmental profile, which indicates that the environmental conditions greatly affected the species that account for differences between studied assemblages.

In the environmental profile, the Mroga and Mrożyca greatly overlap, the Mrożyca adjoins the Moszczenica, the Mroga almost adjoins the Moszczenica, and the Bzura slightly overlaps the Mrożyca and Mroga. All the above is in considerable agreement with the clustering pattern, in which the four rivers form one large cluster (distance 0.53; range 0-1), although the Bzura and Moszczenica are much farther (distances 0.53 and 0.48, respectively) than the most tight sub-cluster (of the whole region) of the Mroga and Mrożyca (distance 0.27). This is mostly in agreement with the ANOSIM-based pattern, because the Mrożyca and Mroga are the second most similar pair of rivers (distance 57.72). The third most similar pair of the ANOSIM-based pattern were the Moszczenica and Mrożyca (distance 67.76), which is also greatly similar to the clustering pattern. Slightly less agreement is presented by the Grabia and Widawka, which are also in a tight sub-cluster (distance 0.28), but do not overlap and only adjoin in the environmental profile, and the pair is far from the other rivers (distance 0.67). A considerable lack of congruence is presented by the Widawka, which slightly overlaps the Bzura and Mroga in the environmental profile, whereas the latter two rivers are in different clusters than the Widawka. The greatest lack of congruence seems to concern the Warta, which is almost completely ‘nested’ within the Widawka in the environmental profile (and slightly overlaps the Bzura), while it is most separate from all other rivers in the clustering pattern (distance 0.79).

However, the above perspective is purely spatial. If it is changed to a spatio-temporal one, i.e. such that month to month variability during the annual sampling cycle is taken into account, then both the large distance of the Warta, considerable distance of the Bzura (0.53) and even that of the Moszczenica (0.48) become explainable by environmental conditions. In the case of the Warta, the large distance to other rivers in the clustering pattern may have resulted from an extremely small dispersion of monthly values of environmental variables, and thus a great stability of environmental conditions over the year. In the case of the Bzura, the considerable distance to other rivers may have resulted from the greatest dispersion, i.e. instability of environmental conditions over the year. The dispersion of the Moszczenica environmental values is intermediate between the extremes of those of the Warta and Bzura, and also smaller than those of the remaining rivers. Yet, the Moszczenica is located far from the Warta and Bzura along axis PC 1 in the environmental profile, which indicates that the occurrence and abundance of its species may have been determined by much higher loads of TPOM and much lower values of dissolved oxygen (Table III).

The clustering and ANOSIM-based patterns are in some respect complementary. An example is the affinity of the Grabia and Widawka, which was identified in the environmental profile. Although the affinity did not manifest itself in the clustering pattern of rivers, it was identified in the ANOSIM-based pattern.

4.5. Group of species accounting for differences in assemblage compositions

Chironomid species of the studied rivers varied in the sensitivity to which they responded to environmental factors, and thus varied in the degree to which they accounted for differences between the rivers. The SIMPER-identified 14-species group presented in Table V are those species that were most sensitive to environmental factors and clearly differ from the rest of the species. As the rest (47) accounted for 43% of variability, then each of them explained on average less than 0.91%. Meanwhile each of the 14-species group explained on average as much as 4.07%, the differences within the 14-species group being moderate (range: 2.873-6.131). As many as 11 species of the 14-species group are of the subfamily Chironominae (eight of the Chironomini tribe, and three of the Tanytarsini tribe). This indicates that this subfamily responds much stronger to the environmental profile of our region than other tribes and subfamilies.

4.6. Univariate alpha species diversity (*species richness, diversity per se, entropy as diversity, dominance, and evenness*) *measures of the studied rivers*

Species diversity assessment is essential for protecting diversity from genes to ecosystems (Koperski 2010; Móra & Szivák 2012; Magurran & McGill 2011), and thus it is also used in this study, in the form of alpha univariate diversity measures (Smith & Wilson 1996; Magurran & McGill 2011). Similarly to the clustering and ANOSIM measures, the univariate diversity measures that we apply here are non-parametric, i.e. not related to the species abundance distribution (SAD) underlying the assemblage that a measure describes. Such univariate diversity measures were chosen to avoid two shortcomings of the parametric measures: difficulty of selecting the correct SAD, and difficulty of comparing assemblages described by SADs (McGill et al. 2007)

However, the univariate species diversity measures also differ greatly from the clustering and ANOSIM-based approaches because the former are absolute while the latter are relative. The relative measures present the compositional distance of each and every river from all other rivers in an abstract space. The absolute measures do not measure such distance, but supply a stand-alone assessment of each river instead (Figure 4). Such stand-alone assessment may be compared with any other similar assessment obtained in this study (and tested for statistical significance by means of bootstrapping and ANOVA, for example) or elsewhere. In contrast, a comparison of the present rivers with others in terms of clustering or ANOSIM would require the recalculation of source data from the present and the other rivers.

While the relative measures displayed the whole compositional difference between rivers, the univariate diversity measures display only that part of diversity (or concentration or evenness) that occurs within given rivers, i.e. the alpha component. This part may be averaged and joined to the beta component (between rivers) to create gamma diversity (Whittaker 1960), i.e. diversity of the region. This estimate is provided in the case of N_0 and N_1 (see Results), though the average alpha, beta and gamma diversity is calculated for the 82 assemblages instead of the seven rivers. Although the measures in Figure 4 may not be informative about the whole compositional difference among rivers they are useful because they provide information about compositional differences that the other measures do not.

In Figure 4, rivers are arranged in each measure according to increasing stream orders and the values of the rivers vary both within and between measures. In the case of species richness, diversity *per se* and Shannon entropy, the rivers present a humpback pattern, with the first and last rivers being the lowest values (or almost the lowest, as in N_0). In the Simpson concentration, the pattern is a vertical mirror image of the humpback pattern, with the first and last rivers being the highest values. Lack of a clear pattern occurs in the two evenness measures, although for the Pielou evenness the first and last rivers are also the lowest values.

In N_0, the values accord with previous studies (Coffman 1989), where an increase in species richness is recorded from stream order 1 through order 3, and stabilization occurs in higher orders. In contrast, in the Warta a clear decrease occurred. This finding is, however, in accordance with the results of other studies conducted worldwide, which indicate that an abrupt change in macroinvertebrate assemblages may frequently be noted in the 4th and/or 5th order streams (Hynes 1970; Minshall & Robinson 1998; Melo 2009). The pattern of N_0 was modified in the diversity *per se* and Shannon measures in such a way that the hump became gradually level, although not to an extent that would make the pattern unidentifiable. This levelling off was an effect of numerous factors, with the most important the decreasing impact of rare species and increasing impact of abundant species from measure to measure.

The values of the two evenness measures (BGS and Pielou) presented in Figure 4 are unexpected, being greatly different from those in the remaining five measures and from each other. While the BGS measure distinguished a homogenous group of three rivers (the Grabia, Widawka, and Warta), each of the rivers belonged to a different group in the Pielou measure. This result of the BGS measure may be explained if we remember that the measure is also the ratio of N_1/N_0 (or N_1/S). The respective divisions are as follows:

Grabia: 5.768(N_1) / 17.716(N_0) = 0.3256,

Widawka: 6.725(N_1) / 18.846(N_0) = 0.3568,

Warta: 3.166(N_1) / 9.339(N_0) = 0.3390.

The results are so similar that the ANOVA (applied to bootstrap pseudo-samples) *post-hoc* test ascribed the three rivers to one group. The results are understandable because the ratios of these three rivers in N_1 and N_0 are similar. Conversely, in the Pielou measure, which is the ratio of the Shannon measure to the natural logarithm of N_0, it was not the case. Although the Shannon measure ratio of these three rivers is also similar to that in N_1, yet the lnN_0 values of the rivers are now greatly changed, hence the outcomes of divisions are also different from those in the BGS measure. Inspect related calculations:

Grabia: 1.724(Shannon) / 2.8744(lnN_0) = 0.5998

Widawka: 1.853(Shannon) / 2.936(lnN_0) = 0.6311

Warta: 1.112(Shannon) / 2.234(lnN_0) = 0.4977

which explain why the ANOVA *post-hoc* test ascribed all three rivers to different groups each. Note that a disparity as small as 1.13 species (between the Grabia and Widawka) was enough to effect a significant difference.

But reverse outcomes as regards the impact of difference in species number also occurred. In the Pielou measure, differences as large as 5.482 species (the Bzura and Warta) and even 7.557 species (the Mrożyca and Grabia) were not large enough to ascribe rivers of each of these pairs to different groups. Consider the related calculations, in which the results of divisions in the former pair and in the latter pair are similar:

Bzura: 0.636(Shannon) / 1.3499($\ln N_0$) = 0.4711
Warta: 1.112(Shannon) / 2.2342($\ln N_0$) = 0.4977
Mrożyca: 1.423(Shannon) / 2.3184($\ln N_0$) = 0.6138
Grabia: 1.724(Shannon) / 2.8744($\ln N_0$) = 0.5998

In other words, if we had relied on the BGS measure only, we would have concluded that the Grabia, Widawka and Warta were quite similar to one another, while all the other rivers greatly different. Conversely, if we had relied on the Pielou measure only, we would have concluded that only the Warta and Bzura, and also the Mrożyca and Grabia were similar to each other, while the Grabia, Widawka and Warta were not. Note that both the Pielou and BGS measures are perfect evenness measures (Jost 2010). However, they indicate different aspects of evenness.

These different aspects have been identified only recently. For many previous decades the BGS measure was considered superior to the Pielou, because the former is replication invariant, i.e. does not change its value when the measure is applied to a dataset that consists of the original assemblage pooled with its copy (as regards SAD) that includes all different species (Alatalo 1981; Taillie 1979), while the Pielou measure does change. Jost's (2010) analysis indicated that a change of perspective renders the importance of the two evenness measures differently. BGS gives the absolute evenness and inequality: when the number of species is higher, a maximally unequal assemblage shows more absolute inequality (less absolute evenness) than when the number of species is low. In contrast, the values of the Pielou measure remain correct relative to the possible range of evenness at a given number of species. Consequently, the Pielou measure should be considered the ideal relative evenness measure (Jost 2010).

To conclude, in a set of lowland rivers with different environmental profiles, chironomid communities were different both in terms of abundance and diversity. Notably some chironomids species, despite the environmental plasticity associated with the family, were absent in some rivers, which may indicate the existence of specific habitat preferences.

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Figure captions

Figure 1. Map of the study area.

Figure 2. Habitat profile of examined rivers in Central Poland depicted by PC scores (average ± standard error).

Figure 3. Clusters of chironomid abundance in the examined rivers of central Poland obtained using the UPGM method and Pearson correlation as a similarity index.

Figure 4. Means (and their standard deviation - whiskers) of bootstrap pseudo-samples of species richness, diversity *per se*, dominance and evenness measures calculated for sets of chironomid assemblages in each studied river. Simple ANOVA was used to assess if the means of the rivers differed significantly. Letters at the standard error values indicate homogeneous groups in each index. The units of the y axes of N_0, N_1,

and N_2 measures are numbers of species. The units of the y axes of the remaining measures are abstract numbers.

Table captions

Table I. Environmental parameters measured/estimated at the study sites located in seven examined rivers in Central Poland ($\bar{x}$ average, CV coefficient of variation).

Table II. The list of identified chironomid species with their mean density (ind. m^{-2}), standard deviations (sd), occurrence frequencies (f) and total number of species from seven examined rivers in Central Poland.

Table III. Loadings (Pearson correlations) of bottom substratum variables on the principal components of principal component analysis (PCA) conducted on data from 82 sampling points in seven rivers in Central Poland. Only components with eigenvalues >1 were retained. Two PCA axes accounted for 64.7% of the total variance. Values with loadings greater than module (0.5) are in bold. NS $P>0{\cdot}05$, $^{*}P<0{\cdot}05$, $^{**}P<0{\cdot}01$, $^{***}P<0{\cdot}001$.

Table IV. Bray-Curtis overall dissimilarity between the structures of given chironomid assemblages that was received from ANOSIM analysis (in the upper triangle of the matrix) and probability of Bonferroni pairwise post-hoc comparisons (below the diagonal).

Table V. Given species' contribution to overall dissimilarity among the chironomid assemblages of the seven examined rivers in Central Poland obtained from SIMPER analysis.

Table I. Environmental parameters measured/estimated at the study sites located in seven examined rivers in central Poland: average/coefficient of variation.

River name Characteristic	Bzura	Mroga	Mrożyca	Moszczenica	Grabia	Widawka	Warta
Water velocity [m s^{-1}]	0.24/0.18	0.06/1.69	0.06/0.17	0.04/0.61	0.36/0.35	0.37/0.31	0.40/0.23
River width [m]	0.74/0.29	3.1/0.23	4.8/0.06	3.9/0.05	15.3/0.06	27.8/0.04	57.0/0.06
River depth [m]	0.07/0.37	0.14/0.78	0.39/0.15	0.28/0.19	0.36/0.08	0.74/0.19	0.56/0.28
SI [mm]	3.4/0.66	4.9/0.46	0.4/0.33	0.3/0.04	20.8/0.22	3.9/0.13	0.8/0.15
BPOM [g m^{-2}]	3092/0.33	5892/0.52	7559/0.58	13951/0.21	404/0.18	1683/0.18	311/0.40
TPOM [g m^{-3}]	131/1.22	12/0.72	15/0.93	17/0.79	31/0.53	44/0.55	13/0.52
Water temperature [ºC]	6.7/0.75	8.9/0.49	9.8/0.53	10.9/0.65	10.8/0.61	10.2/0.73	13.7/0.53
Oxygen content [mg dm^{-1}]	6.1/0.36	6.8/0.31	7.2/0.27	10.5/0.20	8.6/0.28	7.9/0.30	6.9/0.28
Surface of bottom covered by SAM [%]	-	-	-	-	6.9/1.37	2.9/1.39	-

SI – inorganic substrate index, BPOM – benthic and TPOM – transported particulate organic matter, SAM – submersed aquatic macrophytes

Table II. The list of identified chironomid species with their mean density (ind. m^{-2}), standard deviations (sd) and occurrence frequencies (*f*) from seven examined rivers in central Poland.

	Bzura			**Mroga**			**Mrożyca**			**Moszczenica**			**Grabia**			**Widawka**			**Warta**		
	mean	sd	*f*	mean	sd	*f*	mean	sd	*f*	mean	sd	*f*	mean	sd	*f*	mean	sd	*f*	mean	sd	*f*
Tanypodinae																					
Ablabesmyia monilis (Linnaeus)										56	153	0.3	49	48	0.8	41	42	0.8	14	29	0.4
Anatopynia plumipes (Fries)										2	8	0.1									
Apsectrotanypus trifascipennis (Zetterstedt)							2	5	0.1				1	2	0.1						
Conchapelopia melanops (Meigen)	309	518	0.7	30	43	0.4	2	5	0.1	1	3	0.1	2	6	0.1	2	5	0.2			
Macropelopia nebulosa (Meigen)	6	21	0.1	44	55	0.6	31	41	0.6	180	188	0.8	1	3	0.1						
Natarsia punctata (Fabricius)													1	3	0.1	2	7	0.2			
Diamesinae																					
Potthastia gaedii (Meigen)				16	43	0.3							6	9	0.4	2	6	0.1			
Potthastia longimanus Kieffer												0.0	38	61	0.7	33	49	0.6	3	5	0.3
Prodiamesinae																					
Monodiamesa bathyphila (Kieffer)				19	25	0.4	38	52	0.7				18	29	0.7	8	10	0.6			
Odontomesa fulva (Kieffer)				158	318	0.6	23	29	0.5	2	6	0.2	20	27	0.6	19	29	0.6			
Prodiamesa olivacea (Meigen)	2762	2871	0.9	830	766	0.9	714	571	0.8	125	225	0.8	14	12	0.7	254	265	1.0	2	3	0.4
Prodiamesa rufovittata Goetghebuer													15	27	0.6	9	9	0.7			
Orthocladiinae																					
Brillia bifida (Kieffer)							6	16	0.2												
Brillia flavifrons (Johansen)							5	16	0.1	1	3	0.1									
Brillia longifurca Kieffer													31	83	0.3	9	15	0.3			
Cricotopus bicinctus (Meigen)										1	3	0.1	13	20	0.4	13	20	0.4	125	398	0.8
Cricotopus sylvestris (Fabricius)										3	6	0.2	1840	1973	1.0	193	186	1.0			
Diplocladius cultriger Kieffer													9	28	0.2						
Epoicocladius ephemerae (Kieffer)							2	5	0.1												
Eukiefferiella brevicalcar (Kieffer)												0.0	36	43	0.6	30	25	0.9			
Eukiefferiella gracei (Edwards)													1079	997	1.0	4	5	0.5	1	2	0.1
Eukiefferiella sp. 1	3	11	0.1																		
Eukiefferiella sp. 2																2	6	0.1			
Heterotrissocladius marcidus (Walker)	3	11	0.1				72	109	0.5			0.0	55	69	0.7	2	6	0.2			
Heterotrissocladius subpilosus (Kieffer)				11	33	0.2	17	58	0.1												
Nanocladius rectinervis (Kieffer)				4	11	0.2							22	48	0.3				3	9	0.2
Parakiefferiella bathophila (Kieffer)																2	6	0.2			
Paratrichocladius rufiventris (Meigen)																2	5	0.2			
Rheocricotopus fuscipes (Kieffer)	3	11	0.1										20	31	0.4						
Synorthocladius semivirens (Kieffer)							2	5	0.1				55	76	0.5	16	31	0.5			
Thienemanniella clavicornis (Kieffer)													1	4	0.1	16	23	0.5			
Thienemannia gracilis Kieffer										3	8	0.2							3	8	0.2
Tvetenia calvescens (Edwards)										1	3	0.1	20	32	0.4						
Chironominae/Chironomini																					
Chironomus riparius Meigen	7645	6992	1.0	11	23	0.3	2	5	0.1	310	742	0.8				625	671	0.9	2	6	0.1
Chironomus sp. 1										30	53	0.3									
Cryptochironomus borysthenicus (Tshernovskij)							17	58	0.1	50	84	0.4	10	23	0.2				57	92	0.4
Cryptochironomus defectus (Kieffer)	3	11	0.1				29	47	0.6	38	42	0.8	292	312	1.0	103	112	0.9	1	3	0.2

	Bzura			**Mroga**			**Mrożyca**			**Moszczenica**			**Grabia**			**Widawka**			**Warta**		
	mean	sd	*f*	mean	sd	*f*	mean	mean	*f*	mean	sd	*f*	mean	sd	*f*	mean	sd	*f*	mean	sd	*f*
Cryptochironomus supplicans (Meigen)										21	28	0.5									
Dicrotendipes nervosus (Staeger)	6	14	0.2							1	3	0.1							33	88	0.4
Endochironomus albipennis (Meigen)										12	38	0.2							1	2	0.1
Endochironomus sp. 1				3	11	0.1															
Endochironomus sp. 2				15	33	0.3															
Endochironomus sp. 3																			2	8	0.1
Glyptotendipes cauliginellus (Kieffer)	3	11	0.1							7	13	0.3							25	38	0.8
Glyptotendipes paripes (Edwards)				3	11	0.1															
Microtendipes chloris (Meigen)				48	62	0.5	232	386	0.8	60	118	0.6							36	50	0.6
Parachironomus gracilior (Kieffer)							2	5	0.1	1	4	0.1				1	4	0.1	3	9	0.1
Paracladopelma camptolabis (Kieffer)				7	21	0.2	26	42	0.4				11	25	0.2	62	59	0.9	12	40	0.2
Paratendipes albimanus (Meigen)	6	14	0.2	62	158	0.3	179	383	0.4	744	1257	0.6	46	94	0.3	2	5	0.2	82	170	0.5
Paratendipes connectens Lipina										7	23	0.1							196	432	0.6
Polypedilum convictum (Walker)							2064	1656	1.0	19	43	0.3	1071	1186	1.0	1017	485	1.0	1	4	0.1
Polypedilum nubeculosum (Meigen)	6	14	0.2							120	213	0.6	38	39	0.8	34	39	0.8	2	4	0.2
Polypedilum pedestre (Meigen)							2	5	0.1	1	4	0.1				17	16	0.8	4	13	0.1
Polypedilum scalaenum (Schrank)	3	11	0.1	38	50	0.5	1589	1419	1.0	1102	2379	0.9							1	3	0.2
Robackia demeijerei (Kruseman)										11	33	0.2							764	642	1.0
Stictochironomus sticticus (Fabricius)	3	11	0.1	275	229	0.9	434	390	0.8			0.0	138	192	0.7	65	80	0.8	3	9	0.2
Chironominae/Tanytarsini																					
Cladotanytarsus mancus (Walker)				12	42	0.1	162	522	0.2	11	20	0.3	2436	1620	1.0	254	192	1.0			
Micropsectra notescens (Walker)	2166	641	0.2	79	74	0.8	3697	6313	0.9	3	5	0.3	323	313	0.9	41	37	0.9			
Paratanytarsus dissimilis (Johannsen)													3	5	0.3	102	94	1.0	339	816	1.0
Paratanytarsus sp. 1				15	53	0.1				18	62	0.1									
Tanytarsus gregarius Kieffer													384	386	0.8	2	5	0.2	1	4	0.1

Table III. Loadings (Pearson correlations) of bottom substratum variables on the principal components of principal component analysis (PCA) conducted on data from 82 sampling points in seven rivers in Central Poland. Only components with eigenvalues >1 were retained. Two PCA axes accounted for 64.7% of the total variance. Values with loadings greater than module (0.5) are in bold. NS P>0·05, *P<0·05, **P<0·01, ***P<0·001.

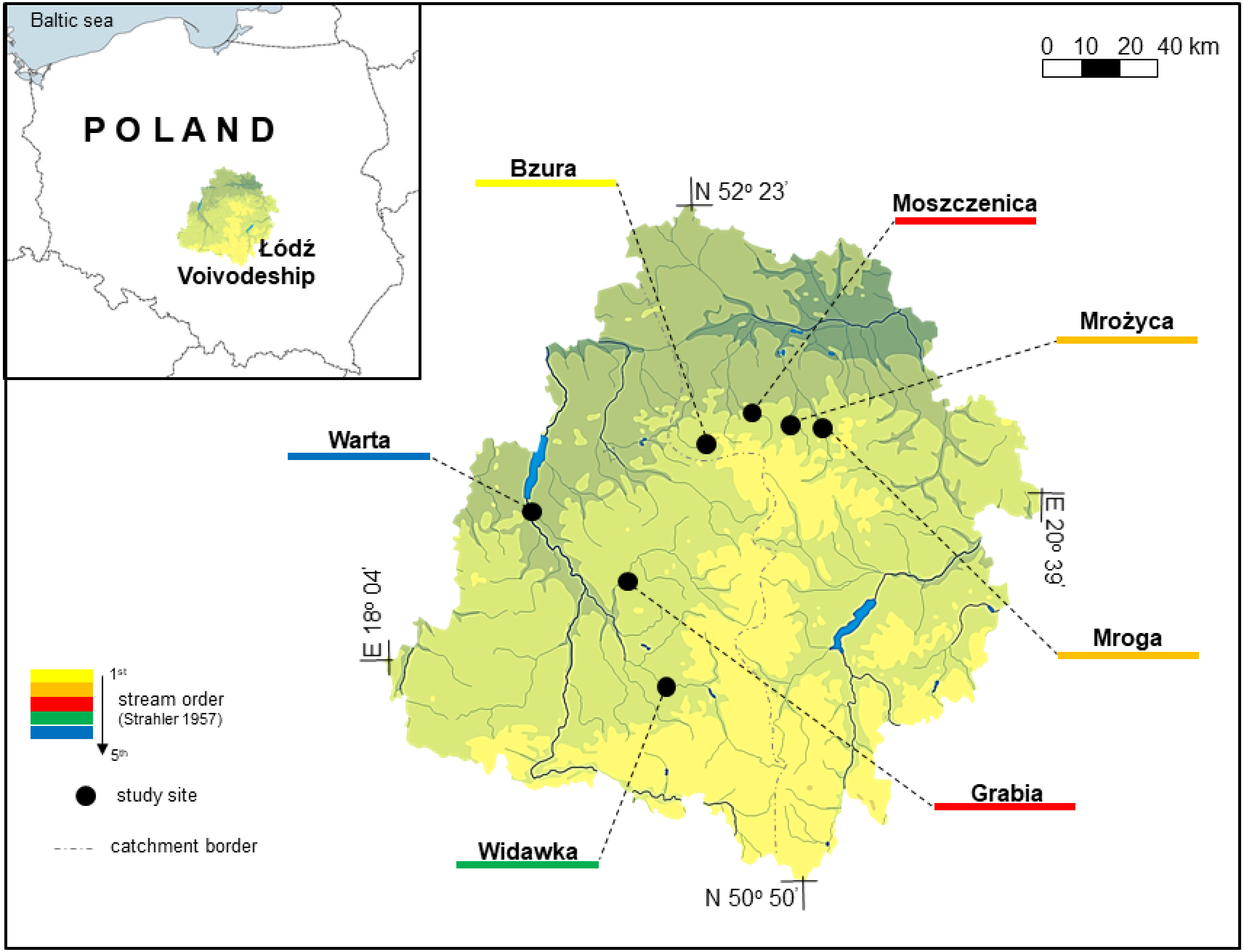
Parameter	PC-1	PC-2
Water velocity (m s^{-1})	**-0.8614*****	-0.0458 ^{ns}
SI	**-0.6589*****	-0.4569***
BPOM (g m^{-2})	**0.8827*****	0.0147 ^{ns}
TPOM (g m^{-2})	-0.3267**	**0.5262*****
Dissolved oxygen (mg dm^{-3})	0.2278^{ns}	**-0.7972*****
eigenvalue	2.114	1.123
% of explained variance	42.279	22.470

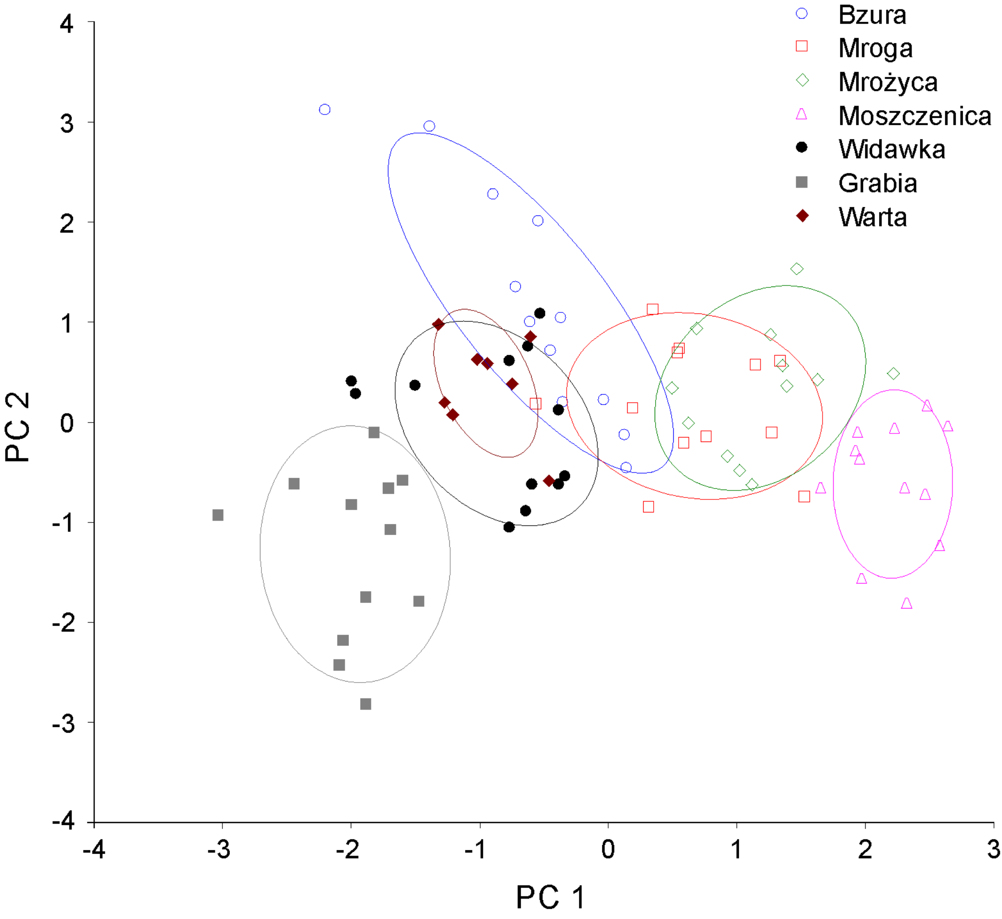
Table IV. Bray-Curtis overall dissimilarity between the structures of given chironomid assemblages that was received from ANOSIM analysis (in the upper triangle of the matrix) and probability of Bonferroni pairwise post-hoc comparisons (below the diagonal).

River	Bzura	Mroga	Mrożyca	Moszczenica	Grabia	Widawka	Warta
Bzura		**72.76**	**82.44**	**74.81**	**92.29**	**76.44**	**94.54**
Mroga	0.0001		**57.72**	**74.64**	**82.00**	**76.53**	**91.84**
Mrożyca	0.0001	0.0001		**67.76**	**68.39**	**85.45**	**89.09**
Moszczenica	0.0001	0.0001	0.0001		**82.14**	**75.47**	**83.47**
Grabia	0.0001	0.0001	0.0001	0.0001		**47.64**	**89.35**
Widawka	0.0001	0.0001	0.0001	0.0001	0.0001		**82.66**
Warta	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	

Table V. Given species' contribution to overall dissimilarity among the chironomid assemblages of the seven examined rivers in central Poland obtained from SIMPER analysis.

Taxon	Average dissimilarity	Contribution %	Cumulative contribution %
C. riparius	4.717	6.131	6.131
P. convictum	4.201	5.460	11.59
P. olivacea	3.963	5.150	16.74
P. scalaenum	3.656	4.751	21.49
M. notescens	3.651	4.745	26.24
S. sticticus	3.399	4.418	30.65
C. mancus	3.118	4.053	34.71
C. defectus	2.711	3.523	38.23
P. albimanus	2.643	3.436	41.67
C. sylvestris	2.614	3.397	45.06
M. chloris	2.511	3.263	48.33
M. nebulosa	2.388	3.104	51.43
P. dissimilis	2.312	3.005	54.44
R. demeijerei	2.211	2.873	57.31


Baltic sea
POLAND
Łódź
Voivodeship
0 10 20 40 km
Bzura
N 52° 23'
Moszczenica
Mrożyca
Warta
E 20° 39'
E 18° 04'
Mroga
Grabia
Widawka
N 50° 50'
1st
stream order
(Strahler 1957)
5th
study site
catchment border


Bzura
Mroga
Mrożyca
Moszczenica
Widawka
Grabia
Warta
PC 2
PC 1
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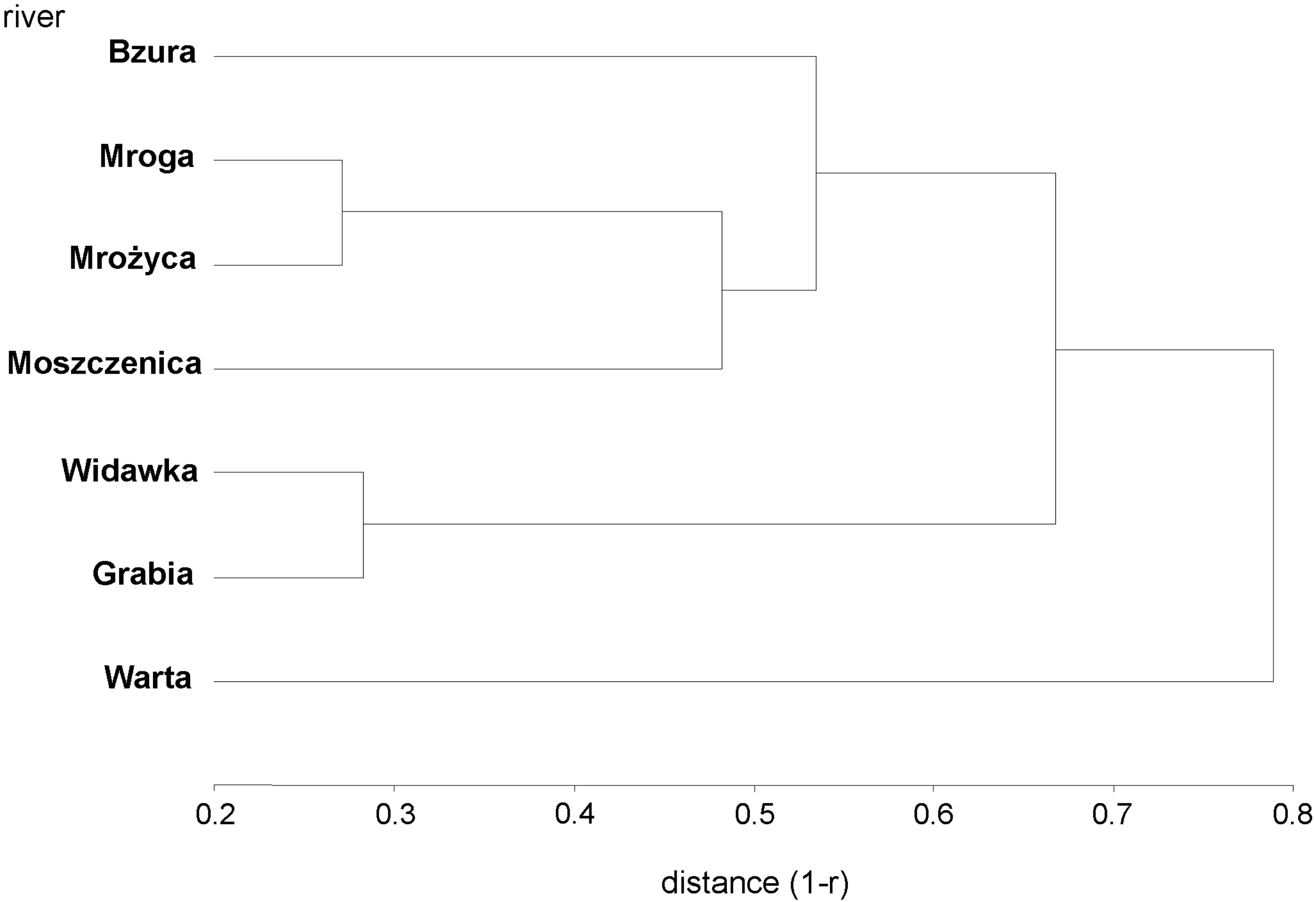
river
Bzura
Mroga
Mrożyca
Moszczenica
Widawka
Grabia
Warta
0.2
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0.4
0.5
0.6
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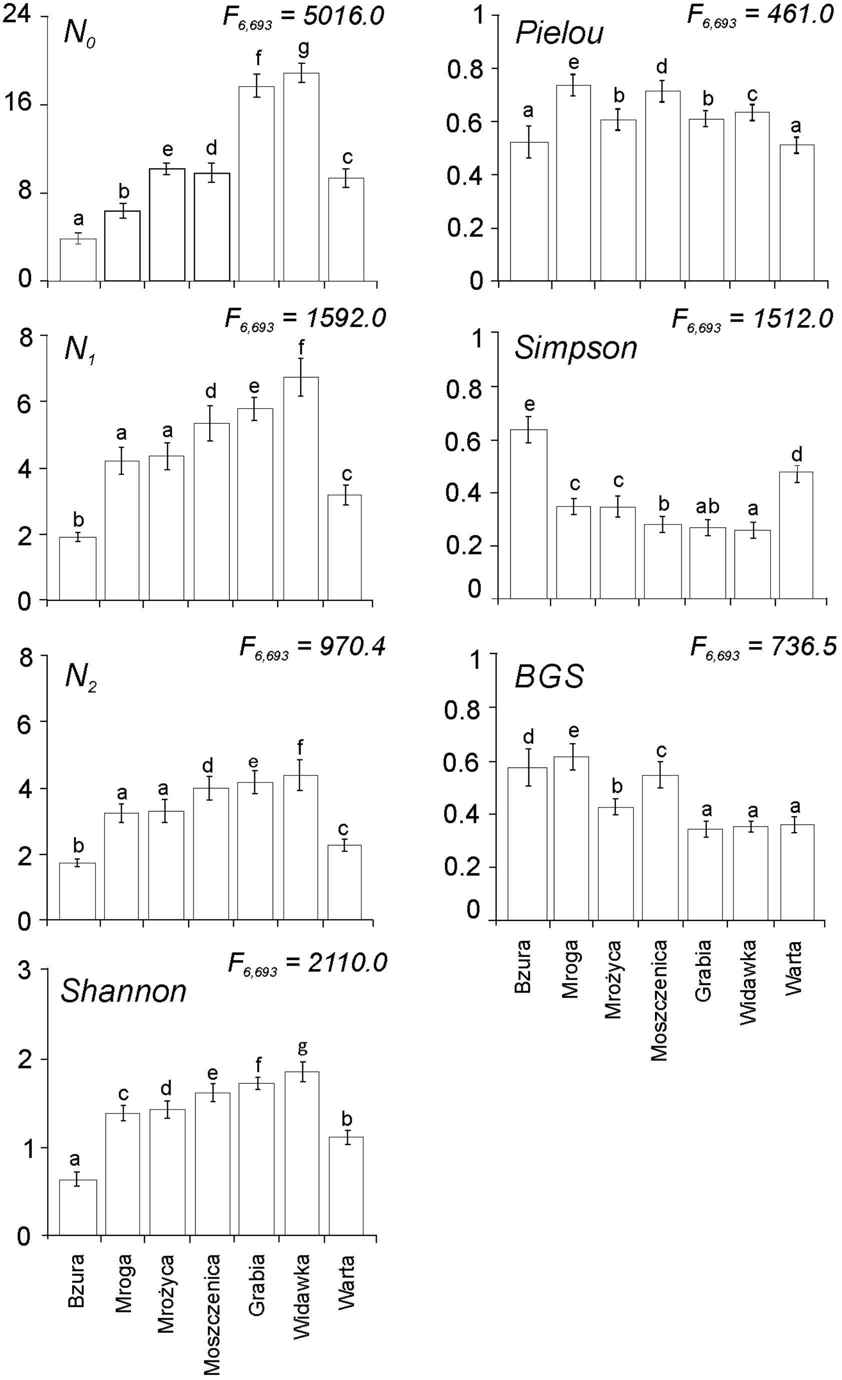
0.8
distance (1-r)


N0
F6,693 = 5016.0
0
8
16
24
a
b
e
d
f
g
c
Pielou
F6,693 = 461.0
0
0.2
0.4
0.6
0.8
1
a
e
b
d
b
c
a
N1
F6,693 = 1592.0
0
2
4
6
8
b
a
a
d
e
f
c
Simpson
F6,693 = 1512.0
0
0.2
0.4
0.6
0.8
1
e
c
c
b
ab
a
d
N2
F6,693 = 970.4
0
2
4
6
8
b
a
a
d
e
f
c
BGS
F6,693 = 736.5
0
0.2
0.4
0.6
0.8
1
d
e
b
c
a
a
a
Shannon
F6,693 = 2110.0
0
1
2
3
a
c
d
e
f
g
b
Bzura
Mroga
Mrożyca
Moszczenica
Grabia
Widawka
Warta

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Factors shaping species richness and biodiversity of riverine macroinvertebrate assemblages at the local and regional scale

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Keywords: Abiotic variables, Aquatic insects, Damming, Landscape fragmentation, (Non-)saturation, Nutrients.

Abstract: The biodiversity and species richness of benthic macroinvertebrate assemblages are under the strong pressure of environmental variables compounded with geographical and historical processes. Numerous studies that have investigated biodiversity and assemblage stability have shown the importance of choosing proper methodologies and paradigms. Consequently, the use of diversity measures and the partitioning of biodiversity at different spatial and temporal scales are of particular significance. Within habitats, only those species whose preferences remain within a tolerable range of the variability of abiotic factors are able to survive. The structure of biocoenosis at the local scale is determined mainly by current velocity/discharge, granulometry of the inorganic bottom substrate, quantity and quality of particulate organic matter, as well as water quality variables. Dispersion plays a key role in shaping regional diversity gradients, which supports the permanent inflow of individuals and their exchange between riverine basins. However, dispersion is also one of the basic aspects of the saturation/non-saturation of local communities with species from the regional species pool; a respective concept tries to determine how, why and to what degree local species richness is dependent on regional species richness.

Nomenclature: Fauna Europaea (2017).

Abbreviations: ENV – Environmental Variables; EPT – Ephemeroptera Trichoptera Plecoptera; LSR – Local Species Richness; OLS – Ordinary Least Squares; POM – Particulate Organic Matter; RSR – Regional Species Richness.

Introduction

Benthic macroinvertebrates play a key role in the circulation of organic matter and the flow of energy in running waters thanks to their feeding preferences, life histories and being prey for consumers at higher trophic levels (Cummins et al. 1983). Meanwhile a sufficiently high level of macroinvertebrate biodiversity is essential to maintain homeostasis in lotic ecosystems (Graça et al. 2004, Duan et al. 2008, 2009). One cause of increasing interest in aquatic macroinvertebrate diversity in recent years has been the intensification of human pressure on the natural environment, which usually results in a decrease in biodiversity (Burgmer et al. 2007, Smith et al. 2009, Rezende et al. 2014, Sokol et al. 2014, Fig. 1). However, reduced biodiversity may also be related to abiotic variables that regulate the abundance and structure of macroinvertebrate assemblages in aquatic ecosystems. The values of these variables can fluctuate considerably in time and space, simply as a result of natural ecological processes (Vannote et al. 1980, Graça et al. 2004, Elliott and Quintino 2007, Clarke et al. 2010, Szczerkowska-Majchrzak and Grzybkowska 2015), but some of them may also influence the environment directionally.

Many different measures are used to assess biodiversity (including macroinvertebrate diversity), the most popular being species richness and the Shannon and Simpson indices, but the partitioning of biodiversity at different spatial scales (i.e., α for local, β for between-habitat, and γ for regional biodiversity: Whittaker 1972, Loreau 2000, Whittaker et al. 2001, Głowacki 2009, 2013) may also be essential. Using the above mentioned measures, hydrobiologists have determined that changes in the structure of macroinvertebrate communities along the course of a river can be connected to biogeographical, temporal and even historical factors operating at various scales (Vannote et al. 1980, Mykra et al. 2007). The measures are used to assess various concepts of species relations, which are mainly dichotomies such as: saturation versus non-saturation, interaction versus non-interaction, emigration versus immigration, local scale versus regional scale, and others.

Nowadays, the assessment of which variables (i.e., spatial environmental and/or temporal environmental) dominate in the structuring of diversity gradients in zoobenthos is also a widely investigated aspect (Heino et al. 2003, Mykra et al. 2007, Heino 2013, Rezende et al. 2014; Fig. 2). Many long-term field or experimental investigations conducted worldwide indicate that riverine macroinvertebrate diversity in particular habitats depends mainly on local abiotic variables, especially inorganic bottom substrate as well as quantity and quality of particulate organic matter – the main food resource for macroinvertebrates. In contrast, the most often distinguished variables that act as main determinants of the struc-

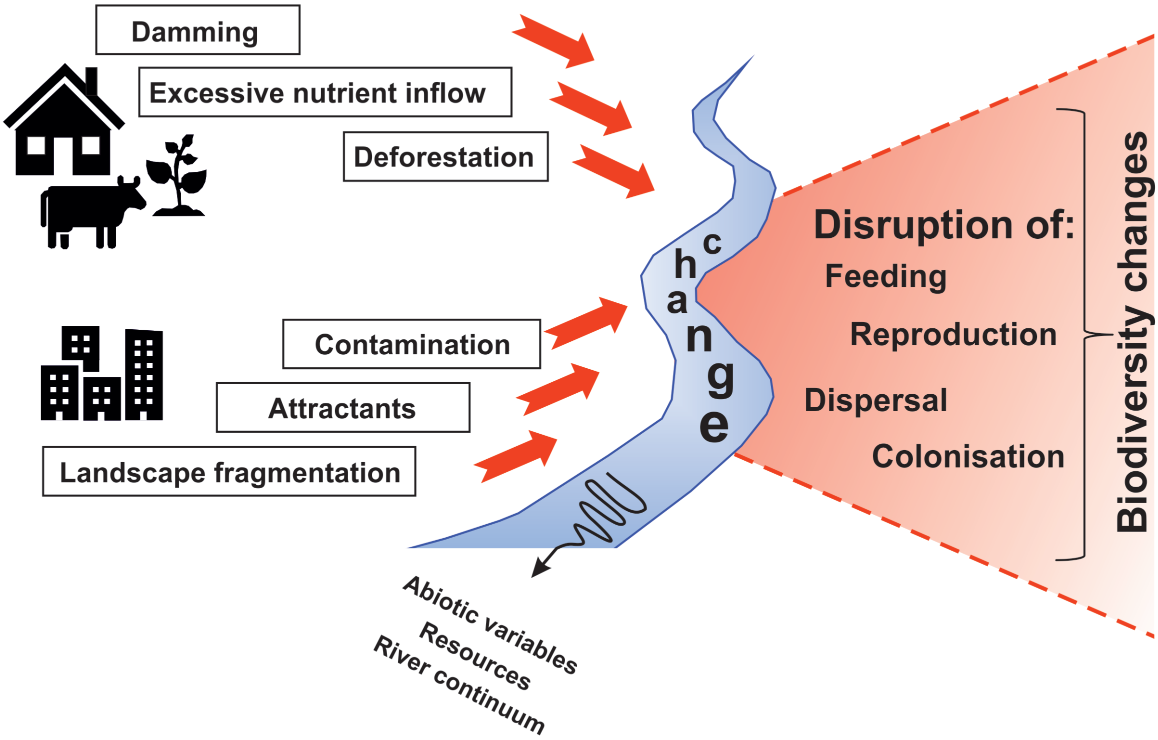

Figure 1. Different types of human impact on the natural environment.

ture of macroinvertebrate communities at the macro scale are discharge or current velocity (Minshall and Robinson 1998, Graça et al. 2004, Costa and Melo 2008, Fig. 2). Influence of environmental factors on freshwater macroinvertebrate diversity is very well investigated in Europe and North America and presented in seminal complex reviews (Malmqvist 2002, Clarke et al. 2008). The assessment of the influence of such factors from the rest of the world is still underdescribed, as was indicated by Schmera et al. (2017).

This review focuses on the impact of selected factors on riverine macroinvertebrate species richness and diversity at different spatial and temporal scales. The term ‘species richness’ refers here to the number of species, while ‘species diversity’ is expressed in diversity indices, which take into consideration both the number of species and their relative proportions. The review is based on the literature published mainly in the recent 20 years to show different and new approaches to the investigating of the relationship between environmental variables or human impact and macroinvertebrate diversity in different parts of the world. A link between well-documented knowledge from Europe and North America, and results of investigations from Asia, South America and Africa, is presented, which is a quite novel approach. The review focuses on: (i) indicating the most often described aquatic macroinvertebrate diversity factors, (ii) defining the scale of their influence (local/regional), (iii) presenting some examples of responses of macroinvertebrate communities to these factors in terms of diversity.

Results

Main factors determining macroinvertebrate diversity at the local scale or in a particular habitat

Inorganic bottom substrate. In general, it has been found that the most conductive substrate fraction for the development of zoobenthos is one consisting of gravel and pebbles, which have a positive influence on the appearance of peryphiton (a food resource for many groups of macroinvertebrates) and act as support shelters (i.e., refuges for small forms and stages of aquatic insects: Grzybkowska and Witczak 1990). This coarse fraction is usually more stable than fine sediments and can more effectively protect organisms from adverse changes in abiotic variables, such as increase in current speed inducing flow from the bottom surface and consequent drifting. This is why diversity of macroinvertebrates is often highest in habitats with substrates consisting of coarse sediments (Rezende et al. 2014).

There is no doubt that the least favourable bottom substrate for the development of macroinvertebrates is fine alluvial sand. Many recent studies (e.g., Szczerkowska-Majchrzak et al. 2010, Leitner et al. 2015, Elbrecht et al. 2016) have considered mass deposition of fine sediment as a threat for the diversity of macroinvertebrate assemblages. Among the many studied variables, a particle size < 2000 µm showed significant and negative correlations with the number of species (Wolmarans et al. 2017). However, it sometimes happens that this fraction is successfully colonised by very small forms of zoobenthos. For example, whilst the coarser

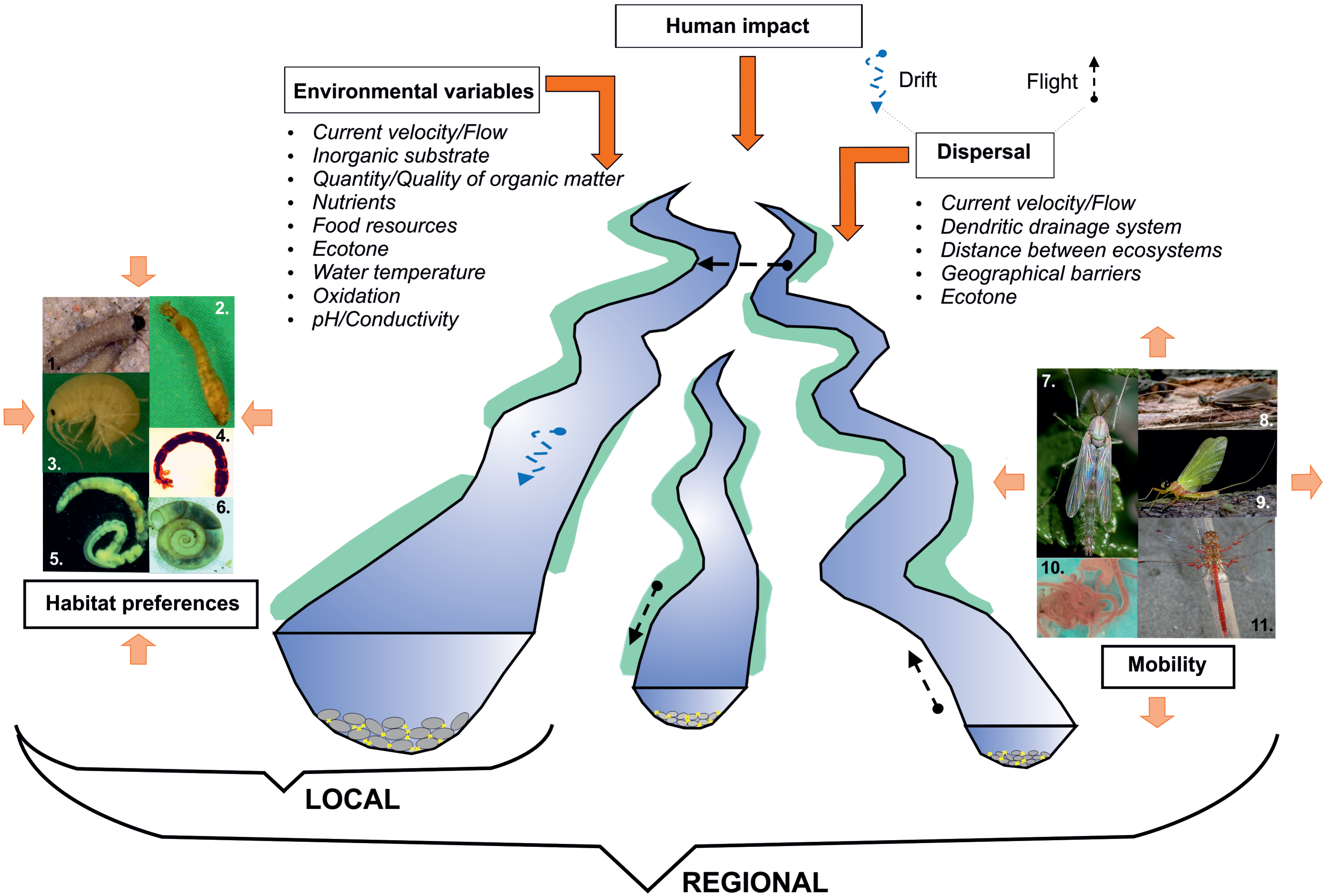

Figure 2. Potential factors determining biodiversity in the environment at various spatial scales (photo credits: 1, 9: K. Majecka; 2, 4, 6: R. Sąsiadek; 3, 5: E. Szczerkowska-Majchrzak; 7–8, 11: R. Jaskuła; 10.: M. Grabowski).

fractions of bottom sediments were preferred by about 40 taxa, good indicators for akal and psammal sediments included only two Chironomidae taxa (Leitner et al. 2015).

In fact, individual species preferences as an effect of morphological and physiological adaptations have a decisive influence on the possibility of maintaining in a given inorganic substrate of particular groups of hydrobionts. But those specific demands that can cause the high density of some organisms on some kinds of bottom can affect their dominance in biocoenoses, and not necessarily diversity (Duan et al. 2009).

Not only grain size can affect macroinvertebrate diversity, but also the structure of riverine bottom. In this respect, macroinvertebrate diversity positively correlated with both interstitial dimensions and substrate porosity, pointing to the important role of streambed heterogeneity as the preferred habitat for a larger number of macroinvertebrate species (Duan et al. 2008).

Organic matter. POM sedimenting on the bottom represents the basic food resource for many taxa and can therefore play a key role in shaping the abundance and diversity gradients of macroinvertebrate assemblages (Graça et al. 2004). Often, an increase in POM biomass can involve a corresponding increase in benthic species richness. In this respect, the number of invertebrate taxa has been found to be positively correlated with the amount of detritus available in particular habitats, hence confirming the above trend (Graça et al. 2004, Costa and Melo 2008).

The results of experiments conducted in last decades of the 20th century are also worth mentioning. Their aim was to overcome labour-intensive and time-consuming research methods for the estimation of zoobenthos abundance, and this was achieved through the use of artificial substrates. For example, Williams (1980) used baskets filled with inorganic substrate (of diverse grain diameter) and POM. This acted as an artificial substrate to obtain representative samples of zoobenthos. After a certain time, a higher biomass and abundance of invertebrates was observed in baskets with higher amounts of organic matter, independently of the heterogeneity of the inorganic bottom substrate.

Autochthonous POM, which mainly comes from decomposition of organic debris within a stream, also plays a key role in shaping species richness and diversity of invertebrates beside allochthonous organic matter, and especially its coarse fraction. Autochthonous POM increases the pool of food resources for shredders and indirectly exerts an influence on the abundance of food (i.e., fine fraction) for other aquatic organisms. Allochthonous coarse POM consists mainly of leaves and branches, which flow seasonally into the river from the ecotone area and gather in shallow, riparian zones or in places where natural flow barriers are located. As a result, a negative correlation between species richness and depth is often noted (e.g., Graça et al. 2004).

Temperature changes. Water temperature is regarded as an essential environmental variable determining the structure of benthic fauna assemblages. Global warming can have a negative impact on the species diversity of many taxa including gastropods, mayflies, beetles, caddisflies and dipterans, even though future likely scenarios are quite hard to predict (Burgmer et al. 2007). Global warming effects, but also other factors related to an increase in the water temperature of lotic ecosystems, can be lessened by canopy cover. This occurs in rivers flowing through dense forests adjoined by abundant vegetation of the ecotone zone. Moreover, canopy cover is profitable also in many other ways, as it stabilises banks, regulates nutrient content, and supports a rich habitat for many taxa (Price et al. 2003).

In the Eriora River in Nigeria, at two study sites with dense riparian vegetation (canopy cover of 70%) located in the nearest area to the source, the highest values in the diversity indices and species richness of benthic fauna were recorded (Arimoro et al. 2012). Also, in the same study, a decrease in canopy cover to 60% caused a considerable decrease in the diversity of macroinvertebrates as compared with that observed at the 70% canopy sites. Similar results were collected in the Pandeiros River (southeastern Brazil), where the lowest species richness and invertebrate diversity occurred at the study sites in which the river flows through deforested areas (Rezende et al. 2014).

Chemical variables of riverine waters. Changes in the chemical composition of riverine waters may be induced by deforestation within the river catchment as well as by other human activities. The consequences of changes in environmental variables, such as dissolved oxygen, pH, conductivity, concentration of nitrates and phosphates for the structure of benthic macroinvertebrate communities have been described (Azrina et al. 2006, Flores and Zafaralla 2012). An investigation conducted on the Mananga River (Philippines), showing that in the upper course, which was subject to weaker human pressure, species richness and diversity of benthic fauna were higher in comparison to sections located far away from the source and characterised by high anthropogenic stress (Flores and Zafaralla 2012). Along the Mananga River, at the study sites located in its lower course, human pressure mainly caused deterioration of water quality, and in particular: an increase in water temperature, in total suspended solids and biological oxygen demand, and a decrease in dissolved oxygen (Flores and Zafaralla 2012).

Differentiation in benthic structure following water quality changes caused by human pressure was also observed in the Langat River in Malaysia (Azrina et al. 2006). In the natural stream sections, 54 taxa of benthic fauna and higher values of diversity indices were recorded compared with sites modified by human activity, where only four taxa occurred. In the natural assemblages, mayflies and chironomids dominated, although caddisflies, stoneflies, dragonflies, beetles as well as other dipterans and gastropods were also present. Conversely, in the modified biocoenoses the dominant organisms were Oligochaeta and Hirudinea. Similar investigations have also been conducted in Poland, where in sections of water courses modified by human pressure Oligochaeta and Chironomidae were mainly noted (Głowacki et al. 2011, Grzybkowska and Głowacki 2011).

Influence of current velocity and flow regime at different spatial scales

Current velocity affects the inorganic structure of the bottom, the transport of organic particles, and the mobility of drifting organisms, and thereby determines species richness and biodiversity of macroinvertebrates at the habitat level (Matthaei et al. 1997). In general, the diverse structure of a biocoenosis and a greater number of macroinvertebrate species are most often connected with high values of current velocity (Grzybkowska and Witczak 1990, Fenoglio et al. 2004, Szczerkowska-Majchrzak and Grzybkowska 2015). In a study conducted in the Marico River in Africa (Wolmarans et al. 2017), the highest taxon richness was observed in habitats characterised by riffles. Only one exception to this trend was noted, namely the lowest macroinvertebrate biodiversity recorded at a site under strong pressure from dam activity, which resulted in irregular releases of water.

A similar influence of current velocity on European macroinvertebrate diversity was confirmed by a mesocosm experiment (Elbrecht et al. 2016), which showed that although reduced current speed did not result in changes in total taxon richness, it still decreased the number of the most sensitive organisms within EPT macroinvertebrates. Also, in the Tibetan-Plateau River, the number of species, diversity and share of EPT in the macroinvertebrate community was found to decrease downstream with decreasing current speed and conductivity (Jiang et al. 2013).

Yet, between particular taxa that are commonly known to be rheophilic (cf. EPT group), distinct preferences for current velocity at the local scale may be observed. These comprise changes in abundance and diversity with increased or decreased current speed. For example, from a comparison of two herbivorous insect larvae, namely the caddisfly *Agapetus boulderensis* and the stonefly *Epeorus* sp. (Plecoptera), it follows that the former favoured lower values of current speed (< 30 cm s^{-1}) whereas the latter preferred fast currents (60–80 cm s^{-1}) (Wellnitz et al. 2001). This correlation between taxa and different values of current velocity was tentatively explained in terms of different taxon mobility. Similarly, in a study on flow velocity tolerance of Limnephilidae (Trichoptera) larvae in a lowland stream, certain species were found to be characterised by different preferences for current speed (de Brouwer et al. 2017). However, for all the above studies values of current velocities of 0.6 m s^{-1}, which are often reached during peak discharges in lowland streams, are critical to maintain suitable habitat for caddisfly species because of their inability to return to the stream bottom as a result of drift.

A decrease in the share of EPT in macroinvertebrate assemblages coupled with an increase in the number of species and abundance of other taxa that are more tolerant to current velocity changes have been recorded (Elbrecht et al. 2016, Jiang et al. 2013). The taxa involved were mostly Chironomidae and Oligochaeta, which are known to be resistant to environmental changes. However, individual species' preferences for current velocity are also found within the Chironomidae family. In this respect, few species of non-biting midges can be indicators of different values of current velocity, with *Polypedilum scalaenum* preferring low current velocities and *Conchapelopia pallidula*, *Orthocladius rubicundus* and *Eukiefierella hospital* being related to moderate ones (Chaib et al. 2013).

Not only current velocity may be essential for macroinvertebrate communities but also flow regime, which nowadays is often disrupted by different human activities. Stream channelisation, which is strictly connected to increase in the speed of runoff and loss of natural riparian zones, is regarded as the most dangerous of human impacts (Verdonschot et al. 2015). Thus, water abstraction results in an overall decrease in the amount of water supplied to rivers in dry summer periods, and this can cause low flows and streambed drying in rivers worldwide, especially in view of global warming. Based on a field experiment in which the flow regime of the river was modified from perennial into intermittent with the creation of three new habitats, namely a stagnant reach, pool and dry streambed it was determined that in the first habitat the richness and abundance of macroinvertebrates experienced a temporal drop (Verdonschot et al. 2015). In the pool, richness decreased but densities increased markedly, whereas in the dry streambed, both richness and invertebrate densities decreased, and only three taxa that were able to survive the entire experimental period in all environments, *Pisidium* sp., *Sialis* sp. and Ceratopogonidae, were distinguished. Although most taxa ($n = 31$) survived in both the control and the stagnant reaches, they were lost from the bottom of the pools or the dry streambed; these included all Ephemeroptera and Plecoptera, and most Trichoptera, as well as many Diptera and Hydracarina. It was also observed that 18 taxa that were not observed in the control samples appeared in the experimental reaches. The majority of these newcomers were not abundant, with the exclusion of mass colonization of pools by *Culex pipiens*, *C. torrentium* and *Chironomus* sp.

The potential link between macroinvertebrate diversity and hydrological regime instability was confirmed also for quite specific perennial streams in rivers of the Middle East (Oman) and Africa. High water and air temperatures and specific flow regimes caused two main taxa that are tolerant to abiotic variables changes, namely Chironomidae and Pulmonata, to survive (Boulaaba et al. 2014). Moreover, the influence of flow regime on macroinvertebrate communities is not only related to the extent of dry periods but also to episodes of heavy rainfalls, which cause local floods. Besides, a negative relationship has been found between EPT abundance and amount of heavy rainfall, suggesting lower EPT abundance during periods of heavy rains and higher densities in dry seasons (Boulaaba et al. 2014).

Saturation versus non-saturation (species pool analysis, local and regional species richness)

This important concept attempts to assess the meaning of regional factors (mainly species pools) and processes for species diversity at the local scale (i.e., its saturation with species), the diversity being understood as species richness. Such assessment is of great value in streams, because they are among the most threatened ecosystems on Earth (Vinson and Hawkins 1998). Initially, saturation or non-saturation was believed to depend mostly on the interaction or non-interaction of species within local communities, which was tested by regressing local species richness (LSR) on regional species richness (RSR). This paradigm was formulated in the 1970s and 1980s (Cornell and Lawton 1992, Srivastava 1999), and appeared as a variant of species diversity analysis (Ricklefs 1987), which was mostly species pool analysis, although the term was coined later. According to it, one extreme of the LSR-RSR relationship is a completely unsaturated case, expressed by a linear, sloppy (and thus significant) regression line, and the other a completely saturated case, expressed by a horizontal line of no dependence. Real local communities are expressed by a curvilinear relation, located between the two above extremes, higher degree of saturation being dependent on higher degree of species interaction within the community.

Although a saturated (i.e., interaction-related) LSR community might be connected to numerous models of niche heterogeneity (classical niche, resource ratio, temporal niche) or spatio-temporal heterogeneity (lottery, random walk, aggregation, disturbance, specialist predator) (Cornell and Lawton 1992) no model was considered usual, indispensable or critical. Gradually, the LSR-RSR assessed saturation/non-saturation concept became more and more deeply related to several other general concepts, such as competitive exclusion, immigration rate versus emigration rate, historical/evolutionary versus ecological time scales, scale-dependence of both local and regional sampling areas, (lack of) speciation, disturbance versus stability, impact of environmental factors, and others. Dozens of studies exploring these concepts to higher or lower extent in the case of numerous species groups appeared in the last decade of the 20th century.

Yet, problems soon began to pile up as regards both the technical and conceptual issues of the LSR-RSR paradigm. Srivastava (1999) discovered that half of 30 such studies were pseudoreplicated, and thus provide unreliable conclusions, which may additionally be biased in frequently unpredictable way by differences in sample size and sampled area, both regional and local. Hillebrand (2005), using theoretical modelling, discovered that lack of relation or curvilinear patterns of the RSR-LRS relationship are unlikely under all but extreme conditions, hence he claimed the regression method was biased. Finally, He et al. (2005), using the island biogeographic model, mathematically formalized the LRS-RSR regression concept, incorporating probability of immigration and emigration (but also the impact of scale), and concluded that the full spectrum of linear and curvilinear relationships may be generated without invoking species interactions at all, the former relationship appearing when colonization rates are higher than extinction ones, while the latter when extinction rates are higher than colonization ones. He et al. (2005) also discovered that changing the sampling scale can make local-regional relationship appear either saturated or unsaturated. It became then obvious that the LSR-RSR concept had to be used with caution, although it cannot be discarded because most accumulated knowledge related to species richness analysis would have to be discarded as well.

In view of the difficulties, and taking them all into account, but also not to break connection with the earlier developments within the LSR-RSR paradigm, Grönroos and Heino (2012) applied a most interesting approach, at least as regards aquatic macroinvertebrates. Sampling 10 sites 50 m^2 in area in each of 10 streams differing in environmental conditions over the distance of up to 2 km from their outlets in Finland, they obtained 167 macroinvertebrate species and divided them into functional guilds. They also employed variance partitioning for a comparison of the impact of over a dozen environmental factors (ENV) with the LSR-RSR approach. Besides, they carried out all analyses for observed (and log-transformed) and for Chao-estimated (as the upper bound) species richness in both the LSR and RSR cases. The results were surprising: although the LSR-RSR relationship was linear in most cases, indicating overall regional species pool effect on LSR, variance partitioning suggested a relatively larger role of local ENV, and several environmental factors turned out significant predictors of LSR.

Although the relative importance of RSR for the guild of predators was much higher than RSR for any of the other guilds (filterers, gatherers, scrapers, and shredders), yet the importance of RSR for LSR never reached that of ENV. In the case of Chao-estimated species richness, less variation was explained than in the case of sampled species richness, but Chao richness estimation depends on rare species. As rare and common species may respond contrastingly to local and regional processes, thus suggesting unnatural results, Chao-estimated richness was further ignored. The study confirmed the hypotheses of strong regional species pool (using LSR-RSR approach) and of strong environmental impact on pooled macroinvertebrates (using variation partitioning), but did not the hypothesis of more curvilinear LSR-RSR relationships within guilds (except gatherers), and of weaker impact of RSR on given guilds, except predators. The last finding may be explained by a lower population density of predators, which increases extinction rates, as a result of which predators must rely to a greater extent on dispersal than other species.

Results that are mostly similar were obtained by Marchant et al. (2006) in Australia. However, their study differed from that of Grönroos and Heino (2012) in several respects. It was concerned with large spatial scales of 25 river basins extending over several hundred thousand square kilometers, relied mostly on the LSR-RSR approach, although considered also several environmental factors, and analysed taxonomic instead of functional macroinvertebrate categories. Besides, the number of taxa recorded was several times higher, bank and channel sites were considered separately, and there were several samples per site, whose number, however, was skillfully standardized and averaged. Despite the great difference in scale, Marchant et al. (2006) found that for all macroinvertebrates and for each of their taxonomic groups the LSR-RSR relationship was linear, as was mostly the case in Grönroos and Heino (2012). However, only conductivity was an environmental factor that was significant, and only for EPT and Coleoptera. When all taxonomic groups were considered, only longitude was related to bank data, and none to channel data. Marchant et al. (2006) also carried out an analysis of the causes of positive rather than zero intercept of the LSR-RSR plots (earlier mentioned by Srivastava 1999), yet the problem turned out too complex for clear generalisations, and thus further research is this respect seems necessary. Grönroos and Heino (2012) and Marchant et al. (2006) seem to confirm the predictions of Hillebrand (2005) that curvilinear LSR-RSR relationships are exceptional, but this is a shortcoming of the approach, and not necessarily indication of lack of saturation in LSR.

Future development in the saturation/non-saturation concept may be related to two shortcomings of the LRS-RSR paradigm never mentioned by any scientist. One is the underestimation of the slope in the LSR-RSR relationship due to the fact that both variables are random, i.e., not controlled by the researcher (Legendre and Legendre 2012, Sokal and Rohlf 2012). Ordinary least squares method (OLS, model I regression), which has only been used so far in this paradigm, always underestimates the slope, although the scale of the underestimation may vary from slight to considerable. Methods of model II regression should be used instead. Unfortunately, at the present state of knowledge there is no model II regression method that may also be used in the case of curvilinear relations, hence new methodological developments are necessary to use model II regression instead of OLS in such cases.

The other shortcoming is parallel to the development in nestedness, a paradigm conceptually similar to the saturation/non-saturation one, although never before discussed in the same context, most probably due to applying a quite different methodology. The nestedness paradigm also relied solely on species richness, in the belief that there was an affinity between a species' frequency of occurrence and its abundance (Atmar and Patterson 1993), as a result of which abundances of species little mattered. Yet, recent developments proved that nestedness indicated by presence-absence (i.e., species richness) data is very rarely confirmed when quantitative data (abundance, for example) are used instead in the same ecosystems (Staniczenko et al. 2013), hence a reevaluation of the whole nestedness concept is necessary. It seems that a similar reevaluation of the saturation/non-saturation might be carried out using quantitative data as well. The reason why this has not been done till now is probably much greater complexity of the quantitative approach, and much more complex methodology that will be necessary.

Connection between dispersal and biodiversity (regional scale)

Environmental factors affecting local assemblages of benthic macroinvertebrates determine the possibility for a species with a particular tolerance range to thrive in a given habitat. For the presence of zoobenthos at the regional scale (γ diversity), mobility has a strong influence, allowing to overcome distance and find suitable habitat (Jocque et al. 2007, Costa and Melo 2008, Fig. 2).

Among the factors that can reduce species richness and macroinvertebrate diversity within different catchments are distance between ecosystems (Costa and Melo 2008), geographical barriers disrupting the continuum of migration corridors (both natural such as mountain ranges and anthropogenic such as reservoirs: Monaghan et al. 2005), type of catchment land use (Sponseller et al. 2001, Smith et al. 2009, Rezende et al. 2014), and geographical location of the river (Costa and Melo 2008), meaning that a water course can be subject to specific climatic conditions (Graça et al. 2004, Burgmer et al. 2007). Overcoming these spatial barriers occurs mainly through dispersal, and permanent migrations between populations allow the free movement of alleles, increasing genetic diversity hence competition for the development of new adaptations (Bilton et al. 2001). Thanks to dipersal, organisms can colonise new habitats, escape from unfavourable abiotic conditions, and enrich neighbouring populations with the addition of new individuals (Smith et al. 2009). Notably, all of these factors play an important role for the structuring of biocenoses (Costa and Melo 2008).

It is sometimes claimed that adults of aquatic insects (females) fly upstream (colonization cycle, Müller 1973) to compensate for the loss of individuals caused by downstream drift (Macneale et al. 2005). Yet, aquatic macroinvertebrates differ in their ability for disperal (mobility), and this concerns both water stages and terrestrial, flying forms. In the case of water stages, dispersal is an effect of downstream transport within the water column and involves:

- Egg masses: some species in the centre of the egg masses have a gas bubble, which helps them flow with the river course for several hundred metres or even more (Williams 1982);
- Youngest larval stage (larvulae): these are predestined by their morphological and physiological features to float in water thanks to a great amount of body fat and the ability to feed on transported POM (Kalugina 1959);
- Individuals with developed legs (mayflies, caddisflies, stoneflies): these not only very easily and actively start to drift, but also manage to stay in suitable habitat patches (i.e., microhabitats).

Other macroinvertebrates also very often enter the drift actively or passively to escape from abiotic disturbances or to avoid predators and interference competition. Why organisms enter the drift and its meaning for riverine ecosystem functioning has been widely discussed since the 1970s (Elliott 1967, Waters 1972, Grzybkowska 2000).

The terrestrial stages of aquatic insects also have a great influence on the dispersal of species. Heino (2013) divided invertebrates according to their ability for active movement into four groups:

- Weak passive dispersers with aquatic adults: Oligochaeta, Hirudinea, Gastropoda, Bivalvia, Aranea and Crustacea;
- Weak aerial dispersers with terrestrial adults: small dipterans (Ceratopogonidae) and Chironomidae;
- Intermediate aerial dispersers with terrestrial adults: Ephemeroptera, Plecoptera, Megaloptera, Trichoptera and other Diptera (Tabanidae, Tipuloidea, Empididae);

- Strong aerial dispersers with terrestrial adults: Odonata, Heteroptera (Corixidae), Coleoptera (Dytiscidae).

In an investigation of the Oulankajoki River, the dispersal of taxa with limited possibility to move (cf. weak passive dispersers) was found to be strongly controlled by spatial factors (Heino 2013). Representatives of this group of invertebrates are not able to move independently to distant lotic ecosystems. This makes their mobility reduced to drifting with current speed within the original ecosystem, so that their occurrence in other rivers is only possible in the presence of connectivity between streams, which is favored by the dendritic network of river systems (Clarke et al. 2010).

In the case of the other groups, the distance between ecosystems ceases to represent a barrier to dispersal once the flying adult stage of the life cycle is reached. The fact that intermediate aerial dispersers are under stronger pressure of environmental variables than weak dispersers is also notable, and can be responsible for transportation over very long distances, as is the case of very light dipterans, such as Ceratopogonidae and Chironomidae. Finally, the dispersal of the most active taxa (e.g., dragonflies as well as some bugs and beetles), is controlled mainly by environmental factors, which make them able to overcome quite long distances above land and selectively choose habitats (Heino 2013).

Although particular taxa are characterised by diverse potential for dispersal, many studies have shown that the adult stages of riverine invertebrates prefer transport in the nearest area of the riverbed, as confirmed by a rapid decrease in the number of individuals together with a drift-away from the riparian zone (Sode and Wiberg-Larsen 1993, Petersen et al. 1999, Briers et al. 2002). Some cases are known when imagines choose a pathway above land to get to a stream that is located far away from the river of origin. This is a strategy that is beneficial from an energetical point of view given the loss of energy involved during flight along a stream to the nearest connection with neighbouring inlets. This type of flight above land has been observed in e.g., the dragonfly *Calopteryx splendens* (Chaput-Bardy et al. 2008) and the stonefly *Leuctra ferruginea* (Macneale et al. 2005).

Changes of land use, especially urbanisation, are becoming a serious impediment for the dispersal of invertebrates, which leads to modification of abiotic variables within the catchment (e.g., direction and strength of wind, intensity of solar radiation or temperature, and humidity gradients). This variability of environmental factors induces organisms to start migrations, and all fluctuations caused by human activity disrupt this process. Moreover, many taxa exhibit preferences to move within forested areas or corridors consisting of riparian vegetation. In this respect, deforestation can lead to loss of migration pathways and consequent reduction of dispersal, resulting in decrease of species diversity in particular river basins (Sponseller et al. 2001, Smith et al. 2009, Rezende et al. 2014). Destruction of the riparian zone, including forest in nearby areas, forces invertebrates to migrate above deforested land, and this results in increased energetic costs, but also possibility of desiccation and exposure to predator pressure (Smith et al. 2009). Moreover, these moving insects may become vulnerable to other dangers, such as road infrastructure, including asphalt, vehicle lights and traffic lampposts, which can function as beacons (Smith et al. 2009).

Besides dispersal, climatic conditions exert an influence on the diversity and species richness of a biocoenosis at the regional scale, and are indirectly responsible for changes in the environmental variables of particular basins. Accordingly, species richness and diversity of benthic fauna were found to be higher in rivers located in northern and central Portugal in comparison to southern streams, and this was explained by a differentiation in riverine abiotic paramaters from other climate zones (Graça et al. 2004). On the contrary, in southern regions, precipitation is usually less heavy but becomes unpredictable. In summer, rivers often dry out resulting in the creation of small ponds, where decaying organic matter and high temperature generate microhabitats suitable for the development of microorganisms, whose physiological requirements contribute to the exhaustion of oxygen resources. The extreme environmental conditions of southern rivers in Portugal were found to allow the survival of only those species that are very resistant to oxygen deficits.

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Research

Population Ecology

Environmental Variables Influencing Chironomid Assemblages (Diptera: Chironomidae) in Lowland Rivers of Central Poland

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Abstract

Chironomids (Diptera: Chironomidae) are a family of dipterans with a global distribution. Owing to their great functional diversity and ability to adapt to a wide range of environmental conditions, they often dominate in freshwater macroinvertebrate communities, playing a key role in the cycling of organic matter and the flow of energy in aquatic ecosystems. Our aim was to analyze the structure of chironomid assemblages and identify the environmental factors, including current velocity, river width, water depth, water temperature, dissolved oxygen, percentage of substrate covered by vascular plants, inorganic bottom substrate, and quantity of benthic (BPOM) and transported (TPOM) particulate organic matter, that underpin variation in species richness across a set of lowland rivers in central Poland, differing by stream order and abiotic parameters. Using an Information Theoretic Approach, we formulated a set of alternative models based on previously published work, with models fitted in a Bayesian framework using Integrated Nested Laplace Approximation. The species richness of chironomids increased with river order, achieving a maximum in third and fourth order rivers, but decreased at higher orders. The best-fitting models included a positive effect of inorganic substrate index and dissolved oxygen on chironomid species richness. The quality structure of chironomid assemblages reflected the assumptions of the River Continuum Concept showing that species richness was under the influence of factors operating at both a micro- (inorganic bottom substrate) and macro-scale (dissolved oxygen).

Key words: riverine macroinvertebrates, species richness, abundance, habitat parameters, Bayesian inference

A major goal of ecology is to understand the patterns and distribution of species diversity (Krebs 2009). The primary driver of contemporaneous variation in diversity is environmental heterogeneity, which is a function of biotic and abiotic environmental variables and their interaction with phylogenetic, geological, and climatic history (Vellend 2016). The Chironomidae (Diptera: Chironomidae) are a taxonomically diverse family of nonbiting dipterans with a global distribution in freshwater lotic ecosystems (Coffman 1995, Ferrington 2008). Chironomids display great functional diversity (e.g., scrapers, gathering collectors, filtering feeders, and predators) and are capable of adapting to a wide range of environmental conditions, typically occurring at high densities and playing a key ecological function in lotic freshwater communities (Benke 1998). As such, this group plays a critical ecological role in cycling organic matter in rivers, in the export of energy to riparian habitats, and offers a valuable model system for understanding which environmental variables drive species richness.

Several studies have attempted to characterize the environmental variables that underpin macroinvertebrate species richness and abundance. Thienemann (1954) proposed water temperature, dissolved oxygen, and current speed as the major factors shaping the community structure of chironomids. In turn, Hynes (1970) formulated a more general list of variables whose influence on aquatic macroinvertebrate assemblages was most visible, including current speed, water temperature, type of substrate, dissolved oxygen, and other physico-chemical parameters, such as pH, conductivity, and the presence of organic matter. Subsequent long-term experimental studies, conducted worldwide, indicated that the impact of environmental variables on the structure of benthic assemblages also depended on the spatial scale of the research (Sponseller et al. 2001, Heino et al. 2004). For example, Feld et al. (2007) distinguished four basic spatial scales: ecoregion, catchment, reach, and site, whereas Sponseller et al. (2001) considered land use practises at five spatial scales within catchments.

In most ecological studies of macroinvertebrate species richness, chironomids have been treated as an undifferentiated group (Armitage et al. 1995), reflecting their difficulty of identification at the species level and making estimation of species richness impossible (Heino et al. 2003, Graça et al. 2004). This problem can be related to the phenomenon of 'extinction of the experience', with a decline in the number of specialists capable of identification to the species level (Cheesman and Key 2007). Another reason is that taxonomy is often treated as knowledge that has little intellectual content, being a primarily descriptive science. However, inexact taxonomic identification can seriously undermine both the conclusions of ecological studies and attempts at biodiversity conservation (Agnarsson and Kuntner 2007).

In this study, we analyze the structure of chironomid assemblages and the dependence of chironomid species richness on environmental variables with taxonomic resolution at the species level. We combine this fine-scale species-level analysis with an Information Theoretic (IT) Approach to evaluate alternate models of species richness (Burnham and Anderson 2002, Burnham et al. 2011) based on previous published work, which we apply in an analysis of seven rivers across central Europe. Models were fitted in a Bayesian framework, which is robust in dealing with complex datasets, unbalanced data, and an inherent lack of dependency due to repeated measures. Bayesian models are flexible in allowing the estimation of a posterior distribution of differences between parameters and across levels of factors. These are relatively straightforward procedures using Bayesian inference, but problematic in a frequentist framework, notwithstanding more general reservations in using frequentist analyses (Allan et al. 2012, Burnham and Anderson 2014).

Materials and Methods

Seven study sites were selected in natural stretches of lowland rivers in central Poland. There were no river impoundments in the study areas. The rivers were the Bzura, Mroga, Mrożyca, Moszczenica, Grabia, Widawka, and Warta. The studied sites differed by order (Strahler 1957) and abiotic parameters: river order being determined on the basis of Czarnecka (2005), which is the most authoritative and up-to-date source of information on the hydrographic partitioning of Poland. A description of all rivers is presented in Table 1 and site locations are illustrated in Fig. 1.

At the study site, benthic samples containing invertebrates and particulate organic and inorganic matter were collected once a month in an annual cycle from two habitats per river: in mid-channel, MC, and close to the bank, BK. Data from these two habitats were added in proportion to the percentages of their areas in their combined area (i.e., a weighted total). In total, 840 samples over the course of the study were collected and 120 from each river (5 samples from each habitat giving 10 samples from a study site per month). Each sample comprised 10 subsamples of 10 cm^2 (100 cm^2 of stream-bed area) taken with a sediment core sampler. Subsamples were uniformly distributed within a given sampling area. To collect a subsample, the sediment core sampler was pushed into the sediment to a depth of 150 mm. At each sampling point, the current velocity,

Table 1. Site characteristics in the seven studied rivers of central Poland

Parameter	Name of river						
	Bzura	Mroga	Mrożyca	Moszczenica	Grabia	Widawka	Warta
River order (Strahler 1957)	1st	2nd	2nd	3rd	3rd	4th	5th
Current velocity (m s^{-1})							
$\bar{x}$	0.24	0.06	0.06	0.04	0.36	0.37	0.40
R	0.20–0.33	0.02–0.38	0.04–0.08	0.02–0.10	0.27–0.61	0.26–0.61	0.26–0.52
Width (m)							
$\bar{x}$	0.74	3.1	4.8	3.9	15.33	27.83	57.0
R	0.20–1.03	2.5–5.0	4.5–5.5	3.5–4.2	14.5–16.5	24.00–31.00	53.0–63.0
Depth (m)							
$\bar{x}$	0.07	0.14	0.39	0.28	0.36	0.74	0.56
R	0.05–0.15	0.08–0.48	0.30–0.47	0.20–0.36	0.26–0.46	0.64–0.80	0.33–0.86
SI (mm)							
$\bar{x}$	3.4	4.9	0.4	0.3	20.8	3.9	0.8
R	0.4–6.8	0.7–7.7	0.3–0.7	0.29–0.34	16.2–24.8	2.4–5.5	0.7–1.0
BPOM (g m^{-2})							
$\bar{x}$	3092	5892	7559	13951	404	1683	311
R	2053–5300	1859–11576	1783–16352	8559–18278	260–500	900–2000	121–504
TPOM (g m^{-3})							
$\bar{x}$	131	12	15	17	31	44	13
R	20–574	2–32	1–51	3–42	18–69	23–99	7–28
Temperature (°C)							
$\bar{x}$	6.7	8.9	9.8	10.9	10.8	10.2	13.7
R	1.0–16.0	2.0–15.3	3.4–16.8	0.0–20.8	0.0–21.0	0.0–18.0	4.0–23.0
Oxygen (mg dm^{-1})							
$\bar{x}$	6.1	6.8	7.2	10.5	8.6	7.9	6.9
R	3.1–9.5	3.0–10.5	3.2–10.1	8.1–14.5	4.5–13.1	5.0–11.0	4.5–9.7
Vascular plants (% of bottom covering)							
$\bar{x}$	0.0	0.0	0.0	0.0	6.9	2.9	0.0
R					0.0–25.0	0.0–10.0	

$\bar{x}$ = annual mean; R = range; SI = inorganic substrate index.

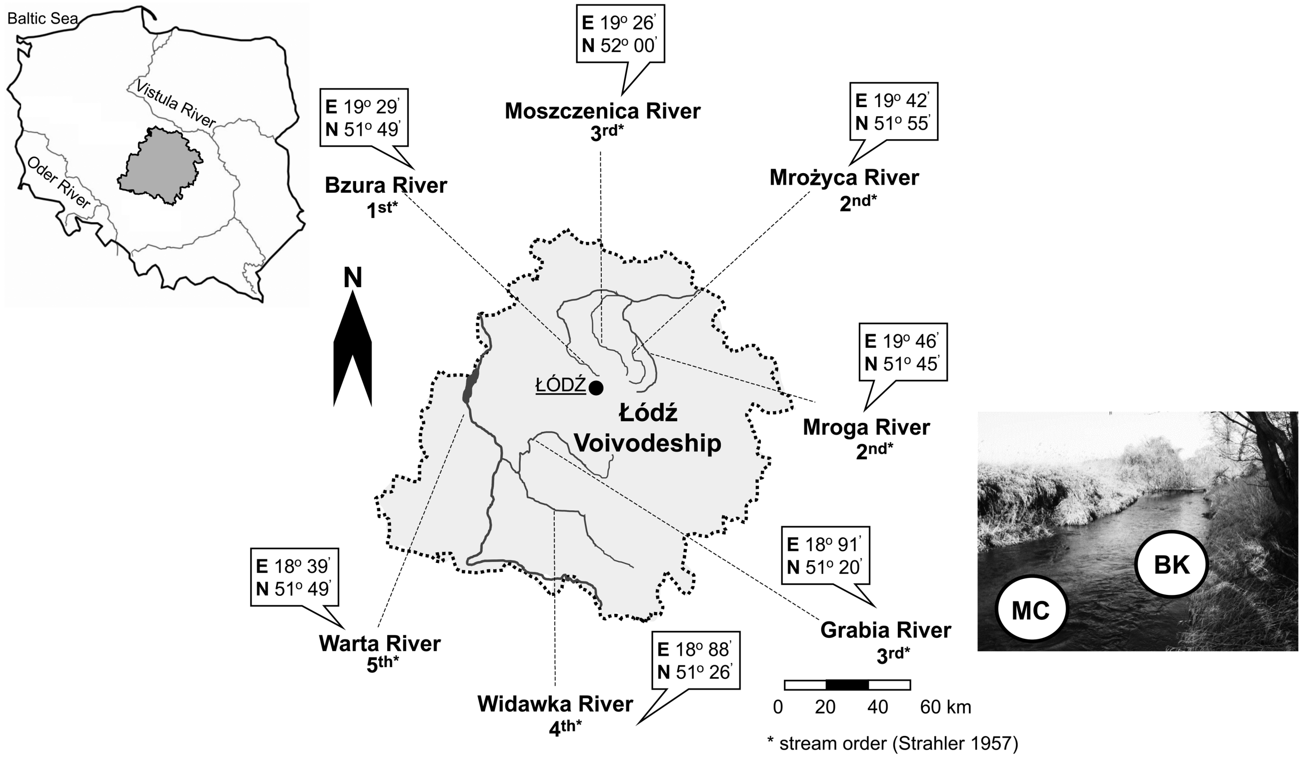

Fig. 1. Study area in the seven investigated rivers with sampled habitats marked: mid-channel (MC) and bank (BK).

river width, water depth, water temperature, dissolved oxygen, and percentage of substrate covered by vascular plants were measured or estimated.

Benthic samples were transferred to the laboratory and invertebrates were sorted from benthic sediment by hand. All chironomids in samples were identified to species level. Since identification of chironomid larvae to species was often impossible, laboratory rearing was conducted. For this purpose, single larvae were placed into small crystallizers with filtered (to avoid the presence of other predators, such as copepods) and aerated river water. They were kept outside the laboratory to experience natural variation in water temperature. On average, every 2 d, larvae were inspected, water was exchanged, and a small portion of detritus or oligochaetes (food base) was added. The containers were covered by netting to prevent adult insects escaping. After 1–14 d, depending on species, eclosion took place. The larval and pupal skins and imago that were obtained, which permitted species-level identification, were collected and preserved in 70% ethanol. To identifiy species, keys by Wiederholm (1983, 1986, 1989) and Nilsson (1997) were used.

After removing all macroinvertebrates, the organic content of samples was determined. To do this, a 1-mm mesh sieve was used to divide benthic particulate organic matter (BPOM) into >1 mm (coarse—BCPOM) and <1 mm (fine—BFPOM; Petersen et al. 1989). The organic matter was dried at 60°C for 2 d, weighed, ashed at 600°C for 2 h, and reweighed. For the purpose of this study, estimates of coarse and fine BPOM were summed. To determine the quantity of transported particulate organic matter (TPOM), water samples of 0.01 m^3 were collected at each site. In the laboratory, samples were filtered through preweighed Whatman GF/C glass-fiber filters (1.2 μm). Samples were subsequently analyzed as described for BPOM (Grzybkowska and Witczak 1990). The granulometry of inorganic substrate was based on the classification of Cummins (1962) and then substrate inorganic index (SI) was estimated. This variable was obtained by summing the mid-point values of grain size classes weighted by their proportional cover (Quinn and Hickey 1990a).

Data were modeled using R (version 3.5.0, R Development Core Team 2018) with models fitted in a Bayesian framework using Integrated Nested Laplace Approximation (R-INLA; Rue et al. 2017). To examine the impact of environmental variables on chironomid species richness, we formulated 12 alternative models (Burnham and Anderson 2002) comprising variables identified as having ecological importance in previously published studies (Table 2). To accommodate temporal dependency in the data, species richness was modeled using a random walk (RW2) trend model fitted for month of year following a Poisson distribution. Rivers were included in the model as a random term to accommodate among-river dependency in the data. Uniform default priors were put on model parameters. The best fitting models were identified with Watanabe–Akaike Information Criterion (WAIC).

Results

The lowest species richness of chironomids was observed in the first-order River Bzura (3–8 species), whereas the highest was recorded in the third- and fourth-order Rivers Grabia and Widawka (15–29 species). In the highest (fifth) order stretch (of the River Warta), an intermediate number of chironomid species was observed (5–15 species; Fig. 2).

In terms of the structure of chironomid communities (subfamilies and tribes), the Rivers Bzura and Mroga were characterized by a high percentage of Prodiamesinae, whereas the dominant groups in the Rivers Moszczenica, Warta, and Widawka were Chironomini larvae (Chironominae). In these five rivers, the density of chironomid larvae achieved between 2,000 and 3,000 ind. m^{-2}. The Rivers Mrożyca and Grabia had approximately three times the highest average density (9,902 and 10,519 ind. m^{-2}, respectively)

Table 2. A priori models to predict macroinvertebrate diversity

Parameter	Source	Region
Discharge/current velocity	Quinn and Hickey (1990b)	New Zealand
	Jiang et al. (2013)	Asia
	Rossaro (1991)	Europe
	Fesl (2002)	Europe
	Karaouzas and Płóciennik (2016)	Europe
	Fenoglio et al. (2004)	South America
	König and Santos (2013)	South America
Inorganic bottom substrate	Liu et al. (2016)	Asia
	Chaib et al. (2013)	Asia/Europe
	Grzybkowska and Witczak (1990)	Europe
	Boulaaba et al. (2014)	Africa
	Graca et al. (2004)	South America
	Rezende et al. (2014)	South America
	Mauad et al. (2017)	South America
Organic matter	Graca et al. (2004)	South America
	König and Santos (2013)	South America
	Mauad et al. (2017)	South America
Temperature	Rossaro (1991)	Europe
	Marziali and Rossaro (2013)	Europe
	Boulaaba et al. (2014)	Africa
	Cusson et al. (2007)	North America
Dissolved oxygen	Liu et al. (2016)	Asia
	Özkan et al. (2010)	Europe
	Buss et al. (2002)	South America
Conductivity, pH	Liu et al.(2016)	Asia
	Chaib et al. (2013)	Asia/Europe
	König and Santos (2013)	South America
	Rezende et al. (2014)	South America
Channel, morphometry: stream order, width, depth	Jiang et al. (2013)	Asia
	Chaib et al. (2013)	Asia/Europe
	Karaouzas and Płóciennik (2016)	Europe
	Graca et al. (2004)	South America
	Mauad et al. (2017)	South America

Studies whose authors' names are in bold concern chironomids, whereas those in normal font concern aquatic invertebrates generally.

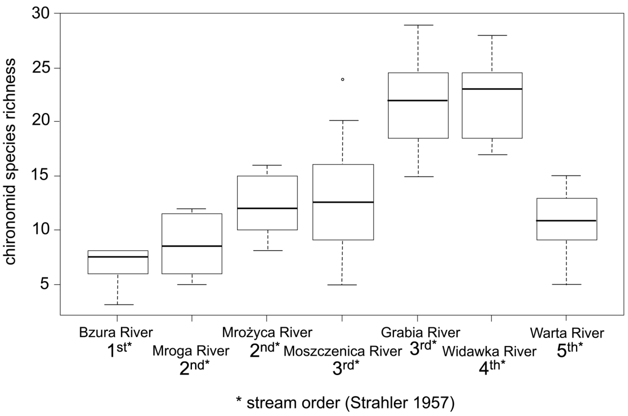

Fig. 2. Chironomid species richness in the seven studied rivers. Bold line indicates the median, squares indicate the 25 and 75% quartiles, and whiskers are data range.

and more even distributions of chironomid taxa among subfamilies than the other rivers. The River Grabia was notable in supporting a high abundance of both Orthocladiinae and Tanytarsini, whereas the River Mrożyca supported a higher abundance of Tanytarsini in comparison to other rivers (Fig. 3).

Six chironomid species achieved the highest mean shares in all investigated rivers: *Prodiamesa olivacea* (Meigen) (20.2%), *Polypedilum convictum* (Walker) (9.1%), *Polypedilum scalaenum* (Schrank) (7.8%), *Micropsectra notescens* (Walker) (6.8%), *Chironomus riparius* Meigen (6.0%), and *Robackia demeijeri* (Kruseman) (5.9%), but the percentage of a particular species differed from river to river, and the total contribution of the six species decreased with river order (Fig. 4).

Two models, M08 and M10, showed the best fit to the data (Table 3). These models were similar, both including an effect of dissolved oxygen and SI, with model M10 also including a nonstatistically important effect of water velocity. Consequently, the simpler of the two models (M08) was selected. This model predicted a positive effect of inorganic substrate granulometry (Table 4; Fig. 5) and dissolved oxygen (Table 4; Fig. 6) on chironomid species richness.

Discussion

Species Richness in Relation to River Order

The structure of assemblages represented in our study by chironomid subfamilies and tribes reflects a trend predicted by the River Continuum Concept (RCC; Vannote et al. 1980, Minshall et al. 1985, Lindegaard and Brodersen 1995), with the dominance of gathering collectors in low- and mid-river orders (Prodiamesinae and Chironomini) and the highest share of grazers and filter feeders in higher order rivers (Orthocladiinae and Tanytarsini). However, a variable stream order is closely associated with other abiotic parameters along a river system. For example, the presence of numerous Tanytarsini species in the River Grabia may be associated with the high current velocity observed in this river. Similarly, the high abundance and availability of mosaic habitats (patches) in the Grabia may explain the appearance of many species of chironomids, mainly Orthocladiinae.

Species richness of chironomids changed with the gradient of river order in a way comparable to trends suggested by Coffman (1989), who observed an increase and then decline in species richness with increasing river order. Notably, the greatest number of species was observed in one of the third order rivers (Grabia), which matched the prediction of Coffman (1989). Although there were exceptions to this rule, with high species richness in the fourth order river (Widawka) and low diversity in the other third order river (Moszczenica), our results broadly indicate a link between species richness and stream order (Fig. 2).

Predictors of Chironomid Species Richness in Lowland Rivers

The best-fitting model indicated an important influence of inorganic bottom substrate on chironomid assemblages. In general, macroinvertebrates prefer a varied coarse substrate consisting mainly of large-grained sand, gravel, and pebbles (Leszczyńska et al. 2017). A positive relationship between the number of taxa and size of inorganic substrate particles was similarly observed by Duan et al. (2008) and Rezende et al. (2014). Leitner et al. (2015) showed that coarser fractions of sediment were preferred by about 40 macroinvertebrate

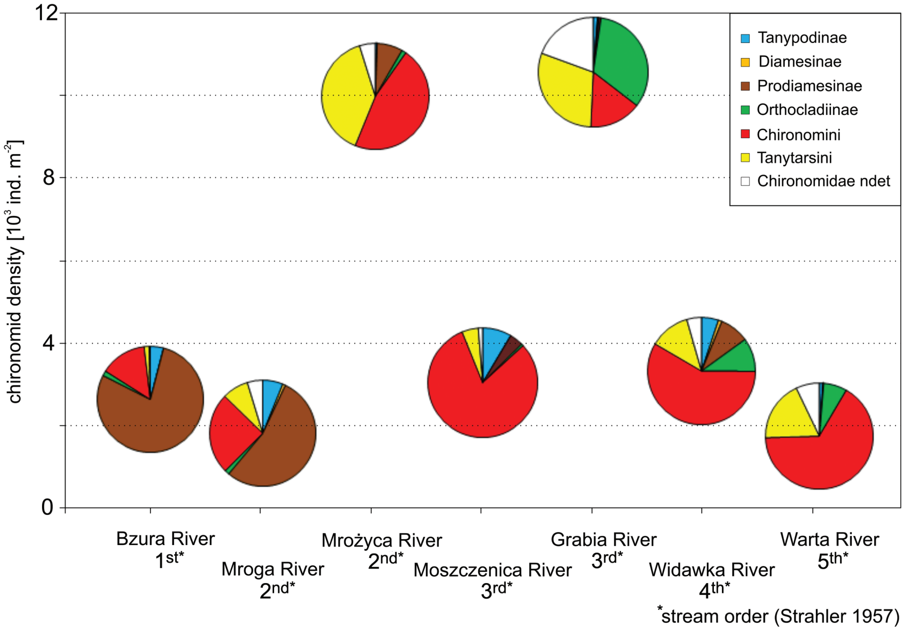

Fig. 3. Mean abundance and the structure of chironomid assemblages showing the proportion of subfamilies (Tanypodinae, Diamesinae, Prodiamesinae, Orthocladiinae, and Chironominae divided into two tribes: Chironomini and Tanytarsini) in the seven studied rivers. The center of each pie chart denotes the density of chironomids.

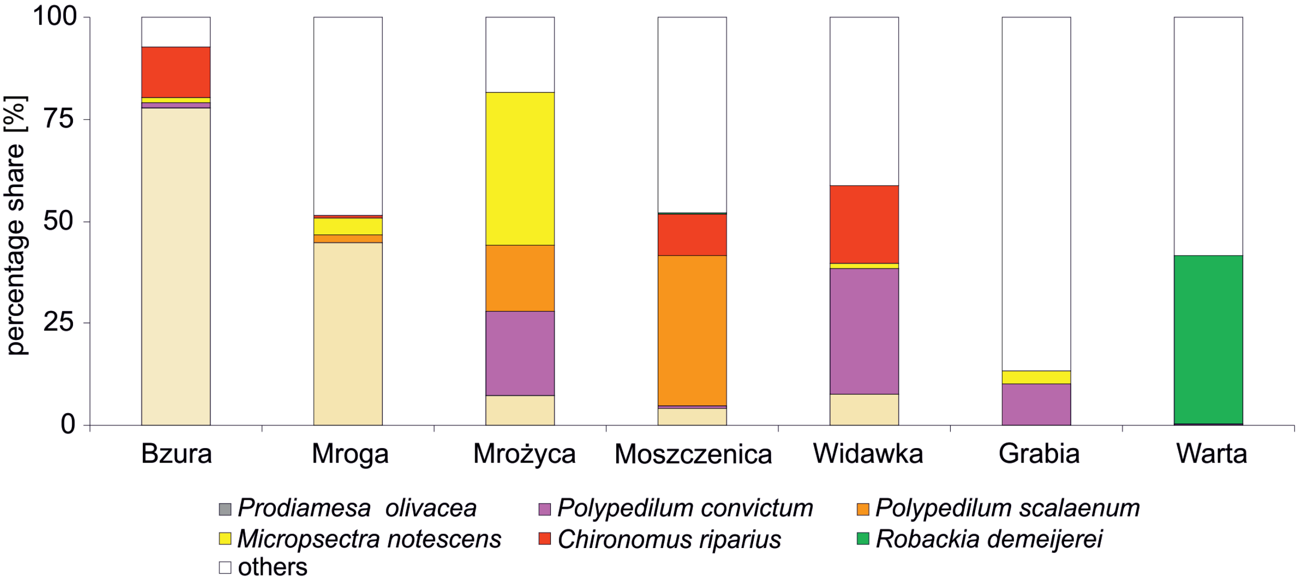

Fig. 4. Mean percentage of dominant chironomid species in the seven studied rivers.

groups, whereas the finest were preferred by only two chironomid taxa. A coarse bottom substrate appears to favor the development of periphyton: an indispensable food resource for many groups of aquatic invertebrates (Grzybkowska and Witczak 1990, Bournaud et al. 1998). Moreover, coarse substrates are relatively stable and offer a suitable size range of interstitial shelters (Rice et al. 2001, Beauger et al. 2006, Duan et al. 2008).

Conversely, large-scale deposition of fine inorganic sediments has been considered a threat to macroinvertebrate diversity (e.g., Szczerkowska-Majchrzak et al. 2010, Leitner et al. 2015, Elbrecht et al. 2016). This phenomenon can be accounted for by the lack of riparian vegetation. Riparian vegetation often stops surface run off by encouraging sheet flow rather than channeled flow. In consequence, the rate of deposition of suspended materials at the riverine bottom decreases. Rooting of vegetation also has a positive influence on soil structure, binding erodible soil, and stabilizing streambeds (Castelle et al. 1994, Broadmeadow and Nisbet 2004). In a study conducted by Wolmarans et al. (2017), a significant negative correlation between a particle size of <2mm and number of species was observed.

Experimental studies by Rabeni and Minshall (1977) and Rae (1987) conducted on chironomid assemblages showed that nonbiting midges chose an intermediate size fraction from available substrates. Rabeni and Minshall (1977), who used coarse substrate in their study (5–70 mm), recorded a higher number of individuals in inorganic substrates with a 30-mm grain size. In turn, according to the results of Rae (1987), who carried out his experiment in a sandy

Table 3. Model comparisons of chironomid species richness in the seven studied rivers showing model number, model formulation, effective number of parameters (*enp*), Watanabe–Akaike information criterion (*WAIC*) and Δ*i*

Model	Model formulation	*enp*	*WAIC*	Δ*i*
M10	velocity + dissolved oxygen + SI	9.2	436.0	0.00
M08	**dissolved oxygen + SI**	**8.8**	**436.4**	**0.40**
M02	velocity + SI	8.5	438.1	2.10
M11	velocity + BPOM + SI	9.3	438.1	2.10
M04	velocity + dissolved oxygen	9.6	439.5	3.50
M07	dissolved oxygen + BPOM	10.2	440.1	4.10
M09	velocity + dissolved oxygen + BPOM	10.5	440.7	4.70
M01	velocity + BPOM	9.4	442.3	6.30
M03	velocity + TPOM	9.5	444.7	8.70
M12	velocity + BPOM + depth	10.1	445.2	9.20
M06	BPOM + TPOM	10.0	445.3	9.30
M05	BPOM + depth	9.8	446.1	10.10

The best-fitting models with *WAIC* <2 shaded. Selected model in bold.

Table 4. Posterior mean estimates for selected model (M08) for chironomid species richness in the seven studied rivers modeled using a Poisson random walk trend model fitted using INLA

Model parameter	Posterior mean	Lower CrI	Upper CrI
Intercept	2.530	2.251	2.804
SI (inorganic substrate index)	0.231	0.046	0.420
Dissolved oxygen	0.090	0.007	0.200

CrI is the 95% Bayesian credible interval. Credible intervals that do not contain zero indicate a statistically important difference.

section of a stream (particle size: 0.25–4 mm), chironomids were most abundant where particle size was 1 mm. In our study, where the range of the diameter of particle sizes was 0.3–25 mm, chironomids were more abundant in the coarse fraction than fine and intermediate particle sizes.

Although the inorganic substrate of the riverine bottom has an important influence on chironomid assemblages, the structure of the stream bed is also a function of other environmental drivers, such as current velocity and discharge (Matthaei et al. 1997). Patterns of river flow shape the structure of the substrate through transport of inorganic and organic particles (Warren et al. 2015). A key role may also be played by the content of organic matter covering the inorganic substrate of the river bed, which is a preferred habitat for many species (Graça et al. 2004). Tolkamp (1982), who divided hydrobionts into several groups according to their substratum demands, proposed that some chironomids are strictly associated with a particular type of substrate. For example, *Prodiamesa olivacea* requires a fine inorganic substrate with a portion of fine organic matter, such as sand with detritus among leaf packages. This observation was confirmed by Bisthoven et al. (1992) and Grzybkowska (1995). Notably, fine benthic particulate organic matter (FPOM) is important in distributing energy and associated nutrients within streams at multiple spatial and temporal scales, but detritus is a rather poor indicator of total macrobenthic density (Corkum 1992).

In addition to a positive relationship with inorganic bottom substrate, the best fitting model indicated an important influence of dissolved oxygen on the structure of chironomid assemblages. The impact of this parameter at a local scale is rarely recorded, but its significance increases on larger scales (Townsend 1989, Fesl 2002). A decrease in the concentration of dissolved oxygen in rivers is often connected with increased values of other parameters, such as pH, conductivity, and concentration of nitrates and phosphates, which can indicate either the impacts of deforestation within a catchment area or pollutant releases into the water (Likens et al. 1978, Carignan and Steedman 2000, Azrina et al. 2006, Popović et al. 2016).

As with other aquatic organisms, the levels of dissolved oxygen that are critical for survival are difficult to pinpoint due to their dependence on temporal patterns and the potentially rapid speed of change of this parameter. Connolly et al. (2004) observed that most macroinvertebrate taxa are able to tolerate short-term low levels of dissolved oxygen (<10% saturation) without any serious change in emergence. However, low oxygen conditions of <20% saturation can cause lethal effects for some sensitive species, such as mayflies (Connolly et al. 2004). For other taxa, such as chironomids, mortalities increased when the level of dissolved oxygen fell to 8% saturation. Some chironomid species show remarkable adaptations to life in terrestrial or aquatic habitats with periodic hypoxia and even anoxic conditions. In these environments, some taxa may switch from aerobic to anaerobic metabolism (Penttinen and Holopainen 1995), which complicates the assessment of the influence of oxygen on chironomids.

Among macroinvertebrates, chironomids express a wide range of tolerances for dissolved oxygen concentrations. The physiological plasticity of many chironomid larvae results from the presence of specific types of hemoglobin in their hemolymph (Osmulski and Leyko 1986, Cranston 1995). These dipterans, such as *Chironomus* sp., are termed oxygen regulators because they have hemoglobin in their blood. They are characterized by an intensive red color of their larvae and possess the ability to maintain a high respiration rate under low oxygen conditions. Taxa without the capacity to regulate are known as oxygen conformers, e.g., *Prodiamesa*, and their internal dissolved oxygen concentrations reflect the external environment (Connolly et al. 2004, Grzybkowska 2006).

Although chironomids are typically considered to be resistant to oxygen fluctuations, in several studies, a significant and positive interaction between dissolved oxygen levels and macroinvertebrate species richness has been observed (Graça et al. 2004, Fenoglio et al. 2004). Our model predicted an increase in the number of chironomid species with elevated dissolved oxygen concentrations in river water. This effect may arise from the appearance of sensitive chironomid species, with higher ecological demands, in the assemblage at higher dissolved oxygen concentrations (Armitage et al. 1995). Notably, in the chironomid assemblages of the Rivers Grabia and Widawka, the highest share of low oxygen intolerant Orthocladiinae species was observed in comparison with the other investigated rivers. In contrast, members of the tribe Chironomini, which are eurythermal and tolerant to low oxygen conditions, were present in each study site independently of oxygen level. However, in the River Moszczenica, where the mean dissolved oxygen concentration was higher than in the Grabia and Widawka, chironomid species richness was relatively low, demonstrating that the influence the other parameters also drives chironomid species richness.

Biotic Factors in Relation to the Impact of Environmental Parameters

High chironomid species richness in rivers can be supported by differences in microhabitats/patches and also by differences in diet and season (Lehmann 1971, Lenat 1987, Lindegaard and Brodersen 1995). In the present study, some chironomid species that we identified on the basis of their morphology may have been species complexes, with each taxon comprising the species

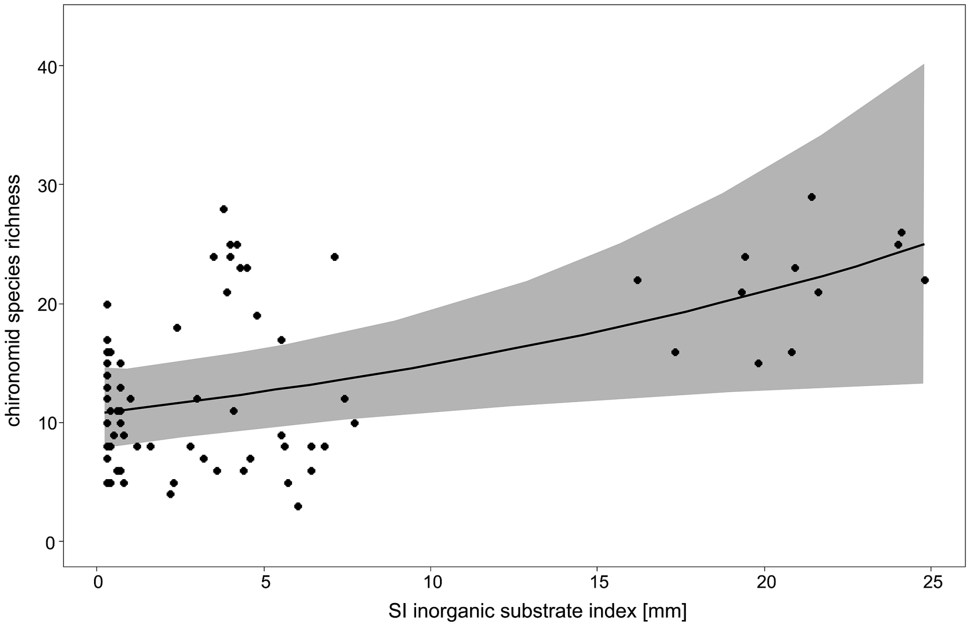

Fig. 5. Fitted values of chironomid species richness (solid line) and 95% Bayesian credible intervals (shaded area) against inorganic substrate index (SI) [mm] in the seven studied rivers modeled using a Poisson random walk trend model fitted using INLA. Black circles are observed values for species richness for each month in each river.

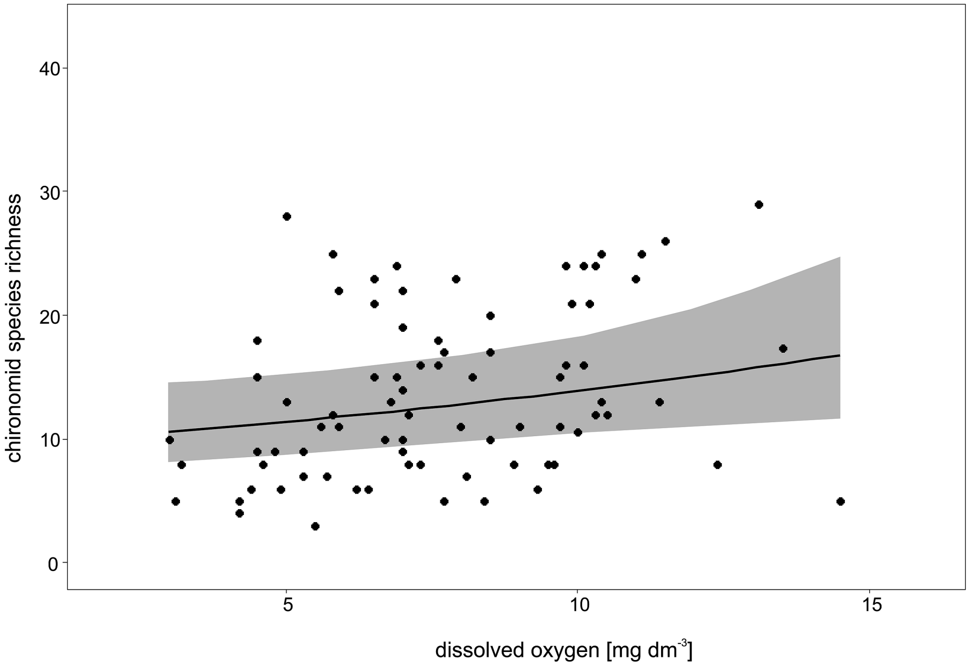

Fig. 6. Fitted values of chironomid species richness (solid line) and 95% Bayesian credible intervals (shaded area) against dissolved oxygen [mg dm^{-3}] in the seven studied rivers modeled using a Poisson random walk trend model fitted using INLA. Black circles are observed values for species richness for each month in each river.

complex expressing different ecological preferences. Unsurprisingly, if Chironomidae are identified to the family level, much of this information about their ecology is lost. A notable ecological pattern within the chironomids, articulated by Thienemann (1954), is that the subfamily Orthocladiinae (mainly periphyton and/or epiphyton scrapers) correlates negatively with that of the Chironomini (tribe of Chironominae, substrate feeders, or filter feeders of BPOM). An outcome is that chironomid species succession along a river reflects the pattern of species distribution predicted by the river continuum concept (Vannote et al. 1980, Lindegaard and Brodersen 1995). However, the impacts of environmental variables such as temperature and flow, as well as anthropological disturbance, on chironomid assemblage structure mean that deviation from broad biotically driven ecological patterns can be masked (Tang et al. 2010).

Heterogeneity in habitat utilization and feeding ecology in the Chironomidae has been comprehensively studied (Berg 1995).

Adaptations of chironomid larvae to heterogeneous habitats are reflected both in the highly diverse morphology of larval mouthparts but also in their feeding behavior (Olafsson 1992). A result of this variability is that many chironomid species cannot be readily classified into a single feeding guild. Many taxa exhibit considerable flexibility in their feeding behavior, switching from filter-feeding to deposit-feeding (gathering collectors) and vice versa in response to the quality and quantity of food resources in the environment (Walshe 1950). In addition, some species change their mouthpart morphology over successive larval stages (during ontogenesis), especially amongst the deposit/filter feeding species, which directly influences the particle sizes ingested (Olafsson 1992). Such versatility in mode of feeding may result in reduced competition both within and among species (Berg 1995).

In summary, our aim was to identify the environmental factors that underpin variation in chironomid assemblages across a set of lowland rivers in central Poland. Chironomid species richness increased with river order, achieving a maximum in third and fourth order rivers, but decreasing at higher orders. Using an IT approach, we identified a positive effect of inorganic substrate index and dissolved oxygen. Our study demonstrates the value of conducting ecological studies on this family at the species level, with species richness contingent on factors operating at both a micro (inorganic bottom substrate) and macro scale (dissolved oxygen).

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ZAŁĄCZNIK II/ APPENDIX II

DOROBEK NAUKOWY/

SCIENTIFIC ACHIEVEMENTS

PUBLIKACJE/PUBLICATIONS

Prace z listy MNiSW (po aktualizacji z dn. 9 lutego 2021 r.):

1. Szczerkowska-Majchrzak E., Lik J., **Leszczyńska J.** 2014. Resistance of riverine macroinvertebrate assemblages to hydrological extremes. *Oceanological and Hydrobiological Studies* 43(4): 402-417.
   punkty MNiSW = 40, IF_{2014} = 0.753

2. Grzybkowska M., Dukowska M., Michałowicz J., **Leszczyńska J.** 2015. Trace metal concentrations in free-ranger, tube-dweller chironomid larvae and a weakly polluted river's sediment. *Oceanological and Hydrobiological Studies* 44: 445-455.
   punkty MNiSW = 40, IF_{2015} = 0.557

3. Grzybkowska M., Szczerkowska-Majchrzak E., Dukowska M., **Leszczyńska J.**, Przybylski M. 2016. *Ephemera danica* (Ephemeroptera: Ephemeridae) As a Resource for Two Commensals: Ciliated Protozoans (Sessilida) and Chironomids (Diptera). *Journal of Insect Science* 16(1): 67, 1-6.
   punkty MNiSW = 70, IF_{2016} = 0.843

4. Grzybkowska M., Kucharski L., Dukowska M., Takeda A.M., Lik J., **Leszczyńska J.** 2017. Submersed aquatic macrophytes and associated fauna as an effect of dam operation on a large lowland river. *Ecological Engineering* 99: 256-264.
   punkty MNiSW (stara) = 100, IF_{2017} = 3.023

5. Lik J., Dukowska M., Grzybkowska M., **Leszczyńska J.** 2017. Summer co-existence of small-sized cyprinid and percid individuals in natural and impounded stretches of a lowland river: food niche partitioning among fishes. *Journal of Fish Biology* 90: 1609-1630.
   punkty MNiSW = 70, IF_{2017} = 1.702

6. **Leszczyńska J.**, Głowacki Ł., Grzybkowska M. 2017. Factors shaping species richness and biodiversity of riverine macroinvertebrate assemblages at the local and regional scale. *Community Ecology* 18(3): 227-236.
   punkty MNiSW = 40, IF_{2017} = 0.943

7. Grzybkowska M., Dukowska M., **Leszczyńska J.**, Lik J., Szczerkowska-Majchrzak E., Przybylski M. 2018. The food resources exploitation by small-sized fish in a riverine macrophyte habitat. *Ecological Indicators* 90: 206-214.
   punkty MNiSW = 140, IF_{2018} = 4.490

8. Marszał L., Grzybkowska M., Błońska D., **Leszczyńska J.**, Przybylski M. 2018. The diet of the endangered spirlin (*Alburnoides bipunctatus*) at the centre of its distribution in Europe. *Marine and Freshwater Research* 69(11): 1712-1723.
   punkty MNiSW = 70, IF_{2018} = 1.859

9. **Leszczyńska J.**, Grzybkowska M., Głowacki Ł., Dukowska M. 2019. Environmental Variables Influencing Chironomid Assemblages (Diptera: Chironomidae) in Lowland Rivers of Central Poland. *Environmental Entomology* 48(4): 988-997.
   punkty MNiSW = 100, IF$_{2019}$ = 1.586

10. Grzybkowska M., **Leszczyńska J.**, Głowacki Ł, Szczerkowska-Majchrzak E., Dukowska M., Szeląg-Wasielewska E. 2020. Some aspects of the ecological niche of chironomids associated with submersed aquatic macrophytes in a tailwater. *Knowledge and Management of Aquatic Ecosystems* 421: 22.
    punkty MNiSW = 100, IF$_{2020}$ = 1.364

11. Kornijów R., Dukowska M., **Leszczyńska J.**, Smith C., Jeppesen E., Hansson L.-A., Ketola M., Irvine K., Nõges T., Sahuquillo M., Miracle M.R., Gross E., Kairesalo T., van Donk E., de Eyto E., García-Criado F., Grzybkowska M., Moss B. 2021. Distribution patterns of epiphytic reed-associated macroinvertebrates across European shallow lakes. *Science of The Total Environment* 760: 144117.
    punkty MNiSW = 200, IF$_{2021}$ = 6.551

12. Pyrzanowski K., Zięba G., **Leszczyńska J.**, Adamczuk M., Dukowska M., Przybylski M. 2021. Food resource partitioning between juvenile and mature weatherfish *Misgurnus fossilis*. *Ecology and Evolution* 00: 000-000 (*w druku*).
    punkty MNiSW = 100, IF$_{2021}$ = 2.392

13. **Leszczyńska J.**, Głowacki Ł., Grzybkowska M., Przybylski M. 2021. Chironomid riverine assemblages at the regional temperate scale – compositional distance and species diversity. *The European Zoological Journal* 00: 000-000 (*po recenzji*).
    punkty MNiSW = 140, IF$_{2021}$ = 1.656

Prace spoza listy MNiSW (po aktualizacji z dn. 9 lutego 2021 r., punkty MNiSW = 5):

1. Lik J., **Leszczyńska J.**, Dukowska M., Szczerkowska-Majchrzak E., Grzybkowska M. 2014. Biocenoza zanurzonych makrofitów w Warcie poniżej tamy. *Roczniki Naukowe Polskiego Związku Wędkarskiego* 27: 103-127.

2. Lik J., Adamczuk M., Dukowska M., Grzybkowska M., **Leszczyńska J.**, Szczerkowska-Majchrzak E. 2015. Przegęszczona płoć i jej baza pokarmowa zasobna w zooplankton poniżej tamy zbiornika Jeziorsko. *Roczniki Naukowe Polskiego Związku Wędkarskiego* 28: 85-104.

3. M. Grzybkowska, **J. Leszczyńska**. 2019. Jak żyć w antropocenie bez szkody dla siebie i planety Ziemia? *Nauka Przyroda Technologie* 13(2): 89-99.

4. M. Grzybkowska, **J. Leszczyńska**, Ł. Głowacki. 2020. Owady na talerzu. *Kosmos* 69(2): 355-360.

Prace w recenzowanych materiałach konferencyjnych:

1. Pyrzanowski K., Dukowska M., Michałowicz J., Grzybkowska M., Szczerkowska-Majchrzak E., **Leszczyńska J.**, Lik J. 2015. Metale ciężkie w osadach dennych nizinnej rzeki Mrogi (w:) Bory Tucholskie i inne obszary leśne. Ochrona i biomonitoring, K. Gwoździński (red.), Wyd. UŁ, Łódź, ss. 128-139, ISBN 978-83-7969-590-4.

KOMUNIKATY ZJAZDOWE/CONFERENCE ABSTRACTS

1. Lik J., Dukowska M., **Leszczyńska J.**, Grzybkowska M., Szczerkowska-Majchrzak E. 2013. Konsekwencje piętrzenia dużej nizinnej rzeki dla bezkręgowców i ryb. Materiały konferencyjne XX Ogólnopolskich Warsztatów Bentologicznych, s. 30.
2. Lik J., Dukowska M., **Leszczyńska J.**, Szczerkowska-Majchrzak E., Grzybkowska M. 2014. Dieta jazgarza (*Gymnocephalus cernuus*) w Warcie, powyżej i poniżej piętrzenia. Materiały konferencyjne XXI Ogólnopolskich Warsztatów Bentologicznych, s. 63.
3. **Leszczyńska J.**, Lik J., Szczerkowska-Majchrzak E.,Woziwoda B. 2014. Przestrzenne zróżnicowanie zgrupowania bentofauny w początkowym odcinku Pichny Szadkowickiej. Materiały konferencyjne XXI Ogólnopolskich Warsztatów Bentologicznych, s 62.
4. Dukowska M., Grzybkowska M., Szczerkowska-Majchrzak E., Lik J., **Leszczyńska J.**, Pyrzanowski K. 2014. Bioakumulacja metali w wybranych bezkręgowcach bentosowych. Materiały konferencyjne XXI Ogólnopolskich Warsztatów Bentologicznych, s. 50-51.
5. Dukowska M., Michałowicz J., Grzybkowska M., Szczerkowska-Majchrzak E., Pyrzanowski K., Lik J., **Leszczyńska J.** 2014. Kumulacja wybranych metali w osadach rzeki Mrogi. Materiały konferencyjne IX Konferencji „Bory Tucholskie – Ochrona Biosfery", s. 10.
6. **Leszczyńska J.**, Grzybkowska M., Dukowska M., Kurzawski M. 2014. Reakcja Chironomidae (Diptera) na piętrzenie niskorzędowych odcinków rzek nizinnych: Bzury, Mrogi i Mrożycy. Materiały konferencyjne IX Konferencji „Bory Tucholskie – Ochrona Biosfery", s. 20.
7. **Leszczyńska J.**, Chrustowicz M., Lik J., Szczerkowska-Majchrzak E. 2015. Dynamika sezonowa bentofauny w początkowym odcinku Pichny Szadkowickiej. Materiały konferencyjne XXII Ogólnopolskich Warsztatów Bentologicznych, s. 50.
8. **Leszczyńska J.**, Pyrzanowski K., Dukowska M., Grzybkowska M., Michałowicz J., Szczerkowska-Majchrzak E., Lik J. Bioakumulacja wybranych metali w różnych stadiach *Prodiamesa olivacea* (Chironomidae, Diptera) z nizinnej rzeki Mrogi. Materiały konferencyjne XXIII Ogólnopolskich Warsztatów Bentologicznych, s. 33-34.
9. Pyrzanowski K., **Leszczyńska J.**, Dukowska M., Grzybkowska M., Michałowicz J., Szczerkowska-Majchrzak E., Lik J. Wynoszenie metali ze środowiska wodnego przez muchówki Chironomidae na przykładzie rzeki Bzury. Materiały konferencyjne XXIII Ogólnopolskich Warsztatów Bentologicznych, s. 40.
10. **Leszczyńska J.**, Pyrzanowski K., Grzybkowska M. 2017. Siedliska nizinnej rzeki Moszczenicy i ich bentofauna. Materiały konferencyjne XXIV Ogólnopolskich Warsztatów Bentologicznych, s. 39.

11. **Leszczyńska J.**, Pyrzanowski K., Szczerkowska-Mjchrzak E. 2017. Sezonowa dynamika dryfu w nizinnej rzece w okresie powrotu do wysokiej częstotliwości zmian przepływu po renaturyzacji. Materiały konferencyjne XXIV Ogólnopolskich Warsztatów Bentologicznych, s. 40.
12. Pyrzanowski K., **Leszczyńska J.**, Zięba G., Dukowska M. 2017. Makrobezkręgowce bentosowe kanału melioracyjnego stanowiące bazę pokarmową dla piskorza *Misgurnus fossilis*. Materiały konferencyjne XXIV Ogólnopolskich Warsztatów Bentologicznych, s. 45.
13. **Leszczyńska J.**, Grzybkowska M., Dukowska M. 2017. Struktura zgrupowań muchówek Chironomidae w nizinnej rzece Moszczenicy. Materiały konferencyjne I Krajowej Konferencji Naukowo-Technicznej „Funkcjonowanie i ochrona wód płynących” PotamON 2017, s. 55.
14. **Leszczyńska J.**, Grzybkowska M. Bioróżnorodność makrobezkręgowców bentosowych w mikrohabitatach rzeki Moszczenicy. Poster prezentowany na IX Konferencji „Interdyscyplinarne Zagadnienia w Inżynierii i Ochronie Środowiska” EKO-DOK 2017.
15. **Leszczyńska J.**, Pyrzanowski K., Grzybkowska M., Głowacki Ł. Chironomid communities of polish lowland rivers: structure, species richness and their environmental determinants. Proceedings of the 7th Aquatic Biodiversity International Conference ABIC 2019, Sybin (Rumunia), s. 12.
16. Pyrzanowski K., **Leszczyńska J.**, Zięba G., Dukowska M., Smith C., Przybylski M. Diel feeding activity, diet and trophic niche of the weatherfish Misgurnus fossilis. Proceedings of the 7th Aquatic Biodiversity International Conference ABIC 2019, Sybin (Rumunia), s. 42.

PROJEKTY BADAWCZE/SCIENTIFIC PROJECTS

1. Wykonawca projektu badawczego NCN nr rej. N N304 023240 pt. „Ocena bioakumulacji wybranych metali w bezkręgowcach bentosowych (Chironomidae) o rozmaitych adaptacjach do środowiska”, kierownik: dr hab. Małgorzata Dukowska (2013-2016 r.).

2. Kierownik „Dofinansowania dla młodych badaczy” ze środków MNiSW (2015-2017 r. 3-krotnie).

ZAŁĄCZNIK III/ APPENDIX III

OŚWIADCZENIA WSPÓŁAUTORÓW/

DECLARATIONS OF CO-AUTHORS ON THEIR CONTRIBUTION TO THE PUBLICATIONS

Leszczyńska J., Głowacki Ł., Grzybkowska M., Przybylski M. 2021. Chironomid riverine assemblages at the regional temperate scale – compositional distance and species diversity. *The European Zoological Journal* 00(0): 000-000 (*po recenzji*).

Łódź, dn. 09.12.2020 r.

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Oświadczam, że jestem współautorem artykułu:

Leszczyńska J., Głowacki Ł., Grzybkowska M., Przybylski M. 2021. Chironomid riverine assemblages at the regional temperate scale – compositional distance and species diversity. *The European Zoological Journal* 00(0): 000-000 (*po recenzji*).

Mój udział w pracy oceniam na 40%. Polegał on na wykonaniu części prac terenowych i laboratoryjnych, uczestnictwie w zaproponowaniu koncepcji artykułu, wstępnym opracowaniu danych oraz przygotowaniu treści manuskryptu (autor korespondencyjny).

Joanna Leszczyńska

Joanna Leszczyńska

Łódź, dn. 09.12.2020 r.

dr hab. Łukasz Głowacki
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Oświadczam, że jestem współautorem artykułu:

Leszczyńska J., **Głowacki Ł.**, Grzybkowska M., Przybylski M. 2021. Chironomid riverine assemblages at the regional temperate scale – compositional distance and species diversity. *The European Zoological Journal*00(0): 000-000 (*po recenzji*).

Mój udział w pracy oceniam na 30%. Polegał on na uczestnictwie w zaproponowaniu koncepcji artykułu, analizie statystycznej danych, przygotowaniu treści manuskryptu oraz jego wstępnej weryfikacji językowej.

Łukasz Głowacki

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Oświadczam, że jestem współautorem artykułu:

Leszczyńska J., Głowacki Ł., **Grzybkowska M.**, Przybylski M. 2021. Chironomid riverine assemblages at the regional temperate scale – compositional distance and species diversity. *The European Zoological Journal* 00(0): 000-000 (*po recenzji*).

Mój udział w pracy oceniam na 15%. Polegał on na wykonaniu prac terenowych i laboratoryjnych, uczestnictwie w zaproponowaniu koncepcji artykułu oraz przygotowaniu treści manuskryptu.

Maria Grzybkowska
Maria Grzybkowska

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Oświadczam, że jestem współautorem artykułu:

Leszczyńska J., Głowacki Ł., Grzybkowska M., **Przybylski M.** 2021. Chironomid riverine assemblages at the regional temperate scale – compositional distance and species diversity. *The European Zoological Journal* 00(0): 000-000 (*po recenzji*).

Mój udział w pracy oceniam na 15%. Polegał on na uczestnictwie w zaproponowaniu koncepcji artykułu, analizie statystycznej danych oraz przygotowaniu treści manuskryptu.

Mirosław Przybylski

Leszczyńska J., Głowacki Ł., Grzybkowska M. 2017. Factors shaping species richness and biodiversity of riverine macroinvertebrate assemblages at the local and regional scale. *Community Ecology* 18(3): 227-236.

Łódź, dn. 09.12.2020 r.

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90-237 Łódź

Oświadczam, że jestem współautorem artykułu:

Leszczyńska J., Głowacki Ł., Grzybkowska M. 2017. Factors shaping species richness and biodiversity of riverine macroinvertebrate assemblages at the local and regional scale. *Community Ecology* 18(3): 227-236.

Mój udział w pracy oceniam na 60%. Polegał on na zaproponowaniu koncepcji artykułu, przeglądzie literatury, wykonaniu szaty graficznej, przygotowaniu treści manuskryptu (autor korespondencyjny).

Joanna Leszczyńska
Joanna Leszczyńska

Łódź, dn. 09.12.2020 r.

dr hab. Łukasz Głowacki
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Oświadczam, że jestem współautorem artykułu:

Leszczyńska J., **Głowacki Ł.**, Grzybkowska M. 2017. Factors shaping species richness and biodiversity of riverine macroinvertebrate assemblages at the local and regional scale. *Community Ecology* 18(3): 227-236.

<u>Mój udział w pracy oceniam na 20%</u>. Polegał on na przeglądzie literatury, przygotowaniu treści manuskryptu oraz jego weryfikacji językowej.

Łukasz Głowacki

Łukasz Głowacki

Łódź, dn. 09.12.2020 r.

prof. dr hab. Maria Grzybkowska
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Wydział Biologii i Ochrony Środowiska
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90-237 Łódź

Oświadczam, że jestem współautorem artykułu:

Leszczyńska J., Głowacki Ł., **Grzybkowska M.** 2017. Factors shaping species richness and biodiversity of riverine macroinvertebrate assemblages at the local and regional scale. *Community Ecology* 18(3): 227-236.

Mój udział w pracy oceniam na 20%. Polegał on na przeglądzie literatury oraz przygotowaniu treści manuskryptu.

MGrzybkowska
Maria Grzybkowska

Leszczyńska J., Grzybkowska M., Głowacki Ł., Dukowska M. 2019. Environmental Variables Influencing Chironomid Assemblages (Diptera: Chironomidae) in Lowland Rivers of Central Poland*. Environmental Entomology* 48(4): 988-997.

Łódź, dn. 09.12.2020 r.

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90-237 Łódź

Oświadczam, że jestem współautorem artykułu:

Leszczyńska J., Grzybkowska M., Głowacki Ł., Dukowska M. 2019. Environmental Variables Influencing Chironomid Assemblages (Diptera: Chironomidae) in Lowland Rivers of Central Poland. *Environmental Entomology* 48(4): 988–997.

Mój udział w pracy oceniam na 50%. Polegał on na uczestnictwie w części prac terenowych i laboratoryjnych, udziale w zaproponowaniu koncepcji artykułu, opracowaniu danych (środowisko R, modelowanie bayesowskie), przygotowaniu szaty graficznej oraz treści manuskryptu (autor korespondencyjny).

Joanna Leszczyńska

Joanna Leszczyńska

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Oświadczam, że jestem współautorem artykułu:

Leszczyńska J., **Grzybkowska M.**, Głowacki Ł., Dukowska M. 2019. Environmental Variables Influencing Chironomid Assemblages (Diptera: Chironomidae) in Lowland Rivers of Central Poland. *Environmental Entomology* 48(4): 988–997.

Mój udział w pracy oceniam na 20%. Polegał on na wykonaniu prac terenowych i laboratoryjnych, uczestnictwie w zaproponowaniu koncepcji artykułu oraz przygotowaniu treści manuskryptu.

M Grzybkowska
Maria Grzybkowska

Łódź, dn. 09.12.2020 r.

dr hab. Łukasz Głowacki
Katedra Ekologii i Zoologii Kręgowców
Wydział Biologii i Ochrony Środowiska
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ul. Banacha 12/16
90-237 Łódź

Oświadczam, że jestem współautorem artykułu:

Leszczyńska J., Grzybkowska M., **Głowacki Ł.**, Dukowska M. 2019. Environmental Variables Influencing Chironomid Assemblages (Diptera: Chironomidae) in Lowland Rivers of Central Poland. *Environmental Entomology* 48(4): 988–997.

Mój udział w pracy oceniam na 15%. Polegał on na przygotowaniu treści manuskryptu oraz jego wstępnej weryfikacji językowej.

Łukasz Głowacki

Łukasz Głowacki

Łódź, dn. 09.12.2020 r.

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Oświadczam, że jestem współautorem artykułu:

Leszczyńska J., Grzybkowska M., Głowacki Ł., **Dukowska M.** 2019. Environmental Variables Influencing Chironomid Assemblages (Diptera: Chironomidae) in Lowland Rivers of Central Poland. *Environmental Entomology* 48(4): 988–997.

<u>Mój udział w pracy oceniam na 15%</u>. Polegał on na wykonaniu części prac terenowych i laboratoryjnych, przygotowaniu bazy danych oraz treści manuskryptu.

Małgorzata Dukowska

STRESZCZENIE

Lokalna i regionalna różnorodność gatunkowa Chironomidae (Diptera) w rzekach centralnej Polski

Ochotki (Chironomidae) są rodziną niewielkich muchówek powszechnie występujących w słodkowodnych, zarówno płynących, jak i stojących ekosystemach całego świata. Pod względem liczebności oraz bogactwa gatunkowego często dominują one w zgrupowaniach makrobezkręgowców bentosowych. Stanowią ważny składnik diety dla wielu organizmów, pełniąc tym samym niezwykle istotną rolę w obiegu materii oraz przepływie energii ekosystemów. Ze względu na trudności w identyfikacji larw do możliwie najniższego poziomu taksonomicznego, dane o Chironomidae często są powierzchowne i ograniczone jedynie do liczby osobników w obrębie całej rodziny. Celem niniejszej rozprawy było uzupełnienie niewystarczającej wiedzy na temat różnorodności zgrupowań Chironomidae oraz czynników determinujących ich występowanie w rzekach położonych w stosunkowo jednorodnym zoogeograficznie regionie centralnej Polski.

Aby zrealizować powyższe cele, próby pobierano w jednym cyklu rocznym (raz w miesiącu) z siedmiu stanowisk wyznaczonych w odcinkach nizinnych rzek o różnej rzędowości: Bzura (I), Mroga (II), Mrożyca (II), Moszczenica (III), Grabia (III), Widawka (IV), Warta (V). Materiał biologiczny stanowiły dane zebrane w ciągu ostatnich 30 lat z każdej rzeki, uzupełnione o próby z nowego stanowiska wyznaczonego w Moszczenicy. W czasie poboru prób mierzono również podstawowe parametry środowiskowe rzek. Wyniki zawarto w dwóch artykułach opublikowanych w czasopismach z listy JCR (*Community Ecology, Environmental Entomology*) oraz jednym manuskrypcie, wysłanym po recenzjach do redakcji *The European Zoological Journal*, kolejnego czasopisma z listy JCR. Sumaryczna wartość współczynnika Impact Factor publikacji wchodzących w skład wynosi 4.221, a suma punktów MNiSW — 280 (bez publikacji *TEZJ*, IF = 2,565, punkty MNiSW = 140).

W toku badań pozyskano 840 prób, w których oznaczono ogółem 61 gatunków Chironomidae z pięciu podrodzin: Tanypodinae, Diamesinae, Prodiamesinae, Orthocladiinae, Chironominae. W badanych zgrupowaniach zidentyfikowano gatunki typowe dla potamalu rzek nizinnych regionu palearktycznego. Analiza SIMPER wyodrębniła grupę 14 gatunków: *Chironomus riparius, Polypedilum convictum, Prodiamesa olivacea, Polypedilum scalaenum, Micropsectra notescens, Stictochironomus sticticus, Cladotanytarsus mancus, Cryptochironomus defectus*, *Paratendipes albimanus*, *Cricotopus sylvestris*, *Microtendipes*

chloris, Macropelopia nebulosa, Paratanytarsus dissimilis, Robackia demeijerei, które wyjaśniały prawie 60% różnic między zgrupowaniami. Wśród nich większość stanowiły gatunki pospolite w zbiorze danych, m. in. obecne w każdej rzece, niezwykle plastyczne i szeroko rozpowszechnione gatunki z rodzajów *Chironomus* i *Polypedilum*.

Pod względem funkcjonalnym, skład zgrupowań Chironomidae nie odbiegał od teorii ciągłości rzeki z dominacją zbieraczy w rzekach o niższej i średniej rzędowości (Prodiamesinae i wiele gatunków Chironomini) oraz wysokim udziałem zdrapywaczy (wiele gatunków Orthocladiinae) i filtratorów (Tanytarsini) w rzekach o wyższej rzędowości. Z kolei bogactwo gatunkowe wzrastało wraz z rzędowością rzeki, osiągając wartości maksymalne w ciekach trzeciego i czwartego rzędu (Grabia, Widawka).

Wartości zastosowanych miar różnorodności/dominacji/równomierności istotnie różniły się zarówno pomiędzy sobą jak i pomiędzy rzekami. Wskazuje to, iż jedynie szeroki wybór tych miar daje relatywnie wiarygodne wyniki w badaniach struktury zgrupowań makrobezkręgowców bentosowych. Struktura zgrupowań muchówek Chironomidae istotnie nawiązywała do profili siedliskowych poszczególnych cieków, ich wielkości oraz przynależności do systemu rzecznego (Wisły i Odry). Decydującymi parametrami były: szybkość prądu, granulacja nieorganicznego podłoża, biomasa bentonicznej cząsteczkowej materii organicznej, zawartość rozpuszczonego w wodzie tlenu, oraz biomasa transportowanej cząsteczkowej materii organicznej. Wszystkie wspomniane zmienne środowiskowe uznawane są przez hydrobiologów za jedne z głównych determinantów występowania makrobezkręgowców bentosowych, w tym Chironomidae. Ponadto, modelowanie bayesiańskie wskazało na istnienie pozytywnej zależności pomiędzy liczbą gatunków Chironomidae a granulacją nieorganicznego podłoża oraz zawartością rozpuszczonego w wodzie tlenu. Bardziej gruboziarnisty substrat oraz większa koncentracja tlenu w wodzie umożliwia kolonizację siedlisk, poza gatunkami oportunistycznymi także gatunkom bardziej wyspecjalizowanym i rzadkim.

Różnorodność Chironomidae (N_1) (gamma γ) całego regionu wyniosła 18,31 gatunków. Została ona rozłożona na średni składnik alfa (α) o wartości 4,04 gatunków i składnik beta (β) o wartości 4,53 zgrupowań.

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SUMMARY

Local and regional species diversity of Chironomidae (Diptera) in rivers of central Poland

Non-biting midges (Chironomidae) are a family of small dipterans, commonly occurring in freshwaters of both lotic and lentic ecosystems around the world. In terms of abundance and species richness they often dominate in benthic macroinvertebrate assemblages. They constitute essential prey for many organisms, thus they play an extremely important role in the circulation of organic matter and in the flow of the energy within ecosystems. Because of some difficulties in identifying chironomid larvae to the lowest possible taxonomic level, data on Chironomidae are often superficial and limited to the number of individuals within the family. The aim of this Ph.D. thesis was to enrich the insufficient knowledge of the diversity of Chironomidae assemblages and of the factors determining their occurrence in rivers located in a zoogeographically homogeneous region of central Poland.

To accomplish the above tasks, chironomid samples were collected in one annual cycle, (once a month), from seven sections of lowland rivers of various orders: the Bzura (I), Mroga (II), Mrożyca (II), Moszczenica (III), Grabia (I), Widawka (IV), and Warta (V). The biological material was collected in the rivers over the recent 30 years; the latest dataset was that obtained in the Moszczenica. During the sampling of chironomids, basic environmental parameters were also measured. The results are contained in two published papers (journals of *Community Ecology* and *Environmental Entomology*) and in one manuscript sent after reviews to the editorial office of a journal (*The European Zoological Journal*). All three journals are from the JCR list. The total value of the Impact Factor of the papers included in the Ph.D. thesis is 4.221, and the sum of points these journals have in the list of the Polish Ministry of Science and Higher Education is 280 (without *TEZJ*, IF = 2.565, PMS&HE score = 140).

In the seven rivers, 840 samples were obtained, from which a total of 61 chironomid species from five subfamilies: Tanypodinae, Diamesinae, Prodiamesinae, Orthocladiinae, Chironominae, were identified. In the composition of the assemblages, species typical of the potamal of lowland rivers of the Palearctic region were observed. The SIMPER analysis identified a group of 14 species: *Chironomus riparius*, *Polypedilum convictum*, *Prodiamesa olivacea*, *Polypedilum scalaenum, Micropsectra notescens, Stictochironomus sticticus,*

Cladotanytarsus mancus, Cryptochironomus defectus, Paratendipes albimanus, Cricotopus sylvestris, Microtendipes chloris, Macropelopia nebulosa, Paratanytarsus dissimilis, Robackia demeijerei that explained almost 60% of the differences between the assemblages. The majority of the above mentioned species were the most common ones in the whole dataset. Among the species present in each river, those of extraordinary flexible and commonly widespread genera of *Chironomus* and *Polypedilum* were recorded.

In terms of functions performed by given species, the composition of chironomid assemblages was similar to this that might be predicted by the river continuum concept, i.e. to a structure characterized by the predominance of collectors in rivers of lower and medium orders (Prodiamesinae and many Chironomini species) and considerable shares of scrapers (many species of Orthocladiinae) and filterers (Tanytarsini) in rivers of higher orders. In turn, the species richness of chironomids increased with the river's order, reaching its maximum values in the third and fourth order streams (Grabia, Widawka).

The values of used diversity/domination/evenness measures differed both from measure to measure and from river to river. This shows that only a comprehensive choice of such measures gives relatively reliable results in the study of the structure of benthic macroinvertebrate assemblages. The structure of chironomid assemblages was related to the habitat profiles of the studied rivers, their size and belonging to a given river system (Vistula and Oder). The most important environmental parameters were current velocity, granulation of the inorganic bottom substrate, biomass of benthic particulate organic matter, content of dissolved oxygen, and biomass of transported particulate organic matter. All above mentioned environmental variables are considered by the hydrobiology specialists as ones of the main determinants of the occurrence of benthic macroinvertebrates, including Chironomidae. Moreover, Bayesian modeling showed a positive relationship between the number of chironomid species and the granulation of the inorganic bottom substrate and the content of dissolved oxygen. Coarse-grained substrate and higher oxygen concentration in water enable not only opportunistic but also more specialized and rare species to colonize habitats.

The diversity of chironomids (N_1) (gamma, γ) of the entire region was 18.31 species. It was decomposed into the average alpha (α) component of 4.04 species and the beta (β) component of 4.53 assemblages.

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