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MAKROZOOBENTOS RÓŻNYCH SIEDLISK ZALEWU WIŚLANEGO

ROZPRAWA DOKTORSKA
składająca się z cyklu artykułów naukowych
w dziedzinie nauk ścisłych i przyrodniczych
w dyscyplinie nauki biologiczne

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Abstrakt

Celem rozprawy doktorskiej było znalezienie odpowiedzi na szereg pytań dotyczących prawidłowości występowania zoobentosu w różnych siedliskach (śródzalewia i litoralu) przymorskiej laguny na przykładzie Zalewu Wiślanego. Badania prowadzono w latach 2010 – 2014. Wyniki opublikowano w czterech pracach z listy JCR. Skład i bogactwo gatunkowe zależały przede wszystkim od stopnia zróżnicowania siedliskowego. Były one najniższe w śródzalewiu, pośrednie w strefie elodeidów i najwyższe w strefie helofitów. Zagęszczenie zoobentosu uwarunkowane było głównie typem osadów (granulacja, zawartości materii organicznej) i dynamiką warunków hydrologicznych. Było ono najniższe wśród elodeidów, wyższe w śródzalewiu i najwyższe w strefie helofitów. Horyzontalne rozmieszczenie fauny w litoralu miało charakter strefowy, zależnie od odległości od pelagialu w gęstym pasie helofitów, odzwierciedlając strefowość zaznaczoną w warunkach fizyczno-chemicznych. Rozmieszczenie pionowe zoobentosu w osadach dennych zależało od odmiennych czynników w poszczególnych siedliskach zalewu. W litoralu były to głównie obecność i stopień upakowania systemów korzeniowych roślin, w strefie śródzalewia granulacja osadów i warunki pokarmowe. W śródzalewiu stwierdzono nieantagonistyczne relacje pomiędzy detrytusożernymi Tubificinae i larwami ochotek w tych samych warstwach osadów dennych. Zaproponowano hipotetyczny model wzajemnych interakcji pomiędzy *C. balatonicus* i Tubificinae oraz ich aktywności życiowej w osadach dennych.

1. Spis publikacji wchodzących w skład rozprawy doktorskiej

Niniejsza rozprawa doktorska składa się z cyklu czterech publikacji, opublikowanych w latach 2019 - 2022 w czasopismach z listy *Journal Citation Reports*. Jedna z nich dotyczy bentosu śródzalewia Zalewu Wiślanego, pozostałe trzy makrofitów i bentosu strefy litoralu. Łączna liczba punktów za publikacje zgodnie z rokiem opublikowania wg MEiN wynosi 370, a sumaryczny *Impact Factor* to 9,8.

1. Kornijów R., Pawlikowski K., Błędzki L.A., Drgas A., Piwosz K., Ameryk A., Całkiewicz J., 2021. **Co-occurrence and potential resource partitioning between oligochaetes and chironomid larvae in a sediment depth gradient.** Aquatic Sciences 83(51): 1-10. https://doi.org/10.1007/s00027-021-00800-z

   IF_{2021} = 2,755 punkty $MEiN_{2021}$ = 100

2. Pawlikowski K., Kornijów R., 2019. **Role of macrophytes in structuring littoral habitats in the Vistula Lagoon (southern Baltic Sea).** Oceanologia 61: 26-37. https://doi.org/10.1016/j.oceano.2018.05.003

   IF_{2019} = 2,198 punkty $MNiSW_{2019}$ = 70

3. Pawlikowski K., Kornijów R., 2022. **Distribution of benthic macroinvertebrates across a reed stand in a brackish Baltic lagoon.** Oceanologia 64: 433-444. https://doi.org/10.1016/j.oceano.2022.02.004

   IF_{2022} = 2,427 punkty $MEiN_{2021}$ = 100

4. Pawlikowski K., Kornijów R., 2022. **Above- and belowground habitat complexity created by emergent and submerged vegetation drives the structure of benthic assemblages.** Oceanologia. https://doi.org/10.1016/j.oceano.2022.10.002

   IF_{2022} = 2,427 punkty $MEiN_{2021}$ = 100

2. Wstęp

Makrozoobentos, czyli bezkręgowce żyjące na dnie lub w osadach dennych o rozmiarach przekraczających 1 mm (Żmudziński et al., 2002), ma istotne znaczenie dla funkcjonowania ekosystemów wodnych. Udział zoobentosu w produkcji wtórnej w zbiorniku wodnym może sięgać 86% (Lindegaard, 1994). Bezkręgowce bentosowe wchodzą w interakcje z innymi zespołami ekologicznymi, oddziałując na zasadzie drapieżnictwa, pasożytnictwa czy konkurencji (Lellak, 1965; Morin et al., 1988; Armitage et al., 1995). Stanowią one też pokarm dla ryb (McCormack, 1970; Craig, 1977; Diehl and Kornijow, 1998; Kornijów, 1997; Kornijow et al., 2005; Kornijów et al., 2016) i nektobentosu (Armitage et al., 1995; Koperski, 1998). Poprzez swoją aktywność, taką jak pobieranie pokarmu i związane z tym przetwarzanie materii organicznej oraz borowanie osadów (bioturbacja), mają też znaczącą rolę w krążeniu materii i kształtowaniu warunków siedliskowych (Charbonneau i Hare 1998; Covich at al., 1999; Urban-Malinga et al., 2013). Poznanie składu gatunkowego, rozmieszczenia, roli i potrzeb zoobentosu w zbiorniku wodnym jest niezbędne dla zrozumienia zachodzących w nim procesów ekologicznych.

Dotychczasowe badania dotyczące makrozoobentosu Zalewu Wiślanego prowadzone były najczęściej w strefie śródzalewia, z pominięciem litoralu (np.: Klimowicz, 1958; Cywińska i Różańska, 1978; Różańska i Cywińska, 1983; Ezhova & Pavlenko, 2001; Ezhova et al., 2005; Ezhova et al., 2012). Wyjątek stanowi praca Żmudzińskiego (1957), w której zawarte są informacje na temat bentosu strefy przybrzeżnej. Także w lagunach i jeziorach przymorskich innych rejonów świata rzadko badano bentos w strefie litoralu (np.: Hansen et al., 2007; Canedo-Arguelles & Rieradevall, 2009; Kotta, 2013). W związku z tym w latach 2010 – 2014 przeprowadzono badania fauny dennej Zalewu Wiślanego ze szczególnym uwzględnieniem litoralu. Jako cel pracy postawiono znalezienie odpowiedzi na następujące pytania:

1. W jaki sposób stopień zróżnicowania siedlisk wpływa na skład i zagęszczenie zoobentosu?
2. Jaki jest wpływ roślinności na warunki siedliskowe i pokarmowe zoobentosu w strefie litoralu?

3. Jak kształtują się i od czego zależą: skład gatunkowy, struktura dominacji, liczebność oraz rozmieszczenie w profilu pionowym osadów dennych w strefach litoralu i śródzalewia?

Postawiono pięć hipotez badawczych:

H_1 Skład gatunkowy i zagęszczenie makrozoobentosu zależą od stopnia zróżnicowania siedliskowego.

H_2 Obecność makrofitów wpływa na warunki siedliskowe i pokarmowe zoobentosu w strefie litoralu.

H_3 Na pionowe rozmieszczenie zoobentosu w profilu osadów dennych wpływa granulacja osadów oraz obecność i stopień upakowania systemów korzeniowych roślin.

H_4 Skład gatunkowy i zagęszczenie zoobentosu w obrębie płatów helofitów zmieniają się zależnie od odległości od pelagialu, odzwierciedlając strefowość zaznaczoną w warunkach fizyczno-chemicznych.

H_5 Występowanie Tubificinae i larw *Chironomus balatonicus* w tych samych warstwach osadów nie ma charakteru antagonistycznego.

Próby pobierano wiosną, latem i jesienią. W śródzalewiu stanowiska badań położone były na głębokości 3 m, gdzie muliste osady denne nie były porośnięte przez roślinność. W litoralu badaniami objęto fragment znajdujący się około 2 km na wschód od Tolkmicka. Roślinność wynurzoną w tym rejonie stanowił pas trzcin (*Phragmites australis* (Cav.) Trin. ex Steud.) o długości ok. 500 m i szerokości 110 m. Strefa roślinności zanurzonej zdominowana była przez płaty rdestnicy przeszytej (*Potamogeton perfoliatus* L.). Wyznaczono szereg stanowisk badawczych w strefach szuwaru trzcinowego oraz elodeidów, w różnej odległości od brzegu, na głębokościach od 25 do 100 cm.

Próby zoobentosu pobierano czerpaczem rurowym o średnicy 4,4 lub 6,0 cm. Pobrane rdzenie miały długość 25 cm. Celem poznania pionowego rozmieszczenia fauny w osadach rdzenie cięto na warstwy o grubości: 2, 3 i 5 cm, odpowiadające głębokościom: 0-2, 2-5, 5-10, 10-15, 15-20 i 20-25 cm przy użyciu specjalnego aparatu (Kornijów, 2013). Osad przesiewano na sicie o średnicy oczka 300 µm.

Poborowi prób towarzyszyły pomiary zasolenia, natlenienia, temperatury i poziomu wody. W wybranych terminach prowadzono również dodatkowe pomiary szeregu innych czynników środowiskowych takich jak: natężenie światła nad powierzchnią wody, skład granulometryczny, zawartość chlorofilu-a i materii organicznej oraz zagęszczenie bakterii w osadach dennych.

Bezkręgowce wybierano z prób makroskopowo i konserwowano w 4% roztworze formaldehydu. Oznaczenia taksonomiczne prowadzono przy użyciu binokularu i mikroskopu do najniższego możliwego taksonu. Przynależność taksonomiczną larw Chironomidae określano za pomocą opracowania Andersen'a et al. (2013), a Oligochaeta według Timm'a (1999). Określono zagęszczenie bezkręgowców i ich biomasę (mokra masa formalinowa) w przeliczeniu na powierzchnię 1 m^2, a w przypadku rozmieszczenia pionowego w osadach w przeliczeniu na dm^3 osadu.

Do analizy zebranego materiału wykorzystano nieparametryczne testy H Kruskala-Wallisa i Chi^2 Friedmana. Stosowano także analizę rarefakcji (Gotelli & Colwell, 2001) do porównania bogactwa gatunkowego i indeksu różnorodności Shannona (H') oraz analizę wielozmiennową (wizualizacja wyników opartych o matryce podobieństwa Bray-Curtis'a za pomocą skalowania wielowymiarowego NMDS) do określenia różnic pomiędzy siedliskami.

3. Omówienie publikacji wchodzących w skład rozprawy doktorskiej

3.1. Kornijów R., Pawlikowski K., Błędzki L.A., Drgas A., Piwosz K., Ameryk A., Całkiewicz J., 2021. **Co-occurrence and potential resource partitioning between oligochaetes and chironomid larvae in a sediment depth gradient.** Aquatic Sciences 83(51): 1-10. https://doi.org/10.1007/s00027-021-00800-z

Interakcje ekologiczne w obrębie zoobentosu niekoniecznie muszą zachodzić wyłącznie na powierzchni lub w całym profilu zasiedlonego osadu. Mogą też mieć miejsce w pewnych specyficznych dla danych grup organizmów warstwach (Whitlatch, 1980). W pracy zbadano bogactwo gatunkowe i zagęszczenia zoobentosu w pionowym profilu osadów, a także międzygatunkowe interakcje pomiędzy detrytusożernymi Tubificinae i larwami ochotek *Chironomus balatonicus* Dévai, Wülker et Scholl, które współwystępują w tych samych warstwach osadów dennych.

Badania prowadzono w latach 2010-2011 na dwu stanowiskach zlokalizowanych w strefie otwartej wody (śródzalewie). Średnie całkowite zagęszczenie makrozoobentosu wynosiło 7044 ± 4493 osobników m^{-2}. Stwierdzono występowanie tylko 7 gatunków makrobezkręgowców, wśród których dominowały: *C. balatonicus*, *Potamothrix hammoniensis* (Mich.) i *Limnodrilus hoffmeisteri* Clapar. Faunę stwierdzano maksymalnie do 25 cm w głąb osadów. Większość bezkręgowców przebywała w górnej 10 cm warstwie osadów. Stwierdzono dodatnią korelację pomiędzy zagęszczeniami Tubificinae i larwami *C. balatonicus* (r^2 = 0,29; $p < 0,05$). Ich współwystępowanie było statystycznie istotne w najpłytszych warstwach (0-2 i 2-5 cm) (Testy χ^2 Pearsona dla tabel 2x2: $\chi^2_{0\text{-}2} = 7$; $p \leq 0,008$; $\chi^2_{2\text{-}5} = 50$; $p < 0,001$). Fakt ten oraz najwyższa frekwencja obu grup w warstwie 0-10 cm, przy obfitości pokarmu w postaci materii organicznej i bakterii, wskazywały na brak antagonistycznych interakcji. Zaproponowano hipotetyczny model wzajemnych interakcji pomiędzy *C. balatonicus* i Tubificinae oraz ich aktywności życiowej w osadach dennych.

3.2. Pawlikowski K., Kornijów R., 2019. **Role of macrophytes in structuring littoral habitats in the Vistula Lagoon (southern Baltic Sea).** Oceanologia 61: 26-37. https://doi.org/10.1016/j.oceano.2018.05.003

Jedną z najbardziej charakterystycznych cech strefy litoralu jest obecność makrofitów (roślin naczyniowych, ramienic i mszaków). W strefie przybrzeżnej najpłycej występują zgrupowania roślin wynurzonych (helofitów), głębiej rośliny z liśćmi pływającymi (nymfeidy) i rośliny zanurzone (elodeidy). Dotychczas w literaturze najczęściej szukano odpowiedzi na pytanie w jaki sposób czynniki siedliskowe wpływają na makrofity (Viaroli et al., 2008; Perez-Ruzafa et al., 2011). Znacznie rzadziej analizowano wpływ roślin na warunki panujące w litoralu. Stąd też w niniejszej pracy podjęto badania nad wpływem różnych form życiowych (helofity, elodeidy) i zagęszczenia makrofitów na warunki siedliskowe w litoralu.

Badania prowadzono w latach 2011-2014 w wycinku litoralu o długości około 500 m i szerokości 110 m. Znajdował się tam pas szuwaru trzcinowego (strefa helofitów), oraz strefa elodeidów z płatami rdestnicy przeszytej. W każdej ze stref badania przeprowadzono w trzech sektorach, różniących się odległością od brzegu.

Pomiędzy strefami wystąpiły różnice w stopniu naświetlenia dna, temperaturze i natlenieniu wody, zawartości materii organicznej, granulacji oraz koncentracji chlorofilu w osadach. Średnia dwumiesięczna temperatury wody była wyższa o ponad 0,5°C w strefie helofitów niż w strefie elodeidów (test T Wilcoxona, $p < 0.01$). Nasycenie wody tlenem było wyższe w strefie elodeidów (110-136%), gdzie występuje swobodne mieszanie się mas wody, niż w strefie helofitów (39-152%). Osady denne w strefie roślin wynurzonych były o mniejszym uziarnieniu (muł) niż w strefie elodeidów (drobny piasek). W obrębie strefy elodeidów nie stwierdzono horyzontalnego zróżnicowania warunków środowiskowych, takich jak: temperatura, natlenienie, zasolenie, uziarnienie osadów i zawartość materii organicznej w osadach dennych. Wystąpiło ono natomiast wyraźnie w pasie trzcinowiska. Tak więc wydaje się, że w Zalewie Wiślanym, w warunkach dużej dynamiki mas wody, na warunki siedliskowe w litoralu znacząco mogą wpływać tylko rosnące zwartym, szerokim pasem helofity. Rola elodeidów, z powodu występowania w płatach o małej powierzchni jest niewielka. W pracy zaproponowano schemat procesów

i zależności związanych z występowaniem makrofitów na badanym obszarze. Przedyskutowano wpływ roślinności mokradeł strefy litoralu na emisję i absorpcję gazów cieplarnianych.

3.3. Pawlikowski K., Kornijów R., 2022. **Distribution of benthic macroinvertebrates across a reed stand in a brackish Baltic lagoon.** Oceanologia 64: 433-444. https://doi.org/10.1016/j.oceano.2022.02.004

Znaczenie trzcinowisk, powszechnie występujących w ekosystemach wodnych jako czynnika determinującego skład i rozmieszczenie zoobentosu w lagunach przymorskich jest słabo poznany (Ostendorp, 1993). Podjęte badania miały na celu uzupełnienie wiedzy na ten temat. Prowadzono je w 2011 roku w płacie trzciny pospolitej o długości 200 m i szerokości około 60 m, w trzech sektorach, różniących się odległością od brzegu i pelagialu.

Większość (ponad 58%) występujących taksonów należała do detrytusofagów. Największe bogactwo jakościowe fauny (24 taksony) stwierdzono w środkowej strefie trzcinowiska, najmniejsze (16 taksonów) w strefie zewnętrznej, przyległej do pelagialu. Także najwyższe całkowite zagęszczenie fauny (do 15 tys. os. m^{-2}) i biomasy (do 107 g mokrej masy m^{-2}) najczęściej obserwowano w strefie środkowej (testy Kruskala-Wallisa dla zagęszczenia: $H = <6, 7>$; $p < 0,05$; dla biomasy: $H = <7, 8>$; $p < 0,04$). Wykazane przestrzenne zróżnicowanie jakościowe i ilościowe fauny korespondowało z wcześniej stwierdzoną strefowością warunków siedliskowych, w tym szczególnie natlenienia wody (Pawlikowski & Kornijów, 2019).

3.4. Pawlikowski K., Kornijów R., 2022. **Above- and belowground habitat complexity created by emergent and submerged vegetation drives the structure of benthic assemblages.** Oceanologia. https://doi.org/10.1016/j.oceano.2022.10.002

Obecność różnych form życiowych roślinności wynurzonej (helofitów) i zanurzonej (elodeidów), ich odmienna fenologia i dynamika rozwoju powodują, że strefy przez nie zajęte cechuje różny stopień strukturalnego zróżnicowania (m.in.: Peterson, 1982; Ságová-Marečková, 2002; Siebert & Branch, 2005, 2007; Fredriksen et al., 2010; Goshima & Peterson, 2012; González-Ortiz et al., 2016). Zależności te, w kontekście wpływu na makrobezkręgowce bentosowe nie są dobrze poznane. Stąd też celem niniejszej pracy było uzupełnienie wiedzy na ten temat.

Badania prowadzono w maju, lipcu i październiku 2013, w wycinku litoralu o długości około 500 m i szerokości 110 m, w którym znajdował się pas helofitów, złożony z trzciny pospolitej i przyległy pas piaszczystego dna z występującymi na nim płatami elodeidów z rdestnicą przeszytą.

Wykazano obecność 27 taksonów należących do: Naididae, Polychaeta, Hirudinea, Gammaridae, Chrysomelidae i Chironomidae. Ponad 92% taksonów należało do detrytusożerców. Wyższe o rząd wielkości zagęszczenia zoobentosu stwierdzono w strefie helofitów (średnie całkowite zagęszczenie w strefie helofitów wynosiło 28 310 ± 2 667 os. m^{-2}, w strefie elodeidów 2550 ± 288 os. m^{-2}) (testy Kruskala-Wallisa: H = <13, 14>; p < 0,001). Także bogactwo taksonomiczne i wartości indeksu Shannona oszacowane metodą rarefakcji były istotnie większe w tej strefie (H' = <1,7; 2,0>) (H' = <1,1; 1,3>). Skalowanie wielowymiarowe i test podobieństwa potwierdziły istotną różnicę (R = 0,658; p = 0,001; podobieństwo Braya-Curtisa < 20) pomiędzy siedliskami. Analizą SIMPER zidentyfikowano taksony, których zagęszczenia najbardziej różnią się pomiędzy strefami litoralu: *Limnodrilus calpaedianus* (19%), *Limnodrilus hoffmeisteri* (16%), *Chironomus* sp. (14%), *Potamothrix hammoniensis* (12%), *Glyptotendipes* sp. (10%), *Limnodrilus profundicola*

(6%) i *Marenzelleria* spp. (5%). Makrobezkręgowce bentosowe w strefie helofitów borowały w dnie płycej (10-15 cm) niż w strefie elodeidów (15-20 cm), prawdopodobnie z powodu obecności gęstego systemu rozłogów i korzeni. Najgłębiej borującym taksonem był występujący tylko w strefie elodeidów wieloszczet *Marenzelleria* spp.

4. Podsumowanie

4.1. Stopień zróżnicowania siedlisk ma wpływ na zoobentos

Stopień zróżnicowania siedliskowego w strefie śródzalewia i w litoralu (strefy helofitów i elodeidów) miał wyraźny wpływ przede wszystkim na bogactwo gatunkowe zoobentosu. Najniższe bogactwo zaobserwowano w śródzalewiu (7 taksonów), nieco wyższe w litoralu w strefie elodeidów (10 taksonów) i najwyższe w trzcinowisku (20 taksonów). Na zagęszczenie fauny większy wpływ miał charakter osadów dennych (granulacja, zawartość materii organicznej) i dynamika warunków hydrologicznych. Najmniej licznie zoobentos występował w litoralu w strefie elodeidów (2550 ± 288 osobników m^{-2}), liczniej w śródzalewiu (7044 ± 4493 os. m^{-2}) i najliczniej w trzcinowisku (28310 ± 2667 os. m^{-2}) (publikacja 1: Kornijów et al., 2021; publikacja 4: Pawlikowski & Kornijów, 2022b). Tym samym hipoteza H_1 okazała się prawdziwa. Wykazano też, że skład gatunkowy i zagęszczenie makrozoobentosu w obrębie płatów helofitów zmieniają się w zależności od odległości od pelagialu, odzwierciedlając strefowość zaznaczoną w warunkach fizyczno-chemicznych (publikacja 3: Pawlikowski & Kornijów, 2022a), co potwierdza prawdziwość założeń hipotezy H_4.

4.2. Roślinność wpływa na warunki siedliskowe i pokarmowe zoobentosu w strefie litoralu

Otrzymane wyniki wskazują na to, że w strefie litoralu przybrzeżnej laguny jaką jest Zalew Wiślany zarówno elodeidy, jak helofity mogą modyfikować warunki siedliskowe (publikacja 2: Pawlikowski & Kornijów, 2019). Jednak tylko w pasie trzcinowiska zaznaczyło się horyzontalne zróżnicowanie warunków środowiskowych, takich jak:

temperatura, natlenienie, zasolenie i zawartość materii organicznej w osadach dennych. Tym samym prawdziwość hipotezy H_2 potwierdzono w całości dla strefy helofitów i częściowo dla strefy elodeidów.

4.3. W profilu pionowym osadów dennych skład, struktura dominacji i liczebność zoobentosu kształtują się odmiennie w różnych siedliskach

Pionowe rozmieszczenie zoobentosu w osadach dennych zależy od odmiennych czynników w poszczególnych siedliskach Zalewu Wiślanego (litoral w strefie helofitów i elodeidów oraz śródzalewie) (publikacja 4: Pawlikowski & Kornijów, 2022b). W strefie litoralu okazały się nimi przede wszystkim granulacja osadów oraz obecność i stopień upakowania systemów korzeniowych roślin. Wynik ten pozwala na przyjęcie hipotezy H_3.

W strefie śródzalewia osady były homogeniczne, a pionowe rozmieszczenie fauny wydawało się zależeć przede wszystkim od warunków tlenowych i możliwości zdobycia pożywienia. Stwierdzono nieantagonistyczne relacje pomiędzy detrytusożernymi Tubificinae i larwami ochotek w tych samych warstwach osadów dennych, co potwierdza słuszność założeń hipotezy H_5. Zaproponowano hipotetyczny model wzajemnych interakcji pomiędzy *C. balatonicus* i Tubificinae oraz ich aktywności życiowej w osadach dennych (publikacja 1: Kornijów et al., 2021).

5. Wnioski

- Różnorodność gatunkowa zoobentosu jest wyższa w cechującej się wyższym stopniem złożoności siedliskowej strefie helofitów niż elodeidów, a najniższa w najbardziej jednorodnej strefie dna otwartego zalewu.

- Gęste płaty roślinności wynurzonej, składające się głównie z trzciny pospolitej znacząco zmieniają warunki środowiskowe w strefie litoralu, w szczególności prowadząc do: zwiększenia temperatury wody, spadku nasycenia wody tlenem, ograniczenia natężenia promieniowania słonecznego docierającego do powierzchni wody oraz wzrostu zawartości materii organicznej w osadach dennych. Ponadto zmniejszają one dobową amplitudę zmian temperatury wody,

ograniczają wpływ falowania i wymianę wody pomiędzy strefą litoralu i otwartym akwenem.

- Roślinność zanurzona, zapewne ze względu na niższą biomasę i pokrycie dna nie ma znaczącego wpływu na zróżnicowanie horyzontalne warunków siedliskowych w Zalewie Wiślanym.

- W śródzalewiu, wysokie zagęszczenia Tubificinae i larw *C. balatonicus* w tych samych warstwach oraz istotne wskaźniki współwystępowania wskazują na brak konkurencyjnych relacji między tymi taksonami.

- *C. balatonicus* i Tubificinae pełnią odmienną rolę w krążeniu materii pomiędzy warstwą powierzchniową osadów i warstwami głębiej położonymi. Larwy Chironomidae jako zbieracze i filtratorzy pobierają pokarm z powierzchni osadu bądź z warstw naddennych wody, po czym niestrawione resztki pokarmowe trafiają w głąb osadu. Korzystają z nich następnie Tubificinae, które żerują w głębokich warstwach osadu, a niestrawione resztki pokarmowe transportują z powrotem na powierzchnię.

- W strefie roślinności wynurzonej, w przeciwieństwie do pozostałych badanych siedlisk, większość bezkręgowców boruje osady stosunkowo płytko z powodu obecności gęstej maty kłączy i korzeni, która ogranicza pionowe przemieszczanie się zwierząt.

- Na skład i bogactwo gatunkowe zoobentosu duży wpływ ma zróżnicowanie strukturalne siedlisk. Zagęszczenie fauny zależy bardziej od charakteru osadów dennych (granulacja, zawartość materii organicznej) i dynamiki warunków hydrologicznych.

6. Bibliografia

Andersen T., Cranston P.S., Epler J.H., 2013. The larvae of Chironomidae (Diptera) of Holarctic region – Keys and diagnoses. Insect Systematics and Evolution Supplements 66, 573 pp.

Armitage P.D., Cranston P.S., Pinder L.C.V., 1995. The Chironomidae. Biology and ecology of non-biting midges. Chapman and Hall: Londyn-Madryt, ISBN 978-94-011-0715-0, 447 pp. https://doi.org/10.1007/978-94-011-0715-0

Canedo-Arguelles M., Rieradevall M., 2009. Quantification of environment-driven changes in epiphytic macroinvertebrate communities associated to *Phragmites australis*. Tesis Doctoral, Universidad de Barcelona 2009.

Charbonneau P., Hare L., 1998. Burrowing behavior and biogenic structures of mud-dwelling insects. Journal of the North American Benthological Society, 17: 239–249. https://doi.org/10.2307/1467965

Covich A.P., Palmer M.A., Crowl T.A., 1999. The role of benthic invertebrate species in freshwater ecosystem. Bio Science, 49: 119-127. https://doi.org/10.2307/1313537

Craig J.F., 1977. Seasonal changes in the day and night activity of adult perch, *Perca fluviatilis* L. Journal of Fish Biology, 11: 161-166.

Cywińska A., Różańska Z., 1978. Zoobenthos of the Vistula Lagoon. Studia i Materiały Oceanograficzne, Biologia Morza, 4: 145–161.

Diehl S., Kornijów R., 1998. Influence of submerged macrophytes on trophic interactions among fish and macroinvertebrates. W: Jeppesen, E., Sondergaard, Ma., Sondergaard, Mo., Christoferssen, K. (red.) Structuring role of submerged macrophytes in lakes. Springer-Verlag, New York, 24-46. https://doi.org/10.1007/978-1-4612-0695-8_2

Ezhova E.E., Pavlenko M.V., 2001. New data on the macrobenthos of the Vistula Lagoon (Baltic Sea). Composition and structure of marine bottom biota, Izd. VNIRO, Moscow, 40–45.

Ezhova E.E., Żmudziński L., Maciejewska K., 2005. Long-term trends in the macrozoobenthos of the Vistula Lagoon, southeastern Baltic Sea. Species composition and biomass distribution. Bulletin of the Sea Fisheries Institute, 1 (164): 55–73.

Ezhova E., Dorokhov D., Sivkov V., Zhamoida V., Ryabchuk D., Kocheshkova O., 2012. Benthic Habitats and Benthic Communities in Southeastern Baltic Sea, Russian Sector. Seafloor Geomorphology as Benthic Habitat: 613-621. https://doi.org/10.1016/B978-0-12-385140-6.00043-8

Fredriksen S., De Backer A., Bostrom C., Christie H., 2010. Infauna from Zostera marina L. meadows in Norway. Differences in vegetated and unvegetated areas. Marine Biology Research, 6, 189-200. https://doi.org/10.1080/17451000903042461

González-Ortiz V., Egea L.G., Jiménez-Ramos R., Moreno-Marin F., Pérez-Lloréns J., Bouma T., Brun F., 2016. Submerged vegetation complexity modifies benthic infauna communities: the hidden role of the belowground system. Marine Ecology, 37, 543-552. https://doi.org/10.1111/maec.12292

Goshima S., Peterson C.H., 2012. Both below- and aboveground shoalgrass structure influence whelk predation on hard clams. Marine Ecology Progress Series, 451, 75-92. https://doi.org/10.3354/meps09587

Gotelli N.J., Colwell R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters, 4: 379-391. https://doi.org/10.1046/j.1461-0248.2001.00230.x

Hansen J.P., Wikström S.A., Kautsky L., 2007. Effects of water exchange and vegetation on the macroinvertebrate fauna composition of shallow land-uplift bays in the Baltic Sea. Estuarine, Coastal and Shelf Science, 77: 535-547.

Klimowicz H., 1958. Mięczaki Zalewu Wiślanego i zależność ich rozmieszczenia od zasolenia. Polskie Archiwum Hydrobiologii, 5(18): 93-123.

Koperski P., 1998. Feeding in epiphytic, carnivorous insects: Resource partitioning and the avoidance of intraguild predation. Archiv fur Hydrobiologie, 142(4): 467-483.

Kornijów R., 1997. The impact of predation by perch on the size-structure of Chironomus larvae - The role of vertical distribution of the prey in the bottom sediments, and habitat complexity. Hydrobiologia, 342-343: 207-213. https://doi.org/10.1023/A:1017067621668

Kornijów R., 2013. A new sediment slicer for rapid sectioning of the uppermost sediment cores from marine and freshwater habitats. Journal of Paleolimnology, 49: 301–304. https://doi.org/10.1007/s10933-012-9655-9

Kornijów R., Measey G.J., Moss B., 2016. The structure of the littoral: Effects of waterlily density and perch predation on sediment and plant-associated macroinvertebrate communities. Freshwater Biology, 61(1): 32-50. https://doi.org/10.1111/fwb.12674

Kornijów R., Pawlikowski K., Błędzki L.A., Drgas A., Piwosz K., Ameryk A., Całkiewicz J., 2021. Co-occurrence and potential resource partitioning between oligochaetes and chironomid larvae in a sediment depth gradient. Aquatic Sciences, 83 (51): 1-10. https://doi.org/10.1007/s00027-021-00800-z

Kornijow R., Vakkilainen K., Horppila J., Luokkanen E., Kairesalo T., 2005. Impacts of a submerged plant (*Elodea canadensis*) on interactions between roach (*Rutilus rutilus*) and its invertebrate prey communities in a lake littoral zone. Freshwater Biology, 50 (2): 262-276. https://doi.org/10.1111/j.1365-2427.2004.01318.x

Kotta J., 2013. Water salinity and benthic macrophyte communities are the key variables defining the distribution pattern of benthic faunal assemblages in the shallow water areas of the Gulf of Riga. Estonian Journal of Ecology, 62 (2): 107-120.

Lellak J., 1965. The food supply as a factor regulating the population dynamics of bottom animals. Internationale Vereinigung für Theoretische und Angewandte Limnologie: Mitteilungen, 13: 128-138.

Lindegaard C., 1994. The role of zoobenthos in energy flow in two shallow lakes. Hydrobiologia, 275/276: 313-322.

McCormack J.C., 1970. Observations on the food of perch (*Perca fluviatilis* L.) in Windermere. Journal of Animal Ecology, 39: 255-267.

Morin P.J., Lawler S.P., Johnson E.A., 1988. Competition Between Aquatic Insects and Vertebrates: Interaction Strength and Higher Order Interactions. Vol. 69, Iss. 5: 1401–1409.

Ostendorp W., 1993. Reed bed characteristics and significance of reed in landscape ecology. W: Ostedorp W., Krumsheid-Plankert P., (red.), Lakeshore deterioration and restoration works in Central Europe, Fischer-Verlag Stuttgart, Germany, 149–161.

Pawlikowski K., Kornijów R., 2019. Role of macrophytes in structuring littoral habitats in the Vistula Lagoon (southern Baltic Sea). Oceanologia 61: 26-37. https://doi.org/10.1016/j.oceano.2018.05.003

Pawlikowski K., Kornijów R., 2022. Distribution of benthic macroinvertebrates across a reed stand in a brackish Baltic lagoon. Oceanologia 64: 433-444. https://doi.org/10.1016/j.oceano.2022.02.004

Pawlikowski K., Kornijów R., 2022. Above- and belowground habitat complexity created by emergent and submerged vegetation drives the structure of benthic assemblages. Oceanologia. https://doi.org/10.1016/j.oceano.2022.10.002

Perez-Ruzafa A., Marcos C., Perez-Ruzafa I.M., Perez-Marcos M., 2011. Coastal lagoons: "Transitional ecosystems" between transitional and coastal waters. Journal of Coastal Conservation, 15 (3): 369-392. https://doi.org/10.1007/s11852-010-0095-2

Peterson C.H., 1982. Clam predation by whelks (Busycon spp.): Experimental tests of the importance of prey size, prey density, and seagrass cover. Marine Biology, 66: 159-170. https://doi.org/10.1007/Bf00397189

Różańska Z., Cywińska A., 1983. Charakterystyka liczebności i biomasy fauny dennej Zalewu Wiślanego. Oceanologia, 14: 187–200.

Ságová-Marečková M., 2002. Distribution of benthic macroinvertebrates in relationship to plant roots, sediment type and spatial scale in fishponds and slow streams. Archiv für Hydrobiologie, 156: 63-81. https://doi.org/10.1127/0003-9136/2002/0156-0063

Siebert T., Branch G.M., 2005. Interactions between *Zostera capensis*, *Callianassa kraussi* and *Upogebia africana*: deductions from field surveys in Langebaan Lagoon, South Africa. African Journal of Marine Science, 27: 345-356. https://doi.org/10.2989/18142320509504094

Siebert T., Branch G.M., 2007. Influences of biological interactions on community structure within seagrass beds and sandprawn-dominated sandflats. Journal of Experimental Marine Biology and Ecology, 340: 11-24. https://doi.org/10.1016/j.jembe.2006.08.007

Timm T., 1999. A guide to the Estonian Annelida. Estonian Academy Publishers, Tallinn, 208 pp.

Urban-Malinga B., Warzocha J., Zalewski M., 2013. Effects of the invasive polychaete *Marenzelleria* spp. on benthic processes and meiobenthos of a species-poor brackish system. Journal of Sea Research, 80: 25-34. https://doi.org/10.1016/j.seares.2013.02.005

Whitlach R.B., 1980. Patterns of resource utilization and coexistence in marine intertidal deposit-feeding communities. Journal of Marine Research, 38: 743-765.

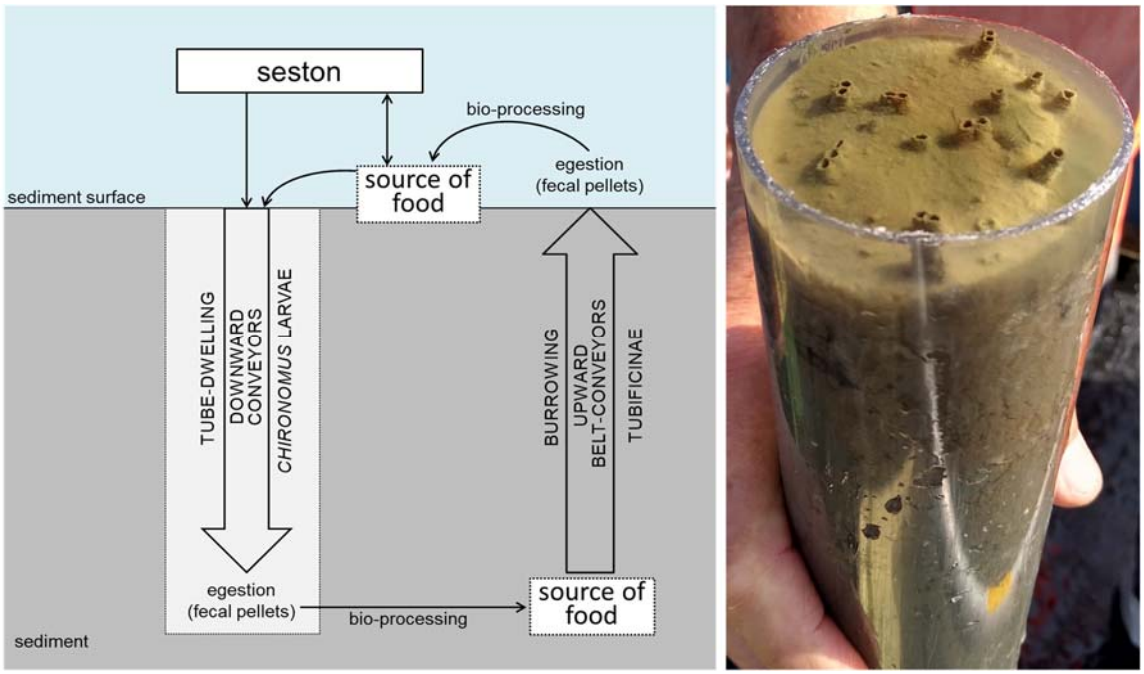
Viaroli P., Bartoli M., Giordani G., Naldi M., Orfanidis S., Zaldivar J.M., 2008. Community shifts, alternative stable states, biogeochemical controls and feedbacks in eutrophic coastal lagoons: a brief overview. Aquatic Conservation, 18 (S1): 105-117. http://dx.doi.org/10.1002/aqc.956

Żmudziński L., 1957. Zoobentos Zalewu Wiślanego. Prace MIR, 9: 453–501.

Żmudziński L., Kornijów R., Bolałek J., Górniak A., Olańczuk-Neymann K., Pęczalska A., Korzeniewski K., 2002. Słownik Hydrobiologiczny (ochrona wód, terminy, pojęcia i interpretacje). Warszawa, PWN.

Kornijów R., Pawlikowski K., Błędzki L.A., Drgas A., Piwosz K., Ameryk A., Całkiewicz J., 2021. **Co-occurrence and potential resource partitioning between oligochaetes and chironomid larvae in a sediment depth gradient.** Aquatic Sciences 83(51): 1-10. https://doi.org/10.1007/s00027-021-00800-z

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Aquatic Sciences

RESEARCH ARTICLE

Co-occurrence and potential resource partitioning between oligochaetes and chironomid larvae in a sediment depth gradient

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Abstract
Although detritivorous Tubificinae and chironomid larvae are important groups in functioning of both, fresh and brackish water ecosystem, their co-occurrence patterns in sediment is weakly known. We carried out two-year-long research in the brackish Vistula Lagoon (southern Baltic Sea), where both Tubificinae (*Limnodrilus hoffmeisteri* and *Potamothrix hammoniensis*) and larvae of *Chironomus balatonicus* occur in high densities. Because of different source of their food, we hypothesized that the ecological interactions between those two groups of detritivores are not antagonistic, thus allowing for their co-occurrence along the depth of sediment profile with lack of competition for space. Here we show that maximum burrowing depth, occasionally reaching 25 cm was significantly affected by the total density of the each group in the entire core. Tubificinae and *C. balatonicus* showed the highest density at 0–10 cm depth, where they co-occurred most frequently, with significant co-occurrence in the layers of 0–2 cm and 2–5 cm. We propose a hypothetical model of interactions between apparently the same functional groups and the complementary role they play in sediment reworking. It points to their coexistence in the shared microhabitat, but using space and food resources differently. Also, the consequences of their activity and habitat structuring are opposite—*Chironomus* larvae mostly affect the deeper layers of the sediments, while Oligochaeta both the deeper and surface layers. Thus, their requirements and ecological roles seem not to overlap, preventing competitive exclusion and allowing for co-occurrence.

Keywords Bioturbation · Detritus-feeders · Macroinvertebrates · Vertical distribution · Zoobenthos · Baltic lagoon

Introduction

Invertebrate benthic communities inhabiting freshwater and brackish water ecosystems are composed of different taxonomic groups. Most of them live on or just below the surface of the bottom sediments, but some burrow sediments to a depth of several dozen cm. The latter particularly include Tubificinae and larvae of several species of Chironomidae, mainly from genus *Chironomus*. They are among the most globally widespread benthic invertebrates (Pinder 1995; Timm and Martin 2015). Because they belong to so-called infauna (deep burrowers), it can be assumed that the ecological interactions can take place not necessarily in the entire inhabited sediment depth but in its specific layers (Whitlatch 1980). However, vertical distribution of these groups in sediments has been rarely studied simultaneously, and suffers the lack of quantitative analysis of the relationships between these groups (Kajak and Dusoge 1971; Milbrink 1973; Newrkla and Wijegoonawardana 1987; Kornijów and Moss 1997). The potential impact of biotic factors driving their distribution has been therefore largely ignored, except for the effect of fish (Van de Bund and Groenendijk 1994; Kornijów 1997; Persson and Svensson 2006) and mainly abiotic factors including pollution (Mucha et al. 2004; Como and Magni 2009), and content of organic matter in sediments (Newrkla and Wijegoonawardana 1987; Mathooko 1995; Magni et al. 2008; Beghelli et al. 2012). In fact, the traditionally perceived role of oligochaetes and chironomid larvae

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primarily involves processing of organic matter as both groups are classified as detritivores (Covich et al. 1999).

Belonging to the same trophic guild can be expected to lead to competition for food resources (Odum 1971). This also was suggested for benthic detritivores such as oligochaetes and chironomids (Brinkhurst and Kennedy 1965; Jónasson 1972; Moss and Timms 1989; Como and Magni 2009; Ojaveer 2017). Vos (2001) hypothesized the ability to avoid competitive interactions between Tubificinae and *Chironomus* larvae due to the possibility of collecting food particles of different sizes, determined by the width of the mouth. Food particles ingested by 4th larvae stage of e.g., *Chironomus balatonicus* Devai, Wuelker & Scholl indeed reach up to 500 µm (Kornijów et al. 2019), i.e. approximately at least twice the value found e.g. in *Limnodrilus* (Juget et al. 1979; Fukuhara 1987). Different source of food can also be considered as an argument precluding the possibility of competing for food. Tubificinae ingest food particles from deeper sediment layers (Davis 1974; Nogaro et al. 2007; Mermillod-Blondin 2011; Timm and Martin 2015), while *Chironomus* larvae feed primarily by filtering the overlying water or by collecting particles from the sediment surface around their burrows (Walshe 1947; McLachlan and Cantrell 1976; McCall and Tevesz 1982; Proulx and Hare 2014).

Given the above, we hypothesize that the interspecific interactions between detritivorous Tubificinae and *Chironomus* larvae at both the individual and community level are not antagonistic, sensu Holland and DeAngelis (2009), allowing for their co-occurrence along the depth of sediment profile with lack of competition for space. In order to test this hypothesis, we conducted two-year-long research in soft bottom sediments of the eutrophicated Vistula Lagoon, where both Tubificinae and C. *balatonicus* larvae occur in high densities (Ezhova et al. 2005; Kornijów and Pawlikowski 2015). Specifically, we expected simultaneous presence of representatives of these groups in both, time and space along the sediment core showing the positive relationship between their densities and co-occurrence.

Materials and methods

Study site

The Vistula Lagoon located in the south-eastern part of the Baltic Sea, is large (838 km^2) but shallow (mean depth 2.5 m; max. depth 5.2 m) and strongly elongated water body, oriented north-east to south-west. The western part of the lagoon with an area of 328 km^2 is located in the Polish territory, whereas the remaining part is in Russia. The lagoon's basin is separated from the Baltic Sea by the Vistula Spit in the north, and connected with the sea by the Baltiysk Strait. Salinity decreases from 6.5 PSU at the Baltiysk Strait to < 1 at the mouth of the large rivers in the western basin. No regular tides occur in the lagoon. The climate is transitional, from moderate maritime to moderate continental.

Concentrations of nutrients in the water column are high ($N_{tot.}$ = 2.1–2.3 mg L^{-1}; $P_{tot.}$ = 0.10–0.11 mg L^{-1}), favouring development of cyanobacteria (Nawrocka and Kobos 2011; Kownacka et al. 2020). Water transparency is low (Secchi depth fluctuates around 50 cm). This is a result of relatively high chlorophyll-*a* concentrations (22.9–54.3 µg L^{-1}), and also high concentrations of total suspended solids (42.7–54.5 mg L^{-1}), caused by frequent resuspension in the shallow area exposed to wind action (Chubarenko and Margoński 2008; Piwosz et al. 2016; Kornijów 2018). Bottom sediments are primarily composed of sand in the hydrodynamic-active, shallow zone at a depth of up to 1.5–2 m. Deeper regions are dominated by fine-grained clayey silt. The near-bottom water layers are well oxygenated, even during long winters under ice cover (Kornijów et al. 2020).

The samples were collected at two sites, in the eastern (54.39190°N, 19.68360°E) and in the middle (54.35010°N, 19.48480°E) part of the open-water area of the Polish part of the lagoon at a depth of approximately 3 m, where soft sediments are composed of clayey silt (Fig. 1). Because the differences in the faunal composition between the sites in this highly homogenous environment were negligible, all the data collected were pooled.

Field survey and laboratory analyses

The field study was conducted in spring, summer, and autumn in 2010 and 2011. On each occasion, from 5 to 15 replicate standardized sediment cores 6 cm in diameter and 30 cm long were taken by means of a gravity sampler (UWITEC Ltd., Austria) equipped with a drive rod. Each core was sectioned into 7 layers with a slicer equipped with a sub-sample holder and centimetre scale (Kornijów 2013). The upper layer of the core was 2 cm thick, the second 3 cm, and the following five 5 cm thick. This interval is corresponding with individual length of worms (Matisoff et al. 1999), and at most twice as large as the length of forth instar of *Chironomus* larvae (Armitage et al. 1995). The volume of core sections ranged from 0.056 to 0.141 L. Each sediment section was washed separately through 0.3 mm mesh. Invertebrates were sorted out by eye on a white tray filled with water, and preserved in 4% formaldehyde solution. Altogether 434 sediment sections were collected and processed. The deepest sediment layer (25–30 cm) was uninhabited by invertebrates, and therefore it was excluded from analysis.

Additional 30 cm long sediment cores for analyses of organic matter and bacteria were sampled simultaneously with macroinvertebrates on each sampling date in the first and the second year, respectively. They were collected and

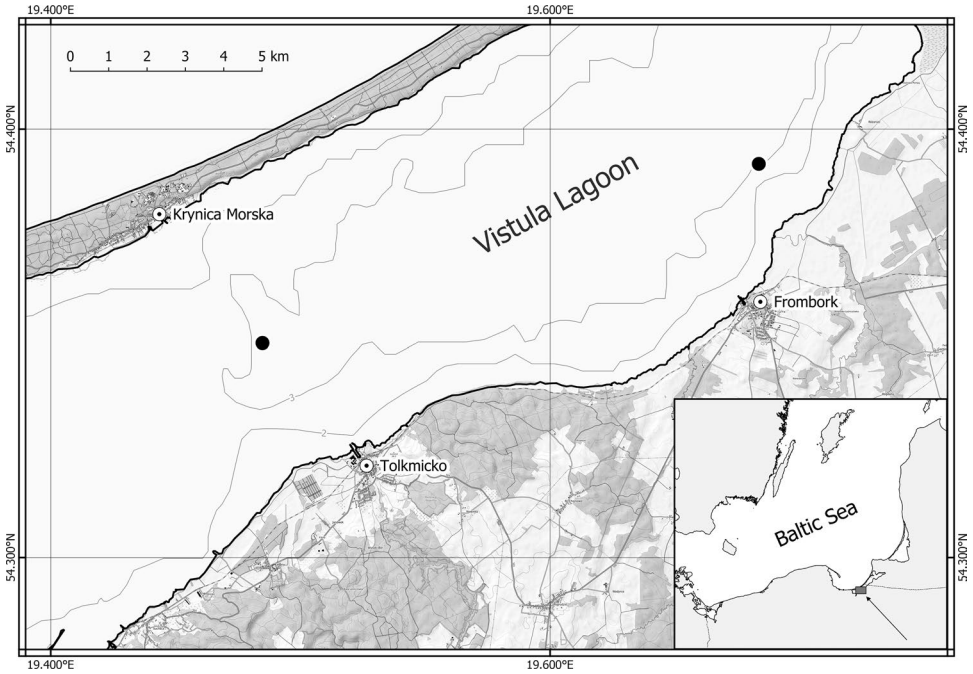


Fig. 1 Research area with sampling stations marked by dots. GIS layers of land cover after OpenStreetMap (2020), bathymetry according to Chubarenko (2008)—modified, and shore line after Maritime Office in Gdynia (2015)—modified

sectioned using the same equipment as in the case of benthic fauna samples. The organic matter and bacteria samples were secured in a cooler with ice immediately after sampling, and later in the laboratory were frozen and stored at − 20 °C until the analysis. The percentage of organic matter was calculated as a percentage weight loss during the ignition (LOI) of dried sediment burned at 550 °C for 24 h. Bacteria in sediments were analysed according to Epstein and Rossel (1995). Bacterial cells from 30 fields of view were counted under 1000 × magnification using epifluorescent microscopy Nikon Eclipse 80i.

Data analyses

Tubificinae and the majority of chironomid larvae were identified according to Timm (1999) and Andersen et al. (2013), respectively. The species affiliation of *Chironomus* (not distinguished morphologically) was adopted based on karyological studies by Markiyanova (2018), indicating that this genus in the central part of the lagoon is represented solely by one species, namely *C. balatonicus*.

Because the sediment layers differed in thickness (and volume), the density of invertebrates in subsequent layers was expressed per sediment L to allow comparison of invertebrates abundance (Kornijów and Pawlikowski 2016). The total density in the entire inhabited core was expressed in the most often used unit in benthos research as the number of individuals per m^2.

Frequency of occurrence was calculated as a percentage of samples (representing a given section of sediment core) in which one of the groups (Tubificinae or larvae of *C. balatonicus*) or two groups occurred together.

Pearson's Chi-Square Test for 2 × 2 tables was performed to check the significance of co-occurrence of the groups with the guidance and assumption given by Gotelli and Ellison (2013). Associations between densities of the fauna and maximum burrowing depth was identified using linear regression. Shapiro–Wilk test for normal distribution and Levene test for equal population variances were conducted. Because of an unequal variances or non-normal distribution several non-parametric tests were used:

- Kruskal–Wallis test (H) was applied for the determination of the effect of sediment depth on the content of organic matter and densities of bacteria.
- Friedman test (χ^2) was applied to test the effect of sediment depth on the density of *C. balatonicus* and Tubificinae, and Friedman post-hoc test after Nemenyi was applied for the detailed analyses.
- Wilcoxon signed-rank test (T) was applied to check the significance of differences in the densities of *C. balatonicus* and Tubificinae between two sampling years.

Statistical tests were performed with the application of STATISTICA 10 software (StatSoft 2011).

Results

Invertebrate density and distribution

The qualitative composition of benthic macroinvertebrates was very poor and consisted of only 7 taxa: *Potamothrix hammoniensis* (M.), *Limnodrilus hoffmeisteri* C. (Tubificinae), as well as larvae of *Chironomus balatonicus*, *Microchironomus tener* (K.), *Procladius* sp. and Tanytarsini juv. (Diptera; Chironomidae). Single specimens of *Potamopyrgus antipodarum* (G.) (Gastropoda) were also encountered. Most samples showed high percentage of Tubificinae and *C. balatonicus*. The mean share of *P. hammoniensis*, *L. hoffmeisteri*, and *C. balatonicus* in the total density of benthic fauna were 42, 7, and 19%, respectively.

Mean total density ± SD (Standard Deviation) of invertebrates was 7044 ± 4493 ind. m^{-2} and ranged from 2806 to 16,269 ind. m^{-2}. During the second sampling year the densities of *C. balatonicus* were significantly lower [Wilcoxon Test: T ($n = 16$) = 23; $p = 0.02$] and those of Tubificinae did not change [Wilcoxon Test: T ($n = 13$) = 28; $p = 0.21$].

Maximum burrowing depth differed between the taxa. Tubificinae and *C. balatonicus* were found to a depth of 25 cm, and the presence of the remaining taxa was limited to the upper 5 cm surface layer (Fig. 2). The depth below 25 cm was uninhabited by macroinvertebrates. The density of Tubificinae and *C. balatonicus* in particular core sections changed with sediment depth in most of the examined seasons (Table 1). In most cases, however, the Friedman post-hoc test did not detect significant differences in density between the particular sediment layers. The exception was *P. hammoniensis*, whose densities significantly differed between the two deepest (15–20 and 20–25 cm) and two shallower layers (2–5 and 5–10 cm) ($p \leq 0.05$). The maximum burrowing depth of both groups was correlated with their total density in the entire core (Fig. 3).

There was a positive correlation between densities of Tubificinae and *C. balatonicus* larvae (Fig. 4). Their co-occurrence was most often recorded up to a depth of 10 cm (Fig. 5) and proved to be significant in the 0–2 cm (Pearson's Chi-Square (df = 1) = 7; $p \leq 0.008$) and 2–5 cm layers (Pearson's Chi-Square (df = 1) = 50; $p < 0.001$). In the two deepest layers (15–20 and 20–25 cm), the frequency of both groups was much lower, and Tubificinae and *C. balatonicus* were never found together in the same sample.

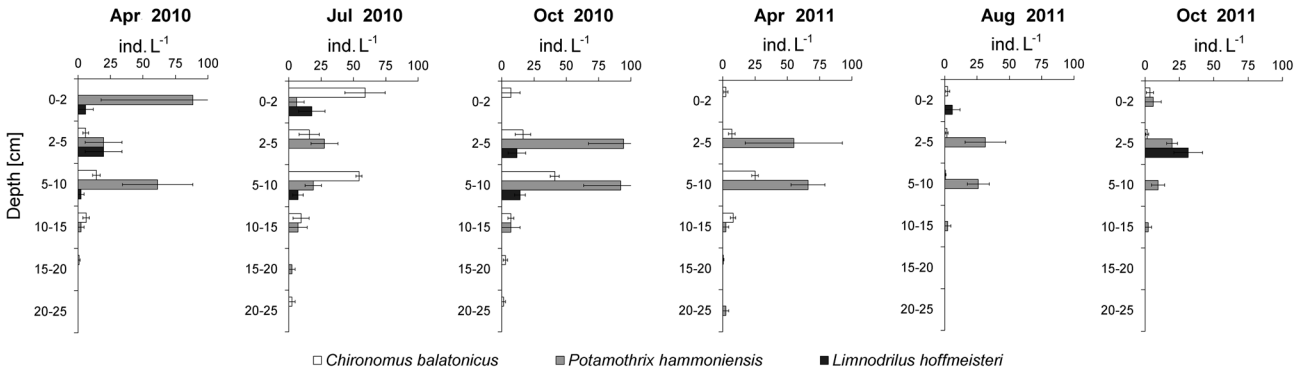


Fig. 2 Density of Tubificinae and *Chironomus balatonicus* larvae along the sediment profile in the Vistula Lagoon. Values are means ± SEM (Standard Error of the Mean) for sampling occasions

Table 1 Friedman Chi-Square (χ^2) test for the effect of sediment depth on the density of *Chironomus balatonicus* and Tubificinae in the Vistula Lagoon

	Apr 2010	Jul 2010	Oct 2010	Apr 2011	Aug 2011	Oct 2011
Chironomus balatonicus	χ^2 ($n = 9$, df = 5) = 24; $p < 0.01$	χ^2 ($n = 7$, df = 5) = 19; $p < 0.01$	χ^2 ($n = 10$, df = 5) = 32; $p < 0.01$	χ^2 ($n = 15$, df = 5) = 46; $p < 0.01$	χ^2 ($n = 15$, df = 5) = 6; NS	χ^2 ($n = 15$, df = 5) = 8; NS
Tubificinae	χ^2 ($n = 9$, df = 5) = 29; $p < 0.0001$	χ^2 ($n = 3$, df = 5) = 9; $p < 0.1$	χ^2 ($n = 5$, df = 5) = 21; $p < 0.0007$	χ^2 ($n = 15$, df = 5) = 52; $p < 0.0001$	χ^2 ($n = 15$, df = 5) = 50; $p < 0.0001$	χ^2 ($n = 15$, df = 5) = 49; $p < 0.0001$

NS not significant

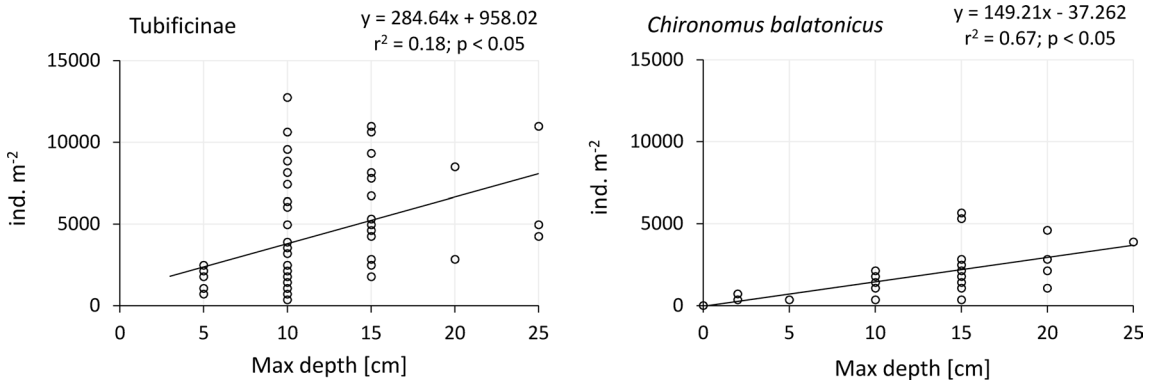


Fig. 3 Linear regression analysis of the relationship between invertebrate density in entire sediment core and maximum burrowing depth in the Vistula Lagoon

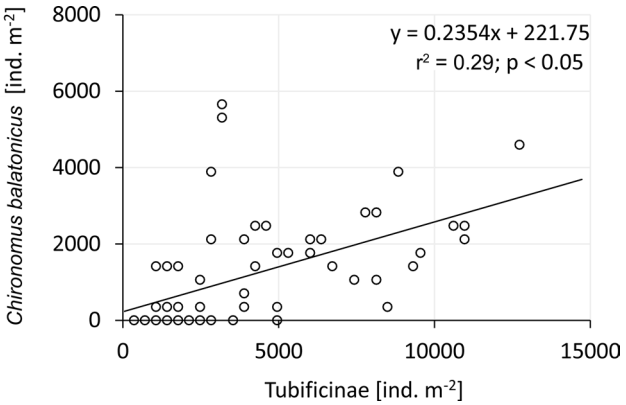


Fig. 4 Relationship between the densities of Tubificinae and *Chironomus balatonicus* larvae in sediment cores

Proxies for nutritional conditions in the sediments

Values of organic matter content in the sediment profile ranged from 8 to 11%, and were aligned in the sediment profile [Kruskal–Wallis H ($n = 21$) = 6; $p = 0.39$]. The concentration of bacteria seemed to be the highest between 15 and 25 cm, but differences between the layers were insignificant [Kruskal–Wallis H ($n = 21$) = 6; $p = 0.42$].

Discussion

The habitat conditions in the Vistula Lagoon, including high concentrations of nutrients and low transparency due to resuspension and the development of phytoplankton corresponded to those in other Baltic costal shallow and highly eutrophic lagoons and estuaries. Their organic matter-rich silty sediments are beneficial particularly for non-selective detritivorous Oligochaeta and chironomid larvae, known to build high densities (Ezhova et al. 2005; Gasiunaite et al. 2008; Radziejewska and Schernewski 2008; Wolnomiejski and Witek 2013; Kornijów and Pawlikowski 2015; Golubkov et al. 2019). However, the mutual distribution of these invertebrates in the sediment is very little known.

In our study the maximum burrowing depth by Tubificinae and *C. balatonicus* larvae in the Vistula Lagoon positively correlated with their densities (Fig. 3). A similar relationship was found for Tubificinae living in rivers (Brinkhurst and Kennedy 1965) and lakes (McCall and

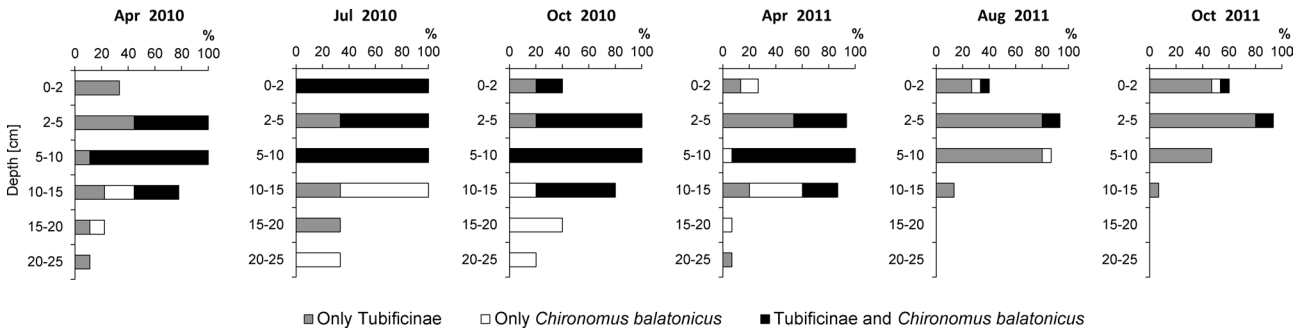


Fig. 5 Frequency (%) of occurrence of Tubificinae alone, *Chironomus balatonicus* alone, or both groups together along the sediment profile in the Vistula Lagoon

Fisher 1980), as well as in experimental conditions (Robbins et al. 1979). According to McCall and Tevesz (1982), deeper burrowing may be related to the rate of exploitation of food resources. At low densities, the rate is low and there is no need for burrowing deeper. The opposite situation might occur at high densities, when food shortage in superficial layers can sooner or later appear. Such situations could take place in the studied lagoon, where the highest density of bacteria was recorded deeper than that of the majority of invertebrates. This could force animals to exploit deeper sediment layers.

The relationship between density and burrowing depth by *Chironomus* larvae might be related to the larval size structure. Because larger individuals tend to burrow deeper (Kajak and Dusoge 1971; Kornijów and Pawlikowski 2015), in a larger population the probability of occurrence of big individuals can be assumed to be greater, and therefore deeper burrowing can be expected.

A general positive relationship was found between densities of Tubificinae and *C. balatonicus* (Fig. 4). The density and joint frequency of occurrence of both groups were highest in the upper 10 cm sediment (Figs. 5 and 6). In addition, only in this depth range co-occurrence proved to be significant. The results suggest lack of antagonistic interactions between Tubificinae and *C. balatonicus*, including lack of competition for space, which supports our hypothesis. A similar conclusion was drawn based on the established correlation between the density of *Chironomus plumosus* (L.) larvae and Tubificinae (mainly *Potamothrix hammoniensis*) in a long-term series of more than twenty years of research in other large and shallow water bodies, namely in the southern Baltic Szczecin Lagoon by Wolnomiejski (1994) and in Estonian Lake Võrtsjärv by Kangur et al. (1998).

The vertical distribution of *C. balatonicus* and Tubificinae in bottom sediments, their distinct diets and modes of physical disturbance suggests their complementary role in the processing of organic matter. A hypothetical model for such role, based on the data of the present study and literature review, is presented in Fig. 7. Tube-dwelling chironomid larvae live in self-ventilated U-shaped, J-shaped, or Y-shaped tubes, and feed on filtered suspension or particles collected from the sediment. A substantial fraction of the detrital material is not assimilated by the animals, and the undigested remains are excreted deeper in the sediment. This applies not only to detritus particles, but partly also to bacteria and certain groups of algae (Kajak and Warda 1968; Baker and Bradnam 1976; Hirabayashi and Wotton 1998). In this way, the larvae, acting as downward conveyors (Mermillod-Blondin 2011; Kristensen et al. 2012), contribute to the transport and decomposition of organic matter to deeper sediment layers.The subsurface sediment enriched by chironomid larvae is in turn a feeding place of Tubificinae. Worms are believed to feed in the upper 15 cm sediment layer (Davis 1974; McCall and Fisher 1980; Fukuhara 1987). They selectively digest some organic components, transport them vertically upward through their gut, and defecate at the sediment surface (biodeposition) (Davis 1974; Fukuhara 1987; Nogaro et al. 2007; Timm and Martin 2015). They are considered upward belt-conveyors enriching the surface sediment layer with fine organic matter (Andersson et al. 1988), which might be of potential importance for chironomid surface collectors. Therefore, *Chironomus* larvae and Tubificinae, representing basically the same trophic guild (detritivores), live in a shared habitat, but use space and food resources differently, and the consequences of their burrowing and feeding behaviour are opposing. As a result of the activity of tube-dwelling *Chironomus* larvae,

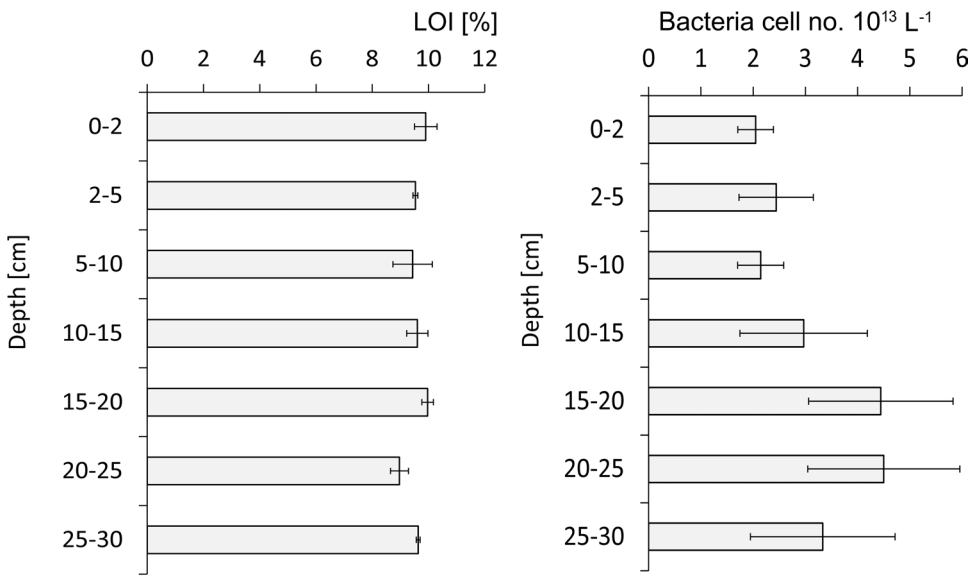


Fig. 6 Percentage of organic matter (LOI) and concentrations of bacteria along the sediment profile in the Vistula Lagoon. Values are means ± SEM for sampling occasions

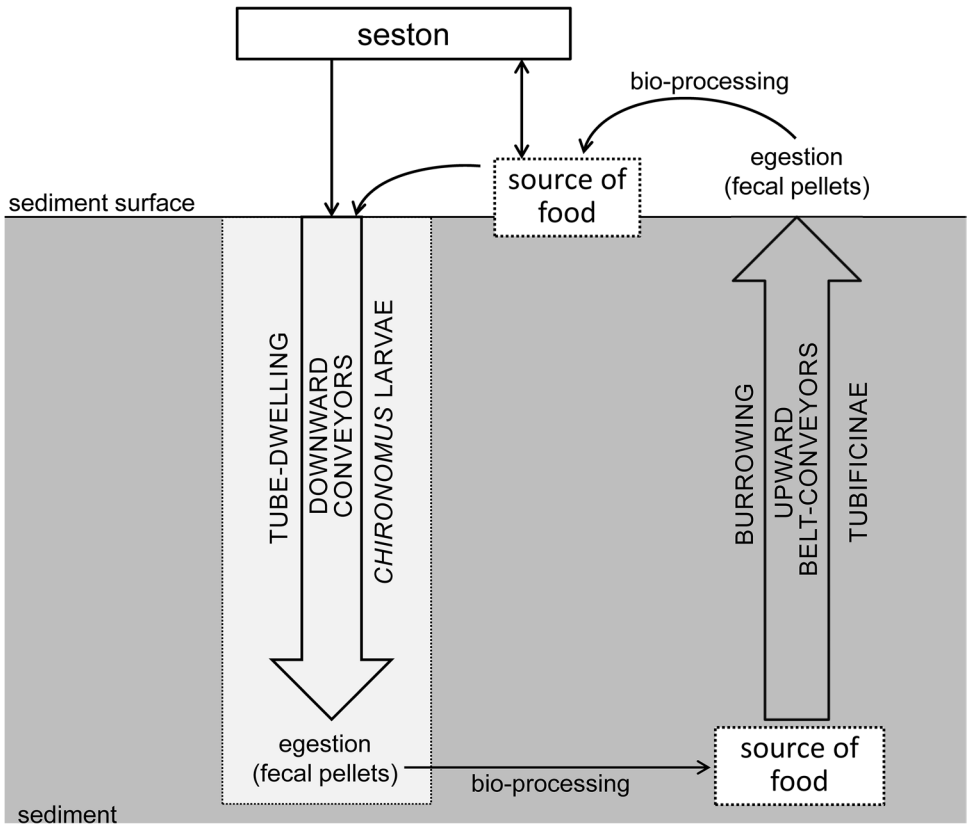


Fig. 7 Conceptual scheme of activity and relationships between Tubificinae and tube-dwelling *Chironomus* larvae, and the resulting direction of matter circulation (arrows). Bio-processing signifies activity of shredders, fungi and bacteria

the nutritional value of surface sediment layers decreases while that of deeper located sediments increases (Lewandowski and Hupfer 2005; Hölker et al. 2015). The effect of worms' activity is the opposite; the top of the sediment becomes covered by fecal pellets, and the underlying layers become more silt-clayish (Timm and Martin 2015). Thus, their requirements and ecological roles (called niches) seem not to overlap, preventing competitive exclusion and allowing for co-occurrence.

It is uncertain to what extent the invertebrates' activity and their environmental structural effect are important for both groups. *Chironomus* larvae are probably less dependent on oligochaetes than vice versa, because they can take food not only from the sediments (enriched by the activity of worms), but also from the water column. Oligochaetes may in turn benefit from sediment enrichment only after the abandoned tubes decay and fecal pellets are processed by meiofauna and bacteria (McLachlan et al. 1979; Van de Bund et al. 1994). Therefore, this relationship can be extended in time. This may explain the fact that in the Vistula Lagoon a strong decrease of the density of *C. balatonicus* larvae in the second year of this study did not result in a simultaneous decrease of the Tubificinae population.

Frequently observed strong dominance, or even the exclusive occurrence of one of the groups, may not to be a result of biotic interactions such as opportunistic predation by *Chironomus* larvae, as suggested by Loden (1974) and Jónasson and Thorhauge (1976), or competition for food, claimed by other authors (Brinkhurst and Kennedy 1965; Jónasson 1972; Moss and Timms 1989). Assuming the constant pressure by fish and invertebrate predators, it may be determined by specific local habitat conditions (e.g. quantity and quality of food, inorganic pollution or organic matter loads and resulting water and sediment oxygenation), to which various invertebrates respond differently. This would be justified by the fact that the density ratio between chironomids and oligochaetes is used in predictive ecology to estimate pollution and/or eutrophication in estuaries (Como and Magni 2009; Silva et al. 2012), lakes (Wiederholm 1980; Lang 1999; Burlakova et al. 2018), and rivers (Goodnight 1973; Rosa et al. 2014; Gorzel et al. 2018). This suggests that research on different drivers of species co-occurrence might be not only of theoretical interest, but can also be a source of new information on the functioning of benthic communities and ecological status of an ecosystem (Cazelles et al. 2016).

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test. We also thank the Editor and two anonymous reviewers who highly contributed to the final version of the article.

Declarations

Conflict of interest The authors declare that they have no conflicts of interest.

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References

Andersen T, Cranston PS, Epler JH (2013) The larvae of Chironomidae (Diptera) of the Holarctic region—keys and diagnoses. Insect Syst Evol 2013:189

Andersson G, Graneli W, Stenson J (1988) The influence of animals on phosphorus cycling in lake ecosystems. Hydrobiologia 170:267–284. https://doi.org/10.1007/Bf00024909

Armitage PD, Cranston PS, Pinder LCV (1995) The Chironomidae. Biology and ecology of non-biting midges. Chapman and Hall, Londyn-Madryt

Baker JH, Bradnam LA (1976) The role of bacteria in the nutrition of aquatic detritivores. Oecologia 24:95–104. https://doi.org/10.1007/bf00572753

Beghelli FGD, dos Santos ACA, Urso-Guimaraes MV, Calijuri MD (2012) Relationship between space distribution of the benthic macroinvertebrates community and trophic state in a Neotropical reservoir (Itupararanga, Brazil). Biota Neotrop 12:114–124. https://doi.org/10.1590/S1676-06032012000400012

Brinkhurst RO, Kennedy CR (1965) Studies on the biology of the Tubificidae (Annelida, Oligochaeta) in a polluted stream. J Anim Ecol 34:429–443. https://doi.org/10.2307/2659

Burlakova LE, Kovalenko KE, Schmude KL et al (2018) Development of new indices of Great Lakes water quality based on profundal benthic communities. J Great Lakes Res 44:618–628. https://doi.org/10.1016/j.jglr.2017.11.004

Cazelles K, Araújo MB, Mouquet N, Gravel D (2016) A theory for species co-occurrence in interaction networks. Theor Ecol 9:39–48. https://doi.org/10.1007/s12080-015-0281-9

Chubarenko BV (2008) The Vistula lagoon. In: Chubarenko BV (ed) Transboundary waters and basins in the south-east Baltic. Terra Baltica, Kaliningrad, pp 37–57

Chubarenko B, Margoński P (2008) The Vistula Lagoon. In: Schiewer U (ed) Ecology of Baltic coastal waters. Ecol St (Anal Synth), vol 197. Springer, Berlin, pp 167–195

Como S, Magni P (2009) Temporal changes of a macrobenthic assemblage in harsh lagoon sediments. Estuar Coast Shelf S 83:638–646. https://doi.org/10.1016/j.ecss.2009.05.024

Covich AP, Palmer MA, Crowl TA (1999) The role of benthic invertebrate species in freshwater ecosystems: zoobenthic species influence energy flows and nutrient cycling. BioScience 49:119–127. https://doi.org/10.2307/1313537

Davis RB (1974) Stratigraphic effects of tubificids in profundal lake sediments. Limnol Oceanogr 19:466–488. https://doi.org/10.4319/lo.1974.19.3.0466

Epstein SS, Rossel J (1995) Methodology of in situ grazing experiments: Evaluation of a new vital dye for preparation of fluorescently labeled bacteria. Mar Ecol Prog Ser 128:143–150. https://doi.org/10.3354/meps128143

Ezhova E, Żmudziński L, Maciejewska K (2005) Long-term trends in the macrozoobenthos of the Vistula Lagoon, southeastern Baltic Sea. Species composition and biomass distribution. Bull Sea Fish Inst 1:55–73

Fukuhara H (1987) The effect of tubificids and chironomids on particle redistribution of lake sediment. Ecol Res 2:255–264. https://doi.org/10.1007/bf02349778

Gasiunaite ZR, Daunys D, Olenin S, Razinkovas A (2008) The Curonian Lagoon. In: Schiewer U (ed) Ecology of Baltic coastal waters, Ecological Studies (Analysis and Synthesis), vol 197. Springer. Berlin, Heidelberg, pp 197–216. https://doi.org/10.1007/978-3-540-73524-3

Golubkov SM, Golubkov MS, Tiunov AV (2019) Anthropogenic carbon as a basal resource in the benthic food webs in the Neva Estuary (Baltic Sea). Mar Pollut Bull 146:190–200. https://doi.org/10.1016/j.marpolbul.2019.06.037

Goodnight C (1973) Use of aquatic macroinvertebrates as indicators of stream pollution. T Am Microsc Soc 92:1–13. https://doi.org/10.2307/3225166

Gorzel M, Kornijów R, Buczyńska E (2018) Quality of rivers: comparison of hydro-morphological, physical-chemical and biological methods. Ecol Chem Eng S 25:101–122. https://doi.org/10.1515/eces-2018-0007

Gotelli NJ, Ellison AM (2013) A primer of ecological statistics, 2nd edn. Sinauer Associates Inc, Sunderland Massachusetts USA

Hirabayashi K, Wotton RS (1998) Organic matter processing by chironomid larvae (Diptera: Chironomidae). Hydrobiologia 382:151–159. https://doi.org/10.1023/a:1003472329603

Hölker F, Vanni MJ, Kuiper JJ et al (2015) Tube-dwelling invertebrates: tiny ecosystem engineers have large effects in lake ecosystems. Ecol Monogr 85:333–351. https://doi.org/10.1890/14-1160.1

Holland JN, DeAngelis DL (2009) Consumer-resource theory predicts dynamic transitions between outcomes of interspecific interactions. Ecol Lett 12:1357–1366. https://doi.org/10.1111/j.1461-0248.2009.01390.x

Jónasson PM (1972) Ecology and production of profundal benthos in relation to phytoplankton in Lake Esrom. Oikos, Suppl, p 14

Jónasson PM, Thorhauge F (1976) Population dynamics of *Potamothrix hammoniensis* in the profundal of Lake Esrom with special reference to environmental and competitive factors. Oikos 27:193–203. https://doi.org/10.2307/3543898

Juget J, Yi BJ, Roux C, Richoux P et al (1979) Structure and functioning manner of the ecosystems in the Upper French Rhone. VII. The hydrographic complex of the Lône des-Pêcheurs, a former bed of the Rhône. Schweiz Z Hydrol 41:395–417

Kajak Z, Dusoge K (1971) The regularities of vertical distribution of benthos in bottom sediments of three Masurian lakes. Ekol Pol 19:485–499

Kajak Z, Warda J (1968) Feeding of benthic non-predatory Chironomidae in lakes. Ann Zool Fenn 5:57–64

Kangur K, Timm H, Timm T, Timm V (1998) Long-term changes in the macrozoobenthos of Lake Võrtsjärv. Limnologica 28:75–83

Kornijów R (1997) The impact of predation by perch on the size-structure of Chironomus larvae—the role of vertical distribution of the prey in the bottom sediments, and habitat complexity. Hydrobiologia 342:207–213. https://doi.org/10.1023/A:1017067621668

Kornijów R (2013) A new sediment slicer for rapid sectioning of the uppermost sediment cores from marine and freshwater habitats. J Paleolimnol 49:301–304. https://doi.org/10.1007/s10933-012-9655-9

Kornijów R (2018) Ecosystem of the Polish part of the Vistula Lagoon from the perspective of alternative stable states concept, with implications for management issues. Oceanologia 60:390–404. https://doi.org/10.1016/j.oceano.2018.02.004

Kornijów R, Karpowicz M, Ejsmont-Karabin J et al (2020) Patchy distribution of phyto- and zooplankton in large and shallow lagoon under ice cover and resulting trophic interactions. Mar Freshw Res 71:1327–1341. https://doi.org/10.1071/MF19259

Kornijów R, Markiyanova M, Lange E (2019) Feeding by two closely related species of *Chironomus* (Diptera: Chironomidae) in south Baltic lagoons, with implications for competitive interactions and resource partitioning. Aquat Ecol 53:315–324. https://doi.org/10.1007/s10452-019-09691-7

Kornijów R, Moss B (1997) Vertical distribution of in-benthos in relation to fish and floating-leaved macrophyte populations. In: Jeppesen E, Søndergaard M, Søndergaard M, Christoffersen K (eds) Structuring Role of Subbmerged Macrophytes in Lakes. Ecol St (Anal Synth). Springer, New York, pp 227–232

Kornijów R, Pawlikowski K (2015) Three-dimensional microdistribution of *Chironomus balatonicus* larvae (Chironomidae, Diptera) in soft sediments from the Vistula Lagoon (South Baltic Sea). Ann Limnol-Int J Lim 51:343–349. https://doi.org/10.1051/limn/2015034

Kornijów R, Pawlikowski K (2016) A common error in calculating the density of invertebrates in sediment core sections of unequal lengths. Ann Limnol Int J Lim 52:301–306. https://doi.org/10.1051/limn/2016017

Kownacka J, Całkiewicz J, Kornijów R (2020) A turning point in the development of phytoplankton in the Vistula Lagoon (southern Baltic Sea) at the beginning of the 21st century. Oceanologia 62:538–555. https://doi.org/10.1016/j.oceano.2020.08.004

Kristensen E, Penha-Lopes G, Delefosse M et al (2012) What is bioturbation? The need for a precise definition for fauna in aquatic sciences. Mar Ecol Prog Ser 446:285–302. https://doi.org/10.3354/meps09506

Lang C (1999) Contrasting responses of oligochaetes (Annelida) and chironomids (Diptera) to the abatement of eutrophication in Lake Neuchatel. Aquat Sci 61:206–214. https://doi.org/10.1007/PL00001324

Lewandowski J, Hupfer M (2005) Effect of macrozoobenthos on two-dimensional small-scale heterogeneity of pore water phosphorus concentrations in lake sediments: a laboratory study. Limnol Oceanogr 50:1106–1118. https://doi.org/10.4319/lo.2005.50.4.1106

Loden MS (1974) Predation by chironomid (Diptera) larvae on oligochaetes. Limnol Oceanogr 19:156–159. https://doi.org/10.4319/lo.1974.19.1.0156

Magni P, De Falco G, Como S, Casu D, Floris A, Petrov AN, Castelli A, Perilli A (2008) Distribution and ecological relevance of fine sediments in organic-enriched lagoons: the case study of the Cabras lagoon (Sardinia, Italy). Mar Pollut Bull 56:549–564. https://doi.org/10.1016/j.marpolbul.2007.12.004

Maritime Office in Gdynia (2015) Urząd Morski w Gdyni—Mapy—Dane GIS/CAD. http://www.umgdy.gov.pl. Accessed 17 August, 2015

Markiyanova MF (2018) Species composition and distribution of sibling species *Chironomus* Meigen (Diptera: Chironomidae) in the Curonian and Vistula lagoons. Oceanology 58:710–716. https://doi.org/10.1134/S0001437018050065

Mathooko JM (1995) Vertical distribution of macrozoobenthos and coarse particulate organic matter in the sediment surface of a pool biotope in the Njoro River Kenya. Arch Hydrobiol 133:95–106

Matisoff G, Wang XS, McCall PL (1999) Biological redistribution of lake sediments by tubificid oligochaetes: *Branchiura sowerbyi* and *Limnodrilus hoffmeisteri/Tubifex tubifex*. J Great Lakes Res 25:205–219. https://doi.org/10.1016/S0380-1330(99)70729-X

McCall PL, Fisher JB (1980) Effects of tubificid oligochaetes on physical and chemical properties of Lake Erie sediments. In: Brinkhurst RO, Cook DG (eds) Aquatic oligochaete biology. Springer, Boston, pp 253–317. https://doi.org/10.1007/978-1-4613-3048-6_16

McCall PL, Tevesz MJS (1982) Chapter 3. The effects of benthos on physical properties of freshwater sediments. In: McCall PL, Tevesz MJS (eds) Animal-sediment relations. Topics in geobiology. Springer, Boston, pp 105–176. https://doi.org/10.1007/978-1-4757-1317-6_3

McLachlan AJ, Cantrell MA (1976) Sediment development and its influence on distribution and tube structure of *Chironomus plumosus* L (Chironomidae, Diptera) in a New Impoundment. Freshwater Biol 6:437–443. https://doi.org/10.1111/j.1365-2427.1976.tb01632.x

McLachlan AJ, Pearce LJ, Smith JA (1979) Feeding interactions and cycling of peat in a bog lake. J Anim Ecol 48:851–861. https://doi.org/10.2307/4198

Mermillod-Blondin F (2011) The functional significance of bioturbation and biodeposition on biogeochemical processes at the water-sediment interface in freshwater and marine ecosystems. J N Am Benthol Soc 30:770–778. https://doi.org/10.1899/10-121.1

Milbrink G (1973) On the vertical distribution of oligochaetes in lake sediments. Institute for Freshwater Research Rep., Drottningholm

Moss B, Timms M (1989) Predation, sediment stability and food availability as determinants of the benthic invertebrate fauna in two shallow lakes. Hydrobiologia 185:249–257. https://doi.org/10.1007/Bf00036613

Mucha AP, Vasconcelos MTSD, Bordalo AA (2004) Vertical distribution of the macrobenthic community and its relationships to trace metals and natural sediment characteristics in the lower Douro estuary, Portugal. Estuar Coast Shelf S 59:663–673. https://doi.org/10.1016/j.ecss.2003.11.010

Nawrocka L, Kobos J (2011) The trophic state of the Vistula Lagoon: an assessment based on selected biotic and abiotic parameters according to the Water Framework Directive. Oceanologia 53:881–894. https://doi.org/10.5697/oc.53-3.881

Newrkla P, Wijegoonawardana N (1987) Vertica distribution and abundance of benthic invertebrates in profundal sediments of Mondsee, with special reference to oligochaetes. Hydrobiologia 155:227–234. https://doi.org/10.1007/Bf00025655

Nogaro G, Mermillod-Blondin F, Montuelle B, Boisson JC, Lafont M, Volat B, Gibert J (2007) Do tubificid worms influence organic matter processing and fate of pollutants in stormwater sediments deposited at the surface of infiltration systems? Chemosphere 70:315–328. https://doi.org/10.1016/j.chemosphere.2007.06.002

Odum EP (1971) Fundamentals of ecology. Toronto, W.B Saunders Company, Philadelphia

Ojaveer E (2017) Life in the Baltic Sea. In: Ojaveer E (ed) Ecosystems and Living Resources of the Baltic Sea. Their assessment and management. Springer, New York, pp 49–208

OpenStreetMap (2020) OpenTopoMap. https://a.tile.opentopomap.org. Accessed via QGIS OSM plugin 18 November 2020

Persson A, Svensson JM (2006) Vertical distribution of benthic community responses to fish predators, and effects on algae and suspended material. Aquat Ecol 40:85–95. https://doi.org/10.1007/s10452-005-9014-2

Pinder LCV (1995) The habitats of chironomid larvae. In: Armitage PD, Cranston PS, Pinder LCV (eds) Chironomidae. Springer, Dordrecht, pp 107–135. https://doi.org/10.1007/978-94-011-0715-0_6

Piwosz K, Kownacka J, Ameryk A, Zalewski M, Pernthaler J (2016) Phenology of cryptomonads and the CRY1 lineage in a coastal brackish lagoon (Vistula Lagoon, Baltic Sea). J Phycol 52:626–637. https://doi.org/10.1111/jpy.12424

Proulx I, Hare L (2014) Differences in feeding behaviour among Chironomus species revealed by measurements of sulphur stable isotopes and cadmium in larvae. Freshw Biol 59:73–86. https://doi.org/10.1111/fwb.12247

Radziejewska T, Schernewski G (2008) The Szczecin (Oder-) Lagoon. In: Schiewer U (ed) Ecology of Baltic Coastal Waters. Ecol St (Anal Synth), vol 197. Springer, Berlin, pp 121–129

Rosa BJFV, Rodrigues LFT, de Oliveira GS, Alves RG (2014) Chironomidae and Oligochaeta for water quality evaluation in an urban river in southeastern Brazil. Environ Monit Assess 186:7771–7779. https://doi.org/10.1007/s10661-014-3965-5

Robbins JA, McCall PL, Fisher JB, Krezoski JR (1979) Effect of deposit feeders on migration of 137Cs in lake sediments. Earth Planet Sci Lett 42:277–287. https://doi.org/10.1016/0012-821X(79)90035-9

Silva ACF, Tavares P, Shapouri M et al (2012) Estuarine biodiversity as an indicator of groundwater discharge. Estuar Coast Shelf S 97:38–43. https://doi.org/10.1016/j.ecss.2011.11.006

StatSoft (2011) Statistica software version 10. StatSoft Inc. http://www.statsoft.com. Accessed 26 May, 2020

Timm T (1999) A guide to the Estonian Annelida. Estonian Academy Publishers, Tallinn

Timm T, Martin PJ (2015) Chapter 21. Clitellata: Oligochaeta. In: Thorp J, Rogers DC (eds) Ecology and general biology, 4th edn. Academic Press, Amsterdam, pp 529–549. https://doi.org/10.1016/B978-0-12-385026-3.00021-8

Van de Bund WJ, Groenendijk D (1994) Seasonal dynamics and burrowing of littoral chironomid larvae in relation to competition and predation. Arch Hydrobiol 132:213–225

Van de Bund WJ, Goedkoop W, Johnson RK (1994) Effects of deposit-feeder activity on bacterial production and abundance in profundal lake sediment. J N Am Benthol Soc 13:532–539. https://doi:https://doi.org/10.2307/1467849

Vos JH (2001) Feeding of detritivores in freshwater sediments. PhD thesis. University of Amsterdam, Amsterdam

Walshe BM (1947) Feeding mechanisms of *Chironomus* larvae. Nature 160:474–474. https://doi.org/10.1038/160474a0

Whitlach RB (1980) Patterns of resource utilization and coexistance in marine intertidal deposit-feeding communities. J Mar Res 38:743–765

Wiederholm T (1980) Use of benthos in lake monitoring. J Water Pollut Control Fed 52:537–547

Wolnomiejski N (1994) Ecological study on muddy bottom macrofauna of the Szczecin Lagoon (1982–1992). Mor Inst Ryb Gdynia, ser. A, Stud Mat, p 31

Wolnomiejski N, Witek Z (2013) Szczecin Lagoon ecosystem: the biotic community of the Great Lagoon and its food web model. De Gruyter. https://doi.org/10.2478/9788376560502

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Gdynia, 2023-01-17

Miejscowość i data

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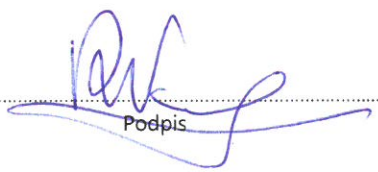
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Mój udział w pracy polegał na:

1. opracowaniu koncepcji,
2. poborze i analizie materiału,
3. napisaniu tekstu manuskryptu,
4. pracach związanych z przedkładaniem manuskryptu do druku (autor korespondencyjny).



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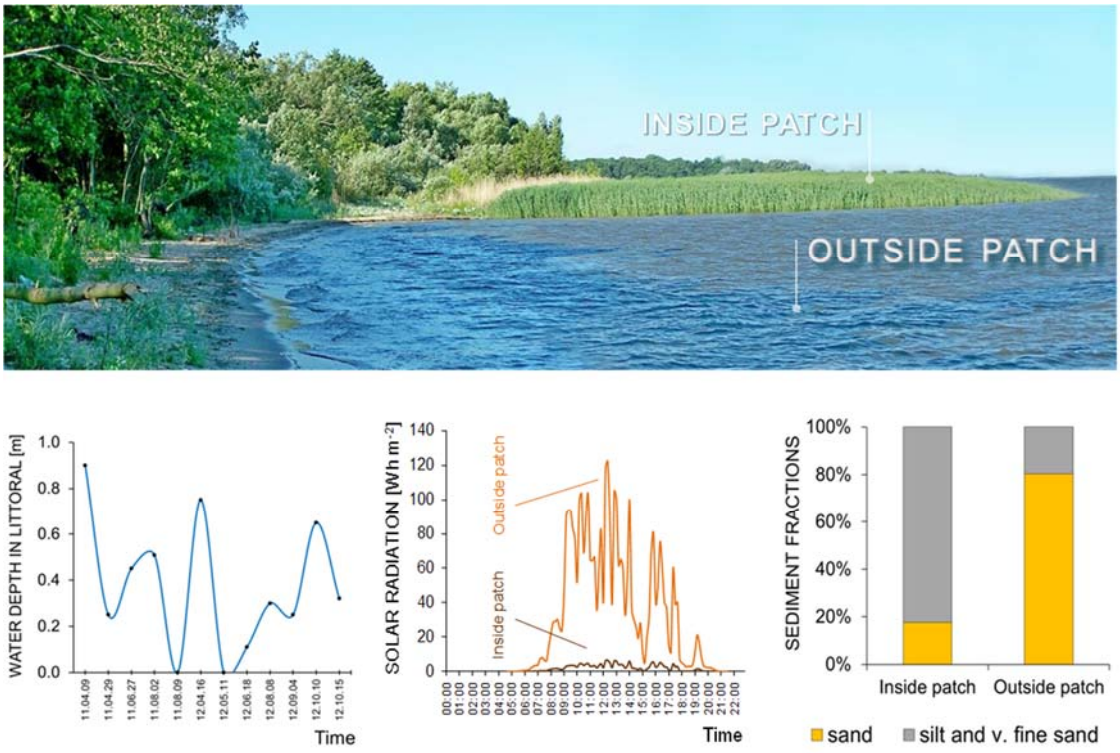
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1. przeprowadzeniu analiz statystycznych wyników dotyczących współwystępowania gatunków,
2. udziale w edycji manuskryptu.

Podpis

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ORIGINAL RESEARCH ARTICLE

Role of macrophytes in structuring littoral habitats in the Vistula Lagoon (southern Baltic Sea)

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KEYWORDS
Submerged and emergent vegetation;
Oxygenation;
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Sediments

Summary The objective of the research conducted in the years 2011—2014 in the near-shore zone of the Vistula Lagoon was the verification of the hypothesis that in the coastal lagoon, similarly as in inland waters, habitat conditions can be substantially modified by macrophytic vegetation, depending on the represented life form and its abundance. The research was conducted in the zone of emergent plants (reed rush composed of *Phragmites australis*) and in the zone of submerged plants occurring as scattered patches of *Potamogeton perfoliatus* and *Stuckenia pectinata*. The hypothesis was supported only in the case of the reed rush which substantially modified water insolation, temperature, and oxygenation, as well as the grain size composition of sediments, and concentration of organic matter contained in the sediments. Patches of submerged vegetation had insufficient surface area and were too scarcely overgrown by plants to considerably affect the habitat conditions and weaken the strong mechanical effect of waves and rate of water exchange between the littoral and open water zone.
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1. Introduction

The littoral is a zone of a water body above the compensation point (Odum, 1971). The most important biotic characteristic of the zone is macrophytic vegetation (vascular flora, stoneworts, bryophytes). It usually occurs in the form of more or less interwinding belts and clusters. The area nearest to the shore is usually occupied by the assemblage of emergent

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plants (helophytes), deeper areas by vegetation with floating leaves (nympheids), and the deepest – vegetation with submerged leaves (elodeids). The presence of such plants indicates the richness of animal communities related to them in various ways (in trophic and paratrophic terms), both invertebrates (epiphytic fauna) and vertebrates (amphibians, reptiles, fish, and birds). In shallow water bodies where the majority of the bottom surface is insolated, the role of macrophytes in the functioning of the entire ecosystem can be sufficiently significant to provide the basis for the designation of one of the alternative regimes – macrophyte-dominated state (Scheffer et al., 1993).

Many papers discuss the impact of different abiotic factors on aquatic vegetation. Considerably fewer publications concern the opposite relations, i.e. the effect of plants on the habitat conditions occurring in the littoral. So far, the issue has been mainly investigated in inland water bodies, and particularly in shallow lakes (Barko and James, 1998; Carpenter and Lodge, 1986; Chen and Barko, 2011; Horppila and Nurminen, 2005; Miranda et al., 2000; Moller and Sand-Jensen, 2012), but very rarely in the conditions of coastal lagoons (Viaroli et al., 1996). It may be caused by among others the popular opinion that in the littoral of lagoons, the habitat conditions are primarily determined by physical parameters, including wave action (Perez-Ruzafa et al., 2011; Viaroli et al., 2008). This paper presents a hypothesis that in a coastal lagoon, like in inland waters, habitat conditions can also be substantially modified by macrophytic vegetation, depending on the represented life form (helophytes, elodeids) and its abundance. The thesis was verified by four years of research in the near-shore zone of the Vistula Lagoon.

2. Study area

The Vistula Lagoon is a brackish lagoon separated from the Gdańsk Bay (Baltic Sea) by the Vistula Spit. The exchange of water masses between the Lagoon and open sea is possible through the Baltijsk Strait. The Vistula Lagoon has an area of 838 km^2 and is divided approximately in half between Poland (south-western part) and Russia (north-eastern part). The lagoon is a shallow water body with a depth usually not exceeding 4 m. The length of the shoreline of the Vistula Lagoon on the Polish side is 92.3 km. Homogenous assemblages of emergent vegetation (EMV) occur along the shoreline, particularly including *Phragmites australis* (Cav.) Trin. ex Steud, and patches of submerged vegetation (SUV), composed mainly of *Potamogeton perfoliatus* L. The greatest degree of vegetation cover occurs in the western part of the lagoon (Fig. 1) (Gajewski, 2010).

Bottom sediments are primarily composed of silt and sand (Zachowicz et al., 1995). The concentrations of total nitrogen and phosphorus in the water are high, and amount to 1.1–4.4 mg dm^{-3} and 0.06–0.19 mg dm^{-3}, respectively. The most frequently recorded water transparency (measured as Secchi disc depth) is approximately 40 cm (Kornijów, 2018). The Vistula Lagoon is classified as a eutrophic water body (Kruk et al., 2012; Nawrocka & Kobos, 2011), and from the viewpoint of alternative stable states theory, the majority of its basin is phytoplankton-dominated, with chlorophyll-*a*

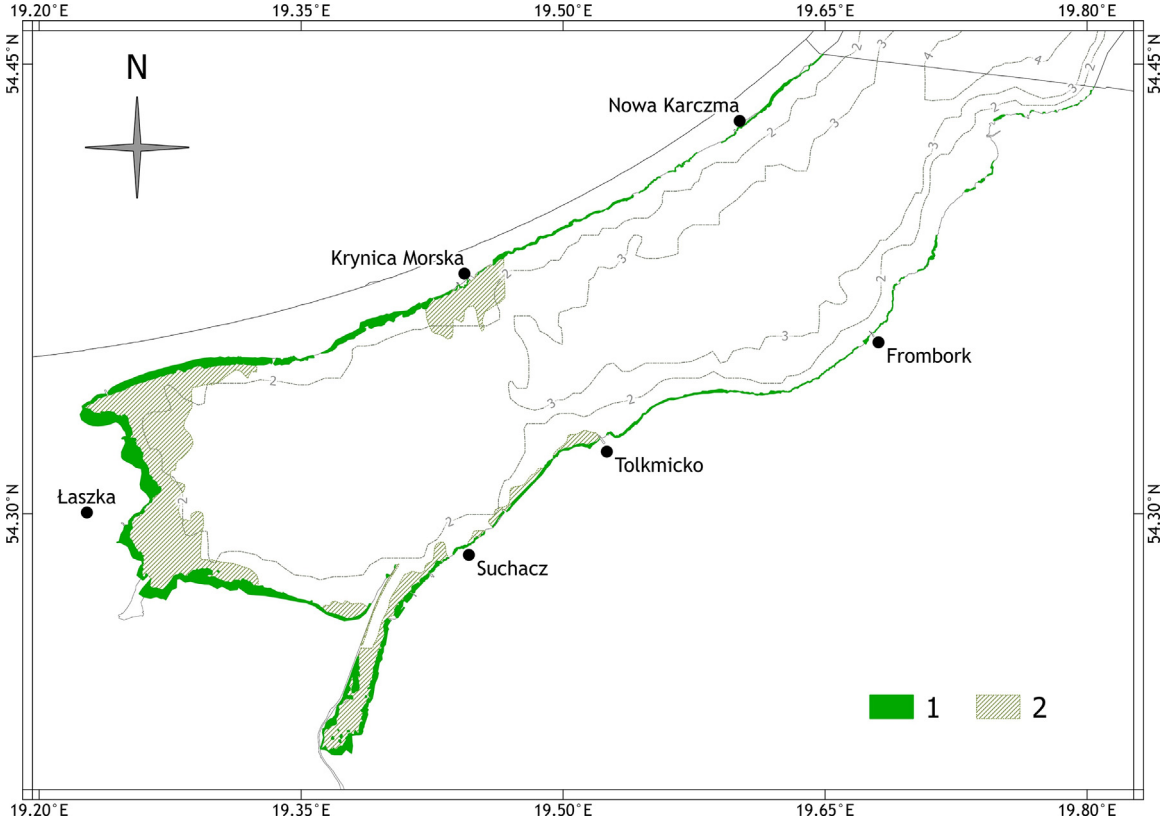


Figure 1 Map of distribution of emergent (1) and submerged vegetation (2) in the Polish part of the Vistula Lagoon. Based on maps elaborated by Gajewski (ed., 2010). Bathymetry adapted from Chubarenko (2008).

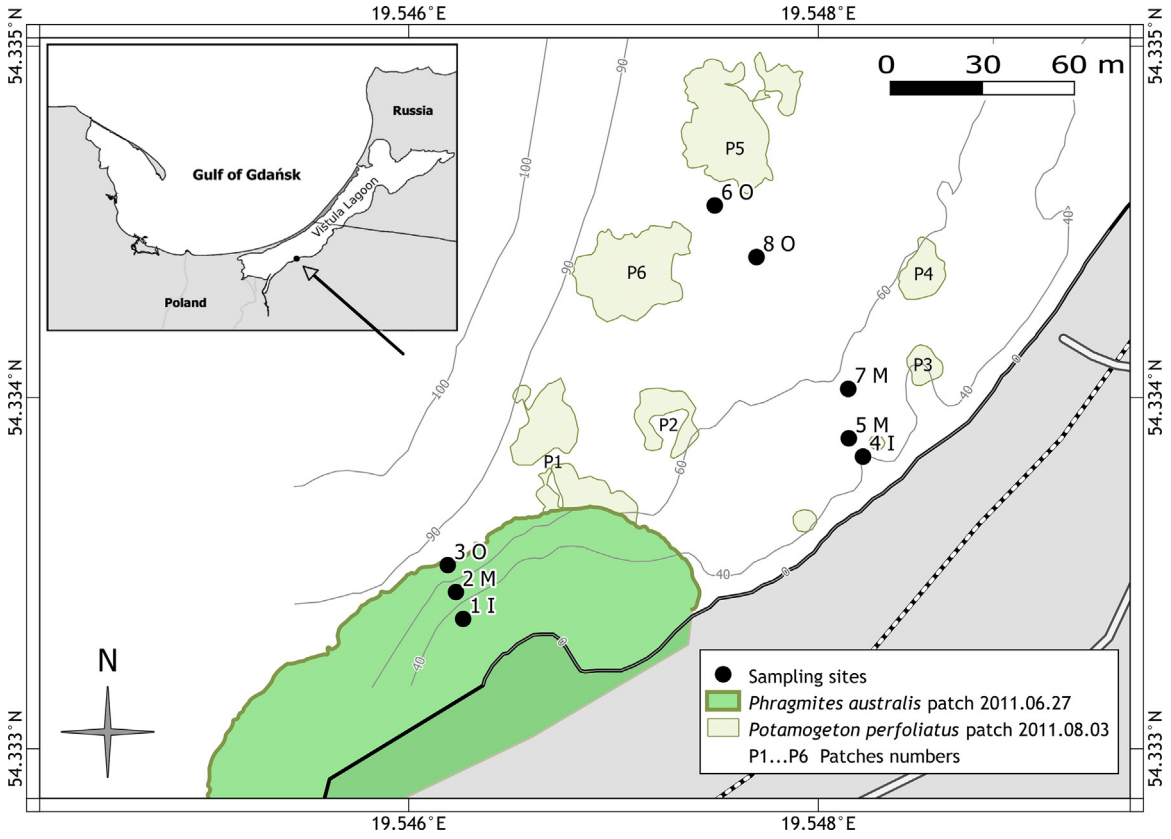


Figure 2 Map of the littoral section studied. For explanation of the site symbols see Table 1.

concentrations between 13 and 107 mg m^{-3} (Kornijów, 2018).

The studied fragment of the littoral (Fig. 2) was located 2 km north-east of the port in Tolkmicko and had a length of approximately 500 m and width of 110 m. A patch overgrown by common reed (*Phragmites australis*) occurred there, with a length of 200 m, as well as a 300 m long section of sandy bottom (psammolitoral) with several patches of submerged vegetation dominated by perfoliate pondweed *Potamogeton perfoliatus*, and more rarely by sago pondweed *Stuckenia pectinata* (L.) Börner. The research was performed at 14 sites selected based on the criterion of depth and occurrence of vegetation (Fig. 2, Table 1). Three sites were located in the zone of emergent vegetation (EMV) overgrown by reed rush, five on the adjacent sandy bare bottom between the patches of SUV macrophytes (herein treated as control), and six within SUV patches (*P. perfoliatus*). The littoral belt was divided into three zones: inner littoral (depth 0–40 cm,

Table 1 Characteristics of the sampling sites: location within the research area, depth, type of sediment, and exposure to wave action. EMV – emergent vegetation, SUV – submerged vegetation.

Site	Zone	Location	Distance from shore [m]	Depth [m] (range in brackets)	Bottom sediment	Exposure to wave action
Site 1 I	EMV (inside the patch)	inner	32	0.25 (0.11–0.51)	silt	weak
Site 2 M	EMV (inside the patch)	mid	40	0.50 (0.26–0.66)	silt	medium
Site 3 O	EMV (inside the patch)	outer	50	0.70 (0.64–0.97)	sand	strong
Site 4 I	SUV (between patches)	inner	13	0.40 (0.23–0.57)	sand	strong
Site 5 M	SUV (between patches)	mid	20	0.50 (0.33–0.67)	sand	strong
Site 6 O	SUV (between patches)	outer	103	0.72 (0.61–0.95)	sand	strong
Site 7 M	SUV (between patches)	mid	31	0.58 (0.36–0.65)	sand	strong
Site 8 O	SUV (between patches)	outer	82	0.71 (0.54–0.78)	sand	strong
Patch P1	SUV (inside patches)	outer	60	0.70	sand	strong
Patch P2	SUV (inside patches)	outer	54	0.70	sand	strong
Patch P3	SUV (inside patches)	inner	22	0.34 (0.17–0.41)	sand	strong
Patch P4	SUV (inside patches)	mid	40	0.59 (0.35–0.66)	sand	strong
Patch P5	SUV (inside patches)	outer	111	0.78 (0.57–0.85)	sand	strong
Patch P6	SUV (inside patches)	outer	103	0.81 (0.67–0.88)	sand	strong

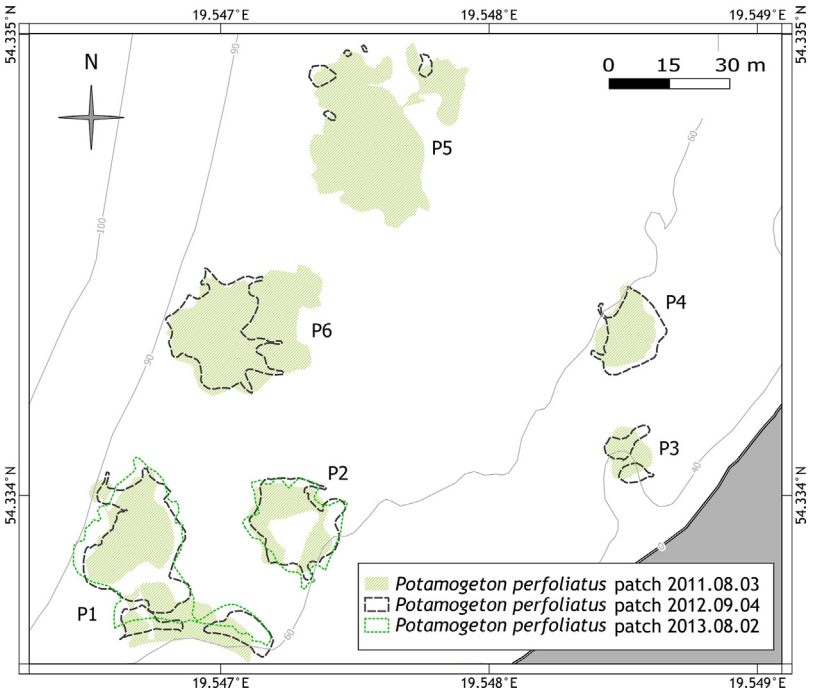


Figure 3 Changes in the surface area occupied by vegetation patches in the period 2011–2013. P1...P6 – numbers of patches.

distance from the shore of approximately 0–40 m), mid-littoral (depth 40–60 cm, distance from the shore of 20–50 m), and outer littoral (depth 60–90 cm, distance from the shore of 50–111 m).

3. Methods

The research was conducted in the years 2011–2014. The estimation of the length of the phytolittoral in the Polish part of the Vistula Lagoon occupied by emergent vegetation (EMV) was performed by means of Google Earth software (Google Inc., 2014–2016). Belts of emergent vegetation were identified, and their length was measured along the shoreline. The length of the shoreline free from reed rush (i.e. belts of artificially altered psammolittoral and littoral) was measured the same way. The identification of vegetation also applied aerial and satellite photographs publicly available online [http://geoportal.gov.pl (Geoportal, 2014), http://www.yandex.ru/maps/ (Yandex, 2014)].

Measurements of the outline of vegetation patches near Tolkmicko were performed by means of a GPS receiver (Garmin GPSMAP 60CSx) by wading along the boundary of vegetation on the water side. Results of the records were preliminarily processed in Garmin MapSource software. The resulting GIS layers were then loaded to Quantum GIS software for final processing and visualisation (Figs. 2 and 3). A density of plants was determined by counting reed stems per 0.25 m^2 plot, designated by means of a wooden frame without one side, which allowed for sliding the device into the thicket of vegetation (Bernatowicz, 1960). At each site, plant measurements were performed on 10 fields located at a distance of several metres from each other.

Research on the vegetation was also conducted along the entire shoreline on the Polish side of the lagoon. While paddling in a boat, the presence of submerged vegetation patches was recorded, and their surface area was estimated. Due to the dispersed character of the patches and their scarce degree of cover, quantitative measurements of density were not performed. Such measurements were performed in reference to reed assemblages at six selected sites (Table 2).

Bathymetric measurements in the littoral near Tolkmicko were performed by means of a ranging rod with accuracy to 1 cm on 2014.09.04. Depth was measured in 154 points with geographic coordinates determined by means of a GPS receiver (Garmin GPSMAP 60CSx). The memory of the receiver also recorded the course of the shoreline (zero depth). The data matrix was loaded to Surfer 10 software in which a detailed bathymetric map of the studied water body was generated by means of the kriging method. The map was then visually processed by means of Quantum GIS software (Figs. 2 and 3).

Water level was measured at study sites: 1I, 2M, 3O, 4I, 5M, and 6O in the years 2011–2012 by means of a gauge with a centimetre scale. In order to demonstrate full water level amplitude, six situations with extreme water levels were selected from maps generated by the hydrodynamic model of the Institute of Oceanography of the University of Gdańsk (Ecohydrodynamic Model, 2016). Readings from the model provided the basis for the calculation of the probable water level at measurement sites. Two sites were selected for the visualisation of water level fluctuations, namely the shallowest site 1I in EMV and one of the deepest ones in SUV – site 6O.

Continuous measurements of water temperature fluctuations at 10-min intervals were performed by means of temperature loggers Seamon Mini in the periods from 2011.07.20 to 2011.10.03 (sites 1I and 2M) and from 2012.04.21 to 2012.09.12 (site 1I). Single temperature and salinity measurements were performed by means of a sonde Saiv A/S STD-CTD model SD-202 or SD-204 at sites 1–6 in four terms in 2011. On 2–3.08.2011, daily water temperature and

Table 2 Density of *Phragmites australis* stems (±SD standard deviation) at sites around the Polish part of the Vistula Lagoon in 2014. Location of the sites in the vicinity of the mentioned municipalities are marked in Fig. 1. Sites sharing the same letter do not differ statistically (post hoc Friedman test).

Name of location near sampling site	Stems density [N m^{-2}] ± SD	Significant difference
Frombork	104 ± 27	c
Tolkmicko	70 ± 11	ac
Suchacz	76 ± 21	ac
Łaszka	62 ± 22	ac
Krynica Morska	56 ± 22	ab
Nowa Karczma	55 ± 17	ab

oxygenation fluctuations were also traced. The measurements were performed by means of a portable sonde at 21:30, 3:30, 9:30, and 14:45 at three sites in EMV (Sites: 1–3) and at three sites in SUV (Sites: 4–6). Measurements of solar radiation were performed in the EMV zone at site 2. They involved the application of two pyranometers of type LI-COR LI-200SA connected to a LI-COR datalogger. One pyranometer was placed on a mast above plant canopies, at a height of 2.73 m above the water surface, and the other at the base of plants, 0.14 m above the water surface. Solar radiation values [Wh m^{-2}] for a 48 h period were recorded between 2012.08.06 at 14:00 and 2012.08.08 at 14:00. Data were logged with 10 min intervals.

For the purpose of determination of the type of bottom sediments and their grain size composition, sediment cores were sampled in both zones (EMV and SUV) by means of a core sampler with a diameter of 4.4 cm, pushed into the bottom to a depth of 25 cm. At the laboratory, the sediments were dried and manually ground in a mortar, and then sieved on a set of geological sieves with the mesh of 2 mm, 1 mm, 0.5 mm, 0.25 mm, 0.125 mm, and 0.063 mm. The obtained data were processed with the application of GRADISTAT software version 8 (Blott and Pye, 2001). Organic matter content in sediment was determined by the direct method of mass losses on ignition at a temperature of 500°C.

Statistical analyses were performed by means of Statistica 10 software (StatSoft Inc, 2011). ANOVA Friedman and Wilcoxon tests were used in order to determine statistical differences (Sokal and Rohlf, 1995).

4. Results

4.1. Vegetation

Particular sections of the Polish shoreline of the Lagoon are occupied by EMV to different degrees: the northern section along the Vistula Spit, from the border to Skowronki, is occupied in 85%, the western section between Skowronki and Suchacz in 99%, and the southern section from the border to Suchacz in 74%.

The density of *P. australis* stems at six sites around the Polish part of the Vistula Lagoon varied from 55 stems m^{-2} ± 17 SD to 104 stems m^{-2} ± 27 (Table 2). The density statistically differed only between the site near Frombork and two sites (near Krynica Morska and Nowa Karczma) on the opposite side of the lagoon at the Vistula Spit [post hoc, ANOVA Friedman test: χ^2 (N = 10, df = 5, p = 0.00613) = 16.26437].

The ranges of the EMV patch, monitored near Tolkmicko, practically did not change in the years 2011–2013, as opposed to the ranges and sizes of SUV patches (Fig. 3). The surface area of *P. perfoliatus* patch 16P in the period 2011–2012 decreased approximately by half, and patch 15P practically entirely declined in 2012. In 2013, all patches inconsiderably increased their surface area.

Seasonal changes in plant density involved a gradual increase in the number of stems during the vegetative season. In the EMV zone, the highest (and relatively even) values of reed density were observed in late summer (132–158 stems m^{-2} in 2011) (Fig. 4).

The density of *P. perfoliatus* stems in the period from June to August only increased in deeper located patches in the mid- and outer littoral zones, and remained unchanged in the inner littoral (Fig. 5). In September, the commencement of the rapid process of dying-off of plants and disappearance of the patches was observed.

4.2. Water level fluctuations

Water level fluctuations were characterised by high dynamics with an amplitude of approximately 40 cm (Fig. 6). Data from the hydrodynamic model show that the performed field measurements did not reflect the full annual amplitude of changes, which could be much greater, leading to periodical exposure of the bottom at the shallowest site.

4.3. Salinity — seasonal changes

Water salinity varied from 1.4 PSU to 3.0 PSU (Fig. 7). Seasonal salinity dynamics, with an evident maximum

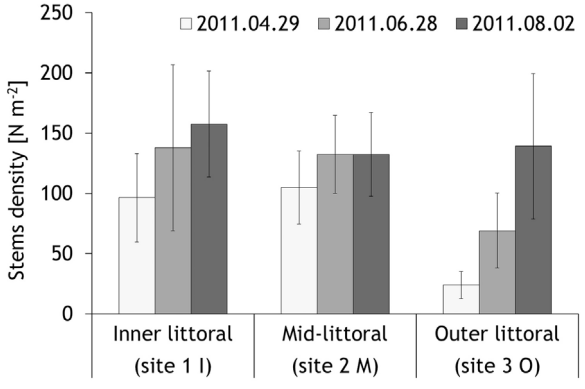


Figure 4 Seasonal changes in the density of *Phragmites australis* stems ± SD in the EMV zone. N — number of stems.

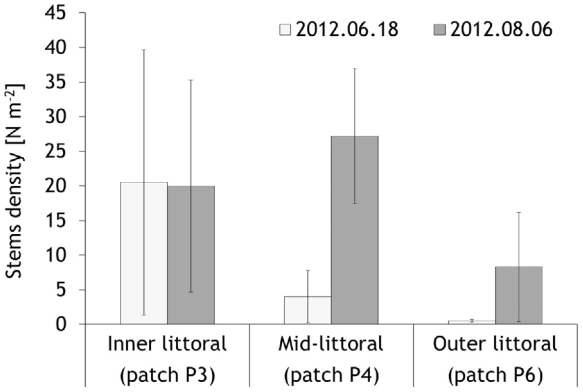


Figure 5 Seasonal changes in the density of *Potamogeton perfoliatus* stems ± SD in the SUV zone. Patch P5 in the outer littoral was not considered due to the very low stem density in June 2012 (0.07 stems m^{-2}) and its later complete disappearance.

recorded in autumn, showed a similar course at all sites, irrespective of the analysed zone, without significant statistic differences [ANOVA Friedman test: χ^2 (N = 3, df = 5, p = 0.095) = 9.37].

4.4. Temperature — seasonal changes

Water temperature changed seasonally [ANOVA Friedman test χ^2 (N = 6, df = 3, p = 0.00094) = 16.89; post hoc]. A greater amplitude of temperature fluctuations was recorded in the EMV zone (15.2–22.0°C) than in the SUV zone (16.4–21.7°C) (Fig. 8). In the EMV zone, water temperature developed differently at the shallowest sites (inner- and mid-littoral) than at the remaining ones, where the temperature distribution had a similar pattern [differences statistically non-significant [ANOVA Friedman test χ^2 (N = 4, df = 3, p = 0.91) = 0.53]. In the elodeid zone (SUV), where the spatial distribution of temperatures was even, no such dependency was observed [ANOVA Friedman test χ^2 (N = 4, df = 5, p = 0.078) = 9.89].

4.5. Temperature — diurnal changes

Water temperature in summer in a diurnal cycle varied from 19.4 to 22.8°C (Fig. 9). Diurnal changes in water temperature at two shallowest sites (shaded, and isolated from the open water zone, located in the reed belt (EMV)) had a different course from the remaining ones in the SUV zone, where they

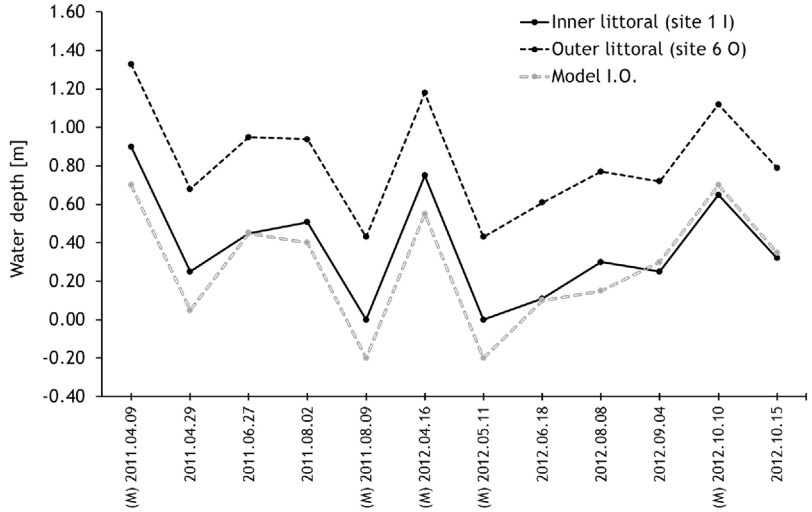


Figure 6 Changes in water depth in the period from 2011.04 to 2012.10 in the EMV zone — inner littoral and in the SUV zone — outer littoral based on field measurements. Additional data (dates marked with letter M) were obtained from the Ecohydrodynamic Model (Model I.O.) developed at the University of Gdańsk, Institute of Oceanography (Ecohydrodynamic Model, 2016).

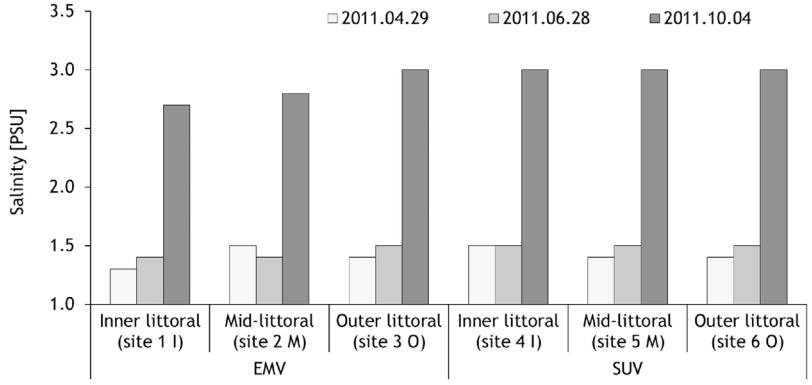


Figure 7 Seasonal changes in salinity in EMV and SUV zones. Numbers of sampling sites in brackets.

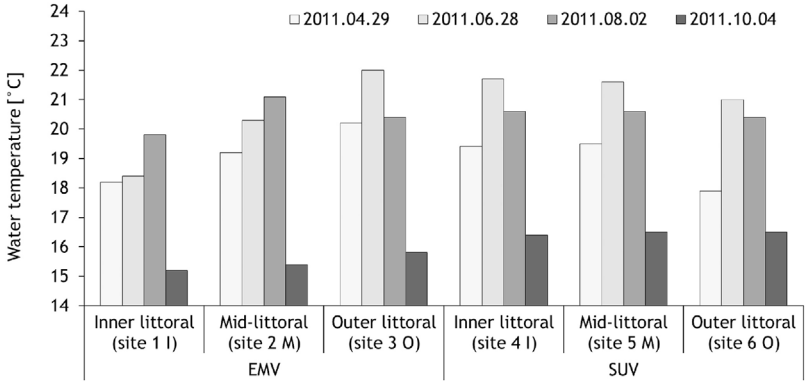


Figure 8 Seasonal changes in water temperature in EMV and SUV zones. Numbers of sites in brackets.

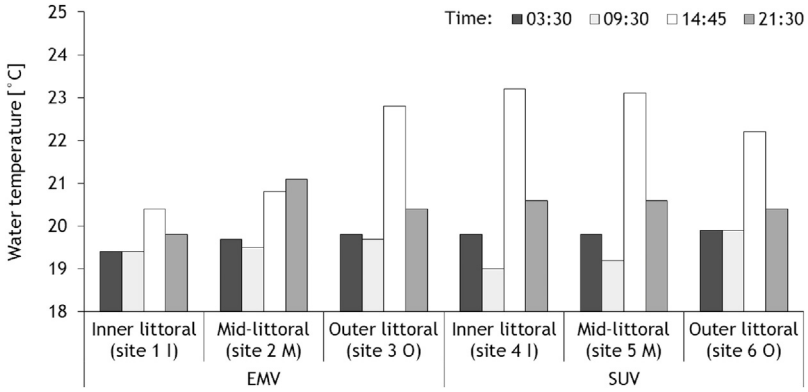


Figure 9 Diurnal changes in water temperature in EMV and SUV zones. Measurements performed on 1.08.—2.08.2011.

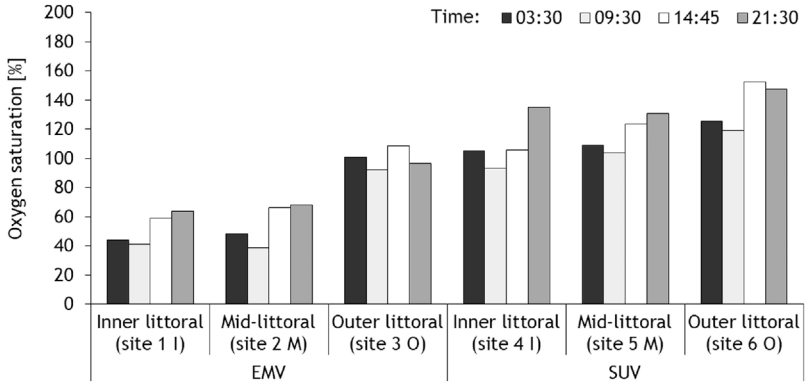


Figure 10 Diurnal changes in oxygen saturation in EMV and SUV zones. Measurements performed on 1.08.—2.08.2011.

developed in a similar way. The differences particularly concerned afternoon hours, when water temperature had relatively low values in the inner- and mid zone of EMV, and considerably higher values at the remaining sites. In the outer littoral zone of EMV, the diurnal amplitude of temperature fluctuations was similar to that at sites in the SUV zone.

4.6. Oxygen — diurnal changes

In summer, in a diurnal cycle, water saturation with oxygen varied from 39% to 152% in the EMV zone, and from 110% to 136% in the SUV zone (Fig. 10). The lowest values of oxygen saturation during the entire day were recorded at two shallowest sites (inner and mid-littoral) in the EMV zone. The course of oxygen saturation in the diurnal cycle was similar at all the sites, irrespective of the zone, with the lowest values in morning hours, and the highest in the evening.

4.7. Solar radiation — diurnal changes

Insolation in the analysed zone changed substantially in the diurnal cycle (Fig. 11). Maximum mean hourly solar radiation

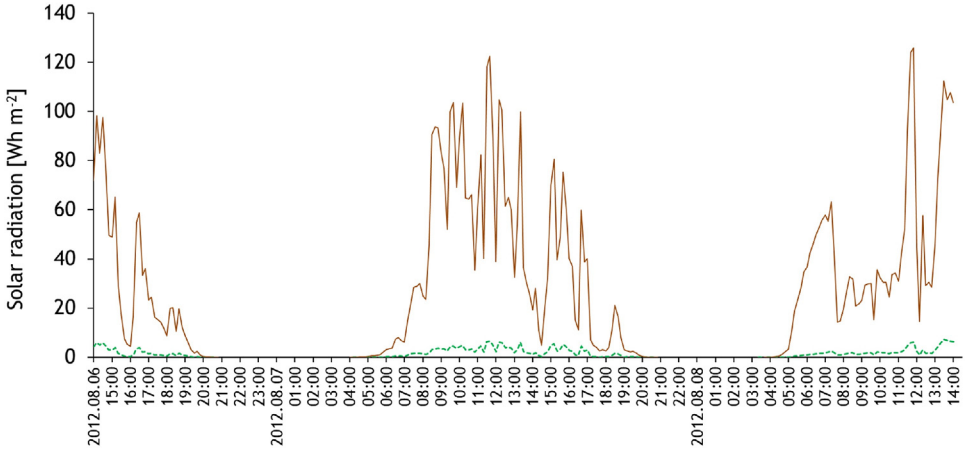


Figure 11 48-hour record of changes in solar radiation reaching the EMV and SUV zones (solid line), and water surface under plant canopies inside EMV (dotted line). Measurements performed on 2012.08.06–08.

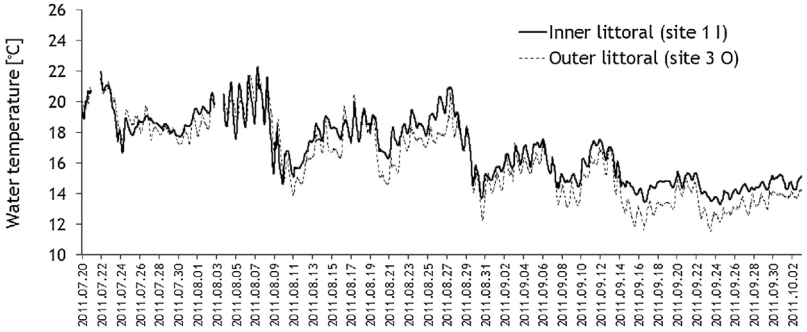


Figure 12 Results of continuous measurements of water temperature fluctuations in the inner- and outer littoral in the EMV zone (2011.07.20–2011.10.02).

amounted to 86.2–104.6 Wh m^{-2}. Under canopies of EMV, right above the water surface, it amounted to (4.7–6.6 Wh m^{-2}) and was considerably lower [Wilcoxon Test: T ($Z = 12.354$, $N = 203$, $p < 0.01$) = 0], constituting only approximately 6% of the total supplied solar radiation.

4.8. Temperature — continuous measurements of energy accumulation

Water temperatures in the majority of terms in the inner littoral zone of EMV near the shore were higher than in the outer littoral zone bordering on the open water zone (Fig. 12). Also mean temperature in the inner littoral (16.92°C) was significantly higher than in the outer littoral zone (16.24°C) [Wilcoxon Test: T ($Z = 70.285$, $N = 10\,597$, $p < 0.01$) = 5 941 811].

4.9. Sediments

In the EMV zone, bottom sediments were primarily composed of fine fractions (very fine sand, very coarse silt) (Fig. 13). In the SUV zone, sediments with coarser grains occurred, in particular, fine sand and medium sand were present. Both zones showed a tendency for increasing contribution of coarse-grained fractions with growing depth and distance from the shore.

Organic matter content in bottom sediments was highest in the inner littoral of the EMV zone (3.1%), and lowest in the mid-littoral of SUV zone (0.4%) (Fig. 14). With growing depth, the recorded values showed a decreasing tendency in EMV and an increasing one in SUV.

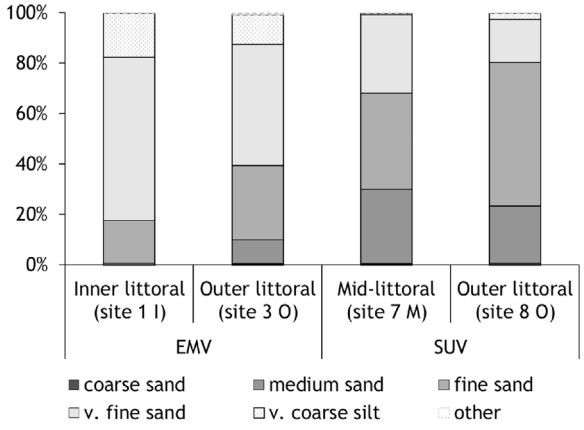


Figure 13 Percentage of particular fractions of bottom sediments in EMV and SUV zones (2012.08.08).

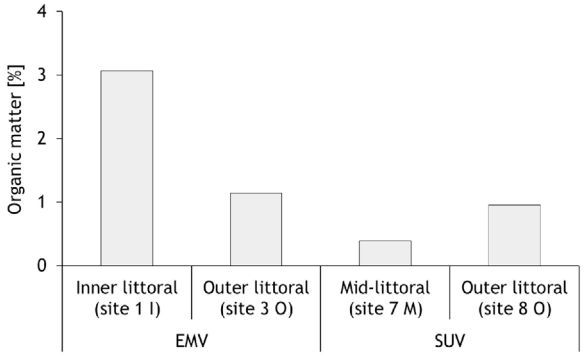


Figure 14 Organic matter content in bottom sediments in EMV and SUV zones (2012.08.08).

5. Discussion

5.1. Impact of vegetation on physical water properties

The research revealed that submerged vegetation has no substantial effect on the habitat conditions in the analysed littoral area. Irrespective of distance from shore, depth, and place within patches, physical water parameters in the SUV zone were similar. This may result from a relatively small surface area of the patches and low plant density, as well as from the observed substantial changes in ranges of the patches in particular years (Fig. 3). The conclusion concerning lack of evident effect of SUV on habitat conditions can be probably transposed to the entire northern and southern shore of the lagoon, where the occurrence of submerged macrophytes is very scarce. A different situation can be expected in the western part of the lagoon, where dense submerged vegetation covers extensive areas (Fig. 1). This is suggested by frequently observed even three times higher water transparency (Różańska and Więcławski, 1978; Szarejko-Łukaszewicz, 1959; Żmudziński and Szarejko, 1955), and approximately a dozen times lower chlorophyll concentrations (Latała, 1978) in the western part of the lagoon than in the remaining areas in spite of similar nutrient concentrations. The dependencies were often associated with the different degree of development of submerged macrophytes (Kornijów, 2018; Latała, 1978; Pliński and Simm, 1978; Renk et al., 2001; Ringer, 1959; Żmudziński and Szarejko, 1955).

Mean density of reed stems determined in the Vistula Lagoon (74 stems $m^{-2} \pm 18$) corresponded with the top values determined in local channels (Boszke et al., 2005), as well as in freshwater and brackish ecosystems of the North America, where reed is an invasive species (Meyerson et al., 2000). It was within the lower range of maximum density values (60–250 m^{-2}) reported from different aquatic environments of Europe by Haslam (1973).

Unlike SUV, the extensive patches of densely growing EMV had a considerable modifying effect on certain physical water parameters (Fig. 15). The effect particularly involved the diversification of lighting conditions and temperature. The energy of solar radiation reaching the reed patch (EMV) was largely reflected and dispersed on the surface of plants, as confirmed by other studies (Grant, 1987; Ondok, 1973). The photosynthetically useful part of the spectrum (PAR) is absorbed by plants and used for photosynthesis (McCree, 1981). The remaining part of the radiation is transformed into heat. Such transformations probably resulted in the observed higher than average water temperature values in the EMV zone.

Differences in temperatures along sections at different distances from the shore and with different depths suggest the variable intensity of water mixing, related to the suppression of the kinetic energy of wave action by densely

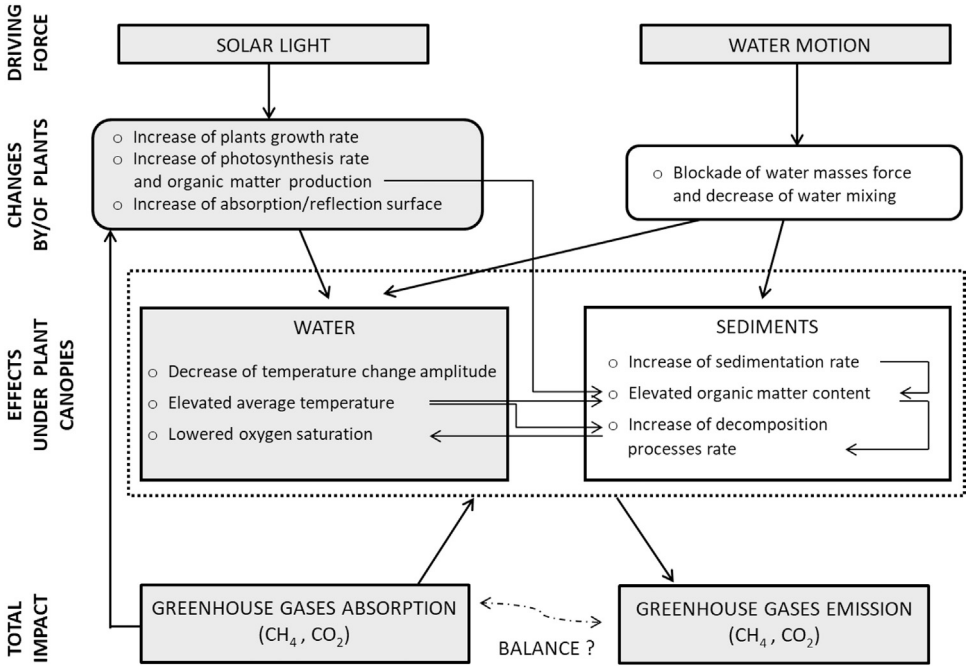


Figure 15 Simplified ideogram of some dependencies and processes related to the presence of macrophytic assemblages in the analysed area. Grey fields concern both SUV and EMV, white fields — only EMV.

growing plant stems. According to Kornijów (2018), the crucial driver regulating the structure and processes occurring in the Vistula Lagoon is wave exposure. Therefore, low rate of water exchange between the littoral and open water zone, and attenuation of the mechanical effect of waves by near-shore vegetation are very important in terms of protection of shores against destructive wave action and erosion (Moller et al., 2011; Rupprecht et al., 2017). Near-shore vegetation is also known to play an important role as a filter for nutrients and organic material flushed from the catchment (Berthold et al., 2018; McGlathery et al., 2007). Moreover, it creates a habitat not only for water organisms, but also for those associated with land, namely amphibians, waterfowl, and mammals.

Due to its high heat capacity, water is a good indicator of energy accumulation in a longer term. The comparison of several months of temperature measurements within EMV and at the boundary of the zone showed that as a result of both a decrease in water mixing and absorption of solar radiation causing air heating within EMV, mean water temperature in summer amongst the reed rush was higher than in the remaining area of the water body. In spring and autumn, the pattern was opposite.

The summer diurnal amplitude of temperature fluctuations in the EMV zone was also lower than in other zones, probably due to the effect of shading by plant canopies and heat inertia of water. It is very likely, that the shading effect by reed stems results in the inhibition of development of other plants in reed rush patches. In consequence, in the Vistula Lagoon, it is primarily composed of a monoculture of *P. australis*, which is interpreted as a manifestation of good condition of the plant assemblage (Haslam, 1973).

Uniform diurnal water oxygenation in the inner and mid-littoral of EMV zone was probably the effect of intensive decomposition processes, as well as a decrease in the intensity of photosynthesis due to very limited access of sunlight to the water surface, as also emphasised by Viaroli et al. (1996). It can also be related to limited water exchange between the rush patch and the open water. In the outer littoral of EMV zone, water oxygenation was considerably higher throughout the day, but it was also uniform in time. This could be determined by continuous mixing with the well-aerated deeper water. Considerable oxygenation drops below 40% can substantially limit the occurrence of animals, both invertebrates and fish (Able and Hagan, 2000; Warren et al., 2001).

No significant differences were observed in salinity within the EMV patch. Water salinity in the Vistula Lagoon is probably not sufficient for a considerable salinity gradient to develop as a result of limiting water mixing by vegetation.

In conclusion, the stated hypothesis in reference to water parameters proved supported only in the case of the reed rush which considerably modified lighting conditions, temperature, and water oxygenation, particularly in warm seasons of the year when reed density was high.

5.2. Impact of vegetation on sediments

Within the SUV zone, no considerable differences were observed in the composition of bottom sediments. This was probably caused by the fact that processes occurring in sediments are largely determined by the mechanical movement of water masses and strong and even insolation the intensity of which could not be affected by macrophytes showing a low degree of cover and density.

In the EMV zone, limited mixing of water masses could favour sediment deposition and permit sedimentation of finer fractions of dead organic matter. This probably led to the observed shallowing and occurrence of sediments with an increased contribution of organic matter. Organic matter content in bottom sediment in the EMV zone, next to limited water mixing, is undoubtedly also determined by the presence of plants dying in masses in autumn (Kuehn et al., 2000).

The stated hypothesis in reference to bottom sediments was supported only in the case of the reed rush which considerably modified the grain size composition of sediments and content of organic matter.

5.3. Total impact

Wetlands are among the most ecologically valuable environments (Mitsch et al., 2013). The key importance of wetlands for the ecosystem, involving e.g. their contribution in primary production, in matter circulation, or water storage, was described by many authors (among others: Kuehn et al., 2000; Mitsch et al., 2013). A particular role in the littoral-wetland environment is played by emergent plant assemblages (Wetzel and Hough, 1973). Their presence influences a number of biochemical processes such as production and decomposition of organic matter (Kuehn et al., 2000), and physical and chemical processes such as release of greenhouse gases: methane (Ding et al., 2005; Olsson et al., 2015) and carbon dioxide (Kuehn and Suberkropp, 1998). Wetlands are among ecosystems absorbing CO_2 (Bekele et al., 2016; Bernal and Mitsch, 2012) and CH_4 (Olsson et al., 2015). The balance of absorption and release of greenhouse gases differs, however, depending on the characteristics of particular wetlands (Bekele et al., 2016; Bernal and Mitsch, 2012; Ding et al., 2005), including the species composition of the vegetation (Kim et al., 1998; Olsson et al., 2015). Plants from genus *Phragmites* belong to the most common plants in wetlands, and rapidly expand the area of its occurrence all over the word (Able and Hagan, 2000; Haslam, 1973; Lelong et al., 2007; Meyerson et al., 2000; Próchnicki, 2005; Warren et al., 2001; Weisner, 1991), also as a result of human activities aimed at limiting areas under agricultural use (Huryna and Pokorny, 2016). Results of the cited studies permit stating the hypothesis that also in the marshy environment of the littoral of the Vistula Lagoon, abundantly covered with vegetation, as well as others lagoons of the Baltic Sea, analogical processes occur that may have a specific impact on climatic changes. The scale of such impact, however, requires further research aimed at among others the determination of the production balance, and release and absorption of greenhouse gases.

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References

Able, K.W., Hagan, S.M., 2000. Effects of common reed (*Phragmites australis*) invasion on marsh surface macrofauna: Response of fishes and decapod crustaceans. Estuaries 23 (5), 633–646, http://dx.doi.org/10.2307/1352890.

Barko, J.W., James, W.F., 1998. Effects of submerged aquatic macrophytes on nutrient dynamics, sedimentation, and resuspension. In: Jeppesen, E., Søndergaard, M., Søndergaard, M., Christoffersen, K. (Eds.), The structuring role of submerged macrophytes in lakes. Ecol. Stu. An., Vol. 131. Springer, New York 197–214, https://doi.org/10.1007/978-1-4612-0695-8_10.

Bekele, T., Lemma, B., Mengistou, S., 2016. Carbon sequestration potentials of selected wetlands at Lake Ziway, Ethiopia. J. Environ. Earth Sci. 6 (9), 1–9.

Bernal, B., Mitsch, W.J., 2012. Comparing carbon sequestration in temperate freshwater wetland communities. Glob. Change Biol. 18 (5), 1636–1647, http://dx.doi.org/10.1111/j.1365-2486.2011.02619.x.

Bernatowicz, S., 1960. Methods of examination of vascular vegetation in lakes. Roczniki Nauk Rolniczych 77 (B-l), 61–78, (in Polish).

Berthold, M., Karstens, S., Buczko, U., Schumann, R., 2018. Potential export of soluble reactive phosphorus from a coastal wetland in a cold-temperate lagoon system: Buffer capacities of macrophytes and impact on phytoplankton. Sci. Total Environ. 616–617, 46–54, http://dx.doi.org/10.1016/j.scitotenv.2017.10.244.

Blott, S.J., Pye, K., 2001. GRADISTAT: A grain size distribution and statistics package for the analysis of unconsolidated sediments. Earth Surf. Proc. Land. 26 (11), 1237–1248, http://dx.doi.org/10.1002/esp.261.

Boszke, P., Bociag, K., Szmeja, J., 2005. Population structure and regeneration of *Phragmites australis* (Cav.) Trin. ex Steud in flood control ditches in the depression wetland (Żuławy Wiślane, Northern Poland). Pol. J. Ecol. 53 (1), 3–12.

Carpenter, S.R., Lodge, D.M., 1986. Effects of submersed macrophytes on ecosystem processes. Aquatic Botany 26, 341–370, http://dx.doi.org/10.1016/0304-3770(86)90031-8.

Chubarenko, B.V., 2008. The Vistula Lagoon. In: Chubarenko, B.V. (Ed.), Transboundary waters and basins in the south-east Baltic, Terra Baltica, Kaliningrad, 37–57, ISBN 978-5-98777-031-3.

Chen, R.L., Barko, J.W., 2011. Effects of fresh-water macrophytes on sediment chemistry. J. Freshwater Ecol. 4 (3), 279–289, http://dx.doi.org/10.1080/02705060.1988.9665177.

Ding, W., Cai, Z., Tsuruta, H., 2005. Plant species effects on CH_4 emissions from freshwater marshes. Atmos. Environ. 39 (18), 3199–3207, http://dx.doi.org/10.1016/j.atmosenv.2005.02.022.

Ecohydrodynamic Model, 2016. Ecohydrodynamic Model. The Gulf of Gdańsk including the Vistula Lagoon. Inst. Oceanograph. Univ. Gdańsk. http://model.ocean.univ.gda.pl/ (accessed 05.11.16.).

Gajewski, L. (Ed.), 2010. Research of the Vistula Lagoon bottom (including the Elbląg Bay).Final Report. Rep. No. 334 by the Maritime Institute in Gdańsk for the Maritime Office in Gdynia, 1–96, (in Polish).

Geoportal, 2014. Geoportal, http://geoportal.gov.pl/, (accessed 2014).

Google Inc., 2014–2016. Google Earth computer software, (accessed 2014).

Grant, L., 1987. Diffuse and specular characteristics of leaf reflectance. Remote Sensing of Environment 22 (2), 309–322, http://dx.doi.org/10.1016/0034-4257(87)90064-2.

Haslam, S.M., 1973. Some aspects of the life history and autecology of *Phragmites communis* Trin. – A review. Pol. Arch. Hydrobiol. 20, 79–100.

Horppila, J., Nurminen, L., 2005. Effects of different macrophyte growth forms on sediment and P resuspension in a shallow lake. Hydrobiologia 545 (1), 167–175, http://dx.doi.org/10.1007/s10750-005-2677-9.

Huryna, H., Pokorny, J., 2016. The role of water and vegetation in the distribution of solar energy and local climate: A review. Folia Geobot. 51 (3), 191–208, http://dx.doi.org/10.1007/s12224-016-9261-0.

Kim, J., Verma, S.B., Billesbach, D.P., Clement, R.J., 1998. Diel variation in methane emission from a midlatitude prairie wetland: Significance of convective through flow in *Phragmites australis*. J. Geophys. Res. – Atmos. 103 (D21), 28029–28039, http://dx.doi.org/10.1029/98JD02441.

Kornijów, R., 2018. Ecosystem of the Polish part of the Vistula Lagoon from the perspective of alternative stable states concept, with implications for management issues. Oceanologia 60 (3), 1–15, http://dx.doi.org/10.1016/j.oceano.2018.02.004.

Kruk, M., Rychter, A., Mróz, M. (Eds.), 2012. The Vistula Lagoon. Environment and its research in the VISLA project. PWSZ, Elbląg, 1–178.

Kuehn, K.A., Suberkropp, K., 1998. Diel fluctuations in rates of CO_2 evolution from standing dead leaf litter of the emergent macrophyte *Juncus effusus*. Aquat. Microbial Ecol. 14 (2), 171–182, http://dx.doi.org/10.3354/ame014171.

Kuehn, K.A., Lemke, M.J., Suberkropp, K., Wetzel, R.G., 2000. Microbial biomass and production associated with decaying leaf litter of the emergent macrophyte *Juncus effusus*. Limnol. Oceanogr. 45 (4), 862–870, http://dx.doi.org/10.4319/lo.2000.45.4.0862.

Latała, A., 1978. Chlorophyll concentration in the waters of the Vistula Lagoon. Stud. Mater. Oceanol. 4 (21), 81–94, (in Polish).

Lelong, B., Lavoie, C., Jodoin, Y., Belzile, F., 2007. Expansion pathways of the exotic common reed (*Phragmites australis*): A historical and genetic analysis. Divers. Distrib. 13 (4), 430–437, http://dx.doi.org/10.1111/j.1472-4642.2007.00351.x.

McCree, K.J., 1981. Photosynthetically active radiation. In: Lange, O.L., Nobel, P.S., Osmond, C.B., Ziegler, H. (Eds.), Physiological plant ecology I. Encyclopedia of plant physiology (New Series) 12/A. Springer, Berlin, Heidelberg, 41–55, http://dx.doi.org/10.1007/978-3-642-68090-8_3.

McGlathery, K.J., Sundback, K., Anderson, I.C., 2007. Eutrophication in shallow coastal bays and lagoons: The role of plants in the coastal filter. Mari. Ecol. Progr. Ser. 348, 1–18, http://dx.doi.org/10.3354/meps07132.

Meyerson, L.A., Saltonstall, K., Windham, L., Kiviat, E., Findlay, S.A., 2000. A comparison of *Phragmites australis* in freshwater and brackish marsh environments in North America. Wetl. Ecol. Manag. 8 (2–3), 89–103, http://dx.doi.org/10.1023/A:1008432200133.

Miranda, L.E., Driscoll, M.P., Allen, M.S., 2000. Transient physicochemical microhabitats facilitate fish survival in inhospitable aquatic plant stands. Freshwater Biol. 44 (4), 617–628, http://dx.doi.org/10.1046/j.1365-2427.2000.00606.x.

Mitsch, W.J., Bernal, B., Nahlik, A.M., Mander, Ü., Zhang, L., Anderson, L., Jørgensen, S.E., Brix, H., 2013. Wetlands, carbon, and climate change. Landscape Ecol. 28 (4), 583–597, http://dx.doi.org/10.1007/s10980-012-9758-8.

Moller, I., Mantilla-Contreras, J., Spencer, T., Hayes, A., 2011. Microtidal coastal reed beds: Hydro-morphological insights and observations on wave transformation from the southern Baltic Sea. Estuar. Coastal Shelf Sci. 92 (3), 424–436, http://dx.doi.org/10.1016/j.ecss.2011.01.016.

Moller, C.L., Sand-Jensen, K., 2012. Rapid oxygen exchange across the leaves of *Littorella uniflora* provides tolerance to sediment anoxia. Freshwater Biol. 57 (9), 1875–1883, http://dx.doi.org/10.1111/j.1365-2427.2012.02849.x.

Nawrocka, L., Kobos, J., 2011. The trophic state of the Vistula Lagoon: An assessment based on selected biotic and abiotic parameters according to the Water Framework Directive. Oceanologia 53 (3), 881–894, http://dx.doi.org/10.5697/oc.53-3.881.

Odum, E.P., 1971. Fundamentals of ecology. W.B. Saunders Co., Philadelphia, London, Toronto, 1–574.

Olsson, L., Ye, S., Yu, X., Wei, M., Krauss, K.W., Brix, H., 2015. Factors influencing CO_2 and CH_4 emissions from coastal wetlands in the Liaohe Delta, Northeast China. Biogeosciences 12 (16), 4965—4977, http://dx.doi.org/10.5194/bg-12-4965-2015.

Ondok, J.P., 1973. Some basic concepts of modeling freshwater littoral ecosystems with respect to radiation regime of a pure *Phragmites* stand. Pol. Arch. Hydrobiol. 20 (1), 101—109.

Perez-Ruzafa, A., Marcos, C., Perez-Ruzafa, I.M., Perez-Marcos, M., 2011. Coastal lagoons: "Transitional ecosystems" between transitional and coastal waters. J. Coast. Conserv. 15 (3), 369—392, http://dx.doi.org/10.1007/s11852-010-0095-2.

Pliński, M., Simm, A., 1978. Seasonal fluctuations in the composition, distribution and quantity of phytoplankton in the Vistula Lagoon in 1974 and 1975. Stud. Mater. Oceanol. 4 (21), 53—80.

Próchnicki, P., 2005. The expansion of common reed (*Phragmites australis* (Cav.) Trin. ex Steud.) in the anastomosing river valley after cessation of agriculture use (Narew River Valley, NE Poland). Pol. J. Ecol. 53 (3), 353—364.

Renk, H., Ochocki, S., Zalewski, M., Chmielowski, H., 2001. Environmental factors controlling primary production in the Polish part of the Vistula Lagoon. Bull. Sea Fish. Inst. 1 (152), 77—95.

Ringer, Z., 1959. An attempt to estimate the biomass of the littoral flora of the Vistula Lagoon based on the studies carried out in 1955. Prace Morskiego Instytutu Rybackiego w Gdyni 10 (A), 193—214.

Różańska, Z., Więcławski, F., 1978. Study of environmental factors of the Vistula Lagoon under human pressure. Studia Mat. Oceanol., Biologia Morza 4 (21), 9—36, (in Polish).

Rupprecht, F., Moller, I., Paul, M., Kudella, M., Spencer, T., Van Wesenbeeck, B.K., Wolters, G., Jensen, K., Bouma, T.J., Miranda-Lange, M., Schimmels, S., 2017. Vegetation—wave interactions in salt marshes under storm surge conditions. Ecol. Eng. 100, 301—315, http://dx.doi.org/10.1016/j.ecoleng.2016.12.030.

Scheffer, M., Hosper, S.H., Meijer, M.L., Moss, B., Jeppesen, E., 1993. Alternative equilibria in shallow lakes. Trends Ecol. Evol. 8 (8), 275—279, http://dx.doi.org/10.1016/0169-5347(93)90254-M.

Sokal, R.I., Rohlf, J., 1995. Biometry: The principle and practice of statistics in biological research. Freeman & Co, New York, 1—887.

StatSoft Inc., 2011. STATISTICA (data analysis software system), version 10. Available from www.statsoft.com.

Szarejko-Łukaszewicz, D., 1959. Hydrographic research on the Vistula Lagoon in 1953—1954. Prace Morskiego Instytutu Rybackiego w Gdyni 10 (A), 215—228, (in Polish).

Viaroli, P., Bartoli, M., Bondavalli, C., Christian, R.R., Giordani, G., Naldi, M., 1996. Macrophyte communities and their impact on benthic fluxes of oxygen, sulphide and nutrients in shallow eutrophic environments. Hydrobiologia 329 (1—3), 105—119, http://dx.doi.org/10.1007/BF00034551.

Viaroli, P., Bartoli, M., Giordani, G., Naldi, M., Orfanidis, S., Zaldivar, J.M., 2008. Community shifts, alternative stable states, biogeochemical controls and feedbacks in eutrophic coastal lagoons: A brief overview. Aquat. Conserv. 18 (S1), 105—117, http://dx.doi.org/10.1002/aqc.956.

Warren, R.S., Fell, P.E., Grimsby, J.L., Buck, E.L., Rilling, G.C., Fertik, R.A., 2001. Rates, patterns, and impacts of *Phragmites australis* expansion and effects of experimental Phragmites control on vegetation, macroinvertebrates, and fish within tidelands of the lower Connecticut River. Estuaries 24 (1), 90—107, http://dx.doi.org/10.2307/1352816.

Weisner, S.E.B., 1991. Within-lake patterns in depth penetration of emergent vegetation. Freshwater Biol. 26 (1), 133—142, http://dx.doi.org/10.1111/j.1365-2427.1991.tb00515.x.

Wetzel, R.G., Hough, R.A., 1973. Productivity and role of aquatic macrophytes in lakes: An assessment. Polish Archive of Hydrobiology 20, 9—19.

Yandex, 2014. Yandex — Maps, https://www.yandex.ru/maps/, (accessed 2014).

Zachowicz, J., Uścinowicz, Sz., Anolik, P., Zaleszkiewicz, L., Krzymińska, J., Jegliński, W., 1995. Geological survey of the Vistula Lagoon area. Archiwum OGM, PIG, Gdańsk, (in Polish).

Żmudziński, L., Szarejko, D., 1955. Hydrographic and biological studies of the Vistula Lagoon. Prace Morskiego Instytutu Rybackiego w Gdyni 8, 284—312, (in Polish).

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3. pobieraniu materiałów i przeprowadzaniu pomiarów w terenie,
4. przeprowadzeniu analiz granulometrycznych osadu oraz zawartości materii organicznej w osadach,
5. opracowaniu danych, przeprowadzeniu analiz statystycznych i wizualizacji wyników,
6. napisaniu tekstu, przygotowaniu manuskryptu do druku,
7. przeprowadzenia procesu korekty po recenzjach i przedkładania pracy do druku (autor korespondencyjny).

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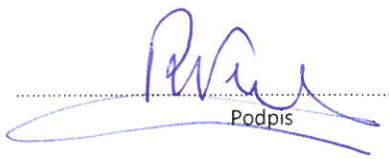
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ORIGINAL RESEARCH ARTICLE

Distribution of benthic macroinvertebrates across a reed stand in a brackish Baltic lagoon

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Abstract The role of reeds in the functioning of ecosystems and their significance for zoobenthos in the coastal lagoons is poorly understood. We hypothesise that next to the spatial zonal differentiation of abiotic factors in the apparently homogeneous habitat of reeds, benthic macroinvertebrate fauna is also unevenly distributed, and differs in taxonomic and functional diversity, as well as density and biomass across the reed stand. The research was carried out in the Vistula Lagoon (southern Baltic) along three designated sectors arranged parallel to the shoreline and differing in distance from the shore and depth. Mean density of reed stems in the analysed stand was within the range of values reported from different American and European wetlands. Regardless of the location within the reeds and the season, the fauna was dominated by detritivorous Tubificinae and larvae of Chironomidae. The highest diversity, density, and biomass of fauna were found in the middle littoral zone, and the lowest in the outer zone adjacent to the open water. The presented data support our hypothesis predicting the existence of a spatial variation pattern in the composition and distribution of macroinvertebrates in response to the changing zonal habitat conditions within the reed stand.
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1. Introduction

Common reed, *Phragmites australis* (Cav.) Trin. ex Steud, is believed to be one of the most widespread riparian plants in a wide range of wetland habitats worldwide. Although the common reed is considered a freshwater species (Ostendorp, 1993), it is well adapted to brackish water conditions (Karstens et al., 2019; Lissner and Schierup, 1997). The plant is considered native to Europe. Beyond the continent, it is often treated as an invasive species (Swearingen and Saltonstall, 2012). There-

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fore, depending on where the reed occurs, its environmental significance and role in wetland vegetation communities may be perceived differently (Gabriel and Bodensteiner, 2011). European literature emphasises the multiple ecosystem functions and services of reeds (Karstens et al., 2019; Mancinelli et al., 2005; Okun and Mehner, 2005; Pawlikowski and Kornijów, 2019). They constitute feeding and breeding places, shape habitat conditions, and determine sediment and water quality for animals and other plants. They also play a role in matter circulation, damp wave energy, and stabilise bottom sediments and banks. In countries where the reed has emerged as an invasive species, particularly in disturbed habitats, its rapid rate of colonisation and tendency to replace other plant and animal species is often considered a nuisance, negatively affecting local biodiversity (Gabriel and Bodensteiner, 2011; Warren et al., 2001). In both cases, however, although for a different reason, it is important to know the role of reeds in the functioning of ecosystems and their significance as a habitat for other organisms. As pointed out by Ostendorp (1993), the latter issue is barely investigated. This is especially true of benthic macroinvertebrates living in sediments overgrown by reeds. One of the reasons could be methodological difficulties in sampling bottom sediments among the tangle of roots and rhizomes (Moss, 1998). The most frequently used methods of sampling include sweeping by hand nets, or collecting a littoral section together with sediments and macrophytes by means of e.g. Surber, Wisconsin, Macan, or Ekman box-samplers (Arnold and Ormerod, 1997; Fell et al., 1998; James et al., 1998; Jayawardana et al., 2006; Jayawardana and Westbrooke, 2010; Miler et al., 2018; Olson et al., 1995; Sychra et al., 2010). Various types of traps are also sometimes used (Fell et al., 1998; Oertli, 1995; Raichel et al., 2003). While such studies provide valuable insight into the general diversity of macroinvertebrates within a stand, they do not reflect the real distribution and quantitative proportions between various invertebrate communities with their distinctive feeding behaviour and diet, such as sediment-living, plant-associated, and free-swimming animals (Moss, 1998). Consequently, such data offer little information on the relationships and drivers that potentially structure truly benthic communities, i.e. those inhabiting bottom sediments. Moreover, the use of different sampling approaches makes it difficult to compare results and draw general conclusions.

Only several papers employ quantitative methods that take into account selective sampling of sediments and, importantly, sampling to a known depth (Cardinale et al., 1998; Kornijów and Gulati, 1992; Okun and Mehner, 2005; Yozzo and Osgood, 2013). These publications focus on benthic invertebrates in reed beds of lakes or rivers. Coastal wetlands have not yet been subject to similar research. The purpose of this work is to fill this gap, and to find a pattern in the distribution of benthic macroinvertebrates within the reed stand.

The structure and processes in lagoon environments are primarily maintained by physical forces, including wave action that can be mediated by dense patches of emergent macrophytes such as reeds (Karstens et al., 2019; Kornijów, 2018; Pawlikowski and Kornijów, 2019; Perez-Ruzafa et al., 2011; Viaroli et al., 1996). This can lead to a spatial gradient of organic matter content in the sediments, and through the consumption of oxygen in decaying processes, also of water oxygenation. The research on abiotic factors in the reeds of the Vistula Lagoon in fact showed low oxygenation of water in the near-shore zone compared to the middle and peripheral part of the patch, adjacent to the open water zone. On the one hand, that was most likely due to the horizontal distribution of sediment organic matter, and on the other hand due to a different rate of water exchange with the pelagic zone (Pawlikowski and Kornijów, 2019). Similar horizontal zonation of oxygen conditions, and other physical and chemical properties of water or sediment, such as pH or salinity within stands of emergent vegetation, were found in various aquatic ecosystems. This suggests the universal character of the phenomenon (Dvorak, 1970; Howard-Williams and Lenton, 1975; Kłosowski, 1992; Suzuki et al., 1995). However, there are exceptions, e.g. water throughout the stand of emergent vegetation in Lake Huron was typically supersaturated with dissolved oxygen, and there was never any evidence of anoxia (Cardinale et al., 1997).

It can be assumed that due to the spatial zonal differentiation of abiotic factors in the apparently homogeneous habitat of reeds, also benthic macroinvertebrate fauna is not evenly distributed, and differs across the reed stand in terms of taxonomy and functional diversity, as well as density and biomass. In order to verify this hypothesis, we carried out seasonal research in the Vistula Lagoon — one of the most important and well-known ecosystems in the southern Baltic coast with extensive reed beds (Karstens et al., 2019).

2. Material and methods

2.1. Study site

The Vistula Lagoon is a brackish coastal lagoon adjacent to the Gulf of Gdansk of the Baltic Sea. The lagoon has a surface area of 838 km^2, including 328 km^2 on the Polish side of the border. The Vistula Lagoon is shallow, with a depth not exceeding 5.2 m in the Russian, and 4 m in the Polish part. The hydrological dynamics of the waters of the lagoon are determined by the inflow of freshwater masses from its extensive catchment area, mixed with salty water inflowing from the Gulf of Gdańsk through the Baltiysk Strait. Salinity varies from 0 to 6.5 PSU. No tides occur, although wind action causes daily water level fluctuations reaching 1 m. The concentrations of total nitrogen and phosphorus in water are high, reaching 1.1—4.4 mg dm^{-3} and 0.06—0.19 mg dm^{-3}, respectively. The most frequently recorded water transparency, measured as Secchi disc depth, fluctuates around 40 cm (Kornijów, 2018). Bottom sediments are primarily composed of silt and sand (Zachowicz, 1985). The lagoon is very productive, with advanced eutrophic processes (Kownacka et al., 2020). It is influenced by both maritime and continental climates, with ice cover persisting for several days in mild winters, and from December until March in the coldest years (Herman, 2018).

The research was conducted in a reed patch with a length of 200 m and width of approximately 60 m (54.33360°N, 19.54700°E), located approximately 2 km north-east of the

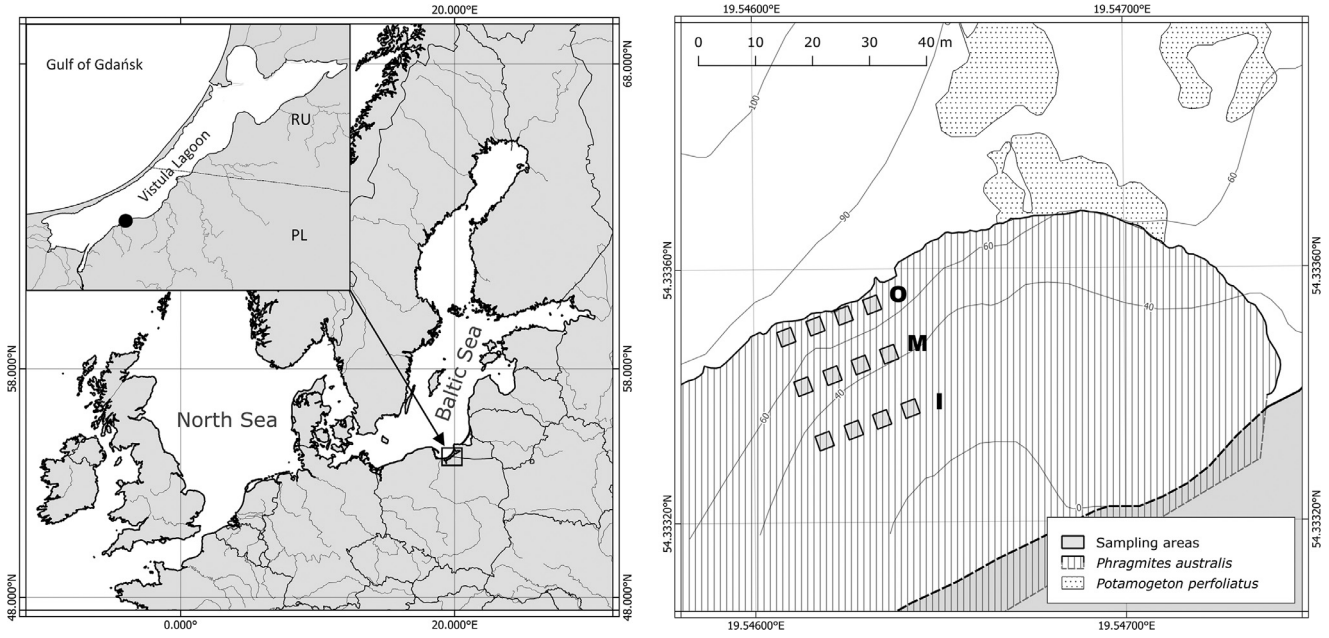


Figure 1 Location of the study area on the map of Northern Europe (left side, marked with a dot). On the right side — detailed map of the analysed reed stand in the Vistula Lagoon. Note that the coastline was drawn conventionally — its range varied as the water level changed. Depths are expressed in centimetres. I — inner zone, M — middle zone, O — outer zone. GIS layers sources for the map of Northern Europe: Europe coastline and rivers: Natural Earth (2020); Country borderlines: NOAA GSHHG (2014); Polish coastline: SIPAM (2020) simplified; Rivers of Vistula Lagoon catchment: OpenStreetMap (2021) modified; Coastline of the Russian part of the Vistula Lagoon: digitized scanned map from Domnin and Chubarenko (2008).

municipality of Tolkmicko at the southern shore of the lagoon (Figure 1). No local changes resulting from human activity such as shoreline alteration were recorded which could potentially interfere with the obtained results (Brauns et al., 2007; Miler et al., 2013). Growth of the macrophytes was seasonal, with regeneration from rhizomes after winter ice-scour. Seasonal changes in reed density involved a gradual increase in the number of stems during the vegetative season, lasting from April until October. The highest and spatially relatively even values of reed density (132—158 stems m^{-2}) in the analysed patch were observed in late summer (Pawlikowski and Kornijów, 2019).

Measurements of physico-chemical properties conducted in 2011 revealed no trends in salinity across the stand (Pawlikowski and Kornijów, 2019). Water oxygenation at the time was generally lower in the near-shore area than in the periphery adjacent to open water. The opposite pattern was observed for water temperature. Water level fluctuations were characterized by high dynamics, with an amplitude of approximately 40 cm (Pawlikowski and Kornijów, 2019).

2.2. Field survey and laboratory analyses

The study was conducted in spring (April), summer (August), and autumn (October) 2011. The width of the analysed reed stand exceeded 60 m, but the sampling area covered a much smaller strip (approx. 30 m wide) due to the shallow depth in the near-shore area and strong water fluctuations. Samples from the reed stand were collected along three designated sectors arranged parallel to the shoreline, at a distance of around 10 m from one another, differing in depth and distance from the shore, depending on geographic distribution and changing water level: inner (depth 0—40 cm, distance from the shore of approximately 30—40 m), middle (depth 40—60 cm, distance from the shore of 40—50 m), and outer (depth 60—90 cm, distance from the shore of 50—60 m) (Figure 1).

Four sampling locations, each of approximately 9 m^2 and spaced 3 m from one another, were established in each sector, referred to as zones. In each sampling location, 3 pooled sediment cores were collected by means of a transparent acrylic tube (length 1.5 m; diameter 4.4 cm) closed from the top with a stopper. In our opinion, the sampler used is appropriate not only for the sampling of sedentary invertebrates, but also for mobile gammarids, and even free-living mysids in turbid lagoon water (Linkowski et al., 2021). The tube was pushed into the bottom to a depth of 25 cm. No fauna occurred deeper in the sediment, as suggested by studies on the vertical distribution of macroinvertebrates in sediments (Pawlikowski and Kornijów, 2022). A total of 36 samples consisting of 108 sediment cores were collected on all sampling occasions. Each sample was washed separately through a net with 0.3 mm mesh size, and transported to the laboratory in plastic containers with no water. We chose such fine mesh to provide accurate community and population estimates given the relatively small size of macro-invertebrates living in estuarine and lagoon ecosystems (Schlacher and Wooldridge, 1996). Invertebrates were sorted live by hand on a white tray filled with water, and preserved with 4% formaldehyde solution. Oligochaeta were treated with Amman's lactophenol solution, and Chironomidae larvae with Faure liquid, and identified to the lowest possible taxon according to Timm (1999) and Andersen et al. (2013), respectively. The nomenclature of Naididae was adopted after

WoRMS (2021). Macrobenthic taxa were assigned to trophic groups based on food preferences documented in the literature (Armitage et al., 1995; Pellan et al. 2016; Savage, 1982; Vaughn, 1982). Categorisation of macroinvertebrates into groups allows a better understanding of the processes of the material cycle and ecosystem function (Cummins, 1973).

Measurements of reed density were carried out in 10 random 0.5 × 0.5 m quadrats within each location, expressed as the number of shoots per square meter and averaged (Pawlikowski and Kornijów, 2019).

Granulometric analyses involved the collection of additional sediment cores with a length of 25 cm in each sampling location in August. The collected sediments were dried and manually ground in a mortar, and then sieved on a set of geological sieves with a mesh of 2 mm, 1 mm, 0.5 mm, 0.25 mm, 0.125 mm, and 0.063 mm. The obtained data were processed with the application of GRADISTAT software version 8 (Blott and Pye, 2001). Organic matter content in sediment was determined by the direct method as a mass loss on ignition (LOI) at a temperature of 500°C for 24 hours.

Bathymetric measurements were performed by means of a ranging rod with an accuracy of 1 cm on 2014.09.04. Depth was measured in 154 points with geographic coordinates determined by means of a GPS receiver (Garmin GPSMAP 60CSx). The memory of the receiver also recorded the course of the shoreline (zero depth). The data matrix was loaded to Surfer 10 software in which a detailed bathymetric map of the studied water body was generated by means of the kriging method. The map was then visually processed by means of QGIS software (Figure 1).

Due to unequal variances or non-normal distribution, the following non-parametric statistics were applied:

- Kruskal-Wallis test (H) was applied for the determination of the effect of different locations within the reed patch on the density and biomass of fauna.
- Friedman test (Chi-Square) was applied for the determination of differences in the density and biomass of fauna between sampling occasions.

T-test was applied for the determination of differences in the density of fauna between 2011 and 2013. For this comparison, we used data from 2013 in zone M on the vertical distribution of macroinvertebrates in sediments (Pawlikowski and Kornijów, 2022), obtained in a similar way as in 2011. Statistical calculations were performed by means of Statistica 10 software (StatSoft, 2011).

3. Results

3.1. Zoobenthos

The material showed the presence of 31 taxa belonging to Chironomidae, Naididae, Hirudinea, Chrysomelidae, Amphipoda, Bivalvia, and Nematoda (Table 1). The highest diversity (24 taxa) was determined in the middle littoral zone, and lowest in the outer zone (16 taxa), adjacent to open water. Depending on the season, the diversity of fauna considerably changed in the middle and outer zones and was relatively stable in the inner zone (Figure 2).

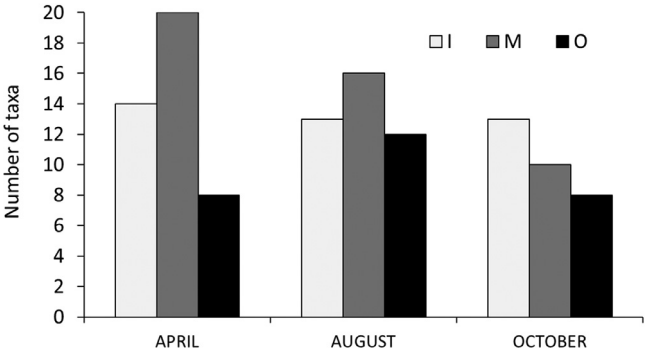


Figure 2 Number of zoobenthos taxa in the inner (I), middle (M), and outer zone (O) of the reed stand in the Vistula Lagoon.

The highest total density of fauna was reached in spring and summer in the middle zone (12 057—15 510 ind. m^{-2}), and lowest, irrespective of the season in the outer zone (4 165—4 658 ind. m^{-2}) (Kruskal-Wallis test H (n = 12) = 6.06 and 7.38; p = 0.04 and 0.02, respectively) (Figure 3). Differences in total density between the zones in autumn were at the threshold of significance (Kruskal-Wallis test H (n = 12) = 5.80; p = 0.06).

Biomass values in spring and autumn were the highest in the middle littoral zone (42—107 g ww m^{-2}), and lowest in the outer zone (8—10 g ww m^{-2}) (Kruskal-Wallis test H (n = 12) = 7.73 and 6.73; p = 0.02 and 0.03, respectively). In summer, differences in biomass between the zones were at the threshold of significance (Kruskal-Wallis test H (n = 12) = 5.54; p = 0.06) (Figure 3).

In terms of percent share, irrespective of the location within the reed stand (with the exception of the middle and outer zone in April), Tubificinae usually dominated (46—79%), and among them particularly *Limnodrilus hoffmeisteri* (Figure 4, Table 1). The second group with the most considerable share were Chironomidae (15—76%) larvae with dominant *Glyptotendipes* sp. (Figure 4, Table 1). The proportions of percent shares between the most abundant taxa varied in particular seasons with no discernible patterns.

Next to Chironomidae and Tubificinae (2—51% and 10—73%, respectively), the biomass contained a high share of Chrysomelidae (*Donacia* sp.) (up to 60%) and Amphipoda (1—42%) (Figure 4). Their contribution varied depending on the study term: in April, the majority of sites were dominated by larvae of *Donacia* sp. (up to 60%) and Chironomidae (22—51%), in August Tubificinae (48—73%) and *Donacia* sp. (23—30%), and in October Amphipoda (up to 42%) and Tubificinae (37—56%).

A large majority of the recorded taxa belonged to detritivores, constituting more than 58% of the fauna abundance (Table 1, Figure 5). The second major trophic group were omnivores constituting up to 34% of the fauna abundance. The percent share of particular trophic groups varied depending on the season and zone. A considerable share of herbivores was observed in spring in the middle zone, and a clear increase in omnivores in summer and autumn in the middle and outer zones.

For the purpose of verification of the stability of benthic communities in the reed belt, their abundances were compared in zone M in 2011 and 2013 (Figure 6). In the second year of the study, the density of zoobenthos was more than

Table 1 Density [ind. m^{-2}] of zoobenthos in the inner (I), middle (M), and outer (O) zones of the reed stand in the Vistula Lagoon in 2011. DETR – detritivores, CARN – carnivores, HERB – herbivores, OMNI – omnivores, n. d. – not determined. Mean values ± SE (Standard Error).

	Taxa	Trophic group	I	M	O
NAIDIDAE					
TUBIFICINAE					
	n. det. without hair chaetae (juvenile or damaged), probably *Limnodrilus* sp.	DETR	3 416 ± 591	5 974 ± 1 463	1 206 ± 346
	n. det. with hair chaetae (juvenile or damaged), probably: *Tubifex* sp., *Potamothrix* sp., *Psammoryctides* sp.	DETR	786 ± 397	877 ± 124	55 ± 39
	Tubifex tubifex (Müller)	DETR	219 ± 127	110 ± 63	0 ± 0
	Limnodrilus hoffmeisteri Clapar.	DETR	1 151 ± 443	347 ± 103	420 ± 116
	Limnodrilus claparedeianus Ratz.	DETR	365 ± 199	512 ± 228	18 ± 18
	Limnodrilus profundicola (Verill)	DETR	110 ± 50	128 ± 63	55 ± 39
	Limnodrilus udekemianus Claparède	DETR	37 ± 25	91 ± 74	0 ± 0
	Potamothrix hammoniensis (Mich.)	DETR	0 ± 0	37 ± 37	0 ± 0
	Potamothrix moldaviensis Vejd.	DETR	0 ± 0	55 ± 55	18 ± 18
	Potamothrix heuscheri (Bretscher)	DETR	18 ± 18	146 ± 87	0 ± 0
	Enchytraeidae n. det.	DETR	0 ± 0	37 ± 37	0 ± 0
NAIDINAE					
	Naidinae n. det.	HERB	0 ± 0	18 ± 18	0 ± 0
TOTAL Naididae			**6 102 ± 1 369**	**8 330 ± 1 652**	**1 772 ± 467**
CHIRONOMIDAE					
	Chironomus sp.	DETR	475 ± 117	183 ± 59	18 ± 18
	Glyptotendipes sp.	DETR	694 ± 134	2 503 ± 454	475 ± 299
	Dicrotendipes sp.	DETR	110 ± 43	91 ± 50	274 ± 90
	Polypedilum scalaneum (Schr.)	DETR	37 ± 25	37 ± 25	0 ± 0
	Cladotanytarsus mancus (Walker)	DETR	18 ± 18	347 ± 128	457 ± 305
	Microchironomus tener (Kieff.)	DETR	0 ± 0	0 ± 0	37 ± 25
	Endochironomus albipennis (Mg.)	DETR	0 ± 0	18 ± 18	0 ± 0
	Parachironomus varus (Goetgh.)	CARN	0 ± 0	0 ± 0	37 ± 37
	Cryptochironomus sp.	CARN	55 ± 29	292 ± 102	201 ± 69
	Procladius sp.	CARN	37 ± 25	73 ± 31	18 ± 18
	Orthocladiinae n. det.	HERB	0 ± 0	0 ± 0	18 ± 18

(*continued on next page*)

Table 1 (*continued*)

	Taxa	Trophic group	I	M	O
TOTAL Chironomidae			**1 425 ± 234**	**3 544 ± 536**	**1 535 ± 567**
CRUSTACEA, MALACOSTRACA					
	Gammaridae n. det. (probably: *G. tigrinus* and *G. duebeni*)	OMNI	201 ± 87	1 754 ± 370	1 005 ± 341
	Asellus sp.	DETR	0 ± 0	37 ± 25	0 ± 0
INSECTA, CHRYSOMELIDAE					
	Donacia sp.	HERB	183 ± 53	457 ± 227	37 ± 25
HIRUDINEA					
	Hirudinea n. det.	CARN	37 ± 37	0 ± 0	0 ± 0
BIVALVIA					
	Dreissena polymorpha (Pallas)	DETR	18 ± 18	37 ± 37	55 ± 39
OTHERS					
	Diptera larvae n. det.	n. d.	91 ± 57	55 ± 39	0 ± 0
	Nematoda n. det.	DETR	18 ± 18	37 ± 25	0 ± 0
TOTAL DENSITY			**8 075 ± 1 449**	**14 249 ± 1 449**	**4 403 ± 811**
NUMBER OF TAXA			**19**	**24**	**16**

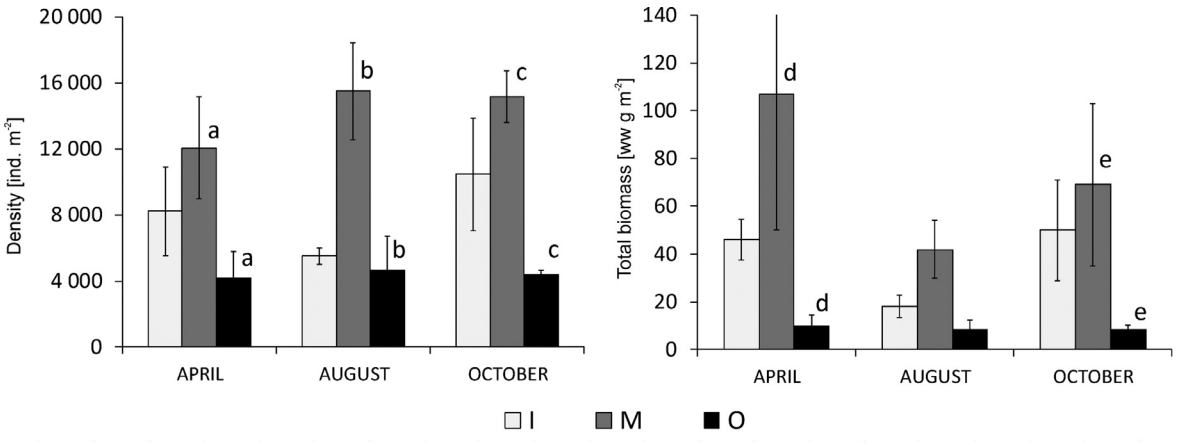


Figure 3 Density [ind. m^{-2}] and total biomass [ww g m^{-2}] of zoobenthos in the inner (I), middle (M), and outer zone (O) of the reed stand in the Vistula Lagoon. Small letters denote significant difference (Post-hoc Kruskal-Wallis test, $p < 0.05$) between areas marked with the same letter. No letter aside bar means no significant difference in density or biomass. Whiskers denote Standard Error.

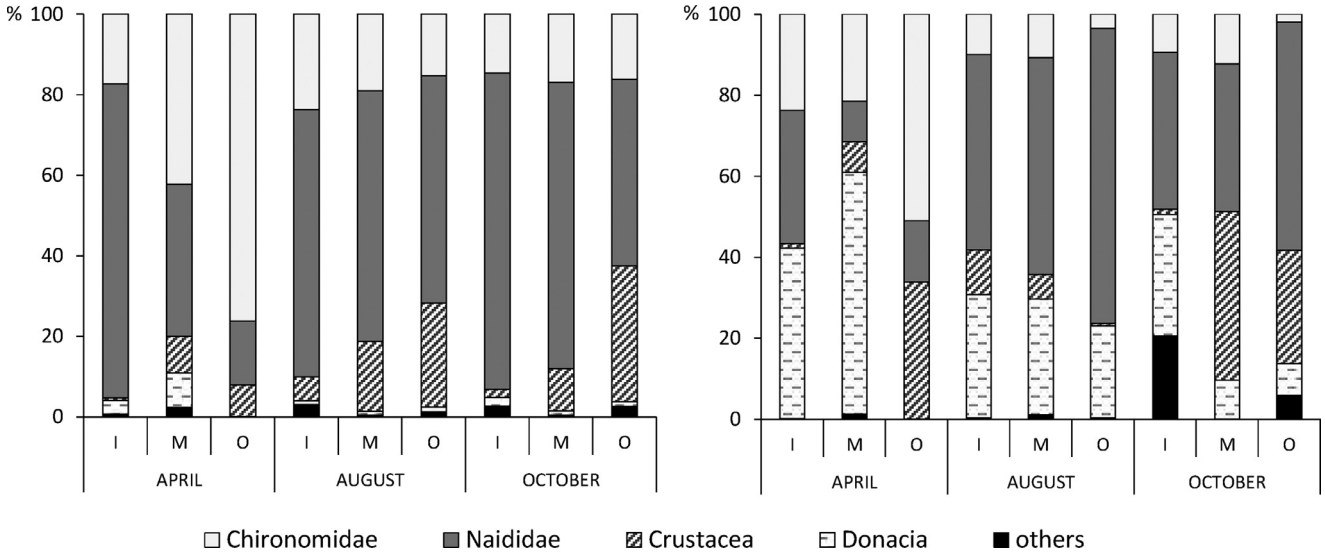


Figure 4 Percent share of the main groups of taxa in total density (left) and total biomass (right) of zoobenthos in the inner (I), middle (M), and outer zone (O) of the reed stand in the Vistula Lagoon.

twice higher (test $t = -3.12$; $p = 0.004$). The quantitative proportions between groups did not change, with evident dominance of Tubificinae and Chironomidae in both years.

3.2. Sediments

Reed grew on sandy-muddy sediments (textural group: slightly gravelly muddy sand) (Table 2). In the inner zone, fine muddy fractions were considerably more abundant (17.4%) than in the middle and outer zones located further from the shore (11.3% and 11.7%, respectively). A similar pattern was recorded in reference to the content of organic matter in the sediment (Table 2).

Table 2 Characteristics of sediments in the inner (I), middle (M), and outer (O) zones of the reed stand in the Vistula Lagoon. LOI — organic matter determined as loss on ignition.

	I	M	O
gravel	0.1%	0.3%	0.5%
sand	82.5%	88.4%	87.7%
mud	17.4%	11.3%	11.7%
LOI	3.1%	1.3%	1.1%

4. Discussion

The diversity of macroinvertebrates found in the lagoon's reed stand was much higher (31 taxa) than that in the open water central part of the lagoon, where only 6 taxa were reported (Kornijów et al., 2021b). It was, however, still much lower than in the littoral of freshwater ecosystems, where many other groups not found in the Vistula Lagoon inhabit the sediments, e.g. Odonata, Ephemeroptera, Trichoptera, Ceratopogonidae, and Gastropoda (Arnold and

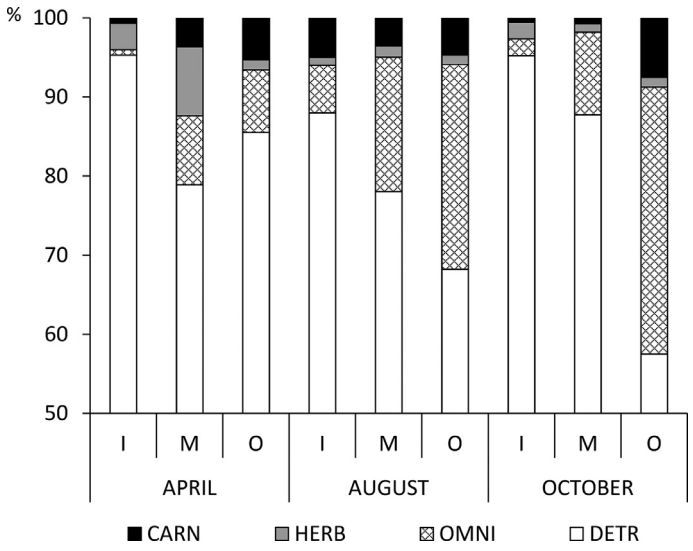


Figure 5 Percent share of particular trophic groups in the total abundance of zoobenthos in the inner (I), middle (M), and outer zone (O). DETR — detritivores, CARN — carnivores, HERB — herbivores, OMNI — omnivores. Note: Y-axis truncated to 50—100% range for clarity.

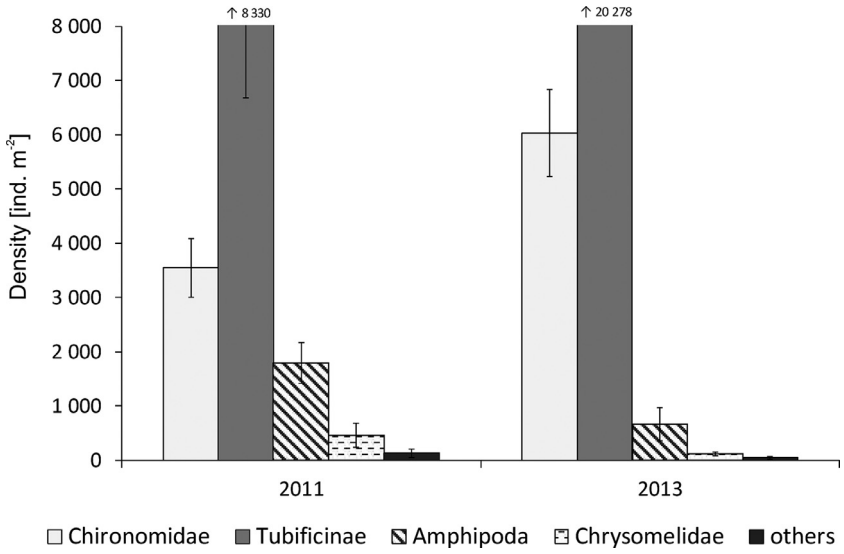


Figure 6 Density [ind. m^{-2}] of the most abundant groups of zoobenthos in the middle zone in 2011 and 2013. The values are means for three sampling occasions. Whiskers denote Standard Error.

Ormerod, 1997; Cardinale et al., 1998; James et al., 1998; Kornijów et al., 2010; Kornijów and Gulati, 1992; Sychra et al., 2010; Yozzo and Osgood, 2013). The reason for this might be elevated salinity which adversely affects some freshwater invertebrates (Arnold and Ormerod, 1997; Brucet et al., 2012; Kornijów et al., 2021a).

In both habitats of the lagoon, namely the littoral and open waters, Tubificinae and chironomid larvae showed the highest abundance. In the reed stand, Tubificinae were dominated by *L. hoffmeisteri*, like in the central part of the lagoon. *Potamothrix hammoniensis*, very abundant in the central part, barely marked its presence in the littoral. Among Chironomidae, the larvae of *Glyptotendipes* sp. were the most abundant in the littoral. As typical dwellers of sediments overgrown with vegetation (Kornijów and Gulati, 1992; Pinder, 1995), they were not present in the central lagoon, where chironomid larvae were instead dominated by *Chironomus balatonicus* Devai, Wuelker & Scholl (Kornijów et al., 2021b). Mean total density was comparable (2 806—16 269 ind. m^{-2} in the central part vs. 4 165—15 510 ind. m^{-2} in the reed stand). Functional feeding groups were dominated by detritus eaters in both habitats.

In the inner littoral zone, the highest densities were reached by a tubificid *L. hoffmeisteri* and *Chironomus* sp. larvae, known for tolerating oxygen deficits and coexisting under such conditions (Kornijów et al., 2021b). A significant percentage of omnivores (mainly *Gammarus* sp.) and herbivores also occurred. The latter were represented almost exclusively by larvae of the root-piercing beetle *Donacia* sp.

The mean density of reed stems in the analysed stand (132—158 stems m^{-2}) was within the mean range of values (60—250 stems m^{-2}) reported from different wetland European habitats (Haslam, 1973), and corresponded with the top determined values, e.g. in freshwater and brackish ecosystems of the North America (Meyerson et al., 2000). Although the reed zones designated in the Vistula Lagoon were separated by a short distance of approx. 10 m, they differed remarkably in terms of habitat conditions. It particularly concerned afternoon water oxygenation the values of which were proportional to the distance from the shoreline and ranged from 59% (5.4 mg dm^{-3}) to 109% (9.5 mg dm^{-3}) (Pawlikowski and Kornijów, 2019).

The relationship between the oxygen conditions and the diversity and density of bottom fauna, regardless of the type of aquatic environment, is a generally known pattern (Berezina and Golubkov, 2008; Jacobsen, 2020; Maasri et al., 2019; Verberk et al., 2011). It was also evident in our research. The highest diversity, density, and biomass were found in the middle zone, where oxygenation was clearly higher than in the inner near-shore zone. The exception was autumn, when the highest diversity was found in the inner zone. It can be assumed that at low water temperature and at plant density too low to impede water circulation, the oxygenation conditions could be aligned across the reed stand, and oxygenation might be no longer the structuring factor for the occurrence of some, at least less oxygen-demanding taxa (Warfe and Barmuta, 2004). A proportion of Amphipoda, known to be sensitive to hypoxia (Meijering, 1991), in the inner zone remained negligible in autumn. The larvae of *Donacia* sp. which rely on the plant for oxygen (Houlihan, 1969) showed the highest biomass in the inner and middle zones, regardless of the season.

Oxygen shortage can be partially compensated by the release of oxygen by macrophyte roots (Reddy et al., 1990; Sand-Jensen et al., 1982) that may support the development of some benthic macroinvertebrates (Sagova-Mareckova and Kvet, 2002). The process, however, was probably insufficient in the stand studied, particularly in summer under the conditions of increased temperature and drying out of the bottom.

A characteristic feature of the littoral of freshwater ecosystems with periodic hypoxia is the occurrence of a high number of invertebrates that respire atmospheric oxygen, such as pulmonate snails or beetles (Dvorak, 1970). They were, however, not present in the brackish waters of the Vistula Lagoon.

Temporary oxygen shortage in shallow coastal Baltic waters seems to be a common phenomenon not only in the reed stand. It can also be the result of the decomposition of drifting algal mats, leading to a strong depletion of benthic macrofauna (Berezina and Golubkov, 2008; Conley et al., 2011).

In the reed stand, a much higher content of organic matter in the sediments of the inner zone was not accompanied by the highest densities of all detritivores, with the exception of *L. hoffmeisteri* and *Chironomus* sp. The probable reason was the astatic nature of this habitat, associated with periodic drying, and the aforementioned strong fluctuations in oxygenation with periodic hypoxia, favoured by the elevated content of sediment organic matter, and limited water exchange with the open water (Cardinale et al., 1997; Dvorak, 1970; Pawlikowski and Kornijów, 2019).

According to Żbikowski et al. (2021), the occurrence and rate of growth of *L. hoffmeisteri* may be determined by the content of the sand fraction with a diameter of 60—160 μm in mud. Swallowed by worms, it may accelerate digestion and nutrient assimilation. Due to the different classification of sand grain size adopted in this paper, however, we could not verify this theory.

The relatively lowest total density and biomass, as well as the diversity of macroinvertebrates in the outer zone adjacent to the well-oxygenated open water, could have resulted from predation pressure by fish migrating here by day from the free water area in search for refugia from predators (Macneil et al., 1999; Okun et al., 2005). An additional factor might be the instability of the habitat conditions due to the strong and frequent wave action that could not damp by the vegetation sufficiently (Kairesalo, 1983). Interestingly, we found no pattern in terms of distribution of invertebrate predators, as previously pointed out by e.g. Dvorak (1970).

In conclusion, with some minor exceptions, the presented data support our hypothesis predicting the existence of a spatial variation pattern in the composition and distribution of macroinvertebrates in response to the changing zonal habitat conditions within the reed stand.

Our main research program lasted for one year. Therefore, in order to verify the long-term stability of the fauna composition, we repeated the research two years later in the middle zone (Pawlikowski and Kornijów, 2022). We recorded a more than double increase in density, but the proportions between the main faunal components did not change much. This suggests that while the density may fluctuate from year to year, the specificity of the assemblage composition remains relatively constant. Our results are generally in agreement with Cardinale et al. (1998), who claimed that distance from open water may be of primary importance for the spatial distributions of macroinvertebrates throughout coastal emergent vegetation.

Declaration of competing interest

The authors declare that they have no conflicts of interest.

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References

Andersen, T., Cranston, P.S., Epler, J.H., 2013. The larvae of Chironomidae (Diptera) of the Holarctic region — Keys and diagnoses. Insect Syst. Evol. Supplement 66, 573 pp.

Armitage, P.D., Cranston, P.S., Pinder, L.C.V., 1995. THE CHIRONOMIDAE. Biology and ecology of non-biting midges. Chapman and Hall, London-Madrid, 447 pp. https://doi.org/10.1007/978-94-011-0715-0.

Arnold, S.L., Ormerod, S.J., 1997. Aquatic macroinvertebrates and environmental gradients in *Phragmites* reedswamps: implications for conservation. Aquat. Conserv. 7 (2), 153—163. https://doi.org/10.1002/(SICI)1099-0755(199706)7:2⟨153::AID-AQC234⟩3.0.CO;2-E

Berezina, N.A., Golubkov, S.M., 2008. Effect of drifting macroalgae *Cladophora glomerata* on benthic community dynamics in the easternmost Baltic Sea. J. Marine Syst. 74, 80—85. https://doi.org/10.1016/j.jmarsys.2008.03.027

Blott, S.J., Pye, K., 2001. GRADISTAT: a grain size distribution and statistics package for the analysis of unconsolidated sediments. Earth Surf. Proc. Land. 26 (11), 1237—1248. https://doi.org/10.1002/esp.261

Brauns, M., Garcia, X.F., Walz, N., Pusch, M.T., 2007. Effects of human shoreline development on littoral macroinvertebrates in lowland lakes. J. Appl. Ecol. 44 (6), 1138—1144. https://doi.org/10.1111/j.1365-2664.2007.01376.x

Brucet, S., Boix, D., Nathansen, L.W., Quintana, X.D., Jensen, E., Balayla, D., Meerhoff, M., Jeppesen, E., 2012. Effects of temperature, salinity and fish in structuring the macroinvertebrate community in shallow lakes: Implications for effects of climate change. Plos One 7 (2), 1—11. https://doi.org/10.1371/journal.pone.0030877

Cardinale, B.J., Brady, V.J., Burton, T.M., 1998. Changes in the abundance and diversity of coastal wetland fauna from the open water/macrophyte edge towards shore. Wetl. Ecol. Manag. 6 (1), 59—68. https://doi.org/10.1023/a:1008447705647

Cardinale, B.J., Burton, T.M., Brady, V.J., 1997. The community dynamics of epiphytic midge larvae across the pelagic-littoral interface: do animals respond to changes in the abiotic environment? Can. J. Fish. Aquat. Sci. 54 (10), 2314—2322. https://doi.org/10.1139/cjfas-54-10-2314

Conley, D.J., Carstensen, J., Aigars, J., Axe, P., Bonsdorff, E., Eremina, T., Haahti, B.M., Humborg, C., Jonsson, P., Kotta, J., Lannegren, C., Larsson, U., Maximov, A., Medina, M.R., Lysiak-Pastuszak, E., Remeikaite-Nikiene, N., Walve, J., Wilhelms, S., Zillen, L., 2011. Hypoxia is increasing in the coastal zone of the Baltic Sea. Environ. Sci. Technol. 45, 6777—6783. https://doi.org/10.1021/es201212r

Cummins, K.W., 1973. Trophic relations of aquatic insects. Annu. Rev. Entomol. 18, 183—206. https://doi.org/10.1146/annurev.en.18.010173.001151

Domnin, D.A., Chubarenko, B.V., 2008. Watershed and administrative division of the Kaliningrad Oblast. In: Chubarenko, B. (Ed.), Transboundary waters and basins in the South-East Baltic. Terra Baltica, Russ. Acad. Sci., P.P. Shirshov Inst. Oceanol., Atlantic Branch, Kaliningrad, 306 pp.

Dvorak, J., 1970. Horizontal zonation of macrovegetation, water properties and macrofauna in a littoral stand of *Glyceria aquatic* (L.) Wahlb. in a pond in South Bohemia. Hydrobiologia 15, 17—30.

Fell, P.E., Weissbach, S.P., Jones, D.A., Fallon, M.A., Zeppieri, J.A., Faison, E.K., Lennon, K.A., Newberry, K.J., Reddington, L.K., 1998. Does invasion of oligohaline tidal marshes by reed grass, *Phragmites australis* (Cav) Trin ex Steud, affect the availability of prey resources for the mummichog, *Fundulus heteroclitus* L.? J. Exp. Mar. Biol. Ecol. 222 (1—2), 59—77. https://doi.org/10.1016/S0022-0981(97)00138-X

Gabriel, A.O., Bodensteiner, L.R., 2011. Ecosystem functions of mid-lake stands of common reed in Lake Poygan. Wisconsin. J. Freshw. Ecol. 26 (2), 217—229. https://doi.org/10.1080/02705060.2011.555202

Herman, A., 2018. The ice cover of the Vistula Lagoon. In: Bolałek, J. (Ed.), The Vistula Lagoon. PWN, Warsaw, 129—133 (in Polish).

Haslam, S.M., 1973. Some aspects of the life history and autecology of *Phragmites communis* Trin. — A review. Pol. Arch. Hydrobiol. 29 (1), 79—100.

Houlihan, D.F., 1969. Respiratory physiology of larva of *Donacia simplex*, a root-piercing beetle. J. Insect Physiol. 15 (9), 1517—1536. https://doi.org/10.1016/0022-1910(69)90173-5

Howard-Williams, C., Lenton, G.M., 1975. The role of the littoral zone in the functioning of a shallow tropical lake ecosystem. Freshw. Biol. 5 (5), 445—459. https://doi.org/10.1111/j.1365-2427.1975.tb00147.x

Jacobsen, D., 2020. The dilemma of altitudinal shifts: caught between high temperature and low oxygen. Front. Ecol. Environ. 18 (4), 211—218. https://doi.org/10.1002/fee.2161

James, M.R., Weatherhead, M., Stanger, C., Graynoth, E., 1998. Macroinvertebrate distribution in the littoral zone of Lake Coleridge, South Island, New Zealand — effects of habitat stability, wind exposure, and macrophytes. N. Z. J. Mar. Freshw. Res. 32 (2), 287—305. https://doi.org/10.1080/00288330.1998.9516826

Jayawardana, J.M.C.K., Westbrooke, M., 2010. Potential effects of riparian vegetation changes on functional organisation of macroinvertebrates in central Victorian streams. Vic. Nat. (Blackburn) 127 (2), 36—48.

Jayawardana, J.M.C.K., Westbrooke, M., Wilson, M., Hurst, C., 2006. Macroinvertebrate communities in *Phragmites australis* (Cav.) Trin. ex Steud. reed beds and open bank habitats in central Victorian streams in Australia. Hydrobiologia 568, 169—185. https://doi.org/10.1007/s10750-006-0103-6

Kairesalo, T., 1983. Dynamics of epiphytic communities on *Equisetum fluviatile* L. In: Wetzel, R.G. (Ed.), Periphiton of freshwater ecosystems, 17. Springer, Dordrecht, 153—160.

Karstens, S., Inacio, M., Schernewski, G., 2019. Expert-based evaluation of ecosystem service provision in coastal reed wetlands under different management regimes. Front. Environ. Sci. 7. https://doi.org/10.3389/fenvs.2019.00063

Kłosowski, S., 1992. Temporal and spatial variation of habitat conditions in the zonation of littoral plant communities. Aquat. Bot. 43 (2), 199—208. https://doi.org/10.1016/0304-3770(92)90043-I

Kornijów, R., 2018. Ecosystem of the Polish part of the Vistula Lagoon from the perspective of alternative stable states concept, with implications for management issues. Oceanologia 60 (3), 390—404. https://doi.org/10.1016/j.oceano.2018.02.004

Kornijów, R., Dukowska, M., Leszczynska, J., Smith, C., Jeppesen, E., Hansson, L.A., Ketola, M., Irvine, K., Noges, T., Sahuquillo, M., Miracle, M.R., Gross, E., Kairesalo, T., van Donk, E., de Eyto, E., Garcia-Criado, F., Grzybkowska, M., Moss, B., 2021a. Distribution patterns of epiphytic reed-associated macroinvertebrate communities across European shallow lakes. Sci. Total Environ. 760, 144117. https://doi.org/10.1016/j.scitotenv.2020.144117

Kornijów, R., Gulati, R.D., 1992. Macrofauna and its ecology in Lake Zwemlust, after biomanipulation. I. Bottom fauna. Arch. Hydrobiol. 123 (3), 337—347.

Kornijów, R., Pawlikowski, K., Błędzki, L.A., Drgas, A., Piwosz, K., Ameryk, A., Całkiewicz, J., 2021b. Co-occurrence and potential resource partitioning between oligochaetes and chironomid larvae in a sediment depth gradient. Aquat. Sci. 83 (51), 1—10. https://doi.org/10.1007/s00027-021-00800-z

Kornijów, R., Strayer, D.L., Caraco, N.F., 2010. Macroinvertebrate communities of hypoxic habitats created by an invasive plant (*Trapa natans*) in the freshwater tidal Hudson River. Fund. Appl. Limnol. 176 (3), 199—207. https://doi.org/10.1127/1863-9135/2010/0176-0199

Kownacka, J., Całkiewicz, J., Kornijów, R., 2020. A turning point in the development of phytoplankton in the Vistula Lagoon (southern Baltic Sea) at the beginning of the 21st century. Oceanologia 62 (4 Pt. A), 538—555. https://doi.org/10.1016/j.oceano.2020.08.004

Linkowski, T.B., Kornijów, R., Karpowicz, M., 2021. Comparison of three methods for nocturnal sampling of predatory zooplankters in shallow waters. Oceanologia 63 (1), 71—79. https://doi.org/10.1016/j.oceano.2020.10.001

Lissner, J., Schierup, H.H., 1997. Effects of salinity on the growth of *Phragmites australis*. Aquat. Bot. 55, 247—260. https://doi.org/10.1016/S0304-3770(96)01085-6

Maasri, A., Schechner, A.E., Erdenee, B., Dodds, W.K., Chandra, S., Gelhaus, J.K., Thorp, J.H., 2019. Does diel variation in oxygen influence taxonomic and functional diversity of stream macroinvertebrates? Freshw. Sci. 38 (4), 692—701. https://doi.org/10.1086/705916

Macneil, C., Dick, J.T.A., Elwood, R.W., 1999. The dynamics of predation on *Gammarus* spp. (Crustacea: Amphipoda). Biol. Rev. (Camb.) 74 (4), 375—395. https://doi.org/10.1017/S0006323199005368

Mancinelli, G., Sabetta, L., Basset, A., 2005. Short-term patch dynamics of macroinvertebrate colonization on decaying reed detritus in a Mediterranean lagoon (Lake Alimini Grande, Apulia, SE Italy). Mar. Biol. 148 (2), 271—283. https://doi.org/10.1007/s00227-005-0091-5

Meijering, M.P.D., 1991. Lack of oxygen and low pH as limiting factors for *Gammarus* in Hessian brooks and rivers. Hydrobiologia 223, 159—169. https://doi.org/10.1007/bf00047637

Meyerson, L.A., Saltonstall, K., Windham, L., Kiviat, E., Findlay, S.A., 2000. A comparison of *Phragmites australis* in freshwater and brackish marsh environments in North America. Wetl. Ecol. Manag. 8, 89—103. https://doi.org/10.1023/A:1008432200133

Miler, O., Czarnecka, M., Garcia, X.F., Jager, A., Pusch, M., 2018. Across-shore differences in lake benthic invertebrate communities within reed stands (*Phragmites australis* (Cav.) Trin. ex Steud.). Int. Rev. Hydrobiol. 103 (5-6), 99—112. https://doi.org/10.1002/iroh.201801955

Miler, O., Porst, G., McGoff, E., Pilotto, F., Donohue, L., Jurca, T., Solimini, A., Sandin, L., Irvine, K., Aroviita, J., Clarke, R., Pusch, M.T., 2013. Morphological alterations of lake shores in Europe: A multimetric ecological assessment approach using benthic macroinvertebrates. Ecol. Indic. 34, 398—410. https://doi.org/10.1016/j.ecolind.2013.06.002

Moss, B., 1998. Ecology of freshwaters. Man and medium, past to future, 3rd edn. Blackwell Science, Oxford, 572 pp.

Natural Earth, 2020. Natural Earth — Free vector and raster map data, https://www.naturalearthdata.com/ (access 2020.12.16).

NOAA GSHHG, 2014. Global self-consistent hierarchical high-resolution geography, https://www.ngdc.noaa.gov/mgg/shorelines/data/gshhg/latest/ (access 2014.12.30).

Oertli, B., 1995. Spatial and temporal distribution of the zoobenthos community in a woodland pond (Switzerland). Hydrobiologia 300, 195—204. https://doi.org/10.1007/Bf00024461

Okun, N., Lewin, W.C., Mehner, T., 2005. Top-down and bottom-up impacts of juvenile fish in a littoral reed stand. Freshw. Biol. 50 (5), 798—812. https://doi.org/10.1111/j.1365-2427.2005.01361.x

Okun, N., Mehner, T., 2005. Distribution and feeding of juvenile fish on invertebrates in littoral reed (*Phragmites*) stands. Ecol. Freshw. Fish. 14 (2), 139—149. https://doi.org/10.1111/j.1600-0633.2005.00087.x

Olson, E.J., Engstrom, E.S., Doeringsfeld, M.R., Bellig, R., 1995. Abundance and distribution of macroinvertebrates in relation to macrophyte communities in a prairie marsh, Swan-Lake, Minnesota. J. Freshw. Ecol. 10 (4), 325—335. https://doi.org/10.1080/02705060.1995.9663455

OpenStreetMap Contributors, 2021. OpenStreetMap — OpenTopoMap. Accessed by OSM plugin in QGIS.

Ostendorp, W., 1993. Reed bed characteristics and significance of reed in landscape ecology. In: Ostedorp, W., Krumsheid—Plankert, P. (Eds.), Lakeshore deterioration and restoration works in Central Europe. Fischer-Verlag, Stuttgart, 149—161.

Pawlikowski, K., Kornijów, R., 2019. Role of macrophytes in structuring littoral habitats in the Vistula Lagoon (southern Baltic Sea). Oceanologia 61 (1), 26—37. https://doi.org/10.1016/j.oceano.2018.05.003

Pawlikowski, K., Kornijów, R., 2022. Patterns of macroinvertebrates distribution in a sediment depth gradient in habitats dominated by emergent and submerged vegetation. Oceanologia Submitted for publication.

Pellan, L., Médoc, V., Renault, D., Spataro, T., Piscart, C., 2016. Feeding choice and predation pressure of two invasive gammarids, *Gammarus tigrinus and Dikerogammarus villosus*, under increasing temperature. Hydrobiologia 781, 43—54. https://doi.org/10.1007/s10750-015-2312-3

Perez-Ruzafa, A., Marcos, C., Perez-Ruzafa, I.M., Perez-Marcos, M., 2011. Coastal lagoons: "transitional ecosystems" between transitional and coastal waters. J. Coast. Conserv. 15 (3), 369—392. https://doi.org/10.1007/s11852-010-0095-2

Pinder, L.C.V., et al., 1995. The habitats of chironomid larvae. In: Armitage, P.S., et al. (Eds.), Chironomidae: biology and ecology of non-biting midges. Chapman & Hall, London, 107—135.

Raichel, D.L., Able, K.W., Hartman, J.M., 2003. The influence of *Phragmites* (common reed) on the distribution, abundance, and potential prey of a resident marsh fish in the Hackensack Meadowlands, New Jersey. Estuaries 26 (2b), 511—521. https://doi.org/10.1007/Bf02823727

Reddy, K.R., Dangelo, E.M., Debusk, T.A., 1990. Oxygen transport through aquatic macrophytes — the role in waste-water treatment. J. Environ. Qual. 19 (2), 261—267. https://doi.org/10.2134/jeq1990.00472425001900020011x

Sagova-Mareckova, M., Kvet, J., 2002. Impact of oxygen released by the roots of aquatic macrophytes on composition and distribution of benthic macroinvertebrates in a mesocosm experiment. Arch. Hydrobiol. 155 (4), 567—584.

Sand-Jensen, K., Prahl, C., Stokholm, H., 1982. Oxygen release from roots of submersed aquatic macrophytes. Oikos 38 (3), 349—354. https://doi.org/10.2307/3544675

Savage, A.A., 1982. The survival and growth of *Gammarus tigrinus* Sexton (Crustacea: Amphipoda) in relation to salinity and temperature. Hydrobiologia 94 (3), 201—212.

Schlacher, T.A., Wooldridge, T.H., 1996. How sieve mesh size affects sample estimates of estuarine benthic macrofauna. J. Exp. Mar. Biol. Ecol. 201, 159—171. https://doi.org/10.1016/0022-0981(95)00198-0

SIPAM, 2020. System informacji przestrzennej administracji morskiej. https://sipam.gov.pl/

StatSoft, 2011. Statistica software version 10. StatSoft Inc., http://www.statsoft.com

Suzuki, N., Endoh, S., Kawashima, M., Itakura, Y., McNabb, C.D., D'Itri, F.M., Batterson, T.R., 1995. Discontinuity bar in a wet land of Lake Huron's Saginaw Bay. J. Freshwater Ecol. 10 (2), 111—123.

Swearingen, J., Saltonstall, K., 2012. *Phragmites* field guide: distinguishing native and exotic forms of common reed (*Phragmites australis*) in the United States. USDA — Natural Resources Conservation Service Boise, TN Plant Materials NO 56 , Idaho. https://www.nrcs.usda.gov/Internet/FSE_PLANTMATERIALS/publications/idpmctn11494.pdf

Sychra, J., Adamek, Z., Petrivalska, K., 2010. Distribution and diversity of littoral macroinvertebrates within extensive reed beds

of a lowland pond. Ann. Limnol. - Int. J. Lim. 46 (4), 281—289. https://doi.org/10.1051/limn/2010026

Timm, T., 1999. A guide to the Estonian Annelida. Estonian Academy Publishers, Tallinn, 208 pp.

Vaughn, C.C., 1982. Distribution of Chironomids in the littoral-zone of Lake Texoma, Oklahoma and Texas. Hydrobiologia 89 (2), 177—188. https://doi.org/10.1007/Bf00006170

Verberk, W., Bilton, D.T., Calosi, P., Spicer, J.I., 2011. Oxygen supply in aquatic ectotherms: Partial pressure and solubility together explain biodiversity and size patterns. Ecology 92 (8), 1565—1572. https://doi.org/10.1890/10-2369.1

Viaroli, P., Bartoli, M., Bondavalli, C., Christian, R.R., Giordani, G., Naldi, M., 1996. Macrophyte communities and their impact on benthic fluxes of oxygen, sulphide and nutrients in shallow eutrophic environments. Hydrobiologia 329 (1—3), 105—119. https://doi.org/10.1007/Bf00034551

Warfe, D.M., Barmuta, L.A., 2004. Habitat structural complexity mediates the foraging success of multiple predator species. Oecologia 141 (1), 171—178. https://doi.org/10.1007/s00442-004-1644-x

Warren, R.S., Fell, P.E., Grimsby, J.L., Buck, E.L., Rilling, G.C., Fertik, R.A., 2001. Rates, patterns, and impacts of *Phragmites australis* expansion and effects of experimental *Phragmites* control on vegetation, macroinvertebrates, and fish within tidelands of the lower Connecticut River. Estuaries 24 (1), 90—107. https://doi.org/10.2307/1352816

WoRMS Editorial Board, 2021. World Register of Marine Species. VLIZ. Available from https://doi.org/10.14284/170

Yozzo, D.J., Osgood, D.T., 2013. Invertebrate communities of low-salinity wetlands: overview and comparison between *Phragmites* and *Typha* marshes within the Hudson River Estuary. Estuar. Coast. 36 (3), 575—584. https://doi.org/10.1007/s12237-012-9543-6

Zachowicz, I.M., 1985. From biostratigraphical studies of sediments from the Vistula Lagoon. Petrobalticum 3, 97—111 (in Polish).

Żbikowski, J., Żbikowska, E., Kobak, J., 2021. The presence of fine sand in the muddy sediments affects habitat selection and accelerates the growth rate of *Limnodrilus hoffmeisteri* and *Limnodrilus claparedianus* (Oligochaeta). Hydrobiologia 848 (11), 2761—2771. https://doi.org/10.1007/s10750-021-04595-w

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2. współudziale w opracowaniu metodyki badań,
3. pobieraniu materiałów w terenie,
4. wykonaniu oznaczeń taksonomicznych makrozoobentosu (w szczególności Oligochaeta),
5. przeprowadzeniu analiz granulometrycznych osadu,
6. opracowaniu danych, przeprowadzeniu analiz statystycznych i wizualizacji wyników,
7. napisaniu tekstu, przygotowaniu manuskryptu do druku,
8. przeprowadzenia procesu korekty po recenzjach i przedkładania pracy do druku (autor korespondencyjny).

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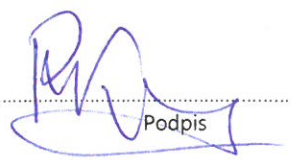
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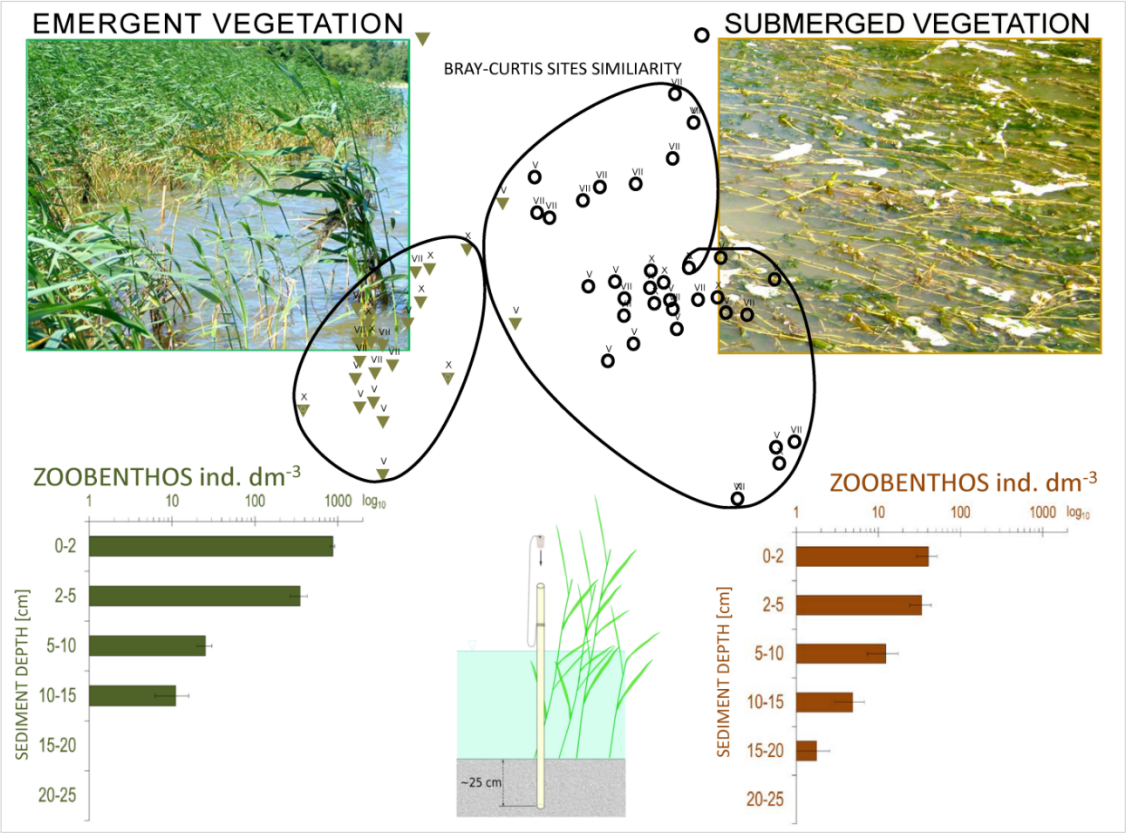
1. opracowaniu koncepcji i pomocy w pobieraniu materiału w terenie,
2. przeprowadzeniu oznaczeń taksonomicznych makrozoobentosu (w szczególności Chironomidae),
3. współudziale w przygotowaniu tekstu manuskryptu.



Podpis

Pawlikowski K., Kornijów R., 2022. **Above- and belowground habitat complexity created by emergent and submerged vegetation drives the structure of benthic assemblages.** Oceanologia. https://doi.org/10.1016/j.oceano.2022.10.002

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ORIGINAL RESEARCH ARTICLE

Above- and belowground habitat complexity created by emergent and submerged vegetation drives the structure of benthic assemblages

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Vistula Lagoon;
Littoral;
Trophic guilds;
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Vertical distribution

Abstract The contrast in habitat complexity between emergent (EMV) and submerged vegetation (SUV) zones in aquatic ecosystems results from the differences in the structure of plant above- and belowground parts, subject to seasonal changes. Comparative studies on the influence of habitat complexity created by vegetation on benthic macroinvertebrates in coastal areas are scarce. In order to fill this knowledge gap, we performed a study on a seasonal basis in the brackish Vistula Lagoon (southern Baltic Sea) in two zones: EMV, dominated by a dense belt of *Phragmites australis* (Cav.) Trin. ex Steud, and SUV, with scattered stands of *Potamogeton perfoliatus* L. We assumed the following: **i.** Species richness, diversity, and density of invertebrates are higher in the EMV zone due to greater and less seasonally variable structural complexity than in the SUV zone, **ii.** High belowground complexity in the EMV zone due to the presence of the rhizome/root matrix, much more robust and denser than in the SUV zone limits the vertical distribution of macroinvertebrates. Both hypotheses were supported. Overall, our results pointing to higher animal diversity and density in more complex aquatic habitats are consistent with other studies, inferred mostly from comparative surveys of bare bottom and that covered with submerged vegetation. The results of this study highlight potentially far-reaching implications for benthic invertebrate fauna and their role in the aquatic ecosystem in the context of increasingly rapid loss of aquatic vegetation due to multiple anthropogenic stressors.
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1. Introduction

Patterns in the spatial distribution of organisms, usually affected by habitat complexity and resource availability, are among the fundamental questions in ecology (Levin, 1992). Structural complexity in freshwater and brackish ecosystems is the highest in the near-shore littoral zone, designated by the presence of macrophytic vegetation (Meerhoff and González-Sagrario, 2021). In the coastal waters of temperate climate, aquatic plants are most commonly represented by two life forms, namely helophytes with strong lignified structures, and more delicately built elodeids. Helophytes form a zone of emergent vegetation (EMV) closer to the shoreline, while elodeids form a zone of submerged vegetation (SUV), usually, but not always, growing deeper, beyond the EMV belt. The aboveground and belowground parts of plants, both elodeids and helophytes, play a distinct role in the functioning of aquatic ecosystems. Aboveground structures provide feeding and reproductive sites, compete with phytoplankton for nutrients, alter nutrient cycling, inhibit wave energy, regulate sedimentation, and provide shelter from visually hunting predators such as crustaceans and fish (Carpenter and Lodge, 1986; Jeppesen et al., 1998; Phillips et al., 2016). The belowground structure stabilises bottom sediments, alters the activity of some burrowers (Goshima and Peterson, 2012; Peterson, 1982; Siebert and Branch, 2005, 2007), and mediates predator-prey relationships (Como et al., 2008; Orth, 1977), influencing both the composition and density of benthic invertebrates (Fredriksen et al., 2010; González-Ortiz et al., 2016; Ságová-Marečková, 2002). Moreover, through metabolic activity, it can have a significant effect on sediment chemistry (Caffrey and Kemp, 1992; Kemp and Murray, 1986) and interacts with bacterial metabolism (Donnelly and Herbert, 1999; Huang et al., 2020), potentially affecting zoobenthos within the rhizosphere (Ságová et al., 1993).

The aboveground and belowground parts of elodeids and helophytes show certain differences. Helophyte stems are partially exposed to the air, while elodeid stems are entirely surrounded by water. Both helophytes and elodeids emerge in spring and die back in fall. While the shoots of the former, after dying off, overwinter and protrude above the water surface for several months the following year, the shoots of the latter sink to the bottom in the autumn of the same year, and are rapidly decomposed by shredders and microorganisms, and then transferred as energy to higher trophic levels (Pieczyńska, 1993). Because of this difference, the habitat conditions in EMV are assumed to be much more stable throughout the year than in the SUV zone.

Another difference is related to belowground structures. In the EMV zone, they comprise a well-developed anchoring system in the form of rhizomes and roots embedded in the sediments (Weisner and Strand, 1996). Some plants growing in the SUV zone often have rhizomes and roots as well, but the organs are usually much more delicate and not as densely packed in the sediment volume (Boström and Bonsdorff, 2000; Fredriksen et al., 2010; Magni et al., 2017; Ozimek et al., 1976; Rodil et al., 2021; Wolfer and Straile, 2004).

Such substantial differences between the zones in terms of the structure and function of the below- and aboveground parts of plants should have implications for macroinvertebrate composition, diversity, and density, as well as their different vertical distribution along the sediment profile. However, comparative studies addressing this issue in the EMV and SUV zones of coastal areas, are scarce. To draw attention to these topics, we conducted research in the littoral of the Vistula Lagoon (southern Baltic Sea) in spring, summer, and autumn. The study covered the emergent vegetation zone in the form of a wide dense belt of reed *Phragmites australis* (Cav.) Trin. ex Steud, and a zone of submerged vegetation with patches of *Potamogeton perfoliatus* L. Both plants are among the most common ones in the studied lagoon (Kornijów, 2018), and show broad global distribution (Kemp et al., 1986; Meyerson et al., 2016). The results presented in this study, although with some caution, can be therefore extrapolated to other aquatic ecosystems, at least in the temperate zone. We assumed the following:

i. Taxonomic richness, diversity, and density of invertebrates are higher in the EMV than in the SUV zone due to greater structural complexity in the former one. This should be particularly evident in autumn when the aboveground parts of the emergent vegetation reach their maximum density, and those of the submerged vegetation disappear after dying off.
ii. High belowground complexity in the EMV zone due to the presence of the rhizome/root matrix, much more robust and denser than in the SUV zone limits the vertical distribution of macroinvertebrates.

2. Material and methods

2.1. Study site

The Vistula Lagoon is a brackish coastal lagoon in the southern part of the Baltic Sea, separated from the Gulf of Gdańsk by the Vistula Spit (Figure 1). The permanent hydrological connection between the Gulf of Gdańsk and the lagoon is provided by the Baltiysk Strait. The total area of the lagoon is 838 km^2. Its mean depth is 2.5 m, and its maximum depth is approximately 5 m. Salinity decreases from 6.5 at the Baltiysk Strait to <1 at the western basin. No tides occur in the lagoon, but daily water level fluctuations due to strong winds may exceed 1 m.

The research covered a fragment of the littoral on the south-western shore of the lagoon (54°20.02′N, 19°32.84′E) with plant communities typically developed in this area (Figure 1). Amongst and outside the large and homogenous stand of EMV, represented exclusively by *Phragmites australis*, patches of SUV with a diameter from 4 to 30 metres occurred, mainly composed of *Potamogeton perfoliatus*. Habitat conditions in this area were characterised in detail in Pawlikowski and Kornijów (2019). The content of organic matter (measured as loss on ignition) in the soft sediments of the EMV zone was multiple times higher than in the sandy sediments of the SUV zone (3.1% and 0.4%, respectively). In summer, in the diurnal cycle, water saturation with oxygen varied more strongly in the EMV zone (39%—152%) than in the SUV zone (110%—136%), with the lowest values in morning hours, and the highest in the evening. Aboveground plant structures appeared in the

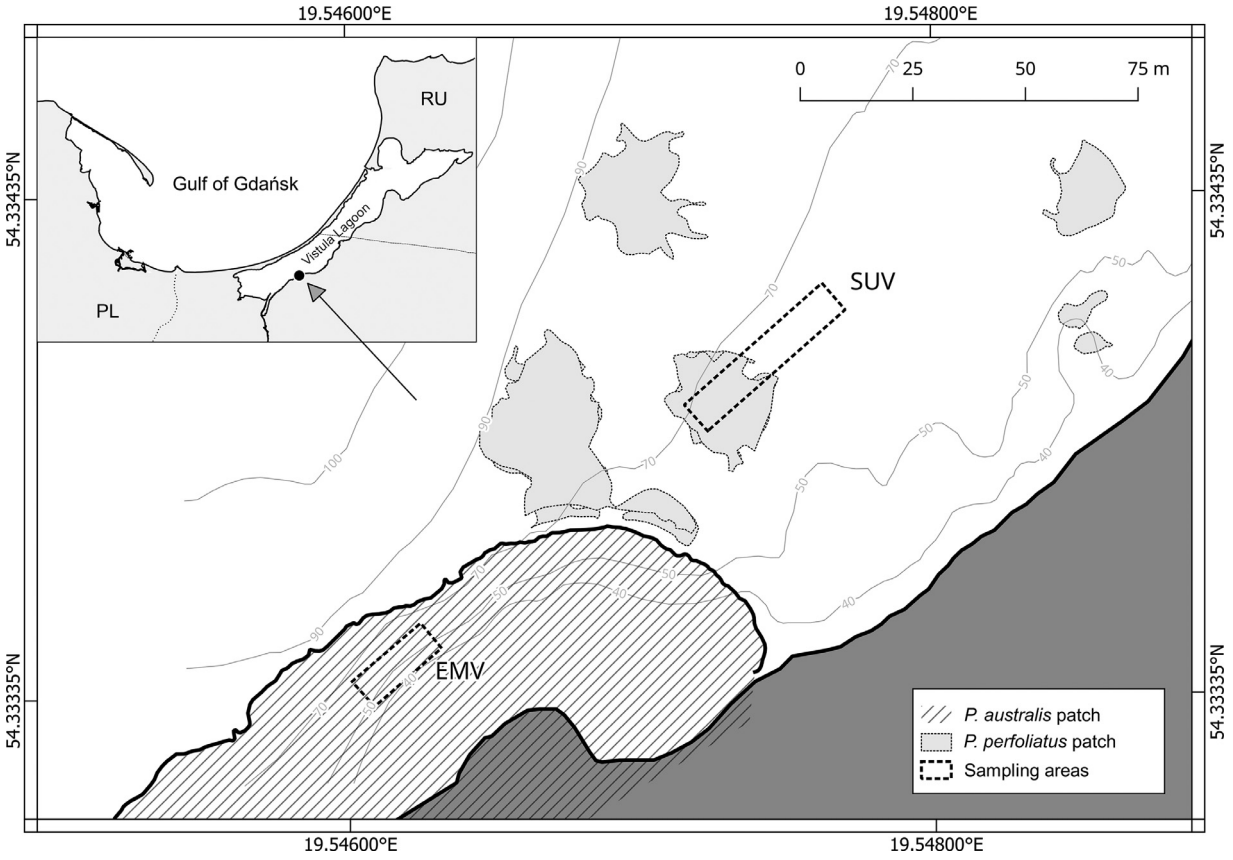


Figure 1 Map of the studied littoral area. EMV — emergent vegetation zone, SUV — submerged vegetation zone.

beginning of May, and began dying off in September. Shoots of *P. perfoliatus* disappeared in October, while the majority of *P. australis* overwintered and gradually declined over the following year. The density of *P. australis* in the peak of the growing season reached 132 ± 35—138 ± 77 shoots m^{-2} (SD; standard deviation), and that of *P. perfoliatus* was 8.3 ± 7.9—27.2 ± 9.8 shoots m^{-2}. Maximum mean solar radiation was much higher in the SUV zone (86.2—104.6 Wh m^{-2}) than under the canopies of EMV (4.7—6.6 Wh m^{-2}) (Pawlikowski and Kornijów, 2019).

2.2. Field survey and laboratory analyses

The material was collected in spring (May), summer (July), and autumn (October) 2013, during two consecutive day sampling events. Zoobenthos was sampled from both the EMV and SUV zones at a depth of 0.4—0.7 m by means of a transparent Plexiglas tube with a length of 1.2 m and a diameter of 6 cm. The corer was sharpened at the lower end to facilitate penetration into the sediment. The sampler was pushed to a depth of 20 or 25 cm. The sampled core was then divided into layers 0—2, 2—5, 5—10, 10—15, 15—20, and 20—25 cm by means of a slicer equipped with a sub-sample holder and centimetre scale (Kornijów, 2013). In the EMV zone, 8 samples (replicates) were collected and sliced each time, and in the SUV zone 16 samples, in each zone at places at least 2 m apart from each other. Cores with a length of more than 30 cm were sporadically collected for the purpose of verification of the occurrence of invertebrates below 25 cm. Each sediment section was washed separately through 0.3 mm mesh. Invertebrates were sorted live in the lab by hand on a white tray filled with water, preserved in 4% formaldehyde buffered with di-Sodium tetraborate, and identified to the lowest possible level. The trophic classification of invertebrates was adopted after Vaughn (1982) and Armitage (1995).

The determination of the grain size and chlorophyll *a* (as a proxy of microalgae biomass) distribution along the sediment profile involved sampling additional cores in both zones in May 2013. The sediment cores were sliced the same way as for benthos research and frozen. At the laboratory, after defrosting the sediments were dried and manually ground in a mortar, and then sieved on a set of geological sieves with mesh of 2 mm, 1 mm, 0.5 mm, 0.25 mm, 0.125 mm, and 0.063 mm. The obtained data were processed with the application of GRADISTAT software version 8 (Blott and Pye, 2001). Furthermore, frozen sediment slices were freeze-dried, and the obtained lyophilisates were suspended in acetone. Chlorophyll *a* concentrations were then determined by the fluorimetric method according to Evans et al. (1983).

2.3. Data analyses

We adopted two indices as a measure of taxonomic diversity in each habitat, namely the number of recorded taxa (taxa richness — S) and the Shannon Diversity Index (*H'*), calculated with natural logarithm. We used rarefaction analy-

sis (Gotelli and Colwell, 2001; Gotelli and Graves, 1996) to compare S and *H'* among sites, using Species Diversity module of EcoSim version 7.71 (Gotelli and Entsminger, 2009). The rarefaction analysis compares both indices standardised by observed abundance (sample size).

Multivariate methods were used to examine the similarity between macroinvertebrate groups in different littoral zones. The analyses were based on Bray-Curtis similarity matrices for square-root transformed abundance data. Non-metric multidimensional scaling (NMDS) and similarity overlay were used for the visualisation of the similarity of the structure of animal communities. A one-way ANOSIM was applied to test the null hypothesis of lack of differences in benthic communities between the zones. The identification of taxa responsible for the differences between the zones employed Similarity Percentage Analysis (SIMPER). All these analyses were carried out using PRIMER 6 version 6.1.15 package (PRIMER-E Ltd, 2007).

Due to unequal variances or non-normal distribution, the following non-parametric statistics were applied:

- Friedman test (Chi-Square) was applied for the determination of the effect of sediment depth on the density of fauna. The results of Friedman analyses is presented in Table 3.
- Kruskal-Wallis (K-W, H_{MAY}, H_{JULY}, $H_{OCTOBER}$) test was applied for the determination of the effect of the zones on the density of fauna.

Kruskal-Wallis and Friedman tests were performed by means of Statistica 10 software (StatSoft Inc, 2011).

3. Results

3.1. Diversity and density of macroinvertebrates

The occurrence of 27 taxa was recorded, belonging to Naididae, Polychaeta, Hirudinea, Gammaridae, Chrysomelidae and Chironomidae (Table 1). In majority, they belonged to detritivores, accounting for more than 92% of the fauna abundance.

During each sampling event, the total number of taxa (S) was much higher in the EMV than in the SUV zone (Table 2). According to the analysis of rarefaction, however, these differences were significant only in October, when structural differences between the habitats were the greatest (Figure 2). Values of Shannon Diversity Index (*H'*) proved higher in the EMV zone in each studied month (Table 2, Figure 2).

Most taxa reached higher densities in the EMV zone. The exception was *Marenzelleria* spp., occurring only in the EMV zone. In consequence, mean total densities of macroinvertebrates in each studied month were significantly higher in the EMV zone, and were not affected by season in either of the zones (K-W tests: H_{MAY} ($n = 24$, $df = 1$) $= 13$; $p < 0.001$; H_{JULY} ($n = 23$, $df = 1$) $= 14$; $p < 0.001$; $H_{OCTOBER}$ ($n = 18$, $df = 1$) $= 13$; $p < 0.001$) (Figure 3).

NMDS ordination evidenced a separation between EMV and SUV zones, with 83.5% dissimilarity (Figure 4) resulting from SIMPER analysis. This finding was further supported by the ANOSIM analysis that pointed to significant differences between the zones ($R=0.658$, $p=0.001$). SIMPER analysis identified taxa that contributed the most to the differentiation between the two zones. They included: *Limnodrilus claparedianus* (19.0%), *L. hoffmeisteri* (16.0%), *Chironomus* sp. (14.2%), *Potamothrix hammoniensis* (11.7%), *Glyptotendipes* sp. (9.6%), *Limnodrilus profundicola* (6.3%), and *Marenzelleria* spp. (5.3%). Average similarity within the EMV was higher (55.8%) than within SUV (42.9%).

3.2. Vertical distribution of macroinvertebrates

In the SUV zone, in all studied months, the sediments were inhabited to a depth between 15 and 20 cm. In the EMV zone, in spring and summer, fauna occurred shallower, to a depth of 10—15 cm, and it was found as deep as in the SUV zone only in autumn (15—20 cm) (Figure 5). The deepest burrowers included: *Tubificinae, Chironomus* sp., and *Marenzelleria* spp. Among the dominant Tubificinae, *Limnodrilus* spp. burrowed at least twice deeper (up to 15—20 cm) than *Potamothrix hammoniensis* and *Psammoryctides barbatus*.

The relative density of taxa clearly changed with sediment depth (Figure 5). It was particularly evident in the SUV zone, where the percentage of *Marenzelleria* spp. increased with depth. Total density changed with sediment depth (Friedman tests results in Table 3). In both zones and in each studied month, the densities were the highest in the near-surface layers, and gradually decreased with depth (Figure 6).

3.3. Characteristics of bottom sediments

Sediment in the EMV and SUV zones differed in terms of grain size composition (Figure 7). The EMV zone was dominated by silt and very coarse silt up to a depth of 10—15 cm. The proportion of sandy fractions increased with depth. In the SUV zone, the situation was the opposite — sandy fractions dominated up to 2—5 cm, and the proportion of silty fractions increased gradually below that depth.

The vertical distribution of chlorophyll *a* in the sediment in both zones was similar, with a strongly marked maximum in the surface layer 0—2 cm, and evidently lower concentrations deeper (Figure 8). The greatest differences were found in the surface layer, where chlorophyll concentration was almost three times higher in the SUV than in the EMV zone.

4. Discussion

4.1. Diversity and density of macroinvertebrates

The taxa richness of benthic macroinvertebrates (27 taxa) in the studied habitat zones was at least twice as high as that in the unvegetated homogenous central part of the lagoon, where only 6 taxa were recorded (Kornijów et al., 2021b). The taxa richness found in this study can still be considered relatively low, e.g. in comparison with lakes (Kornijów and Gulati, 1992; Wolnomiejski and Furyk, 1968). It can be attributed to brackish conditions that are poorly tolerated by many freshwater species (Brucet et al., 2012;

Table 1 Density of benthic macroinvertebrates [ind. m^{-2}] in the submerged (SUV) and emergent vegetation zone (EMV). DETR — detritivores, CARN — carnivores, HERB — herbivores, OMNI — omnivores. Mean values for sampling occasions ± SE (Standard Error).

	Taxa	Trophic group	SUV	EMV
CLITELLATA, NAIDIDAE				
TUBIFICINAE				
	n. det. without hair chaetae (juvenile or damaged), probably *Limnodrilus* sp.	DETR	1390 ± 222	14,793 ± 1 458
	n. det. with hair chaetae (juvenile or damaged), probably: *Tubifex* sp., *Potamothrix* sp., *Psammoryctides* sp.	DETR	33 ± 20	2168 ± 414
	Limnodrilus hoffmeisteri Clapar.	DETR	271 ± 85	1338 ± 297
	L. claparedianus Ratz.	DETR	0	1553 ± 351
	L. profundicola (Verill)	DETR	41 ± 21	308 ± 116
	Potamothrix hammoniensis (Mich.)	DETR	0	62 ± 29
	P. moldaviensis Vejd.	DETR	33 ± 16	0
	Tubificoides heterochaetus (Mich.)	DETR	8 ± 8	0
	Psammoryctides barbatus (Grube)	DETR	0	15 ± 15
	Clitellio arenarius (Müller)	DETR	0	15 ± 15
NAIDINAE				
	Stylaria lacustris (Linné.)	HERB	0	861 ± 445
	Nais elinguis Müller	HERB	8 ± 8	0
	Naidinae n. det.	HERB	132 ± 68	46 ± 34
TOTAL Naididae			**1916 ± 275**	**21,159 ± 2 158**
INSECTA, CHIRONOMIDAE				
	Chironomus sp.	DETR	8 ± 8	3106 ± 478
	Glyptotendipes sp.	DETR	8 ± 8	2353 ± 523
	Dicrotendipes sp.	DETR	8 ± 8	200 ± 117
	Polypedilum nubeculosum Mg.	DETR	8 ± 8	185 ± 70
	P. scalaneum (Schr.)	DETR	0	15 ± 15
	Polypedilum sp.	DETR	0	15 ± 15
	Paratanytarsus austriacus (Kieff.)	DETR	16 ± 11	15 ± 15
	Microchironomus tener (Kieff.)	DETR	0	62 ± 62
	Tanytarsini n. det.	DETR	0	15 ± 15
	Parachironomus varus (Goetgh.)	CARN	8 ± 8	31 ± 21
	Cryptochironomus sp.	CARN	33 ± 20	215 ± 101
	Procladius sp.	CARN	0	77 ± 38
TOTAL Chironomidae			**90 ± 31**	**6289 ± 793**
INSECTA, CHRYSOMELIDAE				
	Donacia sp.	HERB	0	123 ± 42
MALACOSTRACA				
	Gammaridae n. det. (probably: *G. tigrinus*, *G. duebeni*)	OMNI	0	692 ± 326
POLYCHAETA				
	Marenzelleria spp.	DETR	535 ± 80	15 ± 15
CLITELLATA, HIRUDINEA				
	Helobdella stagnalis (L.)	CARN	0	15 ± 15
	Hirudinea n. det.	CARN	8 ± 8	15 ± 15
TOTAL DENSITY			**2550 ± 288**	**28,310 ± 2 667**

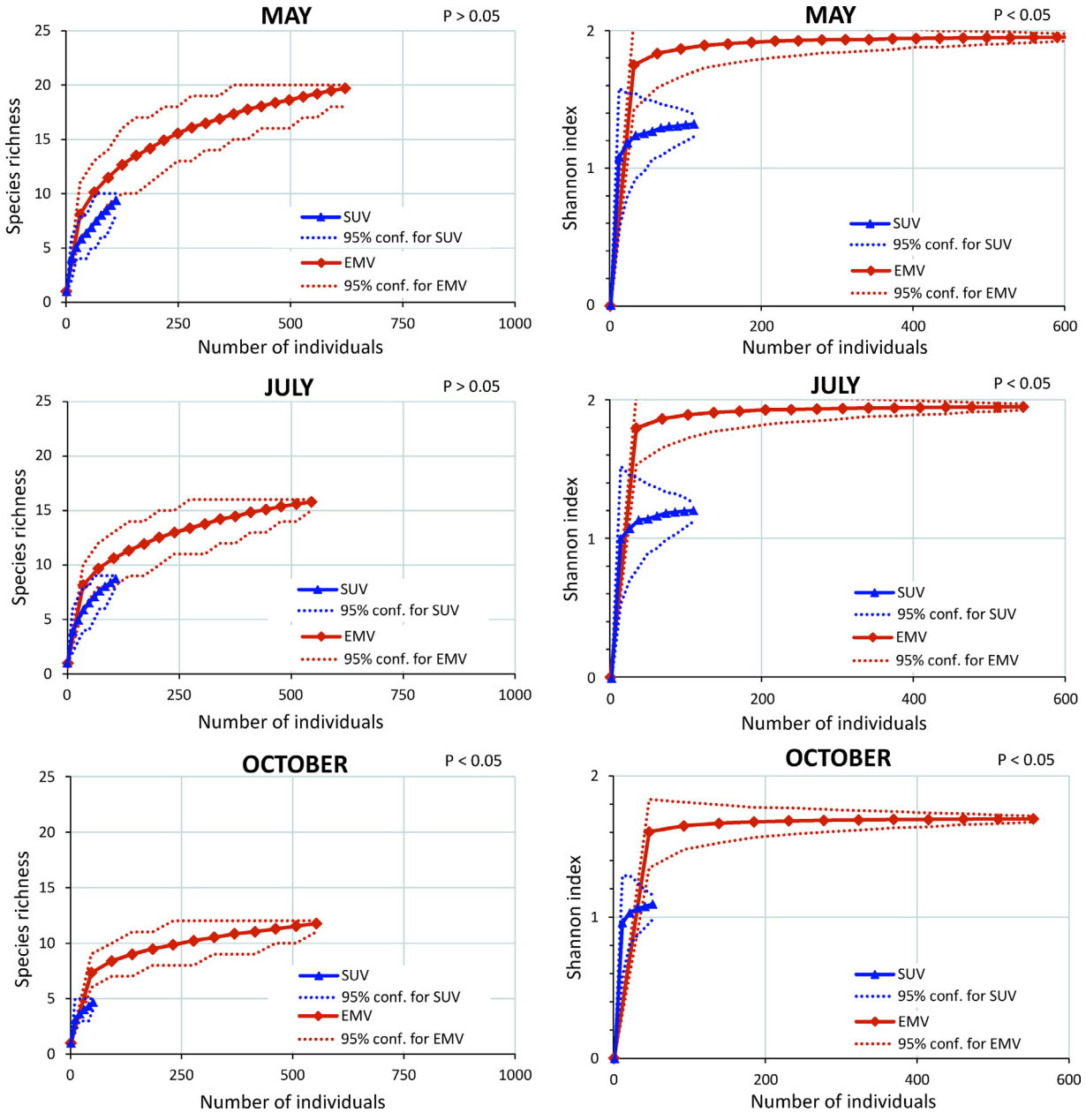


Figure 2 Comparison of species richness and values of the Shannon Diversity Index of macroinvertebrates between the EMV and SUV zones. Overlapping 95%-confidence areas at the end point of the curves, indicates lack of significant differences between species richness.

Kornijów et al., 2021a; Mrozińska et al., 2021; Vidal et al., 2021).

The studied zones highly differed in taxa richness, in favour of EMV. The differences, however, were statistically significant only in autumn, when the aboveground shoots in the EMV zone reached their maximum density, while in the SUV zone they died off and finally disappeared (Pawlikowski and Kornijów, 2019). This result emphasises the positive effect of the habitat complexity created by aboveground plant structures on the macroinvertebrate species richness. This is in line with the results of other studies (González-Ortiz et al., 2014,2016; Takamura et al., 2009). This impact was even more pronounced for the Shannon Diversity Index, with values significantly higher in EMV in each of the months studied, regardless of the difference in the seasonal pattern of development of aboveground plant structures between the zones. The effect of the structural complexity caused by vegetation on infauna richness is probably indirect, for example resulting from increased deposition of detritus and reduced efficiency of predation (Como et al., 2008; Diehl and Kornijów, 1998; Webster et al., 1998).

Trophic groups in both zones were entirely dominated by detritivores, represented mostly by oligochaetes, chironomid larvae, and a non-native polychaete *Marenzelleria* spp. Among considerably less numerous herbivores, only

Table 2 Species richness (S) and Shannon Diversity Index (*H'*) values of benthic macroinvertebrates in the submerged (SUV) and emergent vegetation (EMV) zones.

	S		*H'*	
	SUV	EMV	SUV	EMV
May	10	20	1.3	2.0
July	9	16	1.2	1.9
October	5	12	1.1	1.7

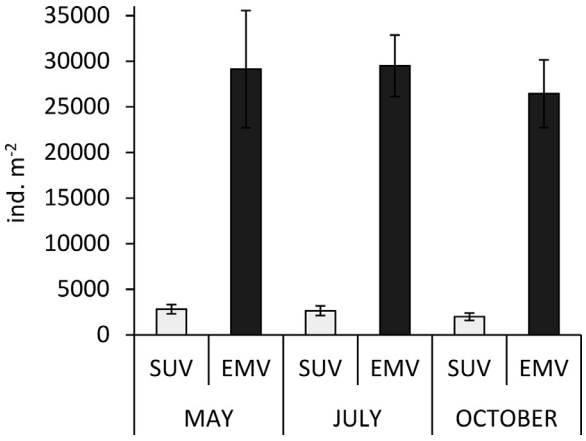


Figure 3 Total density [ind. $m^{-2} \pm SE$] of macroinvertebrates in the submerged (SUV) and emergent vegetation zone (EMV).

Donacia sp. larvae are typical inhabitants of the sediments. Their occurrence is associated with the presence of plant rhizomes/roots (Wolnomiejski and Furyk, 1968) from the tissues of which they obtain food and air for breathing (Hoffman, 1940). The remaining herbivore taxa from the Naidinae group belong to epiphytic fauna that could have been included in benthic samples incidentally, together with fragments of plants, or as a result of dislodging during strong waving.

The majority of taxa reached considerably higher densities in the more complex EMV zone. The exception was *Marenzelleria* spp., much more numerous in the SUV zone with scattered stands of *Potamogeton perfoliatus*. This is in line with the observation by Janas and Kendzierska (2014) that this polychaete avoids vegetated areas. The total density in each studied season was approximately 10 times higher in the EMV zone, a difference that reflected the concentration of organic matter, and pointed to better food conditions for macroinvertebrates domi-

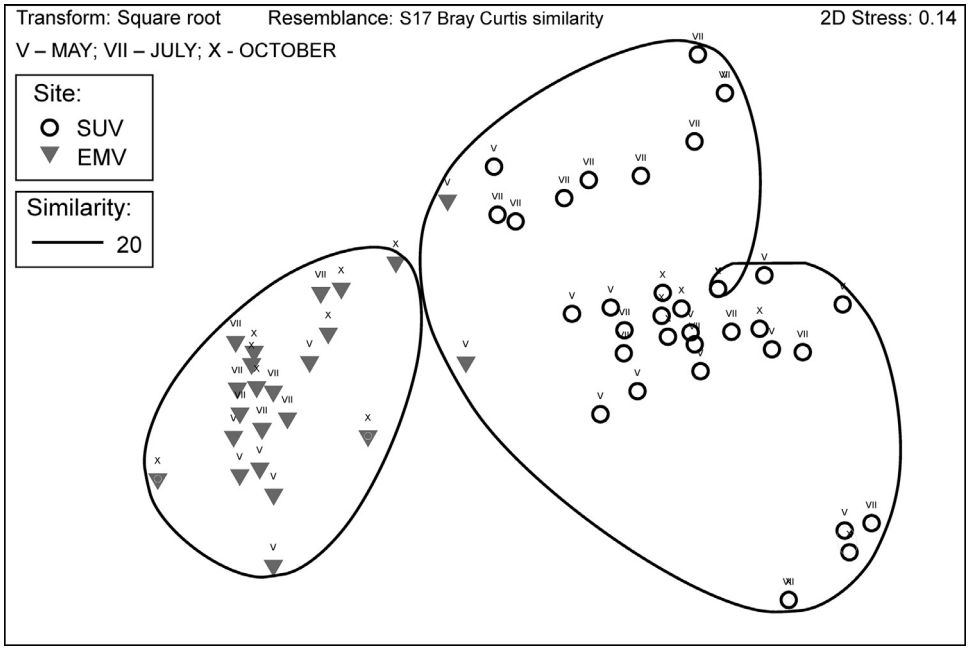


Figure 4 Non-metric multidimensional scaling (NMDS) plot based on Bray-Curtis similarity matrices calculated from the data on macroinvertebrate abundance in the EMV and SUV zones.

Table 3 Friedman tests (Chi-Square) results of the effect of sediment depth on the density of fauna in the submerged (SUV) and emergent vegetation (EMV) zones.

	SUV	EMV
May	Chi-Square ($n = 16$, $df = 5$) $= 53$; $p < 0.05$	Chi-Square ($n = 6$, $df = 5$) $= 28$; $p < 0.05$
July	Chi-Square ($n = 16$, $df = 4$) $= 17$; $p < 0.05$	Chi-Square ($n = 6$, $df = 5$) $= 29$; $p < 0.05$
October	Chi-Square ($n = 10$, $df = 5$) $= 28$; $p < 0.05$	Chi-Square ($n = 6$, $df = 5$) $= 24$; $p < 0.05$

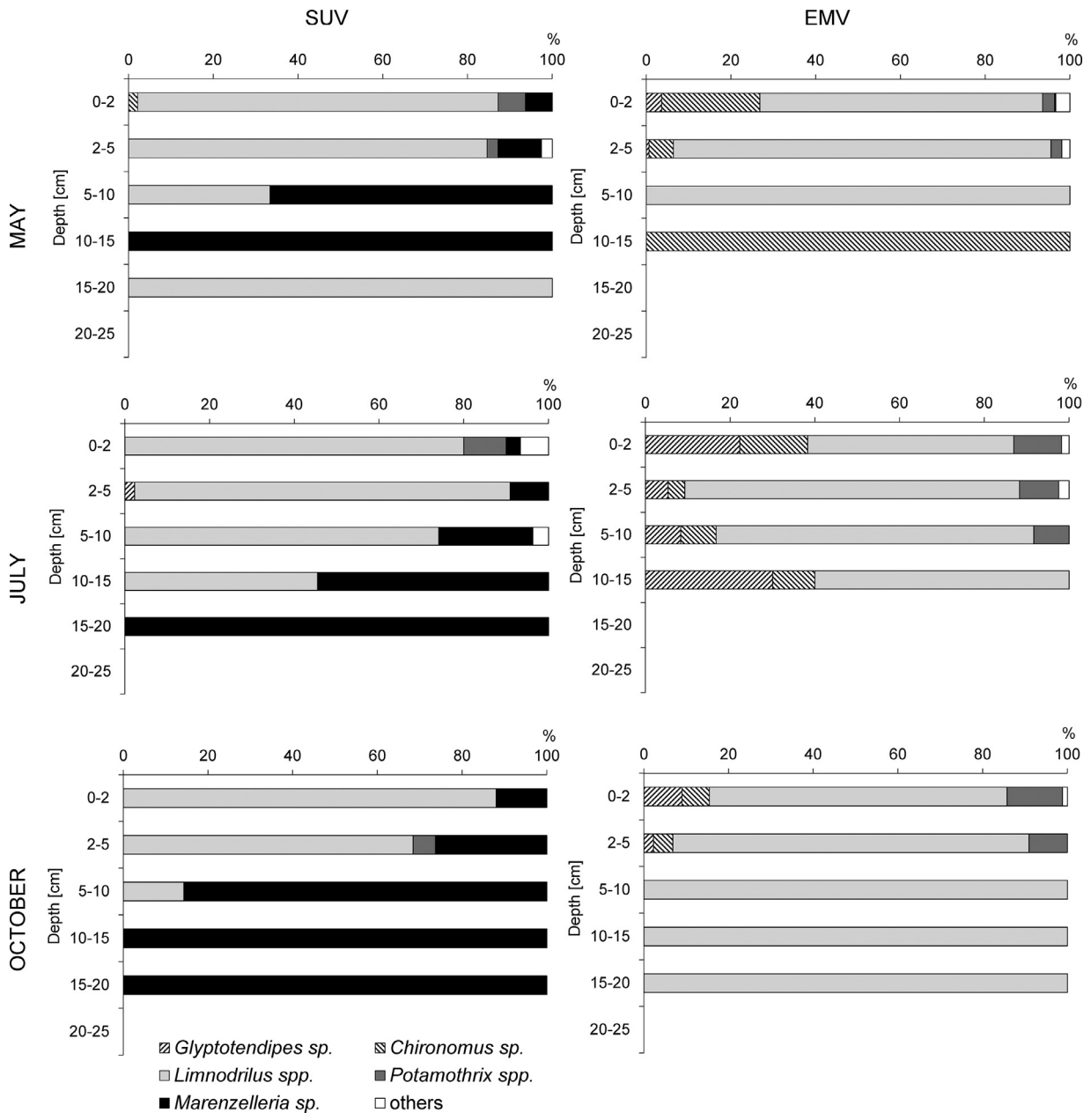


Figure 5 Relative density of dominating detritivores in the vertical sediment profile in the submerged vegetation zone (SUV) and emergent vegetation zone (EMV).

nated by detritivores. It is believed that food sufficiency promotes both high abundance and coexistence of various species with similar food requirements, leading to high diversity (Kangur et al., 1998; Kornijów et al., 2021b; Whitlatch, 1980; Wolnomiejski, 1994).

Next to food conditions, wave action could be another factor influencing the fauna density (James et al., 1998). Wave energy in the littoral of the Vistula Lagoon was effectively attenuated by the dense reed belt (EMV), but not by the scattered stands of the pondweed (SUV). This translated into different spatial variability of physicochemical factors in the two zones (Pawlikowski and Kornijów, 2019). Under hydraulic stress in the SUV, deep burrowers Annelida (Tubificinae and Polychaeta) and *Chironomus* sp. larvae were dominant. A much higher percentage of various chironomid larvae, including several small and shallow-burrowing species, was recorded inside the reeds (Table 1). This agrees with observations made by González-Ortiz et al. (2016) that small organisms may be able to move easily through the rhizosphere mat (and grow there more protected), while the size of the belowground mesh may play a role in impeding the burrowing of larger organisms.

An important factor affecting the faunal composition and density could be fish predation, arguably greater in the SUV zone, particularly in spring and fall when the bottom is devoid of aboveground structures and therefore effective refugia (Diehl and Kornijów, 1998; Van de Bund and Groenendijk, 1994). Potential preys eagerly eaten by

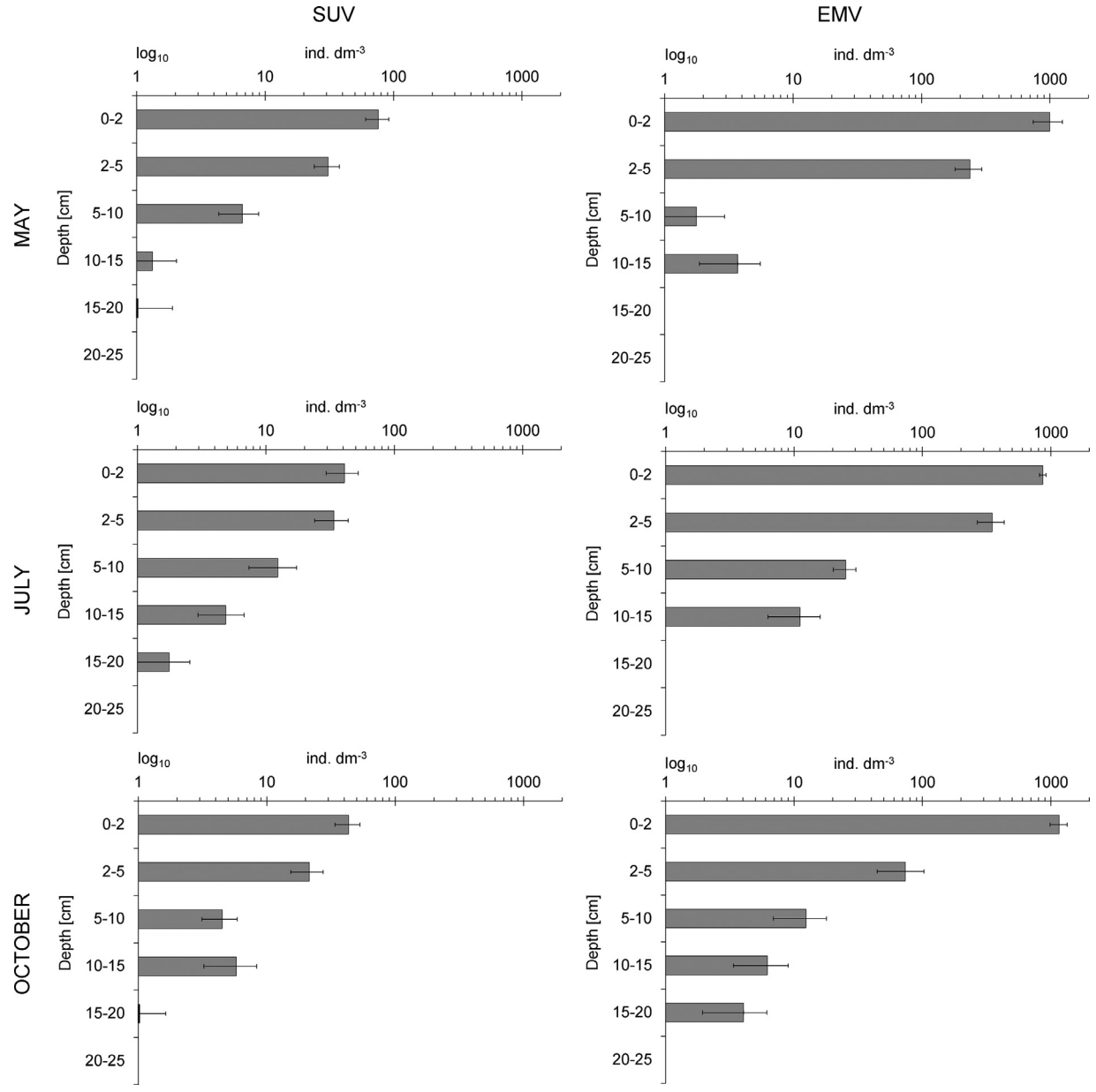


Figure 6 Total density of zoobenthos [ind. $dm^{-3} \pm SE$] in the vertical profile of bottom sediments in the submerged vegetation zone (SUV) and emergent vegetation zone (EMV).

fish included Gammaridae (Gonzalez and Burkart, 2004; Holomuzki and Hoyle, 1990), relatively numerous in the EMV zone and absent in SUV. It is worth emphasising a greater depth of burrowing in the less complex SUV habitat that may also be a response to fish predation under conditions of insufficient refugia (Kornijów and Moss, 1998).

No effect of the season on total faunal density was observed in any of the zones. This can be convincingly explained in the EMV zone, where both below- and aboveground plant structures were present throughout the year, and the habitat complexity appeared unchanged. In the SUV zone, however, the complexity strongly fluctuated seasonally with the development/decay of plant canopies.

The differences in taxa richness, density, and percentage of taxa were reflected by the NMDS ordination model that showed the highest similarities within sites and therefore grouped the fauna assemblages according to the two different habitats: EMV and SUV. Tubificinae, the most numerous Chironomidae larvae, and *Marenzelleria* spp. were the taxa that contributed the most to the differentiation between the EMV and SUV zones, while also indicating their habitat preferences.

4.2. Vertical distribution of macroinvertebrates

The micro-distribution of aquatic invertebrates along the sediment profile is essential for understanding many ecological issues such as community dynamics, competition, resource partitioning (Kornijów et al., 2021b; Whitlatch, 1980), bioturbation (Kristensen et al., 2012; Mermillod-Blondin, 2011), and prey-predator interactions (Kornijów, 1997; Persson and Svensson, 2006;

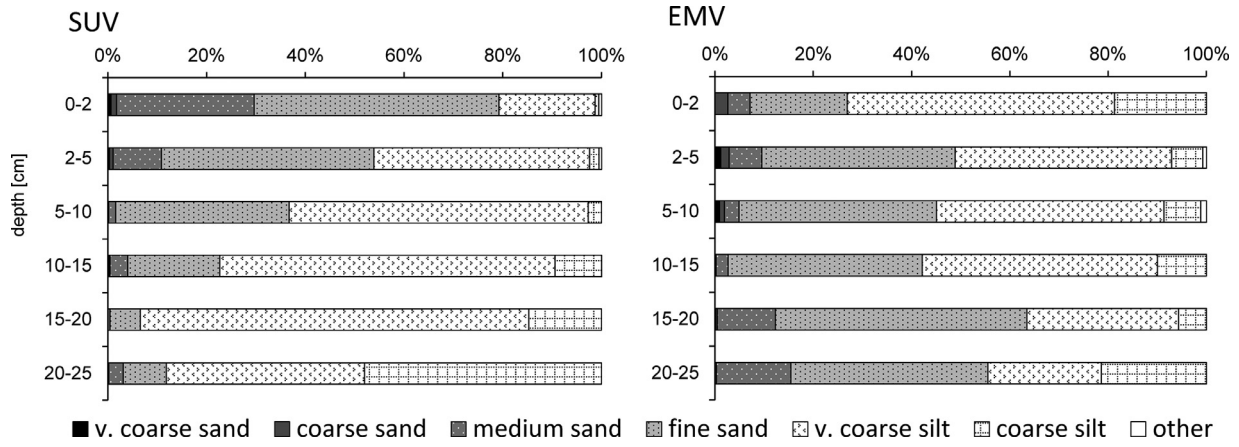


Figure 7 Grain size distribution of bottom sediments in the submerged vegetation zone (SUV) and emergent vegetation zone (EMV).

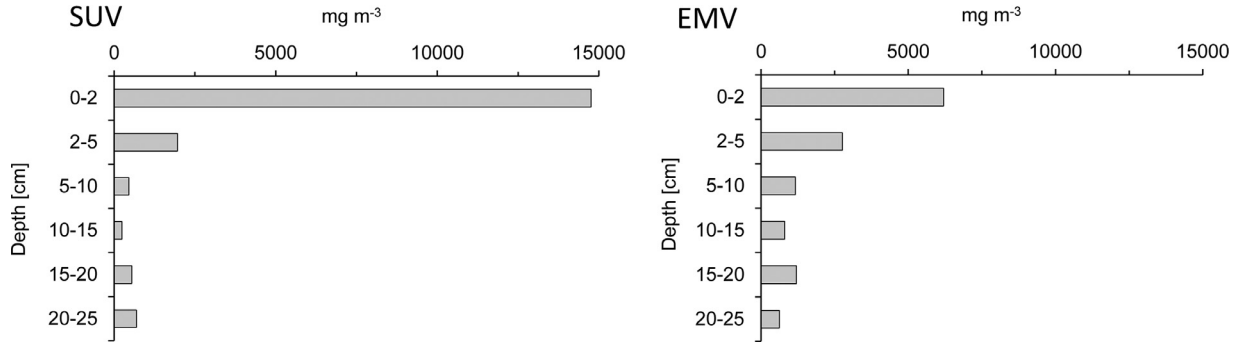


Figure 8 Changes in chlorophyll *a* concentration [mg m^{-3}] along the sediment profile of the submerged (SUV) and emergent vegetation zone (EMV).

Touhami et al., 2018; Van de Bund and Groenendijk, 1994). In both zones, the taxa richness of macroinvertebrates, as well as their density decreased with sediment depth, which is a known pattern (Cardoso et al., 2010; Kajak and Dusoge, 1971). For the vertical distribution of the deepest burrowing *Chironomus* sp. larvae, known as a surface deposit and filter-feeder (Kornijów et al., 2021b; Mermillod-Blondin, 2011), an essential driver could be the concentration of chlorophyll *a*, measured as a proxy of algal presence and nutritive value of the substrate (Kajak, 1988; Kajak and Warda, 1970; Lellak, 1965; Rodil et al., 2008), decreasing along the sediment profile (Fig. 8). Since the highest concentrations of chlorophyll *a* occur in the upper sediment layers, this variable might have been less important for Tubificinae which are deep deposit feeders (Davis, 1974; Kornijów et al., 2021b; Milbrink, 1973; Newrkla and Wijegoonawardana, 1987).

As expected, invertebrates most frequently burrowed sediments deeper (up to 15—20 cm) in the SUV zone with poorly developed root systems than in the EMV zone (mostly up to 10—15 cm) with a dense three-dimensional rhizosphere/root matrix. In sandy littoral sediments without vegetation, zoobenthos can occur even deeper, down to 20—25 cm (Rodil et al., 2008). It can be found at the same depth in soft sediments without vegetation in lagoons and estuaries (Dauer et al., 1987; Kornijów et al., 2021b). The vertical distribution of zoobenthos in reed-covered sediments is much less known. Few studies have been conducted, only in lakes, and they indicate relatively shallow burrowing in reed beds to a depth of 15 cm, like in the current study (Wolnomiejski and Furyk, 1968). This shallower burial is probably related to the densely packed rhizosphere/root matrix produced by the reeds. It stabilises the sediments, and according to several authors, they may limit their penetration, especially by larger invertebrates (González-Ortiz et al., 2016; Goshima and Peterson, 2012; Siebert and Branch, 2005), letting through smaller ones as mentioned above.

Seasonal changes in the relative density of macroinvertebrate communities along the sediment profile were clearly marked only in the EMV zone, despite its relatively stable habitat complexity across seasons, including belowground structures. Their importance for structuring the infaunal community has been emphasised in many studies (González-Ortiz et al., 2014, 2016; Goshima and Peterson, 2012; Orth, 1977; Siebert and Branch, 2005). In the SUV zone, the share of taxa in the total density along the sediment profile underwent no major seasonal changes (considerable depth variations only occurred in the case of *Limnodrilus* spp.), although the seasonal dynamics of aboveground structures and therefore changes in habitat complexity were evident.

5. Conclusions

In conclusion, according to our hypotheses, diversity and density of invertebrate communities were higher in the EMV zone, more complex and more stable throughout the year, than in SUV, less complex and subject to strong seasonal changes. Moreover, macroinvertebrates burrowed reed-covered sediments to lower depths. Our two hypotheses were therefore supported.

Overall, our results are consistent with those of other field and experimental studies that showed a positive relationship between habitat complexity and macroinvertebrate diversity and density (Boström and Bonsdorff, 1997; Como et al., 2008; González-Ortiz et al., 2016; Magni et al., 2017; Sueiro et al., 2011). Different results applied only to selected characteristics (diversity or density), and were rarely reported (Fredriksen et al., 2010; Sueiro et al., 2011). All these studies involved a comparison between macroinvertebrate communities inhabiting the bare bottom and that covered by submerged vegetation. This study shows that the pattern of a generally positive relationship between habitat complexity and faunal diversity and density is also valid when comparing two littoral zones colonised by different forms of plant life. Comparative surveys of the benthos inhabiting the two zones in coastal lagoons are lacking. The results of the scarce studies conducted in lake environments (Kornijów and Gulati, 1992) are consistent with those presented here.

The results of the present study indicate a significant dependence of benthic macroinvertebrates on macrophytes with different structures and seasonal patterns, depending on the vegetation type/life form. In this context, the increasingly rapid loss of aquatic vegetation due to multiple stressors such as eutrophication, land reclamation, and global climate change (Ostendorp, 1989; Zhang et al., 2017) can have potentially far-reaching consequences for the entire ecosystem (Liu et al., 2018; Morris et al., 2003; Phillips et al., 2016), including the diversity and functioning of the benthic system together with its invertebrate inhabitants. The latter aspect has received little attention in the hydrobiological literature to date (Boström and Bonsdorff, 2000; Fredriksen et al., 2010, Rodil et al. 2021).

Declaration of competing interest

The authors declare that they have no conflicts of interest.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.oceano.2022.10.002.

References

Armitage, P.D., Cranston, P.S., Pinder, L.C.V., 1995. The Chironomidae. Biology and ecology of non-biting midges. Chapman and Hall, Londyn-Madryt, 447. https://doi.org/10.1007/978-94-011-0715-0

Blott, S.J., Pye, K., 2001. GRADISTAT: a grain size distribution and statistics package for the analysis of unconsolidated sediments. Earth Surf. Proc. Land. 26, 1237—1248. https://doi.org/10.1002/esp.261

Boström, C., Bonsdorff, E., 1997. Community structure and spatial variation of benthic invertebrates associated with *Zostera marina* (L) beds in the northern Baltic Sea. J. Sea Res. 37, 153—166. https://doi.org/10.1016/S1385-1101(96)00007-X

Boström, C., Bonsdorff, E., 2000. Zoobenthic community establishment and habitat complexity - the importance of seagrass shoot-density, morphology and physical disturbance for faunal recruitment. Mar. Ecol. Prog. Ser. 205, 123—138. https://doi.org/10.3354/meps205123

Brucet, S., Boix, D., Nathansen, L.W., Quintana, X.D., Jensen, E., Balayla, D., Meerhoff, M., Jeppesen, E., 2012. Effects of temperature, salinity and fish in structuring the macroinvertebrate community in shallow lakes: Implications for effects of climate change. Plos One 7. https://doi.org/10.1371/journal.pone.0030877

Caffrey, J.M., Kemp, W.M., 1992. Influence of the submersed plant, *Potamogeton perfoliatus*, on nitrogen cycling in estuarine sediments. Limnol. Oceanogr. 37, 1483—1495. https://doi.org/10.4319/lo.1992.37.7.1483

Cardoso, I., Granadeiro, J.P., Cabral, H., 2010. Benthic macroinvertebrates' vertical distribution in the Tagus estuary (Portugal): The influence of tidal cycle. Estuar. Coast. Shelf S. 86, 580—586. https://doi.org/10.1016/j.ecss.2009.11.024

Carpenter, S.R., Lodge, D.M., 1986. Effects of submersed macrophytes on ecosystem processes. Aquat. Bot. 26, 341—370. https://doi.org/10.1016/0304-3770(86)90031-8

Como, S., Magni, P., Baroli, M., Casu, D., De Falco, G., Floris, A., 2008. Comparative analysis of macrofaunal species richness and composition in *Posidonia oceanica, Cymodocea nodosa* and leaf litter beds. Mar. Biol. 153, 1087—1101. https://doi.org/10.1007/s00227-007-0881-z

Dauer, D.M., Ewing, R.M., Rodi, A.J., 1987. Macrobenthic distribution within the sediment along an estuarine salinity gradient. Int. Rev. Ges. Hydrobiol. 72, 529—538. https://doi.org/10.1002/iroh.19870720502

Davis, R.B., 1974. Stratigraphic effects of tubificids in profundal lake sediments. Limnol. Oceanogr. 19, 466—488. https://doi.org/10.4319/lo.1974.19.3.0466

Diehl, S., Kornijów, R., 1998. Influence of submerged macrophytes on trophic interactions among fish and macroinvertebrates. In: Jeppesen, E., Søndergaard, M., Søndergaard, M., Christoffersen, M. (Eds.), The structuring role of submerged macrophytes in lakes. Ecol. Stud 131. Springer, New York, 24—46. https://doi.org/10.1007/978-1-4612-0695-8_2

Donnelly, A.P., Herbert, R.A., 1999. Bacterial interactions in the rhizosphere of seagrass communities in shallow coastal lagoons. J. Appl. Microbiol. 85, 151S—160S. https://doi.org/10.1111/j.1365-2672.1998.tb05294.x

Evans, C.A., O'Reilly, J.E., 1983. A handbook for the measurement of chlorophyll *a* in netplankton and nannoplankton. In: Biomass handbook No.9. SCAR/SCOR/IABO/ACMRR Group of specialists on living resources of the southern oceans. SCAR, 44 pp.

Fredriksen, S., De Backer, A., Bostrom, C., Christie, H., 2010. Infauna from *Zostera marina* L. meadows in Norway. Differences in vegetated and unvegetated areas. Mar. Biol. Res. 6, 189–200. https://doi.org/10.1080/17451000903042461

González-Ortiz, V., Alcazar, P., Vergara, J.J., Pérez-Lloréns, J., Brun, F.G., 2014. Effects of two antagonistic ecosystem engineers on infaunal diversity. Estuar. Coast. Shelf S. 139, 20–26. https://doi.org/10.1016/j.ecss.2013.12.015

González-Ortiz, V., Egea, L.G., Jiménez-Ramos, R., Moreno-Marin, F., Pérez-Lloréns, J., Bouma, T., Brun, F., 2016. Submerged vegetation complexity modifies benthic infauna communities: the hidden role of the belowground system. Mar. Ecol.-Evol. Persp. 37, 543–552. https://doi.org/10.1111/maec.12292

Gonzalez, M.J., Burkart, G.A., 2004. Effects of food type, habitat, and fish predation on the relative abundance of two amphipod species, *Gammarus fasciatus* and *Echinogammarus ischnus*. J. Great Lakes Res. 30, 100–113. https://doi.org/10.1016/s0380-1330(04)70333-0

Goshima, S., Peterson, C.H., 2012. Both below- and aboveground shoalgrass structure influence whelk predation on hard clams. Mar. Ecol. Prog. Ser. 451, 75–92. https://doi.org/10.3354/meps09587

Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol. Lett. 4, 379–391. https://doi.org/10.1046/j.1461-0248.2001.00230.x

Gotelli, N.J., Entsminger, G.L., 2009. EcoSim: Null models software for ecology, Version 7 edn Acquired Intelligence Inc. & Kesey-Bear. http://www.uvm.edu/~ngotelli/EcoSim/EcoSim.html.

Gotelli, N.J., Graves, G.R., 1996. Null models in ecology. Smithsonian Institution Press, Washington, D.C., 1–368 pp.

Holomuzki, J.R., Hoyle, J.D., 1990. Effect of predatory fish presence on habitat use and diel movement of the stream amphipod, *Gammarus minus*. Freshwater Biol 24, 509–517. https://doi.org/10.1111/j.1365-2427.1990.tb00728.x

Hoffman, C.E., 1940. The relation of Donacia larvae (Chrysomelidae: Coleophera) to dissolved oxygen. Ecol. Evol. 21, 176–183. https://doi.org/10.2307/1930484

Huang, R., Zeng, J., Zhao, D.Y., Cook, K.V., Hambright, K.D., Yu, Z.B., 2020. Sediment microbiomes associated with the rhizosphere of emergent macrophytes in a shallow, subtropical lake. Limnol. Oceanogr. 65, S38–S48. https://doi.org/10.1002/lno.11325

James, M.R., Weatherhead, M., Stanger, C., Graynoth, E., 1998. Macroinvertebrate distribution in the littoral zone of Lake Coleridge, South Island, New Zealand - effects of habitat stability, wind exposure, and macrophytes. New Zeal. J. Mar. Fresh. 32, 287–305. https://doi.org/10.1080/00288330.1998.9516826

Janas, U., Kendzierska, H., 2014. Benthic non-indigenous species among indigenous species and their habitat preferences in Puck Bay (southern Baltic Sea). Oceanologia 56 (3), 603–628. https://doi.org/10.5697/oc.56-3.603

Jeppesen, E., Søndergaard, M., Søndergaard, M., Christoffersen, K., 1998. The structuring role of submerged macrophytes in lakes. Springer, New York, 1–131 pp.

Kajak, Z., 1988. Considerations on benthos abundance in freshwaters, its factors and mechanisms. Int. Rev. Ges. Hydrobiol. 73, 5–19. https://doi.org/10.1002/iroh.19880730103

Kajak, Z., Dusoge, K., 1971. The regularities of vertical distribution of benthos in bottom sediments of three Masurian lakes. Ekol. Pol. 19, 485–499.

Kajak, Z., Warda, J., 1970. Food conditions for. larvae of Chironomidae in various layers of bottom sediments. Bull. Acad. Pol. Sci. 18, 193–196.

Kangur, K., Timm, H., Timm, T., Timm, V., 1998. Long-term changes in the macrozoobenthos of Lake Võrtsjärv. Limnologica 28, 75–83.

Kemp, W.M., Lewis, M.R., Jones, T.W., 1986. Comparison of methods for measuring production by the submersed macrophyte, *Potamogeton perfoliatus* L. Limnol. Oceanogr. 31, 1322–1334. https://doi.org/10.4319/lo.1986.31.6.1322

Kemp, W.M., Murray, L., 1986. Oxygen release from roots of the submersed macrophyte *Potamogeton perfoliatus* L.: Regulating factors and ecological implications. Aquat. Bot. 26, 271–283. https://doi.org/10.1016/0304-3770(86)90027-6

Kornijów, R., 1997. The impact of predation by perch on the size-structure of *Chironomus* larvae - The role of vertical distribution of the prey in the bottom sediments, and habitat complexity. Hydrobiologia 342, 207–213. https://doi.org/10.1023/A:1017067621668

Kornijów, R., 2013. A new sediment slicer for rapid sectioning of the uppermost sediment cores from marine and freshwater habitats. J. Paleolimnol. 49, 301–304. https://doi.org/10.1007/s10933-012-9655-9

Kornijów, R., 2018. Ecosystem of the Polish part of the Vistula Lagoon from the perspective of alternative stable states concept, with implications for management issues. Oceanologia 60 (3), 390–404. https://doi.org/10.1016/j.oceano.2018.02.004

Kornijów, R., Dukowska, M., Leszczynska, J., Smith, C., Jeppesen, E., Hansson, L.A., Ketola, M., Irvine, K., Noges, T., Sahuquillo, M., Miracle, M.R., Gross, E., Kairesalo, T., van Donk, E., de Eyto, E., Garcia-Criado, F., Grzybkowska, M., Moss, B., 2021a. Distribution patterns of epiphytic reed-associated macroinvertebrate communities across European shallow lakes. Sci. Total Environ. 760. https://doi.org/10.1016/j.scitotenv.2020.144117

Kornijów, R., Gulati, R.D., 1992. Macrofauna and its ecology in Lake Zwemlust, after biomanipulation. I. Bottom fauna. Arch. Hydrobiol. 123, 337–347.

Kornijów, R., Moss, B., 1998. Vertical distribution of in-benthos in relation to fish and floating-leaved macrophyte populations, in: Jeppesen, E., Søndergaard, M., Søndergaard, M., Christoffersen, K. (Eds.), The structuring role of submerged macrophytes in lakes. Ecol. Stud 131. Springer, New York, 227–232. https://doi.org/10.1007/978-1-4612-0695-8_12

Kornijów, R., Pawlikowski, K., Błędzki, L.A., Drgas, A., Piwosz, K., Ameryk, A., Całkiewicz, J., 2021b. Co-occurrence and potential resource partitioning between oligochaetes and chironomid larvae in a sediment depth gradient. Aquat. Sci. 83 (51), 1–10. https://doi.org/10.1007/s00027-021-00800-z

Kristensen, E., Penha-Lopes, G., Delefosse, M., Valdemarsen, T., Quintana, C.O., Banta, G.T., 2012. What is bioturbation? The need for a precise definition for fauna in aquatic sciences. Mar. Ecol. Prog. Ser. 446, 285–302. https://doi.org/10.3354/meps09506

Lellak, J., 1965. The food supply as a factor regulating the population dynamics of bottom animals. Verh. Int. Ver. Theor. Angew. Limnol. 13, 128–138.

Levin, S.A., 1992. The problem of pattern and scale in ecology. Ecology 73, 1943–1967. https://doi.org/10.2307/1941447

Liu, W.Z., Jiang, X.L., Zhang, Q.F., Li, F., Liu, G.H., 2018. Has submerged vegetation loss altered sediment denitrification, N_2O production, and denitrifying microbial communities in subtropical lakes? Global Biogeochem. Cy. 32, 1195–1207. https://doi.org/10.1029/2018gb005978

Magni, P., Como, S., Kamijo, A., Montani, S., 2017. Effects of *Zostera marina* on the patterns of spatial distribution of sediments and macrozoobenthos in the boreal lagoon of Furen (Hokkaido, Japan). Mar. Environ. Res. 131, 90–102. https://doi.org/10.1016/j.marenvres.2017.09.013

Meerhoff, M., González-Sagrario, M.A., 2021. Habitat complexity in shallow lakes and ponds: importance, threats, and po-

tential for restoration. Hydrobiologia https://doi.org/10.1007/s10750-021-04771-y
Mermillod-Blondin, F., 2011. The functional significance of bioturbation and biodeposition on biogeochemical processes at the water-sediment interface in freshwater and marine ecosystems. J. N. Am. Benthol. Soc. 30, 770—778. https://doi.org/10.1899/10-121.1
Meyerson, L.A., Cronin, J.T., Pysek, P., 2016. *Phragmites australis* as a model organism for studying plant invasions. Biol. Invasions 18, 2421—2431. https://doi.org/10.1007/s10530-016-1132-3
Milbrink, G., 1973. On the vertical distribution of oligochaetes in lake sediments. Institute for Freshwater Research, Drottningholm, 34—50.
Morris, K., Bailey, P.C., Boon, P.I., Hughes, L., 2003. Alternative stable states in the aquatic vegetation of shallow urban lakes. II. Catastrophic loss of aquatic plants consequent to nutrient enrichment. Mar. Freshwater Res. 54, 201—215. https://doi.org/10.1071/mf02003
Mrozińska, N., Glińska-Lewczuk, K., Obolewski, K., 2021. Salinity as a key factor on the fenthic fauna diversity in the coastal lakes. Animals 11, 3039. https://doi.org/10.3390/ani11113039
Newrkla, P., Wijegoonawardana, N., 1987. Vertical distribution and abundance of benthic invertebrates in profundal sediments of Mondsee, with special reference to Oligochaetes. Hydrobiologia 155, 227—234. https://doi.org/10.1007/Bf00025655
Orth, R.J., 1977. The importance of sediment stability in seagrass communities. In: Coull, B.C. (Ed.), Ecology of Marine Benthos. University of South Carolina Press Columbia, 281—300.
Ostendorp, W., 1989. Die-back' of reeds in Europe: a critical review of literature. Aquat. Bot. 35, 5—26. https://doi.org/10.1016/0304-3770(89)90063-6
Ozimek, T., Prejs, A., Prejs, K., 1976. Biomass and distribution of underground parts of *Potamogeton perfoliatus* L. and *P. lucens* L. in Mikołajskie Lake. Poland. Aquat. Bot. 2, 309—316. https://doi.org/10.1016/0304-3770(76)90028-0
Pawlikowski, K., Kornijów, R., 2019. Role of macrophytes in structuring littoral habitats in the Vistula Lagoon (southern Baltic Sea). Oceanologia 61 (1), 26—37. https://doi.org/10.1016/j.oceano.2018.05.003
Persson, A., Svensson, J.M., 2006. Vertical distribution of benthic community responses to fish predators, and effects on algae and suspended material. Aquat. Ecol. 40, 85—95. https://doi.org/10.1007/s10452-005-9014-2
Peterson, C.H., 1982. Clam predation by whelks (*Busycon* spp.): Experimental tests of the importance of prey size, prey density, and seagrass cover. Mar. Biol. 66, 159—170. https://doi.org/10.1007/Bf00397189
Phillips, G., Willby, N., Moss, B., 2016. Submerged macrophyte decline in shallow lakes: What have we learnt in the last forty years? Aquat. Bot. 135, 37—45. https://doi.org/10.1016/j.aquabot.2016.04.004
Pieczyńska, E., 1993. Detritus and nutrient dynamics in the shore zone of lakes - a review. Hydrobiologia 251, 49—58. https://doi.org/10.1007/Bf00007164
PRIMER-E Ltd, 2007. PRIMER 6 software. 6.1.9. http://www.primer-e.com.
Rodil, I.F., Cividanes, S., Lastra, M., Lopez, J., 2008. Seasonal variability in the vertical distribution of benthic macrofauna and sedimentary organic matter in an estuarine beach (NW spain). Estuar. Coast. 31, 382—395. https://doi.org/10.1007/s12237-007-9017-4
Rodil, I.F., Lohrer, A.M., Attard, K.M., Hewitt, J.E., Thrush, S.F., Norkko, A., 2021. Macrofauna communities across a seascape of seagrass meadows: environmental drivers, biodiversity patterns and conservation implications. Biodivers. Conserv. 30, 3023—3043. https://doi.org/10.1007/s10531-021-02234-3
Ságová-Marečková, M., 2002. Distribution of benthic macroinvertebrates in relationship to plant roots, sediment type and spatial scale in fishponds and slow streams. Arch. Hydrobiol. 156, 63—81. https://doi.org/10.1127/0003-9136/2002/0156-0063
Ságová, M., Adams, M.S., Butler, M.G., 1993. Relationship between plant-roots and benthic animals in three sediment types of a dimictic mesotrophic lake. Arch. Hydrobiol. 128, 423—436.
Siebert, T., Branch, G.M., 2005. Interactions between *Zostera capensis, Callianassa kraussi* and *Upogebia africana*: deductions from field surveys in Langebaan Lagoon, South Africa. Afr. J. Mar. Sci. 27, 345—356. https://doi.org/10.2989/18142320509504094
Siebert, T., Branch, G.M., 2007. Influences of biological interactions on community structure within seagrass beds and sandprawn-dominated sandflats. J. Exp. Mar. Biol. Ecol. 340, 11—24. https://doi.org/10.1016/j.jembe.2006.08.007
StatSoft, 2011. Statistica software version 10. StatSoft Inc. http://www.statsoft.com.
Sueiro, M.C., Bortolus, A., Schwindt, E., 2011. Habitat complexity and community composition: relationships between different ecosystem engineers and the associated macroinvertebrate assemblages. Helgoland Mar. Res. 65, 467—477. https://doi.org/10.1007/s10152-010-0236-x
Takamura, N., Ito, T., Ueno, R., Ohtaka, A., Wakana, I., Nakagawa, M., Ueno, Y., Nakajima, H., 2009. Environmental gradients determining the distribution of benthic macroinvertebrates in Lake Takkobu, Kushiro wetland, northern Japan. Ecol. Res. 24, 371—381. https://doi.org/10.1007/s11284-008-0514-0
Touhami, F., Bazairi, H., Badaoui, B., Benhoussa, A., 2018. Vertical distribution of benthic macrofauna in intertidal habitats frequented by shorebirds at Merja Zerga Lagoon. Thalassas 34, 255—265. https://doi.org/10.1007/s41208-017-0059-5
Van de Bund, W.J., Groenendijk, D., 1994. Seasonal dynamics and burrowing of littoral Chironomid larvae in relation to competition and predation. Arch. Hydrobiol. 132, 213—225.
Vaughn, C.C., 1982. Distribution of chironomids in the Littoral-Zone of Lake Texoma, Oklahoma and Texas. Hydrobiologia 89, 177—188. https://doi.org/10.1007/Bf00006170
Vidal, N., Yu, J.L., Gutierrez, M.F., de Mello, F.T., Tavsanoglu, U.N., Cakiroglu, A.I., He, H., Meerhoff, M., Brucet, S., Liu, Z.W., Jeppesen, E., 2021. Salinity shapes food webs of lakes in semi-arid climate zones: a stable isotope approach. Inland Waters 11, 445—456. https://doi.org/10.1080/20442041.2020.1859290
Webster, P.J., Rowden, A.A., Attrill, M.J., 1998. Effect of shoot density on the infaunal macro-invertebrate community within a zostera marina seagrass bed. Estuar. Coast. Shelf Sci. 47, 351—357. https://doi.org/10.1006/ecss.1998.0358
Weisner, S.E.B., Strand, J.A., 1996. Rhizome architecture in Phragmites australis in relation to water depth: Implications for within-plant oxygen transport distances. Folia Geobot. Phytotx. 31, 91—97. https://doi.org/10.1007/bf02803998
Whitlatch, R.B., 1980. Patterns of resource utilization and coexistence in marine inter-tidal deposit-feeding communities. J. Mar. Res. 38, 743—765.
Wolfer, S.R., Straile, D., 2004. Spatio-temporal dynamics and plasticity of clonal architecture in *Potamogeton perfoliatus*. Aquat. Bot. 78, 307—318. https://doi.org/10.1016/j.aquabot.2003.11.005
Wolnomiejski, N., 1994. Ecological study on muddy bottom macrofauna of the Szczecin Lagoon (1982-1992). Studia i Materiały, Marine Fisheries Institute, Gdynia ser. A, 31, Gdynia, 126 pp., (in Polish).
Wolnomiejski, N., Furyk, A., 1968. The vertical distribution of the bottom fauna in the sediments of the littoral zone of Jeziorak Lake. Zesz. Nauk. UMK w Toruniu, Nauki Mat.-Przyr., Prace Stacji Limnologicznej w Iławie 20, 31—45.
Zhang, Y.L., Jeppesen, E., Liu, X.H., Qin, B.Q., Shi, K., Zhou, Y.Q., Thomaz, S.M., Deng, J.M., 2017. Global loss of aquatic vegetation in lakes. Earth-Sci. Rev. 173, 259—265. https://doi.org/10.1016/j.earscirev.2017.08.013

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5. przeprowadzeniu analiz granulometrycznych osadu,
6. opracowaniu danych, przeprowadzeniu analiz statystycznych i wizualizacji wyników,
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