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# Wpływ zasolenia na różnorodność strukturalną i funkcjonalną zoocenoz oraz zdrowie ekosystemowe jezior

Rozprawa doktorska wykonana

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# Spis treści

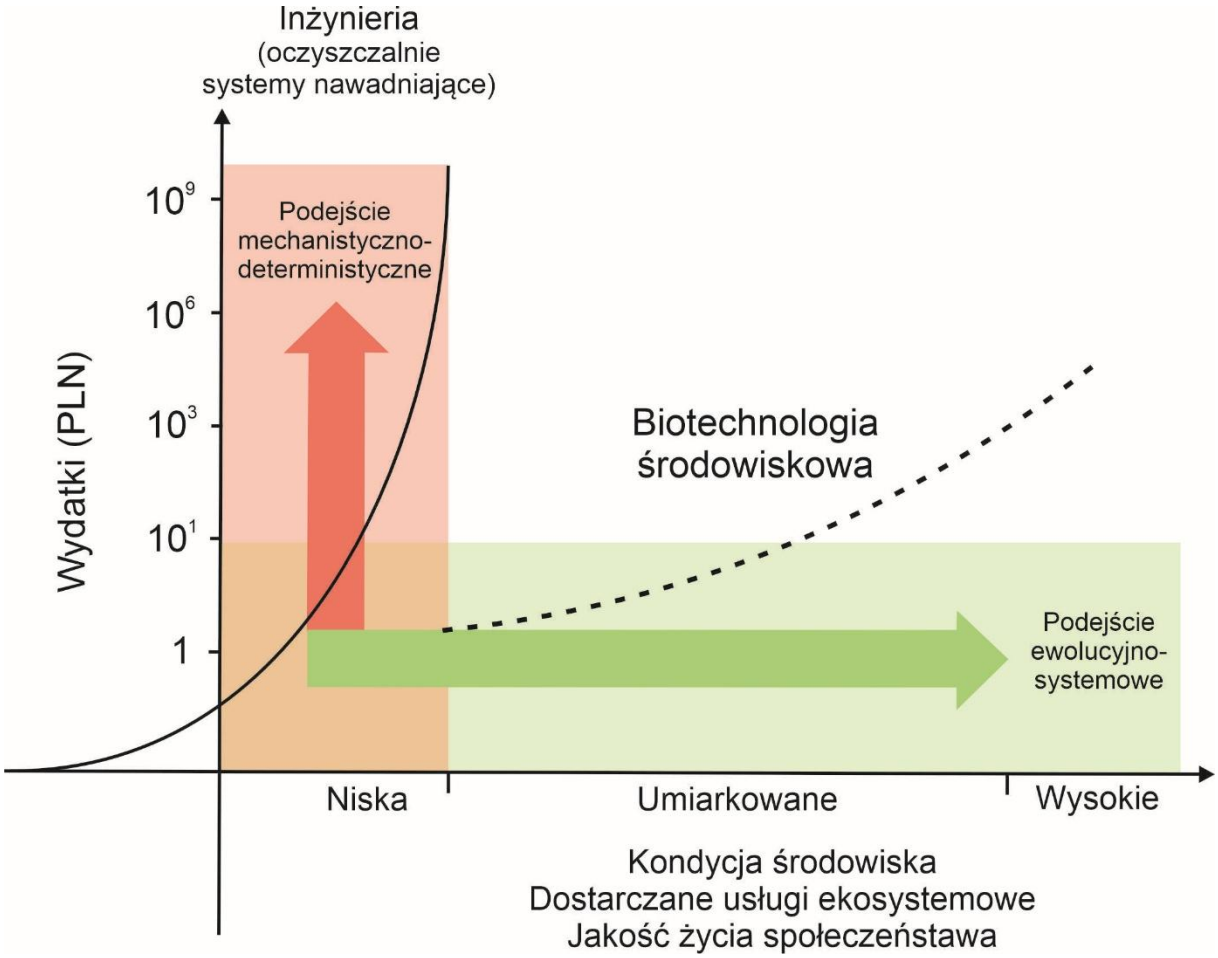
## 1. Wprowadzenie

Ekosystemy stanowią fundamentalną jednostkę strukturalno-funkcjonalną biosfery, zarówno w aspekcie lądowym jak i wodnym. To w nich zachodzą procesy związane z obiegiem materii i przepływem energii, a także dostarczają wielu korzyści dla społeczeństwa i gospodarki, wpływając na dobrostan człowieka (Lynch et al., 2023; Dudgeon & Strayer, 2025). W tym kontekście znaczącą rolę spełniają ekosystemy lentyczne, mimo że stanowią niewielki udział powierzchniowy na Ziemi (około 1%) istotnie kształtują globalną różnorodność biologiczną (Tickner et al., 2020; Lynch et al., 2023; Dudgeon & Strayer, 2025). Zabezpieczenie ich odpowiedniego stanu ekologicznego jest istotnym problemem przed którym stoi świat nauki. Wysokie tempo degradacji rzeki i jezior przekłada się na zaburzenie procesów ekologicznych, co implikuje pogorszenie jakości życia ludzi na globalną skalę (Tickner et al., 2020; Dudgeon & Strayer, 2025). Zgodnie z Living Planet Report 2024 średnia liczebność monitorowanych populacji hydrobiontów związanych z ekosystemami słodkowodnymi zmniejszyła się o 85% w latach 1970–2020. Był to największy spadek spośród analizowanych w raporcie środowisk: słodkowodnego, lądowego i morskiego (Shaw et al., 2024). Dudgeon i Strayer (2025) opisują trzy związane ze sobą zjawiska, które charakteryzują współczesny kryzys bioróżnorodności ekosystemów słodkowodnych,

1) „*great thinning*” zanik populacji i zmniejszanie się zasięgów występowania gatunków;
2) „*great shrinking*” zmniejszanie się rozmiarów ciała organizmów w efekcie selektywnego przełowienia osobników o większych wymiarach;
3) „*great mixing*” ujednolicenie biocenoz na skutek inwazji gatunków obcych.

Procesy te nie odnoszą się wyłącznie do liczby taksonów, ale również do organizacji funkcjonalnej zbiorowisk oraz zdolności ekosystemów do samoregulacji i regulacji po zaburzeniach. Jest to tożsame z terminem *ecological resilience*, czyli zdolnością ekosystemu do absorbowania zaburzeń bez zmiany stanu stabilnego (Tickner et al., 2020; Dudgeon & Strayer, 2025). W odpowiedzi na te wyzwania następuje wyraźne rozszerzenie sposobu opisu i oceny stanu ekosystemów wodnych. Obecne kierują się one w stronę zrozumienia znaczenia relacji pomiędzy bioróżnorodnością, oraz poziomem dostarczanych usług w skali zlewni (Turner et al., 2017; Stefanidis & Papastergiadou, 2024; Fairbrass et al., 2025). Jest to związane z holistycznym podejściem do zrozumienia funkcjonowania ekosystemów, zgodnie ze zmianą podejścia z mechanistyczno-

deterministycznego na ewolucyjno-systemowy (rys. 1). W takim podejściu zarządzanie gospodarka wodną uwzględnia korzyści jakie dostarcza biotechnologia środowiska w minimalizowaniu kosztów działań przy optymalizacji dobrostanu człowieka (Zalewski, 2020).




Rys. 1. Współzależność pomiędzy kondycją środowiska a stosowanymi metodami zachowania jakości ekosystemów wodnych (Zalewski, 2014, zmodyfikowany)

Według IUCN (2024), biomonitoring i bioocena stanowią pojęcia blisko związane, ale nie tożsame. Bioocena ukierunkowana jest na wykrywanie degradacji ekosystemu, a monitoring złożoności biologicznej, dokumentuje pełne spektrum bioty. Z tego powodu **bioróżnorodność** jest powszechnie definiowana jako różnorodność życia we wszystkich jego przejawach. Obejmuje ona zmienność na poszczególnych poziomach organizacji biologicznej - od genów, przez gatunki i populacje, aż po ekosystemy (Gaston & Spicer, 2004). Zatem możemy podzielić ją na trzy fundamentalne poziomy:

1) **różnorodność genetyczną** – odnoszącą się do zmienności warunkującej zdolności adaptacyjne populacji oraz jej odporność na presje środowiskowe ponieważ odnosi się

do dziedzicznej zmienności. W klasycznym ujęciu definiuje się ją jako zróżnicowanie alleli i genotypów obecnych w populacji, przejawiające się w obserwowanych różnicach morfologicznych, fizjologicznych i behawioralnych między osobnikami (Frankham et al., 2002; Toro & Caballero, 2005). Z biochemicznego punktu widzenia Nei (1973) zdefiniował różnorodność genetyczną jako prawdopodobieństwo, że dwa allele losowo pobrane z populacji będą różne, co do dziś stanowi jedno z najczęściej stosowanych ujęć operacyjnych w badaniach populacyjnych. Zmienność genetyczna warunkuje potencjał adaptacyjny organizmów oraz ich zdolność do długoterminowego przetrwania w zmieniających się warunkach środowiskowych, dlatego obfita literatura wskazuje, że jest ona nierozerwalnie związana z ewolucyjną sprawnością populacji, a jej erozja - w wyniku fragmentacji siedlisk, chowu wsobnego czy dryfu genetycznego - niesie poważne konsekwencje demograficzne (DeWoody et al., 2021; Willi et al., 2022). W praktyce badawczej zmienność genetyczna opisywana jest za pomocą wskaźników takich jak heterozygotyczność oczekiwana, bogactwo alleliczne, udział loci polimorficznych oraz miary zróżnicowania między populacjami, które łącznie pozwalają rekonstruować zarówno aktualny stan genetyczny, jak i historię demograficzną badanych populacji (Nei, 1973; Toro & Caballero, 2005).

2) **różnorodność taksonomiczną** – związaną z bogactwem gatunkowym i liczebnością populacji w obrębie zespołu biologicznego. Stanowi najczęściej stosowany poziom opisu bioróżnorodności w badaniach biologicznych, obejmując zróżnicowanie organizmów ujmowane przez pryzmat jednostek systematycznych (Gaston & Spicer, 2004; Magurran, 2004). Magurran (2004) podkreśla, że podstawowym wyrazem różnorodności taksonomicznej jest bogactwo gatunkowe, rozumiane jako liczba gatunków stwierdzonych na danym obszarze lub w obrębie badanej wspólnoty, choć pełniejsze ujęcia uwzględniają odrębność taksonomiczną i relacje systematyczne między taksonami. Wymiar taksonomiczny jest szczególnie użyteczny w inwentaryzacjach przyrodniczych, monitoringu środowiskowym oraz analizach porównawczych między siedliskami, regionami i przedziałami czasowymi (Magurran, 2004; Gaston & Spicer, 2004). Jednocześnie wiadomo, że dwa zbiorowiska o identycznym bogactwie gatunkowym mogą istotnie różnić się pod względem relacji filogenetycznych, funkcji ekologicznych czy wewnętrznej zmienności genetycznej, co potwierdza, że sama różnorodność taksonomiczna nie jest wystarczającym wskaźnikiem stanu układu przyrodniczego (Naeem et al., 2016).

3) **różnorodność funkcjonalną** – wynikającą ze spektrum cech biologicznych organizmów, decydujących o pełnionych rolach troficznych, strategiach życiowych oraz udziale w obiegu materii. Mogą one mieć charakter morfologiczny, fizjologiczny, behawioralny oraz mogą dotyczyć strategii rozrodczych. Aktywność życiowa przejawia się m.in. pobieraniem zasobów, mobilnością, poziomem tolerancji na stresory środowiskowe oraz udziałem w obiegu materii (Gomes et al., 2023). Obecnie takie podejście funkcjonalne jest intensywnie rozwijane w przypadku badań hydrobiologicznych (Martini et al., 2021). Według literatury najczęściej stosowanymi wskaźnikami różnorodności funkcjonalnej są analizy frekwencji cech biologicznych (ang. *Biological Traits Analysis* - BTA); zajmowanej przestrzeni cech (ang. *Functional Richness* - FRic); równomierności rozmieszczenia gatunków w przestrzeni cech (ang. *Functional Evenness* - FEve, *Functional Divergence* - FDiv i *Functional Dispersion* - FDis) (Gomes et al., 2023). Wskazuje się również na odejście od jednowymiarowego opisu bioróżnorodności i wykorzystywania podejścia funkcjonalnego jako zestawu kompletnych miar opisujących różne aspekty organizacji zbiorowisk (Mouillot et al., 2013; Gomes et al., 2023). Szersze zróżnicowanie cech organizmów może wpływać na bardziej efektywne wykorzystywanie zasobów, a pełnienie uzupełniających się ról może wpływać na produktywność, stabilność i wielofunkcyjność ekosystemu. Warto również zauważyć, że utrata przez niego unikalnych cech prowadzi do zaniku konkretnych funkcji nawet w przypadku, gdy gwałtowanie nie spada liczba gatunków (Gomes et al., 2023; Tang et al., 2024). W ekosystemach wodnych ma to znaczenie dla jakości dostarczanych usług ekosystemowych w szczególności tych, które zależą od właściwości funkcjonalnych organizmów (m.in. bioproduktywności, tempa obiegu materii organicznej, kontroli trofii, filtracji materii zawieszonej, dekompozycji materii organicznej, lub odporności ekosystemu na czynniki zaburzające). Ten rodzaj różnorodności może być rozpatrywana jako klucz do zrozumienia mechanizmów działania ekosystemów.

Fundamentalne zagrożenia bioróżnorodności ekosystemów wodnych moją naturę wieloczynnikową i synergiczną (Stefanidis & Papastergiadou, 2024; Dudgeon & Strayer, 2025). Można wśród nich wyróżnić czynniki związane ze zmianami klimatycznymi oraz działalnością człowieka (Tabela 1).

Tabela 1. Główne źródła zagrożeń dla bioróżnorodność ekosystemów wodnych.

| Rodzaj zagrożenia | Mechanizmy oddziaływania |
|---|---|
| **Zmiany klimatu** | Zmiany reżimu wodnego, wzrost temperatury wód, ekstremalne zjawiska długotrwałych susz i nagłych powodzi, wzrost zasolenia wód |
| **Eutrofizacja (nadmierna)** | Zaburzenia struktury troficznej, deficyty tlenowe, niekontrolowane zakwity fitoplanktonu (w tym gatunków produkujących toksyny) |
| **Fragmentacja siedlisk** | Bariery migracyjne, izolacja genetyczna populacji |
| **Inwazje obcych gatunków** | Presja na gatunki rodzime, wysoka odporność i brak naturalnych wrogów, przenoszenie patogenów |
| **Nadmierna eksploatacja** | Przełowienie łowisk, niszczenie dna i zaburzenie transportu osadów przez pozyskiwanie piasku i żwiru |
| **Zanieczyszczenia nowego typu (biologiczne, chemiczne, fizyczne)** | Toksyczność nowych typów zanieczyszczeń dla gatunków wodnych, rozprzestrzenianie się genów odporności antybiotykowej, nieznane szlaki metaboliczne w środowisku i wpływ na ekosystemy |

W ramach oceny dostarczanych **usług ekosystemowych** (ES) analizuje się często wielkość **kapitału naturalnego**, który opisuje przyrodę jako zbiór zasobów, z których może wynikać przepływ dóbr i korzyści dla społeczeństwa i gospodarki (Mandle et al., 2025). W odniesieniu do ekosystemów wodnych śródlądowych obejmuje to przede wszystkim zasoby biologiczne, regulacyjne zdolności oraz wartości niematerialne rzek, jezior i mokradeł (Smith et al., 2017; Lynch et al., 2023; Waikato Regional Council, 2024). Kolejnym krokiem jest ustalenie **potencjału** analizowanego ekosystemu wodnego czyli określenia zdolność tego kapitału do dostarczania ES obecnie i w przyszłości. Jest to w dużej mierze zależne od zasięgu, stanu ekologicznego, odporności i presji środowiskowych/antropogenicznych (Waikato Regional Council, 2024; UN-Water, 2024; Hashemi et al., 2026). Obecnie wskazuje się na to, ażeby nie utożsamiać kapitału naturalnego wyłącznie z wartością monetarną. Kluczowym aspektem jest łączenie danych o stanie ekologicznym z odpornością i rzeczywistym przepływem korzyści dla społeczeństwa. W literaturze najczęściej dzieli się je na trzy główne grupy usług (Millennium Ecosystem Assessment, 2005; Lynch et al., 2023; Ferrini et al., 2025):

a) **Usługi zaopatrzeniowe** – związane m. in. z dostarczaniem wody pitnej, wody do nawodnienia upraw, zasoby biologiczne (ryby, makrofity, małże, itd.), zasoby genetyczne oraz materiały pozyskiwane z organizmów (np. trzcina).

b) **Usługi regulacyjne** – związane m in. z oczyszczaniem wody, retencją osadów i magazynowaniem składników biogennych, przeciwdziałaniem erozji brzegów i kontroli powodzi, wpływem na regulację przepływów bazowych, sekwestrację węgla oraz wpływem na lokalną regulację klimatu.

c) **Usługi kulturowe** – związane m. in. z turystyką i rekreacją, wędkarstwem, walorami estetycznymi krajobrazu, walorami edukacyjnymi i naukowymi, a także z niematerialnymi dobrami takimi jak walory duchowe, artystyczne czy wartości związane z lokalną tożsamością kulturową.

Synergia informacji o stanie ekosystemów i dostarczanych przez nie usług umożliwia dogłębną analizę zachowania przez ekosystem potencjału w długim okresie. Przy opisywaniu kapitału naturalnego według wskazań SEEA-EA (*System of Environmental-Economic Accounting – Ecosystem Accounting*) należy rozdzielać ocenę zasobu od oceny przepływu usługi (Ferrini et al., 2025). Potencjał ekosystemów wodnych wynika z całej organizacji systemu: jakości siedlisk, różnorodności biologicznej, procesów biogeochemicznych i hydrologicznymi, oraz odziaływania pomiędzy zlewnią, a ekosystemem wodnym (Lynch et al., 2023; UN-Water, 2024; Hashemi et al., 2026). Z tej perspektywy możemy traktować jeziora, rzeki i mokradła jako aktywa wspierające bezpieczeństwo wodne, odporność klimatyczną, ochronę różnorodności i trwałość lokalnych źródeł utrzymania (UN-Water, 2024; Hashemi et al., 2026).

Rodzima bioróżnorodność stanowi fundamentalną podstawę dla wszystkich tych kategorii usług (Lynch et al., 2023). Oznacza to, że jej utrata prowadzi nie tylko do zubożenia przyrody, lecz również do obniżenia kondycji ekosystemów do świadczenia istotnych korzyści dla społeczeństwa (Tickner et al., 2020; Lynch et al., 2023; Dudgeon & Strayer, 2025). Aktualnie podkreśla się, że pomiędzy kapitałem naturalnym, potencjałem i usługami ekosystemowymi istnieje relacja przyczynowo skutkowa. Stan i zasoby ekosystemu tworzą fundament do potencjalnego świadczenia usług, a rzeczywisty ich przepływ zależy od świadomości społecznej, dostępności, sposobów użytkowania oraz form zarządzania (Millennium Ecosystem Assessment, 2005; Ferrini et al., 2025; Waikato Regional Council, 2024). Zatem obecność cennego przyrodniczo zbiornika wodnego nie musi wprost przekładać się na pełne wykorzystanie

jego funkcji. Sam wzrost popytu na określoną usługę nie zagwarantuje, że ekosystem zachowa długoterminową zdolność do jej dostarczania (Li and Tsigaris, 2024; Mandle et al., 2025). Jednocześnie wzrost wartości pieniężnej usługi nie zawsze oznacza poprawę stanu przyrody, ponieważ wyceny mogą rosnąć wraz z popytem nawet przy niezmienionej lub pogarszającej się jakości ekosystemu. Aktualnie podkreśla się, że konieczne jest łączenie wyceny ekonomicznej z oceną stanu ekologicznego wraz z analizą trendów zmian w celu wdrażania zasad zrównoważonego rozwoju (Ferrini et al., 2021; Li and Tsigaris, 2024; Mandle et al., 2025).

Praktycznym aspektem wykorzystaniem informacji o poziomie bioróżnorodności ekosystemów wodnych jest próba ustalenie ich zdrowia. Ten stan można zdefiniować jako stopień zachowania prawidłowej struktury i funkcjonowania ekosystemu, określony na podstawie elementów biologicznych, fizykochemicznych i hydromorfologicznych (Dyrektywa 2000/60/WE; Markowski & Wojtasik, 2024). Ważne jest odróżnienie zdrowia ekosystemu od samego monitoringu różnorodności biologicznej. Zgodnie z IUCN tego typu monitoring dokumentuje spektrum bioty i jej zmian, natomiast ocena zdrowia ma bardziej diagnostyczny charakter i jest ukierunkowana na wykrywanie degradacji oraz ocenę przekształcenia ekosystemu (IUCN, 2024). Ocena zdrowia wymaga nie tylko danych o składzie gatunkowym, lecz również powiązania tych danych z presjami środowiskowymi, warunkami siedliskowymi oraz całościowym funkcjonowaniem układu, w tym świadczeń usług jako wymiaru społeczno-ekonomicznego (Stefanidis & Papastergiadou, 2024; IUCN, 2024).

Współczesne badania nad ekosystemami wodnymi wymagają podejścia integracyjnego. Sama analiza różnorodności taksonomicznej okazuje się nie wystarczająca do opisu działania tak złożonego układu jakim jest ekosystem. Analogicznie sama ocena jakości wód nie oddaje pełnego obrazu jego kondycji i zdolności do świadczenia usług ekosystemowych. Konieczne zatem staje się holistyczne podejście, łączące informacje o biocenozach, cechach funkcjonalnych, procesach hydrologicznych, presjach środowiskowych, stanie siedlisk i aspekcie społeczno-gospodarczym opisującym relacje społeczeństwo-przyroda. Tak szeroki model interpretacji pozwala właściwie ocenić potencjał i ograniczenia ekosystemów wodnych w warunkach współczesnych przemian środowiskowych. Takie podejście odpowiada zarówno na potrzebę lepszego zrozumienia procesów ekologicznych, jak i na praktyczne wyzwania związane z bezpieczeństwem wodnym, adaptacją do zmian klimatu oraz optymalizacją renaturyzacji zdegradowanych ekosystemów. Tym wyzwaniom

odpowiada **ekohydrologia**, która jest transdyscyplinarną dziedziną nauki łączącą nauki ścisłe, techniczne i społeczne. Skupia się ona na zależności pomiędzy obiegiem wody w zlewni, a funkcjonowaniem organizmów i ekosystemów (podwójna regulacja pomiędzy czynnikami biotycznymi i abiotycznymi) oraz wykorzystującą tę wiedzę do poprawy jakości wód i potencjału środowiskowego (Zalewski, 2020). Dudgeon i Strayer (2025) ostrzegają jednak, że bez zasadniczej zmiany w świadomości społecznej i politycznej woli działania, przy narastającym kryzysie klimatycznym, nawet te ambitne plany mogą być niewystarczające do zatrzymania utraty słodkowodnej różnorodności biologicznej w najbliższych dekadach. Z tego powodu współczesne wprowadzenie do problematyki ekosystemów wodnych powinno ujmować je nie jako izolowane obiekty przyrodnicze, lecz jako dynamiczne, wielofunkcyjne i podatne na presje systemy społeczno-ekologiczne, których trwałość zależy od zachowania bioróżnorodności, integralności procesów i rozsądnego zarządzania w skali zlewni.

Jednym z coraz wyraźniej zaznaczających się przejawów współczesnych zmian środowiskowych w jeziorach śródlądowych jest **wzrost zasolenia** (=salinizacja), rozumiana jako wzrost stężenia rozpuszczonych jonów w wodzie. Proces ten może być wzmacniany przez ocieplenie klimatu implikujący: (i) wzrost parowania, (ii) deficyt opadów, (iii) obniżanie poziomu wody i (iiii) ograniczenie dopływu oraz antropogeniczne przekształcenia bilansu wodnego. Wraz ze wzrostem zasolenia dochodzi zwykle do selekcji wrażliwych taksonów, spadku bogactwa gatunkowego oraz wzrostu udziału wyspecjalizowanych ekologicznie form euryhalinowych (Williams, 1998). Badania porównawcze potwierdzają, że reakcja biocenoz ma najczęściej charakter filtracji środowiskowej, a nie prostego, liniowego spadku wszystkich parametrów biologicznych (Williams, 1998; Schallenberg et al., 2003; Brucet et al., 2009). Szczególnie dobrze zależności te opisano dla bezkręgowców, które szybko reagują na zmiany składu jonowego wody i dlatego są uznawane za czułe wskaźniki przekształceń siedliskowych. Badania nad zespołami zooplanktonu i zoobentosu jeziornego wykazały, że wzrost zasolenia może prowadzić do zmian bogactwa gatunkowego, przebudowy struktury dominacji, średniej wielkości organizmów oraz relacji w sieciach troficznych (Brucet et al., 2006; Jeppesen et al., 2007; Jeppesen et al., 2010; Brucet et al., 2012; Hébert et al., 2023). Wykazano, że spójne straty liczebności i różnorodności bezkręgowców wraz ze wzrostem zasolenia stanowi jedno z kluczowych zagrożeń dla zróżnicowania biologicznego w pelagialu i bentalu. Z kolei syntetyczne opracowania (np. Williams, 1993; Jeppesen et al., 2015; Jeppesen et al., 2020; Saini & Pandey, 2023)

podkreślają, że dalszy wzrost salinizacji wywołany zmianami klimatu prowadzi do osłabienia odporności ekosystemów wodnych, zawężania puli gatunków oraz deregulacji funkcjonowania jezior w ujęciu globalnym. Z tej perspektywy zasolenie staje się jednym z kluczowych wymiarów interpretacji współczesnych przemian jezior, zwłaszcza w regionach Ziemi szczególnie podatnych na suszę, wzrost temperatury i niestabilność bilansu wodnego. Zastosowanie interdyscyplinarnego podejścia pozwala na pełniejsze zrozumienie mechanizmów kształtujących zmiany w bioróżnorodności, zdrowiu ekosystemów oraz ich zdolności do świadczenia ES.

## 2. Cele badawcze

Głównym celem rozprawy doktorskiej jest wyjaśnienie wpływu zmian klimatycznych, realizujących się między innymi poprzez proces salinizacji, na strukturę zoocenoz wodnych oraz zdrowie ekosystemowe jezior, a także ocena przydatności zintegrowanego podejścia ekosystemowego do identyfikacji mechanizmów odpowiedzialnych za funkcjonowanie, odporność i przekształcenia tego typu ekosystemów.

W odniesieniu do celu głównego wyznaczono następujące cele szczegółowe:

- Określenie zależności między warunkami klimatyczno-hydrologicznymi, a poziomem zasolenia oraz zróżnicowaniem hydrochemicznym badanych jezior.
- Ustalenie roli zasolenia jako jednego z kluczowych filtrów środowiskowych kształtującego strukturę zespołów organizmów wodnych.
- Określenie kierunku zmian liczebności, biomasy oraz składu taksonomicznego biocenoz wodnych wzdłuż gradientu zasolenia.
- Identyfikacja progów zmian środowiskowych, po przekroczeniu których dochodzi do reorganizacji struktury biocenoz jeziornych.
- Ocena wpływu zmian biotycznych i abiotycznych na zdrowie ekosystemowe jezior, rozumiane jako integralność strukturalna, integralność procesów oraz potencjał do świadczenia usług ekosystemowych.
- Określenie znaczenia czynników krajobrazowych, hydrologicznych i ochronnych w kształtowaniu zdrowia ekosystemowego badanych ekosystemów jeziornych**.**

## 3. Hipotezy badawcze

**H1:** Zmiany hydroklimatyczne, w tym wzrost temperatury i deficyty wodne, sprzyjają salinizacji wód jeziornych oraz wtórnym przekształceniom hydrochemicznym, a skala tej odpowiedzi jest modyfikowana przez uwarunkowania krajobrazowe, hydrologiczne i ochronne.

**H2**: Gradient zasolenia stanowi nadrzędny filtr środowiskowy (silniejszy niż czynniki termiczne i geograficzne) kształtujący strukturę biocenoz, gdzie zależność ta ma charakter unimodalny: umiarkowane zasolenie generuje lokalne „gorące punkty" bioróżnorodności, podczas gdy postępująca salinizacja prowadzi do znacznego spadku bogactwa gatunkowego, skrócenia sieci troficznych i dominacji unikalnych, ekologicznie wyspecjalizowanych taksonów halofilnych.

**H3:** Wywołane salinizacją uproszczenie struktury biocenoz oraz zaburzenia procesów biogeochemicznych są związane z obniżeniem składowych zdrowia ekosystemowego oraz potencjału świadczenia usług ekosystemowych, przy czym skala tej zależności jest modyfikowana przez stan zlewni, stref buforowych i presję antropogeniczną.

**4. Artykuły wchodzące w skład cyklu publikacji**

W skład cyklu publikacji, stanowiących podstawę rozprawy doktorskiej jako spójny tematycznie cykl artykułów pt. „Wpływ zasolenia na różnorodność strukturalną i funkcjonalną zoocenoz oraz zdrowie ekosystemowe jezior" zaliczono 5 publikacje, w tym 3 opublikowane oraz 2 w trakcie procedury wydawniczej:

A1. Matela M.✉, Obolewski K. (2022). Structural diagnosis of benthic invertebrate communities in relation to salinity gradient in Baltic coastal lake ecosystems using biological trait analysis. *Scientific Reports*, 12(1), 12750. https://doi.org/10.1038/s41598-022-17002-8 (IF=4.44, 140 pkt MNiSW)

Udział doktoranta w powstaniu opracowania 75%.

A2. Sarmanov A., Matela M. ✉, Sultanov Y., Sergaliyev N., Obolewski K. (2024). Salinisation effects on benthic invertebrate assemblages in shallow lakes in arid and semiarid climate zones. *Scientific Reports*, 14, 30622. https://doi.org/10.1038/s41598-024-82527-z (IF=4.08, 140 pkt MNiSW)
Udział doktoranta w powstaniu opracowania 35%.

A3. Matela M. ✉, Obolewski K. (2026), Quantifying the ecosystem health of Baltic coastal lakes based on a multifaceted index, *Scientific Reports*, 16, 19968 https://doi.org/10.1038/s41598-026-50938-9 (IF=4.9, 140 pkt MNiSW)
Udział doktoranta w powstaniu opracowania 80%.

A4. Sultanov Y., Matela M. ✉, Sarmanov A., Sergaliyev N., Bakiyev S., Obolewski K. (w recenzji), Salinity as the primary driver of zooplankton community shifts in Eurasian arid lakes. *Ecological Indicators*, 000-000 (IF=8.7, 200 pkt MNiSW)

Udział doktoranta w powstaniu opracowania 35%.

A5. Matela M. ✉, Obolewski K. (w recenzji), Quantifying ecosystem services in Baltic coastal lakes under different protection regimes. *Ecosystem Services*, 000-000 (IF=7.9, 140 pkt MNiSW)

Udział doktoranta w powstaniu opracowania 80%.

## 5. Materiały i Metody

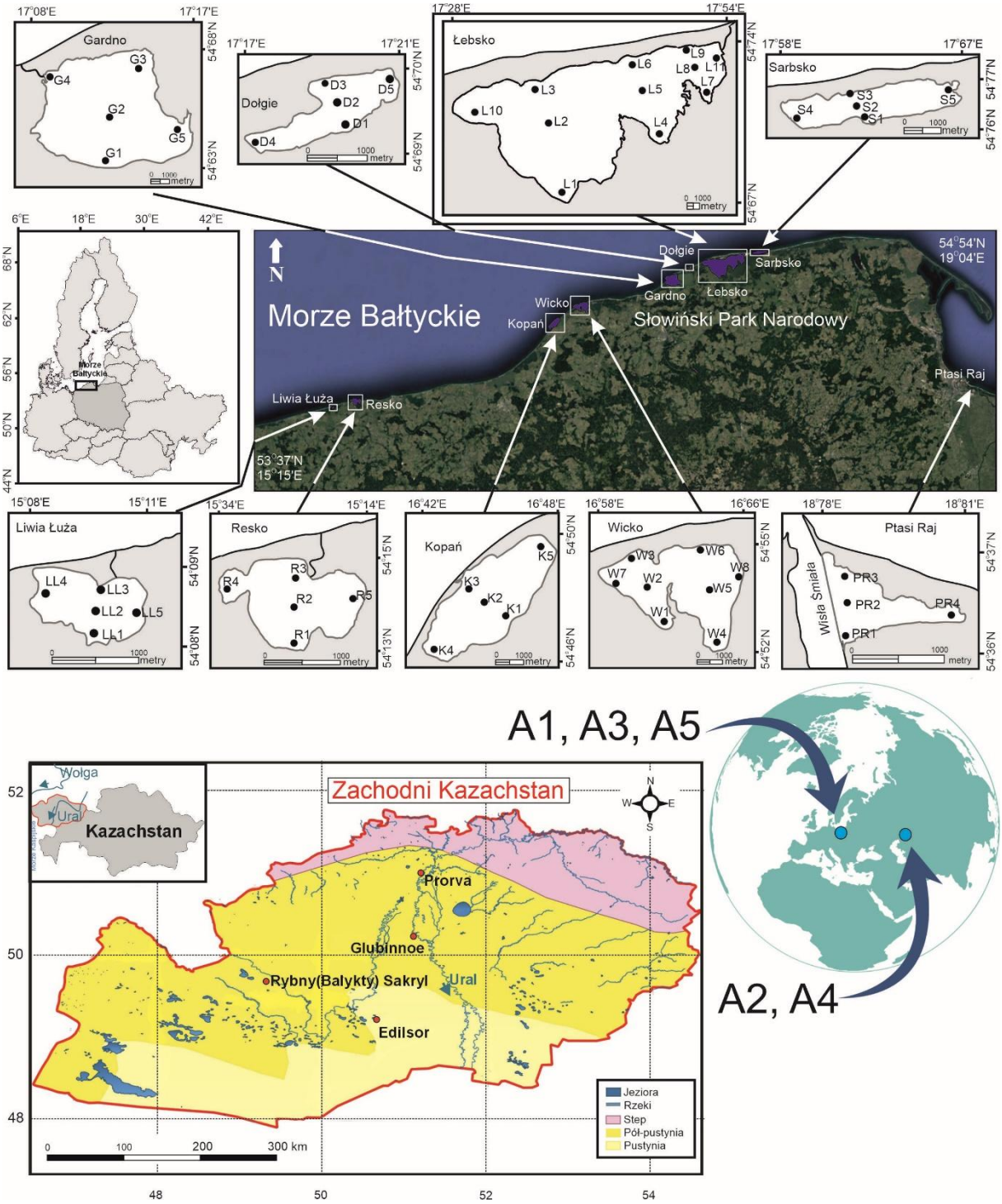
### *5.1. Obiekty badawcze*

Badania ujęte w ramach rozprawy doktorskiej dotyczyły 13 obiektów badawczych – 9 jezior przybrzeżnych południowego Bałtyku oraz 4 jezior w Zachodnim Kazachstanie. Informacje dotyczące charakterystyki badanych zbiorników wodnych przedstawiono w tabeli 2 i na rysunku 2. Pobór prób obejmował łącznie lata 2019–2021. Przeanalizowano łącznie 462 prób biologicznych, w tym 426 prób makrozoobentosu i 36 prób zooplanktonu. Równocześnie jako tło środowiskowe wykorzystano 390 zestawów wyników fizyczno-chemicznych wód badanych jezior oraz 237 geokompleksów i 74 hydrokompleksów dotyczących tych ekosystemów.

Dobór obiektów badawczych miał charakter celowy i wynikał z potrzeby objęcia analizą zbiorników reprezentujących zróżnicowany stopień zasolenia, odmienne uwarunkowania klimatyczne oraz różny poziom presji antropogenicznej i ochrony przyrody. W grupie jezior przybrzeżnych uwzględniono zbiorniki słonawowodne, przejściowe i słodkowodne (wg kryterium łączności z morzem; Venice System, 1959), natomiast w zachodnim Kazachstanie badaniami objęto jeziora reprezentujące gradient od warunków słodkowodnych do mezohalinowych. Tak dobrany zestaw obiektów umożliwił przeprowadzenie analiz porównawczych odnoszących się zarówno do wpływu zasolenia na strukturę biocenoz wodnych, jak i do znaczenia uwarunkowań zlewniowych, przestrzennych oraz ochronnych dla funkcjonowania badanych ekosystemów.

Tabela 2. Charakterystyka obiektów badawczych i odniesienie do artykułów stanowiących podstawę dysertacji

| Jeziora | Położenie geograficzne | Powierzchnia [ha] | $H_{śr.}$ [m] | $H_{max.}$ [m] | Klimat | Poziom zasolenia | Liczba stanowisk | Artykuły |
|---|---|---|---|---|---|---|---|---|
| **Polska** | | | | | | | | |
| Ptasi Raj | 54° 22′ N 18° 48′ E | 53,1 | 1,2 | 2,6 | Umiarkowany | β-mesohalinowy | 4 | A1 |
| Łebsko | 54° 43′ N 17° 25′ E | 7020,0 | 1,6 | 4,7 | Umiarkowany | oligohalinowy | 11 | A1, A3 i A5 |
| Resko | 54° 09′ N 15° 22′ E | 554,1 | 1,6 | 2,6 | Umiarkowany | oligohalinowy | 5 | A1, A3 i A5 |
| Kopań | 52° 29′ N 16° 27′ E | 752,8 | 1,5 | 2,6 | Umiarkowany | oligohalinowy | 5 | A1, A3 i A5 |
| Gardno | 54° 39′ N 17° 07′ E | 2260,8 | 1,4 | 2,2 | Umiarkowany | oligohalinowy | 5 | A1, A3 i A5 |
| Liwia Łuża | 54° 05′ N 15° 06′ E | 172,3 | 1,0 | 1,6 | Umiarkowany | limnetyczny | 5 | A1 |
| Sarbsko | 54° 46′ N 17° 38′ E | 610,6 | 1,2 | 3,2 | Umiarkowany | limnetyczny | 5 | A1 |
| Wicko | 52° 32′ N 16° 37′ E | 977,0 | 2,4 | 4,7 | Umiarkowany | limnetyczny | 8 | A1, A3 i A5 |
| Dołgie Wielkie | 54° 42′ N 17° 12′ E | 135,7 | 1,4 | 2,7 | Umiarkowany | limnetyczny | 5 | A1, A3 i A5 |
| **Kazachstan** | | | | | | | | |
| Prorva | 51°14′ N 51°31′ E | 2,8-3,4 | 1,5 | 4,2 | Umiarkowany kontynentalny (zimnych stepów) | oligohalinowy | 9 | A2 i A4 |
| Glubinnoe | 50°19′ N 51°03′ E | 0,8-6,1 | 1,2 | 1,9 | Półpustynny (zimnych pustyń) | oligohalinowy | 9 | A2 i A4 |
| Balykty Sarkyl | 49°36′ N 49°18′ E | 1270-1600 | 1,6 | 4,2 | Półpustynny (zimnych pustyń) | β-mesohalinowy | 9 | A2 i A4 |
| Edilsor | 49°13′ N, 50°44′ E | 955-1190 | 1,3 | 3,7 | Pustynny (zimnych pustyń) | α-mesohalinowy | 9 | A2 i A4 |




Rys. 2. Lokalizacja badanych jezior.

*5.2. Metody badań*

W ramach badań uwzględnionych w rozprawie doktorskiej przeprowadzono zintegrowane pomiary terenowe, analizy laboratoryjne oraz modelowanie oparte na własnych danych oraz pozyskanych z literatury. Syntetyczne zestawienie zrealizowanych zadań

badawczych przedstawiono w tabeli 3, natomiast szczegółowy opis zastosowanej metodyki zamieszczono w publikacjach stanowiących integralną część niniejszej dysertacji.

Tabela 3. Metody badań terenowych, laboratoryjnych oraz pozostałych analiz przeprowadzonych w pracy doktorskiej.

| PARAMETR | METODA/SPRZĘT | A1 | A2 | A3 | A4 | A5 |
|---|---|---|---|---|---|---|
| BADANIA TERENOWE | | | | | | |
| Tlen rozpuszczony | Wieloparametryczna sonda AquaProbe 7000/ WTW, MultiLine P4 | | | | | |
| Temperatura wody | | | | | | |
| Zasolenie | | | | | | |
| Odczyn pH wody | | | | | | |
| Pobór prób zoobentosu | Czerpak Van Veen'a, siatka o rozmiarze oczek 0,5mm | | | | | |
| Pobór prób zooplanktonu | siatka planktonowa Apsteina (rozmiar oczek 30 µm) | | | | | |
| ANALIZY LABORATORYJNE | | | | | | |
| Twardość wody | Spektrofotometr DR3900, Hach | | | | | |
| Chemiczne zapotrzebowanie na tlen | | | | | | |
| Azotany | | | | | | |
| $Mg^{2+}$ | | | | | | |
| $HCO_3^-$ | | | | | | |
| $SO_4^{2-}$ | | | | | | |
| $Cl^-$ | | | | | | |
| $Ca^{2+}$ | | | | | | |
| ANALIZY GIS/TELEMETRIA | | | | | | |
| Użytkowanie terenu/Pokrycie terenu | QGIS, Corine Land Cover | | | | | |
| Analiza buforu wokół jeziora pod względem charakterystyki geo- i hydrokompleksów | QGIS | | | | | |
| POZOSTAŁE ANALIZY | | | | | | |
| Stopień odporności jeziora na degradację | Wg Bajkiewicz-Grabowska, 1987 | | | | | |
| Potencjał do świadczenia usług ekosystemowych | Wg Krauze K. et al., 2023 | | | | | |
| Różnorodność funkcjonalna | Cechy biologiczne (BTA) | | | | | |
| Różnorodność biologiczna | Analiza zmian bogactwa gatunkowego, zagęszczenia, składu taksonomicznego i bioróżnorodności makrozoobentosu oraz zooplanktonu | | | | | |

W zestawieniu metod oraz analiz statystycznych ujęto wyłącznie procedury zrealizowane bezpośrednio w toku przygotowania rozprawy. Nie przypisywano publikacji składowych

do metod poboru próbek lub oznaczeń laboratoryjnych w przypadkach, gdy wykorzystano wyłącznie dane wtórne (pochodzące z literatury przedmiotu). Specyfikację tych źródeł wydzielono w artykułach stanowiących podstawę niniejszej rozprawy, co pozwoliło na jednoznaczne oddzielenie materiału pozyskanego samodzielnie od danych pochodzących z otwartych repozytoriów, państwowego monitoringu środowiska oraz baz przestrzennych. Dokładne opisy analiz statystycznych znajdują się w opublikowanych pracach.

*5.3. Analizy statystyczne i metody obliczeniowe*

Analizy statystyczne prowadzono w celu opisania struktury i różnorodności biocenoz wodnych, określenia ich związku z gradientem zasolenia i warunkami środowiskowymi oraz oceny zdrowia ekosystemów i potencjału ES. Dobór metod był dostosowany do typu danych (liczebności i biomasy organizmów, obecności taksonów, cech funkcjonalnych, parametrów fizykochemicznych oraz danych przestrzennych), a ich wyniki interpretowano łącznie, z uwzględnieniem ograniczeń wynikających z liczby badanych ekosystemów.

W analizie biocenoz zastosowano podstawowe miary różnorodności taksonomicznej i struktury zespołów, w tym bogactwo taksonomiczne, liczebność, biomasę oraz indeksy różnorodności (wskaźniki α-różnorodności: Simpsona, Shannona, Jaccarda, dominacji; wskaźniki β-różnorodności: SDR-simplex).

Różnorodność funkcjonalną makrozoobentosu opisywano metodą Biological Trait Analysis (BTA). Taksony klasyfikowano na podstawie cech biologicznych, takich jak mobilność, typ siedliska, sposób odżywiania, modyfikowanie siedliska, forma ciała, wielkość ciała i aparat gębowy. Cechy kodowano metodą fuzzy coding, a następnie łączono z liczebnością taksonów, uzyskując macierze częstości modalności cech. Umożliwiło to ocenę reorganizacji funkcjonalnej zespołów niezależnie od samego składu taksonomicznego. Relacje cech z typami jezior wizualizowano dodatkowo za pomocą diagramów cięciwowych (**A1**). Kompletność próbkowania oceniano za pomocą krzywych akumulacji gatunków (SAC), a model Michaelisa–Mentena wykorzystywano do oszacowania asymptotycznego bogactwa taksonów. Pozwalało to odróżnić rzeczywiste różnice biologiczne od możliwych skutków niepełnego wykrycia gatunków lub taksonów rzadkich (**A2**).

Wielowymiarową strukturę danych biologicznych i środowiskowych analizowano z wykorzystaniem metod ordynacyjnych. nMDS stosowano do przedstawienia podobieństwa prób, zespołów organizmów i warunków abiotycznych w przestrzeni zredukowanych wymiarów; dla danych biologicznych wykorzystywano odległość Bray–Curtisa, a dla danych środowiskowych odpowiednie miary odległości euklidesowej (**A1** i **A2**). PCoA oparta

na odległości Gowera służyła natomiast do wizualizacji zróżnicowania cech geo- i hydrokompleksów (**A5**).

Do oceny wielokryterialnej zdrowia ekosystemu zastosowano Analytic Hierarchy Process (AHP) i Fuzzy Comprehensive Evaluation (FCE). AHP służyła do wyznaczenia wag elementów modelu na podstawie porównań parami ocenianych przez ekspertów, a współczynnik spójności CR wykorzystywano do kontroli logicznej zgodności ocen. FCE integrowała dane biologiczne, fizykochemiczne, hydromorfologiczne i dotyczące usług ekosystemowych poprzez funkcje przynależności rozmytej, co umożliwiło przypisanie jezior do klas zdrowia ekosystemowego bez stosowania sztywnych granic klasyfikacyjnych (**A3**). Analizy CA, PCA i DCA wykorzystywano do wstępnego rozpoznania gradientów ekologicznych i wyboru właściwej metody kanonicznej. CCA pozwalała następnie łączyć zmienność składu zooplanktonu ze zmiennymi środowiskowymi; przed budową modeli kontrolowano współliniowość predyktorów współczynnikiem VIF i stosowano procedurę forward selection (**A4**).

Istotność różnic w wielowymiarowej strukturze biocenoz oceniano za pomocą PERMANOVA, ANOSIM oraz, w przypadku danych nieparametrycznych, testu Kruskala–Wallisa. PERMANOVA umożliwiała testowanie wpływu typów jezior, zasolenia, sezonu i innych czynników na strukturę zespołów na podstawie macierzy odległości, bez założenia wielowymiarowej normalności rozkładu. ANOSIM stosowano jako test różnic w podobieństwie między zdefiniowanymi grupami. Dla wskaźników jednowymiarowych test Kruskala–Wallisa uzupełniano testami post-hoc porównań wielokrotnych (Dunna lub porównań średnich rang), przy czym w odpowiednich analizach stosowano korektę Bonferroniego. Homogeniczność wariancji sprawdzano testem Levene'a, a normalność rozkładów testem Shapiro–Wilka, co wspierało wybór testów parametrycznych lub nieparametrycznych (**A1, A2, A4**).

Analizy SIMPER wykorzystywano do dekompozycji średniej niepodobności między grupami na udział poszczególnych taksonów lub wskaźników. Pozwalało to wskazać elementy najsilniej odpowiedzialne za różnice między jeziorami i typami siedlisk. Analizę tę interpretowano jako opis wkładu zmiennych w zróżnicowanie, a nie jako samodzielny test hipotezy. Two-Way Cluster Analysis służyła do równoczesnej klasyfikacji prób i taksonów według wzorców współwystępowania. Beta-różnorodność analizowano metodą SDR-simplex, która rozdzielała udział substytucji gatunków (turnover), zagnieżdżenia i komponentu podobieństwa w regionalnym zróżnicowaniu biocenoz (**A2, A4, A5**).

Związki między zmiennymi analizowano korelacją rang Spearmana, stosowaną do oceny monotonicznej współzmienności parametrów hydrochemicznych, wskaźników biologicznych i cech przestrzennych. W analizach geo- i hydrokompleksów korelacje interpretowano przede wszystkim jako miarę współzmienności i redundancji wskaźników, a nie jako dowód niezależnych zależności przyczynowo-skutkowych. Z uwagi na zagnieżdżenie jednostek przestrzennych w obrębie jezior oraz eksploracyjny charakter części analiz, wartości *p* traktowano pomocniczo (**A2, A5**).

Nieliniowe odpowiedzi biocenoz na zasolenie badano uogólnionymi modelami addytywnymi (GAM). Modele te umożliwiły identyfikację kształtu relacji między zasoleniem a wskaźnikami zooplanktonu oraz wskazanie zakresów wartości, w których następowała wyraźna zmiana trendu. Interpretacja progów ekologicznych miała charakter empiryczny i była odnoszona do danych z badanych jezior, a nie traktowana jako uniwersalna wartość graniczna dla wszystkich systemów (**A4**).

## 6. Wyniki

### *6.1. Zasolenie jako główny czynnik zmian ekosystemowych w jeziorach*

W analizowanych artykułach zasolenie pełni rolę podstawowej osi różnicującej badane ekosystemy, zarówno w jeziorach przybrzeżnych południowego Bałtyku, jak i w jeziorach śródlądowych zachodniego Kazachstanu. W systemach nadbałtyckich (**A1**) gradient ten był związany przede wszystkim ze stopniem łączności hydrologicznej z morzem i intensywnością intruzji wód słonawych, natomiast w jeziorach kazachstańskich (**A2** i **A4**) odpowiadał przejściu od warunków słodkowodnych do mezohalinowych, czemu towarzyszył wzrost mineralizacji wody, stężeń głównych jonów oraz pogorszenie części parametrów tlenowych. W przypadku struktury zooplanktonu jezior zachodniego Kazachstanu (**A4**) zasolenie zostało wskazane jako główny filtr środowiskowy silniej porządkujący strukturę zespołów niż parametry termiczne, a analizy CCA i GAM wyodrębniły zasolenie, pH, siarczany i magnez jako najważniejsze zmienne objaśniające obserwowaną zmienność biologiczną. Analogicznie w badaniu bentosu tego regionu (**A2**) wykazano, że wraz ze wzrostem zasolenia narastały różnice w składzie chemicznym wód, a największe kontrasty dotyczyły właśnie wskaźników mineralizacji i składu jonowego. Wyniki te dowodzą, że poziom zasolenia wód organizowało nie tylko kondycję biotopu, lecz również biologiczną odpowiedź całych ekosystemów.

Wzrost zasolenia ekosystemów śródlądowych staje się coraz istotniejszym problemem ekologicznym wiązanym z efektem globalnych zmian klimatycznych (**A2** i **A4**). Postępująca salinizacja jest w nich bezpośrednio powiązana z rosnącym znaczeniem ewapotranspiracji, ograniczeniem dopływu słodkiej wody oraz zwiększoną niestabilnością bilansu wodnego w strefach pustynnych i półpustynnych. Oznacza to, że zasolenie należy interpretować nie tylko jako lokalny czynnik hydrochemiczny, ale przede wszystkim jako wskaźnik makroskalowych przemian klimatycznych, determinujących strukturę i funkcjonowanie ekosystemów jeziornych.

Wzrost zasolenia nie prowadzi do jednokierunkowego spadku wszystkich miar biologicznych, lecz przede wszystkim zmieniał skład gatunkowy zespołów, udział grup dominujących oraz relacje między bogactwem gatunkowym a liczebnością organizmów. W jeziorach zachodniego Kazachstanu bogactwo gatunkowe makrobezkręgowców bentosowych (**A2**) było najwyższe w jeziorze oligohalinowym, a najniższe w jeziorach mezohalinowych. Pozwoliło to na zidentyfikowanie strefy oligohalinowej jako lokalnego *hotspotu* różnorodności taksonomicznej. W ekosystemach o najwyższej konwersji solnej

obserwowano drastyczne uproszczenie struktury zespołów oraz wzrost udziału taksonów eurytopowych, reprezentowanych głównie przez Diptera i Hemiptera.

W zgrupowaniu zooplanktonu (**A4**) wraz z wyższymi wartościami zasolenia malało bogactwo gatunkowe wrotków oraz obniżała się różnorodność Shannona (*H'*), szczególnie po przekroczeniu progu około 15 PSU. Co istotne, zjawisku temu towarzyszył jednoczesny wzrost całkowitej liczebności zooplanktonu, którego najwyższą obfitość odnotowano w jeziorach silniej zasolonych. Dowodzi to wyraźnego rozdzielenia wzorców bogactwa gatunkowego i biomasy/obfitości organizmów wzdłuż badanego gradientu.

W jeziorach przybrzeżnych południowego Bałtyku (**A1**) odpowiedź bentosu miała bardziej charakter reorganizacyjny, a nie wyłącznie redukcyjny. W jeziorach słonawych odnotowano większą liczbę taksonów niż w jeziorach przejściowych i słodkowodnych, jednak różnice między tymi typami jezior wynikały ze zmiany struktury dominacji oraz udziału gatunków o szerokiej tolerancji ekologicznej (euryhalinowych).

Na poziomie *β*-różnorodności wyniki z jezior kazachstańskich (**A2**) wskazały, że wraz ze wzrostem mineralizacji zespoły stawały się bardziej homogeniczne przestrzennie, a w strukturze zmienności większego znaczenia nabierał proces substytucji gatunków (wymiany taksonomicznej – *turnover*). Tym samym stres solny nie tylko redukował udział gatunków wrażliwych (stenohalinowe), ale również porządkował regionalny rozkład zoocenoz, unifikując strukturę zespołów w warunkach skrajnych środowiskowo.

Najpełniej funkcjonalna odpowiedź biocenoz na zasolenie została pokazana w artykule **A1**, w którym analiza cech biologicznych (*biological traits analysis*) makrozoobentosu wykazała wyraźne różnice między jeziorami słodkowodnymi, przejściowymi i słonawymi. W zbiornikach o wyższej mineralizacji odnotowano preferencję organizmów mobilnych, epifaunowych, reprezentujących gildię troficzną skrobaczy oraz organizmów niemodyfikujących osadów dennych. Z kolei w jeziorach słodkowodnych i przejściowych istotniejszą rolę odgrywały formy osiadłe lub półmobilne, zbieracze, organizmy tubifeksowate (budujące rurki) o ciele robakowatym oraz taksony wyposażone w żuwaczkowy aparat gębowy. Wyniki te wskazują, że wzrost zasolenia zmieniał nie tylko skład taksonomiczny, ale także architekturę funkcjonalną zespołów bentosowych.

Analogiczny wzorzec stwierdzono w strukturze zooplanktonie jezior kazachskich (**A4**). Uniwersalny substytut miary wielkościowej – wskaźnik biomasa/liczebność – wykazywał nieliniową odpowiedź wzdłuż gradientu salinizacji. Odzwierciedlał on sukcesywne przejście od zespołów zdominowanych przez duże skorupiaki planktonowe (głównie Cladocera) do układów zdominowanych przez drobniejsze formy, a następnie częściową odbudowę

struktury wielkości ciała w jeziorach o najwyższym zasoleniu, stymulowaną pojawieniem się wyspecjalizowanych, halotolerancyjnych skorupiaków.

W pracy **A2** podobny kierunek zmian zaobserwowano w przypadku bezkręgowców bentosowych. Wraz ze wzrostem zasolenia nastąpił zanik grupy typowo słodkowodnych i wrażliwych, takich jak mięczaki (Mollusca) i skąposzczety (Oligochaeta), na rzecz taksonów o wyższej tolerancji fizjologicznej i dużej mobilności, zdolnych do szybkiej kolonizacji wolnych nisz ekologicznych. Syntetyzując uzyskane wyniki, gradient zasolenia radykalnie przekształcał strukturę cech biologicznych biocenoz. W tych warunkach stabilne strategie życiowe (typu K), przystosowane do wód słodkich, traciły swoją dominację. Zastępowały je formy oportunistyczne (typu r) oraz organizmy wykazujące wyspecjalizowane adaptacje do siedlisk ekstremalnych.

### *6.2. Zdrowie ekosystemu jako rama integrująca wieloczynnikową zmienność środowiskową i funkcjonalną*

Artykuł **A3** umożliwia osadzenie opisanych wyżej zależności w szerszym paradygmacie zdrowia ekosystemu poprzez aplikację zintegrowanego, wielowskaźnikowego indeksu zdrowia ekosystemowego (*Ecosystem Health Index* – EHI). Wskaźnik ten w spójny sposób łączy trzy główne filary: integralność strukturalną, integralność procesów ekosystemowych oraz potencjał do świadczenia usług ekosystemowych. W tym ujęciu gradient zasolenia pozostawał kluczowym tłem ekologicznym, jednak finalny stan jezior przybrzeżnych jest silnie współkształtowany przez antropopresję w zlewni, stan strefy buforowej, jakość wody i reżim ochrony prawno-przyrodniczej.

W strukturze wagowej modelu EHI najwyższy priorytet przypisuje się integralności procesów, a w obrębie której za kluczowe determinanty składowych uznaje się: efektywność strefy buforowej, stężenie fosforu ogólnego (TP) oraz strukturę użytkowania zlewni. W obrębie komponentu integralności strukturalnej najwyższą czułością i wagą charakteryzuje się kondycja makrozoobentosu, z kolei w spektrum usług ekosystemowych najwyższe oceny uzyskują usługi kulturowe oraz regulacyjne. Wynik ten wykazuje pełną spójność operacyjną z konkluzjami z prac **A1** i **A2**, gdzie to właśnie makrozoobentos (traktowany jako bioindyfikator) najpełniej odzwierciedla presję środowiskową i różnicuje stan ekologiczny analizowanych jezior.

Komparatywna analiza sześciu jezior przybrzeżnych wykazuje wyraźną polaryzację stanu ekosystemów w zależności statusu ochrony obszarowej. Obiekty objęte ścisłą ochroną położone w granicach Słowińskiego Parku Narodowego (SPN) - jeziora Dołgie, Gardno i Łebsko - odznaczają się odmienną specyfiką niż jeziora położone poza strukturą

(Wicko, Kopań i Resko), przy czym w obu kohortach znalazły się jeziora słodkowodne, przejściowe i słonawe. Na poziomie całkowitego zintegrowanego wskaźnika EHI ekosystemy zlokalizowane w SPN osiągały umiarkowane wartości, podczas gdy jeziora pozbawione tej ochrony są klasyfikowane najczęściej jako słabe. Jednocześnie ekosystemy parkowe cechuje istotnie wyższy i bardziej stabilny potencjał do świadczenia kluczowych usług ekosystemowych.

Jednocześnie w artykule **A3** nie stwierdzono związku między stopniem łączności jeziora z morzem, a całkowitym EHI ani potencjałem świadczenia usług ekosystemowych. Oznacza to, że w syntetycznej ocenie zdrowia ekosystemu sam gradient zasolenia nie wyjaśniał całej zmienności między jeziorami przybrzeżnymi, ponieważ jego wpływ był modulowany przez strukturę procesów ekosystemowych oraz sposób zagospodarowania otoczenia jezior.

*6.3. Organizacja przestrzenna geo- i hydrokompleksów vs. potencjał usług ekosystemowych*

Artykuł **A5** rozwija wymiar usług ekosystemowych wskazuje, że potencjał ich świadczenia w jeziorach przybrzeżnych Bałtyku jest silnie powiązany ze sposobem zagospodarowania przestrzeni wokół jezior, opisywanym przez charakterystykę geo- i hydrokompleksów. Analiza obejmowała 29 usług ekosystemowych zgodnych z klasyfikacją CICES V5.1 (Haines-Young & Potschin, 2018), pogrupowanych w usługi zaopatrzeniowe, regulacyjne i utrzymaniowe oraz kulturowe, a ich poziom odnoszono do cech użytkowania terenu, stopnia zmeliorowania, form ochrony, korytarzy ekologicznych, cech linii brzegowej, obecności ekotonów, widoczności jeziora, presji rekreacyjnej oraz infrastruktury hydrotechnicznej.

Zestawienie zmian średnich wartości wskaźników pomiędzy jeziorami pozostającymi poza ścisłą ochroną, a jeziorami objętymi ścisłą ochroną wykazało dodatni kierunek zmian dla wszystkich głównych grup usług ocenianych na podstawie geokompleksów. Średnia zmiana wyniosła +113,8% dla usług zaopatrzeniowych, +50,8% dla usług regulacyjnych oraz utrzymaniowych, +27,1% dla usług kulturowych, +28,7% dla abiotycznych usług regulacyjnych oraz +59,8% dla abiotycznych usług kulturowych. Dowodzi to, że jeziora położone w granicach parku narodowego były osadzone w korzystniejszym układzie przestrzennym z punktu widzenia potencjału usługowego.

Na poziomie poszczególnych ekosystemów najwyższe i najbardziej wyrównane wartości wielu wskaźników geokompleksowych uzyskiwało jezioro Łebsko, a wysokie poziomy są rejestrowane także dla Dołgiego i Gardna. Z kolei Kopań, Resko i Wicko częściej osiągają wartości obniżone lub bardziej zróżnicowane między poszczególnymi wskaźnikami.

Układ ten jest zgodny z wynikami artykułu **A3**, w którym jeziora objęte ścisłą ochroną uzyskiwały wyższy zintegrowany potencjał świadczenia usług ekosystemowych niż jeziora położone poza granicami parku narodowego.

W przypadku hydrokompleksów obraz był bardziej złożony, ponieważ część wskaźników przyjmowała wysokie wartości w większości badanych jezior, a najsilniej różnicujące były wybrane cechy lokalnej organizacji strefy przybrzeżnej. Analizy SIMPER pokazały, że w wielu parach porównań dominującą rolę odgrywał wskaźnik usługi dotyczącej aktywnych form rekreacji i wypoczynku, a w niektórych kontrastach także pasywnych form, oraz możliwości wykorzystania elementów biologicznych do celów reprezentacyjnych lub rozrywkowych. Analiza ta ujawnia również kluczową rolę wskaźników usług związanych z potencjałem jeziora do samooczyszczania i stanowienia siedliska dla bytowania i rozmnażania się gatunków. Wyniki te wskazują na fundamentalne znaczenie lokalnych cech linii brzegowej i bezpośredniego użytkowania otoczenia jeziora dla kreowania potencjału usługowego. Znaczenie tych cech jest zgodne z badaniami wskazującymi, że umacnianie linii brzegowej może prowadzić do redukcji roślinności zanurzonej i wynurzonej, ograniczenia złożoności siedlisk litoralnych oraz zmian w strukturze zespołów ryb i makrobezkręgowców. Wpływ ten nie musi jednak polegać na prostym spadku bogactwa gatunkowego, ponieważ odpowiedź biocenoz zależy od rodzaju umocnienia, właściwości podłoża oraz preferencji poszczególnych grup funkcjonalnych (Chhor et al., 2020). Znaczenie lokalnych cech linii brzegowej potwierdzają również badania prowadzone w jeziorze Raczyńskim, gdzie wzrost presji rekreacyjnej oraz rozwój zabudowy i infrastruktury w bezpośrednim otoczeniu jeziora prowadziły do przekształcenia roślinności litoralnej. Liczne przerwy wykonywane w pasie trzcinowisk pod kąpieliska, pomosty i stanowiska wędkarskie ograniczały funkcję buforową roślinności, sprzyjały dopływowi zanieczyszczeń ze zlewni oraz współwystępowały z pogorszeniem warunków świetlnych i zanikiem większości roślinności zanurzonej (Rosińska & Gołdyn, 2018). Jednocześnie w przypadku geokompleksów różnice między jeziorami są rozproszone między większą liczbą wskaźników. Sugeruje to, że separacja obiektów wynikała z całościowego, wieloskalowego wzorca zagospodarowania przestrzeni wokół zbiorników, a nie z wyizolowanych cechy środowiska.

Wyniki **A5** wskazują więc, że wyższy potencjał świadczenia usług ekosystemowych w jeziorach położonych w granicach parku narodowego jest związany z korzystniejszą strukturą geo- i, w mniejszym stopniu, hydrokompleksów. Oznacza to, że zrównoważony sposób zagospodarowania przestrzeni sprzyja utrzymaniu funkcji zaopatrzeniowych, regulacyjnych i kulturowych ekosystemów jeziornych. Tym samym różnice między trzema

jeziorami położonymi w parku narodowym i trzema poza nim należy interpretować nie tylko w kategoriach formalno-prawnych form ochrony, ale przede wszystkim przez pryzmat przestrzennej i funkcjonalnej organizacji otoczenia tych jezior.

*6.4. Model reorganizacyjny funkcjonowania jezior*

Łącznie wyniki prac składowych wskazują, że gradient zasolenia pełni funkcję głównego czynnika ekologicznego organizującego bioróżnorodność taksonomiczną i funkcjonalną zespołów wodnych. Prowadzi on do ukierunkowanej selekcji taksonów eurytopowych, głębokiej reorganizacji struktury dominacji, uproszczenia nisz ekologicznych w wybranych biocenozach oraz rekonfiguracji strategii funkcjonalnych organizmów. Jednocześnie zdrowie ekosystemu nie jest prostą, liniową funkcją samego zasolenia. Syntetyczna ocena stanu ekologicznego jezior zależy bowiem w równym stopniu od integralności procesów, sprawności ekotonowych stref buforowych, struktury zagospodarowania zlewni oraz finalnego potencjału do świadczenia usług ekosystemowych.

W konsekwencji najbardziej adekwatny obraz badanych układów lentycznych nie wynika z uproszczonego modelu liniowego, w którym wzrost zasolenia oznacza wyłącznie degradację różnorodności i pogorszenie funkcjonowania systemu. Właściwy opis badanych zjawisk zapewnia model reorganizacyjny, w którym gradient zasolenia wyznacza wektor przekształceń biologicznych, natomiast ostateczny poziom zdrowia ekosystemu oraz potencjał świadczenia usług są determinowane przez sposób zagospodarowania przestrzeni wokół zbiorników i stopień zachowania naturalnego charakteru krajobrazu przyjeziornego.

W takim ujęciu zasolenie pozostaje osiowym czynnikiem transformacji ekologicznej, a zdrowie ekosystemu stanowi nadrzędną ramę syntetyczną, która pozwala połączyć zmiany w α-różnorodności, różnorodności funkcjonalnej oraz usługach ekosystemowych w jeden, spójny i komplementarny obraz funkcjonowania jezior przybrzeżnych i śródlądowych.

## 7. Dyskusja

### *7.1. Klimatyczne i krajobrazowe uwarunkowania salinizacji wód jeziornych*

Wyniki uzyskane w ramach niniejszej rozprawy doktorskiej potwierdzają, że zmiany hydroklimatyczne stanowią kluczowy czynnik sprzyjający salinizacji, jednak ich ostateczny wpływ na ekosystemy jeziorne jest nieliniowo modyfikowany przez strukturę makroskali krajobrazowej, co dostarcza przesłanek wspierających hipotezę H1.

Kontekst klimatyczny salinizacji był silniej zarysowany w jeziorach zachodnio-kazachstańskich, gdzie pogłębianie się deficytu wodnego, wzrost parowania i ograniczenie dopływu wody powierzchniowej tworzyły warunki typowe dla nasilającego się procesu klimatycznie uwarunkowanej salinizacji wtórnej (Jeppesen et al., 2020; Saini & Pandey, 2023). Wyniki te pozostają zgodne z ogólnie akceptowalną tezą Williamsa (2001), który wskazał, że jeziora endoreiczne (lub quasiendoreiczne) w strefach suchych i półsuchych są szczególnie wrażliwe na zmienność klimatyczną ze względu na zamknięty bilans wodny i brak możliwości rozcieńczenia.

Niemniej jednak obserwacyjny charakter przeprowadzonych badań nie pozwala na bezpośrednie wnioskowanie przyczynowo-skutkowe; wykazano korelacyjny związek między uwarunkowaniami hydroklimatycznymi, a poziomem zasolenia. Stanowi to istotne uzupełnienie wiedzy o procesie w kontekście zmian klimatycznych, jednak bez możliwości ilościowego rozdzielenia wkładu klimatycznych i antropogenicznych źródeł mineralnych. Przyszłe badania, obejmujące izotopowe śledzenie źródeł jonów lub modelowanie bilansu wodnego, mogłyby pozwolić na pełniejsze wyjaśnienie tych mechanizmów.

Synteza wyników uzyskanych w artykułach **A3** i **A5** dostarcza przesłanek wspierających hipotezę H1, zgodnie z którą odpowiedź jezior na presje związane z salinizacją jest modyfikowana przez uwarunkowania krajobrazowe, hydrologiczne i ochronne. Wyniki wskazują, że oddziaływania środowiskowe nie powinny być interpretowane wyłącznie przez pryzmat właściwości fizykochemicznych wody, ponieważ istotną rolę odgrywa również przestrzenna organizacja zlewni oraz bezpośredniego otoczenia jeziora. Struktura ta wpływa na retencję wody i osadów, dopływ biogenów oraz zanieczyszczeń, ciągłość siedlisk i zdolność ekosystemu do podtrzymywania procesów regulacyjnych.

W artykule **A3** integralność procesów uzyskała najwyższą wagę w strukturze wielowskaźnikowego indeksu zdrowia ekosystemowego (EHI), a w jej obrębie szczególnie istotne były strefa buforowa oraz struktura użytkowania zlewni. Wyższe wartości EHI jezior położonych w granicach Słowińskiego Parku Narodowego, w porównaniu z jeziorami poza

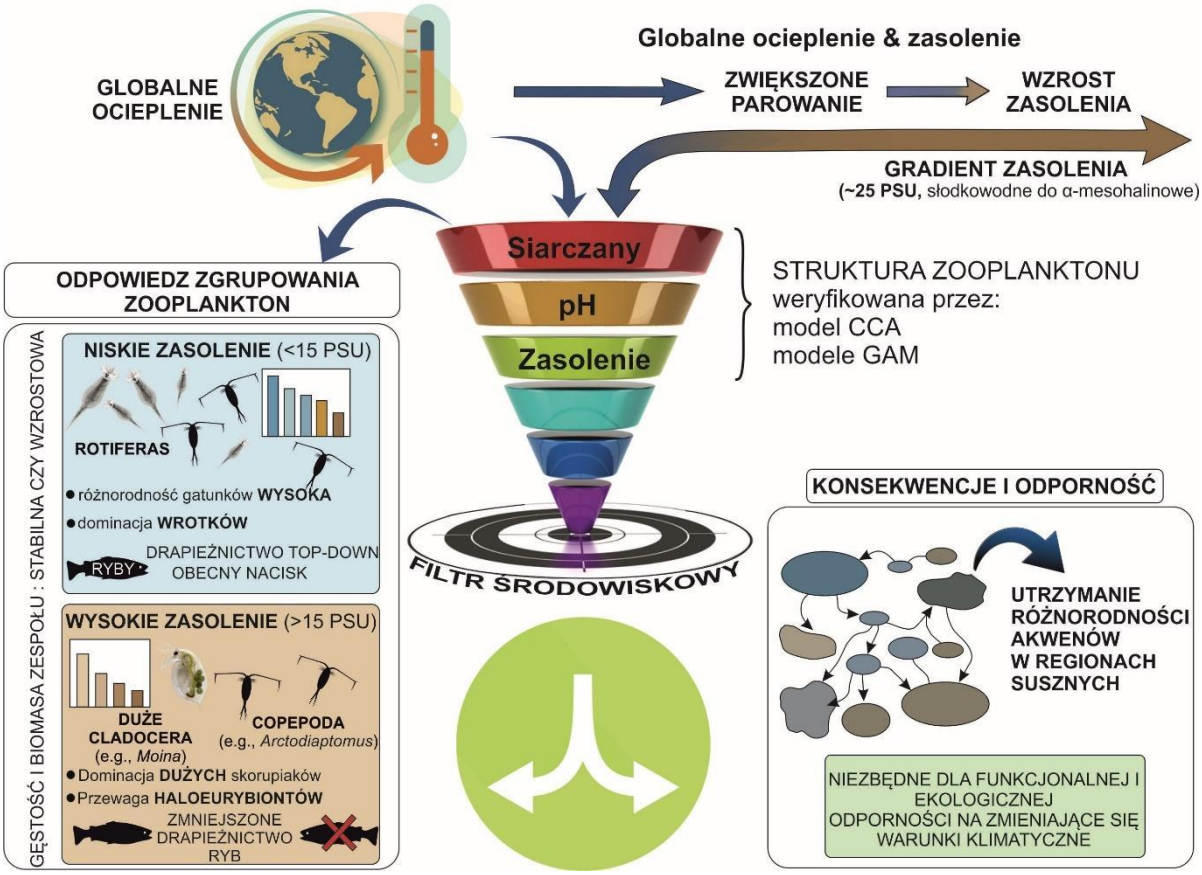
granicami parku, współwystępowały z większym udziałem lasów i mokradeł w 500-metrowej strefie buforowej. Wynik ten jest zgodny z doniesieniami Vagheei i Boano (2025) oraz Moberg i in. (2024) półnaturalne ekotony leśno-mokradłowe mogą pełnić funkcje buforowe, zwiększając retencję wody i osadów, ograniczając dopływ zanieczyszczeń oraz wspierając łączność siedlisk. Ich znaczenie dla odporności całego ekosystemu wymaga jednak interpretacji zależnej od kontekstu zlewniowego. Artykuł **A5** uzupełnił ten obraz o analizę geo- i hydrokompleksów (Krauze et al., 2023), wykazując, że korzystna organizacja przestrzenna otoczenia zwiększa potencjał do świadczenia usług ekosystemowych.

Wysoka łączność hydrologiczna oraz obecność barier buforowych sprawiają, że syntetyczna ocena zdrowia ekosystemu ma właściwości tłumiące: może utrzymywać wartości umiarkowane nawet przy wysokim stresie solnym. Potwierdza to nieliniowy charakter modyfikacji krajobrazowej ujęty w hipotezie H1 – czynniki zlewniowe decydują o tym, czy i kiedy system przekroczy punkt krytyczny (ang. *ecological tipping point*).

*7.2. Gradient zasolenia jako nadrzędny filtr środowiskowy i reorganizacja biocenoz*

Wyniki środowiskowe potwierdzają założenia hipotezy H2, poświadczając, że zasolenie stanowi dominujący gradient ekologiczny porządkujący strukturę biocenoz zarówno w przymorskich systemach południowego Bałtyku, jak i w śródlądowych jeziorach zachodniego Kazachstanu.

Rola zasolenia jako nadrzędnego filtra środowiskowego – silniejszego niż czynniki termiczne czy geograficzne – znajduje odzwierciedlenie w analizach wielowymiarowych prezentowanych w artykule **A4**. Analizy CCA z procedurą *forward selection* i weryfikacją współliniowości (VIF) jednoznacznie wyodrębniły zasolenie, pH, siarczany i magnez jako zmienne objaśniające największą część zmienności struktury zooplanktonu, przy jednoczesnej redundancji temperatury (rys. 3).



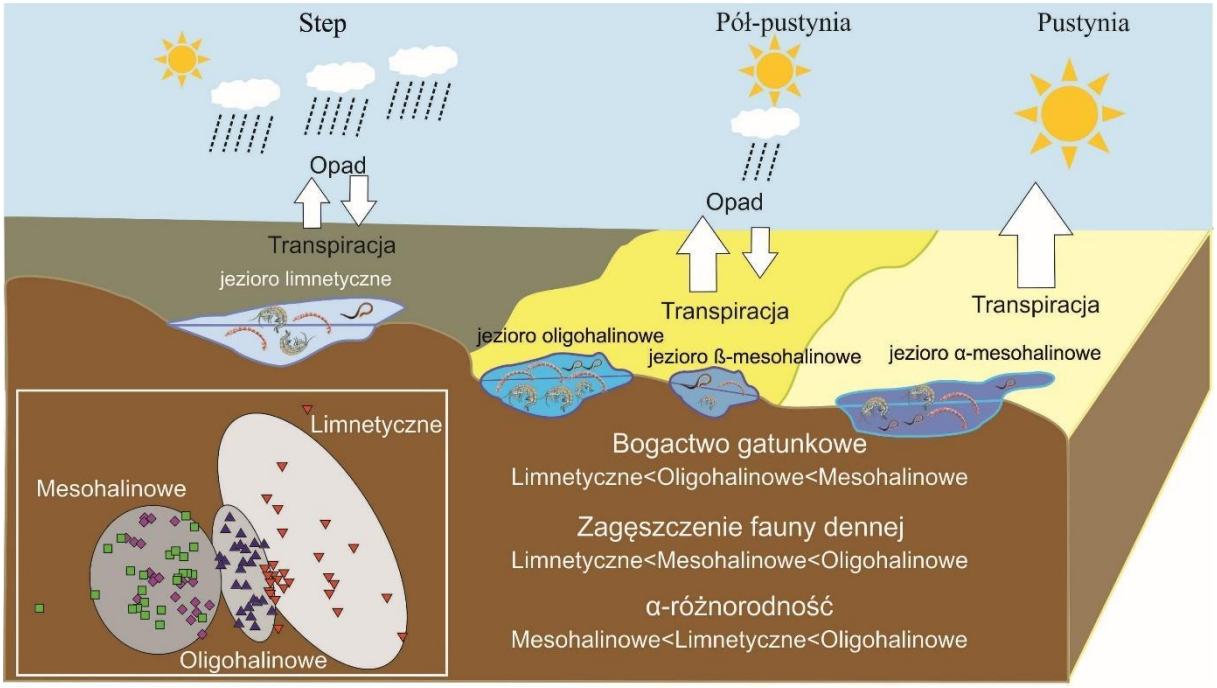

Rys. 3. Model konceptualny reorganizacji struktury zooplanktonu pod wpływem klimatycznie uwarunkowanej salinizacji oraz rola mechanizmów buforujących.

Wynik ten wykazuje wysoką spójność metodologiczną z wnioskami Jeppesena et al. (2015) oraz Bruceta et al. (2009), którzy udowodnili silniejszy wpływ gradientu zasolenia niż temperatury na zooplankton jezior europejskich. Należy jednak zastrzec, że dominacja zasolenia jako predyktora wynikała częściowo ze znacznie szerszego zakresu zmienności tego parametru w doborze obiektów badawczych (57-krotna różnica między słodkowodnym jeziorem Prorva, a mezohalinowym Edilsor).

Weryfikacja H2 ujawniła wyraźny, unimodalny charakter zależności bioróżnorodności od zasolenia, wyznaczany przez specyficzne progi ekologiczne:

- Hotspoty umiarkowanego zasolenia (oligohalinowe): Najwyższe bogactwo gatunkowe makrobezkręgowców bentosowych (artykuł **A2**) stwierdzono w słodkowodnym jeziorze Prorva i oligohalinowym Glubinnoe. Sugeruje to, że strefa umiarkowanego zasolenia tworzy optymalne warunki dla współistnienia w bentalu gatunków słodkowodnych i halotolerancyjnych (rys. 4). Wpisuje się to w hipotezę podwójnego gradientu stresowego (ang. *dual stress hypothesis*), według której umiarkowane nasilenie stresu zwiększa

dostępność nisz ekologicznych, co obserwowali również Schallenberg et al. (2003) w jeziorach nowozelandzkich.




Rys. 4. Model zmian hydroklimatycznych w gradiencie stref krajobrazowych (step – półpustynia – pustynia) oraz ich wpływ na strukturę i zróżnicowanie fauny dennej jezior.

- Postępująca salinizacja i drastyczny spadek bogactwa gatunkowego: Po przekroczeniu zidentyfikowanych progów ekologicznych struktura biocenoz ulega gwałtownemu uproszczeniu. W zooplanktonie kazachstańskich jezior bogactwo gatunkowe wrotków malało statystycznie istotnie po przekroczeniu progu ~15 PSU (analiza GAM, artykuł **A4**), a α-różnorodność obniżała się systematycznie wraz z zasoleniem. W bentosie jezior nadbałtyckich (artykuł **A1**) analizy nMDS i PERMANOVA potwierdziły ostre, asymetryczne rozdzielenie jezior słonawych od słodkowodnych ($p < 0{,}001$).
- Skrócenie sieci troficznych i dominacja specjalistów: W warunkach silnego zasolenia (jeziora mezohalinowe: Balykty Sarkyl i Edilsor) dochodzi do eliminacji wyższych poziomów troficznych i dominacji unikalnych taksonów halofilnych. Mechanizmem amplifikującym te zmiany był efekt uwolnienia spod presji drapieżniczej ryb (ang. *predation release*): powyżej ~6 PSU zanikały ryby karpiowate, a powyżej ~10 PSU sumowate. Skutkowało to drastycznym uproszczeniem sieci troficznej, eliminacją form wrażliwych i masowym rozwojem dużych wioślarek (*Moina micrura*, *M. brachiata*) oraz widłonogów z rodzaju *Arctodiaptomus*. Zjawisko to, opisywane przez Brucet et al. (2006, 2010) oraz Aladina (1999) i Aladina et al. (2005), potwierdza, że ekstremalne poziomy

zasolenia wymuszają głęboką reorganizację struktury funkcjonalnej zoocenoz pelagicznych, działając jako bezwzględny filtr biologiczny (rys. 4).

*7.3. Degradacja stanu ekologicznego i potencjału usług ekosystemowych*

Hipoteza H3 zakładała, że wywołane salinizacją uproszczenie struktury biocenoz oraz zaburzenia biogeochemiczne bezpośrednio obniżają wskaźnik zdrowia ekosystemowego jezior, prowadząc do degradacji ich stanu według kryteriów Ramowej Dyrektywy Wodnej (RDW; Dyrektywa 2000/60/WE, 2000) oraz upośledzenia usług ekosystemowych. Wyniki niniejszej pracy w większości potwierdzają tę hipotezę, aczkolwiek ujawniają znacznie bardziej złożony, nieliniowy mechanizm powiązań strukturalno-funkcjonalnych.

Po pierwsze, analiza zooplanktonu (**A4**) wykazała rozdzielenie wzorców bogactwa gatunkowego i obfitości organizmów: podczas gdy bogactwo taksonomiczne malało, całkowita liczebność zooplanktonu wzrastała wzdłuż gradientu zasolenia (zjawisko zbieżne z obserwacjami Jeppesena et al. 2007 oraz Bruceta et al. 2012). Zgodnie z hipotezą filtracji środowiskowej (*environmental filtering*), stres solny eliminuje wrażliwe gatunki wskaźnikowe kluczowe dla oceny stanu ekologicznego RDW, zwalniając zasoby dla eurybiontów (Schallenberg et al., 2003). Co więcej, odpowiedź wskaźników jakościowych była nieliniowa – wskaźnik wielkościowy B:N wykazywał załamanie w strefie β-mezohalinowej i częściową odbudowę w strefie α-mezohalinowej, odzwierciedlając kaskadowe zaburzenia troficzne. W bentosie (**A1**) wykazano, że wysokie zagęszczenie eurybiontów (*Chironomus plumosus* i *Polypedilum nubeculosum*, stanowiących 62% prób) potrafi maskować rzeczywisty spadek zdrowia ekosystemowego w standardowych indeksach biotycznych, co stanowi krytyczną implikację metodyczną dla monitoringu RDW.

Po drugie, na poziomie zintegrowanego wskaźnika zdrowia ekosystemowego (EHI), wyniki artykułu **A3** dowodzą, że salinizacja bezpośrednio uderza w integralność strukturalną (zwłaszcza kondycję makrozoobentosu). Jednakże wpływ ten nie przekłada się automatycznie w sposób prostoliniowy na degradację całościowego, syntetycznego modelu EHI.

Zgodnie z ramami modelowania przyczynowo-skutkowego SEEA-EA (Hein et al., 2020), stan zasobów biotycznych jest oddzielony od przepływu usług ekosystemowych. Upośledzenie potencjału do świadczenia kluczowych usług zaopatrzeniowych (retencja wody użytkowej), regulacyjnych (samoczyszczenie wód) oraz kulturowych i rekreacyjnych (**A5**) zachodziło najsilniej tam, gdzie presja solna współwystępowała z antropogeniczną degradacją zlewni.

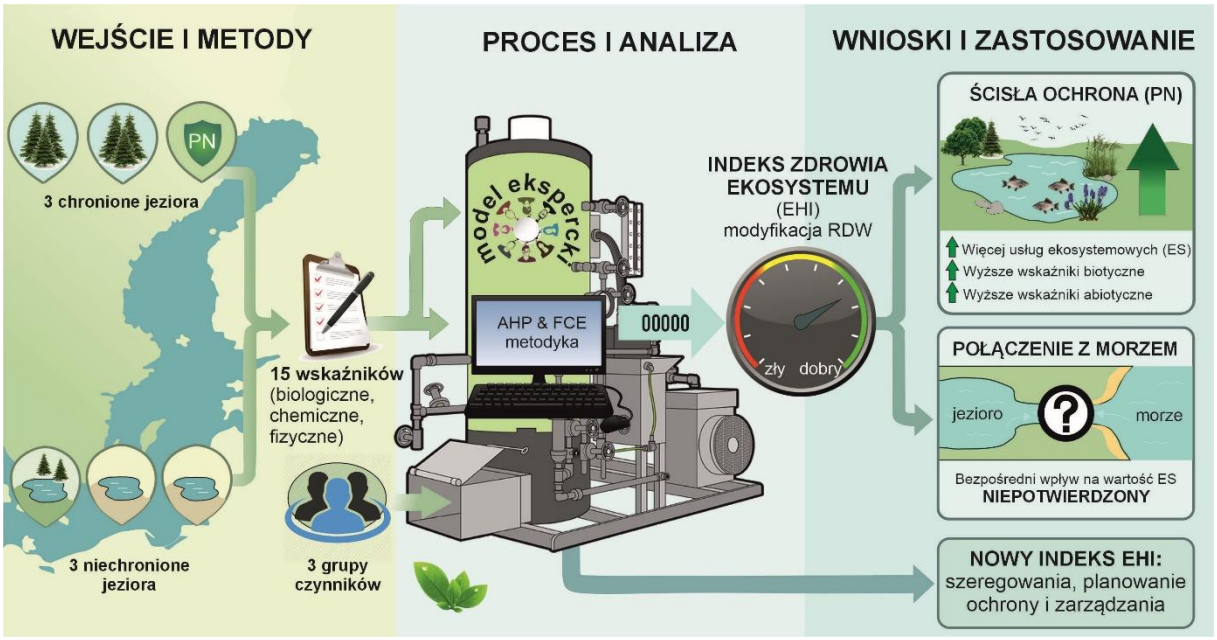
W jeziorach, w których zachowana była półnaturalna strefa buforowa (wysoki wskaźnik zalesienia i obecność mokradeł), procesy samoczyszczenia wód były podtrzymywane pomimo zmian w strukturze gatunkowej biocenoz. Mała próba badawcza (sześć jezior dla modelu EHI) nakazuje ostrożność w statystycznym uogólnianiu tego wniosku, niemniej jednak zebrane dane pozwalają na przeformułowanie i doprecyzowanie hipotezy H3: „Wzrost zasolenia indukuje taksonomiczną reorganizację biocenoz i eliminuje gatunki referencyjne dla klasyfikacji RDW. Jednak tempo i skala ostatecznej degradacji zintegrowanego zdrowia ekosystemowego (EHI) oraz utraty usług ekosystemowych są ściśle sprzężone z kondycją biogeochemiczną zlewni – ekotonowe strefy buforowe i ochrona obszarowa wykazują silne właściwości kompensacyjne, opóźniając nadejście katastrofalnego punktu zwrotnego w funkcjonowaniu geosystemu jeziornego."

*7.4. Nowatorskość metodyczna i wartość naukowa podejścia wielowskaźnikowego*

Niezależnie od weryfikacji poszczególnych hipotez badawczych, niniejsza rozprawa wnosi istotny wkład metodyczny do ekologii jezior słonawych i przybrzeżnych. Po raz pierwszy zastosowano Biological Trait Analysis (BTA) do oceny różnorodności funkcjonalnej makrozoobentosu w jeziorach przybrzeżnych południowego Bałtyku. Metoda ta, intensywnie rozwijana w ekologii wód płynących od lat 90. XX wieku (Usseglio-Polatera et al., 2000; Poff et al., 2006), jest wciąż rzadko stosowana w ekosystemach słonawych. Jej przewaga nad klasycznymi analizami taksonomicznymi polega na zdolności do wykrywania zmian w organizacji funkcjonalnej niezależnie od składu gatunkowego. Stanowi to szczególną wartość w środowiskach zdominowanych przez taksony o szerokiej walencji ekologicznej (eurybionty).

Połączenie procesów analityczno-hierarchicznych (AHP) z logiką rozmytą (FCE) pozwoliło na opracowanie założeń nowatorskiego, syntetycznego Indeksu Zdrowia Ekosystemowego (EHI) (**A3**). Autorskie podejście bazujące na eksperckim ważeniu heterogenicznych grup parametrów skutecznie kompensuje strukturalne ograniczenia metodyczne Ramowej Dyrektywy Wodnej (RDW). Podejście to uzupełnia ograniczenia Ramowej Dyrektywy Wodnej, która w przypadku jezior przybrzeżnych napotyka problem niedostatecznej liczby obiektów do kalibracji wskaźników biologicznych. Zaproponowany indeks, poprzez integrację danych biologicznych, fizykochemicznych i ekosystemowych w ramach jednego spójnego modelu, oferuje możliwość wielofunkcyjnej oceny stanu jezior przybrzeżnych, uwzględniającej zarówno wymogi biooceny, jak i potrzebę wyceny potencjału usługowego (rys. 5). Podejście to wpisuje się w najnowsze, globalne

paradygmaty holistycznego zarządzania środowiskowego (ang. *Ecosystem-Based Management*), dążące do syntezy wskaźników sektorowych w zintegrowane systemy ocen złożonych.




Rys. 5. Schemat koncepcyjny zintegrowanej procedury analitycznej – od danych wejściowych i modelowania eksperckiego (AHP i FCE) po Indeks Zdrowia Ekosystemu (EHI) i zarządzanie jeziorami przybrzeżnymi.

Zastosowanie uogólnionych modeli addytywnych (GAM) w artykule **A4** otworzyło drogę do obiektywnej i matematycznie rygorystycznej identyfikacji progów ekologicznych (ang. *ecological tipping points*) oraz nieliniowych zależności zachodzących na styku skład chemiczny biotopu i struktury biocenozy. Klasyczne analizy ordynacyjne i korelacyjne mogą ograniczać identyfikację złożonych progów oraz kształtów odpowiedzi, dlatego GAM uzupełnia je przez elastyczne modelowanie zależności nieliniowych. Uchwycenie tych progów (np. strefy przełomowej ~15 PSU dla wrotków) ma nie tylko wartość poznawczą, ale i bezpośredni walor wdrożeniowy. Definiuje bowiem precyzyjne ramy i granice bezpieczeństwa ekologicznego akwenu, wskazując menedżerom środowiska moment, w którym interwencja czynna (np. manipulowanie reżimem hydrologicznym, restytucja stref buforowych) staje się bezwzględnie konieczna w celu uniknięcia nieodwracalnego załamania strukturalnego jeziora.

W wymiarze globalnym, zaproponowany w rozprawie wielowskaźnikowy zestaw narzędzi badawczych udowadnia, że nowoczesny monitoring ekologiczny jezior podlegających salinizacji musi łączyć strukturalną głębię analiz funkcjonalnych z systemowym ujęciem procesów zachodzących w skali całej zlewni.

*7.5. Ograniczenia badań i kierunki dalszych badań*

Mimo udokumentowanego wkładu poznawczego i aplikacyjnego, sformułowane w niniejszej rozprawie wnioski należy interpretować z uwzględnieniem obiektywnych ograniczeń metodycznych oraz strukturalnych, które są nieodłącznie związane ze specyfiką analizowanych ekosystemów i przyjętą strategią badawczą. Właściwa parametryzacja tych barier wyznacza jednocześnie naturalne kierunki dla przyszłych, pogłębionych studiów limnologicznych.

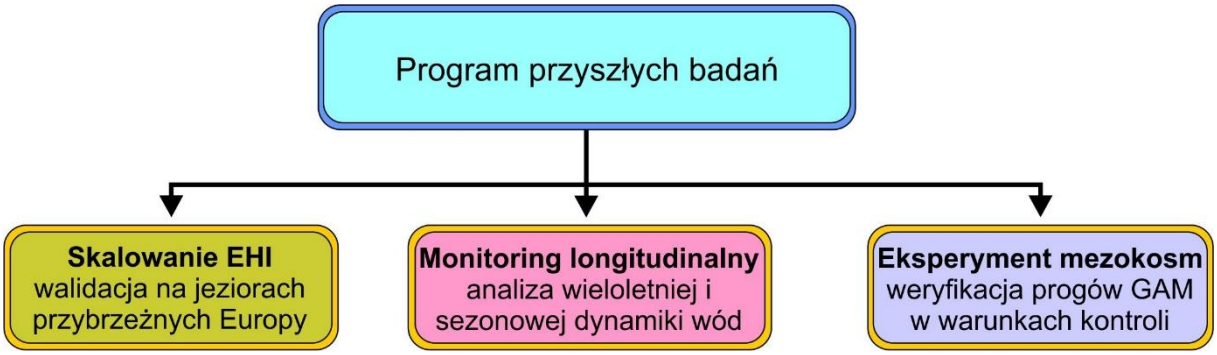
Główne ograniczenia metodologiczne:

- **Korelacyjny charakter relacji hydroklimatycznych**: Dominująco obserwacyjny i przekrojowy (*cross-sectional*) charakter zebranych danych uniemożliwia bezpośrednie, deterministyczne wnioskowanie przyczynowo-skutkowe w sensie eksperymentalnym. Przykładowo, interakcje ujęte w hipotezie H1 (wpływ zmian klimatycznych na salinizację) zrekonstruowano na podstawie sprzężeń korelacyjnych oraz krytycznego przeglądu literatury. Zastosowany aparat badawczy nie pozwolił na precyzyjne, ilościowe rozgraniczenie sygnatury klimatycznej od lokalnej presji antropogenicznej w bilansie mineralnym wód.
- **Paradygmat „przestrzeń zamiast czasu" (*space-for-time substitution*)**: Rekonstrukcja dynamiki reorganizacji biocenoz wzdłuż gradientu zasolenia opierała się na podejściu synchronicznym (przestrzennym). Choć metoda ta jest szeroko akceptowana w ekologii, u jej podstaw leży paradygmatyczne założenie o zbliżonej trajektorii i historii ekologicznej porównywanych obiektów. Warunek ten – z uwagi na drastyczne odrębności ewolucyjne, hydrograficzne i biogeograficzne między basenem południowego Bałtyku oraz pustynnymi, półpustynnymi i stepowymi obszarami zachodniego Kazachstanu – mógł zostać spełniony jedynie częściowo.
- **Reprezentatywność i moc statystyczna próby**: Wolumen obiektów badawczych był restrykcyjnie ograniczony (sześć jezior w artykułach **A3** i **A5**; cztery jeziora w **A2** i **A4**). Stosunkowo niewielka liczebność próby nakłada matematyczne limity na moc statystyczną niektórych testów, co obliguje do traktowania uzyskanych makrotrendów jako modeli kierunkowych, wymagających walidacji na szerszym materiale porównawczym.

- **Subiektywizm ekspercki w procedurach wielokryterialnych**: Matryce wagowe w modelu EHI (opartym na procedurach AHP i FCE) wygenerowano w oparciu o opinie panelu złożonego z 15 ekspertów. Choć proces poddano rygorystycznej standaryzacji i dywersyfikacji pod względem afiliacji specjalistów, wielkość próby eksperckiej wprowadza nieunikniony komponent subiektywizmu, odzwierciedlający aktualne trendy w profilach badawczych osób oceniających.

**Perspektywy rozwoju i kierunki dalszych badań**

W celu weryfikacji sformułowanych modeli oraz operacjonalizacji wypracowanych narzędzi, przyszłe programy badawcze powinny koncentrować się wokół pięciu kluczowych osi:




**1. Skalowanie geograficzne i walidacja modelu EHI**

Konieczne jest przetestowanie i skalibrowanie zintegrowanego indeksu zdrowia ekosystemowego (EHI) na znacznie szerszej grupie jezior przybrzeżnych Europy. Badania te powinny objąć zbiorniki charakteryzujące się odmienną specyfiką hydrologiczną oraz zróżnicowaną strukturą antropopresji (urbanizacja, rolnictwo) w zlewni bezpośredniej.

**2. Przejście na schematy badań wzdłużnych (longitudinalnych) i analizy izotopowe**

Niezbędne jest wdrożenie długoterminowych programów monitoringu ciągłego, zdolnych do uchwycenia reakcji biocenoz na sezonową oraz wieloletnią fluktuację zasolenia. Przejście z modeli korelacyjnych na deterministyczne wymaga integracji numerycznych modeli bilansu wodnego z analizą izotopową jonów oraz analizą długich serii danych meteorologicznych.

**3. Rozszerzenie spektrum funkcjonalnego indeksów biotycznych**

W celu uzyskania w pełni holistycznego obrazu transformacji energetycznych i biogeochemicznych w jeziorach podlegających salinizacji, syntetyczną ocenę zdrowia ekosystemu należy wzbogacić o analizę różnorodności funkcjonalnej pozostałych komponentów biotycznych – w szczególności fitoplanktonu oraz makrofitów.

**4. Weryfikacja genetyczna statusu refugiów**

Zweryfikowanie hipotezy dotyczącej funkcjonowania zbiorników mezohalinowych jako specyficznych refugialnych schronień ekologicznych (*ecological refuges*) wymaga wyjścia poza ramy analizy zagęszczeń i biomasy. Kluczowe będzie zastosowanie zaawansowanych narzędzi genetyki populacyjnej w celu określenia stopnia izolacji, przepływu genów oraz unikalności puli genowej organizmów halotolerancyjnych.

**5. Eksperymentalna weryfikacja progów ekologicznych w mezokosmach**

Wyznaczone za pomocą modeli GAM matematyczne punkty zwrotne (np. próg ~15 PSU) stanowią hipotezy numeryczne, które powinny zostać poddane rygorystycznej walidacji empirycznej. Cel ten może zostać osiągnięty poprzez kontrolowane eksperymenty mezokosmowe, pozwalające na izolację stresu solnego od innych nieliniowo skorelowanych zmiennych środowiskowych (pH, temperatura, biogeny).

## 8. Wnioski - synteza i implikacje dla ochrony ekosystemów wodnych

Wyniki niniejszej rozprawy pozwalają zaproponować spójny model interpretacyjny, łączący gradient zasolenia z bioróżnorodnością taksonomiczną i funkcjonalną, zdrowiem ekosystemu i potencjałem świadczenia usług. Model ten można ująć w postaci dwupoziomowej, hierarchicznej strukturze operacyjnej:

**Poziom I (Lokalny filtr środowiskowy – deterministyczny)**: Na tym poziomie zasolenie działa jako bezwzględny filtr ekologiczny, determinujący strukturę biocenoz. Dokonuje ono kierunkowej selekcji taksonów zdolnych do przetrwania narastającej mineralizacji wody, reorganizuje architekturę funkcjonalną zespołów (BTA), wyznacza krytyczne progi ekologiczne (modele GAM) oraz kaskadowo transformuje relacje troficzne poprzez eliminację wyższych poziomów konsumentów (ryb). Biologiczne i strukturalne skutki salinizacji na tym poziomie charakteryzują się wysoką uniwersalnością biogeograficzną i powtarzalnością – wykazują spójny wektor zmian zarówno w przymorskich jeziorach basenu południowego Bałtyku, jak i w śródlądowych jeziorach zachodniego Kazachstanu.

**Poziom II (Systemowy krajobraz ekosystemu – emergentny):** Na tym poziomie całościowy stan akwenu wyraża się przez syntetyczny wskaźnik zdrowia ekosystemowego (EHI). Jest on wypadkową bezpośredniego, biologicznego wpływu zasolenia (Poziom I), integralności procesów biogeochemicznych (użytkowanie zlewni, dopływ biogenów) oraz stabilności struktury przestrzennej otoczenia determinującej przepływ usług ekosystemowych. Kluczowym wnioskiem płynącym z weryfikacji tego poziomu jest stwierdzenie, że właściwa organizacja makroskali krajobrazowej, wysoka łączność hydrologiczna oraz restrykcyjna ochrona obszarowa wykazują silne właściwości kompensacyjne. Czynniki te potrafią przez określony czas skutecznie tłumić i opóźniać negatywne skutki biologiczne salinizacji na poziomie całego ekosystemu, co odsłania realne perspektywy dla aktywnego zarządzania odpornością jezior w dobie globalnych zmian klimatycznych.

*Implikacje w skali globalnej i aplikacyjnej*

Szeroki kontekst globalny jednoznacznie dowodzi, że zidentyfikowane w pracy wzorce kryzysu i reorganizacji biocenoz pod wpływem stresu solnego nie mają charakteru wyłącznie lokalnego. Wyniki te wykazują pełną konwergencję z najnowszymi doniesieniami literaturowymi – w tym ze skoordynowanymi eksperymentami mezokosmowymi przeprowadzonymi na czterech kontynentach przez Héberta i in. (2023). W badaniu udokumentowano globalny, drastyczny spadek liczebności i zróżnicowania zooplanktonu indukowany wzrostem zasolenia. Potwierdza to, że antropogenicznie i klimatycznie stymulowana salinizacja stanowi obecnie jedno z najbardziej krytycznych, a zarazem wciąż marginalizowanych zagrożeń dla bioróżnorodności wód śródlądowych i przejściowych na świecie.

Niniejsza rozprawa wpisuje się w ten ogólnoświatowy nurt badawczy, wnosząc unikalny, empiryczny wkład w postaci wielofunkcyjnych i wielowskaźnikowych baz danych dla dwóch odmiennych geograficznie, lecz komplementarnych konceptualnie makrosystemów limnicznych.

Wymiar aplikacyjny pracy wyraża się w gotowości wdrożeniowej zaproponowanych narzędzi. Opracowana dwupoziomowa struktura interpretacyjna, autorski indeks EHI oraz wyznaczone matematycznie progi wrażliwości ekologicznej mogą i powinny stanowić instrumentarium diagnostyczne w:

1. Procedurach ewaluacji stanu ekologicznego jezior słonawych, uzupełniając sektorowe ograniczenia Ramowej Dyrektywy Wodnej (RDW);
2. Konstruowaniu i aktualizacji operatów oraz planów ochrony przyrody dla wielkoobszarowych form ochrony (takich jak Słowiński Park Narodowy);
3. Tworzeniu planów zadań ochronnych dla obszarów sieci Natura 2000;
4. Formułowaniu regionalnych dokumentów strategicznych i programów adaptacyjnych sektora gospodarki wodnej wobec postępujących zmian klimatycznych.

## 9. Literatura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# Załączniki

## Zbiór 3 artykułów opublikowanych i 2 będących w procedurze wydawniczej składających się na rozprawę doktorską w przewodzie realizowanym na Wydziale Nauk Biologicznych Uniwersytetu Kazimierza Wielkiego w Bydgoszczy

# A-1

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# Structural diagnosis of benthic invertebrate communities in relation to salinity gradient in Baltic coastal lake ecosystems using biological trait analysis

Mikołaj Matela✉ & Krystian Obolewski✉

**This study is based on biological trait analysis (BTA), which provides a link between the distribution and biological characteristics of species. The paper investigates differences in the structure and functional diversity of benthic fauna in terms of seven biological traits (mobility, habitat, feeding type, habitat modification, body form, body size and feeding apparatus) in nine Baltic coastal lakes whose salinity ranged from 0.1 to 7.3 PSU. Mobile organisms were more common in lakes with higher salinity, while sessile and semi-mobile species preferred low-salinity or freshwater environments. There were also noticeable differences connected with feeding type: collectors and scrapers were more common in brackish lakes, and collectors were significantly dominant in freshwater and transitional ones. This indicates that Baltic coastal lakes are inhabited by similar species of benthic fauna, but that certain biological traits occur with different frequencies. We therefore identified features that may affect the functioning of coastal lakes with a relatively narrow salinity gradient (0.1–7.3 PSU). It seems to confirm the possibility of using BTA methods to determine key characteristics that are helpful for understanding the differences between aquatic ecosystems. The results may provide a basis for further research on changes in the functional diversity of lakes along the southern coast of the Baltic Sea, particularly in view of climate change, given their being small, shallow and less resilient lakes.**

Climate change is encouraging the search for new methods of exploring environmental data that might help to understand the mechanisms that shape the functioning, health and natural potential of coastal ecosystems[1,2]. This is particularly important for small, shallow coastal lakes, including those located along the southern coast of the Baltic Sea (Baltic coastal lakes, BCLs). BCLs are exposed to increasing pressure from human activities. At the same time, progressive climate change may contribute to rapid changes in lake water temperature, degree of seawater intrusion (changes in storm occurrence and intensity), changes in coastal rebuilding processes by the sea, changes in the ratio between evaporation and precipitation within the catchment and lake water balance. These lakes are considered to be priority habitats in the Natura 2000 network (code 3150). Based on their connectivity with the sea, they are divided into three hydro-ecological types: brackish, transitional and freshwater. Previous studies have been based on a mechanistic paradigm, which limited the analyses to determining species composition, taxon abundance and basic biocenological indicators (e.g.[3–6]). However, the increasingly popular evolutionary-systemic approach expands the ability to understand the mechanisms that maintain biodiversity[7–10]. Studies based on defined morphophysiophenological features may predict interactions between community functioning and environmental gradients, thus providing insight into functional changes in ecosystems (including benthic)[11–15]. Therefore, in the field of aquatic ecosystem research, the functional approach has become the preferred method to study the diversity of benthic invertebrate communities (= macrozoobenthos) due to its increasingly well-recognised association with ecosystem functioning and its ability to detect the influence of different stressors[14,16–19]. Nevertheless, organisms with similar ecological roles do not always respond similarly to particular physical, chemical or biological stimuli. This happens because, despite sharing key characteristics, they are differentiated by other, more subtle trophic and non-trophic descriptors[20]. As a result, in many ecosystems (especially marine and transitional), the relationship between environmental changes and the community

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functional diversity is still not well known (e.g.[16,19,21]). Therefore, measuring functional diversity using selected traits can expand our knowledge of how the community responds to environmental factors[14,19,22–24]. Although the impact of single predictors or groups of predictors on the taxonomic structure and abundance of benthic assemblages in estuaries is already well recognized e.g.[5,25–27], there is a lack of complete knowledge on how environmental variability affects functional diversity.

So far, no exclusive, universally accepted method of measuring functional diversity has been adopted. Moreover, for BCLs, there is no complete set of species characteristics that could be used in this method of measuring ecosystem biodiversity[28]. One way of obtaining a comprehensive description of communities is to use biological trait analysis (BTA) alongside a classical taxonomic one[11,14,19,29]. This hybrid method is based on the assumption that phylogenetically unrelated organisms have developed similar traits[30,31]. The research on coastal lakes requires that information on both marine and freshwater fauna species be collected[32,33], which limits the use of BTA[34–36]. This may be why this method has not previously been used to determine the functional diversity of Baltic coastal lakes. In our study, BTA was applied to examine the effect of BCL hydrological connectivity on functional features of macrobenthic communities. The aim was to assess (1) whether the spatial differentiation of functional features was caused by the differing degrees of seawater intrusion, (2) whether these functional features can help to understand mechanisms responsible for the distribution of benthic species along salinity gradients, and (3) whether it is possible to select traits connected with a particular lake type that can provide insight into the evolution of its ecosystem.

## Material and methods

**Study area and sampling design.** The study was conducted on nine polymictic lakes along the southern coast of the Baltic Sea (Fig. 1). The lakes differed in size, hydrological properties and degree of seawater intrusion (= salinity level) (Table 1). Based on the classification proposed by[5], the lakes were divided into three types: freshwater (Wicko, Dołgie Wielkie, Sarbsko), transitional (Liwia Łuża, Kopań, Gardno) and brackish (Resko Przymorskie, Łebsko, Ptasi Raj) (Table 1). All investigated lake ecosystems were in poor condition (e.g.[5,37–39]), due to receiving pollution loads from the catchment which accelerates their eutrophication. They are under strong human impact related to tourism, recreation, municipal pollution, agriculture[40,41].

**Data collection.** The data on taxa and their abundances in the studied BCLs were obtained from an open-access dataset published in studies by[45], where sampling methods and identification procedures were also included. We had to exclude Oligochaeta and Chironomus n. det, as it is impossible to describe their characteristics precisely. The field research for these studies was conducted in three seasons (spring, autumn, summer) in 2019 and 2020. A total of 318 zoobenthos samples were collected, including 120 samples from brackish lakes, 90 samples from transitional lakes, and 108 samples from freshwater lakes.

**Functional trait analysis.** In order to later assess and compare the functional diversity of the ecosystems of the studied lakes by biological trait analysis (BTA)[46], all species were first categorised by biological traits (see Supplementary Table S1). Specifically, based on selected features (mobility, habitat, feeding type, habitat modification, body form, and feeding apparatus), the investigated organisms were first divided into seven groups (traits), further divided into a total of 25 categories (= modalities), as mostly indicated by the literature for species (Table 2) (e.g.[7,21,47,48].). The selected characteristics of each species were then described using information provided by species identification books[49–52], research papers[3,27,53], and web databases[54–56]. These taxa descriptions were then coded using fuzzy coding[57], which assigns a taxon to many categories. The degree of affiliation to a category is assigned on a scale of 0 to 3, with 0 indicating no affiliation and 3 indicating full affiliation[58]; the sum of all category scores for a particular biological trait must be 3. Fuzzy coding is a reliable method because functional features are not necessarily absolute; it is not always possible to assign only one trait category to a species[35]. Via this procedure, each species, based on its biology, was assigned to either one trait modality or multiple distributed modalities[59].

Next, based on thus-coded biological traits, a value was established for each taxon by multiplying the assigned score by the abundance of a taxon on a particular sampling site. The scores for each biological trait were then summed to give us information on "how much of a trait" there is in a given sampling unit[60]. The above technique was applied to all collected material. The frequency tables of biological traits obtained in this way provided a basis for the matrices used in subsequent analyses. The data were square-root transformed, and, due to the occurrence of variables with zero values, the transformation was carried out according to the formula: $(\sqrt{x+1})$. BTA makes it possible to detect differences in the composition of biological traits in whole communities using multivariate ordination. The Bray–Curtis dissimilarity was used to quantify the compositional differences in the frequency of biological traits between the sites/lakes. The obtained dissimilarity matrix was visualized by non-metric multivariate scaling (nMDS). Additionally, the entire procedure was also performed using species abundance (for comparison with the classical species-based analysis) and presence–absence. However, in the latter case, a zero–one data transformation was used (assigning a value of '1' where the result was greater than '0', and for results equal to '0' assigning a value of '0'). The significance of differences in the composition of biological traits and in the species structure of zoobenthos communities was checked using the permutational analysis of variance (PERMANOVA) performed on Bray–Curtis dissimilarity matrices (999 permutations) and the Monte Carlo test. This allowed us to determine the differences in functional diversity between lake types as well as the significance of seasonality, which in the temperate zone is particularly important for the observed changes in the structure of the benthic fauna. Among them are representatives (e.g. Diptera) that migrate from water to terrestrial environments during their development. This results in possible reshuffling of the frequency of appearance of the analysed traits. This problem must therefore be eliminated using measurements taken over

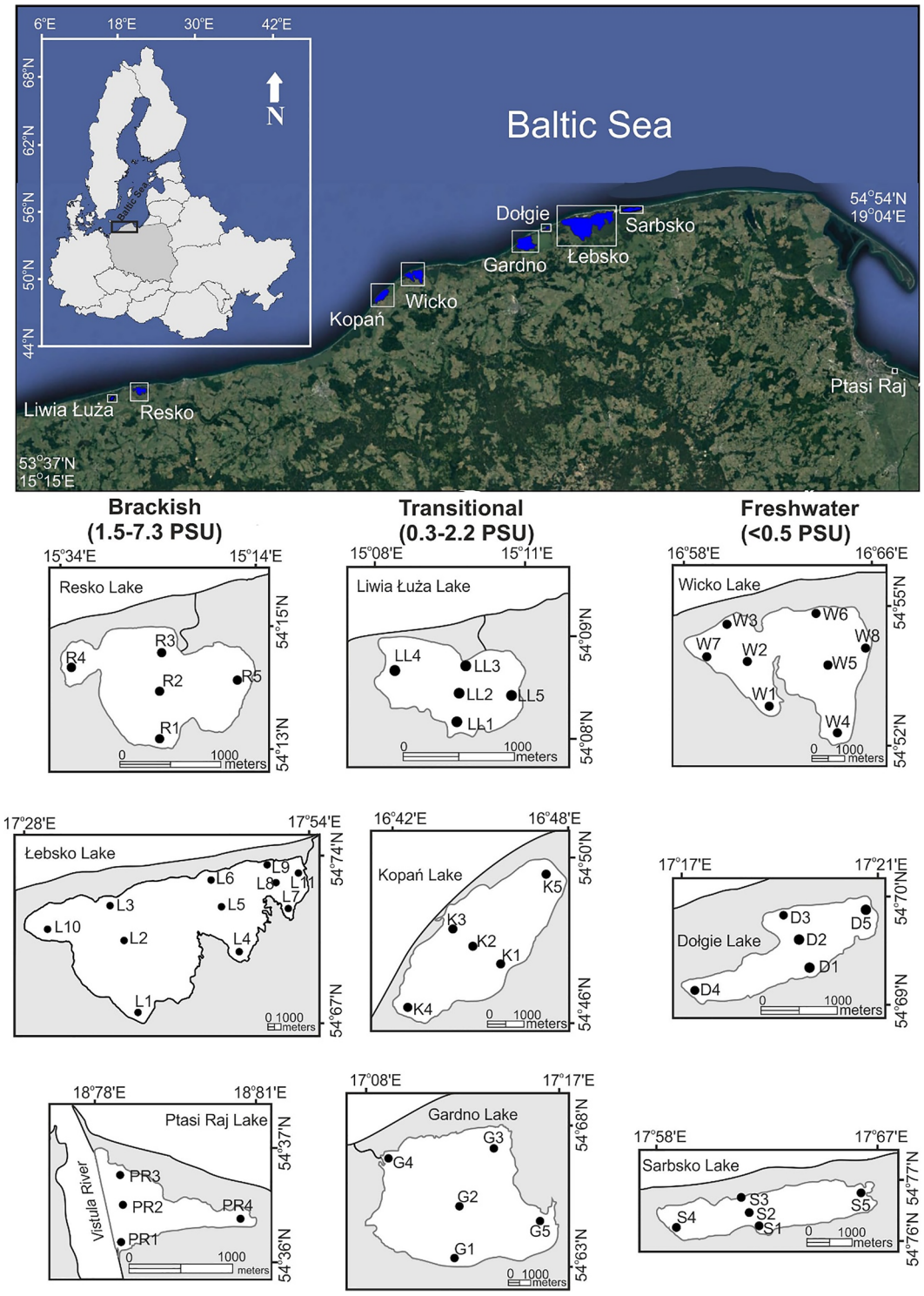


**Figure 1.** Map of the study sites and sampling stations. (The map was created by the authors in CorelDRAW Standard 2020 – version 22.0.0.474 on the basis of private materials. URL link to producer: https://www.coreldraw.com/).

several years in different periods of the year. Non-metric multivariate scaling and permutational analysis of variance were performed using the PRIMER 7 software (by PRIMER-e)[61].

To identify the biological traits that significantly differentiate the lake types, the non-parametric ANOVA Kruskal–Wallis test was used along with the *post-hoc* test of multiple comparisons of mean ranks for all groups; (considering the multiple comparisons, we applied the Bonferroni correction for p-values). The analysis was carried out using Statistica 13 software (TIBCO Software Inc.).

| Type | Lake | Coordination | | Area [ha] | Mean depth [m] | Volume [$10^3$·$m^3$] | Level of salinity [PSU] | Type of hydrological connection with sea | Time of intrusion (days/year) |
|---|---|---|---|---|---|---|---|---|---|
| Brackish | Ptasi Raj | 54° 22′ N | 18° 48′ E | 53.1 | 1.2 | 655.0 | 6.3–7.3 | Permanent seawater intrusion by estuary of the Wisła Śmiała River | 365 |
| | Łebsko | 54° 43′ N | 17° 25′ E | 7020.0 | 1.6 | 113,482.7 | 2.8–3.9 | Permanent seawater intrusion by the Łeba River | 276 |
| | Resko Przymorskie | 54° 09′ N | 15° 22′ E | 554.1 | 1.6 | 8,630.0 | 1.5–3.4 | Permanent seawater intrusion by the Błotnica River | 257 |
| Transitional | Kopań | 52° 29′ N | 16° 27′ E | 752.8 | 1.5 | 11,650.0 | 0.7–2.2 | Periodical seawater by the Kopański Canal | 102 |
| | Gardno | 54° 39′ N | 17° 07′ E | 2260.8 | 1.4 | 31,273.1 | 0.8–1.3 | Periodical seawater intrusion by the Łupawa River | 165 |
| | Liwia Łuża | 54° 05′ N | 15° 06′ E | 172.3 | 1.0 | 1820.0 | 0.3–0.6 | Periodical seawater intrusion by the Liwia Łuża Canal | 20 |
| Freshwater | Sarbsko | 54° 46′ N | 17° 38′ E | 610.6 | 1.2 | 7340.0 | 0.1–0.5 | Occasional seawater intrusion by Chełst Canal and Łeba River | 8 |
| | Wicko | 52° 32′ N | 16° 37′ E | 977.0 | 2.4 | 23,740.0 | 0.1–0.2 | Occasional sea-water intrusion by Główica River | 0 |
| | Dołgie Wielkie | 54° 42′ N | 17° 12′ E | 135.7 | 1.4 | 1918.6 | ~0.1 | Fully isolated from sea | 0 |

**Table 1.** Hydrological connectivity of the studied lakes with the sea and their morphometrics[5,42–44].

| Trait | Category | Code |
|---|---|---|
| Mobility | Semi-mobile | sm |
| | Mobile | mb |
| | Sessile | ss |
| Habitat | Epifauna | ep |
| | Surface infauna | sr |
| | Subsurface infauna | sb |
| Feeding type | Shredders | sh |
| | Filterers | fl |
| | Collectors | cl |
| | Predators | pr |
| | Scrapers | sc |
| Habitat modification | Tube builder | tb |
| | Simple mounds | sj |
| | No | no |
| Body form | Shell | se |
| | Vermiform | vf |
| | Protected | pb |
| Body size | < 10 mm | < 10 |
| | < 50 mm | < 50 |
| | > 50 mm | > 50 |
| Feeding apparatus | Radula | rd |
| | Jawed | jw |
| | Sucker | su |
| | Stinging-sucking | st |
| | Other | ot |

**Table 2.** Biological traits, their categories and their codes.

In the final part of the analysis, a chord diagram was used for displaying relationships between biological traits; it also highlighted traits assigned to a particular lake type. To achieve this, a matrix defining the relationship between the lake type and the biological trait category was first obtained. This was done by summarizing the scores for each trait category in a given lake type, and then calculating percentages of categories in the traits (for each type of lake). The resulting matrix was then processed in the R environment and the RStudio software with the chorddiag library by Matt Flor to generate the chord diagram.

## Results

In total, 46 taxa of benthic invertebrates inhabiting the soft bottom of coastal lakes in the southern Baltic Sea were identified in the study. Only 13 taxa were recorded in all lake types, e.g. *Polypedilum nubeculosum*, *Chironomus plumosus*, *Sergentia coracina*, *Procladius sp.*, *Bezzia nobilis*. In brackish lakes, 34 taxa were identified, with 13 found only in this lake type. In transitional lakes, 24 taxa were identified, with 5 found only in this lake type. In freshwater lakes, 24 taxa were identified, with 5 recorded only in this lake type. Typically, marine species were rare and included *Hediste diversicolor*, *Pygospio elegans*, *Gammarus oceanicus* and *Idotea balthica*. Two euryhalin species, *C. plumosus* and *P. nubeculosum*, predominated in the invertebrate community, with a combined share of 62%.

Non-parametric multivariate analysis (nMDS) (Fig. 2) of biological features (quantitative BTA and presence–absence BTA) highlighted dissimilarities between the studied lake types. The results were similar to those obtained in traditional species-based analysis. In the scatterplot analysis of the quantitative biological traits, more apparent differences were noted between the lakes.

Statistically significant differences in the abundance of benthic fauna of the Baltic coastal lakes were confirmed (Table 3). The most significant differences were found for the brackish lake type. PERMANOVA results based on quantitative BTA indicated the significance of lake type as a factor differentiating the frequency of particular biological traits ($P=0.001$). Pair-wise testing indicated statistically significant differences between the transitional and brackish lakes ($P=0.001$) and between the brackish and freshwater ones ($P=0.004$). The presence–absence BTA again confirmed the significant impact of lake type on the structure of benthic community ($P=0.005$). Compared to other analyses, the p/a BTA showed statistically significant differences only between lakes with extremely different salinity levels ($P=0.001$) Additionally, there were significant differences in impact of seasonality for the analysis based on species abundance ($P=0.001$) Pairwise tests highlighted significant differences between spring and summer ($P=0.043$), and between spring and autumn ($P=0.001$). There were no significant differences when lake type was combined with seasonality ($P=0.124$).

Sessile organisms predominated in freshwater (80.31%) and transitional lakes (70.82%). The greatest variation in mobility was found in brackish lakes, where sessile forms accounted for 43.87%, mobile forms 35.03% and semi-mobile forms 21.09%. Freshwater lakes were dominated by burrowing organisms (71.07%). In transitional lakes, burrowing organisms were common (56.69%), and epiphytic (22.45%) and surface-active (20.86%) organisms occurred with similar frequency. The brackish lakes were characterised by similar proportions of surface-active (40.86%), epiphytic (31.17%) and burrowing invertebrates (27.97%). Collectors were significantly dominant in freshwater lakes (77.71%) and transitional lakes (75.26%). For brackish lakes, collectors (55.31%) and scrapers (27.95%) were most common. Tube-building invertebrates were common in freshwater (67.99%) and transitional lakes (61.47%) with a much lower occurrence of invertebrates non-modifying their habitat (in freshwater 31.98%, in transitional 38.44%). The opposite proportions appeared in brackish lakes, where invertebrates non-modifying their habitat accounted for 61.12%, while tube-builders accounted for 37.55%. Organisms characterised by worm-like bodies totally dominate freshwater (97.96%) and transitional (95.74%) lakes. For brackish lakes the situation was different, worm-like organisms accounted for 65.32% and shell-owning organisms accounted for 28.11%. Medium-sized invertebrates significantly dominated in freshwater (84.29%) and transitional (86.53%) lakes. In brackish lakes, medium-sized invertebrates were common (61.97%), but small-sized invertebrates were also relatively frequent (36.61%). Organisms with a jawed feeding apparatus totally dominated freshwater (97.21%) and transitional lakes (94.72%). Brackish lakes were further characterised by a predominance of organisms with a jawed feeding apparatus (70.00%), but there was also a significant proportion of those with radula (27.95%).

In order to visualize the differences in the frequency of each category in a given trait between BCL types, a chord diagram was created (Fig. 3). Information about the statistical significance of these differences is provided in the table with the results of the Kruskal–Wallis ANOVA test (Table 4).

## Discussion

The growing need to understand the mechanisms shaping ecosystems makes new research techniques, including the assessment of functional diversity, increasingly popular. However, the definition of functional diversity is still ambiguous, which implies the need to develop unified methods to measure its efficiency in various ecosystems. This corresponds with the belief that ecosystems are more important to environmental health than are individual species[21].

In this study, nine Baltic coastal lakes were divided into three types and examined using the classic taxonomic approach and biological trait analysis (BTA). The biological traits selected for this study (including mobility, feeding type, body form, habitat modification) characterize organisms inhabiting the bottom of waterbodies, and they considerably influence processes in coastal ecosystems. The results of the BTA, PERMANOVA permutational analysis of variance, and nMDS results confirmed that seawater intrusion affected the spatial differentiation of the functional diversity of benthic communities in the studied lakes (Table 3, Fig. 2). In this respect, it confirmed the previous results of BCL studies aimed at determining the qualitative and quantitative structure of benthic fauna[5,62,16]. The application of the BTA and assessment of trait frequency facilitated the determining of specific

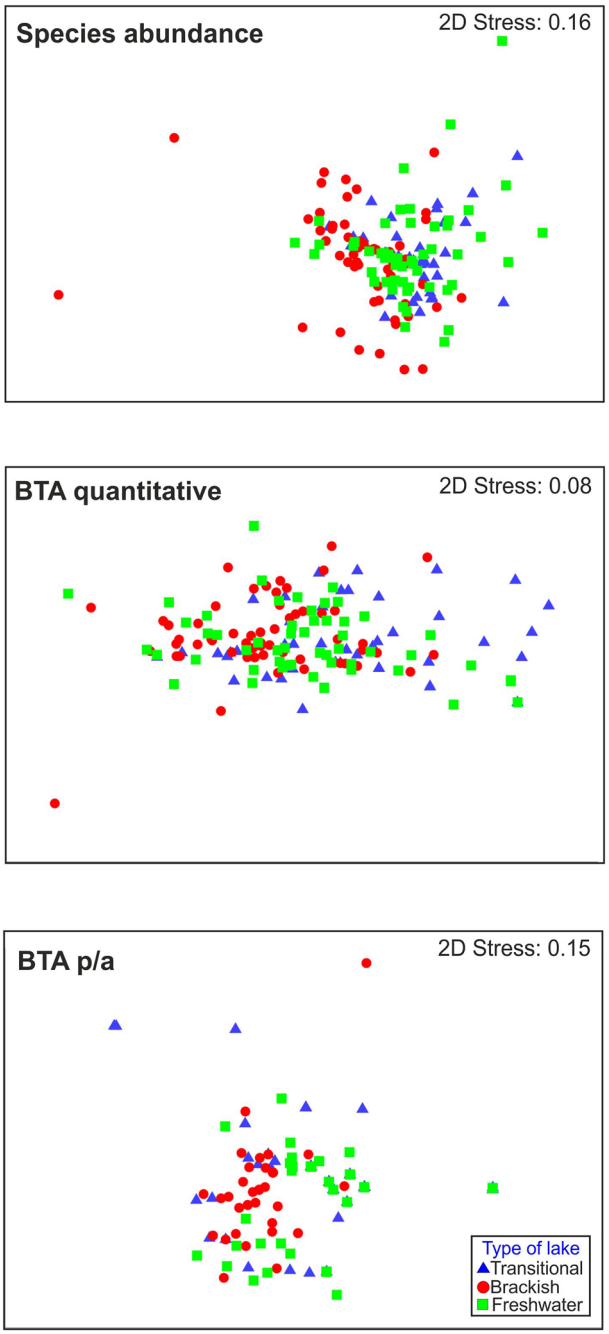


**Figure 2.** NMDS plots based on species abundance, quantitative BTA and presence/absence of biological traits by type of Baltic coastal lake.

configurations of biological traits for each BCL type (Fig. 3). Nevertheless, classical analyses seem necessary to create the basis for further research on functional diversity[16]. It seems that seawater intrusion in the case of the transitional lakes studied by us was too little in relation to their volumes to cause significant changes in the taxonomic and functional structure of benthic communities (in comparison to freshwater lakes). However, we observed that, through their dominance in the lakes studied, two eurybiont species (*C. plumosus*, *P. nubeculosum*) that possess high resilience significantly influence the differentiation between lake types. In the supplementary information (see Supplementary Tables S2–S3 and Supplementary Figs. S1–S2), we considered an approach in which we excluded these two species from the data sets for the same analyses used in this paper. With this approach, statistical analyses revealed significant, meaningful differences between taxonomic and functional structures of benthic communities among all BCLs types.

Benthic organisms found in or on sediment, and near the surface or in deeper waters, are an essential component of aquatic zoocenoses. This implies nutrient flow, bioturbation and sediment stability and structure[63].

| | Source of variation | df | SS | MS | pseudo F-values | p(MC) |
|---|---|---|---|---|---|---|
| **Species abundance** | | | | | | |
| Global test | Type of lake | 2 | 3922.5 | 1961.3 | 6.7184 | **0.001** |
| | Seasons | 2 | 1898.0 | 949.2 | 3.2509 | **0.001** |
| | Type of lake × season | 4 | 1611.4 | 402.9 | 1.3800 | 0.124 |
| Pair-wise test | Transitional × Brackish | | | | | **0.001** |
| | Transitional × Freshwater | | | | | 0.055 |
| | Brackish × Freshwater | | | | | **0.001** |
| Pair-wise test | Spring × Summer | | | | | **0.043** |
| | Spring × Autumn | | | | | **0.001** |
| | Summer × Autumn | | | | | 0.158 |
| **BTA quantitative** | | | | | | |
| Global test | Type of lake | 2 | 9747.6 | 4873.8 | 5.8105 | **0.001** |
| | Seasons | 2 | 1280.1 | 640.1 | 0.7631 | 0.609 |
| | Type of lake × season | 4 | 2597.1 | 649.3 | 0.7741 | 0.680 |
| Pair-wise test | Transitional × Brackish | | | | | **0.001** |
| | Transitional × Freshwater | | | | | 0.070 |
| | Brackish × Freshwater | | | | | **0.005** |
| **BTA p/a** | | | | | | |
| Global test | Type of lake | 2 | 1555.6 | 777.8 | 3.5770 | **0.003** |
| | Seasons | 2 | 390.7 | 195.3 | 0.8983 | 0.497 |
| | Type of lake × season | 4 | 302.6 | 75.7 | 0.3479 | 0.953 |
| Pair-wise test | Transitional × Brackish | | | | | 0.176 |
| | Transitional × Freshwater | | | | | 0.067 |
| | Brackish × Freshwater | | | | | **0.001** |

**Table 3.** Results of permutation analysis of variance (PERMANOVA), effect of BCL type (brackish, transitional, freshwater) and seasonality on abundance of invertebrates and on biological traits (quantitative BTA and presence-absence BTA) in the investigated coastal lakes. Analysis based on Bray–Curtis dissimilarity indices. p(MC): p-value obtained with Monte Carlo permutation test. Bold values indicate significance ($P < 0.05$).

Due to these processes, different functional traits of benthic organisms occur with different frequencies. For instance, foraging behavior (= feeding groups) is so important that it is often considered an essential element of functional diversity of benthic communities and is therefore used in investigating these communities' responses to environmental factors[64–66]. This is possible because trophic guilds combine adaptations, from foraging behavior to diet composition to body modifications, which affects nutrient recycling, energy flow and sediment stability[67]. Mobility is another important ecological trait that affects feeding behavior and defines trophic relationships in benthic communities[36,68]. Basically, it is related to the ability of organisms to move into and out of sediment. In coastal lakes, mobile species were recorded mainly in the lakes with strong seawater intrusion (brackish). This factor can cause abrupt changes in the habitat, thus forcing organisms to migrate to more suitable places. It can also cause the resuspension of bottom sediments and the release of dead organic matter, a potential food source[69] and[70] indicated that the disturbing factor (exploitation of resources) that determines the reconstruction of the habitat structure leads to an increased amount of dead organic matter and an increased number of highly mobile species. Seawater intrusion may have a similar effect in brackish lakes, increasing the mobility and contribution of collectors and scrapers. On the other hand, in freshwater lakes, more stable conditions favor the presence of sessile and semi-mobile organisms (Fig. 3). In our study, the greater share of predators in freshwater and transitional lakes compared to brackish lakes (where collectors and scrapers were dominant) might be connected with the more stable environmental conditions. According to[71] salinity is a stress factor for predators (e.g. lower predation may be a sublethal effect of increased salinity), which results in changes in the composition of invertebrate communities, further lowering trophic levels. Similarly, the variability in the salinity level may decrease predator numbers, which affects the top-down control of the food web, indirectly affecting the trophic cascade[71,72]. [65] and [73], investigating lotic ecosystems, discovered that a low number of predators might be related to the fact that, as specialists, they are more sensitive to disturbances in the environment – unlike generalists, which can eat a variety of foods and thrive in a range of habitats.

Individual body size is also related to life strategy, energy flow and species ecology[74], constituting a good descriptor of the condition of coastal ecosystems[16,75–77]. However, some authors have questioned the accuracy of this notion as the means of describing community functioning[78]. In a number of studies, body size has turned out to be less efficient than other traits in describing the variability of benthic communities in marine and transitional waters[36,46,79]. Nevertheless, we decided to include body size in the list of features used for multivariate analyses. Some functional features, though considered important in determining the community structure, tend to be ignored in studies of benthic communities. The main reason is the scarcity of information in the literature

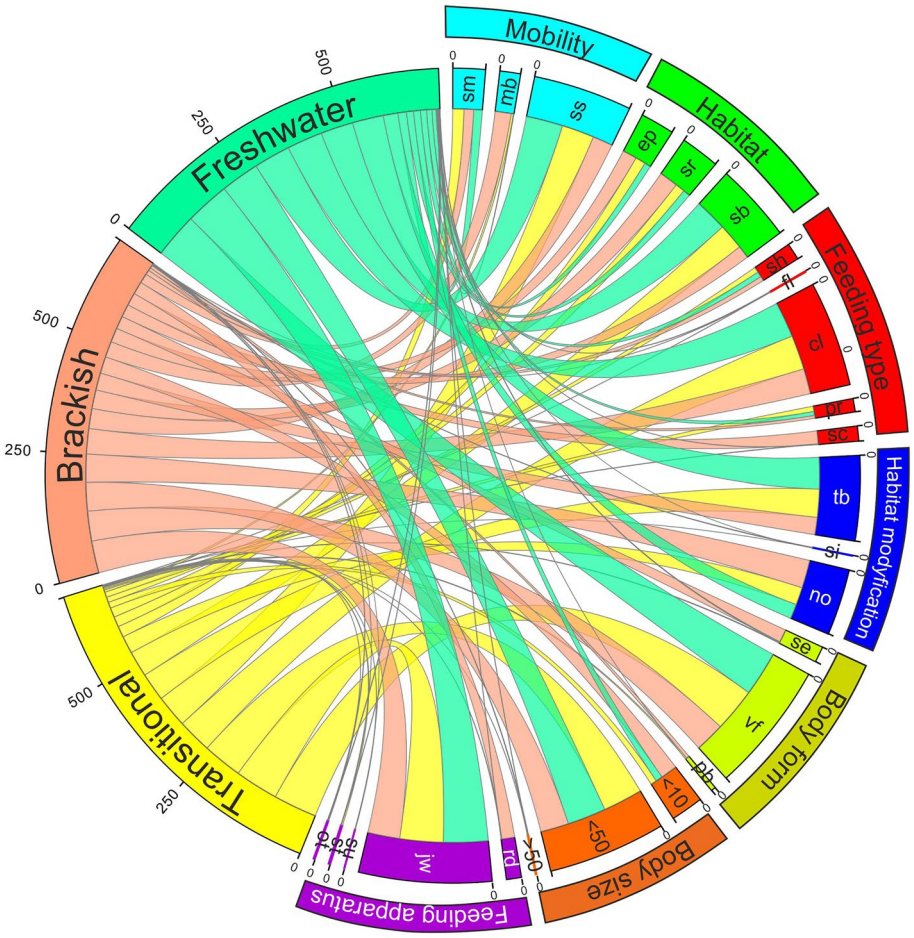


**Figure 3.** Patterns of co-occurrence of different response metrics monitored in studies on functional diversity analyses assigned to brackish, transitional and freshwater BCL types. The base of each ribbon has a width proportional to the importance in lake type in which a particular metric was monitored in combination with the metric at the other end. As the ribbon gets wider, the proportion of that category within the trait is higher.

| Trait | Modalities | ANOVA Kruskal–Wallis test | Post-hoc test |
|---|---|---|---|
| Mobility | sm | H = 12.2925 $P = 0.0021$ | Brackish × Transitional $P = 0.0367$ |
| | mb | H = 24.2625 $P = 0.0000$ | Brackish × Freshwater $P = 0.0010$ |
| | ss | H = 13.2246 $P = 0.0013$ | Brackish × Transitional $P = 0.0210$ |
| Habitat | ep | H = 25.3268 $P = 0.0000$ | Brackish × Transitional $P = 0.0013$ |
| | | | Brackish × Freshwater $P = 0.0015$ |
| | sr | H = 27.0065 $P = 0.0000$ | Brackish × Transitional $P = 0.0001$ |
| | | | Brackish × Freshwater $P = 0.0197$ |
| Feeding type | cl | H = 15.0209 $P = 0.0005$ | Brackish × Transitional $P = 0.0093$ |
| Habitat modification | no | H = 20.4160 $P = 0.0000$ | Brackish × Transitional $P = 0.0010$ |
| Body form | vf | H = 13.0649 $P = 0.0015$ | Brackish × Transitional $P = 0.0226$ |
| | pb | H = 34.3075 $P = 0.0000$ | Brackish × Freshwater $P = 0.0001$ |
| Body size | < 50 | H = 13.5181 $P = 0.0012$ | Brackish × Transitional $P = 0.0234$ |
| Feeding apparatus | jw | H = 17.5465 $P = 0.0002$ | Brackish × Transitional $P = 0.0023$ |

**Table 4.** Results of Kruskal–Wallis analysis of variance, differences in trait categories between types of BCLs were examined. The Bonferroni correction was used for the *P*-value of the post-hoc test; only statistically significant differences were included, $P < 0.05$.

on autecology. As emphasized by[34,36] or[16], this is especially true for rare traits, such as reproductive strategy and life expectancy, and for less common species. In this light, the feature selection proposed in our study combines the load of ecological information verified by previous BTA studies[21,34–36] with the availability of information.

In coastal ecosystems, water salinity and seawater intrusion influence the functioning of benthic communities directly (tolerance to salinity) and indirectly by altering environmental conditions (e.g. increased oxygenation, resuspension of bottom sediments, and distribution of organic matter and contaminants)[2,27,80]. As a result, an ecosystem whose hydrological connectivity with the sea is additionally reinforced by storms is subject to frequent disturbances (changes) that may impair system resilience (e.g.[81–84]). The relationships between the differentiation of functional features of benthic organisms along the salinity gradient and the mechanisms promoting this distribution can be explained by the biology and behavior of individual species (functional groups) and by their interactions with biotic/abiotic factors[15,19,21]. The abundance of nutrients suitable for a particular group, as well as the type and intensity of environmental stressors, determine trophic links and survival strategies. Owing to these relationships, functional traits can provide insights into changes occurring in a given ecosystem[85–87]. This emphasizes the importance of specific anatomical and behavioral characteristics in the functioning of the benthic zone of coastal lakes.

Low species abundance and low taxonomic diversity in transitional ecosystems (coastal lakes, lagoons) cannot be considered reliable indicators of ecosystem functioning, as they result from the presence of tolerant species that are resistant to environmental stressors (e.g. salinity)[36]. [88] also point out that ubiquitous dominant species can buffer the lack of highly specialized ones in biocenoses. As a result, the functional redundancy and zoocenosis immunization against environmental stress may increase. However, the overwhelming dominance of eurybionts (e.g. in terms of foraging behavior) may negatively affect the ability to detect functional changes along natural or anthropogenic gradients, which should be taken into account when developing indicators based on the functional diversity or composition of benthic communities in transitional ecosystems [88]. [34] suggested investigating time-induced changes in relative proportions of biological traits as a potentially reliable way to identify impact-driven alterations in ecosystem diversity. Functional trait analysis, if sufficient knowledge of trait-environment patterns is achieved, may perhaps provide a broader picture of ecosystem functioning than the traditional taxonomic approach, and become an alternative method for determining reference conditions[7]. [89] identified and validated a model of reference conditions for European rivers by establishing patterns of traits that differ predictably depending on certain environmental conditions. As stated by[7], this model could also be adapted to marine ecosystems, although our current understanding of the relationship between these ecosystems and biological traits exhibited by benthic organisms is still insufficient. Therefore, it is assumed that large-scale research involving many different habitats will help to determine biological trait composition, which could be used in general models. The subsequent step would involve examining these models for assumptions and predictive power. Such reference models could provide valuable information on ecosystem management, thus helping to understand biodiversity patterns. Similarly to[7], we see the need for further comprehensive studies aimed at developing reference models for marine and transitional ecosystems. Functional analysis (with modifications) may therefore be a reliable method for assessing ecosystem diversity for coastal lakes. It will also help to conduct a more profound analysis of biological data according to the evolutionary-systemic approach.

Our study is the first to use the functional approach to understand the importance of biological traits of benthic fauna in coastal lakes of the southern Baltic Sea. In this regard, it could be the starting point for future research on BCL functional diversity. In view of ongoing climate change, further analyses may offer a better insight into changes in the frequency of individual biological traits over time. It is possible that transitional water environments may serve as early warning indicators of the effects of climate change in marine ecosystems. For the Baltic Sea, these would be BCLs, which, due to their location and characteristics (small, shallow, less resilient), will probably respond more quickly to changing climate and increasing average water temperatures. Information on the extent and pace of changes in the functional diversity of these waterbodies could facilitate the predicting of future shifts in the Baltic Sea.

## Conclusion

Coastal lakes are characterized by unstable environmental conditions, with macrobenthos being represented by a small number of species. BTA used for the analysis of the benthic communities of the southern Baltic coastal lakes indicated that their biological traits responded to spatial gradients. This response corresponds to differences in hydrological connectivity/degree of seawater intrusion. The functional composition of benthic communities responded visibly to the "Baltic effect": functional diversity increased with increased lake connection to the sea and with increased salinity. At the same time, the functional composition of benthic communities was more homogeneous in isolated lakes. The functional approach provides insight into changes in the frequency pattern of biological traits in relation to salinity levels caused by seawater intrusion. In addition, this method can help to identify which traits may significantly differentiate between BCL ecosystem types. We believe that the functional approach applied in this study (BTA) may be integrated into coastal lake monitoring programs. Moreover, functional approaches are becoming useful tools in determining the relationship between the dominance of specific traits of benthic communities and lake hydrological connectivity with the sea.

## Data availability

A dataset containing the abundance of individual taxa is available at this address: https://www.mdpi.com/2076-2615/11/11/3039#supplementary.

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## Author contributions

M.M., K.O.: Conceptualization; M.M., K.O.: Investigation; M.M., K.O.: Writing-original draft; M.M., K.O.: Writing-review and editing; M.M., K.O.: Supervision.

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## Competing interests

The authors declare no competing interests.

## Additional information

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# Salinisation effects on benthic invertebrate assemblages in shallow lakes in arid and semiarid climate zones

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**Shallow lakes, including those located at the border between Europe and Asia (Kazakhstan), have become very prone to increasing salinity because of climate change. Most of the study area is in one of the fastest-warming parts of the globe. Our research, conducted in four lakes varying in water salinity level and located in western Kazakhstan in the steppe, semi-desert, and desert zones, can be used to predict biodiversity as indicators of the natural potential of ecosystems. This was achieved by assessing the associations of invertebrate communities with environmental conditions based on data collected during nine seasonal measurement campaigns (in May, July, and September of 2019, 2020, and 2021). The multidimensional scaling (nMDS) of biotic and abiotic data enabled us to identify lakes as freshwater (1), oligohaline (1), and mesohaline (2). The key classifier was biotope salinity, irrespective of lake location in the steppe, semi-desert, or desert zones. Twenty-nine taxa were identified in the freshwater lake, 37 in the oligohaline, and 24–28 in the mesohaline lake; these accounted for ~ 80% of their estimated taxonomic composition, according to Species Accumulation Curves (SAC). The differences in the structure of benthic invertebrate assemblages revealed between the lakes are mainly concerned with the density and, to a lesser extent, the diversity of communities (Simpson index). As the salinity of the waters increased, the proportion of Diptera larvae significantly increased, and that of Ephemeroptera larvae decreased. *Sigara assimilis*, accompanied by *Sphaeromas* sp., *Chironomus* sp., and *Saeharia* sp., proved strongly resistant to increased water salinity. Among the studied lakes, the semi-desert lake Balykty Sarkyl (β-mesohaline) is strongly threatened by biodiversity degradation due to unfavourable climatic conditions. Time series analysis for Lake Edilsor (α-mesohaline) shows that it underwent the most rapid salinisation, which has increased the number of taxa tolerant to this predictor (mainly Diptera larvae). The results confirm that detailed taxonomic assessment (including time series) can significantly improve our understanding of lake changes with increasing salinity caused by climate change and/or other stressors.**

**Keywords** Macrozoobenthos, Invertebrate diversity, Degradation of lakes, Kazakhstan

Lentic ecosystems (i.e., wetlands, ponds, and lakes with stationary or relatively still freshwater) are among the elements of the biosphere that are most variable within a relatively short time[1–3]. The biodiversity of lakes, treated as metasystems, strongly depends on hydrological conditions, structure and function, and relative positions in the landscape[4]. The role of lakes as "signallers" of the reaction of the Earth to climate change[5] is a critical element of interest for the United Nations' Intergovernmental Panel on Climate Change (IPCC) and the United Nations Framework Convention on Climate Change (UNFCCC).

Serious environmental consequences of climate change are observed worldwide and will probably worsen[4,6]. The crucial importance of these transformations is attributed to less frequent ice cover, changes in lake water surface temperature, increased evaporation and high productivity[7,8]. All this markedly affects water level and quality, nutrient dynamics, the trophic structure[9], community composition[8,10], and the migratory routes of invasive species[11,12].

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Because of global warming, we can expect changes in the trophic structure and biodiversity of shallow lakes as combined effects of the rise in temperature and salinity. Still, the latter will be particularly noticeable in areas with precipitation deficits and coastal zones[4,7,8,13]. Most of the area of Kazakhstan is characterised by a dry climate and numerous lakes[14], but simultaneously, it is one of the fastest-warming parts of the globe[15–17]. This results in progressing changes in abiotic conditions in aquatic ecosystems, implied directly (climate change) and indirectly (climate-change-intensified eutrophication). The average annual air temperature in Western Kazakhstan is 5.9–6.1 °C for the steppe area, 6.8–7.6 °C for the semi-desert area and 8.2–9.5 °C for the desert area. During the warmest period of the year, the temperature ranges from 21.4 to 21.6 °C in the steppe area, 22.8–23.3 °C in the semi-deserts and 24.4–24.8 °C in the desert. Winters are harshest in the steppe area (-10 °C), followed by the semi-desert area (-8.5 °C), and mildest in the desert area (-7 °C)[16–18].

This remarkably affects the functioning of lake ecosystems because their ecological balance is disturbed [e.g.,[18,19]]. Additionally, the increasing concentrations of dissolved ions in water cause multidirectional changes in the structure and functioning of ecosystems on a global scale[9]. This is generally observed in all extreme habitats, e.g., highly saline lakes, where species composition and diversity decline with increasing salinity [e.g.,[8,20]]. For this reason, lakes with a broad salinity gradient are very attractive study areas for detailed research on transformations of ecological metasystems[21]. The studies, however, should include data on the condition of the biotope and on the assemblages of hydrobionts inhabiting it. In this context, analyses of changes in the species structure of benthic invertebrates can provide beneficial information on how salinity affects ecosystem shifts. Moreover, species of this group are sensitive indicators of changes in aquatic ecosystems [e.g.,[22,23]] because they allow us to assess which structural and functional features linked with endurance and resilience react to rising salinity levels[24]. In general, many organisms are observed in lakes with moderate salinity, with the largest mosaic of microhabitats. However, the speed of climate change may disrupt these patterns[9,17]. Euryhaline species, especially those belonging to the Hemiptera and Diptera order, are observed to have physiological adaptations that allow them to thrive despite a substantial increase in biotope salinity[8].

The role of salinity for the microbiome in coastal and related ecosystems has been widely studied [e.g.,[9,24]], whereas, for inland water bodies, it still requires more investigation. In this study, we have attempted to determine to what extent the gradient of lake salinity (from freshwater to mesohaline) in steppe, semi-desert, and desert zones determines the diversity of benthic fauna. This also allowed us to verify the main hypothesis that an increase in lake salinity (to more than 15 ppt) noticeably limits the abundance and diversity of benthic invertebrates. Thus, we assumed that: (H1) high salinity is preferred only by a narrow group of taxa of invertebrates; (H2) lakes with a moderate level of salinity are the most favourable ecosystems*transit* for benthic invertebrates; (H3) differences in water salinity level, rather than geographic location, increase habitat heterogeneity of lakes in western Kazakhstan.

## Materials and methods

### Study area

The West Kazakhstan Region (WKR), including the study lakes, is located in the north-western part of the Republic of Kazakhstan, mostly within the catchment area of the Caspian Sea (Fig. 1). The region is 425 km long in a north-south direction and 585 km long in an east–west direction, lying at 48°00'–51°35'N and 45°30'–54°35'E. Most of its territory is within the steppe zone. The region is crossed by the Ural River, which flows through the Orenburg Region (Russia) in the north, the Atyrau Region, and the Caspian Sea in the south. The Ural is also a natural border between Europe and Asia. The western part of the West Kazakhstan Region is within the Volga's catchment, the world's largest and longest river that ends in a lake (known as the Caspian Sea)[25].

Lakes of western Kazakhstan are generally shallow water bodies with poorly developed shorelines and are scattered across steppe, semi-desert, and desert zones. The lakes are polymictic[25] but differ in size and water salinity level (Table 1). This causes problems with unambiguously classifying the water bodies, as they have specific features that affect their functioning. The study lakes are located in zones differing in annual precipitation level: Edilsor < 200 mm; Balykty Sarkyl 200–250 mm; Glubinnoe 250–300 mm; and Prorva > 300 mm[16].

### Sampling and processing

Field research was conducted in four lakes in western Kazakhstan: one freshwater – Prorva Lake, one oligohaline – Glubinnoe Lake, one α-mesohaline – Edilsor Lake, and one β-mesohaline – Balykty Sarkyl Lake, in 2019–21. On each lake, three sites were selected along an east–west profile (shore zones and middle of the water bodies) and visited three times a year (in May, July and September). At the 36 sites, 108 lake sediment samples were collected using a Van Veen sampler (sampler area 0.045 $m^2$). The solid samples were sieved through a 0.5-mm mesh and preserved in 70% ethanol. Next, the samples were transported to a Makhambet Utemisov West Kazakhstan University laboratory, where the collected material was transferred to glass trays and sorted under a stereo microscope M60 (Leica, Japan) with 0.8-4.0 magnification. All invertebrates were identified and counted at the lowest possible taxonomic level using proper keys[28–30].

Water sampling for analysis of chemical parameters and in situ measurements (pH and salinity) was carried out at a single point in the middle of the lake using a multiparameter meter (WTW, MultiLine P4). Chemical parameters were assessed spectrophotometrically, according to instructions attached to the instrument (DR3900, Hach): chemical oxygen demand, sulphates, nitrates, chlorides, carbonate hardness, bicarbonates, magnesium, and calcium (expressed in mg $L^{-1}$).

### Data analyses

To classify the sampling plot of the four study lakes, we applied non-metric multidimensional scaling (nMDS) based on matrices of Euclidean distances (abiotic predictors) and Bray–Curtis distances (biological data), using Primer-e v.7.0 software[31]. The method revealed considerable differences in abiotic conditions (Supplementary

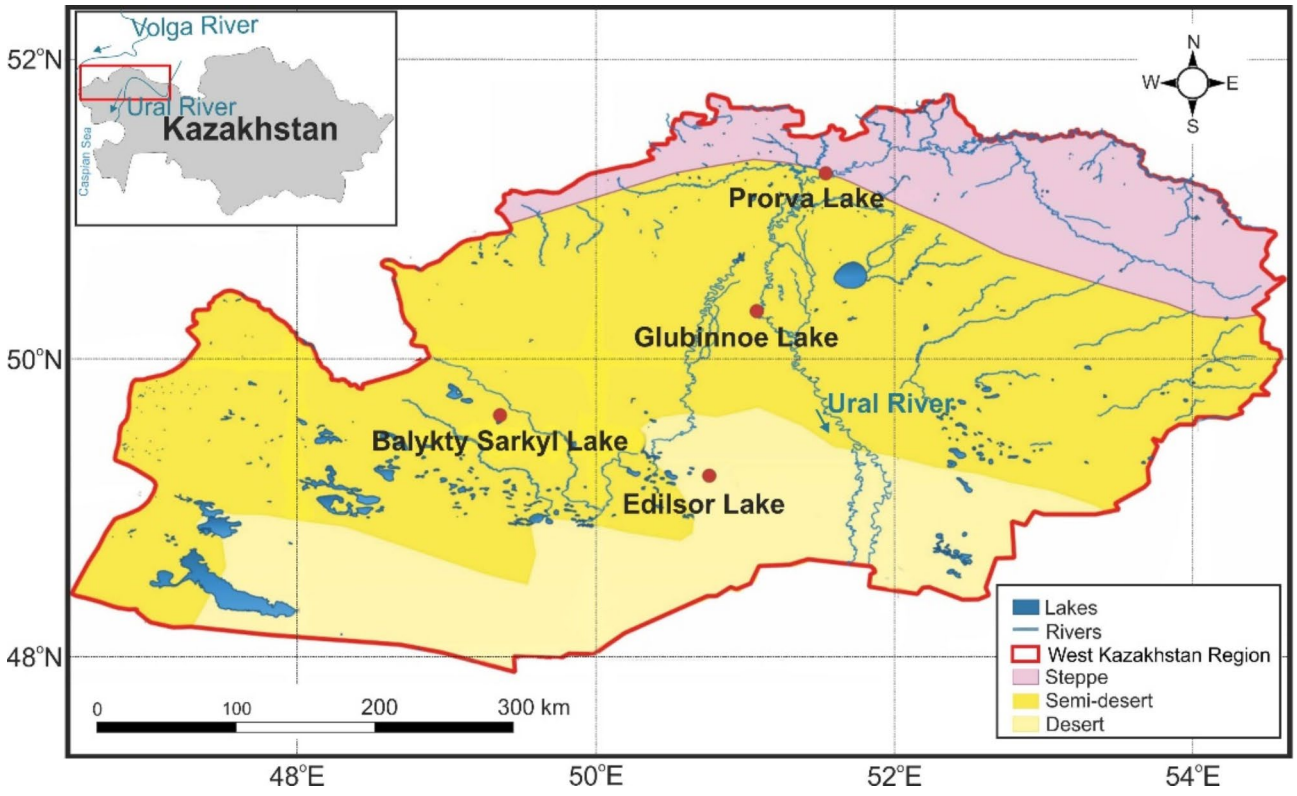


**Fig. 1**. The location of the West Kazakhstan Region indicates study sites. Land-use categories: steppe (pink), semi-desert (dark yellow), and desert (yellow). *Map created with Quantum GIS 3.28. All editions were made on CorelDRAW Graphics Suite EDU 2018.*

| Lake | Range of areas [ha] | Average depth [m] | Max. depth [m] | Capacity [$10^6$ $m^3$] | Level of salinity |
|---|---|---|---|---|---|
| Prorva | 2.8–3.4 | 1.5 | 4.2 | 0.42–0.51 | Freshwater (> 0.5 ppt) |
| Glubinnoe | 0.8–6.1 | 1.2 | 1.9 | 1.00–7.32 | Oligohaline (0.5–5.0 ppt) |
| Balykty Sarkyl | 1270–1600 | 1.6 | 4.2 | 20.32–25.60 | β-mesohaline (5.1–10.0 ppt) |
| Edilsor | 955–1190 | 1.3 | 3.7 | 12.42–15.47 | α-mesohaline (10.1–18.0 ppt) |

**Table 1**. Characteristics of saline inland lakes in West Kazakhstan. Water body type corresponds to salinity level, based on a proposal by Montagna et al.[26]. The range of areas was measured using satellite photographs for the 2019–21 seasons[27].

Fig. S1A) and biotic factors (Supplementary Fig. S1B) of the studied water bodies, except between the most similar lakes, Balykty Sarkyl and Edilsor, which represent α- and β-mesohaline subtypes. Thus, the grouping was consistent with the classification based on salinity[26], and so we started to use the terms "freshwater", "oligohaline", and "mesohaline".

Spearman rank correlation analysis was used to identify correlations between the measured water chemical parameters and verify the normality of the variables' distributions (Shapiro–Wilk test).

Species Accumulative Curves (SAC) were used to test whether the number of samples collected was adequate to determine the richness of the benthic invertebrate community in the study lakes using the "specaccum" function of the "vegan" package in the R environment (in R-Studio software). The methods used to determine SAC were "exact", showing predicted (mean) species richness, and "rarefaction", showing mean accumulating individuals instead of intakes. In addition, the expected species richness was tested by fitting a Michaelis–Menten model. The detailed results are provided in the supplementary material (Supplementary Fig. S2).

An Analysis of Similarities (ANOSIM, 999 permutations) was performed using Bray–Curtis distances to assess differences in the composition of the benthic assemblages among the lake types[32]. If significant differences were found, a similarity percentage analysis (SIMPER)[33] was applied to identify the taxa most responsible for the differences. At that stage, the data were tested for normality (Shapiro–Wilk test) and homoscedasticity (Levene test), and then the $\log(x+1)$ was transformed. Differences between variables for lake types were tested by analysis of variance (ANOVA) with the Kruskal–Wallis test by ranks ($K$–$W$, $p < 0.05$).

Two-way cluster analysis was run independently for groups of samples and invertebrates and then combined into a single diagram to allow observation of associations between lake type in seasons and groups of invertebrates. The input data were analysed with the maximum variable (recommended by PC-ORD), and the matrix of variation was calculated using Bray–Curtis distance. The matrix of agglomerative trees of hierarchical grouping was generated using the flexible beta method (β = -0.25). The significance of differences in the multivariate structure of benthic invertebrates communities was tested using (a) permutational analysis of variance (PERMANOVA)[34] and (b) analysis of variance (ANOVA) with the Kruskal–Wallis test by ranks. The three descriptors of invertebrates were: (a) density (indiv. $m^{-2}$), (b) Simpson index (1-D), and (a) species richness. Determination of differences between types of habitats colonised by invertebrates (permanent categorising factors) and the four study lakes (random factors: 1 freshwater, 1 oligohaline and 2 mesohaline, distinguished in the categorisation) was conducted with the use of permutational (9,999 replications) analysis of variance (PERMANOVA) performed on a matrix of Euclidean distances. All statistical tests used a significance level of α = 0.05.

The heatmap, which presents the preference of identified benthic invertebrate taxa considering the salinity level of the lakes studied, was created using the PRIMER software's "Shade plot" function (based on log(x + 1) density data).

Individual taxa occurrence is relative to the salinity gradient. The relationship between species richness and the degree of lake-water salinity were visualised using the "ggplot2" package in the R environment. A curve fit was performed based on the Self-Starting Non-linear Logistic Model for the relationship between species richness and water salinity.

The final element of the data analyses was to examine the differences in β-diversity index values between the benthic invertebrate communities of the analysed lakes and the change between sampling sites at each site from 2019 to 2021. The entire procedure takes into account Jaccard similarity (S), relative wealth difference (D), and relative species replacement (R), respectively (SDR-simplex), and was carried out according to the methodology proposed by Podani et al.[35].

## Results

### Environmental conditions

The nMDS revealed remarkable differences in the variability of chemical parameters of water in the study lakes (Supplementary Fig. S2A, Supplementary Table S1). Spearman's correlation analysis showed significant relationships between salinity and most of the water chemistry parameters examined. Parameters correlated with salinity showed equally substantial relationships with each other. Only pH and $HCO_3^-$ content (negligible correlation with salinity) showed no correlation with other water parameters (Supplementary Table S2). However, the dispersion of results was most significant for the mesohaline lakes, whereas in freshwater and oligohaline lakes it was much smaller. The most significant differences between the studied of lakes (K–W = 28.83, $p < 0.0001$) concerned salinity level, which was about 44-fold higher in the mesohaline lakes than in the limnetic lake. Other chemical variables differed significantly between the three salinity types of lakes, reaching generally higher values (except for $CaCO_3$ and $Mg^{2+}$) as salinity increased (Table 2). Similarly, concentrations of $Cl^-$, $Mg^{2+}$ and $Ca^{2+}$ were, respectively, about 88-, 16- and three-fold higher in the mesohaline lake. Slightly less significant differences concerned water hardness ($CaCO_3$), $SO_4^{2-}$, COD and pH, and the least significant differences concerned $NO_3^-$ and $HCO_3^-$ in the studied lake. Carbonate water hardness was highest in the oligohaline lake.

### Salinity concentration and assemblage similarities

The biological structure of invertebrates was consistent with the lake classification based on water salinity (Supplementary Fig. S2B). In total, 19,654 individuals of benthic invertebrates were collected, representing 74 taxa (69 species and five genera) (Supplementary Table S3). The highest number of representatives of the benthic invertebrate assemblage was recorded in the oligohaline lake (37), followed by freshwater (29), and the least in mesohaline (24–28). The least diverse assemblage within this range was found in the α-mesohaline lake (Balykty Sarkyl Lake).

| | Unit | Freshwater $n = 9$ | Oligohaline $n = 9$ | Mesohaline $n = 18$ |
|---|---|---|---|---|
| pH*** | – | 7.57 ± 0.51 | 7.61 ± 0.58 | 7.93 ± 0.57 |
| Salinity*** | ppt | 0.40 ± 0.19 | 0.76 ± 0.18 | 15.48 ± 10.26 |
| COD*** | mg $L^{-1}$ | 9.13 ± 8.92 | 19.80 ± 16.20 | 53.66 ± 64.37 |
| $NO_3^-$*** | mg $L^{-1}$ | 0.98 ± 0.87 | 2.27 ± 1.89 | 57.14 ± 100.59 |
| dH*** | mg $L^{-1}$ | 16.7 ± 28.1 | 17.9 ± 23.1 | 108.5 ± 87.4 |
| $HCO_3^-$* | mg $L^{-1}$ | 224 ± 255 | 318 ± 108 | 241 ± 89 |
| $SO_4^{2-}$*** | mg $L^{-1}$ | 142.2 ± 69.6 | 149.9 ± 30.0 | 530.0 ± 467.1 |
| $Cl^-$*** | mg $L^{-1}$ | 51.2 ± 32.5 | 181.1 ± 134.7 | 25,205 ± 4,655 |
| $Mg^{2+}$*** | mg $L^{-1}$ | 56 ± 43 | 47 ± 41 | 724 ± 421 |
| $Ca^{2+}$*** | mg $L^{-1}$ | 79 ± 80 | 83 ± 29 | 381 ± 263 |

**Table 2**. Average chemical water characteristics (mean ± SD) of salinity lakes during 2019–21 ($n = 36$) and results of one-way ANOVA test evaluating differences of results (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

From the Species Accumulation Curves (SAC) and the fitted model, the likely number of species present in a given lake was determined (Supplementary Fig. S2A). The species composition identified during the study was most complete for the β-mesohaline Edilsor Lake (81%), followed by the oligohaline Glubinnoe Lake (79%) and the freshwater Prorva Lake (78%). In contrast, the estimated number of taxa was determined to be least complete for the α-mesohaline Balykty Sarkyl Lake (72%). Considering the rarefaction SAC approach, curves for all the sampled lakes were rapidly reaching asymptotics. (Supplementary Fig. S2B). A small number of rare species was observed in the collected samples. Visualisation of the frequency of occurrence of individual taxa (Fig. 2) in the studied lakes reveals a preference for the salinity level of their biotopes. New species appeared in the most saline lakes, and sporadic and scarce taxa in other lakes increased.

Based on the species richness data collected, it was found that the species richness of the benthic invertebrate communities inhabiting the lakes decreased with increasing salinity levels. Taxa with exceptionally high salinity tolerance included: *Sigara assimilis*, *Sphaeromias* sp., *Chironomus* sp., *Saetheria* sp. (> 40 ppt), *Microchironomus deribae*, *Glyptotendipes paripes*, *Cricotopus trifasciatus*, *Cladotanytarsus mancus*, *Hydrochara flavipes*, *Berosus frontifoveatus*, *Erythromma najas*, *Crocothemis erythraea* (> 18 ppt) (Supplementary Fig. S3).

The taxonomic structure of benthic invertebrates markedly differed among the compared lakes ($R_{ANOSIM}$=0.571, $p$ = 0.001). Results of the SIMPER analysis (Supplementary Table S4) showed that the Odonata (19.1%), Ephemeroptera (17.7%), Hemiptera (17.0%) and Diptera (16.6%) accounted most strongly for the observed differences between freshwater and oligohaline lakes. When comparing freshwater and mesohaline lakes, the differences resulted from the abundance of the Ephemeroptera (20.4%), Diptera (18.1%), Crustacea (13.2%), Hemiptera (13.2%) and Odonata (11.4%). In contrast, for oligohaline vs. mesohaline lakes, they resulted chiefly from the abundance of the Odonata (23.5%), Diptera (15.5%), Hemiptera (15.8%) and Crustacea (14.7%). Simultaneously, the density of the recorded groups of benthic invertebrate assemblages differed significantly between the lake types, reaching the highest values in the oligohaline lake (Table 3). Only in the lake with the lowest water salinity were the Oligochaeta and abundant Mollusca (including Gastropoda and Bivalvia) recorded. At the same time, the Hemiptera and Odonata preferred lakes with a moderate salinity level.

The mesohaline lakes (mainly Edilsor Lake) had the highest density values and freshwater lakes the lowest (Fig. 3A). Ephemeropteran larvae dominated only in the least saline lake (~ 64%), while Diptera larvae dominated in moderately and strongly saline water bodies (46% and 63%, respectively) (Fig. 3B).

Two-way cluster analysis (Fig. 4) showed that the Ephemeroptera were abundant in the limnetic lake, contributing to the appearance of one spring–summer cluster (red frame). In the oligohaline biotope, in spring and autumn, they formed one cluster with the autumn results for the freshwater lake (green frame). This was chiefly due to the high densities of the Odonata and Diptera. High densities of four groups of invertebrates (green frame) caused the isolation of a cluster, including all results for mesohaline lakes and summer results for the oligohaline water body (Fig. 4). Thus, the seasonal variation in biological results was relatively low in lakes with the highest salinity level, as compared to the other lake types.

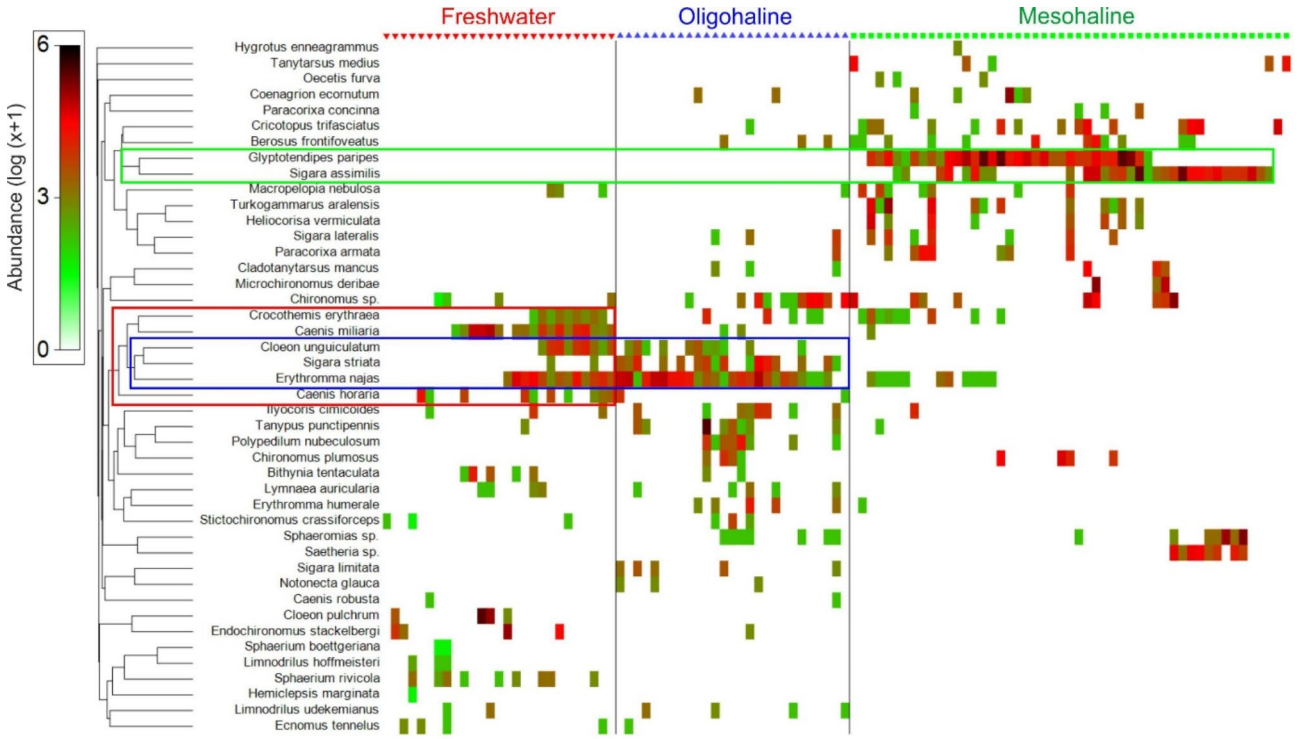


**Fig. 2**. Heatmap of preference of identified benthic invertebrate taxa in terms of salinity level of the lakes studied.

| | Freshwater $n=27$ | Oligohaline $n=27$ | Mesohaline $n=54$ |
|---|---|---|---|
| Oligochaeta* | 2.2 ± 5.9 | 2.4 ± 6.2 | 0.0 |
| Hirudinea | 0.1 ± 0.8 | 0.0 | 0.0 |
| Crustacea*** | 0.0 | 0.0 | 10.9 ± 31.2 |
| Ephemeroptera*** | 70.6 ± 85.4 | 10.1 ± 12.4 | 3.4 ± 18.4 |
| Odonata*** | 29.9 ± 37.1 | 61.6 ± 42.6 | 6.9 ± 21.3 |
| Hemiptera*** | 4.7 ± 12.0 | 47.9 ± 57.9 | 52.6 ± 62.9 |
| Trichoptera | 1.8 ± 4.6 | 0.3 ± 1.5 | 0.7 ± 3.2 |
| Diptera*** | 19.0 ± 35.3 | 58.8 ± 74.6 | 112.8 ± 92.4 |
| Coleoptera** | 0.9 ± 2.6 | 3.9 ± 10.0 | 6.8 ± 16.0 |
| Gastropoda*** | 7.7 ± 11.1 | 2.4 ± 5.8 | 0.0 |
| Bivalvia*** | 5.3 ± 14.0 | 0.9 ± 3.4 | 0.0 |

**Table 3**. Mean density (indiv. $m^{-2}$ ±SD) of groups of benthic invertebrates in lakes of varying salinity in western Kazakhstan ($n=108$) and results of non-parametric Kruskal–Wallis test (* $p<0.05$, *$p<0.01$, ***$p<0.001$).

The results of permutational analysis of variance (PERMANOVA), testing the effects of biotope types on the structure of invertebrates (Table 4), indicated that benthic invertebrates preferred lakes with the highest water salinity values recorded in this study (7.44–47.22 PSU) over those with low values (0.25–0.90 PSU) and moderate ones (0.51–1.04 PSU) (Supplementary Table S1).

The results of the analyses were consistent, regardless of whether they were considered with respect to the presence/absence or relative density of benthic invertebrate groups. Species richness differed significantly among oligohaline vs. mesohaline lakes (Table 4). Results of analysis of variance (ANOVA) with the Kruskal–Wallis test by ranks (K–W, $p<0.05$) for Simpson index (1-D) did not identify statistically significant differences between salinity lake types. However, the mean index value was lowest for the mesohaline lakes and highest for the oligohaline lake.

The analysis results at the beta-diversity level (SDR-simplex) showed variation between lakes and the taxonomic groups inhabiting them. Changes in beta-diversity parameters over the time series were noticeable but occurred differently between lakes. The level of similarity between sampling plots was lowest in the freshwater lake and highest in the two mesohaline lakes (Table 5). During the three-year study of the lakes of western Kazakhstan, there was a clear downward trend in beta-diversity (except in the oligohaline lake). In addition, most lakes (excluding the freshwater lake) showed a significant level of species substitution, the change being biggest in the α-mesohaline lake (from 51.1 to 16.7). All lakes were characterised by high levels of taxonomic richness agreement and high levels of nesting species. This phenomenon was characteristic of lakes with higher levels of biotope salinity, which were particularly strong in the last year of the study.

The similarity between lakes was highest for the occurrence of representatives of Oligochaeta (only between freshwater and oligohaline lakes) and Ephemeroptera, and lowest for Coleoptera. At the same time, Oligochaeta and Trichoptera had the highest species substitution, while this indicator was lowest for the Ephemeroptera. The order Coleoptera had the highest diversity in the lakes studied, whereas Odonata had the lowest. The representatives of Ephemeroptera were strongly attached to a specific lake, and Hemiptera was widely distributed.

## Discussion

Salinity changes the functioning of ecosystems by modifying biotic and abiotic processes[8,36]. The changes in salinity affect aquatic fauna and flora both indirectly and directly. Possibly, fauna and flora react to the same extent to these direct effects and to indirect ionic effects of salt concentrations[5,9,17,24,37]. The taxonomic diversity of the benthic invertebrate assemblage in the lakes of the western region of Kazakhstan fits this pattern, as their distribution was grouped according to the salinity gradient (Supplementary Figs. S1A and B). Our study confirmed the hypothesis H1 that high salinity is preferred only by a narrow group of invertebrate taxa. Of the identified representatives of the invertebrate fauna, only 16% showed significant resistance to high water salinity of > 18 ppt, and only 4% to salinities of > 40 ppt (Supplementary Figs S3A and B). Within this group, only two species were generally observed most frequently and in most significant numbers: *Sigara assimilis* (Hemiptera) and *Glyptotendipes paripes* (Dipter) (Fig. 2). As reported by Knowles and Williams[38], Hemiptera representatives, including those of the Corixa family, are similarly highly tolerant of increases in biotope salinity and possess efficient osmoregulatory properties. Among Corixidae, the species *S. assimilis* colonises mesohaline and polyhaline ecosystems[39] and ends its life cycle at a salinity of 36 g $L^{-1}$[40,41]. The highest salinity tolerance of the various species of dipterans was for the family Chironomidae (to 115 g $L^{-1}$), as documented by some authors in saline water ecosystems in other arid regions of the world[42,43]. High fecundity, ability to migrate, non-specific trophic relationships, high larval mobility, short life cycle and use of food sources in the trophic link that are not used by other organisms decisively contribute to dipterans succeeding under extreme environmental conditions[44]. *Glyptotendipes* spp. represented the Chironomidae family and are constant inhabitants of mesohaline aquatic ecosystems located at the same latitude as the studied water bodies[45]. Small individuals of the genus Chironomus were recorded in the high-salinity samples[46]. Due to *C. salinarius*'s very high salinity

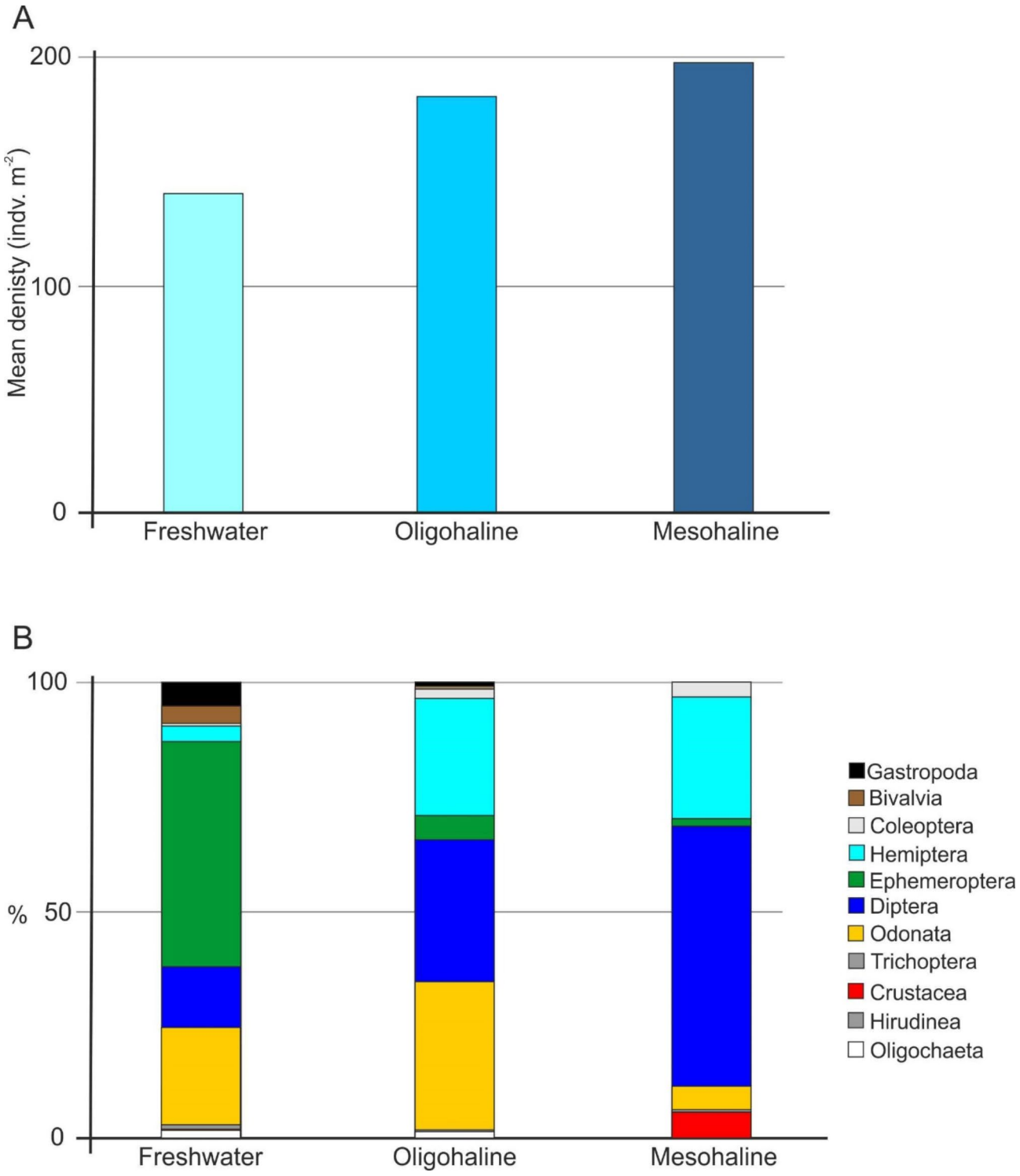


**Fig. 3**. Differences in density (indiv. $m^{-2}$, **A**) and cumulative percentage shares (**B**) of benthic invertebrates inhabiting study lakes along the water salinity gradient.

tolerance, it can be assumed that this species may have occurred mainly in the oligo- and mesohaline lakes studied. The salinity tolerance of their larvae, which inhabit saline rivers, coastal lagoons, seas, and lakes in the 6–80 g $L^{-1}$ salinity range, is well known [e.g.,[46,47]]. The finding of *Saetheria* sp. representatives is shocking and unclear in high-salinity samples, which are treated as freshwater taxa that do not tolerate even low salinity[48]. A specific adaptation is the ability to overcome osmotic stress, as this behaviour is observed in species considered to be prominently freshwater[49]. However, this requires further research, including laboratory studies. As for taxonomic composition, oligochaetes and molluscs were observed only in freshwater lakes, but it is common

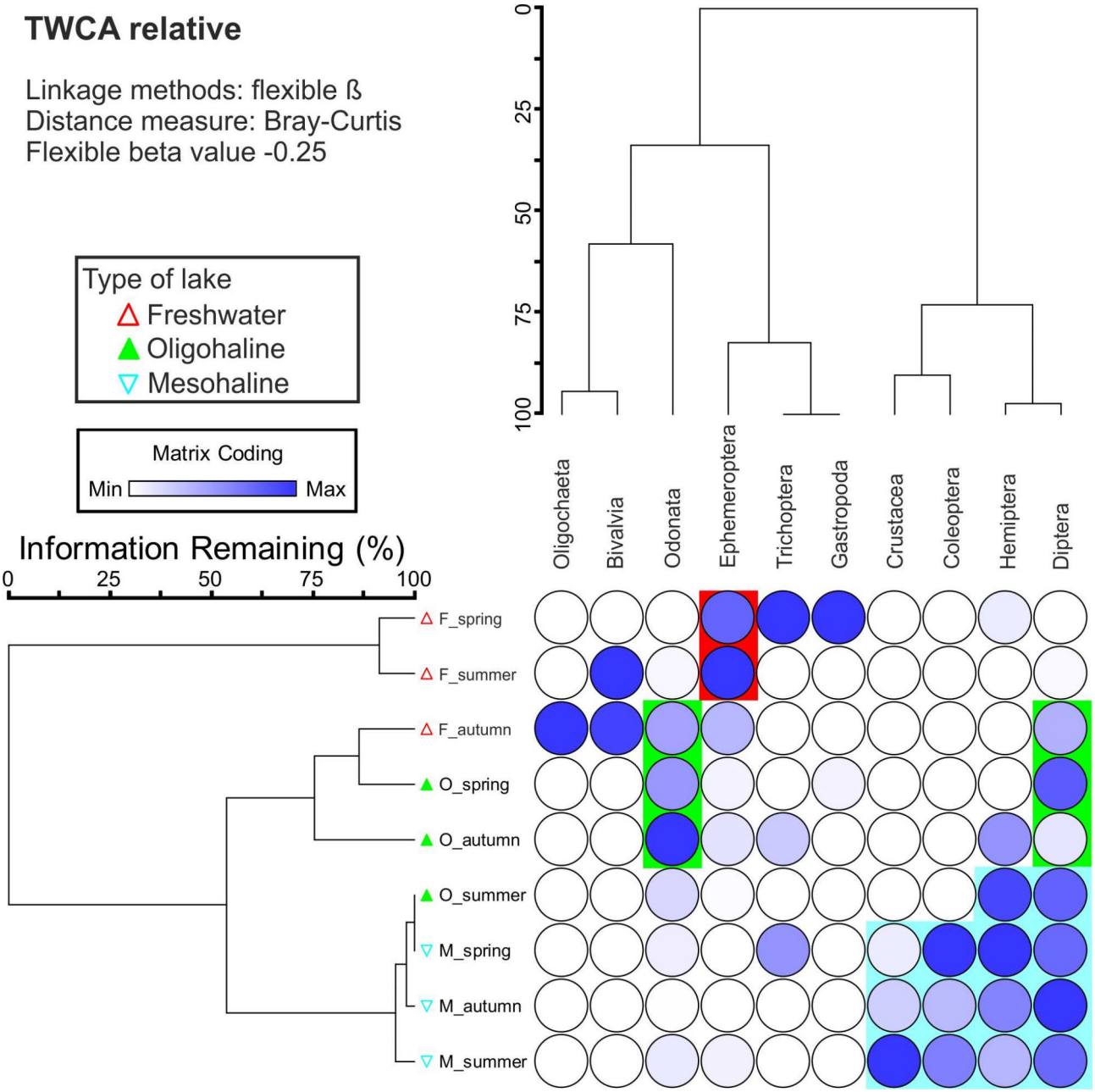


**Fig. 4**. Two-way cluster analysis (TWCA) based on the relative value of seasonal changes in biotic variables in samplings of 3 types of lakes: freshwater (F), oligohaline (O), and mesohaline (M). The horizontal dendrogram groups invertebrates and the principal representatives according to similarity. The vertical dendrogram groups samples according to seasons in each type of lake. Cold map colours indicate the minimum (white) to the maximum (blue) density of benthic invertebrate groups, wherein each element is scaled to its maximum contribution to the total recorded value in a study lake.

knowledge that increasing salinity negatively affects them[50]. In our study, three freshwater Oligochaeta species were reported to tolerate salinities below 5%[48]. It turns out, however, that with increasing water salinity, scorpionfish respond to rapid changes in salinity, not by osmoregulation, but by their behaviour; they venture into the black mud substrate, where the salinity is more stable. In the case of molluscs, the main predictor of their development is the appropriate ionic composition of the water, not just the sum of the ions taken as its salinity. As Brezina[51] pointed out, an unbalanced content of certain cations, especially potassium, limits their development.

In our study, species richness was highest in the oligohaline lake (37 taxa) and lowest for Lake Balykty Sarkyl (17), which represents the β-mesohaline subtype and is located in a semi-desert (Supplementary Table S2). In this respect, the hypothesis H2 was confirmed – lakes with a moderate salinity level are the most favourable places for benthic invertebrates. The intermediate ecosystem (oligohaline), thanks to the higher heterogeneity

| | Sources of variation | Df | SS | MS | Pseudo F values | *p*(MC) |
|---|---|---|---|---|---|---|
| Species richness | salinity lake types | 2 | 77.056 | 38.528 | 3.7807 | **0.03** |
| | lakes | 3 | 129.070 | 43.025 | 4.3954 | **0.004** |
| | Residual | 105 | 1,070.000 | 10.191 | | |
| Pair-wise tests of study lake: | | | | | | |
| Freshwater x oligohaline | | | | | 1.721 | 0.08 |
| Oligohaline x mesohaline | | | | | 2.606 | **0.008** |
| Freshwater x mesohaline | | | | | 0.683 | 0.49 |
| Density | salinity lake types | 2 | 1.05E + 05 | 52,508 | 17.927 | **0.001** |
| | lakes | 3 | 1.20E + 05 | 2807 | 14.276 | **0.001** |
| | Residual | 105 | 2.99E + 05 | 2929 | | |
| Pair-wise tests of study lake: | | | | | | |
| Limnetic x oligohaline | | | | | 3.0282 | **0.001** |
| Oligohaline x mesohaline | | | | | 4.7376 | **0.001** |
| Limnetic x mesohaline | | | | | 4.4086 | **0.001** |

**Table 4**. Permutational analysis of variance (PERMANOVA) results showing the effects of salinity lake types (freshwater, oligohaline and mesohaline) and lakes (1 freshwater, 1 oligohaline and 2 mesohaline) on benthic invertebrate descriptors (species richness and density). Analysis performed based on Bray–Curtis dissimilarity indices. p(MC): p-value obtained with Monte Carlo permutation test. Bold-faced values indicate significant differences at $p < 0.05$.

| | Matrix fill | Similarity 100 S | Relativised species replacement $100R_{Rel}$ | Relativised richness difference $100D_{rel}$ | Relativised beta diversity $100_{\beta}$ | Relativised richness agreement $100A_{rel}$ | Relativised nestedness 100Nrel | Percentage anti-nestedness fraction | Relativised strict nestedness 100Nrel ′ | Percentage richness identity fraction |
|---|---|---|---|---|---|---|---|---|---|---|
| Freshwater lake | | | | | | | | | | |
| 2019 | 63.6 | 47.4 ↓ | 38.7 | 13.9 | 52.6 ↑ | 86.1 | 61.3 | 0 | 61.3 | 0 |
| 2020 | 62.5 | 50.7 ↓ | **39.1** | 10.1 | 49.3 ↑ | 89.9 | 60.9 | 0 | 60.9 | 0 |
| 2021 | 69.2 | 59.5 | 21.4 | 19.1 | 40.5 | 80.9 | 78.6 | 0 | 60.6 | 17.9 |
| Oligohaline lake | | | | | | | | | | |
| 2019 | 63.1 | 45.3 | 46.5 ↑ | 8.2 ↓ | 54.7 | 91.8 ↑ | 53.5 ↓ | 0 | 53.5 ↓ | 0 |
| 2020 | 63.5 | 46.7 | 35.3 ↑ | 18.0 ↓ | 53.3 | 82.0 ↑ | 64.7 ↓ | 0 | 64.7 ↓ | 0 |
| 2021 | 60.8 | 46.2 | 18.7 | **35.1** | 53.8 | 64.9 | 81.3 | 0 | **81.3** | 0 |
| α-mesohaline lake | | | | | | | | | | |
| 2019 | 64.2 | 48.9 ↓ | 35.8 ↑ | 15.2 | 51.1 ↑ | 84.8 | 64.1 ↓ | 0 | 48.7 ↓ | 15.4 ↓ |
| 2020 | **87.8** | 75.8 ↓ | 18.2 ↑ | 6.1 | 24.2 ↑ | 93.9 | 81.8 ↓ | 0 | 54.5 ↓ | 27.3 ↓ |
| 2021 | 83.3 | **83.3** | 0 | 16.7 | 16.7 | 83.3 | **100.0** | 0 | 66.7 | 33.3 |
| β-mesohaline lake | | | | | | | | | | |
| 2019 | 54.2 ↓ | 34.3 ↓ | 38.5 ↑ | 27.1 | **65.6** ↑ | 72.9 | 61.5 ↓ | 0 | 61.5 | 0 |
| 2020 | 71.4 ↓ | 66.7 ↓ | 33.3 ↑ | 0 | 33.3 ↑ | **100.0** | 66.7 ↓ | 0 | 0 | **66.7** |
| 2021 | 83.3 | 74.4 | 16.7 | 8.9 | 25.6 | 91.1 | 83.3 | 0 | 58.3 | 25.0 |
| Invertebrates groups | | | | | | | | | | |
| Oligochaeta | 66.7 | 33.3 | 66.7 | 0.0 | 66.7 | 100.0 | 33.3 | 0 | 0 | 33.3 |
| Odonata | 50.0 | 43.4 | 38.4 | 18.2 | 56.6 | 81.8 | 61.6 | 0 | 56.0 | 5.6 |
| Ephemeroptera | 66.7 | 40.0 | 13.3 | 46.7 | 60.0 | 53.3 | 86.7 | 0 | 86.7 | 0 |
| Trichoptera | 50.0 | 33.3 | 66.7 | 0 | 66.7 | 100.0 | 33.3 | 0 | 0 | 33.3 |
| Hemiptera | 45.0 | 22.7 | 37.6 | 39.5 | 77.3 | 60.5 | 8.3 | 53.8 | 53.8 | 0 |
| Diptera | 54.7 | 36.5 | 46.6 | 17.0 | 63.5 | 83.0 | 53.4 | 0 | 53.4 | 0 |
| Coleoptera | 31.3 | 14.6 | 47.0 | 38.3 | 85.4 | 61.7 | 39.6 | 13.3 | 39.6 | 0 |
| Total taxa | 43.8 | 24.9 | 60.8 | 14.3 | 75.1 | 85.7 | 39.2 | 0 | 39.2 | 0 |

**Table 5**. Percentage matrix fill and percentage contributions from the SDR-simplex analyses of actual ecological data. Boldface numbers emphasise the maximum for each column. Arrows indicate monotone trends.

of conditions, is colonised by the most diverse group of invertebrates, as compared with the other types of lakes with the lowest and the highest salinity levels). Thus, this type of ecosystem can be regarded as a hotspot of species richness. The oligohaline water body was characterised by a high abundance of the diverse Hemiptera in summer and Odonata larvae in autumn (Fig. 3B). Most species of dragonflies[52] are typical inhabitants of fresh waters. However, some taxa can survive in waters of increased and high salinity. Simultaneously, the Hemiptera represented the highest number of species (15) in the studied water bodies, and seven were found in the oligohaline lake (Table S2). Despite this, this did not significantly affect the differences in α-diversity values among the lake types studied (Simpson's index). However, the mean value of the index was lowest for mesohaline lakes represented by Balykty Sarkyl (β-mesohaline subtype) and highest for the oligohaline lakes. Surprisingly, invertebrate abundance increased along the salinity gradient of the water bodies studied and not according to a Gaussian distribution (Fig. 3A). In this respect, H2 was rejected, as the highest density was recorded in the β-mesohaline ecosystem (Edilsor Lake), which can be considered a refugium for the benthic invertebrate assemblage. The susceptibility of small populations to environmental changes is a phenomenon that raises serious concern in conservation biology. This applies mainly to the low density of invertebrates inhabiting the freshwater lake (Table 3). Thus, all the protection measures should be dedicated to maintaining this state of the water body. A salinity rise in the lake, treated as an effect of climate change (i.e., an external factor), forces a dynamic reconstruction of the communities (Table 5). External factors, especially radiation intensity and temperature, are responsible for shaping the framework within which the biological interactions in nature take place[53]. Thus, modifying abiotic conditions changes not only the abundance of species but also species composition, often catastrophically[54,55].

Deserts account for nearly 36% of the territory of Kazakhstan, and the climate is clearly continental, with insufficient humidity. Evaporation prevails over precipitation, especially in the western part, where only 19% of Kazakhstani lakes are located, compared to 45% in the north[56]. Because of the high variation in weather conditions and water balance between years and seasons, large changes are observed in lake area, hydrological regime, total salinity and salt composition in water bodies in this region[25]. Ecosystem heterogeneity, such as the presence of lakes in a given area over a relatively wide salinity gradient, allows changes in biodiversity to be tracked. The number of tolerant taxa increased while the number of sensitive taxa declined, and the structure of benthic invertebrate communities became increasingly homogeneous[24,48,51]. This regularity was observed by analysing the beta-diversity results in a time series (Table 5). It turns out that the location of the studied lakes is no longer such a strong predictor of shaping the benthic invertebrate assemblage as the water salinity level. Thus, the results obtained confirm the formulated hypothesis H3. In this context, the salinity level should be treated as an effect of air temperature and precipitation in particular climatic zones (steppe, semi-desert and desert). During the study, the highest (four-fold) increase in water salinity was recorded in the desert Edilsor Lakes. Such an exchange resulted in selecting a narrow group of euryhaline species with significant abundance. Eliminating freshwater species sensitive to salinity increases (Hirudinea, Ephemeroptera and molluscs) has freed up ecological niches for salinity-tolerant taxa biotopes[41,48]. It is also possible that the presence of few water bodies in the desert area of the WKR forces benthic invertebrates to maximise colonisation at a rapid rate. As a result, the free niches of brackish water are first colonised by the most mobile groups of insects and crustaceans (Fig. 3B).

In our study, most of the lakes were linked with the major river – the Ural – or its tributaries, except for Lake Balykty Sarkyl, which is situated in the catchment area of the Volga. However, all of them were affected by the same climatic factors and were clearly polymictic (Table 1). The region near this lake had the lowest annual precipitation, at 210 mm (the desert area of Edylsor Lake had 250 mm), with an average temperature of 7 °C and a warmest quarter of 22.5–23 °C[16]. This also caused the heterogeneity of lake habitats, as particularly seen in a comparison of results from high-salinity lakes (Lake Edilsor and Lake Balykty Sarkyl) against the freshwater Lake Prorva on the graph of nMDS results (Supplementary Fig. 1A and B). Interestingly, habitat conditions in earlier studied water bodies did not differ significantly between freshwater and brackish (transitional) lakes located in the zone influenced by the sea [e.g., 9,40]. Increasing salinity can affect, for example, water pH, dissolved oxygen and the balance of nutrients that regulate ecological processes. Saline lakes in Kazakhstan are at the final stage of (or have already completed) the removal of calcium and bicarbonates. Simultaneously, magnesium concentration will be increasing continuously as long as evaporation prevails, and the precipitation of sequences of sulphate and chloride minerals is becoming increasingly common[42], which is characteristic of the study lakes. That is why concentrations of the above-mentioned environmental predictors ($Ca^{2+}$, $HCO_3^-$, $Mg^{2+}$ and $Cl^-$) differed most significantly ($p < 0.0001$) between the studied water bodies and were linked with their salinity levels (Table 2, Supplementary Table S1).

Nevertheless, both freshwater and saline habitats are known to be relatively stable[55], which allows a long evolution of diverse organisms that fill the niches in those biotopes (Fig. 2). That is why, using the above assumptions concerning benthic invertebrates diversity, we can conclude that both saline and freshwater lakes of western Kazakhstan are filled with various species but that there is still a gap in biodiversity between them. We can assume that this gap in brackish waters (i.e., transitional stage) has not been filled with appropriate species because of the relatively short time of evolution of these biotopes[8]. In comparison with previous years[25], we observed a decline in qualitative and quantitative indicators of benthic invertebrates (e.g., Crustacea) in the studied sites of water bodies. This may be due to a decrease in water level and lake volume and retreat of the shoreline to below the littoral vegetation zone, which provides shelter, food and breeding sites for some groups of benthic invertebrates so that taller aquatic vegetation supports abundant assemblage[56,57]. All these unfavourable phenomena result from increased evaporation and restructuring of aquatic ecosystems in dry regions. The ecosystems should be so-called "signallers" of future changes expected in other climate zones[5]. High salinity levels are toxic to freshwater organisms and may change their ecological interactions[58,59]. In most

of the studies that assessed the sensitivity of freshwater organisms to salinity, sodium chloride (NaCl) was used, and its concentration was treated as a potentially toxic factor[60].

Despite the efforts to provide comprehensive knowledge of the invertebrate faunal assemblage, some limitations must be pointed out. This shortcoming essentially lies in the need to extend the study to polyhaline and euryhaline lakes to confirm the recorded patterns of dispersal of abundance and richness of benthic invertebrates. In addition, it would be necessary to include more sites at each study site to identify missing, small-bodied species. Although the three-year study presented here provides much information, it should continue. This should provide incontrovertible evidence of the effect of climate change in a susceptible area of Eurasia.

## Conclusions

The use of information solely on the structure of benthic invertebrate communities has limited explanatory power when attempting to predict changes caused by increasing salinity; it has also limited attempts to identify stable ecosystem states of individual lakes in deserts, semi-deserts and steppes. The recorded salinity level of these water bodies is now the dominant predictor determining the structure of benthic invertebrate communities. We found that even a small increase in water salinity (compared to freshwater conditions) initiates significant changes in communities. However, only a narrow group of invertebrates (12 taxa) from the orders Hemiptera and Diptera can be found in highly saline lake biotopes. Therefore, their abundance results in the highest density of benthic invertebrates recorded in the most saline desert lake. This is a shocking observation, since it was assumed that the maximum abundance would be recorded in a transitional (oligohaline) lake, which was the case for taxonomic richness. Thus, the oligohaline lake can be regarded as a hotspot of biodiversity in the study region, whereas the β-mesohaline desert lake is a refugium for the benthic invertebrate assemblage. Such conclusions require further analysis, taking into account the other components of the lake ecosystem of dry Eurasian areas with an even wider salinity gradient.

## Data availability

All data generated or analysed during this study are included in this published article and the supplementary material.

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## Author contributions

Conceptualization, A.S., M.M., N.S., and K.O.; methodology, A.S., M.M., and K.O.; software, M.M., and K.O.; validation, A.S., M.M., and Y.S.; formal analysis, A.S., M.M., and N.S.; investigation, A.S., Y.S., and N.S.; resources, A.S., Y.S., and N.S.; data curation, A.S.; writing—original draft preparation, A.S., M.M., and K.O.; writing—review and editing, K.O. and, M.M.; visualization, K.O., and M.M.; supervision, K.O; project administration, A. S. and Y.S.; funding acquisition, S.N. All authors have read and agreed to the published version of the manuscript.

## Declarations

### Competing interests
The authors declare no competing interests.

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# Quantifying the ecosystem health of Baltic coastal lakes based on a multifaceted index

Mikołaj Matela✉ & Krystian Obolewski

**Quantitative assessment of ecosystem integrity and conservation value is essential to identify the degree of ecosystem degradation and to monitor the outcome of remedial and protective actions. We conducted our study on six Baltic coastal lakes (BCLs), three of which are under strict protection (national park). We analysed 15 indicators grouped into three factors and used them to build an expert-based assessment model combining Fuzzy Comprehensive Evaluation and the Analytic Hierarchy Process. On this basis, we calculated a multifaceted index of the ecosystem health. Our results indicate that strict protection in the form of national parks is associated with higher potential for coastal lakes to provide ecosystem services (ES). Strict protection was also associated with higher biotic indices in freshwater lakes, as well as with higher values of abiotic water quality parameters in all lake types. No association was detected between the degree of hydrological connectivity with the sea and the Ecosystem Health Index or ES provision potential. The proposed Ecosystem Health Index enabled a multifaceted evaluation of the ecological condition of the studied BCLs and allowed them to be ranked along a gradient. The index complements WFD-based ecological assessment by integrating ecosystem services and a weighted multi-criteria synthesis tailored to Baltic coastal lakes. Further validation of the Ecosystem Health Index may enable its widespread implementation as part of conservation and nature management plans currently under development.**

**Keywords** Ecosystem services, Lake ecosystems, Protection area, Poland, Southern Baltic zone

In contemporary times, the global population faces an array of challenges that are intrinsically linked to the detrimental impact of human activity on the natural environment, resulting in a decline in its ecological integrity and biodiversity[1–3]. This is combined with the depletion of natural resources and mass extinction of species, i.e. global deterioration of the biosphere, which necessitates countermeasures. The concept of sustainable development entails developing and implementing measures that simultaneously consider the need for both environmental protection and human well-being. At the same time, it is necessary to apply a perspective based on ecosystem services (ES), which determines the direct and indirect benefits that humans receive from nature[4–6]. This, however, requires that ES be quantified, which allows for the efficient management of social-ecological systems[7]. A proper assessment of the potential accumulated in an ecosystem must be based on identifying relevant indicators, among which the assessment of biodiversity levels appears to be important[8]. At the same time, empirically identifying the links between biodiversity and ES is still the subject of scientific inquiry[9]. The focus is on determining the strength of these linkages, as they are often non-linear, mixed or at the limit of detection. There are many opportunities to analyse the level of biodiversity conservation in biocenotic or functional terms. In recent years, the latter approach has become the leading one.

Among the various types of aquatic ecosystems, coastal ecosystems are particularly susceptible to both anthropogenic and non-anthropogenic changes[10]. They are regarded as highly productive and, thus, one of the most valuable on Earth in terms of potential ecosystem service provision[11,12]. Almost half of the world's population lives near coasts, providing them access to trade, land use, recreational features and food production. Therefore, they represent a valuable element of nature and are more attractive to live in than inland places. In addition, it is noted that coastal wetlands, including lagoons and lakes, store significant amounts of carbon, serve as critical habitats for commercial shellfish and fish, and biologically process terrestrial runoff of nutrients[13,14].

In Poland, the coast is primarily used for agriculture and for nature conservation, subject to national protection measures (Slowinski National Park, Wolinski National Park, and Landscape Parks) and international measures (UNESCO, Ramsar, and Natura 2000 network). For this reason, the coast has never been subjected to heavy industrialisation. At the same time, its natural values also result in extreme tourist traffic in summer. Poland's 524-km-long coastline features 55 municipalities inhabited by one-tenth of the country's human population.

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At the same time, in municipalities with lakes, the population density is less than half the Polish average (121 ind./km$^2$)[15]. The greatest threats to coastal ecosystems are posed by the exploitation of waterbodies (including fishing, energy production and aquaculture), environmental engineering (including artificial structures, flood prevention and construction of waterways and drainage systems) and, in particular, the physical and chemical factors associated with human activities[13,14]. The high pressures in the coastal areas also affect the coastal lakes, which are significant to biodiversity protection and crucial for cultural services support in the region. However, it is yet to be established how Poland's economic development is affecting the ecosystem services that coastal lakes can provide[16].

Under the adopted *Water Framework Directive*(WFD; 2000/60/EC), Poland is obliged to monitor and improve water quality. In practice, WFD-based lake assessments in Poland rely on national methods that commonly apply the one-out, all-out rule, whereby the final class is determined by the lowest-rated element. Unfortunately, there is a paucity of scales and indicators available for analysing the particular ecosystem type of Baltic Coastal Lakes (BCLs). This problem is due to the BCLs being insufficient in number for the statistical methods used to construct appropriate indicators and calibrate scales (Supplementary Fig. 1)[17]. The current approach provides limited differentiation among systems that share naturally low transparency but differ in catchment characteristics, biotic structure and potential to provide ecosystem services. In the case of BCLs, the most common indicator of poor water condition is visibility. However, the low water transparency in these lakes stems directly from their genesis as shallow lakes that often function as a form of "settling tank" for water flowing from the catchment towards the sea[18]. When such problems arise (i.e., classification is impeded by the lakes being too few and environmental parameters being inadequate), expert methods should be used that include procedures for increasing objectivity within a well-defined analytical procedure. This method should also take into account a wide range of biotic, abiotic and socio-economic factors included in the model adopted for the analysis. Adopting a holistic approach across these three domains will facilitate our comprehension of the health of BCL ecosystems. The health of an ecosystem is defined as the state of preservation of its ecosystem integrity, including its capacity for regeneration and stability (resilience) and its potential to provide ecosystem services[19–21].

In this context, lakes are merely part of the hydrological network of a river basin, and their condition is influenced by many factors, including the evolutionary and natural processes to which lakes are subject. However, this approach requires consideration of parameters for determining ecological status in accordance with the *WFD* and of indicators relating to the structure of the direct and total catchment area and ecosystem services.

Strict protection of the highest rank (i.e., national park status) is entailed by the legal conditions at IUCN (International Union for Conservation of Nature) level II, which defines the legal framework for the activities and management of areas subject to protection. In national parks in Poland, legal regulations (Supplementary Table 1) limit the possibility of transforming land cover, introducing changes to the landscape, developing buildings and carrying out most economic activities; they also channel tourist traffic by designating trails and observation points open to visitors. For this reason, strict protection affects land use and the type of land management applied.

With climate change and increasing human environmental impact, there is a clear need to shift from a concept that is typically mechanistic (as in the *WFD*) to one that is mechanistic with dynamic elements (such as ecosystem health). To achieve this, we need long-term studies covering a wide range of data, such as a holistic approach to ecosystem health. This would allow us to observe evolutionary changes in the ecosystem under the influence of environmental and anthropogenic factors. Our study is mechanistic in nature, but we hope it will encourage scientists to multiply their efforts towards long-term research on BCLs. This is essential for the adequate monitoring of the dynamics of biospheric processes, particularly in disturbance-sensitive aquatic ecosystems. To obtain a multilevel, holistic assessment of ecosystem health, it is necessary to synthesise details on the optimal number of components affecting ecosystem state and human well-being. Accordingly, the following research questions were formulated: (i) Does the level of hydrological connections with the sea and the forms of BCL protection affect the biodiversity, ecosystem services and habitat condition of BCLs? and (ii) Does the Ecosystem Health Index (ecosystem services + biodiversity + habitat condition) allow for the identification of differences between lakes of the same ecological status?

## Methods

### Study area

The study included six coastal lakes along the southern coast of the Baltic Sea (i.e., Baltic Coastal Lakes [BCLs]) (Fig. 1). These lakes have different origins: bays that have been closed off by the expansion of sandbars; flow-through lakes that were not previously bays; and isolated lakes that were not initially connected to the sea. This plays an important role in shaping hydromorphological conditions, in particular the type of connection with the sea, where most of the former bays have retained a significant connection with the sea, resulting in frequent seawater intrusion. The remaining BCLs are characterised by periodic intrusion through limited connection to the sea (long or unfavourable for the inflow of brackish water connections between lake and sea, including through artificial channels). The last type of BCL concerns freshwater lakes that are isolated from the sea, preventing intrusion. However, all BCLs are shallow, polymictic lakes.

All the study lakes constitute eminently valuable ecosystems protected under the Habitats Directive (under Natura 2000, habitat 1150) and belong to type 4 lakes within the typology developed for the WFD in Poland. A common feature of these lakes is substantial anthropic impact resulting from tourism, recreation, agriculture and the inflow of pollutants from the catchment area, which generates a trophic state at the eutrophic and hypertrophic levels. At the same time, the lakes differ from one another in terms of their patterns of connectivity to the sea (salinity levels). They also differ in level of protection, in that, while all are subject to Habitats and Landscape protection, three (one of each lake type) are additionally subject to strict legal protection designated as national

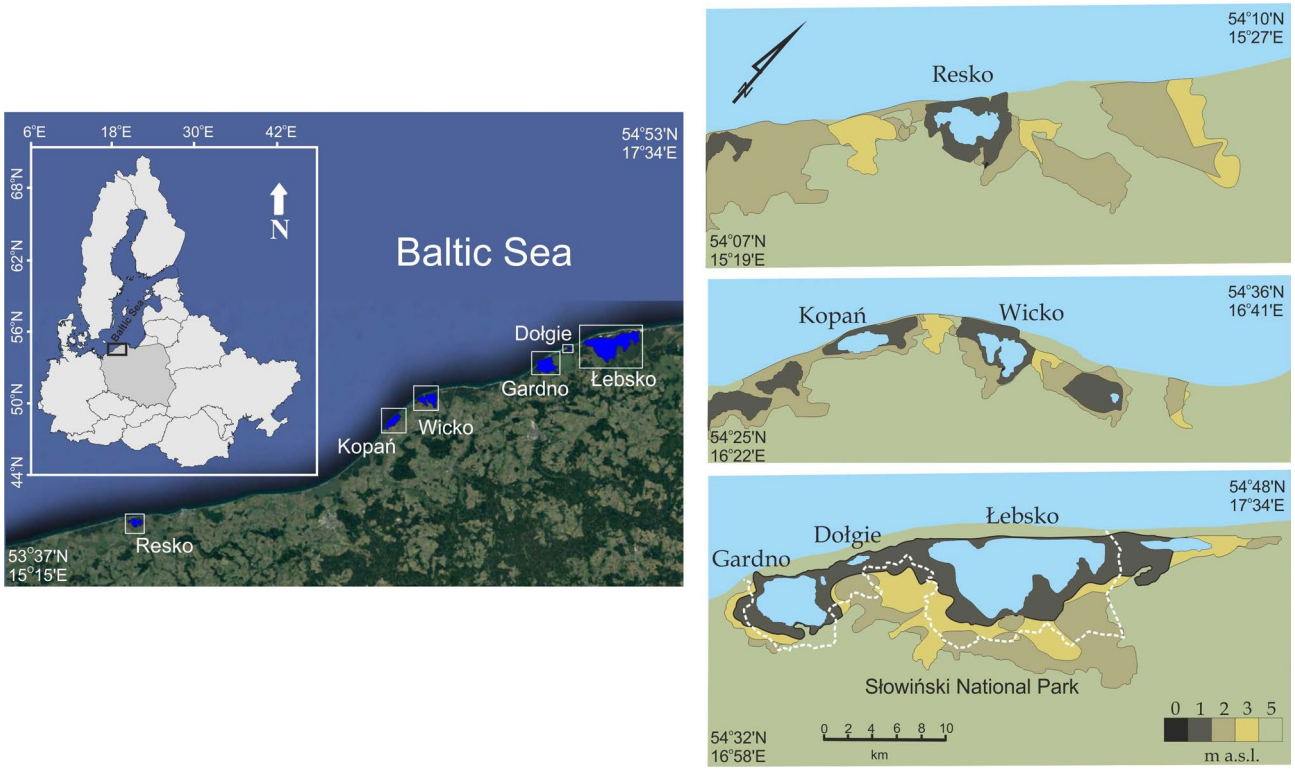


**Fig. 1**. Location of the studied coastal lakes of the southern Baltic Sea (created using QGIS Desktop ver. 3.24.0 https://qgis.org/ and CorelDRAW Standard 2020 https://www.coreldraw.com/).

| Lake | Water body code | Type of lake | Type of protection | | | Trophic state |
|---|---|---|---|---|---|---|
| | | | National park* (IUCN category II) | Habitats** (IUCN category IV) | Landscape*** (IUCN category V) | |
| Resko | PLLW20865 | Brackish | No | Yes | Yes | E |
| Kopań | PLLW20950 | Transitional | No | Yes | Yes | E/H |
| Wicko | PLLW20951 | Freshwater | No | Yes | Yes | E |
| Łebsko | PLLW21045 | Brackish | Yes | Yes | Yes | E |
| Gardno | PLLW21028 | Transitional | Yes | Yes | Yes | E |
| Dołgie | PLLW21046 | Freshwater | Yes | Yes | Yes | H |

**Table 1**. Description of study lakes in terms of hydrological connectivity with the sea, type of protection and trophic status (E-eutrophic, H-hypertrophic)[18,22]. Trophic status was determined based on physicochemical data for BCLs[22] in accordance with the commonly used TSI index scale (Supplementary Table 2). The classification of BCLs into types according to salinity was introduced by[23]. * Slowinski National Park (SNP) (strictly protected), ** habitats protected as Nature 2000 sites, *** landscape parks.

parks (IUCN category II, Slowinski National Park), which entails the most restrictive legal regulations (Table 1). Despite the strict protection status, all six lakes exhibit eutrophic to hypertrophic conditions, as the surrounding catchments extend beyond the protected area boundaries and are subject to intensive agricultural land use. These six lakes were purposively selected to provide a sample set that allows for a comparative assessment of the association between strict protection and differences observed within each of the three lake types. Restrictions resulting from national laws in Poland are presented in Supplementary Table 1.

## Ecosystem health index (EHI) framework for Baltic coastal lakes

The potential of the study lakes was determined by three main groups of factors (structural integrity of the ecosystem [A], integrity of ecosystem processes [B], and ecosystem services [C]) that influence the level of ecosystem health. The fully developed EHI model (prior to adaptation to the BCL case) is presented in Supplementary Fig. 2. Due to the high level of similarity between BCLs in terms of high chlorophyll concentrations in water, frequent blooms and the dominance of cyanobacteria, we recognised information about phytoplankton as a non-differentiating factor for the lakes studied. For this reason, it was not included in the EHI model used in the analysis. Furthermore, the fact that macrophyte flora are species-poor (there is a monoculture of *Phragmites*

*australis* growing mainly in the shore zone of lakes[24]) and the impact of habitat protection on species diversity led us to choose only hydromorphological observations (from a lake habitat modification survey). The EHI model adapted to the case of the analysed lakes is presented in Fig. 2.

The condition of macrozoobenthos (C1) and ichthyofauna communities (C2), along with hydromorphological observations of lake habitats (C3) were selected as indicators for structural integrity, which is understood as the ability of an ecosystem to maintain its structure, i.e. the organisation and interrelationships between biotic and abiotic components. Macrozoobenthos was selected because this group has been proven to be

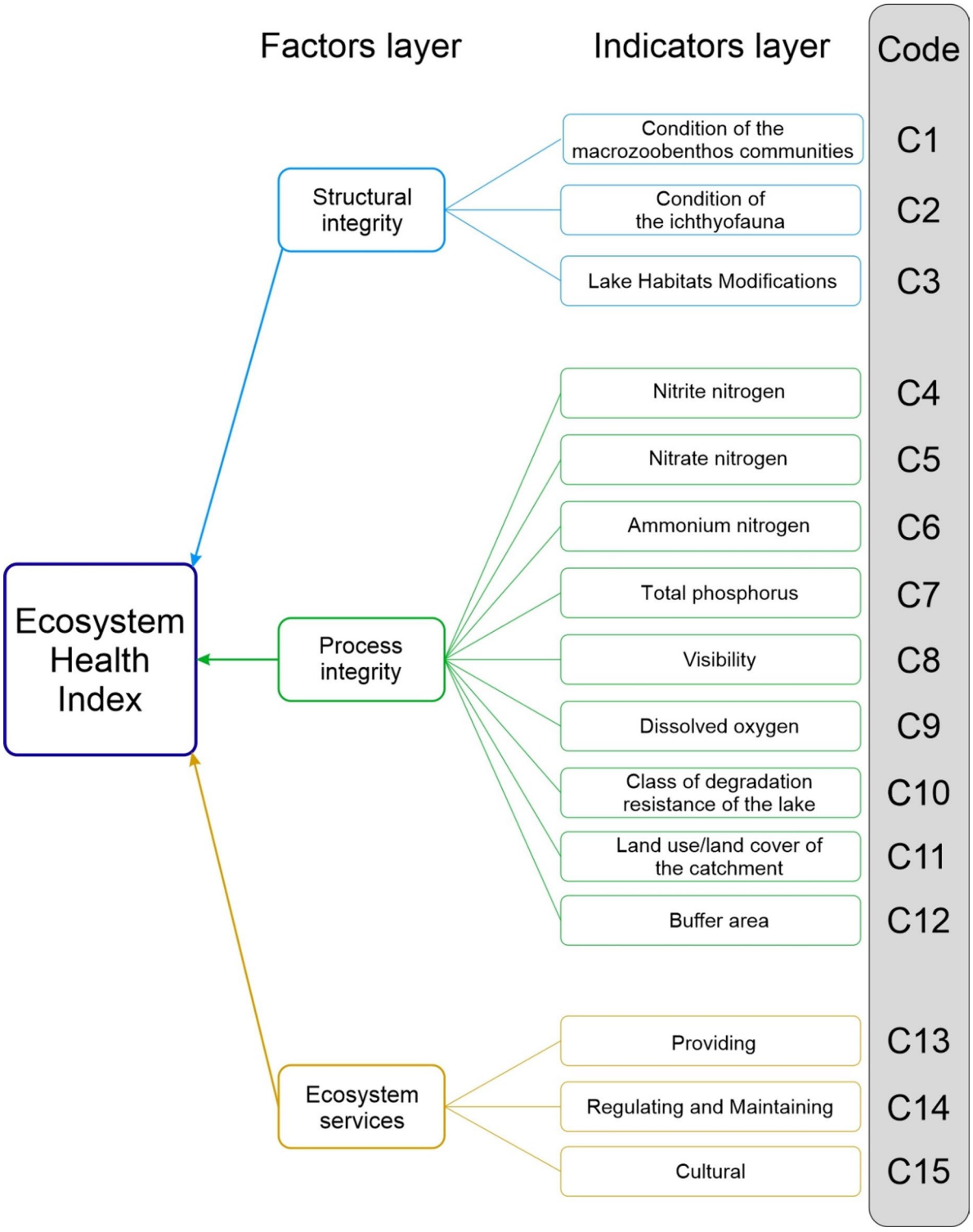


**Fig. 2**. The model of Ecosystem Health Index (EHI) assessment adapted to BCLs case. Note C1-C15 codes for individual basic indicators.

significantly differentiated in these lakes[25,26]. Ichthyofauna was selected due to the sensitivity of changes in the species structure of this group to significant changes in environmental conditions related to pollution from the catchment area and seawater intrusion[27]. Selected physicochemical parameters of water C4-C9 (nitrate nitrogen, ammonium nitrogen, nitrite nitrogen, total phosphorus, Secchi disc visibility, dissolved oxygen concentration), the susceptibility of the lake to degradation (C10), the structure of the catchment area management (C11) and the presence of buffer zones (C12) were selected as indicators for the integrity of ecosystem processes, understood as the ability of the ecosystem to maintain key ecological processes that sustain life and ensure the continuity and resilience of the system and to allow them to function properly. The integrity of ecosystem processes means that processes such as matter and energy cycles, primary production, organic matter decomposition and biogeochemical cycles occur without disruption. Concentrations of nitrogen forms, total phosphorus and visibility were utilised as descriptors of the high trophic status of these lakes, and three parameters related to the impact of the catchment area on the lake were utilised as descriptors of the potential load of surface pollutants and the resilience of the lake[18]. The potential of the ecosystem to support ecosystem services (C13-C15) was adopted as an important socio-economic element of ecosystem health. For this purpose, an analysis based on the methodology described by[28] was used. On this basis, 29 ecosystem services (8 provisioning, 12 regulation & maintenance, 9 cultural) were identified and assessed (Supplementary Table 3). Three ecosystem services indicators were selected from the six main ES categories listed in the CICES V5.1 catalogue; (we reduced the six groups to three by combining corresponding biotic and abiotic categories.)[29] Macrozoobenthos communities condition (C1) was assessed using the Lake Macrozoobenthic Index (LMI), whereas ichthyofauna communities condition (C2) was assessed using the LFI+/LFI-EN lake fish index, based on national monitoring data and methodological manuals developed for WFD implementation. Lake Habitats Modification was assessed using data derived by Lake Habitat Survey method based on hydromorphological observations. Class of degradation resistance of the lake (C10) was determined from morphometric and hydrological characteristics, including mean depth, the ratio of lake volume to shoreline length, water stratification, the ratio of active bottom to epilimnion, annual water exchange intensity, and the Schindler index. Structure of catchment land cover/land use (C11) was determined on the basis of the proportion of individual land cover types and the ratio of semi-natural to anthropogenic types of land cover within the catchment. Buffer area indicator (C12) was based on a 500-m GIS-derived buffer around each lake, within which the proportional cover of forests and wetlands was determined using CORINE Land Cover and BDOT10k data. All indicators we completed are the most typical and widely used indicators in the assessment of aquatic ecosystems, as they provided the broadest possible range of available data and were complete for all six lakes studied. Full methodological details and data sources for all indicators are provided in Supplementary Tables 4 and Supplementary Table 5.

## Assessment of weights: analytic hierarchy process (AHP method)

The Analytic Hierarchy Process (AHP) method was used to determine the weights for the individual indicators in the EHI model. Biological and ecological research involves the analysis of many heterogeneous parameters, both quantitative and qualitative. The AHP method allows these elements to be integrated into a single coherent system[30,31]. There are known cases of studies using this method to assess environmental vulnerability and sustainable management of lakes and lagoons[32,33]. The AHP method has already been used, among other things, to determine the weightings of factors in water quality indices[34-36] The technique described by[37,38] requires the establishment of a hierarchical model and then the assignment of their degree of importance to the individual factors in the model layer. This is done by experts/stakeholders by comparing factors in pairs and assigning them scores ranging from 1 to 9 and 1/9 to 1. The lowest value (1/9) corresponds to the least influential factor, and the highest value (9) corresponds to a very high influential factor. During the workshop, after reviewing the information provided (Supplementary Tables 3–5), experts fill out sheets that allow them to efficiently assign scores to individual pairs of factors in the model layer. On this basis, preference matrices are created. The next step required is to determine the concordance of the assessments, which was obtained by calculating the concordance index (CI) and the concordance ratio (CR). These are defined by the respective formulas: $CI = \frac{\lambda_{max} - n}{n-1}$, $CR = CI/RI$. The symbol $\lambda_{max}$ corresponds to the largest eigenvalue of the preference matrix for the n-parameters. The RI values are defined by [37] as a function for *n*. According to the assumptions of the AHP method, a CR value of less than 0.1 is aimed for. Higher values imply an unreliable result, which requires further rounds of expert assessments until a reliable result is obtained. Each round of expert assessments is preceded by a review of the previous round's results and an open discussion among workshop participants. After a positive test of the reliability of the results, weights are set for all factors at each level of the model.

## Fuzzy comprehensive evaluation method

The Fuzzy Comprehensive Evaluation (FCE) method was used to derive ecosystem health values for individual core indicators, factors and the total EHI[39–41,42]. The fuzzy logic approach is appropriate in cases of uncertainty, complexity and high heterogeneity of biological data[43]. Methods such as FCE allow for the conversion of qualitative expert descriptions into mathematically defined degrees of membership. There are known studies using the fuzzy approach, including FCE, for water quality analysis, toxic substance hazards in the aquatic environment, and environmental status[31,40,44,45]. The fuzzy theory approach makes it possible to mimic better the way humans think and classify different phenomena and objects. Additionally, it is one of the methods used in the multi-objective assessment approach[40].

The first step in determining a set of factors can be described by the formula: $U = \{u_1, u_2, \ldots, u_n\}$, where *u* refers to a specific factor and *n* is the total number of indicators to be evaluated.

The next step is to establish a set of evaluation criteria, which can be described by the formula:

$V = \{v_1, v_2, v_3, v_4, v_5\}$ where the individual values correspond to criteria for five classes of ecosystem health: $v_1 - Excellent$, $v_2 - Good$, $v_3 - Moderate$, $v_4 - Poor$, $v_5 - Bad$. We took ecosystem health values ranging from 0 to 100 and divided them into equal ranges. As it was not possible to establish an appropriate scale for the individual indicators on the basis of statistical data for BCLs due to the insufficient number of existing sites of this lake type, experts were asked to assign class membership factor values with reference to the comment defining the class (Table 2). The class descriptions were developed on the basis of available literature[46,47-48] relating to the indicators analysed in the EHI model, with reference to the general definitions of ecological quality contained in the WFD[49]. A Delphi method[50] procedure was then carried out with the assumption of a 75% similarity threshold in the set of belongingness coefficients for a given indicator. Once compliance exceeded the target threshold (75%) for the set of belongingness coefficients, their average value assigned by experts was adopted as the final value. Class belongingness coefficient values ranged from 0 to 1, and the sum of the belongingness coefficient values for all classes for a given indicator was always equal to 1.

The next step was to construct a fuzzy matrix for each of the subset indicators (according to the established EHI model). The fuzzy relationship matrix ($R$) can be described as:

$$R = \begin{bmatrix} r_{11} & r_{12} & \dots & r_{1j} \\ r_{21} & r_{22} & \dots & r_{2j} \\ \vdots & \vdots & \vdots & \vdots \\ r_{i1} & r_{i2} & \dots & r_{ij} \end{bmatrix}$$

where the element $r_{ij}$ in the $i$-th row and $j$-th column corresponds to the value of the degree to which the indicator in question belongs to a particular ecosystem health class.

To calculate the ecosystem health values for the basic factors from the factors layer (Structural integrity, Process integrity and Ecosystem services [ES]) and the value of the total EHI, the weighted average method was used, according to the formula:

$$S = W \cdot R = (W_1, W_2, \dots, W_n) \begin{bmatrix} r_{11} & r_{12} & \dots & r_{1m} \\ r_{21} & r_{22} & \dots & r_{2m} \\ \vdots & \vdots & \vdots & \vdots \\ r_{n1} & r_{n2} & \dots & r_{nm} \end{bmatrix} = (b_1, b_2, \dots, b_m)$$

where $m$ corresponds to the number of classes and $n$ corresponds to the number of indicators in a given subset. The values of the vector $W$ corresponded to the weights obtained in the AHP.

The final ecosystem health value was calculated according to the formula:

| Index value interval | Class | Characteristics |
|---|---|---|
| 100 – 80 | I (Excellent) | The BCL ecosystem is characterised by a near-natural ecological state, in which both the biocenotic structure and process functions are fully preserved. The balance between biotic and abiotic components remains natural. All trophic levels of the ecosystem maintain continuity and interconnections, enabling self-regulation without disruption. Nitrogen and phosphorus circulation is uninterrupted, with dominant biological retention and denitrification. Eutrophication is minimal and the waters are highly transparent. High potential for providing services such as water purification, biodiversity maintenance, recreation and aesthetic landscape values. Rich EPT (Ephemeroptera, Plecoptera, Trichoptera) communities, macrophyte species indicative of oligotrophic waters, numerous diadromous fish (e.g., *Osmerus eperlanus*, *Perca fluviatilis*, *Rutilus rutilus*). Very high resistance to anthropogenic pressure. The ecosystem shows the ability to fully regenerate after fluctuations. |
| 80 – 60 | II (Good) | The BCL ecosystem retains most of its natural characteristics, but there are minor disturbances in its structure or functions resulting from local human impacts or climate change. Trophic systems remain relatively complete, but symptoms of moderate eutrophication are visible: phytoplankton growth, reduced benthic diversity. Reduction in the area of underwater vegetation due to the expansion of reed beds. Increased concentrations of biogenic compounds (N, P), but self-purification processes still effectively compensate for the excess of organic matter. The ecosystem continues to provide valuable services: filtration, biomass production, recreation, but these are observed to be partially spatially limited. EPT species occur sporadically, molluscs (Bivalvia, Gastropoda) to oxygen depletion dominate. Resilience is moderately high, with the ecosystem responding to environmental stresses with slow but effective regeneration. |
| 60 – 40 | III (Moderate) | The BCL ecosystem in a moderate condition begins to deviate from its proper ecological condition, and ecological processes and biotic structure already show permanent symptoms of disturbance. There is a reduction in the diversity of macrophytes and benthos and an increase in the number of opportunistic species and planktonic cyanobacteria. The trophic network is simplified, and sensitive species of ichthyofauna disappear. Excess phosphorus in bottom sediments initiates the secondary release of biogenic components, causing internal eutrophication. Recreational and landscape potential declines, the risk of massive cyanobacterial blooms increases, and the potential for maintaining biodiversity is reduced. Indicator species (EPT) are scarce or disappear, larvae of Chironomidae, which are resistant to high concentrations of organic matter, predominate. The ecosystem's resistance to disturbances is reduced. The system may lose its ability to self-repair after periods of summer oxygen deficiency. |
| 40 – 20 | IV (Poor) | The BCL ecosystem is characterised by serious degradation of its structure and function: severe eutrophication, oxygenation problems and regression of aquatic vegetation; a simplified trophic network dominated by opportunistic cyanobacteria; the disappearance of underwater vegetation, limiting sediment retention and stability; dominance of anaerobic processes in sediments, release of hydrogen sulphide and methane, internal 'self-poisoning' of the water body; loss of recreational and aesthetic value, limited habitat for waterfowl and fish; species resistant to extreme conditions dominate, e.g. *Chironomus* sp. larvae, Tubificidae larvae. The ecosystem is characterised by low resilience. Any further drop may lead to its collapse. |
| 20 – 0 | V (Bad) | The BCL ecosystem is in a state of profound ecological degeneration, with a complete loss of its ability to self-regulate and provide ecological services. The trophic network has collapsed. Biological communities are dominated by a few species resistant to oxygen deficiency, while predators and filter feeders are disappearing. There are a lack of underwater vegetation and extensive anaerobic zones at the bottom. There is intensive release of phosphorus from bottom sediments. Self-cleaning processes have ceased. With loss of all protective functions, the ecosystem is becoming a source of pollution for the Baltic coastal zone. No tourist or recreational value. The lake is not resistant to disturbances. Restoration is only possible through long-term recultivation works. |

**Table 2**. Characteristics of Ecosystem Health Index (EHI) classes.

$$EHI = \sum b_m \left(s_m + b_m \cdot \left(s_{m+1} - s_m\right)\right)$$

where $m$ corresponds to the class, and the elements $s_{m+1}$ and $s_m$ correspond to the class boundary values.

Fifteen experts (Supplementary Table 6) with good knowledge of the selected research sites took part in this study. They made their assessments based on their own experience in scientific work on BCLs and the monitoring and research data presented to them in addition (Supplementary Tables 3–5). The stages of calculating the Ecosystem Health Index are described schematically in Supplementary Fig. 2 with exemplary calculations in Supplementary Table 7.

Data on the AHP procedure were analysed using XL-Stat software (Addinsoft, New York, NY, USA).

## Results

### Analytic hierarchy process (AHP) weights

Based on the AHP analysis (Fig. 3), on the factors layer of the model, the highest weight was achieved by Process integrity (0.569) and the lowest by Ecosystem Services (0.098). It should be noted that the higher weight assigned to Process integrity may partly reflect the larger number of indicators ($n = 6$) in this subgroup compared to Structural integrity ($n = 3$) and Ecosystem Services ($n = 3$); however, the AHP procedure inherently accounts for relative importance through pairwise expert comparisons, not merely indicator count (see Sect. 2.3). Regarding Structural integrity on the indicators layer, the highest weight was achieved by the Condition of the macrozoobenthos communities (0.692), and the lowest by the Lake Habitats Modification (0.130). Within

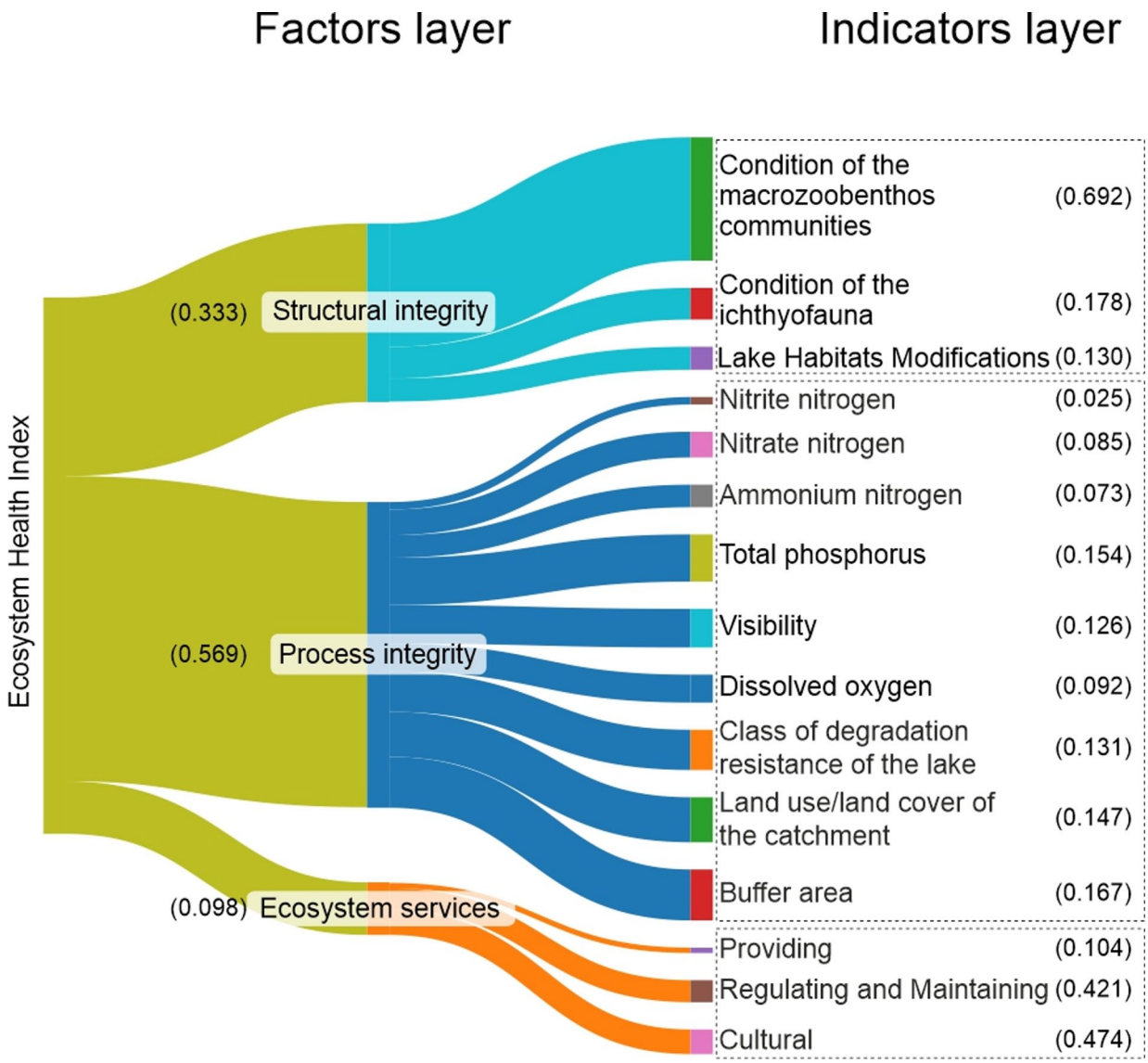


**Fig. 3**. Contribution of indicators in the model. Bundle widths correspond to the relative values of the weights obtained by AHP method. The weights corresponding to the individual subgroups in the factor layer, as determined by the AHP procedure, are given in brackets.

Process integrity on the indicators layer, the highest weights were achieved by Buffer zone (0.167), Total phosphorus (0.154) and Land use/land cover of the catchment (0.147) and the lowest values by Nitrite nitrogen (0.025), Ammonium nitrogen (0.073) and Nitrate nitrogen (0.085). For Ecosystem Services on the indicators layer, Cultural (0.474) achieved the highest weighting and Providing (0.104) the lowest.

### Fuzzy comprehensive evaluation (FCE) results: ecosystem health assessment

Among the analysed basic indices of ecosystem health, only 5.56% were assigned to the best 'excellent' class (three for Lake Dołgie, one for Lake Gardno and one for Lake Łebsko) (Fig. 4). 15.56% of the indices attained the 'good' class level, the highest number corresponding to this class in Lake Dołgie (five), and sporadically in lakes Kopań (one) and Wicko (one). The most frequently attained class was 'moderate' (46.67% of analysed indices), most frequently in the case of Lake Łebsko (10) and least frequently in the case of Lake Dołgie (four). The 'poor' class was attained by 30% of the indicators, with the highest number corresponding to this class in the case of Lake Wicko (7) and the lowest in the cases of Lakes Łebsko (two) and Dołgie (two). The lowest 'bad' class was attained by only 2.22% of the indicators, for Lake Resko (one) and Lake Dołgie (one). Clearly higher scores were achieved more frequently by the indicators for lakes under strict protection in the Slowinski National Park.

The ranges of Ecosystem Health Index values for the Baltic coastal lakes were widest for Buffer zone (from 19.55 to 84.22), Semi-natural land use (from 25.22 to 92.38) and within Ecosystem Services Provisioning (from 43.42 to 86.34). In contrast, ranges were narrowest among indicators within Ecosystem Services Regulation & Maintenance (from 58.37 to 64.83), Integration Processes: visibility (from 19.10 to 25.22) and nitrite nitrogen (from 56.67 to 64.32).

In the freshwater type, 60% of the indicators (three from Structural integrity, five from Process integrity, and one from Ecosystem services) attained a higher class for the strictly protected lake, and only one indicator (from Process integrity) achieved a lower class level for the strictly protected lake. In the transitional type, 40% of the indicators (three from Process integrity, three from Ecosystem services) attained a higher class for the strictly protected lake and two indicators (one from Structural integrity and one from Process integrity) attained a lower class for the strictly protected lake.

On the factors layer (Fig. 5), for 'Structural integrity', the level 'moderate' was attained by the ecosystems of the brackish lakes (Resko and Łebsko) and the freshwater lake in the national park (Dołgie). The level 'poor' concerned transitional-type ecosystems (Kopań and Gardno) and freshwater not under strict protection (Wicko). Within the factor 'Process integrity', the level 'moderate' corresponded only to the ecosystem of the lake Dołgie (freshwater) and Łebsko (brackish), both within the Słowiński National Park, while the remaining ecosystems attained the level 'poor'. As regards the factor 'Ecosystem services', the level of 'good' class corresponded to all ecosystems under strict protection, plus the brackish Resko lake. The ecosystems of the remaining lakes (Kopań and Wicko) provided services at the 'moderate' level.

The total Ecosystem Health Index (Fig. 6) attained 'moderate' values for lakes in Slowinski National Park, while the remaining ecosystems were characterised by 'poor' quality. However, no association was detected between total EHI values and the degree of hydrological connectivity with the sea.

## Discussion

The proposed EHI framework complements, rather than directly modifies, the assessment approach prescribed under the WFD. The WFD establishes a legal framework for determining the ecological status of water bodies (2000/60/EC) but does not prescribe a single unified method; member states develop their own intercalibrated methods within this framework. Importantly, the WFD does encompass hydromorphological and habitat quality elements (e.g., riparian vegetation, bank stability and land use in the surrounding area), contrary to a narrow interpretation focused solely on physicochemical parameters. In the specific case of BCLs, our framework was developed to complement WFD-based assessments by integrating ecosystem services and a weighted multi-criteria synthesis that considers both lake and catchment context. Rather than replacing WFD-based classification, it provides an additional perspective for systems that are difficult to differentiate using conventional assessment alone. This is particularly relevant because final assessments according to the standard WFD-based approach used in Poland may be consistently set low due to a single parameter (e.g., visibility, even when that parameter is naturally low range for this type of lake. Accordingly, we attempted to assess ecosystem health in a broader way than is possible under standard classification alone.

Our results indicate higher levels of ecosystem service provision for lakes under strict protection, consistent with the broader literature on protected area effectiveness. In the analysed lake pairs, lakes located within the national park generally achieved higher ES scores, although the magnitude of this difference varied among lake types. The higher Cultural services score for Resko lake (located out of the national park) may reflect its more intensive recreational use in the absence of strict protection regulations. Within the 500-m buffers analysed around lakes located within the protected area of the SNP, forests and wetlands (averaging 81% of the area) dominate over urbanised and agricultural areas, indicating a high potential for ecosystem service provision. For lakes outside the SNP, forests and wetlands covered an average of only 38% of the area. These patterns are consistent with studies from Europe and North and South America reporting higher ecosystem service potential in protected areas[51–56,57].

The association between strict protection and abiotic water quality conditions was present but modest. This is not surprising, as these are highly eutrophic polymictic lakes, and protection of the shoreline zone does not necessarily imply a clear improvement in abiotic conditions[18]. This pattern is consistent with published observations, such as in the case of Poland's and Portugal's lakes[58,59]. Strict protection of aquatic ecosystems can enhance habitat conditions and biodiversity by minimising human disturbance [51,60,61]. however, numerous cases show no significant improvement, often attributed to factors such as inadequate area size or location, intensive catchment exploitation, lack of buffer zones, excessive tourist pressure, and accumulation of auto-

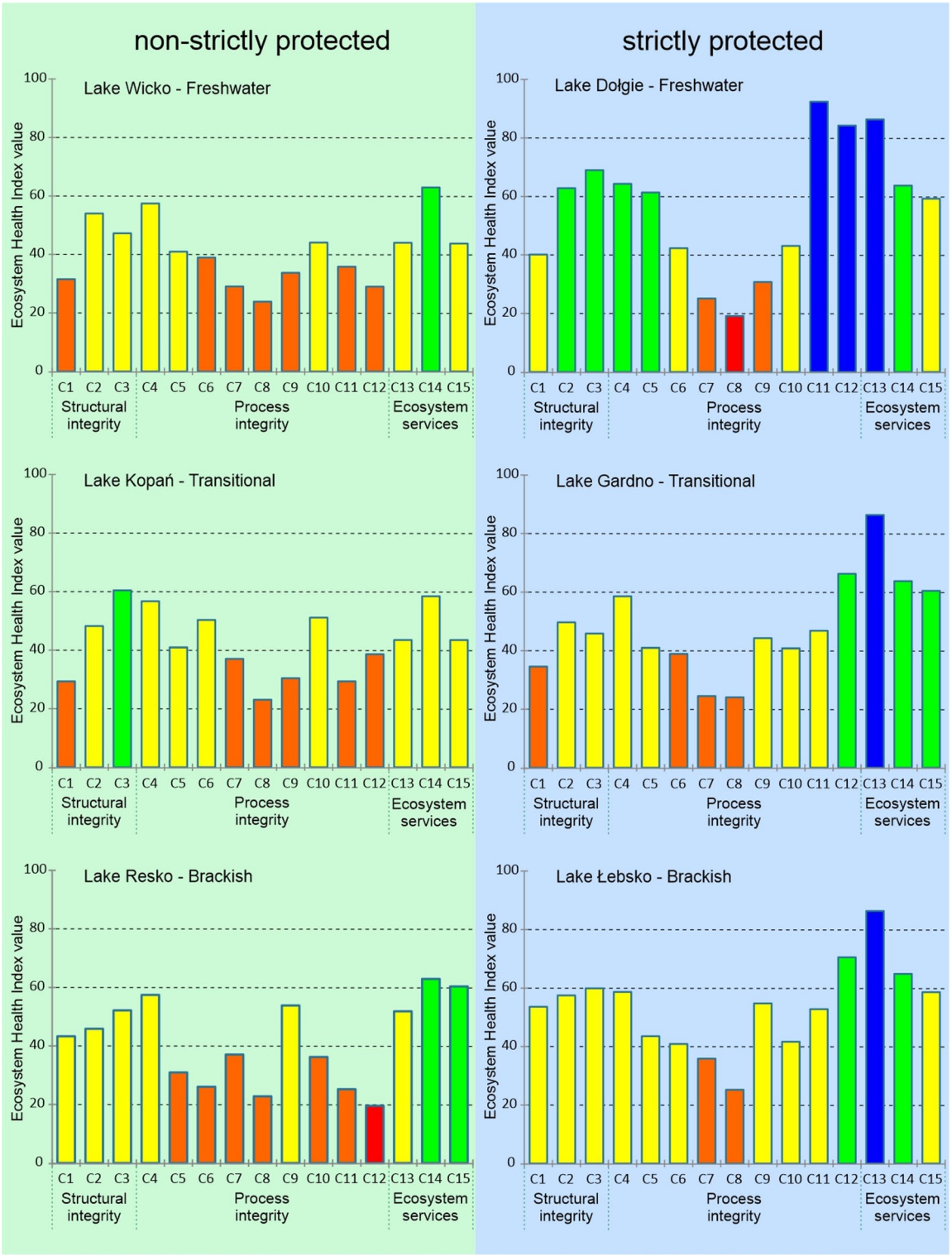


**Fig. 4**. Ecosystem Health Index values calculated using the FCE method for indicator layer elements. On the horizontal axis, the indicators (described as C1–C15) were ordered following their order in the EHI model scheme (Fig. 2). Colours were assigned to ecosystem health classes: red ('bad'), orange ('poor'), yellow ('moderate'), green ('good') and blue ('excellent').

and allochthonous matter[62–64,65]. These shortcomings suggest that the effectiveness of strict protection depends heavily on proper area management, appropriate spatial planning, and enforcement of protection regulations. At the same time, in our study strict protection was associated in some cases with higher scores of biotic components considered within Structural integrity. This pattern was clearest in the freshwater pair, weaker in the transitional

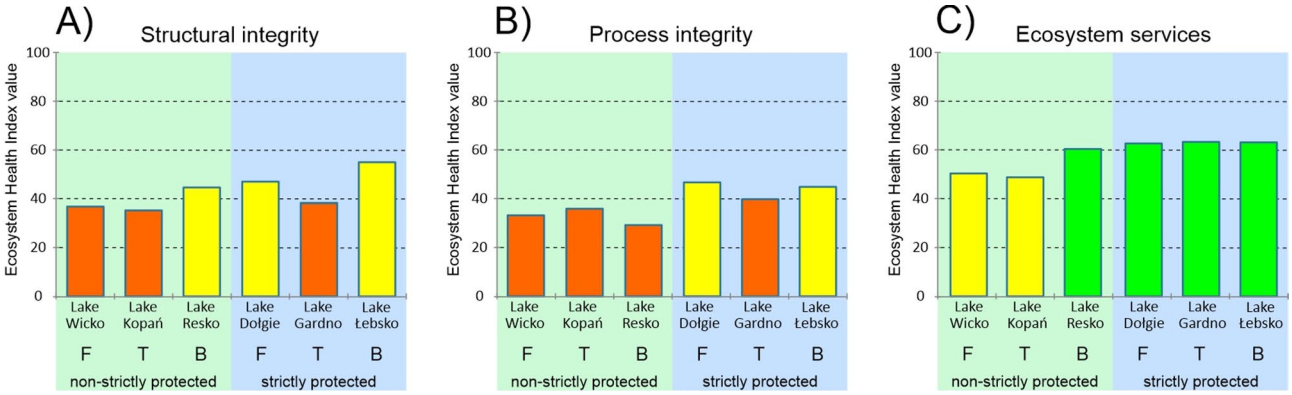


**Fig. 5**. Ecosystem Health Index values calculated using the FCE method for factors layer, where (**A**) Structural integrity, (**B**) Process integrity, (**C**) Ecosystem services. Colours are assigned to ecosystem health classes: orange (class IV), yellow (class III), green (class II). Designations for lake types: F – freshwater, T – transitional, B – brackish.

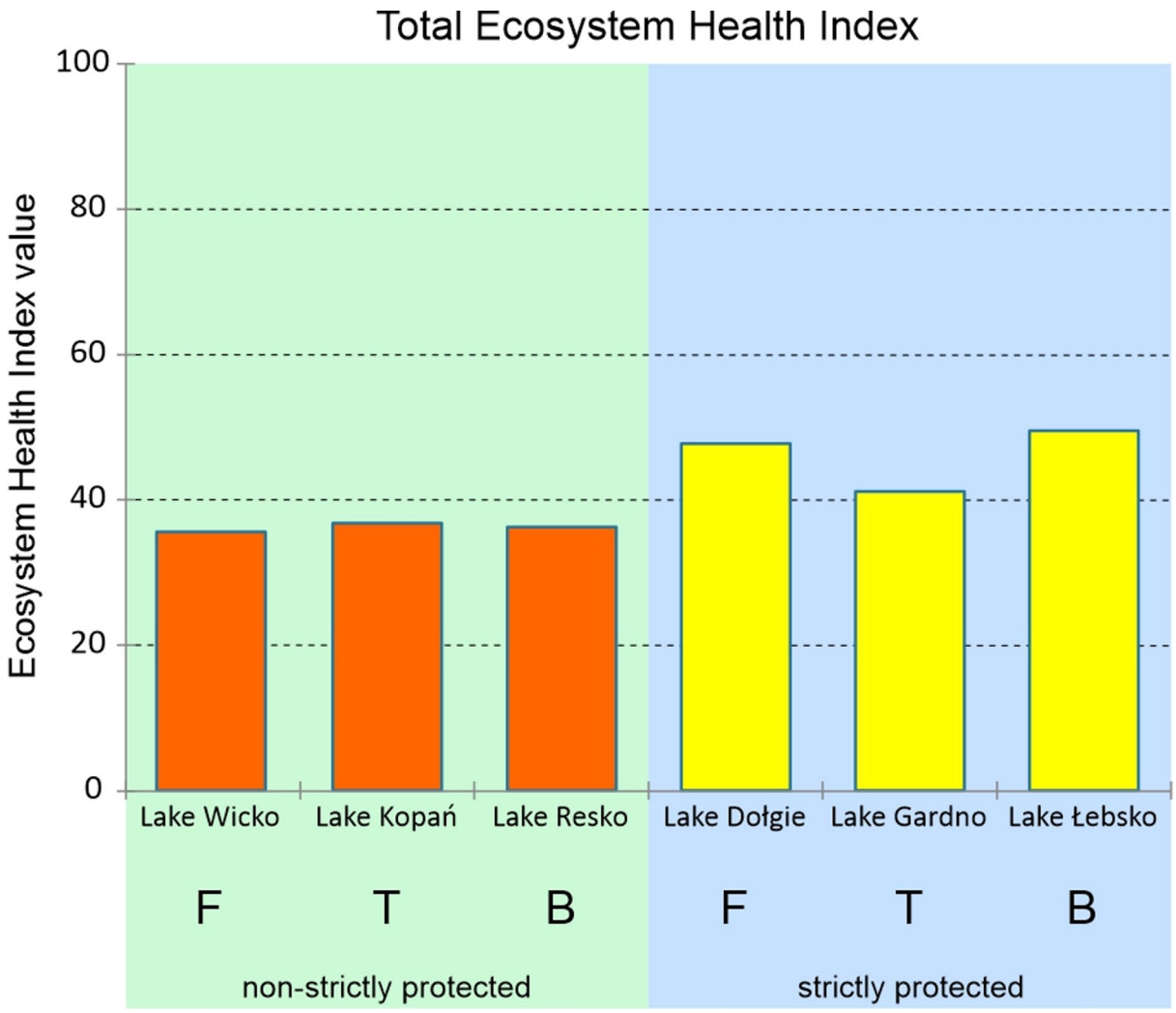


**Fig. 6**. Total Ecosystem Health Index. Colours are assigned to ecosystem health classes: orange (class IV), yellow (class III). Designations for lake types: F – freshwater, T – transitional, B – brackish.

pair, and not evident in the brackish pair. Such type-specific differences are ecologically interpretable, because freshwater lakes may be more sensitive to catchment land-use effects, whereas in brackish and transitional systems biotic assemblages are additionally shaped by salinity-related processes[18,25]. The absence of detectable biotic differences in the brackish pair does not exclude a subtle protective effect, but such an effect may require long-term monitoring to resolve.

Hydrological connectivity with the sea is often discussed as a key factor shaping the condition of coastal ecosystems[66, 67]. In our dataset, hydrological connectivity differentiated some abiotic and biotic parameters, but showed no association with total EHI values or ecosystem-service provision potential. Intrusion likely influences both abiotic and biotic conditions, but in our study this influence did not translate into clear differences in total ecosystem-health scores[14, 18, 24,25]. This may be due to the limited connectivity through estuarine sections of rivers to the sea and the irregular timing of seawater inflows, which prevent the ecological condition of these ecosystems from being markedly altered. As argued previously, the role of the catchment for these ecosystems may therefore be more important than hydrological connectivity alone[18]. It has also been found that maintaining hydrological connectivity with the sea is essential for maintaining the health of BCL ecosystems, which, in their genesis, maintained such connectivity[67]. In addition, it has been observed that loss of connectivity leads to rapid ecological deterioration and a decline in biodiversity. This may imply a reduction in the potential to provide ES, since[68] found that better ecological conditions are positively correlated with the provision of regulatory and cultural ES.

The elevated weight of macrozoobenthos communities condition in the Structural integrity factor of the EHI model, compared with the lower weights of ichthyofauna communities condition and lake habitats modification, may be attributed to the specific characteristics of BCLs being of the crucian carp type, as classified according to the Polish lake fishing typology[69]. *Crucian carp* lakes are characterised by their shallowness (maximum depth of 6 m), the presence of substantial accumulations of silty sediments, and dense growth of macrophytes (in the case of BCLs, it is almost exclusively *Phragmites australis*[24]), particularly in coastal regions. These water bodies are also distinguished by low levels of water visibility. This specificity, in conjunction with elevated trophic levels, results in a decline in species richness and fish biomass, disruptions to the predator–prey balance, and, in the case of lakes connected to the sea, the prevention of the substantial influx of migratory species that are sensitive to environmental conditions. Under such conditions macrozoobenthos appears to be a particularly useful indicator for differentiating between lakes. The enhanced weights assigned to buffer zone, total phosphorus, land use/land cover of the catchment and class of degradation resistance in the Process integrity factor may likewise reflect the strong influence of catchment pressure and trophic status on these ecosystems[18,70]. Furthermore, the dominance of cyanobacteria and high chlorophyll concentrations (frequent blooms) in BCLs were the reasons for not including the phytoplankton group in the proposed EHI model. In the case of the indicators in the Ecosystem Services subgroup, the relatively low weighting for Provision ES may be partly due to limited possibilities for direct use under nature conservation restrictions, whereas the higher weights for Cultural and Regulating & Maintaining ES are likely related to the tourism, educational and retention functions of BCLs.

To summarise the above findings, we can answer the first research question. Based on the results obtained using our proposed approach, we were unable to identify an association between the degree of hydrological connection with the sea and biodiversity, ecosystem services or habitat condition. Regarding protection, our results indicated an association between strict protection and higher scores for biodiversity-related indicators, ecosystem services and habitat condition, although causal inference is beyond the scope of this observational study.

In recent years, many variants for determining ecosystem health have been developed[71]. Some of them adapt expert methods to this need by assigning weights to factors in the model or by applying fuzzy methods in the procedure[40,72]. However, the diversity of factors taken into account in such models and the proprietary nature of many procedures make direct comparison difficult at this stage. Larger-scale implementation of such approaches will therefore require further refinement, validation and eventual standardisation of the framework.

The proposed approach relies on expert knowledge and extensive supporting data, which may limit transferability where only a few specialists are available. In the BCL case, the small expert pool may have increased subjectivity, although the structured AHP and FCE procedures were intended to reduce it. Future applications could benefit from larger expert panels and, where data availability permits, more data-driven calibration of indicator ranges and weights. Due to the observational nature of the present study and the fact that it was based on a small sample of lakes, the observed associations should be interpreted as patterns rather than as cause-and-effect relationships.

The specific characteristics of BCLs do not allow straightforward differentiation using conventional monitoring alone[17]. Additionally, not all parameters selected as basic in monitoring (under the WFD) occur in a given assessment period for all coastal lakes. When a single parameter is likely to downgrade the assessed ecological status, as may be the case for phytoplankton, macrophytes or visibility in BCLs, its impact or lack of measurement may lead to an incorrect assessment. This creates a need for new indicators of a synergistic nature that consider both abiotic and biotic conditions, as well as the potential of ecosystems to provide ES. In the case of the last period (2019–24) of water quality assessment in Poland under the WFD, the studied lakes were classified as follows: Dołgie and Wicko were unclassifiable due to insufficient biotic data, Gardno, Łebsko, and Kopań had poor ecological status, and Resko had moderate ecological status; however, all were ultimately rated as having poor water quality.

In response to the second research question, the proposed EHI assessment scheme enabled the differentiation of BCLs, demonstrating its ability to distinguish among ecosystems that are highly similar in condition by arranging them along a gradient of ecosystem health. It also helps identify missing reference sites, such as Lake Łebsko in the case of Polish Baltic coastal lakes. In this way, the proposed assessment scheme may provide a useful complementary tool for ecosystem comparison, prioritisation and future conservation planning.

## Conclusion

The presence of strict protection in the form of national parks was associated with greater ecosystem-service potential in the studied Polish coastal lakes. Strict protection was also associated with higher biotic indicator scores in freshwater lakes and higher abiotic conditions across all three hydrological lake types. No association was detected between the degree of hydrological connectivity and the Ecosystem Health Index or ES provision potential, though this warrants further investigation with longer-term datasets. However, the proposed Ecosystem Health Index allowed a multifaceted assessment of the ecological condition of the studied BCLs. This provided a broader range of information about the studied water bodies, including the impact of the catchment area and their potential to provide ES as a dimension of the relationship between human wellbeing and the ecosystem. Based on this, the BCLs could be prioritised along a gradient of preserved ecological integrity. Further validation of the Ecosystem Health Index may enable its widespread implementation as part of conservation and nature management plans currently under development.

## Data availability

Data will be made available on request. Please send your request to the corresponding author's email address: matela@ukw.edu.pl.

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## Author contributions
Mikołaj Matela: Writing – review & editing, Writing – original draft, Visualisation, Software, Methodology, Investigation, Formal analysis, Data curation. Krystian Obolewski: Writing – review & editing, Writing – original draft, Visualisation, Formal analysis, Supervision.

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## Declarations

## Competing interests
The authors declare no competing interests.

## Additional information
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# A-4

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Ecological Indicators

# Salinity as the primary driver of zooplankton community shifts in Eurasian arid lakes

--Manuscript Draft--

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| **Manuscript Number:** | ECOLIND-59544R1 |
| **Article Type:** | Research paper |
| **Keywords:** | Zooplankton; Salinisation; environmental filtering; Predation release; Shallow lakes; West Kazakhstan |
| **Corresponding Author:** | Mikołaj Matela<br>Kazimierz Wielki University in Bydgoszcz Department of Hydrobiology<br>POLAND |
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| | Krystian Obolewski |
| **Abstract:** | Global warming significantly impacts Eurasian lake ecosystems, both directly through rising temperatures and indirectly through resultant shifts in salinity. This study examined responses in zooplankton community composition along a salinity gradient (from freshwater to α-mesohaline; max. ~25 PSU) in four lakes across the semi-arid (steppe, semi-desert), and arid zones of western Kazakhstan. Our results demonstrated that salinity, rather than temperature, acts as the primary environmental filter. While community density and biomass remained stable or increased under more saline conditions, species richness declined significantly as salinity exceeded 15 PSU. A distinct taxonomic shift was observed: rotifers dominated low-salinity systems, whereas large-bodied, halotolerant cladocerans and copepods prevailed in mesohaline lakes, likely due to reduced top-down pressure from fish predation. Canonical Correspondence Analysis (CCA) and Generalised Additive Models (GAM) indicated that the key drivers of zooplankton community structure were salinity, pH, and sulphate ($SO_4^{2-}$) concentrations. Notably, local diversity patterns were shaped mainly by geographical isolation and catchment connectivity (Volga vs Ural basins). These findings suggested that, for the functional and ecological resilience of aquatic communities in arid regions to be maintained under changing climatic conditions, maintaining a high diversity of waterbody types is essential. |
| **Response to Reviewers:** | Comments:<br>“Preliminary editorial review: Duplicate submission score of 44%, as this ms was previously submitted (ECOLIND-56778) and rejected for insufficient impact. In this submission, subsections are not numbered. Reference DOI links don't work.”<br><br>Dear Editor,<br>Thank you for your careful assessment of our submission and for bringing the 44% similarity index regarding our previously submitted manuscript to our attention. We fully understand and respect the journal's strict policies regarding originality. However, we would like to provide some context to clarify this overlap and demonstrate that the current manuscript represents a fundamentally new, thoroughly revised, and independent scientific work.<br>Based on previous comments and our own extensive reflections, this paper has been completely rewritten. We have formulated entirely new hypotheses, which fundamentally shifted the narrative of our research. Furthermore, we significantly expanded the scope of our data analyses and meticulously verified and updated the taxonomic database. Because of these comprehensive changes, the ecological implications and the final conclusions of this manuscript are entirely different and offer novel insights into the field. |

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| | The text similarity stems primarily from the specific nature of environmental studies and the necessity to maintain strict methodological precision. The overlapping sections are strictly confined to the description of the study area, the study objects, and foundational methodologies (such as sampling procedures, taxonomic identification, and the collection of physicochemical). Since our current study utilizes a subset of the baseline dataset from the previous submission, the descriptions of these standard procedures must remain consistent to ensure scientific accuracy and reproducibility.<br>Additionally, we would like to inform you that we took this opportunity to improve the manuscript's formatting. We have thoroughly checked and corrected the DOI addresses in the reference list and introduced clear section numbering to facilitate the review process.<br>We hope this explanation fully addresses your concerns regarding the originality of our paper and that you will consider advancing our improved manuscript to the peer-review stage.<br><br>Best regards,<br>Mikołaj Matela<br>On behalf of the co-authors |

Cover letter

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Bydgoszcz, 26th May 2026

Dear Editor,

I am pleased to submit our manuscript entitled “Salinity as the primary driver of zooplankton community shifts in Eurasian arid lakes” for consideration for publication as a research article in *Ecological Indicators*.

This manuscript represents a fundamentally rewritten and substantially expanded evolution of our previous submission to your journal. Based on earlier reviewer feedback and our own extensive reflection, we have completely restructured the research framework. We have formulated entirely new ecological hypotheses, significantly expanded the scope of our data analyses, and meticulously verified the taxonomic database of the observed organisms. As a result, the current paper offers novel insights and a completely different ecological narrative that we believe aligns perfectly with the aims and scope of *Ecological Indicators*.

We would also like to proactively address the 44% similarity index flagged by the editorial system, which relates to our previous submission. The text similarity is strictly confined to the standard descriptions of the study area, the study objects, and foundational methodologies (e.g., sampling procedures, taxonomic identification, and the collection of physicochemical and climatic baseline data). Because this study builds upon a subset of the same baseline dataset, these methodological descriptions must remain consistent to ensure scientific accuracy and reproducibility. Additionally, we have used this opportunity to improve the manuscript’s formatting by adding clear section numbering and correcting DOI addresses in the reference list.

We confirm that this manuscript has not been published elsewhere and is not under consideration by another journal. All authors have approved the manuscript and agree with its submission to *Ecological Indicators*. We have no conflicts of interest to disclose.

Thank you for your time and consideration of our work. We look forward to your positive response and to the opportunity to receive feedback from the reviewers.
We trust that our work will be of great interest to the readers of *Ecological Indicators*.

Thank you for your time and consideration.
Yours sincerely,
Mikołaj Matela (corresponding author)

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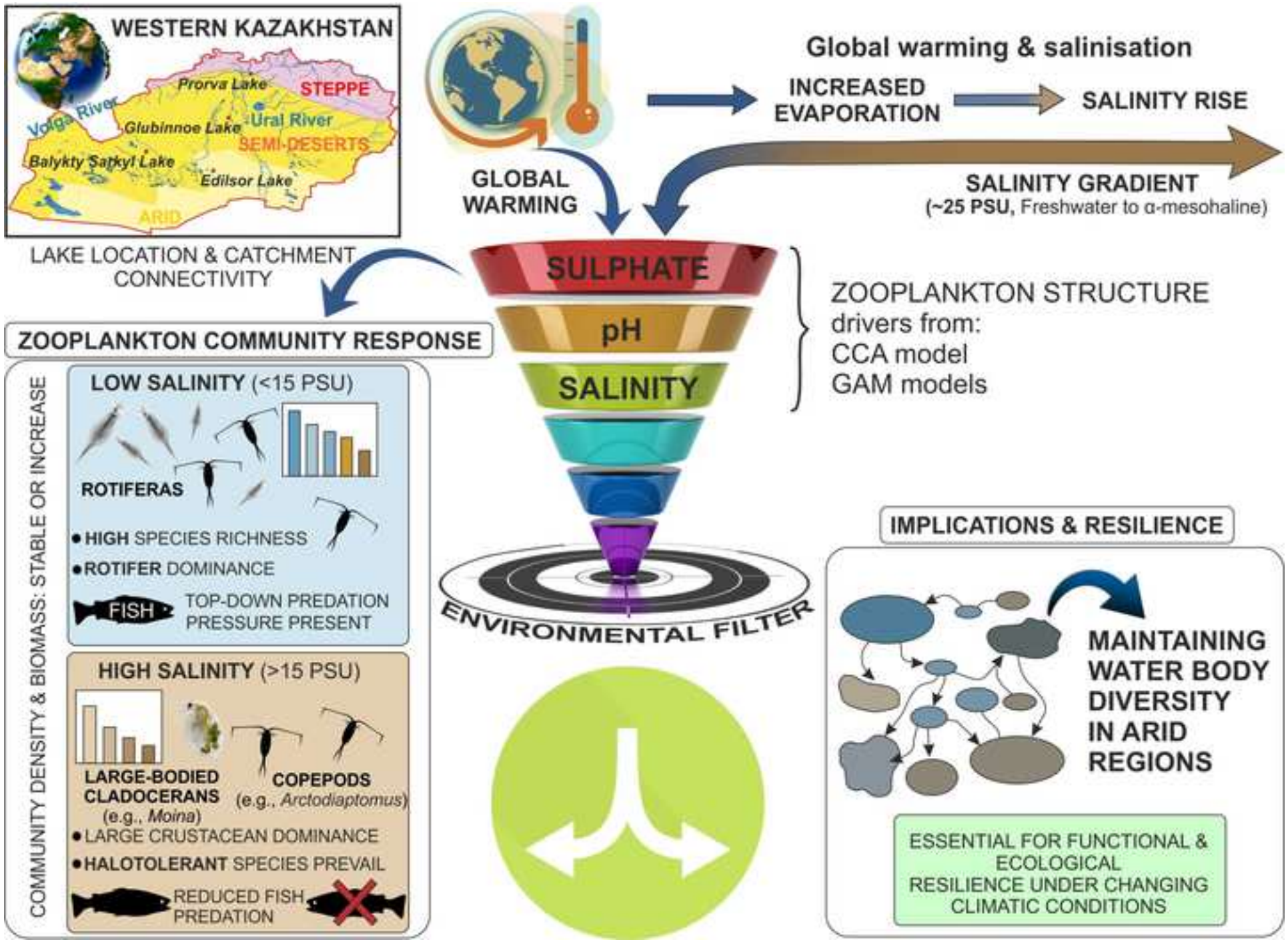
Best regards,

Mikołaj Matela

On behalf of the co-authors

Graphic abstract corrected.jpg



- Salinity, not temperature, is the primary environmental filter.
- Species richness declines significantly above 15 PSU.
- Rotifers shift to halotolerant crustaceans as salinity rises.
- Diverse waterbodies are key to resilience in arid regions.

# Salinity as the primary driver of zooplankton community shifts in Eurasian arid lakes

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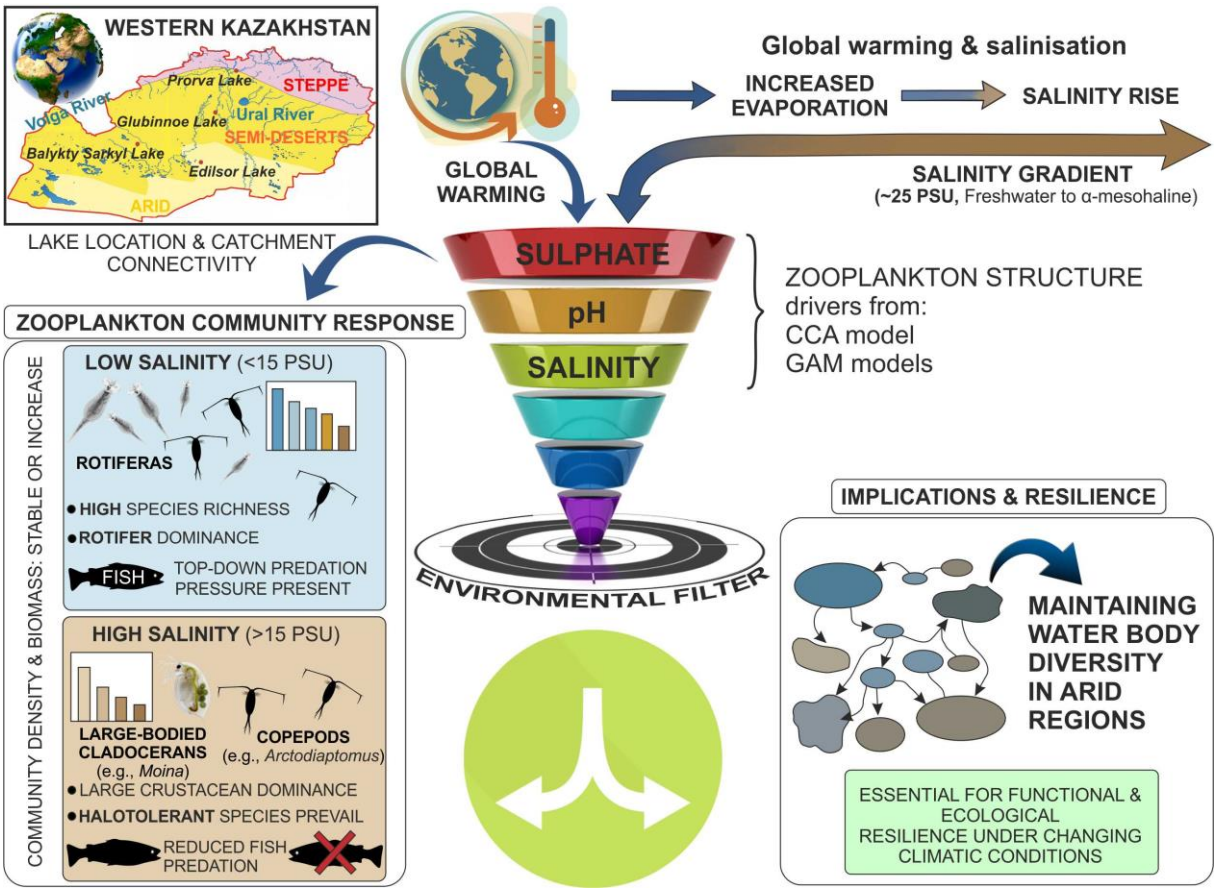


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**Abstract.** Global warming significantly impacts Eurasian lake ecosystems, both directly through rising temperatures and indirectly through resultant shifts in salinity. This study examined responses in zooplankton community composition along a salinity gradient (from freshwater to α-mesohaline; max. ~25 PSU) in four lakes across the semi-arid (steppe, semi-desert), and arid zones of western Kazakhstan. Our results demonstrated that salinity, rather than temperature, acts as the primary environmental filter. While community density and biomass remained stable or increased under more saline conditions, species richness declined

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**Key words:** Zooplankton; Salinisation; Environmental filtering; Predation release; Shallow lakes; West Kazakhstan

## 1. Introduction

In recent years, evidence has increasingly supported that climate change strongly influences the structure and functioning of aquatic ecosystems. This influence results directly from higher temperatures – but also from indirect effects such as salinity changes and eutrophication (e.g., Shurin et al. 2012; Kruk et al. 2021; Scholz et al. 2025). Lakes are among the ecosystems that are changing most quickly in response to climate change and human activity (Sadeghi et al. 2023; Hou et al. 2022; Wu et al. 2022; Saini and Pandey, 2023). This is particularly conspicuous in dry Eurasian regions, where biodiversity is declining dramatically in benthic and pelagic zones alike (Samarkhanov et al. 2021; Sarmanov et al. 2024). The key factors documented as contributing to these changes include rapid snowmelt, changes in lake surface-water temperature, increased evaporation and high productivity (Woolway et al. 2020; Szymańska-Walkiewicz et al. 2024). The development of landscape-level management and biodiversity protection strategies for water bodies requires information

about how diversity is spatially distributed throughout various aquatic habitat types (Obolewski, 2011; Rodil et al. 2021). In this context, crucial insights are provided by investigating zooplankton, owing to their significant role in organic matter cycling and their function as a food source for higher trophic levels. In addition, some zooplanktonic species can serve as sensitive indicators of aquatic environment changes (e.g., Matmuratov et al. 2009; Chen et al. 2010; Ejsmont-Karabin and Karabin 2013) through their utility in assessing which resistance-related structural and functional characteristics react to increasing salinity (Bailey et al. 2004; Tarun 2012).

Studies of brackish lakes show that warming-induced increases in salinity affect zooplankton richness and species composition, thereby changing trophic interactions (Schallenberg et al. 2003; Jeppesen et al. 2007; Barker et al. 2008; Brucet et al. 2009). With increasing lake salinity, zooplankton communities differ increasingly from those of freshwater ecosystems; their taxonomic composition becomes more distinct, with specialised species, genera and families replacing typical freshwater taxa (Williams 1998). In most cases, salinity in inland water bodies increases the proportion of euryhaline fish species, thereby increasing their pressure on zooplankton (Jeppesen et al. 2010). This results in large-sized cladoceran species being consumed and then replaced by rotifers, copepods (mainly calanoids) and small-sized cladoceran species (*Bosmina* and *Chydorus*) (e.g., Jensen et al. 2010; Brucet et al. 2018).

Accordingly, we expect that changes in zooplankton abundance (density and biomass) and diversity in lakes of the West Kazakhstan region are affected by increasing temperatures. However, the pattern of these relations requires more refined understanding because of its dependence on the complex ecological context. A comparison of lakes that differ in water temperature and lie within arid and semi-arid (i.e., semi-desert and steppe) zones can improve our understanding of how global warming affects changes in zooplankton. A concurrent

comparison of lakes along a salinity gradient can aid in determining indirect temperature effects (through salinisation/desalination) on species richness, composition and trophic structure. To conduct two such analyses, we studied lakes differing in salinity (from freshwater to α-mesohaline), within steppe, semi-desert and arid zones of West Kazakhstan. We analysed the variation in species richness, zooplankton composition and community structure in the lakes and analysed how they are influenced by environmental variables. Given the unique hydrochemical characteristics of the lakes in western Kazakhstan, this paper provides a comparative analysis of selected ecosystems representing a salinity gradient. The high frequency of serial measurements allows for a precise determination of the temporal variability within these rarely studied water bodies. We hypothesised that the distinct hydrochemical profiles of the investigated lakes would be reflected in their zooplankton community structures. Specifically, we anticipated that: (i) higher salinity levels would be associated with lower species richness and a significant decline in diversity indices, as the communities became dominated by a few specialised halobionts; (ii) the transition from brackish to hypersaline conditions in these specific systems would lead to a decreased contribution of rotifers in favour of more salt-tolerant cladocerans and copepods; and (iii) the studied high-salinity habitats would support elevated zooplankton density and biomass, reflecting the high productivity potential of these specific arid-zone ecosystems.

## 2. Material and methods

### *2.1 Study area*

Endorheic and floodplain lakes in arid zones are landscape elements of high environmental value (Satybaldiyeva et al. 2023; Sarmanov et al. 2024). They play an important role in maintaining biodiversity by providing water reserves for living organisms and serving as breeding grounds for migratory and sedentary animal species (Obolewski 2011; Ermolaeva et al. 2013). The lakes of West Kazakhstan are generally shallow, with poorly developed

shorelines (Sarmanov et al. 2024), but they differ in size and salinity (Table 1). The study lakes lie in various annual precipitation zones: Prorva >300 mm, Glubinnoe 250–300 mm, Balykty Sarkyl 200–249 mm, and Edilsor <200 mm (https://www.kazhydromet.kz). Many lakes in north-western Kazakhstan are endorheic (including Lake Edilsor and Lake Balykty Sarkyl). Others are floodplain lakes (e.g., Lake Prorva and Lake Glubinnoe) in the Ural River basin, which functioned as disconnected water bodies during the sampling period, having no surface hydrological connection with the river. Both lake types are unstable because seasonal changes in weather conditions (especially precipitation) cause significant fluctuations in size and water level.

**Table 1.** Characteristics of lakes in the West Kazakhstan region. Their area was measured using summer aerial photographs taken in 2019–21. Water-body type corresponds to salinity level (Venice System, 1958).

| Lake | Geographic coordinates | Area [ha] | Average depth [m] | Max. depth [m] | Capacity [$10^6$ $m^3$] | Zone | Salinity level |
|---|---|---|---|---|---|---|---|
| Prorva | 51°14’ N, 51°31’ E | 5.5 | 1.5 | 4.2 | 0.18 | steppe | freshwater |
| Glubinnoe | 50°19’ N, 51°03’ E | 2.2 | 1.2 | 1.9 | 0.02 | semi-desert | oligohaline |
| Balykty Sarkyl | 49°36’ N, 49°18’ E | 1.8 | 1.6 | 4.2 | 30.41 | semi-desert | β-mesohaline |
| Edilsor | 49°13’ N, 50°44’ E | 1.7 | 1.3 | 3.7 | 23.31 | arid | α-mesohaline |

### *2.2 Sample collection and processing*

The data structure relies on repeated measurements within individual salinity-class representatives, and this seasonal approach allows for the capture of ecological processes often overlooked in one-time screening studies. Sampling was conducted seasonally (spring,

142 summer, autumn) over three consecutive years (2019–21). A total of 36 surface samples were
143 collected from four lakes (n=9 per lake) for both qualitative and quantitative analysis of
144 zooplankton. Samples were collected in shallow, open-water areas (~1 m deep) devoid of
145 free-floating macrophytes. For each sample, 100 L of water was filtered through an Apstein
146 plankton net (mesh size 30 µm) and preserved with 4% formalin. Taxonomic identification
147 followed Kutikova (1977), Borutsky et al. (1991), Sinev (2002) and Tsalolikhin (2010).
148 Quantitative analysis of rotifers and crustaceans was performed according to standard
149 methods (Suthers et al. 2009) with modifications. Organisms were counted in subsamples of a
150 specific volume (10–20 mL); after thorough homogenization, 2–3 subsamples of 1 mL were
151 analysed under a microscope. All individuals (excluding larval forms) were identified to
152 species level, and results were expressed as individuals per litre (ind. $L^{-1}$). Species accounting
153 for >10% of the total density within their respective major taxonomic groups (Rotifera,
154 Cladocera, Copepoda) were classified as eudominants. Biomass was estimated by calculating
155 individual weights using established length-weight regression formulas (Keskitalo and
156 Salonen 2004; Hart et al. 2011).

157 Simultaneously with zooplankton sampling, surface water physicochemical parameters
158 were recorded. Water temperature, pH, dissolved oxygen (mg $L^{-1}$), and salinity (PSU) were
159 measured *in situ* using a WTW MultiLine P4 multiparameter meter. Laboratory chemical
160 analyses (Chemical Oxygen Demand [COD], sulphates, nitrates, chlorides, carbonate
161 hardness, bicarbonates, magnesium, and calcium) were performed spectrophotometrically
162 following standard procedures (APHA, 2017).

163 **3. Data analyses**

164 The biomass-to-abundance ratio (B/N) was calculated for each sample to further characterise
165 the community structure. The average individual body mass is given by the ratio of total
166 biomass (B) to total abundance (N) of the zooplankton community. The B/N ratio adds

valuable information on the size distribution and physiological state of the organisms and increases the analytical rigour of the study.

To assess differences in plankton assemblage compositions among the studied lake systems, analysis of similarities (ANOSIM, 999 permutations) was performed using Bray–Curtis distance (Clarke and Warwick, 2001). Where significant differences were found, similarity percentage analysis (SIMPER) was used to identify the taxa that contributed most to the observed dissimilarity. To evaluate the internal variability of physicochemical and biological parameters across the studied lakes, we employed the Kruskal–Wallis test of ranks ($p<0.05$), followed by Dunn's *post-hoc* test. Before analysis, data were tested for homoscedasticity using the Levene test. To further identify patterns in the abundance of invertebrate species, we used Correspondence Analysis (CA) (ter Braak and Šmilauer 2002).

To visualise differences in zooplankton community composition among lakes, a heat map was constructed, and two-way cluster analysis (TWCA) was performed in PC-ORD 6.08 (McCune and Mefford 2011) using the Sørensen (Bray–Curtis) distance measure and flexible-$\beta$ at $-0.25$ as the linkage algorithm. The data were relativised by column.

To investigate the underlying structure of the environmental data and to visualise the covariation of different parameters across the study sites, principal component analysis (PCA) was performed. For biological community data, a detrended correspondence analysis (DCA) was first performed to determine the gradient length of axis 1. The gradient length was >2 standard deviation units, indicating a non-monotonic response (ter Braak 1995). Therefore, canonical correspondence analysis (CCA) was selected to explore relationships between zooplankton descriptors (density, biomass, $\alpha$-diversity) and environmental parameters. To avoid over-fitting, redundancy between predictors in the CCA was tested using the variance inflation factor (VIF), and variables with VIF<10 were retained and a forward selection (FS) algorithm was applied. The significance of the final model was verified using the Monte Carlo

test (999 permutations). Furthermore, generalised additive models (GAM) were employed to model the relationships between community descriptors (abundance, biomass, diversity) and key environmental drivers. All statistical analyses were performed using PC-ORD 6.08 and R (version 4.3.0) using the 'mgcv' package.

## 4. Results

### *4.1 Environmental conditions*

Among the 12 studied descriptors, only $NO_3^-$ exhibited no significant differences among the lakes, whereas four variables associated with water temperature, trophic state and mineralisation were tightly linked to the salinity gradient (Table 2). Detailed physicochemical data are provided in Table S1.

**Table 2.** Summary of water quality characteristics in the study lakes in 2019–21 ($n$=36) and results of the non-parametric Kruskal–Wallis test with *post-hoc* multiple comparisons Dunn's test evaluating differences between the salinity type of lakes

| | | | Freshwater ($n$=9) | Oligohaline ($n$=9) | β-mesohaline ($n$=9) | α-mesohaline ($n$=9) | $p$ |
|---|---|---|---|---|---|---|---|
| $T_w$ | °C | mean | 18.1[a] | 18.9[a] | 18.9[a] | 20.5[b] | <0.001 |
| | | min-max | 16.2-25.4 | 18.3-25.5 | 17.3-26.2 | 19.0-26.1 | |
| pH | | mean | 7.57[a] | 7.64[a] | 7.51[a] | 8.37[b] | 0.001 |
| | | min-max | 7.02-7.95 | 7.10-8.94 | 7.10-8.14 | 7.92-8.61 | |
| Salinity | PSU | mean | 0.40[a] | 0.77[ab] | 15.34[b] | 22.68[b] | <0.0001 |
| | | min-max | 0.25-0.90 | 0.64-1.04 | 7.44-29.98 | 7.94-47.22 | |
| DO | mg $L^{-1}$ | mean | 8.25[a] | 8.50[a] | 7.90[a] | 7.54[b] | 0.01 |
| | | min-max | 7.30-9.20 | 8.00-9.42 | 6.60-8.82 | 6.30-9.22 | |
| COD | mg $L^{-1}$ | mean | 10[a] | 21[ab] | 104[b] | 52[b] | 0.002 |
| | | min-max | 1-24 | 8-52 | 5-240 | 12-149 | |
| $NO_3^-$ | mg $L^{-1}$ | mean | 1.07 | 2.54 | 3.52 | 4.74 | 0.07 |
| | | min-max | 0.00-1.91 | 0.10-5.44 | 0.20-8.96 | 0.10-9.82 | |
| $CaCO_3$ | mg $L^{-1}$ | mean | 18.3[a] | 19.1[a] | 125.4[b] | 145.1[b] | <0.001 |
| | | min-max | 4.3-91.1 | 5.3-78.4 | 8.0-280.4 | 40.3-221.3 | |
| $HCO_3^-$ | mg $L^{-1}$ | mean | 236[a] | 306[b] | 281[a] | 262[a] | <0.02 |
| | | min-max | 122-891 | 134.1-420.9 | 205-354 | 134-354 | |
| $SO_4^{2-}$ | mg $L^{-1}$ | mean | 153.2[a] | 151.3[a] | 590.3[b] | 557.1[b] | <0.001 |
| | | min-max | 54.4-216.3 | 118.4-221.3 | 120.4-1448.0 | 62.3-1350.1 | |
| $Cl^-$ | mg $L^{-1}$ | mean | 53.3[a] | 186.1[ab] | 4015.7[b] | 5134.9[b] | <0.0001 |
| | | min-max | 28.7-114.8 | 43.1-266.0 | 1591.0-11480.0 | 2583.4-8610.3 | |
| $Mg^{2+}$ | mg $L^{-1}$ | mean | 61[a] | 48[a] | 830[b] | 942[b] | <0.0001 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | | min-max | 12-126 | 18-150 | 510-1500 | 258-1876 | |
| $Ca^{2+}$ | mg $L^{-1}$ | mean | 83[a] | 81[ab] | 595[b] | 350[ab] | <0.0001 |
| | | min-max | 40-290 | 20-120 | 320-1010 | 258-1876 | |

Explanations: *p* values modified by the Bonferroni procedure for multiple comparisons show no significant effect. Superscript *a*, *ab* and *b* indicate so-called homogeneous groups: same letters = no significant difference; different letters = significant difference; ab = intermediate group (different from neither "a" nor "b"). $T_w$ – water temperature, DO – dissolved oxygen, COD – chemical oxygen demand

The most important difference between the lakes studied (K–W, $p<0.0001$) was in salinity, which was almost 57 times higher in the α-mesohaline lake than in the freshwater lake. Similarly, water bodies with the lowest and highest salinity differed 96-fold in Cl− concentrations. Cation concentrations varied widely, too: calcium concentrations were 14 times higher in the β-mesohaline lake than in the oligohaline lake, whereas magnesium concentrations were 20 times higher in the α-mesohaline lake than in the oligohaline system. Differences were slightly less significant for water hardness, SO42− content and chemical oxygen demand ($p<0.01$). Conversely, the smallest, yet still significant, differences were observed for pH, dissolved oxygen and $HCO_3^-$ ($p<0.05$). Salinity correlated positively with trophic level ($r=0.91$) and chloride concentration ($r=0.86$), whereas a strong negative correlation was found with dissolved oxygen content ($r=-0.73$).

### *4.2 Zooplankton community composition*

In total, we collected 3,457 adult individuals of pelagic fauna, which represented 62 species, including rotifers (37 species), cladocerans (11) and copepods (14) (Table S2). In all lake types, rotifers were the most diverse group, but their species richness declined with increasing salinity (Table 3).

**Table 3.** Total number of species (richness) and eudominants (D>10% of density) in zooplankton communities in the study lakes of West Kazakhstan in 2019–21

| | Freshwater (*n*=9) | Oligohaline (*n*=9) | β-mesohaline (*n*=9) | α-mesohaline (*n*=9) |
|---|---|---|---|---|
| Rotifera | 25 | 21 | 15 | 14 |

| | | | | |
|---|---|---|---|---|
| Dominant species and % of total density | *Polyarthra vulgaris* (*D*=15%) *Polyarthra longiremis* (*D*=11%) | *Keratella quadrata* (*D*=11%) | *Brachionus quadridentatus* (*D*=17%) *Filinia longiseta* (*D*=12%) | *Brachionus plicatilis* (*D*=12%) |
| Cladocera | 6 | 4 | 5 | 6 |
| Dominant species and % of total density | no | no | *Coronatella rectangular* (*D*=28%) *Ceriodaphnia reticulata* (*D*=14%) | No |
| Copepoda | 6 | 7 | 4 | 8 |
| Dominant species and % of total density | no | no | no | No |

The ratio of biomass to abundance (B/N) showed a distinct non-linear response to increasing salinity. It was characterised by a U-shaped pattern across the salinity zones (Figure 1). In the freshwater and oligohaline zones, high (>100) B/N ratios indicated a high proportion of large-bodied Cladocera in the total biomass.

In the β-mesohaline zone, a critical threshold was found where the B/N ratio fell abruptly to its minimum value (≈30). The decrease in mean body size was due to the near complete disappearance of Cladocera and a community shift to small-bodied Rotifera. Interestingly, in the α-mesohaline zone, the B/N ratio showed a partial recovery (~75), mainly

due to increased relative biomass of Copepoda and some halotolerant Rotifera.

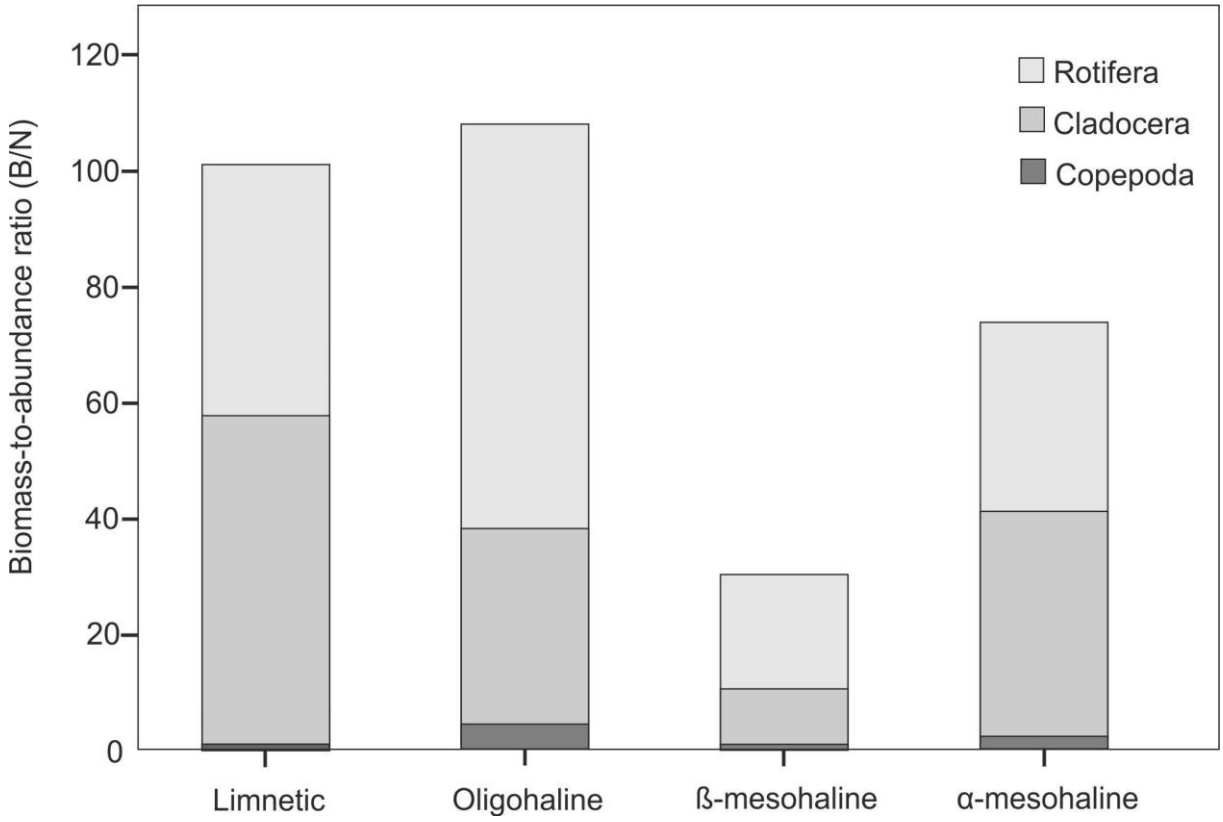


**Figure 1.** The biomass-to-abundance ratio (B/N) of main invertebrate groups in 4 lakes across a salinity gradient. The data represent average values from seasonal sampling in 2019–21. Differences in mean size of individuals across the studied lakes were significant (Kruskal–Wallis test, $p<0.001$).

These results indicate that the relationship between salinity and zooplankton size structure is not a simple linear decline, but rather a complex transition involving the loss of freshwater taxa followed by the emergence of specialised, larger-bodied saline assemblages.

The dominance structure of the zooplankton community exhibited a degree of uniformity across the studied lakes, with a limited number of species prevailing in terms of density. Generally, eudominant taxa (D>10%) were primarily rotifers. A notable shift was observed in the β-mesohaline lake, where cladocerans and rotifers displayed comparable percentage shares (~45% each), together accounting for nearly 90% of the total zooplankton

252 abundance. In the remaining lakes, the combined contribution of these two groups ranged
253 from 70% to 80%. Interestingly, copepods reached their peak taxonomic diversity in the
254 highest salinity habitats, suggesting a high degree of specialisation for hypersaline conditions
255 within this group.

256 Variations in zooplankton community composition among the studied sites were
257 captured by the CA, with the first and second axes explaining 22% of the total inertia. The
258 analysis revealed relatively high uniformity among community structures within the
259 mesohaline habitats, despite significant differences in environmental conditions (Figure 2A).
260 The dominant invertebrate groups identified in each salinity type were consistent with the
261 patterns observed in the univariate analyses. The first axis represented a gradient from taxa
262 with high dispersal and resilience strategies, such as rotifers, toward groups typically
263 associated with more stable environmental conditions, including specific cladocerans and
264 copepods (Figure 2B). Among the identified species, *Moina micrura, Moina brachiata* and
265 *Arctodiaptomus bacillifer* were positioned at the higher end of the salinity gradient, while
266 *Daphnia pulex* and *Mixodiaptomus* sp. showed a clear preference for habitats with less saline
267 concentrations.

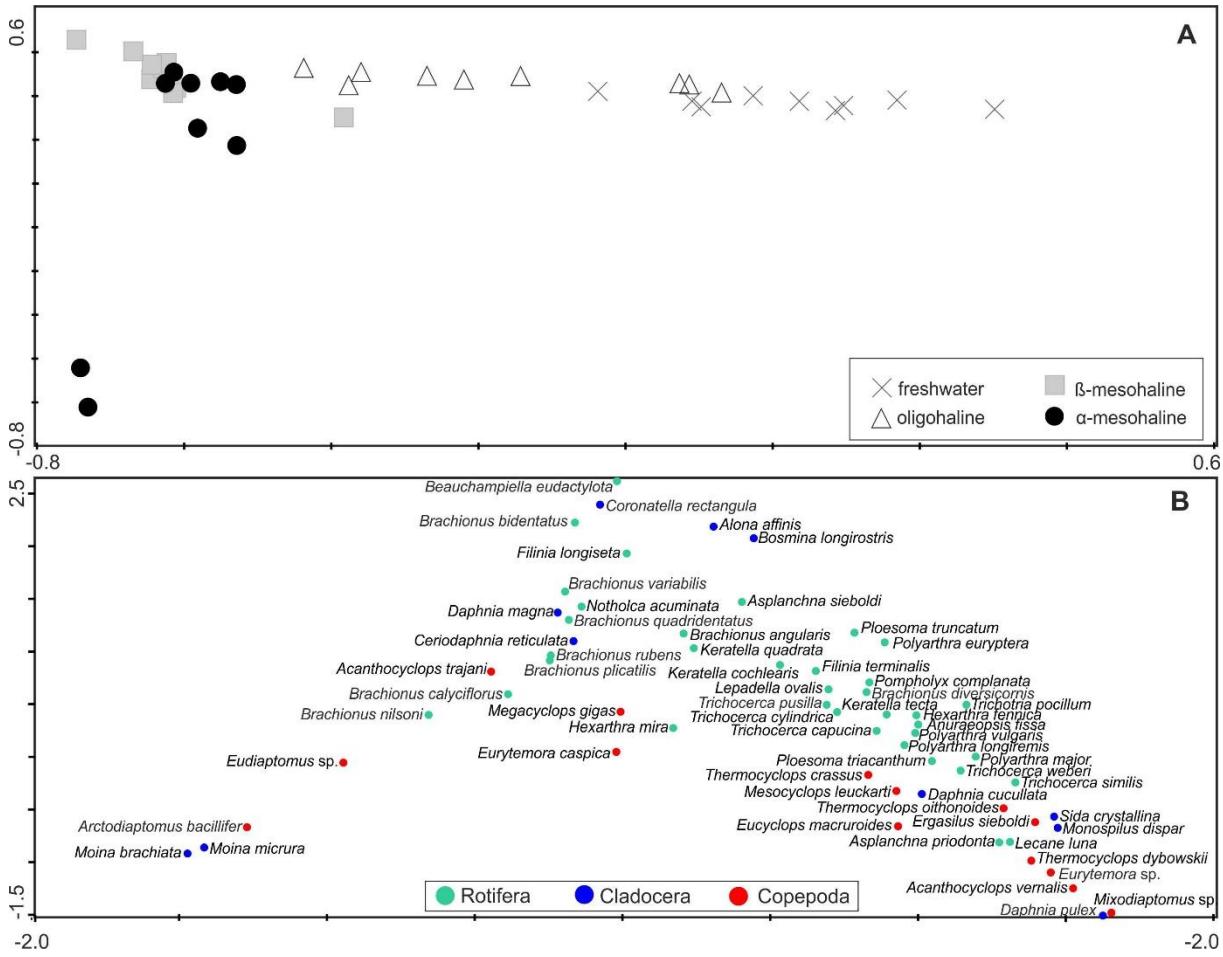


**Figure 2**. Results of Correspondence analysis performed with invertebrate data from the 4 lakes across a salinity gradient. (A): plot of sample scores. (B): plot of species scores

The species composition of zooplankton groups differed markedly among the studied lakes ($R_{ANOSIM}$ = 0.414 – 0.672, $p$=0.001). These differences were most pronounced in copepod assemblages and least evident in cladoceran diversity. SIMPER analysis indicated that rotifer abundance was the primary factor accounting for dissimilarities between the freshwater lake and the other systems, driven by high contributions of *Polyarthra vulgaris* (11.0%), *Brachionus quadridentatus* (10.1%), *Keratella tecta* (7.7%) and *P. longiremis* (7.4%). Dissimilarities between the oligohaline and mesohaline lakes were also predominantly expressed through rotifer taxa, specifically *B. quadridentatus* (12.2%) and *K. tecta* (7.8%). In turn, differences in zooplankton structure between the β-mesohaline and α-mesohaline water

bodies were mainly attributed to the abundances of *B. quadridentatus* (16.6%), *B. plicatilis* (14.5%), *B. calyciflorus* (11.0%) and *Filinia longiseta* (11.3%) (Table S3).

Species richness did not show significant differences across the salinity gradient. However, both the density and biomass of the recorded zooplankton peaked in the α-mesohaline lake (Tables 4 and S4).

**Table 4.** Zooplankton community composition and metrics of the four study lakes in West Kazakhstan in 2019–21. R = Invertebrate richness; N = Total invertebrate abundance; B = Total invertebrate biomass; H' = Invertebrate Shannon diversity; J' = Invertebrate evenness; *P* = significant differences (non-parametric Kruskal–Wallis test, $p \leq 0.05$) among lakes; *a*, *ab* and *b* indicate significant differences (*post-hoc* Dunn's test, $p \leq 0.05$) between lake salinity types: same letters = no significant difference, different letters = significant difference, "ab" = intermediate group (different from neither "a" nor "b")

| | | Freshwater (*n*=9) | Oligohaline (*n*=9) | β-mesohaline (*n*=9) | α-mesohaline (*n*=9) | *P* |
|---|---|---|---|---|---|---|
| R | total | 38 | 32 | 26 | 29 | 0.07 |
| | min-max | 7-21 | 4-15 | 3-14 | 7-16 | |
| N (ind. $L^{-1}$) | mean | 76.5$^{a}$ | 46.8$^{b}$ | 99.3$^{c}$ | 161.6$^{c}$ | 0.01 |
| | min-max | 6.7-319.9 | 8.9-129.3 | 1.8-354.3 | 27.4-298.5 | |
| B (mg $L^{-1}$) | mean | 0.85 | 1.22 | 0.68 | 2.39 | 0.27 |
| | min-max | 0.06-4.09 | 0.03-1.68 | 0.01-1.11 | 0.12-9.09 | |
| H' | mean | 1.82$^{a}$ | 2.06$^{ab}$ | 1.14$^{a}$ | 1.97$^{b}$ | 0.03 |
| | min-max | 1.39-2.49 | 0.83-2.21 | 0.77-1.95 | 1.59-2.53 | |
| J' | mean | 0.43 | 0.58 | 0.35 | 0.51 | 0.94 |
| | min-max | 0.55-0.80 | 0.38-0.90 | 0.27-0.96 | 0.44-0.86 | |
| Density (ind. $L^{-1}$) | | | | | | |
| Rotifera | mean | 58.2 | 27.8 | 43.7 | 93.9 | 0.72 |
| | min-max | 3.9-228.0 | 8.4-90.4 | 1.8-216.4 | 0.5-416.9 | |
| Cladocera | mean | 2.7$^{a}$ | 4.5$^{a}$ | 45.3$^{b}$ | 30.2$^{b}$ | 0.02 |
| | min-max | 0.3-6.8 | 0-30.5 | 0-233.3 | 1.1-91.9 | |
| Copepoda | mean | 15.6 | 14.6 | 10.4 | 37.4 | 0.33 |
| | min-max | 0-25.5 | 0.6-50.5 | 0-39.9 | 1.0-157.3 | |
| Biomass (mg $L^{-1}$) | | | | | | |
| Rotifera | mean | 0.02$^{a}$ | 0.03$^{b}$ | 0.05$^{c}$ | 0.05$^{c}$ | 0.01 |
| | min-max | 0.02-0.40 | 0.01-0.12 | 0.01-0.12 | 0.01-0.10 | |
| Cladocera | mean | 0.16 | 0.16 | 0.43 | 1.24 | 0.21 |
| | min-max | 0.03-0.63 | 0-1.01 | 0-1.80 | 0-7.25 | |
| Copepoda | mean | 0.67 | 1.02 | 0.20 | 1.10 | 0.13 |
| | min-max | 0-4.01 | 0-4.74 | 0-0.89 | 0.02-3.69 | |

Explanations: *p* values modified by the Bonferroni procedure for multiple comparisons show no significant effect.

In contrast to density, total zooplankton biomass, species diversity (H') and evenness (J') remained relatively uniform among the studied lakes. Rotifers dominated in terms of density (58–76%) across most habitats, with the exception of the β-mesohaline lake, where cladocerans were dominant (46%). Cladocera was the only group to show significant density differences among the investigated lakes (Table 4). Regarding biomass, copepods were the dominant group (46–79%), except in the β-mesohaline lake, where cladocerans accounted for 62% of the total biomass. Total zooplankton biomass exhibited a significant, non-linear response across the salinity gradient (Table 4). In the limnetic and oligohaline zones, biomass remained relatively stable at moderate levels. However, a sharp, transient decline was recorded in the β-mesohaline zone, where biomass reached its minimum values, coinciding with the collapse of the B/N ratio and the disappearance of large-bodied Cladocera.

Zooplankton community structures (proportions of zooplankton species/groups, biodiversity index values, etc.) were broadly uniform across all lakes through spring and summer, with the exception of the β-mesohaline lake in summer and the freshwater lake in spring. Autumn was characterised by greater variability in invertebrate abundance across all studied lakes. Two-way cluster analysis (TWCA; Figure 3) revealed that rotifer biomass, as well as cladoceran and copepod abundance, peaked during summer in the limnetic, oligohaline and α-mesohaline habitats (red frame). The β-mesohaline lake, which has the second-highest salinity, also peaked in biomass and abundance during the summer, but the abundance and total biomass of this peak clearly stood out from those of the other three lakes (green frame). In spring, high densities and biomasses of individual zooplankton groups formed an isolated cluster (yellow frame) that included all results from the three high-salinity lakes (Figure 3), indicating strong similarities among these lakes; their biomass and abundances were also high, though slightly less so than in summer. The planktonic

invertebrate communities reached their maximum diversity in autumn, particularly in the lower-salinity habitats (<0.8 PSU).

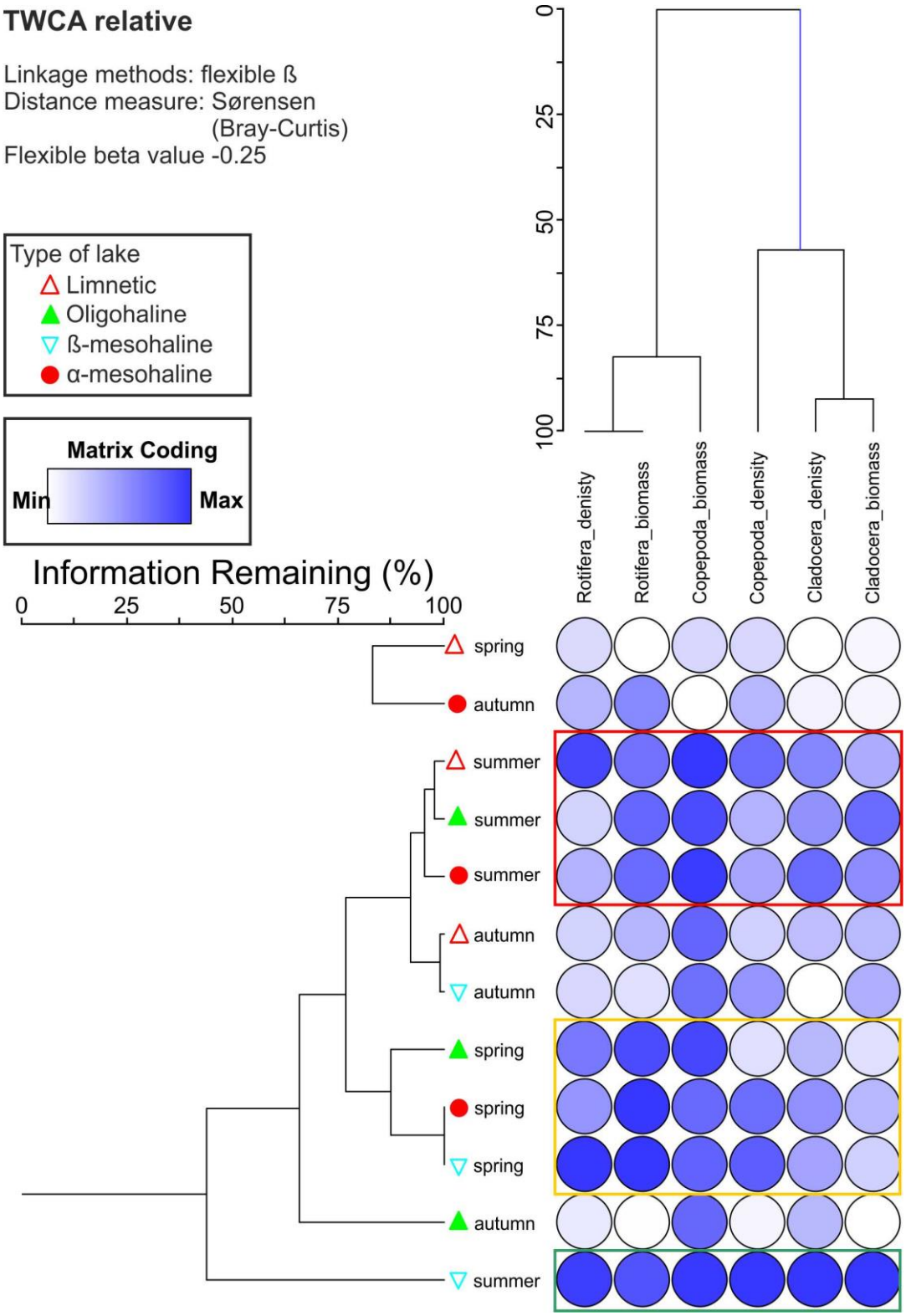


**Figure 3**. Two-way cluster analysis (TWCA) based on the relative values of seasonal changes in biotic variables in samplings from 4 lake habitat types. The vertical dendrogram groups invertebrates by similarity. The horizontal dendrogram groups samples by seasons in each

lake type. Heatmap colour scale indicates the minimum (white) to the maximum (blue) density/biomass of zooplankton groups, wherein each element is scaled to its maximum contribution to the total found value in a lake type.

### *4.3 Environmental variables and zooplankton assemblages*

Of the initial twelve environmental variables, four physicochemical parameters were selected via forward selection as significant drivers, in the descending order: salinity, pH, sulphate ($SO_4^{2-}$) and magnesium ($Mg^{2+}$). The remaining eight variables (temperature, DO, COD, $NO_3^-$, $HCO_3^-$, $CaCO_3$, $Ca^{2+}$ and $Cl^-$) were excluded as redundant. In the CCA model for genus density (Figure 4A), the first and second axes explained 15.7% and 10.6% of the total inertia, respectively (26% combined; Monte Carlo test, F=4.1, $p$=0.001). For genus biomass (Figure 4B), the axes explained 17.9% and 10.4% of the inertia (29% combined; F=4.8, $p$=0.001). In both models, the first axis (CCA1) was strongly associated with salinity and pH, while the second axis (CCA2) was primarily defined by gradients of sulphate and magnesium concentrations. High salinity negatively affected the density and biomass of most genera, with the notable exceptions of *Acanthodiaptomus* (Copepoda) and *Moina* (Cladocera). High sulphate concentrations exerted a similar negative influence on most taxa, except for *Notholca* (Rotifera), *Alona*, and *Ceriodaphnia* (Cladocera).

In the subsequent CCA model, which incorporated major zooplankton groups and community indices (Figure 4C), the first two axes explained 46% of the total inertia (F=5.3, $p$=0.001). Salinity remained the dominant factor along CCA1, while CCA2 was associated with $SO_4^{2-}$ and $Mg^{2+}$. The presence of rotifers and copepods was positively linked to habitats with relatively higher magnesium concentrations and lower overall salinity. Cladocerans, however, reached their highest abundances in the β-mesohaline lake, showing a specific association with elevated sulphate levels.

The analysis of the pie charts in Figure 4D confirmed that the highest values of the H', R, and J' indices for crustaceans (Copepoda, Cladocera) occurred during the summer and

autumn periods. In contrast, the spring aspect played a key role in the development of overall species richness (R) for the Rotifera group.

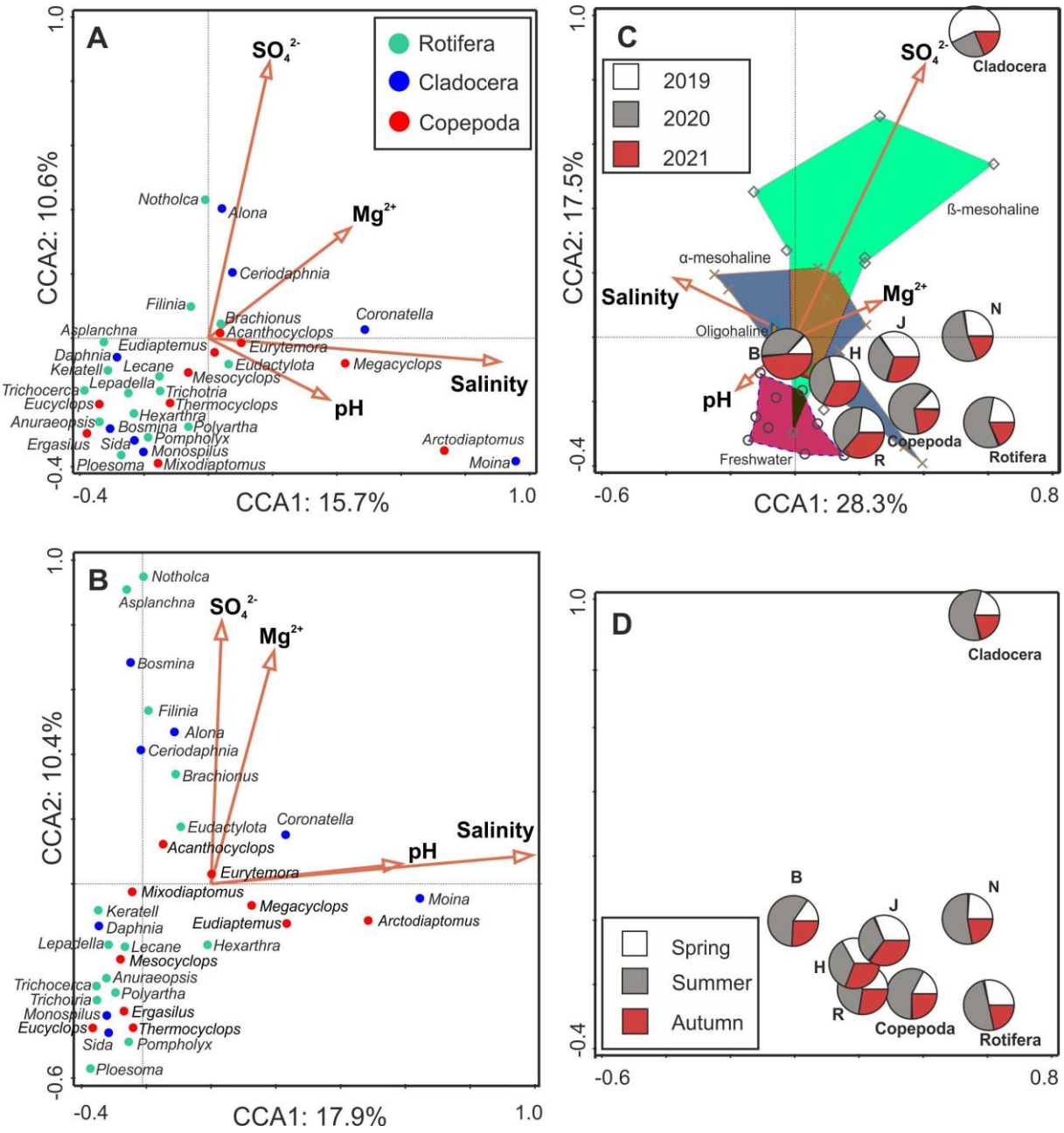


**Figure 4.** Results of canonical correspondence analysis (CCA) performed on invertebrates and environmental data for lake-salinity types using forward selection of variables ($p<0.05$). (A) Biplot of significant environmental variables and density of zooplankton genera; (B) Biplot of significant environmental variables and biomass of zooplankton genera; (C) Triplot of significant environmental variables, samples and percentage shares of each study year of invertebrates within main taxonomic groups, and zoocenotic index values; (D) seasonal dispersion of results describing zooplankton composition. The abbreviations used are explained in Table 4.

The Kruskal–Wallis test and Generalised Additive Models (GAM) indicated that elevated salinity was associated with an increase in total invertebrate abundance (Figure 5A) and cladoceran density (Figure 5C). Rotifer biomass showed a non-linear response, increasing up to ~25 PSU before declining (Figure 5D). Diversity (Shannon index) decreased significantly with rising salinity ($p$=0.02, Figure 5B). Furthermore, GAM models revealed that sulphate concentrations exceeding the threshold of ~700 mg $L^{-1}$ resulted in a significant reduction in rotifer biomass (Figure 5D), while simultaneously fostering a continuous increase in cladoceran abundance (Figure 5C). Shannon diversity showed a strong, systematic decrease in response to rising sulphate concentrations ($p$<0.001, Figure 5B).

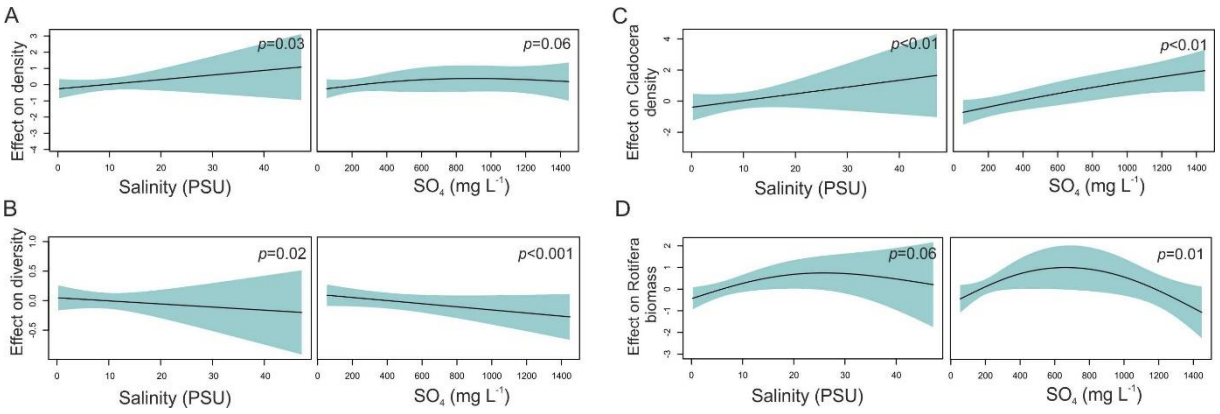


**Figure 5.** Results of Generalised Additive Models (GAM) illustrating the effects of salinity and sulphate concentrations on zooplankton metrics. The solid black line represents the estimated smoothing curve, and the shaded turquoise areas represent the 95% confidence intervals. The *p*-values indicate the statistical significance of each environmental predictor. (A) Effect on total invertebrate density: rank-transformed abundance scores; (B) Effect on Shannon diversity: scores calculated for the zooplankton community; (C) Effect on Cladocera density: rank-transformed density scores; (D) Effect on Rotifera biomass: rank-transformed biomass scores.

## 5. Discussion

### *5.1 Study limitations and ecological context*

Despite the insights gained from our sampling frequency, we acknowledge certain inferential limitations regarding fine-scale temporal dynamics; however, our data remain robust for characterising seasonal patterns in these water bodies. The experimental design, by focusing on a single representative lake for each salinity category, limits our ability to generalise these

findings as universal salinity-driven patterns across all arid-zone ecosystems. This configuration creates a degree of confounding between lake identity and salinity type, a common challenge in the study of unique or geographically isolated salt lakes. However, we believe that the consistent seasonal and annual measurements provide a robust description of the internal variability and ecological stability of these specific systems. Our results should therefore be interpreted as a comprehensive case study of western Kazakhstan's unique hydrochemical gradients, providing a crucial baseline for future multi-lake regional comparisons.

### *5.2 Environmental drivers of zooplankton structure*

In the studied lakes, salinity increased with trophic level and chloride levels but decreased with oxygen levels. Nielson et al. (2003) also found that salinity determines the functioning of aquatic ecosystems because it implies the direction of changes in their biotopes. Planktonic invertebrates – including rotifers, cladocerans and copepods – are extremely sensitive to environmental changes and as a community constitute a perfect indicator of ecosystem health because of their short life cycles and high dispersal potential (Castilho-Noll et al. 2023). Our results align with the "environmental filtering" hypothesis, according to which, salinity acts as a sieve for the regional species pool (Heino et al. 2015). Although some historical studies suggested that salinity only marginally affects trophic dynamics (Williams, 1998), our data support the contrary view that it is the main determinant of for species abundance and richness (Jeppesen et al. 2015; Kruk et al. 2021). Changes in this descriptor directly or indirectly affect zooplankton diversity along the salinity gradient from freshwater to 25 PSU (Modéran et al. 2010). Under extreme environmental conditions (high salinity), the competition from small-bodied freshwater taxa diminishes. This allows a few specialised, often larger-bodied halophilic species to occupy the vacant niches. Examples include specific

413 copepods from the genera *Arctodiaptomus*, which possess a greater individual biomass than
414 the small rotifers dominant in the β-mesohaline zone.

415 *5.3 Taxonomic succession and life strategies*

416 As regards rotifers, salinity in the studied gradient correlated negatively with richness but
417 positively with biomass. This pattern is consistent with the *r*-selection strategy of rotifers
418 (*Brachionus*, *Keratella* and *Filinia*), which, being opportunistic colonisers with short life
419 cycles, thrive in unstable, high-energy saline environments by utilising abundant bacteria and
420 suspended solids (Alprol et al. 2021).

421 A significant finding was the transition in dominance from rotifers to larger
422 crustaceans in specific saline conditions. In the α-mesohaline lake, we observed a substantial
423 share of the cyclopoid copepod *Acanthocyclops trajani* (previously reported as *A.*
424 *americanus*). Following recent taxonomic revisions (Hołyńska et al. 2025), this species is
425 recognised for its invasive potential and high dispersal capacity, often mediated by migratory
426 birds in the dry regions of Kazakhstan.

427 Only in the β-mesohaline lake was *Eudiaptomus* sp. a major contributor to
428 zooplankton density and biomass, being the most common species of calanoid copepods in
429 Europe, tolerating a broad water salinity range (Riccardi and Rossetti 2007). This
430 complements the reports of Krupa and Aubakirova (2021), who consider that the presence of
431 this species in the steppe zone (Volga-Ural province) in Kazakhstan is unconfirmed. In this
432 study the situation was similar, and large-sized specimens of *Coronatella rectangula* were
433 observed in the β-mesohaline lake (Figure 3). It is one of the few members of the Chydoridae
434 that is secondarily adapted to high salinity (10–13 PSU) (Frey 1993), which may explain its
435 appearance in Lake Sarkyl, where salinity exceeds 15 PSU. *C. rectangula* has high dispersal
436 potential, tolerance for a broad range of salinity, and morphological variability (but

437 worldwide similarity of forms) and can be regarded as a species complex at the full phase of
438 expansion and radiation (Van Damme and Dumont 2008).

439 *5.4 Trophic interactions and basin connectivity*

440 The "predation release" mechanism leads to dominance of large-bodied zooplankton in
441 mesohaline lakes. When salinity increases past levels lethal to cyprinids (~6 PSU) and silurids
442 (~10 PSU), these lakes become "fish-free" refuges (Seale et al. 2024). In Lake Edilsor
443 (oligohaline), where salinity is low, a functional fish community dominated by *Perca*
444 *fluviatilis*, 64.3% abundance) maintains intense top-down pressure, shifting zooplankton
445 towards smaller individuals (Sergaliyev et al. 2022). A similar ecological structure likely
446 persists in Lake Prorva (freshwater) and Lake Glubinnoe (oligohaline).

447 On the other hand, in the mesohaline Lake Sarkyl, the environmental filter removes
448 such predators and allows large cladocerans to flourish. Basin isolation further supports this
449 transition; the β-mesohaline lake (Volga catchment) showed different diversity patterns than
450 the Ural River basin, indicating that spatial isolation and basin-scale supply are important
451 determinants of community structure (Connor and McCoy 2017).

452 *5.5 Statistical insights and thresholds*

453 Our CCA ordination confirmed that salinity and pH were the dominant factors shaping genus-
454 level distribution, whereas sulphate ($SO_4^{2-}$) and magnesium ($Mg^{2+}$) gradients defined
455 secondary structural shifts. A surprising result was the positive association of certain
456 cladocerans with high sulphate levels, a finding that warrants further investigation, given the
457 known ionoregulatory stress associated with sulphates (Griffith et al. 2020).

458 The use of Generalised Additive Models (GAM) allowed us to identify critical
459 ecological thresholds. For instance, Shannon diversity showed a marked decline above 15
460 PSU, marking the transition to a community dominated by a few highly specialised
461 halotolerant taxa.

The occurrence of certain morphotypes traditionally associated with freshwater environments (e.g., within the genera *Daphnia* and *Monospilus*) in these saline lakes suggests the potential existence of cryptic lineages with specific osmoregulatory adaptations, a phenomenon previously noted in isolated endorheic basins of Central Asia.

## 6. Conclusions

The selected lakes in Western Kazakhstan, which are both open and endorheic systems, proved an effective choice for studying how biodiversity changes in places rarely frequented by people. Our findings indicate that increased salinity diminishes taxonomic richness but does not consistently reduce overall abundance. Indeed, high salinity can cause biodiversity hotspots to form in very harsh environments. Zooplankton density and biomass peaked at elevated salinity levels (>20 PSU), demonstrating the adaptability of specialized taxa.

Of the species identified, *Moina micrura*, *Moina brachiata* and *Arctodiaptomus* (Rh.) *bacillifer* presented different responses to the salinity gradient. *M. micrura* was broadly halotolerant. *M. brachiata* inhabited ephemeral and small water bodies and was resistant to the great physicochemical oscillations typical of these habitats. Also, *A. bacillifer* was not a true halophile, but it exhibited a high level of tolerance to high electrolytic conductivity, a typical property of Central Asian steppe lakes.

These aquatic systems, regardless of their hydrological connectivity, are highly sensitive to climate-induced changes in the precipitation–evaporation balance. Our results for oligohaline lakes highlight the high degree of uncertainty in transitional waters and provide a baseline for predicting future ecological shifts in arid and semi-arid regions worldwide.

## Data availability

Database data for this article can be accessed online at https://doi.org/10.6084/m9.figshare.31115992 and the supplementary material.

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**Competing interests**

The authors declare no competing interests.

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All authors have read and agreed to the published version of the manuscript.

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# A-5

Matela M. , Obolewski K. (w recenzji), Quantifying ecosystem services in Baltic coastal lakes under different protection regimes. Ecosystem Services, 000-000

Ecosystem Services

# Quantifying ecosystem services in Baltic coastal lakes under different protection regimes

--Manuscript Draft--

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| **Abstract:** | Coastal lakes of the Southern Baltic represent ecologically and socio-economically valuable yet vulnerable transitional ecosystems. Their capacity to provide ecosystem services depends not only on their internal ecological status but also on the spatial configuration of the surrounding landscape. This study evaluated the supply potential of 29 ecosystem services (CICES v5.1 classification) across six coastal lakes (Dołgie Wielkie, Gardno, Łebsko, Wicko, Kopań, and Resko), three protected within a national park and three lacking area-based protection. A two-dimensional geocomplex and hydrocomplex approach was applied within a GIS environment to analyse features across a 500 m buffer zone and the immediate shoreline. Multivariate and spatial analyses (PCoA, Spearman correlation, SIMPER) revealed a consistently higher potential for provisioning, regulating/maintenance, and cultural services in protected lakes compared to unprotected ones (mean difference ranging from +27.1% to +113.8%). Provisioning services exhibited the highest response to protection status, whereas cultural services showed the lowest, albeit positive, gain. Among hydrocomplex indicators, shoreline-related cultural-service potential made the largest contribution to pairwise dissimilarities among lakes. Overall, findings demonstrate that ecosystem service potential is governed less by formal protection status alone and more by the underlying spatial heterogeneity of surrounding geocomplexes and hydrocomplexes. This offers a transferable framework for catchment-scale ecohydrological management and spatial prioritization in threatened transitional waters. |

**Declaration of interests**

☒The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Cover letter

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Bydgoszcz, 04th September 2025

Dear Editor,

On behalf of my co-author, I am pleased to submit the manuscript entitled "Quantifying ecosystem services in Baltic coastal lakes under different protection regimes" for consideration in Ecosystem Services, for the Special Issue "Capturing Interactions Between Services for Ecosystem Management".

The manuscript examines ecosystem services supply potential in six Southern Baltic coastal lakes that differ in area-based protection status and hydrological character. Using a GIS-based, two-dimensional framework, we assessed 29 ecosystem-service indicators according to CICES v5.1 across geocomplex units within 500-m lake buffers and hydrocomplex units along the immediate shoreline. We combined multivariate ordination, SIMPER analysis, and Spearman correlation analysis to examine spatial patterns and interactions among provisioning, regulation and maintenance, and cultural ecosystem-service potentials.

The study makes three main contributions to the Special Issue. First, it provides empirical evidence that lakes located within Słowiński National Park exhibited higher ecosystem-service supply potential across all major service categories than lakes outside the park, with the largest contrast observed for provisioning services. Second, it shows that ecosystem-service interactions differ between spatial scales: geocomplex patterns were distributed across multiple landscape-related indicators, whereas hydrocomplex patterns highlighted the importance of local shoreline conditions. Third, the analysis identified positive associations among selected regulatory and provisioning potentials, as well as spatial trade-offs between indicators of cultural services and selected regulation-and-maintenance functions in shoreline units.

By explicitly linking ecosystem services interactions to geocomplex and hydrocomplex configuration, the manuscript offers a spatially explicit approach for identifying where service synergies and trade-offs may arise in transitional water ecosystems. The findings have direct relevance for ecosystem-based management because they indicate that conservation and restoration measures should consider both catchment-scale landscape structure and the immediate littoral zone. In particular, the results suggest that maintaining semi-natural shoreline conditions may help sustain multiple ecosystem services potentials while accounting for potential tensions between recreational functions and regulation-and-maintenance functions.

This manuscript is original, has not been published previously, and is not under consideration for publication elsewhere. All authors have approved the manuscript and agree with its submission to Ecosystem Services. The authors declare no competing interests.

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Thank you for considering our manuscript for this Special Issue. We believe that its focus on spatially explicit ecosystem-service interactions, including synergies and trade-offs across landscape and shoreline scales, will be of interest to the readership of Ecosystem Services and will contribute to the objectives of the Special Issue.

Sincerely,

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On behalf of all authors

Supplementary Tables S2-S3.xlsx

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**Supplementary material**

Supplementary Tables S2-S3.xlsx

## Highlights

- Protected coastal lakes showed consistently higher ecosystem-service supply potential.
- Local shoreline configuration was closely associated with ecosystem-service potential.
- Shoreline characteristics were associated with cultural-regulating service trade-offs.
- Provisioning services showed the largest contrast across protection regimes.
- Spatially explicit ES mapping can guide coastal-lake conservation planning.

# Quantifying ecosystem services in Baltic coastal lakes under different protection regimes

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## Highlights

- Protected coastal lakes showed consistently higher ES supply potential.
- Local shoreline configuration was closely associated with ES potential.
- Shoreline characteristics were associated with cultural-regulating service trade-offs.
- Provisioning services showed the largest contrast across protection regimes.
- Spatially explicit ES mapping can guide coastal-lake conservation planning.

**Abstract.** Coastal lakes of the Southern Baltic represent ecologically and socio-economically valuable yet vulnerable transitional ecosystems. Their capacity to provide ecosystem services depends not only on their internal ecological status but also on the spatial configuration of the surrounding landscape. This study evaluated the supply potential of 29 ecosystem services (CICES v5.1 classification) across six coastal lakes (Dołgie Wielkie, Gardno, Łebsko, Wicko, Kopań, and Resko), three protected within a national park and three lacking area-based protection. A two-dimensional geocomplex and hydrocomplex approach was applied within a GIS environment to analyse features across a 500 m buffer zone and the immediate shoreline. Multivariate and spatial analyses (PCoA, Spearman correlation, SIMPER) revealed a consistently higher potential for provisioning, regulating/maintenance, and cultural services in protected lakes compared to unprotected ones (mean difference ranging from +27.1% to +113.8%). Provisioning services exhibited the highest response to protection status, whereas cultural services showed the lowest, albeit positive, gain. Among hydrocomplex indicators, shoreline-related cultural-service potential made the largest contribution to pairwise dissimilarities among lakes. Overall, findings demonstrate that ecosystem service potential is governed less by formal protection status alone and more by the underlying spatial heterogeneity of surrounding geocomplexes and hydrocomplexes. This offers a transferable framework for catchment-scale ecohydrological management and spatial prioritization in threatened transitional waters.

**Keywords:** coastal lakes; ecosystem services potential; geocomplexes; hydrocomplexes; protected areas

## 1. Introduction

Coastal lakes represent unique transitional ecosystems located at the interface between marine and terrestrial/freshwater environments, formed in the Southern Baltic region through lagoon isolation processes (Inácio et al., 2018; Uścinowicz, 2003; Woszczyk et al., 2011). Variable hydrological connectivity with the sea (ranging from fully freshwater to brackish conditions) determines their high biodiversity and capacity to provide a broad spectrum of ecosystem services (ES): provisioning, regulating/maintenance, and cultural (Inácio et al., 2018; Obolewski and Glińska-Lewczuk, 2020; Schernewski et al., 2018). In line with contemporary conceptual ES frameworks, biotic services are explicitly separated from abiotic outputs, defining an ecosystem service as the final contribution of ecosystems to human well-being (CICES v5.1; Haines-Young and Potschin, 2018).

Despite their high ecological value, these water bodies face persistent anthropogenic pressures, including nutrient loads, infrastructure expansion, and recreational activities. Their ES supply potential does not depend solely on internal ecological status but is equally shaped by the spatial configuration of the surrounding landscape-a mosaic of land use, drainage networks, and ecological corridors. Conventional monitoring aligned with Water Framework Directive (WFD) requirements often overlooks this spatial dimension. However, empirical evidence demonstrates that landscape features and shoreline hydromorphology can influence ecological status and the translation of biophysical potential into actual service flows to a degree comparable to or exceeding in-lake physicochemical parameters (Kutyła et al., 2024; Wynne and Donohue, 2016). Previous ES assessments in Baltic transitional waters (e.g., Szczecin and Curonian Lagoons) indicated that increasing human pressure reduces provisioning and regulating services while expanding cultural service demands (Inácio et al., 2018; Schernewski et al., 2018). Mapping based on CORINE Land Cover classes and Natura 2000 networks confirmed that forest complexes act as key service hotspots (Kaziukonytė et al., 2021). Furthermore, analyses incorporating macrophyte diversity revealed that the dominance of cultural services (e.g., recreation and tourism) can induce spatial trade-offs with biological conservation, highlighting non-linear relationships between biological health and societal benefits (Robbe et al., 2024). This pattern aligns with a global trend toward prioritizing regulating and cultural services within protected areas (Kalinauskas et al., 2024).

Riparian zones and riverine forests play a critical role in building freshwater ecosystem resilience and mitigating diffuse pollution by serving as ecotonal buffer strips (Dinca et al., 2025; Vagheei and Boano, 2025). The relationship between corridor width, pollutant retention, and species richness is also non-linear-for instance, a 15 m buffer strip retains approximately 67% of pollutants and supports nearly 79% of species relative to wider buffers (Ayala-Torres et al., 2025). Conversely, anthropogenic shoreline alterations (e.g., riprap stabilization, retaining walls) and recreational pressures (pier construction, reed removal) cause habitat homogenization in the littoral zone, restricting submerged macrophyte development and degrading biological communities (Chhor et al., 2020; Rosińska et al., 2018). These impacts reveal ecosystem sensitivity thresholds, although shoreline vegetation exhibits resilience provided structural modifications remain below critical levels and human pressures remain localised. To address the need for precise and repeatable spatial evaluations, a two-dimensional framework based on geocomplexes and hydrocomplexes was recently introduced (Krauze et al., 2023). Geocomplexes parameterize the surrounding buffer zone (land use, drainage, protection status, ecological corridors, and Topographic Wetness Index-TWI; evaluating 23 ES under CICES), whereas hydrocomplexes focus on the immediate shoreline zone (bank stabilization, ecotones, hydrotechnical infrastructure; evaluating 13 ES). This methodology operationalizes IUCN guidelines regarding ecological corridors to maintain connectivity between core habitats (Hilty et al., 2020). This is particularly relevant under the Kunming-Montreal Global Biodiversity Framework (30x30 Target) and recent IUCN reports, which note that while protected areas are vital to halt the drastic decline in freshwater biodiversity (-85% since 1970), they are rarely designed around the specific requirements of inland aquatic systems, and ES assessments frequently miss actual service flows to beneficiaries (Kalinauskas et al., 2024; Moberg et al., 2024).

This study builds directly upon previous research covering six coastal lakes in the Southern Baltic. Earlier evaluations using the Ecosystem Health Index (EHI, based on AHP and FCE) established that lakes located within the Słowiński National Park exhibit higher ecosystem health and service potential than unprotected systems (Matela and Obolewski, 2026). Crucially, the absence of a direct correlation between hydrological connectivity with the sea and the EHI indicated that salinity gradients alone do not explain ecological status variability - a key insight amidst global freshwater salinization and the anthropogenic salt cycle (Herbert et al., 2024;

Kaushal et al., 2023). These findings provided the rationale to explore the spatial mechanisms driving differences in ES potential between strictly protected and unprotected coastal lakes. Specifically, this study addresses three research questions:

1. Does formal protection status (national park vs. unprotected) translate into measurable differences in ecosystem service potential?
2. Which geocomplex and hydrocomplex indicators serve as the primary discriminators among the studied lakes?
3. Is the spatial pattern of ecosystem service potential consistent across all ES categories?

## 2. Methods and Materials

### *2.1 Study area*

The study was conducted on six coastal lakes of the Southern Baltic: Dołgie Wielkie, Gardno, and Łebsko, located within the boundaries of the Słowiński National Park, and Wicko, Kopań, and Resko, which remain without strict area-based protection (Matela and Obolewski, 2026). The selected lakes represent a wide spectrum of hydrological connectivity with the sea, ranging from freshwater to brackish conditions - Dołgie Wielkie and Wicko were classified as freshwater, Gardno and Kopań as transitional, and Łebsko and Resko as brackish - enabling the assessment of protection status effects both independently of and in combination with the salinity gradient, following the classification established in previous investigations of these systems (Obolewski et al., 2018).

### *2.2 Delineation of geocomplexes and hydrocomplexes*

Geocomplexes were delineated within a 500 m buffer zone surrounding each lake using a Geographic Information System (GIS), based on the spatial coherence of five descriptive features: land use, drainage, protection status, ecological corridors, and the Topographic Wetness Index (TWI).

Hydrocomplexes were delineated along the lake shorelines based on the spatial coherence of eleven descriptive features, including land use directly adjacent to the shoreline, drainage status, protected area coverage, shoreline stabilization, presence of an ecotonal zone, ecological corridors, visibility from hiking trails, angling accessibility, presence of hydrotechnical structures, bathing sites, and water intake points. In addition, nine supplementary indicators were

incorporated, covering the number of aquaculture facilities, hotels, marinas/piers/quays, kayaking routes, nature trails, training centres, catering facilities, hydroelectric power plants, and theoretical hydropower potential. This approach builds upon the methodology established for freshwater ecosystem service assessment, wherein hydrocomplexes quantify 13 potential ecosystem services and geocomplexes quantify 23 (Krauze et al., 2023). In total, 29 ecosystem services were identified across the studied Baltic coastal lakes (Matela and Obolewski, 2026).

### *2.3 Data sources*

Spatial data were obtained from high-resolution national and regional repositories: the Topographic Objects Database (BDOT10k), CORINE Land Cover, CIR and RGB orthophotomaps, spatial datasets on nature conservation provided by the General Directorate for Environmental Protection (GDOŚ), a Digital Elevation Model (DEM) used for TWI calculation, and the Map of Hydrographic Division of Poland (MPHP). These data were further validated using OpenStreetMap and Google Maps to identify tourist trails, recreational infrastructure, and accessibility features. This protocol adheres to recommendations favouring high-resolution national spatial databases over lower-resolution pan-European products (such as CORINE Land Cover), whose coarse spatial resolution proves insufficient for localized lake catchment analyses (Kutyła et al., 2024).

### *2.4 Ecosystem Services assessment*

A total of 29 ecosystem services were evaluated according to the Common International Classification of Ecosystem Services framework (CICES v5.1; Haines-Young and Potschin, 2018), categorized into provisioning, regulating and maintenance, and cultural services. This classification system represents one of the most widely applied frameworks for ecosystem service evaluation in transitional and coastal waters, including recent assessments of Baltic coastal lakes and lagoons (Inácio et al., 2018; Kaziukonytė et al., 2021; Robbe et al., 2024; Schernewski et al., 2018). Each service was quantified using specific geocomplex and hydrocomplex indicators, providing a differentiated evaluation of ecosystem service supply potential across the six studied lakes.

### *2.5 Statistical analysis*

Principal Coordinates Analysis (PCoA) based on Gower distance was applied to visualise multivariate similarity patterns among the six coastal lakes across the complete set of

geocomplex and hydrocomplex indicators. Spearman's rank correlation test was used to evaluate relationships between individual spatial indicators. Spearman's rank correlation coefficients ($r_s$) were calculated separately for ES potential indicators assessed in geocomplex and hydrocomplex units. Two-sided p-values were adjusted for multiple testing using the Bonferroni correction within each correlation matrix. Correlations were calculated across all geocomplex or hydrocomplex units, respectively. Similarity Percentage (SIMPER) analysis was used to identify ES indicators contributing to pairwise dissimilarities among geocomplex and hydrocomplex units grouped by lake. The significance of each indicator's average contribution was assessed using 999 unrestricted permutations of lake labels. Indicators were ranked according to their average contribution to between-group dissimilarity. All statistical computing and visualizations were performed in R software (R Core Team, v4.3.2) utilizing the vegan and ggplot2 packages.

## 3. Results

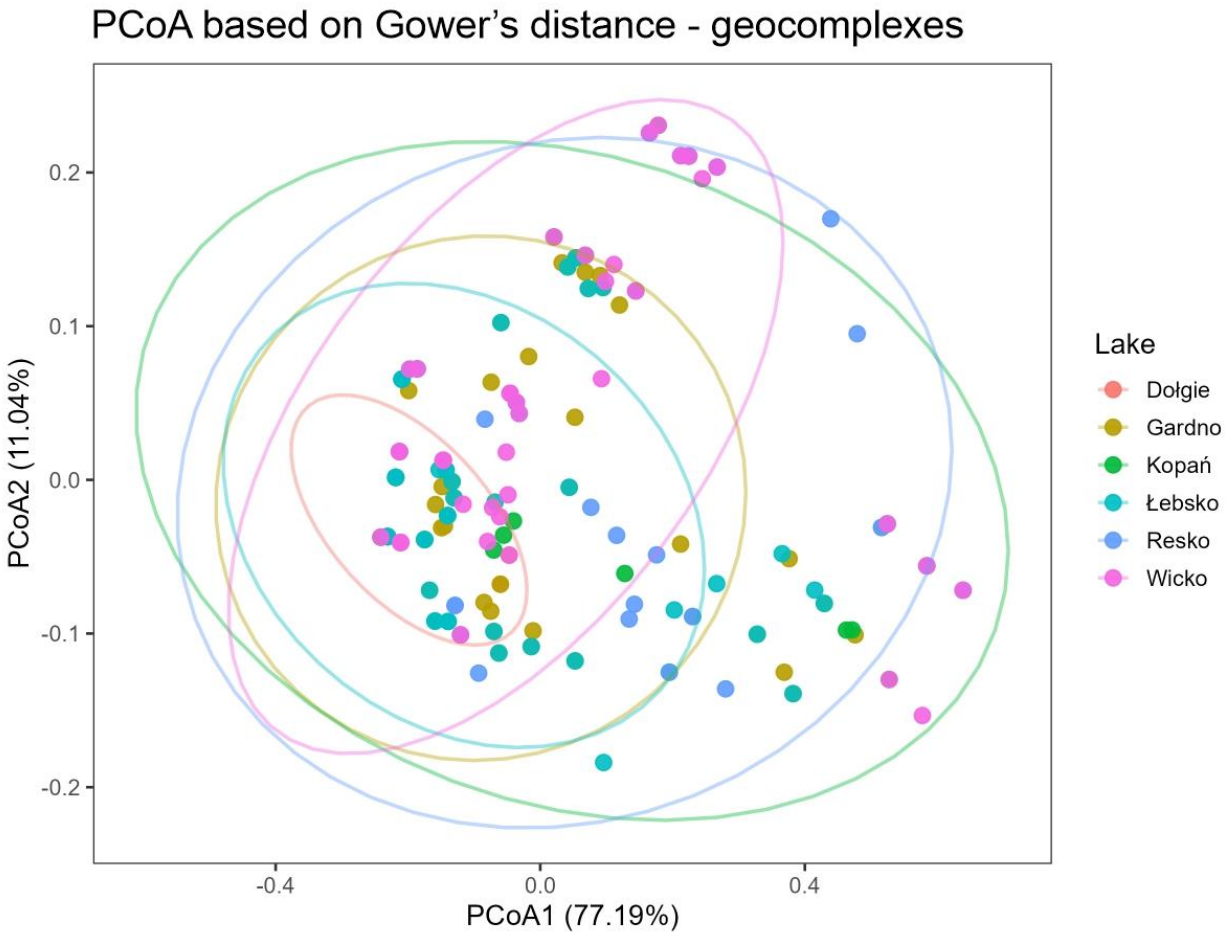
A comparison of the average values of ecosystem service provision potential indices between lakes located within the SPN and those outside it revealed a consistent, positive shift for all major categories of services based on geocomplexes in strictly protected lakes (Supplementary Table S1). The mean difference was +113.8% for provisioning services, +50.8% for regulating and maintenance services, +27.1% for cultural services, +28.7% for abiotic regulatory and maintenance services, and +59.8% for abiotic cultural services, indicating that strictly protected lakes were consistently situated in a more favourable spatial configuration for the provision of ecosystem services than non-strictly protected lakes.

The PCoA ordination based on Gower's distance (Figure 1) revealed distinct patterns of variation in the geo- and hydro-complexes. In the case of the geo-complexes, the first PCoA axis accounted for 79.74% of the variation, whilst the second accounted for 21.83%. The variation in the geo-complexes was therefore predominantly described by the first dimension of the ordination.

The group ellipses for the individual lakes partially overlapped, indicating a lack of complete separation of the objects in the ordination space. Łebsko and Gardno were characterised by a relatively compact distribution of points. Resko showed the greatest dispersion, including a single point clearly situated in the positive region of the PCoA1 axis. Kopań was more elongated along

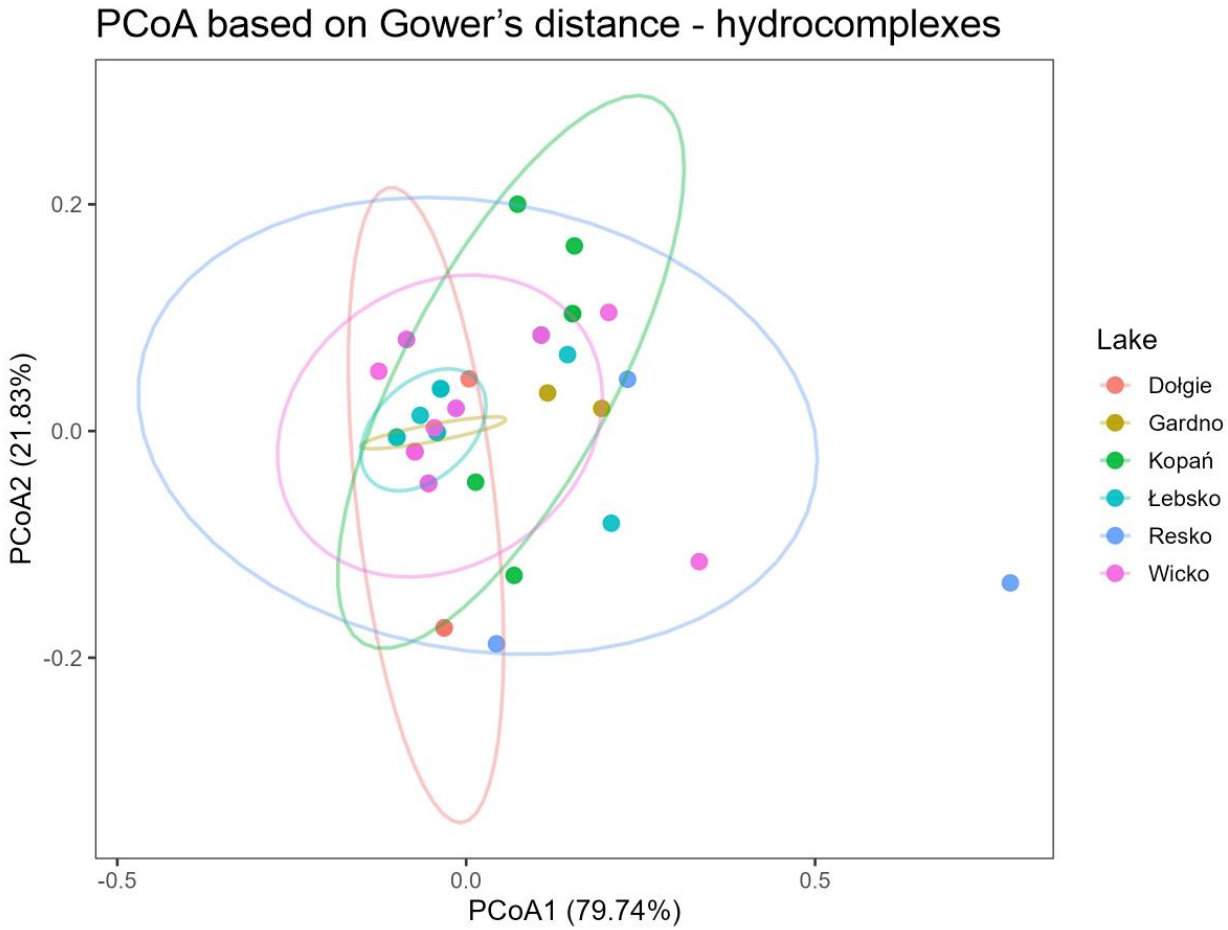
PCoA2, whilst Dołgie Wielkie exhibited greater variability along the vertical axis than the horizontal one.

Figure 1. Results of the PCoA analysis based on Gower's distance for the potential to provide ES by geocomplexes.




For the hydrocomplexes (Figure 2), the first and second PCoA axes explained 77.19% and 11.04% of the variation respectively, totalling 88.23%. The ellipses for the individual lakes overlapped to a significant extent, particularly in the central part of the ordination space. The greatest dispersion of points was observed for Kopań and Resko, whilst Dołgie Wielkie formed a relatively compact cluster. Wicko comprised two distinct clusters: one in the positive region of PCoA2 and the other in the negative region. Łebsko, Gardno and Resko occupied a partially shared ordination space. This result indicates that the characteristics of the immediate littoral zone differed primarily at the level of local hydrocomplex units, rather than exclusively between entire lakes.

Figure 2. Results of the PCoA analysis based on Gower's distance for the potential to provide ES by hydrocomplexes.




The SIMPER analysis (Supplementary Table S2) indicated that pairwise dissimilarities among hydrocomplex units were driven by a small number of ES indicators. The indicator representing opportunities for active and direct contact with nature, including recreation and leisure in the lakeshore environment (CICES 3.1.1.1), made the largest average contribution to dissimilarity in several lake-pair comparisons.

For the indicator representing active and direct contact with nature, the average contribution to dissimilarity was significant in comparisons between Dołgie Wielkie and Gardno ($p_{perm}$ = 0.008), Kopań ($p_{perm}$ = 0.002), Łebsko ($p_{perm}$ = 0.012), Resko ($p_{perm}$ = 0.001) and Wicko ($p_{perm}$ = 0.004) based on 999 permutations. Its percentage contribution to the between-group dissimilarity in these comparisons ranged from 27.7% to 53.4%. In the Dołgie Wielkie-Gardno comparison, this indicator accounted for 50.3% of the average dissimilarity; its mean values were 1.875 and 0.917,

respectively. In comparisons of Dołgie Wielkie with Łebsko and Resko, the corresponding contributions were 53.4% (mean values: 1.875 and 0.619) and 27.7% (mean values: 1.875 and 1.667), respectively.

In the Kopań-Resko comparison, several indicators made significant contributions to between-group dissimilarity, including indicators of active and passive contact with nature, maintenance of freshwater chemical quality, maintenance of habitats and populations, and the potential for harvesting wild aquatic animals ($p_{perm}$ = 0.002-0.030).

For the Łebsko-Resko comparison, indicators related to direct and observational contact with nature contributed significantly to the between-group dissimilarity. In the Resko-Wicko comparison, the indicator representing the maintenance of habitats and populations also contributed to dissimilarity. In the Kopań-Wicko comparison, the indicator related to the intellectual use of nature, including education and learning about the environment, was among the main contributors. No individual indicator made a significant permutation-based contribution to dissimilarity between Gardno and Łebsko.

In contrast to the hydrocomplex analysis, SIMPER results for geocomplex units (Supplementary Table S3) did not identify a single ES indicator that consistently dominated pairwise dissimilarities. For the Dołgie Wielkie-Kopań comparison, the largest contributions to between-group Bray-Curtis dissimilarity were associated with indicators representing the potential for harvesting plant biomass for energy and the use of plant and animal genetic resources. The indicator for harvesting wild plants as an energy source (CICES 1.1.5.3) made a significant permutation-based contribution ($p_{perm}$ = 0.001); its mean values were 3.30 for Dołgie Wielkie and 1.19 for Kopań. This indicator accounted for 5.7% of the average dissimilarity for this comparison.

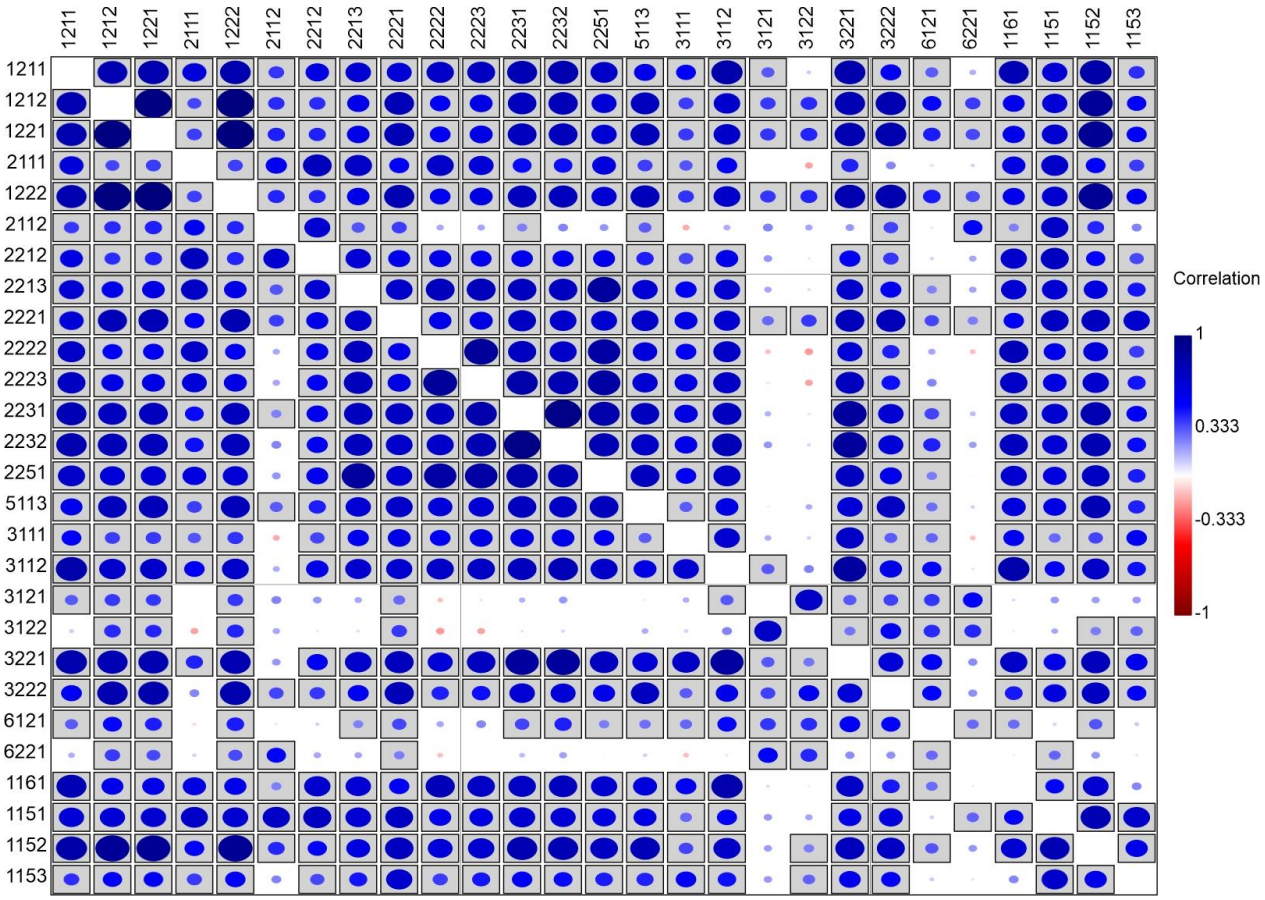
In the Dołgie Wielkie-Gardno comparison, the indicators contributing most to the average dissimilarity represented visual-impact mitigation, habitat maintenance, filtration and retention of pollutants, and plant-biomass harvesting. However, none of these indicators made a significant permutation-based contribution. Similarly, no individual indicator made a significant contribution in the Dołgie Wielkie-Łebsko comparison. These results suggest that the dissimilarity in ES supply potential among geocomplex units was distributed across multiple landscape-related indicators rather than dominated by a single indicator.

Spearman's rank correlation analysis revealed a strong correlation in the potential of many ecosystem services assessed for the geocomplexes (Figure 3). The strongest positive correlations were found for services related to plant and animal genetic resources. This indicates that spatial conditions favourable for the conservation or use of one type of genetic resource co-occurred with conditions favourable for other biological resources.

Clear positive correlations were also found between the potential of regulatory and cultural services. In particular, the potential for mitigating visual disturbances was positively associated with the potential for sustaining habitats and populations, as well as with services enabling passive contact with nature. This implies that, in the case of geocomplexes, some services did not vary independently but reflected a common trend linked to land-use patterns, conservation and the environmental characteristics of the lakes' buffer zones.

Not all services showed a consistent trend. Weak negative correlations were observed between the potential for bioremediation of pollutants and services related to active contact with nature, as well as between the potential for erosion control and selected regulatory and cultural services. However, the strength of these negative correlations was significantly lower than in the dominant group of positively correlated services.

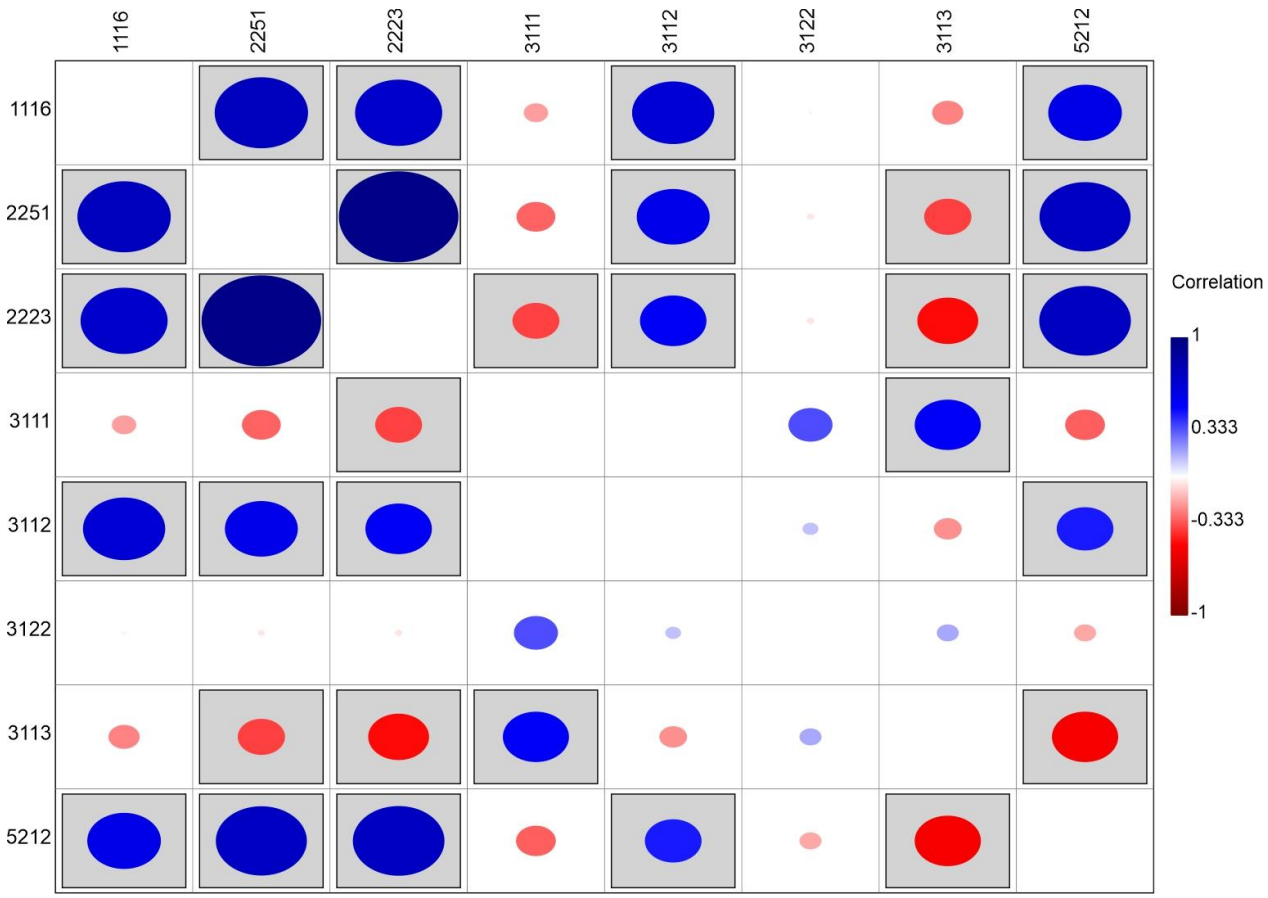
Figure 3. Results of the Spearman's rank correlation analysis for pairs of indicators of the potential for provision of ES by geocomplexes. The codes of ES indicator refer to the CICES v5.1 classification.




In the case of hydrocomplexes, the correlation pattern was more selective (Figure 4). Strong positive correlations were observed between the potential to maintain the chemical quality of freshwater, sustain habitats and populations, and provisioning services related to the harvesting of wild aquatic animals. This suggests that maintaining a well-functioning riparian zone can simultaneously promote the conservation of habitats, water quality and the availability of the ecosystem's biological resources.

A different pattern was observed for cultural services based on direct contact with nature. Their potential was positively correlated with active recreation, but negatively correlated with the potential for habitat maintenance and water quality regulation. This result indicates a partial spatial separation of recreational functions (cultural services) from the closely linked cluster of regulatory and maintenance services in the immediate riparian zone of lakes.

Figure 4. Results of the Spearman's rank correlation analysis for pairs of indicators of the potential for provision of ES by hydrocomplexes. The codes of ES indicator refer to the CICES v5.1 classification.




The detailed results for each pair of services can be found in Supplementary Tables S4-S5.

## 4. Discussion

The results of our study demonstrate that the ES supply potential of Southern Baltic coastal lakes is strongly determined by the spatial configuration of the surrounding landscape, as captured by the geocomplex and hydrocomplex methodology (Krauze et al., 2023). Lakes situated within the Słowiński National Park consistently exhibited higher potentials for provisioning, regulating and maintenance, as well as cultural services compared to unprotected lakes. This confirms that formal area-based protection is associated with a more favourable spatial organization of the adjacent catchment for sustaining ecosystem functions. This finding aligns with IUCN assessments indicating that protected areas can reverse declining trends in freshwater ES potential, provided that effective management and ecological connectivity between core habitats are maintained (Hilty et al., 2020; Moberg et al., 2024).

Crucially, these results directly elucidate and complement prior observations conducted on the same six coastal lakes, which revealed higher Ecosystem Health Index (EHI) values in national

park lakes despite the absence of any relationship between hydrological connectivity to the sea and EHI or ES potential (Matela and Obolewski, 2026). Disaggregating ES potential into geocomplex and hydrocomplex components reveals the spatial mechanism underlying this pattern: the divergence between protected and unprotected lakes stems not from the salinity gradient itself, but from contrasting land-use organization within the buffer zone and along the immediate shoreline. Thus, protection status and salinity represent two largely independent axes of environmental variation, with the former-expressed through geo- and hydrocomplex configurations-being the primary determinant of ES supply potential. This observation aligns with accumulating evidence that freshwater salinization represents a distinct, large-scale process (the anthropogenic salt cycle) operating under spatial and temporal dynamics decoupled from localized land-use organization (Kaushal et al., 2023; Herbert et al., 2024).

The substantial increase in provisioning service potential observed in protected lakes likely reflects greater retention of semi-natural land cover and lower habitat fragmentation supporting fisheries and biological resource extraction. A similar mechanism was documented by Kaziukonytė et al. (2021) in the Nemunas Delta, where forested areas and natural vegetation hotspots yielded the highest overall ES potential. The comparatively smaller, yet positive, gain in cultural services suggests that aesthetic and recreational values are less strictly coupled with formal protection status, as unprotected lakes may retain substantial cultural value through informal recreational use. This pattern corresponds with findings by Inácio et al. (2018) in the Szczecin Lagoon, where anthropogenic pressure decreased provisioning and regulating services while cultural services remained dominant, as well as Robbe et al. (2024), who showed that cultural services dominate actual ES flows in Baltic lagoons regardless of aquatic vegetation state. This heterogeneity between service categories was also reflected in the prior EHI evaluation of these lakes, where cultural and regulating services received the highest expert scores while provisioning services exhibited higher inter-lake variability (Matela and Obolewski, 2026).

The large contribution of hydrocomplex indicator 3111, representing opportunities for active and direct contact with nature, to pairwise dissimilarities highlights the importance of local shoreline conditions for spatial variation in ES supply potential. This association suggests that conservation measures targeting the immediate shoreline may be relevant for maintaining multiple ES potentials. Our finding accords with well-established riparian ecology principles: meta-analyses

demonstrate that even narrow riparian corridors (a few dozen meters) can intercept the majority of diffuse pollutants and sustain significant species richness, pointing to non-linear, threshold-dependent ecological functions. Mechanistically, shoreline modification studies show that replacing natural banks with riprap or retaining walls causes severe losses of littoral vegetation and shifts in fish and benthic macroinvertebrate assemblies (Chhor et al., 2020). From a management perspective, targeted interventions along the immediate shoreline (such as soft-engineering practices, ecotone preservation, and regulation of recreational access) can yield disproportionately large ES benefits relative to their spatial extent. This reinforces the high expert weight assigned to the shoreline buffer zone in maintaining process integrity under the EHI framework (Matela and Obolewski, 2026).

Furthermore, our results align with Kutyła et al. (2024), who demonstrated that land use in the immediate vicinity of flow-through lakes exerts a stronger influence on macrophyte-based ecological status than land use across the wider catchment. This suggests a broader ecological principle: the land-water interface plays a pivotal role in governing overall lake ecosystem functioning relative to its small areal coverage. This concept is foundational to classic lake vulnerability frameworks, which treat direct catchment land use as a primary modifier of lake resilience to external pressures (Bajkiewicz-Grabowska, 1987; Szymańska-Walkiewicz et al., 2024). Similar conclusions emerge from recreational pressure studies, where localized reed belt fragmentation for access points compromises pollutant buffering capacity, even if tourist intensity itself is not the primary driver of littoral biocenosis degradation (Rosińska et al., 2018).

In contrast to hydrocomplexes, ES discrimination based on geocomplexes was distributed across multiple indicators, indicating that catchment-scale protection operates through cumulative, multi-dimensional landscape patterns rather than a single dominant factor. This is consistent with the systematic review by Kalinauskas et al. (2024), which highlighted that regulating, maintenance, and cultural services depend heavily on multi-faceted landscape structures within protected areas.

Synthesised together, this study and the prior EHI analysis (Matela and Obolewski, 2026) demonstrate that the ecological and ES benefits of protecting Baltic coastal lakes operate through a shared mechanism: the preservation of semi-natural shoreline and catchment architecture that simultaneously safeguards biological integrity and ES supply potential. Importantly, this

mechanism operates independently of the salinity gradient-a key environmental filter structuring aquatic communities in coastal systems (Netto and Fonseca, 2017; Obolewski and Glińska-Lewczuk, 2020). Salinity and spatial landscape organization thus act as two distinct dimensions of environmental variation: the former dictates biological community assembly, whereas the latter governs the capacity of the ecosystem to translate its ecological state into socio-economic benefits.

Several limitations of this study should be noted. The small number of research objects (6 lakes) limits statistical power and generalizability to other coastal lake systems. The cross-sectional design precludes assessment of temporal dynamics, and the indicator-based approach relies on expert-derived proxies from geo- and hydrocomplex mapping (Krauze et al., 2023) rather than direct measurements of actual service flows. This constraint aligns with challenges highlighted by Kalinauskas et al. (2024) and Robbe et al. (2024) regarding discrepancies between supply potential and real-world service flow. Future research should expand this methodology to a larger sample of coastal lakes across broader gradients of protection and anthropogenic pressure, while validating proxy-based potentials against empirical measures of service use (e.g., visitor surveys, recreational intensity) and direct biological metrics (Matela and Obolewski, 2022, 2026).

## 5. Conclusions

This study indicates that ES supply potential in the studied Southern Baltic coastal lakes was associated with the spatial organisation of surrounding geocomplexes and hydrocomplexes. Lakes situated within the boundaries of the Słowiński National Park consistently exhibited higher supply potentials across provisioning, regulating and maintenance, and cultural services compared to unprotected lakes, with the most pronounced divergence observed for provisioning services. Among hydrocomplex indicators, the potential for active and direct contact with nature made the largest contribution to pairwise dissimilarities among lakes, underscoring the relevance of local shoreline conditions. Because this indicator is informed by shoreline accessibility and land-use characteristics, its pattern suggests that local shoreline configuration may be important for spatial variation in ES supply potential. Synthesized with prior ecosystem health assessments (EHI) of the same systems (Matela and Obolewski, 2026), these findings strongly justify the integration of geo- and hydrocomplex mapping into conservation planning and catchment-scale management strategies for coastal lakes. This approach offers a transferable, spatially explicit

methodology applicable to similarly threatened transitional water ecosystems beyond the Baltic region.

## 6. Data availability

The raw data for this article is available on request by emailing the corresponding author.

## 7. Competing interests

The authors declare no competing interests.

## 8. Declaration of generative AI and AI-assisted technologies in the manuscript preparation process.

During the preparation of this work, the authors used DeepL, Grammarly, and Perplexity for translation, language editing, literature screening, and support during the revision process. After using these tools/services, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

## 9. CRediT author statement

**Mikołaj Matela:** Writing - review & editing, Writing - original draft, Visualisation, Software, Methodology, Investigation, Formal analysis, Data curation. **Krystian Obolewski:** Writing - review & editing, Writing - original draft, Visualisation, Formal analysis, Supervision.

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