

Uwarunkowania siedliskowe międzygatunkowych różnic w biologii małży z rodziny skójkowatych (Unionidae)

Habitat conditions responsible for interspecific
differences in the biology of mussels of the family
Unionidae

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"If the Lord Almighty had consulted me before embarking on creation, I should have recommended something simpler"

"Gdyby Bóg Wszechmogący skonsultował się ze mną zanim przystąpił do aktu stworzenia, to zaproponowałbym coś prostszego"

Alfonso X, King of Castile

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Spis publikacji

- I Ćmiel A.M., Zając T., Zając K., Lipińska A., Najberek K. 2019. Single or multiple spawning? Comparison of breeding strategies of freshwater Unionidae mussels under stochastic environmental conditions. *Hydrobiologia*. <https://doi.org/10.1007/s10750-019-04045-8>

- II Ćmiel A.M, Zając K., Lipińska A., Zając T. 2019. Is *Pseudanodonta complanata* the most vulnerable of widespread European species of unionids? An intense stress test leading to a massive die-off. *Aquatic Conservation: Marine and Freshwater Ecosystems*. <https://doi.org/10.1002/aqc.3216>

- III Ćmiel A.M., Strużyński A., Wyrębek M., Lipińska A.M., Zając K., Zając T. 2019. Response of freshwater mussel recruitment to hydrological changes in a eutrophic floodplain lake. *Science of the Total Environment*. <https://doi.org/10.1016/j.scitotenv.2019.135467>

Podziękowania

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Streszczenie

Małże słodkowodne to jedna z najszybciej ginących grup zwierząt na Ziemi, a spośród gatunków mięczaków uznanych za globalnie zagrożone, najliczniej reprezentowane są małże z rodziny skójkowatych (Unionidae). Jednocześnie jest to jedna z najsłabiej poznanych grup zwierząt. Niewiele wiadomo na temat ich biologii, wymagań siedliskowych, rozmieszczenia w przestrzeni, interakcji między innymi gatunkami. Małże te żyją w siedliskach słodkowodnych, najsilniej zagrożonych w skali globalnej, zatem kwestia określenia wymagań siedliskowych Unionidae służyć może zarówno ich ochronie gatunkowej, jak i właściwemu zarządzaniu wodami słodkimi.

Prezentowana rozprawa doktorska obejmuje trzy publikacje naukowe dotyczące badań prowadzonych w latach 2013-2018, w Zalewie Pińczowskim (województwo świętokrzyskie). Spośród sześciu rodzimych gatunków małży z rodziny Unionidae występujących w Polsce, aż pięć występuje w Zalewie Pińczowskim: szczeżuja pospolita (*Anodonta anatina*), szczeżuja wielka (*Anodonta cygnea*), szczeżuja spłaszczona (*Pseudanodonta complanata*), skójką malarzy (*Unio pictorum*) i skójką zaostrzoną (*Unio tumidus*). Jest to zatem doskonale miejsce do badania siedliskowych uwarunkowań różnic w biologii poszczególnych gatunków małży z rodziny Unionidae.

W populacjach Unionidae występują bardzo istotne różnice w strategiach reprodukcyjnych, przejawiające się różną liczbą lęgów wyprowadzanych w ciągu roku. W pracy (I) modelowałem, co stałoby się z hipotetyczną populacją małży (pod względem tempa wzrostu populacji i prawdopodobieństwa jej wyginięcia), która uwalnia tę samą liczbę glochidiów (pasożytniczych larw), przystępując do rozrodu od jednego do pięciu razy w trakcie sezonu reprodukcyjnego, w nieprzewidywalnych warunkach siedliskowych, różniących się prawdopodobieństwem zarażenia ryby żywicielskiej. Ocenilem, w jaki sposób warunki siedliskowe oraz liczba lęgów wpływają na parametry populacji istotne z punktu widzenia jej trwałości, tj. na wielkość populacji, wskaźnik wyginięcia, współczynnik zmienności średniej wielkości populacji i średni czas do wyginięcia. Wykazałem, że liczba lęgów jest czynnikiem, który silnie wpływa na dostosowanie osobników.

Jak dotąd znane jest zjawisko bardzo szybkiego zanikania populacji Unionidów, jednak nic nie wiadomo o przyczynach tak szybkiego tempa wymierania, jak również nic nie wiadomo o mechanizmach odpowiedzialnych za różnice w liczebnościach gatunków, co jest zresztą szerszym problemem ekologicznym. W pracy (II) opisałem zjawisko masowego śnięcia około jednej trzeciej z ogólnej liczby osobników małży występujących w Zalewie Pińczowskim, które wystąpiło latem 2018 roku, w ciągu zaledwie kilku dni. Analiza próbek wody pobranych tuż po śnięciu małży, wykazała niezwykle wysokie stężenie fosforanów i azotynów. Sugerowałem, że ruch łodzi motorowej musiał zaburzyć osady jeziorne, negatywnie wpływając na procesy fizjologiczne małży i tym samym powodując ich masową śmiertelność. Najwyższą śmiertelność odnotowano w przypadku *P. complanata* (81%), a następnie *U. pictorum* (58%), *A. cygnea* (26%), *U. tumidus* (15%)

i *A. anatina* (5%). Śmiertelność była istotnie związane z rozmiarem (wiekiem) małży tylko u *A. cygnea*, przy czym śmiertelność była wyższa u mniejszych (młodych) osobników. Uzyskane wyniki wykazały znaczną różnicę w poziomie tolerancji na zaburzenia siedliska między gatunkami małży występującymi w Zalewie Pińczowskim.

Jednym z najszerzej obserwowanych zjawisk, które są powiązane z zanikaniem niektórych małży słodkowodnych, jest brak rekrutacji młodych osobników, jednak niewiele wiadomo o przyczynach tego zjawiska. W pracy (III) opisałem wpływ zmiany przepływu w Zalewie Pińczowskim na rekrutację (obecność i liczebność) młodych małży. Odkryłem, że niewielki wzrost przepływu w zbiorniku po zbudowaniu dodatkowego kanału ulgi, pozytywnie wpłynął na rekrutację u trzech z pięciu gatunków małży występujących w zalewie. Odkryłem również, że po zbudowaniu tego dodatkowego odpływu nisze młodocianych *A. cygnea* i *Unio* spp. zmieniły się, ujawniając różnice w ich wymaganiach hydrologicznych. Pokazałem też, że podobnie jak w wodach płynących, złożone parametry hydrauliczne mają istotne znaczenie dla małży z rodziny Unionidae w wodach stojących.

Powyższe wyniki sugerują, że liczba łęgów należy do czynników najsilniej wpływających na dostosowanie osobników, tymczasem jest to czynnik, który do tej pory nie był nawet opisany dla poszczególnych gatunków, natomiast na skutek interakcji małży z gatunkami ich ryb żywicielskich, jest to czynnik niezwykle zmienny. Wpływ czynników środowiska nieożywionego na występowanie i biologię małży jest znany na bardzo ogólnym poziomie, podczas gdy omawiane badania identyfikują bezpośrednie czynniki: wpływ nagłych zmian własności fizyczno-chemicznych wody na śmiertelność, jak i zmiany warunków hydrologicznych na rekrutację, która jest kluczowym czynnikiem dla dynamiki populacji.

Summary

Freshwater mussels are the fastest dying group of animals on Earth, and Unionidae is the most numerous family of mollusc species recognized as globally endangered. At the same time, these mussels are among the least known groups of animals: little is known about their biology, habitat requirements, spatial distribution or interactions with other species. Freshwater habitats are some of the most endangered worldwide; defining the habitat requirements of unionids will therefore be useful for both species conservation and the appropriate management of freshwaters.

This PhD thesis includes three scientific publications on research conducted in Lake Pińczów (Świętokrzyskie province) between 2013 and 2018. Five of the six species of unionid mussels native to Poland inhabit this lake: duck mussel (*Anodonta anatina*), swan mussel (*Anodonta cygnea*), depressed river mussel (*Pseudanodonta complanata*), painter's mussel (*Unio pictorum*) and swollen river mussel (*Unio tumidus*). It is therefore an excellent place for studying the habitat conditions responsible for interspecific differences in the biology of unionid mussels.

There are very significant differences in reproductive strategies between unionid populations, manifested by the different numbers of broods produced during the year. In the first paper (I) I modelled what would happen to a hypothetical mussel population (in terms of population growth rate and the probability of its extinction) that released the same number of glochidia (parasitic larvae) during one to five reproductive events during a season, in unpredictable habitat conditions differing in the probability of host fish infestation. I evaluated how the number of spawning events would affect population parameters that are important from the point of view of population persistence, i.e. its size, extinction rate, coefficient of variation of mean population size and the mean time to extinction. I showed that the number of broods was a factor strongly influencing individual fitness.

The very rapid disappearance of unionid populations is a familiar phenomenon. Nothing is known, however, about why such extinctions should take place so fast, nor is anything known about the mechanisms causing differences in numbers between species; this is a serious ecological problem. In the second paper (II) I described the massive die-off of approximately one-third of the unionid mussels inhabiting Lake Pińczów that took place within the space of just a few days in the summer of 2018. Analysis of water samples taken immediately after the die-off revealed extremely high concentrations of phosphates and nitrites. I suggested that motorboat movements must have disturbed the lake sediments, negatively affecting the physiological processes of mussels and thereby causing their mass mortality. The highest mortality was recorded in the rarest species *P. complanata* (81%), followed by *U. pictorum* (58%), *A. cygnea* (26%), *U. tumidus* (15%) and *A. anatina* (5%). Mortality was significantly related to the size (age) of the mussels only in *A. cygnea*, and was higher in smaller (young) individuals. The results showed significant differences in levels of tolerance to habitat disturbances between mussel species occurring in this floodplain lake.

One of the most widely observed phenomena associated with the disappearance of some freshwater mussels is the non-recruitment of juveniles, but little is known about why this happens. In the third paper (III) I described the impact of a change in the water regime of Lake Pińczów on the recruitment (presence and number) of young mussels. I found that a slight increase in the discharge from this waterbody, following the construction of an additional outflow pipe, positively influenced recruitment in three of the five mussel species inhabiting the lake. I also found that after this additional outflow had been built, the niches of *A. cygnea* and *Unio* spp. juveniles changed, revealing differences in their hydrological requirements. I also showed that, as in lotic habitats, complex hydraulic parameters are absolutely crucial to unionid mussels in lentic conditions.

The above results suggest that the number of broods is one of the factors strongly affecting the fitness of individual mussels. To date, this factor has not been described even for individual species; it is extremely variable, because of the interaction between mussels and their host-fish species. Although the impact of environmental factors on the occurrence and biology of bivalve molluscs is known at a very general level, these three papers identify direct factors: the impact of sudden changes in the physicochemical properties of water on mortality, as well as changes in hydrological conditions on recruitment, a key factor in population dynamics.

Wstęp

Małże słodkowodne należą do najbardziej zagrożonych grup zwierząt na świecie; dlatego w ostatnich latach zwiększa się liczba badań dotyczących ich ekologii i ochrony, również w Europie (Lopes-Lima i in., 2017, 2018). Małże słodkowodne pełnią wiele ważnych funkcji w ekosystemach wodnych, które określa się terminem usługi ekosystemowe (ang. *ecosystem services*). Do najważniejszych usług ekosystemowych, do których przyczyniają się małże zalicza się: oczyszczanie wody (biofiltracja), obieg i akumulacja składników odżywczych, modyfikacja podłoża i sieci troficznych (Vaughn i Hakenkamp, 2001; Strayer, 2008; Vaughn i in., 2008; Haag, 2012, Vaughn, 2017). Niektóre gatunki (np. *Margaritifera margaritifera*) spełniają kryteria gatunków wskaźnikowych, flagowych i parasolowych, co czyni je idealnymi celami ochrony wód (Geist, 2010). Jednak małże słodkowodne, choć nie tak dawno szeroko rozprzestrzenione i liczne, a nawet wykorzystywane na masową skalę do celów komercyjnych (Williams i in., 1993; Haag, 2012), zanikają (Lydeard i in., 2004), a identyfikacja czynników prowadzących do ich ustępowania, jest nadal poważnym wyzwaniem naukowym (Ferreira-Rodríguez i in., 2019).

Zalew Pińczowski (Fig.1; 50°31'9"N, 20°31'5" E) to niewielki (powierzchnia ok. 11 ha), płytki (maksymalna głębokość 1,5 m), naturalnie eutroficzny zbiornik, który powstał podczas regulacji rzeki Nidy w Pińczowie. Został oddany do użytku w 1973 roku, a następnie zmodernizowany w latach 80. - wykonany został przekop skracający bieg rzeki, a dotychczasowe koryto poszerzono, tworząc w ten sposób zalew. Starorzecze biegnące powyżej przekształcono w doprowadzalnik, a poniżej, po drugiej stronie drogi wojewódzkiej nr 766, wykonano kanał odprowadzający wodę do starorzecza (Strużyński, 2007; Zajac i in., 2016). Jednak wylot wody ze zbiornika nie został wykonany zgodnie z projektem. W trakcie wykonywania robót ziemnych napotkano na pozostałości betonowej konstrukcji dawnego mostu i zamiast dwóch rurociągów o średnicy 80 cm, zastosowano jeden, tej samej średnicy, o wlocie umieszczonym o 36 cm wyżej od rzędnej projektowanej (Strużyński, 2007). W rezultacie tego błędu, kanał wylotowy uniemożliwiał zapewnienie odpowiedniego przepływu wody przez zbiornik. W głównej części zbiornika woda stagnowała, a jej ruch był spowodowany głównie podmuchami wiatru i rozproszaniem ciepła. Niewielka głębokość wody i niewystarczający przepływ spowodowały wystąpienie wielu negatywnych procesów, takich jak zarastanie zbiornika i doprowadzalnika roślinnością wodną, zamulanie się zbiornika i doprowadzalnika, dalsze wypływanie zbiornika i wydłużenie czasu wymiany wody w zbiorniku (Strużyński, 2007; Strużyński i Wyrębek, 2013), co w konsekwencji doprowadziło do pogorszenia jakości wody i coraz większej eutrofizacji zbiornika. Jako rozwiązanie problemu niewystarczającego przepływu, zaproponowano budowę dodatkowego kanału odprowadzającego wodę z zalewu bezpośrednio do Nidy (Strużyński, 2007), który został wybudowany w listopadzie 2013 roku.



Fig.1. Ogólny schemat lokalizacji Zalewu Pińczowskiego wraz z doprowadzalnikiem i odprowadzalnikiem. Strzałki oznaczają kierunek przepływu wody. Czerwonym kolorem zaznaczono lokalizację dodatkowego kanału odprowadzającego zbudowanego w 2013 roku

Zalew pełni funkcję rekreacyjną - przy zalewie znajduje się czynne kąpielisko, a w ciągu prawie całego roku aktywnie funkcjonuje tam także zrzeszenie wędkarzy oraz klub wodny. Jest także obiektem cennym przyrodniczo. Spośród sześciu gatunków Unionidae występujących w Polsce, aż pięć występuje w Zalewie Pińczowskim: szczeżuja pospolita (*Anodonta anatina*), szczeżuja wielka (*Anodonta cygnea*), szczeżuja spłaszczona (*Pseudanodonta complanata*), skójka malarzy (*Unio pictorum*) i skójka zaostzona (*Unio tumidus*). W Polsce, *A. cygnea* i *P. complanata*, są gatunkami zagrożonymi i chronionymi (Zajac, 2004a,b). Z kolei w Europie, *P. complanata* oceniono jako gatunek podatny na zagrożenia (ang. *Vulnerable*; Van Damme, 2011), podczas gdy pozostałe gatunki oceniono jako gatunki "mniejszej troski" (ang. *Least Concern*), chociaż trendy populacji określono jako malejące u *A. anatina* (Lopes-Lima, 2014a) i *A. cygnea* (Lopes-Lima, 2014b).

Czynniki rządzące rozmieszczeniem i liczebnością małży słodkowodnych w ekosystemach wód stojących są słabo poznane. Dotychczas wykazano, że podstawowe parametry zbiorników wodnych, takie jak głębokość wody, odległość od brzegu i wzdłuż brzegu oraz grubość warstwy osadów, mają istotny wpływ na liczebność i rozmieszczenie małży (Zajac i in., 2016). Ponadto jako czynniki wpływające na liczebność i rozmieszczenie małży wymienia się: falowanie (Cyr, 2008), sedymentację (Cyr i in., 2012), rodzaj podłoża (Kat, 1982), dostępność światła, temperaturę wody, dostępność pokarmu i prędkość przepływu wody (Dillon, 2004), napływ różnych związków egzogennych (Richardson i Mackay, 1991), zawartość tlenu (Zajac, 2002), obecność związków toksycznych (Wetzel, 2001) i poziom wody (Dillon, 2004; Gołąb i in., 2010). Mimo, że problem nie został jeszcze wyjaśniony, istnieje coraz więcej dowodów na to, że warunki hydrauliczne odgrywają znaczącą rolę w kształtowaniu siedlisk małży Unionidae. Wiele badań wykazało, że warunki hydrauliczne w pobliżu dna są dobrymi predyktorami odpowiednich mikrosiedlisk dla małży (Statzner i in., 1988; Layzer i Madison, 1995; Lydeard i in., 2008) lub wykazało istotny wpływ ekstremalnych

warunków hydraulicznych np. wysokie i niskie przepływy w trakcie powodzi bądź suszy (Zigler i in., 2008; Allen i Vaughn, 2010; Daraio i in., 2010). Wiadomo również, że małże słodkowodne są szczególnie wrażliwe na zmiany warunków hydrologicznych, które mają szczególne znaczenie w tworzeniu zbiorowisk małży (Strayer i in., 2004; Allen i Vaughn, 2010). Badania te prowadzono jednak w dużych rzekach. Małe, stojące zbiorniki wodne wydają się być zaniebawane, podczas gdy to właśnie starorzecza były typowym miejscem występowania Unionidów w warunkach naturalnej doliny rzecznej (Zajac, 2002), jednak ze względu na brak tego siedliska w krajach rozwiniętych jest ono pomijane w badaniach.

Wśród najważniejszych zagrożeń dla bioróżnorodności ekosystemów słodkowodnych wymienia się: utratę, fragmentację i degradację siedlisk, nadmierną eksploatację populacji, zanieczyszczenie wód, wprowadzanie gatunków obcych i zmiany klimatu (Dudgeon i in., 2006; Geist, 2011). Europejskie małże słodkowodne są podatne na wszystkie te zagrożenia (Lopes-Lima i in., 2017). Jednak inne, nieznanne dotychczas czynniki mogą również odgrywać znaczącą rolę w procesie zanikania populacji małży słodkowodnych. Jednym z dość spektakularnych zjawisk mających bardzo negatywne konsekwencje dla małży są ich masowe śnięcia (ang. *massive die-offs*). Są to epizodyczne zdarzenia, w trakcie których setki, a nawet tysiące małży umiera w krótkim czasie (kilku dni lub tygodni), które w naturze związane są najczęściej z dynamiką populacji tej grupy zwierząt. Jednak częstość występowania masowych śnięć małży wzrasta od 1982 roku i obecnie znacząco przekracza naturalny poziom częstości występowania takich śnięć (Neves, 1987). Etiologia masowych śnięć pozostaje w dużej mierze nieznaną, i podejrzewa się tylko niewielką liczbę czynników o powodowanie tego zjawiska, np. choroby (Neves, 1987), zatrucia (Fleming i in., 1995), powódzie (Hastie i in., 2001; Sousa i in., 2012), susze (Gagnon i in., 2004; Haag i Warren, 2008; Galbraith i in., 2010; Bódis i in., 2014; Sousa i in., 2018) oraz gospodarka wodna (Gołąb i in., 2010). Ponadto w przypadku wielu gatunków małży, zasadniczym problemem jest brak wiedzy na temat ich biologii i wymagań siedliskowych (Lopes-Lima i in., 2018; Ferreira-Rodríguez i in., 2019).

Jednym z najważniejszych symptomów spadku liczby małży słodkowodnych na całym świecie jest brak rekrutacji (Roper i Hickey, 1994; Beasley i Roberts, 1999; Hastie i Toy, 2008). W sprzyjających warunkach Unionidae mogą osiągnąć bardzo duże liczebności i biomasę; jednak w coraz większej liczbie populacji od dziesiątków lat nie obserwowano młodych osobników, co prowadzi do starzenia się tych populacji (Payne i Miller, 1989), i w konsekwencji do ich wyginięcia. Zatem wysoka zmienność w rekrutacji w czasie lub przestrzeni oraz przeżywalności osobników młodocianych, może służyć jako wczesny sygnał ostrzegający o zbliżającej się katastrofie (Strayer, 2014).

Skójkowate (Unionidae) są rozdzielнопłciowe. Samice składają jaja do specjalnie przekształconych płatów zewnętrznych skrzeli (marsupiów), gdzie są zapładniane przez plemniki wciągane wraz ze strumieniem wody. Z zapłodnionych komórek jajowych powstają larwy (glochidia). Cykl życia skójkowatych charakteryzuje się unikalnym okresem pasożytnictwa larwalnego na rybach

żywicielskich (Fig. 2A; Kat, 1984; Haag, 2012; Modesto i in., 2018), który ma kluczowe znaczenie dla pomyślnego rozmnażania (Strayer, 2008; Brodie i in., 2014). Co więcej, cykle życiowe skójek (*Unio*) i szczeżuj (*Anodonta*) różnią się od siebie czasem składania jaj do marsupiów i uwalniania dojrzałych glochidiów z marsupiów (Fig. 2B). U szczeżuj, jaja są składane i zapładniane w drugiej połowie sezonu wegetacyjnego, glochidia są przetrzymywane w marsupiach przez okres zimowy i uwalniane jednorazowo na wiosnę kolejnego roku. Z kolei u skójek, jaja są składane, zapładniane i uwalniane raz lub kilka razy w trakcie tego samego roku (do 2 razy u *Unio pictorum* i *Unio tumidus*, Piechocki, 1999; do 7 razy u *Unio crassus*, Zajac i Zajac, 2018).

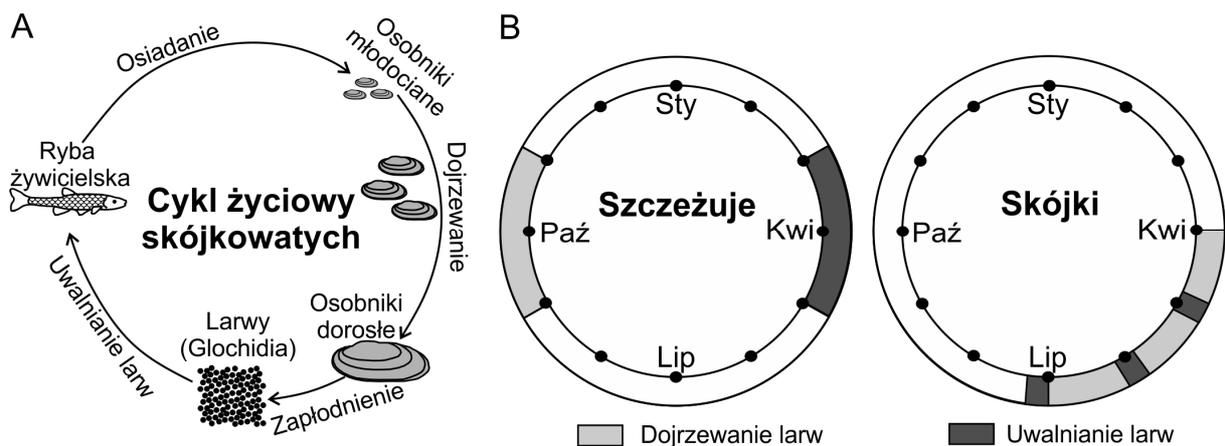


Fig. 2. Cykl życiowy mały skórkowatych Unionidae (A) oraz różnice w czasie składania i uwalniania glochidiów przez szczeżuje i skójki przy założeniu wyprowadzania przez skójki trzech lęgów w sezonie rozrodczym (B). Sty - styczeń, Kwi - kwiecień, Lip - Lipiec, Paź - Październik

Po uwolnieniu z marsupiów, glochidia muszą przyczepić się do odpowiedniego żywiciela, bez którego larwy nie mogą się dalej rozwijać i przekształcać w młode małże. Ten etap ma kluczowe znaczenie w cyklu życiowym mały, ponieważ mimo iż każda samica może uwolnić setki tysięcy glochidiów, to ponad 99,9999% glochidiów nigdy nie trafia na odpowiedniego żywiciela (Young i Williams, 1984; Jansen i Hanson, 1991) i ginie w ciągu 48 godzin. Ponadto, skuteczność zarażenia ryby żywicielskiej może zależeć od reakcji układu odpornościowego gospodarza (Reuling, 1918; Arey, 1932; Chowdhury i in., 2017), wieku i długości ciała gospodarza (Taeubert i in., 2012; Ćmiel i in., 2018) oraz szczepu gatunku ryby żywicielskiej (Taeubert i in., 2010). Co więcej, o sukcesie reprodukcyjnym mogą również decydować warunki siedliskowe panujące w trakcie sezonu rozrodczego, które często dla mały są zupełnie nieprzewidywalne (np. niszówki i wezbrania wód, brak lub pojawienie się odpowiedniego żywiciela).

Dotychczasowe badania nad małżami w Zalewie Pińczowskim (Zajac, 2002, Zajac i in., 2016) wykazały że rozmieszczenie mały w zbiorniku nie jest losowe. Osobniki wszystkich gatunków występują w strefie wzdłuż południowego brzegu jeziora, osiągając najwyższe zagęszczenia na głębokości ok. 0,5 m. Wraz z gradientem odległości wzdłuż południowego brzegu zalewu

zaobserwowano istotny statystycznie spadek liczebności u gatunków *A. anatina* i *U. pictorum*, ale nie u *A. cygnea*, którego liczebność jest stała. Wykazano także, istotną statystycznie, dodatnią korelację liczebności populacji *A. anatina*, *U. pictorum*, i *A. cygnea* z grubością warstwy osadów dennych. Uogólniony model liniowy wpływu odległości od brzegu, odległości wzdłuż brzegu, głębokości wody oraz grubości warstwy osadów na liczebność małży wykazał, że istnieje kompromis (ang. *trade-off*) pomiędzy głębokością wody i odległością od brzegu, który może być odpowiedzialny za występowanie obserwowanej optymalnej strefy występowania małży w Zalewie Pińczowskim (Zajac i in., 2016). Mimo to nadal wiele pytań pozostaje bez odpowiedzi: jak losowe i nieprzewidywalne warunki siedliskowe wpływają na liczebność populacji? Czy katastrofy oddziałują tak samo na wszystkie gatunki? Czy przepływ przez zbiornik ma wpływ na warunki życia małży występujących w zbiorniku? Odpowiedzi na te pytania przedstawia niniejsza rozprawa doktorska.

Ponieważ etap przyczepiania się glochidiów do ryby żywicielskiej jest kluczowy w cyklu reprodukcyjnym małży, w pracy (I) sprawdziłem, jak stochastyczne warunki środowiskowe panujące na tym etapie wpływają na sukces reprodukcyjny małży, w zależności od przyjętej przez nie strategii reprodukcyjnej. Skonstruowałem model matematyczny dla hipotetycznego gatunku małża, który może uwalniać glochidia od jednego do pięciu razy w trakcie sezonu reprodukcyjnego, i który napotyka zmienne i nieprzewidywalne warunki środowiskowe w trakcie każdego epizodu uwalniania glochidiów. Założyłem, że w trakcie uwalniania glochidiów mogą wystąpić warunki "złe", czyli takie które utrudniają skuteczny rozród (np. brak odpowiednich gatunków ryb żywicielskich), warunki "neutralne", które nie wpływają w żaden sposób na rozród małży, oraz warunki "dobre", które umożliwiają skuteczniejszy rozród (np. pojawienie się szczepu ryb żywicielskich, które są bardziej podatne na zarażenie glochidiami). Zamodelowałem pięć scenariuszy: (1) scenariusz "dobry", w którym prawdopodobieństwo wystąpienia dobrych warunków do rozrodu było najwyższe, (2) scenariusz "neutralny", w którym warunki dobre, neutralne i złe mają takie samo prawdopodobieństwo wystąpienia, oraz (3) trzy warianty "złego" scenariusza, w których prawdopodobieństwo wystąpienia złych warunków było wysokie, i wzrastało w kolejnych złych scenariuszach. W każdym scenariuszu modelowano sto kolejnych sezonów reprodukcyjnych, oraz wykonano tysiąc powtórzeń każdego scenariusza. Otrzymane w ten sposób dane analizowałem statystycznie, dzięki czemu mogłem sprawdzić, jaki wpływ w danym scenariuszu ma przyjęcie przez populację małży konkretnej strategii reprodukcyjnej (liczby epizodów reprodukcyjnych) na podstawowe parametry populacji: ostateczną wielkość populacji (po stu sezonach rozrodczych), tempo wzrostu populacji, współczynnik wymierania (jaki procent z tysiąca realizacji każdego scenariusza zakończył się wymarciem populacji przed upływem 100 sezonów rozrodczych), współczynnik zmienności ostatecznej wielkości populacji, oraz średni czas do wymarcia populacji.

W pracy (II) opisałem zjawisko masowego śnięcia małży, które wystąpiło w Zalewie Pińczowskim w lecie 2018 roku. Zaobserwowane zjawisko masowego śnięcia można traktować jako naturalny test skrajnych warunków (ang. *stress test*) na stabilność ekologiczną populacji małży

występujących w zbiorniku. Badania przeprowadzono dwanaście dni po pojawieniu się śniecia małży, przed rozłożeniem się ich ciał, co umożliwiło ilościowe określenie śmiertelności w czasie analizowanego epizodu u wszystkich gatunków małży występujących w Zalewie, wykazując wyraźne, istotne różnice międzygatunkowe, oraz w przypadku jednego gatunku, istotne różnice pomiędzy śmiertelnością młodych i dorosłych osobników. Badania laboratoryjne próbek wody pobranych w trakcie badań pozwoliły ustalić prawdopodobną bezpośrednią przyczynę, która wywołała śniecie małży. Dodatkowo, dla najmniej liczego gatunku w Zalewie Pińczowskim (szczęzui spłaszczonej) ocenilem prawdopodobieństwo wystąpienia efektu Allego w wyniku masowego śniecia osobników tego gatunku.

W pracy (III) opisałem wpływ zwiększenia przepływu wody w Zalewie Pińczowskim, po wybudowaniu dodatkowego kanału odprowadzającego wodę, na rekrutację młodych osobników małży. Wykazałem, że po wybudowaniu dodatkowego kanału odprowadzającego wodę z zalewu, istotnie wzrosła prędkość i turbulencja przepływu. Wykazałem, że zmiana warunków hydraulicznych miała istotny wpływ na występowanie młodych osobników (rekrutów) u trzech z pięciu gatunków małży występujących w Zalewie Pińczowskim, a dla jednego gatunku, również miała istotny wpływ na liczebność rekrutów. Wykazałem także, że po zmianie warunków hydraulicznych, zmieniły się nisze młodocianych osobników tych gatunków, ujawniając wyraźne różnice w ich wymaganiach siedliskowych (pod względem warunków hydraulicznych). Co więcej, praca ta, jako pierwsza na świecie wykazała, że tak samo jak w wodach płynących, warunki hydrauliczne mają istotny wpływ na populacje małży występujące w środowisku wód stojących.

Wnioski

Wyniki symulacji wskazują że, gdy prawdopodobieństwo wystąpienia korzystnych warunków w trakcie uwalniania glochidiów jest wysokie, najlepszą strategią reprodukcyjną jest uwolnienie wszystkich glochidiów w postaci dużego, pojedynczego łęgu. W przypadku gdy prawdopodobieństwo wystąpienia korzystnych, neutralnych i niekorzystnych warunków w trakcie uwalniania glochidiów jest takie samo, wszystkie strategie reprodukcyjne są równie dobre. Natomiast, gdy prawdopodobieństwo wystąpienia niekorzystnych warunków w trakcie uwalniania glochidiów jest najwyższe, strategia uwalniania glochidiów "na raz" jest najgorszą strategią reprodukcyjną, a im wyższe jest prawdopodobieństwo wystąpienia niekorzystnych warunków, tym lepszą strategią reprodukcyjną jest uwalnianie glochidiów w postaci wielu, mniejszych łęgów (artykuł I).

Gatunki stosujące strategię pojedynczego, dużego łęgu (np. szczeżuje), w dobrych siedliskach, powinny osiągać większą liczebność niż gatunki stosujące strategię wielu mniejszych łęgów (np. skójki). Z kolei w gorszych, mniej przewidywalnych siedliskach, to gatunki stosujące strategię wielu mniejszych łęgów (np. skójki) powinny osiągać większą liczebność niż gatunki stosujące strategię pojedynczego, dużego łęgu (np. szczeżuje; artykuł I).

Praktyczne działania ochronne (np. restytucja gatunków), powinny być łatwiejsze i mniej czasochłonne do przeprowadzenia w przypadku gatunków małży stosujących strategię pojedynczego, dużego łęgu, niż w przypadku gatunków stosujących strategię wielu mniejszych łęgów (artykuł I).

Strategia większej liczby łęgów w trakcie sezonu reprodukcyjnego, niezależnie od warunków środowiskowych panujących w trakcie uwalniania glochidiów, charakteryzuje się mniejszą zmiennością liczebności populacji, niż strategia dużego pojedynczego łęgu (artykuł I).

Dla gatunków, które mogą uwalniać glochidia więcej niż raz w trakcie sezonu reprodukcyjnego, najkorzystniejsza jest strategia dwóch łęgów w sezonie rozrodczym (artykuł I).

Najbardziej prawdopodobną przyczyną masowego śnięcia małży w Zalewie Pińczowskim w 2018 roku było uwolnienie ogromnej ilości związków fosforu zdeponowanych w osadach dennych, do którego przyczyniło się pływanie po zalewie łodzią motorową wyposażoną w silnik o zbyt dużej mocy (artykuł II).

Istotne różnice w śmiertelności pomiędzy gatunkami małży występującymi w zalewie świadczą o istotnych różnicach w tolerancji tych gatunków na zaburzenia siedliska, takie jak gwałtowny wzrost stężenia związków fosforu, wzrost mętności wody (artykuł II).

Najbardziej wrażliwym na zaburzenia siedliska okazała się szczeżuja spłaszczona (*Pseudanodonta complanata*). Wysoka wrażliwość tego gatunku na stres środowiskowy sugeruje, że szczeżuja spłaszczona może być uznana za gatunek parasolowy w ochronie współistniejących gatunków małży i naturalnie eutroficznych zbiorników wodnych (siedliska z Dyrektywy Siedliskowej, kod 3150; artykuł II)

Mimo, że dorosłe osobniki szczeżui wielkiej (*Anodonta cygnea*) wykazały wyższą tolerancję na stres środowiskowy niż osobniki młodociane, to kolejne zaburzenia siedliska, prowadzące do masowych śnięć, mogą wypaczyć strukturę wiekową populacji i w dłuższej perspektywie prowadzić do jej starzenia się i wymarcia (artykuł II).

Zaburzenia siedlisk i masowe śnięcia (takie jak to zaobserwowane w Zalewie Pińczowskim), w przypadku małych populacji małży, mogą prowadzić do wystąpienia efektu Allego (artykuł II).

Zwiększenie przepływu przez Zalew Pińczowski po wybudowaniu nowego kanału odprowadzającego wodę, korzystnie wpłynęło na proces rekrutacji u trzech z pięciu gatunków małży występujących w zalewie (*A. cygnea*, *U. pictorum*, *U. tumidus*). Dla pozostałych gatunków (*A. anatina*, *P. complanata*) nowy kanał odprowadzający nie wpłynął istotnie na rekrutację (artykuł III).

Zwiększenie przepływu wody przez zalew istotnie wpłynęło na występowanie młodych osobników *A. cygnea*, *U. pictorum* i *U. tumidus*, ale jedynie w przypadku osobników młodocianych *A. cygnea* istotnie wpłynęło również na ich liczebność. Może to świadczyć, o tym że: (1) pomimo poprawy warunków rekrutacji dla młodych skójek (*U. pictorum* i *U. tumidus*), to nadal nie są to warunki optymalne dla tych gatunków lub (2) istnieje inny, niezbadany czynnik ograniczający ich liczebność.

Przed budową nowego kanału, młode osobniki *A. cygnea*, *U. pictorum* i *U. tumidus* zajmowały bardzo podobne nisze. Zwiększenie przepływu ujawniło wyraźne różnice w wymaganiach hydrologicznych pomiędzy młodymi osobnikami szczeżui wielkiej (*A. cygnea*) a skójkami (*U. pictorum* i *U. tumidus*). Młode osobniki *A. cygnea* preferują miejsca o większej prędkości przepływu i bardziej laminarnym przepływie niż młode skójki (artykuł III).

Warto również podkreślić, że artykuł (III) jest pierwszą tego typu pracą na świecie, która wykazała, że podobnie jak w środowisku wód płynących, warunki hydrauliczne mają istotny wpływ na populacje małży występujących w wodach stojących.

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Artykuł I



Single or multiple spawning? Comparison of breeding strategies of freshwater *Unionidae* mussels under stochastic environmental conditions

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Abstract The life cycle of unionids is characterized by a obligatory period of larval parasitism on a fish host, any disturbance of which might cause a large-scale decline in the mussel population. Because the probability of fish infestation is so important, we modelled what would happen to a population (in terms of population growth and probability of extinction), if the same number of glochidia were released in one or more separate spawning events, by a hypothetical mussel population living in conditions differing in the probability of fish infestation (a “neutral” scenario, a “good” one and three variants of a “bad” one). The single brood strategy was the best in the “good” scenario. However, when the frequency of unfavourable stochastic events increased (“bad” scenarios), all strategies led to population decline, the single brood strategy being the worst. In “good” and moderately

“bad” conditions the double brood strategy performed better than the other multiple brood strategies, but as infestation conditions deteriorated, a greater number of spawning events ensured a slower population decline and longer persistence. Our model can facilitate a better understanding of this problem and set up a framework for further tests in other unionid species and their environmental conditions.

Keywords Extinction · Growth rate · Habitat stochasticity · Modelling · Population size · Population dynamics

Introduction

Important components of aquatic ecosystems (Vaughn & Hakenkamp, 2001; Gutiérrez et al., 2003), freshwater mussels (Unionida) are among the most threatened animal groups on the planet (Lopes-Lima et al., 2017; 2018). The life cycle of unionids is characterized by a unique obligatory period of larval parasitism on a fish host (Kat, 1984; Haag, 2012; Modesto et al., 2018), which is critical for successful reproduction (Strayer, 2008; Brodie et al., 2014); this aspect of their biology remains poorly studied (Ferreira-Rodríguez et al., 2019). The first question that comes to mind is whether the enormous numbers of larvae produced by mussels (from 2,000 to more than 10,000,000 glochidia; Bauer, 1987; Haag, 2013) are released

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during one event or over longer periods. In the former case, a hypothetical mussel significantly increases the density of larvae in the water and, all other things being equal, the probability of infestation will increase. In the latter case, although the multiplication of breeding events reduces the density of larvae released at a given moment, it spreads the risk of complete breeding failure caused by environmental stochasticity (Goodman, 1984). Continuous release is unlikely, because the density of the larvae would then be extremely low.

Most unionid species are reported to produce only a single brood per year, although the production of multiple broods has been described in North America for the genera *Utterbackia*, *Glebula*, *Popenaias* (Haag, 2012 and citations within) and *Elliptio* (one to three broods; Price & Eads, 2011; one to five broods in *Elliptio steinstansana*; Haag, 2012). In Europe, multiple broods has been described for *Unio crassus* (up to five broods; Hochwald, 2001; up to seven broods; Zajac & Zajac, 2018), *U. pictorum* and *U. tumidus* (up to two broods in both species; Piechocki, 1999).

In this study we present a model of a hypothetical unionid species differing in its glochidia-releasing strategies, which faces stochastic variation in the likelihood of fish host presence/infestation. On the basis of this model, we simulated 100 consecutive breeding seasons of this hypothetical mussel population, capable of generating from one to five broods in each season, in unpredictable environmental conditions (affecting infestation probability). This study aims to evaluate how the number of spawning events affects population parameters important from the point of view of population persistence, i.e. its size, extinction rate, coefficient of variation of mean population size and the mean time to extinction in an environment varying in the probability of an event disturbing mussel reproduction.

Methods

Model description

We constructed a population model based on data relating to *Anodonta cygnea*, collected by Zajac (2001) in Lake Zalew Pińczowski, Poland (for a

detailed description of the study area, see Zajac et al., 2016).

Let us suppose that the modelled mussel population consists of $I \in \mathbf{Z}^+$ age classes. Let g be the proportion of glochidia which successfully attach to the host fish, r the glochidial survival rate to the end of the first year, s_i the survival rate of individuals at age i , $A_{i,j}$ the number of individuals at age i during season j and $F_{i,j}$ the number of females at age i during season j . The number of glochidia G_i released by each female in age class i is given by the equation

$$G_i = ae^{bi} \quad (1)$$

where a and b are fixed parameters.

The number of recruits R_j by the end of season j is given by

$$R_j = \sum_{i=1}^{i=I} F_{i,j} G_i g r \quad (2)$$

The number of adult individuals N_j by the end of season j is given by

$$N_j = R_{j-1} + \sum_{i=1}^{i=I} A_{i,j-1} s_i \quad (3)$$

The model's validation and parameterization are given in the Supplementary Materials.

Single versus multiple brood strategy simulations

Let us assume that S spawning events take place during season j , where $S \in \{1, 2, \dots, 5\}$. Let us further assume that during each season, one of three events influencing the proportion of glochidia attached to the host fish (g) occurs during the whole season: (1) a "neutral" one, when the disturbing event does not affect the mussels' breeding; (2) a "good" one, when the disturbing event increases the proportion of attached glochidia (e.g. river not in spate) and (3) a "bad" one, when the disturbing event decreases the proportion of attached glochidia (e.g. river in spate, suitable host fish individuals absent). Let us also assume that n spawning events are disturbed in a given season, where $n \leq S$. Thus, (1) in the case of a "neutral" event, g is set at its default value, (2) in the case of a "good" event, g is multiplied by $1 + \frac{n}{S}$ (e.g. if 2 of 5 spawning events are affected by a "good" event, g is multiplied by 1.4), or (3) in the case of a bad event,

g is multiplied by $\frac{S-n}{S}$ (e.g. if 2 of 5 spawning events are affected by a “bad” event, g is multiplied by 0.6).

Let P_b , P_n and P_g be the respective probabilities of occurrence of a “bad”, “neutral” and “good” event during season j . We simulated a total of five scenarios: (1) a “neutral” scenario, where $P_b = 1/3$, $P_n = 1/3$, $P_g = 1/3$; (2) a “good” scenario, where $P_b = 1/4$, $P_n = 1/4$, $P_g = 1/2$ and three alternative “bad” scenarios: (3a), where $P_b = 1/2$, $P_n = 1/4$, $P_g = 1/4$; (3b), where $P_b = 3/5$, $P_n = 1/5$, $P_g = 1/5$ and (3c), where $P_b = 2/3$, $P_n = 1/6$, $P_g = 1/6$. Simulations were run for 100 consecutive seasons. In each scenario, we modelled five strategies differing in the number of spawning events: the Single Brood Strategy (SBS, 1 spawning event during each season) and four variants of the Multiple Broods Strategy (MBS, from 2 to 5 spawning events during each season). Both events influencing glochidial attachment and the number of spawning events affected by the stochastic event are randomly selected at the beginning of each simulated season. We obtained 1000 realizations of each scenario for each modelled strategy. Below, we present an example of the random selection of an event influencing glochidial infestation and the number of spawning events affected.

To show up the differences between strategies, we compared the final population size (at $t = 100$) for each strategy in each scenario. Also, for each strategy in each scenario, we obtained the extinction rate (E_t)—the percentage of simulation realizations resulting in the extinction of the modelled population, the mean annual growth rate of the population (λ) and the mean time to extinction (E_t), calculated using only realizations resulting in the extinction of the modelled population. We used coefficients of variation of mean population size (CV) to compare the relative variability in the number of individuals between strategies in each scenario.

Example

We exemplify the method of randomly selecting an event influencing glochidial infestation and the number of spawning events affected by the event using the MBS strategy with five spawning events in a “bad” scenario (3c). Since in this scenario $P_b = 2/3$, $P_n = 1/6$, $P_g = 1/6$ and the number of spawning events n equals 5, at the beginning of each season we randomly

draw two numbers x (which will determine the stochastic event) and y (which will determine the number of affected spawning events), where $x \in \{1, 2, \dots, 6\}$ and $y \in \{1, 2, \dots, 5\}$. The selection of a stochastic event occurring during the season is based on the value of x . If $x \leq 4$, then a “bad” event occurs, if $x = 5$, then a “neutral” event occurs and if $x = 6$, then a “good” event occurs. Let us assume that in 3 consecutive draws the randomly selected values are $x_1 = 3$, $y_1 = 4$, $x_2 = 1$, $y_2 = 5$ and $x_3 = 6$, $y_3 = 2$. This means that during the first simulated season a “bad” event occurred, which affected 4 spawning events, during the second season a “bad” event also occurred, affecting all five spawning events, while during the third season, a “good” event occurred, which affected 2 spawning events.

Statistical analysis

The statistical analyses were conducted using Statistica 13. Because the assumption of homogeneity of variance was not fulfilled, the differences in final population size, as well as the differences in mean annual population growth rates and the differences in the mean time to extinction between the simulated strategies in each scenario were tested using the Kruskal–Wallis test. We tested the differences between extinction rates using the test between proportions. We tested the influence of the probability of occurrence of a “bad” event and the number of spawning events on the extinction rate (logit transformed) using a General Linear Model (dependent variable: extinction rate (transformed); continuous predictor: probability of a “bad” event occurring; ordinal predictor: number of spawning events).

Results

Single versus multiple broods strategy simulations

“Neutral” scenario

After a period of initial fluctuations, all the strategies followed a similar trajectory until 60 seasons, when outcomes of the strategies began to differ from each other to a modest extent. The differences in final population size between the strategies were significant (Table 1; Fig. 1A; Kruskal–Wallis test; $H = 28.1$;

Table 1 Basic parameters of populations adopting different breeding strategies in the simulated scenarios: (1) “neutral” scenario, (2) “good” scenario, (3) “bad” scenario

Scenario	Number of spawning events (strategy)	$N_{t=100}$	$SD_{N_{t=100}}$	λ	CV	E_r	E_t
“Neutral” (1)	1 (SBS)	710.8	889.8	0.06	81.5	0	–
	2 (MBS)	716.2	683.7	0.07	67.7	0	–
	3 (MBS)	662.9	601.1	– 0.01	67.9	0	–
	4 (MBS)	750.9	749.7	0.12	64.7	0	–
	5 (MBS)	747.4	839.0	0.11	69.4	0	–
“Good” (2)	1 (SBS)	42821.0	38727.1	4.3	160.6	0	–
	2 (MBS)	26097.9	21703.6	3.7	142.6	0	–
	3 (MBS)	7529.4	8164.2	2.5	127.5	0	–
	4 (MBS)	12018.1	10218.8	2.9	120.9	0	–
	5 (MBS)	10027.9	8314.3	2.7	117.4	0	–
“Bad” (3a)	1 (SBS)	3.0	7.2	– 5.3	152.0	51.4	77
	2 (MBS)	118.4	201.3	– 1.7	88.8	0.2	85
	3 (MBS)	77.9	107.9	– 2.1	87.8	0.5	95
	4 (MBS)	71.4	83.8	– 2.2	88.2	0.1	96
	5 (MBS)	64.3	75.5	– 2.3	88.0	0.2	91
“Bad” (3b)	1 (SBS)	0.03	0.3	– 9.4	208.1	98.4	59
	2 (MBS)	7.7	14.2	– 4.4	133.9	26.9	85
	3 (MBS)	7.9	11.9	– 4.3	129.6	20.4	88
	4 (MBS)	9.4	15.7	– 4.2	126.1	18.2	89
	5 (MBS)	11.1	20.4	– 4.0	122.2	13.4	89
“Bad” (3c)	1 (SBS)	0.0	0.0	– 13.3	240.8	100	43
	2 (MBS)	1.1	3.8	– 6.2	164.6	74	78
	3 (MBS)	1.4	3.3	– 6.0	155.9	67.5	82
	4 (MBS)	2.0	4.0	– 5.7	149.2	55	84
	5 (MBS)	2.6	4.9	– 5.4	145.0	48.5	86

$N_{t=100}$ mean final population size after 100 seasons (at $t = 100$), $SD_{N_{t=100}}$ standard deviation of mean final population size, λ mean annual population growth rate (expressed as a percentage), CV coefficient of variation of mean population size, E_r extinction rate (the percentage of realizations of simulations which resulted in the extinction of the population), E_t mean time to extinction (in seasons) calculated for the realizations of simulations which resulted in the extinction of the population

$P < 0.0001$), whereas the differences in the mean annual population growth rates between the strategies were not significant (Table 1; Fig. 2A; Kruskal–Wallis test; $H = 2.49$; $P = 0.65$). The coefficients of variation were higher in SBS than in MBS (Table 1). None of the realizations of this scenario resulted in the extinction of the modelled population (Table 1), and it was clear that, in the absence of extremely rare coincidences, the population would almost certainly not decrease or become extinct.

“Good” scenario

In a good environment all the strategies differed distinctly from one another (Fig. 1B). The differences in final population size were significant (Table 1; Fig. 1B; Kruskal–Wallis test; $H = 1895.0$; $P < 0.0001$). The final result of the simulations was inversely proportional to the number of broods: the fewer the broods, the larger the final population size (Fig. 1B). A similar pattern was found in the mean annual population growth rate and the coefficient of variation. The differences in mean annual population growth rates between strategies were significant

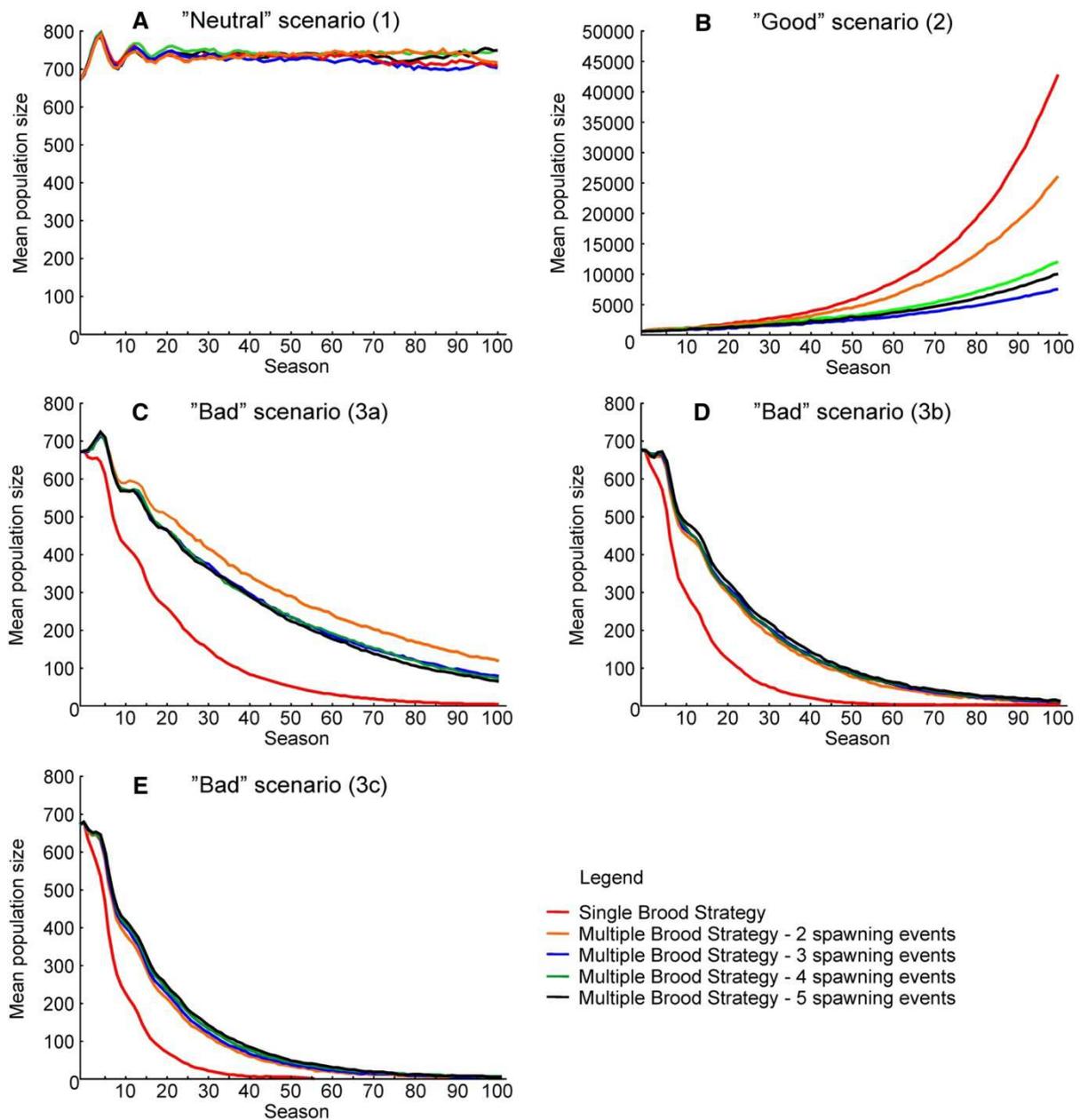


Fig. 1 Effects of breeding strategy on population size over 100 simulated seasons for the "neutral" scenario (**A**), the "good" scenario (**B**) and the 3 variants of the "bad" scenario (**C–E**)

(Table 1; Fig. 2A; Kruskal–Wallis test; $H = 190.3$; $P < 0.0001$). The coefficient of variation was the highest in SBS and the lowest in MBS(5), although the difference was small (Table 1). However, even small differences in population growth rate translated into large differences in population size over 100 seasons (Fig. 1B). None of the realizations of this scenario

resulted in the extinction of the modelled population (Table 1), and it was clear that, in the absence of extremely rare coincidences, the population would almost certainly not decrease or become extinct.

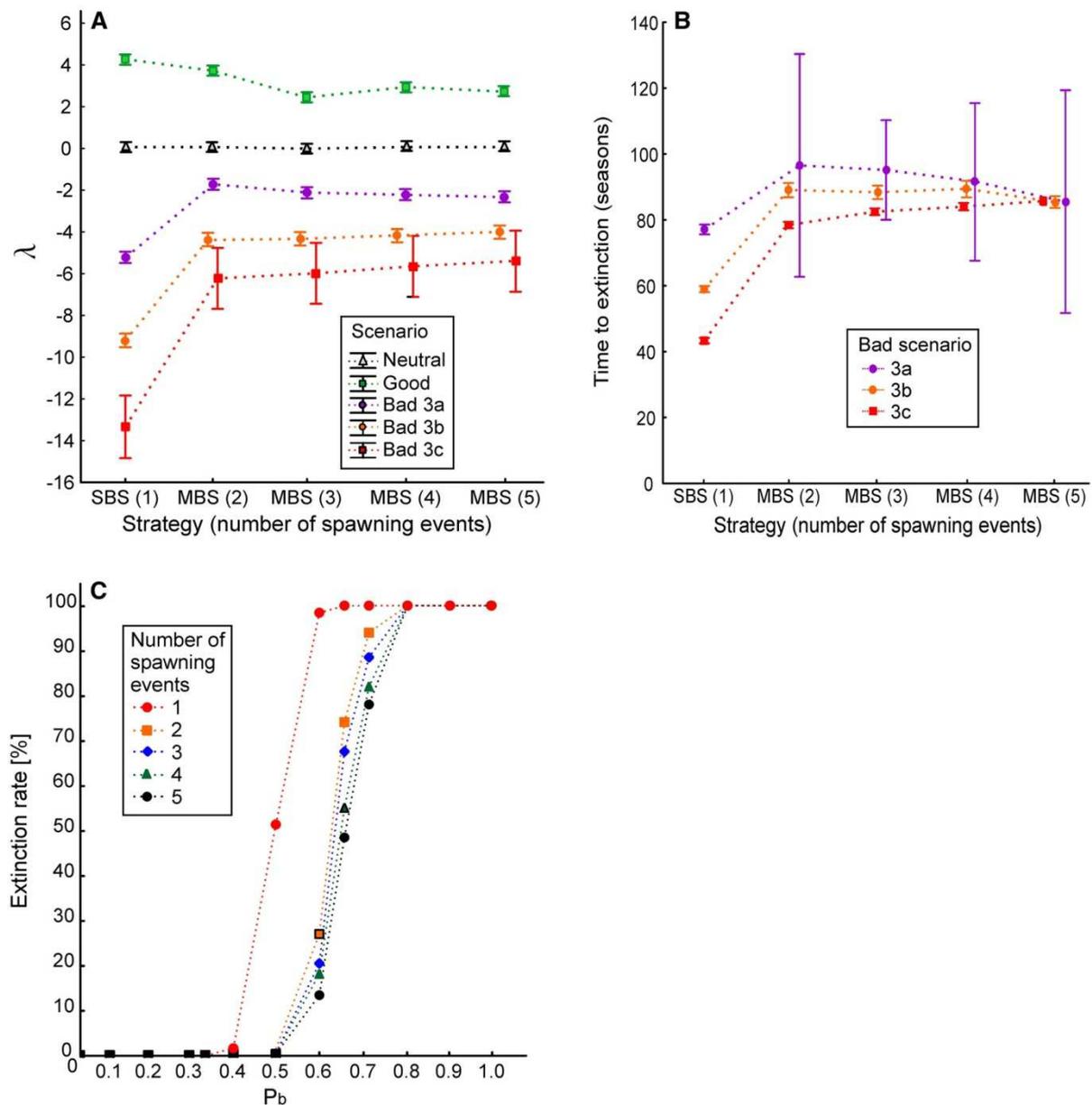


Fig. 2 **A** Differences in mean annual population growth rates (λ) between strategies in the modelled scenarios. **B** Differences in extinction time of a population between strategies in the modelled “bad” scenarios. **C** Relationship between the

probability of a “bad” event (catastrophic reproductive failure) P_b , the number of spawning events during the season and the extinction rate of the population

“Bad” scenarios

In the “bad” scenarios, all the populations declined; nevertheless, the population adopting any variant of MBS reached a much larger population size than the population adopting SBS. SBS decreased the fastest, whereas MBS decreased at a much slower rate

(Fig. 1CDE). An interesting aspect of the bad scenario 3a was that strategy MBS(2) decreased more slowly than all the other MBS variants; in scenarios 3b and 3c, the differences between them disappeared. In all the bad scenarios and in all strategies, the population size decreased more rapidly with increasing probability of bad events (the slowest in 3a, accelerating in 3b and

faster still in 3c). The differences in final population size between strategies were significant in all the modelled scenarios (Table 1; Fig. 1CDE; 3a: Kruskal–Wallis test; $H = 2177.2$, $P < 0.0001$; 3b: Kruskal–Wallis test; $H = 1661.2$, $P < 0.0001$; 3c: Kruskal–Wallis test; $H = 741.3$, $P < 0.0001$).

The differences in mean annual population growth rates between strategies were significant in all the modelled scenarios (Table 1; Fig. 2A; 3a: Kruskal–Wallis test; $H = 203.5$, $P < 0.0001$; 3b: Kruskal–Wallis test; $H = 201.4$, $P < 0.0001$; 3c: Kruskal–Wallis test; $H = 186.1$, $P < 0.0001$). In all the bad scenarios, the biggest difference in population growth rate was found between SBS and MBS(2), where SBS declined more rapidly than MBS(2) (Figs. 1CDE, 2A). Nonetheless, it is worth noting that: (1) the mean annual growth rate did not change much along with the increasing number of broods, (2) strategies MBS(3–5) became slightly worse than MBS(2) in scenario 3a; they did not change in scenario 3b, but increased in scenario 3c together with the number of broods, where MBS(2) lost its predominance and MBS(5) became the best. Even so, these changes were minimal in comparison to the change from SBS to MBS(2).

The differences in the mean time to extinction between strategies were significant in each modelled scenario (Table 1; Fig. 2B; 3a: Kruskal–Wallis test; $H = 12.4$, $P = 0.015$; 3b: Kruskal–Wallis test; $H = 931.9$, $P < 0.0001$; 3c: Kruskal–Wallis test; $H = 1943.3$, $P < 0.0001$). MBS clearly extended the mean time to extinction compared to SBS (from 8 seasons in scenario 3a to 35 seasons in scenario 3c; Table 1).

Coefficients of variation were higher in SBS compared to MBS (Table 1). Also, the extinction rate was significantly higher in SBS than in any variant of MBS in every simulated bad scenario (Table 1; test between proportions; 3a: $P < 0.0001$; 3b: $P < 0.0001$; 3c: $P < 0.0001$).

The extinction rate depended on the probability of occurrence of a “bad” event. If P_b took a value < 0.3 , then $E_r = 0$ in each strategy in each scenario; but if $P_b > 0.8$, then $E_r = 1$ in each strategy in each scenario (Fig. 2C). GLM analysis performed for values of P_b ranging from 0.3 to 0.8 showed that both the number of spawning events (N_{Se}) and the probability of a “bad” event (P_b) had a significant influence on the extinction rate (Fig. 2C; GLM; P_b , $F = 181.9$, $P < 0.0001$; N_{Se} , $F = 13.9$, $P = 0.0009$). The greater the probability of a

“bad” event occurring, the higher the extinction rate, but the more spawning events during the season, the lower the extinction rate (GLM; P_b , $\beta = 0.90$; N_{Se} , $\beta = -0.25$).

Discussion

The natural way of developing a theory is to validate it on the basis of falsifiable predictions, which either confirm the model or suggest that it should be rejected or modified. One can predict that, other things being equal, species adopting SBS should perform much better in good conditions than any of the other strategies; MBS2 is second-best. However, SBS and MBS(2) should also disappear much faster than MBS(3–5) in a “bad” environment. It turns out that in practical conservation actions, it should be easier and faster to restore SBS species, whereas the restoration of MBS species may be slower.

In general, species living in “bad” environmental conditions (in terms of host fish infestation) should be characterized by MBS, whereas species living in “good” conditions should adopt SBS. Nonetheless, since MBS guarantees a less variable population size, the two-brood strategy should be the most effective trade-off between SBS and MBS, and this number of broods should be the most common among species that are capable of producing more than one brood (e.g. *Utterbackia*, *Glebula*, *Popenaias*, *Elliptio*, *Unio*). Some problems in testing the predictions of this model may be related to the boundaries between SBS and MBS, which do not have to be clear-cut. Species can exhibit a more “mixed” strategy than those assumed in this model, like investing more in one spawning event, or saving some energy for later, smaller broods.

By having the capacity to generate from one to seven broods, it seems that *Unio* species may be a good object for studying the factors regulating the occurrence of MBS. A real practical problem arising when we wish to confirm these predictions may derive from the fact that SBSvsMBS strategies are poorly understood in freshwater mussels, because we know hardly anything about their reproductive effort. Hochwald (2001) points out that because temperature affects the mussels’ metabolism, and hence, also their body growth constant and life span, it is quite likely that the number of spawning repetitions is a trait that varies passively in response to environmental factors

(e.g. food, temperature). Also, Haag (2012) suggests that glochidial production is determined mainly by physical and energetic constraints. The possibility of multiple clutches in *Unionidae* mussels is still a matter of discussion. Haag & Staton (2003) suggest that there is no evidence of multiple clutches in *Unionidae*. On the other hand, Piechocki (1999) and Hochwald (2001) show that *Unio* species have the ability to produce up to 5 broods per year, whereas Zajac & Zajac (2018) report 5 broods in *U. crassus* per season in the River San and up to as many as 7 broods per season in the River Biała. Other researchers suggest that multiple peaks in the numbers of glochidia released are attributable to variations in physical conditions stimulating glochidia release events rather than the production of multiple broods (Bruenderman & Neves, 1993; Hove & Neves, 1994) and that only a small percentage of the reproductive complement is released during such events (Haag & Warren, 2000).

One important question that remains to be answered is why an organism should not breed as often as resources allow? We agree that it should, but the consequences will be the same as in the case of some genetically fixed strategies. If the mussel under consideration were an “income breeder” (sensu Stearns, 1992), having no large energy reserves and only accumulating everyday low level energy income during short periods of time to produce many but small broods, the situation of this species would be similar to that of an MBS species. In contrast, a “capital breeder”, having stored energy, e.g. from the previous season, would be able to invest it all in one big spawning event, achieving a high density of larvae and a high infestation rate. The capital breeder would be much more effective in good conditions, but in the face of unpredictable infestation opportunities, the income breeder (analogous to MBS) would perform better, not only because it was better adapted to poorer feeding conditions, but because it could deal better with unpredictable infestation by spreading the risk of failure over a longer period of time.

In this study we present a general mathematical framework of the consequences of adopting a certain reproductive strategy under stochastic environmental conditions. However, we are aware that life history traits in *Unionidae* are highly variable within and among species, and our model must be parameterized and corroborated/falsified using real data. In addition, we have assumed that brood size is the same in each

spawning event in MBS, and that negative population trends in MBS may be compensated for by the increased number of broods (e.g. the mean number of spawning events in *U. crassus* in the River Biała is three, but the maximum can reach as many as seven per season; Zajac & Zajac, 2018). Nevertheless, the total reproductive effort in all strategies in the model must be assumed equal; otherwise, MBS would always result in greater population growth owing to increased reproductive output.

Very little or nothing is known about energy allocation in reproduction and related trade-offs (number vs size of the offspring, parent growth vs reproduction, etc.). Also, we were unable to assess the relative costs (energetic or otherwise) of single versus multiple brood production. Thus, since we lack the required information to make the model more realistic and informative, we were forced to keep it simple. Even so, the results obtained with our model, which formulates the problem explicitly, identifies knowledge gaps and addresses some hitherto unidentified questions, shows that MBS multiple brooding seems to be marginally better in consistently bad conditions, when a population is heading towards extinction. Is this negative trend compensated for by a larger total annual glochidial output in MBS compared to SBS? If so, is reproduction based on stored reserves (allowing for SBS) or current income (forcing MBS)? What is the actual level of environmentally induced variation of infestation success and what level of it would give MBS an advantage over SBS? Field studies answering these questions, though highly desirable (Ferreira-Rodríguez et al., 2019), appear very difficult to carry out. The derivation of explicit mathematical models, validated using field data, can at least clarify the interplay of factors influencing the demography of freshwater mussels, in consequence leading to a better formulation of the problems to be solved and a better understanding of the mussels' ecology.

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Supplementary materials

Model calibration and testing

The model was calibrated using the data collected by Zajac (2001) in Lake Zalew Pińczowski (for a detailed description of the study area, see Zajac et al., 2016). The model was programmed in SciLab 6.0. The number of age classes was set at 10, the initial number of individuals at 673. The age structure of the population in the starting season and the mortality in the age classes are illustrated in figures S1A,B. The relationship between the age of a female and the number of glochidia released is shown in figure S1C. Parameters a and b (eqn 1) were estimated using nonlinear estimation in Statistica 13 and were set at $a=1748.8572$ and $b=0.4046$. The proportion of glochidia which successfully attach to the host fish (g) was set at 0.0001 (0.01%), and the rate of glochidia which survive to the end of their 1st year was set at 0.1. The simulation was run for 100 consecutive seasons.

The results of the deterministic simulation for 100 years showed a fading oscillatory pattern, repeated over 10-season periods, with an increasing population during the first 5 seasons (and a local maximum in the 5th season) and a decreasing population during the next 5 seasons (fig. S1D). This corresponded to the assumed 10-year life span of individuals. The local maximum in the 5th season of the 10-season period was a result of the assumed initial age structure of the modelled population (fig. S1A). The most numerous age class at time $t=0$ (age 4) reached age 10 and, in consequence, the maximum assumed reproductive output at time $t=5$ (fig. S1D). The assumed 100% mortality of individuals at age 10 (fig. S1B) resulted in a decrease in the number of individuals. The fading oscillations were the result of the fixing of the population age structure in the following years (figs. S1E,F,G) caused by the assumed mortality rate, which in consequence caused the number of individuals to stabilize at a value of 745 at time $t=67$ (fig. S1D). The mean number of individuals in the modelled population was 739.83 (SD=12.81; median=741; minimum number of individuals 673; maximum number of individuals 788; fig. S1C).

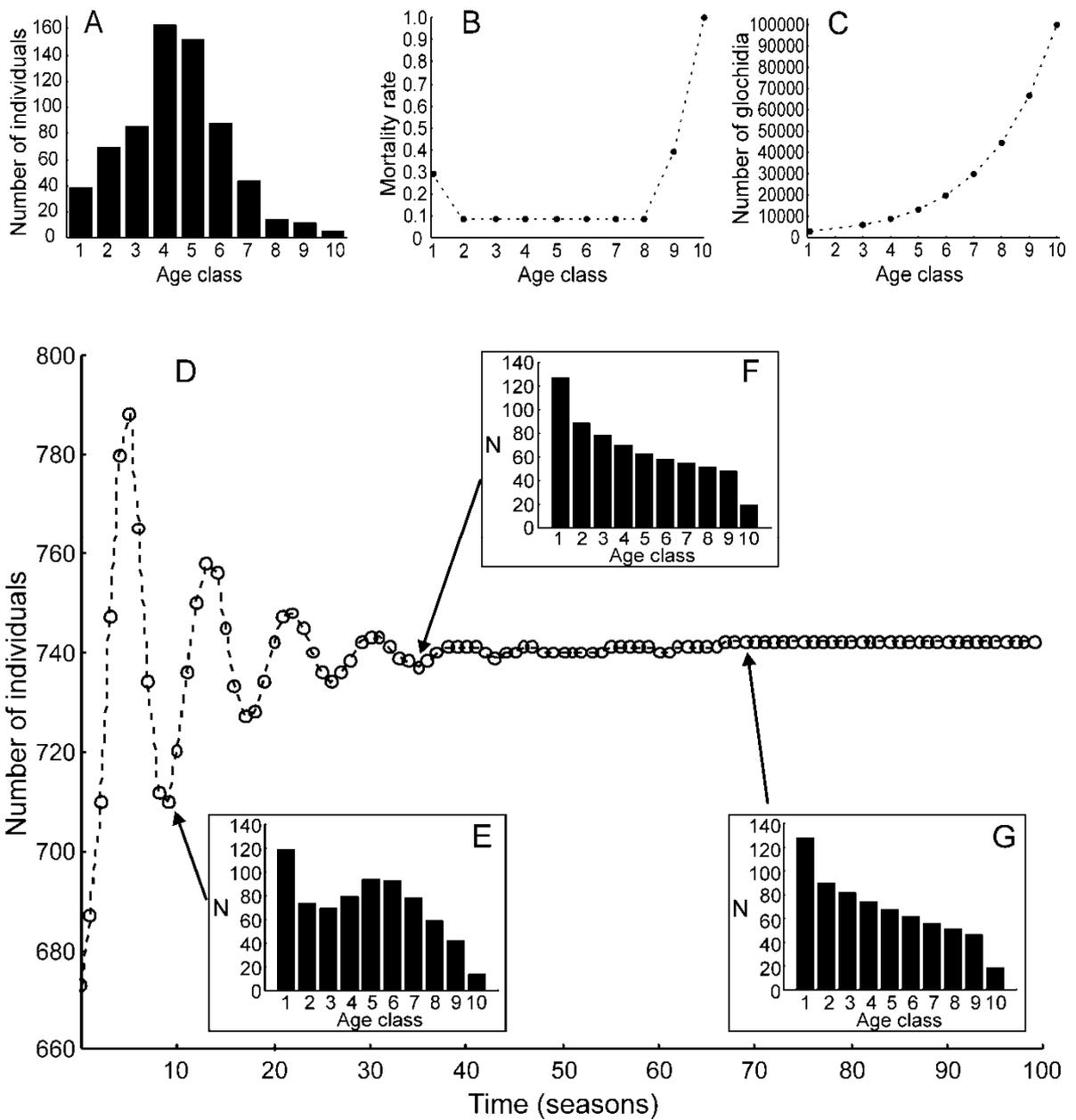


Fig. S1 Starting values, based on field data, and the results of a deterministic simulation to test and calibrate the model: (A) initial age structure of the population (673 individuals in 10 age classes), (B) mortality rate in age classes, (C) the relation between female age and the number of glochidia released, (D) result of model validation, (E) age structure of the population at time $t=10$, (F) age structure of the population at time $t=40$, (G) age structure of the population at time $t=70$.

Artykuł II

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Artykuł III



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Response of freshwater mussel recruitment to hydrological changes in a eutrophic floodplain lake

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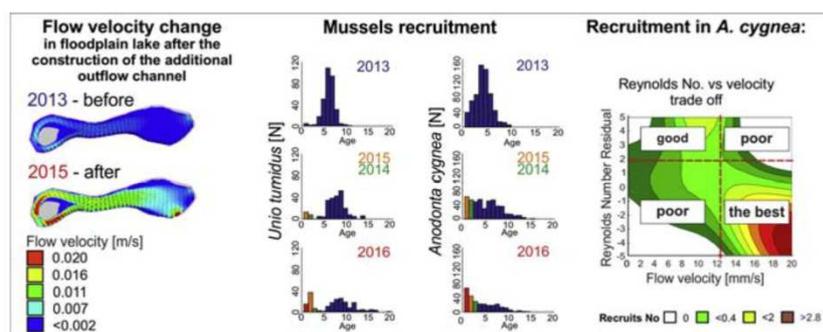
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HIGHLIGHTS

- Additional outflow channel was constructed to reduce the retention time and halt the degradation of a eutrophic lake
- The change in the water regime positively influenced recruitment in three of the five mussel species inhabiting the lake
- The change in the water regime revealed differences in hydrological requirements between mussel species
- As in lotic environments, complex hydraulic parameters are highly significant to unionid mussels in lentic environments

GRAPHICAL ABSTRACT



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ABSTRACT

Although eutrophication of freshwaters is a natural process, the human impact often leads to inland waters becoming overloaded with nutrients, impoverishing many valuable and vanishing habitats, such as floodplain lakes. These changes need to be reversed if the occurrence of endangered aquatic species is to be restored. In this paper we analyse the impact of a change in the water regime of a naturally eutrophic floodplain lake, which harbours a large diversity of Unionidae (large freshwater mussels), a globally threatened taxonomic group that provides important ecosystem functions and services. We found that a slight increase in the discharge from this waterbody, following the construction of an additional outflow pipe, positively influenced recruitment in three of the five mussel species inhabiting the lake. We also found that, after the construction of this additional outflow, the niches of juveniles of *Anodonta cygnea* and *Unio* spp. changed, revealing differences in their hydrological requirements. Our results suggest that, as in lotic habitats, complex hydraulic parameters are highly significant to unionid mussels in lentic conditions.

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1. Introduction

Freshwater lakes provide mankind with many services (Postel and Carpenter, 1997); some of these services, however, are often debilitated by eutrophication (Scharf, 1999), when waterbodies are overloaded with nutrients from external sources. Natural eutrophic floodplain

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lakes (habitat code 3150 in the Habitat Directive) are among the most threatened (Wilk-Woźniak et al., 2019); Even if left intact during river regulation, they are continuously diminishing in area, as they are affected by biological succession. There is no natural mechanism restoring them, because within most floodplains, lateral erosion of channels has been stopped by channel regulation; small lakes separated from the channel by levees seem to diminish at the fastest rate (Zajac, 2001, 2002).

Recent decades have seen a vast improvement in the techniques used to restore shallow eutrophic lakes (Moss et al., 1996; Jeppesen, 1998). Nevertheless, some of these approaches bring about such large disturbances to benthic communities that their structures may be modified (Kornijów and Gulati, 1992). Macroinvertebrates are a critical component of small and shallow lake biotopes, where coupling between benthic and pelagic habitats is very strong (Schindler and Scheuerell, 2002). They interact with fish, periphyton and plants (Jones and Sayer, 2003), as well as with pelagic zooplankton (Burks et al., 2001). Macroinvertebrate assemblages in floodplain lakes are frequently characterised by large biomasses of freshwater mussels from the family Unionidae (Zajac et al., 2016). These are relatively long-lived, sedentary, filter-feeding bivalves found in dense multispecies aggregations inhabiting the sediments of waterbodies. Mussels have a complex life cycle, including an obligatory parasitic phase on a host fish. Moreover, by intensively filtering water, they provide important ecosystem services (Vaughn, 2018) and positively influence ecosystem functions (Gutiérrez et al., 2003). Despite their importance, however, they are among the most endangered groups of animals on the planet (Lydeard et al., 2004). In recent decades a growing number of studies have been conducted concerning their ecology and conservation (Lopes-Lima et al., 2018).

The factors governing the distribution and abundance of freshwater mussels in lentic environments are poorly understood. It has been demonstrated that basic features of lentic waterbodies like water depth, distance from and along the shore, and sediment layer influence their distribution (Zajac et al., 2016). In addition, wave action (Cyr, 2008), littoral zone sedimentation (Cyr et al., 2012), substrate type (Kat, 1982), light, temperature, food and flow rate (Dillon, 2004), inflow of various exogenous compounds (Richardson and Mackay, 1991), oxygen content (Zajac, 2002), toxic compounds (Wetzel, 2001) and falling water level (Dillon, 2004; Gołab et al., 2010) can be considered factors influencing their distribution and abundance. Even though the problem is far from being explained, there is increasing evidence that hydraulics play a significant role in shaping such habitats. A number of studies have demonstrated that near-bed hydraulic conditions are good predictors of suitable microhabitats for mussels (e.g. Layzer and Madison, 1995; Statzner et al., 1988; Lydeard et al., 2008) or the importance of hydraulic conditions during extreme events such as high and low flows (Zigler et al., 2008; Daraio et al., 2010; Allen and Vaughn, 2010); these studies were conducted in large rivers, however. Small, lentic waterbodies in floodplains appear to have been neglected; but since unionid distributions are related to hydraulic conditions, they too may be affected by flow modifications.

One of the most important symptoms of the decline in freshwater mussels around the world is the lack of recruitment (Roper and Hickey, 1994; Beasley and Roberts, 1999; Hastie and Toy, 2008). Under favourable conditions, unionids can achieve very high abundances and biomasses; however, increasing numbers of their formerly abundant populations have become relicts, with a characteristic lack of recruitment, which leads to population ageing and decline (Payne and Miller, 1989). Although this phenomenon is widely reported as being crucial for understanding the decline of unionids, its causes and mechanism are still not understood.

This paper reports on the effects of slight flow changes in the naturally eutrophic floodplain lake Zalew Pińczowski, inhabited by a well-studied (Zajac, 2001; Zajac et al., 2016), formerly abundant and species-rich assemblage of freshwater mussels, which has recently

shown signs of ageing and decline. The aim of this study was to demonstrate how changes in flow velocity and the Reynolds number affected the recruitment (presence and number) of juvenile mussels.

2. Materials and methods

2.1. Study site and water flow regime

The waterbody known as Zalew Pińczowski (Fig. 1A; detailed description in Strużyński, 2007; Zajac et al., 2016) is an old riverbed left after the main channel of the River Nida was straightened in 1973. In the 1980s the old channel was widened. The lake is supplied by a channel following the previous course of the river. The water intake from the Nida is located ca. 1.8 km upstream of the lake. The outflow channel also follows an old channel ca. 1.3 km in length (Strużyński, 2007). The original regulation did not provide adequate water flow through the lake. The main part of it contained almost still water; water movement was caused by wind and dispersion of heat rather than discharge (the retention time was about 8 days). The shallow water and insufficient flow in Zalew Pińczowski caused it to silt up, become shallower, and increased the duration of water exchange (Strużyński and Wyrębek, 2013), which in consequence led to a deterioration in water quality. By way of a solution, an additional spillway with a pipeline connecting the lake directly to the Nida was proposed (Strużyński, 2007) and constructed in November 2013. The maximum water level in the lake stipulated in the water permit from 1991 was 185.80 m a.s.l. The water level in the lake measured on 3 June 2007 was at an altitude of 185.68 m a.s.l., while at the original pipeline mouth it was 184.92 m a.s.l. After the introduction of the second outlet, the elevation of the water surface in the Nida rose. While the weir elevation had been stated at 185.70 m a.s.l., the water elevation measured on 30 November 2015 lied at 185.83 m a.s.l. which was 40 cm below the shore full elevation. Zalew Pińczowski is used by anglers and fish are annually restocked by local angling club in Pińczów.

2.2. Study species and mussel sampling

Zalew Pińczowski is inhabited by five species of freshwater mussels (Unionidae) belonging to two genera: (1) *Unio*: swollen river mussel (*Unio tumidus*) and painter's mussel (*Unio pictorum*) and (2) *Anodonta*: duck mussel (*Anodonta anatina*), swan mussel (*Anodonta cygnea*) and depressed river mussel (*Pseudanodonta complanata*). Two of these species, *A. cygnea* and *P. complanata*, are endangered in Poland and protected by law (Zajac, 2004a, 2004b). In Europe, *P. complanata* was assessed as Vulnerable (Van Damme, 2011), whereas the other species were assessed as Least Concern, although population trends were identified as decreasing in *A. anatina* (Lopes-Lima, 2014a) and *A. cygnea* (Lopes-Lima, 2014b).

The data were collected along the southern shore of Zalew Pińczowski. Thirteen transects, each 10 m long, were delineated perpendicular to the shore at intervals of 50 m from each other. They covered the whole littoral area, extending from the edge of the emergent vegetation to the flat bottom of the lake. On each transect, the water depth and silt layer were both measured every 0.5 m (Fig. 1B). At the same points bottom samples were collected from an area of 0.385 × 1 m using a 38.5 cm wide dredge rake with nylon netting (3 mm mesh). Surveys were performed at the beginning of October in 2013, 2015 and 2016; at this time of year, juveniles are easier to detect because of their shell length (>10 mm).

There is no universal definition of the juvenile life stage in freshwater mussels (Ries et al., 2016). Some studies have defined juveniles based on shell length (e.g. ≤25 mm, Haag and Warren, 2007), whereas others have used age (e.g. ≤1 year old, Jones and Neves, 2011; or even ≤10 years old, Strayer and Malcolm, 2012). Because species of the genus *Anodonta* reach sexual maturity at 1–4 years, and *Unio* species generally mature between 2 and 4 years of age (Lopes-Lima et al.,

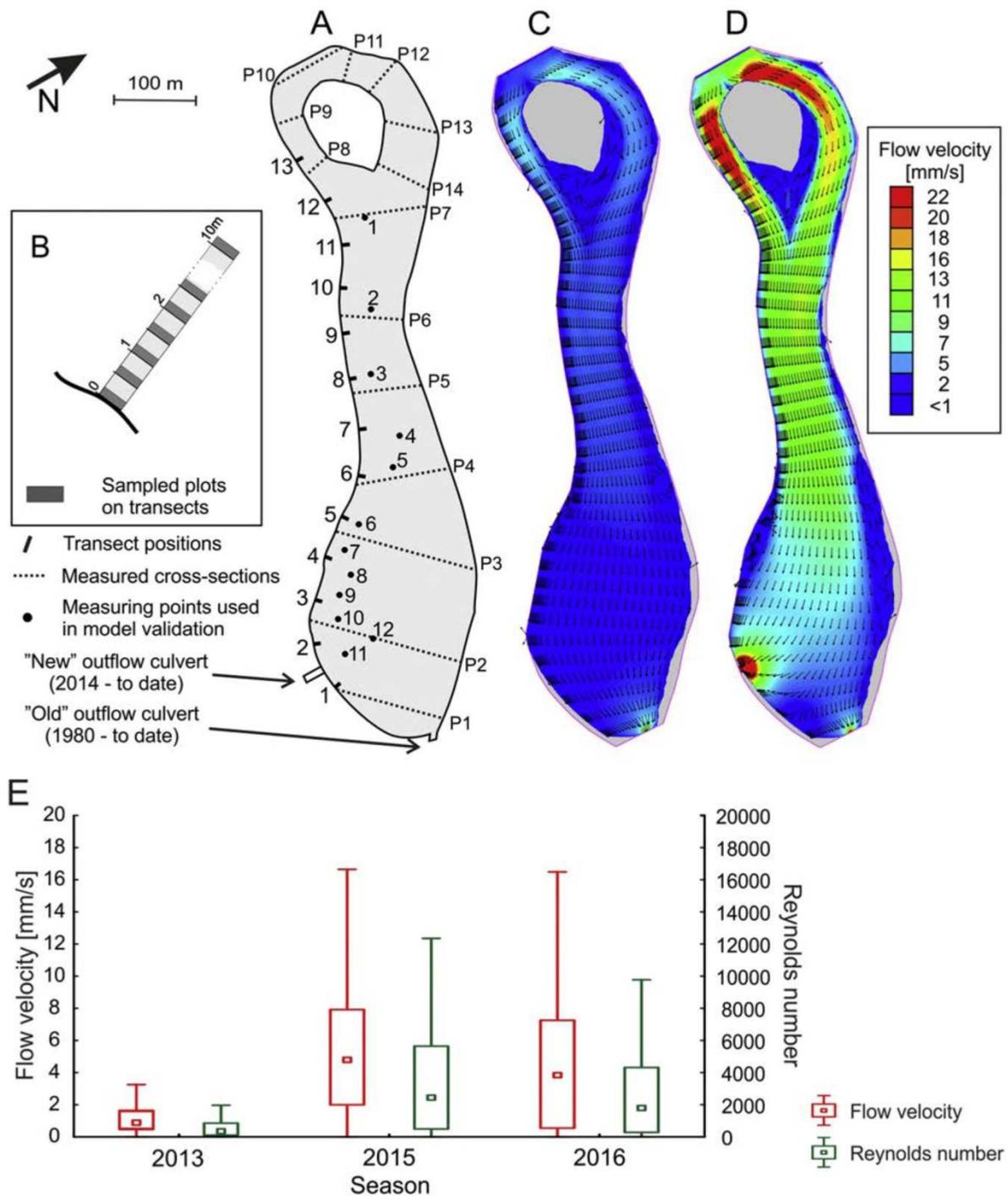


Fig. 1. General view of Zalew Pińczowski, showing the transect positions, measured cross-sections and location of measuring points used in model validation (A), transect sampling scheme (B), flow velocity and direction (obtained from the numerical model) before (C) and after (D) the construction of the new outflow culvert. (E) Box plots of the flow velocity (left Y axis) and Reynolds number (right Y axis) before (2013) and after (2015, 2016) the construction of the new outflow culvert.

2017), individuals aged 1 and 2 were classified in this study as juveniles, while individuals aged 3 or older were classified as adults.

2.3. Hydraulic model

The morphology of the lake bottom was measured using a Humminbird Legend 1000 Realtime Sonar, while geodetic measurements were performed with a Topcon GTS 226 tachymeter. The value characterising the bottom roughness in the reservoir was determined

using Chow (1959) tables. Fourteen cross-sections and a series of shoreline measurements were made to trace the current shape of the lake (Fig. 1A). After the implementation of the additional pipeline, measurements of the overflow geometry and the water conducting culvert were carried out on 30 November 2015, both in the part located in the lake and in the vicinity of the outflow into the Nida.

Flow velocity in the reservoir and in the area of the supply and outlet channels was measured on 1, 3 or 6 measuring levels (depending on the water depth) using a Nautilus Sensa Z300 hydrodynamic sensor at a

frequency of 2 Hz within a period of 1 min. However, the flow velocity measurements made in the reservoir were mostly not successful, because their values were below the level of detection of the used device. For this reason, the actual velocity measurements were used to calculate the average speed in the measuring verticals and the discharge of water supplied and flowing out from the reservoir, while the distribution of water velocity in the reservoir itself was determined using a two-dimensional numerical model obtained in CHE2D software (Zhang, 2006). The model was calibrated based on measurements of the water table in the inlet and outlet channels and in the reservoir itself. After the construction of the additional outflow culvert, the model was validated by comparing the flow velocities obtained by the model to the values measured using a Nautilus Sensa Z300 hydrodynamic sensor at a frequency of 2 Hz within a period of 1 min, at 12 measuring points located along the southern shore of Zalew Pińczowski (Fig. 1A). The results of the validation are presented in the Supplementary materials. The maximum discharge capacity in 2013 was 195 dm³/s, so water flow simulations were carried out for such a discharge. In 2015 and 2016, when the additional outlet was in operation, simulations were performed for the following water distributions: flow in the inlet channel – 1000 dm³/s, flow in the “old” outlet – 195 dm³/s, flow in the “new” outlet – 805 dm³/s. All flow velocity values in the reservoir presented in this study are the result of numerical modelling.

The search for the hydraulic conditions ensuring good conditions for the mussel species was based on the flow velocity and the Reynolds number. The former reflects traction forces, while changes in the latter reflect changes in energy exchange and mixing forces. Reynolds number is one of the basic parameters characterising fluid movement, used to describe the hydrodynamic similarity of various systems. The Reynolds number is used to determine the turbulence of fluid streams (particle vibrations), and thus the intensity of turbulence in the transverse and vertical systems, referred to the main direction of flow vector.

2.4. Statistical analysis

The frequency of unionids found in the bottom samples exhibited a typical Poisson distribution. Thus, the differences in the numbers of juvenile individuals of a given species between years were tested using the Kruskal-Wallis and multiple comparisons of mean ranks for all groups post-hoc tests (Siegel and Castellan, 1988).

The differences in the mean Reynolds number, mean flow velocity and mean silt layer thickness between years were tested using the Kruskal-Wallis test, because the classical ANOVA assumption of homogeneity of variance, even after Box-Cox transformation, was not satisfied.

Because of the high and significant correlation between flow velocity and the Reynolds number (Re ; $N = 742$; $r = 0.93$; $p < 0.0001$), Reynolds number standardised residuals (ReSR; obtained using linear regression between flow velocity and Reynolds number) were used instead of the Reynolds number itself in subsequent statistical models. Using ReSR instead of Re allows us to put it together with flow velocity into one model, which is not possible in case of flow velocity and Re (co-linearity of predictors). The disadvantage of such approach is that we cannot obtain information on direct influence of Re itself on analysed dependent variable, we only can interpret the influence of Re together with flow velocity.

To test the influence of the hydraulic conditions on the presence and number of juvenile mussels, generalized linear models (GLZ; logit; binomial; and GLZ; log; Poisson; respectively) were constructed for each species. The same set of predictors was used in each model; categorical predictor: year; continuous predictors: distance along the shore, distance from the bank, flow velocity, Reynolds number standardised residual, along with interactions between the predictors (which allow the relationship between the response and one predictor to vary with the values of another predictor): distance along shore and distance from the bank, distance along shore and flow velocity, distance along

shore and Reynolds number standardised residual, distance from the bank and flow velocity, distance from the bank and Reynolds number standardised residual, year and flow velocity, year and Reynolds number standardised residual, flow velocity and Reynolds number standardised residual, distance along shore, distance from the bank and flow velocity. The best subset of variables for each species was determined using best subsets model building procedure and Akaike Information Criterion (AIC; Akaike, 1974).

3. Results

Before the construction of the additional outflow culvert, the highest water flow velocities (up to 5 mm/s; Fig. 1C) were recorded in the inlet part of the lake and in the area nearest to the primary (“old”) outlet. Mean water velocities were 2 mm/s in the narrow NW part of the lake, and only 1 mm/s in the wide, main part (over large areas the speed is even lower: 0.8 mm/s, Fig. 1C). After the construction of the additional outflow culvert, water velocities increased to ca. 10 mm/s in the narrow part of the lake, and to ca. 3–4 mm/s in the main, wide part of the lake (ca. 100 m from the outlets, Fig. 1D); within 25 m of the outlet, the water velocity was close to 10 mm/s. A zone of backflows came into existence along the right-hand shore of the lake between the end of the narrow part and secondary outlet (Fig. 1D), but these reversed flow speeds were small (max. 1 mm/s). Basic statistics of flow parameters in 2013, 2015 and 2016 were presented in Table 1.

The differences in mean flow velocity between years were significant (Table 1; Fig. 1E; Kruskal-Wallis test; $H = 194.7$; $p < 0.0001$), and the differences in mean Reynolds number likewise differed significantly between years (Table 1; Fig. 1E; Kruskal-Wallis test; $H = 132.0$; $p < 0.0001$). The differences in mean silt layer thickness between years were not significant (Table 1; Kruskal-Wallis test; $H = 4.01$; $p = 0.1344$) and silt layer thickness was excluded from the subsequent analysis.

A total of 3229 individuals of Unionidae were found. The most numerous population was that of *A. cygnea* (1432 individuals; 44.3%), followed by *U. tumidus* (771 ind.; 23.9%), *U. pictorum* (673 ind.; 20.8%) and *A. anatina* (226 ind.; 7.1%). The least numerous population was of *P. complanata* (127 ind.; 3.9%). The most numerous species among the juvenile individuals (476 ind. in total) was *A. cygnea* (70.2% of all recruits), followed by *U. tumidus* (16.6%), *U. pictorum* (12%), *A. anatina* (0.7%) and *P. complanata* (0.5%). Because of the very small numbers of *A. anatina* and *P. complanata* juveniles, these species were excluded from the subsequent analysis.

The percentage of juveniles in the *A. cygnea* population was 16% in 2013, 24% in 2015 and 39% in 2016. Similarly increasing percentages of juveniles between seasons were found in *U. pictorum* and *U. tumidus*: 3.5% and 2.2% in 2013, 14.5% and 8.8% in 2015 and 12% and 25% in 2016, respectively. The distribution of *A. cygnea*, *U. pictorum* and *U. tumidus* juveniles in Zalew Pińczowski before and after the construction of the additional outflow channel in relation to flow velocity and Reynolds number standardised residual is presented

Table 1

Basic statistics of flow velocity, Reynolds number and silt layer thickness before (2013) and after (2015, 2016) the construction of the additional outflow channel.

Variable	Year	Mean	Standard deviation	Median	Minimum	Maximum
Flow velocity [mm/s]	2013	0.9	0.8	0.7	0.04	3.5
	2015	5.2	3.9	4.8	0	17.6
	2016	4.4	3.7	3.8	0	16.5
Reynolds number	2013	625	705	362	1	3333
	2015	3414	3253	2421	0	12,348
	2016	2732	2820	1814	0	12,434
Silt layer thickness [cm]	2013	12.0	6.6	11.0	0	43.0
	2015	12.8	10.1	10.0	0	75.0
	2016	12.1	10.4	10.0	0	60.0

in the Supplementary materials. The age distribution of the mussel populations in Zalew Pińczowski before and after the construction of the additional outflow channel is illustrated in Fig. 2.

3.1. The influence of flow parameters on the presence and number of juveniles

By using AIC, the top three models supporting the presence of juveniles and top three models supporting the number of juveniles were identified for each mussel species. The detailed summary of model selection procedure was presented in the Supplementary materials (Table S2).

3.1.1. Presence/absence of juveniles

The detailed summary of the influence of predictors selected using best subsets model building procedure on the number of juveniles for each species was presented in the Supplementary materials (Tables S3–S5). In this paper, we present only significant predictors influencing the number of the juveniles of each mussel species (Table 2).

Generalized linear models showed that the Reynolds number standardised residual and change in flow velocity after the construction of the additional outflow channel are positively influencing the occurrence (absence/presence) of juveniles among all the species (Table 2). Nevertheless, each species also had additional specific predictors influencing their occurrence.

For *A. cygnea* juveniles, distance from the bank and the interaction between distance from the bank and distance along shore are positively influencing their occurrence, while the interactions between distance along shore and Reynolds number standardised residuals, distance from the bank and flow velocity and also distance from the bank and Reynolds number standardised residual are negatively influencing the occurrence of *A. cygnea* juveniles (Table 2).

For *U. pictorum* juveniles, distance from the bank has positive, while the interaction between distance from the bank and flow velocity has a negative influence on their occurrence (Table 2).

In the case of *U. tumidus* juveniles, the interaction between distance along the shore and distance from the shore has a positive influence, while the interaction between distance along shore and Reynolds number standardised residuals and the interaction between distance along shore and flow velocity have the negative influence on their presence (Table 2).

3.1.2. Number of juveniles

There were no predictors that were significant for all of the species; moreover, interactions between predictors were rather species specific (Table 2). None of the selected predictors had significant influence on the number of juveniles in either *U. pictorum* and *U. tumidus* in any of the identified models (Supplementary materials).

In *A. cygnea* the interaction between distance along the shore and distance from the bank had positive influence on the number of juveniles, while the interaction between distance from the bank and flow

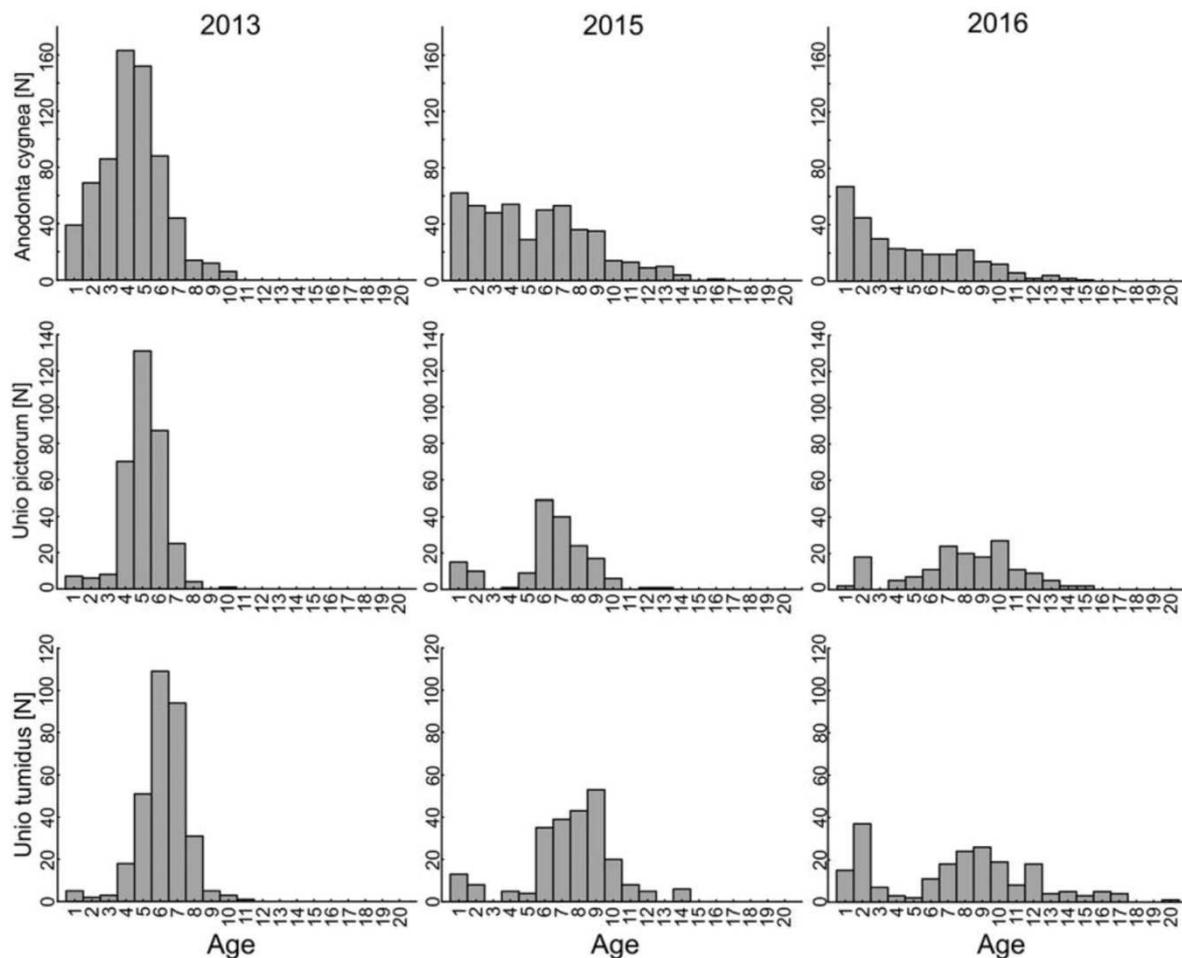


Fig. 2. Age distribution of mussel populations before (2013) and after (2015, 2016) construction of the "new" outflow culvert.

Table 2

The summary of the influence of identified significant predictors and significant interactions between predictors on the number and presence of *Anodonta cygnea* juveniles and presence of *Unio pictorum* and *Unio tumidus* juveniles in Lake Zalew Pińczowski. Green background with "+" symbol indicates the positive influence, while red background with "-" symbol indicate negative influence of a given predictor/interaction between predictors.

Identified significant predictors and significant interactions between predictors	Number of <i>Anodonta cygnea</i> juveniles	Presence of <i>Anodonta cygnea</i> juveniles	Presence of <i>Unio pictorum</i> juveniles	Presence of <i>Unio tumidus</i> juveniles
Distance along shore		+		
Distance from the bank		+	+	
Reynold's number standardised residual		+	+	+
Distance along shore*Distance from the bank	+	+		+
Distance along shore*Reynold's number standardised residual		-		-
Distance from the bank*flow velocity	-	-	-	
Distance from the bank*Reynold's number standardised residual		-		
Change in flow velocity between 2013 and 2015		+	+	+
Distance along shore*flow velocity	-			-

velocity and the interaction between distance along the shore and flow velocity, negatively influence the number of juveniles (Table 2).

4. Discussion

In Europe, eutrophication is a serious environmental problem and an important obstacle to the implementation of the European Water Framework Directive. Many lake restoration projects still involve a large proportion of trial and error, where the mechanisms for successful restoration remain largely blurred (Søndergaard et al., 2007). Moreover, restorations are often conducted primarily to improve water quality and are not designed as a scientific experiment (Mehner et al., 2002).

Freshwater mussels are especially sensitive to changes in hydrological conditions, which are of particular importance in structuring mussel communities (Strayer et al., 2004; Allen and Vaughn, 2010) and may influence recruitment dynamics (Hardison and Layzer, 2001; Morales et al., 2006). Among the many lake restoration techniques used in shallow eutrophic lakes in Europe (e.g. fish removal, sediment dredging or removal, oxygenation, reduction of phosphorous and nitrogen), only flow improvement was applied in Zalew Pińczowski. Preliminary simulations performed by Strużyński (2007) showed that reducing the retention time would be sufficient to halt the slow but on-going degradation of the lake. As he had predicted, the construction of an additional outflow channel increased flow velocity, reducing retention time and increasing the Reynolds number ca. 4-fold. The results showed that both the change in flow velocity between seasons (interaction between year and flow velocity) and the more turbulent flow (Reynolds number standardised residuals) were the key, positive factors that affected the presence of juveniles of all analysed species. Even though the Reynolds number standardised residual itself had a positive influence on the presence of juveniles of all the species, the interaction of Reynolds number standardised residuals with distance along the shore as well as that between distance along the shore and flow velocity both had a negative influence on the presence of juveniles. This is easily

explained by the fact that Zalew Pińczowski is not homogeneous and its width changes with the distance along the shore. Moreover, the narrower parts of the lake were more affected by the change in flow hydraulics.

The change in flow velocity between 2013 and 2015 (before and after the construction of the additional outflow channel) strongly affected the occurrence of juveniles in all analysed mussel species. A key to understanding the underlying mechanism could be the relationship between flow velocity and mussel feeding. In their experiments on the blue mussel (*Mytilus edulis*), Widdows et al. (2002) demonstrated that current velocities >0.06 m/s gave rise to sufficient vertical mixing and a relatively constant algal cell concentration down the water column. At slower currents there was an increasing cell depletion zone within the water column surrounding the mussels' siphons with declining flow velocity. The degree and height of the significantly algal-depleted water extended to 5 cm from the siphons at 0.02 m/s, 10 cm at 0.008 m/s and 15 cm at 0.004 m/s. Their results suggest that before the construction of the new outflow channel, the water velocity in the zone from 0 to 10 m from the shore (ca. 0.005 m/s) could have been slow enough to create an algal-depleted zone, which could have been sufficiently large to prevent filter feeding by juveniles. A low concentration of algal cells owing to the high density of adults, and a too slow flow velocity could have been limiting factors responsible for the low recruitment to populations and in consequence, their ageing. Moreover, as the velocity of water decreases, it loses the ability to carry sediment. Thus, at low flow velocities, floodplain lakes or old river channels may become sediment "traps", eventually smothering mussels that cannot adopt to soft substrates (Isom, 1969).

The possible effects of sediments on unionid mussels are multifold. Mussels are potentially affected by changes in suspended and bed material load, and bed sediment composition associated with increased sediment production and runoff (Brim Box and Mossa, 1999). Increases in fine sediments, whether deposited or suspended, may impact freshwater mussels by interfering with feeding and/or respiration. Widdows

et al. (1979) showed that inorganic silt in suspension reduced the amount of food available to the marine mussel *Mytilus edulis* through dilution, while in another marine species *Mercenaria mercenaria*, increasing sediment loads significantly lowered clearance rates and algal ingestion rates (Bricelj and Malouf, 1984) and significantly lowered growth rates in juveniles (Bricelj et al., 1984). High suspended solids concentrations may also be responsible for observed declines in some mussel populations, by negatively affecting mussels reproduction, regardless of whether they were organic (Gascho Landis et al., 2013) or inorganic (Gascho Landis and Stoeckel, 2016) particles.

A similar mechanism may be in operation in the case of the Reynolds number: this was higher after the second outlet had been built, positively affecting the presence of juveniles, although its interactions with distance from the shore or distance along the shore negatively affected juvenile occurrence. Because the Reynolds number combines mean water column velocity, substrate roughness and kinematic viscosity to describe near-bed turbulence, following Parasiewicz et al. (2012) it may be assumed that it reflects a minimum threshold of turbulence needed to remove waste products. Steuer et al. (2008), too, suggested that the minimum Reynolds number might be required during low flows to deliver food or transport waste products, while Strayer (2014) suggested that the physical energy regime (current speeds, turbulence) are important in determining whether mussel biodeposits remain in place or are swept away. On the other hand, it was demonstrated that small-scale turbulence (Rehmann et al., 2003) and hydrodynamic forces (Horvath and Crane, 2010) could increase the mortality of *Dreissena polymorpha* veligers. It is thus possible that freshly transformed Unionidae juveniles may also be adversely affected by turbulence. Moreover, high boundary turbulence (or shear stress) can displace juvenile mussels. The increase in the mean Reynolds number after the construction of the additional outflow channel appears to have positively affected mussel recruitment in general, although in some specific localities of Zalew Pińczowski, the turbulence may have been too great to permit the successful colonisation of juveniles or high enough to increase juvenile mortality.

Increases in nutrient loading have both positive and negative effects on mussel populations (Strayer, 2014). In very nutrient-poor environments, the quantity and quality of food may be insufficient to support mussels, and increases in food quality and quantity associated with increased nutrient loading could increase mussel growth rates (Reis and Araujo, 2016) and fecundity (Strayer, 2014). Also, fish biomass or productivity generally increase with increased nutrient loading (Kalf, 2001) and could thereby benefit mussel populations by increasing host fish availability for mussels. On the other hand, extreme eutrophication may decrease food quality, prevent juvenile recruitment or even lead to increased mortality of both juveniles and adult mussels (Strayer, 2014). Thresholds of acceptable nutrient loading for freshwater mussels have not yet been specified; however, Strayer (2014) suggested that increased temporal or spatial variability in recruitment or survival of juveniles could serve as an early warning of impending disaster. It is thus possible, that the low level of recruitment observed in Zalew Pińczowski in 2013 was such an early warning of poor habitat conditions, as a result of insufficient flow, and in consequence of an increasing nutrient load in the lake. By increasing retention time, an additional outflow channel could therefore reduce nutrient load and thus have a positive effect on mussel recruitment.

One can also see that the juvenile mussels' niches changed after the construction of the additional outflow channel (Fig. 3). In 2013, before the construction of the channel, juveniles of all species occupied quite similar niches, with flow velocities from 0 to ca. 3.2 mm/s and more turbulent flow (positive Reynolds number standardised residuals). This significantly changed after the change in flow dynamics. It is quite evident (Fig. 3) that *A. cygnea* juveniles did not occur at all in more laminar (negative ReSR) and slower flows (<10 mm/s). It also seems that they did not prefer the more turbulent flows when the flow velocity was >14 mm/s. The highest number of *A. cygnea* juveniles was found

where the velocity of the flow was high but its turbulence the least. However, when the flow velocity was lower (e.g. <10 mm/s) more *A. cygnea* juveniles were found when the flow was more turbulent. Moreover, after the change in water discharge, clear differences in the hydrological requirements between *A. cygnea* and *Unio* spp. juveniles emerged. In the localities preferred by *A. cygnea* juveniles (high flow velocity, the least turbulent flow), only single *Unio* spp. juveniles were found in 2015, and in 2016 no *Unio* spp. juveniles were found at all. Also, there are only slight differences in hydrological requirements between *U. pictorum* and *U. tumidus* juveniles. In 2015, juveniles of both these *Unio* species were found under almost any conditions related to flow velocity and ReSR, albeit in small numbers. In 2016, both *Unio* species occupied similar niches (flow velocity < 18 mm/s), but it appeared that *U. pictorum* juveniles preferred a more turbulent flow (ReSR > ca. -2.5) than *U. tumidus* (ReSR > ca. -3.5). Another interesting result is that the change in hydrology in Zalew Pińczowski influenced mainly the occurrence of juveniles, but did not affect their number (both *Unio* species) or did so only slightly (*A. cygnea*). This suggests that although the hydrology of the lake improved, it may still have been below the optimum.

The life cycle of freshwater mussels includes a parasitic stage, in which the larvae need to attach to fish to continue its development (Modesto et al., 2018), thus the distribution and abundance of host fish may influence the distribution and abundance of mussel juveniles. Mussels species inhabiting Zalew Pińczowski are host generalists (Lopes-Lima et al., 2017) and can use many fish species as hosts. Some fish species, such as Common carp (*Cyprinus carpio*), European perch (*Perca fluviatilis*), Northern pike (*Esox lucius*), Roach (*Rutilus rutilus*), Sander (*Sander lucioperca*) are suitable hosts for all analysed mussels species and are annually restocked in the lake. Electrofishing conducted in 2015 (in April, July and August) showed that suitable host fish are available during the whole reproductive period of mussels and were found in the whole littoral zone of the lake (own, unpublished data). However, host fish species are generally classified as primary or marginal hosts, and they may differ significantly in both infestation intensities and transformation rates of glochidia into juveniles (Haag and Warren, 2003). Moreover, different strains of the same fish species may be characterised by distinct susceptibilities to glochidial infestation (Taeubert et al., 2010). Another major aspect of mussel dispersal is the dispersal biology of the host fish (Schwalb et al., 2010). Dispersal via host fish is important at the catchment scale and at the regional scale, and the abundance of host fish, the movement behaviour of the hosts, influence the dispersal abilities of mussels (Schwalb et al., 2011). Fish movements can vary with season, discharge conditions and ecosystem (Woolnough et al., 2009), host fish home ranges increase exponentially with fish size (Minns, 1995) and fish hosts parasitised with glochidia exhibit altered behavioural patterns in comparison with non-infected fish (Horký et al., 2014). It is thus possible that at a small scale, e.g. a small lake such as Zalew Pińczowski, the spatial distribution and movement behaviour of host fish may affect the mussel distribution. These are issues that should definitely be studied in greater detail in the future (Ferreira-Rodríguez et al., 2019).

An important aspect regarding all the mussel species in 2013 was the ageing of their populations. In that year, the percentages of juveniles in the mussel populations were generally low. Three years later (two years after the change in hydrology), however, the percentage of juvenile individuals increased by ca. 2 times in *A. cygnea*, ca. 4 times in *U. pictorum* and ca. 12 times in *U. tumidus*.

One of the species whose recruitment was not affected by the change in hydrology was *P. complanata*, always the least abundant species in Zalew Pińczowski (since 2003; Zając et al., 2016). It is quite common in the rivers and lakes of Poland, though always in rather small numbers (Zając, 2004b). However, this species is

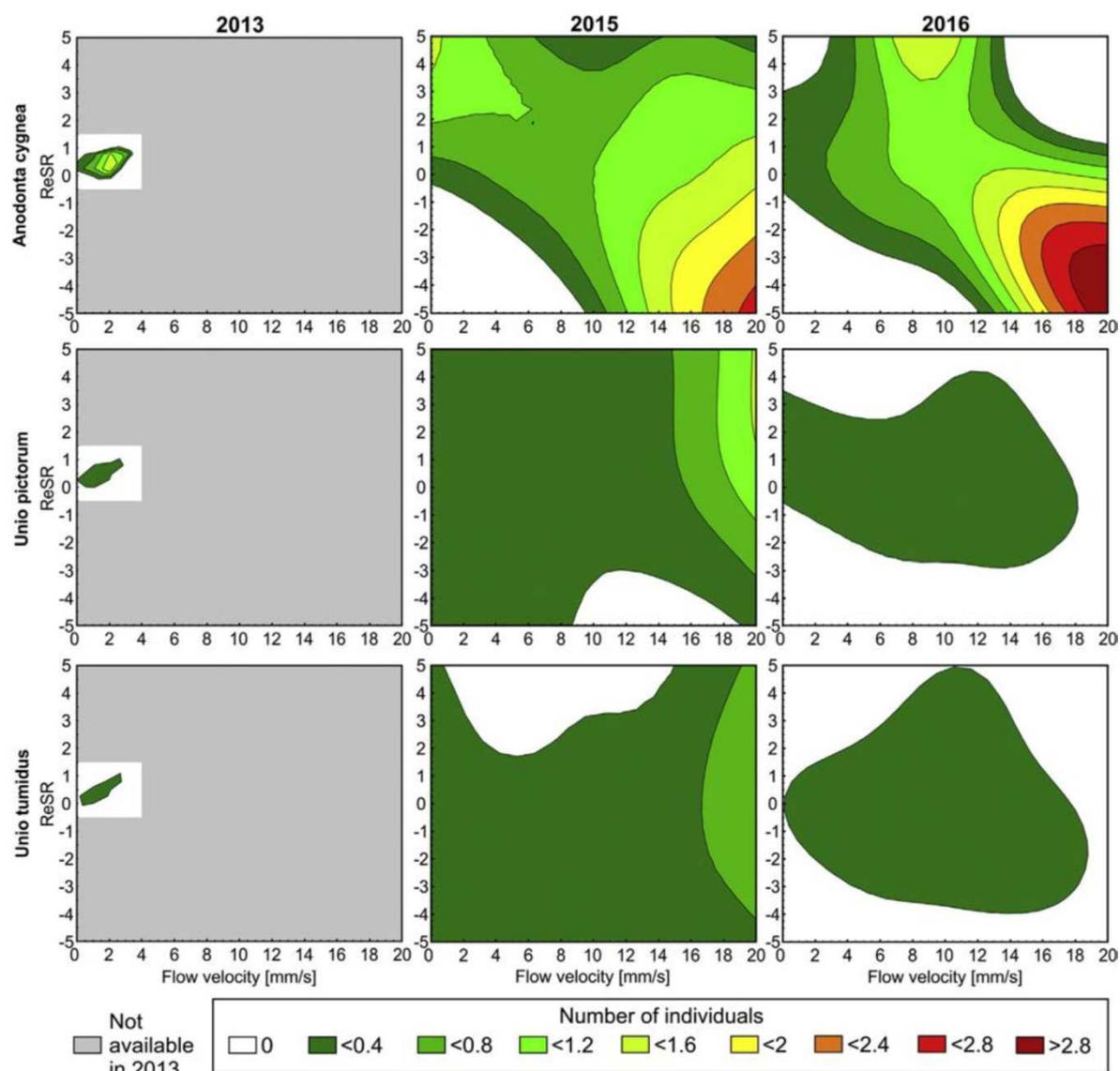


Fig. 3. The influence of Reynolds number standardised residual (ReSR) and flow velocity on numbers of *Anodonta cygnea*, *Unio pictorum* and *Unio tumidus* juveniles, before (2013) and after (2015, 2016) the construction of the additional outflow channel.

usually found in lotic freshwater ecosystems and shows a preference for deeper waters (McIvor and Aldridge, 2007). Thus, it is possible that in Zalew Pińczowski, *P. complanata* occurs in higher numbers farther away from the shore (>10 m), where the water depth and flow velocity are higher, and in consequence, was not detected during the surveys.

The second species whose recruitment was not affected by the change in hydrology was *A. anatina*. This is a generalist species that inhabits both lentic and lotic habitats; it can also exist in both oligotrophic and eutrophic waters (Zettler et al., 2006). Once very common in Zalew Pińczowski (Zajac K. - unpubl. data from 1998, Zajac et al., 2016), it is now in decline and is currently the second-least abundant species in the lake, although to date, no specific threats to *A. anatina* have been reported (Lopes-Lima, 2014a). The only possible explanation is that the population found in the 1990s was a remnant of those that had numerously inhabited the lake in earlier succession stages, and the subsequent silting up of the lake was disadvantageous to *A. anatina*. It will be possible to test this hypothesis over a longer time scale, when siltation and eutrophication of the lake start to decrease as a result of the increased flow.

In conclusion, our results show that additional outflow channel reduced the retention time and significantly changed the water regime in Zalew Pińczowski. The change in the water regime positively influenced recruitment in three of the five mussel species inhabiting the lake, revealed differences in hydrological requirements between mussel species. Our results also showed, that as in lotic environments, complex hydraulic parameters play a significant role with regard to unionid mussels in lentic environments.

Declaration of competing interest

The authors declare no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2019.135467>.

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Supplementary materials

Below we present the results of numerical model validation (Table S1, Fig. S1), and the distribution of *Anodonta cygnea*, *Unio pictorum* and *Unio tumidus* juveniles in Zalew Pińczowski at each sampling point before (2013) and after (2015, 2016) the construction of the additional outflow channel in relation to flow velocity (Fig. S2) and Reynolds number standardised residual (Fig. S3). Also, we present detailed summary of a model selection procedure (Table S2) for each mussel species, and detailed results of Generalized Linear Models (GLZ) of the influence of selected predictors on the presence/absence and number of *Anodonta cygnea* (Table S3), *Unio pictorum* (Table S4) and *Unio tumidus* (Table S5) juveniles.

Model validation

The numerical model of flow through the lake was validated by comparing the flow velocities obtained by the model to the corresponding values measured using a Nautilus Sensa Z300 hydrodynamic sensor, at 12 measuring points located along the southern shore of Zalew Pińczowski (Table S1).

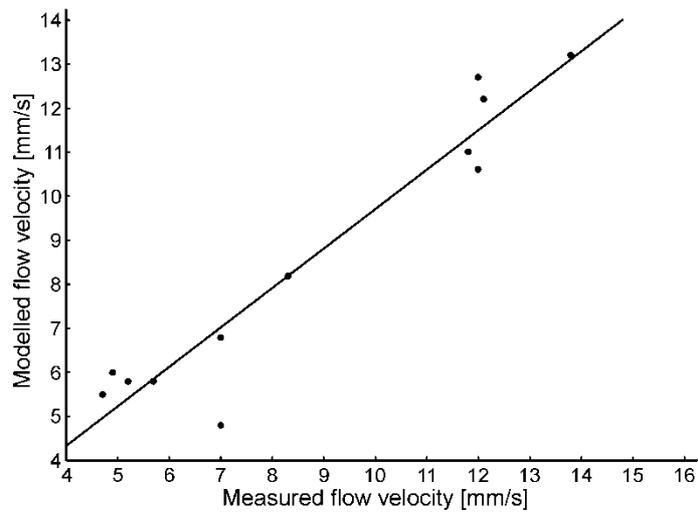
The measured and modelled flow velocities were highly correlated (Fig. S1; Pearson correlation; $r=0.96$; $p<0.001$). The modelled flow velocities fit the measured values very well (Fig. S1; linear regression; $R^2=0.92$; $p<0.001$).

The differences between measured and modelled flow velocities are not significant (t-test for dependent variables; measured mean flow velocity=8.7; SD=3.4; modelled mean flow velocity= 8.6; SD=3.2; $df=11$; $t=0.57$; $p=0.582$).

Table S1. Flow velocities measured using a hydrodynamic sensor and modelled using a numerical hydraulic model at 12 points located along the southern shore of Zalew Pińczowski.

Measuring point	Measured flow velocity [mm/s]	Modelled flow velocity [mm/s]
1	8.3	8.2
2	11.8	11.0
3	12.0	12.7
4	12.1	12.2
5	12.0	10.6
6	7.0	6.8
7	7.0	4.8
8	5.2	5.8
9	4.7	5.5
10	4.9	6.0
11	13.8	13.2
12	5.7	5.8

Fig. S1. Relationship between measured and modelled flow velocities at 12 points located along the southern shore of Zalew Pińczowski.



Distribution of juveniles

Fig. S2. The distribution of *Anodonta cygnea*, *Unio pictorum* and *Unio tumidus* juveniles in Zalew Pińczowski before (2013) and after (2015, 2016) the construction of the additional outflow channel in relation to flow velocity. Black dots - juveniles present, open circles - juveniles absent.

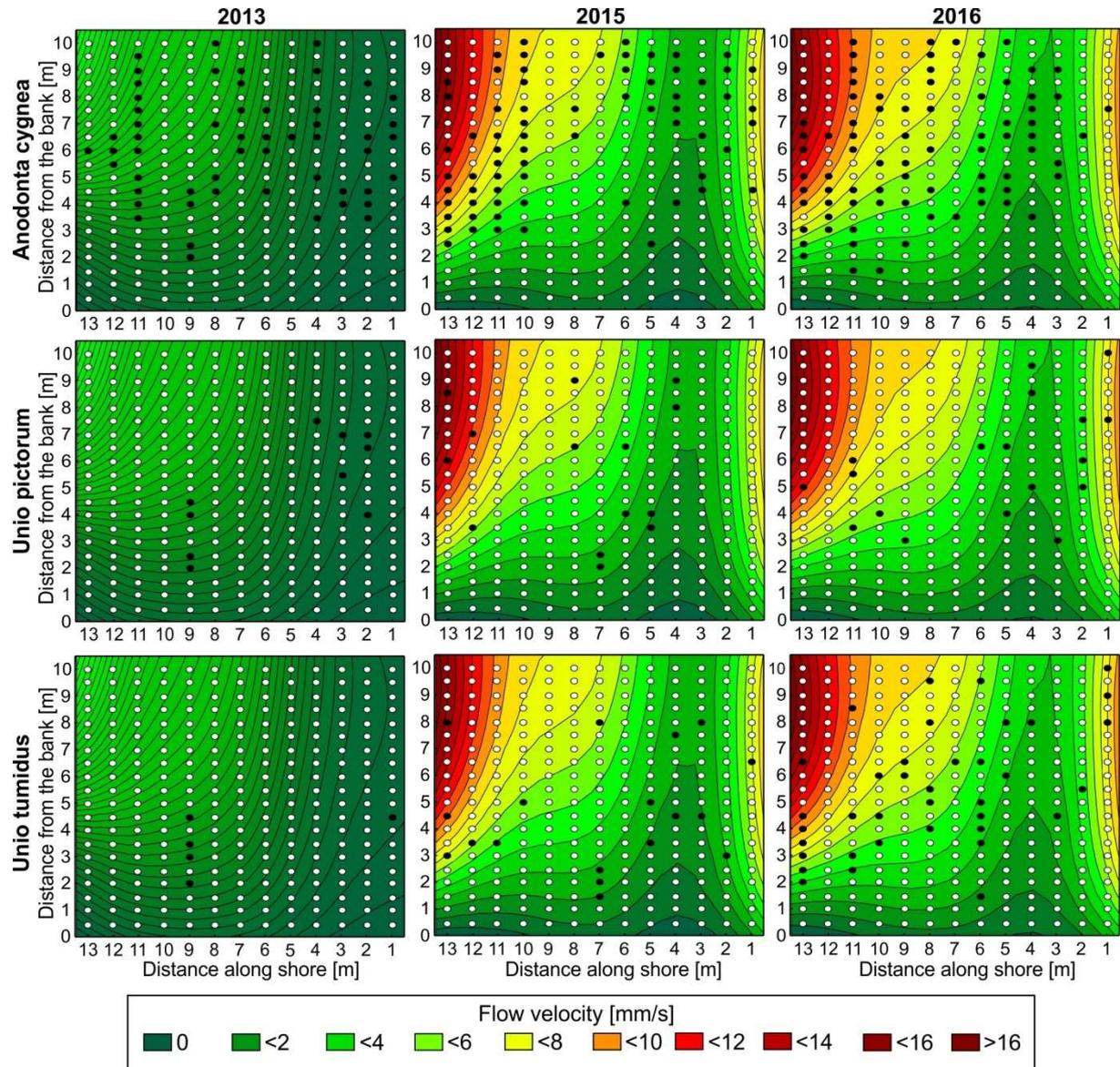
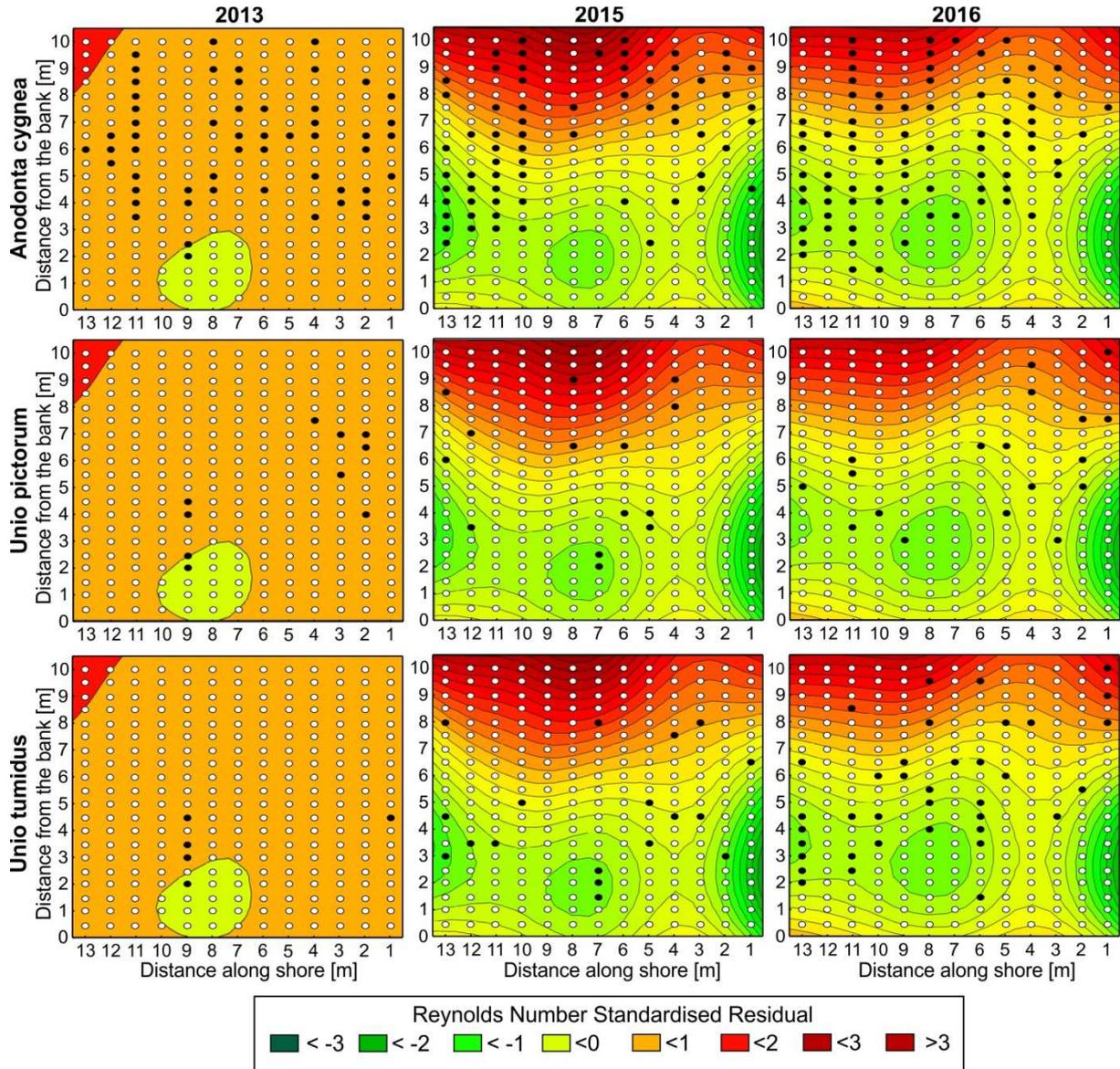


Fig. S3. The distribution of *Anodonta cygnea*, *Unio pictorum* and *Unio tumidus* juveniles in Zalew Pińczowski before (2013) and after (2015, 2016) the construction of the additional outflow channel in relation to Reynolds number Standardised residual. Black dots - juveniles present, open circles - juveniles absent.



Model building procedure and statistical analysis

List of acronyms:

Y - year

Tr - distance along the shore

D - distance from the shore

V - flow velocity

ReSR - Reynolds number standardised residual

df - degrees of freedom

W - Wald statistic

SE - Standard Error of the estimate

For each mussel species we used the same set of predictors and interactions between predictors from which the best fitted sub-sets were selected:

categorical predictor: Y

continuous predictors: Tr, D, V, ReSR

interactions between predictors: Tr*D, Tr*V, Tr*ReSR, D*V, D*ReSR, Y*V, Y*ReSR, V*ReSR, Tr*D*V, Tr*D*ReSR

Model selection method: best subsets using the Akaike Information Criterion (AIC)

The influence of the top 3 best fitted subsets of predictors for each species on the presence/absence of juveniles were analysed using Generalised Linear Models with binomial dependent variable and logit link function (GLZ; binomial, logit).

The influence of the top 3 best fitted subsets of predictors for each species on the number of juveniles were analysed using Generalised Linear Models with Poisson distribution dependent variable and log link function (GLZ; Poisson, log).

Table S2. Summary of model selection using Akaike's Information Criterion (AIC) procedure to examine the influence of flow parameters on the presence or absence (0/1) and number of juveniles in *Anodonta cygnea*, *Unio pictorum* and *Unio tumidus*. Δ AIC - relative difference in AIC value compared to the top-ranked model. Interactions between variables are indicated by *.

Species	Dependent variable	Model	Model rank	Predictors	df	AIC	Δ AIC
<i>Anodonta cygnea</i> juveniles	Presence or absence	GLZ (logit, binomial)	1	D, ReSR, Tr*D, Tr*ReSR, D*V, D*ReSR, Y*V	8	728.1	0
			2	D, ReSR, Tr*D, Tr*ReSR, V*ReSR, D*V, D*ReSR, Y*V	9	728.5	0.4
			3	D, ReSR, Tr*D, Tr*ReSR, D*V, Y*V	7	729.3	1.2
	Number	GLZ (log, Poisson)	1	Tr*D, Tr*ReSR, D*V	3	573.1	0
			2	D, Tr*D, Tr*V, Tr*ReSR	4	573.2	0.1
			3	Tr*D, D*V	2	573.3	0.2
<i>Unio pictorum</i> juveniles	Presence or absence	GLZ (logit, binomial)	1	D, ReSR, Y*V, D*V, D*ReSR	6	334.9	0
			2	Y, D, ReSR, Y*V, D*V, D*ReSR	8	335.7	0.8
			3	D, ReSR, Y*V, D*V, Tr*D*ReSR	6	335.9	1
	Number	GLZ (log, Poisson)	1	ReSR	1	108.8	0
			2	Tr*ReSR	1	108.9	0.1
			3	V*ReSR	1	109.0	0.2
<i>Unio tumidus</i> juveniles	Presence or absence	GLZ (logit, binomial)	1	ReSR, Y*V, Tr*D, Tr*V, Tr*ReSR, D*V	7	370.6	0
			2	ReSR, Y*V, Tr*D, Tr*ReSR, Tr*D*V	6	371.3	0.7
			3	ReSR, Y*V, Tr*D, Tr*ReSR, D*V, Tr*D*V	7	371.5	0.9
	Number	GLZ (log, Poisson)	1	Tr	1	152.4	0
			2	D	1	152.5	0.1
			3	Tr, Tr*V	2	152.9	0.5

Table S3. The influence of selected predictors on the presence/absence and number of *Anodonta cygnea* juveniles. The top 3 ranked Generalised Linear models for juvenile presence/absence data (GLZ; logit; binomial) and juvenile number data (GLZ; log, Poisson) are given. Interactions between variables are indicated by *.

Dependent variable	Model rank	Effect	Estimate	SE	W	p
Juvenile presence/absence GLZ (logit; binomial)	1	Intercept	-3.02	0.28	116.7	<0.001
		D	0.15	0.05	8.6	0.003
		ReSR	1.64	0.49	11.1	0.001
		Tr*D	0.05	0.01	52.7	<0.001
		Tr*ReSR	-0.14	0.04	12.0	0.001
		D*V	-0.04	0.01	16.4	<0.001
		D*ReSR	-0.07	0.04	3.1	0.080
		Y(2015vs2013)*V	0.22	0.05	17.3	<0.001
		Y(2016vs2013)*V	0.22	0.06	15.0	<0.001
	2	Intercept	-3.12	0.30	110.1	<0.001
		D	0.17	0.06	9.9	0.002
		ReSR	1.69	0.51	10.8	0.001
		Tr*D	0.05	0.01	49.5	<0.001
		Tr*ReSR	-0.18	0.05	11.8	0.001
		V*ReSR	0.07	0.06	1.6	0.212
		D*V	-0.05	0.01	18.1	<0.001
		D*ReSR	-0.12	0.06	4.5	0.035
		Y(2015vs2013)*V	0.22	0.05	16.9	<0.001
	Y(2016vs2013)*V	0.21	0.06	14.4	<0.001	
	3	Intercept	-4.63	0.43	117.1	<0.001
		D	0.44	0.06	62.1	<0.001
		ReSR	0.02	0.13	0.0	0.879
		Tr	0.22	0.03	48.8	<0.001
		D*V	-0.04	0.01	14.7	<0.001
		Y(2015vs2013)*V	0.19	0.05	14.9	<0.001
		Y(2016vs2013)*V	0.19	0.05	13.2	<0.001
	Number of juveniles GLZ (log; Poisson)	1	Intercept	-0.10	0.13	0.6
Tr*D			0.02	0.003	33.4	<0.001
Tr*ReSR			-0.009	0.006	2.2	0.135
D*V			-0.006	0.002	7.0	0.008
2		Intercept	0.11	0.22	0.2	0.638
		D	-0.06	0.04	2.1	0.146
		Tr*D	0.02	0.003	32.2	<0.001
		Tr*V	-0.004	0.001	8.3	0.004
3		Tr*ReSR	-0.01	0.008	3.1	0.076
		Intercept	-0.03	0.12	0.1	0.790
		Tr*D	0.01	0.003	31.9	<0.001
		D*V	-0.006	0.002	8.0	0.005

Table S4. The influence of selected predictors on the presence/absence and number of *Unio pictorum* juveniles. The top 3 ranked Generalised Linear models for juvenile presence/absence data (GLZ; logit; binomial) and juvenile number data (GLZ; log, Poisson) are given. Interactions between variables are indicated by *.

Dependent variable	Model rank	Effect	Estimate	SE	W	p
Juvenile presence/absence GLZ (logit; binomial)	1	Intercept	-3.47	0.41	70.1	<0.001
		D	0.16	0.08	4.2	0.041
		ReSR	1.22	0.51	5.8	0.016
		Y(2015vs2013)*V	0.34	0.11	9.0	0.003
		Y(2016vs2013)*V	0.32	0.12	7.4	0.007
		D*V	-0.04	0.02	5.9	0.015
		D*ReSR	-0.13	0.07	3.0	0.083
	2	Intercept	-3.61	0.43	71.0	<0.001
		Y(2015)	-0.69	0.40	2.9	0.089
		Y(2016)	0.35	0.33	1.2	0.282
		D	0.17	0.08	4.8	0.028
		ReSR	1.20	0.50	5.7	0.017
		Y(2015vs2013)*V	0.48	0.15	10.4	0.001
		Y(2016vs2013)*V	0.35	0.15	5.7	0.017
	3	D*V	-0.05	0.02	7.1	0.008
		D*ReSR	-0.11	0.07	2.4	0.120
		Intercept	-3.43	0.42	68.0	<0.001
		D	0.13	0.08	2.9	0.087
		ReSR	0.86	0.37	5.5	0.019
		Y(2015vs2013)*V	0.33	0.12	8.1	0.004
		Y(2016vs2013)*V	0.32	0.12	6.6	0.010
1	D*V	-0.04	0.02	5.5	0.019	
	Tr*D*ReSR	-0.009	0.006	2.4	0.124	
Number of juveniles GLZ (log; Poisson)	1	Intercept	0.25	0.13	3.6	0.059
		ReSR	-0.09	0.14	0.5	0.493
	2	Intercept	0.24	0.13	3.4	0.066
		Tr*ReSR	-0.01	0.02	0.4	0.534
	3	Intercept	0.25	0.13	3.5	0.061
		V*ReSR	-0.009	0.02	0.3	0.568

Table S5. The influence of selected predictors on the presence/absence and number of *Unio tumidus* juveniles. The top 3 ranked Generalised Linear models for juvenile presence/absence data (GLZ; logit; binomial) and juvenile number data (GLZ; log, Poisson) are given. Interactions between variables are indicated by *.

Dependent variable	Model rank	Effect	Estimate	SE	W	p
Juvenile presence/absence GLZ (logit; binomial)	1	Intercept	-3.61	0.358	101.3	<0.001
		ReSR	1.05	0.369	8.1	0.005
		Y(2015vs2013)*V	0.30	0.141	4.4	0.037
		Y(2016vs2013)*V	0.47	0.143	10.9	<0.001
		Tr*D	0.03	0.013	5.8	0.016
		Tr*V	-0.02	0.009	4.0	0.044
		Tr*ReSR	-0.18	0.045	15.9	<0.001
		D*V	-0.03	0.019	3.2	0.072
	2	Intercept	-3.62	0.37	94.8	<0.001
		ReSR	0.65	0.30	4.8	0.029
		Y(2015vs2013)*V	0.10	0.07	2.1	0.149
		Y(2016vs2013)*V	0.27	0.06	19.6	<0.001
		Tr*D	0.03	0.01	4.3	0.039
		Tr*ReSR	-0.14	0.04	13.8	<0.001
		Tr*D*V	-0.003	0.001	3.4	0.067
	3	Intercept	-3.60	0.37	93.4	<0.001
		ReSR	0.86	0.35	6.0	0.014
		Y(2015vs2013)*V	0.22	0.12	3.4	0.063
		Y(2016vs2013)*V	0.40	0.12	10.8	0.001
		Tr*D	0.03	0.01	4.9	0.026
		Tr*ReSR	-0.14	0.04	12.1	<0.001
		D*V	-0.02	0.02	1.6	0.120
		Tr*D*V	-0.003	0.001	3.1	0.076
	Number of juveniles GLZ (log; Poisson)	1	Intercept	-0.008	0.27	0.001
Tr			0.04	0.03	1.5	0.220
2		Intercept	0.59	0.28	4.6	0.032
		D	-0.06	0.05	1.4	0.241
3		Intercept	-0.13	0.30	0.2	0.668
		Tr	0.08	0.05	3.0	0.086
		Tr*V	-0.004	0.003	1.4	0.242