

**Wpływ antropogenicznych przekształceń rzek
na rozmieszczenie i biologię inwazyjnego
raka pręgowatego *Orconectes*
limosus Rafinesque**

The influence of human-mediated river
alteration on the distribution and biology
of the invasive Spiny Cheek
Crayfish *Orconectes limosus* Rafinesque

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SPIS PUBLIKACJI

1. Bonk M., Bobrek R. 2020. Invasion on the doorstep: will the Carpathians remain free from the spiny cheek crayfish *Faxonius limosus* (Rafinesque, 1817)?. *BioInvasions Records* 9 (3): 549–561. DOI: <https://doi.org/10.3391/bir.2020.9.3.10>
2. Bonk M., Bobrek R. 2021. Does river channelization increase the abundance of invasive crayfish? Survey of *Faxonius limosus* in small Central European streams. *Environmental Science and Pollution Research* 28 (24): 31831–31837. DOI: [10.1007/s11356-021-12750-y](https://doi.org/10.1007/s11356-021-12750-y)
3. Bonk M., Amirowicz A. 2022. The body condition of invasive crayfish *Faxonius limosus* (Raf., 1817) (Decapoda: Cambaridae) is better in small rivers than in dam reservoirs in Central Europe. *Environmental Science and Pollution Research*. DOI: <https://doi.org/10.1007/s11356-022-19678-x>

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STRESZCZENIE

Jednym z przejawów ludzkiej aktywności jest przemieszczanie organizmów w związku z różnorodnymi potrzebami. Ze względu na dużą mobilność ludzi, dochodzi do częstego wprowadzania gatunków na tereny, na których dotąd nie występowały. Gatunki, którym udało się zaadaptować do nowego środowiska lub gdy trafią do środowiska podobnego do tego, z którego pochodzą mają szansę stać się gatunkami inwazyjnymi. Inwazje biologiczne są ciekawym obiektem badań jako zjawisko przyrodnicze, jednak znaczenie badań nad tymi organizmami jest większe, gdyż gatunki inwazyjne mają ogromny wpływ na ochronę przyrody i gospodarkę.

W niniejszej rozprawie przedstawiono wybrane aspekty rozmieszczenia i biologii raka pręgowatego *Faxonius limosus* (Rafinesque, 1817) w kontekście warunków środowiskowych. Podczas badań prowadzonych w latach 2018–2019 w rzekach i zbiornikach zaporowych południowej Polski stwierdziłem, że 1) występują geograficzne ograniczenia inwazji raka pręgowatego w środkowej Europie – gatunek ten nie kolonizuje karpackich rzek, 2) liczniej występuje w uregulowanych odcinkach małych cieków niż w odcinkach względnie naturalnych, 3) raki te wykazują zmienną kondycję osobniczą w różnych siedliskach: kondycja raków pochodzących ze zbiorników zaporowych jest niższa niż w rzekach, na których znajdują się te zbiorniki.

Rak pręgowaty mimo znacznego rozpowszechnienia i długiej historii inwazji w Europie wykazuje zatem pewne ograniczenia możliwości dalszej kolonizacji i/lub osiągnięcia dużych zagęszczeń w zależności od warunków siedliskowych. Mimo że przekształcone siedliska oferują mu dobre warunki życia, zbiorniki zaporowe mogą mieć negatywny wpływ na niektóre aspekty jego biologii. Ważnym sposobem ograniczania wpływu inwazji raka pręgowatego na rodzime ekosystemy może być zachowanie naturalnego charakteru siedlisk wodnych, co w szczególności może wspomóc zachowanie zanikających w Europie rodzimych gatunków raków.

SUMMARY

One of the major effects of human activity is both intentional and accidental species displacement resulting in colonizing new areas by species alien to given region. Alien organisms that are flexible enough for coping with challenges of new environment or originating from similar habitats/ecosystems may become invasive. Biological invasion studies are important both in biology, nature conservation and economics as well.

In this dissertation I show some aspects of biology and distribution of the Spiny Cheek Crayfish *Faxonius limosus* (Rafinesque, 1817) in the context of environmental factors. During studies conducted in streams and reservoirs of Southern Poland in 2018–2019 I found that 1) there are geographical limitation for spreading of the studied species – it does not colonize Carpathian rivers, 2) the species is more numerous in channelized sections of small streams compare to natural ones, 3) the studied crayfish revealed body condition related to different habitats, in particular the body condition in dam reservoirs was lower than in streams where these reservoirs are located.

Thus, the Spiny Cheek Crayfish, despite being widely distributed across Europe reveals limitations in colonizing some regions and achieving high population abundance. Despite being well adapted to anthropogenically altered rivers the dam reservoirs may probably affect it negatively. According to presented herein studies, one of the way of mitigating the impact of the spiny cheek crayfish on native ecosystems may be maintaining natural character of aquatic ecosystems. This should be especially valid for European native crayfish conservation.

WSTĘP

Migracje gatunków są procesem naturalnym i zachodzącym od samego początku obecności organizmów żywych na kuli ziemskiej. Jednak, zanim pojawił się człowiek tempo kolonizacji nowych regionów zależało głównie od możliwości dyspersji, migracji i kolonizacji konkretnego gatunku, a także od procesów przyrodniczych odbywających się w różnych skalach czasowych (Tang i Bennet 2010), np. kolonizacji lub rekolonizacji po ustępujących lodowcach, zmianach poziomu morza, wykorzystaniu połączeń pomiędzy lądami w wyniku procesów tektonicznych (np. Segawa et al. 2021). Naturalne bariery straciły jednak na znaczeniu wraz ze wzrostem mobilności człowieka i spowodowanych przez niego modyfikacji środowiska. Szczególne nasilenie przemieszczania się ludzi nastąpiło w epoce wielkich odkryć geograficznych. Od tamtego czasu, na większą niż kiedykolwiek skalę przestrzenną i w bardzo krótkim czasie, nastąpiło celowe i przypadkowe przemieszczanie wielu gatunków roślin i zwierząt (DiCatri 1989). Poza bezpośrednim przenoszeniem gatunków (świadomie lub nie), człowiek wpływa także na mobilność organizmów pośrednio, zmieniając warunki środowiskowe na Ziemi (Davidson et al. 2020, Doherty et al. 2021).

Obecny poziom globalizacji umożliwiający błyskawiczne podróże transkontynentalne, spowodował wzrost częstości i szybkości przemieszczania nowych gatunków na tereny, których być może nigdy nie miałyby szansy skolonizować. Tym samym, zjawisko pojawiania się gatunków obcych dla danego regionu stało się bardzo częste (Seebens et al. 2017). Jednak losy osobników, które trafiły na nowe dla siebie terytoria nie są jednakowe. Część gatunków nie odnosi żadnego sukcesu kolonizacji i proces dyspersji kończy się wówczas wraz ze śmiercią przemieszczonych osobników. W innym przypadku następuje zadomowienie się gatunku w nowym miejscu, ale bez dalszej skutecznej dyspersji. W końcu zdarzają się sytuacje, kiedy następuje szybka dyspersja gatunków obcych, często połączona z wypieraniem rodzimych gatunków, wpływem na przepływ biomasy i energii w ekosystemach, powodowaniem strat w gospodarce i negatywnym wpływem na lokalną różnorodność biotyczną (Pyšek et al. 2020). Ta ostatnia grupa określana jest jako gatunki obce inwazyjne (Weidema 2000). Warto zaznaczyć, że ten ostatni scenariusz nie jest najczęstszy. Gatunek aby stać się inwazyjnym, musi mieć odpowiedni potencjał i trafić do

odpowiedniego siedliska aby mógł rozpocząć proces inwazji. W przybliżeniu około 1 na 10 nowych przybyszów może stać się gatunkiem inwazyjnym (Williamson i Fitter 1996).

Inwazje biologiczne są ważnym zagadnieniem nauk biologicznych i są ściśle związane z ochroną przyrody, ekonomią oraz zdrowiem ludzi i zwierząt (Sujay et al. 2010, Hodgins et al. 2018, Bezerra et al. 2018). Wpływając na procesy przyrodnicze w skali ekosystemów i w odniesieniu do poszczególnych gatunków niosą ze sobą szereg niebezpieczeństw, zarówno dla całych ekosystemów, jak i rodzimych gatunków. Gatunki inwazyjne wypierają gatunki rodzime w wyniku konkurencji i drapieżnictwa (Dueñas et al. 2018), krzyżowania się i utraty unikatowej puli genetycznej (Bay et al. 2021). Mogą także wpływać pośrednio na gatunki rodzime. Przykładem może być przenoszenie chorób i patogenów przez gatunki obce (Foster et al. 2021). Choroby i patogeny mogą nie być szkodliwe dla gatunków je przenoszących (koewoluowały przez tysiąclecia), natomiast mogą być śmiertelne dla gatunków, które wcześniej nie miały z nimi styczności. Takim przykładem jest *Aphanomyces astaci* Schikora, 1906, łęgniowiec powodujący raczą dzumę. Choroba ta cechuje się niską zjadliwością dla północnoamerykańskich raków, natomiast zwykle jest śmiertelna dla gatunków europejskich (Mojžišová et al. 2020). Gatunki obce inwazyjne oddziałują negatywnie nie tylko na gatunki rodzime, ale także na rodzime ekosystemy. Przekształcając środowisko naturalne, w którym się znalazły. Przykładem jest rak Luizjański *Procambarus clarkii* Girard, 1852, który intensywnie kopie nory, co skutkuje znacznymi przekształceniami dna i brzegów siedlisk wodnych oraz wilgotnych terenów lądowych (Emery-Butcher et al. 2020, Correia i Ferreira 1995).

Ważnym aspektem inwazji biologicznych jest ich wpływ na gospodarkę. Szacuje się, że inwazje biologiczne w 2017 r. spowodowały straty ekonomiczne na świecie w wysokości co najmniej 162 miliardów (Diagne et al. 2021). Dlatego badania wyjaśniające sukces inwazji i pozwalające wskazać gatunki z dużym potencjałem inwazyjności są potrzebne.

Spośród dużych grup taksonomicznych zwierząt, w kontekście inwazji biologicznych szczególnie ciekawe są słodkowodne raki (Deapoda: Astacoidea). Jest to licząca około 700 gatunków monofiletyczna grupa dziesięcionogów zamieszkująca głównie słodkie wody obu półkul z centrami bioróżnorodności w Ameryce Północnej i Australii i Oceanii (Crandall i De Grave 2017, Reynolds i Souty-Grosset 2012). Raki słodkowodne są zróżnicowane

ekologicznie. Wśród nich można znaleźć gatunki uzależnione od wód o względnie niskiej temperaturze

i dużym natlenieniu, jak niektóre europejskie gatunki (np. rak szlachetny *Astacus astacus* Linnaeus, 1758 czy rak kamiennik *Austropotamobius torrentium* Schrank, 1803) oraz gatunki związane z terenami bagiennymi, okazjonalnie przemieszczające się po lądzie, czy kopiące nory w pobliżu wody, w środowisku lądowym (np. niektóre amerykańskie raki z rodziny Cambaridae; Reynolds Souty-Grosset 2012). Różne są też rozrodcze strategie gatunków i długość ich życia. Są raki dojrzewające powoli, ale żyjące względnie długo (kilkanaście lat) np. gatunki rodzime dla Europy, lub żyjące krótko (maksymalnie cztery lata) i osiągające szybko dojrzałość płciową, jak raki pręgowate *Faxonius limosus* Rafinesque, 1817, i wiele innych północnoamerykańskich gatunków z rodziny Cambaridae. Co ważne w kontekście inwazji, raki w wielu miejscach świata są ważnym elementem akwakultury i/lub rybactwa śródlądowego, a zatem handlu (Haubrock et al. 2021). Są też częstym obiektem amatorskiej hodowli akwariowej (Weiperth et al. 2019). Zarówno akwakultura jak i branża akwarystyczna sprzyja rozprzestrzenianiu poza ich naturalne zasięgi. Ponadto, ich potencjał kolonizacyjny wynika też z dużej odporności na wysychanie (często mogą przetrwać do kilku dni poza wodą, np. rak Luizjański; Piersanti et al. 2018), co powoduje dużą łatwość w przemieszczaniu żywych osobników przez człowieka, przypadkowo, np. z narzędziami połowowymi, lub intencjonalnie, gdy raki są używane jako przynęty na ryby (Banha i Anastácio 20215). Wiele gatunków jest bardzo płodnych wykazując strategie rozrodcze zbliżone do typu R, a w przypadku gatunków mniej płodnych, duży sukces rozrodczy zapewnia opieka rodzicielska nad jajami i wczesnymi stadiami młodocianymi (wszystkie raki opiekują się potomstwem). U części gatunków występuje też partenogeneza, która umożliwia szybką kolonizację nowych zbiorników wodnych. Jest ona np. jedynym sposobem rozrodu u jednego z najbardziej inwazyjnych raków świata – *Procambarus virginialis* (Lyko 2017). U innych gatunków może też występować okazjonalnie, np. u raka pręgowatego (Buřič et al. 2011).

Skrajne wymagania siedliskowe w obrębie tej grupy zwierząt, pozyskiwanie i handel osobnikami w różnych celach (w tym globalny handel rakami jako zwierzętami akwariowymi), sprawiają, że można tu dostrzec pewien paradoks – wiele gatunków zanika w rodzimych zasięgach (Bland 2017), z drugiej zaś strony część gatunków stała się na obszarach introdukcji groźnymi gatunkami inwazyjnymi zagrażającymi bioróżnorodności

w ogóle (Twardochleb et al. 2013), ale w szczególności innym gatunkom raków. Dobrym przykładem takiej sytuacji jest Europa, gdzie liczba występujących w środowisku gatunków obcych przewyższa obecnie liczbę gatunków rodzimych (Kouba et. al. 2014). Za przyczynę zaniku raków rodzimych poza przekształceniami siedlisk, zanieczyszczeniami i nadmierną eksploatacją, uważa się głównie inwazję obcych gatunków raków, skutkującą konkurencją międzygatunkową i transferem letalnych dla rodzimych raków patogenów.

Obecnie najszerszej rozprzestrzenionym obcym gatunkiem raka w Europie jest rak pręgowaty (pręgowany, amerykański) *Faxonius limosus* Rafinesque, 1817 (do niedawna zaliczany do rodzaju *Orconectes*; Crandall i De Grave 2017). Jest on przedstawicielem rodziny Cambaridae. Jego naturalny zasięg występowania obejmuje północno-wschodnie regiony Stanów Zjednoczonych (Hamr 2002). Gatunek ten osiąga względnie niewielkie rozmiary, żyje zwykle 2–3 lata, przy czym dojrzałość płciową osiąga już pod koniec pierwszego roku życia (rodzime europejskie raki mniej więcej w trzecim roku życia).

Ma stosunkowo niewielkie wymagania siedliskowe i występuje w różnych typach wód, również eutroficznych, niekiedy zanieczyszczonych. Wydaje się jednak, że unika on wód chłodnych np. podgórskich potoków, czy źródłowych odcinków wyżynnych i nizinnych strumieni (Chucholl 2016, Śmietana 2011). Do Europy został sprowadzony w drugiej połowie XIX w., co czyni go gatunkiem raka najwcześniej sprowadzonym na ten kontynent. Jego wprowadzenie było reakcją na zanik rodzimych gatunków raków w wyniku zmian siedliskowych, zanieczyszczenia wód, przełowienia, ale przede wszystkim rozprzestrzeniania się choroby – raczej dżumy (Leńkowa 1962). Rak pręgowaty miał być w akwakulturze substytutem zanikających rodzimych gatunków. Pierwsze introdukcje miały miejsce na terenie dzisiejszej północno-zachodniej Polski (Śmietana 2011). Dalej, intencjonalnie sprowadzono go jeszcze w kilka miejsc na wschód od pierwszych stanowisk. Od tego momentu gatunek ten rozprzestrzenił się na większość krajów Europy, przy czym, o ile w kierunku zachodnim dotarł do Atlantyku (nie wkraczając jednak na większą część Półwyspu Iberyjskiego), to w kierunku wschodnim inwazja przebiegała znacznie wolniej i do tej pory jest gatunkiem jeszcze względnie rzadkim na wschód od granic Polski (Kouba 2014). Biorąc pod uwagę, że jedyna skuteczna introdukcja tego gatunku w Europie była wynikiem wprowadzenia niespełna 100 osobników, co znajduje odzwierciedlenie również w wynikach

badan genetycznych, jest to zwierzę o bardzo dużych możliwościach inwazji (Filipová et al. 2011).

Jednak, pomimo obecności tego gatunku w Europie od ponad stulecia, wiedza o jego biologii, w szczególności na temat czynników wpływających na jego rozmieszczenie i liczebność nie jest duża. Również jeżeli chodzi o jego rozmieszczenie, na mapie Europy występują obszary wskazujące na brak tego gatunku, jednak nie ma pewności, czy rzeczywiście gatunek ten nie występuje tam, czy też jego rozmieszczenie nie zostało wystarczająco dobrze poznane (Kouba 2014). Ciekawym zatem jest, że pomimo zaliczenia *F. limosus* do gatunków obcych inwazyjnych w Europie, w przeglądowej pracy podsumowującej wpływ inwazyjnych gatunków raków na przyrodę skolonizowanych obszarów, brak jest tego gatunku (Twardochleb et al. 2013).

Ze względu na szerokie rozprzestrzenienie i postępującą ekspansję *F. limosus* w Europie oraz niewystarczającą wiedzę na temat biologii i ekologii tego gatunku, istotne jest poznanie czynników sprzyjających jego obecności. Jest to istotne w kontekście naukowym, a także dla sporządzania strategii zarządzania populacjami tego gatunku oraz ochrony rodzimych ekosystemów i gatunków, w szczególności rodzimych europejskich raków słodkowodnych.

CEL BADAŃ I TESTOWANE HIPOTEZY

Celem badań była ocena wpływu wybranych czynników na występowanie, liczebność i biologię raka pręgowatego ze szczególnym uwzględnieniem wpływu antropogenicznych przekształceń rzek.

Aby przetestować wpływ wybranych czynników postawiłem następujące hipotezy:

- 1) Rak pręgowaty nie występuje w naturalnych wodach Karpat – podstawą tej hipotezy jest brak stwierdzeń raka pręgowatego w Karpatach. Mapy rozmieszczenia gatunku dla Polski oraz Europy (Śmietana 2011, Kouba i in. 2014) sugerują, że gatunek dochodzi do podnóży tych gór, jednak nie wkracza na ich obszar. Jedyne potwierdzone do czasu moich badań obserwacje z tego regionu pochodzą z dwóch zbiorników zaporowych: Tresna i Dobczyce, które położone są tuż przy północnej granicy Karpat (Kondracki 2000), a przy tym stanowią silną ingerencję w naturalne

środowisko rzek. Względnie surowy klimat Karpat powinien powstrzymać ten powszechny na niżu gatunek przed przekraczaniem granicy Pogórza (**artykuł 1: Bonk M., Bobrek R. 2020. Invasion on the doorstep: will the Carpathians remain free from the spiny cheek crayfish *Faxonius limosus* (Rafinesque, 1817)?**. *BioInvasions Records* 9 (3): 549–561. DOI: <https://doi.org/10.3391/bir.2020.9.3.10>).

- 2) Hydrotechniczne przekształcenia rzek polegające na prostowaniu koryt sprzyjają zwiększaniu liczebności raka pręgowatego – hipoteza ta została sformułowana na podstawie szeroko rozpowszechnionego przekonania, że ekosystemy zaburzone są bardziej podatne na inwazje biologiczne w porównaniu do ekosystemów o względnie wysokim stopniu naturalności (Byers 2002). W rzekach można to tłumaczyć homogenizacją siedlisk skutkującą ograniczeniem funkcjonalności ekosystemu, np. eliminacją drapieżników i konkurentów gatunku inwazyjnego. Zatem w przypadku odcinków rzek przekształconych i naturalnych (w tym spontanicznie zrenaturyzowanych), większej liczebności raka pręgowatego można się spodziewać na odcinku zmienionym (**artykuł 2: Bonk M., Bobrek R. Does river channelization increase the abundance of invasive crayfish? Survey of *Faxonius limosus* in small Central European streams. *Environmental Science and Pollution Research*: DOI: 10.1007/s11356-021-12750-y**).
- 3) W zbiornikach zaporowych kondycja osobnicza raków pręgowatych jest wyższa w porównaniu do kondycji raków w odcinkach rzek nieprzekształconych w sztuczne jeziora. Kondycja osobnicza (ang. *body condition*) to związek masy ciała zwierzęcia z wybranym wymiarem liniowym (najczęściej długością ciała). Kondycja wskazuje jak skutecznie osobniki korzystają z zasobów troficznych środowiska. W lepszych warunkach siedliskowych, dany gatunek powinien wykazywać lepszą kondycję. Jeżeli więc antropogeniczne przekształcenia rzek w postaci sztucznych zbiorników wpływają dodatkowo na obecność lub liczebność gatunku, należy tam oczekiwać efektu widocznego w jego kondycji (**artykuł 3: Bonk M., Amirowicz A. 2022. The body condition of invasive crayfish *Faxonius limosus* (Raf., 1817) (Decapoda: Cambaridae) is better in small rivers than in dam reservoirs in Central Europe. *Environmental Science and Pollution Research* DOI: <https://doi.org/10.1007/s11356-022-19678-x>**).

METODYKA

Szczegóły metodyki omówiono w każdym z artykułów będących częścią niniejszej rozprawy. Badania przeprowadzone w Karpatach (hipoteza 1, artykuł 1) oparte były na inwentaryzacji wybranych odcinków dużych górskich rzek. Odcinki wybrano tak, aby w danym miejscu badana rzeka była jak najbardziej zbliżona pod względem wielkości zlewni (co przekłada się na wielkość rzeki), odległości od źródła (co determinuje postać ekosystemu rzeki zgodnie z koncepcją rzeczno-kontynuuum) i wysokości nad poziomem morza (co określa warunki termiczne siedliska) do rzeki Raby na wysokości Zbiornika Dobczyckiego. Zbiornik ten jest położony w Karpatach, przy ich północnej granicy, a rak pręgowaty występuje w nim licznie, co najmniej od dekady. Badania terenowe opierały się na poszukiwaniu raków podczas brodzenia w nocy. Skuteczność tej metody w inwentaryzacji występowania raków przetestowałem w pracy nie włączonej do niniejszej rozprawy (Bonk i in. 2019).

Badania dotyczące liczebności raków w zależności od stopnia naturalności rzeki (hipoteza 2, artykuł 2) prowadzone były w sąsiadujących przekształconych i naturalnych odcinkach wybranych rzek Polski południowej. Na pięciu rzekach wyznaczyłem łącznie osiem par odcinków różniących się stanem hydromorfologicznym tj. zmiennością głębokości, liczbą meandrów, liczbą odsypów oraz obecnością korzeni drzew i pokryciem lustra wody makrofitami. Na każdym odcinku wyznaczyłem po pięć punktów, w których latem odławiałem raki w nocy z dna siatką uzbrojoną w metalowe grabie. Analizowałem zmienną zależną (liczba raków w jednym punkcie) w odniesieniu do zmiennych niezależnych: rodzaju siedliska (zmienione vs. naturalne) oraz lokalizacji (jednej lokalizacji odpowiadała jedna para odcinków).

Badania dotyczące kondycji (hipoteza 3, artykuł 3) prowadzone były w trzech parach zbiornik – rzeka, w jednej zlewni (Nida, dopływ górnej Wisły). Każda para znajdowała się na innej rzece. Raki odłowiono ręcznie w ciągu jednego miesiąca jesienią 2019 r. brodząc w nocy. Zarówno w rzekach jak i zbiornikach odłowu prowadzono w typowych dla nich mezohabitatach zbierając wszystkie zauważone osobniki. Złowione raki ważono i mierzono w warunkach laboratoryjnych. Jako wymiar liniowy odzwierciedlający wielkość osobników wykorzystano długość karapaksu. Celem analizy danych biometrycznych było wykrycie

potencjalnych różnic w kondycji osobniczej raków w zależności od dwóch typów siedlisk (zbiornik vs. rzeka) i lokalizacji pary siedlisk, a także płci i wielkości osobników.

WYNIKI I ICH OMÓWIENIE

Brak gatunku w Karpatach jako prawdopodobny wynik górskiego klimatu (hipoteza 1, artykuł 1)

Badania terenowe przeprowadzone w głównych karpackich rzekach nie potwierdziły występowania raka pręgowatego w tym paśmie górskim w rzekach o biegu naturalnym lub nieznacznie zmienionym. Rzeki Skawa, Biała, Wisłoka, Ropa, Jasiołka i Wisłok na odcinkach podobnych pod względem wielkości zlewni, wysokości nad poziomem morza i odległości od źródła do Raby w miejscu występowania raka pręgowatego, były od niego wolne. Jedynym gatunkiem raka stwierdzonym w części z tych rzek był rak szlachetny. Rak pręgowaty został stwierdzony jedynie w Sole, kilkaset metrów powyżej cofki Zbiornika Tresna i w Wiśle w pobliżu północnej granicy Karpat Zachodnich jednak formalnie już poza tymi górami. Przyczym, to ostatnie stanowisko znajdowało się w odległości kilkunastu kilometrów powyżej Zbiornika Goczałkowickiego, który jest znanym miejscem występowania raka pręgowatego. Ponadto, rak pręgowaty został wykryty w Zbiorniku Tresna oraz w dwóch jego mniejszych dopływach w odległości do ok. 2 km od ich ujść do zbiornika. W przypadku Zbiornika Dobczyckiego rak pręgowaty został wykryty w kilku miejscach w samym zbiorniku jednak nie stwierdziłem jego obecności w żadnym z jego dopływów łącznie z rzeką Rabą w pobliżu jej ujścia do tego zbiornika. W wyniku dodatkowych obserwacji dla pozostałych dużych zbiorników: Czorszyńskiego, Rożnowskiego, Klimkówka i Sieniawa-Besko nie stwierdzono tam jego występowania. Wyniki moich badań wskazują, że rak pręgowaty nie jest w stanie skutecznie skolonizować naturalnych rzek Karpat, i tworzy stabilne populacje jedynie w nietypowych dla tego regionu siedliskach wodnych – zbiornikach zaporowych. Wyniki te są zgodne z obserwacjami innych autorów z innych części Europy. Gatunek jest rzadki w Alpach i występuje głównie w zbiornikach wód stojących i w ich pobliżu (Hefti i Stucki 2006). Z kolei w Niemczech modelowanie przeprowadzone przez Chucholla (2016) wykazało, że gatunek ten unika górnych biegów strumieni położonych na terenach podgórskich. Prawdopodobną przyczyną wpływającą na małe możliwości kolonizacji Karpat przez raka pręgowatego jest

niższa temperatura wody w rzekach oraz nie odpowiadające temu gatunkowi warunki hydromorfologiczne w potokach, które zwykle zachowały swój naturalny charakter.

Pozytywny wpływ regulacji rzek na liczebność raka pręgowatego (hipoteza 2, artykuł 2)

Wyniki badań przeprowadzonych w ośmiu parach siedlisk rzecznych (przekształconych i naturalnych) w pięciu rzekach południowej i środkowej Polski sugerują, że gatunek liczniej występuje w odcinkach przekształconych. Zależność nie jest jednak uniwersalna i dotyczy cieków najmniejszych. W większych rzekach (Warta i Kamienna) nie obserwowałem pozytywnego wpływu ingerencji hydrotechnicznych na liczebność osobników. Takie wyniki można tłumaczyć niejednakowym wpływem homogenizacji środowiska na cieki małe i duże. W małym cieku, regulacja powoduje likwidację plos, a więc najgłębszych fragmentów koryta. W efekcie, w przekształconym korycie, w którym pierwotnie mogły występować głębokości sięgające często ponad 1–1.5 m, maksymalne głębokości zwykle nie przekraczają kilkudziesięciu centymetrów. To powoduje zmniejszenie liczby lub całkowitą eliminację siedlisk odpowiednich dla ryb zjadających raki, a więc pośrednio ogranicza presję drapieżniczą na nie. W przekształconych korytach większych rzek głębokości często nadal sięgają 1 m lub więcej, co sprawia, że presja drapieżnicza ze strony ryb może się tam nadal utrzymywać. Choć wyniki wykonanych badań wskazują na to że, że regulacje małych cieków mogą promować występowanie i większą liczebność raków pręgowatych oraz są zgodne z hipotezą o pozytywnym wpływie zaburzeń w środowisku na inwazje biologiczne, to jednocześnie zachęcają do kontynuowania badań w celu precyzyjnego określenia odpowiedzialnych za to czynników.

Wpływ zbiorników zaporowych na kondycje osobniczą raka pręgowatego (hipoteza 3, artykuł 3)

W zbiornikach zaporowych kondycja raków okazała się niższa niż w odcinkach rzek poniżej nich, czyli otrzymane wyniki okazały się sprzeczne z przewidywaniami. Ponadto, kondycja w dużej mierze zależała nie tylko od rodzaju siedliska (zbiornik vs. rzeka), ale też od lokalizacji (istniały różnice w kondycji pomiędzy poszczególnymi parami zbiornik – rzeka). Stwierdziłem zatem, że zbiorniki wpływają na kondycję raków pręgowatych, ale w sposób negatywny. Może się zatem wydawać, że nie sprzyjają one inwazji raków pręgowatych. Jednak wniosek taki byłby sprzeczny z wynikami uzyskanymi w Karpatach (*artykuł 1*) oraz dla raka

sygnałowego *Pacifastacus leniusculus* (Dana, 1852) w USA (Light 2003). Zatem trzeba podkreślić, że zbiorniki mogą sprzyjać inwazji, szczególnie jeżeli budowane są w górnych biegach rzek, zwykle niedogodnych dla gatunku (Chucholl 2016). Są tam środowiskami, gdzie mogą rozwinąć się żywotne populacje lokalne, a raki trafiają do nich zwykle zawlekanie przez wędkarzy jako przynęta. Różnice w kondycji między osobnikami pochodzącymi z rzek i zbiorników można zatem interpretować nie tylko jako negatywny lub pozytywny wpływ danego rodzaju siedliska, a efekt różnej strategii alokacji zasobów w tkankach osobników korzystających z różnych środowisk.

WNIOSKI

Rak pręgowaty jest gatunkiem pospolitym w Polsce i większości krajów Europy. Zajmuje różne siedliska wodne, co świadczy o jego plastyczności ekologicznej. Jego ekspansja jest jednak limitowana przez czynniki działające w skali geograficznej i lokalnej.

Na podstawie wyników moich badań można stwierdzić, że gatunek ten:

- 1) nie kolonizuje siedlisk rzecznych w Karpatach, o ile nie znajduje oparcia w zbiornikach zaporowych,
- 2) ma tendencję do liczniejszego występowania w przekształconych hydrotechnicznie odcinkach małych rzek,
- 3) na wyżynnych obszarach poza Karpatami zbiorniki zaporowe nie zapewniają możliwości osiągnięcia lepszej kondycji osobniczej niż w miejscowych rzekach, zatem nie można tam mówić o ich jednoznacznie pozytywnym wpływie na gatunek.

Pomimo dużego sukcesu kolonizacyjnego w Europie, istnieją siedliska wodne, które są dla raka pręgowatego suboptymalne. Zaliczyć do nich należy rzeki górskie środkowej Europy, co stwierdzam na podstawie obserwacji występowania tego gatunku w Karpatach, gdzie jest spotykany tylko wyjątkowo w sąsiedztwie zbiorników zaporowych.

Brak raka pręgowatego można tłumaczyć tam niższą niż optymalna dla tego gatunku temperaturą wody. Ponadto, szczególnie w niższych położeniach, duże znaczenie może mieć stopień naturalności ekosystemu rzeki – im bardziej naturalny, tym jest mniej podatny na inwazję.

Te suboptymalne siedliska, w szczególności górne odcinki niewielkich potoków są często siedliskiem raka szlachetnego (jedynego gatunku raka notowanego regularnie w karpackich ciekach, zarówno małych potokach jak i dużych rzekach). Można więc wnioskować, że zachowanie naturalnego biegu rzek, a zwłaszcza niewielkich potoków górskich i wyżynnych, może ograniczyć ekspansję raka pręgowatego i ułatwić ochronę rodzimych europejskich gatunków raków związanych z rzekami (w szczególności *A. astacus*, *Austropotamobius torrentium*, i *A. biharensis* (Pârvulescu, 2019)).

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Bonk M., Bobrek R. 2020. Invasion on the doorstep: will the Carpathians remain free from the spiny cheek crayfish *Faxonius limosus* (Rafinesque, 1817)? *BioInvasions Records* 9 (3): 549-561. <https://doi.org/10.3391/bir>. 2020.9.3.10

Research Article

Invasion on the doorstep: will the Carpathians remain free from the spiny cheek crayfish *Faxonius limosus* (Rafinesque, 1817)?Maciej Bonk^{1,*} and Rafał Bobrek²¹Institute of Nature Conservation, Polish Academy of Sciences, al. Adama Mickiewicza 33, 31-120 Kraków, Poland²Polish Society for the Protection of Birds ul. Odrowąża 24, 05-270 Marki, Poland

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Received: 7 January 2020**Accepted:** 13 April 2020**Published:** 12 June 2020**Handling editor:** Christoph Chucholl**Thematic editor:** Karolina Bącela-Spychalska**Copyright:** © Bonk and BobrekThis is an open access article distributed under terms of the Creative Commons Attribution License ([Attribution 4.0 International - CC BY 4.0](https://creativecommons.org/licenses/by/4.0/)).**OPEN ACCESS****Abstract**

The success of biological invasions relies, among other factors, on the abiotic environment. The presence or absence of an invasive alien species in its non-native range may therefore be helpful in understanding the factors facilitating or hampering its invasion. The aim of our study was to determine whether the Carpathians are free from the spiny cheek crayfish *Faxonius limosus* (Rafinesque, 1817), a successful freshwater invader in Europe and locally in Africa. We hypothesised that local factors, mostly climate (i.e. water temperature), have an impact on this species, limiting its spread. However, atypical local habitats with suitable abiotic conditions—in particular artificial reservoirs—might be hubs for *F. limosus*. The study was conducted in 2018 in Carpathian waters. We found that despite being present in plain areas adjacent to the Carpathians for decades, *F. limosus* does not ingress deeper into this mountain range. The exceptions are two dam reservoirs and the lower reaches of some of their tributaries, close to their inflows. The Carpathians are climatically distinct from the surrounding areas, which is also reflected in mean water temperature – ca. 1.5 °C lower than in adjacent lowland areas. Thus, we suggest that relatively severe climate may be the main reason behind the limited range of *F. limosus* in mountains. However, other factors, like current velocity, substrate type, or slope, may contribute to the absence of the species in the studied area. Dam reservoirs providing warmer aquatic habitats and lentic environment may facilitate its invasion related to climate warming.

Key words: biological invasions, climate change, mountain ecosystem, Cambaridae**Introduction**

The recent high volume of international transport leads to enormously fast species dislocation around the World. On a global scale, the number of dislocated species has reached approx. 45,000, and 17,000 of them have successfully colonised non-native ranges (Seebens et al. 2017). Becoming invasive species, they lead to major socio-economic and environmental losses (Gurevitch and Padilla 2004; Clavero and García-Berthou 2005; Pimentel et al. 2005), including in aquatic ecosystems (Keller et al. 2018). The success of the biological invasion depends on a complex set of factors which may be divided in two main categories: 1) species biology and

2) ecosystem susceptibility (Barney and Whitlow 2008). Understanding the factors driving the success of invasive alien species is crucial to both predicting and reducing the threats posed by them (Yonvitner et al. 2020). Furthermore, defining the features of areas free from invaders is important in the context of local biodiversity conservation.

Areas naturally resistant to given species invasion may become more susceptible to invasion when altered by human activity (Marvier et al. 2004). In riverine ecosystems, major alterations are dam reservoirs which turn lotic habitats into lentic ones. Dam reservoirs, as man-made habitats, are more susceptible to colonisation by alien species (Strayer and Dudgeon 2010; Wilk-Woźniak and Najberek 2013). Besides hydromorphological changes, dam reservoirs may provide optimal temperature conditions in relatively cold areas. This is especially important in mountains, where shallow streams and rivers may reach temperatures near 0 °C during the winter, whereas deep dam reservoirs still offer at least approx. 4 °C (Mihu-Pintilie et al. 2014).

Invasions are also related to invading species' colonisation potential. In freshwater ecosystems, some of the most successful invaders are crayfish species, which are among the largest aquatic invertebrates (Twardochleb et al. 2013). It is accepted that more than 30 species of crayfish have been translocated into new areas (Gherardi 2010) due to commercial enterprises as a food source or due to the pet trade (Padilla and Williams 2004; Chucholl and Wendler 2017; Patoka et al. 2018; Yonvitner et al. 2020). A relatively high resistance to dehydration improves their ability to disperse among waterbodies, for example in fishery equipment (Kouba et al. 2016). Thus, some of them are considered to be highly invasive organisms worldwide, and their negative impact on local diversity, including indigenous crayfish, is well documented (Twardochleb et al. 2013). Both in native ranges and the areas of their invasion, they often affect biomass and energy flow in food webs (Pacioglu et al. 2020). North American crayfish are also carriers of crayfish plague, *Aphanomyces astacii*, causing mass mortalities among native European crayfish (Mrugała et al. 2017; Putra et al. 2018).

One of the most successful species of crayfish invader in Europe is the spiny cheek crayfish *Faxonius limosus* (Rafinesque, 1817). This North American cambarid species is native to the Districts of Columbia, Pennsylvania, Maryland, New Jersey, New York, Virginia and West Virginia (Hamr 2002). The introduction into Europe started in 1890, with ca. 100 individuals released in experimental breeding ponds in Berneuchen, Germany (now Baranówko in north-western Poland; Śmietana 2011). Next, the species was transferred to other regions in Poland, Germany, Austria and France (Holdich 2002). Recent genetic analysis supports the hypothesis that the successful introduction in Europe happened only once, and thus this relatively small number of individuals became ancestors of the entire European (meta)population of this species (Filipová et al. 2011). It was

noted that invasion success in this species may result from higher fecundity of females colonising new areas (Pârvulescu et al. 2015), but crayfish plague transmission and successful competition is also important (Lele and Pârvulescu 2017; Pârvulescu et al. 2012). Despite being widely distributed across Europe, there are some observations of uneven occurrence of *F. limosus*. It has been demonstrated that mountains are less invaded than lowlands and lower uplands by this species (Kouba et al. 2014). This is also true for the Carpathians, a region with a distinctly colder climate than the adjacent areas (Hess 1965; Kottek et al. 2006). Besides the climate, the montane or submontane character of the watercourses may also hamper the species' invasion (Petrušek et al. 2006). In this mountain range only records near the edge of the region have been known to date (Pârvulescu et al. 2012; Kouba et al. 2014; Lele and Pârvulescu 2017), with evidence for negative impact on native crayfish species. On the other hand, if global warming progresses further - as the predictions demonstrate (IPPC 2018) - we can also expect an increase in water temperature in mountain rivers. As a result, further invasion of *F. limosus* into mountain rivers by populations living at the edge of the region is possible. However, other factors, like current velocity, substrate type, etc. might negatively affect the invasion.

The purpose of our study was to determine whether rivers of the Carpathians are free from *F. limosus* (Hamr 2002). The second aim was to investigate whether the species is present in large Carpathian dam reservoirs, which feature lentic conditions and warmer water than the prevalent natural streams.

Materials and methods

Study area

We conducted studies at 41 sites located in nine rivers in the Western Carpathians within the Polish borders. All nine (including the Raba river) of the studied streams lie in the Vistula river drainage area and, with the exception of two of them (rivers Ropa and Jasiołka), all drain both the Carpathian and Subcarpathian areas. Additionally, as *F. limosus* was known only from dam reservoirs, we investigated five dam reservoirs in the Carpathians and one adjacent to the northern Carpathian border (see map, Figure 1). We defined the borders of the Carpathians according to Kondracki (2000). The reference site of the field inventory was the Dobczyce dam reservoir, where the presence of *F. limosus* was confirmed several times (A. Amirowicz 2018, *pers. comm.*). For the field inventory in rivers, we looked for localities similar in terms of distance from the source of the river, altitude and drainage area to the Raba river in the location where it has been altered into the Dobczyce reservoir (49.876671°N; 20.083284°E, Figure 1).

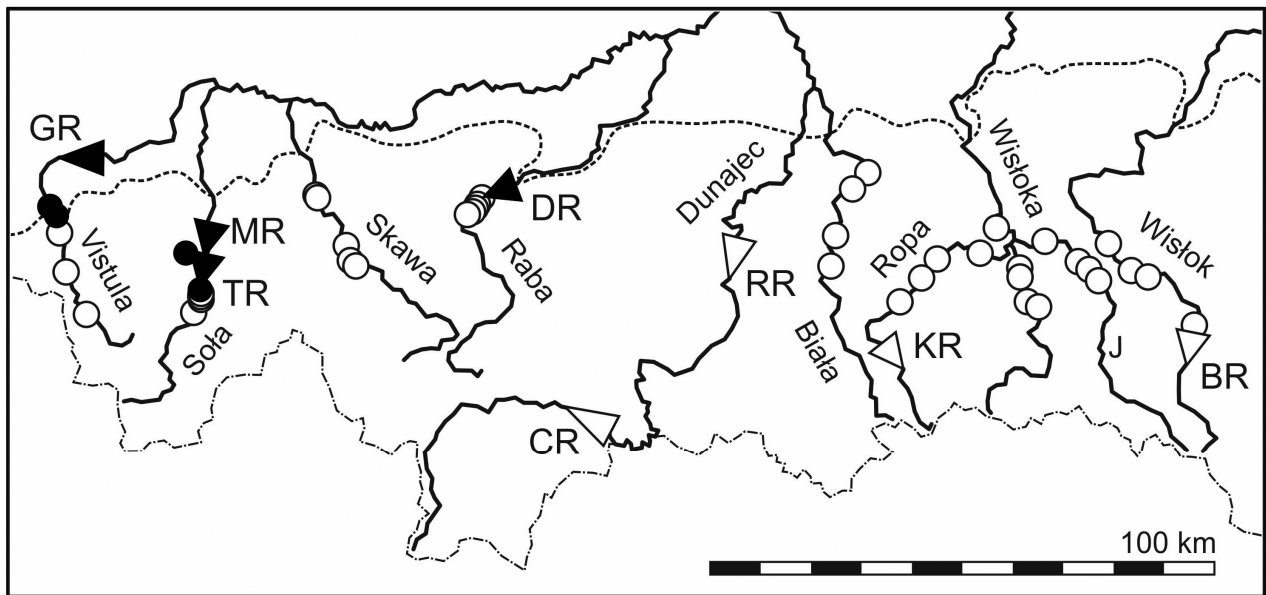


Figure 1. Results of the inventory of *Faxonius limosus* in the main rivers (circles) and reservoirs (triangles) in the Polish part of the Western Carpathians in 2018: J – Jasiołka river, BR – Besko reservoir, CR – Czorsztyń reservoir, DR – Dobczyce reservoir, GR – Goczałkowice reservoir, KR – Klimkówka reservoir, RR – Rożnów reservoir, TR – Tresna reservoir and MB – Międzybrodzkie reservoir. The dashed line shows the northern border of the Carpathians according to Kondracki (2000). Symbols filled with black indicate the presence of the species. *Faxonius limosus* was also detected in two tributaries of the Tresna reservoir, not shown in the map due to picture clarity (see Supplementary Table S1 for details).

Field inventory of crayfish

Within each of the selected river sections, we chose three to five 200–420-m long sampling sites for the crayfish inventory (Supplementary material Table S1). Moreover, we also surveyed the Raba river at five sites located up to about 3 km upstream from its inflow to the Dobczyce reservoir. During the summer of 2018 we searched for crayfish along parts of the rivers where the bottom was clearly visible (visual encounter survey), according to the method described by several authors (Reynolds et al. 2010; Marzec and Okrągła 2018; Bonk et al. 2019). In all the sites we conducted surveys at least several days after rainfall to avoid elevated water level and increased turbidity, and for safety requirements. Apart from the rivers, we also surveyed dam (artificial) reservoirs. In each dam reservoir we conducted at least one 30-minute night check in shallow shore habitats after sunset. The two largest, the Rożnów and the Czorsztyń reservoirs, were checked twice. Due to the already known presence of the species in the Dobczyce reservoir, we also checked eleven 200-m sites on all its six tributaries with the same method as the other river sections. In the Tresna reservoir, after confirmation of *F. limosus* presence, we additionally investigated three sites in two tributaries (Table S1). According to the other observations from stagnant waterbodies (Bonk et al. 2019), the visual encounter survey was assumed to be a satisfactory method for sampling mountain reservoirs.

Water temperature

To describe the water temperature in Carpathian watercourses and adjacent lowlands, we used data of mean temperatures of the Vistula and its tributaries in the Carpathians and the area adjacent to the Carpathians (Data of the Chief Inspectorate of Environmental Protection, referred hereafter as CIEP). In total, we collected temperature data from nine rivers and 59 measuring points. Data were collected from 2008 to 2017. Temperature data were also available for two dam-reservoirs from the period 2011 to 2016. We compared temperatures between lowlands and mountains using the GLM procedure performed in R 3.5.1 (R Core Team 2018) with gamma error distribution.

Results

Field inventory of crayfish

In the range of the Carpathian Mountains we detected *Faxonius limosus* only in one river resembling the Raba river (the Soła river); in this case we found crayfish near the inflow of the dam reservoir (Table S1, Figure 1). At the site in the Vistula river located close to the Carpathian borders, but outside their boundary, we found only one exuvium of a juvenile individual. We also confirmed the presence of *F. limosus* in three reservoirs: one adjacent to the Carpathians (the Goczałkowice reservoir), and two in the Carpathians (the Tresna reservoir and the Dobczyce reservoir, Table S1, Figure 1). Moreover, individuals of *F. limosus* were present in two small tributaries (the Żylica and Łękawka brooks) of a Carpathian reservoir (the Tresna reservoir), upstream from their inflows into the reservoir. In six tributaries of the Dobczyce reservoir (border of the range of the Carpathians), including the Raba river above the reservoir, we did not find any specimens of *F. limosus*. In other studied rivers the species was also not recorded.

Water temperature

Sites located within the Carpathians were on average colder than sites outside the mountain range. The difference between these two categories was on average 1.51 °C ($p < 0.05$, Table S2). The temperatures differed among the rivers, although the interaction between particular rivers and the location of measuring points was not significant, showing that the temperature differences are highly related to the region (Carpathians vs. Subcarpathians). For two dam reservoirs for which data were available and where the inventory for crayfish was conducted, the temperatures were higher by *ca.* 8 °C for the Sieniawa-Besko reservoir compared to the montane sections of Carpathian rivers, and by *ca.* 6 °C for the Goczałkowice reservoir compared to lowland sections of the studied rivers.

Discussion

Faxonius limosus is widespread in Europe (Kouba et al. 2014; Puky and Schád 2006). It is relatively evenly distributed in lowlands near the northern Carpathian border (Kouba et al. 2014; Śmietana 2011; M. Bonk and K. Kukuła 2019, *unpublished data*) and is also present in lowlands southward from the Carpathians (Pârvulescu et al. 2009, 2012, 2015; Lele and Pârvulescu 2017). Despite being found at the margins of the Carpathians, to our best knowledge it does not penetrate submontane/montane river courses within the region, except the Dobczyce reservoir, the Tresna reservoir environs, and in the Międzybrodzie Reservoir (Śmietana et al. 2018). Our findings are consistent with the available species distribution maps for Europe (Kouba et al. 2014) and for Poland (Śmietana 2011). In addition, other contributions concerning crayfish in the area do not confirm *F. limosus* presence therein (Bonk et al. 2014; Bylak and Kukuła 2015). Moreover, the species was also not detected in the Carpathians during the national monitoring of the noble crayfish *Astacus astacus* (Linnaeus, 1758) (GIOŚ 2014, 2018) based on baited traps and a visual encounter survey method (Bonk et al. 2019), and during citizens' crayfish data collection (the data from 20 observers collected from 2013 to 2019 showed only *A. astacus* presence within the Polish part of the Carpathians; M. Bonk 2019, *unpublished data*).

The species has been known from plain landscape adjacent to the Carpathians (the Kotlina Oświęcimska basin, Vistula drainage) for at least five decades (Śmietana 2011); in addition, in the lowlands of Romania near the Carpathians it has been known for at least several years (Pârvulescu et al. 2009). Notably, the maximum yearly spreading rate is estimated at up to 24 km per year (Hudina et al. 2009). Pârvulescu et al. (2012) recorded 14 km distances of spreading of the species. Distribution maps for Poland and Europe from the last decade (Śmietana 2011; Kouba et al. 2014; Śmietana et al. 2018) suggest *ca.* 11 km per year on average (according to the time of the introduction and Euclidean distance from the site of the first stocking to the westernmost European sites in France). Thus, the Carpathians should already have been colonised by *F. limosus*, whereas we detected the species only in three dam reservoirs on the edge of the Carpathians, and only exceptionally found it in montane or submontane watercourses feeding one of these reservoirs. This leads to the question: what are the factors affecting the invasion in this mountain range?

Faxonius limosus is considered to prefer a mild climate. Its breeding success is related to relatively warm temperatures (Dubé and Portelance 1992). Thus, one of the possible explanations of *F. limosus* absence in the studied area may lie in the water temperature. The Carpathians are climatically distinct from adjacent areas in Central Europe. The annual mean temperature decreases with increasing altitude by an average rate of

0.5 °C per every 100 m of elevation (Hess 1965). This results in vertical climatic zones in the mountain range. Climate conditions are also seen in water temperatures in rivers, which are typically lower in their Carpathian reaches of the studied rivers than in the lowland ones – as the monitoring data from the last decade in Poland show. One may argue that extreme temperatures may be more important, however, means reflect also the length of a cold season. In our study both in Subcarpathian and Carpathian reaches extremes reaching 0 °C have occurred during the last decade (CIEP). Additionally, in *F. limosus* individuals recovery after freezing down to –15 °C for 40 minutes was observed (J. Dołęga, M. Bonk *unpublished data*). Thus, an invasive species potentially moving upstream in a Carpathian water course needs to undergo generally more severe climatic conditions than in the surrounding areas, for instance “snow climate, fully humid with warm summer” (Dfb type; Kottek et al. 2006). Notably, the main area of the geographical distribution of *F. limosus* in Europe overlaps with milder “warm temperate climate, fully humid with warm summer” (Cfb type; Kottek et al. 2006), and the spreading was much more successful into the milder climate of Western Europe than the spreading into the more severe eastern part of the continent. According to the published data, the spreading speed of this crayfish is *ca.* 1.5 times higher westwards than eastwards (Kouba et al. 2014). *Faxonius limosus* does not exceed the lower parts of the temperate warm zone (defined by Hess 1965) in the Carpathians, and even there it occurs only occasionally. Thus, the distinctly lower average temperature, including water temperature, may be an important factor explaining the absence of the species in the considered part of the Carpathians.

In the studied area, *F. limosus* reaches an altitude of 358 m a.s.l. (in the Żylica brook; Table S1), which is much lower than records from some other localities from European mountain ranges. According to the map presenting data from the Swiss Alps, *F. limosus* inhabits sites there up to 889 m a.s.l. (Hefti and Stucki 2006). The highest occupied site is the Sihlsee reservoir, followed by two alpine lakes—Lake Brienz and Lake Thun—at 564 and 558 m a.s.l., respectively. This seems to be contrary to our findings. However, the temperatures of the main rivers therein (the Aare and the Rhine rivers) are closer to those obtained recently for the drainage of the upper course of the Vistula river and non-Carpathian parts of its tributaries (Uehlinger et al. 2009, CIEP data), thus resembling the water temperatures in the Subcarpathian lowlands rather than in the Carpathians, even at lower altitudes. Also, the temperate warm zone (as defined by Hess 1965), which is hardly colonised by *F. limosus* in the Carpathians (only within or nearby dam reservoirs), in the Alps starts at higher altitudes (Hess 1965), suggesting the optimal thermal condition for this species in highly located sites. Moreover, the Aare river seems to be incomparable with the studied Carpathian rivers as it is several times larger in terms of distance from the

source and the catchment area. The Aare river downstream from Lake Biel at 429 m a.s.l is the only riverine area for the common occurrence of *F. limosus* in Switzerland (Hefti and Stucki 2006), whereas the majority of records from that area (the Swiss Plateau) originate from lakes at considerably lower altitudes, below 500 m a.s.l. Also, Beran and Petrusek (2006) found this species in the Lipno Reservoir (726 m a.s.l.), far from the next downstream lowland site in the Vltava River at České Budějovice (ca. 380 m a.s.l.). The climate hypothesis is also consistent with the presence of *F. limosus* only within dam reservoirs in the area of our study. According to data from Carpathian rivers and reservoirs, the mean annual temperature for reservoirs may exceed the temperatures in rivers by about 8 °C (CIEP). Studies from the Ropa river and Klimkówka reservoir showed that the reservoir cools the water in the river downstream in summer but increases its temperatures in winter (Wiejaczka 2011). It is also worth noting that the edge of the *F. limosus* range in north-eastern Central Europe, with a relatively severe climate (Dfb type; Kottek et al. 2006), overlaps spatially with glacial lakelands (Kouba et al. 2014; Śmietana 2011; Aklehnovich and Razlutskiy 2013). Also, within the native range of the species, ingression into the relatively severe Dfb climate type (Kottek et al. 2006) overlaps with the lakelands of New York State (Hamr 2002). Dam reservoirs, as stagnant waterbodies, may thus support the occurrence of the species in mountains by providing suitable temperature conditions, supporting the idea that climate is a major factor limiting *F. limosus* dispersion in the mountains.

The recent climate of the Carpathians may hamper *F. limosus* invasion. However, compared to the preindustrial level, global temperature has increased by 1.5 °C, and an increase of 1.4 to 4.9 °C is predicted within the next 100 years (Karl and Trenberth 2003; Easterling and Wehner 2009; IPCC 2018). Also, the temperature of water ecosystems is rising, as observed in the Dobczyce reservoir, where an increase rate of 0.75 °C has been observed for a decade (Amirowicz 2013). If climate is a major obstacle for *F. limosus* to colonise the Carpathians, we cannot exclude further colonisation there independently of dam reservoirs, given that montane areas are considered to be highly prone to climate warming (Pepin et al. 2015). This global process will cause shifts in the vertical pattern of the organisms' distribution, which has also been noted in the Carpathians (Kaczka et al. 2015). As predicted, some warm water invasive crayfish may increase their range in Europe (Capinha et al. 2012) northwards as the climate increasingly warms. Also, most probably, *F. limosus*, avoiding cooler upland streams, may eventually colonise higher elevated regions.

Despite the fact that climate seems to be a one of the factors limiting the colonisation abilities of *F. limosus* in Europe, other factors should also negatively affect the species therein. The Carpathian river systems are dominated by small headwater streams with steep channels and a cobble bottom substrate, often dislocated during flood events. To the contrary,

lowland watercourses near the Carpathians colonised by the species have mostly sandy bottoms (authors' own observations). This may be an additional factor hampering colonisation, as streams with the occurrence of bottom substrate dislocation events are considered to be a suboptimal habitat for *F. limosus* (Hamr 2002 and Peay and Füreder 2011). In our study area, only Carpathians watercourses colonised by this species were, besides the small distances to reservoir, located within a relatively plane region of the Żywiec Basin. A similar explanation was also suggested for another North American crayfish, the signal crayfish *Pacifastacus leniusculus* (Dana, 1852), which is less common in high gradient streams in the upland landscape of California (Light 2003). Notably, the abundance of *P. leniusculus* in that area was also positively related with decreasing distance to artificial reservoirs. Subcarpathian watercourses colonised by *F. limosus* are located in plane or low upland landscapes providing less steep slopes. Again, both climate and landscape-connected factors are mitigated by the stagnant water of dam reservoirs, and thus these man-made habitats may act as hubs for survival and potential upward spreading into Carpathians rivers.

Further studies on more variables, like current velocity, hydromorphology, water chemistry, biotic elements, and variables other than climatic variables, are needed for a better understanding of the absence of *F. limosus* in the Carpathians. This requires sampling from a wider range, including the presence sites near this mountain range. The 41 sites investigated in our study can be used in future for the monitoring of potential colonisation of Carpathian rivers by other invasive crayfish. Assuming the limited spreading of *F. limosus* in the Carpathians (whatever the limiting factors are), due to the potential difficulties in the colonisation of such mountainous regions, such areas create opportunities for preserving indigenous crayfish species. In the Western Carpathians this mostly concerns *A. astacus*, which was the only crayfish species observed during our survey in the main Carpathian rivers (M. Bonk *unpublished data*), as also supported by citizens' data and national monitoring. Other parts of the Carpathians may also be refuge for native stone crayfish *Austropotamobius torrentium* (von Paula Schrank, 1803), and the recently described *Austropotamobius biharensis* Pârvulescu, 2019 (Pârvulescu 2019). On the other hand, reservoirs probably create more optimal conditions for *F. limosus* and facilitate the spreading of the crayfish itself or their diseases, according to the stepping stones population model (Havel et al. 2005). Therefore, preserving the natural conditions of montane rivers should be considered as one of the ways of reducing *F. limosus*' impact on *A. astacus* in the Carpathians. The Carpathian rivers and streams may provide "ark sites" (cf. Peay and Füreder 2011) for the conservation of native and endangered European crayfish. Unfortunately, other invading Europe crayfish species may not be susceptible to the severe Carpathian conditions. This may be especially true for *P. leniusculus*, with

closer to indigenous crayfish species ecology (Chucholl 2016). Nonetheless, stopping the invasion of at least one important invader makes this mountain range of special conservation value in contrast to the lowlands nearby.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Sites controlled in Carpathian rivers and dam-reservoirs with *Faxonius limosus* occurrence (1) and absence (0) data.

Table S2. Water temperatures in Carpathian and Subcarpathian rivers in relation to localisation (Carpathians vs. lowlands).

This material is available as part of online article from:

http://www.reabic.net/journals/bir/2020/Supplements/BIR_2020_Bonk_Bobrek_SupplementaryMaterial.xlsx

Artykuł 1

Supplementary material

Table S1. Sites controlled in Carpathian rivers and dam-reservoirs with *Faxonius limosus* occurrence (1) and absence (0) data. Sites with *F. limosus* presence are marked in bold.

ID	Sites	Coordinates ^a		Altitude [m]	Date	Lenght [m]	Time [min]	<i>F. limosus</i>
		°N	°E					
RIVERS								
1	Biała	49.88194	21.05758	219	10.07.2018	210	17	0
2	Biała	49.7147	20.94971	266	10.07.2018	125	19	0
3	Biała	49.76954	20.96367	247	10.07.2018	220	20	0
4	Biała	49.85239	21.01378	228	10.07.2018	200	32	0
5	Jasiołka	49.67313	21.69162	269	01.08.2018	310	31	0
6	Jasiołka	49.69409	21.66729	262	01.08.2018	210	14	0
7	Jasiołka	49.70942	21.63838	253	01.08.2018	200	18	0
8	Jasiołka	49.74706	21.54733	230	02.08.2018	210	20	0
9	Raba	49.81955	19.93909	287	19.06.2018	290	21	0
10	Raba	49.8269	19.95221	283	19.06.2018	290	20	0
11	Raba	49.83049	19.96175	280	19.06.2018	200	18	0
12	Raba	49.83904	19.96718	275	20.06.2018	200	11	0
13	Raba	49.84991	19.97931	270	04.08.2018	210	22	0
14	Ropa	49.68855	21.19999	271	15.07.2018	200	29	0
15	Ropa	49.64644	21.13855	292	03.08.2018	210	28	0
16	Ropa	49.72216	21.24472	256	03.08.2018	210	n/a	0
17	Ropa	49.73044	21.36506	237	03.08.2018	210	22	0
18	Skawa	49.73041	19.6255	335	12.07.2018	240	28	0
19	Skawa	49.73906	19.60882	327	12.07.2018	220	24	0
20	Skawa	49.76683	19.59762	314	12.07.2018	200	17	0
21	Skawa	49.85778	19.51718	263	18.08.2018	210	15	0
22	Skawa	49.85297	19.51943	265	18.08.2018	200	20	0
23	Soła	49.68816	19.19084	344	08.07.2018	110	12	1
24	Soła	49.68633	19.19322	345	08.07.2018	250	18	0
25	Soła	49.64758	19.17419	368	08.07.2018	240	19	0
26	Soła	49.68302	19.19633	345	08.07.2018	210	20	0
27	Soła	49.67909	19.19638	346	08.07.2018	225	18	0
28	Soła	49.67271	19.1934	351	08.07.2018	230	21	0
29	Vistula	49.64367	18.87521	448	08.08.2018	200	39	0
30	Vistula	49.72099	18.81866	357	08.08.2018	200	36	0
31	Vistula ^b	49.79138	18.8001	295	08.08.2018	200	36	0
32	Vistula^b	49.82268	18.79236	280	09.08.2018	200	30	1
33	Wisłok	49.73913	21.72233	249	08.09.2018	260	51	0
34	Wisłok	49.58722	21.95422	287	08.09.2018	410	68	0
35	Wisłok	49.67659	21.83072	268	24.08.2018	200	48	0

36	Wisłok	49.68888	21.78501	262	24.08.2018	200	32	0
37	Wisłoka	49.63005	21.52443	268	13.07.2018	210	23	0
38	Wisłoka	49.64024	21.49196	259	13.07.2018	210	21	0
39	Wisłoka	49.6851	21.47424	239	13.07.2018	420	30	0
40	Wisłoka	49.70008	21.47494	236	13.07.2018	200	12	0
41	Wisłoka	49.77446	21.41136	216	13.07.2018	320	25	0
RESERVOIRS								
42	Goczałkowice ^b	49.93157	18.87541	257	July 2018	n/a	n/a	1
43	Tresna	49.72312	19.20161	343	08.07.2018	n/a	2	1
44	Dobczyce	49.86963	20.05262	270	20.06.2018	n/a	2	1
45	Czorsztyn	49.4296	20.3139	530	2018.09.12 ^c	n/a	60	0
46	Rożnów	49.75038	20.71294	266	2018.09.13 ^c	n/a	60	0
47	Klimkówka	49.54621	21.09664	395	13.09.2018	n/a	30	0
48	Sieniawa-Besko	49.56059	21.93739	338	27.09.2018	n/a	30	0
DOBCZYCE RESERVOIR TRIBUTARIES								
49	Brzezówka	49.8515	20.06035	273	25.06.2018	200	26	0
50	Brzezówka	49.846	20.0578	282	25.06.2018	200	28	0
51	Bulinka	49.8472	19.98576	274	23.06.2018	200	23	0
52	Bulinka	49.84304	19.98972	279	23.06.2018	200	14	0
53	Ratanica	49.85353	20.02344	280	24.06.2018	200	15	0
54	Słona Woda	49.87153	20.01605	279	23.06.2018	200	19	0
55	Słona Woda	49.86778	20.00198	296	23.06.2018	200	18	0
56	Trzemeśnianka	49.84991	20.00461	277	25.06.2018	200	26	0
57	Trzemeśnianka	49.84391	20.00515	280	24.06.2018	200	18	0
58	Trzemeśnianka	49.84104	20.00958	286	24.06.2018	200	20	0
59	Wolnica	49.90275	20.02324	276	04.07.2018	200	20	0
TRESNA RESERVOIR TRIBUTARIES								
60	Łękawka	49.70916	19.23748	348	08.07.2018	10	1	1
61	Żylica	49.71394	19.16523	350	08.07.2018	20	2	1
62	Żylica	49.7191	19.15877	358	08.07.2018	100	8	1

^a in rivers and streams the location of downstream end of each section is presented

^b site located outside the Carpathians according to borders defined by Kondracki (2000)

Table S2. Water temperatures in Carpathian and Subcarpathian rivers in relation to localisation (Carpathians vs. lowlands). The 'name' reflects to each river considered as a factor in GLM analysis.

Factor	LR Chisq	df	p
Name	6.2595	8	0.62
Region	23.5957	1	<<0.5*
Name:Region	9.6202	6	0.14

Region	N of rivers	N of measure points	mean	1SD	median	max	min
Carpathians	9	32	9.81	6.86	9.3	27.5	0
lowlands	7	27	11.32	7.29	11.3	30.5	0

ARTYKUŁ 2

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Does river channelization increase the abundance of invasive crayfish? Survey of *Faxonius limosus* in small Central European streams

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Abstract

The aim of this study was to assess whether regulated river reaches show higher numbers of the spiny cheek crayfish *Faxonius limosus*, a common freshwater invader in Europe. Man-made alterations of riverine habitats may increase their susceptibility to biological invasions. This phenomenon is commonly studied in the context of dam reservoirs; however, the impact of river channelization and the resulting riverine habitat homogenization on the success of invasive species are mostly lacking. Surveys were conducted in natural and channelised river stretches in five rivers of south-central Poland. General linear mixed model analysis showed that crayfish abundance is usually higher at sites located within regulated reaches. The likely reason for the detected differences in abundance of crayfish may be related to decreased food-web complexity and lack of predators in a homogenised habitat. The results suggest that the channelization of small watercourses may increase the abundance of invasive species *F. limosus* and its pressure on native European crayfish. However, due to limited data obtained in field, our study should be considered as a pilot one.

Keywords River channelization · Decapoda · Cambaridae · Habitat disturbance · River alterations · Freshwater crayfish

Introduction

Biological invasions are a major issue for the economy (Perrings et al. 2002) and in nature conservation (McGeoch et al. 2016). Apart from applied sciences, they are also a major issue in ecological and evolutionary considerations (Mooney and Cleland 2001; Jeschke 2014). These considerations include interactions of invaders with local ecosystems, but have also been of interest in the context of colonization mechanisms in general for several decades (Hengeveld 1988). Invading species are typically ecologically flexible, highly competitive and fertile (Marchetti et al. 2004). On the other hand, successful colonization of a new area requires the

habitat to be adequate for the invading species. An adequate habitat may be defined as similar to the one in the region native for the alien species, which is usually considered in terms of climate (Kriticos 2012). But local undisturbed ecosystems may be relatively resistant to invasion due to biotic ecosystem elements (Naeem et al. 2000). This resistance, however, may be affected by habitat disturbance caused by anthropogenic alteration (Byers 2002). Human alterations often lead to changes in local species composition and abundance, and thus affect ecosystem functionality (Duffy 2002), making them more susceptible to invasion (Malin et al. 2005).

In lotic freshwater ecosystems, one of the most common human-induced is river regulation. According to Ravenga et al. (Allan and Castillo 2007), most of the rivers worldwide have been, to at least some degree, affected by human activity. The regulations include dam reservoirs and other impoundments resulting in turning formerly lotic habitats into lentic ones, but also river channelization, resulting in the elimination of natural meanders, making rivers straighter and shorter than in native state. These actions lead to riverine habitat homogenization (Elosegi et al. 2010). It has been demonstrated that dam reservoirs are highly invasible (Johnson et al. 2008; Liew et al. 2016) and may act as hubs for invaders—for example,

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the abundance of such species decreases with increasing distance to impoundment (Light 2003). There are also many examples of the impact of river regulation on biodiversity (e.g. Poff et al. 2007; Bredenhand and Samways 2009; Clavero and Hermoso 2011). River channelization, eliminating the majority of natural hydromorphological elements, is less studied in the context of biodiversity than dam reservoirs (Aarts et al. 2004; Figarski and Kajtoch 2015). This also concerns biological invasions. Despite numerous papers documenting the invasions of alien plants along altered river channels or valleys in terrestrial habitats (e.g. Mortenson and Weisberg 2010; Calford et al. 2011), there is a lack of knowledge about the invasion process within watercourses.

The aim of the presented contribution was to test whether river channel modification, by straightening the watercourse, may facilitate the invasion of the spiny check crayfish *Faxonius limosus* (Rafinesque). Despite the presence of the species in the non-native European range encompassing the majority of the continent (Kouba et al. 2014) for more than a century, such studies have not been conducted to date. Our prediction was that in the river stretches altered by channelization, this invasive crayfish is more abundant than in natural ones. This contribution is important in the context of identifying riverine habitats susceptible to invasions and reducing the impact of *F. limosus* on small watercourses still inhabited by the declining noble crayfish *Astacus astacus*.

Methods

Study area and surveyed habitats

The studies were conducted in five small- and medium-sized rivers from the Vistula and Oder river drainage areas, located in the lower uplands and lowlands of south-central Poland. In the cases of all rivers, the bottom substrate was dominated by sand or mud, with a minority of pebbles and gravel. In one case, the Kamienna river, the regulated habitat, was dominated by stone.

Eight localities were chosen where two types of habitat (natural vs. regulated) were located directly one after the other. This resulted in eight pairs of two-habitat sections located in five rivers. Natural habitat was defined as containing natural meanders and was preselected using Google Earth maps. Consequently, a subsection without meanders visible on maps was considered regulated. To avoid classifying naturally straight subsections (which are rare in lowland and lower uplands of Poland) as regulated, straight river stretches were included only when oxbows or their remains were visible on the map or found during field observations. For each habitat in each section, 7–13 points were chosen (cross-sections) in which the following data were collected: water depth measured 50 cm from each river bank and at the central point of

the river channel in each point, width of the river channel, number of points where tree roots overgrowing the bank of the watercourse and merging under water were present, percentage of macrophyte cover measured within 7–13 cross-sections as a percent of length of the cross-section covered by plants, number of pools and the number of uncovered deposits along each section. Deposits, pools and tree roots were defined according to Raven et al. (1998). While measuring the habitat features, the water temperatures were recorded in 5–13 points of each section with an accuracy of 0.1 °C.

Crayfish sampling

Crayfish were sampled from 5 July to 21 July 2019 during low water levels. Sampling was performed within 2–3 h after dusk to decrease the effect of crayfish hiding in shelters, which could underestimate the sample. For one night, both regulated and natural habitats were surveyed in one section. In each habitat within a section, five sites, distributed evenly along the stretch, were sampled by dip netting (30 × 50 cm rectangular dip net with rake, mesh approx. 3 mm), including the substrate and macrophytes. At each sampling site, 20 full sweeps were made, always by the same person, and usually 10 sweeps for each river bank within one site. Sweeps were made ensuring the same place was not swept twice. This resulted in 100 sweeps in each section and 200 sweeps within one locality. Crayfish captured in the net were always counted by the same person. Once captured, *F. limosus* individuals were not released as it is forbidden by National law. Thus, resampling of individuals was avoided. One sampling in each habitat/section was made due to limited time and funding resources. An active survey was preferred over trapping as the pilot study in the Sanica river, with 40 baited and unbaited traps, suggested that crayfish are attracted not only by bait, but by the trap as a shelter. In shelter-poor regulated sections, the captured crayfish number could be overestimated. In fact, during two trapping sessions, the number of crayfish was always higher in the regulated section. Moreover, the frequent presence of fish in the traps, i.e., *Perca fluviatilis*, could also affect the crayfish number in the traps (M. Bonk, Bobrek R, Dołęga J. unpublished).

Statistical analysis

A linear-mixed-effects model was used to test for differences in crayfish abundance at sites within regulated and natural subsections. The number of individuals captured at a sampling site ($N = 80$) was the response variable, the habitat type (two levels: natural and regulated) was the fixed factor and the section ID ($N = 8$), referring to the locality, was the random factor. Statistical analysis was performed using the 'glmer' function in the 'lme4' package in R 3.5.1 (2018), with Poisson distribution error. The sum of adult and juvenile

individuals was included in the analysis. For the measured habitat features, the mean values with a variation coefficient were provided to describe habitat variability. Further, the differences in number of meanders $\times 100 \text{ m}^{-1}$, pools $\times 100 \text{ m}^{-1}$, sand deposits $\times 100 \text{ m}^{-1}$, tree root sites $\times 100 \text{ m}^{-1}$, mean temperatures and variation coefficients of water depth and width were tested with the Wilcoxon pairwise test for the significance of the differences between regulated and natural sections. The analyses were conducted in PAST (Hammer et al. 2001).

Results

River habitat description

Field observations confirmed the presumed natural or regulated character of the preselected sections. Subsections considered natural were characterised by more variable habitat features. This was reflected in a higher number of pools ($P = 0.017$) and natural meanders ($P = 0.012$; Table 1), higher values of variation coefficients of the water depth and the watercourse width ($P = 0.017$ and $P = 0.036$, respectively), usually more numerous sand depositions ($P = 0.063$; Table 1) and number of cross-sections with tree roots present ($P = 0.025$; Table 1) reflecting the usually higher tree cover along natural sections. The percentage of macrophyte cover was, on the other hand, usually higher in the regulated subsections; this was probably caused by the higher insulation of such subsections due to tree and shrub removal. Thus, this feature, to our opinion, does not correspond with the natural status of the habitat. Structures protecting the channel edges (like rip-rap) were in general not observed or appeared only sporadically within several meters of each subsection. The exception was the Kamienna river, where the regulated subsection was historically modified by stone embankments, recently destroyed and resulting in stone dominance in the bottom substrate. In the Sanica 2 and Wschodnia regulated sections, one weir was present in each section. However, along a majority of these sections, the flowing character of the watercourses was maintained. The mean temperatures for the section considered natural and regulated did not differ significantly ($P = 0.33$).

Crayfish number

In total, 99 individuals of *F. limosus* were captured. The number of individuals caught per sampling site was low and among-site variation was high (range from 0 to 12 per sampling site, Supp. Tab. 1). The highest number of crayfish was captured in the Sanica and Radna rivers. The mean number of individuals collected at the sampling site was 1.5 (SD = 2.42) for the regulated subsections and 0.93 (SD = 1.25) for

the natural ones. The range of crayfish caught on the regulated and natural subsections (the sum of five sampling sites) ranged from 0 to 21 and from 0 to 7 individuals, respectively (Fig. 1). Usually, there were fewer individuals captured in the natural subsections, with the exceptions of the two largest rivers, where no crayfish were sampled in the regulated subsection (Warta river), or the number was slightly higher in the natural habitat (Kamienna river; Fig. 1, Suppl. Tab 1).

Generalised linear mixed model analysis showed that in general, there is a higher abundance of crayfish per site in the regulated subsections than in the natural ones (SE = 0.2055, z value = 2.511; $P = 0.012$; Fig. 1). However, this effect seems to be most visible in two small rivers belonging to one drainage area (Sanica and Radna rivers), whereas in the largest rivers (the Warta and the Kamienna rivers), the effect was reverse (Fig. 1).

Discussion

Crayfish capture raises several problems. As these animals often hide in any available shelter, the number of collected individuals may be heavily underestimated. In our study, this resulted in a low number of captured individuals. Despite the number of individuals usually being higher in sites located within regulated parts of rivers, the biological significance of this relationship is unclear. In our opinion, the data should be cautiously interpreted and treated as a pilot study that warrants further investigation. Nevertheless, our results were not designed to catch the largest fraction of crayfish, but to use the same method to get comparable results in wild and channelised sections of the same river.

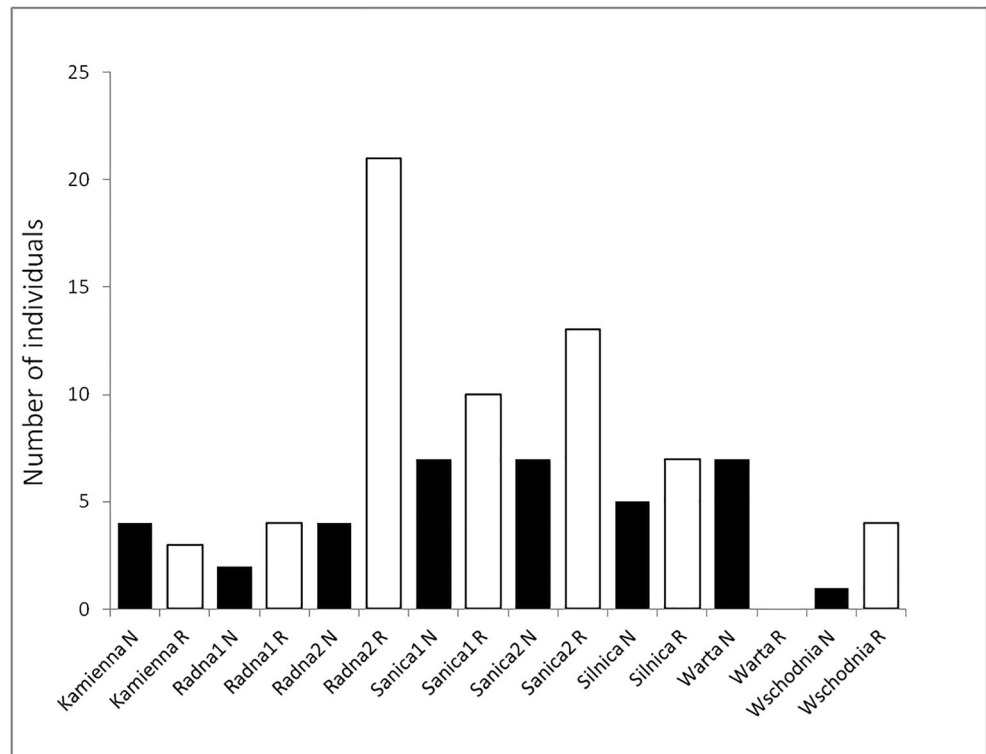
Despite some doubts about the accuracy of the method, our results are consistent with the general knowledge about ecosystem disturbance and its impact on biological invasions (Marvier et al. 2004; Hansen and Clevenger 2005; Elosegı et al. 2010; Case 1990; Levine and D'Antonio 1999; Naem et al. 2000; Kennedy et al. 2002). After anthropogenic alteration of the habitat, native species may lose their superiority, gained through a long history of adaptation to the local environment (Byers 2002). This also seems to be valid in the case of our study.

However, investigating the direct factors related with river channelization, which may affect the crayfish in the studied watercourses, was not a target of our study, potential reasons for that state can be explained according to the already existing literature. The decrease in ecosystem functionality presumed for regulated subsections may be connected with the disappearance of large fish predators from the regulated river sections. Watercourse channelization affects fish diversity and composition, often reducing the abundance of trophic specialists (e.g. predators) (Aarts et al. 2004; Latli et al. 2018). This may result in lower predatory pressure on the invader. It

Table 1 Characteristics of the studied river stretches. In 'habitat', column N refers to natural subsections and R—to regulated subsections. Values in brackets refer to value per 100 m (for meanders, pools, sandy deposits, and tree roots and variation coefficients for mean water depth and mean river width). Symbols refer to river names as follows: K—Kamienka river, R—Radna river, S—Sanica river, Sil—Silnica river, W—Warta river, Ws—Wschodnia river

River name	Habitat	GPS ¹	Section length	Meanders ($\times 100 \text{ m}^{-1}$)	Pools ($\times 100 \text{ m}^{-1}$)	Sandy deposits ($\times 100 \text{ m}^{-1}$)	Tree roots ($\times 100 \text{ m}^{-1}$)	Mean macrophyte cover	Mean water depth (var. coeff.)	Mean river width (var. coeff.)	Mean water temperature [°C]
K	N	51.10906N 20.91073E	412	3 (0.9)	5 (1.5)	7 (2.1)	8 (2.4)	0.19%	39.49 (19.45)	5.08 (0.31)	19.48
	R	51.111002N 20.87892E	331	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	85.50%	53.34 (11.31)	5.22 (0.087)	19.57
R1	N	50.55182N 20.96311E	569	11 (1.9)	12 (2.1)	3 (0.5)	8 (1.4)	30.93%	31.47 (4.85)	2.68 (0.05)	19.70
	R	50.56326N 20.96104E	565	2 (0.4)	0 (0.0)	0 (0.0)	1 (0.2)	62.57%	37.28 (3.91)	3.98 (0.027)	18.06
R2	N	50.5431N 20.94445E	452	7 (1.5)	9 (2.0)	0 (0.0)	5 (1.1)	45.59%	54.33 (7.52)	3.93 (0.10)	22.08
	R	50.54746N 20.954E	480	0 (0.0)	1 (0.2)	0 (0.0)	1 (0.2)	79.00%	55.64 (4.19)	2.72 (0.044)	22.22
S1	N	50.4908N 20.942134E	435	5 (1.1)	13 (3.0)	17 (3.9)	5 (1.1)	12.23%	20.60 (10.47)	4.02 (0.2)	20.65
	R	50.49634N 20.92503E	397	0 (0.0)	0 (0.0)	20 (5.0)	0 (0.0)	5.90%	14.13 (0.06)	3.75 (0.06)	27.90
S2	N	50.51532N 20.88256E	259	6 (2.3)	10 (3.9)	11 (4.2)	5 (1.9)	6.77%	16.10 (3.45)	2.42 (0.049)	22.49
	R	50.51303N 20.8904E	235	0 (0.0)	0 (0.0)	5 (2.1)	6 (2.6)	13.65%	15.15 (3.67)	2.88 (0.11)	22.61
Sil	N	50.85909N 20.55139E	300	6 (2.0)	5 (1.7)	18 (6.0)	4 (1.3)	8.64%	27.7 (16.75)	3.0 (0.38)	22.08
	R	50.858498N 20.5725E	245	0 (0.0)	1 (0.4)	2 (0.8)	3 (1.2)	11%	21.6 (9.56)	3.4 (0.22)	21.50
W	N	50.73889N 19.18124E	286	3 (1.1)	4 (1.4)	2 (0.7)	6 (2.1)	26%	50.28 (13.06)	8 (0.39)	20.80
	R	50.74897N 19.18379E	400	0 (0.0)	1 (0.3)	0 (0.0)	2 (0.5)	33%	59.24 (4.87)	13.1 (0.16)	20.86
Ws	N	50.45459N 21.20616E	493	1 (0.2)	6 (1.2)	20 (4.1)	9 (1.8)	9.14%	31 (15.2)	6.25 (0.8)	21.06
	R	50.4545N 21.191968E	483	0 (0.0)	1 (0.2)	1 (0.2)	2 (0.4)	7.80%	45 (7.16)	7.45 (0.03)	22.98

Fig. 1 Number of *Faxonius limosus* individuals captured within the natural ‘N’ (black bars) and the regulated ‘R’ (white bars) river sections



was shown that the removal of top predators may reduce the resilience of the community to invasion of non-indigenous species (Byers 2002; Reusch 1998; Byers 2002; Ward and Ricciardi 2007). In the investigated rivers, predator elimination, overall biodiversity loss and outcompeting may presumably occur. Some anecdotal data from small rivers in Poland support the idea of a population reduction of predatory fish after river channelization (Wiśniewolski and Gierej 2011). Furthermore, it was found that the density of perch *Perca fluviatilis*, which is a common predator fish in the studied rivers, is higher in unregulated sections of rivers than in regulated ones (Bruylants et al. 1986). Furthermore, even if fish species composition is not altered, small stream channelization leads to the elimination of pools, and as a consequence, deeper microhabitats for older and larger fish (also other than perch) may disappear (Schlosser 1987; Harvey and Stewart 1991; Mallet et al. 2000; Eick 2013).

A fish survey on species composition and size structure within the studied sites was not carried out. However, to some extent, the different results in the smallest and largest rivers may support the existence of a relationship between the amount of deeper microhabitats, preferred by larger predators, and crayfish abundance. In the largest of the studied rivers (Warta and Kamienna), where both the regulated and natural subsections were deep enough (Table 1) to harbour large predatory fish, a positive effect of channelization on invasive crayfish abundance was not observed. In contrast, in the smallest and shallowest rivers (the Radna river and Sanica river), *F. limosus* was less abundant in sections characterised by a

high number of pools. However, the aforementioned reverse effect (or lack of an effect) in large rivers requires further study on a larger number of natural-regulated pairs of river stretches, including broad variations in river size and depth and fish size structure as cofactors. In the case of our study, due to the low number of localities and individuals, such an analysis was not undertaken. In the examined habitats, the regulated subsections differed from the natural ones mostly by characteristics reflecting channel hydromorphology.

In general, *F. limosus* avoids small headwater streams (Chucholl 2016), which may be related to water temperature (Bonk and Bobrek 2020); thus, some of the described sections probably lie near the upper limit of the colonization ability of streams by this species. However, temperature is probably not a major reason for differences in crayfish abundance as in each locality, both regulated and unregulated sections were placed at approximately the same distance from the springs; also, the temperature in one type of section may be related to the temperature within the other due to the short distances between them. This also seems to be supported by the low differences in temperatures measured during our surveys.

F. limosus is a successful invader occurring in most freshwater habitat types across Europe (Holdich and Black 2006; Śmietana 2011; Kouba et al. 2014), including the brackish waters of the southern Baltic Sea (Szaniawska et al. 2017). Our study suggests that despite *F. limosus* being present in both natural and regulated river habitats, watercourse management may have an impact on its abundance and, presumably, the impact of crayfish on local

ecosystems. This is important in the context of observations of several authors (Holdich and Black 2006; Chucholl 2016; Bonk and Bobrek 2020) who showed that *F. limosus* does not ingress into the smallest headwater streams, which are often a refuge of native crayfish (i.e. *Astacus astacus* is present in the Sanica and Radna rivers within the area of our study, M. Bonk, unpublished data). The channelization of such watercourses may increase the pressure of *F. limosus* on native European crayfish by transforming natural small streams into homogenised watercourses and allows its upstream dispersal. As both *F. limosus* and *A. astacus* have occurred in the studied regions in adjacent parts of streams for at least two decades, the transmission of crayfish plague is probably low or non-existent, and *A. astacus* may be competitively disadvantaged by *F. limosus* through habitat alterations. Thus, maintaining the natural character of small watercourses or renaturalising already altered streams may be helpful in maintaining native crayfish populations.

Although our results are in accordance with general knowledge about the impact of habitat disturbance on biological invasions, our data should be regarded with caution and warrant further study.

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Code availability Not applicable.

Declarations

Ethical approval Study has been conducted according to local law.

Consent to participate Not applicable.

Consent for publication Approved.

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

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Artykuł 2

Supplementary material

Supporting tab. 1. Numbers of captured crayfish individuals in the surveyed sites with regards to habitat type

(N – natural subsections, R – regulated subsections), river id and date of sampling.

section id	sample (site)	survey date	N of crayfish	habitat
Kamienna	1	12.07.2019	0	R
Kamienna	2	12.07.2019	1	R
Kamienna	3	12.07.2019	2	R
Kamienna	4	12.07.2019	0	R
Kamienna	5	12.07.2019	0	R
Kamienna	1	12.07.2019	0	N
Kamienna	2	12.07.2019	0	N
Kamienna	3	12.07.2019	1	N
Kamienna	4	12.07.2019	1	N
Kamienna	5	12.07.2019	2	N
Radna 1	1	13.07.2019	1	R
Radna 1	2	13.07.2019	1	R
Radna 1	3	13.07.2019	1	R
Radna 1	4	13.07.2019	0	R
Radna 1	5	13.07.2019	1	R
Radna 1	1	13.07.2019	0	N
Radna 1	2	13.07.2019	1	N
Radna 1	3	13.07.2019	0	N
Radna 1	4	13.07.2019	0	N
Radna 1	5	13.07.2019	1	N
Radna 2	1	9.07.2019	1	R
Radna 2	2	9.07.2019	0	R
Radna 2	3	9.07.2019	12	R
Radna 2	4	9.07.2019	4	R
Radna 2	5	9.07.2019	4	R
Radna 2	1	9.07.2019	0	N
Radna 2	2	9.07.2019	3	N
Radna 2	3	9.07.2019	1	N
Radna 2	4	9.07.2019	0	N
Radna 2	5	9.07.2019	0	N
Sanica 1	1	18.07.2019	6	R
Sanica 1	2	18.07.2019	1	R
Sanica 1	3	18.07.2019	0	R
Sanica 1	4	18.07.2019	2	R
Sanica 1	5	18.07.2019	1	R

Sanica 1	1	18.07.2019	0	N
Sanica 1	2	18.07.2019	5	N
Sanica 1	3	18.07.2019	1	N
Sanica 1	4	18.07.2019	1	N
Sanica 1	5	18.07.2019	0	N
Sanica 2	1	5.07.2019	2	N
Sanica 2	2	5.07.2019	2	N
Sanica 2	3	5.07.2019	2	N
Sanica 2	4	5.07.2019	1	N
Sanica 2	5	5.07.2019	0	N
Sanica 2	1	5.07.2019	3	R
Sanica 2	2	5.07.2019	0	R
Sanica 2	3	5.07.2019	8	R
Sanica 2	4	5.07.2019	1	R
Sanica 2	5	5.07.2019	1	R
Silnica	1	21.07.2019	2	R
Silnica	2	21.07.2019	0	R
Silnica	3	21.07.2019	0	R
Silnica	4	21.07.2019	2	R
Silnica	5	21.07.2019	3	R
Silnica	1	21.07.2019	1	N
Silnica	2	21.07.2019	3	N
Silnica	3	21.07.2019	0	N
Silnica	4	21.07.2019	0	N
Silnica	5	21.07.2019	1	N
Warta	1	17.07.2019	1	N
Warta	2	17.07.2019	1	N
Warta	3	17.07.2019	0	N
Warta	4	17.07.2019	0	N
Warta	5	17.07.2019	5	N
Warta	1	17.07.2019	0	R
Warta	2	17.07.2019	0	R
Warta	3	17.07.2019	0	R
Warta	4	17.07.2019	0	R
Warta	5	17.07.2019	0	R
Wschodnia	1	19.07.2019	3	R
Wschodnia	2	19.07.2019	0	R
Wschodnia	3	19.07.2019	0	R
Wschodnia	4	19.07.2019	1	R
Wschodnia	5	19.07.2019	0	R
Wschodnia	1	19.07.2019	0	N
Wschodnia	2	19.07.2019	0	N
Wschodnia	3	19.07.2019	0	N
Wschodnia	4	19.07.2019	1	N
Wschodnia	5	19.07.2019	0	N

ARTYKUŁ 3

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The body condition of invasive crayfish *Faxonius limosus* (Raf., 1817) (Decapoda: Cambaridae) is better in small rivers than in dam reservoirs in Central Europe

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Abstract

The impact of dam reservoirs on river ecosystems is one of the current major issues in hydrobiology. In addition to the impact on native biodiversity, impoundments may facilitate biological invasions. A successful invasion is presumably related to the individual life history and resource allocation strategy in expanding populations. We tested whether reservoirs affect the body condition of invasive *Faxonius limosus* in upland streams. We found positive allometry of growth in females but more frequent isometric growth in males, and the form factor $a_{3,0}$ was significantly higher in males than in females within populations. Fulton's condition factor (K) was calculated for standard carapace lengths of 20 mm (juvenile) and 40 mm (adult). Both mean $K_{CL\ 20}$ and $K_{CL\ 40}$ were higher in males than in females. Positive allometry of growth in females resulted in a larger mean $K_{CL\ 40}$ than $K_{CL\ 20}$. The majority of the mean K obtained in reservoirs was similar or lower than the respective condition in streams. The condition of adult females was higher in streams in comparison to reservoirs. The obtained results are in contrast to the hypothesis that reservoirs positively affect individual body conditions and show that these man-made lakes do not provide more favourable habitat conditions for *F. limosus* than those in the natural aquatic environments of an upland landscape. An advantageous effect of the presence of reservoirs on invasion spread may be possible in more ecologically harsh landscapes, especially in colder climatic zones. Our study is the first to investigate the relationship of the body condition of *F. limosus* in two contrasting habitats.

Keywords Ecology · Population · Crayfish · Freshwater · Invasive alien species

Introduction

Biological invasions are a significant component of global environmental change. Aquatic invaders influence biodiversity and promote the extinction of native species, may degrade human health and the economy, and can cause considerable expenses to control the invasive species and mitigate their impact (Vitousek et al. 1996). Freshwater ecosystems are among the most invaded in the world (Ricciardi and MacIsaac 2011). In order to take sufficient actions to prevent aquatic invasions, the ecology of the invaders and

the mechanisms of their spread and reaction to various habitats needs to be known. One of the important invasive taxa worldwide are crayfish. Being one of the larger freshwater invertebrates, often reaching high numbers and revealing ecosystem engineering properties, they play a key role in food networks in rivers and stagnant waters worldwide (Reynolds and Souty-Grosset 2012; Linzmaier et al. 2020). Due to their impact on ecosystems, the effects of invasions of crayfish are significant and have been reported for decades (Gherardi and Holdich 1999; Lodge et al. 2000; Holdich et al. 2009; Richman et al. 2015; Souty-Grosset et al. 2016; Meira et al. 2019; Chucholl and Chucholl 2021; Dobler and Geist 2021).

It is often demonstrated that invasive species are promoted by habitats that are created or altered by humans (Marvier et al. 2004; Hansen and Clevenger 2005; Wilk-Woźniak and Najberek 2013; Bonk and Bobrek 2021). In inland waters, dam reservoirs are considered as factor disturbing riverine ecosystems and positively affecting biological invasions in

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ivers (Ellis and Jones 2013; Ellis and Jones 2013; Oliveira et al. 2020; Santos et al. 2021). However, despite examples of the positive impact of impoundments on invasive alien species distribution and abundance (Havel et al. 2005, 2015; Johnson et al. 2008; Beatty et al. 2020), it seems that almost no studies investigated the effect of river habitat alteration on biological traits of invaders (Bonk and Bobrek 2020). Thus, there is a need for testing whether different habitat types interfere with life history traits of invasive alien species, which is important not only for better understanding the ecology of studied organisms but also for better understanding the impact of man-made habitat alterations too.

One of the most successful freshwater invaders in European inland waters is the spiny cheek crayfish *Faxonius limosus* (Rafinesque, 1817) of the Cambaridae family. The species is native to the rivers of the East Coast of North America (Hamr 2002; Filipová et al. 2011). It was brought to Europe in 1890 to a fish pond in Berneuchen village in Germany (now Barnówko in north-western Poland; 52°47' N, 14°46' E) (Kulmatycki 1935). The origin of the stocked individuals was later commonly attributed to the Delaware River in Pennsylvania (Leńkowa 1962). According to Filipová et al. (2011), all the European populations of *F. limosus* probably originated from the single introduction of approximately 100 individuals. There are several life history traits that make this species a successful invader. *Faxonius limosus* has a relatively short life cycle (lifespan up to four years) and long breeding season (Holdich and Black 2007); it is relatively resistant to poor water quality (Holdich and Black 2007; Buřič et al. 2011; Svobodová et al. 2012; Římalová et al. 2014) and is capable to facultative parthenogenesis (Buřič et al. 2011).

In general, the occurrence of *F. limosus* in Europe is mostly recorded in medium and large lowland rivers and stagnant waters (Hamr 2002; Holdich and Black 2007; Římalová et al. 2014), while the occupation of small streams is low (Mickasch 1999; Hefti and Stucki 2006; Petrušek et al. 2006; Chucholl 2016). Moreover, the data on distribution in submountain or mountain areas suggest that stagnant water bodies may be favourable for the species there (Hefti and Stucki 2006; Bonk and Bobrek 2020). However, despite being present for more than a century in Europe, and recently continuing to spread (Kouba et al. 2014), there were no studies comparing life histories of *F. limosus* in different habitats, such as stagnant waters and streams. Literature suggestions that stagnant waters may facilitate the invasion (Bonk and Bobrek 2020) of this species encourage the use of *F. limosus* as an example of a study on the life history traits in different habitats. In this contribution, we tested whether flowing versus stagnant waters have a different impact on the life history and invasion success. We assumed that impounded watercourse would be favourable for the population of this species.

To find out whether dam reservoirs offer a better habitat than streams for *F. limosus*, we used body condition as an indicator of 'well-being' at individual and population levels and adopted Fulton's condition factor, the measure commonly applied in studies on individual conditions (Froese 2006). We hypothesise that the body condition of *F. limosus* is in general better in dam reservoirs in comparison to the small rivers in the upland landscape.

Methods

Selection of study sites

To compare whether individuals in a reservoir differ in condition from individuals living in a riverine habitat, we chose three river–reservoir pairs of sampling sites. Each pair was considered as two forms of the same water course, free-flowing and impounded. All pairs of sites were located in three streams in the drainage basin of the Nida river (left-side tributary of the Vistula, southern Poland; Fig. 1). They are the Belnianka stream with the Borków Reservoir, the Lubrzanka stream with the Cedzyna Reservoir and the Silnica stream with the Kielce Reservoir (Table 1). The mean annual discharge does not exceed $1 \text{ m}^3 \text{ s}^{-1}$ in any of the selected stream reaches. Their width ranges within 2.5–8 m; the dominant bottom substrate is sand with patches of gravel, mud and plant detritus. There are no tributaries between reservoirs and sampling sites in these streams. No precise measurements were conducted to assess the exact areas of each substrate type. Sites in streams were chosen close to the reservoirs but at least 1 km downstream of each dam and were also remote from any other large lentic habitats (sand excavations) that were connected to the stream channels. In the Silnica stream, two sampling sites were located 1 km and 3.8 km from the Kielce Reservoir; in the Belnianka stream, one sampling site was located 1.8 km from the Borków Reservoir and in the Lubrzanka stream sampling site was located 5.4 km from the Cedzyna Reservoir and 1.4 km from a gravel excavation connected with the stream. The studied reservoirs are shallow water bodies with 9–64 ha surface area, sandy bottom and sparse aquatic vegetation. Some portions of their shoreline are strengthened with concrete grid embankments, rip-rap and fascine (bundles of willow branches).

The history of the invasion of the studied area is poorly known due to the lack of regular monitoring or published reports. According to only one publication, *F. limosus* has been present in the study area for at least a decade (Śmietana 2011). However, according to local anglers, this species has been present in the studied rivers and reservoirs for at least two decades.

Fig. 1 Localisation of sampling sites. Triangles refer to reservoirs, and circles refer to sites in streams

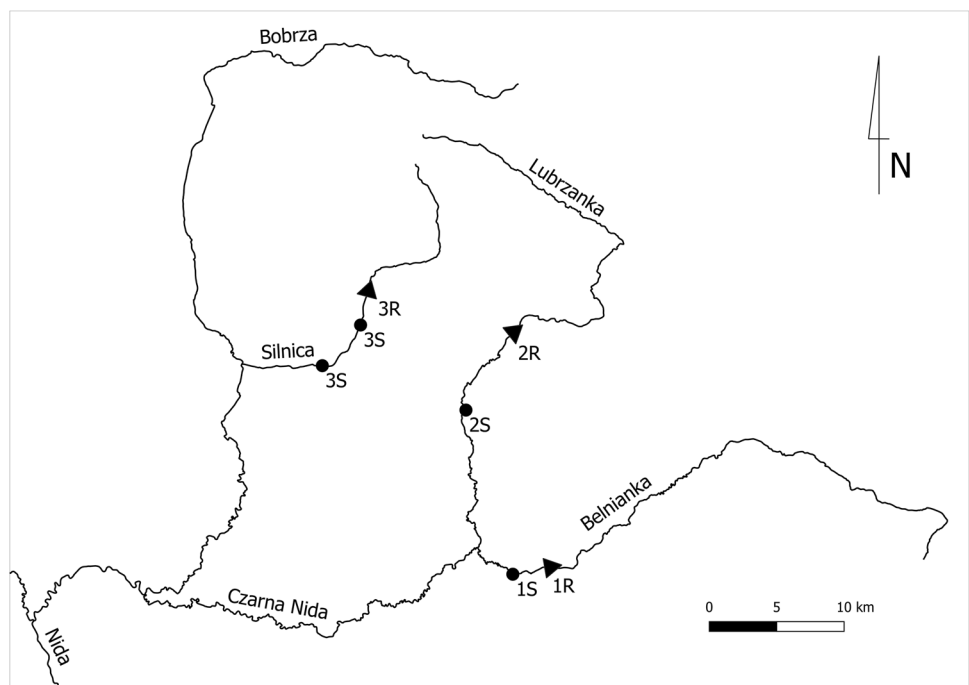


Table 1 Locations of sampling sites, their codes used in this paper and general habitat characteristics

Sampling site	Code	Coordinates of a midpoint		Altitude (m)	Slope ^b (%)	Depth ^c (m)	Macrophyte cover (%)
		°N	°E				
Belnianka Stream	1S	50.772076	20.727502	237–242	1.73	1.5	0
Borków Reservoir	1R	50.773	20.756	246		2	< 10
Lubrzanka Stream	2S	50.839128	20.697289	247	0.23	1	25
Cudzyna Reservoir	2R	50.873	20.733	259		2.5	< 10
Silnica Stream ^a	3S	50.874785	20.627325	241–258	3.09	1	< 10
		50.858793	20.596833				
Kielce Reservoir	3R	50.889	20.633	266		2	< 10

^aIn the Silnica, two stream reaches were sampled

^bThe ratio of vertical (in m) to horizontal (in km) distances between two nearest elevation points marked in stream channel on 1:10,000 topographic map available at <https://mapy.geoportal.gov.pl>

^cPresented values refer to maximum depth in streams and mean depth in reservoirs

Estimation of sample size

Before starting, we estimated the possibility to conduct an adequate investigation and we estimated the variance of Fulton's condition factor in a natural population of *F. limosus* in the area of the intended study. The preliminary sample of 27 females was taken from the Belnianka stream, and the average condition factor value 2.59 ± 0.20 (mean \pm SD; range: 2.15–2.91) was obtained. Then, we estimated the minimum size of a sample, allowing for the detection of a 5% difference from this average condition at the levels of $\alpha = 0.05$ and $1 - \beta = 0.8$, with the calculation method proposed by Dell et al. (2002). The resulting requirement of 39 individuals from each of the compared populations showed us the real

possibility of collecting the appropriate material from a few sites in a narrow time frame.

Crayfish sampling, measuring and weighing

Crayfish were collected from 10 September to 24 October 2019. The water temperature remained within a range of 10–15 °C during this period. Sampling was conducted at night by a visual survey with torchlight. One or two persons waded into each site down to a depth of 0.6 m and captured manually or by hand net any crayfish detected. Caught individuals were placed into wet cloth bags to avoid desiccation and held out of the water all the time until laboratory treatment to preclude retaining water in gill chambers

at weighing (measurements were done up to 24 h from capture).

In the laboratory, the biometric quality of the collected crayfish was evaluated and then they were identified by sex, measured and weighed. Three types of defects resulted in the exclusion of the specimen from the study: (1) broken or distinctly blunted acumen that precludes the correct measurement of the carapace length, (2) lost cheliped that considerably affects the body weight or (3) loss of more than one walking leg that may reduce the locomotory ability and therefore the efficiency of resource acquisition and thus individual condition.

For individual weight–length analysis, we used carapace length (CL) measured with a calliper from the tip of the acumen to the carapace posterior edge with an accuracy of 0.02 mm. Next, the crayfish were wrapped up in a paper towel to remove external moisture and then weighed to the nearest 0.01 g (Kern CM 60-2 N balance).

Data analysis

The data on males and females were processed separately, assuming possible differences in the life history strategies of both sexes, especially in their growth patterns and reproductive investments, which can affect the individual condition. In the analysis, we considered only Form I males. Because Fulton's condition factor is size-dependent in cases of non-isometric growth (Froese 2006), in the analysis, we calculated the condition for two fixed standard sizes, 20 mm CL and 40 mm CL, introduced in this study. At about 20 mm CL, both male and female *F. limosus* are just before sexual maturation or already mature (Smith 1981; Momot 1988). Thus, we considered this size as a biologically reasonable threshold from which the individual condition (1) is affected by the costs of reproduction and (2) is important for reproductive success. The second standard size, 40 mm CL, characterises relatively large older adults close to the medium size of the species in Poland (Szaniawska et al. 2005). *Faxonius limosus* can achieve greater sizes (up to 65.1 mm CL; Chybowski 2007); however, such individuals became scarce in natural populations (Đuriš et al. 2006). Each value of the condition factor (K) in the studied populations was calculated taking (1) the fixed standard carapace length (20 mm or 40 mm) and (2) the body weight (W) obtained for this length with the respective WRL equation. Because the value of Fulton's condition factor in such calculation equals the proportion of estimated W and the constant, 20^3 or 40^3 (i.e., the cube of fixed CL), the expected range limits of the estimated individual condition in the population were obtained as the K values calculated for the limits of 95% confidence intervals of the W estimate. The following equations were used to calculate Fulton's condition factor:

$$K = 10^4 W / CL^3$$

and the form factor (Froese 2006)

$$a_{3.0} = 10^{[\log a - S(b-3)]}$$

where 10^4 is a constant factor to convert small decimals to numbers close to unity, W is body weight in grammes, CL is carapace length in millimetres, a and b are parameters of the weight–length relationship (WLR; $W = a CL^b$), and S is the slope of the regression $\log a$ on b . The WLRs used in this study were the OLS (ordinary least square) regressions that are more appropriate for planned prediction W from the fixed CL value (i.e. 20 mm or 40 mm) than geometric mean regression. The $K_{CL 20}$ and $K_{CL 40}$ abbreviations were used to designate on which length measurement and which standard size the condition factor was calculated. The quality of the obtained WLRs was evaluated by plotting logarithms of coefficient a over exponent b (Froese and Pauly 2000). All points resulting from the respective estimates of a and b values were well fitted to a straight line ($r^2 = 0.993$), evidencing a lack of outlying data sets in our material (Fig. 2). Thus, the slope of this line was used to calculate the values of form factor $a_{3.0}$ for each WLR, i.e. the value that coefficient a would have if exponent b were 3 (Froese 2006).

Next, we fitted a linear mixed-effects model (LMM) estimated using REML and nloptwrap optimizer (R Core Team

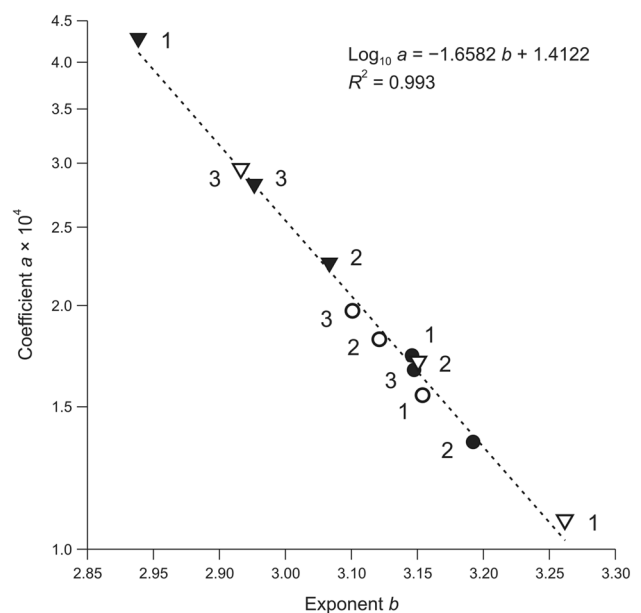


Fig. 2 Plot of logarithms a over b values for WLRs of six populations of *Faxonius limosus* living in streams (full symbols) and reservoirs (open symbols): triangles – Form I males, circles – females. Numbers 1–3 indicate three pairs of sampling sites consisting of a stream and reservoir each (their codes are explained in Table 1). Note the logarithmic scale on the vertical axis

2018) to predict K from CL, habitat and sex including locality as a random effect, according to the formula:

$$K \sim CL + H + S + H : S + (1|L)$$

where H is the kind of habitat (stream or reservoir), S is sex, and L is the pair of compared habitats (i.e. located in the Belnianka, Lubrzanka or Silnica streams); H:S is an interaction of habitat and sex. Statistical analysis was performed using R (R Core Team 2018). The distribution normality was tested with Past 3.26 (Hammer et al. 2001) for testing the CL distribution normality. As in the first approach, the interaction between sex and habitat was not significant; we further excluded interaction from the model. Including CL may, however, be considered confusing, as it is a component of an independent variable. On the other hand, we assumed that it may affect conditions when growth is allometric; thus, we decided to not exclude it from the analysis.

Results

In total, 653 individuals were accepted in this study, 313 of them being collected in streams and 340 in reservoirs (Table 2). Their size ranged between 16.64–51.72 mm CL and 1.01–33.04 g W. The mean value of CL of collected individuals, 31.80 ± 6.05 mm, was located roughly midway between the standard carapace lengths, 20 mm and 40 mm, adopted in this study.

Both isometric and allometric growth patterns were found in the analysed samples (Table 3). Distinct isometric growth prevailed in Form I males, while in females, the positive allometry could not be confirmed formally in only two of the six cases analysed. However, these two respective significance values are close to the accepted threshold of 0.05 (Table 3). Both near-isometric WLRs in females were found only in the reservoir populations. In general, however, as all

calculated values of parameter b are greater than 3.0, we demonstrated that in the studied populations, the growing females become relatively heavier as a rule, regardless of their habitat. Regardless of sex and the iso- or allometry of growth patterns, all the obtained WLRs were very strong (r^2 : 0.96–0.99; Table 3).

The form factor ranged within $2.60\text{--}2.88 \times 10^{-4}$ in the studied populations, being slightly lower in females ($2.60\text{--}2.82 \times 10^{-4}$) than in Form I males ($2.73\text{--}2.88 \times 10^{-4}$) (Table 3). The formal performance of the Wilcoxon signed-rank test suggested the significance of these differences at $p < 0.05$ ($W=0, n=6$).

The expected condition factor in maturing juvenile males, $K_{CL\ 20}$, ranged widely between 2.11 and 3.45, while that of the mature adults, $K_{CL\ 40}$, were between 2.58 and 3.01 only (Table 4). In females, with a range of $K_{CL\ 20}$, 2.20–2.63, was similar but not as wide as in males, while the $K_{CL\ 40}$ range of 2.43–2.84 was noticeably lower than that in adult males. Two significant differences were obtained. Firstly, the mean condition factor calculated for both 20 mm and 40 mm CL standards of Form I males was always higher than in females (Table 4). The Wilcoxon signed-rank test pointed to the significance of these differences at $p < 0.05$ ($W=0, n=6$) in both size standards. Additionally, the apparent tendency to positive allometry of growth in females resulted in significantly larger mean condition values of adult ($K_{CL\ 40}$) than juvenile ($K_{CL\ 20}$) individuals (Wilcoxon signed-rank test; $W=0, n=6$) (Table 4).

The kind of habitat (stream or dam reservoir) had an effect on Fulton’s condition factor of individuals in the studied populations, as the majority of mean K values obtained in reservoirs were similar to or lower than the respective condition in streams, regardless of sex (Table 4). Especially the condition of adult females, which shows a distinct relationship with habitat, always being higher in streams with a range of $K_{CL\ 40}$ values 2.62–2.77 in comparison to 2.56–2.62 in reservoirs. However, a case of a distinctly better condition

Table 2 Distribution of collected individuals of *Faxonius limosus* among categories of carapace length (CL)

CL (mm)	Males						Females						Total
	Streams			Reservoirs			Streams			Reservoirs			
	1S*	2S	3S	1R	2R	3R	1S	2S	3S	1R	2R	3R	
<20					1		6	4	2	1	3	1	18
20–<25		2		1	1	3	2	13	3	6	26	9	66
25–<30	2	2	6	22	3	12	14	20	5	30	21	23	160
30–<35	23	12	20	8	11	5	48	32	20	10	22	12	223
35–<40	9	13	13	2	20	13	6	9	9	4	18	15	131
40–<45	2	3	5	1	4	7	3	1	3	2	8	3	42
≥45					4	1			1	1	1	5	13
Total	36	32	44	34	44	41	79	79	43	54	99	68	653

*Codes of sampling sites are explained in Table 1

Table 3 The parameters of regressions $W = a CL^b$ in the collected samples (CL in mm and W in g), their confidence intervals (95% CI), coefficients of determination (r^2) of these WLRs and values of form factor $a_{3.0}$

Sampling sites	Exponent b			Coefficient a		r^2	Form factor $a_{3.0} \times 10^4$
	b	95% CI b	p	$a \times 10^4$	95% CI $a \times 10^4$		
Males							
1S*	2.8934	2.6869–3.1000	0.302	4.2547	2.0550–8.8092	0.960	2.8326
2S	3.0562	2.9150–3.1975	0.422	2.2431	1.3630–3.6915	0.985	2.7804
3S	2.9924	2.8083–3.1765	0.934	2.8091	1.4656–5.3843	0.962	2.7286
All streams		2.6869–3.1975					
1R	3.2571	3.0130–3.5013	0.040	1.0790	0.4711–2.4711	0.958	2.8800
2R	3.1320	3.0173–3.2466	0.025	1.6966	1.1270–2.5542	0.986	2.8081
3R	2.9810	2.8693–3.0927	0.732	2.9360	1.9832–4.3466	0.987	2.7302
All reservoirs		2.8693–3.5013					
Females							
1S	3.1268	3.0521–3.2016	<0.002	1.7359	1.3438–2.2423	0.989	2.8171
2S	3.1788	3.0780–3.2795	<0.001	1.3568	0.9655–1.9068	0.981	2.6854
3S	3.1285	3.0279–3.2291	<0.02	1.6650	1.1742–2.3610	0.990	2.7198
All streams		3.0279–3.2016					
1R	3.1359	2.9962–3.2756	0.056	1.5503	0.9685–2.4815	0.975	2.6049
2R	3.0991	3.0301–3.1680	<0.01	1.8171	1.4387–2.2950	0.988	2.6524
3R	3.0761	2.9937–3.1585	0.070	1.9699	1.4828–2.6171	0.988	2.6342
All reservoirs		2.9937–3.2756					

*Codes of sampling sites are explained in Table 1

Statistical significance (p) of the deviations of values of regression exponent b from the parametric value $\beta = 3$ was tested with the t -test (the cases regarded as significant are marked with bold type)

in a reservoir habitat was detected, too, in juvenile females in the Cedzyna Reservoir (Table 4). Nevertheless, the highest values in all four mean K categories (i.e. $K_{CL\ 20}$ and $K_{CL\ 40}$ for males and females), as well as those relatively the highest if compared within the studied stream–reservoir pairs, were recorded in the population in the Belnianka stream (Table 4).

The differences found and presented above were confirmed with LMM analysis. The effect of tested variables, sex, habitat and CL, was significant. In habitat, the effect of the reservoir on the condition was negative, and in sex, the higher condition was reported for males (Table 5).

Discussion

Despite the growing amount of literature considering invasive crayfish, their spreading and impact on local ecosystems, there are only a few papers considering the effect of habitat factors on the body condition of these crustaceans, regardless of their status (native vs. invasive). Furthermore, as there is also abundant literature about the impact of the dam reservoirs on riverine ecosystems, including biological invasions, there are almost no papers considering species' biological traits in contrasting habitats (streams vs. reservoirs) of crayfish. Moreover, just a handful of studies refers to the *Faxonius* species. The available data on three species point to the possibility of significant sex-related differences.

In *F. propinquus* (Girard, 1852), collected mainly from natural streams in Indiana, which indicates positive allometry, while remained isometric in females. Contrary to that, in *F. rusticus* (Girard, 1852) collected from their native and introduced range in Indiana and Wisconsin, males also exhibited possible isometry while females tended to positive allometry of growth (Anderson and Simon 2015). In *F. virilis* (Hagen, 1870) living in the basins of the Laurentian Great Lakes and the Ohio River, both sexes exhibited remarkably strong positive allometry (Simon and Stewart 2014). Those results evidence the distinct strategies of the allocation of acquired resources into the growth of body size in males and females, which may be species-specific. In natural populations of *F. limosus*, positively allometric or isometric growth has been found as well. In rivers, streams and small stagnant water bodies in the upper Elbe catchment area in Bohemia, a positive allometric growth was reported (Ďuriš et al. 2006). Also, in two eutrophic lakes in north-eastern Poland, the values of exponent b in the W to total length (TL) relationships were significantly greater than 3.0 in males and females (max. 3.25, 3.21, and 3.17 in Form II males, Form I males, and females, respectively) while those recorded in a mesotrophic lake did not differ from 3.0 in both sexes (Chybowski 2007: table 7). Concerning the range of exponent b values, the results presented by Chybowski (2007) are lower than our values obtained in reservoir populations, i.e. those living in a lacustrine-like environment; however,

Table 4 Fulton’s condition factor (*K*) in the investigated populations of *Faxonius limosus*

Sampling sites	Body weight (g)		Condition factor	
	W_e	95% CI W_e	<i>K</i>	Range for 95% CI of W_e
20 mm CL				
Males				
1S*	2.474	2.215–2.762	3.092	2.769–3.453
2S	2.124	1.965–2.295	2.655	2.457–2.868
3S	2.197	1.985–2.431	2.746	2.481–3.038
All streams				2.457–3.453
1R	1.865	1.685–2.063	2.331	2.107–2.579
2R	2.015	1.882–2.158	2.519	2.353–2.698
3R	2.219	2.087–2.359	2.773	2.608–2.949
All reservoirs				2.107–2.949
Females				
1S	2.030	1.961–2.102	2.538	2.452–2.628
2S	1.855	1.777–1.935	2.318	2.222–2.419
3S	1.958	1.860–2.060	2.447	2.325–2.576
All streams				2.222–2.628
1R	1.864	1.762–1.971	2.329	2.202–2.464
2R	1.956	1.896–2.017	2.445	2.371–2.521
3R	1.980	1.900–2.063	2.474	2.375–2.578
All reservoirs				2.202–2.578
40 mm CL				
Males				
1S	18.380	17.674–19.114	2.872	2.762–2.987
2S	17.666	17.130–18.218	2.760	2.677–2.847
3S	17.480	16.856–18.128	2.731	2.634–2.832
All streams				2.634–2.987
1R	17.829	16.489–19.278	2.786	2.576–3.012
2R	17.668	17.221–18.126	2.761	2.691–2.832
3R	17.516	16.994–18.054	2.737	2.655–2.821
All reservoirs				2.576–3.012
Females				
1S	17.736	17.305–18.179	2.771	2.704–2.840
2S	16.793	16.181–17.429	2.624	2.528–2.723
3S	17.120	16.615–17.640	2.675	2.596–2.756
All streams				2.528–2.840
1R	16.381	15.564–17.241	2.560	2.432–2.694
2R	16.759	16.319–17.212	2.619	2.550–2.689
3R	16.694	16.244–17.157	2.608	2.538–2.681
All reservoirs				2.432–2.694

*Codes of sampling sites are explained in Table 1

The *K* values were calculated for three body weights estimated with respective WRLs for two standards of carapace length, 20 and 40 mm: for W_e (mean weight estimated for the fixed CL) and for limit values of 95% confidence interval (CI) of W_e

the form factors calculated on the basis of these WLRs are close to our results (Table 3). Thus, it can be concluded that (1) our WLR equations are consistent with existing data on

Table 5 Results of the general linear mixed-effects model (LMM) fitted to predict *K* from CL, habitat type (H) and sex (S) including locality as a random effect

	Estimate	SD	t	<i>p</i>
intercept	2.335412	0.047019	49.669	<0.001
CL	0.008571	0.001378	6.218	<0.001
H	−0.06781	0.016122	−4.206	<0.001
S	0.155898	0.017362	8.979	<0.001

F. limosus, (2) positive allometry of growth can be expected in females but not always in Form I males, (3) in general, the stagnant waters may offer less favourable habitats to females of this species where the positive allometry of individual growth is more difficult to achieve than in streams, and (4) the ranges of form factor $a_{3,0}$ values $2.7–2.9 \times 10^{-4}$ in Form I males and $2.6–2.8 \times 10^{-4}$ in females may be introduced as provisional characteristics of body shape in stream and reservoir populations of *F. limosus*. Thus, our study confirms the expected differences in individual body conditions in populations of *F. limosus* living in streams and dam reservoirs, but in the opposite direction than what was assumed. The present study is, to our knowledge, the first comparison of the individual condition of crayfish in the watercourses and the reservoirs located on them. Only Ďuriš et al. (2006) found that individuals from small streams had higher condition values than those from large rivers and isolated water bodies, which is compatible with our findings. However, they did not compare habitats in a pairwise arrangement, thus with no robust conclusions on differences between habitat types. The second achievement of our study is the demonstration of differences in body condition (1) between sexes in juvenile and adult individuals, found both in streams and reservoirs, and (2) between juvenile and adult females within each population, which is concordant with a tendency towards positive allometry of their growth detected in the studied populations of *F. limosus*. Also worthy of note is the lack of a clear positive or negative effect of reservoir habitat on the condition of small individuals. In general, it may be supposed that juveniles are more sensitive to environmental factors than large individuals are and, therefore, some habitat features can affect their condition more distinctly and generate effects that are more variable.

The extensive literature on crayfish aquaculture provides details concerning the pond rearing of juveniles of commercially important species. The main factors affecting their growth rate are stocking density, feed ration and quality, and survival rate during growout. This last factor is related to the availability of shelter that can significantly decrease the mortality of the stock. Therefore, the list of the main factors controlling individual growth can be reduced to current population density and the amount of available food

only. Thus, when the standing stock of *Procambarus clarkii* in a pond exceeds the approximate biomass of 100 g m^{-2} , juvenile growth significantly declines, which may be compensated by an appropriate reduction of density and/or by supplemental feeding (Jarboe and Romaine 1995; McClain 1995a, b). Other cultured crayfish, the three *Cherax* species, exhibited similar density-dependent growth in pond conditions (Mills and McCloud 1983; Morrissy 1992; Jones and Ruscoe 2000). The respective data on *F. limosus* growth were probably neither collected nor published due to the recent lack of interest in the aquaculture of this species, but there is no reason to expect another relationship between the individual growth and the population or habitat characteristics in this crayfish. Thus, the better body condition of juvenile *F. limosus* is more probable where their survival is relatively low and/or the ecosystem productivity is relatively high. The results of our study demonstrated that this is possible both in reservoirs and in stream reaches that have not been impounded. A study on the impact of primary productivity and fish predation on the abundance and individual size in natural populations of *Pacifastacus leniusculus* in streams and lakes in southern Sweden confirms this finding (Nyström et al. 2006). Another study provides evidence that the impact of fish predation on small individuals may be highly effective in the substantial reduction of the crayfish population in sandy lake littoral (Hein et al. 2006). In a study on three *Faxonius* species in shallow littoral, the individuals of 15–18 mm CL were eliminated by fish over 2 times more frequently than those of 23–25 mm CL (DiDonato and Lodge 1993). In laboratory experiments, the 25-cm, long centrarchid fish, the smallmouth bass *Micropterus dolomieu*, selected the smallest *Faxonius propinquus* available (Stein 1977).

The fish predation on juveniles, which can preclude the stunting of a successfully reproducing crayfish population, probably acts in different ways in streams and reservoirs. A stream channel is a spatio-temporal mosaic of habitats defined according to Frissell et al. (1986), which vary in depth, current velocity and bottom substrate (Pringle et al. 1988; Townsend 1989). Individual fish responds to these differences and distributes spatially, showing a relationship between depth and their body size (Harvey and Stewart 1991). As a result, potentially predatory larger individuals (for example, longer than 20 cm) concentrate in deeper pools (Schlosser 1987), while the shallows, especially those with coarse bottom particles or deposited plant debris, may offer refuges for juvenile crayfish. Contrary to that, in reservoirs, predatory fish can penetrate the whole area of a sandy bottom with poor vegetation as a rule due to the fluctuating water level (Krolová et al. 2010). Predation may considerably reduce crayfish density there and additionally can affect their behaviour, making them less active, which causes decreased foraging and growth (Stein

and Magnuson 1976; Collins et al. 1983). The addition of untypical coarse bottom substrate providing appropriate refuge can significantly increase the abundance of the crayfish population in such environments (Johnsen and Taugbøl 2008). Therefore, the presence of any protection from fish predation may be crucial for the survival of juvenile crayfish and, indirectly, for their growth and condition factor in reservoirs. On the other hand, this may not be so important in rivers, where their natural features provide the permanent availability of refuges for crayfish. Possibly some differences in the occurrence of such artificial structures as rip-rap, grid embankments or fascines (made of bundles of willow branches) may affect the abundance of *F. limosus* in the studied reservoirs, despite these differences not being clear in every one of the studied pairs of habitats. There are no studies on the impact of fish foraging on crayfish food resource availability. However, recent studies (Veselý et al. 2021) showed that the diet of crayfish may be shaped by the presence of other crayfish species within the occupied site.

Additionally, the food base available for crayfish is supported in these reservoirs, as they are popular places for recreational fishing. Anglers release considerable amounts of nutritionally enriched ground bait, which may also be appropriate food for omnivorous crayfish and can even alter their isotopic $\delta^{13}\text{C}$ signature, as was demonstrated in Lake Kleiner Döllnsee in Germany (Mehner et al. 2019). In all three reservoirs, ground bait is regularly used, whereas in the studied rivers, such practice is absent (M. Bień 2021, personal communication). Both these anthropogenic factors, artificial shelter and additional food, can impact density and growth in local populations of *F. limosus*, and some differences in their local importance may explain, partly, the wide range of differences in the body condition of juvenile individuals in the studied reservoirs.

The results of our study showed that the dam reservoirs do not provide more favourable conditions for *F. limosus* than those in the natural aquatic environments of an upland landscape; however, they should not be excluded as ‘stepping stones’ for further spread. Their relative significance may depend on local habitat conditions, both within and outside the given reservoir. In fact, some reservoirs, and stagnant water bodies in general, may facilitate *F. limosus* colonising suboptimal regions like mountains (Hefti and Stucki 2006; Petrusek et al. 2006; Bonk and Bobrek 2020). Probably, the positive effect of reservoirs may not be evident if compared to adjacent stream reaches where the habitats are more favourable for *F. limosus*. Moreover, each of the studied reservoirs may not be colonised during the invasion of the river system along with water courses, but can rather act as a ‘gate’ for invasion if these crayfish are used as bait by anglers there. Such practice is regarded among the main factors of crayfish spreading out of their

native ranges in North America (DiStefano et al. 2009), and this effect should also be presumed in Europe.

To conclude, we did not provide the expected evidence that habitats in dam reservoirs enable *F. limosus* to achieve better individual conditions than in natural watercourses of an upland landscape in Central Europe. However, such an advantageous effect may be possible in other, more ecologically harsh landscapes for this crayfish, especially in colder climatic zones (Bonk and Bobrek 2020). Therefore, further studies are needed for a more precise understanding of the impact of habitat features in man-made reservoirs on the body condition measures of *F. limosus*, and crayfish in general. Especially, the reproductive quality of females and their ability to produce abundant cohorts of juveniles seem worth studying because these characteristics may evidence the viability of populations and their invasive potential. Additionally, the decrease of body condition in suboptimal habitats may reveal a range of species plasticity and the ability to adapt by changing resource allocation between growth and reproduction. Furthermore, due to the detected habitat-related variability in body condition, we confirmed that this parameter can be useful for tracking the species traits in different habitats.

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Data availability Provided with tables in the manuscript. Raw data available in authors' databases.

Code availability Not applicable.

Declarations

Ethics approval The study has been conducted according to the "Ethical guidelines for journal publication" (<https://www.elsevier.com/author/policies-and-guidelines>) and local law.

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Consent for publication Approved.

Conflict of interest The authors declare no competing interests.

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Niniejszym zaświadczam, że wersja elektroniczna mojej rozprawy doktorskiej „Wpływ antropogenicznych przekształceń rzek na rozmieszczenie i biologię inwazyjnego raka pręgowatego *Orconectes limosus* Rafinesque” przeznaczona do publikacji w BIP oraz dostarczona na nośnikach cyfrowych, jest tożsama z wersją drukowaną.

Z poważaniem,

