UNIWERSYTET MIKOŁAJA KOPERNIKA W TORUNIU
WYDZIAŁ NAUK BIOLOGICZNYCH I WETERYNARYJNYCH

Piotr Paweł Kłosiński

Rozprawa doktorska

Czynniki kształtujące przewagę konkurencyjną inwazyjnych gatunków ryb babkowatych nad ich rodzimymi odpowiednikami w kontekście zmian klimatycznych

Promotor: prof. dr hab. Tomasz Kakareko

Promotor pomocniczy: dr hab. Łukasz Jermacz, prof. UMK

Katedra Ekologii i Biogeografii

Toruń 2025

Składam serdeczne podziękowania

moim promotorom,
Panu ***prof. dr. hab. Tomaszowi Kakareko*** *i Panu* ***dr. hab. Łukaszowi Jermaczowi,***
prof. UMK
za bezgraniczną życzliwość oraz wszechstronną i nieocenioną pomoc
na każdym etapie realizacji doktoratu;

współautorowi publikacji wchodzących w skład niniejszej rozprawy doktorskiej,
Panu ***prof. dr. hab. Jarosławowi Kobakowi***
za pomoc w realizacji badań i cenne wskazówki merytoryczne
na etapie publikacji uzyskanych wyników

Pracę dedykuję

Moim Najukochańszym Rodzicom,
Najważniejszym Osobom mojego życia,
Mamie Jolancie (1963–2025) i Tacie Jerzemu (1958–2021)*,*
Zmarłym po długich chorobach

Tytuł pracy w języku angielskim:

Factors shaping the competitive advantage of invasive goby fish species over their native counterparts in the context of climate change

Wykaz publikacji wchodzących w skład rozprawy doktorskiej:

1. **Kłosiński, P.**, Kobak, J., & Kakareko, T. (2024). Metabolic rate of two invasive Ponto-Caspian goby species and their native competitors in the context of global warming. Freshwater Biology 69(7), 971–983. https://doi.org/10.1111/fwb.14259. Impact Factor w roku 2023: 2.8, Q1 w kategorii: marine & freshwater biology

2. **Kłosiński, P.**, Kobak, J., & Kakareko, T. (2025a). Effect of hypoxia and acidification on metabolic rate of Ponto-Caspian gobies and their native competitors in the context of climate change. Hydrobiologia. https://doi.org/10.1007/s10750-025-05794-5. Impact Factor w roku 2023: 2.2, Q1 w kategorii: marine & freshwater biology

3. **Kłosiński, P.**, Kobak, J., & Kakareko, T. (2025b). Competitive interactions for food resources between invasive Ponto-Caspian gobies and their native competitors in the context of global warming. NeoBiota 97, 91–119. https://doi.org/10.3897/neobiota.97.134566. Impact Factor w roku 2023: 3.8, Q1 w kategoriach: biodiversity conservation; ecology

Finansowanie badań:

Projekt „Obrona przed drapieżnictwem jako element konkurencyjnej przewagi inwazyjnych gatunków ryb nad rodzimymi: Studium przypadku pontokaspijskich Gobiidae” finansowany przez Narodowe Centrum Nauki (grant nr 2016/23/B/NZ8/00741, kierownik: Tomasz Kakareko). Publikacja 1 i 2.

Program „Inicjatywa doskonałości – uczelnia badawcza” (IDUB), Uniwersytet Mikołaja Kopenika w Toruniu. Publikacja 3.

Spis treści

Streszczenie

Rozprawa doktorska wpisuje się w nurt badań nad inwazjami biologicznymi, czyli procesu ekologicznego, który w wyniku działalności człowieka staje się coraz bardziej powszechny i stanowi zagrożenie dla różnorodności biologicznej oraz funkcjonowania ekosystemów w skali światowej, prowadzącego do postępującej homogenizacji fauny i flory na Ziemi. Inwazjom gatunków obcych mogą sprzyjać globalne zmiany warunków środowiskowych, jak zmiany klimatu. Głównym celem rozprawy doktorskiej było poszerzenie wiedzy na temat wpływu czynników abiotycznych powiązanych ze zmianami klimatu (podwyższona temperatura, hipoksja, acydyfikacja), na metabolizm i behawior współwystępujących w środowisku inwazyjnych i rodzimych gatunków ryb, w kontekście oceny ich przystosowania do ocieplania wód i osiągania przewagi konkurencyjnej w takich warunkach. Wykonano cztery eksperymenty w warunkach kontrolowanych w laboratorium, w których testowano dwa gatunki babek (babka łysa *Babka gymnotrachelus*, babka szczupła *Neogobius fluviatilis*) rozprzestrzeniających się w wodach śródlądowych Europy oraz dwa gatunki rodzime (głowacz białopłetwy *Cottus gobio,* kiełb *Gobio gobio*). W pierwszym eksperymencie badano wpływ podwyższonej temperatury latem (25 vs. 17 °C) na standardowe i maksymalne tempo metabolizmu ryb. Na podstawie tych parametrów określono zakres tlenowy, będący wskaźnikiem wydolności fizjologicznej (tlenowej). W kolejnych dwóch eksperymentach sprawdzono wpływ krótkotrwałej, postępującej hipoksji i acydyfikacji na rutynowe tempo metabolizmu. Ostatni eksperyment dotyczył wpływu podwyższonej temperatury latem (25 vs. 17 °C) na zdolności konkurencyjne ryb o ograniczone zasoby pokarmowe. Badania wykazały, że jakkolwiek w wyższej temperaturze ryby babkowate nie zawsze przewyższały rodzime gatunki pod względem większej wydolności tlenowej, miały jednak niższe koszty utrzymania dzięki utrzymywaniu niższego standardowego tempa metabolizmu. Babki wykazały większą tolerancję na hipoksję w porównaniu z gatunkami rodzimymi. W przypadku acydyfikacji, większą tolerancję na spadki pH odnotowano u babki szczupłej, ale nie babki łysej, w porównaniu z rodzimym konkurentem. Testowane młodociane osobniki babek pomimo tego, że nie wykazywały większej agresji w konfrontacji z rodzimymi gatunkami, aktywniej od nich zdobywały pokarm, niezależnie od temperatury. Wyniki badań sugerują, że pod względem testowanych cech fizjologicznych i behawioralnych, badane gatunki babek są lepiej przystosowane do zmieniających się warunków środowiskowych związanych z globalnymi zmianami klimatycznymi, i wraz z ocieplaniem wód będą utrzymywały przewagę konkurencyjną nad ich

rodzimymi odpowiednikami. Sukces inwazji babki łysej może jednak zostać osłabiony przez postępującą acydyfikację wód.

Abstract

The doctoral dissertation is part of the research stream on biological invasions – an ecological process that is becoming increasingly common due to human activity and poses a threat to biodiversity and the functioning of ecosystems on a global scale, leading to the progressing homogenisation of fauna and flora on Earth. Global changes in environmental conditions, such as climate change, can facilitate invasions of alien species. The main aim of the dissertation was to expand the knowledge on the impact of abiotic factors associated with climate change (elevated temperature, hypoxia, acidification) on the metabolism and behaviour of invasive and native fish species co-occurring in the environment, in the context of assessing their adaptation to water warming and achieving competitive advantage in such conditions. Four experiments were performed under controlled conditions in the laboratory, testing two species of gobies (the racer goby *Babka gymnotrachelus*, the monkey goby *Neogobius fluviatilis*) spreading in inland waters of Europe and two native species (the European bullhead *Cottus gobio*, the gudgeon *Gobio gobio*). The first experiment investigated the effect of elevated summer temperature (25 vs. 17 °C) on the standard and maximum metabolic rate of fish. The aerobic scope was determined based on these parameters, indicating physiological performance (aerobic capacity). The following two experiments examined the effect of short-term progressive hypoxia and acidification on routine metabolic rate. The last experiment concerned the effect of elevated summer temperature (25 vs. 17 °C) on the competitive abilities of fish for limited food resources. Studies have shown that although at higher temperatures, the gobies did not consistently outperform the native species in terms of higher aerobic scope, they had lower living costs by maintaining lower standard metabolic rates. Gobies showed greater tolerance to hypoxia compared to native species. In the case of acidification, greater tolerance to pH drops was noted in the monkey goby but not in the racer goby, compared to the native competitor. Even though the tested juvenile gobies did not show higher aggression than the native species, they more actively accessed food than the latter, regardless of temperature. The results of the studies suggest that in terms of the tested physiological and behavioural traits, the tested goby species are better adapted to changing environmental conditions related to global climate change. With water warming, they will maintain a competitive advantage over their native counterparts. However, the invasion success of the racer goby may be attenuated by progressing water acidification.

Wprowadzenie

Inwazje biologiczne a zmiany klimatu

Wszystkie żywe organizmy mają potencjał do rozprzestrzeniania się, rozszerzenia w sposób naturalny, bez udziału człowieka, zasięgu geograficznego swojego występowania (Solarz, 2007; Wilson i in., 2009; Webber i Scott, 2012). Naturalna ekspansja organizmów ma najczęściej łagodny, powolny przebieg, niekiedy zbliżony do skali czasu geologicznego (Richardson i in., 2000; Solarz, 2007). W odróżnieniu od ekspansji, inwazje biologiczne są procesem, w którym w wyniku bezpośredniej lub pośredniej działalności człowieka – poprzez celowe introdukcje, przypadkowe zawleczenia lub przekształcanie środowiska (Hulme i in., 2008; Nunes i in., 2015) – organizmy są w stosunkowo szybkim tempie wprowadzane poza zasięg swojego rodzimego (naturalnego) występowania (Carlton, 1999; Solarz, 2007), w czasie krótszym niż wynikałoby to z naturalnych mechanizmów ekspansji (Solarz, 2007; Głowaciński i in., 2012). W ciągu ostatnich kilku dekad na całym świecie obserwuje się przyspieszenie takiego sposobu rozprzestrzeniania się organizmów, wynikające głównie z postępującej globalizacji: rozwoju transportu, międzynarodowego handlu i turystyki (Vitousek i in., 1997; Hulme, 2009; Keller i in., 2011; Early i in., 2016). Inwazja gatunku obcego obejmuje szereg następujących po sobie etapów: transportu, introdukcji, zadomowienia i rozprzestrzeniania (Hellmann i in., 2008; Blackburn i in., 2011; Keller i in., 2011). Aby doszło do inwazji, przełamane muszą zostać bariery przemieszczania organizmów – geograficzna oraz związana z oporem środowiska. Przełamanie bariery geograficznej jest głównie efektem działalności człowieka, polegającej na bezpośrednim transporcie gatunków lub usunięciu naturalnej bariery, np. na skutek wybudowania kanału między izolowanymi systemami cieków (Hulme i in., 2008; Pyšek i in., 2010). Barierę mogą stanowić również odmienne abiotyczne warunki środowiskowe. W celu jej przełamania konieczny jest szeroki zakres tolerancji względem czynników środowiskowych. Z kolei przełamanie bariery związanej z elementami biotycznymi środowiska wymaga szeregu przystosowań, np. stwarzających przewagę konkurencyjną nad lokalnymi gatunkami (Rewicz i in., 2014). Część obcych gatunków to gatunki inwazyjne, tj. takie, które w stosunkowo szybkim tempie i dużej liczbie osobników kolonizują nowe tereny, są zdolne utworzyć stabilne, rozmnażające się populacje o odpowiednim zagęszczeniu, i mogą powodować znaczące negatywne zmiany w ekosystemach, a także wywierać szkodliwy wpływ na gospodarkę lub na zdrowie człowieka (Richardson i in., 2000; Blackburn i in., 2011; Głowaciński i in., 2012; Najberek i Solarz, 2016; David i in., 2017). Warto podkreślić, że zgodnie z tzw. „regułą dziesiątek” zaproponowaną przez Williamsona i Fittera (1996) tylko około 10% wszystkich gatunków introdukowanych zadomawia się na nowych terenach, a z tego ponownie około 10% gatunków stanie się inwazyjnymi. Aczkolwiek, istnieją badania pokazujące, że dla wielu taksonów, odsetek ten może przekroczyć nawet 50%, szczególnie w przypadku ekosystemów wodnych (Jeschke i Strayer, 2005; Jeschke, 2008). Wraz z pojawieniem się inwazyjnych gatunków obcych w nowym środowisku odnotowuje się wiele negatywnych skutków w odniesieniu do rodzimych biocenoz. Za najważniejsze uważa się zubożenie puli genowej gatunków rodzimych poprzez drapieżnictwo (Janssen i Jude, 2001; Barton i in., 2005), konkurencję (Kitchell i in., 1997; Blanchet i in., 2007), przenoszenie chorób i pasożytów (Kvach i Ondračková, 2020; Ondračková i in., 2021), przekształcanie siedlisk (Moyle, 1986; Kitchell i in., 1997), a także hybrydyzację oraz introgresję (Costedoat i in., 2004; Gozlan i Beyer, 2006; D'Amato i in., 2007). Gatunki inwazyjne stanowią rosnące zagrożenie dla zachowania bioróżnorodności oraz funkcjonowania ekosystemów w skali globalnej (Rodriguez, 2006; Keller i in., 2011; Lambertini i in., 2011; Simberloff, 2011; Early i in., 2016; Dueñas i in., 2021), co prowadzi do postępującej homogenizacji fauny i flory na Ziemi (Lodge, 1993; Vitousek i in., 1996; Villéger i in., 2011; Simberloff i in., 2013).

W przyszłości inwazje biologiczne mogą przybierać na sile z powodu globalnych zmian środowiskowych, zwłaszcza zmian klimatycznych (Bellard i in., 2012; Luque i in., 2014). Różnice klimatyczne, dotyczące w szczególności temperatury (Früh i in., 2017), są uważane za jedną z najważniejszych barier uniemożliwiających osiedlanie się obcych gatunków na nowych obszarach. Według Międzyrządowego Zespołu ds. Zmian Klimatu (IPCC, 2014, 2018, 2023), w każdej z ostatnich czterech dekad temperatura powierzchni Ziemi była wyższa niż w poprzedniej i jednocześnie wyższa, niż w jakimkolwiek z poprzednich dziesięcioleci od 1850 roku. Obecne scenariusze zmian klimatu zakładają wzrost średniej temperatury powietrza o 2-5 °C do końca tego stulecia (w zależności od scenariusza uwzględniającego emisję dwutlenku węgla do atmosfery), a także zwiększone ryzyko wystąpienia ekstremalnych dobowych wahań temperatury (Estay i in., 2014; IPCC, 2014, 2018, 2023). W konsekwencji oczekuje się, że wzrost temperatury, spowodowany w głównej mierze antropopresją, będzie sprzyjał inwazjom biologicznym (Penk i in., 2016; Hesselschwerdt i Wantzen, 2018). Wyższe temperatury mogą okazać się korzystne dla gatunków ciepłolubnych, umożliwiając im rozprzestrzenianie się na obszarach wcześniej niedostępnych. Stąd przypuszcza się, że inwazyjne gatunki obce w porównaniu z rodzimymi konkurentami mogą być lepiej dostosowane pod względem fizjologicznym do postępujących zmian klimatu, co może sprzyjać ich rozprzestrzenianiu się, kolonizacji przez nie nowych obszarów (Byers, 2002; Thuiller i in., 2007; Hellmann i in., 2008; Rahel i Olden, 2008; Sorte i in., 2013; Sorte, 2014).

Inwazje biologiczne w ekosystemach słodkowodnych a zmiany klimatu

Ekosystemy słodkowodne zajmują tylko około 1% powierzchni Ziemi, ale zapewniają siedliska dla wielu gatunków, w tym około jednej trzeciej wszystkich gatunków kręgowców, i są uznawane za szczególnie narażone na utratę bioróżnorodności na skutek introdukcji gatunków inwazyjnych (Dudgeon i in., 2006; Ricciardi i MacIsaac, 2010; Reid i in., 2019; Bernery i in., 2022). Przewiduje się, że wraz ze wzostem temperatury powietrza w wyniku zmian klimatycznych wzrośnie temperatura wód powierzchniowych (IPCC, 2014; Frölicher i Laufkötter, 2018). Biorąc pod uwagę fakt, że większość organizmów wodnych to organizmy zmiennocieplne (ektotermiczne), takie zmiany termiki wód mogą wywierać na nie poważny wpływ, z uwagi na kluczowe znaczenie temperatury dla ich fizjologii (zwłaszcza metabolizmu), bioenergetyki, behawioru i biogeografii (Rahel i Olden, 2008; Hulme, 2017). Wyniki metaanalizy przeprowadzonej przez Sorte i in. (2013) wskazują, że w ekosystemach wodnych, w odróżnieniu od eksoystemów lądowych, zmienione warunki środowiskowe na skutek zmian klimatu sprzyjają kształtowaniu przewagi konkurencyjnej gatunków obcych nad rodzimymi, co sugeruje większą podatność środowisk wodnych na inwazje biologiczne w porównaniu z lądowymi. Należy zauważyć, że zmiany klimatu to wielowymiarowe zjawisko obejmujące nie tylko zmiany temperatury z epizodami ekstremalnie wysokich temperatur i przedłużającymi się ciepłymi okresami w ciągu roku (Frölicher i in., 2018), ale także zjawiska towarzyszące, jak hipoksja (natlenienie wody na tyle niskie, aby negatywnie wpłynąć na fizjologię i/lub behawior organizmu) (Ficke i in., 2007; Pörtner i Peck, 2010) czy acydyfikacja wód (zakwaszanie wód, spadek pH wody, każdy poziom pH na tyle niski, aby negatywnie wpłynąć na fizjologię i/lub behawior organizmu) (Pörtner i Peck, 2010; IPCC, 2014; Schwieterman i in., 2019). W ten sposób zmieniający się klimat, poprzez kształtowanie warunków abiotycznych środowisk wodnych, może kompleksowo, także pośrednio, wpływać na inwazje biologiczne (Hellmann i in., 2008; Hulme, 2017). Warto podkreślić, że na ogół badania niekorzystnych czynników abiotycznych w środowiskach wodnych, jak podwyższona temperatura, hipoksja i acydyfikacja wód, dotyczą środowisk morskich i oceanicznych a ekosystemy słodkowodne są pod tym względem znacznie słabiej zbadane (Sorte, 2014; Tripp i in., 2022).

W przypadku ekosystemów wodnych, jednymi z najczęściej introdukowanych na świecie zwierząt są ryby słodkowodne (García-Berthou i in., 2005; Bernery i in., 2022). Szacuje się, że inwazyjne ryby słodkowodne stanowią najliczniejszą grupę zwierząt zagrażających gatunkom rodzimym w ekosystemach słodkowodnych w Europie (Genovesi i in., 2015; Xu i in., 2024). W świetle powyższych informacji, zagadnieniem szczególnej wagi dla objaśnienia funkcjonowania, a także ochrony ekosystemów słodkowodnych jest poznanie mechanizmów oraz czynników leżących u podstaw sukcesu inwazyjnych gatunków ryb na nowych terenach. Rośnie liczba artykułów dotyczących mechanizmów rozprzestrzeniania się inwazyjnych słodkowodnych gatunków (np. Hayes i Barry, 2008; Bernery i in., 2022), ale wiele aspektów tego procesu nadal jest słabo poznanych, jak wpływ zmian klimatu na fizjologię czy behawior ryb, tj. właściwości kształtujące np. ich zdolności konkurencyjne czy antydrapieżnicze, ważne dla osiągnięcia sukcesu inwazyjnego. Istotne wydaje się tutaj poznanie tolerancji omawianych organizmów nie tylko na podwyższoną temperaturę, ale także zjawiska towarzyszące ocieplaniu wód, jak hipoksja czy acydyfikacja. Wciąż nikły jest jednak stan wiedzy na temat wpływu tych czynników na metabolizm, a także na behawior współwystępujących w środowisku inwazyjnych i rodzimych gatunków ryb słodkowodnych. Jest to zagadnienie ważne w kontekście oceny ich dostosowania do postępujących zmian klimatu (ocieplanie wód) i przewagi konkurencyjnej obcych przybyszy nad rodzimymi gatunkami.

Inwazje pontokaspijskich Gobiidae w wodach śródlądowych Europy w kontekście zmian klimatu

Wskazuje się, że taksony pochodzące z określonych regionów geograficznych, w których warunki sprzyjały kształtowaniu specyficznych cech organizmów, np. szerokiej walencji ekologicznej, są predysponowane do inwazji (Paiva i in., 2018; Cuthbert i in., 2020; Stern i Lee, 2020). Przykładem jest region pontokaspijski, na który składają się zlewnie mórz Czarnego, Azowskiego i Kaspijskiego, będący jednym z najważniejszych donorów gatunków inwazyjnych, rozprzestrzeniających się w wodach śródlądowych Europy (Bij de Vaate i in., 2002; Galil i in., 2007). Specyficzna historia tego regionu z wielokrotną orogenezą, okresami zlodowacenia i cofania się lodowca czy częstymi fluktuacjami (transgresjami i regresjami) poziomu wód i dynamicznymi zmianami warunków termicznych jak i zasolenia (Mordukhay-Boltovskoy, 1964; Dumont, 1998; Reid i Orlova, 2002; Leroy i in., 2007; Kocovsky i in., 2011; Rewicz i in., 2014), szczególnie w niestabilnych środowiskach nadmorskich limanów (zatok) i estuariów (przyujściowych odcinków miejscowych rzek), wpłynęła na wyewoluowanie eurytopowej fauny. Przykładem są pontokaspijskie ryby z rodziny babkowatych (Gobiidae), rzędu okoniokształtnych (Perciformes) (Nelson i in., 2016). Od lat 90. XX wieku w wodach śródlądowych Zachodniej i Środkowej Europy odnotowuje się nasilone rozprzestrzenianie pontokaspijskich gatunków ryb babkowatych (Copp i in., 2005; Roche i in., 2013). Babkowate wędrują szlakami dużych rzek połączonych ze sobą sztucznymi kanałami (Bij de Vaate i in., 2002; Pauli i Briski, 2018; Soto i in., 2023). Kanały te scalają zlewnie mórz regionu pontokaspijskiego ze zlewniami mórz europejskich (głównie z Morzem Północnym i Morzem

Bałtyckim). W tak utworzonej sieci kanałów można wyróżnić trzy podstawowe korytarze migracji: północny, centralny i południowy (Bij de Vaate i in., 2002; Galil i in., 2007). W wodach śródlądowych Europy stwierdzono sześć inwazyjnych gatunków ryb babkowatych (Copp i in., 2005). Przez Polskę przebiega jeden z najistotniejszych w Europie korytarzy umożliwiających przemieszczanie się na zachód – tzw. korytarz centralny. Należą do niego m.in. Bug, Wisła i Odra (Bij de Vaate i in., 2002). Babka łysa *Babka gymnotrachelus* (Kessler, 1857), babka szczupła *Neogobius fluviatilis* (Pallas, 1814) oraz babka rurkonosa *Proterorhinus semilunaris* (Heckel, 1837) przeniknęły do wód śródlądowych Polski korzystając z tego korytarza (Grabowska i in., 2008, 2010, 2023; Witkowski i Grabowska, 2012). Po raz pierwszy babka łysa pojawiła się w Polsce w 1995 roku w Bugu na odcinku Terespol-Drohiczyn (Danilkiewicz, 1996). W 1997 roku również w Bugu, ale na odcinku Terespol-Mężenin znaleziono po raz pierwszy babkę szczupłą (Danilkiewicz, 1998). Gatunki te szybko rozprzestrzeniły się do Wisły, gdzie już w 2000 (babka łysa) oraz 2001 (babka szczupła) roku zostały odnotowane w Zbiorniku Włocławskim (Kostrzewa i Grabowski, 2001, 2002). Z kolei babka rurkonosa po raz pierwszy pojawiła się w 2008 roku w Zbiorniku Włocławskim (Grabowska i in., 2008). Jak widać, wspomniane trzy blisko ze sobą spokrewnione gatunki ryb babkowatych mogą rozprzestrzeniać się razem, co wskazuje na potencjał tych zwierząt, w przypadku takich wielogatunkowych inwazji, do rozległego kolonizowania nowych terenów, obejmujących różne siedliska. Uwidacznia się to w dorzeczu Wisły, gdzie gatunki te stanowią trwały komponent ichtiofauny w rozmaitych typach siedlisk, zarówno przepływowych jak i lenitycznych, w tym w starorzeczach (Płąchocki i in., 2020; Grabowska i in., 2023). Omawiane pontokaspijskie Gobiidae to ryby bentosożerne o względnie małych rozmiarach ciała (<10 cm długości całkowitej) (Plachá i in., 2010; Kakareko, 2011), pozbawione pęcherza pławnego (Neilson i Stepien, 2011), prowadzące przydenny tryb życia (Teletchea i Beisel, 2018), związane z kryjówkami (Charlebois i in., 1997; Kakareko, 2011; Błońska i in., 2016) o krótkim cyklu życiowym (4-6 lat) (Kakareko, 2011). Wcześnie osiągają dojrzałość płciową (w 1-2 roku życia), mają tarło porcyjne rozciągnięte w czasie a samce sprawują opiekę rodzicielską (Grabowska i Przybylski, 2015). Występują głównie w płytkich obszarach przybrzeżnych rzek jak i wód o wyraźnie spowolnionym przepływie (wysłodzone partie mórz, zbiorniki zaporowe, przepływowe jeziora) (Kottelat i Freyhof, 2007; Kornis i in., 2012; Ulikowski i in., 2021) na głębokości mniejszej niż 1-1,5 m (Erös i in., 2005; Płąchocki i in., 2020) lub 3 m (Kocovsky i in., 2011). Dotychczas wykonane badania wskazują, że babki stanowią zagrożenie dla rodzimych gatunków ryb przydennych: mogą wypierać je z zajmowanych mikrosiedlisk (Dubs i Corkum, 1996; Kornis i in., 2012; van Kessel i in., 2016), skutecznie konkurować z nimi o pokarm (Kakareko i in., 2013; Pawelec-Olesińska, 2020), kryjówki (Jermacz i in., 2015; Błońska i in., 2016; Grabowska i in., 2016) albo zjadać ich ikrę (Dubs i Corkum, 1996). W nowo zasiedlanych ekosystemach babki stają się ważnym ogniwem sieci troficznych, zarówno jako drapieżniki (Janssen i Jude, 2001; Barton i in., 2005), jak i ofiary (Almqvist i in., 2010; Płąchocki i in., 2012). Wpływają też na populacje pasożytów, stając się nosicielami wielu lokalnych, jak i mając potencjał do zwiększania liczebności nowych w środowisku (Kvach i Ondračková, 2020; Ondračková i in., 2021). Badania eksperymentalne wykazały, że pontokaspijskie babki wykazują bardziej odważne zachowania rozumiane jako zdolność do podejmowania ryzyka (opuszczanie kryjówek w nowym środowisku i większa aktywność w eksplorowaniu nowego otoczenia) w porównaniu do rodzimych konkurentów (Augustyniak i in., 2024b). Takie cechy babek z jednej strony mogą sprzyjać ich przemieszczaniu i zajmowaniu przez nie nowych terenów, ale z drugiej strony mogą zwiększać ich podatność na drapieżnictwo, jako czynnik ograniczający ich rozprzestrzenianie się. Jakkolwiek babki mają większe zdolności detekcji drapieżnika na podstawie obserwacji zachowań innych osobników różnych gatunków (Augustyniak i in., 2024a), nie stwierdzono u nich ani silniejszych reakcji na sygnały świadczące o drapieżnictwie (Kłosiński i in., 2022) ani lepszej skuteczności zachowań obronnych w bezpośredniej konfrontacji z drapieżnikiem (Augustyniak i in., 2023) w porównaniu z ich rodzimymi odpowiednikami. Wydaje się zatem, że inwazyjne babki nie mają przewagi konkurencyjnej nad swoimi rodzimymi odpowiednikami w unikaniu drapieżnictwa.

Pontokaspijskie babki stanowią dogodny model do badań wpływu czynników powiązanych ze zmianami klimatycznymi na przebieg inwazji obcych gatunków w zespołach ryb bentosowych w wodach śródlądowych, w tym zwłaszcza w systemach rzecznych Europy, w których spektakularnie się rozprzestrzeniają (Copp i in., 2005). Na duży potencjał babek w dostosowaniu się do skutków postępujących zmian klimatu, wskazuje ich pochodzenie z regionu, gdzie klimat jest cieplejszy niż w Europie Środkowej, Wschodniej i Północnej. Warto wspomnieć o tym, że temperatura w lipcu w limanach i deltach rzek z tego regionu osiąga nawet 29 ºC, co sugeruje wysoką górną granicę tolerancji temperatury lokalnych organizmów (Rewicz i in., 2014) w porównaniu z wymienionymi obszarami Europy. Ewolucja babek, jak już wspomniano, w niestabilnych warunkach siedliskowych limanów i delt dużych rzek wpływających do Morza Czarnego, Azowskiego i Kaspijskiego (Mordukhay-Boltovskoy, 1964; Dumont, 1998; Reid i Orlova, 2002; Leroy i in., 2007; Kocovsky i in., 2011; Rewicz i in., 2014) mogła zaowocować ukształtowaniem się unikalnego zestawu cech, w tym rozwojowi większych zakresów tolerancji środowiskowej, zapewniających przewagę konkurencyjną nad rodzimymi odpowiednikami, pochodzącymi ze stosunkowo chłodniejszego klimatu (Copp i in., 2005; Roche i in., 2013). Spośród babek, jedynie w przypadku babki byczej, znaleźć można stosunkowo wiele opracowań na temat cech fizjologicznych czy behawioralnych, mogących wpływać na sukces inwazyjny gatunku (np. Behrens i in., 2017; Christensen i in., 2021; Backström i Winkelmann, 2022; Quattrocchi i in., 2023; Błońska i in., 2024). W przypadku innych przedstawicieli pontokaspijskich Gobiidae, nikły jest stan wiedzy na ten temat, a przede wszystkim brak jest rozeznania, czy są one lepiej przystosowane do termicznych (podwyższona temperatura) i nietermicznych (hipoksja, acydyfikacja) skutków zmian klimatycznych w ekosystemach wodnych, w porównaniu z rodzimymi konkurentami należącymi do tej samej gildii.

Badania wykonane w ramach rozprawy doktorskiej

Cele badań

Nadrzędnym celem badań było poszerzenie wiedzy na temat wpływu czynników abiotycznych powiązanych ze zmianami klimatu (podwyższona temperatura, hipoksja, acydyfikacja), na metabolizm i behawior współwystępujących w środowisku inwazyjnych, pontokaspijskich ryb babkowatych i ich rodzimych odpowiedników, w kontekście oceny ich przystosowania do ocieplania wód i osiągania przewagi konkurencyjnej w takich warunkach. Dwa gatunki babek rozprzestrzeniające się w wodach śródlądowych Europy, w tym Polski oraz dwa gatunki rodzime z tej samej gildii posłużyły jako model. Cele szczegółowe były wpisane w trzy zadania badawcze oparte na eksperymentach przeprowadzonych w kontrolowanych warunkach laboratoryjnych, w których testowano:

1. Wpływ podwyższonej temperatury latem (25 vs. 17 °C) na standardowe i maksymalne tempo metabolizmu, wydolność fizjologiczną (tlenową) ryb.
2. Wpływ hipoksji i acydyfikacji na rutynowe tempo metabolizmu ryb.
3. Wpływ podwyższonej temperatury latem (25 vs. 17 °C) na zdolności konkurencyjne ryb o ograniczone zasoby pokarmowe.

Podstawę niniejszej rozprawy doktorskiej stanowi zbiór trzech artykułów naukowych, opublikowanych w latach 2024-2025, powstałych w wyniku realizacji powyższych zadań badawczych.

Badane ryby

Do badań wybrano dwie pary gatunków ryb. Każda para składała się gatunku inwazyjnego (pontokaspijskiej babki) oraz jego rodzimego odpowiednika o zbliżonej morfologii i biologii, tj. gatunków współwystępujących w środowisku, zajmujących podobne nisze ekologiczne, należących do tej samej gildii i potencjalnie konkurujących ze sobą w warunkach naturalnych. Były to następujące pary gatunków:

1. Babka łysa *Babka gymnotrachelus* (Kessler, 1857) i głowacz białopłetwy *Cottus gobio* Linnaeus, 1758 (przedstawiciel rodziny głowaczowatych Cottidae)
2. Babka szczupła *Neogobius fluviatilis* (Pallas, 1814) i kiełb *Gobio gobio* (Linnaeus, 1758) (przedstawiciel rodziny karpiowatych Cyprinidae)

Babka łysa i głowacz białopłetwy wykazują wiele podobieństw, przede wszystkim pod względem trybu życia związanego z dnem, w tym m.in. wymagań siedliskowych, pokarmowych i tarłowych, cech takich jak brak pęcherza pławnego (Mills i Mann, 1983; Neilson i Stepien, 2011; Teletchea i Beisel, 2018) czy strategia poruszania się typu „burst-and-hold" polegająca na krótkich okresach aktywnego pływania (specyficzne podskoki do toni wodnej a następnie powolne opadanie na dno), po których następują próby utrzymania nieruchomej pozycji na dnie (Tierney i in., 2011; Egger i in., 2021). W rzekach europejskich babka łysa i głowacz białopłetwy notowane są na tych samych odcinkach, i jakkolwiek zaznacza się selekcja siedlisk pomiędzy tymi gatunkami, ich rozmieszczenie na dnie w znacznym stopniu pokrywa się (Kakareko i in., 2016; Janáč i in., 2018). Eksperymentalne badania laboratoryjne pokazały, że babka łysa jest lepszym konkurentem o pokarm (Kakareko i in., 2013) czy kryjówkę (Jermacz i in., 2015; Błońska i in., 2016; Grabowska i in., 2016) od głowacza białopłetwego, co wskazuje na negatywny wpływ gatunku inwazyjnego na rodzimy. W przypadku drugiej testowanej pary, pomimo tego, że kiełb wykazuje bentopelagiczny tryb życia i jest postrzegany jako gatunek tworzący ławice (Brylińska, 2000; Egger i in., 2021), ma zbliżone wymagania siedliskowe z babką szczupłą. Oba gatunki współwystępują na siedliskach o piaszczystym podłożu (Kottelat i Freyhof, 2007; Jakovlić i in., 2015; Piria i in., 2019; Płąchocki i in., 2020). Stwierdzono, że wraz ze wzrostem udziału babki szczupłej w zespołach ryb następuje spadek udziału kiełbia, co może wskazywać na potencjalną konkurencję i negatywny wpływ gatunku inwazyjnego na rodzimy (Jakovlić i in., 2015; Gertzen, 2016).

Osobniki danej pary gatunków były pozyskiwane do badań z populacji współwystępujących ze sobą w warunkach naturalnych (dorzecze Wisły), a zatem w zbliżonym stopniu uwarunkowanych środowiskiem naturalnym. Do każdego zadania badawczego osobniki tych gatunków były pozyskiwane razem (w tym samym czasie), tą samą metodą, z tych samych lub zbliżonych, sąsiadujących ze sobą siedlisk, w rzece Brdzie (babka łysa, głowacz białopłetwy) oraz rzece Pilicy lub Wiśle (babka szczupła, kiełb). Do badań pozyskiwane były osobniki młodociane, bez oznak dojrzałości płciowej. Połów ryb, transport oraz wszystkie badania zostały zrealizowane z przestrzeganiem obowiązujących norm prawnych, z dbałością o zachowanie wysokiego poziom dobrostanu zwierząt. Każdy z zaplanowanych eksperymentów wykonanych w ramach trzech zadań badawczych przedstawionych w poprzednim podrozdziale, uzyskał zgodę Lokalnej Komisji Etycznej do spraw doświadczeń na zwierzętach w Bydgoszczy: (1) Uchwała Nr 26/2020 z dnia 09.10.2020 r.; (2) Uchwała Nr 27/2021 z dnia 29.06.2021 r.; (3) Uchawała Nr 30/2022 z dnia 22.06.2022 r. Odłów i wykorzystanie głowacza białopłetwego, który jest prawnie chroniony w Polsce (częściowa ochrona gatunkowa), zostało zaakceptowane przez Regionalną Dyrekcję Ochrony Środowiska w Bydgoszczy (nr zezwolenia WOP.6401.4.5.2017. MO, WOP.6401.4. 19.2018.MO, WOP.6401.4.52.2022.MO).

Eksperymenty

Rdzeń prezentowanej rozprawy doktorskiej stanowią cztery eksperymenty przeprowadzone w kontrolowanych warunkach laboratoryjnych, w tym trzy fizjologiczne i jeden behawioralny, na bazie których powstały trzy artykuły naukowe.

W **pierwszym eksperymencie**, przedstawionym w publikacji 1 (Kłosiński i in., 2024) testowano odpowiedzi metaboliczne ryb na podwyższoną temperaturę. Temperatura jest głównym czynnikiem kształtującym warunki życia w ekosystemach wodnych (Estay i in., 2014; Vázquez i in., 2017). W związku z tym, że generalnie ryby są ektotermami, zmiany temperatury wody mają istotny wpływ na ich fizjologię, głównie metabolizm (Pörtner i Knust, 2007; Isaak i Rieman, 2013; Domenici i in., 2019; Jermacz i in., 2020). Metabolizm jest podstawowym, wrażliwym na temperaturę procesem fizjologicznym, podczas którego pobrane i zmagazynowane zasoby są transformowane do różnych struktur biologicznych i aktywności organizmu (Ikeda i in., 2000). Metabolizm można zdefiniować też jako sumę wszystkich reakcji chemicznych zachodzących w komórkach organizmu, z uwolnieniem energii. Energia uzyskana w wyniku tych procesów jest magazynowana wyłącznie w postaci adenozynotrifosforanu (ATP) i wykorzystywana do różnych czynności przez żywe organizmy. ATP powstaje w cyklu kwasu trikarboksylowego. Aby cykl mógł zajść, konieczny jest tlen. Bazując na tych zależnościach, tempo metabolizmu można oszacować metodą respirometryczną, mierząc bezpośrednio tempo zużycia tlenu (Ikeda i in., 2000). Stąd, jedną z najważniejszych zmiennych fizjologicznych służących do porównywania zdolności radzenia sobie z różnymi warunkami abiotycznymi (w tym z podwyższoną temperaturą) przez organizmy stanowi tempo zużycia tlenu, będące miarą całkowitego zużycia energii w czasie (Donelson i in., 2012; Nelson i in., 2016). U zwierząt ektotermicznych metabolizm na ogół wzrasta wraz z temperaturą, generując niekorzystne zmiany w funkcjonowaniu zwierząt (Donelson i in., 2012), głównie z powodu rosnącego zapotrzebowania energetycznego (Rahel i Olden, 2008; Webb i in., 2008; Domenici i in., 2019). Wydolność tlenowa (wydolność fizjologiczna), wyrażona jako zakres tlenowy (AS) (Clark i in., 2013), odzwierciedla zdolność organizmu do wykonywania procesów wymagających tlenu powyżej poziomu niezbędnego do utrzymania spoczynkowego tempa metabolizmu (SMR) w danej temperaturze (Clark i in., 2013). AS to różnica pomiędzy maksymalnym i standardowym (spoczynkowym) tempem metabolizmu (odpowiednio MMR i SMR) (Killen i in., 2021). Przypuszcza się, że niska wydolność tlenowa może stanowić fizjologiczne ograniczenie w rozprzestrzenianiu się i osiedlaniu gatunków na nowo zasiedlonych obszarach (Marras i in., 2015). Stosunkowo wysoki AS może przełożyć się na bardziej elastyczny budżet energetyczny, poprawiając w ten sposób mobilność, wzrost i/lub reprodukcję (Maazouzi i in., 2011; Killen i in., 2016), a w konsekwencji dostosowanie (Claireaux i Lefrançois, 2007).

Biorąc pod uwagę, że inwazyjne ryby babkowate ewoluowały w regionie pontokaspijskim, gdzie klimat jest cieplejszy niż na pozostałych obszarach Europy Środkowej, Wschodniej i Północnej celem eksperymentu było sprawdzenie czy obce w wodach Polski ryby z rodziny babkowatych mają większą wydolność tlenową od współwystępujących z nimi rodzimych gatunków ryb w podwyższonej temperaturze latem (25 vs 17 °C). **Hipotezy testowane w ramach pierwszego eksperymentu były następujące: (hipoteza 1) podwyższona temperatura latem podnosi tempo metabolizmu (zwłaszcza SMR) testowanych gatunków, ograniczając tym samym ich wydolność tlenową wyrażoną jako AS; (hipoteza 2) inwazyjne babki wykazują mniej obniżoną wydolność tlenową w podwyższonej temperaturze latem niż ich rodzime odpowiedniki, ze względu na stosunkowo niższy SMR.**

W **eksperymentach drugim i trzecim**, opisanych w publikacji 2 (Kłosiński i in., 2025a) testowano wpływ hipoksji i acydyfikacji na tempo metabolizmu ryb. Jak już wspomniano wcześniej, zmiany klimatu są wielowymiarowe, zwłaszcza w ekosystemach wodnych i objawiają się nie tylko w postaci wzrostu temperatury (Frölicher i in., 2018), ale także w zjawiskach nietermicznych takich jak hipoksja (Ficke i in., 2007; Pörtner i Peck, 2010) czy acydyfikacja (Pörtner i Peck, 2010; IPCC, 2014; Schwieterman i in., 2019). Podejrzewa się, że rosnąca temperatura wody nasili zjawiska hipoksji w wodach słodkich, zwłaszcza latem (Ficke i in., 2007; Xu i Xu, 2015; Jane i in., 2021; Sampaio i in., 2021) poprzez stymulację mineralizacji materii organicznej (Nixon, 1995; Müller i in., 2012) czy zmniejszenie rozpuszczalności tlenu w wodzie (Deutsch i in., 2011). Z kolei emisja dwutlenku węgla do atmosfery przez człowieka spotęguje, oprócz wzrostu temperatury, spadki pH w ekosystemach wodnych (Feely i in., 2009; Heuer i Grosell, 2014; IPCC, 2014).

Odpowiednim parametrem fizjologicznym służącym do porównania tolerancji organizmów na krótkotrwałe zmiany środowiskowe jest rutynowe tempo metabolizmu (RMR) (Hall i Clark, 2016; Palacios i in., 2016; Onthank i in., 2021). RMR odzwierciedla średnie tempo metabolizmu, podczas którego zwierzę zachowuje typową, spontaniczną aktywność

(Chabot i in., 2016; Metcalfe i in., 2016). Nietermiczne czynniki powiązane ze zmianami klimatu mogą powodować zmiany w metabolizmie ryb, a co za tym idzie, w ich budżecie energetycznym, co może przełożyć się na ich zdolności przystosowania się do zmieniających się wraz z ocieplaniem wód warunków środowiskowych (Rogers i in., 2016; Rosewarne i in., 2016; Nati i in., 2018; Crear i in., 2020).

Reakcje organizmów wobec zmian klimatu, zakresu ich tolerancji środowiskowej, są często powiązane z ich rozmieszczeniem geograficznym, zasięgiem naturalnego występowania (Helmuth i in., 2006; Sorte, 2014). Założono, że inwazyjne babki mają stosunkowo szerokie zakresy tolerancji fizjologicznej ze względu na ewolucję w bardzo niestabilnym, zmiennym pod względem czynników abiotycznych środowisku limanów i ujść rzek (Mordukhay-Boltovskoy, 1964; Dumont, 1998; Reid i Orlova, 2002; Leroy i in., 2007; Kocovsky i in., 2011; Rewicz i in., 2014). Celem przeprowadzonego eksperymentu było sprawdzenie czy obce w wodach Polski ryby z rodziny babkowatych mają większą tolerancję wobec niekorzystnych czynników abiotycznych (krótkotrwałej hipoksji i acydyfikacji), nasilających się w środowisku w wyniku ocieplenia klimatu, od współwystępujących z nimi rodzimych gatunków ryb. Pomiary RMR wykonano w temperaturze 17 °C przy 5 poziomach rozpuszczonego tlenu w wodzie: 95%, 60%, 40%, 30% i 25% oraz przy 5 poziomach pH: 8.5, 8.0, 7.5, 7.0 i 6.5. RMR zawsze porównywano z referencyjnym RMR mierzonym przy 95% rozpuszczonego tlenu lub pH o wartości 8.5. Wszelkie odchylenia (wzrost lub spadek) RMR od referencyjnego uznawano za objaw stresu lub suboptymalnych warunków doświadczanych przez zwierzę (Mandic i in., 2009; Rogers i in., 2016). **Postawione hipotezy testowane w ramach omawianego eksperymentu zakładały, że (hipoteza 3) inwazyjne gatunki ryb babkowatych są fizjologicznie bardziej tolerancyjne na hipoksję i (hipoteza 4) acydyfikację (tj. są zdolne do utrzymania stałego RMR przy niższych wartościach rozpuszczonego tlenu i pH) niż ich rodzime odpowiedniki.**

W **czwartym eksperymencie**, przedstawionym w publikacji 3 (Kłosiński i in., 2025b) testowano wpływ podwyższonej temperatury na interakcje konkurencyjne pomiędzy rybami. Postępujące globalne ocieplenie klimatu poprzez kształtowanie metabolizmu, jednocześnie moduluje funkcjonowanie, czynności życiowe ektotermów, np. ich aktywność lokomotoryczną, odżywianie, reprodukcję (Gillooly i in., 2001; Brown i in., 2004; Savage i in., 2004) czy interakcje konkurencyjne (Taniguchi i in., 1998; Oyugi i in., 2012; Carmona-Catot i in., 2013; Ramberg-Pihl i in., 2023). Dlatego, aby uzyskać kompleksowy obraz wpływu globalnego ocieplenia na ektotermy, celowe jest uwzględnienie w badaniach nie tylko aspektów tego wpływu związanych z metabolizmem, ale także behawiorem (Killen i in., 2014;

Rosewarne i in., 2016). Zwłaszcza behawioralne aspekty związane z interakcjami pomiędzy obcymi i rodzimymi gatunkami, w tym interakcjami konkurencyjnymi, wydają się tutaj ważne, albowiem mogą w sposób znaczący wpływać na zajmowanie nowych terenów, przebieg inwazji. Przyjmuje się, że notowany u gatunków obcych szeroki zakres fizjologicznej tolerancji na czynniki środowiskowe (Kolar i Lodge, 2002; Monaco i Helmuth, 2011) jest cechą, która zwiększa prawdopodobieństwo ich zadomowienia na nowych terenach (Jewett i in., 2005; Keller i in., 2011; Lenz i in., 2011) i skutecznego konkurowania z gatunkami rodzimymi (Liu i van Kleunen, 2017).

Nadrzędnym celem eksperymentu było sprawdzenie czy w warunkach podwyższonej temperatury wody, obce w wodach Polski pontokaspijskie ryby z rodziny babkowatych są lepszymi konkurentami o ograniczone zasoby pokarmowe od rodzimych gatunków ryb. W eksperymencie, konkurencję o ograniczone zasoby pokarmowe (żywe larwy Chironomidae) testowano w parach wewnątrz- i międzygatunkowych, aby poznać różnice w zachowaniach konkurencyjnych między gatunkami, jak i wpływ jednego gatunku na drugi. Rejestrowano zachowania związane z agresją jak i samym żerowaniem (czas dotarcia do pokarmu i czas spędzony na żerowaniu) w dwóch temperaturach (17 i 25 °C). **Postawiono dwie hipotezy: (hipoteza 5) inwazyjne babki, w porównaniu do swoich rodzimych odpowiedników, są lepszymi konkurentami w zdobywaniu pokarmu i w konsekwencji są w stanie pozbawić rodzime gatunki miejsc żerowania. Ich przewaga będzie objawiać się większą agresją wobec rodzimych konkurentów niż wobec przedstawicieli własnego gatunku, szybszym docieraniem do pokarmu i ograniczeniem czasu spędzonego na żerowaniu przez rodzimych konkurentów; (hipoteza 6) różnice te (przewaga konkurencyjna) będą bardziej wyraźne w temperaturze 25 niż 17 °C.**

Wyniki i ich omówienie

W przypadku badań wykonanych w ramach pierwszej części rozprawy doktorskiej (Kłosiński i in., 2024) pierwsza hipoteza (**hipoteza 1**), że podwyższona temperatura (25 °C) spowoduje wzrost spoczynkowego tempa metabolizmu (SMR) skutkujący obniżeniem wydolności tlenowej (AS=MMR–SMR) została potwierdzona w parze babka szczupła-kiełb, ale nie w przypadku pary babka łysa-głowacz białopłetwy. Co ciekawe, chociaż podwyższona temperatura istotnie zwiększyła SMR głowacza i babki łysej, ich AS nie uległ obniżeniu. Druga hipoteza (**hipoteza 2**), że gatunek inwazyjny wykazuje większą wydolność tlenową w podwyższonej temperaturze latem, została potwierdzona również tylko w przypadku pary babka szczupła-kiełb. Warto podkreślić, że chociaż SMR wzrastał w podwyższonej temperaturze, niezależnie od gatunku, to u obu gatunków babek był zawsze niższy niż u ich rodzimych odpowiedników. Natomiast, u żadnego z badanych gatunków podwyższona temperatura nie miała wpływu na maksymalne tempo metabolizmu (MMR). Wyniki wpisują się zatem w hipotezę „*plastic floors and concrete ceilings*" zaproponowaną przez Sandbloma i in. (2016), mającą swoje zastosowanie w odniesieniu do ryb (Rodgers i Franklin, 2021). Zgodnie z tą hipotezą, SMR wykazuje plastyczność fenotypową, podczas gdy MMR jest bardziej stabilne (jest stałe lub wykazuje ograniczoną plastyczność) w kontekście adaptacji do podwyższonych temperatur (Sandblom i in., 2016). Dlatego, zdolność adaptacyjna ryb do ocieplającego się klimatu może być ograniczona przez niższą plastyczność MMR w porównaniu z SMR. Badania potwierdziły, że podwyższona temperatura wpływa na metabolizm (zwłaszcza na SMR) zarówno inwazyjnych jak i rodzimych gatunków ryb. Przeprowadzone testy wykazały, że chociaż inwazyjne ryby babkowate w porównaniu z rodzimymi odpowiednikami nie zawsze miały większą wydolność tlenową, to u każdego z testowanych gatunków babek, SMR był zawsze niższy niż u rodzimych ryb (niezależnie od temperatury). Zdolność babki łysej i babki szczupłej do utrzymywania niższego SMR w porównaniu z rodzimymi odpowiednikami może być kluczową cechą fizjologiczną w kontekście kształtowania się potencjału inwazyjnego babek w warunkach ocieplenia klimatu. Ryby te ponosząc niższe nakłady energetyczne na spoczynkowy metabolizm, mogą uzyskać przewagę konkurencyjną nad rodzimymi gatunkami ryb, albowiem zaoszczędzoną energię mogą alokować na procesy życiowe ściśle związane z dostosowaniem (np. wzrost, rozmnażanie) i aktywności ułatwiające dalszą inwazję.

Badania wykonane w ramach drugiej części rozprawy doktorskiej (Kłosiński i in., 2025a) potwierdziły pierwszą z postawionych hipotez (**hipoteza 3**) – zarówno babka łysa jak i babka szczupła okazały się bardziej tolerancyjne na hipoksję niż ich rodzimi konkurenci, na co wskazuje zdolność babek do utrzymywania rutynowego tempa metabolizmu (RMR) na stabilnym poziomie przy niższych stężeniach tlenu. Jednakże, kolejna hipoteza (**hipoteza 4**), że inwazyjne babki są bardziej fizjologicznie tolerancyjne na spadki pH niż ich rodzime odpowiedniki, została potwierdzona tylko w przypadku pary babka szczupła-kiełb, ale nie w przypadku pary babka łysa-głowacz białopłetwy.

U rodzimych gatunków, w odróżnieniu od inwazyjnych babek, hipoksja wywołała spadek rutynowego tempa metabolizmu, co stanowi reakcję obronną, służącą przeciwdziałaniu negatywnym skutkom niskiego natlenienia wody, oszczędzania limitowanej ilości tlenu. Skutkiem ubocznym, jest ograniczenie wydatków energetycznych na najbardziej podstawowe funkcje życiowe, ale także na czynności związane z dostosowaniem (np. wzrost, rozmnażanie). Wykonane badania wskazują, że inwazyjne babki w warunkach hipoksji mogą nie doświadczać takich szkodliwych skutków w odróżnieniu od ich rodzimych odpowiedników. W przypadku acydyfikacji wzrost RMR u babki łysej i kiełbia wydaje się być wynikiem energetycznie zależnych szlaków regulacji kwasowo-zasadowej (Claiborne i in., 2002; Heuer i Grosell, 2014). W rezultacie ryby te mogą alokować mniej zasobów energetycznych na inne funkcje w porównaniu do swoich środowiskowych konkurentów.

Znaczna tolerancja na hipoksję u ryb z rodziny babkowatych jest ważną cechą ekologiczną, wskazującą na ich potencjał do kolonizacji wód eutroficznych. Szczególnie w takich środowiskach, w wyniku zmian klimatycznych i ocieplania wód, należy spodziewać się występowania coraz częstszych i rozległych deficytów tlenowych. Tolerancja na hipoksję może pozwolić inwazyjnym babkom na wykorzystanie przestrzeni i zasobów niedostępnych dla ich rodzimych konkurentów, współwystępujących w środowisku (Farwell i in., 2007), a także pomagać w unikaniu drapieżnictwa (Rosenberger i Chapman, 1999; Domenici i in., 2007).

Stosunkowo niska tolerancja na niskie pH w przypadku babki łysej wskazuje, że sukces inwazyjny tego gatunku może być w przyszłości osłabiony przez zakwaszenie wody, jeśli ten aspekt globalnych zmian będzie postępował. Obecnie, czynnik ten nie wydaje się kluczowy dla inwazji, zważywszy na znaczne rozprzestrzenienie babki łysej w europejskich wodach śródlądowych (Grabowska i in., 2023).

Rezultaty badań przeprowadzonych w ramach trzeciej części rozprawy doktorskiej i przedstawionych w publikacji 3 (Kłosiński i in., 2025b) potwierdziły pierwszą hipotezę (**hipoteza 5**), że młodociane osobniki babek są skuteczniejszymi konkurentami w zdobywaniu pokarmu niż ich rodzime odpowiedniki. Druga z postawionych hipotez (**hipoteza 6**) nie została potwierdzona – tzn. wpływ podwyższonej temperatury na konkurencję międzygatunkową nie przełożył się na bardziej widoczną dominację babek nad rodzimymi rybami.

Co ciekawe, rodzime ryby, pomimo tego, że wykazywały większą agresję w stosunku do inwazyjnych konkurentów, nie były w stanie skutecznie konkurować z babkami, niezależnie od temperatury. Z kolei, babki okazały się lepszymi konkurentami w rywalizacji o pokarm niż ich rodzime odpowiedniki poprzez szybsze docieranie do źródeł pokarmu i ograniczenie czasu spędzonego na żerowaniu swoim konkurentom, niezależnie od temperatury. Wskazuje to, że konkurencja między młodocianymi osobnikami ryb babkowatych a ich rodzimymi odpowiednikami opiera się na lepszym pozyskiwaniu zasobów pokarmowych, a nie bezpośredniej agresji. Warto podkreślić, że umiejętność oceny swoich szans i unikania bezpośredniego konfliktu z przeciwnikiem pozwala zwierzętom zminimalizować straty energii i ryzyko obrażeń (Parker i Rubenstein, 1981; Moretz, 2003; Poulos i McCormick, 2014), co jest zgodne z nieagresywnym (unikającym walki) zachowaniem młodocianych babek.

Uzyskane wyniki poszerzają wiedzę na temat zagrożeń, jakie stwarzają pontokaspijskie babki dla rodzimych, europejskich ryb słodkowodnych (patrz Grabowska i in., 2023). Okazuje się bowiem, że nie tylko dorosłe osobniki, co wykazano wcześniej (Kakareko i in., 2013), ale także młodociane babki są lepszymi konkurentami pokarmowymi od ich rodzimych odpowiedników (Kłosiński i in., 2025b) przez co mogą stanowić dla nich konkurencyjne zagrożenie w warunkach naturalnych. Uzyskane rezultaty nie dostarczają jednak kolejnych dowodów na to, że podwyższone temperatury wody osłabiają zdolności rodzimych gatunków ryb do konkurowania z gatunkami inwazyjnymi (Taniguchi i in., 1998; Oyugi i in., 2012; Ramberg-Pihl i in., 2023), albowiem efektu temperatury (25 vs 17 °C) w odniesieniu do analizowanych interakcji konkurencyjnych u ryb nie stwierdzono. Pamiętać jednak należy, że w wyższej temperaturze, co wykazano w publikacji 1 (Kłosiński i in., 2024) koszty utrzymania metabolizmu omawianych rodzimych gatunków ryb były wyższe w porównaniu z inwazyjnymi babkami. Z tego powodu, gorsze zdolności konkurencyjne rodzimych gatunków w porównaniu z babkami w odniesieniu do zasobów pokarmowych (Kłosiński i in., 2025b) mogą powodować bardziej niekorzystne skutki dla rodzimych gatunków w podwyższonych temperaturach wody.

Podsumowanie

Najważniejsze wnioski z wykonanych w ramach prezentowanej rozprawy doktorskiej badań inwazyjnych, pontokaspijskich gatunków ryb babkowatych (babka łysa *Babka gymnotrachelus*, babka szczupła *Neogobius fluviatilis*) i ich rodzimych odpowiedników (głowacz białopłetwy *Cottus gobio*, kiełb *Gobio gobio*) w kontekście zmian klimatycznych i ocieplania wód, są następujące:

1. Babki w podwyższonej temperaturze, jakkolwiek generalnie nie osiągają wyższej wydolności fizjologicznej (tlenowej), ponoszą niższe koszty energetyczne, dzięki zdolności do utrzymywania niższego standardowego tempa metabolizmu, i dlatego mogą lepiej funkcjonować w takich warunkach w porównaniu z rodzimymi gatunkami ryb (Publikacja 1).
2. Babki wykazują większą tolerancję na hipoksję od rodzimych gatunków, co wskazuje na ich lepsze przystosowanie do bytowania w warunkach deficytów tlenowych w środowiskach wodnych w porównaniu z rodzimymi gatunkami (Publikacja 2).
3. Większą tolerancję na acydyfikację odnotowano u babki szczupłej, natomiast nie u babki łysej, w porównaniu z rodzimymi gatunkami. Wskazuje to, że babka szczupła jest lepiej przystosowana do postępującej acydyfikacji ekosystemów wodnych w porównaniu z rodzimym konkurentem, tj. kiełbiem. Natomiast inwazje babki łysej mogą ograniczać spadki pH wód w warunkach naturalnych (Publikacja 2).
4. Babki są lepszymi konkurentami w rywalizacji o pokarm niż ich rodzime odpowiedniki poprzez szybsze docieranie do źródeł pokarmu i ograniczenie czasu spędzonego na żerowaniu konkurentom, niezależnie od temperatury. Sugeruje to, że babki mają przewagę konkurencyjną nad rodzimymi gatunkami w odniesieniu do zasobów pokarmowych w warunkach naturalnych, i utrzymają tę przewagę, gdy wody staną się cieplejsze (Publikacja 3).

Uzyskane efekty badań sugerują, że omawiane gatunki babek pod względem testowanych cech fizjologicznych (metabolizm) i behawioralnych (interakcje konkurencyjne), są generalnie lepiej przystosowane do radzenia sobie z globalnymi zmianami klimatu, zarówno termicznymi (podwyższona temperatura wód) jak i nietermicznymi (hipoksja i acydyfikacja wód) i wraz z ocieplaniem wód będą utrzymywały przewagę konkurencyjną nad rodzimymi gatunkami ryb z tej samej gildii. Sukces inwazyjny babki łysej może jednak zostać osłabiony przez postępującą acydyfikację wód.

Bibliografia

Almqvist, G., Strandmark, A. K., & Appelberg, M. (2010). Has the invasive round goby caused new links in Baltic food webs? Environmental Biology of Fishes, 89(1), 79–93. https://doi.org/10.1007/s10641-010-9692-z.

Augustyniak, M., Kobak, J., Jermacz, Ł., Adamiak, A., & Kakareko, T. (2024a). Public information use – are invasive demersal fish species more effective than natives? Behavioral Ecology, 35(6), arae089. https://doi.org/10.1093/beheco/arae089.

Augustyniak, M., Kobak, J., Trojan, M., & Kakareko, T. (2024b). Behavioural responses to environmental novelty in demersal, shelter-associated invasive fish and their native analogues. Animal Behaviour, 208, 111–126. https://doi.org/10.1016/j.anbehav.2023.11.008.

Augustyniak, M., Kołacka, K., Kobak, J., Hliwa, P., Kłosiński, P., Poznańska-Kakareko, M., … Kakareko, T. (2023). Differences in predator-avoidance behavior between two invasive gobies and their native competitors. Current Zoology, 69(6), 727–737. https://doi.org/10.1093/cz/zoac082.

Backström, T., & Winkelmann, C. (2022). Invasive round goby shows higher sensitivity to salinization than native European perch. NeoBiota, 75, 23–38. https://doi.org/10.3897/neobiota.75.86528.

Barton, D. R., Johnson, R. A., Campbell, L., Petruniak, J., & Patterson, M. (2005). Effects of Round Gobies (*Neogobius melanostomus*) on Dreissenid Mussels and Other Invertebrates in Eastern Lake Erie, 2002–2004. Journal of Great Lakes Research, 31(Suppl. 2), 252–261. https://doi.org/10.1016/S0380-1330(05)70318-X.

Behrens, J. W., van Deurs, M., & Christensen, E. A. F. (2017). Evaluating dispersal potential of an invasive fish by the use of aerobic scope and osmoregulation capacity. PLoS ONE, 12(4), e0176038. https://doi.org/10.1371/journal.pone.0176038.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. Ecology Letters, 15(4), 365–377. https://doi.org/10.1111/j.1461-0248.2011.01736.x.

Bernery, C., Bellard, C., Courchamp, F., Brosse, S., Gozlan, R. E., Jarić, I., … Leroy, B. (2022). Freshwater Fish Invasions: A Comprehensive Review. Annual Review of Ecology, Evolution, and Systematics, 53(1), 427–456. https://doi.org/10.1146/annurev-ecolsys-032522-015551.

Bij de Vaate, A., Jazdzewski, K., Ketelaars, H. A. M., Gollasch, S., & Van der Velde, G. (2002). Geographical patterns in range extension of Ponto-Caspian macroinvertebrate species in Europe. Canadian Journal of Fisheries and Aquatic Sciences, 59(7), 1159–1174. https://doi.org/10.1139/f02-098.

Blackburn, T. M., Pyšek, P., Bacher, S., Carlton, J. T., Duncan, R. P., Jarošík, V., … Richardson, D. M. (2011). A proposed unified framework for biological invasions. Trends in Ecology & Evolution, 26(7), 333–339. https://doi.org/10.1016/j.tree.2011.03.023.

Blanchet, S., Loot, G., Grenouillet, G., & Brosse, S. (2007). Competitive interactions between native and exotic salmonids: a combined field and laboratory demonstration. Ecology of Freshwater Fish, 16(2), 133–143. https://doi.org/10.1111/j.1600-0633.2006.00205.x.

Błońska, D., Kobak, J., Kakareko, T., & Grabowska, J. (2016). Can the presence of alien Ponto-Caspian gobies affect shelter use by the native European bullhead? Aquatic Ecology, 50(4), 653–665. https://doi.org/10.1007/s10452-016-9584-1.

Błońska, D., Janic, B., Tarkan, A. S., Piria, M., Bănăduc, D., Švolíková, K. S., … Bukowska, B. (2024). Physiological responses of invasive round goby (*Neogobius melanostomus*) to environmental stressors across a latitudinal span. Biological Invasions, 26(10), 3433–3444. https://doi.org/10.1007/s10530-024-03387-2.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. Ecology, 85(7), 1771–1789. https://doi.org/10.1890/03-9000.

Brylińska, M. (Red.). (2000). Ryby słodkowodne Polski. Warszawa: Wydawnictwo Naukowe PWN.

Byers, J. E. (2002). Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. Oikos, 97(3), 449–458. https://doi.org/10.1034/j.1600-0706.2002.970316.x.

Carlton, J. T. (1999). The scale and ecological consequences of biological invasions in the world's oceans. [W:] O. T. Sandlund, P. J. Schei, & Å. Viken (Red.), Invasive Species and Biodiversity Management (pp. 195–212). Dordrecht: Kluwer Academic Publishers.

Carmona-Catot, G., Magellan, K., & García-Berthou, E. (2013). Temperature-Specific Competition between Invasive Mosquitofish and an Endangered Cyprinodontid Fish. PLoS ONE, 8(1), e54734. https://doi.org/10.1371/journal.pone.0054734.

Chabot, D., Steffensen, J. F., & Farrell, A. P. (2016). The determination of standard metabolic rate in fishes. Journal of Fish Biology, 88(1), 81–121. https://doi.org/10.1111/jfb.12845.

Charlebois, P. M., Marsden, J. E., Goettel, R. G., Wolf, R. K., Jude, D. J., & Rudnika, S. (1997). The round goby *Neogobius melanostomus* (Pallas), A Review of European and North American Literature. Illinois Natural History Survey Special Publication No. 20.

Christensen, E. A. F., Norin, T., Tabak, I., van Deurs, M., & Behrens, J. W. (2021). Effects of temperature on physiological performance and behavioral thermoregulation in an invasive fish, the round goby. Journal of Experimental Biology, 224(1), jeb237669. https://doi.org/10.1242/jeb.237669.

Claiborne, J. B., Edwards, S. L., & Morrison-Shetlar, A. I. (2002). Acid–base regulation in fishes: cellular and molecular mechanisms. Journal of Experimental Zoology, 293(3), 302–319. https://doi.org/10.1002/jez.10125.

Claireaux, G., & Lefrançois, C. (2007). Linking environmental variability and fish performance: integration through the concept of scope for activity. Philosophical Transactions of the Royal Society B: Biological Sciences, 362(1487), 2031–2041. https://doi.org/10.1098/rstb.2007.2099.

Clark, T. D., Sandblom, E., & Jutfelt, F. (2013). Aerobic scope measurements of fishes in an era of climate change: respirometry, relevance and recommendations. Journal of Experimental Biology, 216(15), 2771–2782. https://doi.org/10.1242/jeb.084251.

Copp, G. H., Bianco, P. G., Bogutskaya, N. G., Erős, T., Falka, I., Ferreira, M. T., … Wiesner, C. (2005). To be, or not to be, a non-native freshwater fish? Journal of Applied Ichthyology, 21(4), 242–262. https://doi.org/10.1111/j.1439-0426.2005.00690.x.

Costedoat, C., Pech, N., Chappaz, R., Salducci, M. D., Lim, P., & Gilles, A. (2004). Étude de l’hybridation introgressive entre *Chondrostoma t. toxostoma* et *Chondrostoma n. nasus* (Téléostéen, Cyprinidae) en utilisant une approche multiple. Cybium, 28(1 suppl.), 51–61. https://doi.org/10.26028/cybium/2004-281s-008.

Crear, D. P., Brill, R. W., Averilla, L. M. L., Meakem, S. C., & Weng, K. C. (2020). In the face of climate change and exhaustive exercise: the physiological response of an important recreational fish species. Royal Society Open Science, 7(3), 200049. https://doi.org/10.1098/rsos.200049.

Cuthbert, R. N., Kotronaki, S. G., Dick, J. T. A., & Briski, E. (2020). Salinity tolerance and geographical origin predict global alien amphipod invasions. Biology Letters, 16(9), 20200354. https://doi.org/10.1098/rsbl.2020.0354.

D'Amato, M. E., Esterhuyse, M. M., van der Waal, B. C. W., Brink, D., & Volckaert, F. A. M. (2007). Hybridization and phylogeography of the Mozambique tilapia *Oreochromis mossambicus* in southern Africa evidenced by mitochondrial and microsatellite DNA genotyping. Conservation Genetics, 8(2), 475–488. https://doi.org/10.1007/s10592-006-9186-x.

Danilkiewicz, Z. (1996). Babka łysa (gołogłowa), *Neogobius gymnotrachelus* (Kessler, 1857) Perciformes, Gobiidae – nowy gatunek w ichtiofaunie zlewiska Morza Bałtyckiego. Komunikaty Rybackie, 2, 27–29.

Danilkiewicz, Z. (1998). Babka szczupła, *Neogobius fluviatilis* (Pallas, 1811), Perciformes, Gobiidae – nowy pontyjski element w ichtiofaunie zlewiska Morza Bałtyckiego. Fragmenta Faunistica, 41(21), 269–277.

David, P., Thébault, E., Anneville, O., Duyck, P.-F., Chapuis, E., & Loeuille, N. (2017). Impacts of Invasive Species on Food Webs. [W:] D. A. Bohan, A. J. Dumbrell, & F. Massol (Red.), Advances in Ecological Research (Vol. 56, pp. 1–60). Academic Press. https://doi.org/10.1016/bs.aecr.2016.10.001.

Deutsch, C., Brix, H., Ito, T., Frenzel, H., & Thompson, L. (2011). Climate-Forced Variability of Ocean Hypoxia. Science, 333(6040), 336–339. https://doi.org/10.1126/science.1202422.

Domenici, P., Lefrançois, C., & Shingles, A. (2007). Hypoxia and the antipredator behaviours of fishes. Philosophical Transactions of the Royal Society B: Biological Sciences, 362(1487), 2105–2121. https://doi.org/10.1098/rstb.2007.2103.

Domenici, P., Allan, B. J. M., Lefrançois, C., & McCormick, M. I. (2019). The effect of climate change on the escape kinematics and performance of fishes: implications for future predator–prey interactions. Conservation Physiology, 7(1), coz078. https://doi.org/10.1093/conphys/coz078.

Donelson, J. M., Munday, P. L., McCormick, M. I., & Pitcher, C. R. (2012). Rapid transgenerational acclimation of a tropical reef fish to climate change. Nature Climate Change, 2(1), 30–32. https://doi.org/10.1038/nclimate1323.

Dubs, D. O. L., & Corkum, L. D. (1996). Behavioral interactions between round gobies (*Neogobius melanostomus*) and mottled sculpins (*Cottus bairdi*). Journal of Great Lakes Research, 22(4), 838–844. https://doi.org/10.1016/S0380-1330(96)71005-5.

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z., Knowler, D. J., Lévêque, C., … Sullivan, C. A. (2006). Freshwater biodiversity: importance, threats, status and conservation challenges. Biological Reviews, 81(2), 163–182. https://doi.org/10.1017/S1464793105006950.

Dueñas, M.-A., Hemming, D. J., Roberts, A., & Diaz-Soltero, H. (2021). The threat of invasive species to IUCN-listed critically endangered species: A systematic review. Global Ecology and Conservation, 26, e01476. https://doi.org/10.1016/j.gecco.2021.e01476.

Dumont, H. J. (1998). The Caspian Lake: History, biota, structure, and function. Limnology and Oceanography, 43(1), 44–52. https://doi.org/10.4319/lo.1998.43.1.0044.

Early, R., Bradley, B. A., Dukes, J. S., Lawler, J. J., Olden, J. D., Blumenthal, D. M., … Tatem, A. J. (2016). Global threats from invasive alien species in the twenty-first century and national response capacities. Nature Communications, 7(1), 12485. https://doi.org/10.1038/ncomms 12485.

Egger, B., Wiegleb, J., Seidel, F., Burkhardt-Holm, P., & Hirsch, P. E. (2021). Comparative swimming performance and behaviour of three benthic fish species: The invasive round goby (*Neogobius melanostomus*), the native bullhead (*Cottus gobio*), and the native gudgeon (*Gobio gobio*). Ecology of Freshwater Fish, 30(3), 391–405. https://doi.org/10.1111/eff.12592.

Erős, T., Sevcsik, A., & Tóth, B. (2005). Abundance and night-time habitat use patterns of Ponto-Caspian gobiid species (Pisces, Gobiidae) in the littoral zone of the River Danube, Hungary. Journal of Applied Ichthyology, 21(4), 350–357. https://doi.org/10.1111/j.1439-0426.2005.00689.x.

Estay, S. A., Lima, M., & Bozinovic, F. (2014). The role of temperature variability on insect performance and population dynamics in a warming world. Oikos, 123(2), 131–140. https://doi.org/10.1111/j.1600-0706.2013.00607.x.

Farwell, M., Fox, M. G., Moyes, C. D., & Burness, G. (2007). Can Hypoxia Tolerance Explain Differences in Distribution of Two Co-Occurring North Temperate Sunfishes? Environmental Biology of Fishes, 78(1), 83–90. https://doi.org/10.1007/s10641-006-9079-3.

Feely, R., Doney, S., & Cooley, S. (2009). Ocean Acidification: Present Conditions and Future Changes in a High-CO_2 World. Oceanography, 22(4), 36–47. https://doi.org/10.5670/oceanog.2009.95.

Ficke, A. D., Myrick, C. A., & Hansen, L. J. (2007). Potential impacts of global climate change on freshwater fisheries. Reviews in Fish Biology and Fisheries, 17(4), 581–613. https://doi.org/10.1007/s11160-007-9059-5.

Frölicher, T. L., Fischer, E. M., & Gruber, N. (2018). Marine heatwaves under global warming. Nature, 560(7718), 360–364. https://doi.org/10.1038/s41586-018-0383-9.

Frölicher, T. L., & Laufkötter, C. (2018). Emerging risks from marine heat waves. Nature Communications, 9(1), 650. https://doi.org/10.1038/s41467-018-03163-6.

Früh, D., Haase, P., & Stoll, S. (2017). Temperature drives asymmetric competition between alien and indigenous freshwater snail species, *Physa acuta* and *Physa fontinalis*. Aquatic Sciences, 79(1), 187–195. https://doi.org/10.1007/s00027-016-0489-9.

Galil, B. S., Nehring, S., & Panov, V. (2007). Waterways as Invasion Highways - Impact of Climate Change and Globalization. [W:] W. Nentwig (Red.), Biological Invasions, Ecological Studies No. 193 (pp. 59–74). Berlin, Heidelberg: Springer. https://doi.org/10.1007/978-3-540-36920-2_5.

García-Berthou, E., Alcaraz, C., Pou-Rovira, Q., Zamora, L., Coenders, G., & Feo, C. (2005). Introduction pathways and establishment rates of invasive aquatic species in Europe. Canadian Journal of Fisheries and Aquatic Sciences, 62(2), 453–463. https://doi.org/10.1139/f05-017.

Genovesi, P., Carnevali, L., & Scalera, R. (2015). The impact of invasive alien species on native threatened species in Europe. Rome. Technical report for the European Commission: ISPRA - ISSG.

Gertzen, S. (2016). The ecological niche of invasive gobies at the Lower Rhine in intra- and interspecific competitive and predatory interactions. Dissertation. Universität zu Köln.

Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M., & Charnov, E. L. (2001). Effects of Size and Temperature on Metabolic Rate. Science, 293(5538), 2248–2251. https://doi.org/10.1126/science.1061967.

Głowaciński, Z., Okarma, H., Pawłowski, J., & Solarz, W. (Red.). (2012). Gatunki obce w faunie Polski. Wydawnictwo internetowe Instytutu Ochrony Przyrody PAN w Krakowie.

Gozlan, R. E., & Beyer, K. (2006). Hybridisation between *Pseudorasbora parva* and *Leucaspius delineatus*. Folia Zoologica, 55(1), 53–60.

Grabowska, J., Kakareko, T., Błońska, D., Przybylski, M., Kobak, J., Jermacz, Ł., & Copp, G. H. (2016). Interspecific competition for a shelter between non-native racer goby and native European bullhead under experimental conditions – Effects of season, fish size and light conditions. Limnologica, 56, 30–38. https://doi.org/10.1016/j.limno.2015.11.004.

Grabowska, J., Błońska, D., Ondračková, M., & Kakareko, T. (2023). The functional ecology of four invasive Ponto–Caspian gobies. Reviews in Fish Biology and Fisheries, 33(4), 1329–1352. https://doi.org/10.1007/s11160-023-09801-7.

Grabowska, J., Kotusz, J., & Witkowski, A. (2010). Alien invasive fish species in Polish waters: An overview. Folia Zoologica, 59(1), 73–85. https://doi.org/10.25225/fozo.v59.i1.a1.2010.

Grabowska, J., Pietraszewski, D., & Ondračková, M. (2008). Tubenose goby *Proterorhinus marmoratus* (Pallas, 1814) has joined three other Ponto-Caspian gobies in the Vistula River (Poland). Aquatic Invasions, 3(2), 261–265. https://doi.org/10.3391/ai.2008.3.2.20.

Grabowska, J., & Przybylski, M. (2015). Life-history traits of non-native freshwater fish invaders differentiate them from natives in the Central European bioregion. Reviews in Fish Biology and Fisheries, 25(1), 165–178. https://doi.org/10.1007/s11160-014-9375-5.

Hall, A. E., & Clark, T. D. (2016). Seeing is believing: metabolism provides insight into threat perception for a prey species of coral reef fish. Animal Behaviour, 115, 117–126. https://doi.org/10.1016/j.anbehav.2016.03.008.

Hayes, K. R., & Barry, S. C. (2008). Are there any consistent predictors of invasion success? Biological Invasions, 10(4), 483–506. https://doi.org/10.1007/s10530-007-9146-5.

Hellmann, J. J., Byers, J. E., Bierwagen, B. G., & Dukes, J. S. (2008). Five Potential Consequences of Climate Change for Invasive Species. Conservation Biology, 22(3), 534–543. https://doi.org/10.1111/j.1523-1739.2008.00951.x.

Helmuth, B., Mieszkowska, N., Moore, P., & Hawkins, S. J. (2006). Living on the Edge of Two Changing Worlds: Forecasting the Responses of Rocky Intertidal Ecosystems to Climate Change. Annual Review of Ecology, Evolution, and Systematics, 37(1), 373–404. https://doi.org/10.1146/annurev.ecolsys.37.091305.110149.

Hesselschwerdt, J., & Wantzen, K. M. (2018). Global warming may lower thermal barriers against invasive species in freshwater ecosystems – A study from Lake Constance. Science of The Total Environment, 645, 44–50. https://doi.org/10.1016/j.scitotenv.2018.07.078.

Heuer, R. M., & Grosell, M. (2014). Physiological impacts of elevated carbon dioxide and ocean acidification on fish. American Journal of Physiology. Regulatory, Integrative and Comparative Physiology, 307(9), R1061–R1084. https://doi.org/10.1152/ajpregu.00064.2014.

Hulme, P. E., Bacher, S., Kenis, M., Klotz, S., Kühn, I., Minchin, D., … Vilà, M. (2008). Grasping at the routes of biological invasions: a framework for integrating pathways into policy. Journal of Applied Ecology, 45(2), 403–414. https://doi.org/10.1111/j.1365-2664.2007.01442.x.

Hulme, P. E. (2009). Trade, transport and trouble: managing invasive species pathways in an era of globalization. Journal of Applied Ecology, 46(1), 10–18. https://doi.org/10.1111/j.1365-2664.2008.01600.x.

Hulme, P. E. (2017). Climate change and biological invasions: evidence, expectations, and response options. Biological Reviews, 92(3), 1297–1313. https://doi.org/10.1111/brv.12282.

Ikeda, T., Torres, J. J., Hernandez-León, S., & Geiger, S. P. (2000). Metabolism. [W:] R. Harris, P. Wiebe, J. Lenz, H.-R. Skjoldal, & M. E. Huntley (Red.), ICES Zooplankton Methodology Manual (pp. 455–532). London: Academic Press. https://doi.org/10.1016/B978-0-12-327645-2.X5000-2.

IPCC. (2014). Summary for Policymakers. [W:] C. B. Field, V. R. Barros, D. J. Dokken, K. J. Mach, M. D. Mastrandrea, T. E. Bilir, … L. L. White (Red.), Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (pp. 1–32). Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press.

IPCC. (2018). Summary for Policymakers. [W:] V. Masson-Delmotte, P. Zhai, H.-O. Pörtner, D. Roberts, J. Skea, P. R. Shukla, … T. Waterfield (Red.), Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty. In Press.

IPCC. (2023). Summary for Policymakers. [W:] Core Writing Team, H. Lee, & J. Romero (Red.), Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change (pp. 1–34). Geneva, Switzerland: IPCC. https://doi.org/10.59327/IPCC/AR6-9789291691647.001.

Isaak, D. J., & Rieman, B. E. (2013). Stream isotherm shifts from climate change and implications for distributions of ectothermic organisms. Global Change Biology, 19(3), 742–751. https://doi.org/10.1111/gcb.12073.

Jakovlić, I., Piria, M., Šprem, N., Tomljanović, T., Matulić, D., & Treer, T. (2015). Distribution, abundance and condition of invasive Ponto-Caspian gobies *Ponticola kessleri* (Günther, 1861), *Neogobius fluviatilis* (Pallas, 1814), and *Neogobius melanostomus* (Pallas, 1814) in the Sava River basin, Croatia. Journal of Applied Ichthyology, 31(5), 888–894. https://doi.org/10.1111/jai.12803.

Janáč, M., Roche, K., Šlapanský, L., Polačik, M., & Jurajda, P. (2018). Long-term monitoring of native bullhead and invasive gobiids in the Danubian rip-rap zone. Hydrobiologia, 807(1), 263–275. https://doi.org/10.1007/s10750-017-3398-6.

Jane, S. F., Hansen, G. J. A., Kraemer, B. M., Leavitt, P. R., Mincer, J. L., North, R. L., … Rose, K. C. (2021). Widespread deoxygenation of temperate lakes. Nature, 594(7861), 66–70. https://doi.org/10.1038/s41586-021-03550-y.

Janssen, J., & Jude, D. J. (2001). Recruitment Failure of Mottled Sculpin *Cottus bairdi* in Calumet Harbor, Southern Lake Michigan, Induced by the Newly Introduced Round Goby *Neogobius melanostomus*. Journal of Great Lakes Research, 27(3), 319–328. https://doi.org/10.1016/S0380-1330(01)70647-8.

Jermacz, Ł., Kobak, J., Dzierżyńska, A., & Kakareko, T. (2015). The effect of flow on the competition between the alien racer goby and native European bullhead. Ecology of Freshwater Fish, 24(3), 467–477. https://doi.org/10.1111/eff.12162.

Jermacz, Ł., Nowakowska, A., Kletkiewicz, H., & Kobak, J. (2020). Experimental evidence for the adaptive response of aquatic invertebrates to chronic predation risk. Oecologia, 192(2), 341–350. https://doi.org/10.1007/s00442-020-04594-z.

Jeschke, J. M. (2008). Across islands and continents, mammals are more successful invaders than birds. Diversity and Distributions, 14(6), 913–916. https://doi.org/10.1111/j.1472-4642.2008.00488.x.

Jeschke, J. M., & Strayer, D. L. (2005). Invasion success of vertebrates in Europe and North America. Proceedings of the National Academy of Sciences of the United States of America, 102(20), 7198–7202. https://doi.org/10.1073/pnas.0501271102.

Jewett, E., Hines, A., & Ruiz, G. (2005). Epifaunal disturbance by periodic low levels of dissolved oxygen: native vs. invasive species response. Marine Ecology Progress Series, 304, 31–44. https://doi.org/10.3354/meps304031.

Kakareko, T. (2011). Wpływ wybranych czynników na rozmieszczenie i preferencje siedliskowe babki łysej (*Neogobius gymnotrachelus* Kessler, 1857) i babki szczupłej (*Neogobius fluviatilis* Pallas, 1811), obcych gatunków ryb w Polsce. Rozprawa habilitacyjna. Wydawnictwo Naukowe Uniwersytetu Mikołaja Kopernika.

Kakareko, T., Kobak, J., Grabowska, J., Jermacz, Ł., Przybylski, M., Poznańska, M., … Copp, G. H. (2013). Competitive interactions for food resources between invasive racer goby *Babka gymnotrachelus* and native European bullhead *Cottus gobio*. Biological Invasions, 15(11), 2519–2530. https://doi.org/10.1007/s10530-013-0470-7.

Kakareko, T., Kobak, J., Poznańska, M., Jermacz, Ł., & Copp, G. H. (2016). Underwater evaluation of habitat partitioning in a European river between a non-native invader, the racer goby and a threatened native fish, the European bullhead. Ecology of Freshwater Fish, 25(1), 60–71. https://doi.org/10.1111/eff.12191.

Keller, R. P., Geist, J., Jeschke, J. M., & Kühn, I. (2011). Invasive species in Europe: ecology, status, and policy. Environmental Sciences Europe, 23(1), 23. https://doi.org/10.1186/2190-4715-23-23.

Killen, S. S., Christensen, E. A. F., Cortese, D., Závorka, L., Norin, T., Cotgrove, L., … McKenzie, D. J. (2021). Guidelines for reporting methods to estimate metabolic rates by aquatic intermittent-flow respirometry. Journal of Experimental Biology, 224(18), jeb.242522. https://doi.org/10.1242/jeb.242522.

Killen, S. S., Glazier, D. S., Rezende, E. L., Clark, T. D., Atkinson, D., Willener, A. S. T., & Halsey, L. G. (2016). Ecological Influences and Morphological Correlates of Resting and Maximal Metabolic Rates across Teleost Fish Species. The American Naturalist, 187(5), 592–606. https://doi.org/10.1086/685893.

Killen, S. S., Mitchell, M. D., Rummer, J. L., Chivers, D. P., Ferrari, M. C. O., Meekan, M. G., & McCormick, M. I. (2014). Aerobic scope predicts dominance during early life in a tropical damselfish. Functional Ecology, 28(6), 1367–1376. https://doi.org/10.1111/1365-2435.12296.

Kitchell, J. F., Schindler, D. E., Ogutu-Ohwayo, R., & Reinthal, P. N. (1997). The Nile Perch in Lake Victoria: Interactions Between Predation and Fisheries. Ecological Applications, 7(2), 653–664. https://doi.org/10.2307/2269528.

Kłosiński, P., Kobak, J., Augustyniak, M., Pawlak, R., Jermacz, Ł., Poznańska-Kakareko, M., & Kakareko, T. (2022). Behavioural responses to con- and heterospecific alarm cues by an alien and a coexisting native fish. Hydrobiologia, 849(4), 985–1000. https://doi.org/10.1007/s10750-021-04761-0.

Kłosiński, P., Kobak, J., & Kakareko, T. (2024). Metabolic rate of two invasive Ponto-Caspian goby species and their native competitors in the context of global warming. Freshwater Biology, 69(7), 971–983. https://doi.org/10.1111/fwb.14259.

Kłosiński, P., Kobak, J., & Kakareko, T. (2025a). Effect of hypoxia and acidification on metabolic rate of Ponto-Caspian gobies and their native competitors in the context of climate change. Hydrobiologia. https://doi.org/10.1007/s10750-025-05794-5.

Kłosiński, P., Kobak, J., & Kakareko, T. (2025b). Competitive interactions for food resources between invasive Ponto-Caspian gobies and their native competitors in the context of global warming. NeoBiota, 97, 91–119. https://doi.org/10.3897/neobiota.97.134566.

Kocovsky, P. M., Tallman, J. A., Jude, D. J., Murphy, D. M., Brown, J. E., & Stepien, C. A. (2011). Expansion of tubenose gobies *Proterorhinus semilunaris* into western Lake Erie and potential effects on native species. Biological Invasions, 13(12), 2775–2784. https://doi.org/10.1007/s10530-011-9962-5.

Kolar, C. S., & Lodge, D. M. (2002). Ecological Predictions and Risk Assessment for Alien Fishes in North America. Science, 298(5596), 1233–1236. https://doi.org/10.1126/science.1075753.

Kornis, M. S., Mercado-Silva, N., & Vander Zanden, M. J. (2012). Twenty years of invasion: a review of round goby *Neogobius melanostomus* biology, spread and ecological implications. Journal of Fish Biology, 80(2), 235–285. https://doi.org/10.1111/j.1095-8649.2011.03157.x.

Kostrzewa, J., & Grabowski, M. (2001). Babka łysa (gołogłowa), *Neogobius gymnotrachelus* (Kessler, 1857) (Gobiidae, Perciformes) – nowy gatunek ryby w Wiśle. Przegląd Zoologiczny, 45(1–2), 101–102.

Kostrzewa, J., & Grabowski, M. (2002). Babka szczupła, *Neogobius fluviatilis* (Pallas, 1811), w Wiśle – fenomen inwazji pontokaspijskich Gobiidae. Przegląd Zoologiczny, 46(3–4), 235–242.

Kottelat, M., & Freyhof, J. (2007). Handbook of European Freshwater Fishes. Berlin: Publications Kottelat, Cornol and Freyhof.

Kvach, Y., & Ondračková, M. (2020). Checklist of parasites for Ponto-Caspian gobies (Actinopterygii: Gobiidae) in their native and non-native ranges. Journal of Applied Ichthyology, 36(4), 472–500. https://doi.org/10.1111/jai.14036.

Lambertini, M., Leape, J., Marton-Lefèvre, J., Mittermeier, R. A., Rose, M., Robinson, J. G., … Genovesi, P. (2011). Invasives: A Major Conservation Threat. Science, 333(6041), 404–405. https://doi.org/10.1126/science.333.6041.404-b.

Lenz, M., da Gama, B. A. P., Gerner, N. V., Gobin, J., Gröner, F., Harry, A., … Wahl, M. (2011). Non-native marine invertebrates are more tolerant towards environmental stress than taxonomically related native species: Results from a globally replicated study. Environmental Research, 111(7), 943–952. https://doi.org/10.1016/j.envres.2011.05.001.

Leroy, S. A. G., Marret, F., Gibert, E., Chalié, F., Reyss, J.-L., & Arpe, K. (2007). River inflow and salinity changes in the Caspian Sea during the last 5500 years. Quaternary Science Reviews, 26(25–28), 3359–3383. https://doi.org/10.1016/j.quascirev.2007.09.012.

Liu, Y., & van Kleunen, M. (2017). Responses of common and rare aliens and natives to nutrient availability and fluctuations. Journal of Ecology, 105(4), 1111–1122. https://doi.org/10.1111/1365-2745.12733.

Lodge, D. M. (1993). Biological invasions: Lessons for ecology. Trends in Ecology & Evolution, 8(4), 133–137. https://doi.org/10.1016/0169-5347(93)90025-K.

Luque, G. M., Bellard, C., Bertelsmeier, C., Bonnaud, E., Genovesi, P., Simberloff, D., & Courchamp, F. (2014). The 100th of the world's worst invasive alien species. Biological Invasions, 16(5), 981–985. https://doi.org/10.1007/s10530-013-0561-5.

Maazouzi, C., Piscart, C., Legier, F., & Hervant, F. (2011). Ecophysiological responses to temperature of the "killer shrimp" *Dikerogammarus villosus*: Is the invader really stronger than the native *Gammarus pulex*? Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology, 159(3), 268–274. https://doi.org/10.1016/j.cbpa.2011.03.019.

Mandic, M., Todgham, A. E., & Richards, J. G. (2009). Mechanisms and evolution of hypoxia tolerance in fish. Proceedings of the Royal Society B: Biological Sciences, 276(1657), 735–744. https://doi.org/10.1098/rspb.2008.1235.

Marras, S., Cucco, A., Antognarelli, F., Azzurro, E., Milazzo, M., Bariche, M., … Domenici, P. (2015). Predicting future thermal habitat suitability of competing native and invasive fish species: from metabolic scope to oceanographic modelling. Conservation Physiology, 3(1), cou059. https://doi.org/10.1093/conphys/cou059.

Metcalfe, N. B., Van Leeuwen, T. E., & Killen, S. S. (2016). Does individual variation in metabolic phenotype predict fish behaviour and performance? Journal of Fish Biology, 88(1), 298–321. https://doi.org/10.1111/jfb.12699.

Mills, C. A., & Mann, R. H. K. (1983). The bullhead *Cottus gobio*, a versatile and successful fish. [W:] Fifty-first annual report for the year ended 31st March 1983 (pp. 76–88). Ambleside: Freshwater Biological Association.

Monaco, C. J., & Helmuth, B. (2011). Tipping Points, Thresholds and the Keystone Role of Physiology in Marine Climate Change Research. [W:] M. Lesser (Red.), Advances in Marine Biology (Vol. 60, pp. 123–160). https://doi.org/10.1016/B978-0-12-385529-9.00003-2.

Mordukhay-Boltovskoy, P. D. (1964). Caspian Fauna in Fresh Waters outside the Ponto-Caspian Basin. Hydrobiologia, 23, 159–164. https://doi.org/10.1007/BF00043727.

Moretz, J. A. (2003). Aggression and RHP in the Northern Swordtail Fish, *Xiphophorus cortezi*: The Relationship between Size and Contest Dynamics in Male-Male Competition. Ethology, 109(12), 995–1008. https://doi.org/10.1046/j.0179-1613.2003.00938.x.

Moyle, P. B. (1986). Fish Introductions into North America: Patterns and Ecological Impact. [W:] H. A. Mooney & J. A. Drake (Red.), Ecology of Biological Invasions of North America and Hawaii. Ecological Studies (Vol. 58, pp. 27–43). New York, NY: Springer. https://doi.org/10.1007/978-1-4612-4988-7_2.

Müller, B., Bryant, L. D., Matzinger, A., & Wüest, A. (2012). Hypolimnetic Oxygen Depletion in Eutrophic Lakes. Environmental Science & Technology, 46(18), 9964–9971. https://doi.org/10.1021/es301422r.

Najberek, K., & Solarz, W. (2016). Gatunki obce. Przyczyny inwazyjnych zachowań i sposoby zwalczania. Kosmos, 65(1), 81–91.

Nati, J. J. H., Lindström, J., Yeomans, W., & Killen, S. S. (2018). Physiological and behavioural responses to hypoxia in an invasive freshwater fish species and a native competitor. Ecology of Freshwater Fish, 27(3), 813–821. https://doi.org/10.1111/eff.12394.

Neilson, M. E., & Stepien, C. A. (2011). Historic speciation and recent colonization of Eurasian monkey gobies (*Neogobius fluviatilis* and *N. pallasi*) revealed by DNA sequences, microsatellites, and morphology. Diversity and Distributions, 17(4), 688–702. https://doi.org/10.1111/j.1472-4642.2011.00762.x.

Nelson, J. S., Grande, T. C., & Wilson, M. V. H. (2016). Fishes of the World (Fifth edition). Hoboken, New Jersey: John Wiley & Sons. https://doi.org/10.1002/9781119174844.

Nixon, S. W. (1995). Coastal marine eutrophication: A definition, social causes, and future concerns. Ophelia, 41(1), 199–219. https://doi.org/10.1080/00785236.1995.10422044.

Nunes, A., Tricarico, E., Panov, V., Cardoso, A., & Katsanevakis, S. (2015). Pathways and gateways of freshwater invasions in Europe. Aquatic Invasions, 10(4), 359–370. https://doi.org/10.3391/ai.2015.10.4.01.

Ondračková, M., Bartáková, V., & Kvach, Y. (2021). *Ophiotaenia europaea* Odening, 1963 (Cestoda: Onchoproteocephalidea) adopts a North American brown bullhead catfish *Ameiurus nebulosus* Lesueur, 1819 as intermediate/paratenic host in Europe. BioInvasions Records, 10(4), 948–959. https://doi.org/10.3391/bir.2021.10.4.19.

Onthank, K. L., Trueblood, L. A., Schrock-Duff, T., & Kore, L. G. (2021). Impact of Short- and Long-Term Exposure to Elevated Seawater Pco_2 on Metabolic Rate and Hypoxia Tolerance in *Octopus rubescens*. Physiological and Biochemical Zoology, 94(1), 1–11. https://doi.org/10.1086/712207.

Oyugi, D. O., Cucherousset, J., & Britton, J. R. (2012). Temperature-dependent feeding interactions between two invasive fishes competing through interference and exploitation.

Reviews in Fish Biology and Fisheries, 22(2), 499–508. https://doi.org/10.1007/s11160-011-9243-5.

Paiva, F., Barco, A., Chen, Y., Mirzajani, A., Chan, F. T., Lauringson, V., … Briski, E. (2018). Is salinity an obstacle for biological invasions? Global Change Biology, 24(6), 2708–2720. https://doi.org/10.1111/gcb.14049.

Palacios, M. M., Killen, S. S., Nadler, L. E., White, J. R., & McCormick, M. I. (2016). Top predators negate the effect of mesopredators on prey physiology. Journal of Animal Ecology, 85(4), 1078–1086. https://doi.org/10.1111/1365-2656.12523.

Parker, G. A., & Rubenstein, D. I. (1981). Role assessment, reserve strategy, and acquisition of information in asymmetric animal conflicts. Animal Behaviour, 29(1), 221–240. https://doi.org/10.1016/S0003-3472(81)80170-4.

Pauli, N.-C., & Briski, E. (2018). Euryhalinity of Ponto-Caspian invaders in their native and introduced regions. Aquatic Invasions, 13(4), 439–447. https://doi.org/10.3391/ai.2018.13.4.02.

Pawelec-Olesińska, A. (2020). Ecological and behavioural factors determining relationships between native and invasive species of freshwater fish. Rozprawa doktorska. Uniwersytet Warszawski.

Penk, M. R., Jeschke, J. M., Minchin, D., & Donohue, I. (2016). Warming can enhance invasion success through asymmetries in energetic performance. Journal of Animal Ecology, 85(2), 419–426. https://doi.org/10.1111/1365-2656.12480.

Piria, M., Simonović, P., Zanella, D., Ćaleta, M., Šprem, N., Paunović, M., … Treer, T. (2019). Long-term analysis of fish assemblage structure in the middle section of the Sava River – The impact of pollution, flood protection and dam construction. Science of The Total Environment, 651, 143–153. https://doi.org/10.1016/j.scitotenv.2018.09.149.

Plachá, M., Balážová, M., Kováč, V., & Katina, S. (2010). Age and growth of non-native monkey goby *Neogobius fluviatilis* (Teleostei, Gobiidae) in the River Ipeľ, Slovakia. Folia Zoologica, 59(4), 332–340. https://doi.org/10.25225/fozo.v59.i4.a10.2010.

Płąchocki, D., Kobak, J., & Kakareko, T. (2012). First report on the importance of alien gobiids in the diet of native piscivorous fishes in the lower Vistula River (Poland). Oceanological and Hydrobiological Studies, 41(2), 83–89. https://doi.org/10.2478/s13545-012-0020-4.

Płąchocki, D., Kobak, J., Poznańska-Kakareko, M., & Kakareko, T. (2020). Environmental factors associated with the occurrence of the Ponto–Caspian gobies in a lowland river belonging to the central European invasion corridor. River Research and Applications, 36(1), 25–35. https://doi.org/10.1002/rra.3543.

Pörtner, H. O., & Knust, R. (2007). Climate Change Affects Marine Fishes Through the Oxygen Limitation of Thermal Tolerance. Science, 315(5808), 95–97. https://doi.org/10.1126/science.1135471.

Pörtner, H. O., & Peck, M. A. (2010). Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. Journal of Fish Biology, 77(8), 1745–1779. https://doi.org/10.1111/j.1095-8649.2010.02783.x.

Poulos, D. E., & McCormick, M. I. (2014). Who wins in the battle for space? The importance of priority, behavioural history and size. Animal Behaviour, 90, 305–314. https://doi.org/10.1016/j.anbehav.2014.02.003.

Pyšek, P., Jarošík, V., Hulme, P. E., Kühn, I., Wild, J., Arianoutsou, M., … Winter, M. (2010). Disentangling the role of environmental and human pressures on biological invasions across Europe. Proceedings of the National Academy of Sciences of the United States of America, 107(27), 12157–12162. https://doi.org/10.1073/pnas.1002314107.

Quattrocchi, G., Christensen, E., Sinerchia, M., Marras, S., Cucco, A., Domenici, P., & Behrens, J. W. (2023). Aerobic metabolic scope mapping of an invasive fish species with global warming. Conservation Physiology, 11(1). https://doi.org/10.1093/conphys/coad094.

Rahel, F. J., & Olden, J. D. (2008). Assessing the Effects of Climate Change on Aquatic Invasive Species. Conservation Biology, 22(3), 521–533. https://doi.org/10.1111/j.1523-1739.2008.00950.x.

Ramberg-Pihl, N. C., Klemmer, A. J., Zydlewski, J., Coghlan, S. M., & Greig, H. S. (2023). Smallmouth bass (*Micropterus dolomieu*) suppress Atlantic salmon (*Salmo salar*) feeding activity and increase aggressive behaviours at warmer temperatures. Ecology of Freshwater Fish, 32(3), 606–617. https://doi.org/10.1111/eff.12711.

Reid, A. J., Carlson, A. K., Creed, I. F., Eliason, E. J., Gell, P. A., Johnson, P. T. J., … Cooke, S. J. (2019). Emerging threats and persistent conservation challenges for freshwater biodiversity. Biological Reviews, 94(3), 849–873. https://doi.org/10.1111/brv.12480.

Reid, D. F., & Orlova, M. I. (2002). Geological and evolutionary underpinnings for the success of Ponto-Caspian species invasions in the Baltic Sea and North American Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences, 59(7), 1144–1158. https://doi.org/10.1139/f02-099.

Rewicz, T., Grabowski, M., MacNeil, C., & Bącela-Spychalska, K. (2014). The profile of a 'perfect' invader – the case of killer shrimp, *Dikerogammarus villosus*. Aquatic Invasions, 9(3), 267–288. https://doi.org/10.3391/ai.2014.9.3.04.

Ricciardi, A., & MacIsaac, H. J. (2010). Impacts of Biological Invasions on Freshwater Ecosystems. [W:] D. M. Richardson (Red.), Fifty Years of Invasion Ecology (pp. 211–224). Wiley. https://doi.org/10.1002/9781444329988.ch16.

Richardson, D. M., Pyšek, P., Rejmánek, M., Barbour, M. G., Panetta, F. D., & West, C. J. (2000). Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions, 6(2), 93–107. https://doi.org/10.1046/j.1472-4642.2000.00083.x.

Roche, K. F., Janač, M., & Jurajda, P. (2013). A review of Gobiid expansion along the Danube-Rhine corridor – geopolitical change as a driver for invasion. Knowledge and Management of Aquatic Ecosystems, 411, 01. https://doi.org/10.1051/kmae/2013066.

Rodgers, E. M., & Franklin, C. E. (2021). Aerobic scope and climate warming: Testing the "*plastic floors and concrete ceilings*" hypothesis in the estuarine crocodile (*Crocodylus porosus*). Journal of Experimental Zoology Part A: Ecological and Integrative Physiology, 335(1), 108–117. https://doi.org/10.1002/jez.2412.

Rodriguez, L. F. (2006). Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. Biological Invasions, 8(4), 927–939. https://doi.org/10.1007/s10530-005-5103-3.

Rogers, N. J., Urbina, M. A., Reardon, E. E., McKenzie, D. J., & Wilson, R. W. (2016). A new analysis of hypoxia tolerance in fishes using a database of critical oxygen level (P_{crit}). Conservation Physiology, 4(1), cow012. https://doi.org/10.1093/conphys/cow012.

Rosenberger, A. E., & Chapman, L. J. (1999). Hypoxic wetland tributaries as faunal refugia from an introduced predator. Ecology of Freshwater Fish, 8(1), 22–34. https://doi.org/10.1111/j.1600-0633.1999.tb00049.x.

Rosewarne, P. J., Wilson, J. M., & Svendsen, J. C. (2016). Measuring maximum and standard metabolic rates using intermittent-flow respirometry: a student laboratory investigation of aerobic metabolic scope and environmental hypoxia in aquatic breathers. Journal of Fish Biology, 88(1), 265–283. https://doi.org/10.1111/jfb.12795.

Sampaio, E., Santos, C., Rosa, I. C., Ferreira, V., Pörtner, H.-O., Duarte, C. M., … Rosa, R. (2021). Impacts of hypoxic events surpass those of future ocean warming and acidification. Nature Ecology & Evolution, 5(3), 311–321. https://doi.org/10.1038/s41559-020-01370-3.

Sandblom, E., Clark, T. D., Gräns, A., Ekström, A., Brijs, J., Sundström, L. F., … Jutfelt, F. (2016). Physiological constraints to climate warming in fish follow principles of plastic floors and concrete ceilings. Nature Communications, 7(1), 11447. https://doi.org/10.1038/ncomms11447.

Savage, V. M., Gillooly, J. F., Brown, J. H., West, G. B., & Charnov, E. L. (2004). Effects of Body Size and Temperature on Population Growth. The American Naturalist, 163(3), 429–441. https://doi.org/10.1086/381872.

Schwieterman, G., Crear, D., Anderson, B., Lavoie, D., Sulikowski, J., Bushnell, P., & Brill, R. (2019). Combined Effects of Acute Temperature Change and Elevated $p\mathrm{CO}_2$ on the Metabolic Rates and Hypoxia Tolerances of Clearnose Skate (*Rostaraja eglanteria*), Summer Flounder (*Paralichthys dentatus*), and Thorny Skate (*Amblyraja radiata*). Biology, 8(3), 56. https://doi.org/10.3390/biology8030056.

Simberloff, D. (2011). How common are invasion-induced ecosystem impacts? Biological Invasions, 13(5), 1255–1268. https://doi.org/10.1007/s10530-011-9956-3.

Simberloff, D., Martin, J.-L., Genovesi, P., Maris, V., Wardle, D. A., Aronson, J., … Vilà, M. (2013). Impacts of biological invasions: what's what and the way forward. Trends in Ecology & Evolution, 28(1), 58–66. https://doi.org/10.1016/j.tree.2012.07.013.

Solarz, W. (2007). Inwazje biologiczne jako zagrożenie dla przyrody. Progress in Plant Protection/Postępy w Ochronie Roślin, 47(1), 128–133.

Sorte, C. J. B. (2014). Synergies between Climate Change and Species Invasions: Evidence from Marine Systems. [W:] L. H. Ziska & J. S. Dukes (Red.), Invasive Species And Global Climate Change (pp. 101–116). Wallingford: CABI.

Sorte, C. J. B., Ibáñez, I., Blumenthal, D. M., Molinari, N. A., Miller, L. P., Grosholz, E. D., … Dukes, J. S. (2013). Poised to prosper? A cross-system comparison of climate change effects on native and non-native species performance. Ecology Letters, 16(2), 261–270. https://doi.org/10.1111/ele.12017.

Soto, I., Cuthbert, R. N., Ricciardi, A., Ahmed, D. A., Altermatt, F., Schäfer, R. B., … Briski, E. (2023). The faunal Ponto-Caspianization of central and western European waterways. Biological Invasions, 25(8), 2613–2629. https://doi.org/10.1007/s10530-023-03060-0.

Stern, D. B., & Lee, C. E. (2020). Evolutionary origins of genomic adaptations in an invasive copepod. Nature Ecology & Evolution, 4(8), 1084–1094. https://doi.org/10.1038/s41559-020-1201-y.

Taniguchi, Y., Rahel, F. J., Novinger, D. C., & Gerow, K. G. (1998). Temperature mediation of competitive interactions among three fish species that replace each other along longitudinal stream gradients. Canadian Journal of Fisheries and Aquatic Sciences, 55(8), 1894–1901. https://doi.org/10.1139/f98-072.

Teletchea, F., & Beisel, J.-N. (2018). Alien Fish Species in France with Emphasis on the Recent Invasion of Gobies. [W:] R. Sajal (Red.), Biological Resources of Water (pp. 75–92). IntechOpen. https://doi.org/10.5772/intechopen.73408.

Thuiller, W., Richardson, D. M., & Midgley, G. F. (2007). Will climate change promote alien plant invasions? [W:] W. Nentwig (Red.), Biological Invasions (pp. 197–211). Berlin, Heidelberg: Springer-Verlag.

Tierney, K. B., Kasurak, A. V., Zielinski, B. S., & Higgs, D. M. (2011). Swimming performance and invasion potential of the round goby. Environmental Biology of Fishes, 92(4), 491–502. https://doi.org/10.1007/s10641-011-9867-2.

Tripp, A., Allen, G. J. P., Quijada-Rodriguez, A. R., Yoon, G. R., & Weihrauch, D. (2022). Effects of single and dual-stressor elevation of environmental temperature and P_{CO2} on metabolism and acid-base regulation in the Louisiana red swamp crayfish, *Procambarus clarkii*. Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology, 266, 111151. https://doi.org/10.1016/j.cbpa.2022.111151.

Ulikowski, D., Traczuk, P., Kapusta, A., & Kalinowska, K. (2021). New records of alien monkey goby, *Neogobius fluviatilis* (Pallas, 1814), in the waters of the Great Masurian Lakes system (north-eastern Poland). BioInvasions Records, 10(4), 924–933. https://doi.org/10.3391/bir.2021.10.4.17.

van Kessel, N., Dorenbosch, M., Kranenbarg, J., van der Velde, G., & Leuven, R. (2016). Invasive Ponto-Caspian gobies rapidly reduce the abundance of protected native bullhead. Aquatic Invasions, 11(2), 179–188. https://doi.org/10.3391/ai.2016.11.2.07.

Vázquez, D. P., Gianoli, E., Morris, W. F., & Bozinovic, F. (2017). Ecological and evolutionary impacts of changing climatic variability. Biological Reviews, 92(1), 22–42. https://doi.org/10.1111/brv.12216.

Villéger, S., Blanchet, S., Beauchard, O., Oberdorff, T., & Brosse, S. (2011). Homogenization patterns of the world's freshwater fish faunas. Proceedings of the National Academy of Sciences of the United States of America, 108(44), 18003–18008. https://doi.org/10.1073/pnas.1107614108.

Vitousek, P. M., D'Antonio, C. M., Loope, L. L., Rejmánek, M., & Westbrooks, R. (1997). Introduced species: a significant component of human-caused global change. New Zealand Journal of Ecology, 21(1), 1–16. https://doi.org/10.2307/24054520.

Vitousek, P. M., D'Antonio, C. M., Loope, L. L., & Westbrooks, R. (1996). Biological invasions as global environmental change. American Scientist, 84(5), 218–228.

Webb, B. W., Hannah, D. M., Moore, R. D., Brown, L. E., & Nobilis, F. (2008). Recent advances in stream and river temperature research. Hydrological Processes, 22(7), 902–918. https://doi.org/10.1002/hyp.6994.

Webber, B. L., & Scott, J. K. (2012). Rapid global change: implications for defining natives and aliens. Global Ecology and Biogeography, 21(3), 305–311. https://doi.org/10.1111/j.1466-8238.2011.00684.x.

Williamson, M., & Fitter, A. (1996). The Varying Success of Invaders. Ecology, 77(6), 1661–1666. https://doi.org/10.2307/2265769.

Wilson, J. R. U., Dormontt, E. E., Prentis, P. J., Lowe, A. J., & Richardson, D. M. (2009). Something in the way you move: dispersal pathways affect invasion success. Trends in Ecology & Evolution, 24(3), 136–144. https://doi.org/10.1016/j.tree.2008.10.007.

Witkowski, A., & Grabowska, J. (2012). The Non-Indigenous Freshwater Fishes of Poland: Threats to the Native Ichthyofauna and Consequences for the Fishery: A Review. Acta Ichthyologica Et Piscatoria, 42(2), 77–87. https://doi.org/10.3750/AIP2011.42.2.01.

Xu, M., Li, S., Liu, C., Tedesco, P. A., Dick, J. T. A., Fang, M., … Mu, X. (2024). Global freshwater fish invasion linked to the presence of closely related species. Nature Communications, 15(1), 1411. https://doi.org/10.1038/s41467-024-45736-8.

Xu, Z., & Xu, Y. J. (2015). Determination of Trophic State Changes with Diel Dissolved Oxygen: A Case Study in a Shallow Lake. Water Environment Research, 87(11), 1970–1979. https://doi.org/10.2175/106143015X14362865226716.

Publikacja 1

Kłosiński, P., Kobak, J., & Kakareko, T. (2024). Metabolic rate of two invasive Ponto-Caspian goby species and their native competitors in the context of global warming. Freshwater Biology 69(7), 971–983.

https://doi.org/10.1111/fwb.14259

Tekst opublikowany w czasopiśmie: Freshwater Biology
Wydawnictwo: WILEY
Punktacja według wykazu Ministerstwa Nauki i Szkolnictwa Wyższego (2024): 100
Journal Impact Factor (2023): 2.8
Q1 w kategorii: marine & freshwater biology

Received: 18 January 2023 | Revised: 22 November 2023 | Accepted: 1 May 2024

DOI: 10.1111/fwb.14259

ORIGINAL ARTICLE

Freshwater Biology WILEY

Metabolic rate of two invasive Ponto-Caspian goby species and their native competitors in the context of global warming

Piotr Kłosiński[1] | **Jarosław Kobak**[2] | **Tomasz Kakareko**[1]

[1]Department of Ecology and Biogeography, Faculty of Biological and Veterinary Sciences, Nicolaus Copernicus University in Toruń, Toruń, Poland

[2]Department of Invertebrate Zoology and Parasitology, Faculty of Biological and Veterinary Sciences, Nicolaus Copernicus University in Toruń, Toruń, Poland

Correspondence

Piotr Kłosiński, Department of Ecology and Biogeography, Faculty of Biological and Veterinary Sciences, Nicolaus Copernicus University in Toruń, Lwowska 1, 87-100 Toruń, Poland.

Email: klosinski.piotr@doktorant.umk.pl

Funding information

Narodowe Centrum Nauki, Grant/Award Number: 2016/23/B/NZ8/00741

Abstract

1. In connection with the expansion of alien gobies in European waters, a question arises whether this process can be enhanced or inhibited by global warming. The gobies are of Ponto-Caspian origin, where the climate is warmer than in invaded European areas. Therefore, they are likely to cope physiologically with climate warming better than native species. Our aim was to identify differences in metabolic traits under elevated summer temperature between the invasive gobies and their native counterparts.
2. Using a laboratory respirometer, we compared the effect of elevated summer temperature (25 vs. 17°C) on the metabolic responses of fish in two species pairs consisting of an invasive goby versus its native counterpart from the same ecological guild: the invasive racer goby *Babka gymnotrachelus* versus native European bullhead *Cottus gobio*, and the invasive monkey goby *Neogobius fluviatilis* versus native gudgeon *Gobio gobio*. The paired species share functional traits, including morphological characteristics, despite belonging to different fish families. After 4 weeks of acclimation, standard metabolic rate (SMR), maximum metabolic rate (MMR) and aerobic scope (AS = MMR–SMR) of the fish were determined.
3. We found that SMR increased under elevated temperature irrespective of species, yet it was always lower in the gobies than in natives. The MMR of the racer goby was lower than that of the bullhead across all temperatures, whereas no differences in MMR were found between the gudgeon and monkey goby. On the one hand, the elevated temperature did not affect the AS of the racer goby and bullhead. However, the AS of the racer goby was consistently lower than that of the bullhead across all temperatures. On the other, elevated temperature caused a decrease in AS in both the monkey goby and gudgeon. However, this temperature-induced change in AS was higher in the gudgeon than in the monkey goby.
4. In terms of AS, the invaders did not always outperform the natives at higher temperatures. However, the invaders had lower living costs by maintaining a lower SMR. These results suggest that invasion by gobies may be facilitated by global warming, which is likely to increase their occurrence and effect on local fish communities in freshwater temperate systems.

KEYWORDS
aerobic scope, climate change, intermittent-flow respirometry, invasive species, water temperature

1 | INTRODUCTION

On a global scale, biological invasions and global warming are currently the main causes of biological diversity loss (Bellard et al., 2012; Markovic et al., 2014; Nati et al., 2018). Fresh waters are among the most vulnerable (Dudgeon et al., 2006) owing to their high endemism and the ease of species dispersal through human activity (Chan et al., 2021; Lodge et al., 1998; Vander Zanden & Olden, 2008).

Climatic differences, especially associated with temperature (Früh et al., 2017), provide important barriers to the establishment of alien species in novel areas. The current scenarios of climate change assume an average water temperature increase by 2–5°C by the end of this century, as well as an increased risk of extreme daily temperature fluctuations (Estay et al., 2014; Frölicher & Laufkötter, 2018; IPCC, 2014). Therefore, it is of particular importance to consider the influence of rising temperature on the survival and spread of invasive species, given that invaders can be more tolerant of environmental changes than their native counterparts (Hellmann et al., 2008; Rahel & Olden, 2008) as a consequence of their particular physiological traits (Kelley, 2014). Exposure to conditions beyond the limited temperature range in which animals have evolved may disrupt physiological processes (Pinsky et al., 2019). In ectotherms, metabolism generally increases with temperature, generating favourable or adverse changes in animal functioning (Donelson et al., 2012), mostly as a result of rising energetic demands (Domenici et al., 2019; Rahel & Olden, 2008; Webb et al., 2008).

Physiological performance, expressed as aerobic scope (AS), reflects an organism's capacity to perform oxygen-demanding processes above the basic metabolism maintenance at a given temperature (Clark et al., 2013). It has been suggested as one of the physiological limitations to the spread and establishment of species in newly invaded areas (Marras et al., 2015). AS is a difference between maximum and standard metabolic rate (MMR and SMR, respectively) in a given organism (Killen et al., 2021). A relatively high AS can translate into a more flexible energy budget, enhancing mobility, growth and/or reproduction (Killen et al., 2016; Maazouzi et al., 2011) and, in consequence, fitness (Claireaux & Lefrançois, 2007). The ability to maintain a high AS over a range of temperatures is necessary for the development of thermal tolerance to a changing climate and/or successful establishment in novel areas of different climate (Pörtner, 2001; Weiner, 1992). According to the "plastic floors and concrete ceilings" hypothesis proposed by Sandblom et al. (2016), changes in AS are driven primarily by changes in SMR, which typically increases exponentially with rising temperature (McDonnell & Chapman, 2016), whereas changes in MMR vary depending on species and additional factors (Frisk et al., 2012; Nilsson & Lefevre, 2016; Rubalcaba et al., 2020). On the other hand, MMR has also been found as a primary driver of changes in AS of aquatic ectotherms (Killen et al., 2016; Rodgers & Franklin, 2021), showing that the above-mentioned hypothesis is not a general rule. MMR in fish often increases with rising temperature (Christensen et al., 2021; Crear et al., 2019; Ohlberger et al., 2007; Rubalcaba et al., 2020), although less so in larger species (Rubalcaba et al., 2020). However, MMR can also reach a constant level (phase plateau) or decline at high temperatures, as shown for several fish species (Farrell, 2009; Nilsson et al., 2009; Nilsson & Lefevre, 2016; Verberk et al., 2016).

In the context of global warming, there is a growing need to study eurythermal invasive species invading interconnected river systems, given the potentially large, even continental spatial scale of their spread and the accompanying biocoenotic effects. This applies in particular to the European river network, where connectivity was increased through the construction of canals facilitating the spread of the Ponto-Caspian fauna (Bij de Vaate et al., 2002; Pauli & Briski, 2018; Soto et al., 2023). The Ponto-Caspian region (the catchments of the Black, Azov and Caspian Seas) has undergone a dynamic hydrological history with frequent fluctuations in water level and salinity. This resulted in the evolution of the unique eurytopic fauna, characterized by physiological tolerance to wide spectra of abiotic factors, including temperature and salinity (Dumont, 1998; Mordukhay-Boltovskoy, 1964), and therefore showing a high invasive potential (Bij de Vaate et al., 2002; Rewicz et al., 2014). Indeed, the region constitutes the major source of alien taxa for Europe and North America (Bij de Vaate et al., 2002; Galil et al., 2007), including several species of goby fishes (Gobiidae) (Copp et al., 2005; Roche et al., 2013). Since the 1990s, the range of gobies in Central and Western Europe increased rapidly, and they entered the Laurentian Great Lakes of North America (Kornis et al., 2012). They affect local communities as competitors (e.g., Grabowska et al., 2016; Kakareko et al., 2013; Van Kessel et al., 2016), predators (Barton et al., 2005; Janssen & Jude, 2001), prey (Almqvist et al., 2010) and parasite hosts/vectors (Kvach & Ondračková, 2020; Ondračková et al., 2021).

Might the expansion of invasive gobies in inland waters be enhanced or inhibited by ongoing global warming? The Ponto-Caspian climate is warmer than Central and Western Europe (Rewicz et al., 2014), and the rapid invasion by gobies in Europe is being linked to the progressive increases in mean annual temperatures (Harka & Bíró, 2007). However, it is unclear whether gobies can tolerate elevated temperature and thus cope with climate warming better than their native counterparts. The physiological performance of ectothermic organisms such as fish depends on a number of species traits (e.g., morphological, ecological, behavioural) in addition to temperature, thus the final outcome of the combination of these traits is not obvious. Direct comparisons of metabolic characteristics among invasive and native freshwater fishes are not common in scientific literature. Amongst them, there are examples of both invaders that confer greater physiological resistance to high water temperature than native fish (Marras et al., 2015; Stoffels et al., 2017), as well as those that do not confirm such a tendency (Barker et al., 2018; Vinagre et al., 2014). Interspecific variation of physiological performance in teleost fish species is enormous (by far surpassing the variation in endotherms) and related to lifestyle in the context of locomotor capacity and tolerance to resource (oxygen, food) limitations (Killen et al., 2016). One end of the continuum of ecological lifestyles and corresponding physiological traits in fish is formed by active pelagic foragers with high metabolic rates. At the opposite end, there are sluggish benthic foragers with slow metabolism (Killen et al., 2016). The position of the Ponto-Caspian gobies in this continuum is difficult to define. They represent a specific group of benthic, bladderless freshwater and brackish water fish, associated with shelters (Błońska et al., 2016; Charlebois et al., 1997; Kakareko, 2011) and exhibiting burst-and-hold swimming mode (Egger et al., 2021). Although they live at the bottom, they show dynamic escapes from predation (Augustyniak et al., 2023) and are capable of overcoming currents (Jermacz et al., 2015; Kakareko, 2011). Thus, in contrast to their generally low locomotor and metabolic demands, these fish rely on burst increases in activity. Therefore, physiological capacity to perform oxygen-demanding processes appears to be one of their key characteristics. It follows that there is a need for interspecies comparative studies to understand how climate change may affect such a specific group of invasive benthic fishes, as Ponto-Caspian Gobiidae and their native counterparts. The results will broaden our knowledge of possible scenarios of changes in ichthyofauna in freshwater ecosystems of the temperate zone, especially in Europe. They will also allow a better understanding of the dispersal ability (e.g. in terms of distance and speed of movements) of benthic fish without swim-bladders in general.

In this study, we investigated differences in metabolic responses to an elevated summer temperature (25 vs. 17°C) between alien gobies and their native Central European counterparts. The 17°C value corresponds to mean temperature recorded in the warm half-year in rivers in central Poland (Marszelewski & Pius, 2014, 2016). In turn, 25°C corresponds to the mean annual temperature in the warmest month in the river Vistula (Marszelewski & Pius, 2014, 2016). We used two pairs of fish species that co-occur in European waters and fit well into the above-described context: (1) the native European bullhead *Cottus gobio* Linnaeus, 1758 versus the invasive racer goby *Babka gymnotrachelus* (Kessler, 1857), and (2) the native gudgeon *Gobio gobio* (Linnaeus, 1758) versus the invasive monkey goby *Neogobius fluviatilis* (Pallas, 1814). In European waters, the racer goby is found at the same sites and habitats (rocky and gravely substrata) as the European bullhead (Janáč et al., 2018; Kakareko et al., 2016). The monkey goby enters sandy bottom habitats occupied by the gudgeon (Płąchocki et al., 2020). We made comparisons only within these pairs of co-occurring species that interact in the same environments. We hypothesised that: (1) elevated summer temperature raises the SMR of the test species, limiting their physiological performance (expressed as AS), and (2) invasive gobies show better physiological performance (AS) at elevated summer temperature than their native counterparts, as a consequence of relatively lower SMR.

2 | MATERIALS AND METHODS

2.1 | Animals

We collected the fish from the tributaries of the river Vistula in Poland in July–September 2020. The European bullhead and the racer goby were taken from the river Brda (53°08′52.5″ N 17°58′10.5″ E) with an aquarium net while scuba diving to a depth of 2.5 m. The gudgeon and the monkey goby were collected from the river Pilica (51°45′50.1″ N 21°08′55.5″ E) through electrofishing (EFGI 650; BSE Bretschneider Spezialelektronik) in 2021. All specimens used for the tests were of 0+ age. They lacked symptoms of sexual maturity and thus we did not specify their sex.

Directly after capture, we transported the fish to the laboratory (c. 1–3 h transport time) in polythene bags with oxygenated water. We kept them in 350-L stock tanks in the laboratory, at a density of c. 20–30 individuals of a species per tank, for at least 1 month before the start of acclimation procedure to test temperatures. Tanks were filled with conditioned tap water and equipped with aquarium filters, aerators, and ceramic and stony shelters, but had no bottom substrate. The temperature was maintained by air conditioning at 17°C. The photoperiod was set at 12 hr:12 hr, light:dark with lights on 07:00 hr. We fed the fish daily with frozen chironomid larvae ad libitum. We exchanged c. 30% of water volume in the stock tanks once a week.

2.2 | Acclimation procedure to test temperatures

Fish were acclimated to a specific test temperature in 85-L acclimation tanks 4 weeks before measuring their metabolic rate in experiments. The acclimation tanks were filled with conditioned tap water and equipped with aquarium filters and aerators, but had no bottom substrate. In acclimation tanks, we provided food for the fish every day (frozen chironomid larvae ad libitum) and exchanged water every week. Fish were transferred from the stock tanks and placed in the acclimation tanks in groups of 10–12 individuals, initially at the temperature of the stock tanks (17°C). To control temperature during acclimation to 25°C, we used an aquarium heater with accuracy of 0.25°C (Ultra Heater 150 W; AQUAEL). Temperature was gradually (1°C per day) increased until reaching the required level of 25°C. We controlled the temperature using electronic thermometers placed inside the tanks (to the nearest 0.1°C). The fish tested at 17°C were transferred from the stock tanks to the acclimation tanks, but not subjected to further temperature modifications.

Metabolic traits of fish were measured in so-called post-absorptive state (but not starving) to avoid the confounding effects of ingestion, digestion, absorption and assimilation of a meal on metabolic rate (Ross et al., 1992; Thuy et al., 2010). The above-mentioned activities can cause underestimation or overestimation of respiration rate. To ensure this state (Chabot, Steffensen, & Farrell, 2016), the last feeding took place c. 40 hr before the beginning of the experiment.

Individuals of all four species acclimated to different temperatures did not show unnatural behaviour that might have suggested stopping the experiment, such as no exploration, clinging to the wall of the tank, hiding behind the aquarium filter, or erratic swimming.

Individuals were weighed before the experiment. The fish were gently placed in a bucket with water and weighed to the nearest 0.1 g with a Radwag WPT 3/6 laboratory scale, using the tare weight function, before placing the fish in the bucket. Individual total length was measured with the ImageJ 1.53k program (freeware by W.S. Rasband, U.S. National Institutes of Health: https://imagej.nih.gov/ij), using digital images taken from the top view before the tests. Each species pair was studied independently, comprising species co-existing and interacting in the same environments. The fish used in the experiments were about the same size within each pair (Tables 1, S1 and S2).

2.3 | Experimental set-up

In order to estimate individual metabolic rate (expressed as oxygen consumption rate) of fish, we used an intermittent-flow respirometry glass chamber system (LoligoSystems) according to Svendsen et al. (2016) (Figure S1). Intermittent-flow respirometry is a series of short-term closed respirometry measurements, interrupted by flushing intervals to exchange water in the respirometer. We used custom-made cylindrical borosilicate glass respirometry chambers, which were matched to the size of the fish (inner diameter 14 or 20 mm; length 90 or 100 mm; volume 15 or 34 ml, respectively). Chambers were submerged in a 12.6-L acrylic water bath (length 400 mm; width 225 mm; height 140 mm; water level 100 mm) with oxygenated water (Figure S1). The chambers had two input ports on one side and two output ports on the second. The single chamber was open at one end by a fitted glass stopper, allowing animals to be introduced and, when closed, ensuring that the system was gas- and water-tight. The chamber was mounted in a holder submerged in the water bath, and connected to a recirculating pump on one side and a flush pump on the other side (Figure S1). To connect the chamber to the pumps, we used non-silicone, Tygon E-3603 tubes (inner diameter 3.2 mm) with transparent walls and low gas permeability. Water mixing inside the chamber was obtained by the recirculating pump. Mixing during the measurement is critical for homogenizing oxygen conditions within the respirometric chamber. Fresh oxygenated water from the water bath was provided to the chamber by the flush pump immediately after the measurement phase. The recirculating and flush pumps worked at a rate 800 ml min^{-1}. The recirculating pump worked continuously during the experiment, whereas the flush pump was turned on during the flush phase. We also used a 100-L external tank filled with water to control the water temperature in the water bath. In order to heat or cool the water, water was pumped (a submersible circulation pump, rate 10 L min^{-1}) from the water bath to the external tank, passed through a steel coil (a heat exchanger) and then returned back to the water bath via PVC tubing (inner diameter 13 mm) (Figure S1). Temperature in the external tank was sustained by an aquarium cooler with a built-in heater (TECO 500K).

TABLE 1 Size of fish used in the experiments.

Temperature (°C)	Species	Individual total length (mean ± SD) (cm)
17	European bullhead	5.17 ± 0.29
	Racer goby	5.35 ± 0.47
	Gudgeon	6.30 ± 0.59
	Monkey goby	6.32 ± 0.65
25	European bullhead	5.13 ± 0.45
	Racer goby	5.08 ± 0.31
	Gudgeon	6.39 ± 0.48
	Monkey goby	6.29 ± 0.60

To measure oxygen consumption by fish in the chambers, we used external fibre optic cable sensors (optodes) connected to the Witrox 4 oxygen meter and sensor spots mounted inside the chambers. Oxygen content in chambers was recorded every 1 s during the entire experiment. To control temperature, we submerged a temperature probe with accuracy of 0.15°C (Pt1000 sensor type) in the water bath and connected it to the Witrox 4 meter. Values of oxygen level and temperature were recorded by AutoResp™ software (version 2.3.0; Loligo Systems).

2.4 | Experimental procedure

Each time, we started experiments at 10:00 hr. The laboratory photoperiod was set at 12 hr:12 hr, light:dark with lights on at 08:00 hr. Directly after acclimation (Figure S2), individuals were randomly selected from the acclimation tanks (from 17 or 25°C) and subjected to an exhaustion exercise just before placing them in the chambers (Figure S2). As the selected species are not good steady swimmers (Clark et al., 2013; Norin & Clark, 2016; Reidy et al., 1995), the exhaustion method is optimal for measuring their MMR. The exhaustion exercise were made by manually chasing the fish in a circular tank (diameter 50 cm, water depth 10 cm) for 5 min (Clark et al., 2013; Killen, 2014). Based on preliminary trials, we noticed that 5 min of chasing is sufficient to reduce the fish activity to a minimum and increase the operculum movement. Then, they were put into the respirometric chambers and left for 24 h (Figure S2). The time it took to transfer the fish to the chamber after the exhaustion exercise was approximately 10–15 s. After the test, individuals were gently removed from the respirometric chamber (Figure S2) and transferred to empty tanks with the same water temperature as in the test. To protect the fish from external stimuli, the water bath with the respirometric chambers was curtained off on all sides by Styrofoam screens. Each treatment was replicated 10 times using new individuals for each replicate. Each specimen was tested only once. After the tests, the European bullhead and gudgeon were released into the environment from which they were taken, whereas the racer goby and monkey goby, because of the are invasive fish, had to be euthanized by an overdose of Tricaine Methanesulfonate (MS-222).

The duration of a single measurement cycle (loop) was 450 s and consisted of three phases: flushing with fresh oxygenated water

(45 s), waiting (45 s for stabilization of conditions) and measurement of the oxygen loss in the closed chamber (360 s) (Figure S2). Each replicate included 192 measurement loops. We established the duration of the experiment and its specific phases on the basis of preliminary research and literature (Svendsen et al., 2016). The oxygen concentration during the experiments has never dropped below 6.5 mg O2 L^{-1}, which is within the range of optimal oxygen conditions for the fish species tested (Svobodová et al., 1993).

In order to account for bacterial respiration during the trials, background consumption was measured before and after each trial (replicate) in the respirometry chamber. Throughout all measurements, no bacterial respiration was detected. Before each treatment, we conducted a two-point calibration of oxygen sensors to obtain the most precise level of measurement during the study.

2.5 | Data analysis

Individual oxygen consumption rates were expressed in mg O2 hr^{-1} (Chabot, McKenzie, & Craig, 2016). Immediately after fish exhaustion, we measured its MMR within the first measurement period (360 s) after placing the fish in the respirometric chamber (Figure S2). The entire-animal SMR was assessed as the lowest 10th percentile of measurements carried out during the last 19 hr of the test, the first 5 hr were not included as potentially affected by handling stress and exhaustion exercise (Killen, 2014) (Figure S2). In turn, the AS was calculated as the absolute difference between MMR and SMR.

All oxygen consumption rates were corrected for the volume of the respirometry chamber by subtracting the animal volume (calculated from the measured mass, assuming a density of 1 g ml^{-1}) from the respirometer volume.

In order to analyse factors affecting the dependent variables–individual SMR, MMR and AS–we applied general linear models (GLM) with temperature and species as independent variables, their interaction, as well as animal mass as a covariate (used to control for its effect on metabolic rate). We log-transformed oxygen consumption and mass values to linearise a potentially allometric relationship between mass and metabolism. If needed, significant effects were further explored using sequential Bonferroni corrected LSD *post hoc* tests. We confirmed the normality and homoscedasticity of the data using Shapiro–Wilk and Levene tests, respectively. The level of significance (*p*-values) for all tests was $\alpha = 0.05$. We used SPSS Statistics 27.0 (IBM Inc.) to conduct statistical analyses.

3 | RESULTS

3.1 | European bullhead versus racer goby

SMR increased under the elevated temperature irrespective of species (Figure 1a), as shown by a significant main effect of temperature (Table 2A). Moreover, the SMR of the racer goby was lower than that of the European bullhead across both temperatures (Figure 1b), as shown by a significant main effect of species (Table 2A). Temperature did not affect the MMR of the tested species (Table 2B), but the MMR of the native European bullhead was consistently higher than that of the invasive racer goby across both temperatures (Figure 1c), as shown by a significant main effect of species (Table 2B). Temperature did not affect the AS of the European bullhead and racer goby (Table 2C). However, the AS of the European bullhead was consistently higher than that of the racer goby across all temperatures (Figure 1d), as shown by a significant main effect of species (Table 2C).

3.2 | Gudgeon versus monkey goby

SMR increased under elevated temperature irrespective of species (Figure 2a), as shown by a significant main effect of temperature (Table 3A). Furthermore, the SMR of the monkey goby was lower than that of the gudgeon across both temperatures (Figure 2b), as shown by a significant main effect of species (Table 3A). The MMR of fish depended neither on temperature (Table 3B; Figure 2c) nor species (Table 3B; Figure 2c). However, the elevated temperature caused a significant decrease in the AS of both species (Figure 2d), but the response of the gudgeon was stronger than that of the monkey goby, as indicated by a significant temperature × species interaction (Table 3C; Figure 2d).

4 | DISCUSSION

The first hypothesis, predicting an increase in metabolic rate resulting in decreased AS (resulting from the higher SMR) under the elevated summer temperature was confirmed for the gudgeon–monkey goby pair, but not for the European bullhead–racer goby pair. Interestingly, although the elevated temperature increased the SMR of the European bullhead and racer goby, their AS was not reduced. The second hypothesis, predicting that the invasive species display better physiological performance (AS) at the elevated summer temperature was also confirmed for the gudgeon–monkey goby pair only.

4.1 | Standard metabolic rate

We demonstrated that the elevated summer temperature raised the SMR of all the fish species tested. This is consistent with the fact that ectotherm metabolism increases with temperature (Donelson et al., 2012). The lower SMR of the invasive Ponto-Caspian gobies compared to their native counterparts corresponds the difference in metabolic rate observed between invasive and native amphipods (Becker et al., 2016; Maazouzi et al., 2011). In this situation, the invasive species has an energetic advantage over the native species as a consequence of their lower maintenance costs. This is expected to have a positive effect on fitness according to the compensation

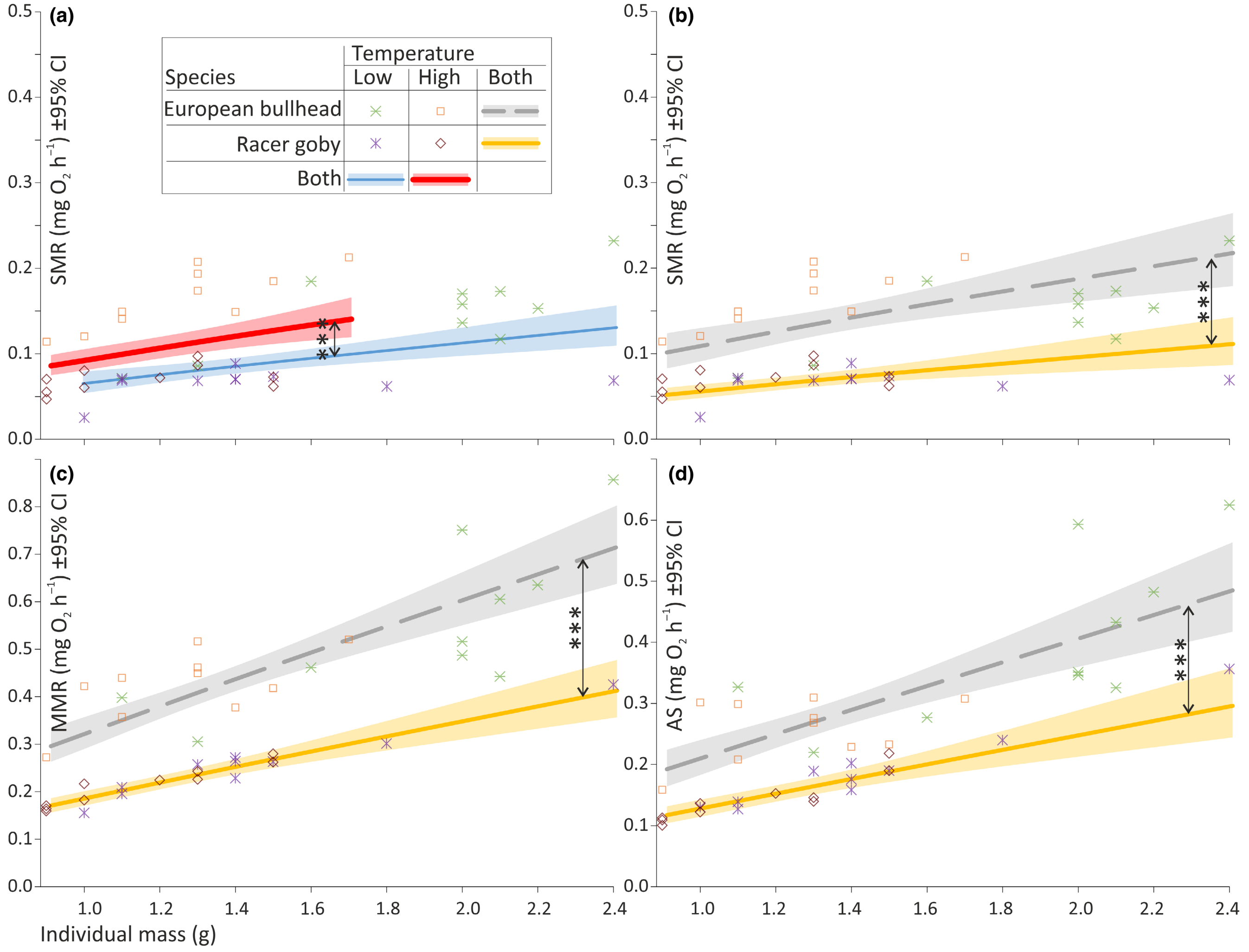


FIGURE 1 Individual standard metabolic rate (SMR) (a, b), maximum metabolic rate (MMR) (c) and aerobic scope (AS) (d) of the racer goby and European bullhead related to individual body mass at a control (17°C) and elevated (25°C) summer temperature. Symbols represent individual data points and lines are predicted by the general linear models (Table 2A–C) for significant main effects of temperature (a) and species (b–d), with shaded areas indicating 95% confidence intervals. The predicted values are back-transformed after the analysis of log-transformed data. Interactions were not significant in all the models. Asterisks indicate statistically significant differences: ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$.

hypothesis (Auer et al., 2015; Burton et al., 2011). On the one hand, a lower SMR can translate into a greater ability to endure periods of restricted and unpredictable food supplies owing to reduced maintenance requirements (Reid et al., 2012). On the other hand, the amount of energy required to maintain a relatively high SMR can diminish the energy resources available for activity (Metcalfe et al., 2016). It is noteworthy that the opposite scenario is also possible, that is, SMR can have a positive effect on fitness, if it fits into the overall higher metabolism and results in a higher rate of resource intake, in line with the increased intake hypothesis (Auer et al., 2015; Burton et al., 2011). However, the results of our study indicate that this scenario does not apply to the Ponto-Caspian gobies achieving such a high invasive success.

The SMR of the invasive gobies is related to the warmer climate of their indigenous area. The water temperature in limans and deltas of big Ponto-Caspian rivers reaches almost 29°C in July, suggesting the high temperature tolerance of local organisms, including goby fish (Rewicz et al., 2014). The ability to maintain a relatively low SMR could be a suitable mechanism enabling such tolerance and life in a warm climate. This relationship was found in populations of threespine stickleback *Gasterosteus aculeatus* by Pilakouta et al. (2020) and in Atlantic cod *Gadus morhua* by Sylvestre et al. (2007), showing that fish from cold habitats exhibit higher SMR than those from warm habitats. Moreover, the SMR of juvenile brown trout *Salmo trutta* developed from eggs incubated in warm water was lower compared to individuals reared in cold water (Durtsche et al., 2021).

4.2 | Maximum metabolic rate

In all of the species tested, the elevated temperature did not affect MMR. Thus, our results support the “plastic floors and concrete

TABLE 2 General linear models to test the effect of the fish species and temperature on standard metabolic rate (SMR), maximum metabolic rate (MMR) and aerobic scope (AS) of the racer goby and European bullhead.

	Dependent variable	Effect		df	MS	*F*	*p*
A	SMR	Experimental factors	Species (S)	1	3.830	71.979	<0.001*
			Temperature (T)	1	0.797	14.976	<0.001*
			(S) × (T)	1	0.100	1.887	0.178
		Covariate	Mass	1	1.168	21.958	<0.001*
		Error		35	0.053		
B	MMR	Experimental factors	Species (S)	1	2.567	140.232	<0.001*
			Temperature (T)	1	0.037	2.016	0.165
			(S) × (T)	1	0.028	1.543	0.222
		Covariate	Mass	1	1.552	84.804	<0.001*
		Error		35	0.018		
C	AS	Experimental factors	Species (S)	1	2.075	65.439	<0.001*
			Temperature (T)	1	0.015	0.469	0.498
			(S) × (T)	1	0.004	0.130	0.721
		Covariate	Mass	1	1.713	54.021	<0.001*
		Error		35	0.032		

*Significant effects ($p < 0.05$).

ceilings" hypothesis proposed by Sandblom et al. (2016). According to this hypothesis, SMRs are thermally phenotypically plastic, whereas MMRs are relatively less flexible in the context of adaptation to elevated temperatures. A study of the European perch *Perca fluviatilis* exposed to acute and chronic heating indicated that thermal flexibility is much more noticeable in resting than in maximum cardiorespiratory capacity of the fish (Sandblom et al., 2016). Nonetheless, the adaptive capacity of fish in a warming climate could be limited by the lower flexibility of MMR compared to SMR. The above-mentioned hypothesis has been demonstrated primarily in the context of fish (Rodgers & Franklin, 2021). However, it is worth noting that, in our study, the MMR of the European bullhead was higher than that of the racer goby, irrespective of temperature. A relatively high maximum oxygen consumption rate by the European bullhead can result from its environment and biology. Although both species are typically benthic, swim-bladderless fish (Egger et al., 2021; Neilson & Stepien, 2011; Teletchea & Beisel, 2018; Vassilev et al., 2012), they show different micro-habitat preferences. Bullhead typically live in well-oxygenated streams and rivers, at temperatures of 2–17°C (Andreasson, 1971; Smyly, 1957; Tomlinson & Perrow, 2003), often occupying habitats close to the main current (Legalle et al., 2005). According to Kakareko et al. (2016), the European bullhead is most abundant in fast-flowing areas of the River Brda with more aerated water (the habitat where European bullhead were caught for the current study) in contrast to the racer goby which, within the same area, occupies mostly sites of lower flow velocities. Thus, presumably, the bullhead is more often forced into burst activity (movement in fast-flowing water, counteracting dislodgement) and usually has access to higher oxygen concentrations compared to the racer goby. This might be the reason why bullhead evolved the ability to temporarily increase their metabolic rate to cope with extreme situations. However, the racer goby depends on sustaining a low metabolic rate to save energetic resources and thrives under lower oxygen concentrations.

4.3 | Aerobic scope

The elevated temperature did not cause any changes in AS of the European bullhead and racer goby in our study. It is worth emphasising that the lower SMR of the racer goby compared to that of the European bullhead did not translate into the higher AS of the former. By contrast, it was the European bullhead that had the higher AS in this species pair, which resulted from its relatively high MMR.

In our study, the physiological performance (expressed as AS) of the gudgeon and monkey goby was reduced at the elevated temperature. However, the size of the decrease in AS in the gudgeon was larger than in the monkey goby. This result follows the common rule that a warming climate causes a gradual decline in physiological performance expressed as AS. This is explained by the fact that the MMR under steady-state conditions does not keep up with the rate of increase SMR (Pörtner & Farrell, 2008). This finding is consistent with the allocation model of energy budgeting (Careau et al., 2008), which states that increased maintenance expenditure can deplete the energy available for other physiological tasks, such as growth or reproduction. When the level of SMR approaches that of MMR, it can lead to mortality of animals (Priede, 1985; Wood et al., 1983). The higher AS of the monkey goby compared to that of the gudgeon, as well as the lower response of the former to elevated temperature, can translate into a higher flexibility of the energy budget and ability to invest in various requiring oxygen activities, such as growth, reproduction and locomotion. All of these energy-demanding activities

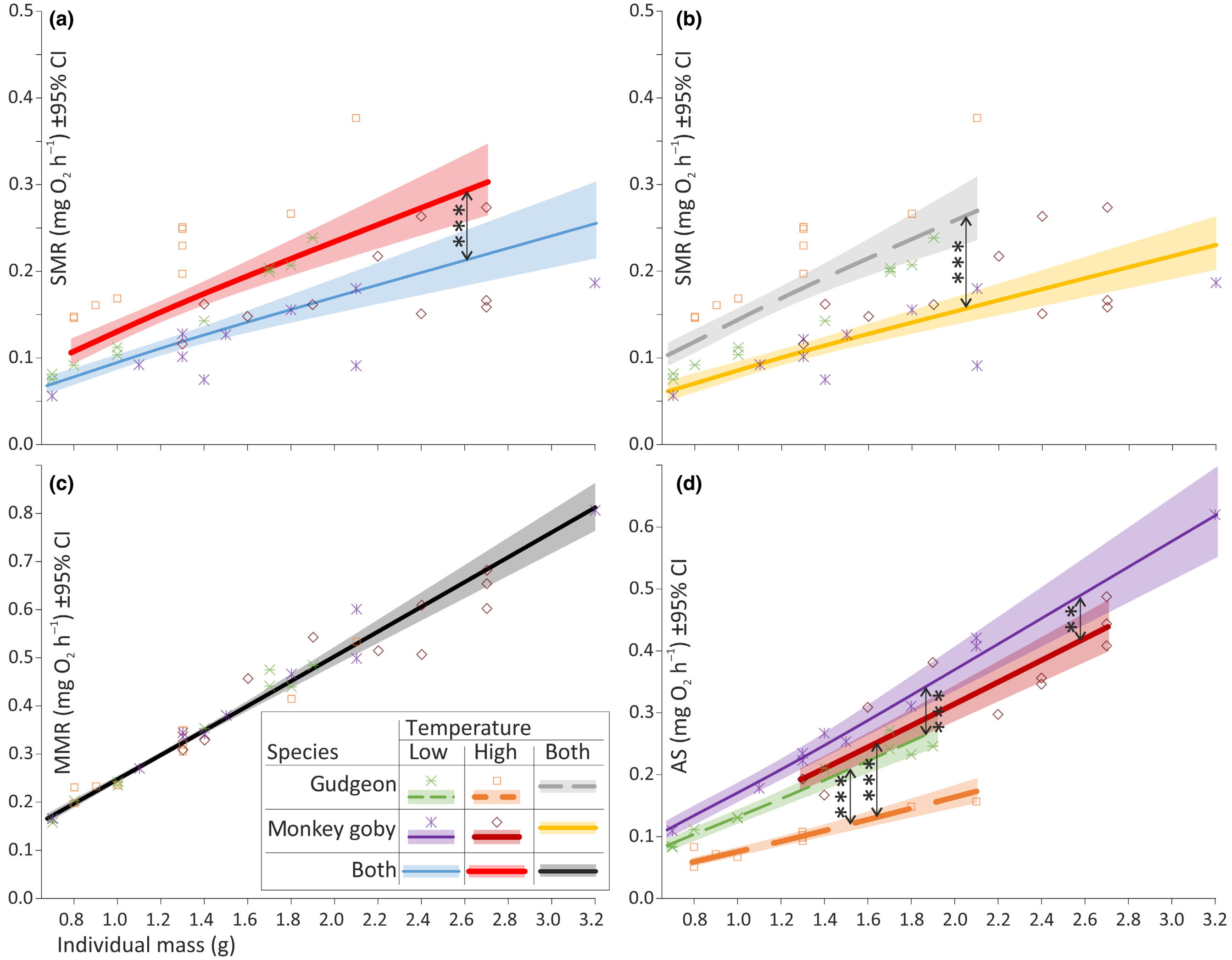


FIGURE 2 Individual standard metabolic rate (SMR) (a, b), maximum metabolic rate (MMR) (c) and aerobic scope (AS) (d) of the monkey goby and gudgeon related to individual body mass at a control (17°C) and elevated (25°C) summer temperature. Symbols represent individual data points and lines are predicted by the general linear models (Table 3A–C) for significant main effects of temperature (a) and species (b), as well as for a species*temperature interaction (d). There were no significant effects of temperature or species on MMR, for which a common line is presented (c). Shaded areas indicate 95% confidence intervals. The predicted values are back-transformed after the analysis of log-transformed data. Asterisks indicate statistically significant differences: ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$.

are relevant and important in the invasion process (Killen et al., 2016; Maazouzi et al., 2011). In general, AS of ectotherms increases exponentially with rising temperature until optimal temperature and then decreases with further temperature growth (Farrell, 2016). The decrease in AS shown by the monkey goby and gudgeon with increasing temperature suggests that a temperature of 25°C is beyond their optimum tolerance range. Despite their multiple ecological and biological similarities, the gudgeon and monkey goby have different water temperature preferences: the gudgeon prefer water of c. 16–20°C (Dawes, 2004; Souchon & Tissot, 2012), whereas the monkey goby prefer values of c. 18–22°C (Dawes, 2004; Hatton et al., 2018). It is worth noting that the greater AS (reflecting the physiological performance) of invasive species compared to native species at elevated temperatures is not a common ecological rule (Marras et al., 2015). Opposite cases, with native species showing higher AS values than their invasive counterparts under elevated temperature, have been reported, for example in the case of an invasive Ponto-Caspian amphipod *Dikerogammarus villosus* and its native counterpart *Gammarus pulex* (Maazouzi et al., 2011).

Although the species in both pairs in our study are similar in terms of body size and shape, and habitat requirements, they show differences in lifestyle, locomotor abilities and micro-habitat preferences. Fish with different lifestyles (e.g., benthic vs. pelagic, sluggish vs. active), from environments differing in resource (e.g., oxygen) availability have different energy requirements (Demer et al., 2012; Eliason et al., 2011; Killen et al., 2016; Sims et al., 2004). Thus, fish species can have different requirements for the allocation of energy resources to various physiological functions. Therefore, the observed variability in SMR, MMR and thus in AS of the species tested in our study can result from these differences. On the one hand, the

TABLE 3 General linear models to test the effect of the fish species and temperature on standard metabolic rate (SMR), maximum metabolic rate (MMR) and aerobic scope (AS) of the monkey goby (MG) and gudgeon (G).

	Dependent variable	Effect		df	MS	*F*	*p*
A	SMR	Experimental factors	Species (S)	1	2.031	61.699	<0.001*
			Temperature (T)	1	0.972	29.536	<0.001*
			(S) × (T)	1	0.130	3.962	0.054
		Covariate	Mass	1	3.376	102.567	<0.001*
		Error		35	0.033		
B	MMR	Experimental factors	Species (S)	1	0.001	0.208	0.651
			Temperature (T)	1	0.001	0.182	0.672
			(S) × (T)	1	0.008	1.504	0.228
		Covariate	Mass	1	4.840	891.154	<0.001*
		Error		35	0.005		
C	AS	Experimental factors	Species (S)	1	1.541	109.735	<0.001*
			Temperature (T)	1	1.222	87.061	<0.001*
			(S) × (T)	1	0.371	26.453	<0.001*
		Covariate	Mass	1	5.686	404.977	<0.001*
		Error		35	0.014		
		(S) × (T) *post hoc* tests					
		G	17°C vs. 25°C				<0.001*
		MG	17°C vs. 25°C				0.006*
		17°C	G vs. MG				<0.001*
		25°C	G vs. MG				<0.001*

*Significant effects ($p < 0.05$).

monkey goby, contrary to the native gudgeon, has no swim bladder (Neilson & Stepien, 2011; Teletchea & Beisel, 2018) and exhibits a burst-and-hold swimming mode (Teletchea & Beisel, 2018). Thus, its lower SMR compared to the native counterpart could be the result of its less active, stationary lifestyle. On the other hand, the racer goby and the European bullhead show a similar lifestyle (swimbladderless, benthic fish). However, the racer goby is associated with more stagnant and oxygen-poor waters than the bullhead. In this case, the lower SMR of the goby could be an adaptation to living in an environment which is less demanding in terms of activity (slow-running waters are easier to swim in than fast-running waters), but also with more limited resources (oxygen concentration).

4.4 | Conclusions

We have shown that elevated temperature affected metabolism, especially SMR of the invasive and native fish species tested. The ability of invasive Ponto-Caspian gobies to keep their SMR at a relatively low level compared to their native counterparts can be a key physiological trait in the context of their invasive potential. In the light of climate warming, the invasive gobiids, having lower metabolic energy expenditure, have a competitive advantage over native fish species from the same area because they can allocate the saved energy into life processes associated with fitness (e.g., growth, reproduction) and other activities associated with their invasiveness. Especially the monkey goby, displaying a weaker reduction in physiological performance (AS) in response to the elevated temperature than the co-occurring native gudgeon, seems likely to increase its competitive advantage over its local counterpart in a warming climate. Perhaps the exception may be habitats with fast-flowing waters, which demand occasional high energy expenditures to counteract the water current. Such locations can become refuges for native counterparts of invasive gobies (Kakareko et al., 2016). Overall, differences in metabolic responses to increasing temperature between the gobies tested in our study and their native counterparts may favour the former, facilitating their successful spread to temperate areas.

AUTHOR CONTRIBUTIONS

Conceptualisation: PK, JK, TK. Developing methods: PK. Conducting the research: PK. Data analysis: PK. Data interpretation: PK, JK, TK. Preparation figures & tables: PK, JK, TK. Writing: PK, JK, TK.

ACKNOWLEDGEMENTS

This research was supported by Polish National Science Centre (NSC grant no. 2016/23/B/NZ8/00741). We sampled and used the fish in accordance with the permit of the Local Committee for Ethics in Animal Research in Bydgoszcz, Poland, statement no. 26/2020 from 9 October 2020 (WOP.6401.4.5.2017.MO, WOP.6401.4.19.2018.MO). The capture and use of the European bullhead, which is protected by law in Poland, was accepted by the Regional Directorate for Environmental Protection in Bydgoszcz, Poland (approval nos

WOP.6401.4.5.2017.MO, WOP.6401.4.19.2018.MO). The procedures conducted within the study met the European Union guidelines on the protection of animals used for scientific purposes (Directive 2010/63/UE). Euthanised fish were disposed according to the Regulation of the Polish Minister of the Environment from 9 September 2011 (Journal of Laws no. 210, item 1260). Killing was carried out by a qualified, certified person (certificate no. 2355/2015 issued by the Polish Laboratory Animal Science Association).

FUNDING INFORMATION

This research was supported by Polish National Science Centre (NSC grant no. 2016/23/B/NZ8/00741).

CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ETHICS STATEMENT

We sampled and used the fish in accordance with the permit of the Local Committee for Ethics in Animal Research in Bydgoszcz, Poland, statement no. 26/2020 from 9 October 2020.

ORCID

Piotr Kłosiński https://orcid.org/0000-0002-6359-9781
Jarosław Kobak https://orcid.org/0000-0001-7660-9240
Tomasz Kakareko https://orcid.org/0000-0001-5054-7416

REFERENCES

Almqvist, G., Strandmark, A. K., & Appelberg, M. (2010). Has the invasive round goby caused new links in Baltic food webs? *Environmental Biology of Fishes*, *89*(1), 79–93. https://doi.org/10.1007/s10641-010-9692-z

Andreasson, S. (1971). *Feeding habits of a sculpin (Cottus gobio L. Pisces) population*. Report of the Institute of Freshwater Research No. 51. Drottningholm, Sweden.

Auer, S. K., Salin, K., Rudolf, A. M., Anderson, G. J., & Metcalfe, N. B. (2015). The optimal combination of standard metabolic rate and aerobic scope for somatic growth depends on food availability. *Functional Ecology*, *29*(4), 479–486. https://doi.org/10.1111/1365-2435.12396

Augustyniak, M., Kołacka, K., Kobak, J., Hliwa, P., Kłosiński, P., Poznańska-Kakareko, M., Jermacz, Ł., & Kakareko, T. (2023). Differences in predator-avoidance behavior between two invasive gobies and their native competitors. *Current Zoology*, *69*(6), 727–737. https://doi.org/10.1093/cz/zoac082

Barker, B. D., Horodysky, A. Z., & Kerstetter, D. W. (2018). Hot or not? Comparative behavioral thermoregulation, critical temperature regimes, and thermal tolerances of the invasive lionfish *Pterois* sp. versus native western North Atlantic reef fishes. *Biological Invasions*, *20*(1), 45–58. https://doi.org/10.1007/s10530-017-1511-4

Barton, D. R., Johnson, R. A., Campbell, L., Petruniak, J., & Patterson, M. (2005). Effects of round gobies (*Neogobius melanostomus*) on dreissenid mussels and other invertebrates in eastern Lake Erie, 2002–2004. *Journal of Great Lakes Research*, *31*, 252–261. https://doi.org/10.1016/S0380-1330(05)70318-X

Becker, J., Ortmann, C., Wetzel, M. A., & Koop, J. H. E. (2016). Metabolic activity and behavior of the invasive amphipod *Dikerogammarus villosus* and two common central European gammarid species (*Gammarus fossarum*, *Gammarus roeselii*): Low metabolic rates may favor the invader. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *191*, 119–126. https://doi.org/10.1016/j.cbpa.2015.10.015

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, *15*(4), 365–377. https://doi.org/10.1111/J.1461-0248.2011.01736.X

Bij de Vaate, A., Jazdzewski, K., Ketelaars, H. A. M., Gollasch, S., & Van der Velde, G. (2002). Geographical patterns in range extension of Ponto-Caspian macroinvertebrate species in Europe. *Canadian Journal of Fisheries and Aquatic Sciences*, *59*(7), 1159–1174. https://doi.org/10.1139/f02-098

Błońska, D., Kobak, J., Kakareko, T., & Grabowska, J. (2016). Can the presence of alien Ponto-Caspian gobies affect shelter use by the native European bullhead? *Aquatic Ecology*, *50*(4), 653–665. https://doi.org/10.1007/s10452-016-9584-1

Burton, T., Killen, S. S., Armstrong, J. D., & Metcalfe, N. B. (2011). What causes intraspecific variation in resting metabolic rate and what are its ecological consequences? *Proceedings of the Royal Society B: Biological Sciences*, *278*(1724), 3465–3473. https://doi.org/10.1098/rspb.2011.1778

Careau, V., Thomas, D., Humphries, M. M., & Réale, D. (2008). Energy metabolism and animal personality. *Oikos*, *117*(5), 641–653. https://doi.org/10.1111/j.2008.0030-1299.16513.x

Chabot, D., McKenzie, D. J., & Craig, J. F. (2016). Metabolic rate in fishes: Definitions, methods and significance for conservation physiology. *Journal of Fish Biology*, *88*(1), 1–9. https://doi.org/10.1111/jfb.12873

Chabot, D., Steffensen, J. F., & Farrell, A. P. (2016). The determination of standard metabolic rate in fishes. *Journal of Fish Biology*, *88*(1), 81–121. https://doi.org/10.1111/jfb.12845

Chan, J., Zeng, Y., & Yeo, D. C. J. (2021). Invasive species trait-based risk assessment for non-native freshwater fishes in a tropical city basin in Southeast Asia. *PLoS One*, *16*(3), e0248480. https://doi.org/10.1371/journal.pone.0248480

Charlebois, P. M., Marsden, J. E., Goettel, R. G., Wolf, R. K., Jude, D. J., & Rudnika, S. (1997). *The round goby, Neogobius melanostomus (Pallas), a review of European and North American literature*. Illinois-Indiana Sea Grant Program and Illinois Natural History Survey. INHS Special Publication No. 20. 76 pp.

Christensen, E. A. F., Norin, T., Tabak, I., van Deurs, M., & Behrens, J. W. (2021). Effects of temperature on physiological performance and behavioral thermoregulation in an invasive fish, the round goby. *Journal of Experimental Biology*, *224*(1), jeb237669. https://doi.org/10.1242/jeb.237669

Claireaux, G., & Lefrançois, C. (2007). Linking environmental variability and fish performance: Integration through the concept of scope for activity. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *362*(1487), 2031–2041. https://doi.org/10.1098/rstb.2007.2099

Clark, T. D., Sandblom, E., & Jutfelt, F. (2013). Aerobic scope measurements of fishes in an era of climate change: Respirometry, relevance and recommendations. *Journal of Experimental Biology*, *216*(15), 2771–2782. https://doi.org/10.1242/jeb.084251

Copp, G. H., Bianco, P. G., Bogutskaya, N. G., Erős, T., Falka, I., Ferreira, M. T., Fox, M. G., Freyhof, J., Gozlan, R. E., Grabowska, J., Kováč, V., Moreno-Amich, R., Naseka, A. M., Peňáz, M., Povž, M., Przybylski, M., Robillard, M., Russell, I. C., Stakėnas, S., … Wiesner, C. (2005). To be, or not to be, a non-native freshwater fish? *Journal of Applied Ichthyology*, *21*(4), 242–262. https://doi.org/10.1111/j.1439-0426.2005.00690.x

Crear, D. P., Brill, R. W., Bushnell, P. G., Latour, R. J., Schwieterman, G. D., Steffen, R. M., & Weng, K. C. (2019). The impacts of warming and hypoxia on the performance of an obligate ram ventilator. *Conservation Physiology*, *7*(1), coz026. https://doi.org/10.1093/conphys/coz026

Dawes, J. (2004). *Akwarystyka słodkowodna*. MULTICO Oficyna Wydawnicza.

Demer, D. A., Zwolinski, J. P., Byers, K. A., Cutter, G. R., Renfree, J. S., Sessions, T. S., & Macewicz, B. J. (2012). Prediction and confirmation of seasonal migration of Pacific sardine (*Sardinops sagax*) in the California current ecosystem. *Fishery Bulletin*, *110*(1), 52–70.

Domenici, P., Allan, B. J. M., Lefrançois, C., & McCormick, M. I. (2019). The effect of climate change on the escape kinematics and performance of fishes: Implications for future predator-prey interactions. *Conservation Physiology*, *7*(1), coz078. https://doi.org/10.1093/conphys/coz078

Donelson, J. M., Munday, P. L., McCormick, M. I., & Pitcher, C. R. (2012). Rapid transgenerational acclimation of a tropical reef fish to climate change. *Nature Climate Change*, *2*(1), 30–32. https://doi.org/10.1038/nclimate1323

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z., Knowler, D. J., Lévêque, C., Naiman, R. J., Prieur-Richard, A. H., Soto, D., Stiassny, M. L., & Sullivan, C. A. (2006). Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biological Reviews*, *81*(2), 163–182. https://doi.org/10.1017/S1464793105006950

Dumont, H. J. (1998). The Caspian Lake: History, biota, structure, and function. *Limnology and Oceanography*, *43*(1), 44–52. https://doi.org/10.4319/lo.1998.43.1.0044

Durtsche, R. D., Jonsson, B., & Greenberg, L. A. (2021). Thermal conditions during embryogenesis influence metabolic rates of juvenile brown trout *Salmo trutta*. *Ecosphere*, *12*(2), e03374. https://doi.org/10.1002/ecs2.3374

Egger, B., Wiegleb, J., Seidel, F., Burkhardt-Holm, P., & Hirsch, P. E. (2021). Comparative swimming performance and behaviour of three benthic fish species: The invasive round goby (*Neogobius melanostomus*), the native bullhead (*Cottus gobio*), and the native gudgeon (*Gobio gobio*). *Ecology of Freshwater Fish*, *30*(3), 391–405. https://doi.org/10.1111/eff.12592

Eliason, E. J., Clark, T. D., Hague, M. J., Hanson, L. M., Gallagher, Z. S., Jeffries, K. M., Gale, M. K., Patterson, D. A., Hinch, S. G., & Farrell, A. P. (2011). Differences in thermal tolerance among sockeye salmon populations. *Science*, *332*(6025), 109–112. https://doi.org/10.1126/science.1199158

Estay, S. A., Lima, M., & Bozinovic, F. (2014). The role of temperature variability on insect performance and population dynamics in a warming world. *Oikos*, *123*(2), 131–140. https://doi.org/10.1111/j.1600-0706.2013.00607.x

Farrell, A. P. (2009). Environment, antecedents and climate change: Lessons from the study of temperature physiology and river migration of salmonids. *Journal of Experimental Biology*, *212*(23), 3771–3780. https://doi.org/10.1242/jeb.023671

Farrell, A. P. (2016). Pragmatic perspective on aerobic scope: Peaking, plummeting, pejus and apportioning. *Journal of Fish Biology*, *88*(1), 322–343. https://doi.org/10.1111/JFB.12789

Frisk, M., Skov, P. V., & Steffensen, J. F. (2012). Thermal optimum for pikeperch (*Sander lucioperca*) and the use of ventilation frequency as a predictor of metabolic rate. *Aquaculture*, *324–325*, 151–157. https://doi.org/10.1016/j.aquaculture.2011.10.024

Frölicher, T. L., & Laufkötter, C. (2018). Emerging risks from marine heat waves. *Nature Communications*, *9*(1), 650. https://doi.org/10.1038/s41467-018-03163-6

Früh, D., Haase, P., & Stoll, S. (2017). Temperature drives asymmetric competition between alien and indigenous freshwater snail species, *Physa acuta* and *Physa fontinalis*. *Aquatic Sciences*, *79*(1), 187–195. https://doi.org/10.1007/s00027-016-0489-9

Galil, B. S., Nehring, S., & Panov, V. (2007). Waterways as invasion highways – Impact of climate change and globalization. In W. Nentwig (Ed.), *Biological invasions, ecological studies No. 193* (pp. 59–74). Springer.

Grabowska, J., Kakareko, T., Błońska, D., Przybylski, M., Kobak, J., Jermacz, Ł., & Copp, G. H. (2016). Interspecific competition for a shelter between non-native racer goby and native European bullhead under experimental conditions – Effects of season, fish size and light conditions. *Limnologica*, *56*, 30–38. https://doi.org/10.1016/j.limno.2015.11.004

Harka, Á., & Bíró, P. (2007). New patterns in Danubian distribution of Ponto-Caspian gobies – A result of global climatic change and/or canalization? *Electronic Journal of Ichthyology*, *1*(1), 1–14.

Hatton, E. C., Buckley, J. D., Fera, S. A., Henry, S., Hunt, L. M., Drake, D. A. R., & Johnson, T. B. (2018). *Ecological temperature metrics for invasive fishes in Ontario and the Great Lakes region*. Science and Research Information Report IR-15. Ontario Ministry of Natural Resources and Forestry. https://doi.org/10.13140/RG.2.2.29219.30244

Hellmann, J. J., Byers, J. E., Bierwagen, B. G., & Dukes, J. S. (2008). Five potential consequences of climate change for invasive species. *Conservation Biology*, *22*(3), 534–543. https://doi.org/10.1111/j.1523-1739.2008.00951.x

IPCC. (2014). *Climate change 2014. Synthesis report. Contribution of working groups I, II and III to the fifth assessment report of the intergovernmental panel on climate*. IPCC.

Janáč, M., Roche, K., Šlapanský, L., Polačik, M., & Jurajda, P. (2018). Long-term monitoring of native bullhead and invasive gobiids in the Danubian rip-rap zone. *Hydrobiologia*, *807*(1), 263–275. https://doi.org/10.1007/s10750-017-3398-6

Janssen, J., & Jude, D. (2001). Recruitment failure of mottled sculpin *Cottus bairdi* in Calumet Harbor, southern Lake Michigan, induced by the newly introduced round goby *Neogobius melanostomus*. *Journal of Great Lakes Resources*, *27*(3), 319–328. https://doi.org/10.1016/S0380-1330(01)70647-8

Jermacz, Ł., Kobak, J., Dzierżyńska, A., & Kakareko, T. (2015). The effect of flow on the competition between the alien racer goby and native European bullhead. *Ecology of Freshwater Fish*, *24*(3), 467–477. https://doi.org/10.1111/eff.12162

Kakareko, T. (2011). *Wpływ wybranych czynników na rozmieszczenie i preferencje siedliskowe babki łysej (Neogobius gymnotrachelus Kessler, 1857) i babki szczupłej (Neogobius fluviatilis Pallas, 1811), obcych gatunków ryb w Polsce (rozprawa habilitacyjna)*. Wydawnictwo Naukowe Uniwersytetu Mikołaja Kopernika.

Kakareko, T., Kobak, J., Grabowska, J., Jermacz, Ł., Przybylski, M., Poznańska, M., Pietraszewski, D., & Copp, G. H. (2013). Competitive interactions for food resources between invasive racer goby *Babka gymnotrachelus* and native European bullhead *Cottus gobio*. *Biological Invasions*, *15*(11), 2519–2530. https://doi.org/10.1007/s10530-013-0470-7

Kakareko, T., Kobak, J., Poznańska, M., Jermacz, Ł., & Copp, G. H. (2016). Underwater evaluation of habitat partitioning in a European river between a non-native invader, the racer goby and a threatened native fish, the European bullhead. *Ecology of Freshwater Fish*, *25*(1), 60–71. https://doi.org/10.1111/eff.12191

Kelley, A. L. (2014). The role thermal physiology plays in species invasion. *Conservation Physiology*, *2*(1), cou045. https://doi.org/10.1093/conphys/cou045

Killen, S. S. (2014). Growth trajectory influences temperature preference in fish through an effect on metabolic rate. *Journal of Animal Ecology*, *83*(6), 1513–1522. https://doi.org/10.1111/1365-2656.12244

Killen, S. S., Christensen, E. A. F., Cortese, D., Závorka, L., Norin, T., Cotgrove, L., Crespel, A., Munson, A., Nati, J. J. H., Papatheodoulou, M., & McKenzie, D. J. (2021). Guidelines for reporting methods to estimate metabolic rates by aquatic intermittent-flow respirometry. *Journal of Experimental Biology*, *224*(18), jeb242522. https://doi.org/10.1242/jeb.242522

Killen, S. S., Glazier, D. S., Rezende, E. L., Clark, T. D., Atkinson, D., Willener, A. S. T., & Halsey, L. G. (2016). Ecological influences and morphological correlates of resting and maximal metabolic rates across teleost fish species. *American Naturalist*, *187*(5), 592–606. https://doi.org/10.1086/685893

Kornis, M. S., Mercado-Silva, N., & Vander Zanden, M. J. (2012). Twenty years of invasion: A review of round goby *Neogobius melanostomus* biology, spread and ecological implications. *Journal of Fish Biology*, *80*(2), 235–285. https://doi.org/10.1111/j.1095-8649.2011.03157.x

Kvach, Y., & Ondračková, M. (2020). Checklist of parasites for Ponto-Caspian gobies (Actinopterygii: Gobiidae) in their native and non-native ranges. *Journal of Applied Ichthyology*, *36*(4), 472–500. https://doi.org/10.1111/jai.14036

Legalle, M., Santoul, F., Figuerola, J., Mastrorillo, S., & Céréghino, R. (2005). Factors influencing the spatial distribution patterns of the bullhead (*Cottus gobio* L., Teleostei Cottidae): A multi-scale study. *Biodiversity and Conservation*, *14*(6), 1319–1334. https://doi.org/10.1007/s10531-004-9673-7

Lodge, D. M., Stein, R. A., Brown, K. M., Covich, A. P., Brönmark, C., Garvey, J. E., & Klosiewski, S. P. (1998). Predicting impact of freshwater exotic species on native biodiversity: Challenges in spatial scaling. *Australian Journal of Ecology*, *23*(1), 53–67. https://doi.org/10.1111/j.1442-9993.1998.tb00705.x

Maazouzi, C., Piscart, C., Legier, F., & Hervant, F. (2011). Ecophysiological responses to temperature of the "killer shrimp" *Dikerogammarus villosus*: Is the invader really stronger than the native *Gammarus pulex*? *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *159*(3), 268–274. https://doi.org/10.1016/j.cbpa.2011.03.019

Markovic, D., Carrizo, S., Freyhof, J., Cid, N., Lengyel, S., Scholz, M., Kasperdius, H., & Darwall, W. (2014). Europe's freshwater biodiversity under climate change: Distribution shifts and conservation needs. *Diversity and Distributions*, *20*(9), 1097–1107. https://doi.org/10.1111/DDI.12232

Marras, S., Cucco, A., Antognarelli, F., Azzurro, E., Milazzo, M., Bariche, M., Butenschön, M., Kay, S., Di Bitetto, M., Quattrocchi, G., Sinerchia, M., & Domenici, P. (2015). Predicting future thermal habitat suitability of competing native and invasive fish species: From metabolic scope to oceanographic modelling. *Conservation Physiology*, *3*(1), cou059. https://doi.org/10.1093/conphys/cou059

Marszelewski, W., & Pius, B. (2014). The impact of changes in air temperature upon the thermal regime of the river Vistula in Toruń (Poland) over the years 1961–2012. In P. Gâştescu, W. Marszelewski, & P. Bretcan (Eds.), *Water resources and wetlands* (pp. 231–236). Romanian Limnogeographical Association.

Marszelewski, W., & Pius, B. (2016). Long-term changes in temperature of river waters in the transitional zone of the temperate climate: A case study of polish rivers. *Hydrological Sciences Journal*, *61*(8), 1430–1442. https://doi.org/10.1080/02626667.2015.1040800

McDonnell, L. H., & Chapman, L. J. (2016). Effects of thermal increase on aerobic capacity and swim performance in a tropical inland fish. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *199*, 62–70. https://doi.org/10.1016/j.cbpa.2016.05.018

Metcalfe, N. B., Van Leeuwen, T. E., & Killen, S. S. (2016). Does individual variation in metabolic phenotype predict fish behaviour and performance? *Journal of Fish Biology*, *88*(1), 298–321. https://doi.org/10.1111/jfb.12699

Mordukhay-Boltovskoy, P. D. (1964). Caspian fauna in fresh waters outside the Ponto-Caspian basin. *Hydrobiologia*, *23*, 159–164. https://doi.org/10.1007/BF00043727

Nati, J. J. H., Lindström, J., Yeomans, W., & Killen, S. S. (2018). Physiological and behavioural responses to hypoxia in an invasive freshwater fish species and a native competitor. *Ecology of Freshwater Fish*, *27*(3), 813–821. https://doi.org/10.1111/EFF.12394

Neilson, M. E., & Stepien, C. A. (2011). Historic speciation and recent colonization of Eurasian monkey gobies (*Neogobius fluviatilis* and *N. pallasi*) revealed by DNA sequences, microsatellites, and morphology. *Diversity and Distributions*, *17*(4), 688–702. https://doi.org/10.1111/j.1472-4642.2011.00762.x

Nilsson, G. E., Crawley, N., Lunde, I. G., & Munday, P. L. (2009). Elevated temperature reduces the respiratory scope of coral reef fishes. *Global Change Biology*, *15*(6), 1405–1412. https://doi.org/10.1111/j.1365-2486.2008.01767.x

Nilsson, G. E., & Lefevre, S. (2016). Physiological challenges to fishes in a warmer and acidified future. *Physiology*, *31*(6), 409–417. https://doi.org/10.1152/physiol.00055.2015

Norin, T., & Clark, T. D. (2016). Measurement and relevance of maximum metabolic rate in fishes. *Journal of Fish Biology*, *88*(1), 122–151. https://doi.org/10.1111/jfb.12796

Ohlberger, J., Staaks, G., & Hölker, F. (2007). Effects of temperature, swimming speed and body mass on standard and active metabolic rate in vendace (*Coregonus albula*). *Journal of Comparative Physiology B*, *177*(8), 905–916. https://doi.org/10.1007/s00360-007-0189-9

Ondračková, M., Janáč, M., Borcherding, J., Grabowska, J., Bartáková, V., & Jurajda, P. (2021). Non-native gobies share predominantly immature parasites with local fish hosts. *Journal of Vertebrate Biology*, *70*(4), 21050. https://doi.org/10.25225/jvb.21050

Pauli, N. C., & Briski, E. (2018). Euryhalinity of Ponto-Caspian invaders in their native and introduced regions. *Aquatic Invasions*, *13*(4), 439–447. https://doi.org/10.3391/ai.2018.13.4.02

Pilakouta, N., Killen, S. S., Kristjánsson, B. K., Skúlason, S., Lindström, J., Metcalfe, N. B., & Parsons, K. J. (2020). Multigenerational exposure to elevated temperatures leads to a reduction in standard metabolic rate in the wild. *Functional Ecology*, *34*(6), 1205–1214. https://doi.org/10.1111/1365-2435.13538

Pinsky, M. L., Eikeset, A. M., McCauley, D. J., Payne, J. L., & Sunday, J. M. (2019). Greater vulnerability to warming of marine versus terrestrial ectotherms. *Nature*, *569*(7754), 108–111. https://doi.org/10.1038/s41586-019-1132-4

Płąchocki, D., Kobak, J., Poznańska-Kakareko, M., & Kakareko, T. (2020). Environmental factors associated with the occurrence of the Ponto–Caspian gobies in a lowland river belonging to the central European invasion corridor. *River Research and Applications*, *36*(1), 25–35. https://doi.org/10.1002/rra.3543

Pörtner, H. O. (2001). Climate change and temperature-dependent biogeography: Oxygen limitation of thermal tolerance in animals. *Naturwissenschaften*, *88*(4), 137–146. https://doi.org/10.1007/s001140100216

Pörtner, H. O., & Farrell, A. P. (2008). Physiology and climate change. *Science*, *322*(5902), 690–692. https://doi.org/10.1126/science.1163156

Priede, I. G. (1985). Metabolic scope in fishes. In P. Tytler & P. Calow (Eds.), *Fish energetics: New perpectives* (pp. 33–64). Croom Helm. https://doi.org/10.1007/978-94-011-7918-8

Rahel, F. J., & Olden, J. D. (2008). Assessing the effects of climate change on aquatic invasive species. *Conservation Biology*, *22*(3), 521–533. https://doi.org/10.1111/j.1523-1739.2008.00950.x

Reid, D., Armstrong, J. D., & Metcalfe, N. B. (2012). The performance advantage of a high resting metabolic rate in juvenile salmon is habitat dependent. *Journal of Animal Ecology*, *81*(4), 868–875. https://doi.org/10.1111/j.1365-2656.2012.01969.x

Reidy, S. P., Nelson, J. A., Tang, Y., & Kerr, S. R. (1995). Post-exercise metabolic rate in Atlantic cod and its dependence upon the method of exhaustion. *Journal of Fish Biology*, *47*(3), 377–386. https://doi.org/10.1111/j.1095-8649.1995.tb01907.x

Rewicz, T., Grabowski, M., MacNeil, C., & Bącela-Spychalska, K. (2014). The profile of a 'perfect' invader – The case of killer shrimp, *Dikerogammarus villosus*. *Aquatic Invasions*, *9*(3), 267–288. https://doi.org/10.3391/ai.2014.9.3.04

Roche, K. F., Janač, M., & Jurajda, P. (2013). A review of Gobiid expansion along the Danube-Rhine corridor – Geopolitical change as a driver for invasion. *Knowledge and Management of Aquatic Ecosystems*, *411*, 1. https://doi.org/10.1051/kmae/2013066

Rodgers, E. M., & Franklin, C. E. (2021). Aerobic scope and climate warming: Testing the "plastic floors and concrete ceilings" hypothesis in the estuarine crocodile (*Crocodylus porosus*). *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology*, *335*(1), 108–117. https://doi.org/10.1002/jez.2412

Ross, L. G., McKinney, R. W., Cardwell, S. K., Fullarton, J. G., Roberts, S. E. J., & Ross, B. (1992). The effects of dietary protein content, lipid content and ration level on oxygen consumption and specific dynamic action in *Oreochromis niloticus* L. *Comparative Biochemistry and Physiology Part A: Physiology*, *103*(3), 573–578. https://doi.org/10.1016/0300-9629(92)90292-X

Rubalcaba, J. G., Verberk, W. C. E. P., Hendriks, A. J., Saris, B., & Woods, H. A. (2020). Oxygen limitation may affect the temperature and size dependence of metabolism in aquatic ectotherms. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(50), 31963–31968. https://doi.org/10.1073/pnas.2003292117

Sandblom, E., Clark, T. D., Gräns, A., Ekström, A., Brijs, J., Sundström, L. F., Odelström, A., Adill, A., Aho, T., & Jutfelt, F. (2016). Physiological constraints to climate warming in fish follow principles of plastic floors and concrete ceilings. *Nature Communications*, *7*, 11447. https://doi.org/10.1038/ncomms11447

Sims, D. W., Wearmouth, V. J., Genner, M. J., Southward, A. J., & Hawkins, S. J. (2004). Low-temperature-driven early spawning migration of a temperate marine fish. *Journal of Animal Ecology*, *73*(2), 333–341. https://doi.org/10.1111/j.0021-8790.2004.00810.x

Smyly, W. J. P. (1957). The life-history of the bullhead or miller's thumb (*Cottus gobio* L.). *Proceedings of the Zoological Society of London*, *128*, 431–453.

Soto, I., Cuthbert, R. N., Ricciardi, A., Ahmed, D. A., Altermatt, F., Schäfer, R. B., Archambaud-Suard, G., Bonada, N., Cañedo-Argüelles, M., Csabai, Z., Datry, T., Dick, J. T. A., Floury, M., Forio, M. A. E., Forcellini, M., Fruget, J.-F., Goethals, P., Haase, P., Hudgins, E. J., … Briski, E. (2023). The faunal Ponto-Caspianization of central and western European waterways. *Biological Invasions*, *25*(8), 2613–2629. https://doi.org/10.1007/s10530-023-03060-0

Souchon, Y., & Tissot, L. (2012). Synthesis of thermal tolerances of the common freshwater fish species in large Western Europe rivers. *Knowledge and Management of Aquatic Ecosystems*, *405*, 3. https://doi.org/10.1051/kmae/2012008

Stoffels, R. J., Weatherman, K. E., & Allen-Ankins, S. (2017). Heat and hypoxia give a global invader, *Gambusia holbrooki*, the edge over a threatened endemic fish on Australian floodplains. *Biological Invasions*, *19*(8), 2477–2489. https://doi.org/10.1007/s10530-017-1457-6

Svendsen, M. B. S., Bushnell, P. G., & Steffensen, J. F. (2016). Design and setup of intermittent-flow respirometry system for aquatic organisms. *Journal of Fish Biology*, *88*(1), 26–50. https://doi.org/10.1111/jfb.12797

Svobodová, Z., Lloyd, R., Máchová, J., & Vykusová, B. (1993). *Water quality and fish health*. EIFAC Technical Paper No. 54. FAO.

Sylvestre, E.-L., Lapointe, D., Dutil, J.-D., & Guderley, H. (2007). Thermal sensitivity of metabolic rates and swimming performance in two latitudinally separated populations of cod, *Gadus morhua* L. *Journal of Comparative Physiology B*, *177*(4), 447–460. https://doi.org/10.1007/s00360-007-0143-x

Teletchea, F., & Beisel, J.-N. (2018). Alien fish species in France with emphasis on the recent invasion of gobies. In R. Sajal (Ed.), *Biological resources of water* (pp. 75–92). IntechOpen. https://doi.org/10.5772/intechopen.73408

Thuy, N. H., Tien, L. A., Tuyet, P. N., Huong, D. T. T., Cong, N. V., Bayley, M., Wang, T., & Lefevre, S. (2010). Critical oxygen tension increases during digestion in the perch *Perca fluviatilis*. *Journal of Fish Biology*, *76*(4), 1025–1031. https://doi.org/10.1111/j.1095-8649.2009.02533.x

Tomlinson, M. L., & Perrow, M. R. (2003). *Ecology of the bullhead*. Conserving Natura 2000 Rivers Ecology Series No. 4. English Nature.

Van Kessel, N., Dorenbosch, M., Kranenbarg, J., van der Velde, G., & Leuven, R. S. E. W. (2016). Invasive Ponto-Caspian gobies rapidly reduce the abundance of protected native bullhead. *Aquatic Invasions*, *11*(2), 179–188. https://doi.org/10.3391/ai.2016.11.2.07

Vander Zanden, M. J., & Olden, J. D. (2008). A management framework for preventing the secondary spread of aquatic invasive species. *Canadian Journal of Fisheries and Aquatic Sciences*, *65*(7), 1512–1522. https://doi.org/10.1139/F08-099

Vassilev, M., Apostolou, A., Velkov, B., Dobrev, D., & Zarev, V. (2012). *Atlas of the Gobies (Gobiidae) in Bulgaria*. Bulgarian Academy of Science.

Verberk, W. C. E. P., Overgaard, J., Ern, R., Bayley, M., Wang, T., Boardman, L., & Terblanche, J. S. (2016). Does oxygen limit thermal tolerance in arthropods? A critical review of current evidence. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *192*, 64–78. https://doi.org/10.1016/j.cbpa.2015.10.020

Vinagre, C., Narciso, L., Cabral, H. N., Costa, M. J., & Rosa, R. (2014). Thermal sensitivity of native and invasive seabreams. *Marine Ecology*, *35*(3), 292–297. https://doi.org/10.1111/maec.12080

Webb, B. W., Hannah, D. M., Moore, R. D., Brown, L. E., & Nobilis, F. (2008). Recent advances in stream and river temperature research. *Hydrological Processes*, *22*(7), 902–918. https://doi.org/10.1002/HYP.6994

Weiner, J. (1992). Physiological limits to sustainable energy budgets in birds and mammals: Ecological implications. *Trends in Ecology & Evolution*, *7*(11), 384–388. https://doi.org/10.1016/0169-5347(92)90009-Z

Wood, C. M., Turner, J. D., & Graham, M. S. (1983). Why do fish die after severe exercise? *Journal of Fish Biology*, *22*(2), 189–201. https://doi.org/10.1111/j.1095-8649.1983.tb04739.x

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Kłosiński, P., Kobak, J., & Kakareko, T. (2024). Metabolic rate of two invasive Ponto-Caspian goby species and their native competitors in the context of global warming. *Freshwater Biology*, *69*, 971–983. https://doi.org/10.1111/fwb.14259

Metabolic rate of two invasive Ponto-Caspian goby species and their native competitors in the context of global warming

Piotr Kłosiński[a, *], Jarosław Kobak[b] and Tomasz Kakareko[a]

[a] Department of Ecology and Biogeography, Faculty of Biological and Veterinary Sciences, Nicolaus Copernicus University in Toruń, Lwowska 1, 87-100, Toruń, Poland

[b] Department of Invertebrate Zoology and Parasitology, Faculty of Biological and Veterinary Sciences, Nicolaus Copernicus University in Toruń, Lwowska 1, 87-100, Toruń, Poland

* Corresponding author: Piotr Kłosiński. E-mail address: klosinski.piotr@doktorant.umk.pl; ORCID iD: https://orcid.org/0000-0002-6359-9781

To compare differences in fish length (Table 1), we performed two separate analyses – each including two species and two temperatures. Length was compared using General Linear Models (GLM) with temperature and species as independent variables (Table S1, S2).

Table S1. Comparisons of the individual total lengths of European bullhead and racer goby used in the experiment

		17 °C	**25 °C**	
		racer goby	**European bullhead**	**racer goby**
17 °C	**European bullhead**	$F_{1, 36} = 0.241$, $P = 0.627$	$F_{1, 36} = 1.584$, $P = 0.216$	Not compared
	racer goby		Not compared	$F_{1, 36} = 1.584$, $P = 0.216$
25 °C	**European bullhead**			$F_{1, 36} = 0.241$, $P = 0.627$

Table S2. Comparisons of the individual total lengths of gudgeon and monkey goby used in the experiment

		17 °C	**25 °C**	
		monkey goby	**gudgeon**	**monkey goby**
17 °C	**gudgeon**	$F_{1, 36} = 0.049$, $P = 0.827$	$F_{1, 36} = 0.026$, $P = 0.874$	Not compared
	monkey goby		Not compared	$F_{1, 36} = 0.026$, $P = 0.874$
25 °C	**gudgeon**			$F_{1, 36} = 0.049$, $P = 0.827$

Metabolic rate of two invasive Ponto-Caspian goby species and their native competitors in the context of global warming

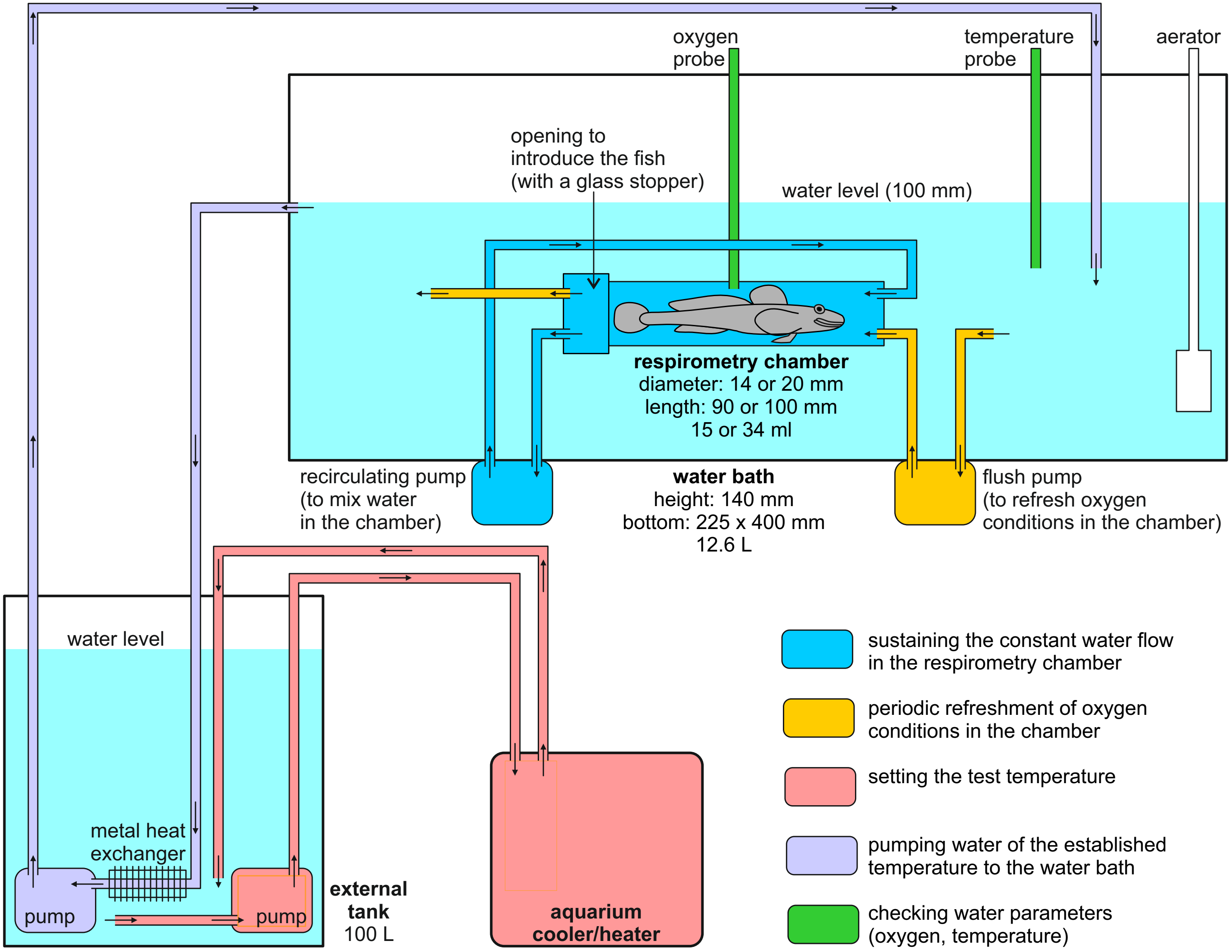
Piotr Kłosiński[a, *], Jarosław Kobak[b] and Tomasz Kakareko[a]

[a] Department of Ecology and Biogeography, Faculty of Biological and Veterinary Sciences, Nicolaus Copernicus University in Toruń, Lwowska 1, 87-100, Toruń, Poland

[b] Department of Invertebrate Zoology and Parasitology, Faculty of Biological and Veterinary Sciences, Nicolaus Copernicus University in Toruń, Lwowska 1, 87-100, Toruń, Poland

* Corresponding author: Piotr Kłosiński. E-mail address: klosinski.piotr@doktorant.umk.pl; ORCID iD: https://orcid.org/0000-0002-6359-9781

Figure S1. Experimental setup


oxygen probe
temperature probe
aerator
opening to introduce the fish (with a glass stopper)
water level (100 mm)
respirometry chamber
diameter: 14 or 20 mm
length: 90 or 100 mm
15 or 34 ml
recirculating pump (to mix water in the chamber)
water bath
height: 140 mm
bottom: 225 x 400 mm
12.6 L
flush pump (to refresh oxygen conditions in the chamber)
water level
metal heat exchanger
pump
pump
external tank
100 L
aquarium cooler/heater
sustaining the constant water flow in the respirometry chamber
periodic refreshment of oxygen conditions in the chamber
setting the test temperature
pumping water of the established temperature to the water bath
checking water parameters (oxygen, temperature)

Metabolic rate of two invasive Ponto-Caspian goby species and their native competitors in the context of global warming

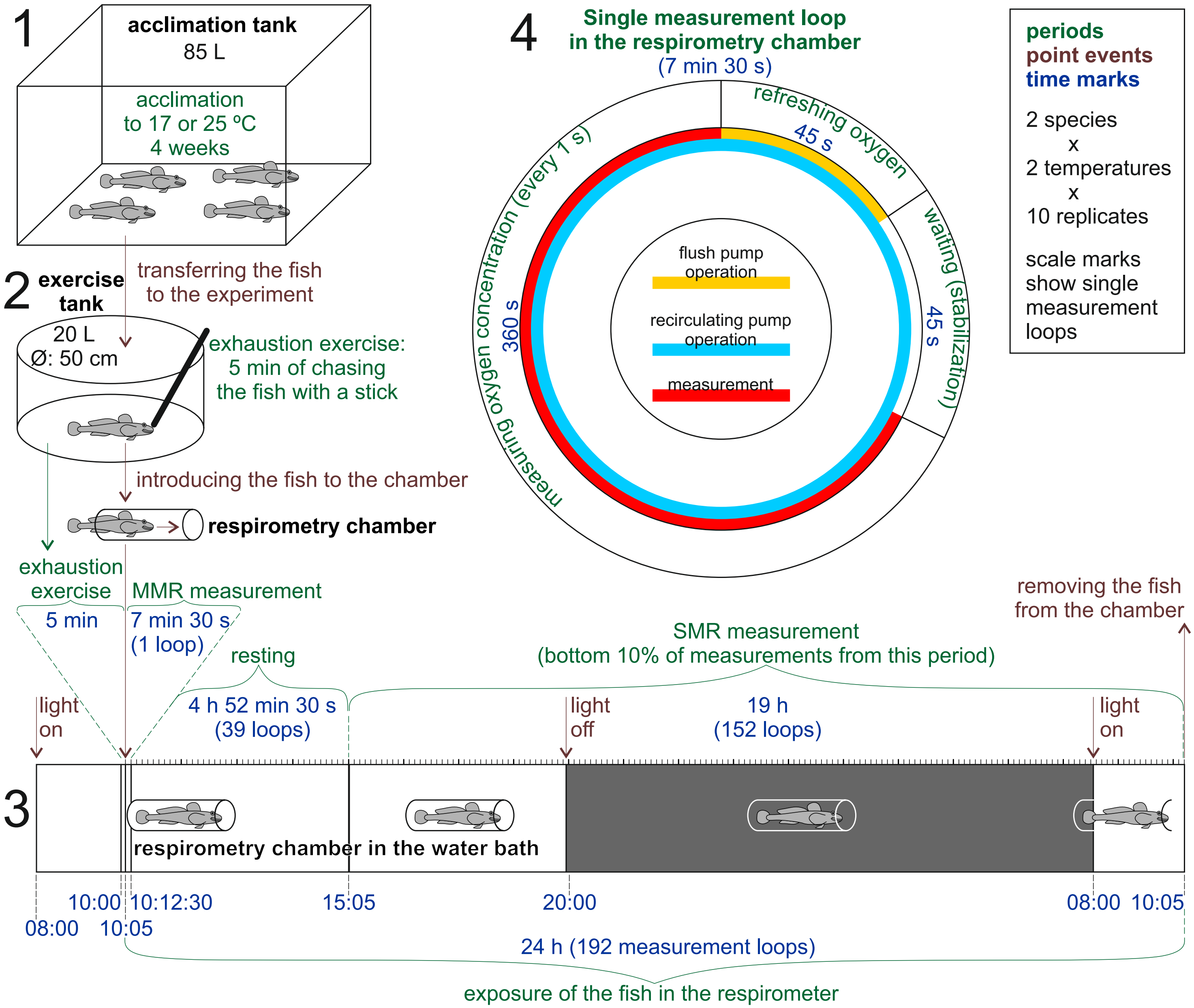
Piotr Kłosiński[a, *], Jarosław Kobak[b] and Tomasz Kakareko[a]

[a] Department of Ecology and Biogeography, Faculty of Biological and Veterinary Sciences, Nicolaus Copernicus University in Toruń, Lwowska 1, 87-100, Toruń, Poland

[b] Department of Invertebrate Zoology and Parasitology, Faculty of Biological and Veterinary Sciences, Nicolaus Copernicus University in Toruń, Lwowska 1, 87-100, Toruń, Poland

* Corresponding author: Piotr Kłosiński. E-mail address: klosinski.piotr@doktorant.umk.pl; ORCID iD: https://orcid.org/0000-0002-6359-9781

Figure S2. Experimental procedure


1
acclimation tank
85 L
acclimation
to 17 or 25 °C
4 weeks
transferring the fish
to the experiment
2
exercise
tank
20 L
Ø: 50 cm
exhaustion exercise:
5 min of chasing
the fish with a stick
introducing the fish to the chamber
respirometry chamber
4
Single measurement loop
in the respirometry chamber
(7 min 30 s)
refreshing oxygen
45 s
waiting (stabilization)
45 s
measuring oxygen concentration (every 1 s)
360 s
flush pump
operation
recirculating pump
operation
measurement
periods
point events
time marks
2 species
x
2 temperatures
x
10 replicates
scale marks
show single
measurement
loops
exhaustion
exercise
5 min
MMR measurement
7 min 30 s
(1 loop)
resting
4 h 52 min 30 s
(39 loops)
SMR measurement
(bottom 10% of measurements from this period)
19 h
(152 loops)
removing the fish
from the chamber
light
on
light
off
light
on
3
respirometry chamber in the water bath
08:00
10:00
10:05
10:12:30
15:05
20:00
08:00
10:05
24 h (192 measurement loops)
exposure of the fish in the respirometer

Publikacja 2

Kłosiński, P., Kobak, J., & Kakareko, T. (2025a). Effect of hypoxia and acidification on metabolic rate of Ponto-Caspian gobies and their native competitors in the context of climate change. Hydrobiologia.

https://doi.org/10.1007/s10750-025-05794-5

Tekst opublikowany w czasopiśmie: Hydrobiologia
Wydawnictwo: SPRINGER
Punktacja według wykazu Ministerstwa Nauki i Szkolnictwa Wyższego (2024): 100
Journal Impact Factor (2023): 2.2
Q1 w kategorii: marine & freshwater biology

Hydrobiologia
https://doi.org/10.1007/s10750-025-05794-5

PRIMARY RESEARCH PAPER

Effect of hypoxia and acidification on metabolic rate of Ponto-Caspian gobies and their native competitors in the context of climate change

Piotr Kłosiński · **Jarosław Kobak** ·
Tomasz Kakareko

Received: 30 May 2024 / Revised: 13 December 2024 / Accepted: 3 January 2025

Abstract Little is known about the non-thermal climate change factors (hypoxia and acidification) in the context of freshwater invasions. It is supposed that invasive Ponto-Caspian gobies have relatively wide environmental tolerance ranges due to their evolution in the highly variable environment of local limans and estuaries. Thus, we assumed that they better tolerate reduced oxygen and pH levels in invaded areas of Central and Western Europe compared to native species. Using a laboratory respirometry assay, we compared the effect of short-term progressive hypoxia and acidification on routine metabolic rate (RMR) of the invasive racer goby *Babka gymnotrachelus* and monkey goby *Neogobius fluviatilis* and their native counterparts sharing similar ecological niches (European bullhead *Cottus gobio* and gudgeon *Gobio gobio*, respectively). The natives displayed a lower hypoxia tolerance compared to the gobies (as changes in their RMR appeared at higher oxygen concentrations), whereas the monkey goby, but not the racer goby, appeared more tolerant to reduced pH than its native competitor. Thus, hypoxia tolerance seems to be a key feature shaping the invasive potential of the monkey and racer goby in benthic fish communities. However, the invasion success of the racer goby may be attenuated by progressing water acidification.

Keywords Biological invasions · Freshwater fishes · Routine metabolism · Dissolved oxygen · pH · Physiological tolerance

Handling editor: Michael Power.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10750-025-05794-5.

P. Kłosiński (✉) · T. Kakareko
Department of Ecology and Biogeography, Faculty of Biological and Veterinary Sciences, Nicolaus Copernicus University in Toruń, Lwowska 1, 87-100 Toruń, Poland
e-mail: klosinski.piotr@doktorant.umk.pl

J. Kobak
Department of Invertebrate Zoology and Parasitology, Faculty of Biological and Veterinary Sciences, Nicolaus Copernicus University in Toruń, Lwowska 1, 87-100 Toruń, Poland

Introduction

Climate change and biological invasions belong to the most important causes of the global biodiversity change in aquatic environments (Poff et al., 2002; Parmesan, 2006). Climate change is a multidimensional phenomenon involving not only temperature changes with episodes of extremely high temperatures and prolonged warm periods throughout the year (Frölicher et al., 2018), but also hypoxic events of increasing severity and frequency (Ficke et al., 2007; Pörtner & Peck, 2010) and drops in pH (Pörtner & Peck, 2010; IPCC, 2014; Schwieterman et al., 2019). Thus, a changing climate, altering abiotic conditions of aquatic environments, can indirectly influence biological invasions (Hellmann et al., 2008; Hulme, 2017), which may create a positive feedback between these two major threats to the aquatic biodiversity.

Freshwater systems, especially shallow waters, have relatively low inertia, as compared to deep locations with large water volumes. That is why freshwaters, particularly stagnant or slowly flowing environments with high trophic level, experience large and rapid fluctuations in oxygen and pH (Cooke et al., 2001; Weiss et al., 2018; Verberk et al., 2022). Decreases in dissolved oxygen (DO) in freshwater ecosystems are 3 to 9 times greater than those observed in deeper and more stable marine waters (Jane et al., 2021), leading more often to local and periodic hypoxic events. Additionally, such hypoxic events are suspected to be enhanced in the future by increasing water temperature in freshwaters, especially in summer (Ficke et al., 2007; Xu & Xu, 2015; Jane et al., 2021; Sampaio et al., 2021). This can be driven by increased microbial respiration (mineralization of organic matter) (Nixon, 1995; Müller et al., 2012), decreased oxygen solubility in water (Deutsch et al., 2011) and enhanced thermal stratification (Straile et al., 2003). Hypoxia can also result from anthropogenic nutrient enrichment (Rogers et al., 2016). In freshwaters, daily pH fluctuations can reach two or more units, in contrast to marine waters, experiencing pH changes of no more than a few tenth parts of units (Simonsen & Harremoës, 1978; Kim et al., 2018; Tagliarolo, 2019). In addition, the decrease in pH is intensified by human emissions of carbon dioxide into the atmosphere (Feely et al., 2009; Heuer & Grosell, 2014; IPCC, 2014). Weiss et al. (2018) suggested that freshwater ecosystems can undergo acidification at a faster rate than oceans.

In European freshwaters, the most common abiotic factors affecting fish distribution are water temperature, oxygenation and pH (Hamilton et al., 2017; Schwieterman et al., 2019; Bandara et al., 2024; Feng et al., 2024). Due to climate change, these parameters change, impairing native species in favour of non-native invaders which are more resistant to new conditions. Therefore, alien species with physiological tolerance to wide ranges of these environmental factors (Kolar & Lodge, 2002; Monaco & Helmuth, 2011; Lagos et al., 2017) are more likely to establish themselves in new habitats (Jewett et al., 2005; Keller et al., 2011; Lenz et al., 2011) and to compete successfully with native species (Liu & van Kleunen, 2017). According to Ferguson et al. (2013) and Lagos et al. (2017), hypoxic conditions can reconfigure competitive ability in marine communities in favour of invasive species resistant to low oxygenation. Taxa from specific regions are predisposed to invasion success (Paiva et al., 2018; Cuthbert et al., 2020; Stern & Lee, 2020). This is particularly true for the species originating from the Ponto-Caspian region, where the highly variable environment (especially recurrent water level fluctuations and salinity changes) of the limans and deltas of the big rivers entering the Black, Azov and Caspian Seas (Mordukhay-Boltovskoy, 1964; Dumont, 1998; Reid & Orlova, 2002; Rewicz et al., 2014) has resulted in the emergence of a unique set of physio-biological features of the local fauna, including several species of goby fish (Copp et al., 2005; Roche et al., 2013). These features make them perfectly pre-adapted to the above-mentioned global changes in environmental conditions (Mordukhay-Boltovskoy, 1964; Dumont, 1998; Reid & Orlova, 2002; Kocovsky et al., 2011).

There are significant gaps in understanding of physiological responses of aquatic ectotherms to non-thermal climate change factors (such as changes in pH or DO in water) (Sorte, 2014), especially in freshwater ecosystems (Tripp et al., 2022). This is particularly important in the context of the aforementioned progressive spread of invasive species, due to their expected greater tolerance to environmental factors and thus competitive advantage (Karatayev et al., 2009; Leuven et al., 2011). Among the Ponto-Caspian Gobiidae, the greatest attention in the context of features contributing to invasion success was devoted to the round goby *Neogobius melanostomus* (Pallas, 1814) (Behrens et al., 2017; Christensen et al., 2021; Puntila-Dodd et al., 2021; Grabowska et al., 2023). Less attention has been given to the other species from the Gobiidae family from the same region that have expanded to many European inland waters, including species being the object of the present study. Moreover, comparative and quantitative comparisons of metabolic tolerance in the context of different stressors associated with non-thermal climate change among invasive and native freshwater fishes are not common in the scientific literature (Fedorenkova et al., 2013). The key physiological parameter suitable for comparing the tolerance of organisms to environmental changes is routine metabolic rate

(RMR) (Hall & Clark, 2016; Palacios et al., 2016; Onthank et al., 2021). RMR refers to the average rate of metabolism when the animal undergoes its normal behaviours (Chabot et al. 2016; Metcalfe et al. 2016).

Our study aimed to determine the impact of short-time progressive hypoxia and acidification on physiological tolerance (measured as changes in RMR) of invasive alien Ponto-Caspian fish and their local counterparts sharing similar ecological niches. Hypoxia/acidification is any level of DO/pH low enough to negatively impact the physiology and/or behaviour of an organism (Pollock et al., 2007). As these thresholds are species-specific, we wanted to find values of DO/pH resulting in hypoxia/acidification for a given species. From a metabolic point of view, hypoxia/acidification occurs when environmental DO/pH values are low enough to disrupt the rate of oxygen uptake by a fish, leaving it unable to sustain its proper oxygen demand (Claireaux & Chabot, 2016; Rogers et al., 2016; Rosewarne et al., 2016; Nati et al., 2018; Crear et al., 2020; Verberk et al., 2022). The invasive species selected for the study are Ponto-Caspian gobies: the racer goby *Babka gymnotrachelus* (Kessler, 1857) and monkey goby *Neogobius fluviatilis* (Pallas, 1814). The racer goby is found at the same sites as the native European bullhead *Cottus gobio* Linnaeus, 1758 (Kakareko et al., 2016; Janáč et al., 2018). In turn, the monkey goby *Neogobius fluviatilis* enters habitats occupied by the gudgeon *Gobio gobio* (Linnaeus, 1758) (Jakovlić et al. 2015; Piria et al. 2016; Płąchocki et al. 2020). We compared results within these co-occurring pairs, as they were composed of species interacting with each other in the same environments. We hypothesized that invasive gobies are more physiologically tolerant to hypoxia and acidification (i.e. are capable of sustaining constant RMR at lower DO and pH values) than their native counterparts.

Materials and methods

Animals

We obtained the fish from two tributaries of the river Vistula in Poland. The racer goby and European bullhead were collected in July–September 2021 from the river Brda (53°08′52.5″N 17°58′10.5″E) by scuba divers using aquarium nets. The gudgeon and monkey goby were collected in September–October 2021 from the river Pilica (51°45′50.1″N 21°08′55.5″E) by electrofishing (EFGI 650, BSE Bretschneider Spezialelektronik, Germany). The individuals of the species compared in our study within a given co-occurring pair (native vs. invasive) were collected at the same time, from the same location and using the same method. All specimens tested were juveniles (no signs of sexual maturity), so we did not determine their sex.

Immediately after capture, we transported the fish to the laboratory (transport time about 1–3 h) in polythene bags with oxygenated water. We kept them in 350-L stock tanks in the laboratory, at a density of about 20–30 individuals of each species per tank, for at least 1 month before the experiments started. The tanks were filled with conditioned tap water and equipped with aquarium filters, aerators and ceramic and stone shelters, but no bottom substrate. The temperature was maintained by air conditioning at 17 °C. The photoperiod was set at 12:12 h light:dark cycle with lights on at 07:00. We fed the fish daily ad libitum with frozen chironomid larvae. Once a week, we exchanged about 30% of water volume in the stock tanks. At the end of the acclimation period, all fish tested did not exhibit unnatural behaviour, such as lack of exploration, clinging to the wall of the tank, hiding behind the aquarium filter or erratic swimming.

Prior to the experiment, the fish were weighed in a container with water to the nearest 0.1 g with a Radwag WPT 3/6 laboratory scale (Radom, Poland). Total fish length was measured with ImageJ 1.53k program (freeware by W.S. Rasband, US National Institutes of Health, Bethesda, Maryland, USA: https://imagej.net/ij/), using digital images taken from the top view before testing. We randomly collected the fish for the experiment, first from the natural environment and then from the stock tanks. The total length of the fish was (mean ± SD) 4.99 ± 0.41 cm for the European bullhead, 5.01 ± 0.35 cm for the racer goby, 4.51 ± 0.39 cm for the gudgeon and 4.43 ± 0.33 for the monkey goby. It did not differ between the species (t-test for independent samples: $t_{46} = -0.118$, $P = 0.907$ and $t_{46} = 0.798$, $P = 0.429$ for the European bullhead–racer goby and the gudgeon–monkey goby pairs, respectively).

Experimental setup

We used a glass intermittent-flow resting respirometry system with 4 chambers (LoligoSystems, Viborg, Denmark) to measure individual oxygen consumption rate and, on this basis, to estimate the metabolic rate of fish, according to Svendsen et al. (2016) (Fig. S1). The basic component of the system was a 12.6-L acrylic water bath (length: 400 mm; width: 225 mm; height: 140 mm; level water: 100 mm) with oxygenated water (Fig. S1). Four custom-made cylindrical respirometry chambers made of borosilicate glass were submerged in the bath. The chambers were matched to the size of individual fish (inner diameter: 14 or 20 mm; length 90 or 100 mm; volume: 15 or 34 ml, respectively). Each chamber had four ports to control the flow: two inlet ports on one side and two outlet ports on the other side (Fig. S1). The ports allowed intermittent-flow respirometry, i.e. a series of short-time respirometric measurements in a closed-circuit, interrupted by flushing intervals to replace the water in the chamber. A single measurement cycle (loop) lasted for 450 s and consisted of three phases: flushing with fresh oxygenated water (45 s), waiting for conditions to stabilize (45 s) and measuring the oxygen loss in the closed chamber (360 s) (Fig. S2). Each replicate included 67 or 68 measurement loops in hypoxia and acidification tests, respectively. We determined the duration of the experiment and its specific phases based on our initial trials and literature data (e.g. Svendsen et al., 2016). The single chamber was opened at one end by removing a fitted glass plug, a fish was placed in the chamber and the chamber was closed, ensuring the system to be gas- and watertight. Each chamber was connected to two pumps: a recirculating pump (mixing the water inside the chamber) and a flush pump (exchanging the water between the bath and chamber) by non-silicone Tygon E-3603 tubes (inner diameter: 3.2 mm) with low gas permeability (Fig. S1). The recirculating pump operated continuously during the experiment, while the flush pump was turned on during the flush phase (Fig. S2). The water flow generated by each pump was 800 ml min^{-1}. To control the temperature in the water bath, a water circulation system was established between the water bath and an external 100-L tank filled with water at a preset temperature maintained by an aquarium cooler with a built-in heater (TECO 500K, Ravenna, Italy). The water from the water bath was pumped at rate 10 L min^{-1} to the external tank by another circulation pump submersed in the tank. In the tank, water passed through a heat exchanger (steel coil) and then was returned back to the water bath via PVC tubing (inner diameter: 13 mm) (Fig. S1). All experiments were conducted at a standardized temperature of 17 °C (Michaelidis et al., 2007; Schwieterman et al., 2019; Collins et al., 2022; Tripp et al., 2022), corresponding to the current mean temperature recorded in the warm half-year in rivers in central Poland (Marszelewski and Pius 2014, 2016). In hypoxia tests, pH was maintained at the level of 8.5. In acidification tests, the DO level was constant at the level of 95%. The photoperiod in the laboratory was 12 h light:12 h dark cycle with lights on at 08:00.

The DO level (in hypoxia tests) was reduced by bubbling nitrogen gas (Rosewarne et al., 2016; Snyder et al., 2016; Crear et al., 2020) from a compressed gas cylinder equipped with an automatic dispensing valve (Fig S1). In turn, the pH value (in acidification tests) was decreased by injecting carbon dioxide (Michaelidis et al., 2007; Schwieterman et al., 2019) from a compressed gas cylinder equipped with an automatic dispensing valve (Fig. S1). Using carbon dioxide in the study allowed us to reduce pH while maintaining the constant DO in the experiment (Michaelidis et al. 2007).

Nitrogen bubbling was controlled by a galvanic oxygen probe (OxyGuard Mini Probe, Farum, Denmark) connected to an oxygen analyser (programmable LED indicator PR5700, PR Electronics, Denmark). Carbon dioxide application was controlled by a pH electrode (TUNZE, Penzberg, Germany) connected to a pH controller (SmartController 7000, TUNZE, Penzberg, Germany, accuracy: 0.05 pH unit) (Fig. S1). The controllers opened a solenoid valve allowing the injection of nitrogen or carbon dioxide from the cylinder into the respirometer when the parameter values rose above a set point (Fig. S1).

External fibre optic cable sensors (optodes) connected to a Witrox 4 oxygen meter and sensor spots mounted inside the chambers were used to measure oxygen consumption by the fish in the chambers every 1 s throughout the experiment. To control the temperature, a temperature probe with accuracy of 0.15 °C (sensor type: Pt1000) was submerged in the water bath and connected to the Witrox 4 oxygen meter. Oxygen level and temperature values were recorded by AutoResp™ software Version 2.3.0 (Loligo Systems, Viborg, Denmark).

Experimental procedure

Metabolic traits of fish were measured ca. 40 h after their last feeding to make sure that they were in post-absorptive state (Chabot et al. 2016; Killen et al. 2021). This allowed us to avoid the interfering effects of ingestion, digestion or assimilation of food, which can result in underestimation or overestimation of metabolic rate (Ross et al., 1992; Thuy et al., 2010).

Experimental procedure started at 09:00 am. The photoperiod in laboratory was set at 12:12 h light:dark cycle with lights on at 08:00. Immediately prior to the start of the experimental procedure, individuals were randomly taken from the stock tanks, placed in the chambers and left for 4 h to familiarize themselves with the experimental conditions (Fig. S3, Fig. S4). In each treatment, we tested simultaneously four individuals of the same species placed in the separate chambers submerged in the bath. We ran three independent rounds of such measurements with separate individuals for each species and treatment. Exposure to hypoxia lasted in total 4 h 22 min 30 s (35 measurement loops) and started from 95% oxygen saturation, which was then gradually reduced at a rate of 0.67% per min (Fig. S3). In turn, exposure to acidification lasted 4 h 30 min (36 measurement loops) and started from pH of 8.5, which was then gradually lowered at a rate of 0.5 pH unit per 30 min (Fig. S4). Metabolic rate measurements were taken at DO levels of 95%, 60%, 40%, 30%, and 25% for hypoxia and at pH values of 8.5, 8.0, 7.5, 7.0, and 6.5 for acidification. Every time, after obtaining the desired value of DO/pH, we measured the RMR of the fish for 30 min (4 measurement loops) (Fig. S3, Fig. S4). We established the experimental conditions and event timing based on preliminary research and literature data for hypoxia (Simonsen & Harremoës, 1978; Killen et al., 2012; Xu & Xu, 2015; Nati et al., 2018) and acidification (Michaelidis et al. 2007; Onthank et al., 2021). The water bath with the respirometric chambers was covered by Styrofoam screens on all sides to isolate the fish from external stimuli. Twelve individuals of each species were exposed to the tested range of decreasing oxygen concentrations, and another 12 individuals of each species were tested across the range of decreasing pH values.

To account for microbial respiration, background oxygen consumption was measured before and after each trial in the empty respirometry chamber (without fish). Throughout all measurements, no detectable microbial respiration was found. At the end of the test, fish were removed from the chambers and transferred to separate post-experimental tanks with the same water temperature as in the test.

Data analysis

Individual oxygen consumption rates were expressed in mg O_2 h^{-1} per individual (Chabot et al., 2016). All oxygen consumption rates were corrected for the volume of the respirometry chamber by subtracting the animal volume (calculated from the measured mass, assuming a density of 1 g ml^{-1}) from the chamber volume according to Svendsen et al. (2016). After obtaining the desired value of DO or pH, we measured the RMR of the fish tested (Fig. S3, Fig. S4). RMR was always compared to the reference RMR measured at 95% DO or pH of 8.5. If the measured RMR was different from the reference RMR, this indicated that the animal could no longer maintain a constant rate of oxygen uptake (Mandic et al., 2009; Rogers et al., 2016). Thus, any deviation in oxygen uptake in both directions (increase or decrease) can be considered a symptom of stress or suboptimal conditions experienced by the animal.

To analyse factors affecting the RMR of fish (each pair separately), we applied a General Linear Mixed Model (GLMM) with species (categorical between-subject factor), treatment (oxygenation or acidification level) (a categorical repeated measures factor with 5 levels), animal mass (we included animal mass as a covariate in the model to control for the effect of mass on metabolic rate) and their interactions as fixed effects, as well as fish identity and experimental round (nested in species) as random factors. We log-transformed oxygen consumption and mass values to linearize a potentially allometric relationship between mass and metabolism. Initially, we included all main effects and interactions and then applied backward simplification of the models by removing non-significant higher-order interactions. Significant effects we further explored using sequential Bonferroni-corrected LSD post hoc tests to compare RMR at particular levels of hypoxia and acidification with that observed at normoxic conditions and control pH, respectively. We confirmed the normality and homoscedasticity of the data using Shapiro–Wilk and Levene tests, respectively. The level of significance was $\alpha = 0.05$ (p-value). We used IBM SPSS Statistics 29.0 (IBM Inc., USA) to conduct statistical analyses.

Results

Hypoxia tolerance

Under progressive hypoxia, the routine metabolic rate (RMR) of fish in both tested pairs of species depended on fish species * oxygenation interactions (Table 1A–B). For the European bullhead, the oxygen consumption rate dropped below the normoxic routine metabolic rate at a DO level of 30% (c.a. 3 mg O_2 l^{-1}) (Fig. 1, Table S1A). In turn, the RMR of the racer goby did not change across all tested DO levels (Fig. 1, Table S1A). The RMR of the gudgeon decreased significantly at a DO level of 60% (Fig. 2, Table S1B), whereas the RMR of the monkey goby became lower than the normoxic RMR at a DO level of 25% (c.a. 2.5 mg O_2 l^{-1}) (Fig. 2, Table S1B).

Acidification tolerance

Under progressive acidification, the RMR of both tested pairs of fish species depended on fish species * acidification interactions (Table 2A–B). Decreasing pH resulted in the increased RMR of the European bullhead at a pH of 6.5 (Fig. 3, Table S2A). The RMR of the racer goby was raised within the pH range of 7–8 and then, at a pH of 6.5, was reduced back to the level observed in reference conditions (pH of 8.5) (Fig. 3, Table S2A). The RMR of the gudgeon followed the pattern exhibited by the racer goby (an increase within the pH range of 7–8 followed by a reduction at a pH of 6.5) (Fig. 4, Table S2B). The RMR of the monkey goby did not change across all tested pH levels (Fig. 4, Table S2B).

Discussion

Hypoxia tolerance

In accordance with our hypothesis, both the racer goby and monkey goby turned out more tolerant to hypoxia than their native competitors, as indicated by their ability to maintain constant RMR at lower oxygen concentrations.

Actually, the RMR of the racer goby was not affected at all by hypoxic conditions in our study, even at DO of 25%. This suggests that the racer goby can tolerate even lower values of DO. According to Kakareko (2011), severe oxygenation deficits significantly influenced the spatial distribution of the racer goby in their natural conditions. Moreover, the racer goby shows an affinity for muddy substratum (Kakareko, 2011), commonly associated with low oxygenation of the near-bottom water layer. This is consistent with the high tolerance of this species to hypoxia, observed in our study, and can be one of the factors facilitating its colonization in dam reservoirs (Brylińska, 2000; Kakareko, 2011). Moreover, the racer goby is associated with dense vegetation (Didenko, 2013). This type of habitat often experiences low DO at night due to daily oxygen fluctuations. On the other hand, the monkey goby is generally associated with shallow sandy areas (Kottelat & Freyhof, 2007; Płąchocki et al., 2020) with relatively

Table 1 General Linear Mixed Model to test the effect of hypoxia on routine metabolic rate (RMR) of two pairs of fish species: A. European bullhead and racer goby; B. gudgeon and monkey goby. Asterisks indicate significant effects ($P < 0.05$)

	Tested species	Effect	*df1*	*df2*	*F*	*P*
A	European bullhead and racer goby	Fish species (S)	1	5	0.963	0.370
		Oxygenation (DO)	4	30	6.348	< 0.001*
		Mass[#]	1	17	8.460	0.010*
		(S) x (DO)	4	30	10.168	< 0.001*
B	Gudgeon and monkey goby	Fish species (S)	1	4	61.677	0.001*
		Oxygenation (DO)	4	19	3.415	0.029*
		Mass[#]	1	19	11.865	0.003*
		(S) x (DO)	4	19	2.999	0.045*

[#] Covariate

Fig. 1 Individual routine metabolic rate (RMR) of the racer goby and European bullhead in response to progressive hypoxia. The presented values (back-transformed after the analysis of log-transformed data) are means ± 95% C.I. (calculated for an individual of the mean mass of 2.29 g) predicted by the General Linear Mixed Model (Table 1) for a significant fish species x oxygenation interaction. Smaller and lighter symbols represent individual data points. Asterisks indicate significant differences compared to DO level of 95%: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$

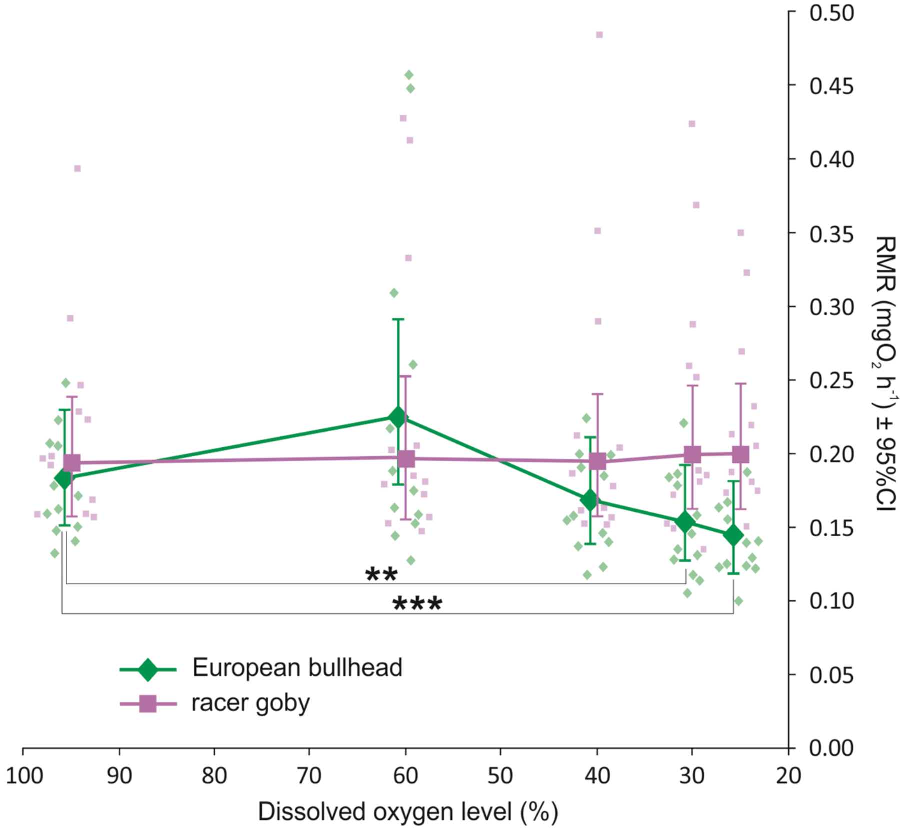


Fig. 2 Individual routine metabolic rate (RMR) of the gudgeon and monkey goby in response to progressive hypoxia. The presented values (back-transformed after the analysis of log-transformed data) are means ± 95% C.I. (calculated for an individual of the mean mass of 1.09 g) predicted by the General Linear Mixed Model (Table 1) for a significant fish species x oxygenation interaction. Smaller and lighter symbols represent individual data points. Asterisks indicate significant differences compared to DO level of 95%: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$

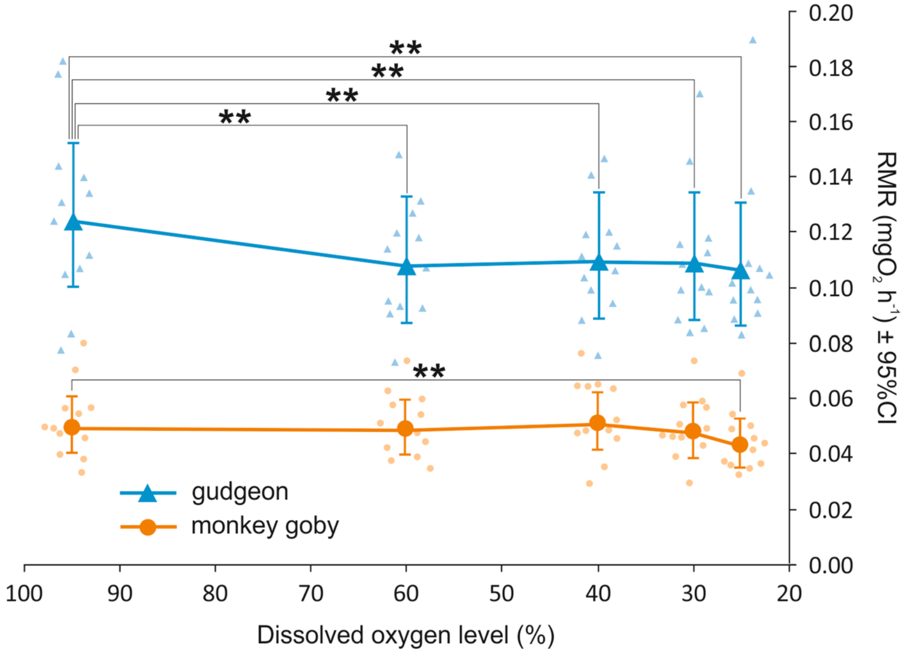


Table 2 General Linear Mixed Model to test the effect of acidification on routine metabolic rate (RMR) of two pairs of fish species: A. European bullhead and racer goby; B. gudgeon and monkey goby. Asterisks indicate significant effects ($P < 0.05$)

	Tested species	Effect	*df1*	*df2*	*F*	*P*
A	European bullhead and racer goby	Fish species (S)	1	5	15.602	0.010*
		Acidification (pH)	4	28	13.748	< 0.001*
		Mass#	1	20	0.225	0.640
		(S) x (pH)	4	28	21.251	< 0.001*
B	Gudgeon and monkey goby	Fish species (S)	1	4	10.919	0.031*
		Acidification (pH)	4	28	2.875	0.041*
		Mass#	1	20	10.538	0.004*
		(S) x (pH)	4	28	3.067	0.033*

Covariate

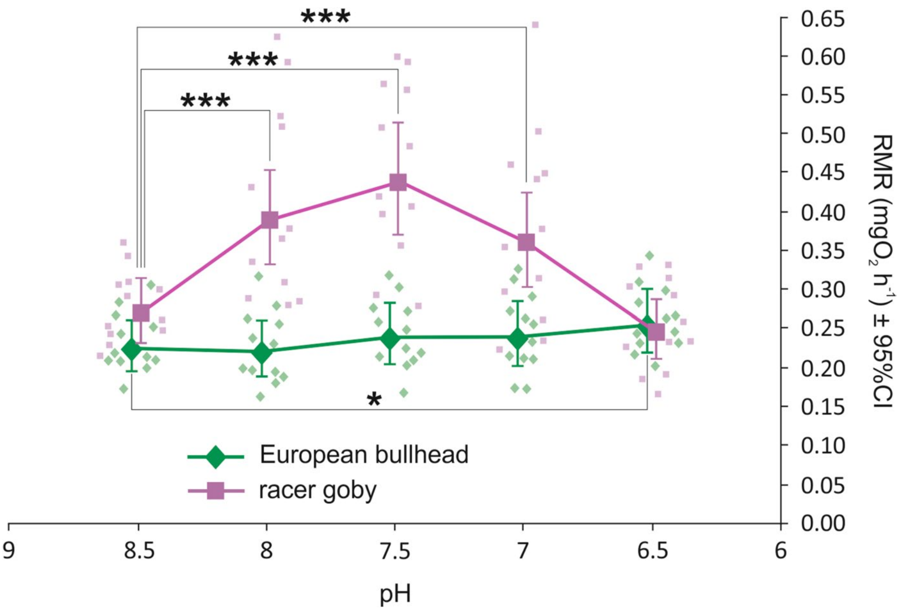
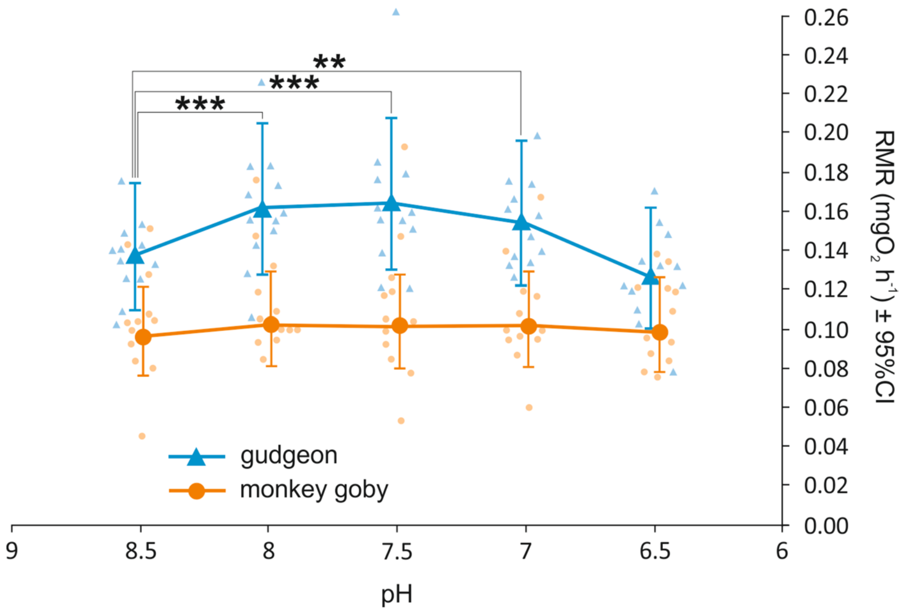


Fig. 3 Individual routine metabolic rate (RMR) of the racer goby and European bullhead in response to progressive acidification. The presented values (back-transformed after the analysis of log-transformed data) are means ± 95% C.I. (calculated for an individual of the mean mass of 2.60 g) predicted by the General Linear Mixed Model (Table 2) for a significant fish species x acidification interaction. Smaller and lighter symbols represent individual data points. Asterisks indicate significant differences compared to pH of 8.5: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$

good oxygen conditions. However, in our study, the monkey goby also displayed relatively high tolerance to hypoxia compared to its native counterpart. Thus, our study showed that the monkey goby is more tolerant to hypoxia than it has been commonly assumed (Smirnov, 1986; Pinchuk et al., 2003). Halačka (2015) proved that the monkey goby has more erythrocytes than other invasive gobies, such as the round goby *Neogobius melanostomus* and the bighead goby *Ponticola kessleri* (Günther, 1861), which can be responsible for its hypoxia tolerance (Moyle & Cech, 2004). Moreover, this fact can account for the ability of the monkey goby to bury itself in the sand to avoid predators (Erös et al., 2005; Čápová et al., 2008; Jakubčinová et al., 2017), even for as long as three hours (Smirnov, 1986; Holčík et al., 2003). Moreover, high hypoxia tolerance of the monkey goby can explain its high densities observed occasionally on muddy substrate (Sindilariu et al., 2006). Both the racer goby and monkey goby are capable of maintaining constant RMR up to very low oxygen levels, which can favour their colonization of habitats experiencing hypoxic events with oxygen drops below 4–5 mg O_2 l^{-1}, considered harmful to most freshwater fishes in Central Europe (Ficke et al., 2007; Boyd, 2015; Marium et al., 2023).

The native species (European bullhead and gudgeon) were more susceptible to hypoxia compared to their invasive counterparts. The European bullhead inhabits clean shallow rivers and streams with high oxygen content (Smyly 1957; Lelek 1987; Tomlinson and Perrow 2003). Its distribution is often limited by low oxygen levels (Hänfling et al., 2002). On the other hand, despite its

Fig. 4 Individual routine metabolic rate (RMR) of the gudgeon and monkey goby in response to progressive acidification. The presented values (back-transformed after the analysis of log-transformed data) are means ± 95% C.I. (calculated for an individual of the mean mass of 1.10 g) predicted by the Generalized Linear Mixed Model (Table 2) for a significant fish species x acidification interaction. Smaller and lighter symbols represent individual data points. Asterisks indicate significant differences compared to pH of 8.5: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$



high oxygen requirements, in our study, the European bullhead was able to maintain stable RMR at relatively low DO values, i.e. above 30%. It may be associated with their capability of fast increasing in their erythrocyte number (even twofold in just a few dozen hours) in response to low DO (Moyle & Cech, 2004; Halačka et al., 2012; Halačka, 2015). Our study showed that the gudgeon is not able to sustain constant RMR at DO values below 60%. This fact is consistent with the study by Wunder (1936), who classified the gudgeon as a species requiring well-oxygenated water for normal respiration. Thus, the gudgeon appears to be an exception among the other species in the family Cyprinidae, which generally exhibit high tolerance to hypoxia and anoxia (see Killen et al., 2016).

To survive periods of low DO levels, the native fish in our experiments had to limit their use of environmental oxygen and switch to anaerobic energy production (Boutilier, 2001; Richards, 2009), which is 30 times less efficient than aerobic metabolism, resulting in reduced ability to bear high energetic costs (Rogers et al., 2016). This way, they can compensate for low oxygen content in the environment through lower oxygen consumption (Carlson & Parsons, 2003; Crear et al., 2020). Otherwise, quick exhaustion of O_2 would induce cellular death (Mandic et al., 2013).

Acidification tolerance

Our hypothesis, predicting that the invasive gobies are more physiologically tolerant to acidification than their native counterparts, was confirmed for the gudgeon–monkey goby pair, but not for the European bullhead–racer goby pair. We demonstrated that the invasive monkey goby and native European bullhead were more tolerant to acidification compared to their competitors (gudgeon and racer goby, respectively) as indicated by their ability to maintain constant RMR across wider pH ranges. Furthermore, only in the case of the monkey goby, RMR was stable across all pH levels tested, suggesting that this species can tolerate even lower pH values. In turn, the RMRs of the racer goby and gudgeon increased within the pH range of 7–8, which was followed by a reduction at a pH of 6.5. The RMR of the European bullhead only increased slightly at a pH of 6.5.

Tolerance to pH changes by the fish species can be linked to their habitats and distribution patterns in river systems. The pH value in flowing waters is fundamentally influenced by catchment, climate and human factors, such as annual precipitation, bedrock geology, land cover (Rothwell et al., 2010; Lauerwald et al., 2013), land use (Degerman & Appelberg, 1992; Saarinen et al., 2013) and episodic weather events, such as melting snow in spring (Laudon et al.,

2000) or summer droughts (Laudon & Bishop, 2002). An important feature in this context is a watercourse gradient with concomitant effects on water chemistry, more specifically carbonate buffering conditions shaping the ability to resist pH changes. In general, small headwater catchments have lower buffering capacity than large rivers (Stets et al., 2014). Thus, a lower pH and its greater fluctuations tend to be observed in mountain and upland streams compared to lowland rivers (Rothwell et al., 2010). This explains the relatively high pH tolerance found in the European bullhead, which evolved in headwater systems and inhabits many types of running waters, including both high-altitude and lowland streams (Tomlinson and Perrow, 2003; Vezza et al., 2014). There are reports of the species occurrence in upland streams with pH of c.a. 7, as well as in lowland chalk streams with pH of c.a. 9 (Philippart, 1979; Nocita et al., 2009). The ability of the European bullhead to keep the constant RMR within a wide pH range suggests its highly efficient acid–base regulation mechanisms. Philippart (1979) reported its high tolerance to acidification, with the lower pH tolerance limit being as low as 4.7. Indeed, ecotoxicological studies conducted by McCahon and Pascoe (1989) have shown that the European bullhead is able to tolerate a 24-h exposure to pH of 4.87. Moving on to discuss the monkey goby, our demonstration of high pH tolerance of this species is a new finding indicating a capacity of the goby to colonize waters prone to acidification, even high-altitude streams. It should be pointed out that the monkey goby does not seem as adapted to fast-flowing waters as the European bullhead: its preferred habitats are open areas of sand substrate, often devoid of vegetation (Erős et al., 2005; Kottelat and Freyhof 2007; Jakovlić et al., 2015; Szalóky et al., 2015; Płąchocki et al., 2020), i.e. waters with slow to moderate flow rate. However, climate change and the associated droughts and water flow reductions may encourage them to expand upstream into areas that are currently not occupied, which has already been observed in submountain locations (Carpathian) rivers (Bylak & Kukuła, 2024).

The racer goby, contrary to monkey goby, is mainly found in stagnant or slowly flowing waters of pools and old river beds (Płąchocki et al., 2020) with muddy substrate and well-vegetated habitats of high complexity (Kottelat and Freyhof 2007; Didenko 2013). These habitats are usually associated with lowland, eutrophic, alkaline environments with high bicarbonate buffering capacity (Verspagen et al., 2014; Boyd, 2015; Boyd et al., 2016). Diurnal and local fluctuations in pH and oxygen concentration do occur in such waters due to intensive biological processes that use (photosynthesis) or release (respiration, mineralization) carbon dioxide into water, especially in densely vegetated areas (Simonsen and Harremoës 1978; Kim et al., 2018). However, apparently this has not been a critical factor for the goby species to develop broader tolerance to pH changes. The fact that we have shown resistance to oxygen depletion in the racer goby does not contradict the low pH tolerance of this species. Physiological adaptation to acidification is species-specific (Munday et al., 2012) and tolerances to low DO and to low pH do not always correlate with each other, as shown for copepod species (Deconinck & Willett, 2022), suggesting that the mechanisms of tolerance to each stressor are different. The gudgeon is found in the same sandy bottom habitats as the monkey goby (Jakovlić et al., 2015; Vilizzi et al., 2019; Płąchocki et al., 2020). However, in contrast to the monkey goby, it is also associated with stagnant (including lakes), shallow waters with vegetated bottom (Kottelat and Freyhof, 2007) with higher carbonate buffering, which can partly explain why the gudgeon did not evolve tolerance to low pH. According to McDonald et al. (1991) cyprinid fish exhibit a low tolerance to pH drops and thus they have been recommended as useful indicators of acidification. This is consistent not only with our present work but also with the study by Rahel and Magnuson (1983), in which cyprinids were the fish group that turned out to be the most sensitive to decreasing pH and were absent in northern Wisconsin lakes already below pH of 6.2.

Long-term acidification can constitute a limiting factor for fish by decreasing plasma pH under decreasing pH and simultaneously causing loss of the haemoglobin–oxygen affinity (Berenbrink, 2011; Verde et al., 2011). Thus, to prevent the detrimental effect of acidification, organisms try to counteract pH changes to maintain homeostasis. Therefore, the increase in RMR of the racer goby and gudgeon is the result of energy-dependent acid–base regulation pathways (Claiborne et al., 2002; Heuer & Grosell, 2014). As a result, fish can partition less energetic resources into other physiological functions such as foraging, growth and reproduction. On the other hand, pH decreases often trigger acute behavioural responses (Nagelkerken & Munday, 2016). Thus, the observed increase in RMR could be caused by increased activity (Schwieterman et al., 2019; Onthank et al., 2021), due to an attempt to escape from the area of low pH (Onthank et al., 2021).

Vulnerability to climate change: summary remarks

Climate change provokes changes in fish metabolism and therefore their energy budget, which may translate into their ability to cope with future changes in environmental conditions. Both the racer goby and monkey goby turned out to be more tolerant to hypoxia than their native competitors. The capacity of the invasive Ponto-Caspian gobies to sustain constant RMR at lower DO values than their native counterparts can be a key ecological trait in terms of their invasive potential and, specifically, the ability to colonize eutrophic waters. In the native species, hypoxia will likely induce a decrease in metabolism to counteract negative effects of low DO levels and thus save energy. Lower routine metabolic rate of the native species at low DO levels can effectively limit oxygen demand, but simultaneously impair life activities. Low oxygenation results in exhaustion, and since there is less energy for the most basic life functions, such as maintaining metabolism, there is also no energy for fitness-related activities (e.g. growth, reproduction). The invasive gobies keep constant energy expenditures on regulation of their metabolism rate under hypoxia, and this way the gobies, in contrast to their native counterparts, can allocate more energy to growth and reproduction. In addition, hypoxia tolerance can allow the invasive gobies to use space and food resources unavailable to their native counterparts (Farwell et al., 2007). Moreover, gobies can avoid predation by using hypoxic habitats as refuges (Rosenberger & Chapman, 1999; Domenici et al., 2007).

In the context of global warming, hypoxia resistance may be important for withstanding high temperatures because these two factors are related in aquatic environments. DO concentration in water is inversely related to temperature. Because aerobic metabolic rates of ectotherms increase with temperature, an increase in temperature will decrease the DO supply and simultaneously increase the oxygen demand (Ficke et al., 2007). Therefore, the decreased supply of oxygen cannot meet the increased demand by fish under elevated water temperatures associated with climate change. Our results suggest that adaptation to hypoxia can be a key feature shaping the invasive potential of monkey and racer goby in benthic fish communities, especially in the light of the increased probability of higher temperatures resulting from climate warming. As, despite its relatively low tolerance to low pH, the racer goby has successfully expanded to many European inland waters (Grabowska et al., 2023); indeed, the tolerance to acidification seems to be less important for the invasion success, at least nowadays. Nevertheless, it cannot be excluded that the future invasion success of the racer goby may be attenuated by water acidification, especially as this aspect of global change is going to progress.

The monkey goby were more tolerant to acidification compared to the gudgeon enabling the goby to allocate saved energy to maximize fitness. Thus, the high pH tolerance of the monkey goby suggests that with climate change and droughts reducing water flows, this species may increase its invasion success and move even into upstream, weakly buffered waters, which are currently unavailable to the goby because the flow is too fast (see Bylak and Kukuła 2024).

Our findings contribute to the growing body of knowledge on competitive potential of the invasive gobies against their native counterpart species. Additional research on this topic has been focused on the anti-predatory capacity of the fish. Both weaker effectiveness of behavioural defences (Augustyniak et al., 2023) and lower responsiveness to predation cues (Kłosiński et al., 2022) of the racer and monkey goby compared to their native counterparts were shown by experimental studies. These findings suggest that the invasive gobies have no competitive advantage over their native analogues in avoiding predation. Thus, anti-predator defence is not the mechanism lying at the base of their invasion success. Here, we showed for the first time that the two invasive gobies tested in our study may have an advantage over their native counterparts through physiological adaptations to challenging environmental abiotic conditions, mostly associated with hypoxia.

It should be noted that physiological performance (Marras et al., 2015), most often expressed as aerobic scope (Clark et al., 2013), has been suggested as one of the physiological limitations to spreading and establishing species in newly invaded areas. Thus, determining this parameter in the context of hypoxia and acidification would be helpful in the full assessment of the invasive potential of the racer and monkey goby, including their capability to expand their ranges, thrive in new areas and thus compete with native fish. Nevertheless, our results do show that invasive gobies, compared to their native competitors, seem to be better physiologically adapted to changing environmental conditions associated with global warming. From the point of view of metabolism, especially the monkey goby, displaying a weaker reduction in physiological performance in response to the elevated temperature (25 vs. 17 °C) (Kłosiński et al., 2024), as well as a greater tolerance to hypoxia and acidification than the co-occurring native gudgeon, seems likely to increase its competitive advantage over its local counterpart with ongoing climate change.

Authors' contributions Piotr Kłosiński was involved in conceptualization, resources, methodology, investigation, formal analysis, data interpretation, visualization and writing—original draft preparation. Jarosław Kobak was responsible for conceptualization, resources, formal analysis, data interpretation and writing—reviewing and editing. Tomasz Kakareko took part in conceptualization, resources, methodology, data interpretation, writing—reviewing and editing, supervision and funding acquisition.

Funding This research was supported by the National Science Centre, Poland (NSC Grant No. 2016/23/B/NZ8/00741).

Data availability The data that support the findings of this study are available from the corresponding author, PK, upon reasonable request.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare no competing interests.

Ethical approval We collected and used the fish in accordance with the permit of the Local Committee for Ethics in Animal Research in Bydgoszcz, Poland, statement no. 27/2021 from 29 June 2021. In addition, the capture and use of the European bullhead, which is protected by law in Poland, were accepted by the Regional Directorate for Environmental Protection in Bydgoszcz, Poland (approval numbers: WOP.6401.4.5.2017.MO, WOP.6401.4.19.2018.MO). The procedures carried out within the study met the European Union guidelines on the protection of animals used for scientific purposes (Directive 2010/63/UE). The housing conditions guaranteed a high level of animal welfare, which was manifested by the overall condition of the fish during the study period. The fish were active, foraged, occupied shelters and did not show any external signs of stress or disease. Each individual was used only once in the experiment. Upon completion of the study, the European bullhead and gudgeon were released into the wild at the site from which they had been taken, while the racer goby and monkey goby, as invasive species, had to be euthanized by an overdose of tricaine methanesulphonate (MS-222) and disposed according to the Regulation of the Polish Minister of the Environment from 9 September 2011 (Journal of Laws No. 210, item 1260). Killing was carried out by a qualified, certified person (certificate No. 2355/2015 issued by the Polish Laboratory Animal Science Association).

Consent to participate Not applicable.

Consent for publication Not applicable.

References

Augustyniak, M., K. Kołacka, J. Kobak, P. Hliwa, P. Kłosiński, M. Poznańska-Kakareko, Ł. Jermacz & T. Kakareko, 2023. Differences in predator-avoidance behavior between two invasive gobies and their native competitors. Current Zoology 69: 727–737. https://doi.org/10.1093/cz/zoac082.

Bandara, R. M. W. J., E. Curchitser & M. L. Pinsky, 2024. The importance of oxygen for explaining rapid shifts in a marine fish. Global Change Biology 30: e17008. https://doi.org/10.1111/gcb.17008.

Behrens, J. W., M. van Deurs & E. A. F. Christensen, 2017. Evaluating dispersal potential of an invasive fish by the use of aerobic scope and osmoregulation capacity. PLoS ONE 12: e0176038. https://doi.org/10.1371/journal.pone.0176038.

Berenbrink, M., 2011. Transport and exchange of respiratory gases in the blood | Evolution of the Bohr Effect. In Farrell, A. P. (ed), Encyclopedia of Fish Physiology: From Genome to Environment Elsevier, Amsterdam: 921–928.

Boutilier, R. G., 2001. Mechanisms of cell survival in hypoxia and hypothermia. Journal of Experimental Biology 204: 3171–3181. https://doi.org/10.1242/jeb.204.18.3171.

Boyd, C. E., 2015. Water Quality, Springer, Cham: 357 pp. https://doi.org/10.1007/978-3-319-17446-4.

Boyd, C. E., C. S. Tucker & B. Somridhivej, 2016. Alkalinity and hardness: critical but elusive concepts in aquaculture. Journal of the World Aquaculture Society 47: 6–41. https://doi.org/10.1111/jwas.12241.

Brylińska, M. (ed), 2000. Ryby słodkowodne Polski. Wydawnictwo Naukowe PWN, Warszawa: 520 pp.

Bylak, A. & K. Kukuła, 2024. Remarkable monkey goby expansion through a new invasion route into submountain rivers. Biological Invasions 26: 1303–1312. https://doi.org/10.1007/s10530-024-03261-1.

Čápová, M., I. Zlatnická, V. Kováč & S. Katina, 2008. Ontogenetic variability in the external morphology of monkey goby, *Neogobius fluviatilis* (Pallas, 1814) and its relevance to invasion potential. Hydrobiologia 607: 17–26. https://doi.org/10.1007/s10750-008-9361-9.

Carlson, J. K. & G. R. Parsons, 2003. Respiratory and hematological responses of the bonnethead shark, *Sphyrna tiburo*, to acute changes in dissolved oxygen. Journal of Experimental Marine Biology and Ecology 294: 15–26. https://doi.org/10.1016/S0022-0981(03)00237-5.

Chabot, D., J. F. Steffensen & A. P. Farrell, 2016. The determination of standard metabolic rate in fishes. Journal of Fish Biology 88: 81–121. https://doi.org/10.1111/jfb.12845.

Christensen, E. A. F., T. Norin, I. Tabak, M. van Deurs & J. W. Behrens, 2021. Effects of temperature on physiological performance and behavioral thermoregulation in an invasive fish, the round goby. Journal of Experimental Biology 224: jeb237669. https://doi.org/10.1242/jeb.237669.

Claiborne, J. B., S. L. Edwards & A. I. Morrison-Shetlar, 2002. Acid-base regulation in fishes: cellular and molecular mechanisms. Journal of Experimental Zoology 293: 302–319. https://doi.org/10.1002/jez.10125.

Claireaux, G. & D. Chabot, 2016. Responses by fishes to environmental hypoxia: integration through Fry's concept of aerobic metabolic scope. Journal of Fish Biology 88: 232–251. https://doi.org/10.1111/jfb.12833.

Clark, T. D., E. Sandblom & F. Jutfelt, 2013. Aerobic scope measurements of fishes in an era of climate change: respirometry, relevance and recommendations. Journal of Experimental Biology 216: 2771–2782. https://doi.org/10.1242/jeb.084251.

Collins, M., M. Truebano & J. I. Spicer, 2022. Consequences of thermal plasticity for hypoxic performance in coastal amphipods. Marine Environmental Research 177: 105624. https://doi.org/10.1016/j.marenvres.2022.105624.

Cooke, G. D., P. Lombardo & C. Brant, 2001. Shallow and deep lakes: determining successful management options. Lakeline 21: 42–46.

Copp, G. H., P. G. Bianco, N. G. Bogutskaya, T. Erős, I. Falka, M. T. Ferreira, M. G. Fox, J. Freyhof, R. E. Gozlan, J. Grabowska, V. Kováč, R. Moreno-Amich, A. M. Naseka, M. Peňáz, M. Povž, M. Przybylski, M. Robillard, I. C. Russell, S. Stakėnas, S. Šumer, A. Vila-Gispert & C. Wiesner, 2005. To be, or not to be, a non-native freshwater fish? Journal of Applied Ichthyology 21: 242–262. https://doi.org/10.1111/j.1439-0426.2005.00690.x.

Crear, D. P., R. W. Brill, L. M. L. Averilla, S. C. Meakem & K. C. Weng, 2020. In the face of climate change and exhaustive exercise: the physiological response of an important recreational fish species. Royal Society Open Science 7: 200049. https://doi.org/10.1098/rsos.200049.

Cuthbert, R. N., S. G. Kotronaki, J. T. A. Dick & E. Briski, 2020. Salinity tolerance and geographical origin predict global alien amphipod invasions. Biology Letters 16: 20200354. https://doi.org/10.1098/rsbl.2020.0354.

Deconinck, A. & C. S. Willett, 2022. Hypoxia tolerance, but not low pH tolerance, is associated with a latitudinal cline across populations of *Tigriopus californicus*. PLoS ONE 17: e0276635. https://doi.org/10.1371/journal.pone.0276635.

Degerman, E. & M. Appelberg, 1992. The response of stream-dwelling fish to liming. Environmental Pollution 78: 149–155. https://doi.org/10.1016/0269-7491(92)90023-4.

Deutsch, C., H. Brix, T. Ito, H. Frenzel & L. Thompson, 2011. Climate-forced variability of ocean hypoxia. Science 333: 336–339. https://doi.org/10.1126/science.1202422.

Didenko, A. V., 2013. Gobiids of the Dniprodzerzhynsk reservoir (Dnieper River, Ukraine): distribution and habitat prferences. Acta Ichthyologica Et Piscatoria 43: 257–266. https://doi.org/10.3750/AIP2013.43.4.01.

Domenici, P., C. Lefrançois & A. Shingles, 2007. Hypoxia and the antipredator behaviours of fishes. Philosophical Transactions of the Royal Society B: Biological Sciences 362: 2105–2121. https://doi.org/10.1098/rstb.2007.2103.

Dumont, H. J., 1998. The caspian lake: history, biota, structure, and function. Limnology and Oceanography 43: 44–52. https://doi.org/10.4319/lo.1998.43.1.0044.

Erős, T., A. Sevcsik & B. Tóth, 2005. Abundance and night-time habitat use patterns of Ponto-Caspian gobiid species (Pisces, Gobiidae) in the littoral zone of the River Danube, Hungary. Journal of Applied Ichthyology 21: 350–357. https://doi.org/10.1111/j.1439-0426.2005.00689.x.

Farwell, M., M. G. Fox, C. D. Moyes & G. Burness, 2007. Can hypoxia tolerance explain differences in distribution of two co-occurring north temperate sunfishes? Environmental Biology of Fishes 78: 83–90. https://doi.org/10.1007/s10641-006-9079-3.

Fedorenkova, A., J. A. Vonk, A. M. Breure, A. J. Hendriks & R. S. E. W. Leuven, 2013. Tolerance of native and non-native fish species to chemical stress: a case study for the River Rhine. Aquatic Invasions 8: 231–241. https://doi.org/10.3391/ai.2013.8.2.10.

Feely, R. A., S. C. Doney & S. R. Cooley, 2009. Ocean acidification: present conditions and future changes in a high-CO_2 world. Oceanography 22: 36–47. https://doi.org/10.5670/oceanog.2009.95.

Feng, X., A. T. Peterson, L. J. Aguirre-López, J. R. Burger, X. Chen & M. Papeş, 2024. Rethinking ecological niches and geographic distributions in face of pervasive human influence in the Anthropocene. Biological Reviews 99: 1481–1503. https://doi.org/10.1111/brv.13077.

Ferguson, N., C. R. White & D. J. Marshall, 2013. Competition in benthic marine invertebrates: the unrecognized role of exploitative competition for oxygen. Ecology 94: 126–135. https://doi.org/10.1890/12-0795.1.

Ficke, A. D., C. A. Myrick & L. J. Hansen, 2007. Potential impacts of global climate change on freshwater fisheries. Reviews in Fish Biology and Fisheries 17: 581–613. https://doi.org/10.1007/s11160-007-9059-5.

Frölicher, T. L., E. M. Fischer & N. Gruber, 2018. Marine heatwaves under global warming. Nature 560: 360–364. https://doi.org/10.1038/s41586-018-0383-9.

Grabowska, J., D. Błońska, M. Ondračková & T. Kakareko, 2023. The functional ecology of four invasive Ponto-Caspian gobies. Reviews in Fish Biology and Fisheries 33: 1329–1352. https://doi.org/10.1007/s11160-023-09801-7.

Halačka, K., 2015. Differences in haematology and respiratory system morphology at three neogobiid species. Open Life Sciences 10: 514–520. https://doi.org/10.1515/biol-2015-0053.

Halačka, K., T. Vítek, L. Vetešník & P. Spurný, 2012. Epidermis structure and blood parameter differences between sculpin *Cottus gobio* and Siberian sculpin *Cottus poecilopus* from the Morava watershed. Folia Zoologica 61: 9–16. https://doi.org/10.25225/fozo.v61.i1.a3.2012.

Hall, A. E. & T. D. Clark, 2016. Seeing is believing: metabolism provides insight into threat perception for a prey species of coral reef fish. Animal Behaviour 115: 117–126. https://doi.org/10.1016/j.anbehav.2016.03.008.

Hamilton, S. L., C. A. Logan, H. W. Fennie, S. M. Sogard, J. P. Barry, A. D. Makukhov, L. R. Tobosa, K. Boyer, C. F. Lovera & G. Bernardi, 2017. Species-specific responses of juvenile rockfish to elevated $p\mathrm{CO}_2$: from behavior to genomics. PLoS ONE 12: e0169670. https://doi.org/10.1371/journal.pone.0169670.

Hänfling, B., B. Hellemans, F. A. M. Volckaert & G. R. Carvalho, 2002. Late glacial history of the cold-adapted freshwater fish *Cottus gobio*, revealed by microsatellites. Molecular Ecology 11: 1717–1729. https://doi.org/10.1046/j.1365-294X.2002.01563.x.

Hellmann, J. J., J. E. Byers, B. G. Bierwagen & J. S. Dukes, 2008. Five potential consequences of climate change for invasive species. Conservation Biology 22: 534–543. https://doi.org/10.1111/j.1523-1739.2008.00951.x.

Heuer, R. M. & M. Grosell, 2014. Physiological impacts of elevated carbon dioxide and ocean acidification on fish. American Journal of Physiology - Regulatory Integrative and Comparative Physiology 307: R1061–R1084. https://doi.org/10.1152/ajpregu.00064.2014.

Holčík, J., I. Stráňai & J. Andreji, 2003. The further advance of *Neogobius fluviatilis* (Pallas, 1814) (Pisces, Gobiidae) upstream of the Danube. Biologia - Section Zoology 58: 967–973.

Hulme, P. E., 2017. Climate change and biological invasions: evidence, expectations, and response options. Biological Reviews 92: 1297–1313. https://doi.org/10.1111/brv.12282.

IPCC, 2014. Climate change 2014: synthesis report. In Meyer, R. K. & L. A. Pachauri (eds), Core Writing Team, Contribution of Working Groups I II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, Geneva, Switzerland: 151.

Jakovlić, I., M. Piria, N. Šprem, T. Tomljanović, D. Matulić & T. Treer, 2015. Distribution, abundance and condition of invasive Ponto-Caspian gobies *Ponticola kessleri* (Günther, 1861), *Neogobius fluviatilis* (Pallas, 1814), and *Neogobius melanostomus* (Pallas, 1814) in the Sava River basin, Croatia. Journal of Applied Ichthyology 31: 888–894. https://doi.org/10.1111/jai.12803.

Jakubčinová, K., P. Simonović, B. Števove, J. Čanak Atlagić & V. Kováč, 2017. What can morphology tell us about ecology of four invasive goby species? Journal of Fish Biology 90: 1999–2019. https://doi.org/10.1111/jfb.13283.

Janáč, M., K. Roche, L. Šlapanský, M. Polačik & P. Jurajda, 2018. Long-term monitoring of native bullhead and invasive gobiids in the Danubian rip-rap zone. Hydrobiologia 807: 263–275. https://doi.org/10.1007/s10750-017-3398-6.

Jane, S. F., G. J. A. Hansen, B. M. Kraemer, P. R. Leavitt, J. L. Mincer, R. L. North, R. M. Pilla, J. T. Stetler, C. E. Williamson, R. I. Woolway, L. Arvola, S. Chandra, C. L. DeGasperi, L. Diemer, J. Dunalska, O. Erina, G. Flaim, H. P. Grossart, K. D. Hambright, C. Hein, J. Hejzlar, L. L. Janus, J. P. Jenny, J. R. Jones, L. B. Knoll, B. Leoni, E. Mackay, S. I. S. Matsuzaki, C. McBride, D. C. Müller-Navarra, A. M. Paterson, D. Pierson, M. Rogora, J. A. Rusak, S. Sadro, E. Saulnier-Talbot, M. Schmid, R. Sommaruga, W. Thiery, P. Verburg, K. C. Weathers, G. A. Weyhenmeyer, K. Yokota & K. C. Rose, 2021. Widespread deoxygenation of temperate lakes. Nature 594: 66–70. https://doi.org/10.1038/s41586-021-03550-y.

Jewett, E. B., A. H. Hines & G. M. Ruiz, 2005. Epifaunal disturbance by periodic low levels of dissolved oxygen: native vs. invasive species response. Marine Ecology Progress Series 304: 31–44. https://doi.org/10.3354/MEPS304031.

Kakareko, T., 2011. Impact of selected factors on the distribution and habitat preferences of two non-native fish species in Poland: racer goby *Neogobius gymnotrachelus* (Kessler, 1857) and monkey goby *Neogobius fluviatilis* (Pallas, 1811). Habilitation thesis (in Polish with English sum). Nicolaus Copernicus University Press, Toruń: 139 pp.

Kakareko, T., J. Kobak, M. Poznańska, L. Jermacz & G. H. Copp, 2016. Underwater evaluation of habitat partitioning in a European river between a non-native invader, the racer goby and a threatened native fish, the European bullhead. Ecology of Freshwater Fish 25: 60–71. https://doi.org/10.1111/eff.12191.

Karatayev, A. Y., L. E. Burlakova, D. K. Padilla, S. E. Mastitsky & S. Olenin, 2009. Invaders are not a random selection of species. Biological Invasions 11: 2009–2019. https://doi.org/10.1007/s10530-009-9498-0.

Keller, R. P., J. M. Drake, M. B. Drew & D. M. Lodge, 2011. Linking environmental conditions and ship movements to estimate invasive species transport across the global shipping network. Diversity and Distributions 17: 93–102. https://doi.org/10.1111/J.1472-4642.2010.00696.x.

Killen, S. S., S. Marras, M. R. Ryan, P. Domenici & D. J. McKenzie, 2012. A relationship between metabolic rate and risk-taking behaviour is revealed during hypoxia in juvenile European sea bass. Functional Ecology 26: 134–143. https://doi.org/10.1111/j.1365-2435.2011.01920.x.

Killen, S. S., D. S. Glazier, E. L. Rezende, T. D. Clark, D. Atkinson, A. S. T. Willener & L. G. Halsey, 2016. Ecological influences and morphological correlates of resting and maximal metabolic rates across teleost fish species. American Naturalist 187: 592–606. https://doi.org/10.1086/685893.

Killen, S. S., E. A. F. Christensen, D. Cortese, L. Závorka, T. Norin, L. Cotgrove, A. Crespel, A. Munson, J. J. H. Nati, M. Papatheodoulou & D. J. McKenzie, 2021. Guidelines for reporting methods to estimate metabolic rates by aquatic intermittent-flow respirometry. Journal of Experimental Biology 224: jeb242522. https://doi.org/10.1242/jeb.242522.

Kim, J. H., E. J. Kang, K. Kim & K. Y. Kim, 2018. A continuous-flow and on-site mesocosm for ocean acidification experiments on benthic organisms. Algae 33: 359–366. https://doi.org/10.4490/algae.2018.33.11.10.

Kłosiński, P., J. Kobak, M. Augustyniak, R. Pawlak, Ł. Jermacz, M. Poznańska-Kakareko & T. Kakareko, 2022.

Behavioural responses to con- and heterospecific alarm cues by an alien and a coexisting native fish. Hydrobiologia 849: 985–1000. https://doi.org/10.1007/s10750-021-04761-0.

Kłosiński, P., J. Kobak & T. Kakareko, 2024. Metabolic rate of two invasive Ponto-Caspian goby species and their native competitors in the context of global warming. Freshwater Biology 69: 971–983. https://doi.org/10.1111/fwb.14259.

Kocovsky, P. M., J. A. Tallman, D. J. Jude, D. M. Murphy, J. E. Brown & C. A. Stepien, 2011. Expansion of tubenose gobies *Proterorhinus semilunaris* into western Lake Erie and potential effects on native species. Biological Invasions 13: 2775–2784. https://doi.org/10.1007/s10530-011-9962-5.

Kolar, C. S. & D. M. Lodge, 2002. Ecological predictions and risk assessment for Alien Fishes in North America. Science 298: 1233–1236. https://doi.org/10.1126/science.1075753.

Kottelat, M. & J. Freyhof, 2007. Handbook of European Freshwater Fishes, Publications Kottelat, Cornol and Freyhof, Berlin: 646 pp.

Lagos, M. E., D. R. Barneche, C. R. White & D. J. Marshall, 2017. Do low oxygen environments facilitate marine invasions? Relative tolerance of native and invasive species to low oxygen conditions. Global Change Biology 23: 2321–2330. https://doi.org/10.1111/gcb.13668.

Laudon, H. & K. Bishop, 2002. Episodic stream water pH decline during autumn storms following a summer drought in northern Sweden. Hydrological Processes 16: 1725–1733. https://doi.org/10.1002/hyp.360.

Laudon, H., O. Westling & K. Bishop, 2000. Cause of pH decline in stream water during spring melt runoff in northern Sweden. Canadian Journal of Fisheries and Aquatic Sciences 57: 1888–1900. https://doi.org/10.1139/f00-131.

Lauerwald, R., J. Hartmann, N. Moosdorf, S. Kempe & P. A. Raymond, 2013. What controls the spatial patterns of the riverine carbonate system?—A case study for North America. Chemical Geology 337–338: 114–127. https://doi.org/10.1016/j.chemgeo.2012.11.011.

Lelek, A., 1987. The Freshwater Fishes of Europe, Vol. 9. Threatened Fishes of Europe. Aula-Verlag, Wiesbaden: 343 pp.

Lenz, M., B. A. P. da Gama, N. V. Gerner, J. Gobin, F. Gröner, A. Harry, S. R. Jenkins, P. Kraufvelin, C. Mummelthei, J. Sareyka, E. A. Xavier & M. Wahl, 2011. Non-native marine invertebrates are more tolerant towards environmental stress than taxonomically related native species: results from a globally replicated study. Environmental Research 111: 943–952. https://doi.org/10.1016/j.envres.2011.05.001.

Leuven, R. S. E. W., A. J. Hendriks, M. A. J. Huijbregts, H. J. R. Lenders, J. Matthews & G. van der Velde, 2011. Differences in sensitivity of native and exotic fish species to changes in river temperature. Current Zoology 57: 852–862. https://doi.org/10.1093/czoolo/57.6.852.

Liu, Y. & M. van Kleunen, 2017. Responses of common and rare aliens and natives to nutrient availability and fluctuations. Journal of Ecology 105: 1111–1122. https://doi.org/10.1111/1365-2745.12733.

Mandic, M., A. E. Todgham & J. G. Richards, 2009. Mechanisms and evolution of hypoxia tolerance in fish. Proceedings of the Royal Society B: Biological Sciences 276: 735–744. https://doi.org/10.1098/rspb.2008.1235.

Mandic, M., B. Speers-Roesch & J. G. Richards, 2013. Hypoxia tolerance in sculpins is associated with high anaerobic enzyme activity in brain but not in liver or muscle. Physiological and Biochemical Zoology 86: 92–105. https://doi.org/10.1086/667938.

Marium, A., A. M. M. Chatha, S. Naz, M. F. Khan, W. Safdar & I. Ashraf, 2023. Effect of temperature, pH, salinity and dissolved oxygen on fishes. Journal of Zoology and Systematics 1: 1–12. https://doi.org/10.56946/jzs.v1i2.198.

Marras, S., A. Cucco, F. Antognarelli, E. Azzurro, M. Milazzo, M. Bariche, M. Butenschön, S. Kay, M. Di Bitetto, G. Quattrocchi, M. Sinerchia & P. Domenici, 2015. Predicting future thermal habitat suitability of competing native and invasive fish species: from metabolic scope to oceanographic modelling. Conservation Physiology 3: cou059. https://doi.org/10.1093/conphys/cou059.

Marszelewski, W. & B. Pius, 2014. The impact of changes in air temperature upon the thermal regime of the river Vistula in Toruń (Poland) over the years 1961–2012. In Gâştescu, P., W. Marszelewski & P. Bretcan (eds), Water Resources and Wetlands Romanian Limnogeographical Association, Tulcea, Romania: 231–236.

Marszelewski, W. & B. Pius, 2016. Long-term changes in temperature of river waters in the transitional zone of the temperate climate: a case study of Polish rivers. Hydrological Sciences Journal 61: 1430–1442. https://doi.org/10.1080/02626667.2015.1040800.

McCahon, C. P. & D. Pascoe, 1989. Short-term experimental acidification of a Welsh stream: toxicity of different forms of aluminium at low pH to fish and invertebrates. Archives of Environmental Contamination and Toxicology 18: 233–242. https://doi.org/10.1007/BF01056208.

McDonald, D. G., J. Freda, V. Cavdek, R. Gonzalez & S. Zia, 1991. Interspecific differences in gill morphology of freshwater fish in relation to tolerance of low-pH environments. Physiological Zoology 64: 124–144. https://doi.org/10.1086/physzool.64.1.30158516.

Metcalfe, N. B., T. E. Van Leeuwen & S. S. Killen, 2016. Does individual variation in metabolic phenotype predict fish behaviour and performance? Journal of Fish Biology 88: 298–321. https://doi.org/10.1111/jfb.12699.

Michaelidis, B., A. Spring & H. O. Pörtner, 2007. Effects of long-term acclimation to environmental hypercapnia on extracellular acid-base status and metabolic capacity in Mediterranean fish *Sparus aurata*. Marine Biology 150: 1417–1429. https://doi.org/10.1007/S00227-006-0436-8.

Monaco, C. J. & B. Helmuth, 2011. Tipping points, thresholds and the keystone role of physiology in marine climate change research. Advances in Marine Biology 60: 123–160. https://doi.org/10.1016/B978-0-12-385529-9.00003-2.

Mordukhay-Boltovskoy, P. D., 1964. Caspian fauna in fresh waters outside the Ponto-Caspian basin. Hydrobiologia 23: 159–164.

Moyle, P. B. & J. J. Cech, 2004. Fishes: an introduction to ichthyology, 5th ed. Prentice Hall, Englewood Cliffs, NJ: 726 pp.

Müller, B., L. D. Bryant, A. Matzinger & A. Wüest, 2012. Hypolimnetic oxygen depletion in eutrophic lakes. Environmental Science and Technology 46: 9964–9971. https://doi.org/10.1021/es301422r.

Munday, P. L., M. I. McCormick & G. E. Nilsson, 2012. Impact of global warming and rising CO_2 levels on coral reef fishes: what hope for the future? Journal of Experimental Biology 215: 3865–3873. https://doi.org/10.1242/jeb.074765.

Nagelkerken, I. & P. L. Munday, 2016. Animal behaviour shapes the ecological effects of ocean acidification and warming: moving from individual to community-level responses. Global Change Biology 22: 974–989. https://doi.org/10.1111/gcb.13167.

Nati, J. J. H., J. Lindström, W. Yeomans & S. S. Killen, 2018. Physiological and behavioural responses to hypoxia in an invasive freshwater fish species and a native competitor. Ecology of Freshwater Fish 27: 813–821. https://doi.org/10.1111/eff.12394.

Nixon, S. W., 1995. Coastal marine eutrophication: a definition, social causes, and future concerns. Ophelia 41: 199–219. https://doi.org/10.1080/00785236.1995.10422044.

Nocita, A., A. Massolo, M. Vannini & G. Gandolfi, 2009. The influence of calcium concentration on the distribution of the river bullhead *Cottus gobio* L. (Teleostes, Cottidae). Italian Journal of Zoology 76: 348–357. https://doi.org/10.1080/11250000902806631.

Onthank, K. L., L. A. Trueblood, T. Schrock-Duff & L. G. Kore, 2021. Impact of short- and long-term exposure to elevated seawater Pco_2 on metabolic rate and hypoxia tolerance in *Octopus rubescens*. Physiological and Biochemical Zoology 94: 1–11. https://doi.org/10.1086/712207.

Paiva, F., A. Barco, Y. Chen, A. Mirzajani, F. T. Chan, V. Lauringson, M. Baltazar-Soares, A. Zhan, S. A. Bailey, J. Javidpour & E. Briski, 2018. Is salinity an obstacle for biological invasions? Global Change Biology 24: 2708–2720. https://doi.org/10.1111/gcb.14049.

Palacios, M. M., S. S. Killen, L. E. Nadler, J. R. White & M. I. McCormick, 2016. Top predators negate the effect of mesopredators on prey physiology. Journal of Animal Ecology 85: 1078–1086. https://doi.org/10.1111/1365-2656.12523.

Parmesan, C., 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics 37: 637–669. https://doi.org/10.1146/annurev.ecolsys.37.091305.110100.

Philippart, J. C., 1979. A study of the fish populations in three oligotrophic trout streams in the upper Roer basin (Belgium). Bulletin of the Royal Society of Liege 48: 212–227.

Pinchuk, V. I., E. D. Vasil'eva, V. P. Vasil'ev, & P. Miller, 2003. *Neogobius fluviatilis* (Pallas, 1814) The freshwater fishes of Europe. Vol. 8/I Mugilidae, Atherinidae, Atherionopsidae, Blennidae, Odontobutidae, Gobiidae 1. AULA-Verlag, Wiesbaden: 225–252.

Piria, M., G. Jakšić, I. Jakovlić & T. Treer, 2016. Dietary habits of invasive Ponto-Caspian gobies in the Croatian part of the Danube River basin and their potential impact on benthic fish communities. Science of the Total Environment 540: 386–395. https://doi.org/10.1016/j.scitotenv.2015.05.125.

Płąchocki, D., J. Kobak, M. Poznańska-Kakareko & T. Kakareko, 2020. Environmental factors associated with the occurrence of the Ponto-Caspian gobies in a lowland river belonging to the central European invasion corridor. River Research and Applications 36: 25–35. https://doi.org/10.1002/rra.3543.

Poff, N. L., M. M. Brinson, & J. W. Day, 2002. Aquatic ecosystems and global climate change: potential impacts on inland freshwater and coastal wetland ecosystems in the United States. Pew Center on Global Climate Change, Arlington, VA 44: 1–36.

Pollock, M. S., L. M. J. Clarke & M. G. Dubé, 2007. The effects of hypoxia on fishes: from ecological relevance to physiological effects. Environmental Reviews 15: 1–14. https://doi.org/10.1139/A06-006.

Pörtner, H. O. & M. A. Peck, 2010. Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. Journal of Fish Biology 77: 1745–1779. https://doi.org/10.1111/j.1095-8649.2010.02783.x.

Puntila-Dodd, R., D. Bekkevold & J. W. Behrens, 2021. Estimating salinity stress via hsp70 expression in the invasive round goby (*Neogobius melanostomus*): implications for further range expansion. Hydrobiologia 848: 421–429. https://doi.org/10.1007/s10750-020-04449-x.

Rahel, F. J. & J. J. Magnuson, 1983. Low pH and the absence of fish species in naturally acidic Wisconsin Lakes: inferences for cultural acidification. Canadian Journal of Fisheries and Aquatic Sciences 40: 3–9. https://doi.org/10.1139/f83-002.

Reid, D. F. & M. I. Orlova, 2002. Geological and evolutionary underpinnings for the success of Ponto-Caspian species invasions in the Baltic Sea and North American Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 59: 1144–1158. https://doi.org/10.1139/f02-099.

Rewicz, T., M. Grabowski, C. MacNeil & K. Bącela-Spychalska, 2014. The profile of a 'perfect' invader–the case of killer shrimp, *Dikerogammarus villosus*. Aquatic Invasions 9: 267–288. https://doi.org/10.3391/ai.2014.9.3.04.

Richards, J. G., 2009. Metabolic and molecular responses of fish to hypoxia. In Richards, J. G., A. P. Farrell & C. J. Brauner (eds), Hypoxia, Academic Press, Amsterdam, Boston: 444–485.

Roche, K. F., M. Janač & P. Jurajda, 2013. A review of Gobiid expansion along the Danube-Rhine corridor-geopolitical change as a driver for invasion. Knowledge and Management of Aquatic Ecosystems 411: 01. https://doi.org/10.1051/kmae/2013066.

Rogers, N. J., M. A. Urbina, E. E. Reardon, D. J. McKenzie & R. W. Wilson, 2016. A new analysis of hypoxia tolerance in fishes using a database of critical oxygen level (P_{crit}). Conservation Physiology 4: cow012. https://doi.org/10.1093/conphys/cow012.

Rosenberger, A. E. & L. J. Chapman, 1999. Hypoxic wetland tributaries as faunal refugia from an introduced predator. Ecology of Freshwater Fish 8: 22–34. https://doi.org/10.1111/j.1600-0633.1999.tb00049.x.

Rosewarne, P. J., J. M. Wilson & J. C. Svendsen, 2016. Measuring maximum and standard metabolic rates using intermittent-flow respirometry: a student laboratory investigation of aerobic metabolic scope and environmental hypoxia in aquatic breathers. Journal of Fish Biology 88: 265–283. https://doi.org/10.1111/jfb.12795.

Ross, L. G., R. W. McKinney, S. K. Cardwell, J. G. Fullarton, S. E. J. Roberts & B. Ross, 1992. The effects of dietary protein content, lipid content and ration level on oxygen consumption and specific dynamic action in *Oreochromis niloticus* L. Comparative Biochemistry and Physiology Part A: Physiology 103: 573–578. https://doi.org/10.1016/0300-9629(92)90292-X.

Rothwell, J. J., N. B. Dise, K. G. Taylor, T. E. H. Allott, P. Scholefield, H. Davies & C. Neal, 2010. Predicting river water quality across North West England using catchment characteristics. Journal of Hydrology 395: 153–162. https://doi.org/10.1016/j.jhydrol.2010.10.015.

Saarinen, T., S. Mohämmädighävam, H. Marttila & B. Kløve, 2013. Impact of peatland forestry on runoff water quality in areas with sulphide-bearing sediments; how to prevent acid surges. Forest Ecology and Management 293: 17–28. https://doi.org/10.1016/j.foreco.2012.12.029.

Sampaio, E., C. Santos, I. C. Rosa, V. Ferreira, H. O. Pörtner, C. M. Duarte, L. A. Levin & R. Rosa, 2021. Impacts of hypoxic events surpass those of future ocean warming and acidification. Nature Ecology & Evolution 5: 311–321. https://doi.org/10.1038/s41559-020-01370-3.

Schwieterman, G., D. Crear, B. Anderson, D. Lavoie, J. Sulikowski, P. Bushnell & R. Brill, 2019. Combined Effects of Acute Temperature Change and Elevated $p\mathrm{CO}_2$ on the Metabolic Rates and Hypoxia Tolerances of Clearnose Skate (*Rostaraja eglanteria*), Summer Flounder (*Paralichthys dentatus*), and Thorny Skate (*Amblyraja radiata*). Biology 8: 56. https://doi.org/10.3390/biology8030056.

Simonsen, J. F. & P. Harremoës, 1978. Oxygen and pH fluctuations in rivers. Water Research 12: 477–489. https://doi.org/10.1016/0043-1354(78)90155-0.

Sindilariu, P. D., J. Freyhof & C. Wolter, 2006. Habitat use of juvenile fish in the lower Danube and the Danube Delta: Implications for ecotone connectivity. Hydrobiologia 571: 51–61. https://doi.org/10.1007/s10750-006-0216-y.

Smirnov, A. I., 1986. Perciformes (Gobioidei), Scorpaeniformes, Pleuronectiformes, Gobiesociformes, Lophiiformes. Fauna Ukrainy 8. Ryby (5). Naukova Dumka, Kiev.

Smyly, W. J. P., 1957. The life-history of the bullhead or miller's thumb (*Cottus gobio* L.). Proceedings of Zoological Society of London 128: 431–453.

Snyder, S., L. E. Nadler, J. S. Bayley, M. B. S. Svendsen, J. L. Johansen, P. Domenici & J. F. Steffensen, 2016. Effect of closed *v.* intermittent-flow respirometry on hypoxia tolerance in the shiner perch *Cymatogaster aggregata*. Journal of Fish Biology 88: 252–264. https://doi.org/10.1111/jfb.12837.

Sorte, C. J. B., 2014. Synergies between climate change and species invasions: evidence from marine systems. In Ziska, L. H. & J. S. Dukes (eds), Invasive Species and Global Climate Change, CABI, Wallingford: 101–116. https://doi.org/10.1079/9781780641645.0101.

Stern, D. B. & C. E. Lee, 2020. Evolutionary origins of genomic adaptations in an invasive copepod. Nature Ecology & Evolution 4: 1084–1094. https://doi.org/10.1038/s41559-020-1201-y.

Stets, E. G., V. J. Kelly & C. G. Crawford, 2014. Long-term trends in alkalinity in large rivers of the conterminous US in relation to acidification, agriculture, and hydrologic modification. Science of the Total Environment 488–489: 280–289. https://doi.org/10.1016/j.scitotenv.2014.04.054.

Straile, D., K. Jöhnk & H. Rossknecht, 2003. Complex effects of winter warming on the physicochemical characteristics of a deep lake. Limnology and Oceanography 48: 1432–1438. https://doi.org/10.4319/lo.2003.48.4.1432.

Svendsen, M. B. S., P. G. Bushnell & J. F. Steffensen, 2016. Design and setup of intermittent-flow respirometry system for aquatic organisms. Journal of Fish Biology 88: 26–50. https://doi.org/10.1111/jfb.12797.

Szalóky, Z., V. Bammer, I. György, L. Pehlivanov, M. Schabuss, H. Zornig, A. Weiperth & T. Erős, 2015. Offshore distribution of invasive gobies (Pisces: Gobiidae) along the longitudinal profile of the Danube River. Fundamental and Applied Limnology 187: 127–133. https://doi.org/10.1127/fal/2015/0768.

Tagliarolo, M., 2019. Acidification in Aquatic Systems Encyclopedia of Ecology, Elsevier: 6–13. https://doi.org/10.1016/B978-0-12-409548-9.10958-3.

Thuy, N. H., L. A. Tien, P. N. Tuyet, D. T. T. Huong, N. V. Cong, M. Bayley, T. Wang & S. Lefevre, 2010. Critical oxygen tension increases during digestion in the perch *Perca fluviatilis*. Journal of Fish Biology 76: 1025–1031. https://doi.org/10.1111/j.1095-8649.2009.02533.x.

Tomlinson, M. L. & M. R. Perrow, 2003. Ecology of the Bullhead. Conserving Natura 2000 Rivers. Ecology Series No. 4, English Nature, Peterborough: 18 pp.

Tripp, A., G. J. P. Allen, A. R. Quijada-Rodriguez, G. R. Yoon & D. Weihrauch, 2022. Effects of single and dual-stressor elevation of environmental temperature and P_{CO2} on metabolism and acid-base regulation in the Louisiana red swamp crayfish, *Procambarus clarkii*. Comparative Biochemistry and Physiology, Part A : Molecular and Integrative Physiology 266: 111151. https://doi.org/10.1016/j.cbpa.2022.111151.

Verberk, W. C. E. P., J. F. Sandker, I. L. E. van de Pol, M. A. Urbina, R. W. Wilson, D. J. McKenzie & F. P. Leiva, 2022. Body mass and cell size shape the tolerance of fishes to low oxygen in a temperature-dependent manner. Global Change Biology 28: 5695–5707. https://doi.org/10.1111/gcb.16319.

Verde, C., D. Giordano, R. Russo & G. di Prisco, 2011. Transport and exchange of respiratory gases in the blood | Hemoglobin Differentiation in Fishes. In Farrell, A. P. (ed), Encyclopedia of Fish Physiology: From Genome to Environment, Elsevier, Amsterdam: 944–950. https://doi.org/10.1016/B978-0-12-374553-8.00111-8.

Verspagen, J. M. H., D. B. Van De Waal, J. F. Finke, P. M. Visser, E. Van Donk & J. Huisman, 2014. Rising CO_2 levels will intensify phytoplankton blooms in eutrophic and hypertrophic lakes. PLoS ONE 9: e104325. https://doi.org/10.1371/journal.pone.0104325.

Vezza, P., P. Parasiewicz, O. Calles, M. Spairani & C. Comoglio, 2014. Modelling habitat requirements of bullhead (*Cottus gobio*) in Alpine streams. Aquatic Sciences 76: 1–15. https://doi.org/10.1007/s00027-013-0306-7.

Vilizzi, L., G. H. Copp, B. Adamovich, D. Almeida, J. Chan, P. I. Davison, S. Dembski, F. G. Ekmekçi, Á. Ferincz, S. C. Forneck, J. E. Hill, J. E. Kim, N. Koutsikos, R. S. E. W. Leuven, S. A. Luna, F. Magalhães, S. M. Marr, R. Mendoza, C. F. Mourão, J. W. Neal, N. Onikura, C. Perdikaris, M. Piria, N. Poulet, R. Puntila, I. L. Range, P. Simonović, F. Ribeiro, A. S. Tarkan, D. F. A. Troca, L. Vardakas, H. Verreycken, L. Vintsek, O. L. F. Weyl, D. C. J. Yeo & Y. Zeng, 2019. A global review and meta-analysis of applications of the freshwater Fish Invasiveness Screening Kit. Reviews in Fish Biology and Fisheries 29: 529–568. https://doi.org/10.1007/s11160-019-09562-2.

Weiss, L. C., L. Pötter, A. Steiger, S. Kruppert, U. Frost & R. Tollrian, 2018. Rising pCO_2 in freshwater ecosystems has the potential to negatively affect predator-induced defenses in *Daphnia*. Current Biology 28: 327–332. https://doi.org/10.1016/j.cub.2017.12.022.

Wunder, W., 1936. Physiologie der Süsswasserfische Mitteleuropas, E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart: 340 pp.

Xu, Z. & Y. J. Xu, 2015. Determination of trophic state changes with diel dissolved oxygen: a case study in a shallow lake. Water Environment Research 87: 1970–1979. https://doi.org/10.2175/106143015x14362865226716.

Effect of hypoxia and acidification on metabolic rate of Ponto-Caspian gobies and their native competitors in the context of climate change

Journal: Hydrobiologia

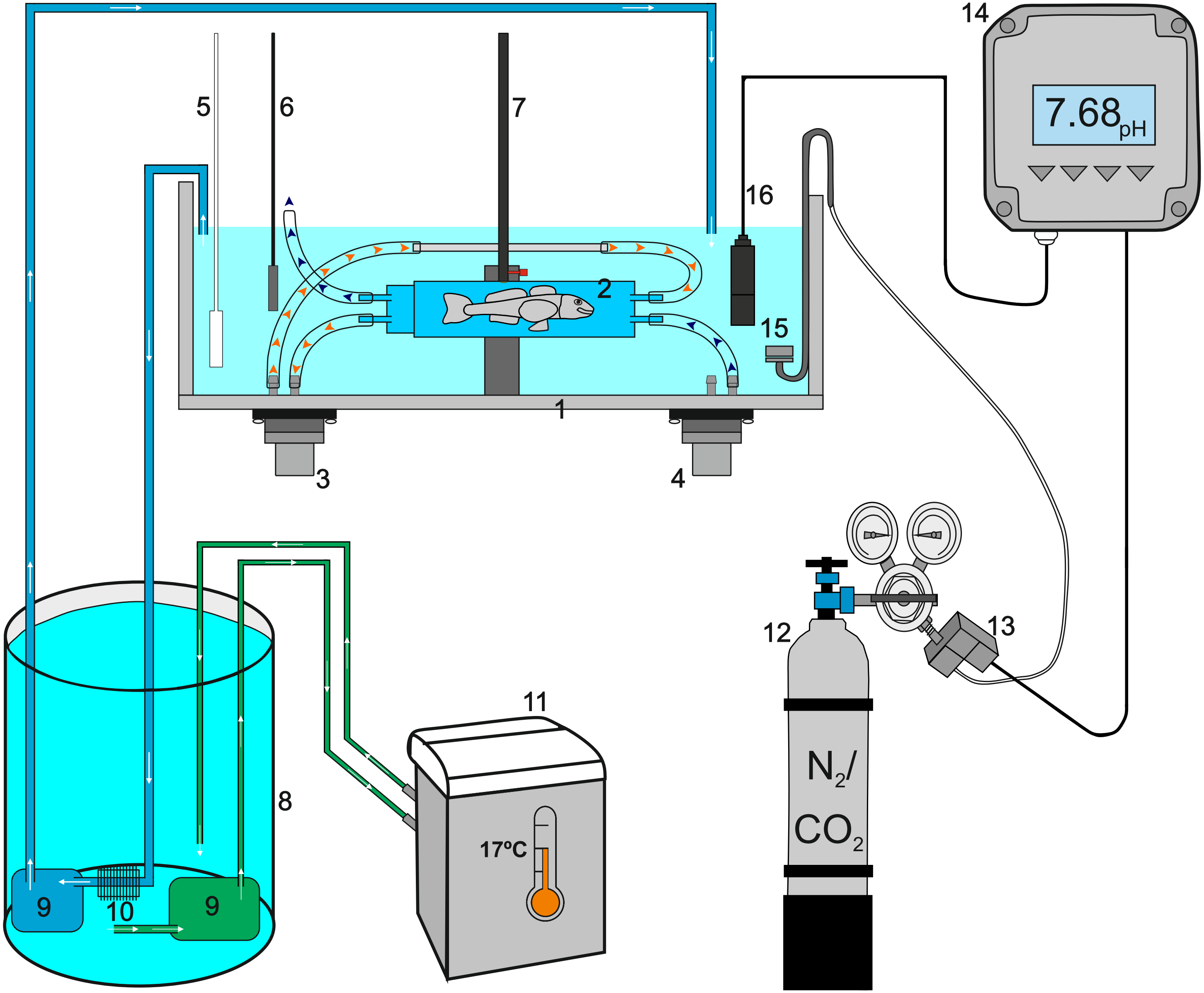
Piotr Kłosiński[a, *], **Jarosław Kobak**[b] **and Tomasz Kakareko**[a]

[a] Department of Ecology and Biogeography, Faculty of Biological and Veterinary Sciences, Nicolaus Copernicus University in Toruń, Lwowska 1, 87-100, Toruń, Poland

[b] Department of Invertebrate Zoology and Parasitology, Faculty of Biological and Veterinary Sciences, Nicolaus Copernicus University in Toruń, Lwowska 1, 87-100, Toruń, Poland

* Corresponding author: Piotr Kłosiński. E-mail address: klosinski.piotr@doktorant.umk.pl; ORCID iD: https://orcid.org/0000-0002-6359-9781

Figure S1. Experimental setup: 1 – water bath, 2 – respirometry chamber, 3 – recirculating pump, 4 – flush pump, 5 – aerator, 6 – temperature probe, 7 – oxygen probe, 8 – external tank, 9 – pump, 10 – metal heat exchanger, 11 – aquarium cooler/heater, 12 – gas cylinder, 13 – solenoid valve, 14 – oxygen analyzer/pH controller, 15 – diffuser, 16 – galvanic oxygen probe/pH electrode



14
7.68pH
5
6
7
16
2
15
1
3
4
12
13
N2/
CO2
11
17ºC
8
9
10
9

Effect of hypoxia and acidification on metabolic rate of Ponto-Caspian gobies and their native competitors in the context of climate change

Journal: Hydrobiologia

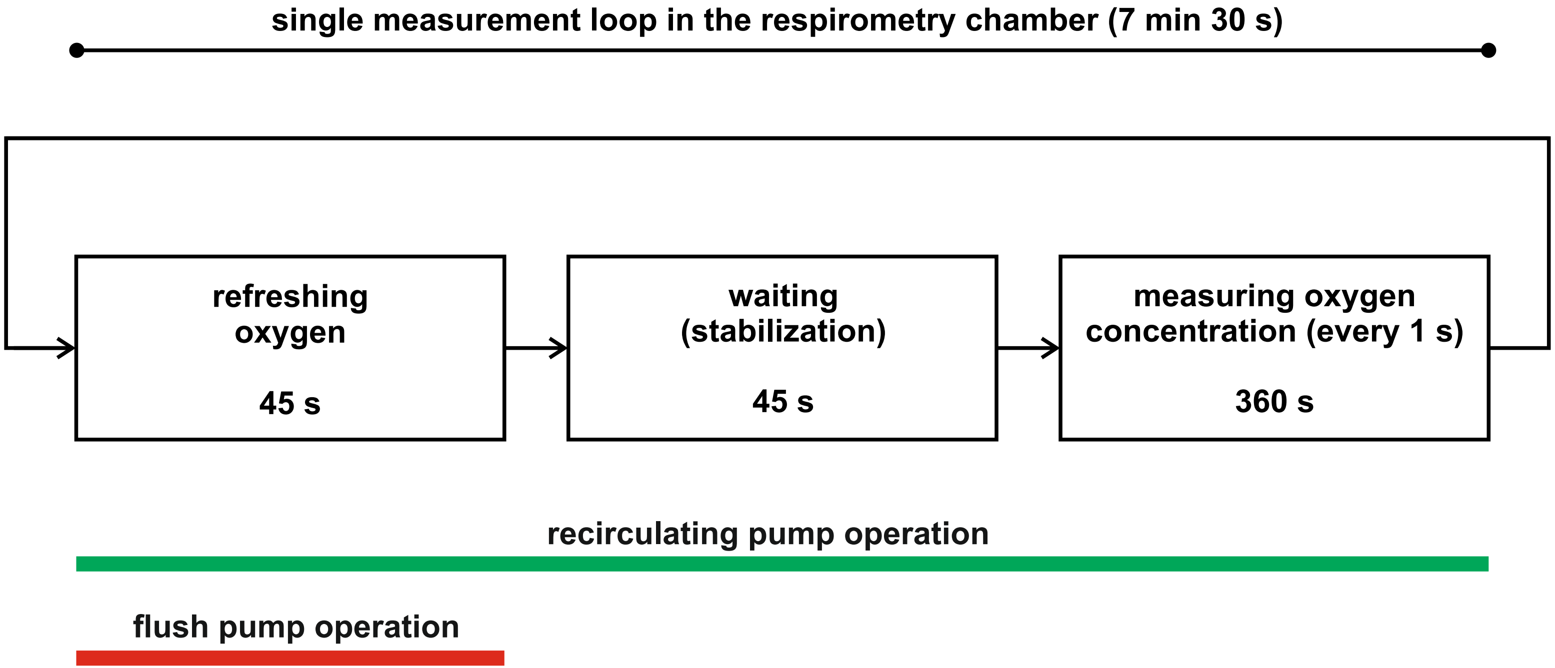
Piotr Kłosiński[a, *], Jarosław Kobak[b] and Tomasz Kakareko[a]

[a] Department of Ecology and Biogeography, Faculty of Biological and Veterinary Sciences, Nicolaus Copernicus University in Toruń, Lwowska 1, 87-100, Toruń, Poland

[b] Department of Invertebrate Zoology and Parasitology, Faculty of Biological and Veterinary Sciences, Nicolaus Copernicus University in Toruń, Lwowska 1, 87-100, Toruń, Poland

* Corresponding author: Piotr Kłosiński. E-mail address: klosinski.piotr@doktorant.umk.pl; ORCID iD: https://orcid.org/0000-0002-6359-9781

Figure S2. Single measurement loop in the respirometry chamber


single measurement loop in the respirometry chamber (7 min 30 s)
refreshing oxygen
45 s
waiting (stabilization)
45 s
measuring oxygen concentration (every 1 s)
360 s
recirculating pump operation
flush pump operation

Effect of hypoxia and acidification on metabolic rate of Ponto-Caspian gobies and their native competitors in the context of climate change

Journal: Hydrobiologia

Piotr Kłosiński[a, *], Jarosław Kobak[b] and Tomasz Kakareko[a]

[a] Department of Ecology and Biogeography, Faculty of Biological and Veterinary Sciences, Nicolaus Copernicus University in Toruń, Lwowska 1, 87-100, Toruń, Poland

[b] Department of Invertebrate Zoology and Parasitology, Faculty of Biological and Veterinary Sciences, Nicolaus Copernicus University in Toruń, Lwowska 1, 87-100, Toruń, Poland

* Corresponding author: Piotr Kłosiński. E-mail address: klosinski.piotr@doktorant.umk.pl; ORCID iD: https://orcid.org/0000-0002-6359-9781

Figure S3. The outline presenting a step-by-step procedure to test fish tolerance to progressive hypoxia

	Times & durations	Loops
Introduction of a single fish to respirometer	09:00	
Fish acclimation to experimental conditions	4 h	32
Measurement of RMR at a DO level of 95%	13:00 - 13:30	4
Gradually reducing of DO level from 95 to 60% at a rate of 0.67% per min	1 h	8
Measurement of RMR at a DO level of 60%	14:30 - 15:00	4
Gradually reducing of DO level from 60 to 40% at a rate of 0.67% per min	30 min	4
Measurement of RMR at a DO level of 40%	15:30 - 16:00	4
Gradually reducing of DO level from 40 to 30% at a rate of 0.67% per min	15 min	2
Measurement of RMR at a DO level of 30%	16:15 - 16:45	4
Gradually reducing of DO level from 30 to 25% at a rate of 0.67% per min	7 min 30 s	1
Measurement of RMR at a DO level of 25%	16:52:30 - 17:22:30	4

Effect of hypoxia and acidification on metabolic rate of Ponto-Caspian gobies and their native competitors in the context of climate change

Journal: Hydrobiologia

Piotr Kłosiński[a, *], Jarosław Kobak[b] and Tomasz Kakareko[a]

[a] Department of Ecology and Biogeography, Faculty of Biological and Veterinary Sciences, Nicolaus Copernicus University in Toruń, Lwowska 1, 87-100, Toruń, Poland

[b] Department of Invertebrate Zoology and Parasitology, Faculty of Biological and Veterinary Sciences, Nicolaus Copernicus University in Toruń, Lwowska 1, 87-100, Toruń, Poland

* Corresponding author: Piotr Kłosiński. E-mail address: klosinski.piotr@doktorant.umk.pl; ORCID iD: https://orcid.org/0000-0002-6359-9781

Figure S4. The outline presenting a step-by-step procedure to test fish tolerance to progressive acidification

	Times & durations	Loops
Introduction of a single fish to respirometer	09:00	
Fish acclimation to experimental conditions	4 h	32
Measurement of RMR at pH of 8.5	13:00 - 13:30	4
Gradually reducing of pH from 8.5 to 8.0 at a rate of 0.5 pH per 30 min	30 min	4
Measurement of RMR at pH of 8.0	14:00 - 14:30	4
Gradually reducing of pH from 8.0 to 7.5 at a rate of 0.5 pH per 30 min	30 min	4
Measurement of RMR at pH of 7.5	15:00 - 15:30	4
Gradually reducing of pH from 7.5 to 7.0 at a rate of 0.5 pH per 30 min	30 min	4
Measurement of RMR at pH of 7.0	16:00 - 16:30	4
Gradually reducing of pH from 7.0 to 6.5 at a rate of 0.5 pH per 30 min	30 min	4
Measurement of RMR at pH of 6.5	17:00 - 17:30	4

Effect of hypoxia and acidification on metabolic rate of Ponto-Caspian gobies and their native competitors in the context of climate change

Journal: Hydrobiologia

Piotr Kłosiński[a, *], Jarosław Kobak[b] and Tomasz Kakareko[a]

[a] Department of Ecology and Biogeography, Faculty of Biological and Veterinary Sciences, Nicolaus Copernicus University in Toruń, Lwowska 1, 87-100, Toruń, Poland

[b] Department of Invertebrate Zoology and Parasitology, Faculty of Biological and Veterinary Sciences, Nicolaus Copernicus University in Toruń, Lwowska 1, 87-100, Toruń, Poland

* Corresponding author: Piotr Kłosiński. E-mail address: klosinski.piotr@doktorant.umk.pl; ORCID iD: https://orcid.org/0000-0002-6359-9781

Table S1. Results of post-hoc comparisons for the significant effect of a species*oxygenation (DO) interaction from the model testing fish responses to hypoxia (Table 1). * – significant difference (sequential Bonferroni-corrected Fisher LSD tests).

			DO = 95% vs			
	Tested species	Species	60	40	30	25
A	European bullhead & racer goby	European bullhead	0.033	0.101	0.001*	<0.001*
		Racer goby	0.797	0.894	0.534	0.311
B	Gudgeon & monkey goby	Gudgeon	0.013*	0.009*	0.003*	0.001*
		Monkey goby	0.797	0.555	0.368	0.003*

Effect of hypoxia and acidification on metabolic rate of Ponto-Caspian gobies and their native competitors in the context of climate change

Journal: Hydrobiologia

Piotr Kłosiński[a, *], Jarosław Kobak[b] and Tomasz Kakareko[a]

[a] Department of Ecology and Biogeography, Faculty of Biological and Veterinary Sciences, Nicolaus Copernicus University in Toruń, Lwowska 1, 87-100, Toruń, Poland

[b] Department of Invertebrate Zoology and Parasitology, Faculty of Biological and Veterinary Sciences, Nicolaus Copernicus University in Toruń, Lwowska 1, 87-100, Toruń, Poland

* Corresponding author: Piotr Kłosiński. E-mail address: klosinski.piotr@doktorant.umk.pl; ORCID iD: https://orcid.org/0000-0002-6359-9781

Table S2. Results of post-hoc comparisons for the significant effect of a species*acidification (pH) interaction from the model testing fish responses to acidification (Table 2). * – significant difference (sequential Bonferroni-corrected Fisher LSD tests).

			pH = 8.5 vs			
	Tested species	Species	8.0	7.5	7.0	6.5
A	European bullhead & racer goby	European bullhead	0.666	0.393	0.410	0.028*
		Racer goby	<0.001*	<0.001*	<0.001*	0.085
B	Gudgeon & monkey goby	Gudgeon	<0.001*	<0.001*	0.010*	0.200
		Monkey goby	0.092	0.227	0.155	0.611

Publikacja 3

Kłosiński, P., Kobak, J., & Kakareko, T. (2025b). Competitive interactions for food resources between invasive Ponto-Caspian gobies and their native competitors in the context of global warming. NeoBiota 97, 91–119.

https://doi.org/10.3897/neobiota.97.134566

Tekst opublikowany w czasopiśmie: NeoBiota
Wydawnictwo: PENSOFT PUBLISHERS
Punktacja według wykazu Ministerstwa Nauki i Szkolnictwa Wyższego (2024): 140
Journal Impact Factor (2023): 3.8
Q1 w kategoriach: biodiversity conservation; ecology

A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

NeoBiota 97: 91–119 (2025)
DOI: 10.3897/neobiota.97.134566

Research Article

Competitive interactions for food resources between invasive Ponto-Caspian gobies and their native competitors in the context of global warming

Piotr Kłosiński[1], Jarosław Kobak[2], Tomasz Kakareko[1]

1 *Department of Ecology and Biogeography, Faculty of Biological and Veterinary Sciences, Nicolaus Copernicus University in Toruń, Lwowska 1, 87-100, Toruń, Poland*
2 *Department of Invertebrate Zoology and Parasitology, Faculty of Biological and Veterinary Sciences, Nicolaus Copernicus University in Toruń, Lwowska 1, 87-100, Toruń, Poland*
Corresponding author: Piotr Kłosiński (klosinski.piotr@doktorant.umk.pl)

OPEN ACCESS

Academic editor: Nicola Smith
Received: 13 August 2024
Accepted: 24 December 2024
Published: 3 February 2025

Citation: Kłosiński P, Kobak J, Kakareko T (2025) Competitive interactions for food resources between invasive Ponto-Caspian gobies and their native competitors in the context of global warming. NeoBiota 97: 91–119. https://doi.org/10.3897/neobiota.97.134566

Abstract

Climate warming can modify the process of biological invasions by affecting the outcomes of competition between alien species and their native counterparts in invaded environments. Inland freshwaters are particularly vulnerable to the intensification of such phenomena due to the accumulation of invaders, including thermophilic species that may benefit from warming. We intended to check whether an elevated summer temperature (25 vs. 17 °C) affects the abilities of the Ponto-Caspian gobies to compete for food. These fish are considered temperature-tolerant, highly invasive freshwater fish in Europe. In laboratory experiments, we tested single- and two-species pairs of juvenile specimens of two goby species and their native counterparts from the same ecological guild (the racer goby *Babka gymnotrachelus* versus European bullhead *Cottus gobio*, and monkey goby *Neogobius fluviatilis* versus native gudgeon *Gobio gobio*). The fish competed for food (live chironomidae larvae provided at rates below satiation) for 1 hour at night. We analysed behaviours associated with direct interactions (aggression acts) and foraging activity (time to enter the feeder and the time spent in the feeder). We found that although the gobies did not show higher aggression than the natives, they more actively accessed food compared to the latter, irrespective of temperature. Our results suggest that, in the wild, the invasive fish have a competitive advantage over the native ones due to better resource allocation (gaining food without incurring the costs of aggression) and will maintain this advantage as water warming continues.

Key words: Aggressive behaviour, biological invasions, climate change, food competition, freshwater species, nonnative species

Introduction

Nowadays, biological invasions constitute a leading threat to global biodiversity (Chandra and Gerhardt 2008; Lambertini et al. 2011; Ricciardi et al. 2013; Reid et al. 2019) with adverse impact on native populations (Dudgeon et al. 2006). This is especially true for freshwater ecosystems exposed to strong human impact (Reid et al. 2019; Bernery et al. 2022), which have been colonised by non-native species to a greater extent than human-affected terrestrial habitats (Dudgeon et al. 2006; Ricciardi and MacIsaac 2010).

Invasions of alien species can be aided by changes in environmental conditions, such as climate warming (Walther et al. 2009; Bellard et al. 2013; Chown et al.

2015; Früh et al. 2017). Climate warming is a global phenomenon that causes multiple changes in the functioning and distribution of organisms, including animals (Isaak and Rieman 2013; Estay et al. 2014; Vázquez et al. 2017). Current scenarios predict an average temperature increase by 2–5 °C (depending on the assumed carbon dioxide emission) by the end of this century (Estay et al. 2014; IPCC 2014). It is worth noting that ectothermic animals are especially sensitive to temperature changes, as their physiology (Vinagre et al. 2014; Marras et al. 2015; Stoffels et al. 2017; Barker et al. 2018) and behaviour (Briffa et al. 2013; Magellan et al. 2019) depend on the ambient temperature. Many invasive species evolved under warmer conditions than their native counterparts, therefore their establishment in novel areas is correlated with ongoing global warming (Hellmann et al. 2008; Rahel and Olden 2008; Jones and Cheung 2015; Hesselschwerdt and Wantzen 2018).

The Ponto-Caspian region constitutes the major donor of alien taxa for European waters (Bij de Vaate et al. 2002; Galil et al. 2007), including several species of goby fish (Gobiidae) (Copp et al. 2005; Roche et al. 2013). The Ponto-Caspian invaders migrate to inland waters of Central and Western Europe through the European river network connected by artificial canals (Bij de Vaate et al. 2002; Pauli and Briski 2018; Soto et al. 2023). Since the 1990s, gobies have quickly increased their ranges throughout Europe (Bij de Vaate et al. 2002; Galil et al. 2007), exerting a strong impact on the environment. The gobies evolved in limans and deltas of Ponto-Caspian rivers where the water temperature reaches 29 °C in July, suggesting the higher upper-temperature tolerance limit of local organisms (Rewicz et al. 2014) compared to central, eastern, and northern European areas. Thus, the invasion of the Ponto-Caspian gobies in Central and Western Europe seems to be linked to the progressive increase in the mean annual temperature (Harka and Bíró 2007).

The success of the Ponto-Caspian gobies is often linked to their effective competition (Kakareko et al. 2013; Jermacz et al. 2015; Grabowska et al. 2016, 2019). Due to their competition with local ichthyofauna, they change the abundance and taxonomic composition of the local benthic fish communities (Gurevitch and Padilla 2004; Kornis et al. 2012; Jakovlić et al. 2015), sometimes contributing to the displacement of native species (Kakareko et al. 2013; Grabowska et al. 2016). The latest studies have shown that the outcomes of interspecific competition between Ponto-Caspian gobies and their native counterparts are variable and can depend on species, size, and reproductive status (Kakareko et al. 2013; Jermacz et al. 2015; Błońska et al. 2016; Grabowska et al. 2016). For example, the racer goby *Babka gymnotrachelus* (Kessler, 1857) revealed greater aggressiveness than the native European bullhead *Cottus gobio* Linnaeus, 1758 of comparable size, being a stronger competitor (Kakareko et al. 2013). On the other hand, the monkey goby *Neogobius fluviatilis* (Pallas, 1814) did not exhibit competitive advantage against European bullhead (Błońska et al. 2016).

Ongoing global warming can reconfigure interspecific interactions between invasive species and their native counterparts (Taniguchi et al. 1998; Oyugi et al. 2012; Carmona-Catot et al. 2013; Ramberg-Pihl et al. 2023), potentially increasing existing and generating new negative effects of invasions (Taniguchi et al. 1998; Carmona-Catot et al. 2013; Ramberg-Pihl et al. 2023). The ability of the Ponto-Caspian gobies to maintain their resting metabolism (SMR) within a range of 17–25 °C at a constant and relatively low level compared to their native counterparts can be an important trait responsible for their invasive potential (Kłosiński et al. 2024). This way, the gobies can allocate saved energy to interspecific food competition and have an advantage over native species from the same ecological guild.

The tolerance to elevated temperature and competitive efficiency are separate issues which likely interact with each other, but their interacting effects are unknown. Therefore, we aimed to study these interactions experimentally. First, we assumed that interspecific competition between alien gobies and their native counterparts belonging to the same ecological guild is an effect of overlapping food niches (Peiman and Robinson 2010). Second, we assumed that the invasive status of the gobies has been already determined by earlier studies (Copp et al. 2005; Roche et al. 2013; Vilizzi et al. 2019, 2021), and we are looking for their traits contributing to their invasive potential, i.e. their capability to expand and thrive in new areas. In our study, we compared behaviours associated with interference (aggression) and consumptive (exploitative) competition (rapid access to the food source and time spent on feeding) at two different summer temperatures (17 and 25 °C). A temperature of 17 °C reflects the mean temperature recorded in the warm half-year in rivers in central Poland (Marszelewski and Pius 2014, 2016). In turn, 25 °C refers to the mean annual temperature in the warmest month in rivers in central Poland (Marszelewski and Pius 2014, 2016), but is expected to occur more and more often, and for longer periods with ongoing climate change. In contrast to the native species, the invasive gobies had a chance to evolve mechanisms that enabled them to tolerate relatively high temperatures. We hypothesized that the invasive gobies, compared to their native counterparts, are superior in a direct competition for food. Their advantage will be manifested by higher aggression towards their native competitors than towards conspecifics, visiting the food source faster, spending more time in the feeding area, and limiting the access of the natives to the feeding ground. Moreover, we hypothesized that this competitive advantage of gobies over the native species will become more pronounced at 25 than 17 °C.

Materials and methods

Animals

We tested two goby species of Ponto-Caspian origin, the racer goby and monkey goby, paired with their coexisting native competitors: the European bullhead and gudgeon *Gobio gobio* (Linnaeus, 1758), respectively. These two pairs of species were chosen as they co-occur in the same habitats of European freshwater environments sharing similar biology and ecology (Kakareko et al. 2016; Piria et al. 2016; Janáč et al. 2018; Płąchocki et al. 2020). Thus, interspecific competition between the alien gobies and their native counterparts can be an effect of their overlapping food niches (Peiman and Robinson 2010). The test species have similar food preferences: benthic invertebrates, especially chironomid larvae (Welton et al. 1991; Declerck et al. 2002; Grabowska and Grabowski 2005; Kakareko et al. 2005; Grabowska et al. 2009, 2024). We obtained juvenile fish from lowland rivers in October-November 2022. European bullhead and racer goby were caught in the River Brda (53°08'52.5"N, 17°58'10.5"E), a tributary of the lower River Vistula, by scuba divers using aquarium nets. At this locality, both species are quite common and reach similar densities (ca. 60 specimens per 100 m^2 each) on the river bottom. There is some habitat overlap between small (juvenile) individuals of the two species, with an inverse relationship between their densities, suggesting that competition among them is likely (Kakareko et al. 2016). We collected the fish from four sites (each of about 25 m^2) from areas of a depth of ca. 1–2 m and moderate (0.3–0.6 m s^{-1}) water velocity over small stones and gravel, i.e. where their co-occurrence is most pronounced (Kakareko et al. 2016). Gudgeon and monkey goby were collected by electrofishing (EFGI 650, BSE Bretschneider Spezialelektronik, Germany) in the lower River Vistula (52°26'23.9"N, 19°56'32.5"E). Both species are, in general, common in the river, with the monkey goby considered more abundant than gudgeon in the near-shore fish assemblages (Kakareko et al. 2009; Błażejewski et al. 2022). We collected these species from several sites accessible from the shore by wading, with sandy or sandy-muddy bottoms, and low to moderate flow. Directly after capture, fish were transported to the laboratory (ca. 1–3 h transport time) in polythene bags with oxygenated water. In the laboratory, the fish were placed in 350-L stock tanks with 20–30 individuals of each species per tank, at a temperature measured in the wild (10 °C). After a few days, the temperature in the stock tanks was gradually raised to 17 °C. All specimens used for the tests were of 0+ age. They had no external signs of sexual maturity, thus we did not determine their sex. The stock tanks were filled with conditioned tap water and equipped with aquarium filters, aerators and stony and ceramic shelters, but no bottom substrate. The temperature was maintained by air conditioning at 17 °C. We fed the fish daily with unfrozen chironomid larvae *ad libitum* and uneaten prey were removed from the stock tanks. We exchanged ca. 30% of water volume in the stock tanks once a week. The fish were allowed to adapt to laboratory conditions for at least 1 month before the start of temperature acclimation.

Acclimation procedure to test temperatures

Fish were transferred from the stock tanks to 85-L acclimation tanks in groups of 10–12 individuals, at an initial temperature of 17 °C (as in the stock tanks). The acclimation tanks were filled with conditioned (24 h aged, aerated) tap water and furnished in the same way as the experimental tanks (see below, “Experimental setup”). The progressive adjustment of a temperature up to 25 °C was reached within 8 days using aquarium heaters with an accuracy of 0.25 °C (AQUAEL Ultra Heater 150 W; Suwałki, Poland). During acclimation, fish were fed *ad libitum* once a day with unfrozen chironomid larvae and uneaten prey were removed from the acclimation tanks. Food was delivered with a small amount of water to the acclimation tank on the Petri dish (a feeder placed on the bottom) through the PVC hose and the transparent glass tube. The fish to be tested at 17 °C were transferred from the stock tanks to the acclimation tanks for the same amount of time, but not subject to other temperature alterations. After 8 days in the acclimation tanks, when the temperature reached 25 °C, the fish were transferred to the experimental tanks.

Experimental setup

Experiments were carried out in 27-L tanks (30 × 30 × 30 cm) filled with aged (24 h), aerated tap water. To reduce the effects of handling and visual disturbance on the test fish, the experimental tanks were isolated on all sides by Styrofoam screens. Each tank was furnished with an aerator, two shelters, aquarium heater (between the shelters), and feeder (Suppl. materials 1, 2). Each shelter was made of a PVC tile leaned against the tank wall at an angle of 49 degrees) in the corner of the tank. The two shelters ensured a refuge for both fish outside the feeding periods to mitigate competitive tensions them. The feeder was located opposite the shelters and heater. The feeder consisted of a Petri dish (attached to the experimental tank bottom with silicone glue), a transparent glass tube (attached to the tank wall with silicone glue, suspended 0.5 cm above the Petri dish bottom) and a PVC hose (coming out of the glass tube on the top and extending beyond the tank) (Suppl. material 1). Food (live chironomid larvae) was flushed with a small volume of water into the Petri dish through the hose and glass tube. The construction allowed us to apply food while minimizing the disturbing effect of the experimenter's presence on the fish. We recorded the experiment using an IP video camera (SNB–6004P, Samsung, Changwon, South Korea) suspended 0.8 m above the water level. Because the test species are nocturnal (see below, "Experimental procedure"), we used infrared lamps (MFL-I/ LED5-12 850 nm, eneo, Rödermark, Germany) for recording in darkness.

Experimental procedure

We took the fish for the research randomly, firstly from the field and then from the stock tanks. The total length of the fish was measured from digital photographs taken during tests using ImageJ 1.53k (freeware by W.S. Rasband, U.S. National Institutes of Health, Bethesda, Maryland, USA: https://imagej.net/ij/). Mean (± SD) total lengths (TL) were: 4.68 ± 0.58 cm, 4.87 ± 0.67 cm, 4.70 ± 0.69 cm and 5.31 ± 0.52 cm for the racer goby, bullhead, monkey goby and gudgeon, respectively. Within each species pair, the fish were tested in dyads of similar TL (average difference in TL of 0.10–0.26 cm). Mean TLs of fish in pairs were not significantly different between the species (Student's *t* tests for dependent samples; see Suppl. material 3 for details). The fish were tested either at 17 or 25 °C in (1) single species treatments: two conspecifics, invasive or native; and (2) mixed species treatments: one individual of the invasive species and one individual of the native species. Altogether, we used 71 individuals of the racer goby, 65 individuals of the European bullhead, 78 individuals of the monkey goby and 78 individuals of the gudgeon. In total, we conducted 146 replicates (*n* for a specific treatment = 7–14, see Suppl. material 3 for specific numbers of replicates in particular treatments).

The last feeding took place 40 h before the beginning of the experiment. Two fish (depending on the treatment) were selected from the acclimation tanks and placed in the experimental tank 16 h (at 15:00) before the start of the trial to get familiar with the experimental arena (the adaptation period) (Suppl. material 2). The air stone was turned off before the beginning of the experimental test to prevent water surface movement, which could disturb the video analysis. The tests were always conducted on the following day at 07:00. In the stock, acclimation, and experimental tanks, the photoperiod was set at 12:12 h light:dark cycle with lights on at 10:00 and off at 22:00. Experiments were carried out during the nighttime because the test species are nocturnal and thus their activity (including foraging) is highest at night (Prenda et al. 2000; Erös et al. 2005; Grabowska and Grabowski 2005; Kobler et al. 2012;

Kakareko et al. 2013; Grabowska et al. 2016; Nowak et al. 2019, our preliminary observations). The video camera was turned on at 07:00 and immediately the food (live chironomidae larvae) was delivered manually to the feeder (Suppl. material 2). Fish behaviour was recorded for the next 1 h (07:00–08:00) (Suppl. material 2). This timing was established based on preliminary research, and literature data (Bachman 1984; Taniguchi et al. 1998). Food dose was established as 20–25 mg of live chironomid larvae (2.12–2.65% of the fish weight), which was below the satiation level for one individual (estimated based on preliminary observations). This allowed us to maintain competitive tension between the individuals for limited food resources at the start of the test. Specimens were used only once during the experiments, and subsequently transferred to separate post-experimental tanks with the same water temperature as in the test (Suppl. material 2). After the tests, the elevated temperature in post-experimental tanks was gradually decreased to 17 °C.

Processing video data

Analysis of all the video recordings of fish behaviour was carried out manually, always by the same person, to avoid bias due to differences in the interpretation of fish behaviour. We noted one variable related to aggression and two variables related to foraging: (1) the number of aggressive actions directed towards the opponent, when one fish moved quickly towards the other, which ended in a physical contact between the individuals, such as hitting or pushing (so, the opponents had to touch each other at some moment of the interaction to count the event as aggression). This allowed us to establish clear, strict and objective criteria of aggressiveness, which did not raise any doubts about their correct assessment by the observer; (2) the time to enter the feeder for the first time by each individual; (3) the percentage of time spent by the fish directly in the feeder, which was used as a proxy for food consumption, as it was challenging to observe it directly in darkness. We assume this as a good proxy for foraging, especially in the initial period of the exposure, directly after the food application, when the food was present in the feeder for sure. The animal needed to be present inside the feeder at this moment to have access to the food. In the one-species treatments, because of the visual similarity of the individuals, it was not possible to track them without mistaking particular individuals on video frames. Instead, the two individuals of the same species were tracked together and the final response consisted of summed up and averaged responses of these individuals.

Statistical analysis

We conducted the following types of statistical analyses: (i) comparison between the species within each pair in their single-species treatments (to test differences between the species); (ii) comparison between the species within each pair in the mixed-species treatment (to check which species has an advantage over the other when they are confronted in the same area); (iii) comparison of the behaviour of each species between the mixed vs. single species treatments (to test the impact of one species on the other). Dependent variables tested in the analyses were as follows: (i) the number of aggression events determined in six consecutive 10-min periods during the exposure (analysed using a General Linear Mixed Model; the use of a Generalized Linear Model designed for count data was not possible due to non-integer data points averaged for single species pairs); (ii) the time spent in the feeder (analysed using a General Linear Mixed Model); (iii) the time to enter the feeder (analysed using a Cox proportional hazard regression to account for the individuals that did not enter the feeder at all). Independent variables were as follows: (i) species (in the comparisons between the species); (ii) treatment (in the comparison between the mixed vs. single species treatments for each species); (iii) temperature (17 and 25 °C); (iv) exposure time counted since the food introduction to the feeder (for the models testing the number of aggression events and time spent in the feeder, a continuous covariate: 10, 20, 30, 40, 50, 60 min), (v) individual pair ID as a random factor (to group repeated measurements for each pair of individuals). Species was a within-subject factor when the species tested in mixed-species treatments were compared to each other. The summary of all the models used in the study is shown in Suppl. material 4. In the above-mentioned models, we included all main effects and interactions and then applied backward simplification of the models by removing non-significant higher-order interactions. To meet the assumptions of the General Linear Model, we tested normality with a Shapiro-Wilk test as well as homoscedasticity with a Levene test. We log-transformed the exposure time, time spent in the feeder and number of aggression events to achieve normality. To disentangle significant interactions between exposure time and categorical factors, we used partial models to check: (1) significances of regression slopes for each categorical level; (2) differences between pairs of significant slopes for different categorical levels; (3) differences between the intercepts (means) of parallel or non-significant slopes for different categorical levels. We conducted all statistical analyses using the SPSS 29.0 statistical package (IBM Inc., USA).

Results

The number of aggression events (racer goby vs. European bullhead)

In all treatments, the number of aggression events exhibited by the racer goby and European bullhead decreased with time (a significant effect of exposure time), but was independent of temperature (Table 1, Fig. 1A–D). The number of intraspecific aggression events exhibited by these fish in the single-species treatments (Fig. 1A) depended on a significant main effect of species (Table 1): the racer goby revealed a significantly greater number of aggression events towards conspecifics (0.8 aggressive events on average during the entire 1-h exposure) than the European bullhead (0.1 events on average).

The numbers of interspecific aggression events displayed by the racer goby and European bullhead in the mixed-species treatment (Fig. 1B, 0.7 events on average) did not differ between the species (Table 1).

The racer goby showed similar levels of intra- and interspecific aggression (Fig. 1C), as shown by a non-significant effect of treatment (single vs. mixed-species) (Table 1). Whereas, the number of interspecific aggression events exhibited by the European bullhead was higher than that directed towards conspecifics (Fig. 1D), as shown by a significant effect of treatment (Table 1).

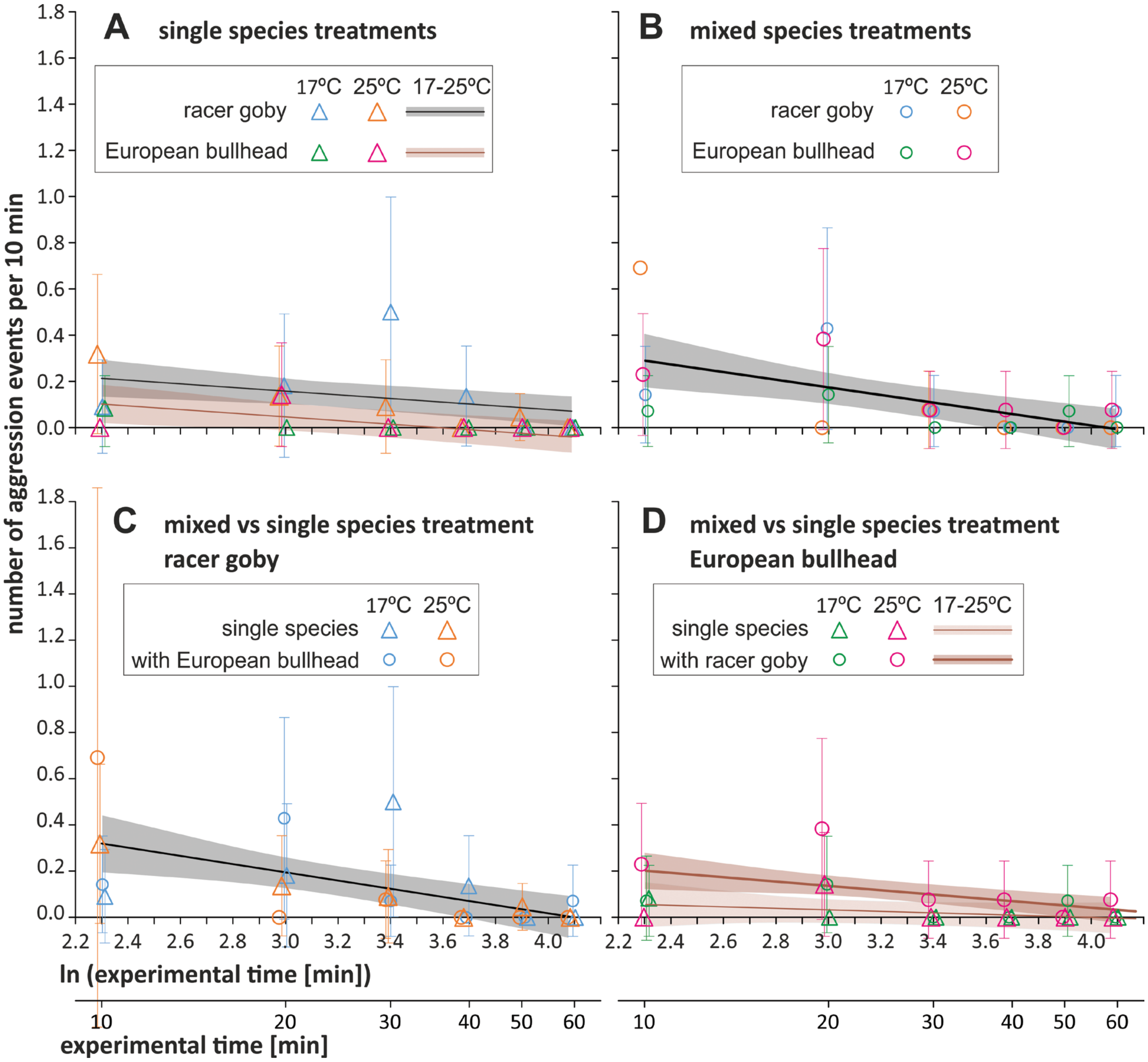


Figure 1. Numbers of aggression acts per 10 min (a single observation period) shown by the racer goby and European bullhead kept in separate single-species treatments (**A**) or together in the mixed-species treatment (**B**). Panels **C, D** present comparisons of the behaviour of the racer goby and European bullhead, respectively, between the single- and mixed-species treatments. Symbols represent raw data (means ± 95%CI) for each species, temperature and period. Lines are predicted by the models (with 95%CI as shaded areas). Common slopes were predicted for groups of data that did not differ significantly from each other in the models.

The number of aggression events (monkey goby vs. gudgeon)

In the single-species treatments (Fig. 2A), the monkey goby and gudgeon displayed similar levels of intraspecific aggression (0.3 aggression events on average during the 1-h exposure), irrespective of temperature, but decreasing with time (Table 2, Fig. 2A).

The number of interspecific aggression events displayed by these fish in the mixed-species treatment (Fig. 2B) depended on an interaction between species and exposure time, but was independent of temperature (Table 2, Suppl. material 5). This resulted from the significantly greater interspecific aggression of the gudgeon (1.8 aggression events on average during the entire 1-h exposure, including 0.8 events within the first 10 min) compared to that displayed by the monkey goby (0.1 events, all during the first 10 min) at the beginning of the exposure.

Table 1. General Linear Mixed Models to test the impact of treatment, temperature, exposure time and species on the number of aggressive events shown by the racer goby and European bullhead. Non-significant higher order interactions were removed from the models in a simplification procedure.

Analysis	Effect	*df*	*F*	*P*
Racer goby vs European bullhead from single-species treatments	Species	1, 38	8.43	0.006*
	Temperature	1, 38	0.43	0.519
	Exposure time ^{C}	1, 204	7.85	0.006*
Racer goby vs European bullhead from the mixed-species treatment	Species^{WS}	1, 295	0.33	0.565
	Temperature	1, 25	0.75	0.395
	Exposure time^{C}	1, 295	13.78	<0.001*
Racer goby from mixed- vs single-species treatments	Treatment	1, 46	0.001	0.976
	Temperature	1, 46	0.09	0.766
	Exposure time^{C}	1, 244	13.40	<0.001*
European bullhead from mixed- vs single-species treatments	Treatment	1, 43	4.81	0.034*
	Temperature	1, 43	3.81	0.057
	Exposure time^{C}	1, 229	8.69	0.004*

^{WS} – within-subject effect, ^{C} – continuous covariate.

Table 2. General Linear Mixed Models to test the impact of treatment, temperature, exposure time and species on the number of aggressive events shown by the monkey goby and gudgeon. Non-significant higher order interactions were removed from the models in a simplification procedure.

Analysis	Effect	*df*	*F*	*P*
Monkey goby vs gudgeon from single-species treatments	Species	1, 47	0.11	0.746
	Temperature	1, 47	0.06	0.806
	Exposure time^{C}	1, 249	13.73	<0.001*
Monkey goby vs gudgeon from the mixed-species treatment	Species^{WS} (Spec.)	1, 305	17.58	<0.001*
	Temperature	1, 26	1.06	0.313
	Exposure time^{C} (Time)	1, 305	17.28	<0.001*
	Spec.^{WS}*Time	1, 305	12.18	0.001*
Monkey goby from mixed- vs single-species treatments	Treatment	1, 50	1.88	0.177
	Temperature	1, 50	1.41	0.241
	Exposure time^{C}	1, 264	9.05	0.003*
Gudgeon from mixed- vs single-species treatments	Treatment (Treat.)	1, 279	9.42	0.002*
	Temperature (Temp.)	1, 279	1.56	0.212
	Exposure time (Time)^{C}	1, 261	19.98	<0.001*
	Treat.*Temp.	1, 279	6.06	0.014*
	Treat.*Time	1, 261	6.36	0.012*
	Temp.*Time	1, 261	1.28	0.259
	Treat.*Temp.*Time	1, 261	5.12	0.024*

^{WS} – within-subject effect, ^{C} – continuous covariate.

The monkey goby displayed similar levels of intra- and interspecific aggression (single vs. mixed-species treatments) irrespective of temperature (Fig. 2C), but decreasing with exposure time (Table 2).

On the other hand, the number of aggression events shown by the gudgeon (Fig. 2D) depended on an interaction between treatment (single vs. mixed-species), temperature and exposure time (Table 2). The aggression of gudgeon directed towards the monkey goby at 17 °C (2.2 events on average during the entire exposure, including 1.7 events within the first 20 min) was higher than that directed towards conspecifics (0.2 events, all within the first 20 min) at the beginning of the exposure, and decreased later, as shown by its significant slope (Suppl. material 5,

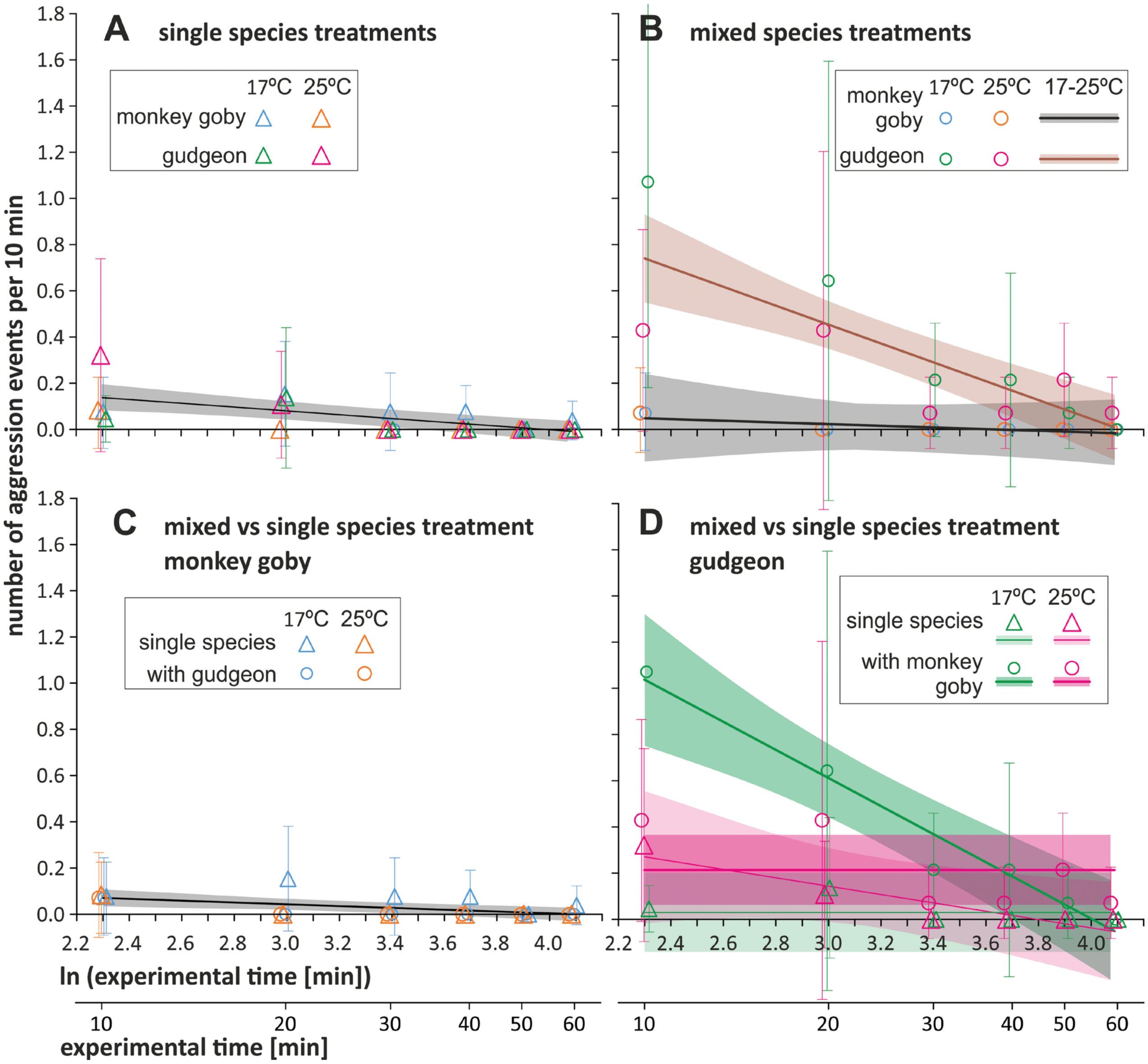


Figure 2. Numbers of aggression acts per 10 min (a single observation period) shown by the monkey goby and gudgeon kept in separate single-species treatments (**A**) or together in the mixed-species treatment (**B**). Panels **C, D** present comparisons of the behaviour of the monkey goby and gudgeon, respectively, between the single- and mixed-species treatments. Symbols represent raw data (means ± 95%CI) for each species, temperature and period. Lines are predicted by the models (with 95%CI as shaded areas). Common slopes were predicted for groups of data that did not differ significantly from each other in the models. Horizontal lines indicate non-significant slopes.

Fig. 2D). At 25 °C, the gudgeon showed similarly low levels of intra- and interspecific aggression (0.1 events, Fig. 2D).

Time to enter the feeder (racer goby vs. European bullhead)

In the single-species treatments (Fig. 3A) the racer goby entered the feeder earlier (after 2 min on average) than European bullhead (9 min), irrespective of temperature (Table 3).

In the mixed-species treatment (Fig. 3B), the racer goby entered the feeder faster (4.5 min and 13 min at 17 and 25 °C, respectively) than the European bullhead (22.5 min and 36.5 min, respectively), and both species appeared in the feeder faster at 17 vs. 25 °C (Table 3).

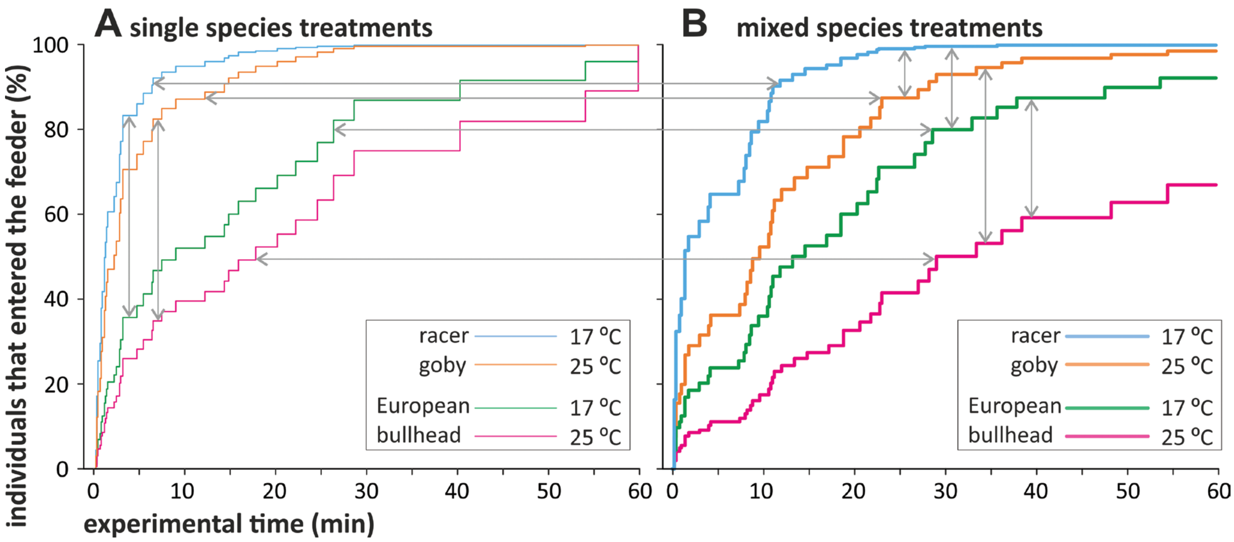


Figure 3. Times to enter the feeder by the racer goby and European bullhead kept in separate single-species treatments (**A**) or together in the mixed-species treatment (**B**). Arrows indicate groups significantly differing from each other.

Table 3. Cox proportional hazard regression models to test the effect of treatment, temperature and species on the time to enter the feeder by the racer goby and European bullhead.

Analysis	Effect	*df*	χ^2	*P*
Racer goby vs European bullhead from single-species treatments	Species	1	12.92	<0.001*
	Temperature	1	1.16	0.282
Racer goby vs European bullhead from the mixed-species treatment	Species	1	17.54	<0.001*
	Temperature	1	6.99	0.008*
Racer goby from mixed- vs single-species treatments	Treatment	1	4.96	0.026*
	Temperature	1	4.45	0.035*
European bullhead from mixed- vs single-species treatments	Treatment	1	10.58	<0.001*
	Temperature	1	0.63	0.429

The racer goby reached the feeder earlier in the presence of conspecifics than with the European bullhead (Table 3, Fig. 3A, B). The European bullhead also entered the feeder earlier in the presence of conspecifics than with the racer goby, irrespective of temperature (Table 3, Fig. 3A, B).

Time to enter the feeder (monkey goby vs. gudgeon)

In the single-species treatments (Fig. 4A), the monkey goby entered the feeder earlier (9 min and 3.5 min at 17 and 25 °C, respectively) than the gudgeon (21 min and 7.5 min, respectively), and both species appeared in the feeder faster at 25 vs. 17 °C (Table 4).

In the mixed-species treatment (Fig. 4B), the monkey goby entered the feeder earlier (8 min) than the gudgeon (19.5 min) irrespective of temperature (Table 4).

The entry time to the feeder shown by the monkey goby and gudgeon was independent of the species identity of the other individual in the pair (Table 4, Fig. 4A, B).

Time spent in the feeder (racer goby vs. European bullhead)

In the single-species treatments (Fig. 5A), both the racer goby and European bullhead spent more time in the feeder at 17 than 25 °C (3.4 vs. 1.9% of the total exposure time) throughout the exposure time as indicated by a significant main

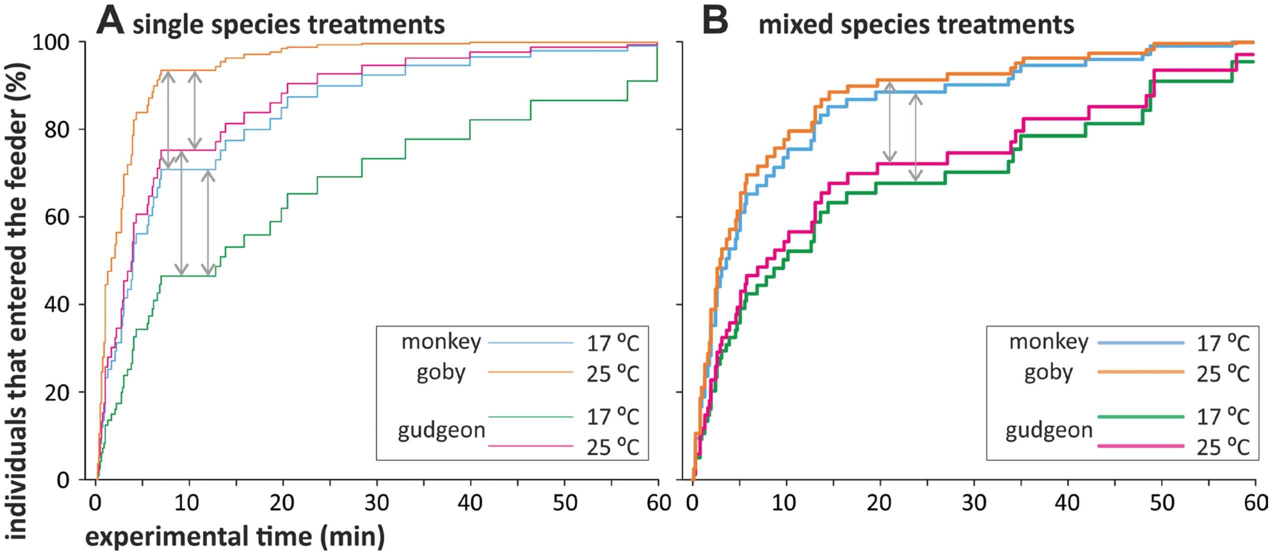


Figure 4. Times to enter the feeder by the monkey goby and gudgeon kept in separate single-species treatments (**A**) or together in the mixed-species treatment (**B**). Arrows indicate groups significantly differing from each other.

Table 4. Cox proportional hazard regression models to test the effect of treatment, temperature and species on the time to enter the feeder by monkey goby and gudgeon.

Analysis	Effect	*df*	χ^2	*P*
Monkey goby vs gudgeon from single-species treatments	Species	1	5.33	0.021*
	Temperature	1	6.42	0.011*
Monkey goby vs gudgeon from the mixed-species treatment	Species	1	4.74	0.029*
	Temperature	1	0.18	0.671
Monkey goby from mixed- vs single-species treatments	Treatment	1	0.56	0.454
	Temperature	1	0.10	0.754
Gudgeon from mixed- vs single-species treatments	Treatment	1	1.51	0.219
	Temperature	1	7.84	0.005*

effect of temperature (Table 5). Moreover, time spent in the feeder decreased with time (Fig. 5A, Table 5), but differently for each species, which resulted in a significant interaction between species and exposure time (Table 5, Suppl. material 6). The racer goby spent more time in the feeder than the European bullhead at the beginning of exposure (10.0 vs. 2.7% during the first 10 min of the exposure), but not at the end (Fig. 5A).

The presence of heterospecifics in the mixed-species treatment (Fig. 5B, C) did not affect the time spent in the feeder by the racer goby and European bullhead, compared to their behaviour in the single-species treatments, as shown by a non-significant effect of treatment (Table 5).

Time spent in the feeder (monkey goby vs. gudgeon)

In the single-species treatments (Fig. 6A), time spent by the monkey goby and gudgeon in the feeder depended on species*exposure time and temperature*exposure time interactions (Table 6). Time spent in the feeder by both species decreased with time at different rates, depending on species and temperature (Suppl. material 6). At the beginning of the exposure, both species spent more time in the feeder at 25 °C than at 17 °C (4.9 vs. 2.1% of time during the first 20 min of the exposure),

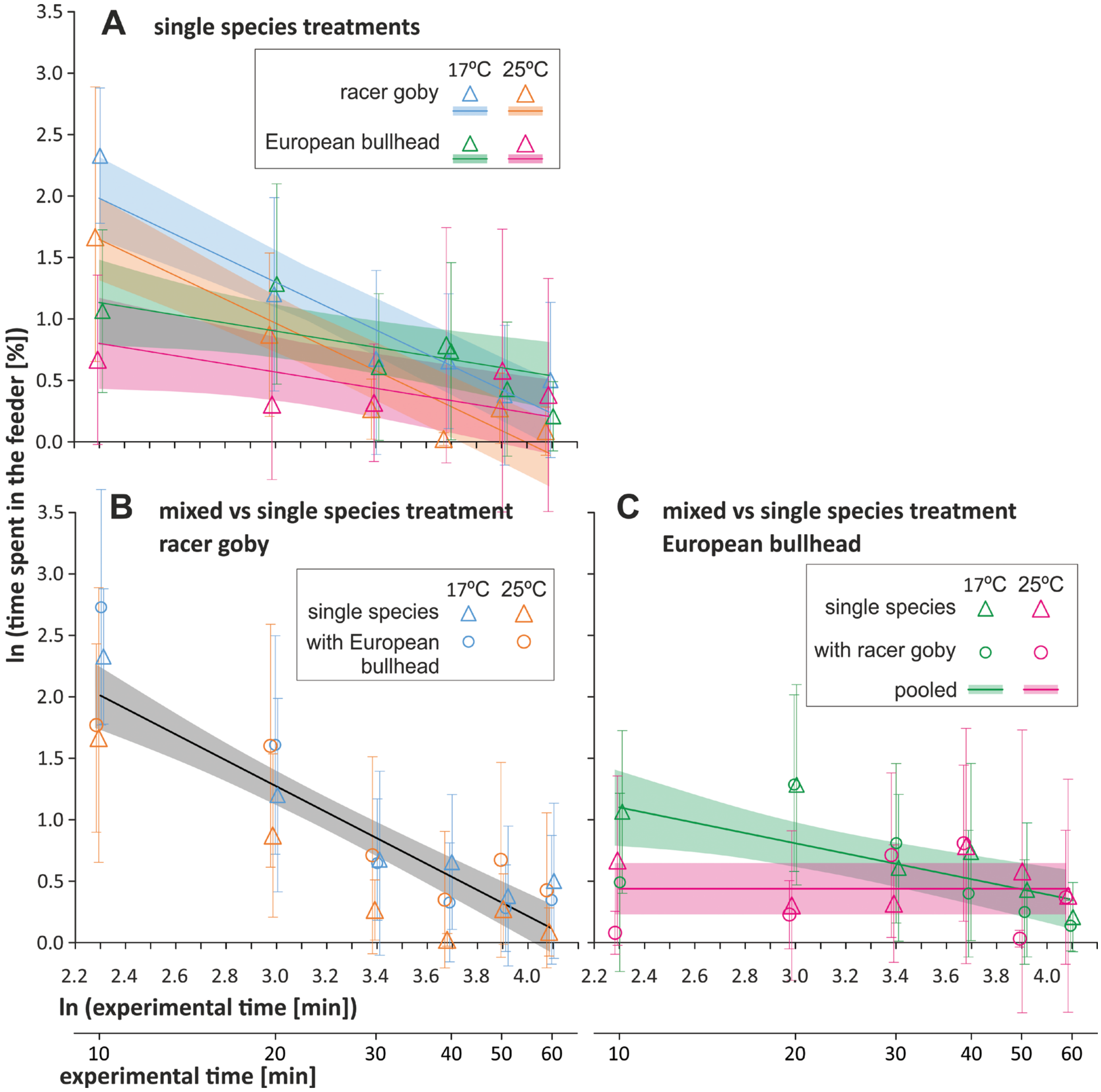


Figure 5. Times spent in the feeder (as percentage of the total exposure time) by the racer goby and European bullhead kept in separate single-species treatments (**A**). Panels **B, C** present comparisons of the behaviour of the racer goby and European bullhead, respectively, between the single- and mixed-species treatments. Symbols represent raw data (means ± 95%CI) for each species, temperature and period. Lines are predicted by the models (with 95%CI as shaded areas). Common slopes were predicted for groups of data that did not differ significantly from each other in the models. Horizontal lines indicate non-significant slopes.

and the monkey goby spent more time in the feeder than the gudgeon (4.7 vs. 2.3% of time during the first 20 min of the exposure).

The feeder was occupied for a longer time by the monkey goby in the presence of the gudgeon in the mixed-species treatment (6.9% of the total exposure time, Fig. 6B) than in the single-species treatment (2%) throughout the exposure duration, as shown by a significant main effect of treatment (Table 6).

Whereas the gudgeon spent more time in the presence of conspecifics than with the monkey goby, but only at the beginning of exposure at 25 °C (6.7 vs. 4.0% of time during the first 20 min of the exposure, Fig. 6C), as shown by a significant interaction between treatment (single vs. mixed-species treatment), temperature and exposure time (Table 6, Suppl. material 6).

Table 5. General Linear Mixed Models to test the impact of treatment, temperature, exposure time and species on the feeder occupancy time shown by the racer goby and European bullhead. Non-significant higher order interactions were removed from the models in a simplification procedure.

Analysis	Effect	*df*	*F*	*P*
Racer goby vs European bullhead from single-species treatments	Species (Spec.)	1, 220	14.44	<0.001*
	Temperature	1, 38	6.74	0.013*
	Exposure time (Time)^{C}	1, 203	55.08	<0.001*
	Spec.*Time	1, 203	13.30	<0.001*
Racer goby from mixed- vs single-species treatments	Treatment	1, 46	2.43	0.126
	Temperature	1, 46	2.95	0.093
	Exposure time^{C}	1, 244	103.98	<0.001*
European bullhead from mixed- vs single-species treatments	Treatment	1, 43	1.32	0.258
	Temperature (Temp.)	1, 246	9.10	0.003*
	Exposure time (Time)^{C}	1, 228	3.19	0.075
	Temp.*Time	1, 228	7.59	0.006*

^{C} – continuous covariate.

Table 6. General Linear Mixed Models to test the impact of treatment, temperature, exposure time and species on the feeder occupancy time shown by the monkey goby and gudgeon. Non-significant higher order interactions were removed from the models in a simplification procedure.

Analysis	Effect	*df*	*F*	*P*
Monkey goby vs gudgeon from single-species treatments	Species (Spec.)	1, 264	27.41	<0.001*
	Temperature (Temp.)	1, 264	20.27	<0.001*
	Exposure Time (Time)^{C}	1, 247	91.76	<0.001*
	Spec.*Time	1, 247	24.71	<0.001*
	Temp.*Time	1, 247	17.78	<0.001*
Monkey goby from mixed- vs single-species treatments	Treatment	1, 50	8.28	0.006*
	Temperature	1, 50	0.03	0.871
	Exposure time^{C}	1, 264	108.14	<0.001*
Gudgeon from mixed- vs single-species treatments	Treatment (Treat.)	1, 290	0.06	0.803
	Temperature (Temp.)	1, 290	8.10	0.005*
	Exposure time (Time)^{C}	1, 261	14.47	<0.001*
	Treat.*Temp.	1, 290	3.58	0.060
	Treat.*Time	1, 261	0.02	0.889
	Temp.*Time	1, 261	6.28	0.013*
	Treat.*Temp.*Time	1, 261	4.00	0.046*

^{C} – continuous covariate.

Discussion

Present work supported the first hypothesis that the non-native gobies are more successful food competitors than their native counterparts. Although the invaders did not consistently outperform the natives in terms of higher aggression, they revealed faster and longer food access compared to the natives. However, the second hypothesis was not confirmed. The effect of an elevated temperature on interspecific competition did not translate into a more apparent dominance of the gobies over the native fish.

Aggression

In single-species treatments, the racer goby was more aggressive than the European bullhead. In contrast, the gudgeon and monkey goby did not differ in level of aggression in the second pair of co-existing species. This finding suggests that aggressive

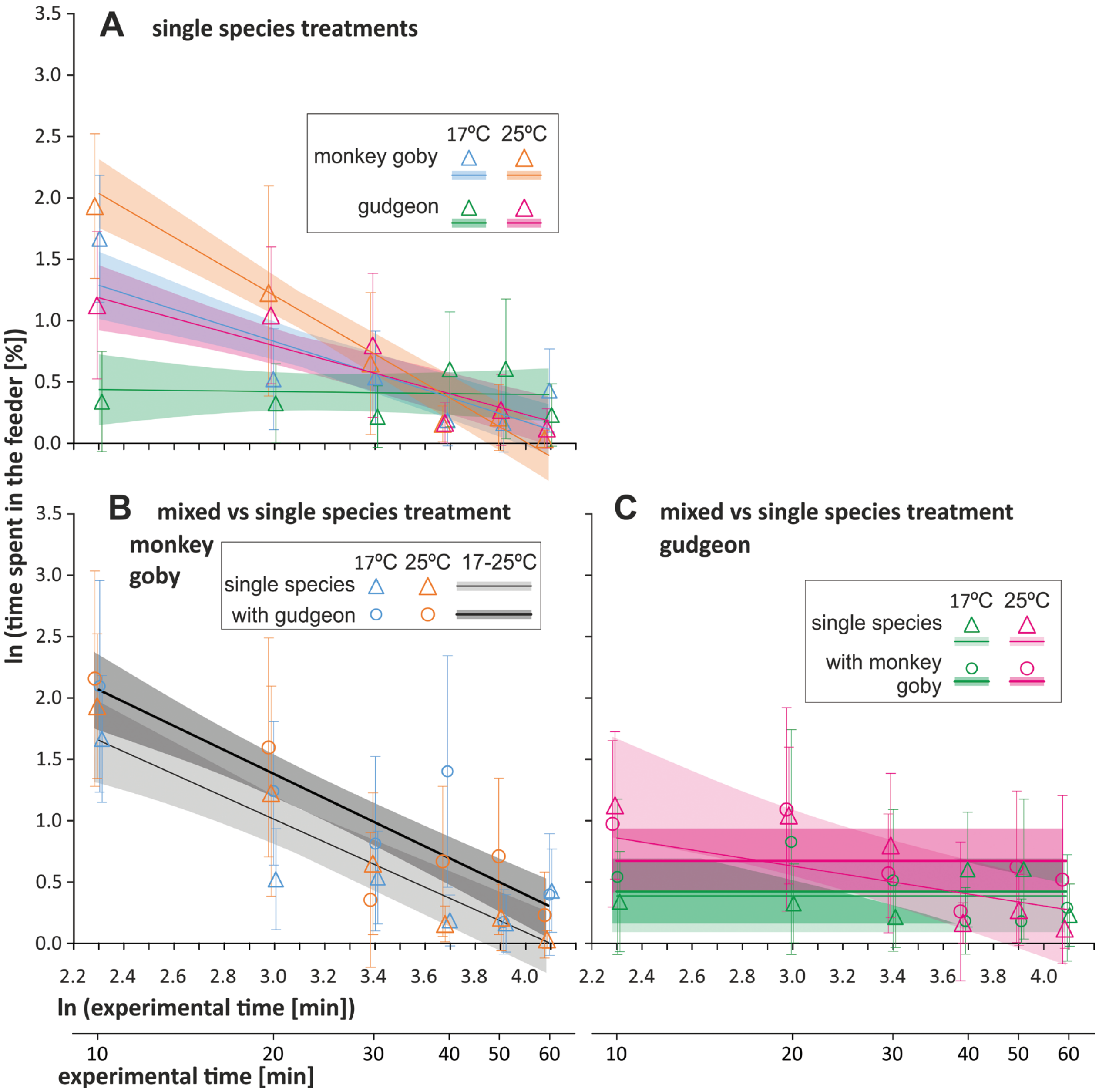


Figure 6. Times spent in the feeder (as percentage of the total exposure time) by the monkey goby and gudgeon kept in separate single-species treatments (**A**). Panels **B, C** present comparisons of the behaviour of the monkey goby and gudgeon, respectively, between the single- and mixed-species treatments. Symbols represent raw data (means ± 95%CI) for each species, temperature and period. Lines are predicted by the models (with 95%CI as shaded areas). Common slopes were predicted for groups of data that did not differ significantly from each other in the models. Horizontal lines indicate non-significant slopes.

behaviour is of primary importance for establishing intra-species dominance in the racer goby, while it is not so in the other species tested. Interestingly, relatively higher aggression was revealed in inter-species interactions in these species in our study (Ladich 1988, 1990, 1997; Hadjiaghai and Ladich 2015; Horvatić et al. 2016, 2021; Fattorini et al. 2023). According to the resource overlap hypothesis (Connell 1983; Britton et al. 2010; Peiman and Robinson 2010), intraspecific aggression is usually stronger than interspecific one because of the greater niche similarity between conspecifics compared to heterospecifics (Kornis et al. 2014). While, in the present work, the native species increased their aggression in the presence of their invasive counterparts. Moreover, the gudgeon was more aggressive towards the monkey goby than the other way round. These findings are also surprising in the light of the fact that, in general, invasive fish species have been found to display higher levels of aggression than native fish species (Blanchet et al. 2007; Martin et al. 2010; Kakareko et al. 2013), which is considered an important behavioural mechanism determining the competitive superiority of successful invaders (Pintor et al. 2008; Hudina et al. 2014; Silva et al. 2019). Although the opposite situations can be found e.g., in native cichlids: the Kariba tilapia *Oreochromis mortimeri* (Chifamba and Mauru 2017) and the Mexican mojarra *Cichlasoma istlanum* (Archundia and Arce 2019), these are rather rare. In the case of the Ponto-Caspian gobies, earlier laboratory experiments on adult individuals have demonstrated that the higher aggressiveness allowed them to gain an advantage over native species (Kakareko et al. 2013; Jermacz et al. 2015; Grabowska et al. 2016). Nevertheless, relatively high aggression of invasive gobies in those experiments could depend on their larger size (associated with older age and maturity) than that of the gobies tested in the present work (Logue et al. 2011; Funghi et al. 2015; Beltrão et al. 2021; Diatroptov and Opaev 2023), especially during the spawning period (Grabowska et al. 2016). On the contrary, we showed that juvenile specimens of the invasive gobies exhibited lower aggression against their native counterparts (except the gudgeon at 25 °C). It is worth noting that aggression can depend on metabolic traits (Seth et al. 2013; Killen et al. 2014). Species with relatively high standard (resting) metabolism displayed more aggression (Metcalfe et al. 1995; Cutts et al. 1998). Indeed, our findings are supported in this respect by the results of Kłosiński et al. (2024), who showed that the native species from the same populations and similar in size to those studied in this work exhibit a higher resting metabolism compared to the invasive gobies. This indicates that juveniles of native gudgeon and European bullhead have a potential to expend energy on activities associated with aggressive behaviour. Although such behaviour, as mentioned earlier, is not displayed by the natives in intra-population interactions, it is activated when confronted with juvenile gobies (less aggressive than older individuals). This suggests that the native fish treat juvenile gobies as weaker opponents than conspecifics when assessing the risk of defeat before deciding to start fighting. Nevertheless, in our study, despite the aggression displayed by the natives, the invasive gobies could reach the feeder more efficiently than their native competitors. Thus, the aggression of the native fish turned out to be ineffective against the alien competitors.

The relationship between temperature and aggression acts can be variable. Elevated temperature can either increase (Wilson et al. 2007; Seebacher et al. 2013) or decrease aggression level (White et al. 2019), or cause no changes in aggression (White et al. 2020). In our study, the gudgeon was less aggressive against the monkey goby at 25 °C than at 17 °C. This inability to maintain the constant level of aggression could be accounted for by the temperature elevated beyond its physiological tolerance (Kłosiński et al. 2024), causing a relatively high energy demand. Thus, the gudgeon might have suppressed costly aggressive acts in favour of reaching the feeder earlier to compensate for metabolic costs associated with elevated temperature (Morgan et al. 2001). From the metabolic point of view, aggressive behaviours are associated with relatively high energetic expenditures (Briffa and Sneddon 2007; Seebacher et al. 2013; Fisher et al. 2021), which are expected to have adverse consequences for fitness in the natives.

Regarding the first pair of fish studied, we found that the aggression shown by the European bullhead and racer goby was independent of temperature. This indicates the potential of the European bullhead to survive in warming waters, assuming they have access to abundant food resources and meet increased energy needs under such conditions. According to Killen et al. (2013), the greater the metabolic scope, the faster the recovery after the effort, and the lower probability that aggressive behaviour is constrained by maximal metabolic capacity. A higher aerobic scope shown by the European bullhead compared to the racer goby, both at 17 and 25 °C (Kłosiński et al. 2024), can allow it to show a greater flexibility in energy allocation (Maazouzi et al. 2011; Killen et al. 2016). On the other hand, allocating too much energy in aggression can lead to the depletion of energy resources for other life activities, such as anti-predatory defences or foraging (Sneddon et al. 1999; Seebacher et al. 2013; Chifamba and Mauru 2017). Therefore, aggression can be beneficial if food resources are possible to defend (Peiman and Robinson 2010). However, our study suggests this is not the case for juvenile European bullhead facing the racer goby invasion in the wild. This is because, in our experiment, the bullhead aggression was insufficient to effectively defend the food resource against the invasive competitor (see the subchapter below).

Foraging

We posit that the time to enter the feeder and the time spent in the feeder should be considered together. These two behaviours are likely to act together in the same direction to enhance the probability of success in food resource competition. Both gobies tended to reach the feeder before their native counterparts. This was likely to limit foraging of their native competitors and provided the invasives with better access to the richest food resources (directly after the food application), which has also been shown for larger (adult) European bullhead and racer goby (Kakareko et al. 2013). Thus, competition between invasive gobies and their native counterparts is likely to depend on the exploitation of resources by the invaders, successfully reducing the foraging time of the natives (Keiller et al. 2021). This has been demonstrated in our study for the monkey goby-gudgeon pair. Alternatively, even if the native species spent the same time in the feeder as their invasive counterparts, the food could have already been eaten by the gobies, being earlier visitors in the feeder. This has been shown in the racer goby-European bullhead pair in our study.

An elevated temperature delayed the time to enter the feeder by the invasive racer goby, despite the fact that this species originates from a warmer climate than that in its invaded range. Hence, increased temperature may have a disruptive effect not only on natives, but also on invasive species. However, the native species, being less adapted to elevated temperatures, can use even more energy or even limit their foraging (thus causing difficulties with obtaining energy) at 25 °C. Therefore, in the longer term, indirect (exploitation) competition (Vonshak et al. 2012; Newman et al. 2020) may adversely affect native species more than invasives as waters become warmer. It is worth emphasising that of the Ponto-Caspian Gobiidae, the round goby (*Neogobius melanostomus*) has received the greatest attention in terms of successfully competing for food with native fish (Grabowska et al. 2023). Janssen and Jude (2001) proposed that interference competition, rather than exploitation competition, was the primary mechanism for declines in the mottled sculpin populations following the round goby invasion. Less attention has been given to the other goby species from the Ponto-Caspian region, which have expanded to many European inland waters. For the first time, we showed that interspecific competition between juvenile individuals of these gobies and their native counterparts is based on the ability to gain better (faster and longer) access to food resources rather than on direct aggression. Moreover, the ability to assess their chances and avoid a direct conflict with an opponent allows animals to minimize their energy loss and risk of injuries (Parker and Rubenstein 1981; Moretz 2003; Poulos and McCormick 2014), which is consistent with the non-aggressive (fight-avoiding) behaviour of juvenile invasive gobies in our experiment.

Final remarks

Our study has shown that, regardless of summer temperatures (normal or elevated) that occur in Central European rivers, the juvenile invasive gobies are more effective than their native counterparts in competing for access to limited food resources. This finding broadens the knowledge of the threat posed by the Ponto-Caspian gobies towards native European freshwater fishes (see a review by Grabowska et al. 2023), although it does not support the growing evidence for the negative influence of elevated temperatures on native fish species in competitive interactions with invasive species (Taniguchi et al. 1998; Oyugi et al. 2012; Ramberg-Pihl et al. 2023). In our study, the native fish, although more aggressive, could not effectively compete with the juvenile individuals of the gobies irrespective of temperature. This suggests that, in the wild, the juveniles of the invasive gobies have a competitive advantage over natives, gaining better access to food without the cost of aggression, and will maintain this advantage as waters get warmer. It is worth bearing in mind that the gobies have been proven to outperform the natives in other aspects of global warming. They have lower living costs by keeping a lower resting metabolism at the elevated temperature (Kłosiński et al. 2024) and show a greater physiological tolerance to hypoxia (Kłosiński et al. 2025), which is considered another effect of global warming in fresh waters (Ficke et al. 2007; Jane et al. 2021). Therefore, the future invasion success of the alien gobies owing to efficient food competition may be even enhanced by warming waters, although further studies are needed to confirm this.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

We sampled and used the fish by the permit of the Local Committee for Ethics in Animal Research in Bydgoszcz, Poland, statement no. 30/2022 from 22 June 2022. In addition, the capture and use of the European bullhead, which is protected by law in Poland, was accepted by the Regional Directorate of Environmental Protection in Bydgoszcz, Poland (approval number: WOP.6401.4.52.2022.MO). The procedures conducted within the study met the ASAB/ABS guidelines for the use of animals in research (ASAB Ethical Committee and ABS Animal Care Committee 2019). The housing conditions guaranteed a high level of animal welfare, which was manifested by the overall activity and food intake of the fish throughout the research period. The fish had no external signs of stress or disease. Each specimen was used only once. After the experiments, the European bullhead and gudgeon were released into the wild from which they were caught. In turn, racer goby and monkey goby, as invasive species were euthanized by an overdose of buffered Tricaine Methanesulfonate (MS-222) and disposed of according to the Regulation of the Polish Minister of the Environment from 9 September 2011 (Journal of Laws No. 210, item 1260). Killing was conducted by a qualified, certified person (certificate No. 2355/2015 issued by the Polish Laboratory Animal Science Association).

Funding

This research was supported by “The Excellence Initiative – Research University” programme at Nicolaus Copernicus University in Toruń, Poland.

Author contributions

PK: Conceptualisation, Resources, Methodology, Investigation, Formal analysis, Data interpretation, Visualisation, Writing-Original draft preparation. JK: Conceptualisation, Resources, Formal analysis, Data interpretation, Visualisation, Writing-Review & Editing. TK: Conceptualisation, Resources, Methodology, Data interpretation, Writing-Review & Editing, Supervision.

Author ORCIDs

Piotr Kłosiński https://orcid.org/0000-0002-6359-9781
Jarosław Kobak https://orcid.org/0000-0001-7660-9240
Tomasz Kakareko https://orcid.org/0000-0001-5054-7416

Data availability

The data that support the findings of this study are available from the corresponding author, PK, upon reasonable request.

References

Archundia M, Arce E (2019) Fighting behaviour in native fish: the Mexican mojarra (*Cichlasoma istlanum*) wins when confronted with the non-native convict cichlid fish (*Amatitlania nigrofasciata*). Journal of Ethology 37(1): 67–73. https://doi.org/10.1007/s10164-018-0569-5

ASAB Ethical Committee, ABS Animal Care Committee (2019) Guidelines for the treatment of animals in behavioural research and teaching. Animal Behaviour 147: I–X. https://doi.org/10.1016/j.anbehav.2018.12.015

Bachman RA (1984) Foraging behavior of free-ranging wild and hatchery brown trout in a stream. Transactions of the American Fisheries Society 113(1): 1–32. https://doi.org/10.1577/1548-8659(1984)113<1:FBOFWA>2.0.CO;2

Barker BD, Horodysky AZ, Kerstetter DW (2018) Hot or not? Comparative behavioral thermoregulation, critical temperature regimes, and thermal tolerances of the invasive lionfish *Pterois* sp. versus native western North Atlantic reef fishes. Biological Invasions 20(1): 45–58. https://doi.org/10.1007/s10530-017-1511-4

Bellard C, Thuiller W, Leroy B, Genovesi P, Bakkenes M, Courchamp F (2013) Will climate change promote future invasions? Global Change Biology 19(12): 3740–3748. https://doi.org/10.1111/gcb.12344

Beltrão P, Godinho C, Lourenço R, Pereira PF (2021) Behavioural repeatability in Sardinian warblers (*Sylvia melanocephala*): larger individuals are more aggressive. Acta Ethologica 24(1): 31–40. https://doi.org/10.1007/s10211-020-00358-3

Bernery C, Bellard C, Courchamp F, Brosse S, Gozlan RE, Jarić I, Teletchea F, Leroy B (2022) Freshwater fish invasions: A comprehensive review. Annual Review of Ecology, Evolution, and Systematics 53: 427–456. https://doi.org/10.1146/annurev-ecolsys-032522-015551

Bij de Vaate A, Jazdzewski K, Ketelaars HAM, Gollasch S, Van der Velde G (2002) Geographical patterns in range extension of Ponto-Caspian macroinvertebrate species in Europe. Canadian Journal of Fisheries and Aquatic Sciences 59(7): 1159–1174. https://doi.org/10.1139/f02-098

Blanchet S, Loot G, Bernatchez L, Dodson JJ (2007) The disruption of dominance hierarchies by a non-native species: An individual-based analysis. Oecologia 152(3): 569–581. https://doi.org/10.1007/s00442-007-0668-4

Błażejewski M, Król J, Kakareko T, Mierzejewska K, Hliwa P (2022) Daily and seasonal dynamics of littoral zone fish communities in the lowland Włocławek Reservoir (central Poland), with a special emphasis on alien invasive gobies. Journal of Limnology 81(1): 2059. https://doi.org/10.4081/jlimnol.2022.2059

Błońska D, Kobak J, Kakareko T, Grabowska J (2016) Can the presence of alien Ponto-Caspian gobies affect shelter use by the native European bullhead? Aquatic Ecology 50(4): 653–665. https://doi.org/10.1007/s10452-016-9584-1

Briffa M, Sneddon LU (2007) Physiological constraints on contest behaviour. Functional Ecology 21(4): 627–637. https://doi.org/10.1111/j.1365-2435.2006.01188.x

Briffa M, Bridger D, Biro PA (2013) How does temperature affect behaviour? Multilevel analysis of plasticity, personality and predictability in hermit crabs. Animal Behaviour 86(1): 47–54. https://doi.org/10.1016/j.anbehav.2013.04.009

Britton JR, Cucherousset J, Davies GD, Godard MJ, Copp GH (2010) Non-native fishes and climate change: Predicting species responses to warming temperatures in a temperate region. Freshwater Biology 55(5): 1130–1141. https://doi.org/10.1111/j.1365-2427.2010.02396.x

Carmona-Catot G, Magellan K, García-Berthou E (2013) Temperature-specific competition between invasive mosquitofish and an endangered cyprinodontid fish. PLoS ONE 8(1): e54734. https://doi.org/10.1371/journal.pone.0054734

Chandra S, Gerhardt A (2008) Invasive species in aquatic ecosystems: issue of global concern. Aquatic Invasions 3(1): 1–2. https://doi.org/10.3391/ai.2008.3.1.1

Chifamba PC, Mauru T (2017) Comparative aggression and dominance of *Oreochromis niloticus* (Linnaeus, 1758) and *Oreochromis mortimeri* (Trewavas, 1966) from paired contest in aquaria. Hydrobiologia 788(1): 193–203. https://doi.org/10.1007/s10750-016-2997-y

Chown SL, Hodgins KA, Griffin PC, Oakeshott JG, Byrne M, Hoffmann AA (2015) Biological invasions, climate change and genomics. Evolutionary Applications 8(1): 23–46. https://doi.org/10.1111/eva.12234

Connell JH (1983) On the prevalence and relative importance of interspecific competition: evidence from field experiments. American Naturalist 122(5): 661–696. https://doi.org/10.1086/284165

Copp GH, Bianco PG, Bogutskaya NG, Erős T, Falka I, Ferreira MT, Fox MG, Freyhof J, Gozlan RE, Grabowska J, Kováč V, Moreno-Amich R, Naseka AM, Peňáz M, Povž M, Przybylski M, Robillard M, Russell IC, Stakėnas S, Šumer S, Vila-Gispert A, Wiesner C (2005) To be, or not to be, a non-native freshwater fish? Journal of Applied Ichthyology 21(4): 242–262. https://doi.org/10.1111/j.1439-0426.2005.00690.x

Cutts CJ, Metcalfe NB, Taylor AC (1998) Aggression and growth depression in juvenile Atlantic salmon: The consequences of individual variation in standard metabolic rate. Journal of Fish Biology 52(5): 1026–1037. https://doi.org/10.1111/j.1095-8649.1998.tb00601.x

Declerck S, Louette G, De Bie T, De Meester L (2002) Patterns of diet overlap between populations of non-indigenous and native fishes in shallow ponds. Journal of Fish Biology 61(5): 1182–1197. https://doi.org/10.1111/j.1095-8649.2002.tb02464.x

Diatroptov M, Opaev A (2023) Bigger male Eurasian nuthatches (*Sitta europaea*) behave more aggressively in playback-simulated territorial intrusion. Journal of Ethology 41(2): 185–193. https://doi.org/10.1007/s10164-023-00784-3

Dudgeon D, Arthington AH, Gessner MO, Kawabata ZI, Knowler DJ, Lévêque C, Naiman RJ, Prieur-Richard AH, Soto D, Stiassny MLJ, Sullivan CA (2006) Freshwater biodiversity: Importance, threats, status and conservation challenges. Biological Reviews 81(2): 163–182. https://doi.org/10.1017/S1464793105006950

Erös T, Sevcsik A, Tóth B (2005) Abundance and night-time habitat use patterns of Ponto-Caspian gobiid species (Pisces, Gobiidae) in the littoral zone of the River Danube, Hungary. Journal of Applied Ichthyology 21(4): 350–357. https://doi.org/10.1111/j.1439-0426.2005.00689.x

Estay SA, Lima M, Bozinovic F (2014) The role of temperature variability on insect performance and population dynamics in a warming world. Oikos 123(2): 131–140. https://doi.org/10.1111/j.1600-0706.2013.00607.x

Fattorini N, Lovari S, Franceschi S, Chiatante G, Brunetti C, Baruzzi C, Ferretti F (2023) Animal conflicts escalate in a warmer world. Science of The Total Environment 871: 161789. https://doi.org/10.1016/j.scitotenv.2023.161789

Ficke AD, Myrick CA, Hansen LJ (2007) Potential impacts of global climate change on freshwater fisheries. Reviews in Fish Biology and Fisheries 17(4): 581–613. https://doi.org/10.1007/s11160-007-9059-5

Fisher DN, Kilgour RJ, Siracusa ER, Foote JR, Hobson EA, Montiglio PO, Saltz JB, Wey TW, Wice EW (2021) Anticipated effects of abiotic environmental change on intraspecific social interactions. Biological Reviews 96(6): 2661–2693. https://doi.org/10.1111/brv.12772

Früh D, Haase P, Stoll S (2017) Temperature drives asymmetric competition between alien and indigenous freshwater snail species, *Physa acuta* and *Physa fontinalis*. Aquatic Sciences 79(1): 187–195. https://doi.org/10.1007/s00027-016-0489-9

Funghi C, Leitão A V., Ferreira AC, Mota PG, Cardoso GC (2015) Social dominance in a gregarious bird is related to body size but not to standard personality assays. Ethology 121(1): 84–93. https://doi.org/10.1111/eth.12318

Galil BS, Nehring S, Panov V (2007) Waterways as Invasion Highways - Impact of Climate Change and Globalization. In: Nentwig W (Ed.) Biological Invasions, Ecological Studies No. 193. Springer, 59–74. https://doi.org/10.1007/978-3-540-36920-2_5

Grabowska J, Grabowski M (2005) Diel-feeding activity in early summer of racer goby *Neogobius gymnotrachelus* (Gobiidae): A new invader in the Baltic basin. Journal of Applied Ichthyology 21(4): 282–286. https://doi.org/10.1111/j.1439-0426.2005.00676.x

Grabowska J, Grabowski M, Kostecka A (2009) Diet and feeding habits of monkey goby (*Neogobius fluviatilis*) in a newly invaded area. Biological Invasions 11(9): 2161–2170. https://doi.org/10.1007/s10530-009-9499-z

Grabowska J, Kakareko T, Błońska D, Przybylski M, Kobak J, Jermacz Ł, Copp GH (2016) Interspecific competition for a shelter between non-native racer goby and native European bullhead under experimental conditions - Effects of season, fish size and light conditions. Limnologica 56: 30–38. https://doi.org/10.1016/j.limno.2015.11.004

Grabowska J, Zięba G, Przybylski M, Smith C (2019) The role of intraspecific competition in the dispersal of an invasive fish. Freshwater Biology 64(5): 933–941. https://doi.org/10.1111/fwb.13275

Grabowska J, Błońska D, Ondračková M, Kakareko T (2023) The functional ecology of four invasive Ponto–Caspian gobies. Reviews in Fish Biology and Fisheries 33(4): 1329–1352. https://doi.org/10.1007/s11160-023-09801-7

Grabowska J, Płóciennik M, Grabowski M (2024) Detailed analysis of prey taxonomic composition indicates feeding habitat partitioning amongst co-occurring invasive gobies and native European perch. NeoBiota 92: 1–23. https://doi.org/10.3897/neobiota.92.116033

Gurevitch J, Padilla DK (2004) Are invasive species a major cause of extinctions? Trends in Ecology and Evolution 19(9): 470–474. https://doi.org/10.1016/j.tree.2004.07.005

Hadjiaghai O, Ladich F (2015) Sex-specific differences in agonistic behaviour, sound production and auditory sensitivity in the callichthyid armoured catfish *Megalechis thoracata*. PLoS ONE 10(3): e0121219. https://doi.org/10.1371/journal.pone.0121219

Harka Á, Bíró P (2007) New patterns in Danubian distribution of Ponto-Caspian gobies – a result of global climatic change and/or canalization? Electronic Journal of Ichthyology 1: 1–14.

Hellmann JJ, Byers JE, Bierwagen BG, Dukes JS (2008) Five potential consequences of climate change for invasive species. Conservation Biology 22(3): 534–543. https://doi.org/10.1111/j.1523-1739.2008.00951.x

Hesselschwerdt J, Wantzen KM (2018) Global warming may lower thermal barriers against invasive species in freshwater ecosystems – A study from Lake Constance. Science of The Total Environment 645: 44–50. https://doi.org/10.1016/j.scitotenv.2018.07.078

Horvatić S, Cavraro F, Zanella D, Malavasi S (2016) Sound production in the Ponto-Caspian goby *Neogobius fluviatilis* and acoustic affinities within the *Gobius* lineage: Implications for phylogeny. Biological Journal of the Linnean Society 117(3): 564–573. https://doi.org/10.1111/bij.12696

Horvatić S, Malavasi S, Vukić J, Šanda R, Marčić Z, Ćaleta M, Lorenzoni M, Mustafić P, Buj I, Onorato L, Ivić L, Cavraro F, Zanella D (2021) Correlation between acoustic divergence and phylogenetic distance in soniferous European gobiids (Gobiidae; *Gobius* lineage). PLoS ONE 16(12): e0260810. https://doi.org/10.1371/journal.pone.0260810

Hudina S, Hock K, Žganec K (2014) The role of aggression in range expansion and biological invasions. Current Zoology 60(3): 401–409. https://doi.org/10.1093/czoolo/60.3.401

IPCC (2014) Climate change 2014: synthesis report. In: Core Writing Team, R. K. Meyer, L. A. Pachauri (Eds) Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Geneva, Switzerland, 151 pp.

Isaak DJ, Rieman BE (2013) Stream isotherm shifts from climate change and implications for distributions of ectothermic organisms. Global Change Biology 19(3): 742–751. https://doi.org/10.1111/gcb.12073

Jakovlić I, Piria M, Šprem N, Tomljanović T, Matulić D, Treer T (2015) Distribution, abundance and condition of invasive Ponto-Caspian gobies *Ponticola kessleri* (Günther, 1861), *Neogobius fluviatilis* (Pallas, 1814), and *Neogobius melanostomus* (Pallas, 1814) in the Sava River basin, Croatia. Journal of Applied Ichthyology 31(5): 888–894. https://doi.org/10.1111/jai.12803

Janáč M, Roche K, Šlapanský L, Polačik M, Jurajda P (2018) Long-term monitoring of native bullhead and invasive gobiids in the Danubian rip-rap zone. Hydrobiologia 807(1): 263–275. https://doi.org/10.1007/s10750-017-3398-6

Jane SF, Hansen GJA, Kraemer BM, Leavitt PR, Mincer JL, North RL, Pilla RM, Stetler JT, Williamson CE, Woolway RI, Arvola L, Chandra S, DeGasperi CL, Diemer L, Dunalska J, Erina O, Flaim G, Grossart HP, Hambright KD, Hein C, Hejzlar J, Janus LL, Jenny JP, Jones JR, Knoll LB, Leoni B, Mackay E, Matsuzaki SIS, McBride C, Müller-Navarra DC, Paterson AM, Pierson D, Rogora M, Rusak JA, Sadro S, Saulnier-Talbot E, Schmid M, Sommaruga R, Thiery W, Verburg P, Weathers KC, Weyhenmeyer GA, Yokota K, Rose KC (2021) Widespread deoxygenation of temperate lakes. Nature 594(7861): 66–70. https://doi.org/10.1038/s41586-021-03550-y

Janssen J, Jude D (2001) Recruitment failure of mottled sculpin in calumet habor, southern Lake Michigan, induced by the newly introduced round goby *Neogobius melanostomus*. Journal of Great Lakes Resources 27(3): 319–328. https://doi.org/10.1016/S0380-1330(01)70647-8

Jermacz Ł, Kobak J, Dzierżyńska A, Kakareko T (2015) The effect of flow on the competition between the alien racer goby and native European bullhead. Ecology of Freshwater Fish 24(3): 467–477. https://doi.org/10.1111/eff.12162

Jones MC, Cheung WWL (2015) Multi-model ensemble projections of climate change effects on global marine biodiversity. ICES Journal of Marine Science 72(3): 741–752. https://doi.org/10.1093/icesjms/fsu172

Kakareko T, Żbikowski J, Żytkowicz J (2005) Diet partitioning in summer of two syntopic neogobiids from two different habitats of the lower Vistula River, Poland. Journal of Applied Ichthyology 21(4): 292–295. https://doi.org/10.1111/j.1439-0426.2005.00683.x

Kakareko T, Płąchocki D, Kobak J (2009) Relative abundance of Ponto-Caspian gobiids in the lower Vistula River (Poland) 3- to 4 years after first appearance. Journal of Applied Ichthyology 25(6): 647–651. https://doi.org/10.1111/j.1439-0426.2009.01301.x

Kakareko T, Kobak J, Grabowska J, Jermacz Ł, Przybylski M, Poznańska M, Pietraszewski D, Copp GH (2013) Competitive interactions for food resources between invasive racer goby *Babka gym-*

notrachelus and native European bullhead *Cottus gobio*. Biological Invasions 15(11): 2519–2530. https://doi.org/10.1007/s10530-013-0470-7

Kakareko T, Kobak J, Poznańska M, Jermacz L, Copp GH (2016) Underwater evaluation of habitat partitioning in a European river between a non-native invader, the racer goby and a threatened native fish, the European bullhead. Ecology of Freshwater Fish 25(1): 60–71. https://doi.org/10.1111/eff.12191

Keiller ML, Lopez LK, Paijmans KC, Wong MYL (2021) Behavioural plasticity in a native species may be related to foraging resilience in the presence of an aggressive invader. Biology Letters 17(3): 20200877. https://doi.org/10.1098/rsbl.2020.0877

Killen SS, Marras S, Metcalfe NB, McKenzie DJ, Domenici P (2013) Environmental stressors alter relationships between physiology and behaviour. Trends in Ecology and Evolution 28(11): 651–658. https://doi.org/10.1016/j.tree.2013.05.005

Killen SS, Mitchell MD, Rummer JL, Chivers DP, Ferrari MCO, Meekan MG, McCormick MI (2014) Aerobic scope predicts dominance during early life in a tropical damselfish. Functional Ecology 28(6): 1367–1376. https://doi.org/10.1111/1365-2435.12296

Killen SS, Glazier DS, Rezende EL, Clark TD, Atkinson D, Willener AST, Halsey LG (2016) Ecological influences and morphological correlates of resting and maximal metabolic rates across teleost fish species. American Naturalist 187(5): 592–606. https://doi.org/10.1086/685893

Kłosiński P, Kobak J, Kakareko T (2024) Metabolic rate of two invasive Ponto-Caspian goby species and their native competitors in the context of global warming. Freshwater Biology 69(7): 971–983. https://doi.org/10.1111/fwb.14259

Kłosiński P, Kobak J, Kakareko T (2025) Effect of hypoxia and acidification on metabolic rate of Ponto-Caspian gobies and their native competitors in the context of climate change. Hydrobiologia. https://doi.org/10.1007/s10750-025-05794-5

Kobler A, Humblet Y, Knaepkens G, Engelen B, Eens M (2012) Diel movement of bullhead (*Cottus perifretum*) in a lowland stream. Ecology of Freshwater Fish 21(3): 453–460. https://doi.org/10.1111/j.1600-0633.2012.00564.x

Kornis MS, Mercado-Silva N, Vander Zanden MJ (2012) Twenty years of invasion: a review of round goby *Neogobius melanostomus* biology, spread and ecological implications. Journal of Fish Biology 80(2): 235–285. https://doi.org/10.1111/j.1095-8649.2011.03157.x

Kornis MS, Carlson J, Lehrer-Brey G, Vander Zanden MJ (2014) Experimental evidence that ecological effects of an invasive fish are reduced at high densities. Oecologia 175(1): 325–334. https://doi.org/10.1007/s00442-014-2899-5

Ladich F (1988) Sound production by the gudgeon, *Gobio gobio* L., a common European freshwater fish (Cyprinidae, Teleostei). Journal of Fish Biology 32(5): 707–715. https://doi.org/10.1111/j.1095-8649.1988.tb05411.x

Ladich F (1990) Vocalization during Agonistic Behaviour in *Cottus gobio* L. (Cottidae): An Acoustic Threat Display. Ethology 84(3): 193–201. https://doi.org/10.1111/j.1439-0310.1990.tb00797.x

Ladich F (1997) Agonistic behaviour and significance of sounds in vocalizing fish. Marine and Freshwater Behaviour and Physiology 29(1–4): 87–108. https://doi.org/10.1080/10236249709379002

Lambertini M, Leape J, Marton-Lefèvre J, Mittermeier RA, Rose M, Robinson JG, Stuart SN, Waldman B, Genovesi P (2011) Invasives: A Major Conservation Threat. Science 333(6041): 404–405. https://doi.org/10.1126/science.333.6041.404-b

Logue DM, Takahashi AD, Cade WH (2011) Aggressiveness and size: A model and two tests. American Naturalist 177(2): 202–210. https://doi.org/10.1086/657978

Maazouzi C, Piscart C, Legier F, Hervant F (2011) Ecophysiological responses to temperature of the “killer shrimp” *Dikerogammarus villosus*: Is the invader really stronger than the native *Gammarus pulex*? Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology 159(3): 268–274. https://doi.org/10.1016/j.cbpa.2011.03.019

Magellan K, Bonebrake TC, Dudgeon D (2019) Temperature effects on exploratory behaviour and learning ability of invasive mosquitofish. Aquatic Invasions 14(3): 502–517. https://doi.org/10.3391/ai.2019.14.3.09

Marras S, Cucco A, Antognarelli F, Azzurro E, Milazzo M, Bariche M, Butenschön M, Kay S, Di Bitetto M, Quattrocchi G, Sinerchia M, Domenici P (2015) Predicting future thermal habitat suitability of competing native and invasive fish species: From metabolic scope to oceanographic modelling. Conservation Physiology 3(1): cou059. https://doi.org/10.1093/conphys/cou059

Marszelewski W, Pius B (2014) The impact of changes in air temperature upon the thermal regime of the river Vistula in Toruń (Poland) over the years 1961–2012. In: Gâştescu P, Marszelewski W, Bretcan P (Eds) Water Resources and Wetlands. Romanian Limnogeographical Association. Tulcea, Romania, 231–236.

Marszelewski W, Pius B (2016) Long-term changes in temperature of river waters in the transitional zone of the temperate climate: a case study of Polish rivers. Hydrological Sciences Journal 61(8): 1430–1442. https://doi.org/10.1080/02626667.2015.1040800

Martin CW, Valentine MM, Valentine JF (2010) Competitive interactions between invasive nile tilapia and native fish: The potential for altered trophic exchange and modification of food webs. PLoS ONE 5(12): e14395. https://doi.org/10.1371/journal.pone.0014395

Metcalfe NB, Taylor AC, Thorpe JE (1995) Metabolic rate, social status and life-history strategies in Atlantic salmon. Animal Behaviour 49(2): 431–436. https://doi.org/10.1006/anbe.1995.0056

Moretz JA (2003) Aggression and RHP in the Northern Swordtail Fish, *Xiphophorus cortezi*: The Relationship between Size and Contest Dynamics in Male-Male Competition. Ethology 109(12): 995–1008. https://doi.org/10.1046/j.0179-1613.2003.00938.x

Morgan IJ, McDonald DG, Wood CM (2001) The cost of living for freshwater fish in a warmer, more polluted world. Global Change Biology 7(4): 345–355. https://doi.org/10.1046/j.1365-2486.2001.00424.x

Newman RM, Henson FG, Richards C (2020) Competition between invasive ruffe (*Gymnocephalus cernua*) and native yellow perch (*Perca flavescens*) in experimental mesocosms. Fishes 5(4): 33. https://doi.org/10.3390/fishes5040033

Nowak M, Klaczak A, Koščo J, Szczerbik P, Fedorčák J, Hajdú J, Popek W (2019) Diel changeover of fish assemblages in shallow sandy habitats of lowland rivers of different sizes. Knowledge and Management of Aquatic Ecosystems 420: 41. https://doi.org/10.1051/kmae/2019037

Oyugi DO, Cucherousset J, Britton JR (2012) Temperature-dependent feeding interactions between two invasive fishes competing through interference and exploitation. Reviews in Fish Biology and Fisheries 22(2): 499–508. https://doi.org/10.1007/s11160-011-9243-5

Parker GA, Rubenstein DI (1981) Role assessment, reserve strategy, and acquisition of information in asymmetric animal conflicts. Animal Behaviour 29(1): 221–240. https://doi.org/10.1016/S0003-3472(81)80170-4

Pauli NC, Briski E (2018) Euryhalinity of Ponto-Caspian invaders in their native and introduced regions. Aquatic Invasions 13(4): 439–447. https://doi.org/10.3391/ai.2018.13.4.02

Peiman KS, Robinson BW (2010) Ecology and Evolution of Resource-Related Heterospecific Aggression. The Quarterly Review of Biology 85(2): 133–158. https://doi.org/10.1086/652374

Pintor LM, Sih A, Bauer ML (2008) Differences in aggression, activity and boldness between native and introduced populations of an invasive crayfish. Oikos 117(11): 1629–1636. https://doi.org/10.1111/j.1600-0706.2008.16578.x

Piria M, Jakšić G, Jakovlić I, Treer T (2016) Dietary habits of invasive Ponto-Caspian gobies in the Croatian part of the Danube River basin and their potential impact on benthic fish communities. Science of The Total Environment 540: 386–395. https://doi.org/10.1016/j.scitotenv.2015.05.125

Płąchocki D, Kobak J, Poznańska-Kakareko M, Kakareko T (2020) Environmental factors associated with the occurrence of the Ponto–Caspian gobies in a lowland river belonging to the central European invasion corridor. River Research and Applications 36(1): 25–35. https://doi.org/10.1002/rra.3543

Poulos DE, McCormick MI (2014) Who wins in the battle for space? The importance of priority, behavioural history and size. Animal Behaviour 90: 305–314. https://doi.org/10.1016/j.anbehav.2014.02.003

Prenda J, Rossomanno S, Armitage PD (2000) Changes in depth distribution and activity in small benthic riverine fishes under gradually changing light intensities. Limnetica 18(1): 75–80. https://doi.org/10.23818/limn.18.06

Rahel FJ, Olden JD (2008) Assessing the effects of climate change on aquatic invasive species. Conservation Biology 22(3): 521–533. https://doi.org/10.1111/j.1523-1739.2008.00950.x

Ramberg-Pihl NC, Klemmer AJ, Zydlewski J, Coghlan SM, Greig HS (2023) Smallmouth bass (*Micropterus dolomieu*) suppress Atlantic salmon (*Salmo salar*) feeding activity and increase aggressive behaviours at warmer temperatures. Ecology of Freshwater Fish 32(3): 606–617. https://doi.org/10.1111/eff.12711

Reid AJ, Carlson AK, Creed IF, Eliason EJ, Gell PA, Johnson PTJ, Kidd KA, MacCormack TJ, Olden JD, Ormerod SJ, Smol JP, Taylor WW, Tockner K, Vermaire JC, Dudgeon D, Cooke SJ (2019) Emerging threats and persistent conservation challenges for freshwater biodiversity. Biological Reviews 94(3): 849–873. https://doi.org/10.1111/brv.12480

Rewicz T, Grabowski M, MacNeil C, Bącela-Spychalska K (2014) The profile of a 'perfect' invader – the case of killer shrimp, *Dikerogammarus villosus*. Aquatic Invasions 9(3): 267–288. https://doi.org/10.3391/ai.2014.9.3.04

Ricciardi A, MacIsaac HJ (2010) Impacts of Biological Invasions on Freshwater Ecosystems. In: Richardson DM (Ed.) Fifty Years of Invasion Ecology. Wiley, 211–224. https://doi.org/10.1002/9781444329988.ch16

Ricciardi A, Hoopes MF, Marchetti MP, Lockwood JL (2013) Progress toward understanding the ecological impacts of nonnative species. Ecological Monographs 83(3): 263–282. https://doi.org/10.1890/13-0183.1

Roche KF, Janač M, Jurajda P (2013) A review of Gobiid expansion along the Danube-Rhine corridor – geopolitical change as a driver for invasion. Knowledge and Management of Aquatic Ecosystems 411: 01. https://doi.org/10.1051/kmae/2013066

Seebacher F, Ward AJW, Wilson RS (2013) Increased aggression during pregnancy comes at a higher metabolic cost. Journal of Experimental Biology 216(5): 771–776. https://doi.org/10.1242/jeb.079756

Seth H, Gräns A, Sandblom E, Olsson C, Wiklander K, Johnsson JI, Axelsson M (2013) Metabolic Scope and Interspecific Competition in Sculpins of Greenland Are Influenced by Increased Temperatures Due to Climate Change. PLoS ONE 8(5): e62859. https://doi.org/10.1371/journal.pone.0062859

Silva J da, Matono P, Barata EN, Bernardo JM, Costa AM, Ilhéu M (2019) Behavioural interactions between the endangered native fish saramugo, *Anaecypris hispanica*, and the invasive bleak, *Alburnus alburnus*. Limnetica 38(2): 517–533. https://doi.org/10.23818/limn.38.30

Sneddon LU, Taylor AC, Huntingford FA (1999) Metabolic consequences of agonistic behaviour: Crab fights in declining oxygen tensions. Animal Behaviour 57(2): 353–363. https://doi.org/10.1006/anbe.1998.0982

Soto I, Cuthbert RN, Ricciardi A, Ahmed DA, Altermatt F, Schäfer RB, Archambaud-Suard G, Bonada N, Cañedo-Argüelles M, Csabai Z, Datry T, Dick JTA, Floury M, Forio MAE, Forcellini M, Fruget JF, Goethals P, Haase P, Hudgins EJ, Jones JI, Kouba A, Leitner P, Lizée MH, Maire A, Murphy JF, Ozolins D, Rasmussen JJ, Schmidt-Kloiber A, Skuja A, Stubbington R, Van der Lee GH, Vannevel R, Várbíró G, Verdonschot RCM, Wiberg-Larsen P, Haubrock PJ, Briski E

(2023) The faunal Ponto-Caspianization of central and western European waterways. Biological Invasions 25(8): 2613–2629. https://doi.org/10.1007/s10530-023-03060-0

Stoffels RJ, Weatherman KE, Allen-Ankins S (2017) Heat and hypoxia give a global invader, *Gambusia holbrooki*, the edge over a threatened endemic fish on Australian floodplains. Biological Invasions 19(8): 2477–2489. https://doi.org/10.1007/s10530-017-1457-6

Taniguchi Y, Rahel FJ, Novinger DC, Gerow KG (1998) Temperature mediation of competitive interactions among three fish species that replace each other along longitudinal stream gradients. Canadian Journal of Fisheries and Aquatic Sciences 55(8): 1894–1901. https://doi.org/10.1139/f98-072

Vázquez DP, Gianoli E, Morris WF, Bozinovic F (2017) Ecological and evolutionary impacts of changing climatic variability. Biological Reviews 92(1): 22–42. https://doi.org/10.1111/brv.12216

Vilizzi L, Copp GH, Adamovich B, Almeida D, Chan J, Davison PI, Dembski S, Ekmekçi FG, Ferincz Á, Forneck SC, Hill JE, Kim JE, Koutsikos N, Leuven RSEW, Luna SA, Magalhães F, Marr SM, Mendoza R, Mourão CF, Neal JW, Onikura N, Perdikaris C, Piria M, Poulet N, Puntila R, Range IL, Simonović P, Ribeiro F, Tarkan AS, Troca DFA, Vardakas L, Verreycken H, Vintsek L, Weyl OLF, Yeo DCJ, Zeng Y (2019) A global review and meta-analysis of applications of the freshwater Fish Invasiveness Screening Kit. Reviews in Fish Biology and Fisheries 29(3): 529–568. https://doi.org/10.1007/s11160-019-09562-2

Vilizzi L, Copp GH, Hill JE, Adamovich B, Aislabie L, Akin D, Al-Faisal AJ, Almeida D, Azmai MNA, Bakiu R, Bellati A, Bernier R, Bies JM, Bilge G, Branco P, Bui TD, Canning-Clode J, Cardoso Ramos HA, Castellanos-Galindo GA, Castro N, Chaichana R, Chainho P, Chan J, Cunico AM, Curd A, Dangchana P, Dashinov D, Davison PI, de Camargo MP, Dodd JA, Durland Donahou AL, Edsman L, Ekmekçi FG, Elphinstone-Davis J, Erős T, Evangelista C, Fenwick G, Ferincz Á, Ferreira T, Feunteun E, Filiz H, Forneck SC, Gajduchenko HS, Gama Monteiro J, Gestoso I, Giannetto D, Gilles AS, Gizzi F, Glamuzina B, Glamuzina L, Goldsmit J, Gollasch S, Goulletquer P, Grabowska J, Harmer R, Haubrock PJ, He D, Hean JW, Herczeg G, Howland KL, İlhan A, Interesova E, Jakubčinová K, Jelmert A, Johnsen SI, Kakareko T, Kanongdate K, Killi N, Kim JE, Kırankaya ŞG, Kňazovická D, Kopecký O, Kostov V, Koutsikos N, Kozic S, Kuljanishvili T, Kumar B, Kumar L, Kurita Y, Kurtul I, Lazzaro L, Lee L, Lehtiniemi M, Leonardi G, Leuven RSEW, Li S, Lipinskaya T, Liu F, Lloyd L, Lorenzoni M, Luna SA, Lyons TJ, Magellan K, Malmstrøm M, Marchini A, Marr SM, Masson G, Masson L, McKenzie CH, Memedemin D, Mendoza R, Minchin D, Miossec L, Moghaddas SD, Moshobane MC, Mumladze L, Naddafi R, Najafi-Majd E, Năstase A, Năvodaru I, Neal JW, Nienhuis S, Nimtim M, Nolan ET, Occhipinti-Ambrogi A, Ojaveer H, Olenin S, Olsson K, Onikura N, O'Shaughnessy K, Paganelli D, Parretti P, Patoka J, Pavia RTB, Pellitteri-Rosa D, Pelletier-Rousseau M, Peralta EM, Perdikaris C, Pietraszewski D, Piria M, Pitois S, Pompei L, Poulet N, Preda C, Puntila-Dodd R, Qashqaei AT, Radočaj T, Rahmani H, Raj S, Reeves D, Ristovska M, Rizevsky V, Robertson DR, Robertson P, Ruykys L, Saba AO, Santos JM, Sarı HM, Segurado P, Semenchenko V, Senanan W, Simard N, Simonović P, Skóra ME, Slovák Švolíková K, Smeti E, Šmídová T, Špelić I, Srėbalienė G, Stasolla G, Stebbing P, Števove B, Suresh VR, Szajbert B, Ta KAT, Tarkan AS, Tempesti J, Therriault TW, Tidbury HJ, Top-Karakuş N, Tricarico E, Troca DFA, Tsiamis K, Tuckett QM, Tutman P, Uyan U, Uzunova E, Vardakas L, Velle G, Verreycken H, Vintsek L, Wei H, Weiperth A, Weyl OLF, Winter ER, Włodarczyk R, Wood LE, Yang R, Yapıcı S, Yeo SSB, Yoğurtçuoğlu B, Yunnie ALE, Zhu Y, Zięba G, Žitňanová K, Clarke S (2021) A global-scale screening of non-native aquatic organisms to identify potentially invasive species under current and future climate conditions. Science of The Total Environment 788: 147868. https://doi.org/10.1016/j.scitotenv.2021.147868

Vinagre C, Narciso L, Cabral HN, Costa MJ, Rosa R (2014) Thermal sensitivity of native and invasive seabreams. Marine Ecology 35(3): 292–297. https://doi.org/10.1111/maec.12080

Vonshak M, Dayan T, Hefetz A (2012) Interspecific displacement mechanisms by the invasive little fire ant *Wasmannia auropunctata*. Biological Invasions 14(4): 851–861. https://doi.org/10.1007/s10530-011-0122-8

Walther GR, Roques A, Hulme PE, Sykes MT, Pyšek P, Kühn I, Zobel M, Bacher S, Botta-Dukát Z, Bugmann H, Czúcz B, Dauber J, Hickler T, Jarošík V, Kenis M, Klotz S, Minchin D, Moora M, Nentwig W, Ott J, Panov VE, Reineking B, Robinet C, Semenchenko V, Solarz W, Thuiller W, Vilà M, Vohland K, Settele J (2009) Alien species in a warmer world: risks and opportunities. Trends in Ecology and Evolution 24(12): 686–693. https://doi.org/10.1016/j.tree.2009.06.008

Welton JS, Mill CA, Pygott JR (1991) The effect of interaction between the stone loach *Noemacheilus barbatulus* (L.) and the bullhead *Cottus gobio* (L.) on prey and habitat selection. Hydrobiologia 220(1): 1–7. https://doi.org/10.1007/BF00017487

White SL, Kline BC, Hitt NP, Wagner T (2019) Individual behaviour and resource use of thermally stressed brook trout *Salvelinus fontinalis* portend the conservation potential of thermal refugia. Journal of Fish Biology 95(4): 1061–1071. https://doi.org/10.1111/jfb.14099

White DP, Nannini MA, Wahl DH (2020) Examining the effects of chronic, lake-wide elevated temperatures on behavioural expression in largemouth bass, *Micropterus salmoides*. Journal of Fish Biology 97(1): 39–50. https://doi.org/10.1111/jfb.14313

Wilson RS, Hammill E, Johnston IA (2007) Competition moderates the benefits of thermal acclimation to reproductive performance in male eastern mosquitofish. Proceedings of the Royal Society B: Biological Sciences 274(1614): 1199–1204. https://doi.org/10.1098/rspb.2006.0401

Supplementary material 1

Experimental setup

Authors: Piotr Kłosiński, Jarosław Kobak, Tomasz Kakareko

Data type: tif

Explanation note: Experimental setup (all the dimensions are given in mm).

Link: https://doi.org/10.3897/neobiota.97.134566.suppl1

Supplementary material 2

Experimental procedure

Authors: Piotr Kłosiński, Jarosław Kobak, Tomasz Kakareko

Data type: tif

Explanation note: Experimental procedure.

Link: https://doi.org/10.3897/neobiota.97.134566.suppl2

Supplementary material 3

Numbers of replicates and individual size differences in particular experimental treatments

Authors: Piotr Kłosiński, Jarosław Kobak, Tomasz Kakareko

Data type: docx

Explanation note: Numbers of replicates (*n*) and individual size (total length, TL) differences in particular experimental treatments (pairs of fish in particular species configurations tested at specific temperatures). Individual sizes were compared between the species within each species pair in each experimental treatment using t-tests for dependent samples.

Link: https://doi.org/10.3897/neobiota.97.134566.suppl3

Supplementary material 4

The summary of all the models used in the study

Authors: Piotr Kłosiński, Jarosław Kobak, Tomasz Kakareko

Data type: docx

Explanation note: The summary of all the models used in the study.

Link: https://doi.org/10.3897/neobiota.97.134566.suppl4

Supplementary material 5

Tests of slope significance for particular levels of categorical factors interacting with exposure time in their effects on the number of aggression events shown by the monkey goby and gudgeon (see Table 2)

Authors: Piotr Kłosiński, Jarosław Kobak, Tomasz Kakareko

Data type: docx

Explanation note: Tests of slope significance for particular levels of categorical factors interacting with exposure time in their effects on the number of aggression events shown by the monkey goby and gudgeon (see Table 2).

Link: https://doi.org/10.3897/neobiota.97.134566.suppl5

Supplementary material 6

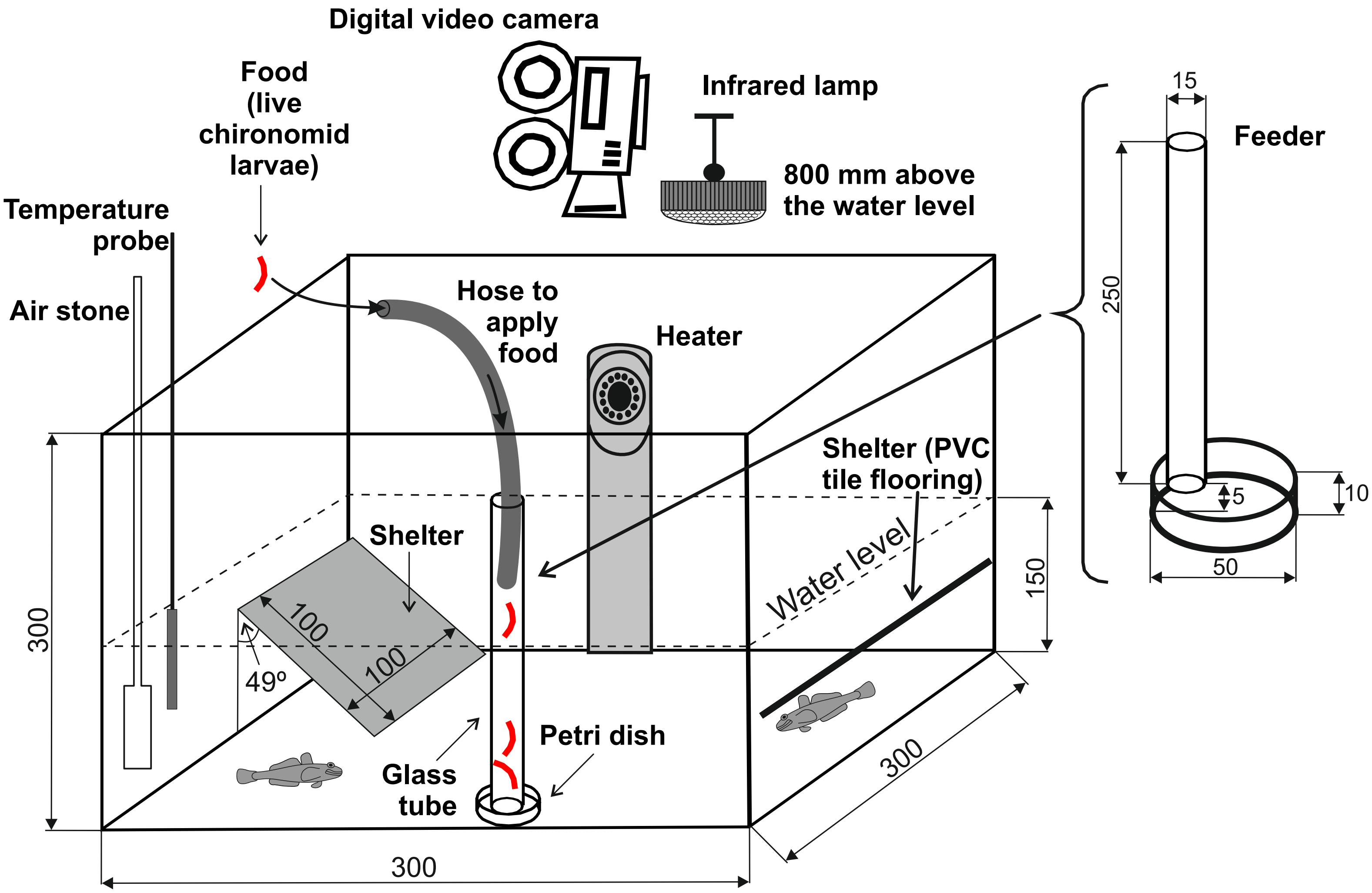
Tests of slope significance for particular levels of categorical factors interacting with exposure time in their effects on the time spent in the feeder by the racer goby and European bullhead (see Table 5), as well as by the monkey goby and gudgeon (Table 6)

Authors: Piotr Kłosiński, Jarosław Kobak, Tomasz Kakareko

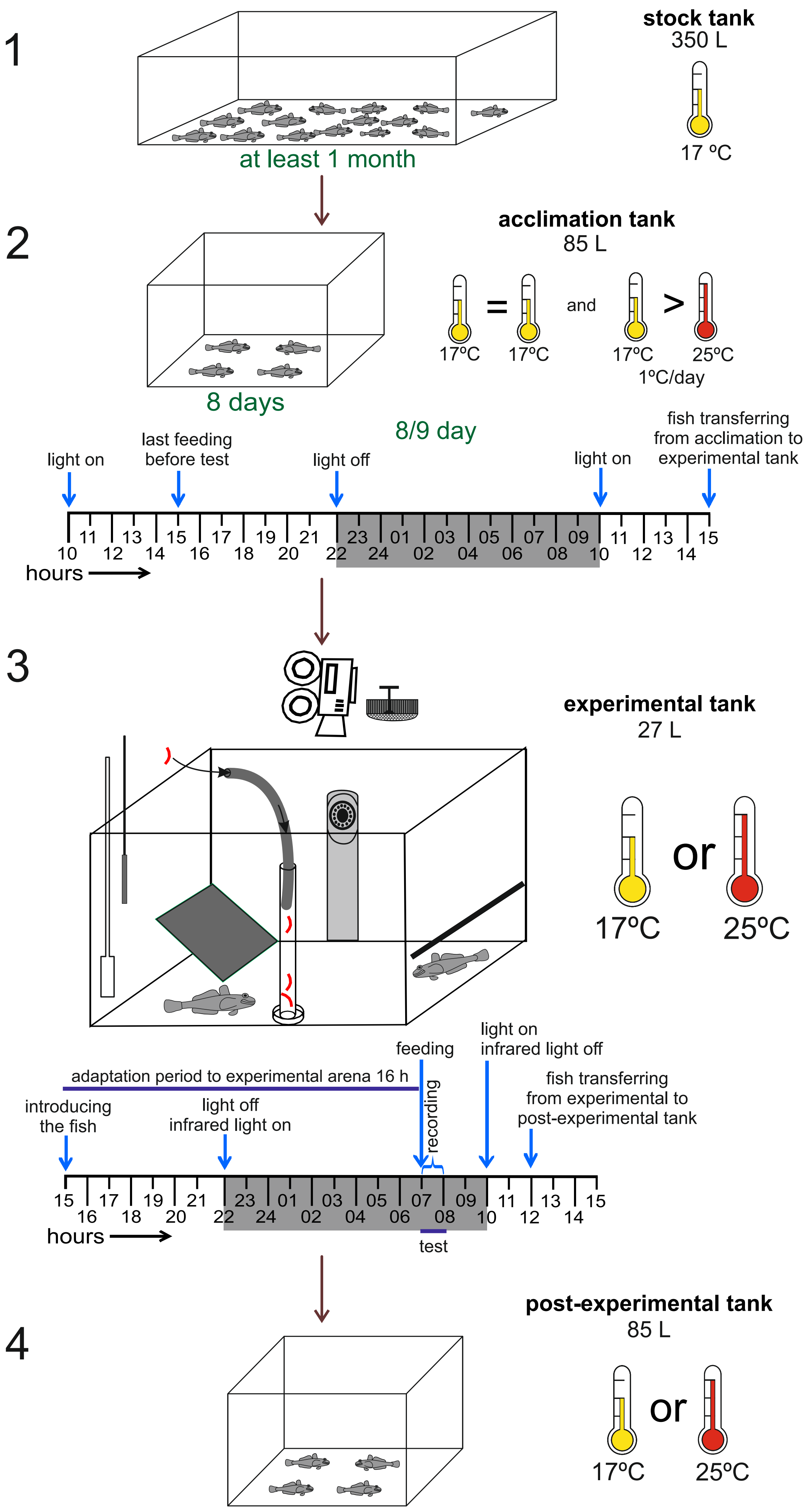
Data type: docx

Explanation note: Tests of slope significance for particular levels of categorical factors interacting with exposure time in their effects on the time spent in the feeder by the racer goby and European bullhead (see Table 5), as well as by the monkey goby and gudgeon (Table 6).

Link: https://doi.org/10.3897/neobiota.97.134566.suppl6



Supplementary material 1. Experimental setup (all the dimensions are given in mm)



Supplementary material 2. Experimental procedure

Supplementary material 3. Numbers of replicates (*n*) and individual size (total length, TL) differences in particular experimental treatments (pairs of fish in particular species configurations tested at specific temperatures). Individual sizes were compared between the species within each species pair in each experimental treatment using t-tests for dependent samples

Temp.	Treatment	*n*	Average difference in TL between tested individuals [cm]	Maximum difference in TL between tested individuals [cm]	*df*	*t*-statistic	*P*-value
17 °C	RG vs EB	14	0.24	0.51	13	0.591	0.565
	RG vs RG	11	0.21	0.41			
	EB vs EB	12	0.18	0.42			
	MG vs GG	14	0.26	0.42	13	-1.758	0.102
	MG vs MG	13	0.25	0.51			
	GG vs GG	11	0.15	0.35			
25 °C	RG vs EB	13	0.25	0.58	12	-0.109	0.915
	RG vs RG	11	0.15	0.28			
	EB vs EB	7	0.24	0.62			
	MG vs GG	14	0.10	0.23	13	0.000	1.000
	MG vs MG	12	0.17	0.34			
	GG vs GG	14	0.15	0.35			

RG – racer goby, EB – European bullhead, MG – monkey goby, GG – gudgeon

Supplementary material 4. The summary of all the models used in the study

Data range	Purpose of the models	Model/test type	Dependent variable	Independent variables
Single species treatments (separate model for each species pair)	Comparisons between the traits of the species within each pair: intraspecific aggression and foraging traits	GLMM	Ln(Number of aggression acts)	Species, Temperature, Ln(Experimental time) (cov), Replicate ID (random)
		GLMM	Ln(Time in feeder)	As above
		Cox	Time to enter the feeder	Species, Temperature
Single vs mixed species treatment (separate model for each species)	Effects of one species on the other in the pair: comparisons of the behaviour of individuals accompanied by conspecifics vs heterospecifics: intra- vs interspecific aggression, changes in foraging behaviour	GLMM	Ln(Number of aggression acts)	Treatment, Temperature, Ln(Experimental time) (cov), Replicate ID (random)
		GLMM	Ln(Time in feeder)	As above
		Cox	Time to enter the feeder	Treatment, Temperature
Mixed species treatments (separate model for each species pair)	Direct comparisons between heterospecifics kept together to check which species has an advantage in a direct interaction: interspecific aggression, rapidness of accessing the food source	GLMM	Ln (Number of aggression acts)	Species (WS), Temperature, Ln(Experimental time) (cov), Replicate ID (random)
		Cox	Time to enter the feeder	Species, Temperature

GLMM - General Linear Mixed Model, Cox - Cox proportional hazard regression

Ln – log transformation

Cov – continuous covariate, WS – within-subject factor

Supplementary material 5. Tests of slope significance for particular levels of categorical factors interacting with exposure time in their effects on the number of aggression events shown by the monkey goby and gudgeon (see Table 2)

Analysis	Effect			*df*	*F*	*P*
	Temperature	Treatment	Species			
MG vs G from the mixed-species treatment (interaction species* exposure time)	–	–	MG	1, 139	6.85	0.010*
	–	–	G	1, 139	14.94	<0.001*
G from the mixed vs single-species treatments (interaction temperature*treatment* exposure time)	17 °C	Mixed	–	1, 69	12.62	0.001*
	17 °C	Single	–	1, 54	1.67	0.201
	25 °C	Mixed	–	1, 82	3.04	0.085
	25 °C	Single	–	1, 82	9.02	0.004*

MG – monkey goby, G – gudgeon

Supplementary material 6. Tests of slope significance for particular levels of categorical factors interacting with exposure time in their effects on the time spent in the feeder by the racer goby and European bullhead (see Table 5), as well as by the monkey goby and gudgeon (Table 6)

Analysis	Effect			*df*	*F*	*P*
	Temperature	Treatment	Species			
RG vs EB from the single-species treatments (interaction species*exposure time)	–	–	RG	1, 109	82.26	<0.001*
	–	–	EB	1, 94	5.41	0.022*
EB from the mixed- vs single-species treatments (interaction temperature*exposure time)	17 °C	–	–	1, 129	10.03	0.002*
	25 °C	–	–	1, 99	0.55	0.462
MG vs G from the single-species treatments (interaction species* exposure time)	–	–	MG	1, 146	108.55	<0.001*
	–	–	G	1, 123	9.53	0.002*
	17 °C	–	–	1, 140	15.17	<0.001*
	25 °C	–	–	1, 128	89.14	<0.001*
G from the mixed- vs single-species treatments (interaction temperature*treatment* exposure time)	17 °C	Mixed	–	1, 69	2.71	0.104
	17 °C	Single	–	1, 64	0.29	0.592
	25 °C	Mixed	–	1, 69	3.67	0.059
	25 °C	Single	–	1, 69	24.31	<0.001*

RG – racer goby, EB – European bullhead, MG – monkey goby, G – gudgeon