

Journal Pre-proof

Functional responses of an invasive mud crab across a salinity gradient

Ross N. Cuthbert, Elizabeta Briski



PII: S0048-9697(21)06760-7

DOI: <https://doi.org/10.1016/j.scitotenv.2021.151684>

Reference: STOTEN 151684

To appear in: *Science of the Total Environment*

Received date: 27 August 2021

Revised date: 10 November 2021

Accepted date: 10 November 2021

Please cite this article as: R.N. Cuthbert and E. Briski, Functional responses of an invasive mud crab across a salinity gradient, *Science of the Total Environment* (2021), <https://doi.org/10.1016/j.scitotenv.2021.151684>

This is a PDF file of an article that has undergone enhancements after acceptance, such as the addition of a cover page and metadata, and formatting for readability, but it is not yet the definitive version of record. This version will undergo additional copyediting, typesetting and review before it is published in its final form, but we are providing this version to give early visibility of the article. Please note that, during the production process, errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

© 2021 Published by Elsevier B.V.

Short communication

Functional responses of an invasive mud crab across a salinity gradient

Ross N. Cuthbert^{1*}, Elizabeta Briski¹

¹GEOMAR Helmholtz-Zentrum für Ozeanforschung Kiel, Düsterbrookweg 20, 24105

Kiel, Germany

Abstract

Environmental gradients may alter the ecological impacts of invasive alien species. In marine systems such as the Baltic Sea, current salinity is variable and seawater freshening is projected in future, potentially facilitating novel keystone predators. Here, we examine the influence of salinity variation in the western Baltic Sea (i.e. ambient 10, then 7 and 4 ppt) on the functional response (FR) of the Harris mud crab *Rhithropanopeus harrisii* towards benthic macroinvertebrate prey at different densities. *Rhithropanopeus harrisii* displayed a Type II FR across salinities towards larval chironomids, due to a consistently high resource consumption rate at low prey densities. Feeding rates were significantly reduced at 4 ppt (mean 6 chironomid prey killed day⁻¹) compared to 10 ppt and 7 ppt (9 killed day⁻¹). Search efficiencies tended to be greatest at 10 ppt, whereas handling times were shortest — and maximum feeding rate highest — at the intermediate 7 ppt. These results suggest a slight reduction in predatory impact by *R. harrisii* at lower salinities. Nevertheless, across most prey densities, FRs were not significantly different, indicating sustained interaction strength across a range of salinity regimes.

Key words: Baltic Sea; Chironomidae; desalinisation; functional responses; predator-prey interaction; *Rhithropanopeus harrisii*

Introduction

Biological invasions are a major component of global change that is eroding biodiversity and driving massive socio-economic impacts worldwide (Simberloff et al., 2013; Bellard et al.,

2016; Cuthbert et al., 2021a; Diagne et al., 2021). Aquatic ecosystems are particularly at risk of anthropogenic impacts such as from invasion (Darwall et al., 2018; Anton et al., 2019), with resident communities in the aquatic realm highly vulnerable, for example, to novel predators (Cox and Lima, 2006; Anton et al., 2020). Environmental change is likely to alter invasion rates and impacts, but there remains an inadequate basis to predict potential synergies between environmental gradients and invasive alien species (IAS) effects (Ricciardi et al., 2013; Ricciardi et al., 2021). In particular, widespread shifts in salinity patterns already occur or have been projected in many seas (Durack et al., 2012), with potential implications for both the success and impacts of IAS (Paiva et al., 2018; Dickey et al., 2021).

The Baltic Sea is particularly sensitive to salinity regime shifts (Meier and Kauker, 2003), with natural variability of between 2 and 24 ppt (Leppäkoski et al., 2002) and projected widespread freshening in future owing to alterations of precipitation patterns (Meier et al., 2012). There are presently over 100 IAS in this system (Leppäkoski et al., 2002; Casties et al., 2016), and these are likely growing in line with rising detection rates of aquatic invaders on the global scale in the last decades (notwithstanding time lags in detection in recent years; Seebens et al., 2017; Bailey et al., 2020). Sea freshening may favour the establishment of euryhaline IAS in particular, causing the demise of native taxa which historically may be more adapted to fully marine conditions (Paiva et al., 2018). However, very little information is available on the implications of current salinity regime gradients for ecological impacts of high profile IAS.

Crabs are mobile keystone species with generalist dietary preferences, which exert substantial top-down control on benthic organisms at large scales with potential for wider trophic cascades (Paine, 1966; Levinton and Kelaher, 2004; Kotta et al., 2018). One of the most successful invasive decapods worldwide is the Harris mud crab *Rhithropanopeus harrisii* (Gould, 1841), with a native range along the Eastern seaboard of North America,

from Canada (New Brunswick) to Mexico (Veracruz), and a tolerance to low salinity (i.e. of the current/future Baltic Sea). Corroborating the ecology of ‘sleepers’ (Spear et al., 2021), the mud crab was first detected in the Baltic Sea in the 1930’s (in Germany), but did not become widely established in all basins until the 1990’s (Fowler et al., 2013). In many low salinity parts of the Baltic Sea, this species represents a novel predator archetype (Forsström et al., 2015), with no trophically-analogous native crabs, and thus it may cause substantial cascades to ecological communities through shifts from bottom-up to top-down processes (Kotta et al., 2018). Accordingly, prey species may be particularly vulnerable to their impacts due to a lack of co-evolutionary adaptation that facilitates anti-predator responses (Leonard et al., 1999; Anton et al., 2020). This crab species has been found to broadly consume both sessile (e.g. bivalves) and mobile (e.g. snails) fauna, although ecological effects can differ between the laboratory and field (Forsström et al., 2015).

The present study examines how local salinity variations alter the ecological impacts of *R. harrisii* using a comparative functional response (FR) approach. We examine how FRs (resource use as a function of resource density) change under salinity regimes in a site from the western Baltic Sea towards chironomid prey. Functional responses have been shown to be robust predictors of IAS ecological impacts (Dick et al., 2017; Cuthbert et al., 2019), including for crabs (e.g. Howard et al., 2018; Ens et al., 2021), and can allow for inferences of how environmental change influences ecological impacts and population stability (Lavery et al., 2017). We hypothesise that *per capita* potential ecological impacts of *R. harrisii* will be sustained under alterations to salinity regime, given its euryhalinity (Keith, 2008; Roche et al., 2009). We also expect the crab to exhibit Type II FRs, characterised by high rates of resource consumption at low prey densities, which may destabilise prey populations under certain conditions.

Materials and methods

Animal collection and experimental design

The predators, *R. harrisii* (0.9 – 1.0 cm carapace width) of mixed sex, were obtained from Travemünde, Lübeck, Germany in August 2021 by dredging benthic areas using a kick net. The ambient salinity of this site is around 10 ppt, but can be much lower due to variations in runoff from an adjoining waterway (Trave river). Being an estuary, salinity at this site can extend approximately 6 ppt below the ambient level (i.e. down to 4 ppt; E. Briski, personal observation) due to seasonal differences in precipitation. Port areas such as Travemünde are at high risk of invasion due to ship traffic (Bailey et al., 2020). Crabs were separated from other macroinvertebrates in the field and transported to a controlled environment chamber (18 °C; 12:12 light and dark regime) at GEOMAR Helmholtz Centre for Ocean Research Kiel, Germany in source water. In the chamber, crabs were housed in 56 L aquaria containing filtered Baltic Sea water from Kiel Fjord that was mixed with aged tap water to reach the desired ambient salinity of the collected population (10 ppt). The tank contained boulders to provide shelter for crabs, and individuals were acclimated for one week under these conditions on a diet of live chironomid larvae. Larvae of chironomids were obtained commercially (ZOO and Co. Kautzen, Kiel). After one week, crabs were transferred to separate 5 L tanks (6 ind. aquaria⁻¹) with one of three salinities (10, 7 or 4 ppt) for acclimation to experimental conditions over one further week, and fed *ad libitum* with chironomids as before. All crabs survived this salinity transition. A 50 % water change was performed on each second day per tank. This range of salinity regimes reflects current variability in the sampled location in the western Baltic Sea. Furthermore, our range of salinities accounts for very high annual variability in nearshore areas and river mouths (Pansch and Hiebenthal, 2019). In particular, owing to variations in runoff of the adjoining waterway, short-term salinity variations can be marked at the crab collection location (i.e. down to 4 ppt). Short-term salinity variation of 8 ppt has also been recorded nearby in the

western Baltic (Pansch and Hiebenthal, 2019).

In the controlled environment chamber, FRs of *R. harrisii* towards live chironomid larval prey (total length: 1.1 – 1.5 cm) were quantified factorially under three salinities (10, 7, 4 ppt) and five prey densities (2, 4, 8, 16, 32, i.e. 1 – 16 prey L⁻¹). Prey were not pre-acclimated to these salinities, however, chironomids comprise a large share of the wider macrozoobenthos of the Baltic Sea (Brodin et al., 2013) and have been shown to tolerate salinities beyond those examined here in experimentation (Cuthbert et al., 2021b). Controls consisted of prey in the absence of predators under each salinity and density treatment, to quantify non-predatory background mortality rates. Four replicates were conducted per experimental group. Crabs were unfed for 24 hours prior to experimentation to standardise hunger levels in 500 mL circular, transparent arenas (12 cm dia.) with the appropriate salinity regime. Experiments were conducted in transparent, rectangular 500 mL arenas (~5 cm water depth), with chironomid prey introduced at one of the five densities before the crabs. Experimental arenas had no shelter as we did not aim to examine effects of habitat complexity on feeding rates. Following the 24 h starvation, predators were added to aquaria containing each prey density and allowed to feed for 24 hours. After this period, crabs were removed and remaining live prey enumerated to quantify those killed *via* predation. Feeding conditions were 18 °C and under a 12:12 light and dark regime.

These experimental conditions were selected to provide a standardised feeding setup for crabs, such that we could examine the effects of salinity and prey density without experimental confounds related to other factors. We note that here we consider FRs phenomenologically rather than mechanistically given the nature of our comparative laboratory experiment, with our approach used as a tool to examine treatment effects without determining the underlying processes of predator or prey behaviour (Dick et al., 2014). Last, we note that the broad range of prey densities selected was essential to fit FR models to the

data, by allowing sufficient resolution at low densities to measure the search coefficient, and an overabundance at high prey densities to enable an asymptotic plateau in the model.

However, in some treatments, feeding rates did not reach a clear asymptotic plateau and therefore the provisioning of higher prey densities, or a shorter experimental duration, could have elicited a greater maximum feeding rate per unit time.

Statistics

Median levels of prey mortality in predator-free controls at each prey density and salinity were used to qualify consumption rates in those treatments containing predators (i.e. *via* subtraction of control mortality from predator-driven mortality; mean control mortality across each salinity treatment ranged from 8 to 11%). Consumption rates (proportions of available prey killed) were analysed using generalised linear models assuming a quasi-binomial error distribution and logit link, as a function of salinity and prey density as well as their interaction. The quasi-binomial family was used owing to residual overdispersion (residual deviance exceeded degrees of freedom). Analysis of deviance was used to perform *F*-tests on the resulting model, with Type III sums of squares (Fox and Weisberg, 2019). Tukey comparisons were used *post-hoc* for pairwise comparisons (Lenth, 2020). Non-significant terms were manually removed from the full model step-by-step, such that the final one included only significant terms (Zuur et al., 2009).

Crab FR Types (I, II or III) were categorised using binomial generalised linear models with logit links for each salinity treatment separately, with consumption rates (proportion of prey killed) analysed as a function of initial prey density. Because prey were not replaced as they were killed, we fit a flexible form of the FR to the data which accounts for non-replacement of prey (Real, 1977; Pritchard et al., 2017):

$$N_e = N_0 (1 - \exp(bN_0^q(hN_e - T))) \quad (1)$$

where N_e is the number of prey eaten, N_0 is the initial prey density, b is the search coefficient,

q is the scaling coefficient, h is the handling time and T is the experimental duration (24 h).

Where a categorical Type II FR is evidenced, the scaling exponent q may be fixed at 0, whilst responses are increasingly sigmoidal (i.e. Type III) where $q > 0$. If crab functional responses were equivocal in type (i.e. non-significant first order term), different scaling exponents (q fixed at 0; q fixed at 1; q free to vary) were fit and corresponding models compared *via* Akaike's Information Criterion, with the lowest value indicating the best fit. For each salinity level separately, the selected model was non-parametrically bootstrapped 2000 times to predict 95 % confidence intervals around the FR curves. All analyses were computed in R v4.0.2 (R Core Team, 2020), with significance inferred at an α of 0.05.

Results

Proportions of chironomid prey killed by *R. harrisii* differed significantly among salinity regimes ($F_{2,56} = 7.52, p < 0.01$). Significantly fewer prey were killed at 4 ppt compared to 10 and 7 ppt (both $p < 0.01$), which were in turn not significantly different ($p > 0.05$). On average, 9 prey were killed by *R. harrisii* under the two higher salinity regimes, but only 6 prey at 4 ppt over the total experimental period (Figure 1). Proportional predation rates reduced significantly as prey density increased ($F_{1,56} = 8.43, p < 0.01$), and for all salinities as there was no significant 'salinity \times density' interaction term ($F_{2,54} = 1.02, p > 0.05$).

First order terms were significantly negative under 10 ppt (estimate = -0.07, $z = 4.06, p < 0.001$) and 4 ppt (estimate = -0.04, $z = 2.99, p < 0.01$), thus clearly evidencing Type II FRs. However, at 7 ppt, the first order term was not significantly negative (estimate = -0.02, $z = 1.15, p > 0.05$). Nevertheless, fitting various FR model exponents to the 7 ppt feeding data indicated that fixing scaling exponent q at 0 (i.e. analogous to Type II FR) minimised information loss compared to q being fixed at 1 or being free to vary ($\Delta AIC \geq 20.56$). Accordingly, all FRs were deemed to be Type II across salinity regimes, with q fixed at 0 in all models.

Functional response search coefficients were generally highest at 10 ppt compared to 7 ppt and 4 ppt (Figure 2), whereas handling times were shortest (and thus maximum feeding rates highest) at 7 ppt, with 10 ppt being intermediate and 4 ppt the longest. Nevertheless, irrespective of salinity regime, FR confidence intervals always overlapped, with the exception of 10 ppt and 4 ppt at intermediate prey densities (Figure 3). Accordingly, that effects of salinity on *R. harrisii* FRs were not statistically clear across the majority of prey densities; although, variability was high at the lowest salinity (Figure 3).

Discussion

The present study found significant predatory FRs of the invasive Harris mud crab *R. harrisii* towards benthic macroinvertebrates across changeable current salinity regimes. Feeding rates of *R. harrisii*, however, were highest at elevated salinity levels (10 ppt), corroborating ambient conditions of the sampled population. Nevertheless, hyperbolic Type II FRs were exhibited by crabs across all salinity regimes, indicating consistently high search efficiency towards prey, even when relatively rare in the environment. In turn, this FR type could allow for prey population extirpation at low densities (Dick et al., 2014), and particularly in relatively simple communities where predators cannot switch between prey (McCard et al., 2021) or prey cannot seek physical refuge (Barrios-O'Neill et al., 2016). *Per capita* feeding rates of crabs varied from 6 (4 ppt) to 9 (7-10 ppt) prey day⁻¹.

Our results thus suggest predatory impact by *R. harrisii* across the varying salinities of the western Baltic Sea sampling location, with a slight tendency for greater impacts at higher salinities. Our results also capture seasonal variability in the sampled nearshore area due to runoff. The highest feeding rates, found under the higher salinity regimes (10 and 7 ppt), may reflect improved predatory performance at higher salinities, corroborating the brackish native habitat of these crabs (i.e. North American Atlantic coast). Alternatively, they may reflect population-level characteristics and local adaptations, given that 10 ppt reflects

the predominant conditions of the sampling locations to which the collected crabs may be best adapted. Populations in the Baltic Sea may have arrived from multiple independent introductions, resulting in high intraspecific heterogeneity that could alter responses to climate change. As such, a longer period of acclimation to the lower salinities, or experimentation on different populations, could have yielded greater feeding similarities at the reduced salinities compared to the ambient level. Future research should examine the behavioural aspects that underpin feeding responses to salinity variation in this and other crab predators, to gain a mechanistic understanding of trends. Changes to salinity can be demanding due to energy expenditure to maintain ion and osmotic balance, with salinity previously found to reduce specific metabolic rates in *R. harrisii* (Normant and Gibowics, 2008). We nevertheless caution that our results are based on a single population of this species collected at a particular point in time, in terms of making broader inferences. Further, we caution that laboratory impacts can differ from those in the field due to context-dependencies (Forsström et al., 2015). They may also change with alternative prey types, such as small bivalves, isopods and amphipods which are also readily consumed (Forsström et al., 2015), as well as associated prey and predator behavioural or physiological responses to salinity gradients which require elucidation.

Nonetheless, FKE can have high in-field predictive potential (Dick et al., 2017). In parts of the native range, in Chesapeake Bay, *R. harrisii* has been reported to tolerate salinities between ~ 2 and 18 ppt (Ryan, 1956); in Newport River Estuary, North Carolina, the crab has also been found between 0.5 and 25 ppt (Cronin, 1982). This thus indicates a potential capacity to withstand conditions across the entirety of the Baltic Sea (i.e. as low as 2 ppt), and at even lower salinities. Furthermore, while crab larvae may be more sensitive to low salinities than adults (Gonçalves et al., 1995), breeding populations and larval survival have been found at salinities below 1 ppt (Keith, 2008; Roche et al., 2009). In future, the

effects of salinity on abundance and fecundity of these crabs should be further discerned to determine responses at the population-level in a range of abiotic conditions (Dick et al., 2017), as FRs inform only as to *per capita* effects. Feeding rates under a larger salinity gradient representative of the current and future Baltic Sea should also be discerned. In that context, *R. harrisii* has been found to display ‘boom-bust’ dynamics, with recruitment also potentially aided by climate change and mediated by biotic resistance from resident predators (Forsström et al., 2018). Accordingly, population-level impacts could vary spatiotemporally across the invasion process for this species.

Functional response parameters discerned here — the search coefficient and handling time — also differed among salinities. Mud crabs exhibited the highest search efficiencies at the highest salinity (i.e. 10 ppt), indicating that their abilities to detect and capture prey are greatest in these conditions, but reduced below that ambient level. As the search coefficient corresponds to the initial slope of FR curves, crabs may be particularly destabilising to low density prey in these situations, but freshening could mediate these interactions. However, importantly, the addition of habitat structure could also impart refuge for prey in benthic experimental conditions (Barrios O'Neill et al., 2018), irrespective of salinity, and dampen search efficiencies. Handling times were contrastingly shortest at the intermediate salinity level (i.e. 7 ppt), suggesting that the capacity for *R. harrisii* to process prey items potentially peaks unimodally in this range of conditions. Yet, this low handling time may also be an artefact of the lack of clear feeding plateau in that experimental treatment, with equivocal evidence for a saturating Type II FR exhibited.

Conclusions

Overall, the results of the present study show consistent predatory behaviour across salinities in *R. harrisii*, relevant to the variation of the sampling location (i.e. 10 – 4 ppt). This invader is known to exert significant predation pressure on native macroinvertebrate

communities, and also responds positively to warming (Forsström et al., 2015; Nurkse et al., 2018). Further work should examine the capacity for *R. harrisii* to interact mutualistically with other invaders, such as has been suggested with the zebra mussel *Dreissena polymorpha* and round goby *Neogobius melanostomus* (Nurkse et al., 2018; Kotta et al., 2018) in the context of invasion meltdown, and combined effects of multiple climatic stressors (e.g. warming and desalination) on impact at the population-level.

Acknowledgements

This study received funding from the Alexander von Humboldt Foundation. We acknowledge input from four anonymous reviewers that improved the manuscript.

References

- Anton A, Geraldi NR, Ricciardi A, Dick JTA (2020) Global determinants of prey naiveté to exotic predators. *Proceedings of the Royal Society B: Biological Sciences* 287: 2978.
- Anton, A., Geraldi, N.R., Lovelock, C.E., Apostolaki, E.T., Bennett, S., Cabrien, J., et al. (2019) Global ecological impact of marine exotic species. *Nature Ecology and Evolution* 3: 787–800.
- Bailey SA, Brown L, Campbell ML, Canning-Clode J, Carlton JT, Castro N, et al. (2020) Trends in the detection of aquatic non- indigenous species across global marine, estuarine and freshwater ecosystems: A 50- year perspective. *Diversity and Distributions* 26: 1780–1797.
- Barrios-O'Neill D, Kelly R, Dick JTA, Ricciardi A, MacIsaac HJ, Emmerson MC (2016) On the context- dependent scaling of consumer feeding rates. *Ecology Letters* 19: 668–678.
- Bellard C, Cassey P, Blackburn TM (2016) Alien species as a driver of recent extinctions. *Biology Letters* 12: 0623.
- Brodin Y, Ejdung G, Strandberg J, Lyrholm T (2013) Improving environmental and

- biodiversity monitoring in the Baltic Sea using DNA barcoding of Chironomidae (Diptera). *Molecular Ecology Resources* 13: 996–1004.
- Casties I, Seebens H, Briski E (2016) Importance of geographic origin for invasion success: A case study of the North and Baltic Seas versus the Great Lakes–St. Lawrence River region. *Ecology and Evolution* 6: 8318–8329.
- Cox JG, Lima SL (2006) Naivete and an aquatic-terrestrial dichotomy in the effects of introduced predators. *Trends in Ecology and Evolution* 21: 674–680.
- Cronin TW (1982) Estuarine retention of larvae of the crab *Rhithropanopeus harrisii*. *Estuarine Coastal and Shelf Science* 15: 207–220.
- Cuthbert RN, Briski E (2021b) Temperature, not salinity, drives impact of an emerging invasive species. *Science of the Total Environment* 780: 146640.
- Cuthbert RN, Dickey JWE, Coughlan NE, Joyce JW S, Dick JTA (2019) The Functional Response Ratio (FRR): advancing comparative metrics for predicting the ecological impacts of invasive alien species. *Biological Invasions* 21: 2543–2547.
- Cuthbert RN, Pattison Z, Taylor NG, Verbrugge L, Diagne C, Ahmed DA et al. (2021a) Global economic costs of aquatic invasive alien species. *Science of the Total Environment* 775: 145228.
- Darwall W, Bremerich W, De Wever A, Dell AI, Freyhof J, Gessner MO et al. (2018) The alliance for freshwater life: A global call to unite efforts for freshwater biodiversity science and conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems* 28: 1015–1022.
- Diagne C, Leroy B, Vaissière AC, Gozlan RE, Roiz D, Jarić I et al. (2021) High and rising economic costs of biological invasions worldwide. *Nature* 592: 571–576.
- Dick JTA, Alexander ME, Jeschke JM, Ricciardi A, MacIsaac HJ, Robinson TB, et al. (2014) Advancing impact prediction and hypothesis testing in invasion ecology using a

- comparative functional response approach. *Biological Invasions* 15: 837–846.
- Dick JTA, Lavery C, Lennon JJ, Barrios-O'Neill D, Mensink PJ, Britton JR, Medoc V et al. (2017) Invader Relative Impact Potential: a new metric to understand and predict the ecological impacts of existing, emerging and future invasive alien species. *Journal of Applied Ecology* 54: 1259–1267.
- Dickey JWE, Cuthbert RN, Steffen GT, Dick JTA, Briski E (2021) Sea freshening may drive the ecological impacts of emerging and existing invasive non- native species. *Diversity and Distributions* 27: 144–156.
- Durack PJ, Wijffels SE, Matear RJ (2012) Ocean salinities reveal strong global water cycle intensification during 1950 to 2000. *Science* 336: 455–458.
- Ens NJ, Lim EG, Howard BR, Eastham TM (2021) A comparison of the predatory impacts of an invasive and native crab species using a functional response approach. *Biological Invasions* 23: 2329–2336.
- Fox J, Weisberg S (2019) *An R companion to applied regression*. Sage, Thousand Oaks.
- Fowler AE, Forsström T, von Numers M, Vesakoski O (2013) The North American mud crab *Rhithropanopeus harrisi* (Gould, 1841) in newly colonized Northern Baltic Sea: distribution and ecology. *Aquatic Invasions* 8: 89–96.
- Forsström T, Fowler AE, Manninen I, Vesakoski O, (2015) An introduced species meets the local fauna: predatory behavior of the crab *Rhithropanopeus harrisi* in the Northern Baltic Sea. *Biological Invasions* 17: 2729–2741.
- Forsström T, Vesakoski O, Riipinen K, Fowler AE (2018) Post-invasion demography and persistence of a novel functional species in an estuarine system. *Biological Invasions* 20: 3331–3345.
- Gonçalves F, Ribeiro R, Soares AMVM (1995) Laboratory study of effects of temperature and salinity on survival and larval development of a population of *Rhithropanopeus*

- harrisii* from the Mondego River Estuary, Portugal. Marine Biology 121: 639–645.
- Howard BR, Barrios-O'Neill D, Alexander ME, Dick JTA, Therriault TW, Robinson TB, Côte IM (2018) Functional responses of a cosmopolitan invader demonstrate intraspecific variability in consumer-resource dynamics. PeerJ 6: e5634.
- Keith DE (2008) Occurrence of *Rhithropanopeus harrisii* (mud crab) in Texas inland impoundments. Occurrence of *Rhithropanopeus harrisii* (mud crab) in Texas inland impoundments. Tarleton State University, Texas.
- Kotta J, Wernberg H, Jänes I, Kotta K, Nurkse M, Pärnoja et al. (2018) Novel crab predator causes marine ecosystem regime shift. Scientific Reports 8: 4956.
- Laverty C, Brenner D, McIlwaine C, Lennon JJ, Dick JTA, Lucy FE, Christian KA (2017) Temperature rise and parasitic infection interact to increase the impact of an invasive species. International Journal for Parasitology 47: 291-296.
- Leonard GH, Bertness MD, Yund P (1999) Crab Predation, waterborne cues, and inducible defenses in the blue mussel, *Mytilus edulis*. Ecology 80: 1–14.
- Leppäkoski E, Gollasch S, Gruszká P, Cjaveer H, Olenin S, Panov V (2002) The Baltic- A sea of invaders. Canadian Journal of Fisheries and Aquatic Sciences 59: 1175–1188.
- Lenth R (2020) emmeans: estimated marginal means, aka least-squares means. R package version 1.4.8.
- Levinton J, Kelaher B (2004) Opposing organizing forces of deposit-feeding marine communities. Journal of Experimental Marine Biology and Ecology 300: 65–82.
- McCard M, South J, Cuthbert RN, Dickey JWE, McCard N, Dick JTA (2021) Pushing the switch: functional responses and prey switching by invasive lionfish may mediate their ecological impact. Biological Invasions 23: 2019–2032
- Meier HEM, Kauker F (2003) Sensitivity of the Baltic Sea salinity to the freshwater supply. Climate Research 24: 231–242.

- Meier HEM, Hordoir R, Andersson HC, Dieterich C, Eilola K, Gustafsson BG et al. (2012) Modelling the combined impact of changing climate and changing nutrient loads on the Baltic Sea environment in an ensemble of transient simulations for 1961-2099. *Climate Dynamics* 39: 2421–2441.
- Normant M, Gibowics M (2008) Salinity induced changes in haemolymph osmolality and total metabolic rate of the mud crab *Rhithropanopeus harrisii* Gould, 1841 from Baltic coastal waters. *Journal of Experimental Marine Biology and Ecology* 355: 145–152.
- Nurkse K, Kotta J, Orav-Kotta H, Ojaveer HA (2016) A successful non-native predator, round goby, in the Baltic Sea: generalist feeding strategy, diverse diet and high prey consumption. *Hydrobiologia* 777: 271–281.
- Nurkse K, Kotta J, Rätsep M, Kotta I, Kreitsberg P (2018) Experimental evaluation of the effects of the novel predators, round goby and mud crab on benthic invertebrates in the Gulf of Riga, Baltic Sea. *Journal of the Marine Biological Association of the United Kingdom* 98: 25–31.
- Paine RT (1966) Food web complexity and species diversity. *American Naturalist* 100: 65–75.
- Paiva F, Barco A, Chen Y, Mirzajani A, Chan FT, Lauringson V et al. (2018) Is salinity an obstacle for biological invasions? *Global Change Biology* 24: 2708–2720.
- Pansch C, Hiebenthal C (2019) A new mesocosm system to study the effects of environmental variability on marine species and communities. *Limnology and Oceanography: Methods* 17: 145–162.
- Pritchard DW, Paterson RA, Bovy HC, Barrios- O'Neill D (2017) FRAIR: An R package for fitting and comparing consumer functional responses. *Methods in Ecology and Evolution* 8: 1528–1534.

- R Core Team (2020) R: A language and environment for statistical computing. R foundation for statistical computing, Vienna.
- Real LA (1977) The kinetics of functional response. *American Naturalist* 111: 289–300.
- Ricciardi A, Hoopes MF, Marchetti MP, Lockwood JL (2013) Progress toward understanding the ecological impacts of nonnative species. *Ecological Monographs* 83: 263–282.
- Ricciardi A, Iacarella JC, Aldridge DC, Blackburn TM, Carlton JC, Catford JA et al. (2021) Four priority areas to advance invasion science in the face of rapid environmental change. *Environmental Reviews* (in press).
- Roche DG, Torchin ME, Leung B, Binning SA (2009) Localized invasion of the North American Harris mud crab, *Rhithropanopeus harrisii*, in the Panamá Canal: implications for eradication and spread. *Biological Invasions*, 11: 983–993.
- Ryan EP (1956) Observations on the life histories and the distribution of the Xanthidae (mud crabs) of Chesapeake Bay. *The American Midland Naturalist* 56: 138–162.
- Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, et al. (2017) No saturation in the accumulation of alien species worldwide. *Nature Communications* 8: 14435.
- Simberloff D, Martin J, Genovesi P, Maris V, Wardle DA, Aronson J et al. (2013) Impacts of biological invasions: what's what and the way forward. *Trends in Ecology and Evolution* 28: 58–66.
- Spear MJ, Walsh JR, Ricciardi A, Vander Zanden MJ (2021) The invasion ecology of sleeper populations: prevalence, persistence, and abrupt shifts. *BioScience* 71: 357–369.
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. First edition. Springer, New York, New York, USA.

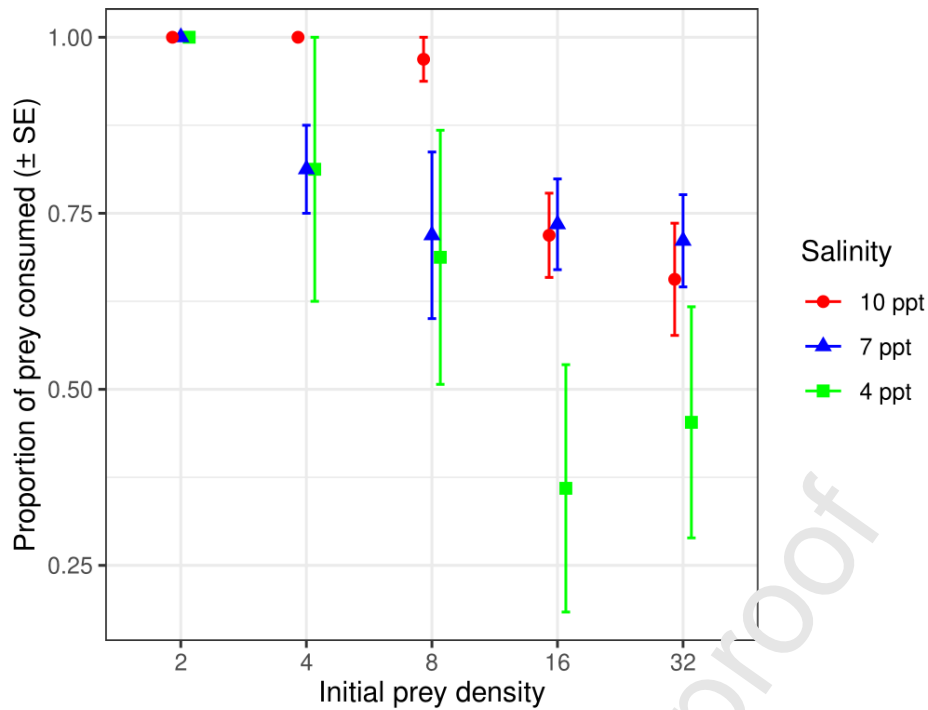


Figure 1. Proportions of chironomid prey consumed by *Rhithropanopeus harrisii* across prey densities (2, 4, 8, 16, 32) and salinity regimes over 24 h. Means are \pm SE ($n = 4$ per experimental group). Feeding rates differed significant among salinities (GLM: $F_{2,56} = 7.52$, $p < 0.01$) and across prey densities (GLM: $F_{1,56} = 8.43$, $p < 0.01$).

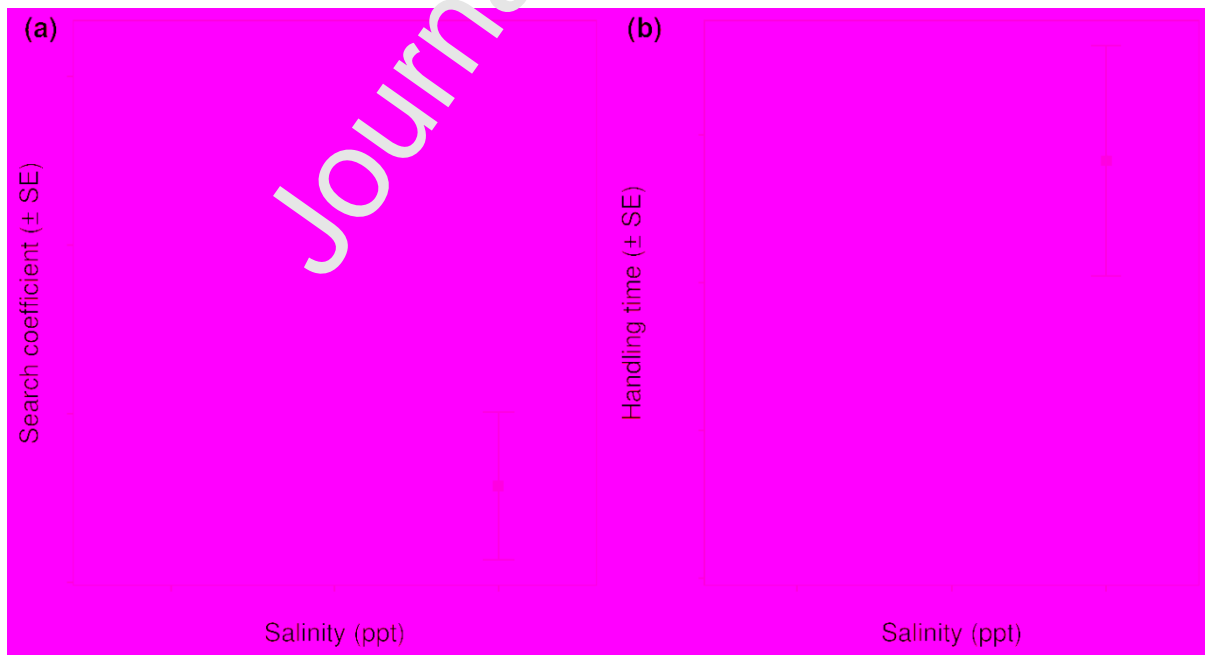


Figure 2. Functional response parameters from the flexible statistical model with scaling exponent q fixed at 0 — search coefficients b (a) and handling times h (b) — across salinity

regimes by *Rhithropanopeus harrisii* towards chironomid prey over 24 h at different prey densities (2, 4, 8, 16, 32). Means are \pm SE.

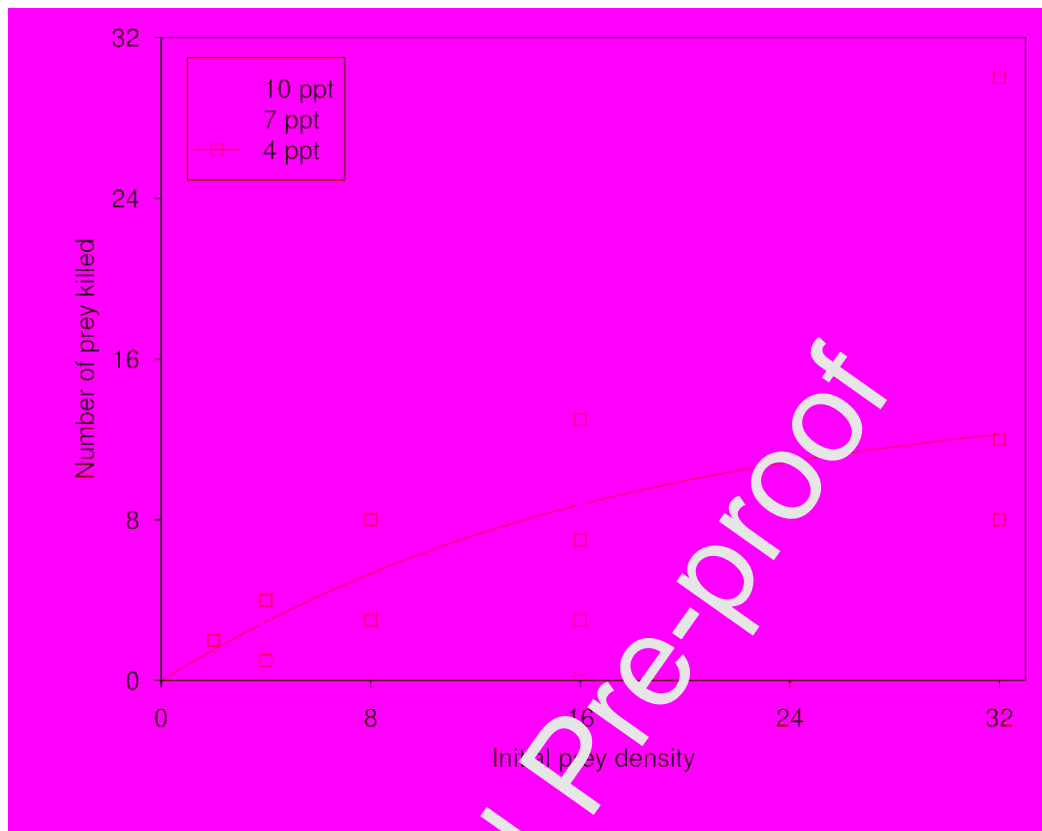


Figure 3. Type II functional response of *Rhithropanopeus harrisii* towards chironomid prey over 24 h at different prey densities (2, 4, 8, 16, 32), among salinity regimes. Shaded areas are non-parametric bootstrapped 95 % confidence intervals ($n = 2000$ iterations) and points are raw data. Divergences in confidence intervals indicate significant differences.

Declaration of competing interests

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

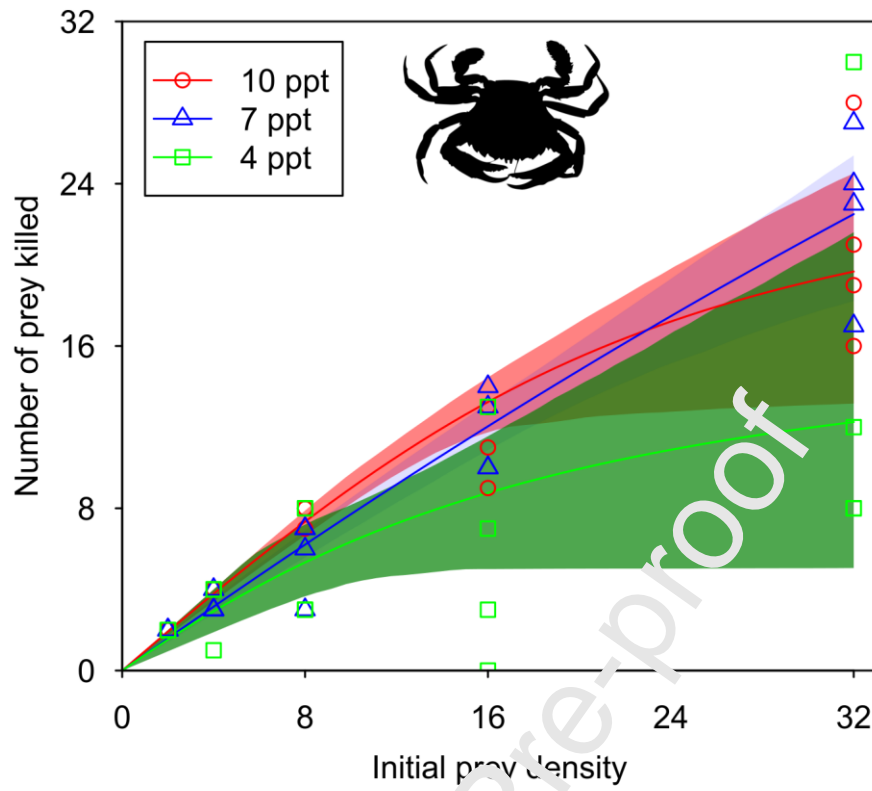
☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

CRedit author contributions statement

All authors: Conceptualisation. RNC: Data curation, Formal analysis, Visualisation. RNC:

Writing – original draft. EB: Investigation. All authors: Writing – review & editing.

Graphical abstract



Highlights

- Salinity can be highly variable spatiotemporally in enclosed sea systems
- Functional response of invasive mud crab *Rhithropanopeus harrisii* quantified
- Invasive crab feeding followed a hyperbolic Type II functional response
- Feeding rates were highest at 10 ppt and 7 ppt compared to 4 ppt
- Ecological impacts are reduced at the lowest salinity level