



Lack of anti-predator recognition in a marine isopod under the threat of an invasive predatory crab

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Received: 28 August 2021 / Accepted: 11 May 2022 / Published online: 1 July 2022
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Abstract The prey naïveté hypothesis suggests that the failure of prey to recognize novel predators as a threat is caused by a lack of anti-predator adaptations. We tested this hypothesis in a unique natural setting, where the isopod *Idotea balthica* encountered the rapidly spreading invasive crab, *Rhithropanopeus harrissii*. Earlier research had indicated high mortality of the isopods during exposure to *R. harrissii*. The isopod exerted no co-evolutionary history with any littoral crabs and thus the strong impact could be caused by lack of pre-adaptations towards the new predator species. We tested this hypothesis by studying the anti-predator responses of the

isopods with water-born cues of *R. harrissii* and of the native predatory fish *Perca fluviatilis*. Compared to control water, the isopods lowered their activity when exposed to the fish cue. Instead crab cue did not induce anti-predator behaviour. We also tested the hypothesis that mortality caused by novel predator, similar to predation by *P. fluviatilis*, would result in differential selection for the two sexes and contribute to the evolution of personalities. However, we found no differences in anti-predator behaviour nor in mortality between the sexes or personalities of the isopods. The outcomes reveal an interesting evolutionary scenario, where predation by a local predator induce soft selection on prey characteristics, but an invasive species cause hard selection without differentiating between prey individuals. Our study—conducted in the dawn of the population outbreak of *R. harrissii*—provides an excellent reference point for studies resolving the evolutionary impacts of invasive predators on naïve prey.

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Keywords Anti-predator adaptations · *Idotea balthica* · Littoral community · Personality · *Rhithropanopeus harrissii* · Sex-specific adaptations

Introduction

Species are introduced to a new environment intentionally (e.g., for aquaculture), naturally (e.g., via rafting), or accidentally (e.g., via ballast water) The

introduction may not be successful, but in some cases, the species establish a new population. A successful introduction can have profound effects on native species and/or communities (Ruiz et al. 1997; Lepäköski et al. 2002; Bax et al. 2003; Molnar et al. 2008) because it brings species into contact that do not share common evolutionary history (Freeman and Byers 2006). Hence, impacts of species invasions can be positive or negative. Negative impacts appear e.g., through reduced native biodiversity, which may cascade into erosion of habitats and ecological communities and loss of ecosystem services (Goodenough 2010; Katsanevakis et al. 2014; Doherty et al. 2016; Jormalainen et al. 2016; Lima et al. 2018; Anton et al. 2019). Invasive generalist predators are one of the main factors contributing to the decline of native species globally, as they often exert impacts that are far greater than those attributed to their native counterparts (e.g., Snyder and Evans 2006; Monceau et al. 2013; Brzeziński et al. 2019).

An introduced species can have a pronounced impact on the recipient community if the local prey species lack anti-predator responses, i.e., native prey species fail to recognize introduced predator species as a threat and/or lack appropriate defence (e.g., Anton et al. 2020). The prey naïveté hypothesis assumes that this is attributed to insufficient co-evolutionary exposure, which facilitates the establishment of the new predator and at the same time exacerbates its impacts on prey populations (Diamond and Case 1986; Cox and Lima 2006; Freeman and Byers 2006). This particularly applies when the invaded community does not include any evolutionary history with such functional predator species, and thus the prey species lack pre-adaptations towards such predators. This is the case in the Northern Baltic Sea, where the American white-fingered mud crab *Rhitropanopeus harrissii* invaded in the year 2009 an area where no native crab species had previously existed (Ojaveer et al. 2007; Kotta and Ojaveer 2012; Fowler et al. 2013).

Predation is a powerful selective force to develop anti-predator defences (reviewed e.g. in Lima and Dill, 1990) including, for example, protective armour and/or behaviour adaptations towards the predator species (DeWitt et al. 1999; Pettersson et al. 2000; Hammill et al. 2008), including freezing when predators are around (Jormalainen and Tuomi 1989) or hiding or fleeing. At the early stage of encounter,

individuals that become exposed to a novel predator may not express very effective defences. Effective anti-predator adaptations need time to evolve. For instance, Freeman and Byers (2006) showed that invaded mussel beds of *Mytilus edulis* evolved inducible morphological defences in the form of shell thickening within 15 years of the introduction of the invasive Asian shore crab *Hemigrapsus sanguineus*.

Inter-individual differences in anti-predator behaviour could be related to personality variation within the prey. Animal personality has been studied a great deal in the past decade and today personality differences are an established paradigm in behavioural ecology (Wolf and Weissing 2012; Dall et al. 2012; Sih et al. 2004a, b, 2015). Consistent inter-individual differences in behaviour are known to influence inter-specific interactions (e.g., Sih et al. 2015). For example, some individuals can be bolder in the presence of predators. Boldness can be measured as an activity which indeed may be advantageous, e.g., when locating mates, optimizing feeding rates, or maximizing territorial defence (Magnhagen 1991; Lind and Cresswell 2005; Biro et al. 2006; Stamps 2007) but can also be harmful in the presence of predators. These life-history trade-offs are assumed to be a major driving force for the maintenance of animal personalities (Stamps 2007; Wolf et al. 2007). There is a growing body of studies showing that personality differences affect prey species survival, but this new framework of individual variation in anti-predator adaptation has not yet been adopted for studies clarifying the selection pressure caused by invasive predators. Our take is that invasive predators can have drastic effects on certain personality types of the prey, and thus pose a new selective regime for personality variation in the prey species.

Furthermore, as the behaviour of males and females often differ, the selection pressure by predators often varies between the sexes. This is studied in detail in the marine isopod *Idotea baltica*, where anti-predator responses are sex-specific (Vesakoski et al. 2008). Sexes often differ due to their dimorphic traits (e.g., colour morphs, body size, ornaments) that can alter the ability of predators to find, capture, and subdue prey (Brown 1999; Croft et al. 2006). However, physical attributes are not the only sexually dimorphic traits that impact predation risk. Sex-differences in behaviours also influence the odds of survival. For instance, in *I. baltica* differences between activity

(e.g., Jormalainen and Tuomi 1989; Vesakoski et al. 2008), habitat choice (e.g., Merilaita and Jormalainen 1997, 2000; Jormalainen et al. 2001; Vesakoski et al. 2008) and feeding patterns (e.g., Merilaita and Jormalainen 2000; Vesakoski et al. 2008) can result in sex-related unequal survival rates. Yli-Renko et al. (2018) applied this knowledge on personality studies and found that isopods' personality, measured as activity, influenced their survival in the presence of *P. fluviatilis*, namely that in highly active individuals, survival was lower in males than in females.

Herein, we tested the prey naïveté hypothesis in the Northern Baltic Sea with the mud crab *R. harrissii*, as an invasive prey. *Rhitropanopeus harrissii* is a small brachyuran crab, which tolerates a wide range of temperatures (4–35 °C) and salinities (0.5 to >40 PSU) (Costlow et al. 1966; Forward 2009), making it an ideal invader. One particular and common grazer within the littoral community of the Northern Baltic Sea is the isopod *Idotea balthica*. It is a generalist herbivore, living associated with reed, seagrass, and macroalgae (Bostrom et al. 2006) and is preyed upon several visually hunting fish species, one of them is the European perch (*Perca fluviatilis*) but also by the mud crab (Forsström et al. 2015). Jormalainen et al. (2016) showed a drastic decrease of isopods in nature during the time that the crab density skyrocketed. We conducted this study at the dawn of the population outbreak of *R. harrissii* (the year 2012), when only 0–2 generations of isopods had experienced coexistence with the crab, i.e., experienced an early stage of the co-evolutionary process. This provided an excellent foundation to study the prey naïveté hypothesis, as well as serving a reference point for future studies resolving the evolution of anti-predator responses and evolutionary impacts of invasive predators on naïve prey.

Based on the above considerations, the aim of the current study was to experimentally evaluate whether the high mortality of *I. balthica* under predation pressure of the novel introduced mud crab *R. harrissii* was caused by lack of anti-predation responses. We were particularly interested in determining whether (i) isopods are able to recognize the invasive predator and whether they consequently (ii) show anti-predator responses. We further ask whether (iii) the invasive predator selects for a certain personality type or deviates between the sexes of the isopod.

Material and methods

Prey species

The isopod *I. balthica* is a colour polymorphic, generalist herbivore. In our study area, the Northern Baltic Sea (locational details below), the isopod has a lifespan of 13 to 15 months (Salemaa 1979). In earlier studies we have shown that isopod activity can be considered as a personality trait, with consistency of the behaviour over time (Yli-Renko et al. 2015). Moreover, personality is related to the overwintering survival in the laboratory (without predator presence) but also to the survival in the presence of native predators (Yli-Renko et al. 2015; 2018). This makes *I. balthica* an optimal model species to explore how personality can influence the survival of a native prey species in the presence of an invasive predator.

Invasive and native predator species

The North American white-fingered mud crab (*R. harrissii*) is a small omnivorous benthic crustacean, native to the Atlantic coast of North America (Williams 1984), from where it has expanded around the globe, mostly via ballast waters (Roche and Torchin 2007). In the Finnish Archipelago Sea (Northern Baltic Sea), where this study was conducted, it was first found in 2009 (Fowler et al. 2013) and has since been expanding its local range, occupying multiple habitats (Fowler et al. 2013; Kotta et al. 2018). Within the Finnish Archipelago, the crab not only forages on mussels and snails but also on amphipods and isopods (Forsström et al. 2015), which provoked a shift in the invertebrate community (Forsström et al. 2015; Jormalainen et al. 2016). Recently, it was shown that the crab prefers the shelter of rocky bottoms independent of food availability (Riipinen et al. 2017), and also that they are likely to negatively impact nest-building fishes by taking over their occupied nests (Lehtonen et al. 2018).

The European perch (*Perca fluviatilis*) is a common native predatory fish and forages on *I. balthica*. The fish hunts visually within littoral environments of the Northern Baltic Sea and has been used successfully in former studies as a model predator under experimental conditions (see e.g., Engström-Öst et al. 2009; Yli-Renko et al. 2018).

Field collections

In May 2012, we sampled all species used herein for experimentation within the Finnish Archipelago Sea. All experiments were conducted at the Archipelago Research Institute, University of Turku (ARI: 60°14'N, 21°58' E). The isopod and the native fish species were collected in the vicinity of ARI, while the invasive mud crab was collected in its invasive range within the Finnish Archipelago Sea (see Fowler et al. 2013). The isopods collected were exposed to maximum of three generations of the introduced crab as the first individual crabs were observed only in 2009, but the population expansion took place in 2010 and 2011.

A total of 116 adult isopods (77 males, 39 females) were collected by hand from bushes of *Fucus vesiculosus*, while the crabs (a total of 72) were collected using habitat traps. Both sexes (42 males and 30 females) were used in the experiments. The native fish predator (N=5) was caught via nets and traps that were installed at the same sites where isopods were collected. All species were transported in buckets and quickly brought to the laboratory at ARI and kept in plastic aquaria.

Prior to experimentation, all test species were maintained in a temperature-controlled laboratory room at ~13 °C, which corresponds to the in situ water temperatures during early spring. The light/dark rhythm inside the laboratory was adjusted to natural conditions (14 h day, 10 h night). Sexes of the crabs and the isopods were determined, and their carapace width (crabs) and weight (isopods) were measured, respectively.

Experimental setup

Activity measurements

A total of N=116 isopods were kept individually in plastic aquaria (dimensions 23 cm × 13 cm × 14 cm; without aeration 2.7 L) for 12 h to ensure that we measured their activity rather than their exploration behaviour in a novel environment. Activity has been shown to be a personality trait (Yli-Renko et al. 2015), and was measured for each isopod by observing their movements and locations repeatedly every 20 min following the protocol developed and used by Yli-Renko et al. (2015). Each aquarium had sand

and a small rock on the bottom to mimic their natural habitat. In addition, an apical piece and a basal piece of *F. vesiculosus* were placed at the opposite ends of the aquaria to provide shelter and food. This decoration (sand-rock-apical piece/basal piece) also made the observations of the isopod location straightforward. We observed the location of each isopod over one day (from 8:00 am to 8:20 pm local time) with a total of 37 observations per individual. The isopod could be in one of the following positions: interacting with the 'apical' or 'basal' piece of the alga; resting on the sand near the 'apical' or 'basal' piece of the alga; buried in the sand; moving along the sides of the aquaria; or resting on the rock. We quantified the individual activity as the number of changes of location that the isopod made during the 37 observations. Hence, we obtained the activity of each isopod, which was then used for experimentation.

Cue of invasive and native predators

For the anti-predator response experiment, we selected a total of 72 isopods with 43 males and 29 females. For *I. balthica*, it has been reported that inactivity is an anti-predator response (Jormalainen and Tuomi 1989). Therefore, we measured their anti-predator response cues by comparing their movements in the same aquaria (see above) but now with predator cues. The cues were either 35 ml of water taken from tanks containing the invasive crab, the native fish *P. fluviatilis* or control water (without any predator cue), which were added to experimental aquaria. After the cue water was carefully added to the experimental aquaria, we waited for 30 s before the location of isopods was observed. For each isopod we observed its number of movements repeatedly every 20 min. These measurements were conducted over 4 h (from 4:40 pm to 8:40 pm local time) with a total of 12 observations per individual. In every trial, i.e., at 20 min intervals, new cue water was added.

Predation experiment with the invasive crab

To study the survival of isopods with different activity levels (=personality), we continued the experiment and added into each of the aquaria (N=72) one *R. harrissii* individual of varying size. We then measured the isopod survival over four days. Within the

first two days of experimentation, isopod survival was checked twice per day and afterwards only once per day, which was sufficient to gather the survival data. Crabs used in the predation experiment were not fed for 12 h before the experiment.

Statistical analyses

In order to study whether the cue of invasive and native predators or control water affected the activity of isopods, we ran a generalized linear mixed model (GLMM) with negative binomial distribution and log link function. The different cues (native, invasive, and control), sex, and personality (activity level=resting on rock/sand, moving, interacting with algae) were treated as fixed factors. Isopod body size (weight) was included as a covariate. To avoid multicollinearity in our analyses we first calculated Spearman's rank correlation coefficient for body size and activity as these two are continuous factors. We did not find any correlation between these factors and thus both can be used as a fixed factor in the analysis (Spearman rank correlation: $r_s = -0.07$; $p = 0.54$). First, we also included in the model the interaction sex x cue as we were interested in whether isopod sexes responded differently to the predator cues. However, based on p-values, the interaction was not significant and therefore we simplified the model and removed the interaction from the final analysis.

To compare the probability of survival within the isopod personality types and sexes in the presence of the invasive crab species, we also ran a GLMM, but this time with a binomial error distribution (alive-dead) and logit link function (a total of $N = 72$ isopods from which $N = 19$ were found dead, and not eaten, which were excluded from the analyses). We treated isopod personality (activity) and sex as fixed factors. Earlier laboratory studies showed that the size of the crab affected the impact on prey items (Forsström et al. 2015), while the size of the isopods affected their survival in the presence of a predatory fish (Jormalainen and Tuomi 1985). Thus, the body size of crabs and isopods were included as covariates (weight for isopods and carapace width for crabs). All analyses were carried out using SAS Enterprise Guide (6.1, Cary, NC, USA).

Results

Cue of invasive and native predators

There was an indication of an anti-predator behaviour (pronounced as reduced activity) towards the native-fish predator cue, but not towards the invasive-crab predator cue (Fig. 1A). Even though this main effect was higher than the general threshold of 0.05 ($F_{(2, 66)} = 2.64$, $p = 0.08$), pairwise comparisons revealed that there were significant differences between the control treatment and the native predator cue treatment ($F_{(2, 66)} = -2.30$, $p = 0.02$) but not between the control and the invasive predator cue treatment ($F_{(2, 66)} = -0.94$, $p = 0.35$). Isopod activity under incasive predator cue treatment was between the control treatment and native predator cue treatment, but native predator cue treatment and invasive predator cue treatments did not differ statistically from each other ($F_{(2, 66)} = -1.38$, $p =$

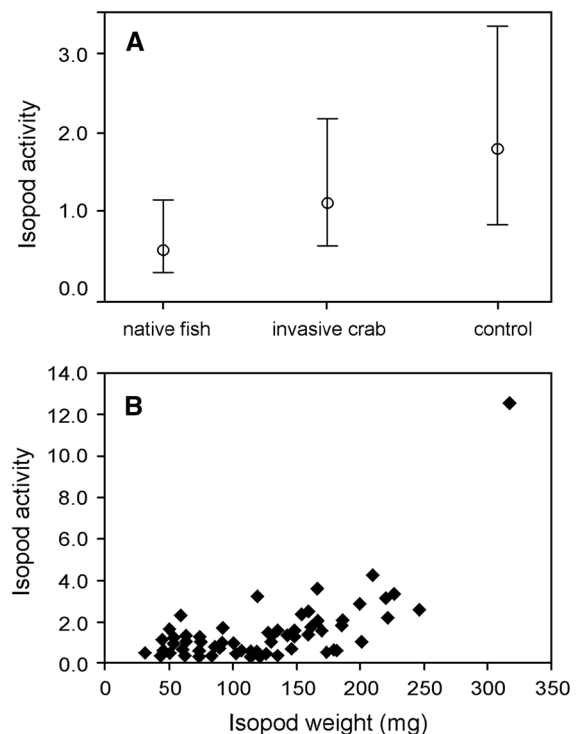


Fig. 1 Activity of individual isopods (movements) when treated with cues from the native fish (*Perca fluviatilis*), the invasive mud crab (*Rhithropanopeus harrissii*) and with control water (A) as well as the relation of isopod activity to isopod size throughout the treatments (B). Least square means for isopod activity with 95% confidence limits are shown

0.17). Neither sex ($F_{(1, 66)} = 0.44$, $p = 0.51$) nor personality ($F_{(1, 66)} = 1.72$, $p = 0.19$) affected the activity of the isopods. However, the size of the isopods significantly affected their activity level, showing that larger individuals were more active throughout all treatments ($F_{(1, 66)} = 1.72$, $p = 0.03$; Fig. 1B).

Survival in relation to personality and sex of the isopods

During the predation experiment, 15 of the 53 isopods were consumed by the crabs. Neither the personality of isopods ($F_{(1, 48)} = 0.10$, $p = 0.75$) nor their sex ($F_{(1, 48)} = 0.23$, $p = 0.62$) and body size ($F_{(1, 48)} = 0.92$, $p = 0.34$) affected their survival. Only the size of the crabs predicted the mortality: isopod survival was significantly reduced in the presence of large crabs ($F_{(1, 48)} = 4.75$, $p = 0.03$; Fig. 2).

Discussion

The prey naïveté hypothesis assumes that due the absence of evolutionary history between non-native predators and native prey species, prey species have ineffective anti-predator behaviours, which increases the impact of non-native predators (Diamond and Case 1986; Cox and Lima 2006; Freeman and Byers 2006). We had a unique opportunity to test this hypothesis at the dawn of the invasion of *R. harrissii* to the Northern Baltic Sea, where the littoral community had historically never experienced any equivalent

predator, which further increases the relevance of this system to study the impact of invasive species. A field study indicated a drastic effect of the invasive predator *R. harrissii* on its littoral community (Jormalainen et al. 2016) and a laboratory experiment suggested that the removal of *I. balthica* was due to direct predation (Forsström et al. 2015). Earlier studies done with *I. balthica* have revealed that they respond to the vicinity of a predator via freezing (Jormalainen and Tuomi 1989). In our study the freezing behaviour was apparent and was triggered by the sole chemical cue of the native predatory fish. However, the anti-predator response (inactivity) was not elicited through cue of the novel predator. Instead, the isopods maintained their activity level under the crab treatment. Our findings support the prey naïveté hypothesis in explaining the drastic effects that some invasive species can have on local fauna. More specifically, this is the first study that experimentally tested the ultimate reason for the noteworthy effects of the invasive *R. harrissii*—a lack of prey behavioural adaptation against the novel predator.

Based on our earlier studies on isopods' personality variation and personality-dependent survival (Yli-Renko et al. 2015, 2018), we hypothesized that anti-predator response would depend on the personality of the prey species. However, the variation in isopod personality did not influence the anti-predator behaviour nor the survival in the presence of the predatory crab (i.e. the isopods did not lower their activity under the chemical cue of *R. harrissii*). We also assumed that the isopod survival would have varied between the sexes, as the isopods showed between-sex variation also in their survival in the presence of *P. fluviatilis* (Yli-Renko et al. 2018) and habitat-use patterns (Merilaita and Jormalainen 1997, 2000; Vesakoski et al. 2008). However, there were no differences in survival between the sexes, nor there was any interaction between sex and treatment. This indicates that *R. harrissii* poses a so-called hard selection on *I. balthica*. Soft selection selects between individuals causing potentially evolutionary alternations to the population gene frequencies, but hard selection simply lowers the population numbers. Thus, the novel predator does not induce evolutionary pressures on personality variation in *I. balthica*, even though selection by the European perch (*Perca fluviatilis*) does (Yli-Renko et al. 2018).

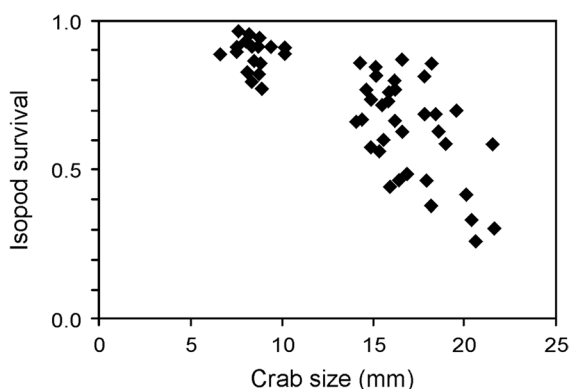


Fig. 2 Individual isopod survival in relation to the carapace width (mm) of the invasive mud crab

Evolution of personality variation is a strongly debated study area in behavioural ecology (Sih et al. 2004a, b; Réale et al. 2007; Wolf and Weissing 2012) and multiple drivers have been suggested. One of the propositions is that life-history trade-offs are the major driving force for the maintenance of animal personalities (Stamps 2007; Wolf et al. 2007; Biro and Stamps 2008; Reale et al. 2010). We have shown earlier that in *I. balthica* wintertime survival was lower for high-activity individuals (Yli-Renko et al. 2015) and that survival due to a natural predator (the same fish species as tested herein) was lower for active males than for active females (Yli-Renko et al. 2018). As previous studies have associated isopod activity with fecundity (Jormalainen and Tuomi 1989) it has been assumed that counteracting selective forces between fecundity and survival are the main driving force in maintaining personality variation (discussed also in Yli-Renko et al. 2015, 2018).

Mortality of the isopods was predicted only by the size of *R. harrissii*, meaning that the larger crabs were more likely to kill the prey. The impact of crab size on isopods has been noted also in earlier laboratory experiments (Forsström et al. 2015). This indicates that not only the absolute number of crabs in the area but especially their size distribution is an important factor in predicting their community impacts.

In many regions worldwide, drastic effects of invasive predators on local communities have been reported (e.g., Zaret and Paine 1973; Ogutu-Ohwayo 1990; Albins and Hixon 2008; Anton et al. 2019, 2020 and references therein). This is also the case in the Northern Baltic Sea, where this study was conducted and where populations of the mud crab *R. harrissii* have been found to increase alongside an extreme drop in prey communities (Jormalainen et al. 2016). That is, former communities dominated by herbivores together with periphyton-grazing gastropods and crustaceans have shifted to a mussel-dominated community with overall low abundances of herbivores (Jormalainen et al. 2016). A similar decline in invertebrate biomass and richness due to the invasive mud crab was recently also reported for the north-eastern Baltic Sea (Kotta et al. 2018). Based on our findings, the deep impacts of *R. harrissii* in the Northern Baltic Sea may occur through lack of anti-predator responses in local prey species. In summary, we have demonstrated here a lack of anti-predator behaviour by isopods against a new invasive predator

species and suggest that the high mortality of *I. balthica* when predated by *R. harrissii* is according to the prey naïveté hypothesis. Neither personality nor sex affected the isopod survival, suggesting that *R. harrissii* poses hard selection towards *I. balthica*, and that predation by the crabs does not contribute to the evolution of the personality variation of the isopods, unlike the selective predation by the native fish predator *P. fluviatilis*. In the long run, predation by *R. harrissii* should result in selection for better anti-predator responses. At the time of acceptance of this paper, isopods have approximately 11 generations of selection for more effective anti-predator behaviour. This natural experiment calls for studies that follow the evolution of anti-predator traits.

Acknowledgements We are grateful to the students from the experimental marine ecology course held at the Archipelago Research Institute (by University of Turku) in the spring 2012 for their assistance with the experiments. Research infrastructure facilities were provided by FIN-MARI (Finnish Marine Research Infrastructure consortium), and we thank Veijo Jormalainen for additional equipment. We greatly appreciate the comments of the two anonymous reviewers on the manuscript. Financial support was obtained through the Emil Aaltonen Foundation (MY-R), the Ella and Georg Ehrnrooth Foundation (MY-R), the Finnish Cultural Foundation (MY-R) as well as the Finnish Foundation for Nature Conservation (MY-R).

Author contributions MY-R, JP and OV contributed to the study conception and design, and collected the data. Analysis were performed by MY-R and JP. The first draft of the manuscript was written by MY-R and all authors improved the previous versions of the manuscript. ER finalized the manuscript. All authors read and approved the final manuscript.

Funding Open Access funding provided by University of Turku (UTU) including Turku University Central Hospital. Besides of salaries of the mentioned departments (author's affiliations), financial support was obtained through the Emil Aaltonen Foundation (MY-R), the Ella and Georg Ehrnrooth Foundation (MY-R), the Finnish Cultural Foundation (MY-R) as well as the Finnish Foundation for Nature Conservation (MY-R).

Data availability On request.

Code availability On request.

Declarations

Conflict of interest The authors have not disclosed any competing interests.

Ethics approval All animals were treated with respect and skills. Ethical permission was not relevant for non-invertebrata studies.

Consent to participate All the authors consented to participate.

Consent for publication All the authors consented to submit the manuscript.

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