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Competição interespecífica entre o siri nativo *Callinectes danae* e o siri invasor *Charybdis hellerii* em um cenário de aumento de temperatura

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Resumo

As mudanças climáticas e a invasão biológica são dois dos principais fatores responsáveis pela perda de biodiversidade. Quando estabelecidas, espécies invasoras competem pelos mesmos recursos que espécies nativas, frequentemente monopolizando-os devido a sua alta agressividade em situações de competição direta (interferência comportamental). A temperatura desempenha um papel fundamental na fisiologia e comportamento de espécies ectotérmicas marinhas, com espécies invasoras frequentemente apresentando maior resistência a estressores climáticos em comparação a espécies nativas. Dessa forma, o aumento da temperatura em cenários climáticos futuros pode intensificar a exclusão competitiva de espécies nativas com nicho ecológico semelhante ao das espécies invasoras. O presente estudo avaliou se a temperatura afeta as interações agonísticas e a aquisição de recursos entre a espécie de siri nativo *Callinectes danae* (siri-azul) e a espécie de siri invasora *Charybdis hellerii* (siri-capeta), de nicho ecológico similar. Simulamos uma situação de competição entre a espécie nativa e o competidor invasor por um único item alimentar (mexilhão *Perna perna*) na temperatura controle (27,1°C) e no cenário climático RCP 8.5 (+4,3°C; 31,4°C), avaliando a interação agonística e a aquisição de recursos de ambas as espécies. A temperatura do cenário climático RCP 8.5 reduziu agressões sem contato, sugerindo uma escalada mais rápida da agressividade nos confrontos, independentemente do competidor presente. Contudo, agressões com e sem contato foram mais intensas entre competidores conspecíficos do que competidores invasores, independente da temperatura utilizada. A menor intensidade das lutas com competidores invasores pode estar associada à percepção de ameaça devido ao maior tamanho das quelas da espécie invasora em relação à espécie nativa. A aquisição de alimento também não foi afetada pela temperatura e pela presença da espécie invasora, enquanto a presença de um competidor conspecífico reduziu o tempo de monopolização do alimento pela espécie nativa. Nossos resultados sugerem que as temperaturas projetadas em cenários climáticos futuros não afetarão significativamente a dinâmica competitiva entre as espécies *C. danae* e *C. hellerii*.

Palavras-chave: Interferência comportamental; mudanças climáticas; interação agonística; aquisição de recursos; recurso alimentar

Abstract

Climate change and biological invasions are two major drivers contributing to biodiversity loss. Once established, invasive species overlap ecological niches with native species, frequently monopolizing resources due to their aggressiveness during direct competition. Temperature plays a critical role in the physiology and behaviors of marine ectothermic species, with invasive species exhibiting greater resistance to abiotic stressors compared to native species, potentially intensifying competitive exclusion under future climate change scenarios. This study evaluates whether temperature affects agonistic interaction and resource acquisition between native and invasive swimming crab's species during food resource competition. Similar-sized individuals of the native blue crab *Callinectes danae* were exposed to the similar niche invasive swimming crab *Charybdis hellerii* in a competition situation for a single food item (*Perna perna* mussel) under control (27.1°C) and climate scenario RCP 8.5 (+4,3°C; 31.4°C). Our results suggest that future climate change scenario temperatures may not significantly alter interactions with the invasive species. However, higher temperatures decreased non-contact aggressions, indicating a quicker escalation of fights regardless of the competitor's present. Physical aggressions were significantly more intense with conspecifics competitor than with invasive competitors. The lower intensity of fights with invasive species may be attributed to the threat posed by the invasive's larger weapon size (cheliped) relative to the native species. Food acquisitions were also not affected by temperature or by the invasive species presence, despite the conspecific competitor led to a reduction in the native species food monopolization time. While the invasive species exhibited slower feeding initiation than the native species, it maintained similar food holding time. These findings suggest that projected climate change scenarios are unlikely to substantially alter the competitive dynamics between *C. danae* and *C. hellerii*.

Keywords: temperature; *Callinectes danae*; *Charybdis hellerii*; behavioral interference; feeding efficiency.

Sumário

Competition between tropical native and invasive crabs in climate change scenarios: can global warming interact with biological invasion?

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1. Introduction

Climate change and biological invasion are two key drivers contributing to biodiversity loss (Wernberg et al. 2011; Mollot et al. 2017; Hillebrand et al. 2018). The intensification of globalization in recent decades has led to increasingly higher amounts of CO^2 and greenhouse gas emissions (Rehman et al. 2022), resulting in an increase in the sea surface temperatures up to 4.3ºC by the end of the century (IPCC 2023). Furthermore, maritime traffic and international maritime trade have increased, facilitating the dispersion and settlement of invasive species through ballast water in marine ecosystems (Keller et al. 2011; Sardain et al. 2019). Consequently, more species are being reported outside their natural range (Seebens et al. 2018). Once well-established these species unbalance ecosystems by changing interspecific interactions (*e.g.* competition and predation (Sura and Mahon 2011; Svenning et al. 2014) and affecting community structure (David et al. 2017; Bradley et al. 2019). However, invasive species may present a higher thermal limit than native species (Sorte et al. 2013; Liu et al. 2020), which may promote competitive advantages during competition with native species in future climate

change scenarios by affecting some species more than others (Kordas et al. 2011; Lauchlan et al. 2019).

Interspecific interactions are important abiotic factors regulating populations in marine ecosystems (Lindegren et al. 2011). Invasive species can compete with native species for the same resources, e.g. food resources (Richter-Boix et al. 2013; Zengeya et al. 2015; Yalçın Özdilek et al. 2019), overlapping their ecological niche. Whether directly (interference competition; (Le Louarn et al. 2016)) or indirectly (exploitative competition; (Damas-Moreira et al. 2020)), these interactions can impact the fitness of native species, leading to population declines through the process of competitive exclusion (Bøhn et a'l. 2008; Catford et al. 2018). However, interference competition (or behavioral interference) has a more pronounced effect on the fitness of native species as it involves resource monopolization through aggressive behaviors (Grether et al. 2017) such as food steal (Damas-Moreira et al. 2020) and agonistic disputes (Sanches et al. 2012; Culbertson and Herrmann 2019). As invasive species often exhibit a high aggressiveness (Hudina et al. 2014), their coexistence can lead to the displacement of less aggressive native competitors and, hence, to niche partitioning in the short term (Polo-Cavia et al. 2011; Britton et al. 2018; Culbertson and Herrmann 2019).

Temperature is one of the main abiotic stressors for marine ectothermic animals by affecting physiology and, consequently, the behaviors of individuals (Su et al. 2020; Vianna et al. 2020). Species may exhibit different thermal ranges for their activities, with behaviors being more affected when the temperature is close to their thermal limit due to a higher metabolic rate (Vinagre et al. 2015; Sunday et al. 2019). In this situation, crucial behaviors for resource acquisition may be negatively affected, reducing the food consumption and foraging activity (Nowicki et al. 2012). However, when the temperature is within the species' thermal optimum, it may intensify behaviors, with individuals

increasing fight intensity (Su et al. 2020) and enhancing foraging performance (Hu et al. 2021). Invasive species are often more tolerant of thermal stress, which could imply less negative impacts on physiology and behavior compared to native species (Zerebecki and Sorte 2011; Kelley 2014). For the invasive freshwater Mosquitofish (*Gambusia holbrooki*), higher temperatures induce higher aggressiveness than in the endangered Iberian toothcarp (*Aphanius iberius*), intensifying interference competition of the native species (Carmona-Catot et al. 2013). Despite this, moderate levels of climate changes warming were not sufficient to change aggressive behavior on the invasive crab *Carcinus maenas* (Lauchlan et al. 2019).

Although understanding individual responses to future climate change scenarios is important for predicting the ecological impacts of invasive species on native species, it is still poorly understood how temperature may directly impact resource acquisition and ecological interactions between invasive and native marine tropical species. Our study is the first to assess temperature effects on competition between invasive and native crab species of tropical regions. As invasive species may exhibit greater resistance to climatic stressors than native species (Yu et al. 2012), we hypothesized that in future climate change scenarios, the native species would reduce fight intensity, but the invasive species would maintain similar aggressiveness. Consequently, the native species would have less success in obtaining food resources. Thus, our objective is to evaluate whether the temperature (climate change scenario RCP 8.5; + 4.3°C) affects agonistic interaction and resource acquisition by a native species during competition for food resources with an invasive competitor.

2. Material and Methods

Biological models, collection and maintenance

We opt to use two species of swimming crabs (Brachyura; Portunidae) with similar ecological niche as animal models of our study due to their complex aggressive behaviors (Weis 2010) and to the strong pressure that invasive crustaceans exert on native species populations decline (Anton et al. 2019). We chose *Charybdis hellerii* as the invasive species and competitor model due to its presence as a well-established invasive species at the southwestern Atlantic Santos-São Vicente estuarine-bay complex (Sant'Anna et al. 2012). This species has demonstrated ecological interference in several native species both through competition (Oliveira 2016) and predation (Izar et al. 2023). *Charybdis hellerii* originates from the Indo-Pacific (Ferreira and Rosso 2009) and occurs associated with rocky shores ecosystems. This species is highly aggressive (Oliveira 2016), making it a strong competitor that directly competes with various native species of crustaceans (Vinagre et al. 2018).

One of the native species that competes with *C. hellerii* is the blue crab *Callinectes danae* (Oliveira 2016). This native species is an important fishery resource along the Brazilian coast (Pereira et al. 2009; Joyeux et al. 2010) and occur in a variety of habitats (Pereira et al. 2009; Araújo et al. 2012) but competes with the invasive species in habitats near to rocky shore ecosystems (Sant'Anna et al. 2012; Oliveira 2016). Species of the genus *Callinectes* also exhibit highly aggressive behavior (MacDonald et al. 2007), making it a good native species model.

Both species were collected from rocky shores in three cities along the São Paulo State coast (Santos, São Vicente, and Itanhaém), southeast Brazil. The collections during low-tide periods involved active search, while during high-tide periods, ring nets baited with fish were used. Only healthy males in the intermolt stage and all pereopods, with a carapace width of 7.12 (± 0.9 cm) were selected. Standardization of males was necessary

due to sexual dimorphism present in both species (Mantelatto and Garcia 2001; Marochi et al. 2013).

Species were acclimatized in monospecific stock systems (180 L; 50 X 89 X 48,5 cm) in a temperature-controlled room with systems separated by temperature treatment (control = 27,1ºC or RCP8.5 = 31,4ºC) for 21 days prior to the initial of experimental trials. Temperature was maintained constantly using 100 W thermostats, and measurements were taken twice daily using a precision digital thermometer. Water quality was kept stable through physical and biological filtration, with salinity kept at 25 using synthetic sea salt Veromar to avoid chemical interference during experiments. The individuals were fed on alternate days with entire *Perna perna* mussels (adapted from Matheson and Gagnon 2012), which are one of the food items consumed for both species in rocky shore ecosystems (Oliveira 2016) and were also used as food resource in experimental trials.

The initial temperature of the stock systems was maintained similar to the field conditions and then increased by 1°C per day until reaching the target temperature (Su et al. 2020). If the stock was already at the acclimation temperature (27,1ºC or 31,4ºC), newly collected individuals were acclimatized using 80 L aquariums until they reached the stock temperature, and then transferred on acclimatized stocks. Shelters were provided within the stocks to reduce agonistic interactions and maintain at a maximum density of 8 individuals per system. The temperature control of 27,1ºC was established based on the mean sea surface temperatures from the last 5 summers using the National Oceanic and Atmospheric Administration (NOAA) meteorological database (adapted of Marochi et al. 2021), covering all collection municipalities. We used the most pessimistic climate change scenario RCP8.5 (IPCC 2022) as future climate change scenario of our

experiments, adding the projection of +4,3ºC to the control temperature obtained, resulting in a projected future climate change scenario of 31,4 °C.

Experimental design

To evaluate the impact of warming on future climate change scenarios on agonistic interactions and resource acquisition by a native species competing with an invasive species, we simulated a competitive scenario involving a single food resource (*Perna perna* mussel) under two climate scenarios [control (27,1 °C) and RCP 8.5 (31,4°C); Fig. 1]. The experiment involved exposing one focal animal individual (native species; *Callinectes. danae*) to a competitor [conspecific (*Callinectes danae* against *Callinectes danae*; DXD) or invasive (*Callinectes danae* against *Charybdis hellerii*; DXC)] in an experimental arena with one individual of mussel (food item) placed at the center (Fig. 2). We used focal animals and competitors of similar carapace width (±2 %) (MacDonald et al. 2007) to avoid size asymmetry interference during fights.

To assess the agonistic interaction with the invasive competitor to each climate change scenario, we exposed the native species to an invasive (DXC; $n^{control} = 6$, $n^{RCP\ 8.5} = 6$) or a conspecific competitor (DXD; $n^{control} = 9$, $n^{RCP\ 8.5} = 8$). We quantified aggressive behaviors of each individual separately (both the focal animal and competitor) to assess each native and invasive species behavior.

To assess the resource acquisition of the native species during competition with the invasive competitor under each climate change scenario, we exposed the native species to an invasive (DXC; $n^{control} = 6$, $n^{RCP\ 8.5} = 6$) or conspecific competitor (DXD; $n^{control} = 9$, $n^{RCP\ 8.5} = 8$), using isolated individuals of each species [isolated *C. hellerii*

(CISO; $n^{control}$ = 9, $n^{RCP\ 8.5}$ = 6); isolated *C. danae* (DISO; $n^{control}$ = 9, $n^{RCP\ 8.5}$ = 8)] to compare feeding behavior with and without competitors.

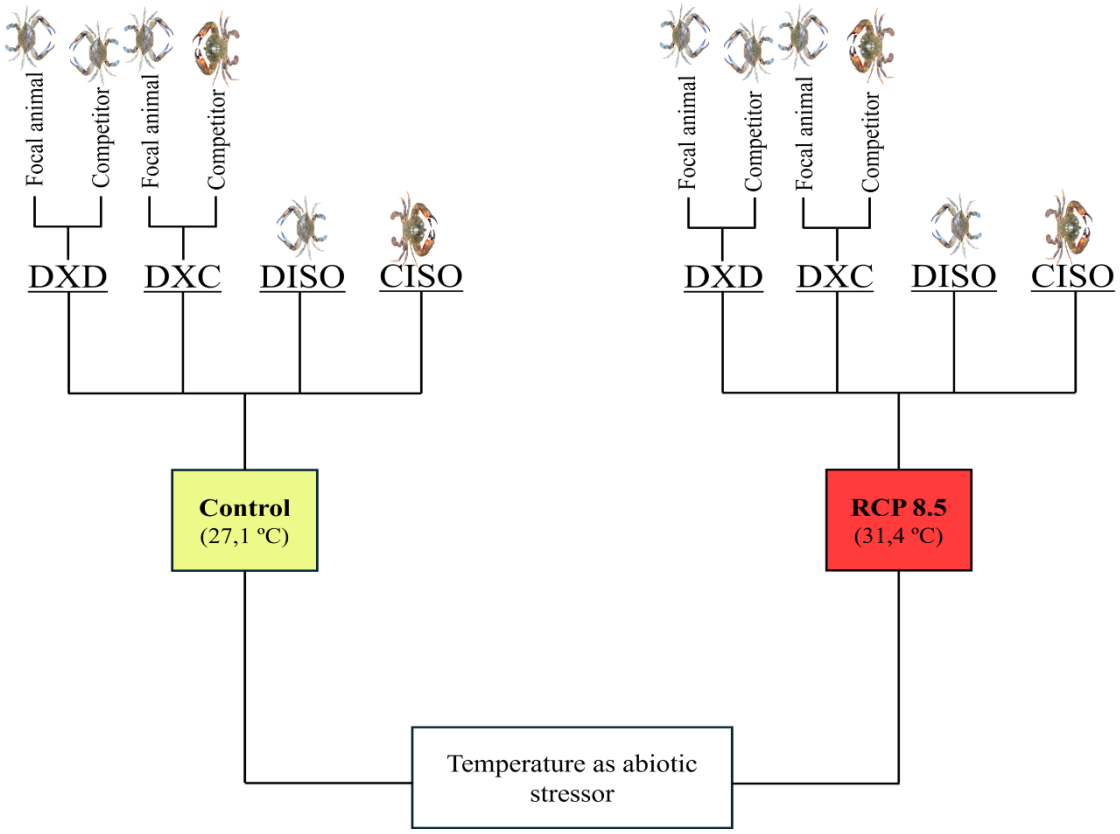

Fig. 1: Factors (temperature; control and RCP 8.5) and factor levels (competitors; DXD, DXC, DISO and CISO) of the experimental designs. DXD indicates conspecific competitor treatment (*Callinectes danae* against *C. danae*), DXC indicates invasive competitor treatment (*C. danae* against *Charybdis hellerii*), DISO indicates isolated *C. danae* treatment and CISO indicates isolated *C. hellerii* treatment. For treatments with competitors (DXD and DXC), focal animal and competitor (observer individual) were used as factors.

Experimental protocol

Before starting the experiments, individuals stayed for 72-hour individualized acclimatization period (Fig. 1) to reduce the effects of previous social interaction (Hsu et al. 2006; Kuo et al. 2019). Individuals were selected from stocks maintained at the same

temperature as the acclimatization aquaria, measured (carapace width; cm), and then individually housed in 22-liter acclimation aquaria (40 X 24 X 23 cm) with 3 cm of sand that had been previously washed with chlorine and dechlorinated to remove chemical cues (identical to the experimental arena conditions). Acclimation aquarium conditions were maintained similar to the stocks tanks, with food provided in the same manner as in the stock system and a 24-hour fasting period prior to the experimental trial.

A 40-liter aquarium (45 X 35 X 20 cm) at the same condition of the acclimatization aquarium was used as neutral arena (without prior residence) for experimental trials. We used sand as substrates to facilitate locomotion during fights. Before starting the experimental trial, the individuals were placed on opposite corners of the arena, with the food item (standardized as 2/3 of the carapace width to facilitate handling) positioned at the center (Fig. 2). They were then acclimatized for 5 minutes in the experimental arena using an opaque square enclosure with holes to allow chemical perception (Fig. 2). The upper part of the enclosure was identified as F or C to differentiate focal animal from competitor at behavioral analysis. After 5 minutes, the enclosures were removed at the same time, starting a 45-minute experimental trial (Fig. 2). The experiments were recorded to avoid observer interference and allowing later behavioral analysis. No individual was seriously injured or died during the experiments.

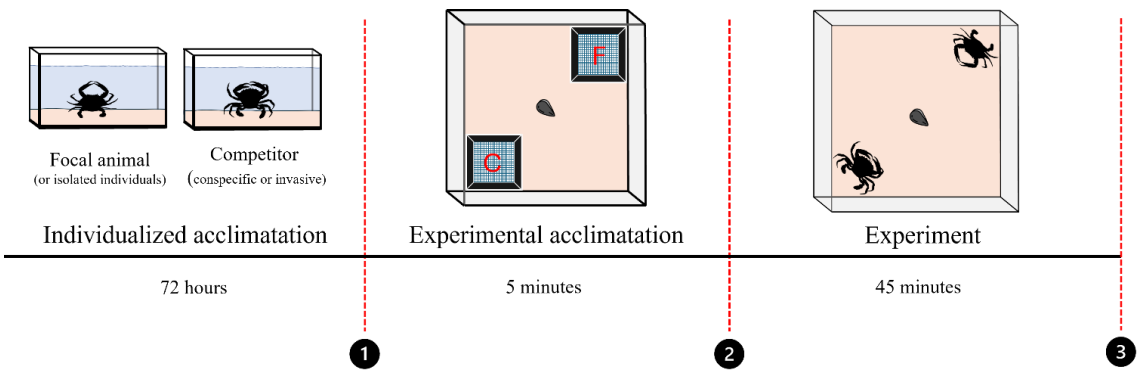

Fig. 2: Chronological sequence of events in the climate change competition experiment. Focal animals represent the native species *Callinectes danae* and the invasive (*Charybdis hellerii*) or conspecific competitor (*C. danae*). The horizontal bar indicates the stages of the experiment and the duration. Number 1 indicates the beginning of the experimental acclimatation in the experimental aquarium (neutral arena), with black squares being the opaque shields used, and the food item (*Perna perna*) placed at the center. Letter "F" indicate the opaque shields identified to focal animals and "C" to competitors. Number 2 indicates the beginning of the experiments, with the removal of the opaque shields. Number 3 indicates the end of the experiment.

Agonistic interactions

As temperature may affect energy output during fights, we opted to separate aggression behaviors by absence or presence of physical contact. We used non-contact aggression and physical aggression to assess fight intensity, while aggression latency was used to assess fight motivation. Non-contact aggression was measured by the sum of two displayed aggressive behaviors with no physical contact: chelipeds display and threat (Table 1). Physical aggression was measured by the sum of three aggressive behaviors with physical contact and potential damage to the opponent: strike, grasp and wrestles (Table 1). Aggression latency was considered as the time, in seconds, taken by the individual (focal animal and competitor) to display the first aggressive behavior with physical contact (strike, grasp or push).

Table 1: Aggressive behavioral measures of intra and interspecific crustacean fights (adapted from Sneddon et al. 1997; Su et al. 2020).

Behavior	Description	Aggressive variables
Chelipeds display	Chelipeds are held out in front with the chalae open or closed	Non-contact aggression
Threat	One crab quickly approaches the other, with the opponent retreats	Non-contact aggression
Strike	One crab suddently hits out at the other with one or both chelips	Physical aggression
Grasp	One crab uses its chelae to pinch the carapace, chelipeds or legs of the other crab	Physical aggression
Wrestles	Both crabs interlock theis chelae, pushing against each other	Physical aggression

Due to dependence (two individuals of the same trial) and non-parametric data, we used Generalized Estimation Equations (GEE) for aggressive variables. GEE analysis consists of a marginal model for correlated structure with non-normally distribution data, making it a suitable approach for behavior analysis with dependent data (for further detail see Pekár and Brabec 2018). All analyses were performed using the 'geepack' package (Halekoh et al. 2006) in R (R Core Team 2023).

The fixed factors used were the temperature (2 levels: control or RCP 8.5), competitors (2 levels: DXD and DXC) and the observed individuals (2 levels: focal animal or competitor). We selected regression models with exchangeable structures ("exchangeable" function) with the Poisson family and Log function. The Wald test was used to test the significance of fixed factors, with statistical significance set at $p < 0.05$. A *post hoc* Tukey test was applied to all aggressive variables to assess differences between factor levels when observing differences in factor interaction. Outliers' data were removed from the analysis using the Chauvenet test.

Resource acquisition

As feeding behavior variables we used feeding latency to assess feeding motivation and handling time to assess the monopolization of the food resource. Feeding latency was considered as the time, in seconds, taken by the individual to start handling

the food item. Handling time was considered as the time, in seconds, that the individual spent handling the food item. We analyzed focal animal and competitor behaviors separately, with the focal animal analysis representing data only from native species, and the competitor's analysis allowing us to compare the invasive and native species feeding behavior. Thus, we excluded dependent data from feeding behavior analysis, allowing us to compare treatments with competitors (DXC and DXD) to each species isolated (CISO and DISO).

For the focal animal feeding behavior analysis, we used as fixed factors temperature (2 levels: control or RCP 8.5) and competitor (3 levels: DISO, DXC – focal animal, DXD – focal animal). For the competitor's analysis we used as fixed factors temperature (2 levels: control or RCP 8.5) and competitor (4 levels: CISO, DISO, DXC – competitor, DXD – competitor). We used General Linear Models (GLM) with Poisson family distribution and Log function due to non-parametric data. Outliers' data were removed from the analysis using the Chauvenet test and data was transformed to avoid overdispersion when necessary. A *post hoc* Tukey test was applied to assess differences between factor levels.

3. Results

Aggressive behavior

The non-contact aggression was significantly affected by temperature (GEE: Wald test, $\chi^2 = 13.9$, $p < 0.001$; Fig. 3), being 2.5 times less intense at the RCP8.5 climate (mean of 11.9) change scenario compared to the control temperature (mean of 26.1), regardless of the competitor and the observed individual (GEE: Temperature:Competitor:Observed individual Wald test, $\chi^2 = 0.15$, $p < 0.694$). Non-contact aggressive behaviors was also 2.5

times more frequent during conspecifics fights (mean of 25.6) than with invasive competitors (mean of 10.1) (GEE: Competitor Wald test, $\chi^2 = 21.3$, $p < 0.001$; Fig. 3), with similar aggressiveness displayed by focal animal and competitors (GEE: Competitor:Observed individual Wald test, $\chi^2 = 0.63$, $p = 0.427$; Fig. 3).

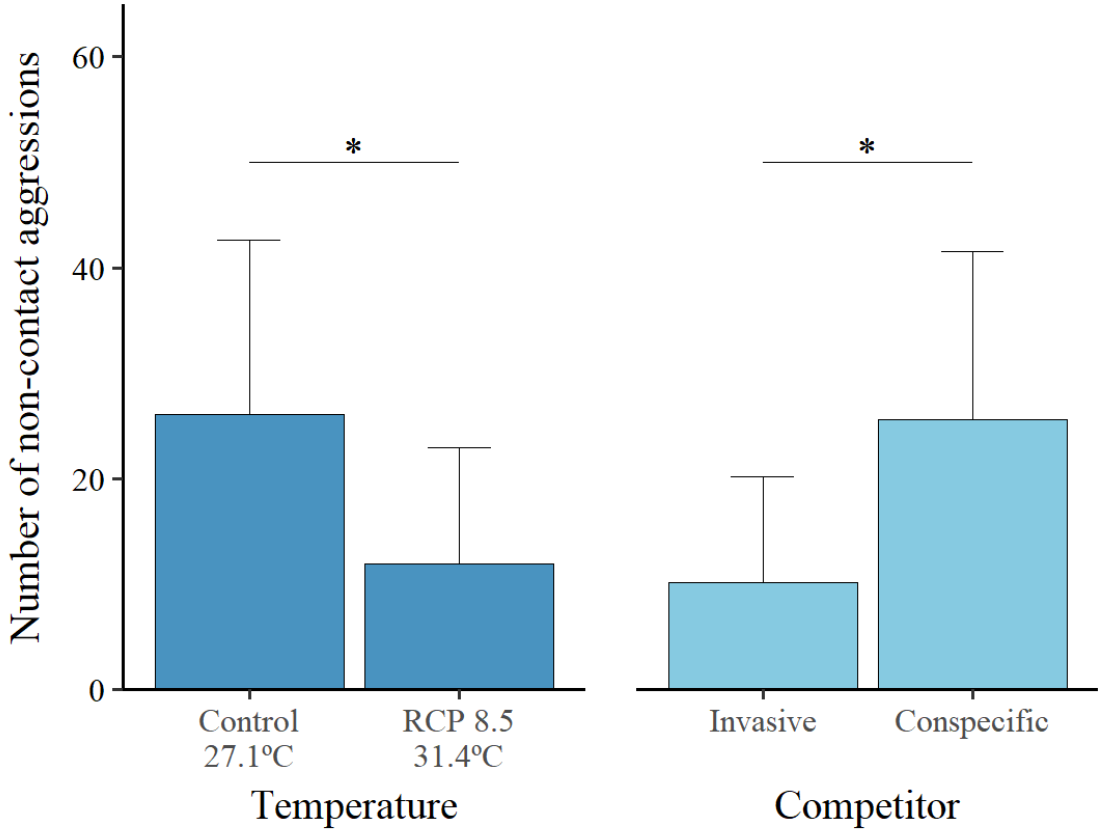

Fig. 3: Number of non-contact aggressions (chelipeds display and threat) by temperature (left bar graph; dark blue) and type of competitor (right bar graph; light blue). The left graph represents the total non-contact aggressive behaviors of both invasive and conspecific fights for each temperature used. The right graph represents the sum of focal animal and competitor non-contact aggressions during the invasive (DXC; *Callinectes danae* against *C. hellerii*) and conspecific (DXD; *C. danae* against *C. danae*) fights, regardless of the temperature used. Asterisks (*) represent statistical significance ($p < 0.05$). The upper limit of the bar indicates the mean value, while the whiskers represent the standard deviation of the data.

Physical aggression was significantly influenced by the type of competitor (GEE: Competitor Wald test, $\chi^2 = 111.6$, $p < 0.001$; Fig. 4), being nearly tenfold higher during conspecific (mean of 17) encounters compared to those with invasive competitors (mean of 1.75), regardless of temperature (GEE: Temperature:Competitor Wald test, $\chi^2 = 0.0$, $p = 0.953$; Temperature Wald test, $\chi^2 = 1.1$, $p = 0.287$). There was no significant interaction involving the observed individual (GEE: Temperature:Competitor:Observed individual Wald test, $\chi^2 = 0.1$, $p = 0.734$), suggesting that both focal and competitor individuals exhibited similar levels of aggression, irrespective of temperature. Although less intense, fights with invasive competitors were initiated with similar latency as those with conspecifics, as indicated by the non-significant effects of competitor type (GEE: Competitor Wald test, $\chi^2 = 1.957$, $p = 0.16$), individual identity (GEE: Competitor:Observed individual Wald test, $\chi^2 = 0.171$, $p = 0.68$), and temperature (GEE: Temperature Wald test, $\chi^2 = 0.041$, $p = 0.91$). These results suggest a similar motivation to initiate fights, despite the higher intensity of conspecific interactions.

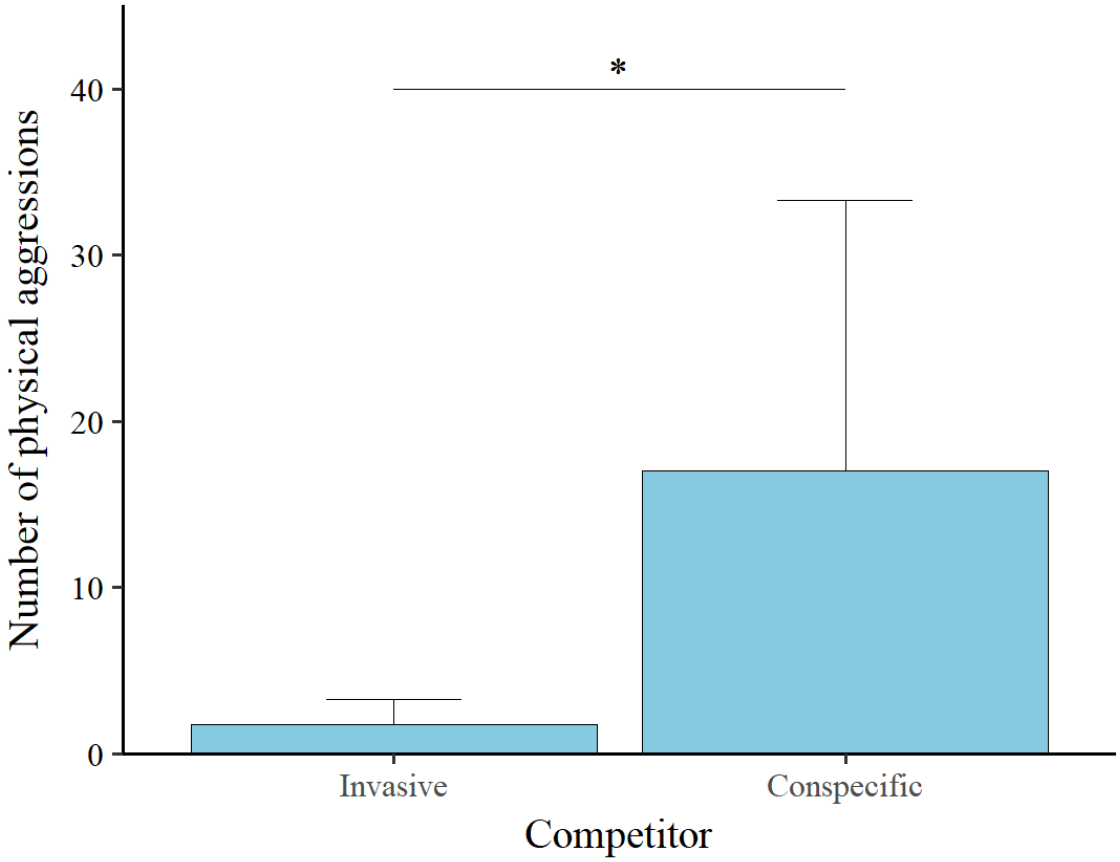

Fig. 4: Number of physical aggressions by the type of competitor. The graph represents the sum of focal animal and competitors' physical aggressions during the invasive (DXC; *Callinectes danae* against *C. hellerii*) and conspecific (DXD; *C. danae* against *C. danae*) fights, independently of the temperature used. Asterisks (*) represent statistical significance ($p < 0.05$). The upper limit of the bar indicates the mean value, while the whiskers represent the standard deviation of the data.

Feeding behavior

While agonistic interactions were more intense with conspecific competitors, the native species exhibited similar feeding latency regardless of competitor type (GLM: Competitor; Deviance = 49.2, $p = 0.077$) or temperature (GLM: Temperature; Deviance = 53.3, $p = 0.631$). Handling time of the focal animal was unaffected by temperature (GLM: Temperature; Deviance = 93.3, $p = 0.251$) but was significantly influenced by

competitor type (GLM: Competitor; Deviance = 83.3, p = 0.006; Fig. 5). The native species spent three times longer handling food items in the absence of competitors (DISO; mean of 615) compared to when a conspecific competitor was present (DXD; mean of 190) (Tukey: Z = -3.17, p = 0.0042; Fig. 5). Handling time during fights with invasive competitors was similar to both, when the native species was alone (Tukey: Z = -1.42, p = 0.32; Fig. 5) and to the conspecific competitor treatment (Tukey: Z = -1.55, p = 0.26; Fig. 5), suggesting that individuals monopolized the food item less during competition with conspecific than to an invasive competitor.

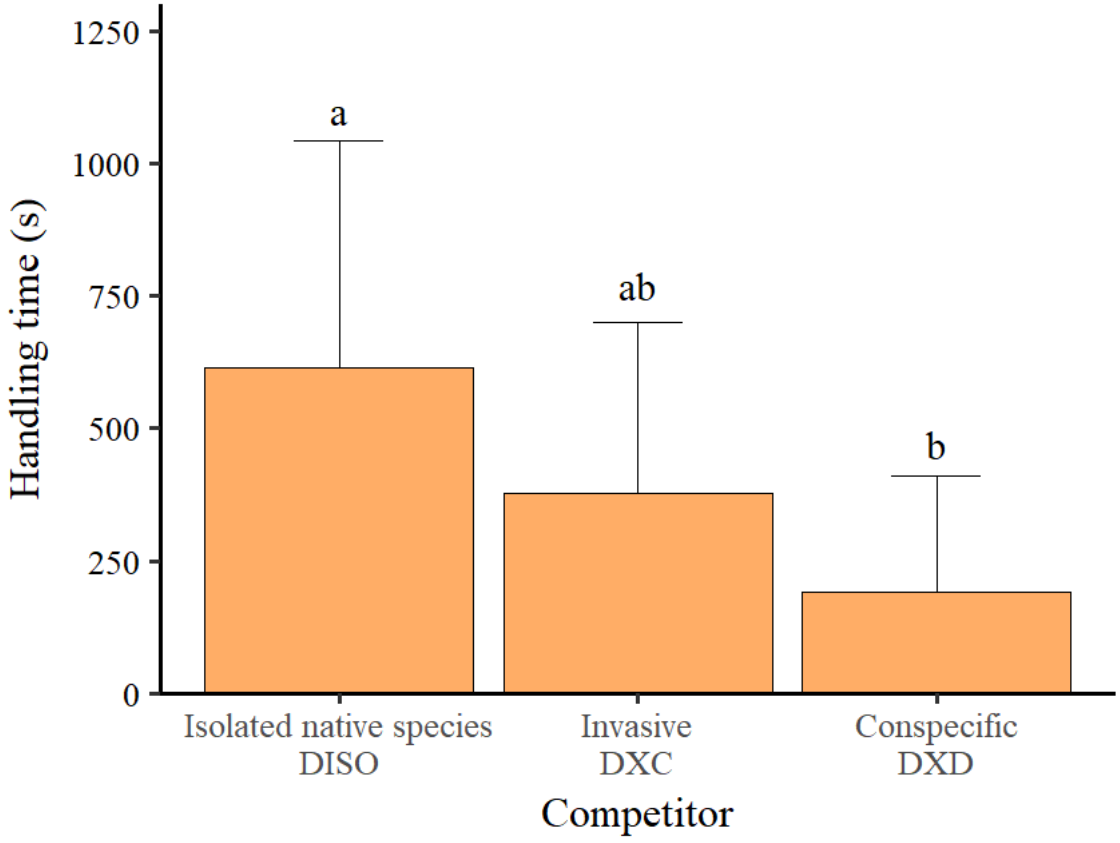

Fig. 5: Food item handling time (seconds) of the focal animals to the invasive competitor treatment (DXC), conspecific competitor treatment (DXD) and isolated native species (DISO). Different letters represent statistical significance ($p < 0.05$). The upper limit of the bar indicates the mean value, while the whiskers represent the standard deviation of the data.

Competitor feeding latency was unaffected by temperature (GLM: Temperature; Deviance = 57.9, p = 0.67) but varied significantly with competitor type (GLM: Competitor; Deviance = 58.1, p < 0.001; Fig. 6), showing that the invasive species used as a competitor (DXC; mean of 1018) took nearly five times longer to initiate feeding compared to native competitors (DXD; mean of 210) (Tukey: Z = -3.04, p = 0.013; Fig. 6) and nine times longer than isolated native species (DISO; mean of 111) (Tukey: Z = 4.75, p < 0.001; Fig. 6). Additionally, the isolated invasive species (CISO; mean of 341) took three times longer to initiate feeding compared to the isolated native species (Tukey: Z = 2.56, p = 0.050; Fig. 6), indicating superior foraging efficiency of the native species. Although the native species accessed the food item more quickly, competitor handling time was unaffected by temperature (GLM: Temperature; Deviance = 88.9, p = 0.36) or competitor type (GLM: Competitor; Deviance = 83.9, p = 0.17), suggesting similar food monopolization duration.

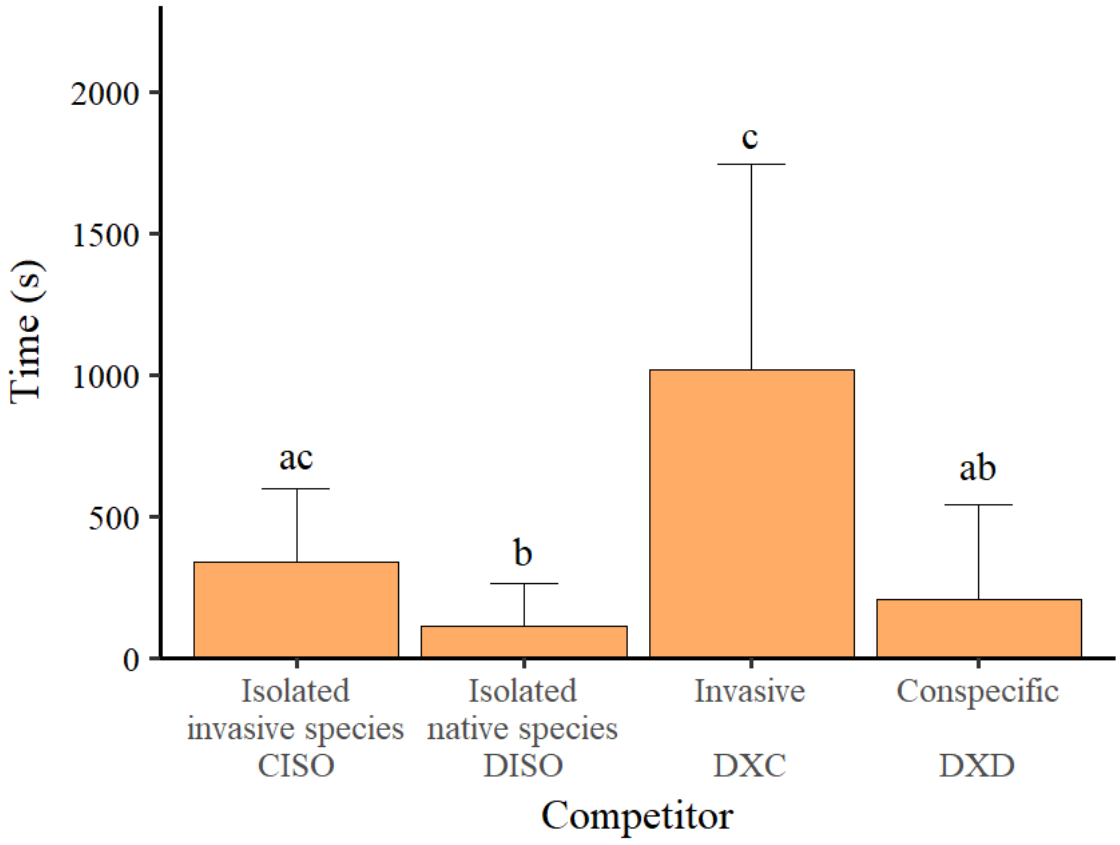

Fig. 6: Feeding latency (seconds) of competitors (DXC – *Charybdis hellerii*; DXD – *Callinectes danae*) and isolated individuals (CISO and DISO). Different letters represent statistical significance ($p < 0.05$). The upper limit of the bar indicates the mean value, error bars represent the standard deviation.

4. Discussion

Our results indicate that projected future climate change scenarios do not significantly impact the intensity of aggressive behaviors or resource acquisition during competition with an invasive competitor. While we observed a decrease in non-contact aggressive behaviors under warmer conditions, this effect was independent of the presence of an invasive competitor. Fights with conspecific competitors resulted in more intense aggressive interactions compared to invasive competitors. Both species initiated fights similarly, regardless of temperature, suggesting reactive responses to opponent aggression. Neither species' feeding behavior was significantly affected by temperature or competitor type. The presence of the invasive competitor did not influence the native species' feeding latency or handling time, but the presence of a conspecific competitor led to a reduction in the native species' food monopolization time. While the invasive species exhibited slower feeding initiation, it maintained similar food holding time, even in the absence of a competitor. Our findings suggest that future climate change scenarios are unlikely to significantly alter the competitive dynamics between these species.

Temperature in our study influenced non-contact aggressive behaviors, such as aggressive displays, which are commonly used by crustaceans to signal resource-holding potential (RHP) before engaging in fights with an opponent (Briffa 2013) indicating aggressive intent (Elwood et al. 2006). However, temperature did not significantly affect physical aggressive interactions. suggesting a reduction in signaling aggressive behavior

under warmer conditions for both conspecific and invasive fights. Hence, individuals may escalate to physical confrontations more readily under warmer conditions.

Our findings on aggressive behaviors align with Lauchlan et al. (2019), who reported no significant changes in agonistic intensity for both native and invasive species under future climate change scenarios. However, our results contrast with Su et al. (2020), who observed increased cheliped displays and physical contact aggression in the swimming crab *Portunus trituberculatus* at elevated temperatures (32°C). Other studies, such as Da Silva-Pinto et al. (2020), have reported shifts in aggressive behavior, with damselfish adjusting from high-energy-cost displays to more economical strategies under warmer conditions. Thus, the influence of temperature on aggressive behavior appears to vary among ectothermic species, potentially explaining the observed discrepancies. While increased temperature can elevate metabolic rates in crabs (Vianna et al. 2020) and alter metabolite concentrations like glucose and lactate (Su et al. 2020), physiological responses and subsequent behavioral changes may be more pronounced near thermal limits (Sinclair et al. 2016).

Non-contact and physical aggressive behaviors indicate that agonistic interactions were more intense during competition with conspecific competitors than with invasive competitors. This may suggest that native individuals perceive a greater threat from conspecifics than from invasive competitors. The reduced threat perception towards invasive species may be due to a lack of recognition, as previously reported by Dufour et al. (2020). To minimize injury risk, individuals often assess opponents based on factors like recognition and resource-holding potential (e.g., body size and weapon size) before engaging in fights (Grether et al. 2009). In crustaceans, weapon size, particularly cheliped size, is a crucial factor in assessing fighting ability (Barki et al. 1997; Sneddon et al. 1997). For hermit crabs, cheliped size is a more reliable predictor of fighting ability than

body size (Yoshino et al. 2011). The invasive species *C. hellerii* exhibits a higher weapon allometry coefficient (propodus length × carapace width) of 1.40 compared to 1.25 for the native *C. danae* (Mantelatto and Garcia 2001; Marochi et al. 2013), suggesting a higher energy investment in cheliped development for *C. hellerii* and potentially resulting in larger weapons relative to body size. Consequently, smaller individuals of *C. hellerii* may be able to compete effectively for resources with larger *C. danae* individuals.

The feeding behavior of the native species suggests that the invasive competitor does not significantly interfere with its feeding behavior, regardless of the climate scenario. This is supported by the similar time taken to obtain and handle food, both in the absence of competitors and in the presence of the invasive competitor. Furthermore, there were no significant differences between treatments with invasive and conspecific competitors. The increased monopolization of the food item during conspecific competition suggests that conspecifics pose a stronger competitive threat to *C. danae* than invasive competitors. Although temperature did not significantly impact feeding behavior in our study, the combined effects of pH and temperature under future climate change scenarios may influence feeding behavior. For instance, the native swimming crab *Portunus armatus* experienced reduced feeding time, while the invasive *Carcinus maenas* remained unaffected. Similarly, the Japanese stone crab (*Charybdis japonica*) exhibited faster food discovery under future climate scenarios (Wu et al. 2017). Similar responses have been observed in other taxa. For example, while juvenile *Siganus doliatus* remained unaffected by warmer conditions, the congeneric species *Siganus lineatus* required less time to find food (LaMonica et al. 2021). Such species-specific contrasting responses may be attributed to differences in thermal tolerance and resistance to abiotic stressors (Vinagre et al. 2016).

In contrast, the feeding behavior of the competitors reveals that the invasive species takes longer to begin feeding than the native species, but this does not affect the time spent monopolizing the contested resource. Future climate change scenarios also did not affect the feeding behavior of the invasive species. The native species was the first to start feeding in five of the six trials under control temperature conditions and in three of the six trials under the RCP8.5 temperature scenario, demonstrating a faster food resource acquisition in the native species. These results suggest that the population growth of the invasive species may be more influenced by resource exploitation and ecological opportunism than by interference competition or the competitive superiority on the native species (Sol et al. 2011). Individual characteristics of invasive species, such as higher food intake and greater energy efficiency, may contribute to enhanced reproductive performance (Zaviezo et al. 2019; Ode et al. 2022), enabling rapid population growth even in the absence of strong competitive interactions.

In conclusion, our findings indicate that the projected temperature changes by the end of the century do not significantly impact interspecific competition between the studied invasive and native marine tropical species. Therefore, our initial hypothesis was not supported. However, future studies investigating the effects of longer-term projections with more extreme temperature scenarios may reveal different outcomes. As the difference in the cheliped size of the invasive and native species also may have influenced agonistic interaction, further studies may incorporate body size asymmetry and weapon size symmetry on fight outcomes between invasive and native crabs. Our study provides novel insights into the aggressive and feeding behaviors of the invasive species *Charybdis hellerii* during competition with a native swimming crab *Callinectes danae*. While temperature did not significantly impact these behaviors, future research should consider the potential effects of temperature on the metabolism of both species, with physiological

assessment being an important tool to predict indirect effect on the fitness of native species. Additionally, exploring the role of body size asymmetry and weapon size in shaping the outcome of competitive interactions between invasive and native crabs could provide further valuable insights.

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