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ORIGINAL PAPER

Feeding ecology of an invasive swimming crab: how feeding patterns favors invasion success

Vinícius Soares Correa da Costa[1,2,3] · **Vivian de Mello Cionek**[1,3] · **Joaquim Olinto Branco**[1,2,4]

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Abstract

The feeding ecology of invasive species provides essential information on trophic interactions within invaded ecosystems. This study evaluated the feeding ecology of the invasive swimming crab *Charybdis (Charybdis) hellerii* (A. Milne Edwards, 1867) from a sexual, ontogenetic, and seasonal perspective in Southern Brazil. We collected 410 individuals between May 2021 and April 2022, once a month, using Jereré-type traps (top-opening traps, with 10 mm mesh size, baited with fresh fish). The Feeding Index (IAi) was calculated using the frequency of occurrence and the proportion of each prey in the stomach. The invasive population consumes mostly Crustacea and Mollusca, and did not show a significant difference in the feeding consumption pattern between males and females, among ontogenetic development stages, nor throughout the year. The absence of diet variation among different individuals from the invasive population might represent a good strategy for invasion success because all individuals are able to feed on the most available prey items in the region. This is an important result because the invasive population is well adapted and growing in ecosystems that host a large diversity of native crabs, essential for aquaculture and fishing, that might be threatened by the invader.

Keywords Stomach content · Natural diet · Predation · Invasive species · Non-indigenous

Introduction

Biological invasions are considered one of the primary threats to global biodiversity (Kolar and Lodge 2001; Lopes and Villac 2009; Calizza et al. 2021). In the marine environment, introductions occur more easily through ballast water from ships, transportation on vessel hulls, aquaculture, aquarium discharge, and intentional or accidental release (Carlton 1996; Blackburn et al. 2011; Clarke et al. 2020). Invasive species compete with native ones for food, space, and sunlight, potentially leading to the reduction and even local extinction of native populations (Strona 2022). Additionally, they can alter the structure and function of marine habitats (Pyšek et al. 2020), cause changes in nutrient cycles (Zhang et al. 2019), disrupt food chains, and negatively impact fishing and tourism activities (Faraudello et al. 2021).

Predation on a specific prey affects its abundance, prompting other predators to alter their diet (Kotta et al. 2018; Izar et al. 2023). The theory of optimal foraging, for example, indicates that predators should maximize energy during foraging. Therefore, the preference for consumption of specific preys may reflect their higher energy content, leading to intra-guild predation interactions (Charnov 1976; Stephens and Krebs 1986; Liu et al. 2019). Trophic interactions, reproduction, and niche allocation play a crucial role in the establishment of introduced species (Lockwood et al. 2005), and therefore, help in the assessment

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✉ Vinícius Soares Correa da Costa
vinissc@hotmail.com

[1] Graduate Program in Environmental Science and Technology, Polytechnic School, Universidade do Vale do Itajaí (UNIVALI), Rua Uruguai, 458, Itajaí 88302-901, Santa Catarina, Brazil

[2] Laboratory of Zoology, Polytechnic School, Universidade do Vale do Itajaí (UNIVALI), Rua Uruguai, 458, Itajaí 88302- 901, Santa Catarina, Brazil

[3] Laboratory of Community Ecology, Polytechnic School, Universidade do Vale do Itajaí (UNIVALI), Rua Uruguai, 458, Itajaí 88302-901, Santa Catarina, Brazil

[4] Center for Biological and Health Sciences (CCBS), Graduate Program in Ecology and Natural Resources (PPGERN), Universidade Federal de São Carlos (UFSCAR), São Carlos, São Paulo, Brazil

of environmental pressure, and potential impacts on the invaded ecosystem, such as the reduction of prey species, reduction of native species that compete for the same food resources, and changes in community structure (Molnar et al. 2008).

Swimming crabs are one example of keystone species capable of controlling energy flow in invaded environments (Lockwood et al. 2007) and understanding the diet of invasive swimming crabs helps evaluate their trophic role and pressure exerted on natives over resources, especially in areas where native crab communities are of socioeconomic importance. The Portunidae *Charybdis (Charybdis) hellerii* (A. Milne-Edwards, 1867) is native to the Indo-Pacific Ocean, accidentally introduced to Brazil around 1996, possibly through the transportation of larvae in ballast water (Carqueija and Gouvêa 1996). It has become the second most recorded invasive species on the coast (Teixeira and Creed 2020), occurring across 14 Brazilian states (Cintra et al. 2023). Several bioecological characteristics contributed to the success of the species' invasion, including a long larval development of 44 days, which allows for resistance and reduced energy demands during long distance dispersal (Dineen et al. 2001). It presents a generalist feeding capability, allowing it to explore a variety of available food resources (Sant'anna et al. 2015), and multiple spawns from a single copulation event, reducing the need for frequent reproductive events. The species also presents the capacity for polyandry, ensuring greater genetic variability (Watanabe et al. 2022).

The invasion success of the species might be facilitated by their feeding habits and is context-dependent. Generalist species are more prone to explore a wide variety of prey in the invaded system, depending on the competitiveness of the native species community. Resistant native species communities might induce a niche specialization of the invader, while vulnerable native communities might lose prey resources to the invader (Hisam et al. 2020). Sex-specific morphological features such as claws, that can break and manipulate hard-shelled prey more effectively, might give a competitive advantage in obtaining food. Ontogenetic variation in feeding contributes to the success of the population by preventing intraspecific competition. It is also expected that smaller individuals will feed on small invertebrates and as they grow, they will feed on larger invertebrates and teleosts (De Lestang et al. 2010; Kunsook et al. 2014). Seasonal variation in prey availability can also be expected due to alterations in available resources in the ecosystem (Iglesias et al. 2023).

The evaluation of seasonal variations and feeding differences between gender and ontogenetic phases of *C. (C.) hellerii*, enables a better understanding of the overall dynamics of the invasive crab within the invaded environment, 25 years after its first record in the South of Brazil in Santa Catarina (Mantelatto & Dias 1999). Evaluating variation in feeding behavior can provide guidance on the management strategies of the invader, as it can direct monitoring efforts of native prey and vulnerable ecosystems. The study of feeding behavior can also help design monitoring activities and implement control measures at strategic times, such as low foraging times when individuals are more vulnerable (Triay-Portella et al. 2022). The objective of this study is to evaluate the feeding ecology of the invasive swimming crab *C. (C.) hellerii* from a sexual, ontogenetic, and seasonal perspective in Southern Brazil.

Materials and methods

Study area and sampling procedure

Sampling was conducted once a month from May 2021 to April 2022 in Armação do Itapocoroy, southern coast of Brazil (26° 46' 51.37 "S; 48° 36' 12.99 ''W) (Fig. 1). Twelve Jereré-type traps (top-opening traps, mesh size of 10 mm) baited with fresh fish were used, with the bait protected by two nylon bags to prevent ingestion and avoid influencing stomach content analysis (Branco et al. 2002). The traps were placed on non-consolidated rocky substrate at depths ranging from one to two meters. Given that *C. (C.) hellerii* is a cryptic species and has nocturnal habits, collections began at 5 p.m., with the traps being checked every 30 minutes until 10 p.m. The capture of *C. (C.) hellerii* was authorized by the System for Authorization and Information in Biodiversity (SISBIO), under license number 77938-2.

Swimming crabs were captured at night (17:00–23:00) using traps checked every half hour. The captured specimens were placed in a thermal box, immersed in ice to inhibit digestion, and kept frozen until laboratory analysis (Williams 1981; Sant'anna et al. 2015).

Stomach analysis and taxonomic identification prey

All captured crabs were measured for carapace width (CW) using digital calipers (precision of 0.01 mm) and identified as males or females (Williams 1974).

Stomachs were removed with tweezers and scissors, and their weight was recorded, using a 0.01 g precision analytical balance. The stomach contents were placed on a Petri dish and analyzed fresh under a stereomicroscope. To facilitate comparison with other diet studies on invasive and native species, food items were classified at the order/infraorder level into broad taxonomic groups. Items that could not be

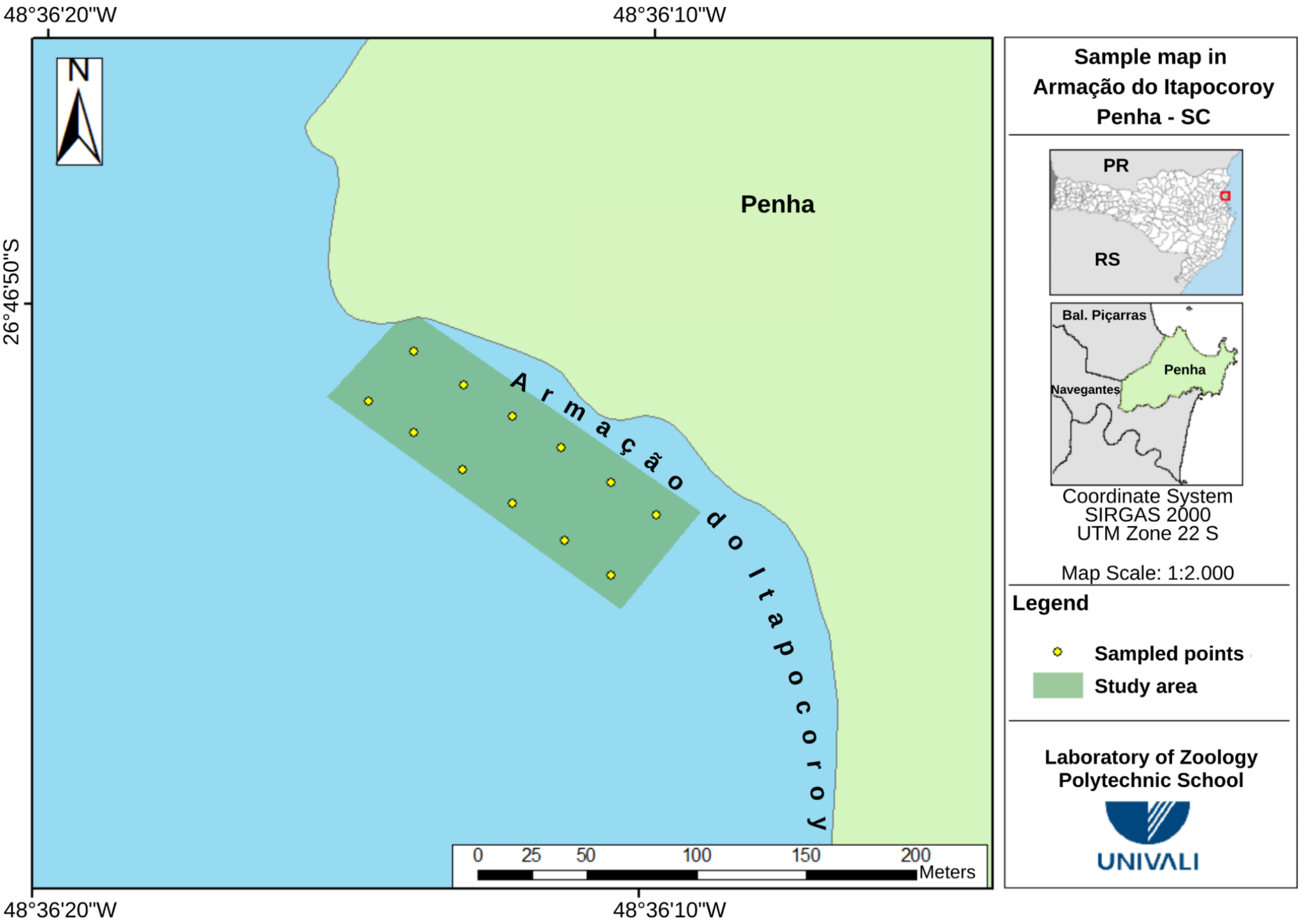

Fig. 1 Map of the Sampling Location in Penha, Santa Catarina - Brazil

identified due to elevated levels of digestion were grouped as Unidentified Debris (UD).

After stomach opening, the degree of fullness was visually assessed on a five-category scale (Haefner 1990), modified by Branco and Verani (1997): 1 = empty stomach, 2 = partially empty (25% filled), 3 = half full (50% filled), 4 = partially full (75% filled), and 5 = full (completely filled). The repletion index (RI), which analyzes the amount of food in the stomach, expressed as a percentage, was determined according to Eq. 1, where We = stomach weight (g) and Wt = individual weight (g) (Santos 1978).

$$RI = \frac{We}{Wt} \tag{1}$$

The composition of the natural diet was determined using the methodology proposed by Branco and Verani (1997), also employed in the study by Sant'anna et al. (2015). This method complements the Point Method (PM) proposed by Williams (1981) and Frequency of Occurrence (F_i) proposed by Hyslop (1980). The PM was obtained by assigning points ranging from 2 to 100 (%), depending on the degree of fullness, representing the proportion of each food item based on abundance. Stomachs with no food items were disregarded. The F_i was calculated using Eq. 2, where E_A = the quantity of stomachs with item A, and E = the total number of analyzed stomachs (Hynes 1950).

$$F_i = \left(\frac{E_A}{E}\right) \times 100 \tag{2}$$

Combining these two methodologies allowed the determination of the Alimentary Index (IAi) (Kawakami and Vazzoler 1980), adapted according to Eq. 3, where i = food item; F_i = frequency of occurrence (%) of the item, and P = point (%) of the item.

$$IAi = \left[\frac{(Fi\,x\,Pi)}{(\sum(Fi\,x\,Pi))}\right] \times 100 \tag{3}$$

The diet composition was defined for the entire population based on gender (male/ female), ontogenetic groups (juvenile/ adult/ old adult), and seasons (summer/ autumn/ winter/ spring). Ontogenetic groups were defined based on the estimate of the first physiological maturation (L50) and the largest recorded individual. Thus, "juveniles" presented CW < 46.7 mm (females) and < 62.1 mm (males). The "adult" category included individuals with CW ranging between 46.7 and 56.7 mm for females and 62.1 to 72.1 mm for males. Individuals with CW above 56.7 and 72.1 mm for females and males, respectively, were considered "old adults" (Triay-Portella et al. 2022). This category is considered the largest individual captured for the studied population, with a CW of 81.5 mm.

Statistical analysis

To assess whether there was a significant relationship between stomach degree of repletion and sex or season, we employed the chi-square test of independence. To visualize potential diet composition variation between genders, ontogenetic phases, and seasons, a Non-Metric Multidimensional Scaling (NMDS) analysis was applied separately for each factor. Alimentary Index (IAi) values of each item were considered as the response variable, and gender, ontogeny, and seasons were considered as categorical variables. IAi values for each level of the investigated categories were calculated monthly and considered as replicates. The assessment of the most important items for group separation was performed using the envfit function. To test whether the observed variation was significant, permutational multivariate analysis of variance (PERMANOVA, with 999 permutations) was applied to the data, separately for gender, ontogeny, and seasons (Anderson et al. 2017). The response variables were the IAi values of each item, and the fixed factors were gender (males and females), ontogenetic phases (juvenile, adult and old adult), and seasons (summer (January, February, March), autumn (April, May, June), winter (July, August, September) and spring (October, November, December).

Results

For the characterization of food items, 410 stomachs of *C. (C.) hellerii* were analyzed, of which 115 (28.04%) were empty (8 females, 107 males), and were therefore excluded from the characterization. The relation between stomach degree of repletion and sex was significant (x^2 (8, $N=410$) = 24.64, $p=0.0017$). Non-ovigerous females are more likely to present partially full stomachs, while males and ovigerous females are more likely to present partially empty and empty stomachs. There was no association between stomach degree of repletion and season (x^2 (12, $N=410$) = 20.23, $p=0.06$). Seasonality did not influence stomach fulfillness, although a small prevalence of empty stomachs was registered during winter.

Among the 295 stomachs with content, 51 were from females (17.28%) and 244 from males (82.72%). Of this total, 142 were juveniles (females CW < 46.7 mm, males < 62.1 mm), 123 were adults (females: 46.7–56.7 mm, males: 62.1–72.1 mm), and 30 were stomachs from individuals considered "old adult" (females > 56.7 mm, males > 72.1 mm).

Stomach contents included sediment and plastic, as well as food items such as annelids, crustaceans, echinoderms, sponges, mollusks, fishes, and Unidentified Debris (UD) (Fig. 2). Taxonomic identification resulted in the characterization of 13 taxa distributed among class, order, and infraorder (Fig. 3, Table A.1).

There was no significant difference in diet composition between males and females ($F=0.999$, $p=0.375$) (Fig. 3, Table A.2) nor among ontogenetic development stages ($F=0.850$, $p=0.575$) (Fig. 4, Table A.3). Crustacea was the most consumed prey by the *C. (C.) hellerii* population in general, followed by Unidentified debris.

Although there were no significant differences in diet composition, juvenile and adult crabs consumed more mollusks, especially Bivalvia. On the other hand, older individuals showed a preference for Brachyura (Table A.1), while juveniles utilized a more diversified range of prey. Males exhibited a broader trophic spectrum than females, that, on the other hand consumed more algae compared to males although this difference was not statistically significant.

There were no significant seasonal differences in diet composition ($F=1.24$, $p=0.247$), with an annual preference for Crustacea consumption that was more evident during summer, winter and spring. During autumn diet composition was more evenly distributed with similar contributions of Unidentified Debris and Mollusca. Although less consumed, sediment grains, annelids, and fish were most consumed during summer (Fig. 5). Crustaceans prevailed during winter. Algae and mollusk were mostly consumed during autumn (Fig. 5).

Discussion

C. (C.) hellerii is a generalist omnivorous mesopredator in the invaded system, with a tendency to consume animal prey, primarily feeding on crustaceans, mollusks, and annelids. Despite exhibiting distinct ecological behavior depending on the life stage (Bauer 2018), juveniles, adults, and old adults showed similar predatory activities, as do males and females. Seasonal diet shifts, however, might be following seasonal population dynamics of prey items. Evidence shows that in other Brazilian coastal areas *C. (C.) hellerii*

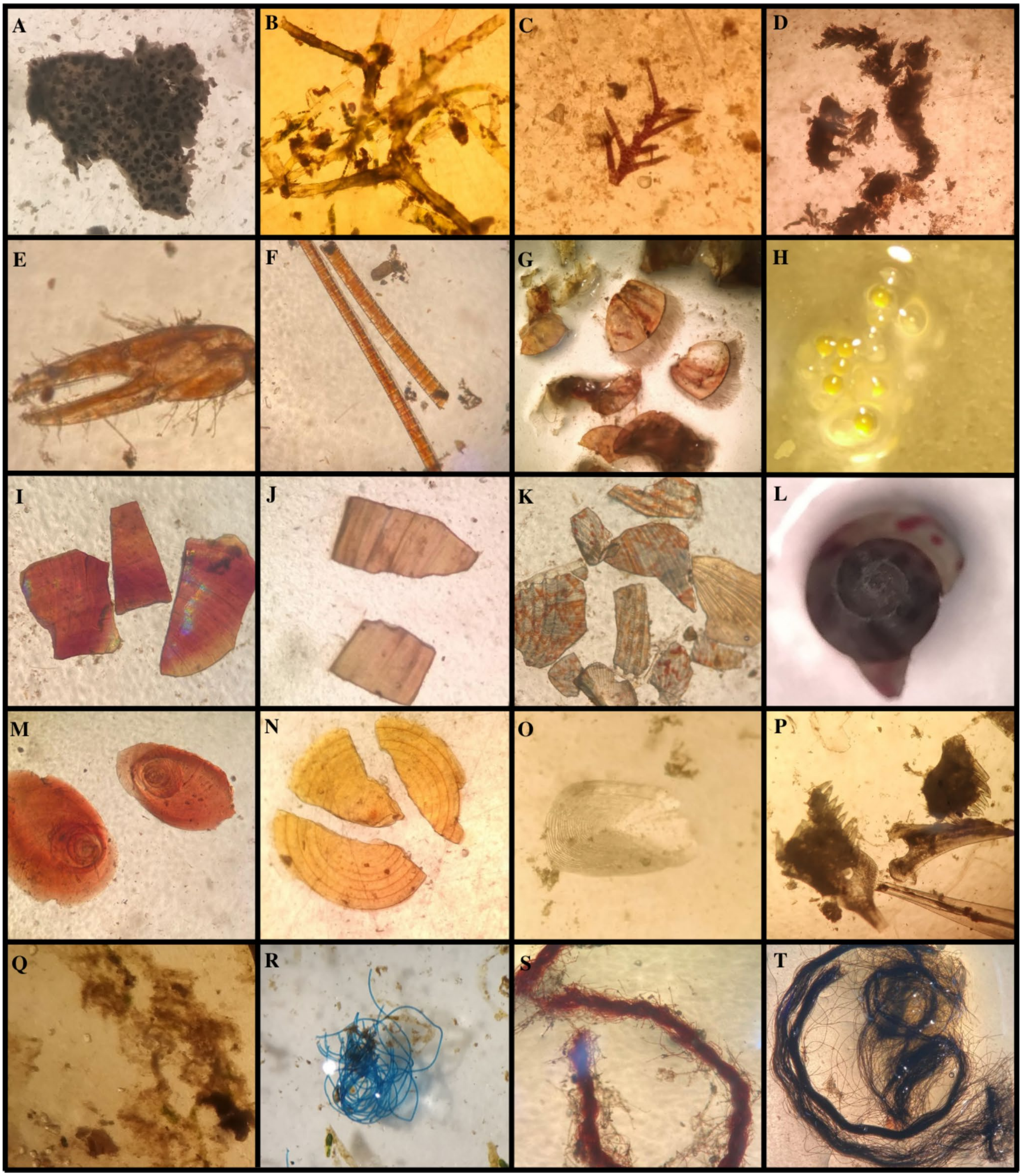

Fig. 2 Food items found in the stomach of *Charybdis (Charybdis) hellerii* sampled in Armação do Itapocoroy, Penha (SC). (**A**) Fragment of Haplosclerida; (**B** - **C**) Fragments of algae; **D**) Echinodermata; (**E** - **H**) Fragments of Crustacea: (**E**) Cheliped chela; (**F**) Antenna; (**G**) Uropod; (**H**) Eggs; (**I**, **J**, and **K**) Fragment of Mollusca, Bivalvia; (**L**, **M**, and **N**) Fragment of Mollusca, Gastropod; (**O**) Scale of Perciformes; (**P**) Mandibular bones of Perciformes; (**Q**) Unidentified Debris (UD); (**R** - **T**) Fragments of plastic

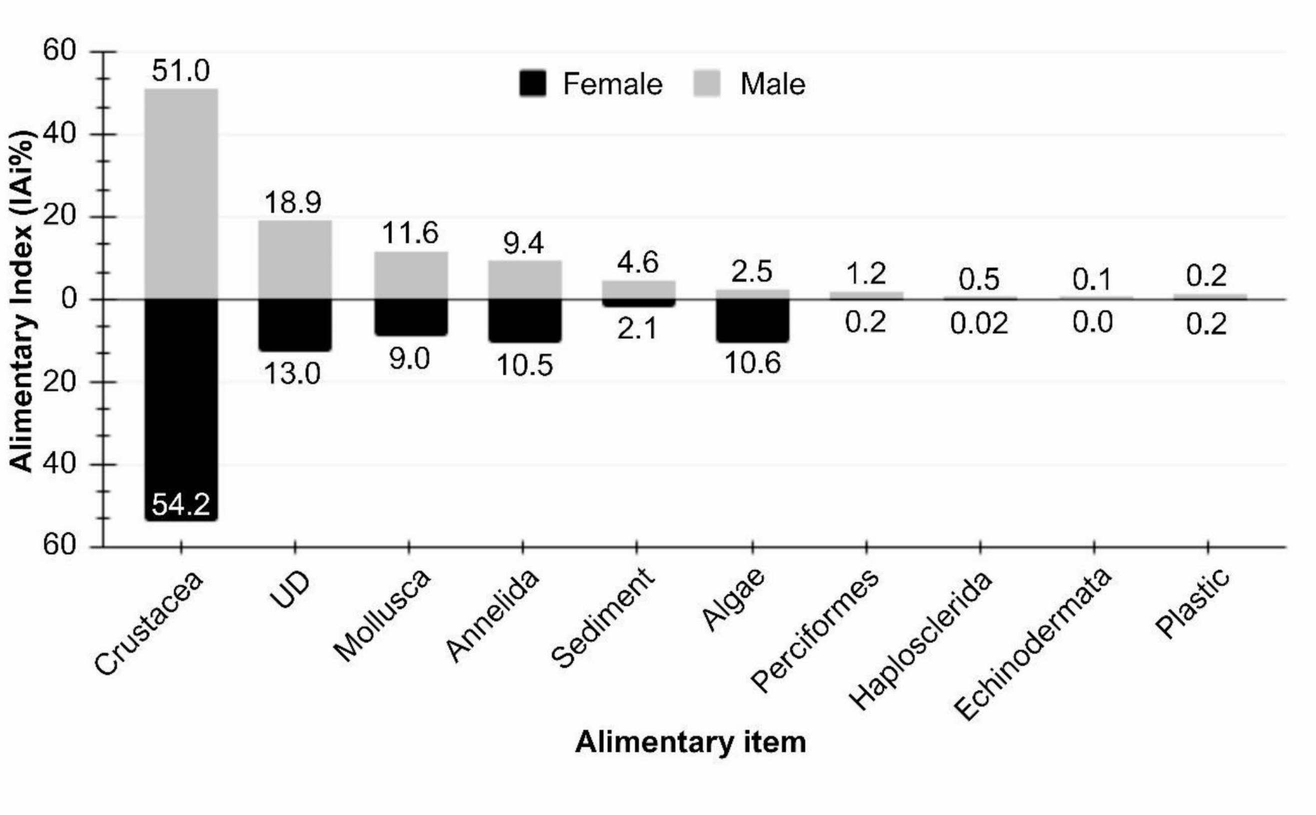

Fig. 3 Importance Alimentary Index (IAi %) identified in the stomach of *Charybdis (Charybdis) hellerii* separated by gender (male and female) in a population from southern Brazil. UD: Unidentified Debris

can be considered an active predator with a strong tendency for animal prey, mainly for highly sedentary prey with low escape ability (Iza et al. 2023), and that predation pressure varies according to prey type, indicating a potential adaptability to local conditions (Iza et al. 2023).

Generalist diets with a carnivorous tendency have been observed in other invasive portunids worldwide, such as *Carcinus maenas* (Siegenthaler et al. 2022), *Callinectes sapidus* (Prado et al. 2022), and *Cronius ruber* (Triay-Portella et al. 2022). These species can exert ecological pressure on marine ecosystems through the predation of specific prey, and trophic interactions with various species affecting productivity and species diversity, consequently forcing native predators to alter their diet (Ricklefs 2012; Kotta et al. 2018). Because the *C. (C.) hellerii* population presented similar feeding habits among ontogenetic stages and sex, it might be exerting pressure over native prey populations that are also preyed by native portunids in the studied area (Branco et al. 2002; Madambashi et al. 2005). This is concerning, considering the potential trophic niche overlap, which could cause direct and indirect impacts on native populations and local ecosystem balance (Ricciardi et al. 2013). For example, native portunids that inhabit the area, such as *Achelous spinimanus* (Latreille, 1819), presents similar feeding preferences, consuming more Crustacea, followed by Osteichthyes, Echinodermata and Mollusca (including Bivalvia and Cephalopoda), (Branco and Lunardon-Branco 2002).

Females of *C. (C.) hellerii* showed a higher proportion of full stomachs than males, especially ovigerous females that can store energy for reproduction (Tuomi et al. 1983; Barki 2008). This strategy could be supported by two hypotheses related to food availability. The first suggests that the female feeds continuously while ovulating (Brown 2009), which seems to be the case in Penha, allowing the female to obtain enough energy to fertilize and develop her eggs. The second hypothesis is related to the time interval between spawning, where longer intervals would allow the female to obtain enough energy to deposit her eggs on the pleopods successfully, without the need to forage for food while ovulating (McLay and Becker 2015).

A decade ago, algae ranked as the third least preferred food item for *C. (C.) hellerii* in Penha (Sant'anna et al. 2015). In this study, this preference shifted to polychaetes, which previously ranked fifth. The presence of algae, although of intermediate importance, may reflect accidental consumption due to the species' habitat exploration. This becomes more evident when associating the predation of mollusks,

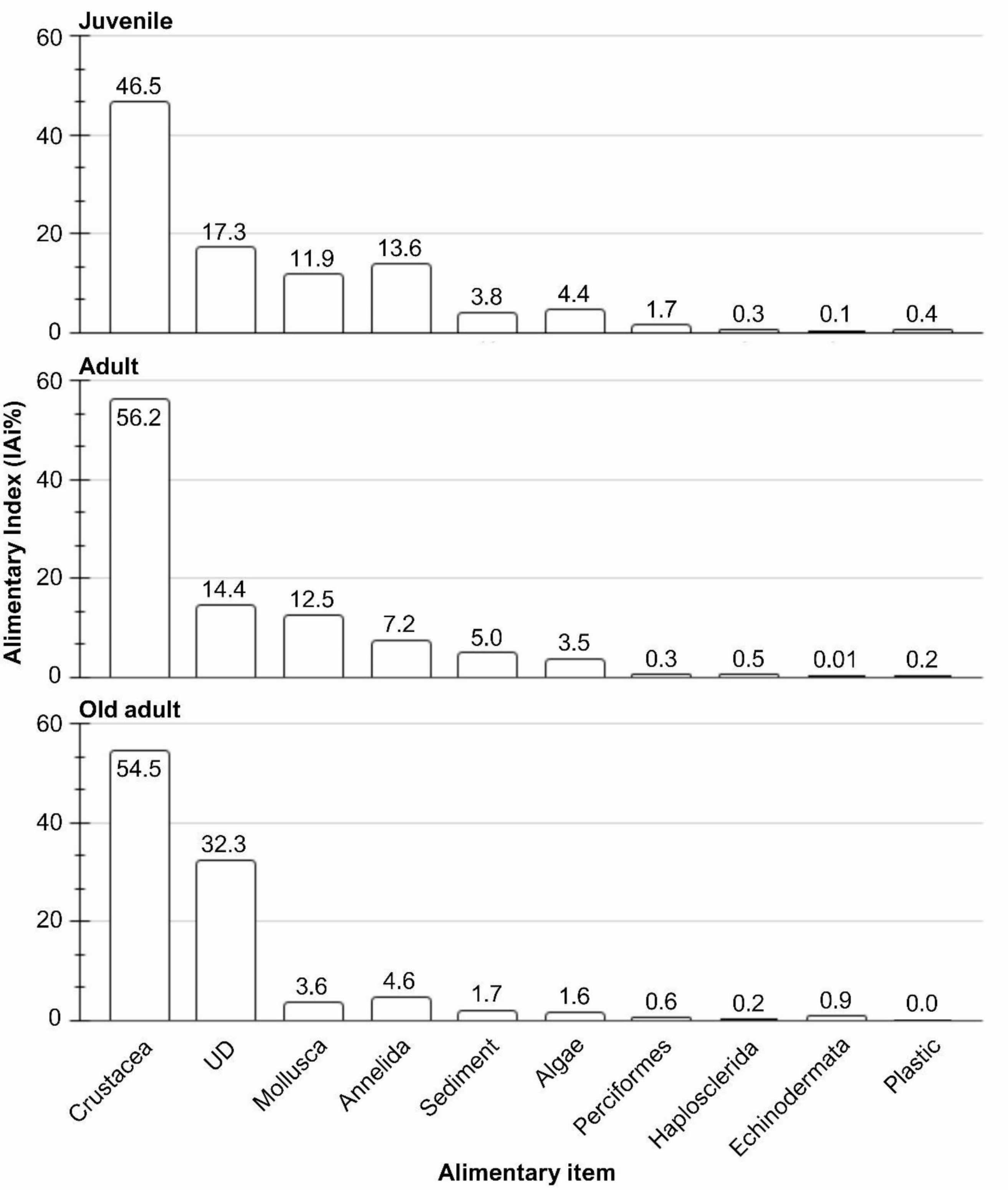

Fig. 4 Importance Alimentary Index (IAi %) of prey items of *Charybdis (Charybdis) hellerii* separated by ontogeny (juvenile, adult, and old adult) in a population from southern Brazil. UD: Unidentified Debris

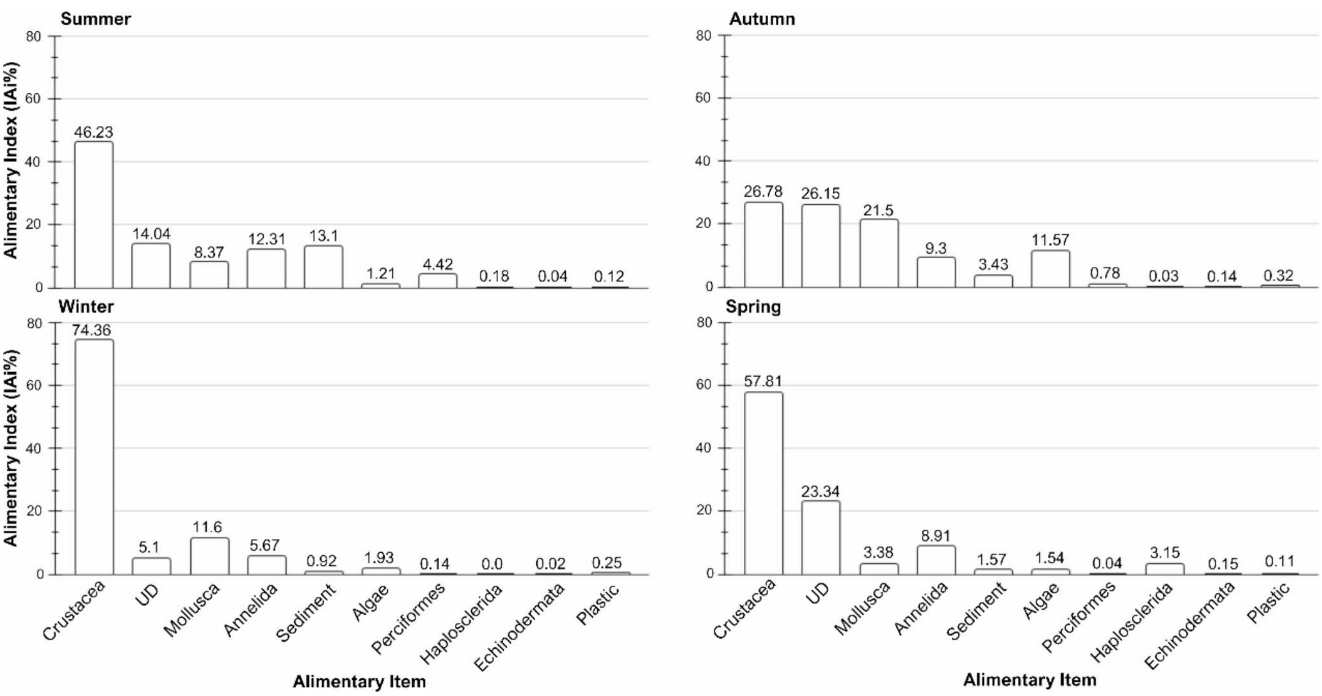

Fig. 5 Importance Alimentary Index (IAi %) in the diet of *Charybdis (Charybdis) hellerii*, separated by season, in a population from southern Brazil. UD: Unidentified Debris. Seasons: ummer (January, February, March), autumn (April, May, June), winter (July, August, September) and spring (October, November, December)

which live in direct contact with substrate containing algae, and because we identified a simultaneous increase in the consumption of mollusks and algae in autumn. Similar results were found for *Cronius ruber* and were attributed to the type of habitat occupied and preference for foraging locations (Triay-Portella et al. 2022). For *Liocarcinus puber* and *L. holsatus*, the high consumption of algae was considered the main food source in the warmer months, related to the molting period (Choy 1986). Throughout the sampled year, individuals of *C. (C.) hellerii* in the molting period were not collected or observed.

Ontogenetic diet shifts were expected due to habitat shifts during ontogeny for swimming crabs. Young or small-sized crabs inhabit shallow waters and migrate to deeper water when they grow larger (Hisam et al. 2020). Although the invaders' diet did not change significantly through ontogenetic development, old adult crabs tend to consume fewer mollusks, preferring crustaceans. This might give a fitness advantage because of the consumption of more energy-rich items. On the other hand, smaller individuals forage for bivalves, likely because they require less energy for manipulation, considering that juveniles need to feed more for their growth. The prevalence of sediment grains in stomachs in summer may be related to the predation of annelids, which was higher in the same season. Sediment contains a wide variety of associated fauna, e.g., polychaetes, which end up being ingested accidentally by macrocrustaceans (Branco and Verani 1997). Thus, the associated fauna is often consumed together with substrate. Additionally, sediment grains may be ingested deliberately to increase food maceration and digestive efficiency in the gastric mill (Loureiro et al. 2016). Fish consumption was identified by the presence of scales and bones, being especially high during summer, when the occurrence of fish in the intertidal zone was higher and associated with temperature elevation.

Crustaceans were the most abundant prey item in the swimming crab's diet in all seasons. The increase in bivalves and gastropod consumption could reflect both the absence of crustacean's availability, and the availability of easier-to-capture prey, such as molluscs in the autumn, and annelids and perciformes in the summer. Moreover, the contribution of mollusks to the diet, as well as any other soft-bodied individual, such as annelids, may have been underestimated since their soft bodies are easily digested, being included in the category of Unidentified Debris (UD) (Prado et al. 2020).

In this study, 11 individuals were observed with a high quantity of filamentous plastic fragments, some of them large enough to fill the stomach cavity of the individuals. The region has a high incidence of fishermen and mariculturists, and many fishing nets are lost or abandoned. Since the invader has cryptic habits and lodges under rocks, there is an increased potential for the accidental ingestion of these items (Sant'anna et al. 2015). The ingestion of plastic and microplastics affects both the health and fitness of marine organisms, usually through reduced food digestion, decreased nutrient synthesis, and starvation (Galgani et al. 2010). Wójcik-Fudalewska et al. (2016) found fishing net filaments in about 13% of the stomachs of *Eriocheir sinensis* in the coastal waters of the Baltic Sea in Poland and the Tejo estuary in Portugal and attributed it to a possible reproductive decline and compromised feeding capacity. Crooks et al. (2019) suggest that the ingestion of microplastics results in high rates of adsorption of toxic compounds - polycyclic aromatic hydrocarbons, which can bioaccumulate in the food chain (McLeod et al. 2015).

Although *C. (C.) hellerii* is an invasive species, evidence of the consumption of net and plastic fragments demonstrates that the area is under pressure from anthropogenic use related to tourism and fishing, with great potential to affect native marine animals and the human population that consumes fishery products. Toxic compounds may bioaccumulate in the food chain, including fish, birds and mammals that feed on crabs, eventually reaching local communities that rely on this food resources (Miller et al. 2020; Huang et al. 2021; Rakib et al. 2023).

C. (C.) hellerii was first registered in 1999 in the study region, and the population evolution was tracked during 2006 and 2010, indicating unchanged population abundance and occurrence of ovigerous females, and an increase of juveniles (Sant'anna et al. 2015). In this study, ovigerous females were registered thought the year, indicating that the population is better established in Penha (Costa 2023). Diet composition did not change significantly over decades although preferences were distinct in the early establishment stages. Males where more frequent in the study area most likely due to their preference for lower salinity found near shore, while ovigerous females might be conducting short reproductive migratory behavior and were not fully sampled.

Conclusion

The generalist feeding habits of the invader *C. (C.) hellerii* can represent a mechanism that facilitates the success of invasion. *C. (C.) hellerii* diet did not change much after 25 years from the invasion and might reflect an adaptation process of the invader that is thriving in the region. Temporal monitoring of invasive populations is essential to track the evolution of the invasion process. Seasonal changes in diet composition are reflecting natural prey availability, while the similarity of diet composition between sex and ontogenetic stages can be due to two hypotheses: (i) the population foraging amplitude might be limited by native swimming crab populations, or (ii) the species rely on the most available prey on the region.

It is not possible to state that a shift in feeding habits of the species have occurred two decades after the invasion, but monitoring the population to assess potential for interference in ecological processes and biological interactions with native species is essential. Future effects of their establishment could include competition for food and space, displacing native species of commercial interest and disturbing the ecosystem balance in the region. It is recommended that future studies include investigating the effects of the invasive species on populations of native swimming crabs and on mollusk crops in the region.

Deeper investigations into the feeding ecology of *C. (C.) hellerii* over time could help identify specific prey that are critical to its survival and reproduction. This could provide targeted management strategies, such as manipulating prey availability. Investigating the potential impact of *C. (C.) hellerii* on commercial crops, such as shellfish, is essential to understanding how the invasion could affect the local economy and the communities that depend on these resources.

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Author contributions All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Vinícius Soares Correa da Costa and Vivian de Mello Cionek. The first draft of the manuscript was written by Vinícius Soares Correa da Costa and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

Ethics approval The collection of *Charybdis hellerii* was authorized by the Ministry of the Environment, SISBIO-ICMBio, under license number 77938-2. This study did not involve the removal of threatened or protected species.

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