Ocean and Coastal Research

ORIGINAL ARTICLE

http://doi.org/10.1590/2675-2824074.24060
ISSN 2675-2824

Dietary similarities between native swimming crab *Achelous spinimanus* (Latreille, 1819) and invasive *Charybdis (Charybdis) hellerii* (A. Milne-Edwards, 1867) in Santa Catarina, South Brazil

Vinícius S. Correa da Costa[1,2,3*], Vivian de Mello Cionek[1,3,4], Nicole Muriel Filipini[1,3], Lívia Garcia Prado[1,3], Alessandro Franchini[4], Joaquim Olinto Branco[1,2,5]

[1] Programa de Pós-graduação em Ciência e Tecnologia Ambiental (PPCTA) – Escola Politécnica – Universidade do Vale do Itajaí (Itajaí – Rua Uruguai, 458 – 88302-901 – SC – Brazil).
[2] Laboratório de Zoologia – Escola Politécnica – Universidade do Vale do Itajaí (Itajaí – Rua Uruguai, 458 – 88302-901 – SC – Brazil).
[3] Laboratório de Ecologia de Comunidades Aquáticas – Escola Politécnica, Universidade do Vale do Itajaí (Itajaí – Rua Uruguai, 458 – 88302-901 – SC – Brazil).
[4] Graduação em Ciências Biológicas – Escola de Ciências da Saúde, Universidade do Vale do Itajaí (Itajaí – Rua Uruguai, 458 – 88302-901 – SC – Brazil).
[5] Programa de Pós-graduação em Ecologia e Recursos Naturais – Universidade Federal de São Carlos (São Carlos – Rodovia Washington Luís, s/n – 13565-905 – SP – Brazil).

* Corresponding author: vinissc@hotmail.com

ABSTRACT

Achelous spinimanus (Latreille, 1819) constitutes an ecologically and commercially important species along the South America coast. Over the last three decades, this native species has been exposed to the introduction of *Charybdis* (*Charybdis*) *hellerii* (A. Milne-Edwards, 1867), a potential competitor for the same substrate. Invasive species often show significant dietary adaptability which can impact native species and coastal ecosystems. This study compares the diet composition of *C.* (*C.*) *hellerii* and the native *A. spinimanus*. The stomachs of 66 *A. spinimanus* and 180 *C.* (*C.*) *hellerii* were analyzed, and the Alimentary Importance Index (IAi) was calculated. Trophic comparison was assessed using the Pianka index. Crustacean represented the most important food item, followed by mollusks for both species, which exhibited high similarity, suggesting a possible competition for resources. Results reveal dietary overlap and highlight the generalist feeding strategy of the invasive species during its establishment phase. These patterns suggest potential long-term ecological impacts on native crab populations. Overall, the study offers a baseline for future assessments on trophic interactions and the consequences of biological invasions in coastal environments.

Keywords: Bioinvasion, Coastal conservation, Diet, Trophic Ecology, Fishing

Submitted: 16-May-2024
Approved: 01-Apr-2026

Associate Editor: Abilio Soares-Gomes

© 2026 The authors. This is an open access article distributed under the terms of the Creative Commons license.

INTRODUCTION

Competition for food between swimming crabs plays an important role in shaping the ecology of coastal communities, often triggering the development of physical or behavioral adaptations

that enable species to exploit distinct ecological niches (McDonald et al., 2001; Rato et al., 2021; Yeoh, 2020). Consequently, it can lead to habitat segregation, with species occupying specific areas such as beaches, rocky substrates, or mangroves, reducing resources overlap and minimizing direct competition. Evidence suggests that aggressive species can displace more sensitive ones, leading to significant changes in the dynamics and composition of local communities (Rato et al., 2021; Siddiqui et al., 2021). Swimming crabs may also exhibit morphological adaptations, including differences in claw size and shape, allowing them to target various food sources or outcompete other organisms (Lim et al., 2016; Yamada and Boulding, 1998). For example, while smaller organisms can access tight spaces under rocks to escape predators, larger crabs with stronger claws are better equipped to consume hard-shelled prey (Bashevkin and Morgan, 2020).

In this context, *Achelous spinimanus* stands out as a native species of high ecological and commercial importance along the Brazilian coast, acting as an intermediate predator in shallow environments and contributing to regulate benthic prey populations (Rodrigues-Filho et al., 2023). Despite its relevance, reports of declining abundance in certain regions and changes in capture frequency suggest that the species may be vulnerable to additional competitive pressures, particularly when invasive species occupy the same microhabitats and exploit similar prey resources (Branco and Lunardon-Branco, 2002; Ripoli et al., 2007). The ecological literature point to dietary overlap as one of the primary mechanisms through which species may engage in exploitative competition, especially when resource availability fluctuates temporally and spatially (Holt et al., 1994; Yang, 2020). Although such overlap does not provide direct evidence of competition, it is considered a robust indicator of potential interspecific interaction and has been widely applied in studies evaluating the impacts of biological invasions (Ricciardi et al., 2013; Triay-Portella et al., 2022).

This variety of foraging strategies underscore their pivotal role in marine coastal ecosystems, significantly contributing to both the food chain and local economies (Rodrigues-Filho et al., 2023; Susanto, 2021; Yulianto et al., 2024). Swimming crabs are important predators, feeding on small fish, mollusks and other crustaceans (Prado et al., 2020). They help maintain coral reefs and mangroves by controlling prey populations, thereby supporting ecological balance (Arceo-Carranza, et al., 2021; Yulianto et al., 2024). They are also important sources of food for coastal communities (Branco et al., 2002; Mesquita, 1972; Santos et al., 1995a) where fishing activities provide employment and livelihoods for local fishers (Rodrigues-Filho et al., 2023).

Interactions mediated by swimming crabs can become imbalanced due to the introduction of Invasive Alien Species (IAS), posing severe threats to local biodiversity (Lockwood et al., 2013; Ricciardi et al., 2021). For example, the invasive swimming crabs *Charybdis* (*Charybdis*) *hellerii*, originally from the Indo-Pacific, were likely introduced via maritime transport, with larvae being carried in ballast water. Over time, viable and self-sustaining populations have been established along various regions of the Brazilian coast (Negri et al., 2018; Teixeira and Creed, 2020). In southeastern Brazil, a reduction in the frequency of *Cronius ruber* records has been reported since the mid-1990s, coinciding with the first observations of *C.* (*C.*) *hellerii* in the region (Mantelatto and Dias, 1999; Sant'anna et al., 2012). Competition between invasive and native species not only disrupts regional ecological balance but also directly impacts the fishing economy.

The southern Brazilian coast, which depends on fishing and mariculture, generates substantial income for municipalities and attracts tourism. The region is responsible for 98% of national mollusk production (Andrade, 2016), making the region economically and socially vulnerable to disruptions in these activities. In 2007, researchers reported damage to oyster production lanterns caused by *C.* (*C.*) *hellerii* in southern Brazil, which led to financial losses for local fisheries (Frigotto and Serafim-Júnior, 2007). Trophic niche assessment has become a crucial tool for evaluating the potential impact of invasive species on native fauna (Izar et

al., 2023; Sant'anna et al., 2015; Triay-Portella et al., 2022). By examining food interactions between species, researchers can better understand invasion effects on ecosystems (David et al., 2017; Ricciardi et al., 2013). Although comparing the diets of invasive and native species in natural environments is challenging and considering that similar diets do not necessarily indicate direct competition for food resources, the comparison can provide valuable insights into potential interspecific interactions (Prado et al., 2020; Sant'anna et al., 2015; Triay-Portella et al., 2022). Significant overlap in resource use may signal potential competition, leading to changes in native species' abundance or distribution, ultimately influencing coastal community dynamics (Costa et al., 2022; Rocha-Barreira and Rosa-Filho, 2023; Yang, 2020). Thus, this study evaluates the trophic similarity between the native species of commercial importance *Achelous spinimanus* and the invasive species *C.* (*C.*) *hellerii,* established in Armação do Itapocoroy, Penha, Santa Catarina state, for at least a decade, since both species occupy the same rocky substrate (Sant'anna et al., 2015).

METHODS

Study Area

The municipality of Penha is located on the north-central coast of Santa Catarina state (26º40'-26º47'S – 48º36'-48º38'W). Covering an area of 60.30 km², it is bordered by Navegantes to the south, Piçarras to the west, and the Atlantic Ocean to the north and east. The climate is classified as humid subtropical, with average annual temperatures ranging from 15°C to 25°C. Summer is hot and humid, while winter is milder and less rainy. The Armação do Itapocoroy bay is a semi-circular inlet open to the northeast, located 2.5 km from the coast. Its geographical position provides protection from waves generated by eastern winds (Araújo et al., 2006). The bay is bordered by Penha Hill to the west and Ponta da Vigia to the east (Figure 1). The region experiences low tidal amplitudes, typically varying between 1 and 2 meters. This semi-diurnal tidal pattern, with two high and two low tides per day, is influenced by the lunar position and local weather conditions, affecting coastal dynamics and marine habitats.

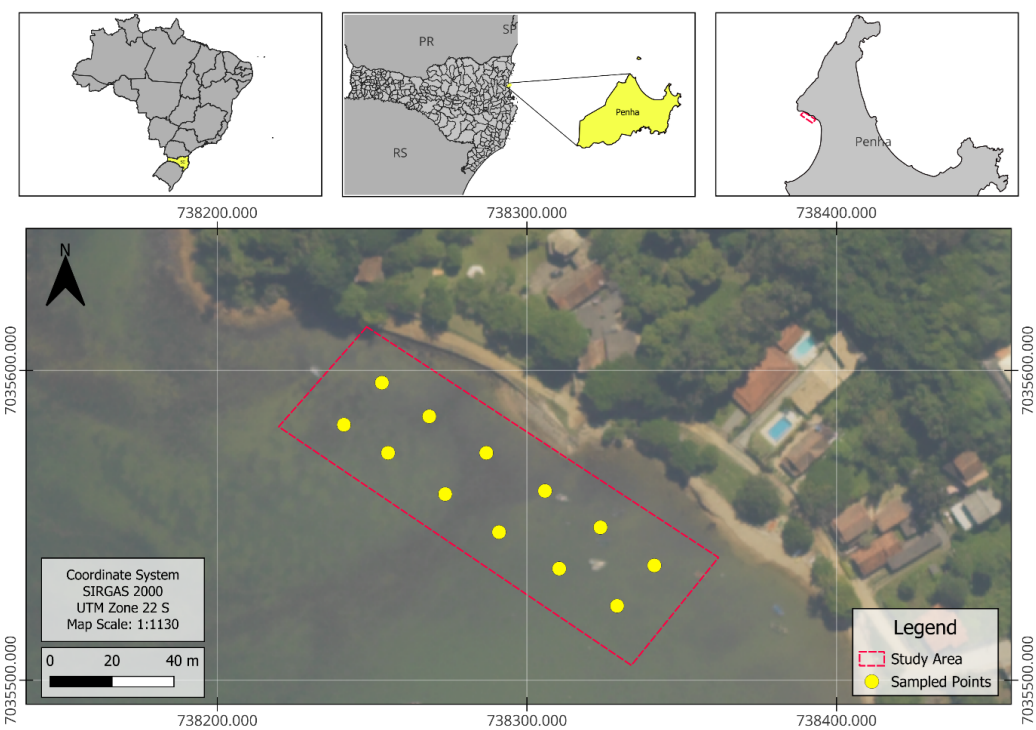


Figure 1. Map of the sampling site in Penha, Santa Catarina - Brazil.

The region receives significant contributions from small rivers and streams that carry nutrients and sediments into the marine environment, altering coastal salinity. *Charybdis* (*Charybdis*) *hellerii* thrives in such coastal environments, particularly intertidal zones and coral reefs, where it easy finds shelter and food (Dineen et al., 2001). Ovigerous females migrate to saltier, open-sea environments to release their larvae (Kobayashi and Vazquez-Archdale, 2018). Thus, the natural reefs and rocky areas in the study region provide a suitable substrate for these species, which is also adapted to nutrient-rich shallow waters.

Sampling

Sampling was conducted in May, September, October and December 2021 and January 2022. Twelve Jereré-type traps (top-opening traps, mesh size of 10 mm) were used, baited with fresh fish. The baits were enclosed in two nylon bags to prevent ingestion and avoid influencing stomach content analysis (Branco et al., 2002). The traps were placed on a heterogeneous substrate composed of unconsolidated sediments and consolidated rocky formations at depths of one to two meters.

Due to the nocturnal habits of crabs, traps were deployed between 5pm and 11pm, and checked every half hour. Captured specimens were immediately placed in a cooler and immersed in ice to inhibit digestion and kept frozen until laboratory analysis (Sant'anna et al., 2015; Williams, 1981).

Capture of the *Achelous spinimanus* and *Charybdis* (*Charybdis*) *hellerii* specimens was authorized by the Biodiversity Authorization and Information System (SISBIO) under license no. 77938-2.

Analysis of stomach contents and taxonomic identification of prey

The stomachs of all swimming crabs were removed using tweezers and scissors, and their weight were recorded. Stomach contents were examined under a stereomicroscope and classified into broad taxonomic groups at the order or infraorder level for comparative purposes. Plastics were recognized by their uniform appearance, shine and sharp edges, and only large fragments unlikely to be confused with organic prey were included. Sediments were characterized by granular textures and varying grain sizes, typical of natural inorganic materials. Items that could not be identified due to advanced digestion were grouped into Unidentified Debris (UD) (Branco et al., 2002).

Stomach fullness was assessed visually using a five-category scale (Haefner Junior, 1990), modified by Branco and Verani (1997) as follows: 1= empty stomach, 2= partially empty (25% filled), 3= medium (50% filled), 4= partially full (75% filled) and 5= full (completely filled). Repletion Index (RI), expressing the percentage of food relative to the individual weight, was calculated using equation 1, in which We = stomach weight (g) and Wt = individual weight (g) (Santos, 1978):

Equation 1: $$RI = \left(\frac{We}{Wt} \right)$$

Natural diet composition was determined following the methodology proposed by Branco and Verani (1997), also used by Sant'anna et al. (2015), which complements the Point Method (PM) proposed by Williams (1981) and the Frequency of Occurrence (FO) proposed by Hyslop (1980). Points were assigned based on repletion degree, ranging from 2 to 100 points (%), depending on the abundance of each food item. Stomachs with no identifiable food items were excluded. FO was calculated using equation 2, in which EA = number of stomachs containing item A, and E = total number of stomachs analyzed (Hynes, 1950):

Equation 2: $$FO = \left(\frac{EA}{E} \right) x100$$

The Alimentary Importance Index (IAi) (Kawakami and Vazzoler, 1980) was adapted and calculated using equation 3, in which i = food item; F = frequency of occurrence (%) of the item and P = point (%) of the item:

Equation 3: $$IAi = \left[\frac{(FixPi)}{\sum (Fi \; x \; Pi)} \right] x100$$

Monthly diet compositions were analyzed for both *A. spinimanus* and *C. (C.) hellerii* populations for comparative purposes.

Data analysis

To visualize potential differences in diet composition between *A. spinimanus* and *C. (C.) hellerii*, an NMDS was applied to the data, using IAi values of each item as a response variable and species origin (native or invasive) as categorical variable. The most important items for explaining dietary variability between species were evaluated using the envfit function. To test whether there is significant variation in diet composition between *A. spinimanus* and *C. (C.) hellerii*, we applied a PERMANOVA to the data, taking the IAi values of each item as the response, and the origin of the species (native or invasive) as the categorical variable. We calculated the distance matrix using the Bray-Curtis method. To test whether potential differences in diet composition between species could be due to intraspecific data dispersal, as an assumption test to validate the permanova interpretation, we used a permutational dispersal test (permutest) (Anderson & Walsh, 2013), which revealed no significant dispersal within species (F = 2.901, p=0.168).

The Pianka index was calculated to assess niche overlap between the species, ranging from 0 (no overlap) to 1 (total overlap). This index measures resource competition or sharing using equation 4:

Equation 4: $$O_{jk} = \frac{\sum \left(Pij \; x \; Pik\right)}{\sqrt{\sum \left(P^2 ij\right) \sum \left(P^2 jk\right)}}$$

In which, Ojk = Pianka's measure of food overlap between species j and k; Pij = proportion of food resource i in the total resources used by species j; Pik = proportion of food resource i in the total resources used by species k.

RESULTS

Diet composition

To characterize the food items, 66 stomachs of *Achelous spinimanus* (19 (28.78%) from females and 47 (71.21%) from males) and 180 of *Charybdis (Charybdis) hellerii* (152 (84.44%) from females and 28 (15.56%) from males) were analyzed. Food items analysis revealed consistent patterns between the metrics used (Alimentary Importance Index (IAi%), Point Method (MP%), Frequency of Occurrence (FO%)), allowing for a robust diet characterization for *Achelous spinimanus* and *C.* (*C.*) *hellerii* in Armação do Itapocoroy. Overall, items with higher IAi% values also presented high percentages in MP% and FO% (SM1), indicating that these food resources were not only recurrent but also volumetrically relevant for both species. All individuals were adults, with sizes ranging from 27 to 81 mm. Recorded food items included sediment, plastic, and various prey types such as annelids, crustaceans, echinoderms, sponges, mollusks, fish, and Unidentified Debris (UD) (Figure 2). Taxonomic identification resulted in the characterization of seven distinct taxa (Figure 3).

Decapod crustaceans, identified primarily by their carapace and antennae (e.g., shrimp), were among the most important diet components, representing the most frequently ingested item for both species. Various morphotypes of green, brown and red algae, as well as the presence of algae filaments in different decomposition stages were found, especially in the stomachs of *A. spinimanus*.

Fragments from mussels and other bivalve shells, as well as remains of gastropod shells and opercula, were identified as mollusk parts. UD was common, especially in *C. (C.) hellerii*, indicating frequent feeding. Less frequent were the presence of fish scales and bone fragments.

Inorganic matter such as sediment and gravel were found in small quantities and were likely ingested accidentally during feeding. Additionally, plastic fragments (probably from fishing nets) were found in the stomachs of ten *A. spinimanus* and four *C. (C.) hellerii* specimens.

Analysis found no significant differences in diet composition between the native and invasive swimming crab species (PERMANOVA: DF = 1, F = 0.527, p = 0.737) (Table 1).

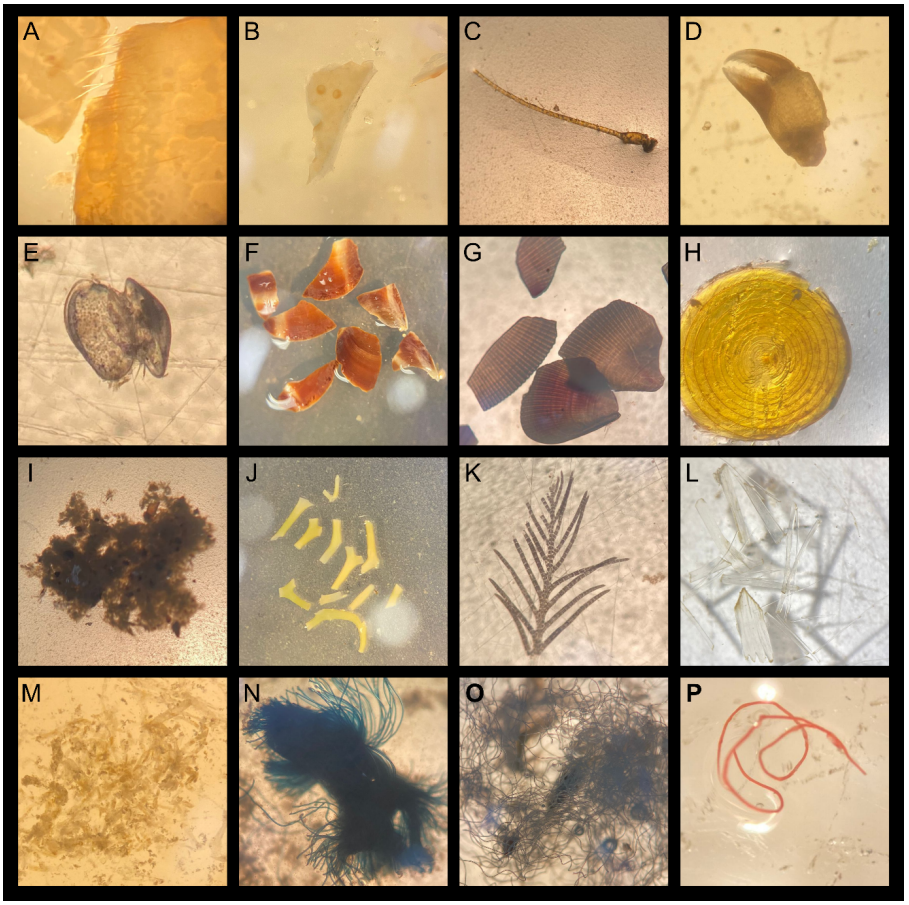


Figure 2. Food items found in the stomachs of *Charybdis (Charybdis) hellerii* and *Achelous spinimanus* sampled at Armação do Itapocoroy, Penha, Santa Catarina. **A** and **B**: crustacean carapace fragment; **C**: crustacean antenna; **D**: crustacean cheliped chela; **E**: ostracode; **F** and **G**: bivalve fragment; **H**: gastropod operculum; **I**: decomposing polychaete; **J** and **K**: algae fragment; **L**: fish bone fragments; **M**: Unidentified Debris (UD); **N**, **O** and **P**: plastics.

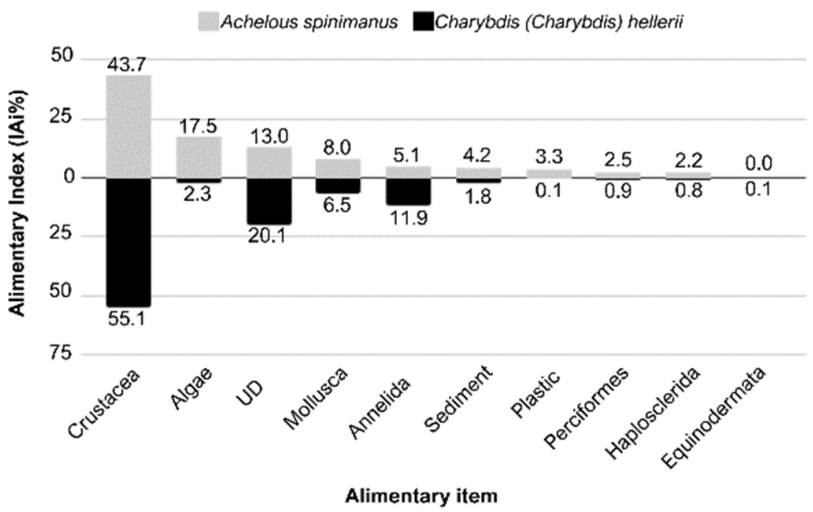


Figure 3. Alimentary Importance Index (IAi %) for the total sampled population of *Achelous spinimanus* and *Charybdis (Charybdis) hellerii* at Armação do Itapocoroy, Penha, Santa Catarina, Brazil. UD = Unidentified Debris.

Table 1. Analysis of differences in diet composition (IAi) between native and invasive species. DF = Degrees of Freedom, SQ = Sum of Squares, R2 = R-squared, F = F-statistic, Pr(>F) = P-value.

	DF	SQ	R2	F	Pr(>F)
Origin	1	0.061	0.06	0.527	0.737
Residuals	8	0.930	0.93		
Results	9	0.991	1.00		

Temporal dynamics of dietary overlap

Monthly IAi values revealed strong fluctuations for both species (Figure 4, Table 2). Peaks in crustacean consumption occurred in May and October for *C*. (*C*.) *hellerii* and in May for *A. spinimanus*, whereas annelids and algae showed pronounced month-specific contributions for each species. These shifts resulted in temporal differences in trophic structure despite the overall similarity between species.

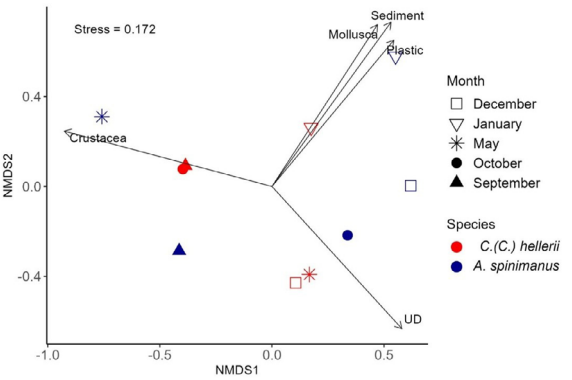


Figure 4. NMDS based on the IAi of the dietary items of the native (*Achelous spinimanus*) and invasive (*Charybdis (Charybdis) hellerii*) species. UD = Unidentified Debris.

Table 2. Alimentary Importance Index (IAi%) of dietary categories identified in the stomach contents of the swimming crabs *Achelous spinimanus* and *Charybdis (Charybdis) hellerii* in Armação do Itapocoroy, Penha, Santa Catarina, Brazil. Dec = December, Jan = January, Oct = October, Sep = September, UD = Unidentified Debris.

Group	*Achelous spinimanus* (n=66)					*Charybdis* (*Charybdis*) *hellerii* (n=180)				
	IAi (%)					IAi (%)				
	Dec	Jan	May	Oct	Sep	Dec	Jan	May	Oct	Sep
Crustacea	23.03	21.13	90.91	38.87	54.09	32.77	36.50	29.55	73.91	70.59
Algae	27.33	0.00	0.00	24.45	2.92	0.50	0.32	8.83	2.28	1.52
UD	19.70	17.37	0.00	20.18	7.02	32.14	17.92	31.58	13.19	10.12
Mollusca	6.03	26.06	0.00	4.58	0.58	3.48	14.94	6.18	2.03	8.99
Annelida	5.26	0.00	0.00	0.16	33.33	15.75	6.51	20.44	7.12	8.32
Sediment	6.70	20.66	0.00	2.51	1.17	1.44	14.23	2.69	0.47	0.00
Plastic	7.17	11.27	0.00	0.20	0.00	0.00	0.11	0.10	0.22	0.00
Perciformes	1.91	3.52	9.09	0.71	0.88	0.25	9.27	0.66	0.00	0.21
Haplosclerida	2.87	0.00	0.00	8.35	0.00	13.55	0.32	0.00	0.49	0.00
Equinodermata	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.07	0.52	0.26

Pianka's index showed a consistently high overall overlap (0.97) between species; however, the monthly calculation revealed that overlap was not uniformly high throughout the sampling period. Overlap increased substantially in months when both species concentrated on crustacean prey (May, October), and decreased when one or both species incorporated algae, annelids, or sediments at higher proportions (e.g., September and December). These results indicate that dietary overlap is dynamic rather than static, influenced by temporal fluctuations in resource availability. NMDS ordination illustrated that temporal variation, rather than species identity, accounted for most of the dispersion in dietary space. Envfit analysis reinforced that crustaceans, algae, annelids, and UD were the primary contributors to the observed temporal structure. Collectively, the results indicate that although the invasive and native swimming crab species share similar prey categories, their resource use varies through time, suggesting that trophic interactions are modulated

by seasonal changes rather than constant direct competition.

DISCUSSION

The invasive population of *Charybdis* (*Charybdis*) *hellerii* presents a high trophic niche overlap (97%) with the native species *Achelous spinimanus*, both of which prefer crustaceans and mollusks. Although the results point to resource sharing, the seasonal variation in diet, especially in May and October, suggests dietary flexibility rather than constant direct sharing. This dynamic indicates that the adults adjust their trophic strategies according to prey availability. Costa et al. (2025) observed similar results, highlighting the role of dietary plasticity in the ecological success of invasive swimming crabs. The high overlap seems to reflect high trophic plasticity which might mitigate direct competition over time. Nonetheless, this overlap raises concerns about possible future impacts on native populations, especially if prey supply becomes limited (Ricciardi et al., 2013). Although resource sharing may be viable in environments with an abundance of prey (Dayton and Hessler, 1972; Holt et al., 1994), this mechanism may not fully explain the observed dynamics in Armação do Itapocoroy. Self-sustaining populations of *C.* (*C.*) *hellerii* have been established along the Southwestern Atlantic coast (Tavares and Mendonça, 2004). In Ubatuba, southeastern Brazil, *C.* (*C.*) *hellerii* remains less abundant than native portunid species (Fransozo et al., 1992; Mantelatto and Fransozo, 1999). However, this pattern is not universal; in other areas such as Baía de Todos os Santos (Bahia state), *C.* (*C.*) *hellerii* has become more abundant than the native *Callinectes marginatus*.

Seasonal variation in prey availability is a well-documented driver of temporal shifts in trophic interactions, particularly in dynamic coastal systems (Yang, 2020). These fluctuations can reshape foraging strategies throughout the year, leading species to modify their level of dietary overlap without necessarily altering their fundamental trophic roles. In this study, the strong seasonal signals observed, especially in May and October, align with ecological expectations that benthic invertebrate reproduction, algal turnover, and habitat structure influence short-term resource use (Rodrigues-Filho et al., 2023). These mechanisms help explain why overlap remains high overall even though specific prey groups dominate different months, reinforcing that trophic similarity cannot be interpreted as constant or uniform through time.

Achelous spinimanus is commonly caught at high depths, ranging from 82 to 393 meters (Felder et al., 2009), but some studies also show that this species can be caught in shallow environments along the Brazilian coast. In Ubatuba, São Paulo state, juvenile individuals of *A. spinimanus* are frequently caught in waters from 4 to 15 meters deep, and adult individuals above 15 meters, suggesting an ontogenetic distribution related to depth (Santos et al., 1995b). At Ilha do Frade, Espírito Santo state, specimens (including ovigerous females) were caught with hand trawls in coastal areas up to 2 meters deep, highlighting the use of these habitats as breeding areas (Ripoli et al., 2007). Thus, the species makes good use of shallow waters and coastal zones, reinforcing its habit of occupying coastal and estuarine environments often associated with coarse sand and gravel substrates, as is the case of Armação do Itapocoroy. Reports from local fishers indicate a decline in *A. spinimanus* abundance and a simultaneous increase in *C.* (*C.*) *hellerii* presence in artisanal fisheries. Despite evidence indicating that both species have been consuming similar prey for at least one decade (Branco and Lunardon-Branco, 2002; Sant'anna et al., 2015), diet similarity alone does not imply direct competition for resources or niche overlap, but it does raise a concern about the status of the native species, which appears to be in decline at the study site. In southeastern Brazil, invasive *C.* (*C.*) *hellerii* have reduced native *Cronius ruber* populations (Sant'anna et al. 2012). Observations suggest aggressive behavior by the invasive species, contributing to the apparent decline of native populations. The widespread carnivorous diet of *C.* (*C.*) *hellerii* increases pressure on native species, positioning it as both a predator and a competitor for food resources. However, detailed studies have yet to be conducted to confirm and quantify these impacts on native communities.

Several biological attributes that have already been studied evince the invasive success of *C.* (*C.*) *hellerii*, such as a prolonged larval phase, rapid growth, the ability to store sperm to produce multiple broods in a short period of time, high fecundity, a generalist carnivorous diet, the ability to colonize a wide variety of habitats, and early sexual maturity with a carapace width of only 35 mm (Dineen et al., 2001; Mantelatto and Garcia, 2001). Another relevant factor is that *C.* (*C.*) *hellerii* has no commercial value and is not consumed by local communities, unlike native portunids which are subject to fishing exploitation. Gurevitch et al. (2000) showed how competition for resources, including food, can be modified by the arrival of invasive species, potentially leading to declines in native populations due to shifts in competition dynamics. The trophic overlap between *C.* (*C.*) *hellerii* and native species might represent a likely mechanism for invasion success in tropical coastal regions. This is a plausible hypothesis because Costa et al. (2025), studying the same site, documented that invasive population reproduces year-round with a high success rate, a stark contrast to the seasonal reproductive cycles observed a decade ago (Sant'anna et al., 2015). The generalist feeding habits and continuous spawning cycles of *C.* (*C.*) *hellerii* indicate that the species has successfully established itself in the region, posing a significant threat to small-scale fisheries.

C. (*C.*) *hellerii* is also considered a threat to local fauna along the São Paulo coast (Izar et al., 2023). This species is an active predator with a strong preference for animal prey, particularly those with a low ability to escape, such as mussels. Laboratory studies show that while no linear relationship exists between predator density and predation pressure, *C.* (*C.*) *hellerii* exerts greater predation pressure on smaller prey, such as small bivalve mollusks, than on other swimming crabs, regardless of ontogenetic stage (Izar et al., 2023). These behaviors may have a cascading impact on mussel bed-associated fauna, affecting intertidal biodiversity. Previous studies have shown *A. spinimanus* preference for bivalves (Branco and Lunardon-Branco, 2002), but we found crustaceans as their primary dietary component, suggesting a dietary shift potentially driven by reduced availability of easier-to-capture prey. Invasive species are known for their broad feeding habits, adapting effectively to various ecological conditions and prey availability (Wu et al., 2017). Changes in prey density or water temperature can influence the food preferences among swimming crabs (Zhu et al., 2021).

This study represents the first comparative analysis of diet composition between the native swimming crab *Achelous spinimanus* and the invasive *C.* (*C.*) *hellerii* in the southwest Atlantic Ocean. Analyses were conducted exclusively in the coastal region of Penha, focusing on unconsolidated substrate in shallow waters, with depths varying between 1 and 2 meters. The sampling strategy was based on standardized collections with baited traps, performed at fixed points along the intertidal zone and shallow sublittoral. The size range of the individuals analyzed was limited to adult specimens within a previously determined carapace range, which restricts inferences about other age classes.

Considering this temporal perspective is essential for evaluating potential competitive outcomes. Temporal fluctuations in overlap suggest that resource sharing may increase during periods of high prey abundance but relax during seasonal prey bottlenecks, a pattern described across marine invasive systems (Ricciardi et al., 2013; Triay-Portella et al., 2022). Thus, interpreting trophic overlap solely from aggregated data can obscure ecologically meaningful dynamics. A temporally explicit view provides a more accurate approximation of how invasive species like *C*. (*C*.) *hellerii* interact with native fauna and the likelihood that competition will emerge under changing environmental conditions.

These findings are particularly relevant to the area studied, where native swimming crabs are preferentially caught by local fishermen. The establishment of *C.* (*C.*) *hellerii* in the region and its generalist feeding behavior during the initial invasion phase indicate a potential for long-term negative impacts on native populations. Although the direct effects of overlapping diets on the sustainability of native species cannot yet be fully assessed, this study offers an initial insight into how these two species exploit available trophic resources,

providing important input for future research and for understanding the ecological impacts associated with the introduction of invasive alien species.

AI Use statement

AI tools were used solely for language editing and translation (from Portuguese to English), specifically using Academic Assistant Pro. No AI tools were used in study design, data analysis, interpretation of results, or manuscript conceptualization. All scientific content and conclusions are the sole responsibility of the authors.

Data availability statement

The data that support the findings of this study consist of biometric measurements of the analyzed individuals. These data are available from the corresponding author upon reasonable request, subject to any applicable restrictions.

Supplementary material

No supplementary material is associated with this article.

Acknowledgments

We thank all the Zoology Lab and Community Ecology Lab members that assisted with field sampling and laboratory procedures, especially the Oceanography undergraduate students Ádyla Katilla Quintiliano da Silva and Maria Eduarda de Jesus Oliveira. We also thank Murilo Soares (first version) and Jullia Comicholi (published version) for creating the map, and Brenda Ramires for spell-checking.

Funding

We thank the Brazilian Federal Agency for Support and Evaluation of Graduate Education (CAPES) for supporting VSCC under Grant (88887.603759/2021-00) and the National Council for Scientific and Technological Development (CNPq) for providing a Productivity Grant to JOB.

Author contributions

V.S.C.C.: Conceptualization; Methodology; Software; Formal Analysis; Investigation; Writing – original draft; Writing – review & editing.

V.M.C.: Methodology; Software; Formal Analysis; Investigation; Writing – review & editing.

N. M. F.: Investigation; Methodology; Data Curation; Writing – Review & Editing.

L. G. P.: Investigation; Methodology; Data Curation; Writing – Review & Editing.

A.F.: Methodology; Writing – review & editing.

J.O.B.: Supervision; Resources; Project Administration; Funding Acquisition; Writing – review & editing.

Conflicts of interest

The authors declare that they have no conflicts of interest.

REFERENCES

Anderson, M. J. & Walsh, D. C. I. 2013. PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing? *Ecological Monographs*, 83, 557-74. DOI: https://doi.org/10.1890/12-2010.1

Andrade, G. J. P. O. 2016. Maricultura em Santa Catarina: A cadeia produtiva gerada pelo esforço coordenado de pesquisa, extensão e desenvolvimento tecnológico. *Extensio: Revista Eletrônica de Extensão*, 13, 204-217. DOI: https://doi.org/10.5007/1807-0221.2016v13n24p204

Arceo-Carranza, D., Chiappa-Carrara, X., Chávez López, R. & Yáñez Arenas, C. 2021. Mangroves as feeding and breeding grounds. *Mangroves: Ecology, Biodiversity and Management*, 63-95. DOI: https://doi.org/10.1007/978-981-16-2494-0_3

Bashevkin, S. M. & Morgan, S. G. 2020. Predation and competition. *The natural history of the Crustacea*, 7, 360-382. DOI: https://doi.org/10.1093/oso/9780190648954.003.0013

Branco, J. O. & Lunardon-Branco, M. J. 2002. Ecologia trófica de *Portunus spinimanus* Latreille (Decapoda, Portunidae) na Armação do Itapocoroy, Penha, Santa Catarina, Brasil. *Revista Brasileira de Zoologia*, 19, 723-729. DOI: https://doi.org/10.1590/S0101-81752002000300009

Branco, J. O., Lunardon-Branco, M. J., Verani, J. R., Schveitzer, R., Souto, F. X. & Vale, W. G. 2002. Natural diet of *Callinectes ornatus* Ordway, 1863 (Decapoda, Portunidae) in the Itapocoroy inlet, Penha, SC, Brazil. *Brazilian Archives of Biology and Technology*, 45, 35-40. DOI: https://doi.org/10.1590/S1516-89132002000100006

Branco, J. O. & Verani, J. R. 1997. Dinâmica da alimentação natural de *Callinectes danae* Smith (Decapoda, Portunidae) na Lagoa da Conceição, Florianópolis, Santa Catarina, Brasil. *Revista brasileira de Zoologia*, 14, 1003-1018. DOI: https://doi.org/10.1590/S0101-81751997000400014

Costa, L. L., Soares-Gomes, A. & Zalmon, I. R. 2022. Sandy beach heterogeneity: intertidal and supralittoral communities. *In*: Gonçalves, S. C. & Ferreira, S. M. F. (Ed.). *Sandy beaches as endangered ecosystems* (pp. 1-25). Boca Raton: CRC Press.

Costa, V. S. C., Cionek, V. M. & Branco, J. O. 2025. Feeding ecology of an invasive swimming crab: how feeding

patterns favors invasion success. *Marine Biology*, 172, 1-11. DOI: https://doi.org/10.1007/s00227-024-04589-x

David, P., Thebault, E., Anneville, O., Duyck, P. F., Chapuis, E. & Loeuille, N. 2017. Impacts of invasive species on food webs: a review of empirical data. *Advances in ecological research*, 56, 1-60. DOI: https://doi.org/10.1016/bs.aecr.2016.10.001

Dayton, P. K. & Hessler, R. R. 1972. Role of biological disturbance in maintaining diversity in the deep sea. *Deep Sea Research and Oceanographic Abstracts*, 19(3), 199-204. DOI: https://doi.org/10.1016/0011-7471(72)90031-9

Dineen, J. F., Clark, P. F., Hines, A. H., Reed, S. A. & Walton, H. P. 2001. Life history, larval description, and natural history of *Charybdis hellerii* (Decapoda: Brachyura: Portunidae), an invasive crab in the western Atlantic. *Journal of Crustacean Biology*, 21, 774-805. DOI: https://doi.org/10.1651/0278-0372(2001)021[0774:LHLDAN]2.0.CO;2

Fransozo, A., Mantelatto, F. L. M. & Santos, S. 1992. Composition and distribution of decapod crustaceans in Fortaleza Bay, Ubatuba, SP, Brazil. *Revista Brasileira de Biologia*, 52, 667–675. DOI: https://doi.org/10.20950/1678-2305.2016v42n2p307

Felder, D. L., Alvarez, F., Goy, J. W. & Lemaitre, R. 2009. Decapoda (Crustacea) of the Gulf of Mexico, with comments on the Amphionidacea. *In*: Felder, D. L. & Camp, D. K. (Ed.). *Gulf of Mexico - Origins, Waters, and Biota: Volume 1, Biodiversity*. (pp. 1019-1104). College Station: Texas A&M University Press.

Frigotto, S. F. & Serafim-Junior, M. 2007. Primeiro registro de *Charybdis hellerii* (Milne Edwards, 1867) (Crustacea) no litoral do estado do Paraná. *Estudos de Biologia*, 29(67), 227-230. DOI: https://doi.org/10.7213/reb.v29i67.22771

Gurevitch, J., Morrison, J. A. & Hedges, L. V. 2000. The interaction between competition and predation: a review of the evidence. *Ecological Monographs*, 70, 371-397. DOI: https://doi.org/10.1086/303337

Haefner Junior, P. A. 1990. Natural diet of *Callinectes ornatus* (Brachyura: Portunidae) in Bermuda. *Journal of Crustacean Biology*, 10, 236-46. DOI: https://doi.org/10.1163/193724090X00069

Holt, R. D., Grover, J. & Tilman, D. 1994. Simple rules for interspecific dominance in systems with exploitative and apparent competition. *The American Naturalist*, 144, 741-771. DOI: https://doi.org/10.1086/285705

Hynes, H. B. N. 1950. The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*) with a review of methods used in studies of the food fishes. *Journal of Animal Ecol*ogy, 19(1), 36-58. DOI: https://doi.org/10.2307/1570

Hyslop, E. J. 1980. Stomach contents analysis—a review of methods and their application. *Journal of fish biology*, 17, 411-429. DOI: https://doi.org/10.1111/j.1095-8649.1980.tb02775.x

Izar, G. M., Oliveira, D. N., Laurino, I. R. A., Zara, F. J. & Christofoletti, R. A. 2023. Is the population increase of an invasive portunid crab (*Charybdis hellerii*) a concern? The effect on native prey. *Estuarine, Coastal and Shelf Science*, 282, 108249. DOI: https://doi.org/10.1016/j.ecss.2023.108249

Kawakami, E. & Vazzoler, G. 1980. Método gráfico e estimativa de índice alimentar aplicado no estudo de alimentação de peixes. *Boletim do Instituto Oceanográfico*, 29(2), 205-207. DOI: https://doi.org/10.1590/S0373-55241980000200043

Kobayashi, S. & Vazquez-Archdale, M. 2018. Growth and reproductive ecology of the portunid crab *Charybdis japonica* in an open seacoast and an inland bay in Fukuoka, Japan. *Journal of Sea Research*, 142, 52-65. DOI: https://doi.org/10.1016/j.seares.2018.09.006

Lim, S. S., Yong, A. Y. & Christy, J. H. 2016. Ontogenetic changes in diet and related morphological adaptations in *Ocypode gaudichaudii*. *Invertebrate Biology*, 135, 117-126. DOI: https://doi.org/10.1111/ivb.12122

Lockwood, J. L., Hoopes, M. F. & Marchetti, M. P. 2013. *Invasion ecology*. Hoboken: John Wiley & Sons.

Mantelatto, F. L. M. & Dias, L. L. 1999. Extension of the known distribution of *Charybdis hellerii* (A. Milne-Edwards, 1867)(Decapoda, Portunidae) along the western tropical South Atlantic. *Crustaceana*, 72(6), 617-620. Available from: https://brill.com/view/journals/cr/72/6/article-p617_6.xml. Access date: 2026 apr. 12.

Mantelatto, F. L. M. & Fransozo, A. 1999. Reproductive biology and moulting cycle of the crab *Callinectes ornatus* (Decapoda, Portunidae) from the Ubatuba region, São Paulo, Brazil. *Crustaceana*, 72(1), 63–76. Available from: https://brill.com/view/journals/cr/72/1/article-p63_7.xml. Access date: 2026 apr. 12.

Mantelatto, F. L. M. & Garcia, R. B. 2001. Biological aspects of the non-indigenous portunid crab Charybdis hellerii in the western tropical South Atlantic. *Bulletin of Marine Science*, 68(3), 469-477. Available from: https://www.ingentaconnect.com/contentone/umrsmas/bullmar/2001/00000068/00000003/art00008. Access date: 2026 apr. 12.

McDonald, P. S., Jensen, G. C. & Armstrong, D. A. 2001. The competitive and predatory impacts of the nonindigenous crab *Carcinus maenas* (L.) on early benthic phase Dungeness crab *Cancer magister* Dana. *Journal of Experimental Marine Biology and Ecology*, 258, 39-54. DOI: https://doi.org/10.1016/s0022-0981(00)00344-0

Mesquita, A. L. L. 1972. Dados biométricos do siri canela *Portunus spinimanus* Latreille, 1819 (Decapoda, Brachyura, Portunidae). *Arquivos de Ciências do Mar*, 12, 88-90. DOI: https://doi.org/10.32360/acmar.v12i1.32530

Negri, M., Schubart, C. D. & Mantelatto, F. L. 2018. Tracing the introduction history of the invasive swimming crab *Charybdis hellerii* (A. Milne-Edwards, 1867) in the Western Atlantic: evidence of high genetic diversity and multiple introductions. *Biological invasions*, 20(7), 1771-1798. DOI: https://doi.org/10.1007/s10530-018-1660-0

Prado, P., Peñas, A., Ibáñez, C., Cabanes, P., Jornet, L., Álvarez, N. & Caiola, N. 2020. Prey size and species preferences in the invasive blue crab, *Callinectes sapidus*: Potential effects in marine and freshwater ecosystems. *Estuarine, Coastal and Shelf Science*, 245, 106997. DOI: https://doi.org/10.1016/j.ecss.2020.106997

Rato, L. D., Crespo, D. & Lemos, M. F. 2021. Mechanisms of bioinvasions by coastal crabs using integrative approaches–A conceptual review. *Ecological Indicators*, 125, 107578. DOI: https://doi.org/10.1016/j.ecolind.2021.107578

Ricciardi, A., Hoopes, M. F., Marchetti, M. P. & Lockwood, J. L. 2013. Progress toward understanding the ecological impacts of nonnative species. *Ecological monographs*, 83, 263-282. DOI: https://doi.org/10.1890/13-0183.1

Ricciardi, A., Iacarella, J. C., Aldridge, D. C., Blackburn, T. M., Carlton, J. T., Catford, J. A., Dick, J. T. A., Hulme, P. E., Jeschke, J. M., Liebhold, A. M., Lockwood, J. L., MacIsaac, H. J., Meyerson, L. A., Pyšek, P., Richardson, D. M., Ruiz, G. M., Simberloff, D., Vilà, M. & Wardle, D. A. 2021. Four priority areas to advance invasion science in the face of rapid environmental change. *Environmental Reviews*, 29, 119-141. DOI: https://doi.org/10.1139/er-2020-0088

Ripoli, L. V., Fernandes, J. M., Rosa, D. M. & Araújo, C. C. V. 2007. Dinâmica populacional de *Portunus spinimanus* Latreille, 1819 (Crustacea, Portunidae) em um trecho litorâneo da Ilha do Frade, Vitória - ES. *Boletim do Instituto de Pesca*, 33(2), 205-212. Available from: https://institutodepesca.org/index.php/bip/article/view/755/737. Access date: 2026 apr. 12.

Rocha-Barreira, C. A. & Rosa-Filho, J. S. 2023. Biological Interactions. *In*: Amaral, A. C. Z., Checon, H. H. & Corte, G. N. (Ed.). *Brazilian Sandy Beaches*. (pp. 199-222). Cham: Springer International Publishing.

Rodrigues-Filho, J. L., Macêdo, R. L., Sarmento, H., Pimenta, V. R., Alonso, C., Teixeira, C. R., Pagliosa, P. R., Netto, S. A., Santos., N. C. L., Daura-Jorge, F. G., Rocha, O., Horta, P., Branco, J. O., Sartor, R., Muller, J. & Cionek, V. M. 2023. From ecological functions to ecosystem services: linking coastal lagoons biodiversity with human well-being. *Hydrobiologia*, 850, 2611-2653. DOI: https://doi.org/10.1007/s10750-023-05171-0

Sant'anna, B. S., Branco, J. O., Oliveira, M. M. D., Boos, H. & Turra, A. 2015. Diet and population biology of the invasive crab *Charybdis hellerii* in southwestern Atlantic waters. *Marine Biology Research*, 11, 814-823. DOI: https://doi.org/10.1080/17451000.2015.1024134

Sant'anna, B. S., Watanabe, T. T., Turra, A. & Zara, F. J. 2012. Relative abundance and population biology of the non-indigenous crab *Charybdis hellerii* (Crustacea: Brachyura: Portunidae) in a southwestern Atlantic estuary-bay complex. *Aquatic Invasions*, 7, 347-356. DOI: https://doi.org/10.3391/ai.2012.7.3.006

Santos, E. P. 1978. *Dinâmica de populações aplicada à pesca e piscicultura*. São Paulo, Edusp. Available from: https://www.sidalc.net/search/Record/KOHA-OAI-FCF:19808/Description. Access date: 2026 Apr. 28.

Santos, S., Negreiros-Fransozo, M. L. & Pandovani, C. R. 1995a. Relação do peso do corpo em função da largura da carapaça do siri candeia *Portunus spinimanus* Latreille, 1819 (Decapoda, Portunidae). *Arquivos de Biologia e Tecnologia*, Curitiba, 38, 715-724.

Santos, S., Pires, M. & Fransozo, A. 1995b. Decapod crustaceans associated with a *Halodule wrightii* Aschers. (Cymodoceaceae) meadow in Ubatuba Bay, Brazil. *Journal of Coastal Research*, Fort Lauderdale, 11(2), 413–419.

Siddiqui, J. A., Bamisile, B. S., Khan, M. M., Islam, W., Hafeez, M., Bodlah, I. & Xu, Y. 2021. Impact of invasive ant species on native fauna across similar habitats under global environmental changes. *Environmental Science and Pollution Research*, 28, 54362-54382. DOI: https://doi.org/10.1007/s11356-021-15961-5

Susanto, G. N. 2021. Crustacea: the increasing economic importance of crustaceans to humans. *In*: Ranz, R. E. R. (Ed.). *Arthropods - Are They Beneficial for Mankind?* (pp. 01-10). London: IntechOpen. DOI: http://dx.doi.org/10.5772/intechopen.96255

Tavares, M. & Mendonça Jr., J. B. 2004. *Charybdis hellerii* (A. Milne Edwards, 1867) (Brachyura: Portunidae), eighth nonindigenous marine decapod recorded from Brazil. *Crustacean Research*, 25, 151-157. DOI: https://doi.org/10.18353/crustacea.25.0_151

Teixeira, L. M. & Creed, J. C. 2020. A decade on: an updated assessment of the status of marine non-indigenous species in Brazil. *Aquatic Invasions*, 15(1), 30-43. DOI: https://doi.org/10.3391/ai.2020.15.1.03

Triay-Portella, R., Martín, J. A., Luque, L. & Pajuelo, J. G. 2022. Relevance of feeding ecology in the management of invasive species: Prey variability in a novel invasive crab. *Estuarine, Coastal and Shelf Science*, 274, 107949. DOI: https://doi.org/10.1016/j.ecss.2022.107949

Williams, M. J. 1981. Methods for analysis of natural diet in portunid crabs. (Crustacea: Decapoda: Portunidae). *Journal of Experimental Marine Biology and Ecology*, 52(1), 103-113. DOI: https://ui.adsabs.harvard.edu/link_gateway/1981JEMBE..52..103W/doi:10.1016/0022-0981(81)90174-X

Wu, F., Wang, T., Cui, S., Xie, Z., Dupont, S., Zeng, J., Gu, H., Kong, H., Hu, M., Lu., W., Lu, W. & Wang, Y. 2017. Effects of seawater pH and temperature on foraging behavior of the Japanese stone crab *Charybdis japonica*. *Marine Pollution Bulletin*, 120, 99-108. DOI: https://doi.org/10.1016/j.marpolbul.2017.04.053

Yamada, S. B. & Boulding, E. G. 1998. Claw morphology, prey size selection and foraging efficiency in generalist and specialist shell-breaking crabs. *Journal of experimental marine biology and ecology*, 220, 191-211. DOI: https://doi.org/10.1016/S0022-0981(97)00122-6

Yang, L. H. 2020. Toward a more temporally explicit framework for community ecology. *Ecological Research*, 35, 445-462. DOI: https://doi.org/10.1111/1440-1703.12099

Yeoh, L. H. 2020. Behavioural competition in the intertidal shore crab, *Petrolisthes elongatus* (Doctoral dissertation). Wellington: Victoria University of Wellington.

Yulianto, H., Ihsan, Y. N., Sumiarsa, D. & Ansari, A. 2024. Assessing the sustainability of the blue swimming crab (*Portunus pelagicus*) on the Eastern Coast of Lampung: a holistic approach to conservation and resource stewardship. *Frontiers in Marine Science*, 11, 1304838. DOI: https://doi.org/10.3389/fmars.2024.1304838

Zhu, B., Lu, Y., Wang, F., Liu, D., Su, X. & Shang, Y. 2021. Will swimming crab change their territoriality when prey density increases?. J*ournal of Experimental Marine Biology and Ecology*, 539, 151546. DOI: https://doi.org/10.1016/j.jembe.2021.151546