

Predation of portunid crabs *Callinectes sapidus* and *Callinectes ornatus* (Crustacea, Decapoda) on the medusa *Lychnorhiza lucerna* (Cnidaria, Scyphozoa)

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Jellyfishes (pelagic medusozoans and ctenophores) have a limited number of specialized predators, such as the leatherback turtle (*Dermochelys coriacea*), the ocean sunfish (*Mola mola*) and some comb jellyfishes (*Beroe* spp.); however, an increasing number of pelagic and benthic species have been reported feeding on jellyfishes (reviewed by Ates, 2017; Hays et al., 2018). Non-specialized jellyfish consumers include fishes, birds, and marine mammals, as well as many invertebrates, such as crabs, amphipods, other jellyfish, sea anemones, etc. These recent studies have indicated that predation and scavenging on jellyfish are widespread, contradicting a previous paradigm in which jellyfish were considered the “dead ends” of marine trophic webs (Hays et al., 2018). Under this new view, the energy channelized for the production of large jellyfish blooms can be naturally driven toward multiple sets of consumers (Sweetman et al., 2014; Hays et al., 2018). This topic is, however, widely unknown and many questions remain unsolved, such as what is the importance of jellyfish for the energy intake of these consumers? Which populations of jellyfish predators take advantage of jellyfish blooms?

Many marine animals are found together with large jellyfishes in associations that may result in multiple benefits, such as protection against

predation, transport in the water column, and food acquisition from jellyfish tissues or captured prey (Purcell and Arai, 2001; Fleming et al., 2014). When the jellyfish are not affected by their “hitchhikers”, such association is considered phoresis (e.g. Martinelli et al., 2008). In some cases, these symbionts also provide benefits to their hosts, by cleaning jellyfish ectoparasites (Towanda and Thuesen, 2006). In contrast, some studies have suggested that jellyfishes are consumed by their symbionts (D’Ambra et al., 2015) or that symbionts ingest food particles captured by the jellyfish (Gonçalves et al., 2020). Brachyuran crabs are often found with scyphomedusae in coastal and estuarine areas (Farr, 1978; Moyano et al., 2012; Ates, 2017; Gonçalves, et al. 2020). These symbioses usually involve the megalopae or young crabs, but adults were also reported on top of the jellyfish bells. Information on the possible trophic role of these symbiotic relationships is scattered or unavailable in many cases. Moyano et al. (2012) reviewed 28 studies on associations involving 18 jellyfish and nine crab species; only nine studies provided evidence of predation on the jellyfish hosts, ranging from direct observations of predation *in situ* (Farr, 1978), laboratory experiments (Esser et al., 2004), analysis of crab gut contents (Gonçalves et al., 2020), to trophic markers such as stable isotopes (Mancinelli et al., 2017). Although these studies may reveal an important trophic link, the potential damage these symbionts may cause and whether jellyfish populations can be affected by these crabs remain unsolved.

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Portunid crabs of the genus *Callinectes* are among the most common macrobenthic invertebrates in tropical and subtropical coastal areas (William, 1974; Guerra-Castro et al., 2007). The diets of these opportunist omnivorous crabs are influenced by food availability (Oliveira et al., 2006; Silveira et al., 2020). Common *Callinectes* prey include benthic organisms, coastal vegetation, and small fish (Branco et al., 2002; Oliveira et al., 2006). Species such as *Callinectes sapidus* Rathbun, 1896 are considered estuarine dependent, because their adults inhabit estuarine zones, whereas larvae development occurs in coastal and ocean areas (Epifanio, 2007; Yeager et al., 2007). *Callinectes ornatus* Smith 1869 inhabits sand and mud bottoms in brackish waters (Melo, 1996). Because of their abundance, these crabs play an important role as consumers in coastal food webs, potentially controlling populations of their prey (Hines, 2007).

The rhizostome medusa *Lychnorhiza lucerna* Haeckel, 1880 is one of the most common jellyfish in the Southwest Atlantic, occurring from Colombia to the northern Argentinean coast (Schiariti et al., 2008). The species is particularly abundant in coastal areas under the influence of estuaries, and can be dominant in the pelagic environment during its seasonal population peaks (Colombo et al., 2003; Schiariti et al., 2008; Nagata et al., 2009). Newly released ephyrae were recently found in a Brazilian estuary (Nogueira Jr. et al., 2019), which reinforces the importance of such ecosystems to the species life cycle. *L. lucerna* is a key consumer of mesozooplankton and captures thousands of prey in their filtrating oral arms (Nagata et al., 2016; Nagata and Morandini, 2018); however, the species' predatory impacts and role in coastal trophodynamics are widely unknown. Large individuals of *L. lucerna* often reach 30 cm in bell diameter; their oral arms and subgenital cavities offer many microhabitats that can be inhabited by innumerable symbionts, such as cleaner shrimp *Periclimenes paivai* (Martineli et al., 2008) and the spider crabs *Libinia ferreirae* (Nogueira Jr. and Haddad, 2005) and *Libinia spinosa* (Moyano et al., 2012). To the best of our knowledge, this study is the first record of an association between the medusa *L. lucerna* and portunid crabs of the genus *Callinectes*. We also analyzed the gut contents of the crabs, providing evidence of medusae consumption.

One aggregation of *L. lucerna* was found on the surface water of an embayment on the southernmost part of the Patos Lagoon, south Brazil (Figure 1A), on 25 March 2019. Medusae (N = 33) and associated crabs (N = 4) were collected individually using a dip net aboard small boats. Specimens were photographed, immediately preserved in 4% formaldehyde solution and transported to the Laboratory of Zooplankton at the Universidade Federal do Rio Grande (FURG). Biometric data of the carapace length between consecutive spines (LC2) was taken with the aid of a pachymeter (± 0.01 mm). The weight of the crabs was estimated (± 0.01 g). The stomachs of crabs were removed through a section on their carapace and the gastric contents were analyzed on slides under an inverted microscope at 1,000 \times magnification. After the identification of cnidae in the gastric content, these were compared with the cnidae of *L. lucerna*, obtained from tissues of the medusa oral arms and marginal lappets and analyzed on slides under a microscope at 1,000 \times magnification. These cnidae were compared and classified according to Östman (2000). The analyzed material was stored in the collection of the Laboratory of Zooplankton of FURG.

We found three medusae of *L. lucerna* in association with individuals of the blue crab *Callinectes sapidus* and one medusa with one crab of the species *Callinectes ornatus*. In all cases, only one crab was found per medusa (Figure 1 B and C). Both crab species were found on the subumbrella of the medusae and were juveniles, two females and two males. The mean carapace length (LC2) was 1.70 cm (0.97–2.05 cm) and the mean weight was 0.65 g (0.09–0.97 g). Gut content analyses of crabs revealed nematocysts of *L. lucerna* in all stomachs. These nematocysts were classified as oval-shaped small isorhiza and rhopaloids (Figure 1 C). The small (<10 μ m) isorhizae were characterized by an isodiametric tubule, without a proximal shaft, but the presence of spines could not be confirmed at 1000 \times magnification of the compound light microscope employed. The rhopaloids were characterized by a clearly distinct shaft and a coiled thinner tubule (Figure 1 D). The same nematocysts were found on oral arms and bell margins of *L. lucerna* (Figure 1 E) and both were similar in shape and size to those described for the rhizostome species *Catostylus mosaicus* and *Phyllorhiza punctatata* (Peach and Pitt, 2005). These

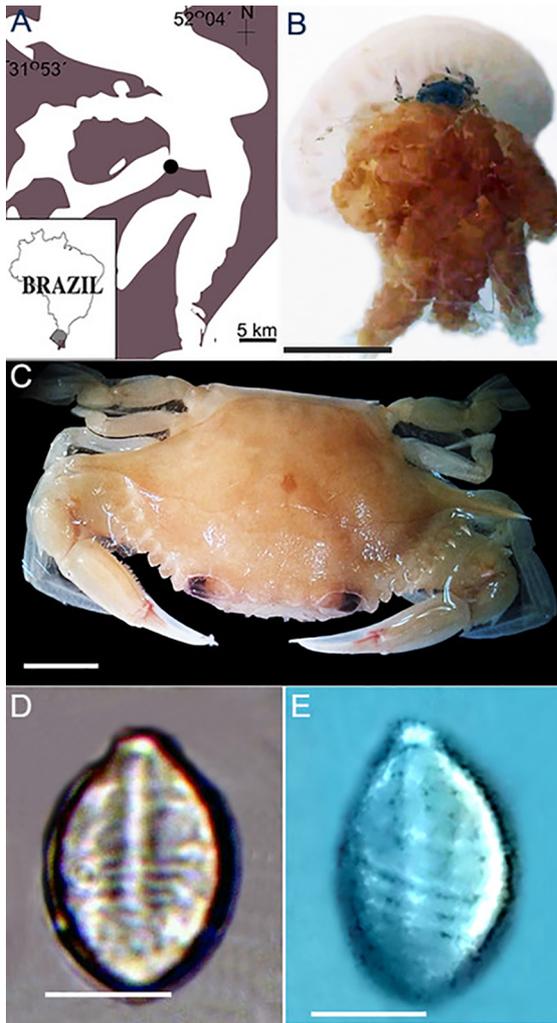


Figure 1 - A - Study site, in the Patos Lagoon Estuary, south Brazil. B - Specimen of *Lychnorhiza lucerna* with a crab *Callinectes sapidus* on its bell, scale: 4 cm. C - Detail of one specimen of *Callinectes sapidus*, found with *L. lucerna*, scale: 0.25 cm. D - Rhopaloid nematocyst from oral arms of *Lychnorhiza lucerna*, scale bar: 5 μ m. E - Rhopaloid nematocyst found in gut content of *Callinectes sapidus*, scale bar: 5 μ m.

nematocysts were the only prey item found in the gut contents of crabs, which characterized an opportunistic predation of scyphozoan jellyfish.

The extent of the damage caused by decapods feeding on jellyfishes can be varied. For spider crabs of the genus *Libinia*, it has been suggested that the damage to the hosts is not substantial and that nematocysts of *L. lucerna* found in the gut contents could have been incidentally ingested along with prey captured by the jellyfish (Moyano et al., 2012; Gonçalves et al., 2020). In contrast, decapods such as *Carcinus maenas*, *Crangon crangon*, and *Pagurus bernhardus* were able to actively capture and

consume comb jellyfish in laboratory experiments (Esser et al., 2004) or in the field (Ramussen, 1973; Farr, 1978). Predation by decapod crabs on jellyfish was reported even on occasions when other prey items were available (Ates, 2017). This is in contrast with the idea that jellyfish are consumed only in the absence of energy-richer prey (Farr, 1978). Specifically, regarding *Callinectes* crabs, Farr (1978) described individuals of *C. sapidus* actively feeding on the bells and oral arms of the medusae *Cyanea capillata* and *Stomolophus meleagris*. Based on this evidence, as well as the data, it was concluded that portunid crabs may consume large jellyfish, but it is not possible to determine whether the large number of dead or damaged jellyfish found without oral arms during sampling was a consequence of such predation.

Another non-exclusive explanation for the large number of dead/damaged jellyfish is the senility of individuals in this population during late summer. Although there is no study on the population dynamics of *L. lucerna* at the Patos Lagoon Estuary, other populations along the Southwest Atlantic are seasonal, as are most scyphozoan species (Schiariti et al. 2008; Nogueira Jr. & Haddad 2017). An evaluation of the jellyfish feeding structures suggested that most individuals showed a non-feeding post-reproductive condition, because of the lack or reduction of oral arms and the absence of digitata, the finger-like projections on oral arms that capture prey. This feature is common in scyphozoan jellyfishes that shed their reproductive and feeding structures and rapidly became senescent (Henschke et al. 2017). It is possible, therefore, that both factors (predation and senescence) contributed to the mortality of these jellyfishes. To clarify the role of predation by crabs and the interplay of this factor with the senescence of *L. lucerna*, further studies should investigate crab feeding rates and the extent of their damage to the jellyfishes. Even if the predation is less important to the jellyfish mortality, as suggested by the low frequency of crabs found on the latter (~12%), our study demonstrates an important fate for the large biomass that is seasonally produced by scyphozoan species in coastal areas.

The predation of benthic organisms may be increased when jellyfish aggregations are stuck in shallow enclosed waters and become more vulnerable to crabs, as well as to other consumers, such as hyperiid

amphipods, shrimps, free-living or parasitic anemones, and echinoderms (reviewed by Ates, 2017). In the Patos Lagoon Estuary, the tides are small amplitude (<40 cm); therefore, the entrance of coastal/oceanic waters with jellyfishes depends on the wind stress and lower rainfall (Odebrecht et al., 2017). After salinization of the estuary, the southernmost part of the Patos Lagoon can hold pockets of saltwater with aggregations of *L. lucerna* for weeks within small shallow (<2 m) embayments. In the Patos Lagoon Estuary, such episodes may be more frequent during the warmer months (December to May) when the rainfall is lower. These enclosed/shallow areas may act as sinks for aggregations/blooms of gelatinous organisms. In addition, research has shown that benthic consumers can control jellyfish populations (Esser et al., 2004) and alter pelagic food web structures (Sullivan et al., 1991). These interactions can be enhanced by turbulence (Esser et al., 2004), by the behavior of *L. lucerna* aggregating close to the bottom (Alvarez Colombo et al., 2003), and by the fact that these crabs can feed on pelagic prey (Rady et al., 2018).

Finally, the results demonstrate that portunid crabs of the genus *Callinectes* actively feed on *L. lucerna* and may benefit from blooms/aggregations of this species. The possible role of these crabs in controlling jellyfish populations is still unknown and should be further investigated. Because these crabs are key species in estuaries and coastal areas, they may act as intermediate consumers, driving the energy produced by jellyfish to other consumers, such as the fishes *Micropogonias furnieri*, *Genidens* spp., and *Paralichthys brasiliensis*, which are known predators of *Callinectes* (Figueiredo and Vieira, 2005; Bemvenuti and Colling, 2010). This trophic relationship illustrates examples of benthic–pelagic coupling and the contribution of coastal/oceanic production to the estuarine food web, which can also be found in many similar coastal ecosystems.

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AUTHOR CONTRIBUTIONS

T.L.V.: Conceptualization; Data curation; Formal analysis; Writing - Original draft; Writing - review & editing.

S.S.: Formal analysis; Investigation; Writing - review & editing;

R.M.N.: Investigation; Methodology; Formal Analysis; Supervision; Writing - review & editing.

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