**WHO PREYS ON CHITONS? CHITON PREDATORS AND A NEW CASE TO THE BRAZILIAN REEF OCTOPUS.**

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**Abstract**

Chitons are a eight-shelled mollusks group that has thrived in oceans worldwide for at least 540 million years, playing a crucial ecological role in regulating populations of algae and other benthic organisms. Despite this, chitons remain relatively unfamiliar to the general public, and even details about their predators are notably absent from major undergraduate invertebrate biology textbooks. In this study, we review the scientific literature to identify the main groups of animals that prey on chitons, specifying the predator species involved, the contexts of these predator-prey interactions, methods of observation, and the chiton species targeted. Additionally, we present a new field record of an interaction between a juvenile Brazilian reef octopus, *Octopus insularis*, and the endemic West Atlantic chiton *Ischnoplax pectinata*, a species with limited ecological data. Our survey identified fish, starfish, crabs, birds, octopuses, sea snails, polychaetes, and lobsters as the primary predators of chitons. Predation was predominantly observed in manipulative experiments or inferred through indirect methods, with only two studies documenting predation in natural habitats. In our field observations, a juvenile octopus preyed on an adult chiton hiding beneath a boulder. The chiton’s head plate was disarticulated and partially retained by the girdle, with no visible drill holes were observed on its shell. Chitons are notoriously difficult to prey upon due to their strong attachment to hard substrates, especially when disturbed. Predators can use different foraging and prey-handling strategies based on their own traits and the specific characteristic of their prey and habitat. Fish may peck or bite, birds deliver sharp jabs with their beaks, crabs use their claws to grip and crush, and sea snails drill hole into their prey’s shells. Octopuses combining tactics similar to those of crabs and snails. The Brazilian reef octopuses’ juveniles emerge as prominent predators in intertidal reefs in northeastern Brazil. Our field observation of an octopus preying on a chiton beneath boulders challenges the assumption that hiding under boulders provides reliable protection from predators. Despite being preyed upon by a wide range of predators, chiton have thrived evolutionary. Understanding the interactions between cryptic species, like octopuses and chitons, is essential for understanding the structure, dynamics, and vulnerabilities of tropical reef ecosystems. This knowledge is important for guiding conservation and management efforts in boulder reef systems amid the challenges posed by climate change and biodiversity loss.

**Key words**: Borehole, Boulder fields, Cephalopoda, Drill hole, Intertidal reefs, Polyplacophora.

# Introduction

Predation is considered a powerful evolutionary force that drives adaptive radiation, inducing genetic variation and promoting phenotypic diversity (Bond and Kamil 2002; Nosil and Crepi 2006; Tigreros et al. 2021). As an ecological mechanism, its effect is noticeable at different ecological scales, shaping prey distributions, habitat use, population dynamics, food webs, and ensuring the flow of energy through ecosystems (Guo et al. 2023; Johnson-Bice et al. 2023; Carroll et al. 2024; Orrick et al. 2024). Being preyed upon may be the most tearing fate an individual can face in its lifetime. Avoiding predation is therefore critical to individual's fitness (Palmer and Packer 2021). Evolution offers remarkable examples of how natural selection has shaped strategies for organisms to prevent predator detection or defend themselves after being detected (Ruxton et al. 2018). The former associate phenotypical variations, such as color patterns, transparency, and morphological outgrowths, with behavioral changes that help organisms avoid detection or be misidentified as an inedible object like sticks, leaves, seaweed, or bird-droppings (Arias et al. 2019; Cuthill 2019; Stevens and Ruxton 2019). Additionally, the latter make organisms unprofitable for predators, such as developing spines, stingers, toxins, or even warning signals (Ruxton et al. 2018). In this way, the presence of predators in a given community can force prey to make behavioral choices between vital activities, such as feeding, and avoiding contact with predators by reducing activity or seeking refuge (Chauhan et al. 2024; Liao et al. 2024).

Chitons, or polyplacophorans, are eight-shell plate-bearing mollusks that are strongly associated with hard marine substrates (Eernisse 2007). As a lineage, polyplacophorans have survived major climate changes and transformation of Earth’s surface throughout its history (Wanninger and Wollesen 2019). Their articulating shell-armature are similar to ancestral chitons species from the early Cambrian (ca. 540 Mya) and has been well-conserved in the living chitons lineages from the early Carboniferous ca. 340 mya (Sigwart 2009; Parkhaev 2017). Chitons occupy a diverse array of environments, including rocky shores, coral reefs, sandstone reefs, boulder fields, pebbles, rhodolith beds, and seagrass meadows, as well as unconventional deep habitats such sunken woods, whale bones, and hydrothermal vents [(Kangas and Shepherd 1984; Schwabe and Sellanes 2004; Konar et al. 2006; Saito et al. 2008; Barros et al. 2013; Reyes-Gómez et al. 2017; Sigwart 2017; Barboza 2019)](https://www.zotero.org/google-docs/?RLRcNX). They use an iron-mineralized radula to scrape food from the substrate, often ingesting various organisms or even sediment particles in the process (Fulton 1975; Joester and Brooker 2016). As a result, many intertidal chitons capable of digesting both animal and plant matter are considered browsing omnivorous (Latyshev 2004; Sigwart and Schwabe 2017). Ecologically, chitons can regulate algae growth through grazing, while also exerting an unintentional “bulldozing-effect” on larvae and post-metamorphic invertebrate stages, influencing heterogeneity and community composition (Aguilera and Navarrete 2007, 2012; Aguilera et al. 2015; Liversage and Kotta 2019).

Details on chiton predators are not included in major undergraduate textbooks on invertebrate biology (Brusca et al. 2023). This information is scattered throughout scientific literature of various fields, including zoology, ecology, and animal behavior, and may even be unknown to chiton researchers who are confined to literature of their specific group. Most studies focus on the diets of other animals, where chitons are merely one of the food items found in the species’ stomach/gut contents (Irons et al. 1986; Petracci et al. 2004). Additionally, chitons are often overlooked by the untrained eye and are deemed ‘rare’ by conventional marine ecology methods. This probably is because chitons are typically negatively photosensitive, hiding in crevices, holes, depressions, or under rocks during daylight low tides – the period when the most marine ecology studies are conducted (Miller and Ambrose, 2000; Vermeiren and Seaves, 2014; Montes et al. 2021). On intertidal boulder reefs, they are often seen crawling and feeding on the side surfaces of boulders during nighttime low tides (Jörger et al. 2008; Liversage and Benkendorff 2017), though their activity patterns seem to vary by species and habitat type (Demopulos, 1975; Kangas and Shepherd 1984; Cretchley et al. 1997). Chitons’ activity patterns are influenced by a variety of tidal and non-tidal rhythms, such as tidal regimes, the light-dark daily cycle, season, and climate [(Glynn 1970; Ng and Williams 2006; Yoshioka and Fujitani 2006)](https://www.zotero.org/google-docs/?2jjeDf). These patterns seem to be related to protecting them from direct solar radiation, and preventing high temperature and desiccation [(Shick 2007)](https://www.zotero.org/google-docs/?NLCAIl). Ecologically, it is assumed that the chitons’ permanence under boulders during daylight provides not only physiological benefits to fitness but also protection from potential visual guided predators [(Schmitt 1982; Rodrigues and Absalão 2005)](https://www.zotero.org/google-docs/?yXrAci).

Octopuses are a prominent shallow-water predator adapted for foraging and feeding in complex marine habitat such as boulder reefs [(Mather 2021)](https://www.zotero.org/google-docs/?VH4lF4). They use multiple sensory information to perceive their surroundings and navigate within their environment, including vision, mechanoreception, and chemical sensing [(Buresch et al. 2022)](https://www.zotero.org/google-docs/?kepkmI). Octopus predation is probably a major cause of mortality for many benthic marine species, especially for crabs, bivalves, and gastropods [(Anderson et al. 2008)](https://www.zotero.org/google-docs/?V14Uoy). Chitons can also be included in octopus's diet, although they seem to be a less preferred prey [(Mather 1991)](https://www.zotero.org/google-docs/?NMWwvf). The Brazilian reef octopus, *Octopus insularis* [(Leite et al. 2008)](https://www.zotero.org/google-docs/?C4zT6i), is a diurnal species [(O’Brien et al. 2023)](https://www.zotero.org/google-docs/?Jipmvt) with juveniles commonly found in intertidal reefs in northeastern Brazil [(Batista and Leite 2016)](https://www.zotero.org/google-docs/?tOucQb). Their diet consists of small crustaceans, bivalves, and gastropods, with occasional consumption of large preys (Dantas et al. 2022). Chitons may also be a frequent part of their diet (Dantas et al. 2020), but details about which chiton species are targeted, conditions and habitat where this interaction occur, and life stages involved remain unknown.

Here, we present a mini-review of the species and animal groups that prey on chitons, based on a literature survey of studies documenting chiton predator-prey relationships. We describe the species that prey on chitons, the conditions under which observations were made, and the chiton species targeted. Additionally, we also documented a direct field observation of the interaction between the Brazilian reef octopus (*O. insularis*) and a endemic West Atlantic chiton species, *Ischnoplax pectinata* (G.B.Sowerby II, 1840), with scarce ecological data.

# Materials and methods

## Study site

Observation occurred along an intertidal reef in Santa Rita beach (05°41′S, 35°11′W), Rio Grande do Norte, Brazil (Fig. 1). The region presents a tropical humid climate, with rainfall occurring during the austral spring [(Vital et al. 2016)](https://www.zotero.org/google-docs/?7JdAi3). Winds come predominantly from the southeast [(Silva et al. 2002)](https://www.zotero.org/google-docs/?aVvwit). Tides are semidiurnal with meso-tidal regime (Vital et al. 2016). Siliciclastic sands predominantly dominate the beaches [(Vital 2009)](https://www.zotero.org/google-docs/?wHqIrS). The Santa Rita reef is a linear formation along the coast of limited height (no more than 1m). It is characterized by rocky outcrops and irregular boulders, red or black iron-colored, which can either be loosely distributed on the sediment or other rocks [(Barboza 2019)](https://www.zotero.org/google-docs/?eOJlwS).

## Field procedures

As part of the field study on the chiton species *I. pectinata* (in preparation), measurements of water temperature and tide level relative to the base of the boulder were taken before handling the boulder, while weight was measured as the final step after handling. Water temperature was recorded with a thermometer over five minutes, and tide level was measured using a measuring tape. The boulder’s weight was determined by placing it inside a cloth bag and weighing it with a handheld scale. Visual field identification used to determine the octopus’s species (*O. insularis*) was based on distinct red/white body patterns and habitat [(O’brien et al. 2021)](https://www.zotero.org/google-docs/?wWYeH7). The chiton was identified as *I. pectinata*, based on their convex valves sculptured by radial ribs [(Gomes 2015)](https://www.zotero.org/google-docs/?9wieHS).

## Bibliographic survey

A bibliographic survey was conducted in the Scopus database using the search term “chiton” OR “polyplacophora” AND “prey” applied to the article title, abstract, and keywords sections. The search was limited to articles and conference papers within the subject area of Biological, Environmental, and Planetary Sciences, restricted to English and Spanish languages, covering the period from 1900 to 2024. The primary survey results were filtered by examining the title and abstracts. Papers were further filtered after a thorough reading. Additionally, a secondary survey was conducted using references from the articles obtained in the primary survey. Additional references were provided by the authors and through contacts with researchers.

# Results

## Field observation

On April 13, 2021 (10:50 am), during our ecological fieldwork with *I. pectinata* at Santa Rita Reef (Fig. 2A), we encountered a juvenile *O. insularis* (~2 cm eye distance) feeding on a chiton beneath a boulder we overturned (Fig. 2B). Due to the disturbance, the octopus quickly fled, leaving behind fresh chiton remains (Fig. 2C). T). The boulder (3kg) was situated in the lower mesolittoral zone, resting on a bed of sand and silt. It was exposed during low tide (0.3), but a shallow layer (0.9 cm) of warmer water (30°C) covered its lower portion. The chiton remains (length: 3cm, Fig. 2C), identified as *I. pectinata*, exhibited freshness, including foot tissue, gills, and mantles with the head plate (Plate I) disarticulated and partially held by the girdle (Fig. 2D). We did not observe any apparent drill holes.

## Chiton predators

Chitons can be preyed upon by several animals from different taxa, including other members of the phylum Mollusca (Table 1). There are sixty four recorded species that prey on chitons, although some records do not specify the exact chiton species consumed. The main groups of predators are fishes (30 sp.), starfishes (9 sp.), crabs (8 sp.), birds (6 sp.), octopuses (5 sp.), sea snails (4 sp.), polychaetes (1 sp.), and lobsters (1 sp.). Fish are the most diverse predators of chitons, with species including grunts, wrasses, porgies, blennies, puffers, groupers, boxfish, damselfish, triggerfish, tilefish, squirrelfish, and goatfish. Starfish are also an important predatory group of chitons, although their diversity of predator’s species is predominantly concentrated in the Asteridae family. Among crabs, the richness of species reflected greater family diversity. For birds, the primary predators are gulls, black oystercatchers, harlequin ducks, and common eiders. Among mollusks, all sea snail species, except *L. dirum*, are muridic gastropods, while 1all octopuses belongs to the genus *Octopus*. Only one species of polychaetes, the bearded fireworm, was recorded as preying on chitons and only the Caribbean spine lobster was recorded with chitons in its gut content.

Forty-seven species of chitons were either consumed directly or found in the stomach/gut contents of predators. For most predators, only species-specific relationships with chitons have been documented. However, the fish species *Notolabrus tetricus* and *Diplodus vulgaris* notably prey on a wide variety of chiton species, with the former potentially being a key predator of chitons in boulder field habitats. In these habitats, only octopuses, crabs, and fish have been identified as predator of boulder-dwelling chitons species. Most studies rely on indirect methods such as analyzing stomach or gut content, regurgitation pellets, fecal samples, drill holes (boreholes), or prey remain. Studies reporting direct interactions typically occur under limited or artificial condition, such as prey choice experiments in laboratory or natural settings. Only two studies report *in situ* observations I which starfish directly feeding on chitons

# Discussion

Chitons are fascinating mollusks found in oceans worldwide, closely associated with hard marine substrates. They play a crucial ecological role in regulating populations of algae and other benthic organisms. Despite of their importance, chitons are relatively unknow to the general public and often overlooked even by biologists. Much of the knowledge about their biology, ecology, and behavior remains scattered across the scientific literature and has not been systematized in major invertebrate biology textbooks, this including details about their predators. In this study, we compile information on species and animal groups that prey on chitons, the contexts of these predator-prey interactions, methods of observation, and the chiton species targeted. The primary predators identified include fish, starfish, crabs, birds, octopuses, sea snails, polychaetes, and lobsters. Additionally, we present a new field record of an interaction between a juvenile Brazilian reef octopus, *Octopus insularis*, and the endemic West Atlantic chiton *Ischnoplax pectinata*, a species with limited ecological data. This observation is the first documented interspecific relationship between *O. insularis* and *I. pectinata*, highlighting the role of juvenile Brazilian reef octopuses as prominent predators in intertidal boulder field habitat in northeastern Brazil. Although the Brazilian reef octopus are indirectly known to consume chitons [(Dantas et al. 2020)](https://www.zotero.org/google-docs/?ckqMEC), the latter are likely less preferred or opportunistically preyed upon, as the octopuses’ diet mainly consists of small crustaceans, bivalves, and gastropods [(Batista and Leite 2016; Leite et al. 2016)](https://www.zotero.org/google-docs/?hYWb4X).

In our survey, we found only two studies reporting predation on chitons in their natural habitats. These studies focused on sea star species, which typically feed by spreading their stomachs over their prey, secreting digestive enzymes, and ingesting the partially digested mixture [(Brusca et al. 2022)](https://www.zotero.org/google-docs/?sXQ33M). For the remaining studies, predation on chitons was only observed in manipulative experiments or through indirect methods, such as analyzing stomach/gut contents, regurgitation pellets, drill holes, stable isotopes, and prey remains. This highlights the challenge of directly observing predation and prey selection *in nature* (Smith and Ruxton 2020). This is especially evident with invertebrates, where visually cryptic species further complicate field studies, necessitating significant effort and financial resources [(Sunderland 1988; Birkhofer et al. 2017)](https://www.zotero.org/google-docs/?xe78bg). Predation events under natural conditions are seldom observed, even in octopuses’ studies where visual search methods and *in situ* dives are heavily employed [(Leite et al. 2009a, 2016)](https://www.zotero.org/google-docs/?LzuuXS). In such cases, opportunistic recording can be a valuable tool for gaining insight into the true nature of predator-prey interactions.

Chitons are notoriously difficult to prey upon due to their resistance to removal from hard substrates, especially when disturbed [(Linsenmeyer 1975; Brusca et al. 2022)](https://www.zotero.org/google-docs/?eSCGra). The shear force required to dislodge a 5 cm long chiton is five times greater than that required to dislodge a sea urchin of approximately the same diameter [(Irons et al. 1986)](https://www.zotero.org/google-docs/?X53u4R). Predators can use different foraging and prey-handling strategies based on their own traits and the specific characteristic of their prey and habitat [(Grisley et al. 1999; Buresch et al. 2022)](https://www.zotero.org/google-docs/?Hi7UX8). It is likely that birds feeding on mollusks with habits similar to chitons, such limpets, use comparable foraging strategies. For example, oystercatchers deliver sharp jabs with their beaks to the edges of limpet shells to crack them, making it easier to dislodge the animal from the rock surface (Hartwick 1973). Likewise, gulls have been observed prying chitons off rocks with their beaks, either swallowing them whole or removing the soft tissue from their feet and gills ([Burnaford 2004](https://www.zotero.org/google-docs/?9rQKeQ), *personal observation*[)](https://www.zotero.org/google-docs/?a0CBTa). In many reef fish, morphological adaptations of teeth are closely linked to their feeding habits (Santic et al. 2007). Fish primarily capture prey through pecking or biting (Corn et al. 2022). Their robust molar teeth are specifically adapted for crushing the hard exoskeletons and hard shell of decapods and mollusks (Deng et al. 2022). It is possible that the chiton-rich diet of *N. tetricus* and *D. vulgaris* is a specialization associated with the large number of molars in their jaws (Pallaoro 2006). However, the diversity of chiton species in diet of the Blue-throated wrasse, *N. tetricus*, may also be related to a methodological bias, as the researchers turned over the boulders, thereby exposing the cryptic species to predation (Shepherd and Clackson, 2001). Crabs likely use strategies similar to those employed with limpets to handle chitons, using their claws to grasp, crush, leverage, and pull their prey [(Silva et al. 2008)](https://www.zotero.org/google-docs/?PooCNL). Non-chelate crustaceans like spiny lobsters probably uses its mandibles in the place of a claw to crash chitons shell (Randall 1964; Lau, 1987). This probably occurs at the late juvenile-adult stage of lobsters, when they have a carapace length of between 45–80 mm. At this stage, the jaws are more calcified, with more defined molar and incisor processes, being able to easily crush the resistant chitinous exoskeletons of large mollusks (Cox et al. 2008).

Among mollusks, many predatory snails use their radula to rasp and drill holes through the shells of their prey, effectively killing them [(Mondal et al. 2021)](https://www.zotero.org/google-docs/?YllfoW). The most notable drilling gastropod belong to the families Naticidae, Muricidae, Thaididae, and Nassariidae (Reyment 1967). Variations in the shape of the hole allow the identification of the predator at the family level (Carriker and Yochelson 1968). For example, naticid snails drill distinctively tapered-parabolic hole, whereas muricid snails produce holes with nearly straight sides; Carriker 1981). Notably, chitons plates with boreholes have been documented in the Late Pleistocene fossil record ([Rojas et al. 2014)](https://www.zotero.org/google-docs/?i05d7c). Octopuses can also drill the shells of their preys. As an muscular long-armed mollusks, they can employ several foraging strategies and multimodal sensing techniques adapted to different natural prey context, combining tactics similar to those used by both crabs and snails [(Mather 1991; Leite et al. 2009a; Buresch et al. 2022)](https://www.zotero.org/google-docs/?9hU5lH). These abilities make them a truly remarkable predator. For example, they may initially try to forcibly detach the chiton from the substrate by pulling it, like crabs do. If this method fails, they may drill a hole in the shell and inject a secretory substance to make the chiton release its hold on the substrate, similar to how snails do [(Nixon et al. 1980; Mondal et al. 2021)](https://www.zotero.org/google-docs/?5Uvaka). However, chitons do not necessarily need to be drilled to be ingested [(Cortez et al. 1998)](https://www.zotero.org/google-docs/?RFu1YO). According to [Mather and Nixon (1990)](https://www.zotero.org/google-docs/?CPhz6E), when referring to juvenile *O. insularis* (identified as *O. vulgaris*) from Bermuda´s shallow waters*,* “sometimes the octopus consumed the internal organs of the chiton and discarded the valves held together by the girdle”, which is similar to our findings with juvenile *O. insularis*.

Many marine intertidal organisms, such as chitons, brittle stars, and worms, are habitat specialist species that exhibit phototropic cryptic behavior (Sumner-Rooney et al. 2021). They hide under boulders and within crevices during the daytime to avoid solar radiation, high temperatures, and dissection (Denny 2007). This strategy of seeking refuge beneath boulder is considered particularly effective against visually guided predators [(Grayson and Chapman 2004)](https://www.zotero.org/google-docs/?yqygKS). However, intertidal boulders are often naturally overturned by waves, storms, and hurricanes [(McGuinness 1987b; Etienne et al. 2011; Li et al. 2023)](https://www.zotero.org/google-docs/?GoFb8x), or even by animals [(Randall 1967; Webb and Whiting 2006; Liversage and Benkendorff 2017)](https://www.zotero.org/google-docs/?BhhaHQ). Consequently, the risk of predation likely exerts strong selection pressure on chitons to avoid smaller boulders that are more easily overturned (Schmitt 1982). Our field observation of octopus predation on a chiton during low tide challenges the assumption that hiding beneath boulders offers reliable protection from visual predators. In this instance, the octopus preyed on the chiton without the need to overturn the boulder. Although shallow-water octopuses possess an excellent visual system, they are also highly adapted to hunting cryptic prey

(Buresch et al. 2024). When visual cues are unavailable, octopuses utilize chemo- and mechanoreceptors in their arms to "blindly" search for prey hidden in rock holes, crevices, or beneath boulders, bypassing the need to turn them over (Buresch et al. 2024). This behavior is particularly evident in *Octopus insularis*, a species that hunts during narrow daylight windows (O’Brien et al. 2023). It prioritizes fast, easily captured small prey over larger, more challenging prey (Leite et al. 2009b, 2016). Our observation suggests that boulder-dwelling chitons are vulnerable to predation not only at night, when they are apparently active on the lateral side of boulders (Liversage and Benkendorff 2017), but also during the day. This could help refine estimates of octopus predation rates on chitons in intertidal boulder fields (Sunderland 1988).

# Conclusions

The West Atlantic chiton *I. pectinata* is a cryptic species with limited ecological information. Understanding its ecological relationships is crucial for assessing its impact on individual growth, survival, and reproduction. Additionally, it allows us to recognize their role in structuring communities and ecosystem functions.

Despite their ecological significance, little is known about the natural interactions between chitons and their predators. Most studies exploring these relationships have been conducted in controlled laboratory or experimental conditions, often requiring the manipulation of species and scenarios to facilitate encounters. Much of the current knowledge is derived from indirect methods, such as dietary analyses of predators where chitons were not the primary focus. Consequently, field observations under natural conditions remain invaluable for uncovering the true nature of these predator-prey interactions.

The fact that chitons are preyed upon by a wide range of predators has not hindered their evolutionary success. This ancient group has thrived in seas worldwide for at least 540 million years (Wanninger and Wollesen, 2019). Understanding these interactions with cryptic species is essential for piecing together the larger ecological puzzle (Scheibling et al., 2009). It provides critical insights into the structure, dynamics, and vulnerabilities of tropical ecosystems, guiding conservation and management efforts amid the challenges of climate change and biodiversity loss (Gross, 2023).

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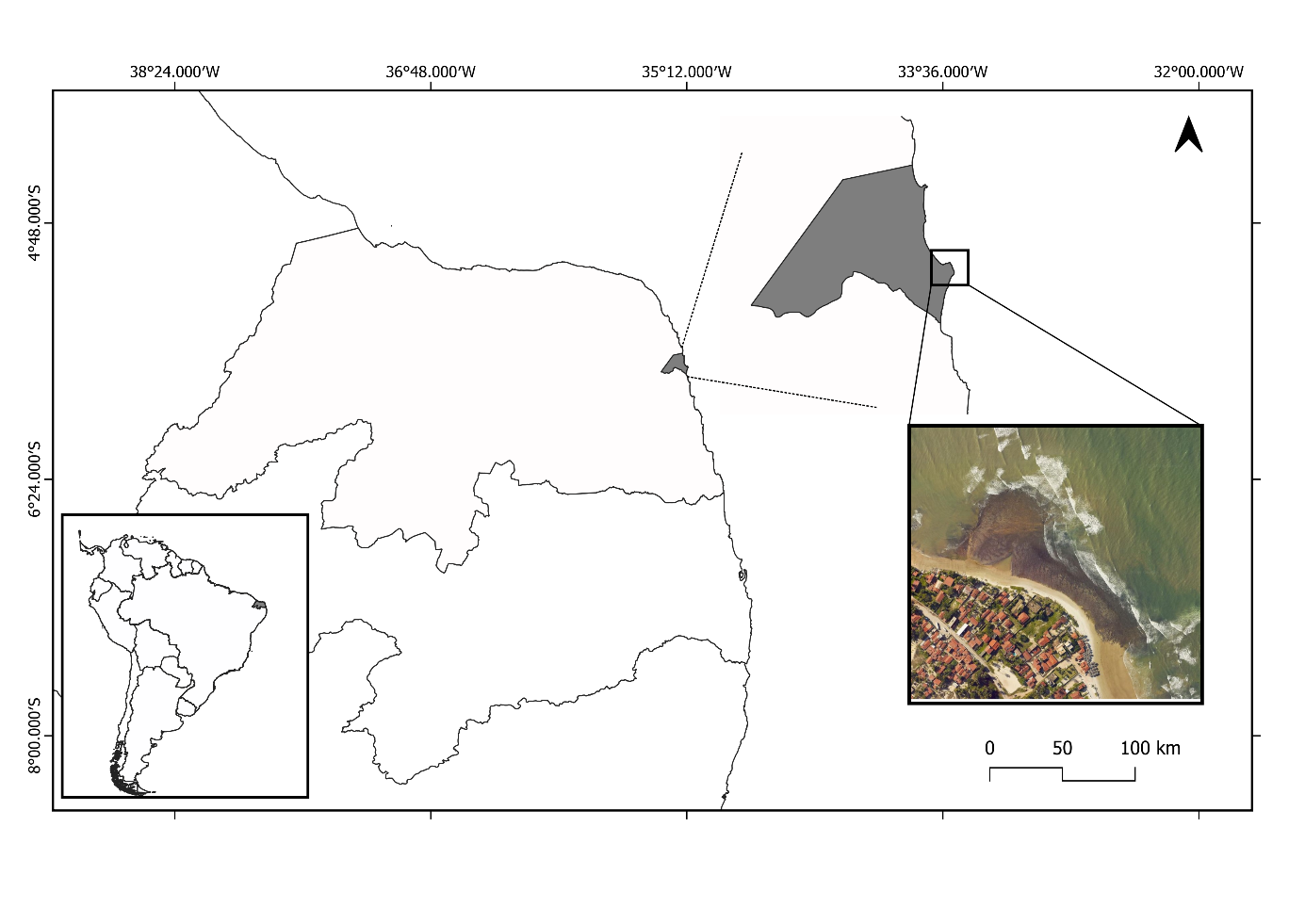
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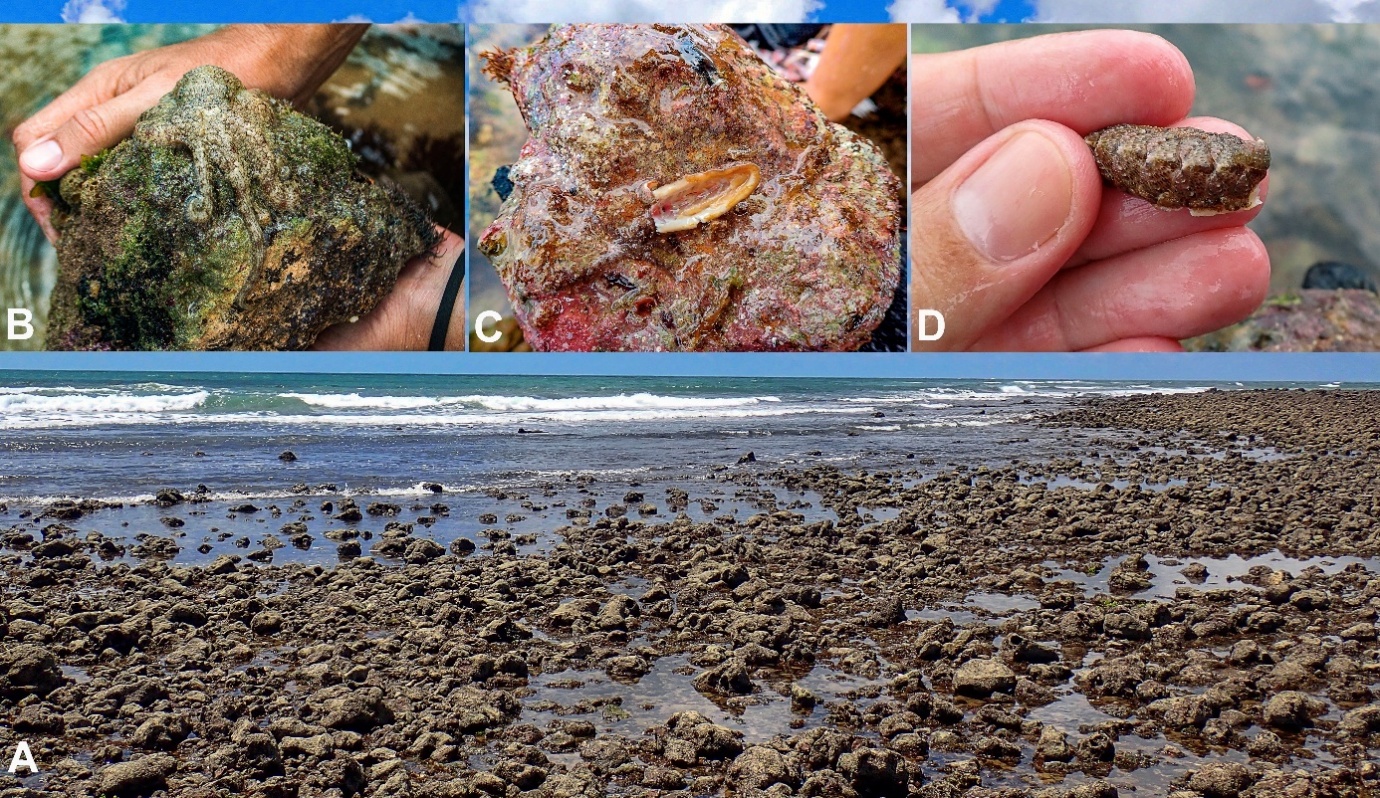
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**Fig. 1.** Intertidal reef in Santa Rita beach (05°41′S, 35°11′W), Rio Grande do Norte, Brazil.



**Fig. 2.** A. Santa Rita reef during low tide, Rio Grande do Norte, Brazil. B. The Brazilian reef octopus (Octopus insularis). C. The remains of the chiton (Ischnoplax pectinata) in ventral view, with traces of gills, foot tissue, and mantles. Dorsal view, showing the disarticulated cephalic valve is discarded the held together by the girdle. Image: R. Guidi

**Table 1:** Studies reporting chiton predators. The scientific names were used according to the currently accepted nomenclature in WoRMS. In table footnote, boulder chitons and their respective studies.

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| **Predators** | **Chitons** | **Method** | **Reference** |
| **Snails** |  |  |  |
| *Amplidrupa clathrata* | No specified | Gut content | Taylor (1983) |
| *Drupa morum* | No specified | Gut content | Taylor (1983) |
| *Lirabuccinum dirum* | *Katharina tunicata* | Manipulative experiment | Louda (1979) |
|  | *Tonicella lineata* | Manipulative experiment | Louda (1979) |
| *Sistrum ricinus* | No specified | Gut content | Taylor (1983) |
| **Octopuses** |  |  |  |
| *Octopus sp.* | *Achantopleura granulata¥* | no specified | Wodinsky (1969) |
|  | *Stenoplax conspicua¥* | no specified | Wodinsky (1969) |
| *O. bimaculatus* | *S. conspicua¥* | Manipulative experiment/ Prey remains | Pilson & Taylor (1961); Ambrose (1984) |
|  | *Callistochiton* sp. | Prey remains | Ambrose (1984) |
| *O. bimaculoides* | *S. conspicua¥* | Manipulative experiment | Pilson & Taylor (1961) |
| *O. insularis* | No specified | Stable isotopes | Dantas *et al.* (2020) |
|  | *Chiton tuberculatus¥* | Prey remains | Mather & Nixon (1990) |
| *O. mimus* | *Chiton granosus* | Manipulative experiment | Cortez *et al.* (1998) |
|  | *Enoplochiton echinatus* | Manipulative experiment | Cortez *et al.* (1998) |
| **Worms** |  |  |  |
| *Hermodice carunculata* | *Rhyssoplax olivácea* | Manipulative experiment | Simonini *et al.* (2018) |
| **Crabs** |  |  |  |
| *Carcinus maenas* | *Lepidochitona cinerea¥* | Manipulative experiment/ Stomach content | Silva *et al.* (2010a); Mendonça *et al.* (2016) |
| *Cancer pagurus* | *L. cinerea¥* | Stomach content | Silva *et al.* (2010a) |
| *Eriphia verrucosa* | *L. cinerea¥* | Stomach content | Silva *et al.* (2010b) |
| *Hemigrapsus nudus* | *Cyanoplax hartwegii* | Manipulative experiment | DeBevoise (1975) |
| *Maja squinado* | *Acanthochitona crinita* | Gut content | Bernárdez *et al.* (2000) |
| *Necora puber* | *L. cinerea¥* | Stomach content | Silva *et al.* (2010a) |
| *Pachygrapsus crassipes* | *C. hartwegii* | Manipulative experiment | DeBevoise (1975) |
| *P. marmoratus* | *L. cinerea¥* | Stomach content | Silva *et al.* (2009) |
| **Lobsters** |  |  |  |
| *Panulirus argus* | *Acanthochitona* spp. | Gut content | Cox *et al.* (1997) |
| **Starfishes** |  |  |  |
| *Anasterias antarctica* | *Plaxiphora aurata* | Direct observation | Laptikhovsky *et al.* (2015) |
|  | *Tonicia* spp. | Direct observation | Laptikhovsky *et al.* (2015) |
| *Astrostole scabra* | *Chiton glaucus* | Manipulative experiment | Town (1980) |
|  | *Ischnochiton maorianus* | Manipulative experiment | Town (1980) |
|  | *Onithochiton neglectus* | Manipulative experiment | Town (1980) |
| *Dermasterias imbricata* | *T. lineata* | Stomach content | Mauzey *et al.* (1968) |
| *Leptasterias pusilla* | *C. hartwegii* | Manipulative experiment | DeBevoise (1975) |
| *Meyenaster gelatinosus* | *Chiton* spp. | Direct observation | Ortiz *et al.* (2003) |
| *Orthasterias koehleri* | No specified | Stomach content | Mauzey *et al.* (1968) |
| *Patiria miniata* | *C. hartwegii* | Manipulative experiment | DeBevoise (1975) |
| *Pisaster ochraceus* | *C. hartwegii* | Manipulative experiment | DeBevoise (1975) |
|  | *K. tunicata* | Stomach content | Mauzey (1966) |
|  | *T. lineata* | Stomach content | Mauzey (1966) |
|  | *Mopalia sp.* | Stomach content | Mauzey (1966) |
| *Stylasterias forreri* | *T. lineata* | Stomach content | Mauzey *et al.* (1968) |
| **Fishes** | *Stenoplax* spp. | Gut content | Cox *et al.* (1997) |
| *Abudefduf taurus* | No specified | Stomach content | Randall (1967) |
| *Anisotremus virginicus* | No specified | Stomach content | Randall (1967) |
| *Balistes vetula* | No specified | Stomach content | Randall (1967);  Reinthal *et al.* (1984) |
| *Bodianus rufus* | *Calloplax janeirensis* | Stomach content | Randall (1967) |
| *Calamus calamus* | No specified | Stomach content | Randall (1967) |
| *Coris gaimard* | No specified | Gut content | Shibuno *et al.* (1994) |
| *Diplodus caudimacula* | No specified | Stomach content | Randall (1967) |
| *D. vulgaris* | *Acanthochitona fascicularis* | Gut content | Pallaoro *et al.* (2006) |
|  | *Callochiton laevis* | Gut content | Pallaoro *et al.* (2006) |
|  | *Rhyssoplax corallina* | Gut content | Pallaoro *et al.* (2006) |
|  | *Rhyssoplax olivácea* | Gut content | Pallaoro *et al.* (2006) |
|  | *Ischnochiton rissoi* | Gut content | Pallaoro *et al.* (2006) |
|  | *Lepidopleurus cajetanus* | Gut content | Pallaoro *et al.* (2006) |
| *Epinephelus adscensionis* | *Acanthochitona hemphilli* | Stomach content | Randall (1967) |
| *Haemulon album* | No specified | Stomach content | Randall (1967) |
| *H. carbonarium* | *Ischnochiton papillosus* | Stomach content | Randall (1967) |
| *H. flavolineatum* | *Acanthochitona pygmaea* | Stomach content | Randall (1967) |
| *H. plumierii* | *Ischnochiton papillosus* | Stomach content | Randall (1967) |
| *Halichoeres bivittatus* | *A. pygmaea* | Stomach content | Randall (1967) |
|  | *Ischnochiton sp.* | Stomach content | Randall (1967) |
| *H. garnoti* | No specified | Stomach content | Randall (1967) |
| *H. maculipinna* | No specified | Stomach content | Randall (1967) |
| *H. poeyi* | *I. papillosus* | Stomach content | Randall (1967) |
| *H. radiatus* | *I. papillosus* | Stomach content | Randall (1967) |
| *Holocentrus rufus* | *A. pygmaea* | Stomach content | Randall (1967) |
| *Gobioclinus guppyi* | No specified | Stomach content | Randall (1967) |
| *Lactophrys trigonus* | *Acanthochitona sp.* | Stomach content | Randall (1967) |
| *L. triqueter* | No specified | Stomach content | Randall (1967) |
| *Lipophrys pholis* | *L. cinearea¥* | Gut content | Mazé *et al.* (1999) |
|  | Acanthochitona crinita | Gut content | Mazé *et al.* (1999) |
| *Malacanthus plumieri* | *Choneplax lata* | Stomach content | Randall (1967) |
| *Mulloidichthys martinicus* | *A. pygmaea* | Stomach content | Randall (1967) |
| *Neoniphon vexillarium* | *C. lata* | Stomach content | Randall (1967) |
| *Notolabrus tetricus* | *Rhyssoplax diaphora¥* | Stomach content | Shepherd & Clarkson (2001) |
|  | *Cryptoplax striata¥* | Stomach content | Shepherd & Clarkson (2001) |
|  | *Ischnochiton australis¥* | Stomach content | Shepherd & Clarkson (2001) |
|  | *Ischnochiton cariosus¥* | Stomach content | Shepherd & Clarkson (2001) |
|  | *Ischnochiton elongatus¥* | Stomach content | Shepherd & Clarkson (2001) |
|  | *Ischnochiton lineolatus¥* | Stomach content | Shepherd & Clarkson (2001) |
|  | *Notoplax speciosa¥* | Stomach content | Shepherd & Clarkson (2001) |
| *Salaria pavo* | *R. olivácea* | Stomach content | Santic *et al.* (2007) |
|  | *R. corallina* | Stomach content | Santic *et al.* (2007) |
| *Sphoeroides spengleri* | No specified | Stomach content | Randall (1967) |
| *Thalassoma lutescens* | No specified | Gut content | Gushima *et al.* (1991) |
| **Birds** |  |  |  |
| *Haematopus bachmani* | *K. tunicata* | Prey remains | Bergman *et al.* (2013) |
|  | *Mopalia muscosa* | Prey remains | Bergman *et al.* (2013) |
| *Histrionicus histrionicus* | *Mopalia* spp. | Esophagi/Gizzard content; Fecal sample | Gaines & Fitzner (1987); Rodway & Cooke (2000) |
|  | *T. lineata* | Fecal sample | Rodway & Cooke (2002) |
| *Larus dominicanus* | No specified | Regurgitation pellets | Petracci *et al.* (2004) |
| *L. glaucescens* | *K.tunicata* | Regurgitation pellets/ Manipulative experiment | Irons *et al.* (1986) |
|  | *Mopali*a sp. | Regurgitation pellets/ Manipulative experiment | Irons *et al.* (1986) |
| *L. occidentalis* | *K. tunicata* | Regurgitation pellets | Moore (1975) |
|  | *M. muscosa* | Regurgitation pellets | Moore (1975) |
|  | *Nuttallina californica* | Regurgitation pellets | Moore (1975) |
| *Somateria mollissima* | *Tonicella marmórea* | Stomach content | Kristjansson *et al.* (2013) |
|  | *Boreochiton ruber* | Stomach content | Kristjansson *et al.* (2013) |
|  | *Stenosemus albus* | Stomach content | Kristjansson *et al.* (2013) |
|  |  |  |  |
| *¥*Boulder chitons: *A. granulata* (Glynn, 1970), *C. diaphorus* (Kangas & Shepherd, 1984; Liversage & Benkendorff, 2013), *C. tuberculatus* (Glynn, 1970), *I. australis* (Kangas & Shepherd, 1984; Smith & Otway, 1997; Chapman, 2002, 2005; Grayson & Chapman, 2004; Liversage *et al*., 2012; Palmer, 2012; Liversage & Benkendorff, 2013), *I. cariosus* (Kangas & Shepherd, 1984; Chapman, 2002; Liversage & Benkendorff, 2013), *I. elongatus* (Smith & Otway, 1997; Chapman 2002, 2005; Grayson & Chapman, 2004; Liversage & Benkendorff, 2013), *I. lineolatus* (Kangas & Shepherd, 1984; Liversage & Benkendorff, 2013), *L. cinerea* (Evans, 1951; Mendonça *et al*., 2016), *N. speciosa* (Kangas & Shepherd, 1984), and *S. conspicua* (Schmitt, 1982). | | | |
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