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SHORT REVIEW

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What do we know about *Cassis tuberosa* (Mollusca: Cassidae), a heavily exploited marine gastropod?

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ABSTRACT

Cassis tuberosa is a key species in reefs and sandy beaches, where it plays an essential role as a predator of sea urchins and sand dollars. Due to the beauty of its shell, it is one of the most exploited species for trade as marine souvenirs throughout its distribution in the Western Atlantic. Despite its ecological importance, there is little available information about population and biological data or the impacts of its removal from its natural habitats. Considering the economic and ecological importance of this species, this study provides a short review of existing studies and highlights research and conservation needs for this highly exploited marine gastropod.

Keywords: Brazil; Predatory Gastropod; Marine Curio Trade; Species Conservation; Shell Trade

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INTRODUCTION

The king helmet *Cassis tuberosa* (Linnaeus 1758) (Figure 1) is a large marine gastropod mollusk belonging to the family Cassidae and is distributed from North Carolina to Brazil (Rios 2009), including the Gulf of Mexico, Caribbean and Cape Verde Islands, Western Africa (Tewfik and Scheuer 2013). In Brazil, it is found from Pará to Espírito Santo states (Rios 2009). The species has a heavy and large shell, reaching up to 30 cm in total length (Ardila et al. 2002), and occurs from 1 to 10 m deep (Rios 2009). Due to the beauty of its shell in all growth stages (Figure 1), *C. tuberosa* has been the target of fishing for decades for ornamental purposes and to supply trade in souvenirs and marine curiosities (Dias et al. 2011).

Although it is a large species, is broadly distributed along the eastern Atlantic coast

and is economically relevant, *Cassis tuberosa* biology and ecology is poorly known. Little is known about its representativeness in the ornamental shell trade, and this is one of the probable reasons for the population decline that has been reported for this species in Brazil and the Caribbean (Dias et al. 2011; Tewfik 2015).

This short review presents the main information available in the literature published in scientific journals, books and book chapters that address this species. The literature used was searched in Google Scholar and on journal websites. Some full papers published in the Proceedings of Scientific Events were also included.

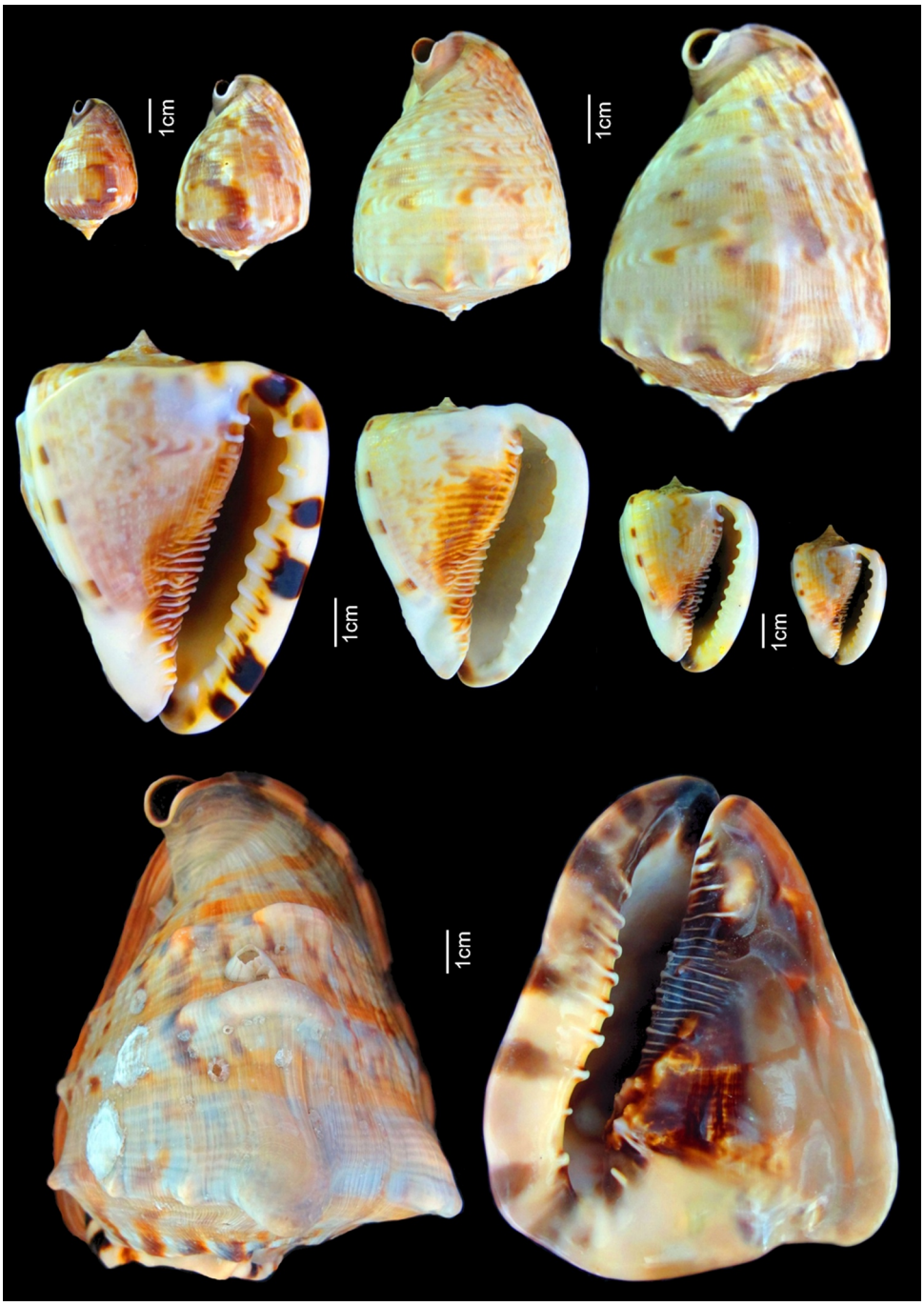

Figure 1. *Cassis tuberosa* growth series illustrating shell characteristics from the young phase to the adult phase (Photos: Thelma Dias).

Shell morphology, habitat and ecology

Cassis tuberosa has one of the most admired shells by collectors in the Western Atlantic (Figure 2a–b). As described by Matthews and Coelho (1972), the form of the shell is subtriangular, with a low spire and it is cream in general coloration with dark brown spots. The dorsal surface is ornamented by fine growth lines cut by fine spiral lines, producing a canceled effect. The opening is narrow and long, with an outer lip containing strong dark teeth. The margin of the columella has strong crimps that extend through the opening. The small corneal operculum is elongated, with rounded ends and is light brown in color (Figure 2c).

In the soft part, the ample ventral muscular foot constitutes a great part of the visceral mass (Figure 2d). Although the siphonal canal is short, the siphon of large caliber can extend to reach the dorsal side of the shell, as reported by Hughes and Hughes (1971). According to these authors, the taenioglossate radula of *Cassis tuberosa* is reinforced with seven strong teeth per row, with a central spinal tooth and heavily spit lateral teeth. Details of the morphology of the digestive tract are shown by Hughes and Hughes (1981).

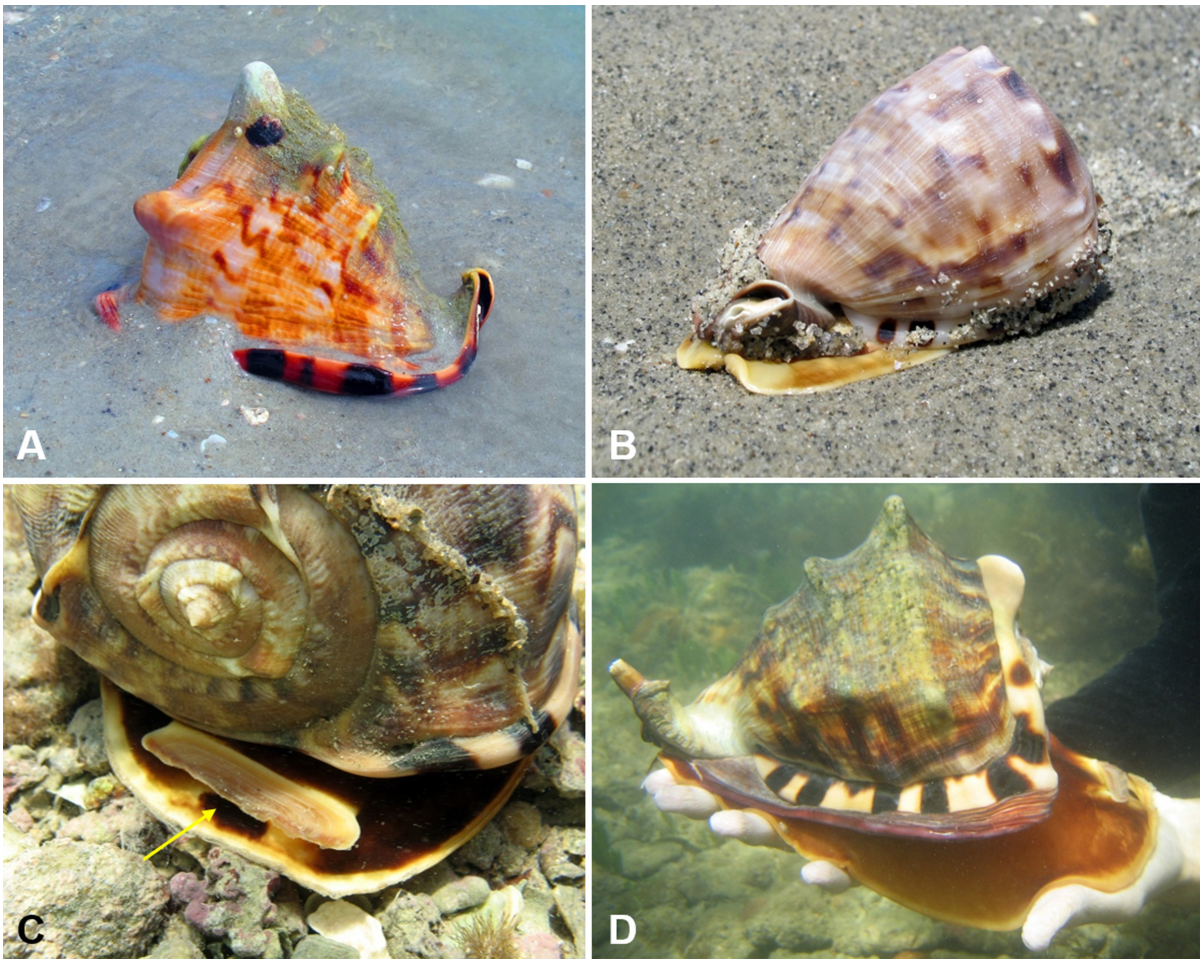

Figure 2. (A) Adult individual emerges on a sandy beach during low tide and (B) Young moving on sandy bottom at Macau, state of Rio Grande do Norte, NE Brazil. (C) View of the back of *Cassis tuberosa* with detail on the reduced operculum (yellow arrow) and (D) Adult with wide distended foot at Cabo Branco reefs, João Pessoa, state of Paraíba, NE Brazil (Photos: Thelma Dias).

Cassis tuberosa is considered a solitary species (Moore 1956) but may be observed in larger numbers, such as while searching for prey (Matthews and Coelho 1972; Tewfik 2015). It inhabits shallow coastal waters occurring in sandy beaches and reef environments, where it lives associated with seagrass beds, macroalgae banks, rhodolith beds and coral rubble (Schroeder 1962; Nieto-Bernal et al. 2013; Tewfik and Scheuer 2013; Tewfik 2015; Dias and Mota 2015; Grun and Nebelsick 2017). Figure 3a–e illustrates *C. tuberosa* using different habitat types.

The king helmet is known as a nocturnal predator that remains buried in unconsolidated substrates during the day. According to Grun and Nebelsick (2017), *Cassis tuberosa* is mainly semi-epifaunal and rests semi-buried, leaving an exposed portion of the shell, which is encrusted by macroalgae, other smaller gastropod molluscs and crustaceans. On the other hand, some studies report the feeding activity of *C. tuberosa* in the diurnal period (e.g. McClintock and Marion 1993; Levitan and Genovese 1989), which, according to Grun and Nebelsick (2017), would classify this species as metaturnal, feeding during the day and at night.

Several decades ago, the king helmet was once considered one of the most abundant gastropod species in Northeastern Brazil (Matthews and Coelho 1972) and common in the West Indies (Schroeder 1962). Currently, the few studies that mention the abundance of this species have revealed a low number of individuals. In the Turks and Caicos Islands, the density of *Cassis tuberosa* associated with dense seagrass beds (*Thalassia testudinum*) ranged from 2.6 to 15.8 individuals/ha (Tewfik and Scheuer 2013; Tewfik 2015), while in La Guajira (Colombia), Nieto-Bernal et al. (2013) recorded a density ranging from 0.3 to 0.8 individuals/ha. A low density of this predator was also reported by Engstrom (1982), who mentioned one individual/660 m^2 (=15 individuals/ha) in Pitahaya and one individual/14,000 m^2 (=0.7 individuals/ha) in Guayacan, both in Puerto Rico. Other studies that mention the abundance of *C. tuberosa* report a low number of individuals (e.g. Hughes and Hughes 1971; McClintock and Marion 1993; Levitan and Genovese 1989; Grun and Nebelsick 2017).

Young individuals of *Cassis tuberosa* are rarely reported in the literature (e.g. Pequeno and Matthews-Cascon 2001; 2011). On the other hand, recently Dias and Mota (2015) first recorded an adult of this species depositing their spawn in the Tamandaré reefs (State of Pernambuco), located in a marine protected area in the northeast of Brazil. The spawn was released on a border of macroalga of the genus *Padina* at 2 m depth during the day. According to Dias and Mota (2015), the oothecae was arranged in a single layer consisting of a mass of eggs with approximately 200 vasiform capsules that were orange in color (Figure 3f). According to these authors, the spawn of *C. tuberosa* resembles that of other Cassidae, especially that of its congener, *C. madagascariensis*. Dias and Mota (2015) also reinforced the importance of macroalgae banks as a spawning substrate and suggest that measures of protection of this species should include this type of habitat to maintain wild populations of *C. tuberosa*.

Diet and predatory behavior

One of the best-known aspects about *Cassis tuberosa* is its diet and feeding behavior. It is a carnivorous predator that feeds exclusively on echinoid echinoderms

(Figure 4). There are at least 14 species of prey consumed by *C. tuberosa* in the laboratory and in the wild (e.g. Foster 1947; Moore 1956; Snyder and Snyder 1970; Pequeno and Matthews-Cascon 2010; Tewfik and Scheuer 2013), but the most frequently cited are the sea urchins *Diadema antillarum, Echinometra lucunter, Lytechinus*

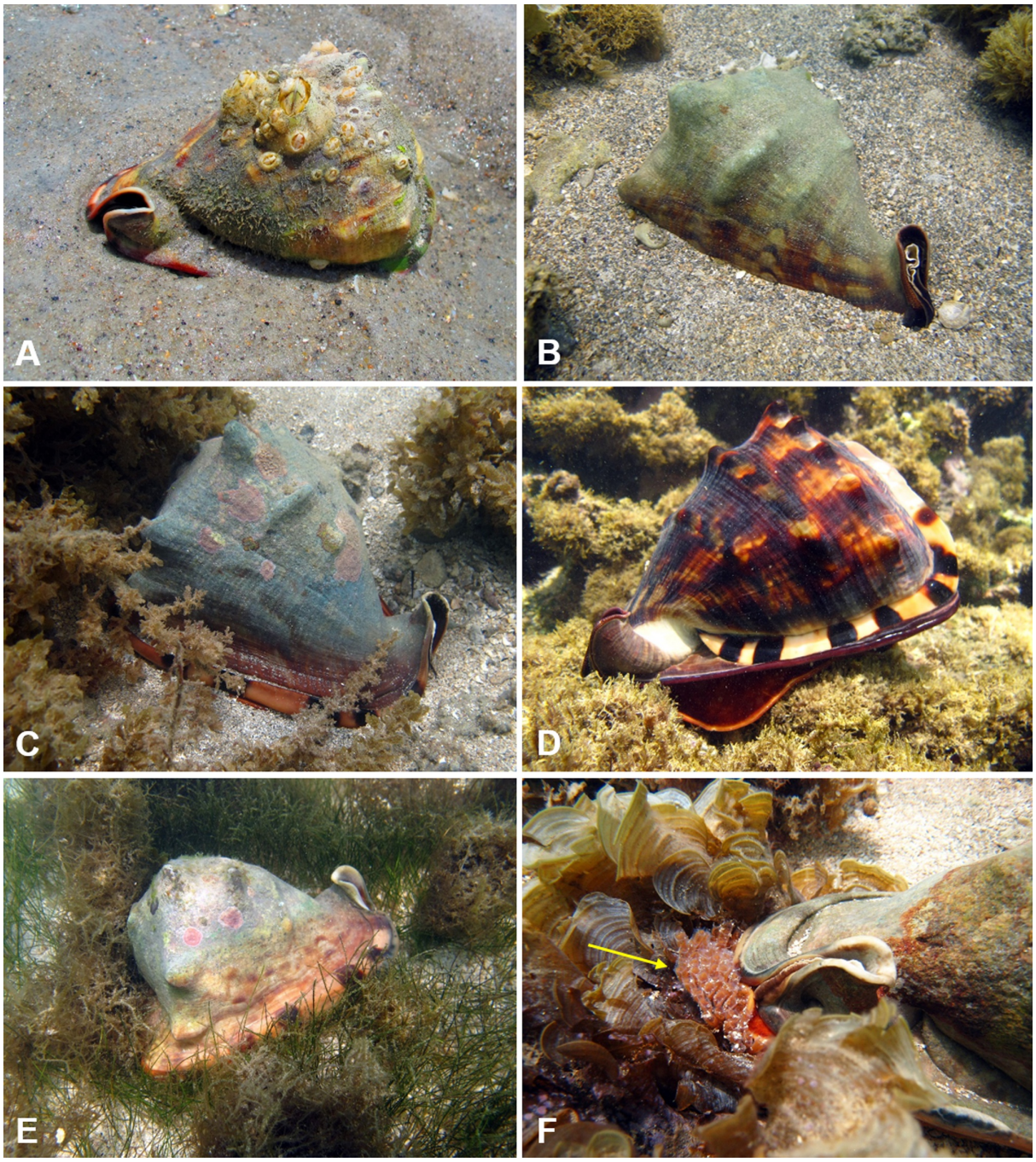

Figure 3. Adult *Cassis tuberosa* on different substrates and behaviors. (A) Resting on sandy beach at Macau, state of Rio Grande do Norte, Brazil. (B) Partially buried in sandy bottom, (C) Resting on sandy and gravel bottom near macroalgae, (D) Moving on rocks in a reef environment, (E) Moving on seagrasses in a reef environment, and (F) Spawning (yellow arrow) on macroalgae of the genus *Padina* at Tamandaré reefs, state of Pernambuco, Brazil (Photos: Thelma Dias).

variegatus and *Tripneustes ventricosus* (Schroeder 1962; Hughes and Hughes 1971, 1981; Gladfelter 1978; Levitan and Genovese 1989; Gerace and Lindsay 1992), and the sand dollars *Mellita quinquiesperforata* (Work 1969; Pequeno and Matthews-Cascon 2001) and *Leodia sexiesperforata* (McClintock and Marion 1993; Grun 2017).

To find and subdue its prey, *Cassis tuberosa* performs an elaborate hunting behavior. According to Hughes and Hughes (1971, 1981), when the hunt begins, the animal extends the siphon and tentacles forward while moving at a speed of 0.3 cm/s. Once the prey is detected, *C. tuberosa* raises the front portion of the foot and quickly expands it over the animal, holding it firmly. The proboscis is then extended and the small head rests on the foot (Hughes and Hughes 1971). When the echinoid prey is a sea urchin, after subjugating it, the predator uses the anterior portion of the muscular foot to break the spines of a small test area where it drills a small hole (about 0.5 cm in diameter) to access soft tissues of prey (Hughes and Hughes 1971, 1981). Figure 4 illustrates different stages of the

Figure 4. Predatory behavior of *Cassis tuberosa*. (A) Adult searching for prey with tentacles extended forward (yellow arrow) and (B) Adult preying on sea urchin *Echinometra lucunter* in reef environment at Cabo Branco beach, João Pessoa, state of Paraíba, Brazil. (C) Adult preying on sea urchin *Lytechinus variegatus* in a patch reef at Praia Formosa, Cabedelo, state of Paraíba, Brazil. (D) Young preying on the sand dollar *Mellita quinquiesperforata* on sandy beach at Macau, state of Rio Grande do Norte, Brazil (Photos: Thelma Dias).

predatory behavior of *C. tuberosa* in natural habitat.

The toxic properties of the saliva of *Cassis tuberosa* probably act during the immobilization of the prey and the drilling of the test. According to Cornman (1963), the toxic oral secretion of *C. tuberosa* can incapacitate the organs of the surface of the long-spined sea urchin *Diadema antillarum*, decreasing its mobility and the effectiveness of its spines and ambulacral feet. The active component of saliva appears to be a neurotoxin that blocks the response to light and touch. Cornman (1963) suggests that this effect would apply to other prey species and other species of Cassidae, such as *C. flammea* and *C. madagascariensis*, which probably have comparable toxicity.

Predation by *Cassis tuberosa* leaves a characteristic bore hole from testing echinoid prey. This typical hole has been recorded for other Cassidae from the Upper Cretaceous and the Tertiary (Ceranka and Złotnik 2003; Grun 2017), being a characteristic of the family. The time of ingestion varies depending on the type and size of the prey. Under laboratory conditions, Hughes and Hughes (1971) recorded a time of consumption of a sea urchin between 1 and 3 hours. Hughes and Hughes (1981) reinforce that the predator consumes all the prey's inner tissue, except the stomach contents and the tissue around the Aristotle's lantern.

Uses and trade

Specimens of the gastropod *Cassis tuberosa* (hole animal or empty shells) are used in traditional medicine, as marine curiosities and ornamental shells, as handicrafts, tools and in magic-religious rituals (Gasparini et al. 2005; Alves and Dias 2010; Dias et al. 2010, 2011; Léo-Neto et al. 2012; Alves et al. 2017). In Northeastern Brazil, the medical use is focused on the treatment of asthma (Alves and Dias 2010).

The king helmet also plays an important cultural role directly connected to local communities and their cultural and religious traditions. Shells of this species are among the main ornaments used to decorate orixás altars in the afro-Brazilian religion named Candomblé, which considers the shell of *Cassis tuberosa* an item of great value and esteem, as a wealth of the seas with which it presents itself to the orixás. In addition, the shells are used to decorate tables on which realized rituals, called 'games of shells,' are conducted (Léo-Neto et al. 2012).

Regarding its use as a food source, Ardila et al. (2002) highlight the consumption of *Cassis tuberosa* by local fishermen from Colombia. Moreover, the use of this species as a tool has historical records. Ancient populations used whole shells as a musical instrument and for communication. Pieces of the shells were also used as spoons (McKenzie and Stehlik 2001). According to Abbott (1968), for many centuries in the Caribbean region, shells of *C. tuberosa* were used as the raw material for cameos.

Among the several uses involving *Cassis tuberosa*, trade in ornamental shells (live and mainly empty shells) is the most documented activity, although these records are still scarce considering the important role of this species in the trade of marine curiosities. In Brazil, Gasparini et al. (2005) cite *C. tuberosa* as one of the main species of marine invertebrates exploited for the trade of souvenirs, and they are captured mainly through bottom trawls. In the northeast of Brazil, according to Dias et al. (2011), large *C. tuberosa* shells are the main targets for use in the manufacture of table lamps and for sale of individual shells in outdoor markets. In addition, some littoral

states are used in crafts (Figure 5). The ornamental and handicraft trade using *C. tuberosa* is also mentioned throughout its distribution in the Caribbean and Florida (Leal 2002; Nieto-Bernal et al. 2013; Tewfik and Scheuer 2013).

Ecological role

The king helmet, *Cassis tuberosa*, is part of a specialized group of large meso-predatory gastropods that inhabit the shallow waters of the Gulf of Mexico and the

Figure 5. (A) Live specimens of *Cassis tuberosa* caught by fishermen on the coastal reef of Cabo Branco beach, João Pessoa, state of Paraíba, Brazil. (B) Table lamp made with two shells of *C. tuberosa.* (C) Shells of *C. tuberosa* for sale in a beach tent in Coqueirinho beach, Conde, State of Paraíba, Brazil (Photos: Thelma Dias).

Caribbean (Tewfik 2015), and in the other areas where it is distributed in the Atlantic Ocean. Because it is a target species for several purposes, knowing its ecological function is essential for assessing the impacts of its removal from the environment.

As a meso-predator, *Cassis tuberosa* causes high predation pressure on populations of sea urchins and sand dollars in some areas of the Caribbean, significantly influencing the mortality of these populations (Engstrom 1982; Gladfelter 1978; McClintock and Marion 1993). In addition, it is a food resource for top predators in the marine food chain (Tewfik 2015). According to Tewfik (2015), their ecological function includes the control of large populations of herbivorous (e.g. sea urchins) that can cause significant damage to the ecosystem, such as reef bioerosion. Grun and Nebelsick (2017) also demonstrated that the shell of *C. tuberosa* can act as a substrate for the recruitment of organisms, such as coralline algae, green algae and small invertebrates, such as the crab *Mithraculus sculptus*, and limpets.

Conservation concerns and future studies

The conservation status of *Cassis tuberosa* is not known throughout its distribution. Only in Colombia the species is included in the Red Book of Endangered Invertebrates as 'Vulnerable' (Ardila et al. 2002). In 2014, ICMBio (2014) evaluated the species as 'Near Threatened' with extinction in Brazil. According to the MMA (2014), by being classified into this category, the species does not qualify to be in threat categories (e.g. vulnerable, threatened) but approximates the quantitative thresholds of the criteria and is likely to fit in a threat category in the near future.

Websites selling shells in various countries around the world (e.g. Brazil, Italy, Canada, USA, Belgium) market this species using individuals exclusively captured in the wild, since it is not cultivated. Specimens are imported and exported without regulation and the biological and ecological impacts of this activity remain unknown.

According to the MMA (2014), in Brazil, *Cassis tuberosa*, as well as other species evaluated as 'Near Threatened', is considered a priority species for research on conservation status. In this sense, studies that provide data about its biology, ecology and its ecological role in the habitats where it occurs are of special relevance, in addition to the documentation and quantification of the trade involving this species and other meso-predatory gastropods.

Although the feeding behavior and diet of *Cassis tuberosa* are well documented, their food preference remains little studied. In areas where there is a varied availability of prey, the possible factors that would lead to the choice of a particular prey are not known. This information is very important considering the susceptibility of prey consumed by *C. tuberosa* to processes such as acidification of ocean water, imbalance of macroalgal communities, which are the crucial food of sea urchins, and erosion and decharacterization of sandy beaches, which are among the essential habitats of the sand dollars. Although shell size structure data are important for interpreting the size and possibly age of individuals (Tewfik and Scheuer 2013), exact information on growth, size at first sexual maturation and essential habitat of recruits, young and adults, are non-existent.

In the Colombian Caribbean, *Cassis tuberosa* is caught by fishermen manually by snorkeling or SCUBA diving, and catch by fishing boats is common, although this activity has not been quantified (Ardila et al. 2002). From the ethnobiological point of

view, aspects inherent to the local ecological knowledge of human populations that have some kind of relationship with *C. tuberosa* remain scarce and restricted to certain areas of their occurrence. Table 1 indicates the main published studies on *C. tuberosa* so far.

CONCLUSIONS

This short review has highlighted the ecological and economic importance of the large heavily exploited marine gastropod, *Cassis tuberosa*, throughout its distribution, which is restricted to a portion of the western

Table 1. Main published studies on the gastropod *Cassis tuberosa*.

Study type	Locality	References
Field observation of feeding on an echinoid	South Bimini, Bahamas	Foster (1947)
Observations of predation on echinoids	Florida Keys, USA	Moore (1956)
Analysis of toxic properties of the saliva on echinoids	Bimini, Bahamas	Cornman (1963)
Predatory behavior on sea urchins	Florida, USA	Schroeder (1962)
Experimental observations of predation on sea urchins	Six-Men's Bay, Barbados, Lesser Antilles – collection of specimens	Hughes and Hughes (1971)
General aspects of the Cassidae found in NE Brazil	NE Brazil	Matthews and Coelho (1972)
Morphology and behavior related to feeding in the Cassidae	Barbados, Lesser Antilles – collection of specimens	Hughes and Hughes (1981)
Field and experimental observations of predation on sea urchins and sand dollars	San Salvador, Bahamas	Gerace and Lindsay (1992)
Observations of predation on sand dollars	San Salvador, Bahamas	McClintock and Marion (1993)
Experimental observations of predation by young *C. tuberosa* on sand dollars	Icapuí, Ceará (NE Brazil) – collection of specimens	Pequeno and Matthews-Cascon (2001)
Experimental observations of predation by young *C. tuberosa* on sea urchins	Icapuí, Ceará (NE Brazil) – collection of specimens	Pequeno and Matthews-Cascon (2010)
Density, shell size, predation and habitat in the wild	South Caicos, Turks and Caicos Islands, Caribbean Sea	Tewfik and Scheuer (2013)
Density and food sources of predatory gastropods in the wild	Islands of Central Bahamas	Tewfik (2015)
Spawning in the wild and oothecae description	Tamandaré reefs, NE Brazil	Dias and Mota (2015)
Shell fouling and burrowing behavior	San Salvador, Bahamas	Grun and Nebelsick (2017)
Analysis of the traces of cassid predation on the tests of sand dollars (*Leodia sexiesperforata*)	San Salvador, Bahamas	Grun (2017)

Atlantic Ocean and Cape Verde Islands (eastern Atlantic Ocean). Biological and ecological aspects of the species are poorly known and their role as a fishing resource is virtually unknown. Population density is estimated for restricted areas of its distribution and suggest that wild populations are sparse, especially considering studies conducted in the last decade. Anecdotal information obtained from fishermen and traders suggests a decline in the abundance of *C. tuberosa* in the last two decades, which has been reflected in the international trade in ornamental shells.

Few countries recognize that *Cassis tuberosa* needs more attention regarding its conservation. However, once biological, ecological and shell trade research is carried out, they may contribute to a better assessment of conservation status and the development of management measures directed to species that will go beyond the areas researched. Among the many aspects that lack attention, studies that evaluate the ecological role of *C. tuberosa* in reef habitats and in sandy beaches are essential for understanding the impact of the removal of these meso-predators from wild. In addition, in order to maintain viable populations, it is essential to know their essential habitat in the various ontogenetic phases.

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