

Losing the Shell Game: Consequences of Seascapes without Predatory Gastropods

Perdiendo el Juego de la Cáscara: Consecuencias de Marinos sin Depredadores Gastrópodos

Perdre le Jeu Shell : Conséquences des Paysages Marins sans Gastéropodes Prédateurs

ALEXANDER TEWFIK

Wildlife Conservation Society – Belize, 1755 Coney Drive, Belize City, Belize. atewfik@wcs.org.

ABSTRACT

A number of large, predatory gastropods including Chanks (Turbinellidae), Helmets (Cassidae), and Tritons (Ranellidae) are targeted by fishers supplying the trade in collectible shells, components of decorative souvenirs, and a source of food in some areas. However, the over-harvesting of these predators is considered a contributing factor in population increases of their prey resulting in the alteration of shallow-water ecosystem dynamics and loss in biodiversity. Similar cascading effects have been documented in a number of other marine systems in which over-harvesting of predators (e.g. fish, lobsters, sea otters) have resulted in the release of prey and fundamental shifts in benthic communities. Given our limited understanding of predatory gastropods this overview intends to: (1) highlight the importance of predatory gastropods within complex Caribbean seascapes; (2) demonstrate how assessments of gastropod predators may be integrated into existing benthic resource surveys; and (3) provide new information on the ecology and status of several species of predatory gastropods (*Cassis flammea*, *Cassis tuberosa*, *C. madagascariensis*, *Charonia variegata*, *Turbinella angulata*) inhabiting seagrass habitats in The Bahamas, Belize and the Turks and Caicos Islands.

KEY WORDS: trophic cascade, meso-predator, fisheries, population assessment, ecological function

INTRODUCTION

The removal of predators and subsequent trophic cascades (Figure 1a) have been recognized as causing significant restructuring of marine ecosystems, loss of biodiversity and impacts on associated livelihoods especially where fisheries are concerned (Frank et al. 2005, Salomon et al. 2009, Terborgh and Estes 2010). The cascading effects of predator removals have been documented for changes in both apex and meso-predators (occupy trophic levels below apex predators) and may result in non-linear or unpredictable dynamics throughout complex systems (Figure 1b) with resulting loss in ecological function and formation of alternate states (Pinnegar et al. 2000, Myers et al. 2007, Ritche and Johnson 2009). The overharvesting of gastropod predators has contributed to population increases of echinoderms, including *Acanthaster planci* (Crown-of-thorns seastar), resulting in significant changes in coral reef community structure (Endean 1982, McClanahan and Muthiga 1988). Cascading effects have also been documented in macrophyte-dominated systems (kelp, seagrass) in which overfishing of various echinoid predators (fish, lobsters, Sea Otter) have resulted in the release of prey and shifts in benthic community structure (Steneck 1998, Pinnegar et al. 2000, Eklof et al. 2008).

A specialized group of large, meso-predatory univalve molluscs inhabit shallow-waters of the Caribbean and Gulf of Mexico (Figure 1). The species include some of the largest members of the families Cassidae (Helmets), Fasciolaridae (True tulips), Ranellidae (Tritons), and Turbinellidae (Chanks) which are all sought-after collectable shells in the global marine ornamental trade as well as being components of decorative souvenirs, and harvested for food through largely unregulated fisheries (Abbott 1980, Engstrom 1982, Wood and Wells 1988, Poulsen 1995, Gosling et al. 2004, Dias et al. 2011, Stephenson et al. 2013). The geographic distribution of the six largest species overlaps significantly, with some notable exceptions (Figure 2). Of the three Helmet species *Cassis flammea* has the most limited range, to Southern Florida (Figure 2a), while both *Cassis madagascariensis* (Figures 2b, 3a) and *Cassis tuberosa* (Figures 2c, 3c) exhibit more extensive ranges to North Carolina and Bermuda. The West Indian Chank (*Turbinella angulata*) (Figures 2d, 3b) and Florida Horse conch (*Triplofusus giganteus*), the largest univalve in the region (up to 600 mm shell length) (Paine 1963), have largely separate ranges but do co-occur around the coasts of the Yucatan and Belize (Figures 2d, e). The distribution of the Atlantic Triton's Trumpet (*Charonia variegata*) (Figure 1d) largely coincides with all five other species mentioned (Figure 2f).

We generally have a poor understanding of predatory gastropod ecology, status, and consequences of their loss in the region. This paper intends to:

- i) Highlight the various ecological functions that predatory gastropods perform within complex Caribbean seascapes,
- ii) Demonstrate how assessments of predatory gastropods may be integrated into existing benthic resource surveys, and
- iii) Provide new information on the feeding ecology and occurrence of several species of predatory gastropods (*Cassis flammea*, *Cassis tuberosa*, *C. madagascariensis*, *Charonia variegata*, *Turbinella angulata*) inhabiting seagrass habitats in The Bahamas, Belize and the Turks and Caicos Islands.

METHODS

Seagrass communities were examined for predatory gastropods at a number of sites across the central Bahamas (n = 24: Andros, Bimini, Berry Islands and the Exuma Cays), Belize (n = 16, South Water Caye Marine Reserve) and the Turks and Caicos Islands (n = 1) between April 2012 and September 2014 (Figure 2a). These assessments were all part of broader scoping environmental monitoring and resource assessment activities conducted during day light hours. Densities of all mega-invertebrates (> 25 mm) were assessed using snorkeling and SCUBA within two meters along either side of 50, 60 or

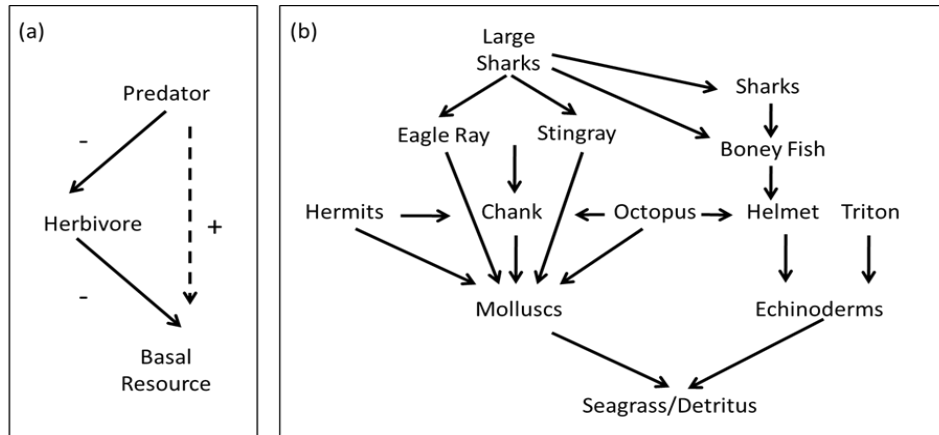


Figure 1. Trophic dynamics: (a) Basic trophic cascade, the predator and herbivore have negative (-) effects on the trophic level immediately below, the predator has an indirect (broken arrow), positive (+) effect on the basal resource (modified from Pinnegar et al. 2000); (b) Simplified seagrass foodweb including predators (apex - large sharks, meso- e.g. Stingray, Helmet shell), herbivores (principal prey of predatory gastropods, e.g. echinoderms) and basal resource (seagrass). Solid arrows represent direct, negative interactions. Horizontal arrows represent intra-guild interactions. Arrow between hermit crabs and predatory gastropods (Chank, Helmet, Triton) also represents potential use of shell resources. A number of other direct and indirect interactions are not illustrated.

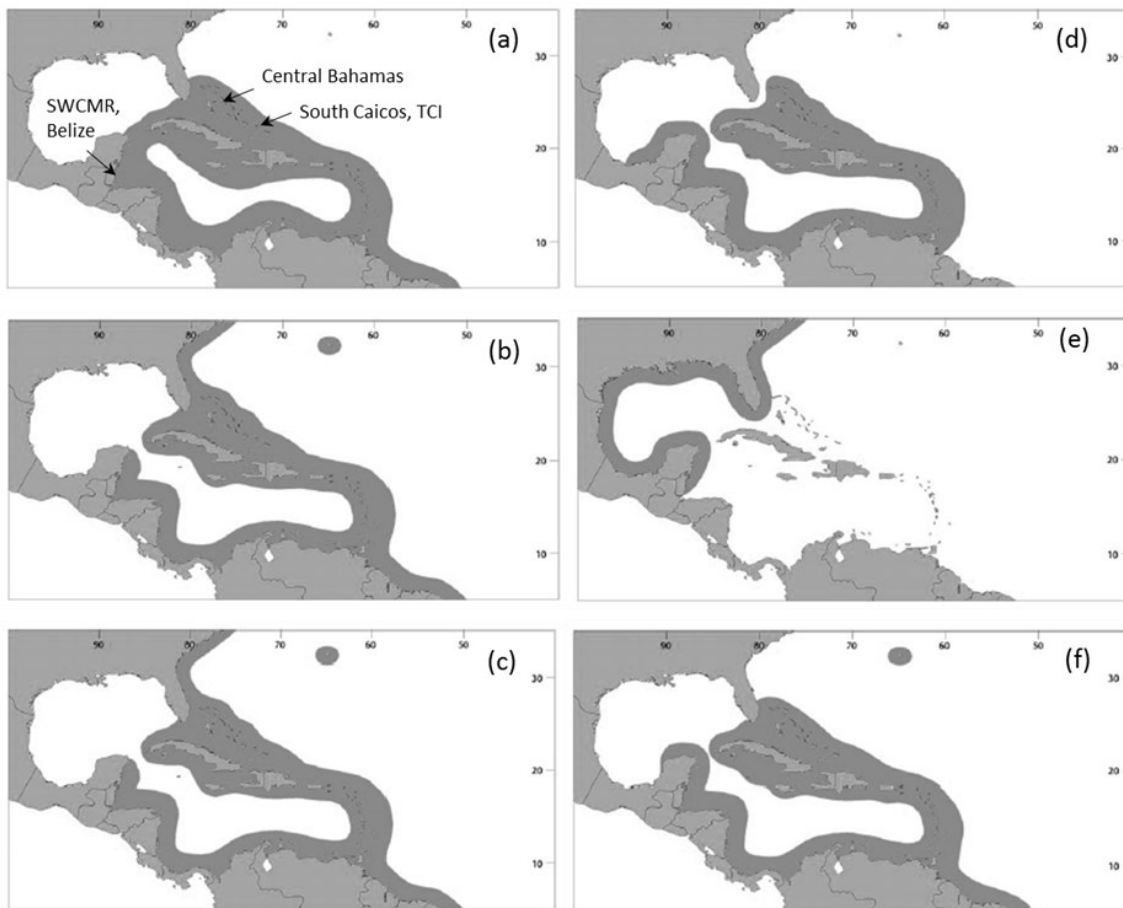


Figure 2. Sampling sites (a) and geographic distribution of large predatory gastropod species of the Caribbean and Gulf of Mexico: (a) Flame Helmet - *Cassiss flammea* (Linnaeus, 1758); (b) Emperor Helmet - *Cassiss madagascariensis* (Lamarck, 1822); (c) King Helmet - *Cassiss tuberosa* (Linnaeus, 1758); (d) West Indian Chank - *Turbinella angulata* (Lightfoot 1786); (e) Florida Horse Conch - *Triplofusus gigantea* (Kiener, 1840) (aka *Pleuroploca gigantea*), and (f) Atlantic Triton's Trumpet - *Charonia variegata* (Lamarck, 1816). Maps modified from Leal 2002. Notes: SWCMR = South Water Caye Marine Reserve; Central Bahamas = Andros, Bimini group, and Exuma Cays; TCI = Turks and Caicos Islands.

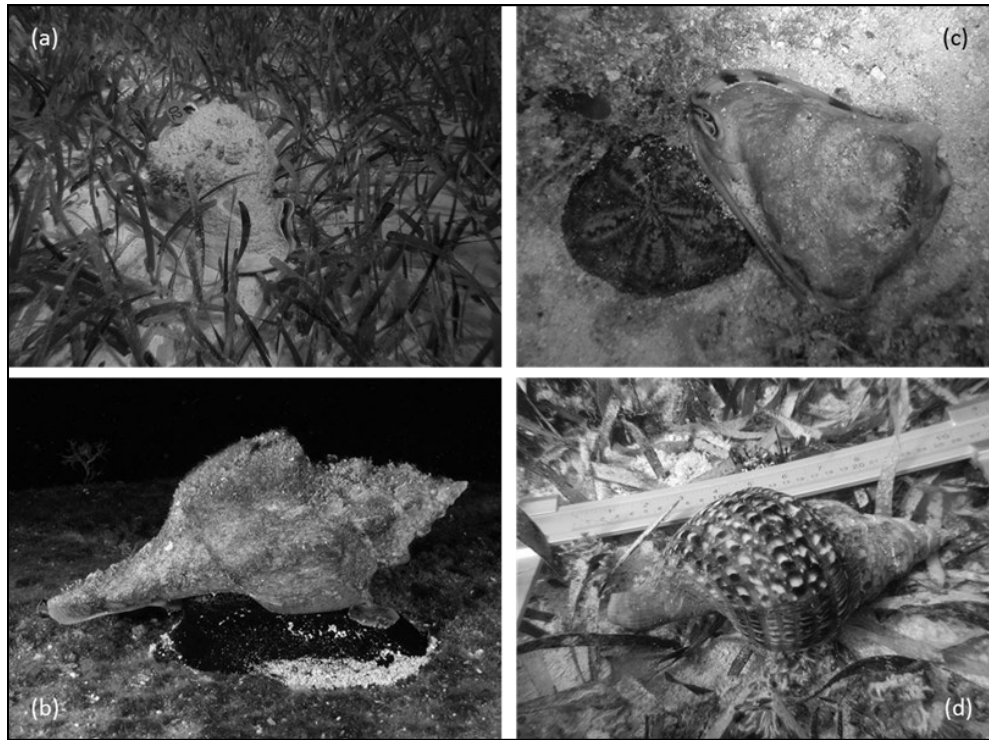


Figure 3. Large predatory gastropods of the Caribbean: (a) Emperor Helmet - *Cassis madagascariensis* (Lamarck, 1822), Andros, Bahamas; (b) West Indian Chank - *Turbinella angulata* (Lightfoot 1786), Cozumel, Mexico*; (c) King Helmet - *Cassis tuberosa* (Linnaeus, 1758) preying on *Meoma ventricosa*, Exuma Cays, Bahamas; (d) Atlantic Triton's Trumpet - *Charonia variegata* (Lamarck, 1816), South Water Caye Marine Reserve, Belize. *<http://chemistry.csudh.edu/faculty/jim/cozaug2010webpics/chank.jpg>.

300 m long transects, depending on site specific conditions, and extrapolated to individuals per hectare (Tewfik et al. 2007, Tewfik and Scheuer 2013, Tewfik 2014). Coverage of macrophytes, primarily seagrass, along transects was characterized using a mean of three to five 25- x 25-cm quadrats (% cover \pm 5%). All sites were assessed as medium (30 – 70% cover) or dense (> 70%) seagrass (Mumby and Harborne 1999, Tewfik and Scheuer 2013, Tewfik 2014) and will not be discussed further. All mega-invertebrates were measured (150 or 300 mm Vernier calipers \pm 1 mm) along the longest body axis, shell length (SL, tip of the spire to siphonal canal) for all gastropods. Two sites (Fresh Creek Cays, Andros, Bahamas; East Bay, South Caicos, Turks & Caicos Is.) had additional data collected haphazardly by snorkeling in order to encounter the greatest number of predatory gastropods for the purposes of tagging and identification of active predation events (Tewfik and Scheuer 2013). Observations included prey species under attack as well as presence of broken, crushed or empty predatory gastropod shells and identification of potential predators of predatory gastropods (e.g. Spotted Eagle ray).

RESULTS AND DISCUSSION

Meso-predatory gastropods perform a number of critical ecological functions within shallow-water, coastal systems (Figure 4). The ecological connections and associated functions involving these species is likely significant but underappreciated given the limited quantitative research conducted, with a few exceptions (Paine 1963), on rates of predation or interaction strengths (Figure 1b). Perhaps the most obvious function these species serve is as predators on a variety of primary consumers, principally herbivores and detritivores, in both seagrass and coral reef systems. The Helmet shells (i.e. Cassids) prey on a variety of regular and irregular echinoid species including *Clypeaster rosaceus* (Inflated Sea Biscuit), *Diadema antillarum* (Long-spined Urchin), *Echinometra lucunter* (Rock-boring Urchin), *Leodia sexiesperforata* (Six-keyhole Sand Dollar), *Lytechinus variegatus* (Variegated Urchin), *Meoma ventricosa* (Red Heart urchin) (Fig. 1c), *Mellita quinquesperforata* (Five-keyhole Sand Dollar), and *Tripeustes ventricosus* (West Indian Sea Egg) (Foster 1947, Schroeder 1962, Chesher 1969, Hughes and Hughes 1971, Engstrom 1982, Levitan and Genovese 1989, McClintock and Marion 1993, Pequeno and Matthews-Cascon 2001, Tewfik and Scheuer 2013). Almost half of all *Cassis* spp. individuals encountered at Fresh Creek Cays, Bahamas were actively feeding on *Meoma ventri-*

cosa (Figure 5) while at East Bay, Turks & Caicos Islands 30% of *Cassid* *turberosa* individuals and all *C. flammea* were feeding on *Clypeaster rosaceus* (Inflated Sea Biscuit). Both *M. ventricosa* (1177/ha) and *C. rosaceus* (82/ha) were the most abundant potential prey species at each site receptively and suggests that Cassids are opportunistic predators within a broader echinoid species specialty (Tewfik and Scheuer 2013).

The West Indian Chank (*T. angulata*) and the Florida Horse conch (*T. giganteus*), two species often confused, appear to be molluscan prey specialists. *Triplofusus giganteus* includes both bivalves (*Crassostrea virginica*, *Artemia rigida*) and gastropods, which may be smaller predators (*Fasciolaria tulipa*, *Busycon* spp), in its diet (Paine 1963, Kuhlmann 1994). However, this study did not observe *T. gigantea* at any site which may be due to the more northern distribution of Horse conch when compared to Chank shells (Figures 2d, e). Classic competitive exclusion theory may help explain the largely discontinuous distributions of the two molluscan specialists (Hardin 1960, Pianka 1974). The Chank (*T. angulata*) feeds on all sizes of strombid conchs (e.g. *Lobatus gigas*, aka *Strombus gigas*), which was observed in this study, and may also include smaller predatory gastropods in its diet. However, the lack of strombid prey at Fresh Creek Cays may explain why only a single living *T. angulata* was observed amongst many Cassids (Figure 5). Finally, *Charonia*

variegata appears to specialize on asteroids - *Echinaster sentus*, *Linckia guildingi*, *Ophidiaster ophidianus* and *Oreaster reticulatus* (Percharde 1972, Lipe and R.T. 1991, Morton 2012). This specialization is similar to its more well-known con-generic *Charonia tritonis* (Pacific Giant Triton) which is the principle predator of the Crown-of-thorns seastar (*Acanthaster planci*) throughout the Indo-Pacific (Endean 1977, Poulsen 1995). An asteroid resource specialization may explain the significant geographic overlap and co-existence of *C. variegata* (Figure 1d) with echinoid hunting Cassids. However, *C. variegata* has also been reported to prey on echinoids (Pencil urchin, *Eucidaris tribuloides*), holothurians, bivalves and gastropods (e.g. *Fasciolaria tulipa*) (Percharde 1972) indicating a more generalized diet and overlapping niche with all Cassids and *T. angulata*. No predation events were observed for the Atlantic Triton in this study. It should be noted that if the Cushion seastar, *Oreaster reticulatus*, is an important prey for an asteroid specialist such as the Atlantic Triton the targeted collection of *O. reticulatus* in many areas for the curio trade may have a significant impact on Triton populations.

Predatory gastropods also serve as prey to a variety of invertebrate and fish predators (Figure 1b). Smaller sized individuals may be targeted by common shell crushing



Figure 4. Ecological functions and cultural uses of predatory gastropods: (a) Predator - Atlantic Triton's Trumpet (*Charonia variegata*) stalking Cushion seastar (*Oreaster reticulatus*), Bocas del Toro, Panama; (b) Prey - *Octopus* sp. consuming King Helmet (*Cassid tuberosa*), Cozumel, Mexico* (c) Shelter - Giant Hermit crab (*Petrochirus diogenes*) with West Indian Chank shells (*Turbinella angulata*), Andros, Bahamas; Cultural - Shell artifacts including Chank (*T. angulata*) and Helmet (*Cassid* sp.) shells from Mayan ruins at Lamanai, Northern Belize. *<http://chemistry.csudh.edu/faculty/jim/cozumelaug06small/octopus.jpg>.

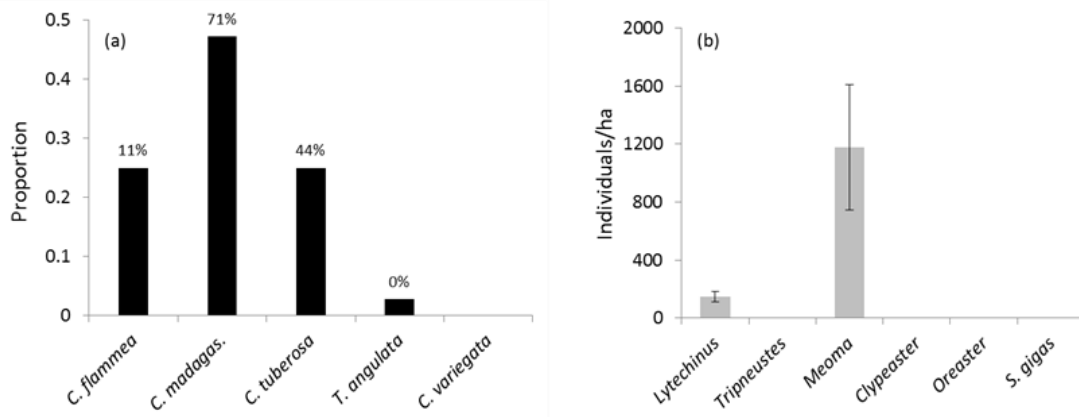


Figure 5. Proportion of (a) large predatory gastropods and (b) densities (indiv./ha) of their potential prey (see text for details) sampled within moderate (30 – 70% cover) to dense (> 70% cover) seagrass beds at Fresh Creek Cays, Andros, Bahamas (November 2013). Error bars are +/- standard error. Percent values above columns in (a) indicate proportion of predatory gastropod species actively feeding. All observations of feeding were on *Meoma ventricosa* (Red Heart urchin).

crustaceans (e.g. Hermit crabs; Spiny lobster, *Panulirus* spp.) (McLean 1983) as well as *Octopus* spp. (Figure 4b) and inter-guild predatory gastropods mentioned previously. A number of invertivorous fish (e.g. Hogfish, *Lachnolaimus maximus*; Porcupinefish, *Diodon hystrix*) may also prey on smaller size classes (Palmer 1979). The Spotted Eagle Ray (*Aetobatus narinari*), Stingrays (*Dasyatis* spp.) and the Nurse Shark (*Ginglymostomacirratum*) may also crush even the largest predatory gastropods during their benthic foraging activities with such prey potentially forming a significant part of their diets (Randall 1967). Large Helmet shell fragments were observed at field sites in the Bahamas, Belize, and TCI and are reasonably caused by large ray and nurse shark predation. The release of these larger meso-predators from apex sharks may increase foraging on a number of benthic populations (Myers et al. 2007, Ritche and Johnson 2009, Vaudo and Heithaus 2011).

The shells of predatory gastropods will also be an important part of the broader shell resource that helps shape the structure of benthic communities (McLean 1983). This includes providing attachment opportunities for sponges and cnidarians in areas of limited hard substrate as well as shelter for lobsters, octopus and fish (McLean 1983). Hermit crabs have an especially strong link to shell resources given their need for protective armor (McLean 1983). Hermit crabs, including *Petrochirus diogenes* (Giant Hermit), were observed utilizing *T. angulata* and Cassids for food and shell armor (Fig. 4c). Large predatory gastropods have also played an important role in human culture and society. Helmets, Chanks, and Tritons have been found at Mayan ruins dating back 3000 years (Miller 1977, Andrews 1969). These shells were used as practical household items and ceremonial artifacts (Figure 4d). More recently, approximately 5000 species of molluscs are traded as collectable shells and materials for souvenirs, with the largest species described here being some of the most sought-after (Abbott 1980, Wood and Wells 1988, Poulsen 1995, Gossling et al. 2004, Dias et al. 2011). Predatory gastropods may also be used as food and

form significant fisheries, supported by limited quantitative information, in some areas (Dias et al. 2011, Nieto-Bernal et al. 2013, Stephenson et al. 2013).

The King Helmet, *Cassid tuberosa*, was the most widely distributed species of the large predatory gastropods, occurring at 29% of sites surveyed, followed by *T. angulata* (20%), *C. flammea* (5%), *C. madagascariensis* (2%) and *C. variegata* (2%). Although *C. madagascariensis* only occurred at a single site (Fresh Creek Cays, Bahamas) a total of 17 individuals were found. This is in stark contrast to the single Atlantic Triton observed at South Water Caye Marine Reserve, Belize at an overall density of 0.7 indiv./ha ($n = 16$ sites) (Figure 6). Densities for Cassids were highest (41.6 individuals/ha) for *C. tuberosa* at a single site in the Bahamas with associated prey (*Clypeaster rosaceus*) at 3396 indiv./ha. Overall densities of *C. tuberosa* were much lower, 2.6 to 15.8 indiv./ha (Figure 6). The abundance of the Chank Shell was also highest at a single site in the Bahamas, 31.2 indiv./ha, with associated prey (*Strombus gigas*) at 115 indiv./ha and overall densities ranging from zero to 7.3 indiv./ha (Figure 6). The occurrence of higher densities of predatory gastropods seems to be associated with the presence of abundant prey, as noted for a number of sites, but significant correlations could not be formulated across the larger data set (Figure 6). Establishing such correlations may be confounded by the simultaneous release of larger meso-predators (e.g. Eagle rays) from apex predators and cascading increased predation on predatory gastropods (Figure 1b). The impacts of opportunistic or targeted fisheries for a number of benthic invertebrate prey of predatory gastropods (e.g. *Strombus gigas*, *Oreaster reticulatus*) may also limit the ability to detect patterns and require further field studies.

Data available from a recent investigation of targeted fisheries for gastropod populations in the Caribbean waters of Columbia indicate generally low densities for *Cassid* spp. ranging between 0.5 and 1.4 indiv./ha, with no observations of the Atlantic Triton (Nieto-Bernal et al. 2013) and are in general agreement with this study. In

addition to observations of low densities the impacts of fisheries may also be illustrated by the lack of large individuals in populations. Limited sampling in this study indicate that *C. flammaea* do exhibit larger sizes up to 111 mm SL (Figure 7a) as do samples of *C. tuberosa* from all areas, reaching known maximums of 250 mm SL (Fig. 7) (Leal 2002). In contrast, the largest sizes observed for *C. madagascariensis* in this study (210 mm SL, Fig. 7b) are far below maximums of 350 mm SL (Leal 2002). Maximum observed sizes for *T. angulata* (265 mm SL) and *C. variegata* (230 mm SL) were also well below the known maximum sizes for both species which can exceed 350 mm SL (Leal 2002) (Figure 7). The data presented here would tend to support the contention that predatory gastropod populations in the areas surveyed are under some level of exploitation with the possible exception of *C. tuberosa* in East Bay, TCI where populations were quite high (Tewfik and Scheuer 2013). However, the most recent information from East Bay indicated that this population, including 79 tagged individuals (Tewfik and Scheuer 2013), had been totally removed.

CONCLUSIONS

Data and observations presented in this study were compiled from a number of broader scoping environmental monitoring and resource assessment surveys and demonstrate the opportunities to evaluate poorly studied populations of predatory gastropods during more targeted activities (e.g. Queen conch, seagrass surveys). This study highlights new information from areas not previously assessed including main prey species, maximum sizes and essential ecological functions of a number of large and conspicuous predatory gastropods. The ecological functions include the control of large populations of grazers that may cause significant habitat damage if left unchecked as well as prey to larger meso-predators. It is very likely that populations of predatory gastropods are being impacted by poorly regulated fisheries, targeting both meat and highly prized shells, as has been documented in other areas (Dias et al. 2011, Nieto-Bernal et al. 2013, Stephenson et al. 2013). It is hoped that this work, along with previous studies, will stimulate ongoing efforts to conduct research leading to meaningful and sustainable use and protection of predatory gastropod populations.

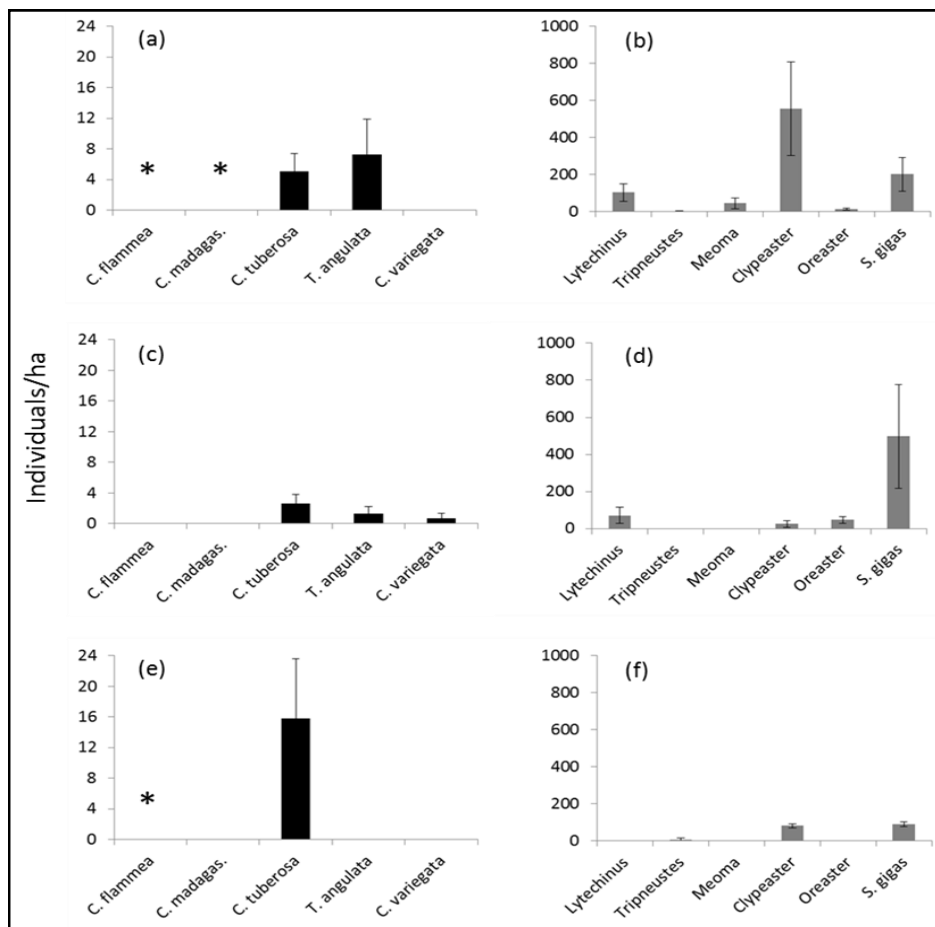


Figure 6. Densities (indiv./ha) of large predatory gastropods and their potential prey (see text for details) sampled within moderate (30 – 70% cover) to dense (> 70% cover) seagrass beds in the Bahamas (N=23)(a, b), Belize (N = 16) (c, d) and the Turks and Caicos Islands (N = 1) (e, f) between 2012 and 2014. Error bars are +/- standard error across sites with the exception of TCI which represents within site error. * Species observed during haphazard sampling for individuals to be tagged, no density calculations obtained. *C. madagas* = *Cassia madagascariensis*. No observations of *Triplofusus gigantea* were made at any site.

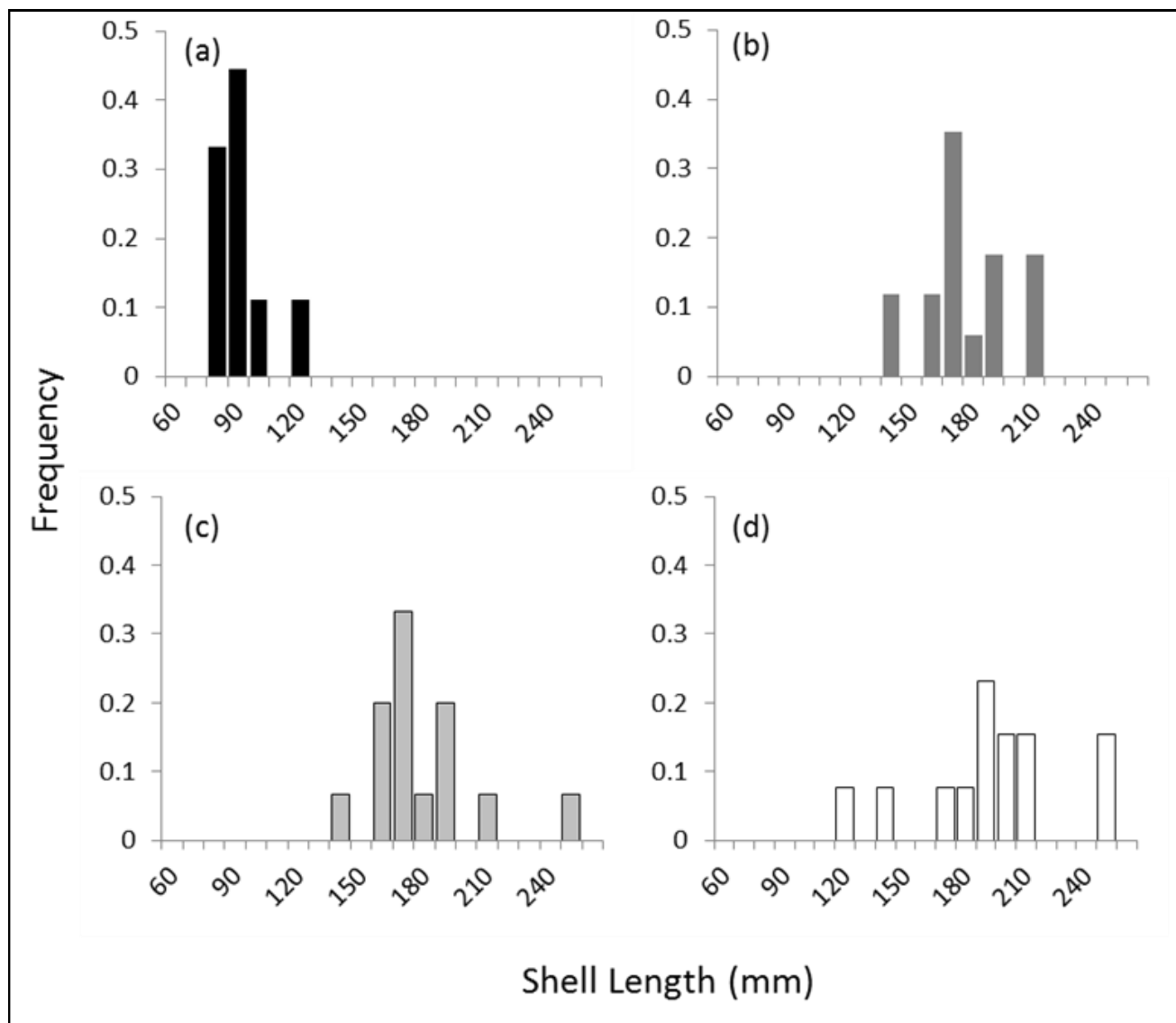


Figure 7. Frequency distribution of shell length (mm) for large predatory gastropods observed in the Central Bahamas during 2013: (a) *Cassis flammea* (n = 9); (b) *Cassis madagascariensis* (n = 17); (c) *Cassis tuberosa* (n = 15); (d) *Turbinella angulata* (n = 13).

ACKNOWLEDGEMENTS

This work was made possible through a number of data collection and funding opportunities. **Belize** - Long-term monitoring efforts conducted by the Wildlife Conservation Society (WCS) at South Water Caye Marine Reserve funded by the Oak and Summit Foundations, **The Bahamas** - Funded by Daniel P. Haerther Center for Conservation and Research, John G. Shedd Aquarium and the Paul M. Angell Family Foundation, and **Turks and Caicos Islands** - School for Field Studies (SFS), Center for Marine Resource Studies, South Caicos. Many thanks to Virginia Burns (WCS) and other data collectors in Belize, James Clark of Shedd Aquarium and other staff and volunteers data collectors working from R/V Coral Reef II, and the members of the seagrass directed research team at the SFS, Spring 2012. All work was conducted through institution (WCS, Shedd, SFS) associated research permits issued by national government bodies responsible for fisheries resources in Belize, The Bahamas and Turks and Caicos Is. All photos © A. Tewfik except where noted otherwise.

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