

ORIGINAL RESEARCH

## Assessing the ecological vulnerability of Western Atlantic marine benthic gastropods

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**ABSTRACT.** Assessing the extinction risk in marine invertebrates poses serious challenges to conservation biology, due to the magnitude of marine biodiversity, the inaccessibility of most of the marine realm, and the lack of appropriate data on population dynamics and ecology for most species. However, simple life history traits have a huge potential for preliminary screening criteria for assessing large numbers of species whose status is harsh or impossible to evaluate. Body size and trophic position could be strong predictors of extinction risk providing a general framework for the assessment of species vulnerability. We analyzed the Body Size-Trophic Position (BS-TP) relationship along 1,067 genera representing 4,256 nominal species of western Atlantic benthic gastropods. We found that a carnivore diet characterizes 67% of the genera and that, supporting theoretical predictions, the probability of being carnivores as a function of size showed a unimodal trend. For species with adult body sizes larger than 5 cm, a negative association between trophic position and body size was detected. This result points to an energetic restriction for the viability of large species, implying that organisms placed near the BS-TP boundary are extremely vulnerable to environmental changes. With this result, 109 genera from 42 families of carnivore gastropods and 33 genera from 19 families of herbivore gastropods that may be more vulnerable from the analyzed perspective were identified and ranked. Supporting these results, while the most vulnerable genera are not represented in global IUCN assessments, all our 'top 10' vulnerable families are being considered in National or Regional Red Lists. Prior to conducting regional or global conservation assessments for invertebrate taxa, screening methods should be strongly considered.

**Key words:** Extinction risk, body size-trophic position relationship, conservation biology.



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### Evaluación de la vulnerabilidad ecológica de los gasterópodos bentónicos marinos del Atlántico Occidental

**RESUMEN.** Evaluar el riesgo de extinción de los invertebrados marinos plantea serios desafíos para la biología de la conservación, debido a la magnitud de la biodiversidad marina, la inaccesibilidad de la mayor parte del ámbito marino y la falta de datos apropiados sobre la dinámica de población y la ecología de la mayoría de las especies. Sin embargo, los rasgos simples de la historia de vida tienen un gran potencial como criterios preliminares de selección para evaluar un gran número de especies cuyo estado es difícil o imposible de evaluar. El tamaño del cuerpo y la posición trófica podrían ser fuertes predictores del riesgo de extinción proporcionando un marco general para la evaluación de la vulnerabilidad de las especies. Analizamos la relación Tamaño Corporal-Posición Trófica (BS-TP) a lo largo de 1.067 géneros que representan 4.256 especies nominales de gasterópodos bentónicos del Atlántico Occidental. Encontramos que una dieta carnívora caracteriza al 67% de los géneros y que, apoyando las predicciones teóricas, la probabilidad de ser carnívoros en función del tamaño mostró una tendencia unimodal. Para especies con tamaños corporales adultos mayores de 5 cm, se

detectó una asociación negativa entre la posición trófica y el tamaño corporal. Este resultado apunta a una restricción energética para la viabilidad de las especies grandes, lo que implica que los organismos ubicados cerca del límite BS-TP son extremadamente vulnerables a los cambios ambientales. Con este resultado, se identificaron y clasificaron 109 géneros de 42 familias de gasterópodos carnívoros y 33 géneros de 19 familias de gasterópodos herbívoros que pueden ser más vulnerables desde la perspectiva analizada. Respaldando estos resultados, mientras que los géneros más vulnerables no están representados en las evaluaciones globales de la UICN, todas nuestras “10 principales” familias vulnerables están siendo consideradas en las Listas Rojas Nacionales o Regionales. Antes de realizar evaluaciones de conservación regionales o globales para taxones de invertebrados, se deben considerar seriamente los métodos de detección.

**Palabras clave:** Riego de extinción, relación tamaño corporal-posición trófica, biología de la conservación.

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## INTRODUCTION

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Despite the widespread global threats to marine ecosystems (Halpern et al. 2007), rates of registered marine neo-extinctions have been so far relatively low, with a 9-fold lower marine extinction rate compared to terrestrial systems (Webb and Mindel 2015). In fact, only five marine mollusc species or subspecies have been mentioned as possible extinct in recent historical times (Dong et al. 2015). However, the pace of marine habitat deterioration is accelerating, thus increasing already apparent threats to marine biodiversity, with nearly 66% of the ocean and 77% of national jurisdictions showing increased human impact (Halpern et al. 2015). Further, it should be noticed that only a small number of marine animals has been evaluated by the IUCN, and many assessed species were determined to be data deficient. Thus, reported numbers of extinct and endangered marine fauna should be considered as conservative (Régnier et al. 2009; Pimm et al. 2014).

Gastropods are an incredibly diverse and widespread group, with representatives found in virtually all aquatic and terrestrial environments, ranging from shallow to deep regions of the ocean, freshwater, and most land areas. Nevertheless, the ocean remains their predominant habitat, with the highest number of species concentrated in marine benthic environments. Gastropod species have a variety of different feeding styles. Some species are seaweed-eating herbivores or suspension

feeders, while others are predatory carnivores or internal parasites (Todd 2001). Most aquatic gastropods spend adult life in the benthic realm, from intertidal rocky shores to abyssal plains and hydrothermal vents. The evolutionary success of gastropods can be largely attributed to the structural and functional plasticity of the feeding apparatus (Purchon 1977; Kohn 1983).

To date, only 11,2% species of gastropods in the IUCN red list are marine. Most of these species are represented in the Red List owing to the first comprehensive global assessment of a marine taxon, namely the 632 valid species of the tropical marine gastropod Genus *Comus* (Peters et al. 2013). However, there is a huge potential for simple life history traits to be used as preliminary screening criteria for the assessment of large numbers of species whose status is harsh or impossible to evaluate, such as the 32,000-40,000 known described species and the estimated 85,000-105,000 undescribed species in marine Gastropoda (Appeltans et al. 2012).

In this vein, body size is closely and predictably related to a wide array of species traits, thus synthesizing a large amount of biological information (Brown et al. 2004). Larger animals live longer, expend more energy, and have higher metabolic rates, affecting resource demands and population growth rate and density (McNab 2002; Brown et al. 2004; White et al. 2007). Additionally, the hierarchy in trophic interactions, in which free-living predators consume smaller prey, is a well-reported empirical pattern and a main determinant of food web structure

(Brose et al. 2006a, 2006b). Congruently, it was found that extinction threat for molluscs in modern oceans is strongly associated with large body size, whereas past extinction events were non-selective or preferentially affected smaller-bodied taxa (Payne et al. 2016). In addition, whereas habitat zone and feeding mode do not appear to be associated with threats in the modern ocean, previous mass extinctions have disproportionately removed pelagic species. This suggests that organisms that live in the benthic realm may face the same threats as their open sea nektonic and planktonic counterparts.

When the phylogenetic, temporal or spatial scales are large enough, a hump-shaped relationship between trophic position and body size is expected (Arim et al. 2007a) and reported (Burness et al. 2001, 2016; Segura et al. 2015a, 2016). Despite this, there have been numerous reports of positive relationships within taxonomic groups. (Arim et al. 2010; Romanuk et al. 2011). The BS-TP relationship would be positive as morphological restrictions on consumption disappear at larger sizes; however, the relationship would be negative because high trophic positions have increased energetic demands and decreased resources (Arim et al. 2007a). Positive correlations arise since larger sizes can provide several advantages, including escape from predation and/or the ability to engage in more 'daring' behaviours, which can expand the range of available prey. With body size comes an increase in the ability to capture and dominate prey, the maximum distance between meals (in space or time), and the length of the digestive tract (resulting in longer digestion times and more resources extracted per gram of prey consumed), which translates into greater processing opportunities. (McNab 2002). This may be enhanced by the also increasing absolute size of the organs associated with prey (and predator) identification and thus the species ability to differentiate between resources and distances and detection thresholds in the environment (Pawar 2015). All these factors led to an important expansion of the

quantity and quality of resources that can be exploited. However, the negative relationship often found at the extreme of body-size distributions may imply that species placed near the boundary are extremely vulnerable to any shift in resource availability, which could drive these species to extinction. This is of utmost importance for conservation biologists, since most processes related with biodiversity loss (e.g. fragmentation, pollution, overfishing, etc.) produce said shifts in resource availability and quality (Segura et al. 2015b, 2016). In this sense, there may be important conservation applications for identifying species and/or clades that are susceptible to energetic constraints.

Most of the published examples on BS-TP focus on taxonomically restricted assemblages, typically freshwater or marine fishes (e.g. Layman et al. 2005; Akin and Winemiller 2008; Lucifora et al. 2009; Arim et al. 2010; Romanuk et al. 2011; Segura et al. 2015b; Burrell et al. 2016; Ou et al. 2017; Dantas et al. 2019). Further, BS-TP curves may show non-trivial idiosyncratic patterns according to clade identity, feeding ecologies and the broader environmental setting. However, no study has analysed the BS-TP relationship for marine gastropods to date. Gastropods span four orders of magnitude in linear dimensions and eight orders in mass (volume). From Triphoridae, presenting adult sizes generally ranging between 2-10 mm, with a few species exceptionally reaching 40-50 mm (Albano et al. 2011), to *Syrinx aruanus*, the largest living gastropod (more than 90 cm maximum adult size), marine gastropods are a remarkably well suited group to study the BS-TP relationship. Further, gastropods exploit a wide array of feeding ecologies, often very conserved at genus, family, or even superfamily level. This implies that a feeding strategy may be more that reasonably inferred given the taxonomic identity of a given species. In the present study, we evaluated the relationship between body size and trophic position along genera of western Atlantic marine benthic gastropods. By detecting a hump-

shaped pattern that support energetic constraints, species prone to be affected by the ongoing change in the energetic scenario, e.g. productivity, resource diversity and distribution, temperature, pollutants, among others, were identified. Finally, results were contrasted to the existing conservation assessments for marine gastropods.

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## MATERIAL AND METHODS

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### Database structure

Species-level data and associated taxonomy for western Atlantic benthic gastropods were obtained from Malacolog 4.1.1, a database created for research on the systematics, biogeography and diversity of molluscs (Rosenberg 2009). Malacolog geographical coverage ranges from Greenland to Antarctica, attempting to document all names that have ever been applied to marine molluscs in the western Atlantic and providing species identity and taxonomy, maximum adult length (hereafter body size), bathymetric and geographic ranges and relevant references supporting each assignment. However, there is no currently available dietary information in this database.

### Dietary information

Species-level information derived from Malacolog was later combined with dietary information based on Todd (2001), derived and modified from the trophic classifications of Hughes (1980) and Taylor and Reid (1984) for Neogene Neotropical Gastropods. This trophic classification recognizes seven categories: Predatory carnivores, browsing carnivores, herbivorous omnivores, herbivores, herbivores on rock, rubble or coral substrates, herbivores on plant or algal substrates, and suspension feeders (Table 1). Each species in the Malacolog database was assigned to one of the above-described categories combining them on

the general categories of Carnivore-Non Carnivore (Arim et al. 2007b, 2010; Segura et al. 2016).

### Data analysis

Considering that the feeding ecology is highly conserved at generic level, the BS-TP analysis was analysed at this taxonomic resolution. The trophic position of each genera (carnivorous versus non-carnivorous) was linked to the mean body size of the genera. The occurrence of carnivorous genera was related to the average body size using a logistic regression (Zuur et al. 2009). Three logistic models were fitted to: i) a model considering only a constant intercept, in which diet and body size are independent; ii) a model that included the effect of body size, reflecting a monotonic association between variables; and iii) a model with body size and its quadratic value as independent variables, considering the theoretical expectation of a humped association between the probability of being carnivorous and body size (Arim et al. 2007a). Models were ranked from their AIC values and the weight of evidence:  $w_i = \exp(-0.5 \cdot (AIC_i - \min(AIC))) / \sum \exp(-0.5 \cdot (AIC_i - \min(AIC)))$  (Burnham and Anderson 2002). Model weights indicate the probability that the model is the best for the data in comparison to the other models considered.

### Priorities for conservation

Genera were ranked in order to identify conservation priorities. The first component of the ranking was based on the difference between the maximum body size in the dataset and the mean body size for each genus. Specifically, the calculation involves subtracting the mean body size from the maximum body size, resulting in a numerical value that represents the difference between the two measurements. This difference was calculated for each genus, allowing for comparisons of the size variation within and between different genera. Thus, the largest carnivorous or non-car-

Table 1. Diet categories for Gastropoda used in this study, based in Hughes (1980), Taylor and Reid (1984), and Todd (2001).

| Non carnivores  | Carnivores  |
|---|---|
| Herbivorous omnivores: browsing macroherbivores with unselective omnivory, typically of epifauna attached to macroalgae.  | Predatory carnivores: predators that consume entire sedentary or mobile macro-organisms, killing them in the process and also selective foraminifera ingesters (foraminiferivores). Include scavengers which, with scant exceptions, display predatory characteristics. These organisms possess the ability to modulate their feeding behaviour in response to the availability of carrion. |
| Herbivores on fine-grained substrates: microalgivores, detritivores, microphages and unselective deposit feeder. Also included here is a miscellany of herbivorous non-HR and HP categories, including those living on wood or mangrove substrates. | Browsing carnivores: predators that consume sedentary, clonal animals such as corals and cnidarians, sponges, and ascidians, without causing their immediate death, fall under this category. Additionally, the group includes ectoparasites that live on larger sedentary or mobile prey.  |
| Herbivores on rock, rubble or coral substrates: microalgivores.   |   |
| Herbivores on plant or algal substrates: micro-and macroalgivores and detritivores on macroalgal and seagrass substrates.   |   |
| Suspension feeders: includes taxa feeding solely or dominantly upon suspended particles, including mucociliary feeders.   |   |

nivorous genus was assigned a rank value of 1. The ranking then proceeds with the assumption that the number of species within genera is negatively correlated with extinction risk and takes into account the species richness within each genera. As a result, less speciose genera will be ranked higher at any given body size. The analysis was done for both carnivores and non-carnivores separately.

#### Online search on conservation status

Finally, the overlap between genera/families here identified was assessed 1) on a global scale with the IUCN red Lists Global Assessment, and

2) on a regional scale with other non-IUCN national or regional assessments or national red lists from countries within the western Atlantic Ocean, when available.

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## RESULTS

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The database included data on maximum reported adult body size and dietary information for 4,256 species belonging to 1,067 genera of western Atlantic benthic gastropods. Once the holoplanktonic gastropods were removed, the database consisted of 1,047 genera, with 350 gen-

era (33%) classified as non-carnivores and 697 genera (67%) classified as carnivores. The distribution of species richness within genera was highly skewed, with approximately 43% of the genera being monospecific, while the maximum generic diversity corresponded to *Conus*, with some 121 species.

Both carnivorous and non-carnivorous species covered a large range of overlapping body sizes (Figure 1 A). However, the probability density of carnivorous genera surpassed that of herbivorous at intermediate body sizes. This trend is particularly evident in the logistic regression analysis (Figure 1 B). A quadratic model in which carnivorous incidence is maximum at intermediate body sizes was the one that best matched the data. This model presented the lower AIC values and its associated weight of evidence outperformed alternative linear or monotonic models ( $w_{\text{quadratic}} = 0.999$ ;  $w_{\text{linear}} = 7.2e-06$ ;  $w_{\text{intercept}} = 5.9e-26$ ). This result supports the existence of an association between the incidence of carnivorous genera and body size, and also that this association involves a hump-shaped relationship (Figure 1 B).

Once identified the theoretical threshold after

which energetic constraints operate (around 5 cm maximum adult body size) and ranked species as previously described, 109 genera from 42 families of carnivore gastropods and 33 genera from 19 families of herbivore gastropods that may be more vulnerable from the analyzed perspective were classified. Among the overall ranking, seven out of 10 genera assigned top priorities were carnivorous, the exception being *Titanostrombus*, *Aliger* and *Syphonota* (Table 2). *Titanostrombus*, *Syphonota*, *Aliger*, *Lentigo*, *Cittarium*, *Bursatella*, *Macrocypraea*, *Dolabrifera*, *Entemnotrochus* and *Aplysia* were the most vulnerable of the herbivorous genera (Table 3). *Triplofusus*, *Charonia*, *Zidona*, *Pachycymbiola*, *Turbinella*, *Adelomelon*, *Cassis*, *Pugilina*, *Platydorid* and *Pleuroploca* species ranked amongst the more threatened carnivorous genera.

### Online search on conservation status

The IUCN currently lists 643 species of marine gastropods. From these, as mentioned above, 617 species belong to the Genus *Conus* (Peters et al. 2013). Data deficient and least concern species

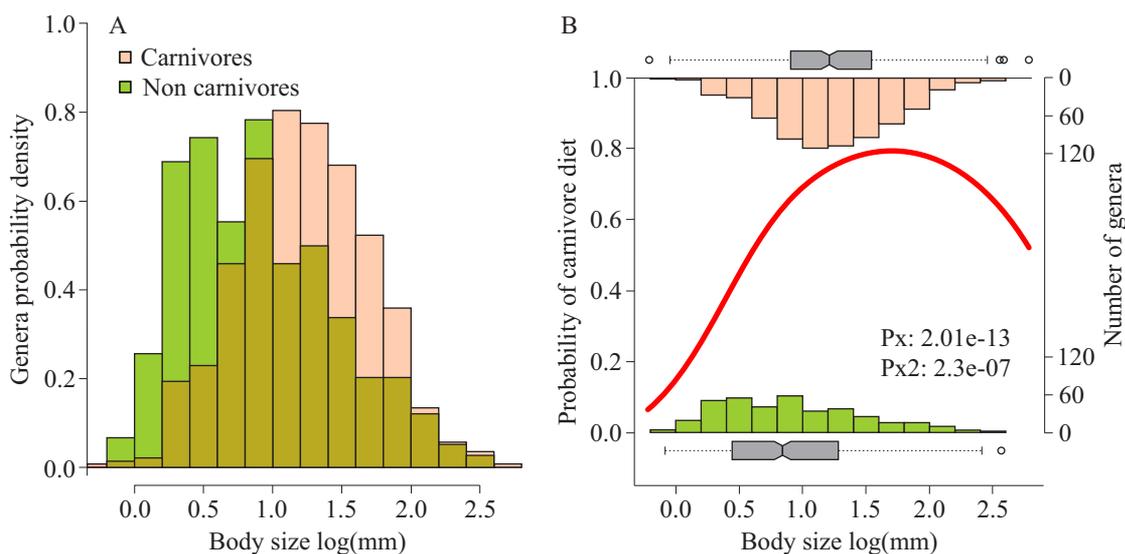


Figure 1. Size-frequency distribution for carnivorous and non-carnivorous gastropod genera (A) and the probability density of a carnivorous diet from logistic regression analysis (B).

Table 2. Marine gastropod genera most affected by energetic constraints, based in species richness (SR) within genera and average maximum adult size. C = carnivores; H = non-carnivores.

| Family          | Genus                 | Species richness | Mean size (cm) | Diet | Rank |
|-----------------|-----------------------|------------------|----------------|------|------|
| Fascioliariidae | <i>Triplofusus</i>    | 1                | 609            | C    | 1    |
| Strombidae      | <i>Titanostrombus</i> | 1                | 380            | H    | 2    |
| Charoniidae     | <i>Charonia</i>       | 2                | 382            | C    | 3    |
| Volutidae       | <i>Zidona</i>         | 1                | 270            | C    | 4    |
| Volutidae       | <i>Pachycymbiola</i>  | 2                | 200            | C    | 5    |
| Volutidae       | <i>Adelomelon</i>     | 3                | 362            | C    | 6    |
| Turbinellidae   | <i>Turbinella</i>     | 2                | 280            | C    | 7    |
| Cassidae        | <i>Cassis</i>         | 3                | 288            | C    | 8    |
| Aplysiidae      | <i>Syphonota</i>      | 1                | 170            | H    | 9    |
| Strombidae      | <i>Aliger</i>         | 2                | 274            | H    | 10   |

Table 3. Non-carnivore marine gastropod genera most affected by energetic constraints.

| Higher clade    | Number of families | Family          | Genus                 | Species richness |
|-----------------|--------------------|-----------------|-----------------------|------------------|
| Aplysioidea     | 2                  | Aplysiidae      | <i>Syphonota</i>      | 1                |
|                 |                    |                 | <i>Bursatella</i>     | 1                |
|                 |                    |                 | <i>Aplysia</i>        | 6                |
|                 |                    | Dolabriferidae  | <i>Dolabrifera</i>    | 1                |
| Cypraeoidea     | 1                  | Cypraeidae      | <i>Macrocypraea</i>   | 2                |
| Pleuromarioidea | 1                  | Pleuromarioidea | <i>Entemnotrochus</i> | 2                |
| Stromboidea     | 1                  | Strombidae      | <i>Titanostrombus</i> | 1                |
|                 |                    |                 | <i>Aliger</i>         | 2                |
|                 |                    |                 | <i>Lentigo</i>        | 1                |
| Trochoidea      | 1                  | Trochidae       | <i>Cittarium</i>      | 1                |
| Total           | 6                  |                 |                       | 18               |

accounts for ca. 90% of the assessed species. Taxonomically, nine families are represented (Table 4), although most of the families include mainly freshwater and/or brackish species (e.g. Stenothyridae and Hydrobiidae). However, 39 species from 16 families are represented in regional and/or national assessments (Table 5). Results were retrieved from Rio Grande do Sul,

Brazil (ICMBio 2018), Guatemala (CONAP no date), Colombia (Ardila et al. 2002) and Venezuela (Rodríguez et al. 2015). Scientific names provided in Table 5 were updated using the latest nomenclature available in the World Register of Marine Species WORMS (Ahyong et al. 2023), and some names may differ from those utilized in the original publication.

Table 4. Families of marine gastropods represented in the IUCN Red List as data deficient (DD), least concern (LC), near threatened (NT), vulnerable (VU), endangered (EN), and critically endangered (CR).

| Family        | DD        | LC         | NT        | VU        | EN        | CR       | Total      |
|---------------|-----------|------------|-----------|-----------|-----------|----------|------------|
| Assimineidae  | 2         | 2          | 0         | 0         | 0         | 0        | 5          |
| Conidae       | 85        | 465        | 25        | 25        | 11        | 3        | 617        |
| Ellobiidae    | 3         | 0          | 0         | 0         | 0         | 0        | 3          |
| Haliotidae    | 0         | 0          | 0         | 0         | 0         | 1        | 1          |
| Hydrobiidae   | 0         | 1          | 0         | 0         | 0         | 0        | 1          |
| Iravadiidae   | 0         | 1          | 0         | 0         | 0         | 0        | 1          |
| Neritidae     | 1         | 7          | 0         | 0         | 0         | 0        | 8          |
| Stenothyridae | 1         | 4          | 0         | 0         | 0         | 0        | 5          |
| Thiaridae     | 0         | 2          | 0         | 0         | 0         | 0        | 2          |
| <b>Total</b>  | <b>92</b> | <b>482</b> | <b>25</b> | <b>25</b> | <b>11</b> | <b>4</b> | <b>643</b> |

Table 5. Western Atlantic Marine Gastropods species included in available national assessments as data deficient (DD), least concern (LC), near threatened (NT), vulnerable (VU), endangered (EN) and critically endangered (CR). Scientific names may differ from those originally published. See references in the text.

| Family        | Species                               | Red list category | Country   |
|---------------|---------------------------------------|-------------------|-----------|
| Cassidae      | <i>Cassis flammea</i>                 | VU                | Colombia  |
| Cassidae      | <i>Cassis madagascariensis</i>        | VU                | Colombia  |
| Cassidae      | <i>Cassis madagascariensis</i>        | EN                | Guatemala |
| Cassidae      | <i>Cassis tuberosa</i>                | VU                | Colombia  |
| Charoniidae   | <i>Charonia variegata</i>             | DD                | Brazil    |
| Charoniidae   | <i>Charonia variegata</i>             | VU                | Colombia  |
| Columbellidae | <i>Anachis coseli</i>                 | VU                | Colombia  |
| Cypraeidae    | <i>Muracypraea mus</i>                | VU                | Venezuela |
| Cypraeidae    | <i>Propustularia surinamensis</i>     | VU                | Colombia  |
| Fasciolaridae | <i>Fasciolaria tulipa</i>             | EN                | Guatemala |
| Melongenidae  | <i>Melongena melongena</i>            | VU                | Guatemala |
| Melongenidae  | <i>Melongena patula</i>               | VU                | Guatemala |
| Melongenidae  | <i>Pugilina morio</i>                 | LC                | Brazil    |
| Olividae      | <i>Olivancillaria contortuplicata</i> | CR                | Brazil    |
| Olividae      | <i>Olivancillaria teaguei</i>         | CR                | Brazil    |
| Olividae      | <i>Olivancillaria vesica vesica</i>   | NT                | Brazil    |
| Olividae      | <i>Olivancillaria auricularia</i>     | DD                | Brazil    |
| Olividae      | <i>Olivella formicacorsii</i>         | DD                | Brazil    |
| Cymatiidae    | <i>Cymatium femorale</i>              | DD                | Brazil    |

Table 5. Continued.

| Family        | Species                          | Red list category | Country   |
|---------------|----------------------------------|-------------------|-----------|
| Strombidae    | <i>Aliger gallus</i>             | DD                | Brazil    |
| Strombidae    | <i>Aliger gigas</i>              | VU                | Colombia  |
| Strombidae    | <i>Aliger gigas</i>              | VU                | Guatemala |
| Strombidae    | <i>Aliger gigas</i>              | VU                | Venezuela |
| Strombidae    | <i>Titanostrombus goliath</i>    | VU                | Brazil    |
| Strombidae    | <i>Macrostrombus costatus</i>    | VU                | Brazil    |
| Strombidae    | <i>Macrostrombus costatus</i>    | VU                | Guatemala |
| Strombidae    | <i>Macrostrombus costatus</i>    | VU                | Brazil    |
| Strombidae    | <i>Strombus pugilis</i>          | VU                | Guatemala |
| Strombidae    | <i>Titanostrombus goliath</i>    | VU                | Brazil    |
| Tegulidae     | <i>Cittarium pica</i>            | VU                | Colombia  |
| Tegulidae     | <i>Cittarium pica</i>            | VU                | Venezuela |
| Terebridae    | <i>Hastula cinerea</i>           | LC                | Brazil    |
| Tonnidae      | <i>Tonna galea</i>               | LC                | Brazil    |
| Tonnidae      | <i>Tonna pennata</i>             | DD                | Brazil    |
| Turbinellidae | <i>Turbinella angulata</i>       | EN                | Guatemala |
| Turbinellidae | <i>Turbinella laevigata</i>      | DD                | Brazil    |
| Vermetidae    | <i>Petalconchus myrakeenae</i>   | CR                | Brazil    |
| Volutidae     | <i>Adelomelon beckii</i>         | DD                | Brazil    |
| Volutidae     | <i>Adelomelon riosi</i>          | DD                | Brazil    |
| Volutidae     | <i>Adelomelon ancilla</i>        | NA                | Brazil    |
| Volutidae     | <i>Odontocymbiola americana</i>  | LC                | Brazil    |
| Volutidae     | <i>Odontocymbiola simulatrix</i> | DD                | Brazil    |
| Volutidae     | <i>Pachycymbiola brasiliiana</i> | LC                | Brazil    |
| Volutidae     | <i>Voluta ebraea</i>             | DD                | Brazil    |
| Volutidae     | <i>Voluta musica</i>             | VU                | Venezuela |
| Volutidae     | <i>Zidona dufresnei</i>          | LC                | Brazil    |

## DISCUSSION

The present study contributes to both applied marine conservation initiatives and food web theory. A complementary approach useful for the identification and prioritization of a number of gastropod genera was derived from the empirical evidence supporting the predicted humped trend

between organism trophic position and body size in benthic marine gastropods.

### Theoretical implications

The expected trophic position trend along the body size gradient was significant and covered a large variation in the proportion of carnivorous species. However, it has to be noted that carnivorous diets do not reach a zero incidence among

larger gastropods, as reported for other taxa as mammals, birds, and fishes (Arim et al. 2011; Segura et al. 2016). This suggests that in spite of being a strategy that became progressively more difficult to sustain, it represents a frequent strategy even among the larger gastropod species.

It was concluded that larger species were considered as particularly vulnerable to extinction. The claim that large consumer at higher trophic position are particularly vulnerable to extinction is not new (May et al. 1995). However, trophic position and body size were considered as positively related, thus providing redundant information for vulnerability assessments. Still, the detection of a humped trophic position-body size association supports the opposite pattern, showing a negative association between trophic position and body size among large and vulnerable species. This implies that large herbivorous could be equally or more vulnerable to environmental change than carnivorous species (Segura et al. 2016). More generally, the negative trophic position-body size association along intermediate to larger body sizes involves an explicit mechanistic understanding of the energetic constrain, potentially affecting species local persistence or extinction susceptibility (Burness et al. 2001; Valkenburgh et al. 2004; Arim et al. 2007a).

So far it is known, the negative association between trophic position and body size emerge from the balance between energetic population demands and the available energy in the environment for each population (Brown et al. 1993; Marquet and Taper 1998; Burness et al. 2001; Arim et al. 2007a, 2016). This balance is affected by environmental variables such as temperature due to its effects on metabolism (Arim et al. 2007a). Similarly, since more energy has to be incorporate into the population to reach the minimum viable population size, predation rates are expected to increase energetic constrains (Arim et al. 2011). The total amount of local energy in the food web is determined by the interaction between area and productivity at the community

or ecosystem level (Schoener 1989), and landscape features determines how individuals move among local populations, integrating spatial patches of resources (Urban and Keitt 2001; McCann 2005, 2012). Finally, pollutants negatively affect individual's metabolism, energetic demands and resource allocation (Garay-Narváez et al. 2013). Consequently, the negative association between trophic position and body size herein reported is likely to encompass multiple drivers of energetic imbalance at individual, population, community and ecosystem levels. The observed pattern is therefore connecting ongoing environmental trends with the persistence of particular species close to the 'boundary' of energetic constraints. However, it should be noticed that these mechanisms cannot be equally invoked if there is no positive association between trophic position and body size (Dantas et al. 2019).

### Practical implications

This being said, we found a poor match between the genera identified here as being close to the energetic imbalance and the IUCN Red List marine gastropods. Not only is none of the families currently assessed by the IUCN present in our 'top 10' assessment, but our analysis suggests that most species listed may not be affected by energetic constraints. In contrast, all of our 'top 10' vulnerable families and genera are much often represented on the national or regional list. We are not saying, in any case, that species listed in the IUCN are not genuine conservation targets, yet rather suggesting new avenues for identifying endangered species. In this line, a new addition to the IUCN Red List, the scaly-foot snail or sea pangolin (*Chrysomallon squamiferum*), exemplifies how Red List criteria can be applied to organisms in deep water, poorly known habitats without baseline population data (Sigwart et al. 2019). However, it is worth noting that several species included in national or regional Red Lists does not rank high in our vulnerability assessment, such as

the olivid gastropods *Olivancillaria teaguei* and *O. contortuplicata* (see e.g. Scarabino 2004), highlighting that the causes of species declines are complex and often interconnected, and encouraging more local or regional assessment of gastropod species.

### Caveats

This approach aims to provide an initial screening for a large number of species and therefore it is beyond the scope of this paper to carefully review the nomenclature provided in the database. This may have important implications, since the establishment of a new genera, the description of new species, and the identification of synonymies may modify our ranking. Further, taking into consideration that most species are probably microgastropods (Albano et al. 2011), the database can be regarded as biased towards large-sized species. For example, in an unprecedented massive collecting effort involving 400 person-days at a single site in New Caledonia, SW Pacific, 2,738 species of marine molluscs were recorded (Bouchet et al. 2002). Small-sized species made up the majority of the diversity, while over 50% of the species had adult sizes below 10 mm. Top five families in terms of species richness were 'Turridae' (specialist polychaete hunters), Eulimidae (echinoderm parasites), Pyramidellidae (invertebrate ectoparasites), Triphoridae and Cerithiopsidae (specialist feeders on sponges). These five families together accounting for 29.5% of the mollusc diversity at the study site. There are thus reasons to expect that any in-depth study of the diversity of gastropods in the western Atlantic should also follow this pattern. However, even taking into account the large number of unreported small gastropods and associated taxonomic uncertainties (e.g. genus or family-level assignment of species), our results should be robust since no changes in the shape of the curve are expected unless a large number of previously unknown large carnivore gastropods species is discovered.

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## CONCLUSIONS

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Mechanistic theories provide a better framework for the management of applied problems with comparatively less demand of empirical information. The humped trend in trophic position with body size support the existence of both morphological restriction to trophic position among smaller species and an energetic constrain for large species. It is interesting to note that few empirical evidence support the humped association when was originally proposed. However, the analysis at large taxonomic and spatial scale is progressively supporting its occurrence in different ecosystems. Equally or more important, when the humped pattern is not observed, the operation of additional mechanisms become evident. In this sense, a theory based on basic principle provides a mechanist understanding of biodiversity patterns, even when it fails. The taxonomic biases in the analysis of the TP-BS relationship and more generally on the environmental determinants of food chain length are a matter of concern. The bulk of evidence about the trophic position-body size relationship is based on fishes. The analysis of different organisms, with different traits and inhabiting different environment is essential for the validation of general mechanisms and/or the identification of novel mechanisms to be included on theory. Our analysis of the trophic position-body size relationship for marine gastropods attempts to be a step in this direction, which provide in this case, mechanistic based suggestions for the identification of species of conservation concern.

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