CIM.UH Centro de Investigaciones Marinas Universidad de La Habana

Revista de Investigaciones Marinas

RESEARCH ARTICLE

Exploring marine mollusc drilling predation: insights into predator-prey dynamics and selective pressures in gastropod shell assemblages of Playa Guardalavaca, Cuba

Explorando la depredación por perforación en moluscos marinos: perspectivas en las dinámicas depredador-presa y presiones selectivas en ensambles de conchas de gasterópodos de Playa Guardalavaca, Cuba

Yander L. Diez[1,2,*]
Yodanis Rodríguez-Santos[3]
Alejandro Catalá[3]
Sandra Gordillo[4]

[1] Museum of Nature Hamburg – Zoology, Leibniz Institute for the Analysis of Biodiversity Change (LIB), Martin-Luther-King-Platz 3, D-20146, Hamburg, Germany.

[2] Hasselt University, Centre for Environmental Sciences, Research Group Zoology: Biodiversity and Toxicology, Universitaire Campus Gebouw D, B-3590 Diepenbeek, Belgium.

[3] Universidad de Oriente, Biology and Geography Department, Ave. Patricio Lumumba s/n, Santiago de Cuba, Cuba. CP 90500.

[4] IDACOR, CONICET. Universidad Nacional de Córdoba. Avda. Hipólito Yrigoyen 174, X5000JHO, Córdoba, Argentina.

Corresponding author::
yanderluis87@gmail.com

Editor:
Beatriz Martínez-Daranas (CIM-UH)

Received: 02.06.2023
Accepted: 12.12.2023

Abstract

Predation marks by drilling molluscs serve as evidence for feeding activity. This behaviour has been extensively studied to understand predator-prey relationships. The objective of this study is to characterise the mollusc drilling predation on gastropods from Playa Guardalavaca, Cuba. We examined the species richness and abundance of drilled and non-drilled shells and calculated predation rates and its relationship with prey size. To compare drilled and non-drilled shells, we used the median and interquartile range due to the asymmetric distribution of the measurements. Furthermore, we employed a Kolmogorov-Smirnov test to compare the size distribution frequencies. A total of 114 morphospecies and nine species groups were identified. Five species were identified as new records for the area. A total of 5,795 shells were quantified, out of which 24.4% displayed drillholes. The most abundant species are not the most preyed upon, presenting a distinct pattern compared to bivalve assemblages in this and other locations. The highest predation rate was observed among individuals of medium size, may be attributed to the predators' ability to manipulate their prey. Smaller shells may not offer sufficient food resources, resulting in lower predation rates. Statistical analyses revealed significant differences in predation related to shell size for six out of the 11 tested species. Potential predators were identified, some of which exhibit drillholes themselves. In general, drilling predation in gastropods from the studied area appears to be influenced by a combination of factors, including high species richness of both predators and prey, prey abundance, specialised feeding strategies of predators, and habitat diversity.

Keywords: biotic interactions, Caribbean Sea, drillholes, feeding behaviour, Gastropoda, Mollusca, thanatocoenosis.

Resumen

Las marcas de depredación por perforación de moluscos sirven de evidencia de la actividad alimentaria. Este comportamiento ha sido extensamente estudiado para comprender las relaciones depredador-presa. El objetivo de este estudio es caracterizar la depredación por perforación de moluscos gasterópodos de Playa Guardalavaca, Cuba. Se examinó la riqueza de especies y abundancia de conchas perforadas y no perforadas y se calculó la tasa de depredación y su relación con el tamaño de las presas. Para comparar las conchas perforadas y no perforadas se utilizó la mediana y el rango intercuartil dada la distribución asimétrica de las mediciones. Además, se empleó una prueba de Kolmogorov-Smirnov para comparar las frecuencias de distribución de tamaño. En total 114 morfoespecies y nueve grupos de especies fueron identificadas. Cinco especies fueron identificadas como nuevos registros para el área. Se cuantificaron 5 795 conchas, de las cuales 24,4 % presentaron perforaciones. Las especies más abundantes no son las más depredadas, presentando un patrón distinto comparado con los ensambles de bivalvos en esta y otras localidades. La mayor tasa de depredación fue observada entre individuos de tamaño medio, atribuido a la habilidad de los depredadores para manipular sus presas. Conchas pequeñas podrían no ofrecer suficiente alimento, resultando en tasas de depredación menores. Los análisis estadísticos revelaron diferencias significativas de depredación en relación al tamaño de la concha en seis de las 11 especies evaluadas. Depredadores potenciales fueron identificados, algunos de los cuales también mostraron perforaciones. En general, la depredación por perforación en los gasterópodos del área estudiada parece estar influenciada por una combinación de factores, incluyendo la alta riqueza de especies de depredadores y presas, la abundancia de las presas, estrategias especializadas de alimentación de los depredadores y la diversidad de hábitats.

Palabras clave: interacciones bióticas, Mar Caribe, perforaciones, comportamiento alimentario, Gastropoda, Mollusca, tanatocenosis.

Introduction

Marine molluscs serve as a key group for studying predator-prey interactions, primarily due to the long-term preservation of their shells, which retain evidence of predation. One such piece of evidence is the drillholes in shells. These interactions among molluscs have been studied using both fossil and extant species (e.g., Pahari *et al*., 2016; Bardhan *et al*., 2021; Mondal *et al*., 2021a; Zuschin *et al*., 2022) and drilling predation was shown to play a crucial role in the evolution of both predators and their prey (Kowalewski *et al*., 1998; Kowalewski, 2002). In addition, the rate at which this type of predation occurs varies over time. For instance, during the Palaeozoic era, predation intensities were generally low to moderate, with predominantly sessile and benthic prey species (Klompmaker *et al*., 2017). The Ordovician period in the Palaeozoic era represents a peak in predation intensity (Huntley & Kowalewski, 2007), whereas drilling predation was relatively low during the Mesozoic (Fürsich & Jablonski, 1984). The highest predation rates occurred during the Cenozoic and persist to the present day (e.g., Kelley & Hansen, 2006; Sarkar *et al*., 2016; Mondal *et al*., 2019).

Mollusc drilling predation has predominantly been investigated in the context of mollusc prey, including gastropods, bivalves, and scaphopods (Taylor, 1998; Archuby & Gordillo, 2018; Gordillo & Malvé, 2021). However, drilling molluscs also engage in predation on other shelled invertebrates such as polychaetes (Morton & Harper, 2009), barnacles (Mondal *et al*., 2019, 2021b), brachiopods (Delance & Emig, 2004), brachyuran crabs (Huelsken, 2011), and echinoderms (Grun *et al*., 2017). Among the gastropod families, most of drilling activity is attributed to representatives of Muricidae (Thomas & Day, 1995; Morton *et al*., 2007) and Naticidae (Kabat, 1990; Kelley & Hansen, 1993; Gordillo *et al*., 2020). However, representatives of Cassidae (Hughes & Hughes, 1981; Grun *et al*., 2017), Cominellidae (Peterson & Black, 1994; Morton, 2006), Marginellidae (Ponder & Taylor, 1992), Nassariidae (Morton & Chan, 1997; Chiu *et al*., 2010), and several other families also employ this feeding strategy (for a comprehensive overview, see Harper, 2003). Additionally, octopuses are also known to exhibit drilling predation behaviour (Blustein & Anderson, 2016; Greenwell *et al*., 2019; Gordillo *et al*., 2022).

Studies on thanatocoenoses imply the analysis of mixed organisms proceeding from several biocoenoses (Kidwell, 2001). The shells found in the thanatocoenosis represent non-contemporary generations since they are generated from the mixture of organisms in space over a period. The abundance of death shells in the supratidal does not indicate food availability for predators. However, several studies have demonstrated that thanatocoenoses preserve the ecologic fidelity of the communities from which the shells come. Furthermore, the thanatocoenoses represent the accumulation of shells for years; therefore, they are not affected by anomalies or extreme conditions. Analysing the shell abundance in the thanacoenosis does not allow the analysis of the relative abundance of a population but the accumulative effect of different populations (Tomašových & Kidwell, 2009; Kidwell, 2002, 2013; Archuby *et al*., 2015).

Research on drilling predation by marine molluscs in Cuba is relatively recent. Gordillo *et al*. (2019) provided the first comprehensive description of this interaction in the Cuban archipelago. These authors observed a higher predation rate on bivalves and noted that predation appeared to be non-elective and was determined by prey abundance. Recently, Diez *et al*. (2023) investigated this phenomenon on bivalve shell deposits and found that the predation rate was also related to the size and external morphology of prey. Moreover, drilling predation has been studied in the Cuban fossil record of serpulid polychaetes (Villegas-Martín *et al*., 2016), and drillholes were attributed to naticid gastropods.

Building upon these previous studies, the objective of this research is to provide a comprehensive description of drilling predation on marine gastropods, specifically those occurring on Playa Guardalavaca, Holguín.

Material and methods

Study area and sampling

Sampling took place in June 2019 at Playa Guardalavaca, located in Banes Municipality, Holguín Province, Cuba. The sampling site was chosen based on the presence of a high concentration of shells in a supratidal point of a sandy beach (21°07’17.2”N; 75°50’22.9”W). For a detailed map of the sampled area and its ecological characteristics, the reader is referred to Diez *et al*. (2023) and references therein.

Two samples, each weighing approximately 2 kg, were collected from the supratidal thanatocoenosis (death assemblage of marine organisms) and transported to the Zoology Laboratory of Universidad de Oriente, where they were washed and dried at room temperature. Shells were separated from sand under a stereoscopic microscope (Novel NSZ-606), and gastropod shells were selected for analysis. Species were identified following Warmke and Abbott (1962), Abbott (1974), and Espinosa *et al*. (2012), and updated taxonomic names were obtained from WoRMS (2023).

Data analysis

The specific richness (S_{obs}) of gastropods (Ludwing & Reynolds, 1988) was determined based on the number of species identified in the sample, and it was differentiated into two groups: the total number of species and the number of species showing drilling marks. Two types of drilling marks were considered: complete holes, which penetrate the prey’s shell and reach the soft tissues, and incomplete holes, which do not pierce the prey’s shell. To estimate the predation rate, the percentage of specimens with drillholes was calculated globally and for each species.

Shell length measurements were taken using a digital ABS Digimatic Vernier calliper (Mitutoyo, Japan; Instrumental error ±0.02 mm). Due to the asymmetric distribution of the measurements, the median and interquartile range were calculated to compare drilled and non-drilled shells among 11 taxa [*Cerithium lutosum*

Menke, 1828, *C. litteratum* (Born, 1778), *Zebina* spp., *Rissoina* spp., *Suturoglypta* spp., *Steironepion* sp., *Gibberula* spp., *Brachycythara* sp., *Olivella acteocina* Olsson, 1956, *O. minuta* (Link, 1807), and *Acteocina* spp.]. Other species were not included in the size analyses because they presented specimens in one or two size ranges and/or their size differences were lower than the used interval range of 1 mm. Results were visualised with a boxplot graph, using a sinaplot arrangement of drawn points, performed in the application Extended Boxplot Graphics (Denis & Ramirez-Arrieta, 2020; Ramirez-Arrieta, 2020). Distribution histograms were constructed to illustrate the predation preferences of these 11 taxa based on prey size.

Statistical differences in central tendency statistics of the shells' size were tested using the two independent samples Wilcoxon test. The frequency distributions of size for each species (drilled and non-drilled shells) were evaluated using a Kolmogorov-Smirnov test to compare two independent distributions (two-sample K-S test). These analyses were carried out in R v.4.2.1 with the RStudio interface v.2022.02.3+492 (2009–2022), using the packages Rcmdr and RcmdrPlugin.UCA. A significance level of 0.05 was applied (Fox, 2005, 2017; Fox & Bouchet-Valat, 2022; Munoz-Marquez, 2022).

Results

Species richness and taxonomic composition

A total of 114 morphospecies of gastropods were identified, along with nine species groups that could not be assigned to a single species (*Eulithidium* spp., *Zebina* spp., *Schwartziella* spp., Rissoinidae spp., *Suturoglypta* spp., *Gibberula* spp., *Volvarina* spp., *Acteocina* spp., and *Odostomia* spp.) (Table 1). These species belong to 84 genera and 52 families. The families with the highest species richness were Fissurellidae, Columbellidae, and Pyramidellidae, each with eight species. Among the genera, *Melanella*, *Crassispira*, and *Echinolittorina* had the highest species richness, with four species each.

Several species were recorded for the first time on the northeastern coast of Cuba, including *Finella dubia* (d'Orbigny, 1840), *Lucapinella limatula* (Reeve, 1850), *Phrontis alba* (Say, 1826), *Retusa sulcata* (d'Orbigny, 1841), and *Turbonilla pupoides* (d'Orbigny, 1841).

Abundance and drill holes

A total of 5,795 gastropod shells were collected, out of which 1,416 displayed complete drillholes (total drillhole rate 24.4%). Incomplete drillholes were not observed. Among the collected gastropods, 50 species (32.5%) did not exhibit any evidence of drillholes. The most abundant species encountered was *Cerithium lutosum*, accounting for 1,421 shells (24.6% of the total abundance). This was followed by *Olivella acteocina* with 381 shells (6.6%), *Smaragdia viridis* with 286 shells (5%), and *Trochomodulus carchedonius* with 227 shells (3.9%) (Table 1).

Among the species with 10 or more collected shells, the highest drillhole rates were observed in *Iniforis* sp. 1 (70%), *Astyris* sp. 2 (62%), *Brachycythara* sp. (60%), *Pyrgocythara* sp. 1 (58%), *Triptychus niveus* (53%), and *Steironepion* sp. (52.4%). Some species displayed higher predation rates (75–100%), but low abundances (less than 4 shells), and thus were not considered in this analysis. The most abundant species did not show the highest drillhole rate, e.g., *C. lutosum* (32%), *O. acteocina* (22%), and *S. viridis* (9%). Additionally, 39 species did not show any evidence of drillholes (Table 1). Figure 1 provides examples of the drillholes found in the collected shells.

Prey size

Central tendency statistics revealed no significant differences between drilled and non-drilled shells size in most species ($p > 0.05$), with the exception of *C. litteratum*, *C. lutosum*, and *Suturoglypta* spp. (Fig. 2). This analysis suggests that there is a different consumption pattern related to size, with the higher predation rates in size classes where prey are more abundant, according

Table 1. Number of shells, drilled shells and predation rate (% of the abundance), and habitat of the gastropods from Playa Guardalavaca, Holguín, Cuba, collected in June 2019. Abbreviations: s- seagrass, sb- sublittoral soft bottoms (sandy, sandy-muddy), sr- sublittoral rocky bottoms (including coral rubble), ir- intertidal rocky bottoms, sl- rocky supralittoral, fi- feeders on invertebrates (i.e. sponges), p- parasitic (feeding on echinoderms), ma- mangroves, mr- marshes, and ga- grazing on algae. The habitat was taken from the literature for species identification and WoRMS.

Tabla 1. Número de conchas, conchas perforadas, tasa de depredación (% de la abundancia) y hábitat de los gasterópodos de Playa Guardalavaca, Holguín, Cuba, recolectados en junio de 2019. Abreviaturas: s- pastos marinos, sb- fondos blandos sublitorales (arenosos, arenosos-fangosos), sr- fondos rocosos sublitorales (incluyendo restos de coral), ir- fondos rocosos intermareales, sl- supralitoral rocoso, fi- comedores de invertebrados (i.e. esponjas), p- parásitos (succionadores en equinodermos), ma- manglares, mr- ciénagas, and ga- raspadores en algas.

Species	Family	Known habitat	Total abundance	Drilled shells	Predation rate (%)
Cerithium lutosum	Cerithiidae	s, sb	1,421	447	31.5
Eulithidium spp.	Phasianellidae	s, sb	965	95	9.8
Olivella acteocina	Olividae	s, sb	381	83	21.8
Zebina spp.	Zebinidae	s, sb, sr	314	113	36.0
Smaragdia viridis	Neritidae	s, sb	286	26	9.1
Trochomodulus carchedonius	Modulidae	s, sb	227	63	27.8
Hipponix antiquatus	Hipponicidae	sb	192	27	14.1
Cerithium litteratum	Cerithiidae	s, sb	191	59	30.9
Schwartziella spp.	Zebinidae	s, sb, sr	143	29	20.3
Eulithidium bellum	Phasianellidae	s, sb, sr	128	17	13.3
Acteocina spp.	Tornatinidea	s, sb	127	73	57.5
Olivella minuta	Olividae	s, sb	124	15	12.1
Rissoinidae spp.	Rissoinidae	s, sb	111	47	42.3
Gibberula spp.	Cystiscidae	s, sb, sr	103	22	21.4
Puperita pupa	Neritidae	sl	91	22	24.2
Suturoglypta spp.	Columbellidae	s, sb	89	38	42.7
Eoacmaea pustulata	Eoacmaeidae	sr	55	10	18.2
Bulla occidentalis	Bullidae	s, sb	54	1	1.9
Olivella sp.	Olividae	s, sb	44	3	6.8
Zafrona cf. *pulchella*	Columbellidae	s, sb	43	15	34.9
Phrontis alba	Nassariidae	s, sb	40	17	42.5
Diodora minuta	Fissurellidae	sr	37	7	18.9
Caecum insularum	Caecidae	s, sb	32	8	25.0
Odostomia spp.	Pyramidellidae	s, sb	32	9	28.1
Columbella mercatonia	Columbellidae	s, sb	31	10	32.3
Bittiolum varium	Cerithiidae	s, sb, sr	30	7	23.3
Brachycythara sp.	Mangeliidae	sb, sr	25	15	60.0
Finella adamsi	Scaliolidae	s, sb	24	6	25.0
Lottia albicosta	Lottiidae	sr, ir	21	-	-
Steironepion sp.	Columbellidae	s, sb	21	11	52.4
Volvarina spp.	Marginellidae	sr	18	4	22.2
Triptychus niveus	Pyramidellidae	s, sb	17	9	52.9
Melanella sp. 1	Eulimidae	p	16	3	18.8
Persicula pulcherrima	Cystiscidae	sr	15	5	33.3
Pyrgocythara cinctella	Mangeliidae	s, sb, sr	15	5	33.3
Arene sp.	Areneidae	sr	14	4	28.6
Seila adamsii	Cerithipsidae	sr	14	6	42.9
Hemimarginula pumila	Fissurellidae	sr	13	1	7.7

Species	Family	Known habitat	Total abundance	Drilled shells	Predation rate (%)
Melanella sp. 3	Eulimidae	p	12	4	33.3
Natica sp.	Naticidae	s, sb	12	-	-
Pyrgocythara sp.	Mangeliidae	sr	12	7	58.3
Iniforis sp. 1	Triphoridae	rs, fi	10	7	70.0
Fissurella barbadensis	Fissurellidae	sr, ir	9	-	-
Meioceras nitidum	Caecidae	s, sb	9	2	22.2
Tegula gruneri	Tegulidae	s, sb, sr	9	4	44.4
Astyris sp. 2	Columbellidae	s, sb	8	5	62.5
Fissurella angusta	Fissurellidae	sr, ir	7	-	-
Hinea lineata	Planaxidae	sr	7	2	28.6
Litiopa melanostoma	Litiopidae	ga	7	1	14.3
Parviturbo weberi	Skeneidae	sb, sr	7	1	14.3
Cerithiopsis sp. 2	Cerithipsidae	rs, fi	6	1	16.7
Diodora dysoni	Fissurellidae	sr	6	-	-
Lottia leucopleura	Lottiidae	sr, ir	6	-	-
Alvania sp. 3	Rissoidae	s, sb	5	2	40.0
Dentimargo sp.	Marginellidae	sr	5	-	-
Melanella conoidea	Eulimidae	p	5	-	-
Pilsbryspira sp.	Pseudomelatomidae	s, sb, sr	5	-	-
Turbonilla sp. 1	Pyramidellidae	s, sb, sr	5	3	60.0
Agathotoma sp. 2	Mangeliidae	s, sb, sr	4	3	75.0
Atys sp.	Haminoeidae	s, sb	19	4	21.1
Cosmotriphora melanura	Triphoridae	rs, fi	4	3	75.0
Hemitoma octoradiata	Fissurellidae	sr, ir	4	-	-
Pedipes mirabilis	Ellobiidae	sl	4	-	-
Polinices lacteus	Naticidae	s, sb	4	1	25.0
Tegula fasciata	Tegulidae	s, sb, sr	4	2	50.0
Modulus modulus	Modulidae	s, sb	4	1	25.0
Finella dubia	Scaliolidae	s, sb	4	-	-
Conella ovulata	Columbellidae	s, sb	3	-	-
Echinolittorina mespillum	Littorinidae	ir, sl	3	-	-
Granulina sp.	Granulidinae	s, sb, sr	3	1	33.3
Lithopoma phoebium	Turbinidae	sr	3	-	-
Lucapina sowerbii	Fissurellidae	sr	3	-	-
Polinices hepaticus	Naticidae	s, sb	3	1	33.3
Turbonilla sp. 2	Pyramidellidae	s, sb, sr	3	1	33.3
Teinostoma semistriatum	Teinostomatidae	sb	3	-	-
Alvania sp. 2	Rissoidae	s, sb, sr, ga	2	-	-
Cerithiopsis sp. 1	Cerithipsidae	rs, fi	2	2	100.0
Conus sp.	Conidae	s, sb, sr	2	-	-
Crassispira sp. 4	Pseudomelatomidae	s, sb, sr	2	1	50.0
Echinolittonina meleagris	Littorinidae	ir, sl	2	-	-
Ithycythara sp.	Mangeliidae	s, sb, sr	2	2	100.0

Species	Family	Known habitat	Total abundance	Drilled shells	Predation rate (%)
Melanella sp. 2	Eulimidae	p	2	2	100.0
Nerita tessellata	Neritidae	ir, sl	2	-	-
Opalia sp.	Epitoniidae	s, sb	2	-	-
Plesiothyreus hamillei	Phenacolepadidae	sr	2	1	50.0
Prunum sp.	Marginellidae	s, sb	2	-	-
Retilaskeya bicolor	Newtoniellidae	sr	2	-	-
Rissoina sp.	Rissoinidae	s, sb, sr	2	1	50.0
Synaptocochlea picta	Trochidae	sr	2	-	-
Trabecula krumpermani	Pyramidellidae	s, sb, sr	2	-	-
Turridae sp. 3	Turridae	s, sb, sr	2	1	50.0
Agathotoma sp. 1	Mangeliidae	s, sb, sr	1	1	100.0
Alvania sp. 1	Rissoidae	s, sb, sr, ga	1	-	-
Astyris sp. 1	Columbellidae	s, sb	1	1	100.0
Caecum textile	Caecidae	s, sb	1	1	100.0
Cerithideopsis sp.	Potamididae	ma, mr	1	1	100.0
Cheilea equestris	Hipponicidae	sr	1	-	-
Crassispira sp. 1	Pseudomelatomidae	s, sb, sr	1	1	100.0
Crassispira sp. 2	Pseudomelatomidae	s, sb, sr	1	1	100.0
Crassispira sp. 3	Pseudomelatomidae	s, sb, sr	1	1	100.0
Echinolittorina angustior	Littorinidae	ir, sl	1	-	-
Echinolittorina tuberculata	Littorinidae	ir, sl	1	-	-
Engina turbinella	Pisaniidae	ir, sr	1	1	100.0
Epitonium sp. 1	Epitoniidae	s, sb	1	-	-
Epitonium sp. 2	Epitoniidae	s, sb	1	1	100.0
Iniforis sp. 2	Triphoridae	rs, fi	1	1	100.0
Aliger gigas	Strombidae	s, sb	1	1	100.0
Lucapinella limatula	Fissurellidae	sr	1	1	100.0
Mitromorpha sp.	Mitromorphidae	s, sb, sr	1	-	-
Phrontis candissima	Nassariidae	s, sb	1	1	100.0
Probata barbadensis	Mitridae	rb	1	-	-
Pyramidella dolabrata	Pyramidellidae	s, sb	1	-	-
Pyramidella sp.	Pyramidellidae	s, sb	1	1	100.0
Teinostoma sp.	Teinostomatidae	sb	1	-	-
Turbonilla pupoides	Pyramidellidae	s, sb, sr	1	1	100.0
Turridae sp. 1	Turridae	s, sb, sr	1	-	-
Turridae sp. 2	Turridae	s, sb, sr	1	1	100.0
Zafrona cf. *idalina*	Columbellidae	s, sb	1	-	-
Retusa sulcata	Retusidae	s, sb	1	1	100.0
Mumiola gradatula	Pyramidellidae	s, sb, sr	1	-	-
Liotia microgrammata	Liotiidae	sb	1	1	100.0
Teinostoma nesaeum	Teinostomatidae	sb, sr, ma	1	-	-
Acteon sp.	Acteonidae	s, sb	1	-	-
Total			5,795	1,416	24.4

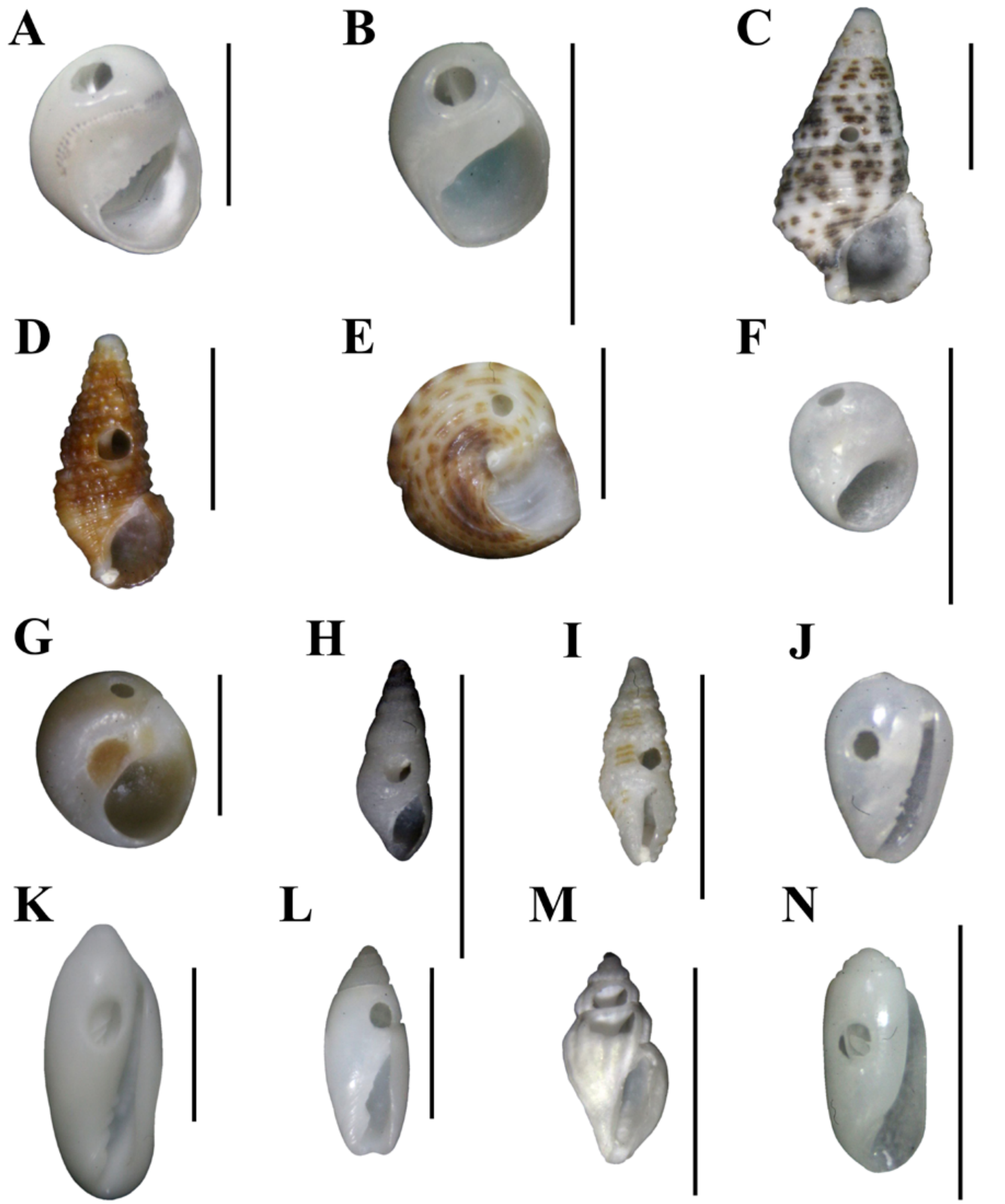

Fig. 1. Examples of drilled shells of the collected species. A: *Puperita pupa,* B: *Smaragdia viridis,* C: *Cerithium litteratum,* D: *Cerithium lutosum,* E: *Trochomodulus carchedonius,* F: *Polinices lacteus,* G: *Polinices hepaticus,* H: Rissoinidae sp., I: *Steironepion* sp., J: *Gibberula* sp., K: *Volvarina* sp., L: *Olivella* sp. 1, M: *Brachycythara* sp., and N: *Acteocina* sp. Scale bars = 0.5 cm.

Fig. 1. Ejemplos de conchas perforadas de las especies recolectadas. A: *Puperita pupa*, B: *Smaragdia viridis*, C: *Cerithium litteratum*, D: *Cerithium lutosum*, E: *Trochomodulus carchedonius*, F: *Polinices lacteus*, G: *Polinices hepaticus*, H: Rissoinidae sp., I: *Steironepion* sp., J: *Gibberula* sp., K: *Volvarina* sp., L: *Olivella* sp. 1, M: *Brachycythara* sp. y N: *Acteocina* sp. Barras de escala = 0.5 cm.

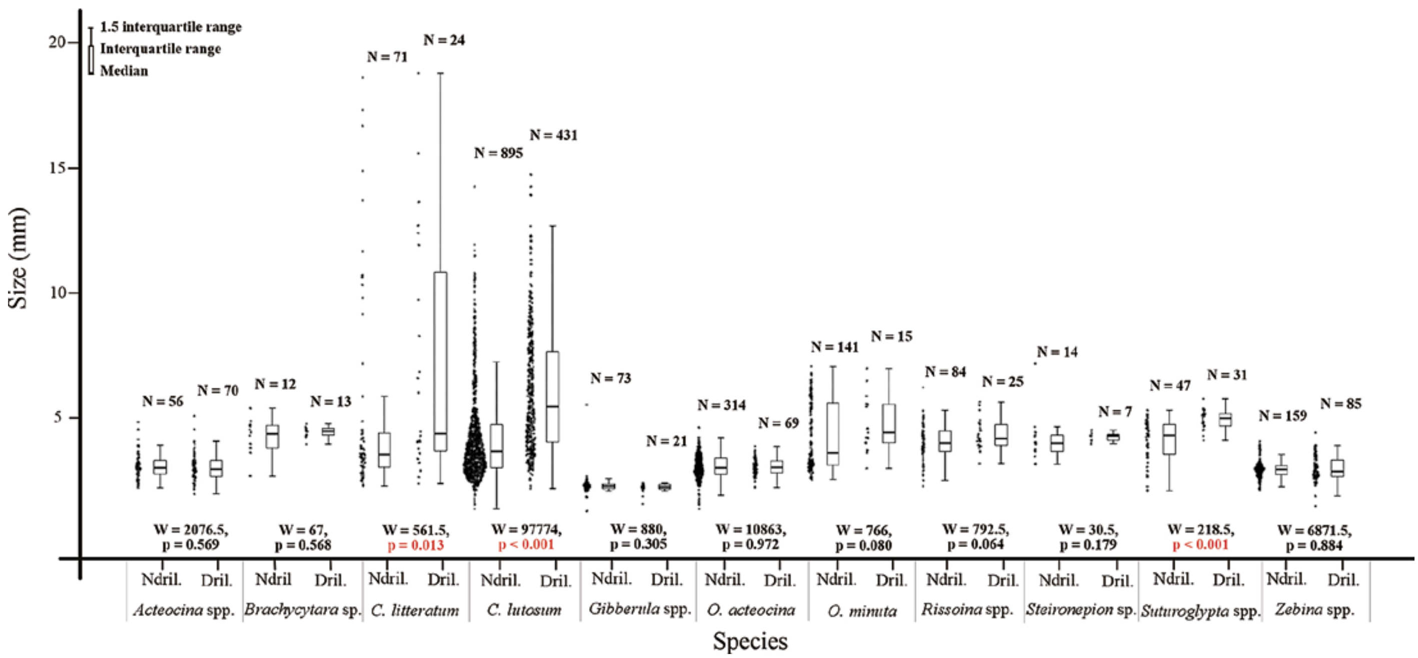

Fig. 2. Median and interquartile range of the distribution comparison between drilled and non-drilled shells. The values of the two-independent samples Wilcoxon test (W) and probabilities (p) are represented. Statistically significative p-values are highlighted in red colour.
Fig. 2. Comparación de la distribución de la media y rango intercuartir entre conchas perforadas y no perforadas. Los valores de la prueba de Wilcoxon para dos muestras independientes (W) y las probabilidades (p) son presentadas. Los valores significativos de p son resaltados en color rojo.

to the results of the Wilcoxon test (Fig. 2). Size distribution histograms (Figs. 3-4) show a decreasing abundance as size increases, indicating a general pattern of a higher predation rate in medium-sized specimens of each species, considering the size of specimens (Table 2; Fig. 4).

For the most abundant species, *Cerithium lutosum*, the predation rate exceeds 50% in medium-sized shells

Tabla 2. Drilling predation rate (% of the abundance) according to the size range of selected species of gastropods from Playa Guardalavaca, Holguín, Cuba, collected in June 2019.
Tabla 2. Tasa de depredación por perforación (% de la abundancia) en correspondencia con el rango de talla de las especies de gasterópodos seleccionadas de Playa Guardalavaca, Holguín, Cuba, recolectadas en junio de 2019.

Species	Predation rate (%) and distribution size (mm)																		
	0,0-0,99	1,0-1,99	2,0-2,99	3,0-3,99	4,0-4,99	5,0-5,99	6,0-6,99	7,0-7,99	8,0-8,99	9,0-9,99	10,0-10,99	11,0-11,99	12,0-12,99	13,0-13,99	14,0-14,99	15,0-15,99	16,0-16,99	17,0-17,99	18,0-18,99
Cerithium lutosum	-	0	6	22	33	50	55	57	62	71	33	56	100	100	67	-	-	-	-
Cerithium litteratum	-	-	16	12	35	0	100	0	100	33	0	50	100	50	0	100	50	0	50
Rissoinidae spp.	-	-	0	19	29	33	0	-	-	-	-	-	-	-	-	-	-	-	-
Zebina spp.	-	100	33	37	50	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Suturoglypta spp.	-	-	0	0	39	83	-	-	-	-	-	-	-	-	-	-	-	-	-
Steironepion sp.	-	-	-	13	50	-	-	0	-	-	-	-	-	-	-	-	-	-	-
Gibberula spp.	-	40	21	-	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-
Olivella acteocina	-	0	18	18	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Olivella minuta	-	-	4	4	26	12	13	0	-	-	-	-	-	-	-	-	-	-	-
Brachycythara sp.	-	-	0	20	67	0	-	-	-	-	-	-	-	-	-	-	-	-	-
Acteocina spp.	-	100	58	53	50	100	-	-	-	-	-	-	-	-	-	-	-	-	-

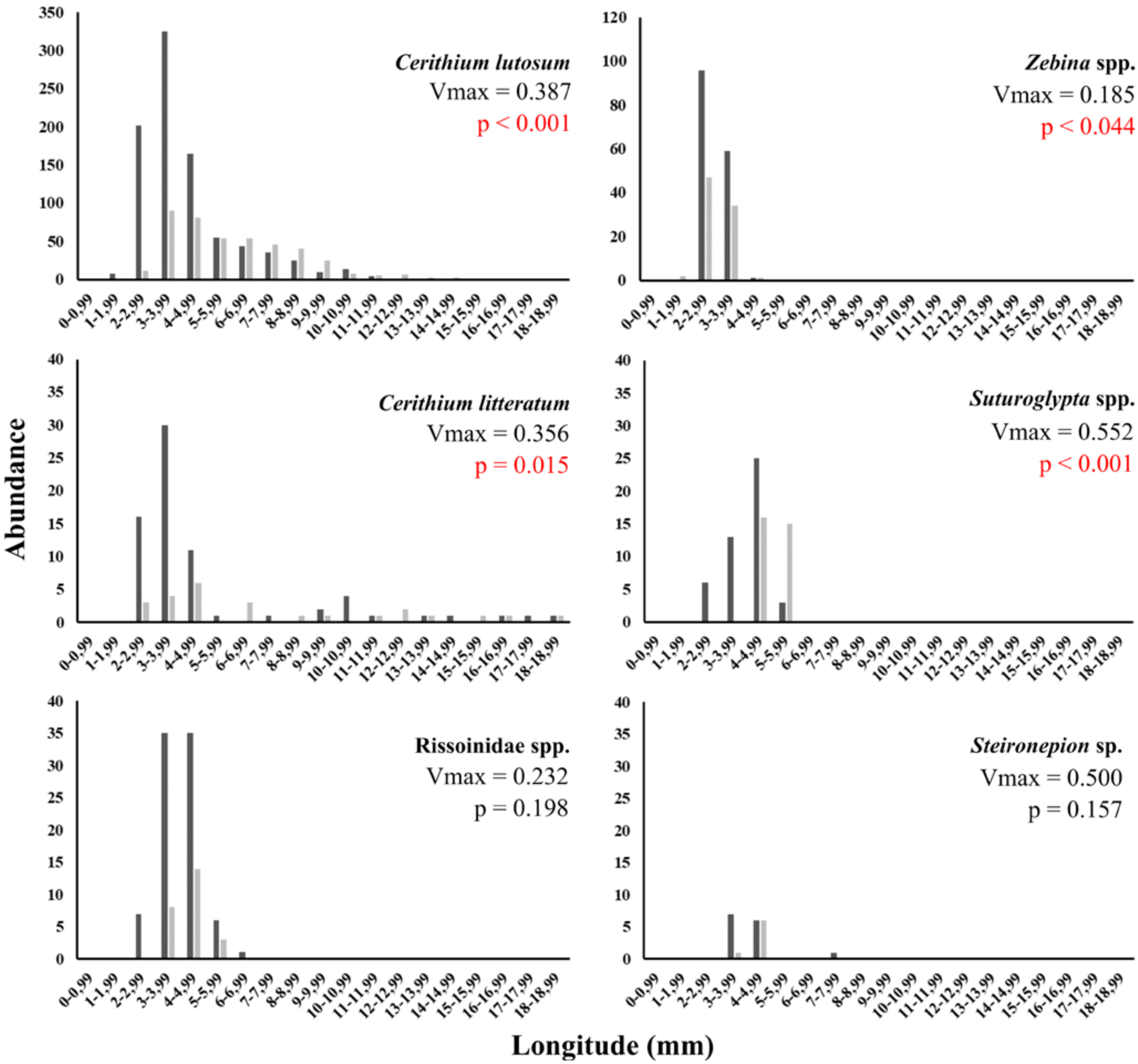

Fig. 3. Size distribution histograms of the drilled (dark-grey bars) and non-drilled (light-grey bars) gastropod shells collected in Playa Guardalavaca in June 2019. The values of the Kolmogorov-Smirnov test (Vmax) and probabilities (p) are represented. Statistically significative p-values are highlighted in red colour.

Fig. 3. Histogramas de la distribución de tallas de las conchas perforadas (barras gris oscuro) y no perforadas (barras gris claro) de los gasterópodos recolectados en Playa Guardalavaca en junio de 2019. Los valores de la prueba de Kolmogorov-Smirnov (Vmax) y las probabilidades (p) son presentadas. Los valores de p estadísticamente significativos son resaltados en color rojo.

(5.00–11.99 mm) (Fig. 3, Table 2). A similar pattern was observed in *Acteocina* spp., with a predation rate of 50–58% in shells measuring 2.00–4.99 mm. The highest predation rates were observed in *Suturoglypta* spp., reaching 83% for shells measuring 5.00-5.99 mm, and in *Brachycythara* sp., with a predation rate of 67%

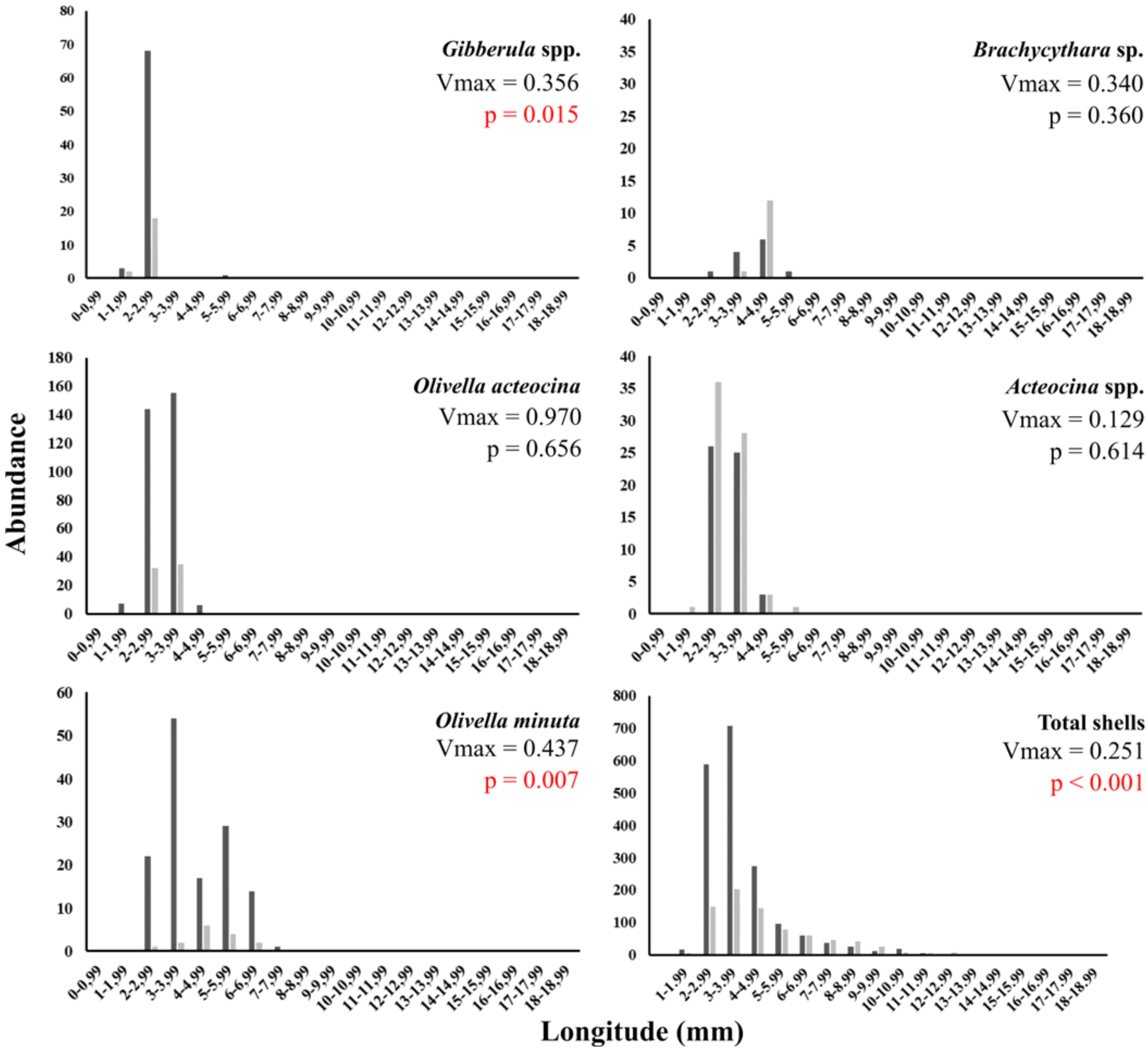

Fig. 4. Size distribution histograms of the drilled (dark-grey bars) and non-drilled (light-grey bars) gastropod shells collected in Playa Guardalavaca in June 2019. The values of the Kolmogorov-Smirnov test (Vmax) and probabilities (p) are represented. Statistically significative p-values are highlighted in red colour.

Fig. 4. Histogramas de la distribución de tallas de las conchas perforadas (barras gris oscuro) y no perforadas (barras gris claro) de los gasterópodos recolectados en Playa Guardalavaca en junio de 2019. Los valores de la prueba de Kolmogorov-Smirnov (Vmax) y las probabilidades (p) son presentadas. Los valores de p estadísticamente significativos son resaltados en color rojo.

for shells measuring 4.00-4.99 mm (Figs. 3 and 4 respectively; Table 2). The Kolmogorov-Smirnov test indicated statistically significant differences in the size distribution between drilled and non-drilled shells of *C. lutosusm*, *C. litteratum*, *Zebina* spp., *Suturoglypta* spp., *Gibberula* spp., and *O. minuta* (Figs. 3-4).

Discussion

According to Diez *et al*. (2022), the area where the present study was conducted has recorded 232 species of marine molluscs. Therefore, we have detected approximately half of them, and 70% when considering gastropods alone (166 species; see Diez & Jover, 2012; Diez *et al*., 2022). With the addition of the five species recorded for the first time in the area, the species richness of Guardalavaca reaches 237 species, including 171 gastropods. Note, however, that the reported species richness is underestimated due to the inclusion of nine species groups, each of which encompasses multiple species. For example, the group *Eulithidium* spp. includes specimens of *E. adamsi* (R. A. Philippi, 1853), *E. affine* (C. B. Adams, 1850), and *E. thalassicola* (R. Robertson, 1958). These specimens were lumped because many of them were damaged, making it impossible to identify them to species level. Similar reasons led us to report *Zebina* spp., *Acteocina* spp., *Gibberula* spp., *Odostomia* spp., *Suturoglypta* spp., and *Volvarina* spp. as containing at least two species each. The other two species groups, Rissoinidae spp. and *Schwartziella* spp., are common and diverse in Cuban waters. The former includes 17 species, and the latter includes nine species (Espinosa & Ortea, 2002; Rolán & Fernández-Garcés, 2010; Espinosa *et al*., 2012). Species of Rissoinidae are difficult to identify when the protoconch is missing and/or the shell sculpture is damaged. Until now, *Acteon*, *Brachycythara*, *Gibberula*, *Granulina*, *Mitromorpha*, *Schwartziella*, *Suturoglypta*, and *Zebina* had not been recorded from the area. Therefore, we anticipate that the reported gastropod species richness of the area will increase in the future as more fresh shells of these taxa are studied.

Given that 68.5% of the collected species exhibit drillholes, drilling predation may play an important role in shaping the characteristics of the mollusc assemblages in Guardalavaca. This argument is further supported by the high total predation rate (24.5%), which reaches even higher values for particular species. Our results for the study locality in Guardalavaca support the notion that predation rate on gastropods is similar to the situation in bivalves (22%; Diez *et al*., 2023). In other published studies, this parameter varies between 7% and 37% (Pruss *et al*., 2011), whereas in northern of Cuba, the recorded predation rates range from 19% to 29% (Gordillo *et al*., 2019).

Identifying the predators is challenging since no shells with incomplete drillholes were found. Both naticids and muricids, which are known as the primary perpetrators of mollusc drilling predation, appear well represented in the area (Diez *et al*., 2023). This is evident from the prevalence of their typical signature drill holes, characterized by a central hump in the case of naticids and a flat bottom in the case of muricids (Carriker, 1981; Kong *et al*., 2017).

However, the situation in this specific locality may be more complex due to the presence of several species of Cassidae, Marginellidae, and Nassariidae (Diez & Jover, 2012; Diez *et al*., 2022) which also display this feeding behaviour (Ponder & Taylor, 1992; Morton & Chan, 1997; Grun *et al*., 2017). Some of these potential predators themselves fell prey to drilling, as evidenced by the observed drillholes in representatives of Marginellidae (*Volvarina* spp.), Naticidae (*Polinices hepaticus* and *P. lacteus*), and Nassariidae (*Phrontis alba* and *P. candissima*). In Nassariidae, drilling predation may even be a consequence of cannibalism (Chiu *et al*., 2010). Additionally, the presence of octopuses in the area (Diez & Jover, 2012) adds another possibility, as these animals also employ drilling as a predation strategy (Greenwell *et al*., 2019; Gordillo *et al*., 2022).

The predator-prey relationships can also be influenced by the diversity of habitats in Playa Guardalavaca (see Diez *et al*., 2022, 2023). As discussed in Diez *et al*. (2023), certain muricids documented in the area, such as *Claremontiella nodulosa* (C. B. Adams, 1845), are commonly found in subtidal rocky beds, while *Plicorpurpura patula* (Linnaeus, 1758) typically inhabits the rocky intertidal, and *Phyllonotus pomum* (Gmelin, 1791) is associated with seagrass habitats.

Other potential predators display a preference for rocky bottoms (Marginellidae), while representatives of Cassidae, Nassariidae, and Naticidae are predominantly found in seagrass beds and various sandy substrates. Consequently, these species have the opportunity to feed on prey that inhabit these specific habitats. Most of the species reported in this study are commonly found in soft substrates and seagrass habitats (Table 1). Based on these factors, it is reasonable to suspect that naticids may be primarily responsible for the majority of the drillholes observed on the shells.

Our findings regarding the selectivity of predators based on prey shell size reveal a general trend of higher predation rates on small and medium-sized shells, considering the total assemblage of shells. However, this pattern lacks statistical support across five of the 11 investigated species. While some studies have reported similar findings (*e.g*., Sawyer & Zuschin, 2010; Pahari *et al*., 2016), other research has shown that drilling success was higher in smaller specimens but with a higher intensity of incomplete holes compared to larger specimens (Chattopadhyay & Dutta, 2013). It has been proposed that small or miniaturised shells represent a strategy to avoid predation (Chattopadhyay *et al*., 2020). Since we did not encounter shells with incomplete holes in our study, potential predators in this area are inferred to be highly efficient.

A promising area of further investigation is the selectivity of predators in drilling specific areas of the prey's shell surface. It is well established that predators can target different regions of the shell based on the prey's shell morphology and muscle location (Morton *et al*., 2007; Pahari *et al*., 2016). The decision to drill holes near the main muscle area can be influenced by the thickness of the shell in that region, which may require more effort from the predator (Thomas & Day, 1995). Given the morphological diversity observed in the shells studied here, it is expected that predators may employ varied drilling strategies based on their prey's shell characteristics, such as ornamentation, the proportion of the body whorl with respect to the spire, and thickness. However, previous research suggests that differences in shell ornamentation are not necessarily adaptations to drilling predation, there may not be significant differences in predation intensity between shells with low or high sculpturing (Allmon *et al*., 1990).

Overall, it can be stated that drilling predation in the gastropod assemblages of Guardalavaca is influenced by the high diversity of both prey and predators. The diverse habitats present in the area contribute to the complexity of this behaviour, as prey and predators may exhibit preferences for different substrates, such as sandy or rocky bottoms, seagrass beds, coral rubble, etc. Predators may employ different strategies depending on the morphology, abundance, and microhabitat (epifaunal, infaunal) of prey.

Acknowledgements

We thanks Marlies Monnens (Hasselt University, Belgium) for her kindly revision of the English writing. Gratitude is extended to two anoymous reviewers for their valuable contributions in revising an earlier draft of this manuscript.

Statements

Funding

This research has been partially supported by the institutional project 9136 'VLIR P1. Valorisation of environmental scientific services for climate stress mitigation in eastern of Cuba' (Universidad de Oriente, Cuba) and 'Project P1 - Risk mitigation plan for biodiversity and food production to face climatic change in the eastern region of Cuba' (Universidad de Oriente – VLIR, Belgium). YLD is currently supported by a Georg Forster Research Fellowship (Alexander von Humboldt Foundation, Germany, grant number 3.2 - CUB - 1226121 - GF-P).

Conflict of interest

The authors have no financial or non-financial conflicts of interest to declare that are relevant to the content of the manuscript. Currently, YR-S is working at 'Delegación Territorial del CITMA, Mayarí, Holguín, Cuba'.

Ethical behaviour

The authors have followed all applicable international, national, and institutional recommendations related to the use and handling of animals for research.

Permits for sampling and other permits

No permits were required for the conduct of this research.

Statement of authors' contributions

Conceptualization, YLD; Methodology, YLD and SG; Software, YLD, YR-S and AC; Formal Analysis, YLD, YR-S, AC and SG; Resources and Funding Acquisition, YLD; Writing – Original Draft Preparation, YLD, YR-S, AC and SG; Writing - Review and Editing, YLD and SG.

References

Abbott, R. (1974). *American Sea Shells*. New York, USA: Van Nostrand Reinhold.

Allmon, W.D., Nieh, J.C., Norris, R.D. (1990). Drilling and peeling of turritelline gastropods since the Late Cretaceous. *Palaeontology*, *33*, 595-611.

Archuby, F., Gordillo, S. (2018). Drilling predation traces on recent limpets from northern Patagonia, Argentina. *Palaeontol. Electron.*, *21*, 1-23.

Archuby, F.M., Adami, M., Martinelli, J.C., Gordillo, S., Boretto, G.M., Malve, M.E. (2015). Regional-scale compositional and size fidelity of rocky intertidal communities from the Patagonian Atlantic coast. *Palaios*, *30*(8), 627-643.

Bardhan, S., Saha, S., Das, S.S., Saha, R. (2021). Paleoecology of naticid–molluscan prey interaction during the Late Jurassic (Oxfordian) in Kutch, India: evolutionary implications. *J. Paleontol.*, *95*(5), 974-993.

Blustein, D.H., Anderson, R.C. (2016). Localization of octopus drill holes on cowries. *Am. Malacol. Bull.*, *34*(1), 61-64.

Carriker, M. (1981). Shell penetration and feeding by naticacean and muricacean predatory gastropods: a synthesis. *Malacologia*, *20*(2), 403-422.

Chattopadhyay, D., Dutta, S. (2013). Prey selection by drilling predators: a case study from Miocene of Kutch, India. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, *374*, 187-196.

Chattopadhyay, D., Kella, V.G.S., Chattopadhyay, D. (2020). Effectiveness of small size against drilling predation: Insights from lower Miocene faunal assemblage of Quilon Limestone, India. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, *551*, 109742.

Chiu, J.M., Shin, P.K., Wong, K.P., Cheung, S.G. (2010). Sibling cannibalism in juveniles of the marine gastropod *Nassarius festivus* (Powys, 1835). *Malacologia*, *52*(1), 157-161.

Delance, J.H., Emig, C.C. (2004). Drilling predation on *Gryphus vitreus* (Brachiopoda) off the French Mediterranean coasts. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, *208*(1-2), 23-30.

Denis, D., Ramirez-Arrieta, V.M. (2020). Si una imagen vale más que mil palabras: ¿cuanto puede decir un gráfico de cajas? *Rev. Jard. Bot. Nac.*, *41*, 57-69.

Diez, Y.L., Jover, A. (2012). Moluscos marinos del sector Bahía de Puerto Padre-Bahía de Nipe, Cuba. *Amici Molluscarum*, *20*(1), 17-28.

Diez, Y.L., García-Mora, O., Batista-Zaldívar, C.D. (2022). New records of marine molluscs for the northeastern coast of Cuba. *Rev. Invest. Mar.*, *42*(2), 47-53.

Diez, Y.L., García-Mora, O., Catalá, A., Gordillo, S. (2023). Drilling predation on bivalve shell assemblages at Playa Guardalavaca, Cuba. *Rev. Invest. Mar.*, *43*(1), 55-68.

Espinosa, J., Ortea J. (2002). Descripción de cuatro nuevas especies de la familia Rissoinidae (Mollusca: Gastropoda). *Avicennia*, *15*, 141-146.

Espinosa, J., Ortea, J., Sánchez, R., Gutiérrez, J. (2012). *Moluscos marinos de la Reserva de la Biósfera de la Península de Guanahacabibes*. La Habana, Cuba: Instituto de Oceanología.

Fox, J. (2005). The R Commander: A Basic Statistics Graphical User Interface to R. *J. Stat. Softw.*, *14*(9), 1-42.

Fox, J. (2017). *Using the R Commander: A Point-and-Click Interface or R*. Florida, USA: Chapman and Hall/CRC Press.

Fox, J., Bouchet-Valat, M. (2022). *Rcmdr: R Commander*. R package version 2.8-0.

Fürsich, F.T., Jablonski, D. (1984). Late Triassic naticid drillholes: carnivorous gastropods gain a major adaptation but fail to radiate. *Science*, *224*, 78-80.

Gordillo, S., Diez, Y.L., Espinosa, J. (2019). Marcas de depredación por perforación en bivalvos y gasterópodos de la costa norte de Cuba. *Rev. Invest. Mar.*, *39*(1), 66-75.

Gordillo, S., Malvé, M.E. (2021). Drilling predation on Antarctic tusk shells: first records on Recent scaphopods from the Southern Hemisphere. *Antarct. Sci.*, *33*(4), 344-348.

Gordillo, S., Malvé, M.E., Morán, G.A., Boretto, G.M. (2020). Naticid drilling predation from tidal flats in northern Patagonia, SW Atlantic. *J. Mar. Biol. Assoc. UK*, *100*(6), 909-919.

Gordillo, S., Morán, G.A., Malvé, M.E. (2022). Octopuses and drilling snails as the main suspects of predation traces on shelled molluscs in West Antarctica. *Polar Biol.*, *45*(1), 127-141.

Greenwell, C.N., Loneragan, N.R., Admiraal, R., Tweedley, J.R., Wall, M. (2019). Octopus as predators of abalone on a sea ranch. *Fish. Manag. Ecol.*, *26*(2), 108-118.

Grun, T.B., Kroh, A., Nebelsick, J.H., Zamora, S., Rahman, I.A. (2017). Comparative drilling predation on time-averaged phosphatized and nonphosphatized assemblages of the minute clypeasteroid echinoid *Echinocyamus stellatus* from Miocene offshore sediments (Globigerina Limestone Formation, Malta). *J. Paleontol.*, *91*(4), 633-642.

Harper, E.M. (2003). Assessing the importance of drilling predation over the Palaeozoic and Mesozoic. *Palaeogeogr.*, *Palaeoclimatol.*, *Palaeoecol.*, *201*(3-4), 185-198.

Huelsken, T. (2011). First evidence of drilling predation by *Conuber sordidus* (Swainson, 1821) (Gastropoda: Naticidae) on soldier crabs (Crustacea: Mictyridae). *Moll. Res.*, *31*(2), 125-132.

Hughes, R.N., Hughes, H.P.I. (1981). Morphological and behavioral aspects of feeding in the cassidae (Tonnacea, Mesogastropoda). *Malacology*, *20*, 385-402.

Huntley, J.W., Kowalewski, M. (2007). Strong coupling of predation intensity and diversity in the Phanerozoic fossil record. *Proc. Natl. Acad. Sci. USA*, *104*, 15006-15010.

Kabat, A.R. (1990). Predatory ecology of naticid gastropods with a review of shell boring predation. *Malacologia*, *32*(1), 155-193.

Kelley, P.H., Hansen, T.A. (1993). Evolution of the naticid gastropod predator-prey system: an evaluation of the hypothesis of escalation. *Palaios*, *8*(4), 358-375.

Kelley, P.H., Hansen, T.A. (2006). Comparisons of class and lower taxon level patterns in naticid gastropod predation, Cretaceous to Pleistocene of the US Coastal Plain. *Palaeogeogr.*, *Palaeoclimatol.*, *Palaeoecol.*, *236*, 302-320.

Kidwell, S.M. (2001). Preservation of species abundance in marine death assemblages. *Science*, *294*(5544), 1091-1094.

Kidwell, S.M. (2002). Time-averaged molluscan death assemblages: palimpsests of richness, snapshots of abundance. *Geology*, *30*(9), 803-806.

Kidwell, S. M. (2013). Time-averaging and fidelity of modern death assemblages: building a taphonomic foundation for conservation palaeobiology. *Palaeontology*, *56*(3), 487-522.

Klompmaker, A.A., Kowalewski, M., Huntley, J.W., Finnegan, S. (2017). Increase in predator-prey size ratios throughout the Phanerozoic history of marine ecosystems. *Science*, *356*, 1178-1180.

Kong, D.-Y., Lee, M.-H., Park, C.H., Lee, S.J. (2017). Boreholes on three bivalve species found on the sand beach at Sagot. *J. Asia-Pac. Biodivers.*, *10*, 441-447.

Kowalewski, M. (2002). The fossil record of predation: An overview of analytical methods. *Paleont. Soc. Pap.*, *8*, 3-42.

Kowalewski, M., Dulai, A., Fürsich, F.T. (1998) A fossil record full of holes: the Phaneorozoic history of drilling predation. *Geology*, *26*, 1091-1094.

Ludwig, J., Reynolds, J. (1988). *Statistical Ecology*. New York, USA: John Wiley and Sons.

Mondal, S., Chakraborty, H., Paul, S. (2019). Latitudinal patterns of gastropod drilling predation intensity through time. *Palaios*, *34*, 261-270.

Mondal, S., Chakraborty, H., Saha, S., Dey, S., Sarkar, D. (2021a). High biogeographic and latitudinal variability in gastropod drilling predation on molluscs along the eastern Indian coast: Implications on the history of fossil record of drillholes. *PLoS ONE*, *16*(8), e0256685.

Mondal, S., Maitra, A., Bose, K., Goswami, P., Bardhan, S., Mallick, S. (2021b). Substrate-controlled naticid gastropod drilling predation on recent barnacles from Chandipur, India and its Palaeontological implications. *Hist. Biol.*, *33*(7), 1029-1042.

Morton, B. (2006). Diet and predation behaviour exhibited by *Cominella eburnea* (Gastropoda: Caenogastropoda: Neogastropoda) in Princess Royal Harbour, Albany, Western Australia, with a review of attack strategies in the Buccinidae. *Moll. Res.*, *26*(1), 39-50.

Morton, B., Chan, K. (1997). First report of shell boring predation by a member of the Nassariidae (Gastropoda). *J. Moll. Stud.*, *63*(3), 476-478.

Morton, B., Harper, E.M. (2009). Drilling predation upon *Ditrupa arietina* (Polychaeta: Serpulidae) from the Mid-Atlantic Açores, Portugal. *Açoreana*, suppl. *6*, 157-165.

Morton, B., Peharda, M., Harper, E. M. (2007). Drilling and chipping patterns of bivalve prey predation by *Hexaplex trunculus* (Mollusca: Gastropoda: Muricidae). *J. Mar. Biol. Assoc. UK*, *87*(4), 933-940.

Munoz-Marquez, M. (2022). RcmdrPlugin.UCA: UCA Rcmdr Plug-in_. R package version 5.1-1, https://CRAN.R-project.org/package=RcmdrPlugin.UCA.

Pahari, A., Mondal, S., Bardhan, S., Sarkar, D., Saha, S., Buragohain, D. (2016). Subaerial naticid gastropod drilling predation by *Natica tigrina* on the intertidal molluscan community of Chandipur, Eastern Coast of India. *Palaeogeogr.*, *Palaeoclimatol.*, *Palaeoecol.*, *451*, 110-123.

Peterson, C.H., Black, R. (1994). Drilling by buccinid gastropods of the genus *Cominella* in Australia. *Veliger*, *38*, 37-42.

Ponder, W.F., Taylor, J.D. (1992). Predatory shell drilling by two species of *Austroginella* (Gastropoda: Marginellidae). *J. Zool.*, *228*(2), 317-328.

Pruss, S., Stevenson, M., Duffey, S. (2011). Drilling predation and taphonomy in modern mollusk death assemblages, San Salvador Island, Bahamas. *Palaeogeogr.*, *Palaeoclimatol.*, *Palaeoecol.*, *311*, 74-81.

Ramirez-Arrieta, V.M. (2020). Extended Boxplot Graphics. https://vmra.shinyapps.io/univariados/. Revised February 14, 2023.

Rolán, E., Fernández-Garcés, R. (2010). The shouldered species of the Rissoininae (Mollusca: Rissooidea) in the Caribbean with the description of three new species. *Novapex*, *11*(4), 83-91.

Sarkar, D., Bardhan, S., Mondal, S., Das, A., Pahari, A., Buragohain, D., Saha, S. (2016) Predation on Recent terebrid gastropods from the Indian subcontinent and a spatiotemporal reappraisal based on a revised global database. *Malacologia*, *59*, 271-303.

Sawyer, J.A., Zuschin, M. (2010). Intensities of drilling predation of molluscan assemblages along a transect through the northern Gulf of Trieste (Adriatic Sea). *Palaeogeogr.*, *Palaeoclimatol.*, *Palaeoecol.*, *285*(3-4), 152-173.

Taylor, J.D. (1998). Understanding biodiversity: adaptive radiations of predatory marine gastropods. In *The marine biology of the South China Sea* (pp. 187–206). Hong Kong: Hong Kong University Press.

Thomas, M., Day, R. W. (1995). Site selection by a small drilling predator: Why does the gastropod *Haustrum baileyanum* drill over muscle tissue of the abalone *Haliotis rubra*? *Mar. Freshw. Res.*, *46*(3), 647-655.

Tomašových, A., Kidwell, S.M. (2009). Fidelity of variation in species composition and diversity partitioning by death assemblages: time-averaging transfers diversity from beta to alpha levels. *Paleobiology*, *35*(1), 94-118.

Villegas-Martín, J., Rojas-Consuegra, R., Klompmaker, A.A. (2016). Drill hole predation on tubes of serpulid polychaetes from the Upper Cretaceous of Cuba. *Palaeogeogr.*, *Palaeoclimatol.*, *Palaeoecol.*, *455*, 44-52.

Warmke, G., Abbott, R. (1962). *Caribbean Seashells*. Pennsylvania, USA: Livingston Publishing Company.

WoRMS (2023). *Mollusca*. https://www.marinespecies.org/aphia.php?p=taxdetails&id=51. Revised March 10, 2023.

Zuschin, M., Nawrot, R., Dengg, M., Gallmetzer, I., Haselmair, A., Wurzer, S., Tomašových, A. (2022). Scale dependence of drilling predation in the Holocene of the northern Adriatic Sea across benthic habitats and nutrient regimes. *Paleobiology*, *48*(3), 462-479.

How to cite this article

Diez, Y.L., Rodríguez-Santos, Y., Catalá, A., Gordillo, S. (2024). Exploring marine mollusc drilling predation: insights into predator-prey dynamics and selective pressures in gastropod shell assemblages of Playa Guardalavaca, Cuba. *Rev. Invest. Mar.*, *44*(1), 01-17.