

RESEARCH ARTICLE

Drilling predation on bivalve shell assemblages at Playa Guardalavaca, Cuba

Depredación por perforación en ensambles de conchas de bivalvos de Playa Guardalavaca, Cuba

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Abstract

Drilling predation plays an important role in the evolution and diversification of organisms, and is one of the most studied biotic interactions in fossil and modern records. Marks of drilling predation on mollusc shells are proof of food activity and the selective pressure of one taxon on another. In this study, we explore drilling predation on preserved bivalve death assemblages (thanatocoenosis) at Playa Guardalavaca, Cuba. We characterize the taxonomic composition, relative abundance and incidence of drilling. Furthermore, geometric morphometric tools were used to test whether there was a preference for any particular form of shell. Forty-eight species were identified, and a little less than half (21) showed drilling predation marks. The families with the highest species richness were Lucinidae and Tellinidae, with 11 species each. A total of 1,726 valves were quantified, estimating an abundance of 863 specimens. 190 valves showed drilling marks (22% of the abundance). The most abundant species were *Lucina* sp. (464 shells), *Divalinga quadrisulcata* (328), *Americardia media* (242), *Ctena imbricatula* (156), and *Chione* spp. (117). However, the most predated species were *Epicodakia* sp. (100%), *Acorylus gouldii* (56%), and *Eurytellina* sp. (44%). The highest predation rate occurs on small and medium-sized valves (≤ 7 mm); however, according to the Kolmogorov-Smirnov test, this result is only statistically significant in *Lucina* sp. ($p < 0.001$). The morphometric analysis showed predation preferences for species with semi-circular rather than elliptical shells. These results elucidate that drilling predation on bivalves is not only determined by the abundance of prey, but also by their external morphology and size, suggesting highly specialised feeding behaviour by predators.

Keywords: biodiversity, drill holes, drilling predation, feeding behaviour, thanatocoenosis.

Resumen

La depredación por perforación juega un importante papel en la evolución y diversificación de los organismos y es una de las interacciones bióticas más estudiadas en el registro fósil y

actual. Las marcas de depredación por perforación en las conchas de los moluscos son evidencias y pruebas de la actividad alimentaria y la presión selectiva de un taxón sobre el otro. En este estudio, se explora la depredación por perforación en ensamblajes preservados de bivalvos muertos (tanatocenosis) en Playa Guardalavaca, Cuba. Se caracteriza la composición taxonómica, su abundancia relativa y la incidencia de perforaciones. Además, técnicas de morfometría geométrica fueron utilizadas para evaluar si existe preferencia por alguna forma particular de las conchas. Cuarenta y ocho especies fueron identificadas, y poco menos de la mitad (21) presentaron marcas de depredación por perforación. Las familias con mayor riqueza de especies fueron Lucinidae y Tellinidae con 11 cada una. Un total de 1 726 valvas fueron cuantificadas, estimando una abundancia de 863 ejemplares. De estas 190 valvas presentaron marcas de perforación (22% de la abundancia). Las especies más abundantes fueron *Lucina* sp. (464 conchas), *Divalinga quadrilucata* (328), *Americardia media* (242), *Ctena imbricatula* (156) y *Chione* spp. (117). No obstante, las especies más depredadas fueron *Epicodakia* sp. (100%), *Acorylus gouldii* (56%) y *Eurytellina* sp. (44%). La mayor tasa de depredación se encontró en conchas pequeñas y medianas (≤ 7 mm); no obstante, acorde a la prueba de Kolmogorov-Smirnov, este resultado es estadísticamente significativo solo para *Lucina* sp. ($p < 0.001$). El análisis morfo-métrico mostró preferencias de depredación por especies con conchas semicirculares en lugar de las elípticas. Estos resultados evidencian que la depredación por perforación en bivalvos no está solo determinada por la abundancia de presas, sino también por su morfología externa y tamaño, sugiriendo comportamientos de alimentación altamente especializados de los depredadores.

Palabras clave: biodiversidad, perforaciones, depredación por perforación, comportamiento alimentario, tanatocenosis.

Introduction

Predation has played an important role in the evolution and diversification of organisms (Vermeij, 1987). Molluscs as prey represent one of the most important

sources for the study of fossil evidence of predation due to their abundance and the good preservation of their shells (Vermeij, 1987; Kowalewski, 2002). There are four general mechanisms of predation associated with these animals: 1- fragmentation of the shells, 2- ingestion of the whole shell, 3- insertion of mouth structures and extraction of the animal soft tissues, and 4- drilling (Harper & Skelton, 1993). However, drilling predation is considered the most specialised feeding method (Ruiz, 2017), and drilling marks on molluscs and other marine invertebrates have been used to identify the predators and infer their selectivity patterns (Vermeij, 1987).

Drilling predation in molluscs is characterised by predator use of chemical secretions and physical rasping by the radula, which leaves characteristic drill holes on the shelled prey (Carriker, 1981; Kabat, 1990). Predation marks produced by drilling molluscs are evidence of their feeding activity and their feeding selectivity over other molluscs (Aiken & Risk, 1988; Pastorino & Ivanov, 1996; Martinelli *et al.*, 2013). These marks are usually also related to the prey size and the relative position on the shell (Hughes & Dunkin, 1984). However, most studies on selectivity have been conducted at the intraspecific level.

Most molluscs secrete a protective calcareous exoskeleton: the shell. However, some molluscs such as naticids and muricids have developed the capacity to drill by using a combination of both the radula and acids secreted by accessory organs. The main drilling molluscs are gastropods from the families Naticidae and Muricidae (Gordillo & Amuchastegui, 1998; Stafford, 2010). Naticids are considered the most effective drilling predators on soft bottoms, and muricids on rocky bottoms (Vermeij, 1987), although muricids also coexist in different substrates, and are potential predators of bivalves living within soft substrates (Gordillo 1998; Gordillo & Archuby, 2014). Some octopuses have also developed drilling feeding strategies (Carriker, 1981), but they use other methods that either do not leave traces, or if traces (breaks) are present, they are more

difficult to interpret. In marine snails, observations under laboratory conditions have shown that some species, such as the muricid *Acanthina monodon* (Pallas, 1774) from southern South America (Gordillo, 2001), are able to use two different strategies for feeding (drilling shells or using the labral spine to open the valves), depending on the prey and their size.

Predator-prey interactions allow the ecosystem to be kept in balance, and affect its structure and the species abundance and distribution (Barbosa & Castellanos, 2005). To study the drilling predation interactions of molluscs, shell deposits or mollusc death assemblages are used (thanatocoenosis to differentiate it from biocoenosis; Kidwell & Bosence, 1991). These deposits represent non-contemporary generations since they have been generated as a result of the mixture of organisms over a period of time, preserving the ecological fidelity of the communities from which they came (Kidwell, 2013). As they are not equivalent to one year, but rather represent a set of years or averages, they are

not affected by extreme conditions. Thus, they provide biological signals for these communities, which makes them function as valuable biological and environmental indicators (Tomašových & Kidwell, 2009; Kidwell, 2013; Archuby *et al.*, 2015).

Cuban marine molluscs are the best studied in the Caribbean. However, most of these studies are taxonomical (e.g. Espinosa *et al.*, 2020, 2021), rather than ecological (e.g. Diez & Reyes, 2014; Jover, 2021), with only one previous record of mollusc drilling activities in the archipelago (Gordillo *et al.*, 2019). In this paper, we therefore provide new information on drilling predation of mollusc assemblages and explore the relationship between this predation behaviour and the morphology of the prey.

Material and methods

Study area and sampling

Sampling was conducted at Playa Guardalavaca, Banes Municipality, Holguín Province (Fig. 1). The samples

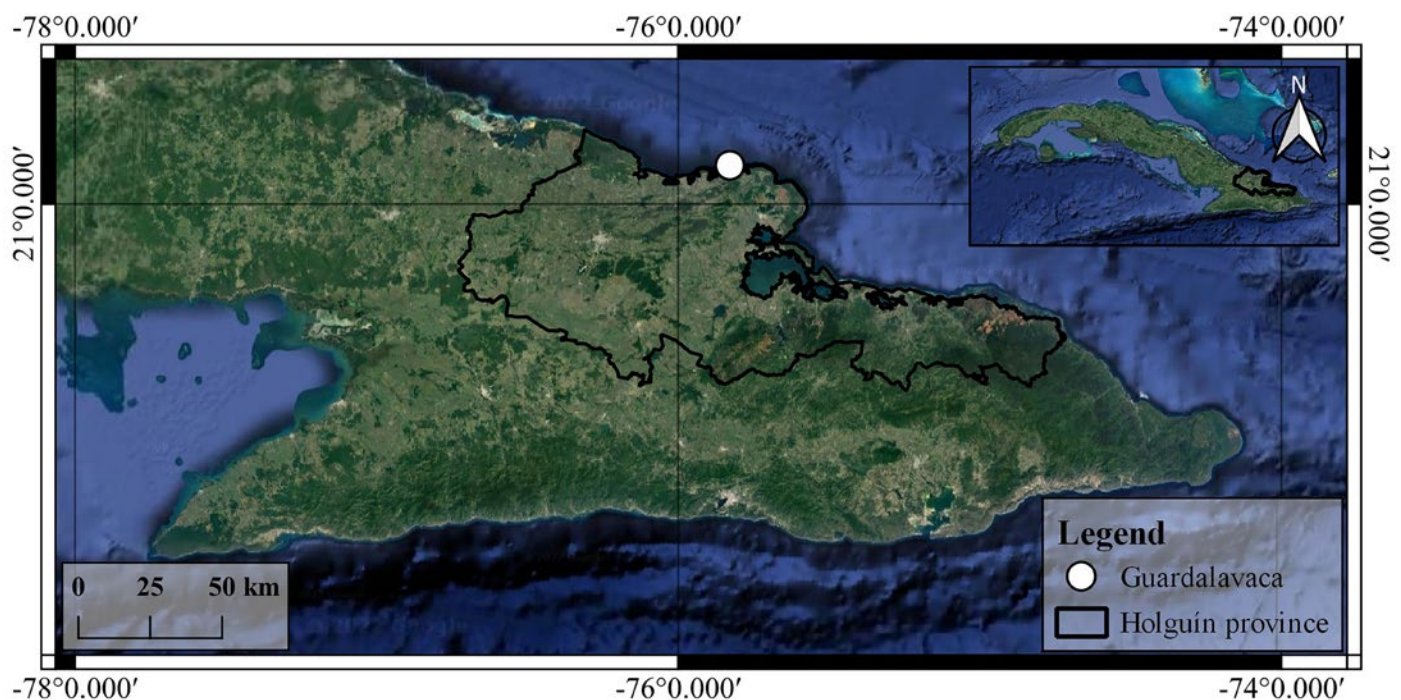


Fig. 1. Location of the sampled locality.

were taken at a point where we found a concentration of valves (21°07'17.2"N; 75°50'22.9"W). This locality is a beach with biogenic white sands of about 800 m long, and is an important tourist destination with several hotels. Ecologically, it is a reef lagoon surrounded by coral promontories, with a sandy bottom covered by grass (*Thalassia testudinum* Koenig and *Syringodium filiforme* Kützing). Previous studies in this area included the diversity of macroalgae (Zayas *et al.*, 2002) and molluscs (Diez & Jover, 2012; Diez *et al.*, 2022), and the ecology of *Ocypride quadrata* (Fabricius, 1787) [Ocaña *et al.*, 2012].

Two samples of about 2 kg each were taken in the supratidal thanatocoenosis. Samples were washed in the laboratory and dried at room temperature. A stereoscopic microscope (Novel NSZ-606) was used to separate the mollusc shells from the sand. Bivalve shells with no breaks were selected for the analyses. The species were identified using Warmke and Abbott (1962), Abbott (1974), Espinosa *et al.* (2012) and Taylor and Glover (2016). The names of the taxa were actualised using WoRMS (2022).

Data analysis

The specific richness (S_{obs}) of bivalves (Ludwing & Reynolds, 1988) was determined according to whether the shells had drilling marks or not. We considered the possible existence of two types of drilling marks: complete holes (the drillholes pierce the prey's shell reaching the soft tissues) and incomplete ones (the drillholes do not pierce the prey's shell). In order to make our study comparable with others, we divided the total number of valves by two in order to estimate the number of specimens. To estimate the predation rate, the percentage of specimens with drill holes was calculated (globally and for each species). Abundance-range curves (Whittaker, 1965) of the total species and the species with drill holes were built to assess dominance. Predation preferences by prey size were tested using size distribution histograms of the most abundant species (*Lucina* sp.,

Americardia media (Linnaeus, 1758), *Ctena imbricatu-la* (C. B. Adams, 1845), *Chione* spp., *Transennella* sp., *Acorylus gouldii* (Hanley, 1846), *Arcopsis adamsi* (Dall, 1886), and Lucinidae sp. 3. We excluded *Codakia orbicularis* (Linnaeus, 1758) from this analysis because of the disparity in the size distribution of the valves, with few valves measuring up to 71.6 mm. Shells length were measured with a digital ABS Digimatic Vernier calliper (Mitutoyo, Japan; Instrumental error ± 0.02 mm). The statistical differences of the size distribution of each species were assessed using a Kolmogorov-Smirnov test to compare two samples (two-sample K-S test), performed in STATISTICA v. 8. (StatSoft, 2007).

Geometric morphometry

We recorded the morphology of the left valve (internal view) of 16 species, randomly selecting up to 30 shells of each. Geometry morphometric tools were used to study the relationship between the shape of the valves and the predation rate. On the valves of the 16 selected species, 10 landmarks were located (Fig. 2) using the software tpsDig 2.17 (Rohlf, 2008). These landmarks

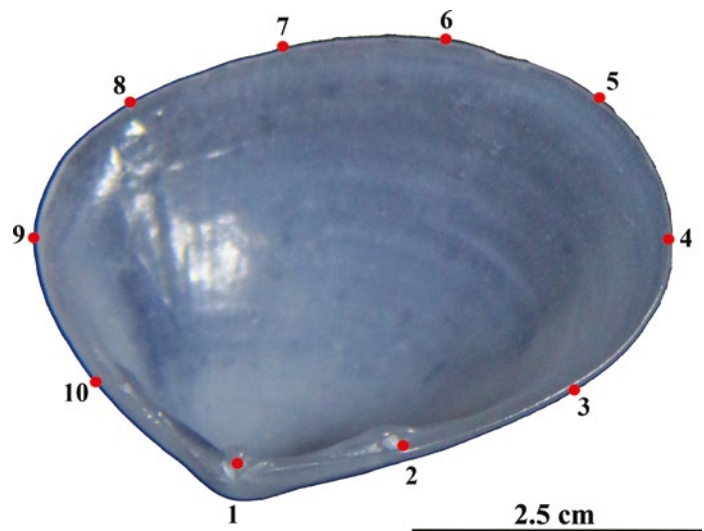


Fig. 2. Distribution of the landmarks in the left valve of *Acorylus gouldii*. The same pattern was applied to all analysed species (landmarks type I [1], type II [4 and 9], and type III [2, 3, 5, 6, 7, 8, and 10]).

were classified as type I, II or III using the anatomic and geometric criteria of Bookstein (1991). A single type I landmark (landmark 1) was located in the beak of each valve. Type II landmarks (landmarks 4 and 9) were located over the maximum curvature of the lateral margins. The other landmarks (type III) were located equidistantly over the valve margin.

A generalized Procrustes overlay was applied to landmark settings in MorphoJ v. 1.07a (Klingenberg, 2011). The procedure was carried out to eliminate information not related to shape and associated with differences in scale, position and rotation. This method transposes all landmark configurations until they share the same centre of gravity, transforms them to the same scale, and rotates them through an iterative process. This process minimises the squared distances between corresponding landmarks, taking a configuration as a reference (Klingenberg, 2013). The coordinates obtained after the Procrustes transformation were subjected to a Principal Component Analysis (PCA) using the MorphoJ program. This analysis reduces the number of variables to compare when obtaining the percentage of species showing drill holes. The first three principal components (PC), which represent more than 80% of the variance, were used in a multivariate analysis of variance by permutations (NPERMANOVA; 10,000 permutations) using PAST v. 1.99 (Hammer *et al.*, 2001) to test for differences in shell shape. After the NPERMANOVA, we tested the differences between species with pairwise comparisons of the corrected Bonferroni analysis (Armstrong, 2014). In all statistical analyses, we considered a significant level for a value of $p \leq 0.05$.

Results

Species richness and taxonomic composition

Forty-eight bivalve species belonging to 13 families and 34 genera were identified. The families with the highest species richness were Lucinidae and Tellinidae, with

11 species each, and Veneridae, with six species. The families Nuculidae, Crassatellidae, Glycymerididae, Semelidae, and Basterotiidae were represented by a single species. Twelve species were identified at generic level and six to family level. *Chione* spp. was used to name specimens of *C. cancellata* (Linnaeus, 1767) and *C. elevata* (Say, 1822) that are mostly impossible to differentiate when the shells are damaged (as usual in the thanatocoenosis). One juvenile specimen was not assigned to any taxa. Some of these species are new records for Cuba or the north-eastern coast; however, this taxonomical information will be discussed in separate papers (i.e. Diez *et al.*, 2022).

Relative abundance and drill holes

A total of 1,726 valves (863 estimated specimens) were quantified, with the most abundant species being *Lucina* sp. (464 valves; 27%), *Divalinga quadrisulcata* (d'Orbigny, 1846) (328; 19%), *A. media* (242; 14%), *C. imbricatula* (156; 9%), and *Chione* spp. (117; 7%). Eight species were represented by 21 to 63 valves and 35 species by 1 to 18 valves (Table 1). Species of Lucinidae were the most abundant (59% of the total valves), followed by Cardiidae (14%), and Veneridae (13%). The range-abundance curves of the total species showed few dominant species, and most species are either medium or low dominant (Fig. 3).

Twenty-two percent of the estimated specimens (95 specimens; 190 valves) presented complete drill holes (Table 1). Specimens showing incomplete drill holes were not found. These valves belong to 21 species (44%). Fig. 4 shows some examples of drilled valves. Species with a high number of drilled valves were *Lucina* sp. and *D. quadrisulcata* with 43 each (19% and 26% of their abundance, respectively). However, the highest drilled rate (considering species with five or more specimens) was found in *Epicodakia* sp. (100%), *A. gouldii* (56%), and *Eurytellina* sp. (44%) (Table 1). The range-abundance curves of the species with drill holes showed few dominant species,

Table 1. Number of valves, drilled valves and predation rate (% of the abundance) of the bivalves from Playa Guardalavaca, Holguín, Cuba, collected in June 2019.

Species	Family	Total valves	Perforated valves	Predation rate (%)
<i>Lucina</i> sp.	Lucinidae	464	43	19
<i>Divalinga quadrisulcata</i>	Lucinidae	328	43	26
<i>Americardia media</i>	Cardiidae	242	19	16
<i>Ctena imbricatula</i>	Lucinidae	156	19	24
<i>Chione</i> spp.	Veneridae	117	16	28
<i>Transennella</i> sp.	Veneridae	63	3	10
<i>Acorylus gouldii</i>	Tellinidae	40	11	56
<i>Semelina nuculides</i>	Semelidae	31	1	6
<i>Codakia orbicularis</i>	Lucinidae	30	6	40
<i>Barbatia domingensis</i>	Arcidae	28	2	14
<i>Arcopsis adamsi</i>	Arcidae	27	5	38
Lucinidae sp. 3	Lucinidae	23	4	34
<i>Brachidontes exustus</i>	Mytilidae	21	1	10
<i>Chioneryx pygmaea</i>	Veneridae	18	2	22
<i>Transennella cubaniana</i>	Veneridae	17	2	24
<i>Scissula candeana</i>	Tellinidae	15	3	40
<i>Barbatia candida</i>	Arcidae	11	1	18
<i>Epicodakia</i> sp.	Lucinidae	10	5	100
<i>Eurytellina</i> sp.	Tellinidae	9	2	44
<i>Gouldia cerina</i>	Veneridae	8	-	-
<i>Strigilla mirabilis</i>	Tellinidae	8	-	-
<i>Brachidontes modiolus</i>	Mytilidae	4	-	-
<i>Crassinella</i> sp.	Crassatellidae	4	-	-
<i>Crenella divaricata</i>	Mytilidae	4	-	-
Lucinidae sp. 2	Lucinidae	4	-	-
<i>Nucula proxima</i>	Nuculidae	4	-	-
<i>Tampaella mera</i>	Tellinidae	4	-	-
Tellinidae sp. 2	Tellinidae	4	-	-
<i>Chama</i> sp.	Chamidae	3	-	-
<i>Eulopia</i> sp.	Lucinidae	3	-	-
<i>Tellina radiata</i>	Tellinidae	3	-	-
<i>Anadara</i> sp. 2	Arcidae	2	1	100
<i>Botula fusca</i>	Mytilidae	2	-	-
Lucinidae sp. 4	Lucinidae	2	-	-
<i>Scissula similis</i>	Tellinidae	2	-	-
<i>Transennella stimpsoni</i>	Veneridae	2	-	-
<i>Tucetona pectinata</i>	Glycymerididae	2	-	-
<i>Clathrolucina costata</i>	Lucinidae	1	1	100
<i>Anadara</i> sp. 1	Arcidae	1	-	-

Species	Family	Total valves	Perforated valves	Predation rate (%)
<i>Basterotia quadrata</i>	Basterotiidae	1	-	-
<i>Chama macerophylla</i>	Chamidae	1	-	-
<i>Dallocardia</i> sp.	Cardiidae	1	-	-
<i>Tellinella listery</i>	Tellinidae	1	-	-
<i>Laevicardium</i> sp.	Cardiidae	1	-	-
Lucinidae sp. 1	Lucinidae	1	-	-
<i>Strigilla</i> sp.	Tellinidae	1	-	-
Tellinidae sp. 1	Tellinidae	1	-	-
Bivalvia sp.	?	1	-	-
Total		1,726	190	22

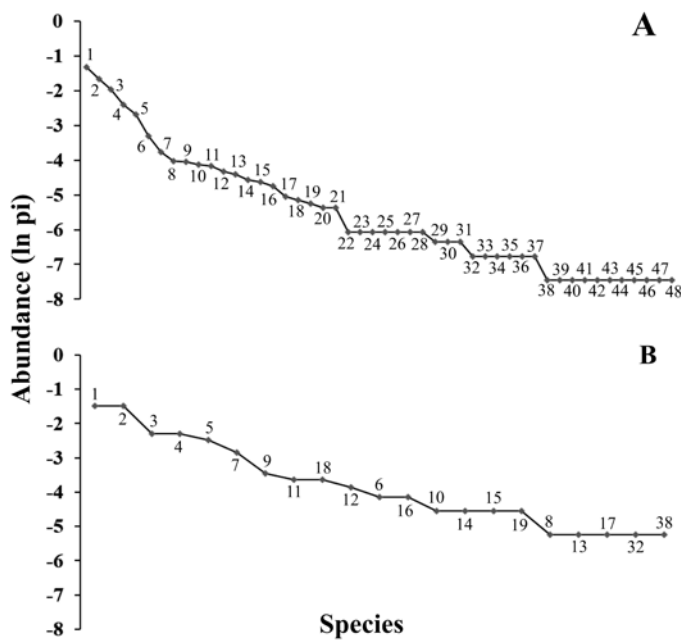


Fig. 3. Range-abundance curves of the total bivalves (A) and drilled bivalves (B) collected in Playa Guardalavaca in June 2019. 1- *Lucina* sp., 2- *Divalinga quadrisulcata*, 3- *Americardia media*, 4- *Ctena imbricatula*, 5- *Chione* spp., 6- *Transennella* sp., 7- *Acryolus gouldii*, 8- *Semelina nuculides*, 9- *Codakia orbicularis*, 10- *Barbatia dominguiensis*, 11- *Arcopsis adamsi*, 12- Lucinidae sp. 3, 13- *Brachidontes exustus*, 14- *Chioneryx pygmaea*, 15- *Transennella cubaniana*, 16- *Scissula candeana*, 17- *Barbatia candida*, 18- *Epicodakia* sp., 19- *Eurytellina* sp., 20- *Gouldia cerina*, 21- *Strigilla mirabilis*, 22- *Brachidontes modiolus*, 23- *Crassinella* sp., 24- *Crenella divaricata*, 25- Lucinidae sp. 2, 26- *Nocula proxima*, 27- *Tampaella mera*, 28- Tellinidae sp. 2, 29- *Chama* sp., 30- *Eulopia* sp., 31- *Tellina radiata*, 32- *Anadara* sp. 2, 33- *Botula fusca*, 34- Lucinidae sp. 4, 35- *Scissula similis*, 36- *Transennella stimpsoni*, 37- *Tucetona pectinata*, 38- *Anadara* sp. 1, 39- *Basterotia quadrata*, 40- Bivalvia sp., 41- *Chama macerophylla*, 42- *Clathrolucina costata*, 43- *Dallocardia* sp., 44- *Tellinella listery*, 45- *Laevicardium* sp., 46- Lucinidae sp. 1, 47- *Strigilla* sp., and 48- Tellinidae sp. 1.

A and most species are either medium or low dominant (Fig. 3).

Drilling and prey size distribution

The size distribution histograms showed a general pattern of a higher predation rate in the specimens of small to medium size, while the largest specimens were scarcely predated (Fig. 5). Species such as *C. imbricatula* and *A. gouldi* showed drilled valves in all size intervals. Notwithstanding, the Kolmogorov-Smirnov test only showed statistically significant differences in the size distribution of *Lucina* sp. ($K_{max} = 0.354$; $p < 0.001$).

Geometric morphometry

The PCA produced 16 components, thus reducing the number of initial shape variables. Of the total components, the first three were taken for the hypothesis testing, which represents more than 80% of the variance of the data. The NPERMANOVA showed significant differences in the shape of the shell between the species ($n_{AcGo} = 17$; $n_{ArAd} = 13$; $n_{BaCa} = 10$; $n_{BaDo} = 16$; $n_{ChPy} = 11$; $n_{CoOr} = 12$; $n_{EpPe} = 10$; $n_{BrEx} = 10$; $n_{Lus3} = 14$; $n_{ScCa} = 10$; $n_{SeNu} = 12$; $n_{TrCu} = 10$, and $n_{AmMe} = n_{CtIm} = n_{Chsp} = n_{Lusp} = 30$; $F = 132,200$; $p = 0,0001$). A summary of the p-values of the corrected Bonferroni test is shown in Table 2.

PC 1 and PC 2, which represent 76.85% of the variance, are shown in Fig. 6. Fig. 6A shows the component scores; note that *Brachidontes exustus* (Linnaeus,

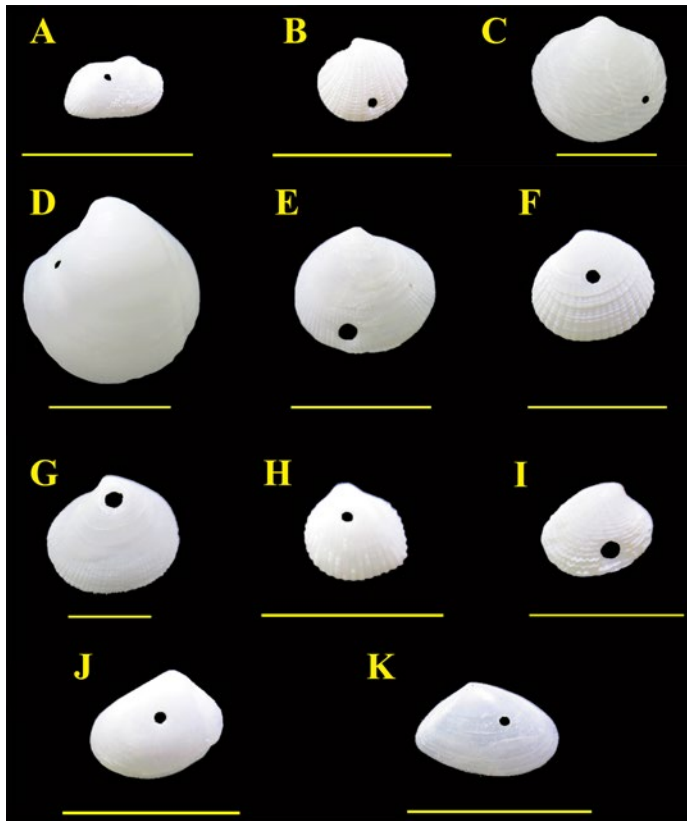


Fig. 4. Examples of drilled valves of the collected species. A- *Arcopsis adamsi*, B- *Clathrolucina costata*, C- *Divalinga quadri-sulcata*, D- *Lucina* sp., E- *Codakia orbiculatis*, F- *Ctena imbricata*, G- *Epicodakia* sp., H- *Americardia media*, I- *Chione* spp., J- *Tampaella mera*, and K- *Scissula candeana*. Scale bars = 1 cm.

1758) is separated from the rest of the species in PC 2, whereas the other species are separated in PC 1. Shell shape variability is represented in the negative (Figs. 6B & 6D) and positive direction (Figs. 6C & 6E) of PC 1 and PC 2, respectively. The species with semi-circular shells group towards the middle of both PCs, and those that segregate tend to have elliptical shapes. See Fig. 7 for a comparison of the predation rate with respect to the shell's morphology.

Discussion

This study allows us to analyse the drilling predation patterns on the bivalves of Playa Guardalavaca. Species richness was similar (i.e. 48) to the previous record for

the same locality (44 species; Diez & Jover, 2012) and represents 14% of the 338 bivalves recorded in Cuba (Espinosa *et al.*, 1995). This richness value is also higher than that recorded in the first report on drilling predation behaviour in Cuba (42 species; Gordillo *et al.*, 2019). These slight differences in the number of species could be the result of the different collecting techniques used; Gordillo *et al.* (2019) collected conspicuous shells (≥ 0.5 mm) deposited at the high tide mark, whereas in this study, small species (≤ 0.5 mm) were collected in sand samples.

The taxonomical composition of the bivalves reflects the ecological conditions of the locality. Playa Guardalavaca is a reef lagoon with sandy bottoms and grass; therefore, it is expected to find a predominance of bivalves typical of these habitats, such as the most species-rich families Lucinidae and Tellinidae (Hauser *et al.*, 2007; Dame, 2011; Taylor *et al.*, 2014). Few species are found in rocky bottoms attached to rocks via the byssus (i.e. *B. exustus* and species of *Barbatia*), perforating (*Botula fusca*), or cementing one of the valves to the rocks (species of *Chama*) (Espinosa *et al.*, 2012).

The mean predation rate value of 22% is, comparatively, moderately high taking into account that this index varies between 7% and 37% (Pruss *et al.*, 2011). The pattern of dominances, recovered in the range-abundance curves, correspond with the species of families that are also very abundant on soft bottoms, particularly lucinids (Taylor *et al.*, 2014; Taylor & Glover, 2016). A similar pattern of dominance was found in the analysis of the valves with drilling marks; 64% of the shells with drill holes are lucinids. However, the higher predation rate was not found in the most abundant species (*Epicodakia* sp. [100%], *A. gouldii* [56%], and *Eurytellina* sp. [44%]). This finding does not match the previous results by Gordillo *et al.* (2019), where the most abundant species were the most predated, suggesting that other variables, maybe size, are also determining factors.

In this regard, the histograms of size distribution suggest that there is preferential predation on small

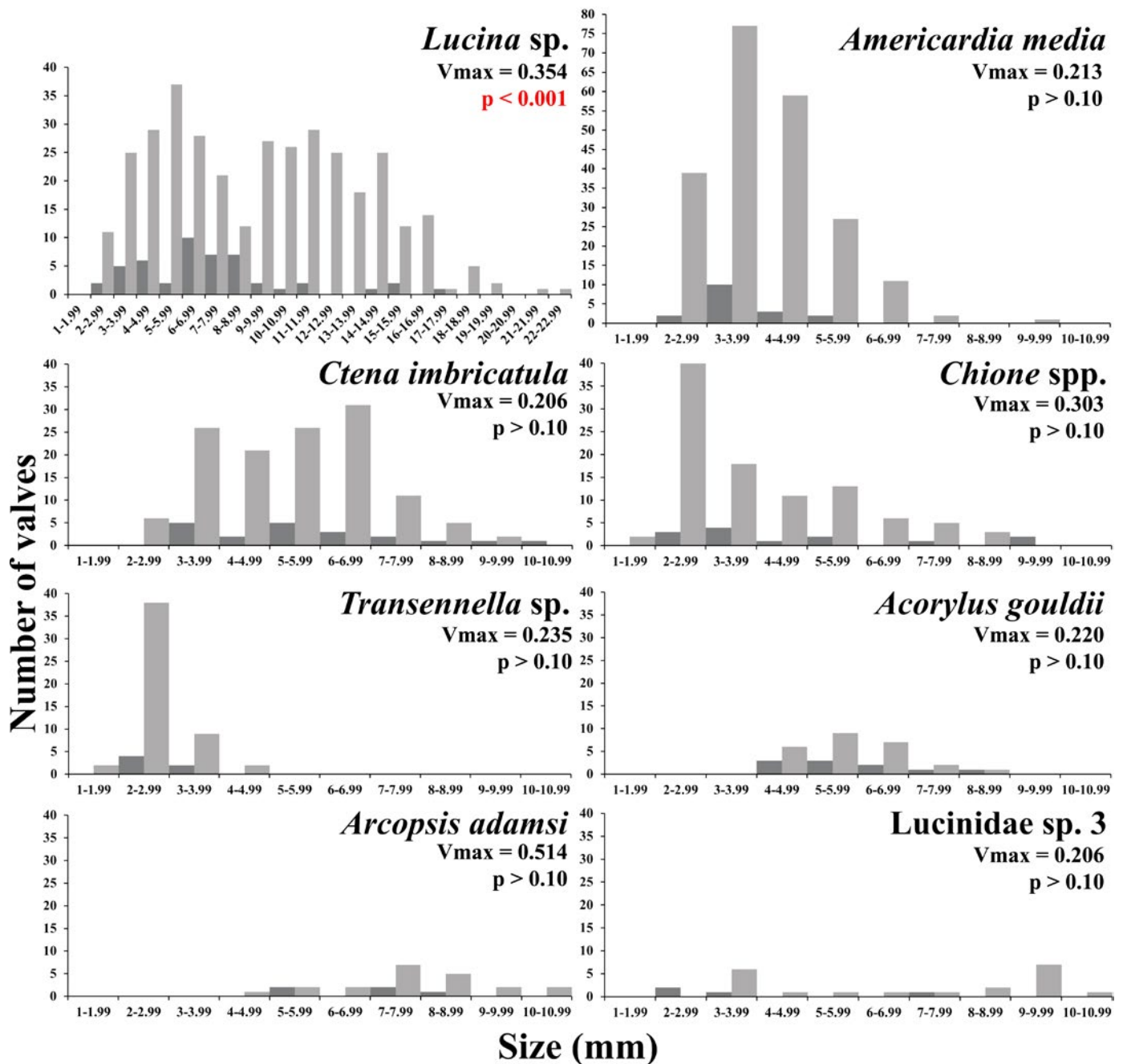


Fig. 5. Size distribution histograms of the drilled (dark-grey bars) and non-drilled (light-grey bars) bivalve shells collected in Playa Guadalavaca in June 2019. The values of the Kolmogorov-Smirnov test (Vmax) and probabilities (p) are represented. Statistically significant p-values are highlighted in red colour.

and medium-sized shells (≤ 7 mm). This fact could be determined by the ability of predators to manipulate smaller prey, or the efficiency of drilling thinner and

softer shells. We did not find drilling evidence on the larger shells of most species, including the largest, *C. orbicularis*. Other studies also show that site selectivity

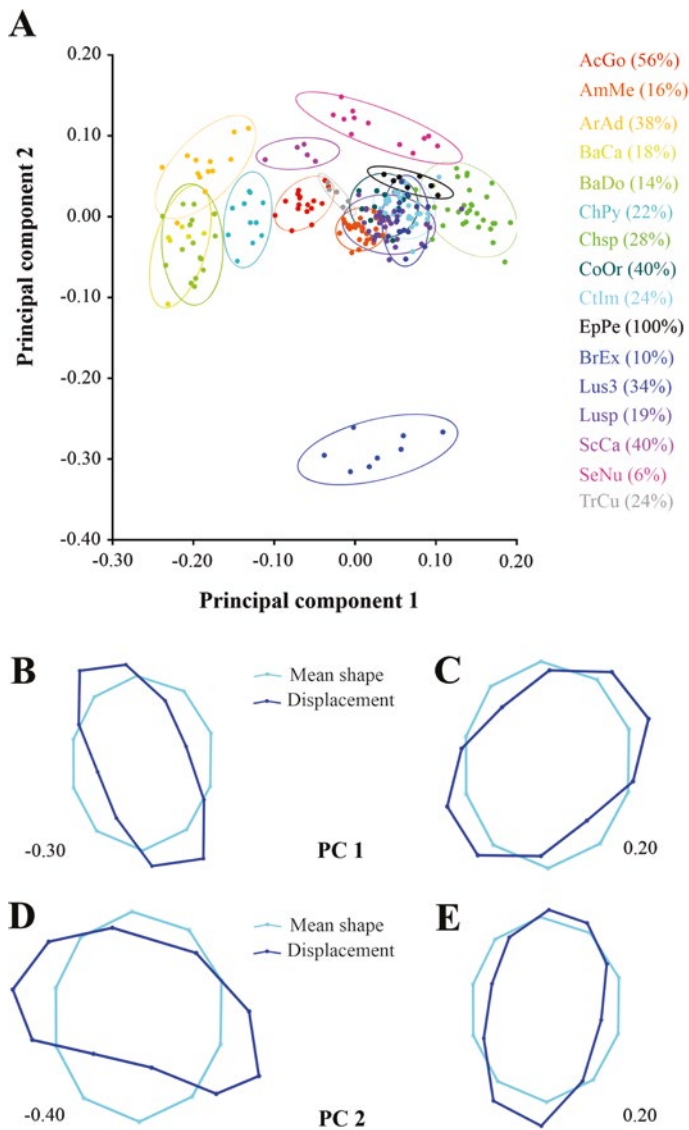


Fig. 6. A- Representation of the principal components 1 and 2 of the shape variation. The predation rate (%) is represented beside the acronym of each species. B- displacement of 0.30 units to the negative direction in PC 1. C- displacement of 0.20 units to the positive direction in PC 1. D- displacement of 0.40 units to the negative direction in PC 2. E- displacement of 0.20 units to the positive direction in PC 1. AcGo- *Acorylus gouldii*, AmMe- *Americardia media*, ArAd- *Arcopsis adamsi*, BaCa- *Barbatia candida*, BaDo- *Barbatia dominguensis*, BrEx- *Brachidontes exustus*, ChPy- *Chioneryx pygmaea*, Chsp- *Chione* spp., CoOr- *Codakia orbicularis*, Ctlm- *Ctena imbricatula*, EpPe- *Epicodakia* sp., Lus3- *Lucinidae* sp. 3, Lusp- *Lucina* sp., ScCa- *Scissula candeana*, SeNu- *Semelina nuculoides*, and TrCu- *Transennella cubaniana*.

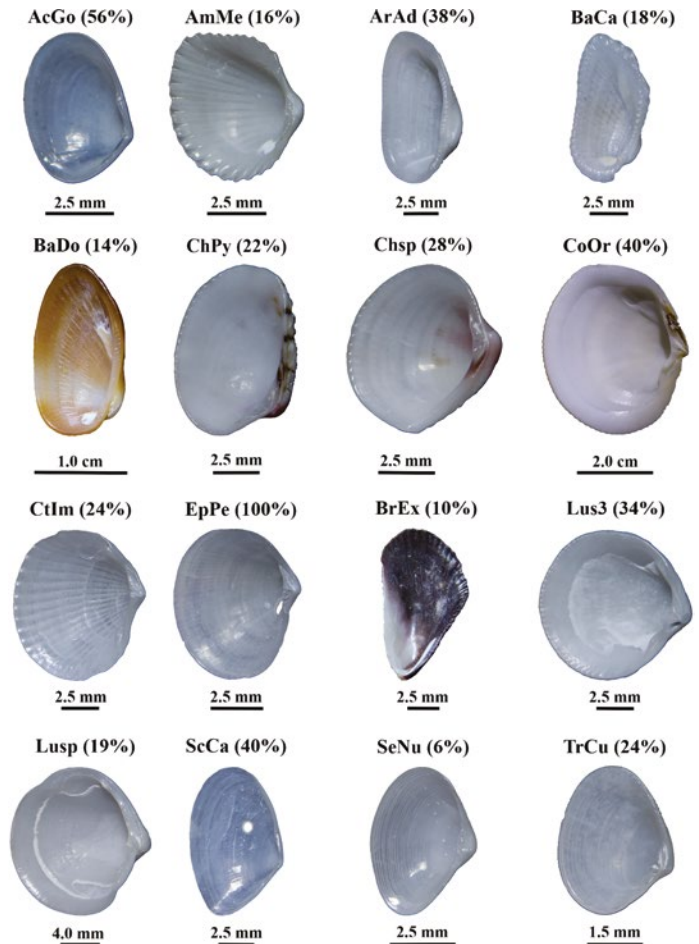


Fig. 7. Left valve of the species included in the morphometric analysis. On the upper side of the shells are the acronym name of the species and the predation rate. AcGo- *Acorylus gouldii*, AmMe- *Americardia media*, ArAd- *Arcopsis adamsi*, BaCa- *Barbatia candida*, BaDo- *Barbatia dominguensis*, BrEx- *Brachidontes exustus*, ChPy- *Chioneryx pygmaea*, Chsp- *Chione* spp., CoOr- *Codakia orbicularis*, Ctlm- *Ctena imbricatula*, EpPe- *Epicodakia* sp., Lus3- *Lucinidae* sp. 3, Lusp- *Lucina* sp., ScCa- *Scissula candeana*, SeNu- *Semelina nuculoides*, and TrCu- *Transennella cubaniana*.

or drilled area of the valves depends, at least partially, on the prey size (Chiba & Sato, 2011), but this pattern varies and can be different for each prey (Valdez & Araiza, 2015). The morphometric analysis differentiated two groups of shells: semi-circular and elliptical. Species with elliptical shells such as *B. exustus* showed the lowest predation rates. These results suggest that the shape and size could be a key trait in the selection of

Table 2. Summary of the p-values of the pairwise comparisons of the corrected Bonferroni test. AcGo- *Acorylus gouldii*, AmMe- *Americardia media*, ArAd- *Arcopsis adamsi*, BaCa- *Barbatia candida*, BaDo- *Barbatia dominguensis*, BrEx- *Brachidontes exustus*, ChPy- *Chioneryx pygmaea*, Chsp- *Chione* spp., CoOr- *Codakia orbicularis*, Ctlm- *Ctena imbricatula*, EpPe- *Epicodakia* sp., Lus3- *Lucinidae* sp. 3, Lusp- *Lucina* sp., ScCa- *Scissula candeana*, SeNu- *Semelina nuculoides*, and TrCu- *Transennella cubaniana*.

Species	AcGo	AmMe	BaCa	BaDo	Chsp	ChPy	CoOr	Ctlm	EpPe	BrEx	Lusp	Lus3	ScCa	SeNu	TrCu	ArAd
AcGo	-	0	0.8438	0.9747	0.7932	0.1375	0	0	0.047	0.5241	0.037	0.0001	0.0221	0.0198	0.0153	0.0003
AmMe	0	-	0.0042	0	0.2637	0	0.0988	0.1484	0.3081	0.0001	0.6336	0.6211	0.127	0.4115	0.0958	0
BaCa	1	0.504	-	0.3712	0	0.0002	0.4643	0.3846	0.0007	0.0003	0.9048	0.5998	0.0024	0	0.0016	0.0014
BaDo	1	0	1	-	0	0	0.5059	0.5228	0	0	0.8581	0.6866	0.0001	0	0	0
Chsp	1	1	0	0	-	0	0.9991	0.9064	0	0	0.9982	0.9932	0	0	0	0
ChPy	1	0	0.024	0	0	-	0.0001	0	0	0	0.7211	0.0013	0.0005	0	0.0002	0
CoOr	0	1	1	1	1	0.012	-	0.09	0.8255	0.4408	0.1539	0.1044	0.0444	0.9564	0.0924	0
Ctlm	0	1	1	1	1	0	1	-	0.7065	0.4426	0.9228	0.4235	0.106	0.6531	0.0047	0
EpPe	1	1	0.084	0	0	0	1	1	-	0	0.8899	0.7335	0.0009	0	0.0033	0
HoEx	1	0.012	0.036	0	0	0	1	1	0	-	0.8697	0.5539	0.0009	0	0.0004	0
Lusp	1	1	1	1	1	1	1	1	1	1	-	0.1095	0.4491	0.8489	0.7974	0.5981
Lus3	0.012	1	1	1	1	0.156	1	1	1	1	1	-	0.1117	0.7974	0.0341	0.0001
ScCa	1	1	0.288	0.012	0	0.06	1	1	0.108	0.108	1	1	-	0.0001	0.0065	0
SeNu	1	1	0	0	0	0	1	1	0	0	1	1	0.012	-	0.0016	0
TrCu	1	1	0.192	0	0	0.024	1	0.564	0.396	0.048	1	1	0.78	0.192	-	0
ArAd	0.036	0	0.168	0	0	0	0	0	0	0	1	0.012	0	0	0	-

prey, and are evidence that selective and specialised predation occur. Specialised predation has been found in Brazil, where gastropods can feed on different bivalves depending on the prey's morphology and shell thickness (López *et al.*, 2010).

Regarding potential predators, both naticids and muricids have been recorded in the study area (Diez & Jover, 2012). Naticids are common predators on soft bottoms and are generally small animals: *Natica livida* Pfeiffer, 1840 (maximum size 0.75 cm long), *Polinices lacteus* (Guilding, 1834) (max. size 3.7 cm), and *Naticarius canrena* (Linnaeus, 1758) (max. size 5.0 cm) (Warmke & Abbott, 1962). Therefore, they may predate small molluscs such as bivalves. However, some muricids recorded in the area are larger such as *Plicorpurpura patula* (Linnaeus, 1758) (max. size 9.0 cm) and *Phyllonotus pomum* (Gmelin, 1791) (max. size 12.0 cm), and may preferentially feed on larger molluscs. However, their juvenile specimens can also predate small molluscs. The habitat of both predators and prey can also determine their interactions

and predation behaviour. Whereas naticids live in soft bottoms, muricids are commonly found on rocky bottoms. Muricids also exhibit broad habitat preferences; for example, *P. patula* is commonly found in the intertidal, *P. pomum* in muddy sublittoral and grasses, and the small *Claremontiella nodulosa* (C. B. Adams, 1845) inhabit subtidal rocky beds. The last mentioned species (max. size 2.5 cm; Warmke & Abbott, 1962) also has been recorded from the study locality (Diez & Jover, 2012).

In general, our results support the hypothesis that drilling predation does not only depend on the availability of prey; other aspects such as size and shape also have implications for prey selection. More complex predation behaviours can include specialised feeding determined by the prey size and shape. In addition, the type and size of predators would influence the selection of prey on different substrates. Further studies are therefore needed to address the different situations in Cuba's coastal environments.

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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.

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.

Authors' contributions

Author Contribution: Conceptualization and Methodology, YLD, AC and SG; Field collecting and Formal Analysis, YLD and OG-M; Resources and Funding Acquisition, YLD and SG; Writing - Original Draft Preparation, YLD, OGM and AC; Writing - Review and Editing, YLD and SG.

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