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Profiling abundance, size, and shell utilization patterns of *Coenobita clypeatus* (Fabricius, 1787) (Decapoda: Anomura: Coenobitidae) in protected and highly frequented beaches in Puerto Rico

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ABSTRACT

The coastal Caribbean is a well-known harbor for biodiversity, yet it is mainly valued for its ample resources and services. Economic interests typically supersede conservation efforts, introducing anthropogenic-related factors such as noise, chemical pollution, and geographical disturbances into the littoral zone, where ecological diversity is abundant. Although human activity is known to be detrimental to biodiversity across habitats, the effect of conservation measures that limit anthropogenic activity on coastal populations remains understudied. To measure the benefit of conservation in the littoral environment, we sampled populations of the hermit crab *Coenobita clypeatus* (Fabricius, 1787) of highly frequented (non-protected) and protected beaches in northern Puerto Rico. We profiled 1,119 individuals by using transects, describing their size and shell utilization patterns during winter and summer. The *C. clypeatus* population was larger ($P < 0.0001$ during both seasons) and more abundant ($P = 0.0006$ during winter, $P < 0.0038$ during summer) in the protected beach than in the non-protected beach, with no effect of season. Shell utilization patterns were more consistent in the protected beach, likely due to the greater availability of gastropod shells. These results suggest that the conservation measures implemented in the protected beach promote the survival, reproduction, and growth of hermit crabs in the location. Expansion of protected habitats through governmental and civilian efforts should enhance the conservation of the biodiversity of protected areas.

KEY WORDS: anthropogenic factors, conservation, Crustacea, natural reserves, West Indies

INTRODUCTION

An outstanding characteristic of the coastal regions of the Caribbean region is its rich biological diversity (Beatley, 1991; Anadon-Irizarry *et al.*, 2012). In particular, the littoral zone harbors several unique animal species, including molluscs, echinoderms, and crustaceans (Göltenboth *et al.*, 2006). The economic value of the littoral zone, however, attracts anthropogenic activity through tourism and urbanization, the effects of which may threaten the integrity of coastal ecosystems (Chan & Blumstein, 2011; Ke *et al.*, 2011). The destruction of the ecosystem, replacement by structures, and disruption by chemical and noise pollution may disturb the behavior of various animal species in urbanized coastal regions (Beatley, 1991; Neves & Bemvenuti, 2006; Dauvin, 2008; Pine *et al.*, 2016). Anthropogenic-related factors increase energy expenditure when searching for food, shelter (Stillman & Goss-Custard, 2002), and mates (Butler & Maruska, 2020), impacting fitness and decreasing population density. Increasing the number and area of protected habitats or natural reserves is a viable strategy to regulate urban development and preserve biodiversity (Beatley, 1991; Ke *et al.*, 2011). More empirical data on the population of coastal organisms occupying the understudied littoral zone is necessary to better understand the effects of urbanization and promote local legislation for coastal conservation.

The Caribbean hermit crab, *Coenobita clypeatus* (Fabricius, 1787), is a semi-terrestrial decapod crustacean that inhabits the supralittoral zone of tropical regions, including the Bahamas (Morrison & Spiller, 2006), Jamaica (Warner, 1969), and Puerto Rico (Nieves-Rivera & Williams, 2003). A variety of factors

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related to human presence, such as chemical contamination and physical disturbances, adversely alter the population dynamics of hermit crabs and other animals of the littoral zone (Schlacher *et al.,* 2016). Previous studies have reported that the marine hermit crab, *Pagurus bernhardus* (Linnaeus, 1758) is slower and more hesitant to change from a suboptimal to an optimal shell when exposed to reduced sea water pH, indicating the potential vulnerability of resource assessment and decision-making to environmental stressors (de la Haye *et al.,* 2011). Another environmental stressor, sound pollution, was also found to alter social behavior in *P. bernhardus*, depending on the size of the shell occupied (Tidau & Briffa, 2019). Ryan *et al.,* (2012) showed that short bursts of elevated levels of sound had a detrimental effect on the response of *C. clypeatus* to predators. Roberts (2021) characterized chirp events in *Coenobita compressus* (H. Milne Edwards, 1837), which occurred during shell fights and in the presence of conspecifics. Despite these findings, differences in the population dynamics of coastal organisms, such as *C. clypeatus,* in protected and non-protected environments are yet to be documented.

We used the transect method to compare differences in the patterns of abundance, size, and shell utilization by *C. clypeatus* in a non-protected, highly frequented beach and in a protected natural reserve on the northern coast of Puerto Rico. We hypothesized that *C. clypeatus* is less abundant and smaller in size in the non-protected beach in comparison to a protected beach. Our goal is that the presented data will promote local legislation to preserve the coastal region and increase the size and number of protected coastal areas. Furthermore, our research may establish *C. clypeatus* as a local bioindicator (Holt & Miller, 2010) to study the effects of regulations in the littoral zone.

METHODS

Study site

We selected two study sites in the northern coast of the main island of the Puerto Rican archipelago. Both sites have a similar topography, vegetation, tidal activity, and weather conditions, but with differences in anthropogenic activity (Fig. 1). The analyzed beaches were Puerto Nuevo in Vega Baja (18.490103º N, –66.3945295º W), a non-protected and highly frequented beach, and Hacienda La Esperanza in Manatí (18.4808763º N, –66.5196964º W), the largest natural reserve of its type in northern Puerto Rico. The two study sites are approximately 13.52 km apart. Both beaches include subtidal environments populated by seagrass meadows and aeolianite rock formations. The beaches also share similar land vegetation (grasses, vines, *Coccoloba uvifera*, *Calophyllum antillarum*). Puerto Nuevo and La Esperanza beaches, nevertheless, differ in the anthropogenic effects along the study sites, where the former is located near a commercial and residential area, as well as a main road, whereas the latter is located farther from less densely populated urban areas. We defined a non-protected beach as an area with constant anthropogenic activity and minimal regulation mediated by governmental or non-governmental organizations. In contrast, we define a protected beach as an area where ecological features are preserved, and anthropogenic activity is regulated by governmental or non-governmental organizations. The implementation of conservation measures in La Esperanza is managed and monitored by the non-profit organization, Para la Naturaleza (https://www.paralanaturaleza.org/).

The field studies were conducted in cycles and were completed in the morning over two consecutive days in each beach. Annual differences in tide levels, as well as littoral dynamics may vary per season within the same studied beach. Beach-visitation patterns were also likely to differ due to seasonal variations in weather and anthropogenic activity. For these reasons, field studies were conducted during January (winter) and July (summer).

Transect sampling

The broadest ecological diversity of the littoral area can be found in the supralittoral zone, which is defined by the onset of coastal vegetation on the shore inward (Peters & Lodge, 2009). We used the transect and quadrats method (see Bertness, 1981) to assess hermit crab abundance, size, and shell utilization patterns, in the supralittoral zones of the studied beaches. Five transects, each 5 m long, were laid parallel to each other and 5 m apart from each other. Each transect was composed of five 1 m^2 × 1 m^2 quadrats. Transects were positioned perpendicular to the shoreline and began within the supralittoral zone. Hermit crabs were counted and analyzed from odd quadrats at 8:00, 9:00, 10:00, 11:00, and 12:00 noon. Hermit crab individuals were retained after each period of quadrat sampling until all transects were completed to avoid recounting individuals. Crabs were relocated and distributed within the studied site following data collection.

Measurements of crab size and percentage of shell occupation

The major chela of hermit crab individuals was measured in the field as a morphological character to estimate size with minimal disturbance (see Colón-Piñeiro *et al.,* 2021; Morrison & Spiller, 2006). We measured the length of the major chela with calipers ± 0.01mm. To evaluate shell utilization patterns, we photographed the occupied gastropod shell to identify the species. The hermit crab's dry body weight was estimated from a linear regression correlating dry body weight and chela length: Y= 0.231 + 2.995 * *x*, where Y = dry body weight and x = measured chela length in mm (Morrison & Spiller, 2006). The percentage of shell occupation per season was calculated by dividing the number of hermit crabs that occupied the shell of a particular species of gastropod, over the total number of hermit crabs profiled in both the highly frequented and protected beach, during winter or summer.

Statistical analysis

A two-way repeated measures ANOVA was used to compare crab abundance differences in the non-protected and protected beaches (Fig. 2). A mixed-effects two-way ANOVA was used to compare differences between chela length and dry body weight measurements in the non-protected and protected beaches (Fig. 3). Post-hoc Šídák's tests were used when there was a main effect of beach type or an interaction between beach type and season (Figs. 2, 3).

We performed linear regressions to visualize slopes between beach types and seasons, as well as to make an initial probe of the relationship between chela length (mm) and shell aperture length (mm). Because chela length (mm) has a positive

Figure 1. Study site topography is similar between Puerto Nuevo (18.490103º; -66.3945295º W; Google Earth, https://earth.google.com/web/search/Hacienda+La+Esperanza+Para+la+Naturaleza,+Calle+La+Esperanza,+Manat%C3%AD,+Puerto+Rico/@18.47520438,-66.52260072,16.00127533a,3274.35212106d,35y,-0h,0t,0r/data=CigiJgokCZ4W3asvgDJAEU6lvKmgfDJAGbRsMeqnmFDAISgze6pNmlDA) (**A**) and La Esperanza (18.4808763º N, –66.5196964º W; Google Earth, https://earth.google.com/web/@18.4937774,-66.39811953,6.56378605a,2444.42792695d,35y,-0h,0t,0r) (**B**). Google © Maxar Technologies Data SIO, NOAA, U.S. Navy, NGA, GEBCO TerraMetric.

relationship with dry body weight (g) and serves as a proxy for crab size, we explored whether chela length would also correlate positively with shell aperture length. Linear regression analyses were used (Fig. 4, Table 1).

To evaluate the relationship of shell aperture length with chela length, beach type, and season, we performed a generalized linear model (GLM). To establish which predictive variable had the higher correlation, we calculated the percent of variation

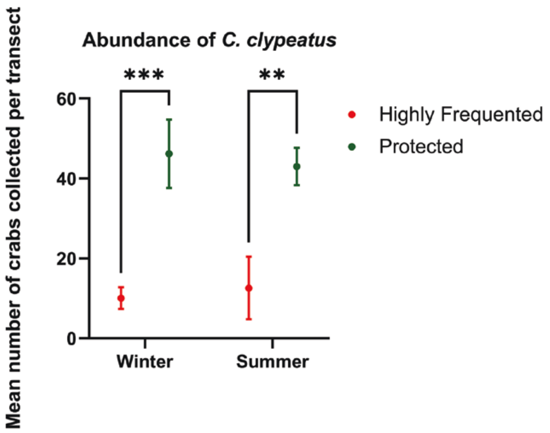

Figure 2. The abundance of *Coenobita clypeatus* according to the beach type and season.

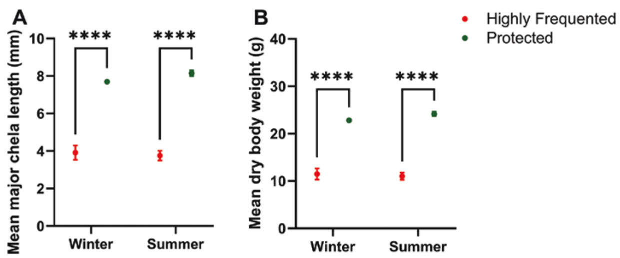

Figure 3. Major chela size (**A**) and body weight (**B**) of *Coenobita clypeatus* by beach type and season.

explained by each variable included in the model, dividing the regression sum of squares for each predictive variable by the total sum of squares (Acevedo-Charry & Aide, 2019; Colón-Piñeiro *et al.*, 2021). GLM analysis summary is included in Table 2.

To verify whether the number of gastropod-shell types varied significantly between the studied beaches, we performed a Chi-square test of independence comparing the frequency of the most occupied shells during both winter and summer seasons. Differences were considered statistically significant when probability values were ≤ 0.05.

RESULTS

A two-way ANOVA revealed a significant effect of beach type on the number of crabs collected in each transect ($F_{(1,18)} = 26.42$, $P < 0.0001$). We found no effect of season nor interaction between season and beach type on the number of crabs collected in each transect ($F_{(1,18)} = 0.003039$, $P = 0.9566$, $F_{(1,18)} = 0.2015$, $P = 0.659$, respectively). Šídák's multiple comparisons test revealed that more crabs were collected on average in each transect at the protected beach compared to the non-protected, highly frequented beach for both the winter and summer seasons ($t_{(36)} = 3.983$, $P = 0.0006$, $t_{(36)} = 3.354$, $P < 0.0038$, respectively) (Fig. 2). The total number of crabs identified during winter and summer was 101 and 126 in the non-protected beach, 462 and 430 in the protected beach, respectively.

A mixed-effects two-way ANOVA revealed a significant effect of beach type ($F_{(1,1115)} = 338.1$, $P < 0.0001$) on chela length in the two types of beaches analyzed. No effect of season ($F_{(1,1115)} = 0.4026$, $P = 0.5259$) or season *versus* beach ($F_{(1,1115)} = 1.780$, $P = 0.1824$) was detected. Šídák's multiple comparisons test revealed that crabs collected from the protected beach are larger, as measured by chela length, compared to those from the non-protected beach for both the winter and summer seasons ($t_{(1115)} = 11.41$, $P < 0.0001$, $t_{(1115)} = 14.34$, $P < 0.0001$, respectively) (Fig. 3A). Since dry body weights were not measured in the field, we used the formula ($Y = 0.231 + 2.995 * x$) (Morrison & Spiller, 2006) to estimate the crabs' dry body weight. Similarly, mixed-effects two-way ANOVA revealed a significant effect of beach type ($F_{(1,1115)} = 338.1$, $P < 0.0001$). No effect of season ($F_{(1,1115)} = 0.4026$, $P = 0.5259$) or season *versus* beach ($F_{(1,1115)} = 1.780$, $P = 0.1824$) was detected. Šídák's multiple comparisons test also revealed that crabs collected from the protected beach have a higher dry body weight compared to those from the non-protected beach for both seasons ($t_{(1115)} = 11.41$, $P < 0.0001$, $t_{(1115)} = 14.34$, $P < 0.0001$, respectively) (Fig. 3B). Since dry body weight estimates were calculated using the formula of Morrison & Spiller (2006), which uses chela length as the explanatory variable, the statistics obtained from the mixed-effects two-way ANOVA and Šídák's multiple comparisons test are the same. Overall, these findings suggest that both dry body weight and major chela length are accurate estimates of crab size.

Linear regression analyses of the relationship between chela length and shell-aperture length revealed that in both the protected and non-protected beach, regardless of season, there is a significant and positive relationship between the two variables (Table 1). We used a generalized linear model (GLM) to assess the statistical significance of major chela length, location, and season as predictors for shell aperture length. The GLM test revealed that chela length is the most important predictive variable in the model, predicting most of the variance (76%) in shell-aperture length (Table 2).

To assess shell-occupation patterns in the field, each shell was photographed, and the gastropod identified. During winter, hermit crabs in the non-protected beach utilized 24 genera of gastropod shells, of which 11 were unique to Puerto Nuevo. In the protected beach, hermit crabs occupied 36 different genera of gastropods, and of these, 24 were only found in La Esperanza. During summer, hermit crabs of the non-protected beach utilized 23 genera of gastropods, where only three were unique to Puerto Nuevo. In the protected beach, 39 different gastropod genera were occupied by crabs, and 19 of these shells were only documented in La Esperanza. Shell occupation was measured in percentage of occupation of each identified gastropod shell observed per season (Supplementary material Tables S1, S2), for winter and summer, respectively. Measuring the frequency of shell use by beach type, the most used shells in the non-protected beach during winter were the land snail *Bulimulus guadalupensis* (Bruguière, 1789) (18.8%), the tessellated nerite *Nerita tessellata* (Gmelin, 1791) (11.9%), and the green star shell *Astraea tuber* (Linnaeus, 1767) (9.9%). During summer, the most used shells in the non-protected beach were the glossy dove shell *Nitidella nitida* (Lamarck, 1822) (34.1%), *N. tessellata* (9.5%), and *A. tuber* (6.4%). The most used shells in the protected beach during winter were *A. tuber* (34.9 %), *N. tessellata* (11.5 %), and the beaded periwinkle *Tectarius muricatus* (Linnaeus, 1758) (7.6 %), and following the same

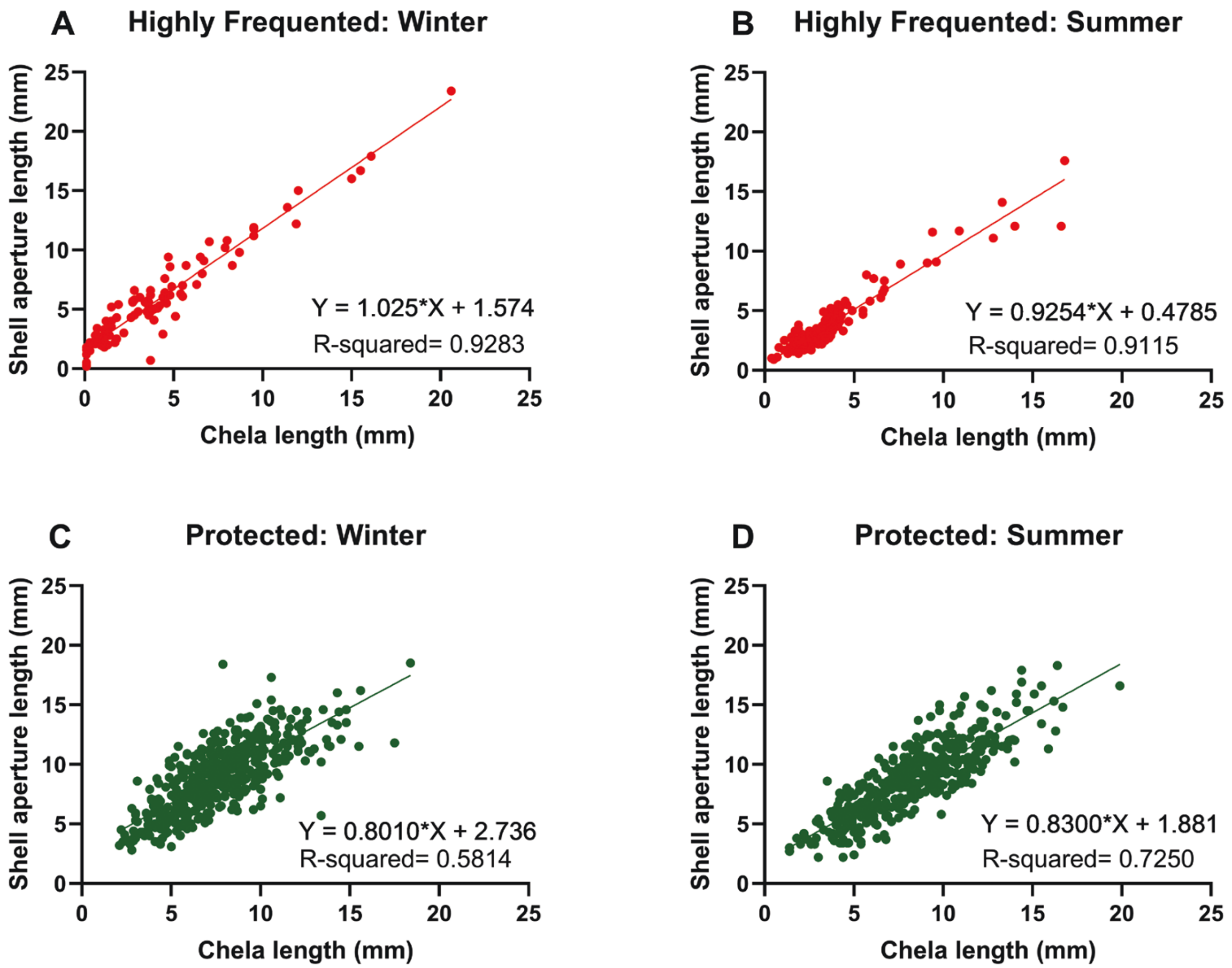

Figure 4. Linear relationship between chela length (mm) and shell aperture length (mm) of *Coenobita clypeatus* by beach and season.

Table 1. Linear regression analyses of the relationship between the chela length and aperture length of occupied gastropod shells by the *C. clypeatus* population of conserved and non-conserved beaches.

Beach type	Season	DFn, DFd	Intercept	Slope	R^2	*P*
Highly Frequented	Winter	1, 99	1.574	1.025	0.9283	< 0.001
Highly Frequented	Summer	1, 124	0.4785	0.9254	0.9115	< 0.001
Protected	Winter	1, 460	2.736	0.8010	0.5814	< 0.001
Protected	Summer	1, 428	1.881	0.8300	0.7250	< 0.001

Table 2. Generalized linear-model analysis of the effects of chela length, beach type, season, and the interaction between beach type and season on the aperture length of shells occupied by *C. clypeatus* populations in non-conserved and conserved beaches.

	Estimate + SE	Pr(> |t|)	% Variance explained
Intercept	1.64955 ± 0.15351	< 0.001	NA
Chela	0.85848 ± 0.01619	< 0.001	76.31%
Beach	0.91986 ± 0.17997	< 0.001	0.004%
Season	0.64446 ± 0.10962	< 0.001	1.35%
Beach * Season	0.85175 ± 0.24411	< 0.001	0.23%
Residuals			21.72%

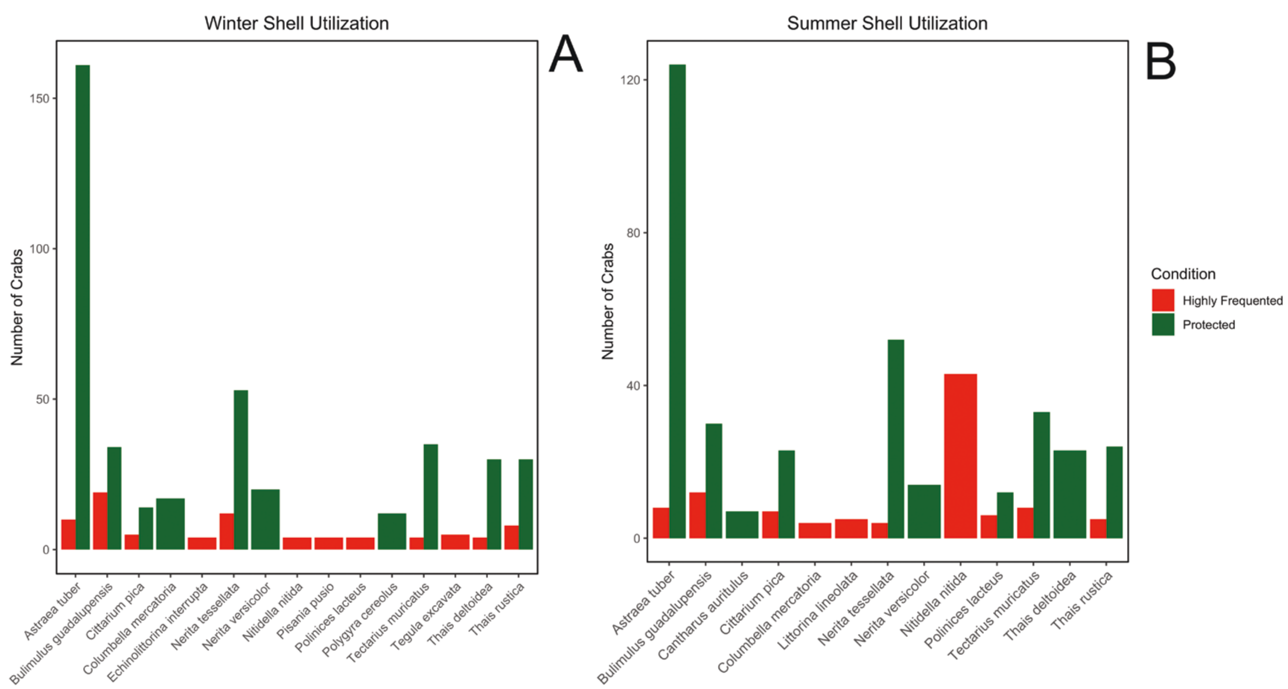

Figure 5. Ten most utilized gastropod shells by *Coenobita clypeatus* by season and beach type.

pattern, *A. tuber* (28.8%), *N. tessellata* (12.1%), and *T. muricatus* (7.7%) during summer.

The Chi-square test of independence indicated significant differences in the frequency of identified shells between the protected and non-protected beaches during winter ($P > 0.0001$) and summer ($P > 0.0001$). During winter, shells of *A. tuber* and *N. tessellata* were less abundant than expected in the non-protected beach, and fewer shells of *A. tuber* and more of *B. guadalupensis* than expected were identified in the non-protected beach during summer. More shells of *B. guadalupensis* than expected were also identified in the non-protected beach but less abundant than expected in the protected beach during summer. The expected frequencies of shell occupancy were based on the residuals (< −5 and > 5) from the Chi-square test. The most frequently occupied shells during winter (Fig. 5A) and summer (Fig. 5B) are also shown.

DISCUSSION

There is global concern over the effects that the increase in urbanization and other anthropogenic-related factors have on biodiversity (Roy *et al.*, 2003; Worm *et al.*, 2006; Alonso *et al.*, 2008; McDonald *et al.*, 2008; Morris, 2010). To promote thoughtful and effective legislation that protects biodiversity, empirical data that evidence the negative consequences of anthropogenic activity on animal abundance in the littoral zone are particularly required in the Caribbean. We used *C. clypeatus* as a bioindicator to assess differences in populations in relation to the conservation status of particular areas because of the ubiquity of the species across the coasts of Puerto Rico and its susceptibility to disturbed-environment cues (Nieves-Rivera & Williams, 2003; Ryan *et al.*, 2012). Although Puerto Nuevo has been recognized as a Blue Flag beach (https://blueflag.us/), a certification reserved for beaches that meet environmental safety and quality standards, our results show that there are significantly fewer and smaller hermit crabs with more varied shell use between seasons in this highly frequented beach when compared to the protected beach. These results may be due to the differences in regulatory systems that control anthropogenic activity in the beaches, suggesting that conservation measures have a positive impact on the population dynamics of animals in the littoral zone.

Coenobita clypeatus was more than twice as abundant in the protected beach than in the highly frequented, non-protected beach during both seasons (Fig. 2). Differences in its abundance may reflect migration to other littoral regions induced by the species' inability to properly adapt to anthropogenic disturbances. The status of Puerto Nuevo as a Blue Flag beach (https://www.vegabaja.gov.pr/) marks it as a popular tourist attraction, with up to 15,000 beachgoers a month visiting during the tourist season. Studies have shown that marine and non-aquatic vertebrates, such as the harbor porpoise, *Phocoena phocoena* (Linnaeus, 1758) and the northern saw-whet owl, *Aegolius acadicus* (Gmelin, 1788) change routes and location due to acoustic pollutants (Kastelein *et al.*, 2013; Dyndo *et al.*, 2015; Mason *et al.*, 2016; Mamo *et al.*, 2018). Decapod crustaceans are not exempt from the effect of acoustic disturbance. Wale *et al.* (2013) showed that the ability of the brachyuran crab, *Carcinus maenas* (Linnaeus, 1758) to evade predators is disrupted by boat noise. Another study showed that the withdrawal response of *C. clypeatus*, a defensive anti-predator behavior, is sensitive to prolonged innocuous sound exposure (Stahlman *et al.*, 2011). This effect was referred to by Chan *et al.* (2010) as the distracted prey hypothesis, which states that the limited attentional resources an animal possesses are occupied by anthropogenic noise, increasing predation risk. The distracted prey hypothesis, as well as migration towards unaffected regions, could apply to local *C. clypeatus* and other littoral animals, and may partially explain the reduced number of hermit crabs in the non-protected beach.

Another potential factor influencing the abundance and size of *C. clypeatus* is a reduced availability of gastropod shells in the littoral zone. Shells play a pivotal role in the survival and social and reproductive behaviors of hermit crabs. The abdominal region lacks the protective exoskeleton of the cephalothorax, and shells protect the vulnerable abdominal region from desiccation, predation, and abrasion (i.e., Szabó, 2012). Molting and subsequent growth are chiefly dependent on the internal volume of the shell, which crabs obtain via scavenging or shell exchange (Elwood, 2022). The clutch size of a female hermit crab is also dependent on the size of the occupied shell (Conover, 1978; Bertness, 1981; Hazlett, 1981). Due to the value of this resource, hermit crabs have evolved to thoroughly examine each shell encountered, selecting a shell that corresponds to their general size in order to maximize their individual fitness (Hazlett, 1981; Szabó, 2012).

Shell selection is an example of a decision-making process that is affected by external factors (Reese, 1963; Conover, 1978; Bertness, 1981; Hazlett, 1981; McClintock, 1985; Lewis & Rotjan, 2009; Rotjan *et al.*, 2010). The shell utilization data indicates that the type of shells used by *C. clypeatus* in the protected beach does not vary substantially between seasons, favoring the green star shell (*A. tuber*), a preference that was also observed in Puerto Rico by Colón-Piñeiro *et al.* (2021). Hermit crabs of the highly frequented beach, conversely, showed greater variation in the type of shell used in both seasons sampled. Although natural differences in the abundance and species of gastropods in the studied beaches may impact shell occupation in *C. clypeatus* (Colón-Piñeiro *et al.*, 2021), the studied beaches are similar environments, containing aeolianite rock formations and seagrass meadows, as well as comparable tidal activity and land vegetation. The observed differences in shell utilization patterns are thus less likely to be due to natural variation in distribution of gastropod species in each area. Given these observations, along with those of other studies (Lange *et al.*, 2013; Bloch & Klingbeil, 2016), it is instead probable that gastropod populations and shell availability are impacted by human activity, influencing shell utilization, and subsequently, the potential abundance and size of *C. clypeatus.*

Analysis of major chela length as a general indicator of size (Morrison & Spiller, 2006; Colón-Piñeiro *et al.*, 2021) demonstrated that hermit crabs at the non-protected and highly frequented beach are significantly smaller than those in the protected beach. The proportions of the shells occupied by *C. clypeatus* as measured by the shell aperture length (mm) scaled positively with hermit crab size, as measured by chela length (mm). These results are supported by Colón-Piñeiro *et al.* (2021) showing a positive relationship between shell proportions and crab size. This is not surprising considering that shell aperture length is a quality assessed by *C. clypeatus* to appropriately select a shell that meets the necessary dimensions to protect from desiccation and predation (Szabó, 2012). As hermit crabs have evolved to be entirely dependent on the shells available, this trait has the drawback of needing a constant supply of shells of increasing size, which crabs must continually scavenge and evaluate (Morrison & Spiller, 2006). Fewer larger shells available per beach are therefore a limiting growth factor for animals inhabiting both sampled beaches. Gastropods and their shells are frequently collected for their gastronomic and aesthetic value, limiting their availability in the beach (Roy *et al.*, 2003). Gastropods such as *Cittarium pica, Astraea tuber,* and *Nerita tessellata* grow to medium and large sizes and are often collected for consumption, a practice that goes unregulated in the non-protected beach. This indirect anthropogenic interaction should be evaluated in future studies, as these may contribute to the reduced size and abundance of hermit crabs from highly frequented beaches when compared to those of the protected beaches.

The impact of anthropogenic factors on coastal areas, and the interactions between humans and the littoral zone, are complex and far-reaching. Although hermit crabs and humans have been shown to be capable of forming mutualistic relationships (Barnes, 2001), the potential benefit of increased anthropogenic activity in the non-protected littoral zone is not reflected by our findings. The *C. clypeatus* profile generated herein suggests that the protected beach harbors more optimal conditions for the hermit crab population than the highly frequented beach. This may be due to the variety of factors and anthropogenic activities that threaten the ecological integrity of the coastal region, which is minimized in protected beaches (Ke *et al.*, 2011). Determining the specific anthropogenic factors inducing the observed differences in the *C. clypeatus* population, was beyond the scope of our study. Potential anthropogenic-related factors may include but are not limited to pollution, overexploitation of resources, introduction of invasive species, governmental management issues, and even human perception of coastal ecosystems (Beatley, 1991; Suchanek, 1994; Lande, 1998; Reid *et al.*, 2005; Forster *et al.*, 2011). Although any of these factors could adversely alter the population dynamics of animals in the littoral zone, pollution is known to be a significant contributor to biodiversity loss, specifically in coastal regions (Wafar *et al.*, 2011). Exposure to common coastal contaminants, such as heavy metals, adversely affects the social behavior and reproduction of hermit crabs, which in turn impacts abundance (Aghabozorgi Nafchi & Chamani, 2019). The effects of copper exposure in the fighting behavior of *P. bernhardus* (White *et al.*, 2013), and the cardiac and respiratory function of the brachyuran crab, *Carcinus maenas* have been described (Mh, 1984). Tributyltin, a historically common antifouling agent, provokes morphological disruption of the ovaries in female *Clibanarius vittatus* (Bosc, 1801) (Sant'Anna *et al.*, 2012). The negative ecological impact that anthropogenic factors impose on the behavior of coastal organisms, not only threatens biodiversity, but also impacts their sustainability and capability to meet human resource demands (Worm *et al.*, 2006). Immediate action, in the form of increased conservation measures, must be taken to limit the noxious consequences of anthropogenic activities in the littoral zone and prevent further biodiversity loss (Alonso *et al.*, 2008).

Anadon-Irizarry *et al.*, (2012) identified key biodiversity areas along Caribbean coastlines, including the coastal regions of Puerto Rico. Expansion of protected areas, such as natural reserves, can help to protect biodiversity and benefit the local population via the sustainable use of natural resources (Burgess *et al.*, 2017; van Schalkwyk *et al.*, 2019). Proper conservation methods also require a robust catalog of the local flora and fauna. These efforts typically focus on vertebrate and plant species so a broader number of taxa must be considered to effectively preserve biodiversity. Conservation measures, such as those implemented in the Hacienda La Esperanza, provide optimal conditions to hermit crab populations. Our study has shown that *C. clypeatus* can serve as a useful model organism to study the benefits of conservation measures in littoral organisms. These findings, along with further research, should encourage legislative measures to expand the area and number of littoral protected areas to mitigate the impact of anthropogenic activity for the protection of coastal biodiversity.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Crustacean Biology* online.

Table S1. Gastropod shells utilized by *Coenobita clypeatus* in the protected (La Esperanza) and highly frequented beach (Puerto Nuevo) during late winter.

Table S2. Gastropod shells utilized by *Coenobita clypeatus* in the protected (La Esperanza) and highly frequented beach (Puerto Nuevo) during summer

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REFERENCES

Acevedo-Charry, O. & Aide, T.M. 2019. Recovery of amphibian, reptile, bird and mammal diversity during secondary forest succession in the tropics. *Oikos*, **128**: 1065–1078.

Aghabozorgi Nafchi, M. & Chamani, A. 2019. Physiochemical factors and heavy metal pollution, affecting the population abundance of Coenobita scaevola. *Marine Pollution Bulletin*, **149**: 110494 [https://doi.org/10.1016/j.marpolbul.2019.110494].

Alonso, D., Ramírez, L.F., Segura-Quintero, C., Castillo-Torres, P., Diaz, J.M. & Walschburger, T. 2008. *Prioridades de conservación in situ para la biodiversidad marina y costera de la plataforma continental del Caribe y Pacífico colombiano*. Instituto de Investigaciones Marinas y Costeras, Santa Marta, Colombia.

Anadon-Irizarry, V., Wege, D.C., Upgren, A., Young, R., Boom, B., Leon, Y.M., Arias, Y., Koenig, K., Morales, A.L. & Burke, W. 2012. Sites for priority biodiversity conservation in the Caribbean Islands Biodiversity Hotspot. *Journal of Threatened Taxa*, **4**: 2806–2844.

Barnes, D.K.A. 2001. Hermit crabs, humans and Mozambique mangroves. *African Journal of Ecology*, **39**: 241–248.

Beatley, T. 1991. Protecting biodiversity in coastal environments: Introduction and overview. *Coastal Management*, **19**: [https://doi.org/10.1080/08920759109362128].

Bertness, M.D. 1981. The influence of shell-type on hermit crab growth rate and clutch size (Decapoda, Anomura). *Crustaceana*, **40**: 197–205.

Bloch, C.P. & Klingbeil, B.T. 2016. Anthropogenic factors and habitat complexity influence biodiversity but wave exposure drives species turnover of a subtropical rocky inter-tidal metacommunity. *Marine Ecology*, **37**: 64–76.

Bosc, L.A.G. 1801. *Histoire naturelle des Crustacés, contenant leur description et leurs moeurs; avec figures dessinées d'après nature*, **Vol. 1**. Déterville, Paris.

Burgess, N.D., Malugu, I., Sumbi, P., Kashindye, A., Kijazi, A., Tabor, K., Mbilinyi, B., Kashaigili, J., Wright, T.M., Gereau, R.E., Coad, L., Knights, K., Carr, J., Ahrends, A. & Newham, R.L. 2017. Two decades of change in state, pressure and conservation responses in the coastal forest biodiversity hotspot of Tanzania. *Oryx*, **51**: 77–86.

Butler, J. M. & Maruska, K. P. 2020. Underwater noise impairs social communication during aggressive and reproductive encounters. *Animal Behaviour*, **164**: 9–23.

Chan, A.A.Y.-H., Giraldo-Perez, P., Smith, S. & Blumstein, D.T. 2010. Anthropogenic noise affects risk assessment and attention: The distracted prey hypothesis. *Biology Letters*, **6**: 458–461.

Chan, A.A.Y.-H. & Blumstein, D.T. 2011. Attention, noise, and implications for wildlife conservation and management. *Applied Animal Behaviour Science*, **131**: 1–7.

Colón-Piñeiro, Z., Nieves-Álvarez, J.J. & Rodríguez-Fourquet, C. 2021. Demography and shell use of the terrestrial hermit crab *Coenobita clypeatus* Fabricius, 1787 (Decapoda: Anomura: Coenobitidae) in two marine protected areas in Puerto Rico. *Journal of Crustacean Biology*, **41**: [https://doi.org/10.1093/jcbiol/ruaa101].

Conover, M. R. 1978. The importance of various shell characteristics to the shell-selection behavior of hermit crabs. *Journal of Experimental Marine Biology and Ecology*, **32**: 131–142.

Dauvin, J.-C. 2008. Effects of heavy metal contamination on the macrobenthic fauna in estuaries: The case of the Seine estuary. *Marine Pollution Bulletin*, **57**: 160–169.

de la Haye, K. L., Spicer, J. I., Widdicombe, S. & Briffa, M. 2011. Reduced sea water pH disrupts resource assessment and decision making in the hermit crab *Pagurus bernhardus*. *Animal Behaviour*, **82**: 495–501.

Dyndo, M., Wiśniewska, D.M., Rojano-Doñate, L. & Madsen, P.T. 2015. Harbour porpoises react to low levels of high frequency vessel noise. *Scientific Reports*, **5**: 11083 [https://doi.org/10.1038/srep11083].

Elwood, R.W. 2022. Hermit crabs, shells, and sentience. *Animal Cognition*, **25**: [https://doi.org/10.1007/s10071-022-01607-7].

Fabricius, J.C. 1787. *Mantissa insectorum sistens eorum species nuper detectas adjectis characteribus genericis, differentiis specificis, emendationibus, observationibus*, **Vol. 1**. Impensis Christ. Gottl. Proft., Hafniae [= Copenhagen].

Forster, J., Lake, I.R., Watkinson, A.R. & Gill, J.A. 2011. Marine biodiversity in the Caribbean UK overseas territories: Perceived threats and constraints to environmental management. *Marine Policy*, **35**: 647–657.

Göltenboth, F., Schoppe, S. & Widmann, P. 2006. Sea shores and tidal flats. In: *Ecology of insular Southeast Asia* (F. Goltenboth, K. Timotius, P. Milan & J. Margraf, eds.), pp. 171–186. Elsevier, Amsterdam.

Hazlett, B.A. 1981. The behavioral ecology of hermit crabs. *Annual Review of Ecology and Systematics*, **12**: 1–22.

Holt, E.A. & Miller, S.W. 2010. Bioindicators: Using organisms to measure environmental impacts. *Nature Education Knowledge*, **3**: 1–8.

Kastelein, R.A., van Heerden, D., Gransier, R. & Hoek, L. 2013. Behavioral responses of a harbor porpoise (*Phocoena phocoena*) to playbacks of broadband pile driving sounds. *Marine Environmental Research*, **92**: 206–214.

Ke, C.-Q., Zhang, D., Wang, F.-Q., Chen, S.-X., Schmullius, C., Boerner, W.-M. & Wang, H. 2011. Analyzing coastal wetland change in the Yancheng National Nature Reserve, China. *Regional Environmental Change*, **11**: 161–173.

Lande, R. 1998. Anthropogenic, ecological and genetic factors in extinction and conservation. *Population Ecology*, **40**: 259–269.

Lange, C.N., Kristensen, T.K. & Madsen, H. 2013. Gastropod diversity, distribution and abundance in habitats with and without anthropogenic disturbances in Lake Victoria, Kenya. *African Journal of Aquatic Science*, **38**: 295–304.

Lewis, S.M. & Rotjan, R.D. 2009. Vacancy chains provide aggregate benefits to *Coenobita clypeatus* hermit crabs. *Ethology*, **115**: 356–365.

Linnaeus, C. 1758. *Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis*. **Vol. 1**, Edn. 10. Reformata. Laurentii Salvii, Holmiae [= Stockholm].

Mamo, L.T., Kelaher, B.P., Coleman, M.A. & Dwyer, P.G. 2018. Protecting threatened species from coastal infrastructure upgrades: The importance of evidence-based conservation. *Ocean & Coastal Management*, **165**: 161–166.

Mason, T., McClure, C. & Barber, J. (2016). Anthropogenic noise impairs owl hunting behavior. *Biological Conservation*, **199**: 29–32.

McClintock, T.S. 1985. Effects of shell condition and size upon the shell choice behavior of a hermit crab. *Journal of Experimental Marine Biology and Ecology*, **88**: 271–285.

McDonald, R.I., Kareiva, P. & Forman, R.T.T. 2008. The implications of current and future urbanization for global protected areas and biodiversity conservation. *Biological Conservation*, **141**: 1695–1703.

Mh, D. 1984. Disruption of circulatory and respiratory activity in shore crabs (*Carcinus maenas* (L)) exposed to heavy metal pollution. *Comparative Biochemistry and Physiology C*, **78**: 445–459.

Milne Edwards, H. 1837. *Histoire naturelle des Crustacés, comprenant l'anatomie, la physiologie et la classification de ces animaux*, **Vol. 2**. Librairie Encyclopédique de Roret, Paris.

Morris, R.J. 2010. Anthropogenic impacts on tropical forest biodiversity: A network structure and ecosystem functioning perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**: 3709–3718.

Morrison, L.W. & Spiller, D.A. 2006. Land hermit crab (*Coenobita clypeatus*) densities and patterns of gastropod shell use on small Bahamian islands. *Journal of Biogeography*, **33**: 314–322.

Neves, F.M. & Bemvenuti, C.E. 2006. The ghost crab *Ocypode quadrata* (Fabricius, 1787) as a potential indicator of anthropic impact along the Rio Grande do Sul coast, Brazil. *Biological Conservation*, **133**: 431–435.

Nieves-Rivera, Á.M. & Williams, E.H. 2003. Annual migrations and spawning of *Coenobita clypeatus* (Herbst) on Mona Island (Puerto Rico) and notes on inland crustaceans. *Crustaceana*, **76**: 547–558.

Peters, J.A. & Lodge, D.M. 2009. Littoral zone. In: *Encyclopedia of inland waters*, pp. 79–87. Elsevier, Amsterdam.

Pine, M.K., Jeffs, A.G., Wang, D. & Radford, C.A. 2016. The potential for vessel noise to mask biologically important sounds within ecologically significant embayments. *Ocean & Coastal Management*, **127**: 63–73.

Reese, E.S. 1963. The behavioral mechanisms underlying shell selection by hermit crabs. *Behaviour*, **21**: 78–124.

Reid, W.V., Capistrano, D., Carpenter, S.R., Chopra, K., Cropper, A. & Mooney, H.C. 2005. *Millennium Ecosystem Assessment. Ecosystems and human well-being: synthesis.* Island Press, Washington, DC.

Roberts, L. 2021. Substrate-borne vibration and sound production by the land hermit crab *Coenobita compressus* during social interactions. *Journal of the Acoustical Society of America*, **149**: 3261–3272.

Rotjan, R.D., Chabot, J.R. & Lewis, S.M. 2010. Social context of shell acquisition in *Coenobita clypeatus* hermit crabs. *Behavioral Ecology*, **21**: 639–646.

Roy, K., Collins, A.G., Becker, B.J., Begovic, E. & Engle, J.M. 2003. Anthropogenic impacts and historical decline in body size of rocky intertidal gastropods in southern California. *Ecology Letters*, **6**: 205–211.

Ryan, K.M., Blumstein, D.T., Blaisdell, A.P. & Stahlman, W.D. 2012. Stimulus concordance and risk-assessment in hermit crabs (*Coenobita clypeatus*): Implications for attention. *Behavioural Processes*, **91**: 26–29.

Sant'Anna, B.S., Santos, D.M. dos, Marchi, M.R.R. de, Zara, F.J. & Turra, A. 2012. Effects of tributyltin exposure in hermit crabs: *Clibanarius vittatus* as a model. *Environmental Toxicology and Chemistry*, **31**: 632–638.

Schlacher, T.A., Lucrezi, S., Connolly, R.M., Peterson, C.H., Gilby, B.L., Maslo, B., Olds, A.D., Walker, S.J., Leon, J.X., Huijbers, C.M., Weston, M.A., Turra, A., Hyndes, G.A., Holt, R.A. & Schoeman, D.S. 2016. Human threats to sandy beaches: A meta-analysis of ghost crabs illustrates global anthropogenic impacts. *Estuarine, Coastal and Shelf Science*, **169**: 56–73.

Stahlman, W.D., Chan, A.A. Y.-H., Blumstein, D.T., Fast, C.D. & Blaisdell, A.P. 2011. Auditory stimulation dishabituates anti-predator escape behavior in hermit crabs (*Coenobita clypeatus*). *Behavioural Processes*, **88**: 7–11.

Suchanek, T.H. 1994. Temperate coastal marine communities: biodiversity and threats. *American Zoologist*, **34**: 100–114.

Stillman, R.A. & Goss-Custard, J.D. 2002. Seasonal changes in the response of oystercatchers *Haematopus ostralegus* to human disturbance. *Journal of Avian Biology*, **33**: 358–365.

Szabó, K. 2012. Terrestrial hermit crabs (Anomura: Coenobitidae) as taphonomic agents in circum-tropical coastal sites. *Journal of Archaeological Science*, **39**: 931–941.

Tidau, S. & Briffa, M. 2019. Anthropogenic noise pollution reverses grouping behaviour in hermit crabs. *Animal Behaviour*, **151**: 113–120.

van Schalkwyk, J., Pryke, J., Samways, M. & Gaigher, R. 2019. Complementary and protection value of a Biosphere Reserve buffer zone for increasing local representativeness of ground-living arthropods. *Biological Conservation*, **239**: 108292 [https://doi.org/10.1016/j.biocon.2019.108292].

Wafar, M., Venkataraman, K., Ingole, B., Khan, S.A. & LokaBharathi, P. 2011. State of knowledge of coastal and marine biodiversity of Indian Ocean countries. *PLoS ONE*, **6**:. e14613 [https://doi.org/10.1371/journal.pone.0014613].

Wale, M., Simpson, S. & Radford, A. 2013. Noise negatively affects foraging and antipredator behaviour in shore crabs. *Animal Behaviour*, **86**: 111–118.

Warner, G. F. 1969. The occurrence and distribution of crabs in a Jamaican mangrove swamp. *Journal of Animal Ecology*, **38**: 379–389.

White, S.J., Pipe, R.K., Fisher, A. & Briffa, M. 2013. Asymmetric effects of contaminant exposure during asymmetric contests in the hermit crab *Pagurus bernhardus*. *Animal Behaviour*, **86**: 773–781.

Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C., Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J. & Watson, R. 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science*, **314**: 787–790.