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CHARACTERIZATION OF FOOD GUILDS OF THE CLASS GASTROPODA ON THE NORTHEAST ROCKY COAST OF THE GULF OF CALIFORNIA

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ABSTRACT. Few detailed studies are available on the ecology of Class Gastropoda in rocky intertidal areas of the Gulf of California, or conducted embracing wide latitudinal scales. This paper analyses differences in density (individuals/2 m2), of five different food guilds of the macrogastropod community (≥1 cm) found in the three different sections of the intertidal, and in 13 coastal sites of the northeast Gulf of California (latitudes 27° N - 31° N). Density was calculate through visual census in transects perpendicular to the coast, surveyed with 2 m2 quadrants over each intertidal level (upper, middle, and lower). A total of 5 823 individuals of 41 species were found, and of the five trophic guilds, algivores stood out with the highest (50.87%) abundance, followed by specialist carnivores (19.22%), carnivores (14.19%), omnivores (14.51%) and microalgivores (less than 2% of the total). In the intertidal zone, the abundance of algivores was higher in the upper section, while carnivores were well represented in middle and lower tide levels. Trophic diversity only showed lower significant values in the upper intertidal band while in latitudes and sites they were similar. A non-metric multidimensional scaling demonstrated four groups that separate algivores, predator carnivores, omnivores and carnivores. This study shows for the first time the distribution of the diversity of trophic macromollusc guilds northeast of the Gulf of California, and evidence that changes in its composition occur at latitudinal and intertidal spatial scales, which highlights the importance and necessity of generating a solid base for detailed class research in the region.

Keywords: benthos, macroinvertebrates, malacology, gastropods, carnivores, algivores.

Characterization of food guilds of the class Gastropoda on the rocky coasts northeast of the Gulf of California

RESUMEN. Existen pocos estudios detallados sobre la ecología de la Clase Gastropoda en áreas rocosas intermareales del Golfo de California y en los últimos 30 años ninguno ha sido a escala latitudinal significativa para laregión. Este trabajo busca caracterizar los gremios de alimentación de la comunidad de macrogasterópodos (≥1 cm)presentes en el intermareal rocoso de 13 sitios costeros del noreste del Golfo de California (latitudes 27° N - 31° N),mediante censos visuales en transectos de 40 m perpendiculares a la costa con cuadrantes de 2 m2 cada 20 m. Los resultados acumularon un total de 5823 conteos referentes a 41 especies. La clasificación por tipo de alimentación incluye cinco gremios, y destacan los alguívoros con la mayor abundancia 50.87%; los carnívoros depredadores representan el 19.22% de la riqueza de especies; carnívoros 14.19%, omnívoros 14.51% y microalguívoros con menos del 2% del total. En la zona intermareal la abundancia de alguívoros disminuye significativamente en el nivel inferior, mientras los carnívoros son bien representados en los niveles medio e inferior. Latitudinalmente la distribución de los gremios de alimentación es heterogénea sin un patrón latitudinal especifico, sin embargo, la diversidad trófica tiende a ser mayor en sitios de las latitudes 29° N - 30° N. El Análisis de escalamiento multidimensional no-métrico demuestra cuatro principales áreas que agrupan a alguívoros, carnívoros depredadores, omnívoros y carnívoros (estrés= 0.1). El esfuerzo de este trabajo demuestra por primera vez la diversidad de gremios tróficos de macromoluscos en el noreste del Golfo de California y resalta la importancia y necesidad de generar una base sólida para estudios detallados para la clase en la región.

Palabras clave: bentos, macroinvertebrados, malacología, gasterópodos, carnívoros, alguívoros.

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INTRODUCTION

The Class Gastropoda is the group of Phylum Mollusca with major species abundance exceeding 50 000 *taxa* (García-Cubas & Reguero, 2004). Within the Gulf of California (GC) (specifically the Central and North fauna regions) these molluscs maintain their dominance and exceed 1 500 species described in different habitats (Brusca *et al.,* 2005; Ríos-Jara *et al.,* 2015). These *taxa* are well represented in the GC benthos -specifically in hard substrates- gastropod diversity tends to be higher (Keen, 1971; Brusca, 1980; Hendrickx *et al.,* 2005; 2014; Houart and Hendrickx, 2020; Houart and Löser, 2020). These organisms have noticeable ecological plasticity despite having a relatively generalised form; they possess the ability to occupy different levels in a trophic web because of their presence in several different food guilds, such as algivores, carnivores, omnivores, detritivores, among others (Vermeij, 2015; Stafford *et al.,* 2015). Several investigations have described the role of marine gastropods in different trophic guilds. An example is the work of Chim and Ong (2012) where they analysed predatory habits of *Semiricinula fusca* (synonym of *Morula fusca*) (Muricidae) (WORMS, 2020) by observations of perforated shells collected in rocky intertidal areas of St John's Island, Singapore. Their results highlight the preference for small-sized preys, mainly members of the family Siphonariidae, *Siphonaria guamensis* and *S. javanica*. On the other hand, Chattopadhyay *et al.* (2014) observed under experimental conditions the predatory preferences and cannibalism tendencies of *Paratectonatica tigrina* (Naticidae) (synonym of *Natica tigrina*) (WORMS, 2020) found in intertidal zones of Chandipur, India. Their results and conclusions demonstrated an evi-

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dent preference for bivalves (Cardium sp.) before attacking members of their own species, regardless of size and ontogenetic stages, but a high frequency of cannibalism is evident in adult stages compared to early ones of the taxon. Pawar *et al.* (2017) estimated gastropod diversity in rocky intertidal zones on the coasts of Uran, India for two years, and their results showed higher species richness in the pre- and post-monsoon seasons. They also mentioned the presence of 60 species and that herbivore and carnivore guilds had the greatest taxonomic richness (25% and 23.33% respectively). In México, few studies have focused on outlining food guilds of these organisms; Cruz-Abrego *et al.* (1994) analysed the community of marine gastropods in the Contoy Island of the Mexican Caribbean by benthic trawling over sandy substrate and calcareous biogen. They described 46 species and determined that the proportion of carnivorous and herbivorous *taxa* constituted more than 70% of malacological abundance. On the other hand, Siqueiros-Beltrones *et al.* (2004) determined the diet of the species *Haliotis fulgens* and *Haliotis corrugata* in the Mexican Pacific with organisms that belong to rearing areas in the east coast of Baja California Sur, Mexico. These *taxa* were considered grazers, but the results indicated that these molluscs were not limited to only consuming diatoms facilitated by the rearing treatment; the previous is the result of the significant presence of macroalgal content in stomach. Additionally, within the region of the GC in Puerto Peñasco, Sonora, Mexico, Lively and Raimondi (1987) evaluated the interspecific interactions among *Chthamalus anisopoma* (Crustacea), *Brachidontes semilaevis* (Bivalvia) and *Claremontiella nodulosa* (Gastropoda) over rocky intertidal zone during low summer tides. Their observations indicated that mussels have a negative effect on barnacle densities. However, gastropods have a mutualistic relation with crustaceans. These last ones attract settlement and facilitate mussel survival, while gastropods decrease competence among them by feeding themselves from bivalves.

Most of the work on gastropod community ecology has been specific, and assemblages have not been described from a functional point of view. Thus, the assembly of trophic guilds in the NEGC is modified according to the coastal latitudinal heterogeneity and their respective intertidal levels. Therefore, the objective of this study was to describe distribution and abundance of gastropod feeding guilds in the intertidal zone of 13 locations along the northeast Gulf of California (NEGC).

MATERIALS AND METHODS

Field work. The research area is located in the rocky shores in the NEGC (integrated by 13 sites) where field activities were conducted (latitudes 27° N 31° N) (Fig. 1). The tidal dynamics of the region is distinguished with semi-diurnal and mixed tides, generally two per day with variable tidal levels. The moon influence is evident at new and full moons when tidal levels reach extreme peaks, while dead tides appear in quarter moon phases (Hupp & Malone, 2015). The substrate in intertidal and subtidal zones is noticeably heterogeneous. It is primarily composed of limestone blocks, volcanic tuff, rhyolite, pebbles, fine gravel, sandy patches and substrates that are composed by coquina and limestone (Brusca *et al.,* 2004; Turk-Boyer *et al.,* 2014). In addition, low tides frequently uncover more than 50 m of intertidal benthos in the selected sites; these characteristics allow an easy access to work on the substrate (Moreno-Báez, *et al.,* 2010; 2012; Hupp & Malone, 2015). On the other hand, temperatures are extreme; during winter they average from 8°C to 12°C and in summer they rise over 40°C (Brusca *et al.,* 2004).

Figure 1. Sampling sites along the northeast Gulf of California in Sonora, Mexico.

Data collection. The research sites were visited only once during the months with the highest low tidal effects per year: March and November 2018; and on February and March 2019 during six-day intervals that matched with extreme tides (according to the tide prediction calendar of Centro de Investigación Científica y Estudios Superiores de Ensenada, Mexico (CICESE) (González & Ochoa, 2009) in a way that it offered a wide range of available time to work on the exposed substrate. In every low tide the approximate time period for data gathering was six hours and all observations were done during afternoon and night in low tides. In every site work was performed in three intertidal areas: high (superior level), low (inferior level), and intermediate area between both, defined directly on site and based on the separation of transect ends (intermediate intertidal level). In these areas, three perpendicular transects to the coastline were deployed. (N = 9 per site). In each one of them two quadrants of polyvinyl chloride (PVC) were marked with an area of 1 m^2 on each side of the transect band (54 m^2 total per site), in which conspicuous live gastropods were identified and counted. The organisms were found in substrate in hollows, cracks, tidal pool, green, red and calcareous alga patches. Taxonomic identifications were conducted in the field by the

same person with the purpose of reducing criterium error (Keen, 1971; Brusca, 1980; Brusca *et al.,* 2004; Bouchet & Rocroi, 2005; Hupp & Malone, 2015; Bertsch & Aguilar-Rosas, 2016). A total of 117 band transects with a length of 40 m were traced (4 680 lineal m) with cumulative 351 quadrants (702 m^2).

Numerical analyses. After field work, data were arranged in a species x site matrix to determine the most abundant and frequent. Afterwards, the information was grouped on the basis of the feeding guild of each species, as defined by predatory carnivores (active, specialists, large gastropods that usually attack other mollusc species), carnivores (generalist species), algivores (usually feed on fastened or detached algal fronds), microalgivores (consumers of algal turf and diatom algal films growing over rocks and other hard substrata), and omnivores (diet includes both animal and algal items). From this new arrangement, the abundance per quadrant of each of the five feeding guilds was determined, and with these data, the Shannon-Wiener diversity index (Hutcheson, 1970) was calculated as a measure of trophic diversity of the assemblage. The abundance of the different gastropod feeding guilds and trophic diversity per quadrant were compared separately among tide levels and latitudinal belts using the Kruskal-Wallis non-parametric analysis of variance, and Mann-Whitney as *a posteriori* test (Zar, 2010). These statistics were chosen because in all cases data were heteroscedastic. Additionally and with the intention of robusting statistical analyses, the Bray-Curtis coefficient was calculated, which is widely used for the analysis of communities in ecology because of its robustness with respect to the characteristics that distinguish the community data (high proportion of zeros and outliers). However, density data were transformed to a fourth root to compensate for the high levels of the mostly abundant species and the low numbers of rare species. Therefore, the average similarity of the data was evaluated according to species identity, trophic guild and abundance in each spatial scale (Bray & Curtis, 1957; Clarke & Gorley, 2015); from there, a non-metric multidimensional scaling was applied to determine possible groupings on the basis of feeding characteristics of the local assemblages. Finally, a three-way nested permutational multivariate analysis of variance (PERMANOVA) (latitudes, sites and intertidal zones) was implemented to test the simultaneous response and determine the variation differences in the structure of the trophic guilds that the Gastropoda class community represents on the different spatial scales. Likewise, *a posteriori* multiple pairwise comparisons were made between factor levels to identify the significant similitude of the spatial levels (Clarke et al., 2014).

RESULTS

During field work, a total of 5 823 individuals from 41 species of 25 genera and 15 families were found in the 351 quadrants (Table 1). The most abundant gastropod was *Nerita funiculata* (18.79% of the total 5 823 specimens), followed by *Turbo fluctuosus* (16.43%) and *Mexacanthina angelica* (10.05%), while the most commonly found was *T. fluctuosus* (28% of 351 sampling units), followed by *N. funiculata* (23%) and *Pusio elegans* (18%) (Table 1).

The species (N = 41) were arranged in five feeding guilds (Table 1): algivores (with the highest abundance; 2 962 of 5 823 total individuals; 50.87%), predatory carnivores (most species 19.22%), omnivores (14.51%), carnivores (14.19%), and microalgivores (just one species adding 1.22% of total abundance).

The statistical analysis for algivores in relation to tidal level (Fig. 2) showed that the low level had significantly lower abundance than the other two (Kruskal-Wallis test, KW = 10.38, p = 0.005); in contrast, predatory carnivores gastropods were more numerous in the mid- and lower tidal levels (KW = 37.30, p = 0.000); the omnivores did not show significant differences (KW = 4.94, p = 0.084) and carnivores recorded significantly low differences in the upper band (KW = 71.15, p = 0.000) showing higher numbers in mid- than in lower and upper levels, while for microalgivores, they only had presence in the upper band (KW = 16.32, p = 0.000) (Fig. 2).

The results from the latitudinal comparison were more heterogeneous (Fig. 3). For omnivores, quadrants conducted at latitudes 27º N, 28° N and 31º N had less gastropods than at latitudes 29º and 30º N (KW = 50.44, p = 0.000) while in predator carnivores the largest significant difference was observed at latitude 29 ° N (KW = 44.43, p = 0.000) and carnivores had the lowest count of gastropods per quadrant at latitude 27º N (KW = 66.69, p = 0.000). In microalgivores, latitude 28º N had the highest abundance of the rest (KW = 13.06, p = 0.000), while for algivores the largest statistically significant difference stands out at latitude 27 ° (KW = 60.15, p = 0.000).

Finally, trophic diversity was significantly less in the upper than in mid- and lower tidal levels (KW = 54.16, p < 0.000). And latitudinally, significant lower values were shown in the 31° N band (KW = 19.17, p < 0.000).. In addition, the NMDS had a stress of 0.1 (meaning that the results were acceptable) and showed that sites followed a latitudinal arrangement based on the numerically dominant feeding guild, chiefly separating four areas where algivores, carnivores, omnivores and predatory carnivores prevailed (Fig. 4).

The PERMANOVA (three-way nested) analysis for distribution variation of trophic guilds based on the interactions of different spatial levels showed significant differences at the latitudinal level and intertidal zones by sites (PERMANOVA Pseudo-F = 6.052; P = 0.000 and Pseudo-F = 7.419; P = 0.000). However, no differences were recorded in the interaction between sites and latitude (PERMANOVA Pseudo-F = 0.579; P = 0.912) (Table 2).

Table 1. Gastropod species observed at the intertidal zone of the northeast Gulf of California, Mexico (27º N to 31º N). List arranged on the basis of feeding guild and total number of individuals. Key: AL: Algivore, CA: Carnivore, MI: Microalgivore, OM: Omnivore, PC. Predatory carnivore; Percentages calculated from 5 823 individuals and 351 quadrants.

Family	Specie	Feeding guild	N	(%)	Ocurr.	(%)
Strombidae	*Persististrombus granulatus*	AL	5	0.09	3	0.01
Cerithiidae	*Liocerithium judithae*	AL	33	0.57	3	0.01
Cerithiidae	*Cerithium atromarginatum*	AL	33	0.57	9	0.03
Neritidae	*Nerita funiculata*	AL	1094	18.79	79	0.23
Neritidae	*Nerita scabricosta*	AL	444	7.62	50	0.14
Neritidae	*Vitta luteofasciata*	AL	39	0.67	7	0.02
Tegulidae	*Tegula rugosa*	AL	179	3.07	33	0.09
Tegulidae	*Tegula felipensis*	AL	2	0.03	2	0.01
Turbinidae	*Turbo fluctuosus*	AL	957	16.43	99	0.28
Turbinidae	*Uvanilla unguis*	AL	176	3.02	36	0.10
Cypraeidae	*Pseudozonaria annettae*	CA	23	0.39	10	0.03
Ovulidae	*Jenneria pustulata*	CA	7	0.12	5	0.01
Triviidae	*Pseudopusula californiana*	CA	25	0.43	15	0.04
Triviidae	*Pseudopusula sanguinea*	CA	2	0.03	1	0.00
Pisaniidae	*Pusio elegans*	CA	433	7.44	62	0.18
Mitridae	*Atrimitra idae*	CA	2	0.03	1	0.00
Muricidae	*Vasula speciosa*	CA	32	0.55	15	0.04
Muricidae	*Claremontiella nodulosa*	CA	302	5.19	51	0.15
Lottiidae	*Lottia stanfordiana*	MI	71	1.22	8	0.02
Littorinidae	*Echinolittorina aspera*	OM	93	1.60	10	0.03
Littorinidae	*Echinolittorina modesta*	OM	51	0.88	21	0.06
Columbellidae	*Columbella paytensis*	OM	15	0.26	1	0.00
Columbellidae	Columbella fuscata	OM	103	1.77	19	0.05
Columbellidae	*Columbella major*	OM	489	8.40	45	0.13
Columbellidae	*Columbella strombiformis*	OM	92	1.58	19	0.05
Columbellidae	*Columbella haemastoma*	OM	2	0.03	1	0.00
Conidae	*Conasprella perplexa*	PC	94	1.61	8	0.02
Conidae	*Conasprella ximenes*	PC	14	0.24	5	0.01
Conidae	*Conus brunneus*	PC	4	0.07	3	0.01
Conidae	*Conus princeps*	PC	21	0.36	8	0.02
Conidae	*Conus nux*	PC	6	0.10	4	0.01
Muricidae	*Mexacanthina angelica*	PC	585	10.05	39	0.11
Muricidae	*Stramonita haemastoma*	PC	147	2.52	33	0.09
Muricidae	*Stramonita biserialis*	PC	52	0.89	2	0.01
Muricidae	*Mexacanthina lugubris*	PC	2	0.03	1	0.00
Muricidae	*Neorapana tuberculata*	PC	161	2.76	38	0.11
Muricidae	*Plicopurpura columellaris*	PC	25	0.43	9	0.03
Muricidae	*Hexaplex erythrostomus*	PC	1	0.02	1	0.00
Muricidae	*Hexaplex nigritus*	PC	4	0.07	4	0.01
Muricidae	*Hexaplex princeps*	PC	3	0.05	3	0.01

DISCUSSION

The information in this research shows for the first time the trends of abundance and occurrences of the different trophic guilds of 41 intertidal species within the Gulf of California. According to Brusca et al. (2005) and Brusca & Hendrickx (2008) the taxonomic richness in the gulf region maintains the presence of at least 135 families of the class Gastropoda and have been defined: especially 1 317 *taxa* were considered benthic. The gathered information for this research demonstrates the presence of 15 families (11.85% of the total for the GC and 3.11% of the total benthic *taxa* for the gulf) of rocky intertidal zones of the NEGC. However, based on the work of different authors, a lower malacological richness would be expected in sites of subtropical marine regions, such as those in this study (Roy *et al.,* 2000; Sevilla *et al.,*

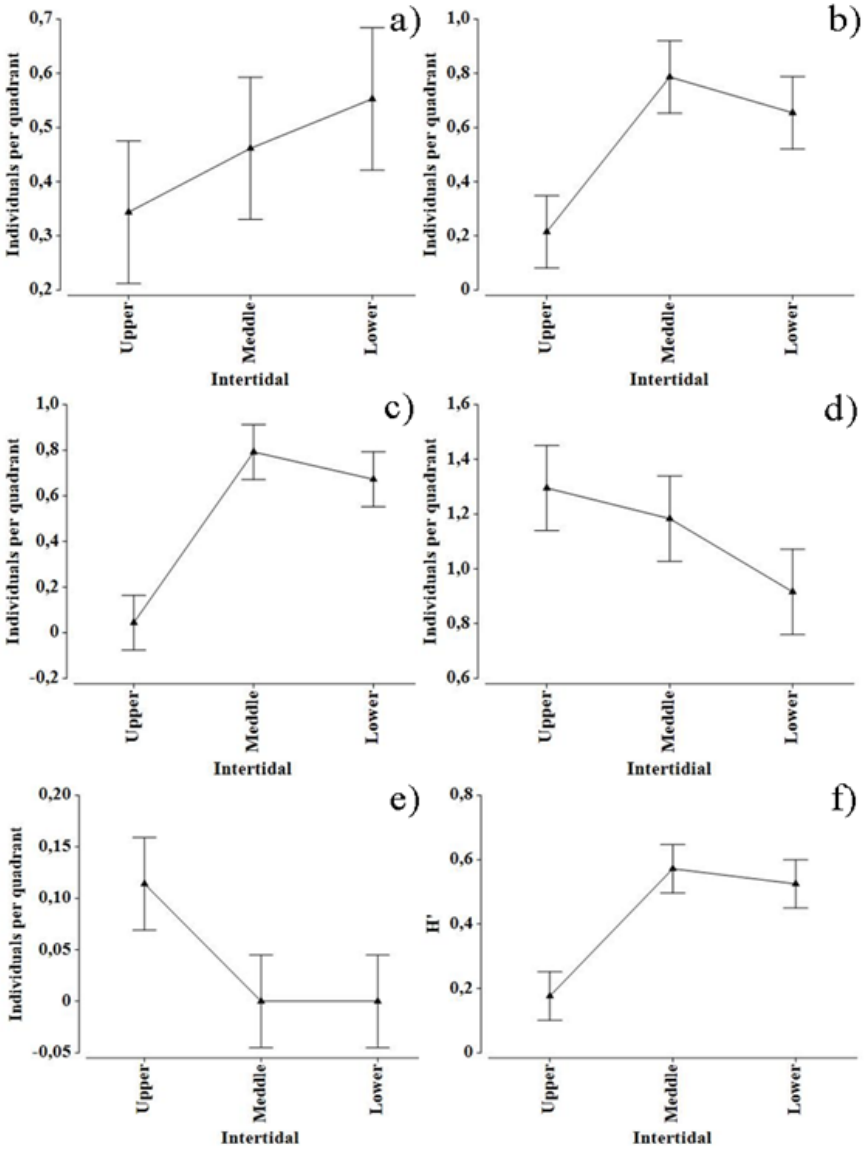

Figure 2. Abundance of intertidal gastropods per sampling unit (2 m^2 quadrants), feeding guild: (a) omnivores; (b) predatory carnivore*; (c) carnivores*; (d) algivores*; (e) microalgivore*; and (f) trophic diversity* (Shannon-Wiener index) at three tide levels in the northeast Gulf of California, Mexico (latitudes 27º N to 31º N). The asterisks in the names of the trophic guilds indicate significant differences ($P \leq 0.05$). Notice the difference in scale in Y axis.

2003; Ríos-Jara *et al.,* 2015). In contrast, the difference between the values from the Caribbean Sea and Indian coasts (tropical latitudes) (Cruz-Abrego *et al.,* 1994; Pawar *et al.,* 2017) was low, which confirmed the high species richness of the malacological fauna in rocky substrates of the GC (Brusca *et al.,* 2004, Hump & Malone 2015; Skoglund 2002). On the other hand, Roy et al. (1994) defined that mollusc diversity in the East Pacific (including the GC) does not obey a latitudinal correlation according to the Rapoport rule. This rule stipulates that species are correlated between the size of geographic areas and latitudes, and proposes that the species best adapted to climate seasonality are able to cover a wide range of latitudinal distribution. Therefore, and based on the observed values, This study infers that the particular and temporal (biotic, abiotic and climatic) conditions within the GC favour a wide distribution of the species that inhabit it, as is the case of the species *T. fluctuosus*, *N. funiculata*, *P. elegans* and *Claremontiela nodulosa*.

Regarding the representativeness of taxonomic richness by trophic guild, this study found, in general, that algivores and carnivores dominated (52.09% and 33.44%, respectively; Table 1, Fig. 4). When these results were contrasted with different studies, it was evident that the malacological richness values by food guild in the GC behave similarly to that reported

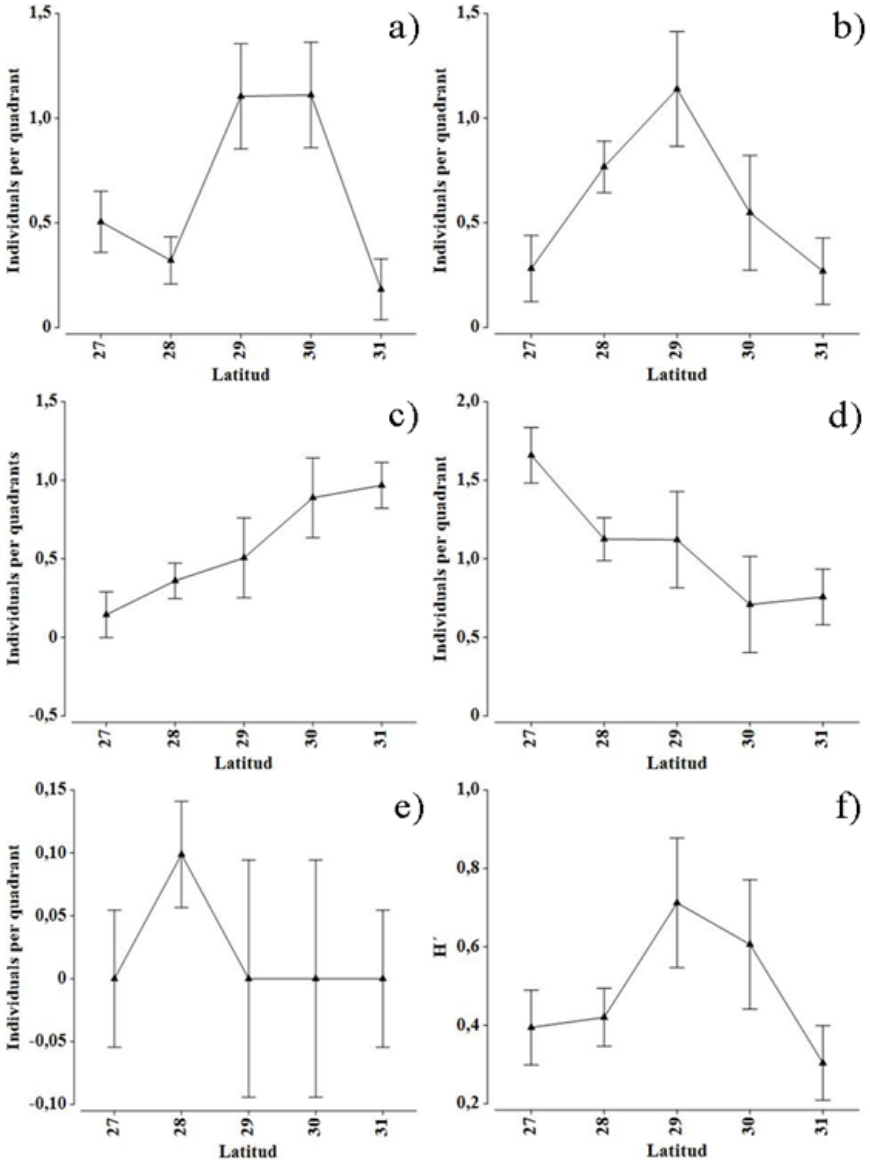

Figure 3. Abundance of intertidal gastropods per sampling unit (2 m2 quadrants), feeding guild: a) omnivore*, b) predatory carnivore*, c) browser carnivores*, d) macroalgivore*, e) microalgivore*; and f) trophic diversity (Shannon-Wiener index) at five latitudinal degrees in the northeastern Gulf of California, Mexico. The asterisks in the names of the trophic guilds indicate significant differences ($P \leq 0.05$). Notice the difference in scale in Y axis.

in other areas worldwide, since the highest taxonomic richness was expressed in herbivore and carnivore guilds. For instance, Cruz-Abrego *et al.* (1994) analysed the composition of the class Gastropoda in Isla Contoy in the Mexican Caribbean, highlighting the presence of 47 species and dominant food guilds were carnivore and herbivore with 40% and 36% of species richness, respectively. On the other hand, Aldea & Valdovinos (2005) described intertidal malacological fauna in points of the central-south coast of Chile (South Pacific). Their results showed that Gastropoda reached 15 families composed by 55 *taxa*, of which 58.18% of the taxonomic richness were herbivores, 25.45% carnivores, 1.82% omnivores and 14.55% among other guilds. Moreover, Pawar *et al.* (2017) made manual gastropod collections on intertidal rocky areas in a locality on the Uran coast in India from 2013-2015 and defined the presence of 25 families that included 60 species. The proportions by food guild in their results showed a higher taxonomic richness for herbivores with 46.67%; carnivores reached 41.68%, omnivores 8.33% and 3.32% for detritivores.

Values per intertidal level. The analysed information regarding the distribution of gastropod trophic

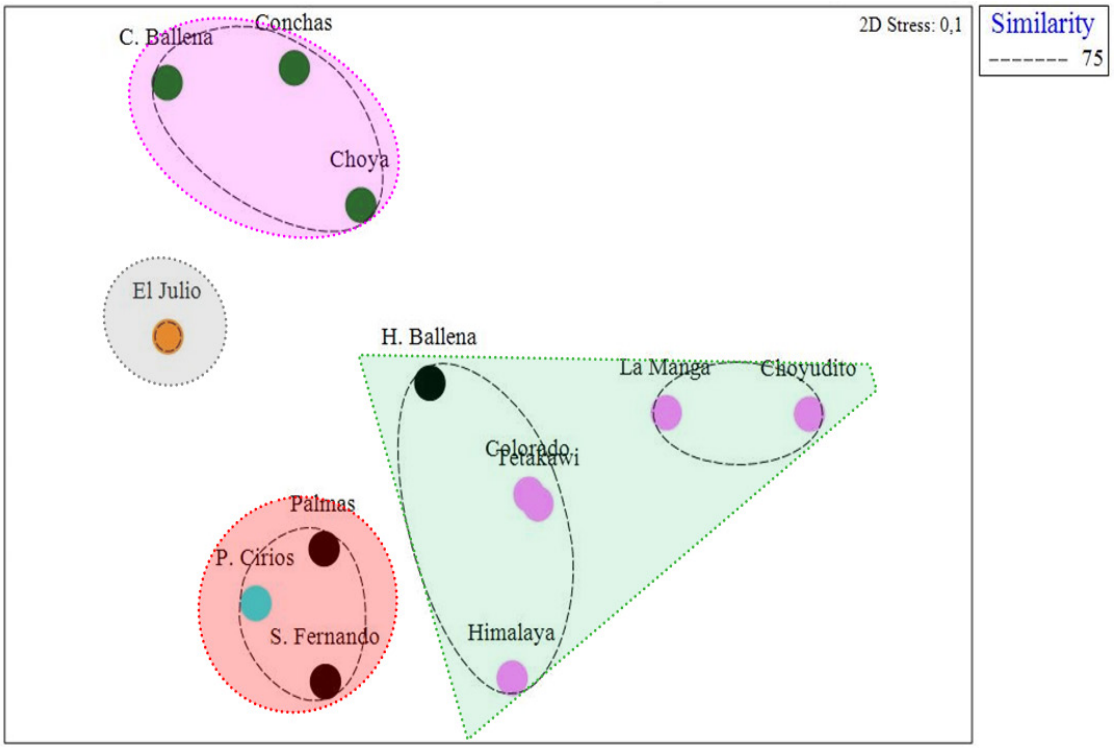

Figure 4. Non-metric multidimensional scaling of sampling sites in the northeast Gulf of California, Mexico based on average abundance of intertidal gastropod feeding guilds. The black line ovals indicate 75% similarity. The coloured figures on the groups indicate areas where the species assemblage is numerically dominated by algivores (green dotted line), predatory carnivores (red dotted line), omnivores (gray dotted line) and carnivores (pink dotted line). Colour of dots depict latitudinal belt. Pink: 27º N; Black: 28 ° N; Blue sky: 29º N; Orange 30º N and Green: 31ºN.

guilds in the intertidal zones of the NEGC showed there is a pattern according to what some authors have shown in other studies outside the gulf. The analyses showed that algivores maintained high abundances at the upper intertidal level, and in this guild, *N. funiculata* was *taxa* with the highest abundance (Table 1, Fig. 2), in agreement with Sturm *et al.* (2006) who mentioned that the upper and intermediate intertidal levels have a great abundance of conspicuous gastropods and predominance of the Trochoidea and Neritidae families (algivores) due to food disposition, especially green, red and calcareous algae on the hard substrate (Table 1). On the other hand, the representativeness of carnivores and predatory carnivores had higher abundances in the middle and low intertidal levels (Fig. 3) and were mostly represented by the Muricidae family (34.14% of the total; Table 1). The most abundant representative species in this family was *Mexacanthina angelica* (10.05% of the total), species that specialises in predating the abundant barnacles found in the intertidal middle part mainly (Bertsch & Aguilar-Rosas, 2016). Another work that describes these patterns was that of Baharuddin *et al.* (2018) who described the diversity of benthic molluscs on the rocky intertidal zone of the east coast of Malaysia. These authors found a total species rich-

Table 2. Three-way nested permutational multivariate analysis of variance (PERMANOVA) results for abundances of gastropod trophic guilds at different spatial levels within the Northeast Gulf of California (NEGC) and the corresponding levels of variation by factor (%). The asterisk indicates the significant differences $P < 0.05$.

PERMANOVA table of results

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Latitude	4	135000	33751	6,0521	0,0003*	9815
Sites(Latitude)	8	44613	5576,7	0,57985	0,9128	9927
Intertidal(Sites(Latitude))	26	250050	9617,4	7,4194	0,0001*	9862
Residual	312	404430	1296,3			
Total	350	834100				

ness of 28 *taxa* and pointed out that the families Littorinidae (algivore) and Muricidae (carnivore) were the best represented in the three (upper, middle, lower) intertidal zones.

Latitudinal representation. Taylor and Taylor (1977) explained that the distribution of predatory gastropods on the Atlantic coasts attends an increase in diversity from latitude 40° N, attributing it to the drastic change in abiotic factors that positively influence the presence of generalist predatory families. Likewise, Rivadeneira *et al.* (2015) mentioned that species richness of these benthic molluscs (Gastropoda and Bivalvia) is accentuated in the tropical latitudinal gradients, based on extrapolations of intertidal taxon richness. On the other hand, Roy *et al.* (1994) defined that mollusc (including gastropod) diversity in the East Pacific (including the GC) does not obey a latitudinal correlation according to the Rapoport rule, as previously mentioned – species are correlated between the size of the geographic areas and latitudes – proposing that the species better adapted to climate seasonality are able to cover a wide range of latitudinal distribution.

In contrast to the results in this study, the heterogeneity of food guilds showed by the class Gastropoda in the latitudinal gradient of the NEGC (27 ° N - 30 ° N) could be supported by the peculiar oceanographic dynamics that occur in the north and central GC according to Roy *et al.* (1994) and Simison (2005), influencing the peculiar faunal distribution described by Brusca *et al.* (2005). This result is evident with the increase in diversity values in the north latitudes 29 ° N - 31 ° N with an increase in omnivore and carnivore gastropod diversity according to Taylor & Taylor (1977). Likewise, specifically the specialist carnivores (predatory carnivores) were better represented at latitude 30 ° N (Fig. 3) located in the centre of the north GC faunal region indicated by Brusca *et al.* (2005), while herbivores were more representative in south latitudes 27 ° N - 29 ° N. These facts allow inferring that the main trophic guilds present in the GC cover geographic areas in which they are highly adapted: carnivores such as *M. angelica*, *P. elegans* and *C. nodulosa* dominate latitudes where climate factors are highly extreme (temperature, dissection time and seasonality) (Brusca *et al.,* 2005). Whereas algivores *T. fluctuosus, N. funiculata* are distributed in latitudes with mostly homogeneous climate variability that allows greater stability in food disposition (Readdie *et al.,* 2006; Rivadeneira *et al.,* 2015; Baharuddin *et al.,* 2019) in intertidal marine environment. The foregoing is also evident and is supported by the demonstrated groupings of the NMDS (Fig. 4), in which the trophic guilds are clearly grouped latitudinally.

In conclusion, the assemblage of Gastropoda trophic guilds at latitudinal gradient and intertidal zones of the NEGC demonstrates significant changes at these scales. And the algivorous and carnivorous guilds predominated in the southern and northern latitudes, respectively. Regarding trophic diversity, it only presents differences at the intertidal level, specifically in the upper fringe.

The study demonstrates the need to strengthen efforts to characterize and comprehend in detail the ecological plasticity of Gastropoda, as a way to improve the understanding of this mollusc group, which is a significant part of the benthos.

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