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Diversity and seasonal variation of the molluscan community associated with the seagrass *Halodule wrightii* in a marine protected area in the southern Gulf of California

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Abstract The structural complexity of *Halodule wrightii* enhances the abundance and diversity of mollusks in the marine protected area of Bahía Balandra, in the southern Gulf of California. Marine mollusks are considered ecosystem engineers because they create, modify, and maintain habitats. Taxonomical and functional analyses of the mollusk community were carried out from May 2016 to 2017. The total abundance in all sampled periods was 7284 individuals and comprised 52 families, 69 genera, and 89 species. The Gastropoda class showed the highest number of species (61 species, 68.53%), followed by Bivalvia (24 species, 26.96%) and Scaphopoda (4 species, 4.49%). The highest density of mollusks was in the summer of 2016 (*ca.* 6500 ind. m^{-2}), while the highest richness was found in spring 2017 (60 species). Five trophic levels were identified. All trophic groups were present in all the seasons with carnivores showing the highest species richness and herbivores the highest abundance, followed by filter-feeders. A positive and moderate relationship between the total biomass of seagrass and gastropod richness was found, while the relationship between gastropod abundance and seagrass biomass was negative. *Halodule wrightii* in the Gulf of California represents a unique niche that supports a high mollusk biodiversity and offers great variability of resources for this group. *Halodule wrightii* represents a suitable habitat for reproduction, metamorphosis, nursery, refuge, and feeding for mollusks. Finally, the functional group concept was applied to evaluate the ecosystem seagrass health of Bahía Balandra resulting in a moderate score.

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Introduction

Sustainable use of marine and coastal living resources cannot be adequately established without a good knowledge of biodiversity (Hendrickx et al. 2007). The links among changes in species diversity, ecosystem functions, and services are relevant in marine systems, particularly in coastal areas where an accelerated decrease of mangroves, coral reefs, and seagrass beds have been reported (e.g., seagrass loss of 110 km^2 yr^{-1}) (Fortes 1988; Short and Wyllie-Echeverria 1996; Orth et al. 2006; Waycott et al. 2009). Many marine mollusks are considered ecosystem engineers because they create, modify, and maintain habitats (Jones et al. 1994, 1997). Shell-producing mollusks can structure benthic habitats by modifying and increasing their heterogeneity and complexity, ultimately making resources available for other organisms (Jones et al. 1997; Gutiérrez et al. 2003; Fortunato 2015). Mollusks that live as epifauna or infauna are functionally important in trophic webs and are key species in benthic marine ecosystems (Webster et al. 1998; Hemminga and Duarte 2000). The marine mollusks (gastropods, bivalves, scaphopods, and cephalopods, among others; Haszprunar and Wanninger 2012) have been classified according to the trophic guild to which they belong, e.g., suspension feeders (Rosa et al. 2018), herbivores (Buschbaum 2000), parasites (Høisæter 2014), carnivorous predators (Young 1985; Valentine et al. 2002), and detritivores (Brusca et al. 2016). They are interconnected by energy flow patterns and deposition processes that help to balance the trophic structure of the community (Hootsmans and Vermat 1985; Greenway 1995; Peterson and Heck 2001). Consequently, marine mollusks create a network that promotes plant–animal–plant interactions, both positive and negative (Gagnon et al. 2020).

Seagrasses are present in temperate and tropical marine regions (Hemminga and Duarte 2000), being a critical component of coastal communities in shallow waters. They promote ecologically important functions and services, such as modifying the hydrodynamic environment, stabilizing the sediment, providing oxygen, and acting as important carbon source. In addition, the seagrass biomass is key in the energy flow and food webs of coastal ecosystems (den Hartog 1970; Heck and Valentine 1995; Hemminga and Duarte 2000; Mosbahi et al. 2018). Knowledge of functional feeding groups is key to understanding the structure and function of the ecosystem (Peng et al. 2013). According to Gamito and Furtado (2009) in seagrass healthy areas almost all feeding groups are present; in contrast, in areas affected by environmental or anthropogenic negative effects, the dominance of feeding groups will change showing frequently a reduction in the number of groups.

The structure of seagrasses (leaves and rhizomes/roots) creates suitable microhabitats that maintain high levels of biodiversity, thus increasing the primary and secondary productivity of coastal ecosystems (Kaldy and Dunton 2000; Somerfield et al. 2002; Spalding et al. 2003; Bouma et al. 2005; Koch et al. 2006; Mateo et al. 2006). The studies about the relationship between seagrasses (primary producers) and their associated fauna (e.g., mollusks) are essential to developing suitable management of coastal biological resources because the results generate valuable information to establish biodiversity conservation strategies, in ecosystems affected by human activity; this issue is of particularly great priority, since reverting human impacts can contribute to preserving ecological functions of degraded and fragmented marine habitats (Bentley et al. 2000; Hauser et al. 2006).

In the Gulf of California, populations of the seagrass *Halodule wrightii* are located in the northernmost range along the Mexican Pacific Ocean coast, showing a patchy distribution (Santamaría-Gallegos 2016). In this region, the first record of *H. wrightii* was reported 41 years ago and since then at least there are populations identified in six localities from Baja California Sur, Mexico; recently, *H. wrightii* was listed as threatened species in Mexico (Pérez-Estrada et al. 2021; NOM-059-SEMARNAT-2010, DOF 2019). Given that Bahía Balandra is a natural protected area, we assumed that seagrass in this zone has a healthy environment and high mollusk diversity with all feeding groups represented, whereas if the environment is degraded, a few groups will generally dominate it. Based on this assumption, the objective was to provide a taxonomic inventory of mollusks associated with seagrass populations in Bahía

Balandra, contributing with information leading to the identification of diverse key species, with emphasis in the potential changes in the seasonal variability in the biodiversity, abundance, and density of mollusks in the region.

Study area

The study was carried out on the shallow coast of Bahía Balandra, in the southern region of the Baja California Peninsula, Mexico (24°18′54.8″ N; 110°19′39.3″ W, Fig. 1). Bahía Balandra comprises a coastal lagoon, rocky reefs, and mangrove communities; the sandy substrate is mostly composed of the remaining invertebrate shells and calcium carbonate (Torres-Alfaro 2010; CONANP 2016). The tidal pattern is semi-diurnal and oscillates between 1 and 1.5 m; salinity values vary between 34.4 and 36.42 UPS (CONANP 2016; Urquidi-Gaume 2018; Pérez-Estrada et al. 2021). The sea surface temperature reaches minimum values during winter (12–20 °C), peaking in summer (29–39.5 °C) (Mendoza-Salgado 1983; Sicard et al. 2012). Bahía Balandra is in a subtropical arid zone where tropical cyclones and hurricanes typically occur every year with a wide range of frequency and intensity (Pérez-Estrada et al. 2021). In this area, the community of primary producers is composed of patches of *H. wrightii* and several species of algae. Monospecific perennial patches of *H. wrightii* have a scattered distribution (both intertidal and subtidal) in the area. For this study, only subtidal patches of *H. wrightii* at 0.4–0.75 m depth at low tide were sampled (Fig. 1) (Pérez-Estrada et al. 2021). Proliferations of two species of macroalgae have been reported in the area (*Caulerpa sertulariodes* and *Spyridia filamentosa*). These species covered considerable extensions in the sandy areas attached to the

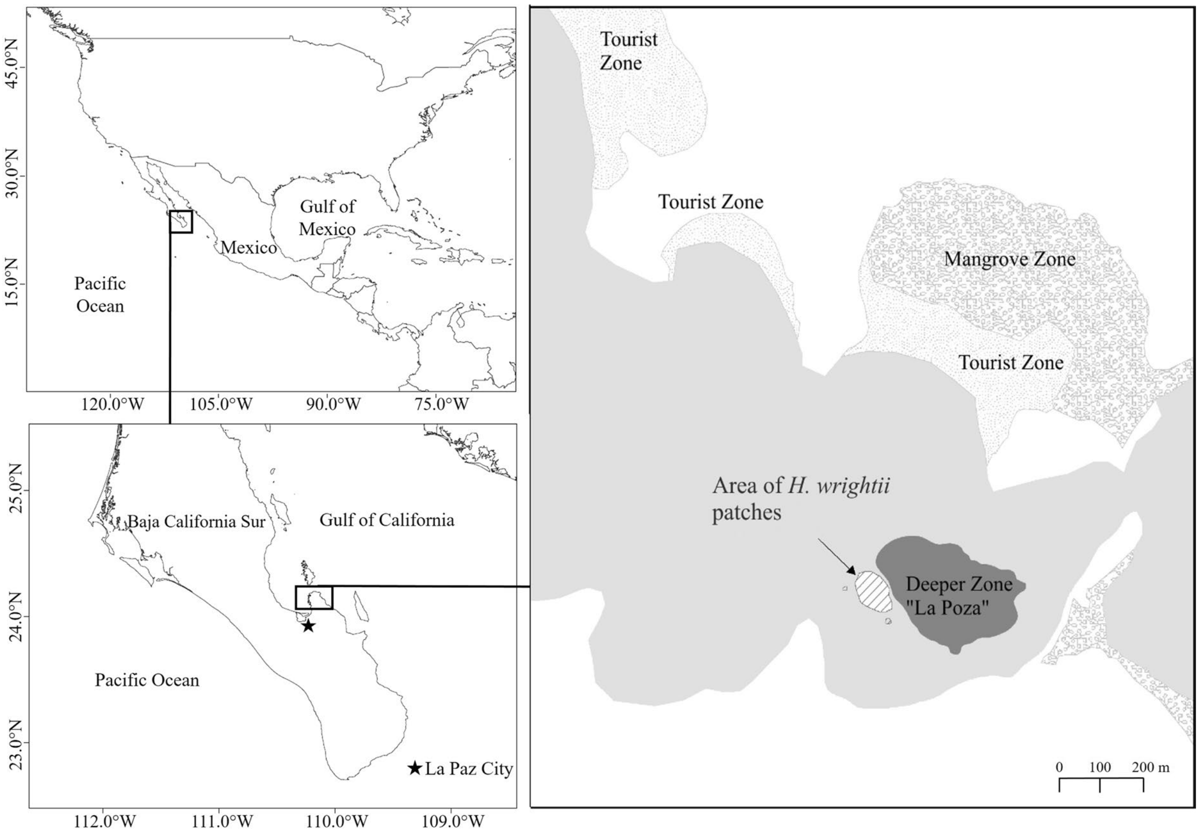


Fig. 1 Spatial distribution of patches of *Halodule wrightii* in the marine protected area of Bahía Balandra located in the southern region from the Baja California Peninsula, Mexico

mangrove swamp, and the records were accompanied by *Polysiphonia simplex* (Huerta-Múzquiz and Mendoza-González 1985). Epiphytic algae predominated in April, July, and January (i.e., *Ceramium* sp. and diatoms) and cyanobacterial proliferation of *Lyngbya* sp. and *Anabaena* sp. occur mainly during "El Niño" events or after rain.

Material and methods

Abiotic data collection

The environmental variables measured in the study area were water temperature (°C), salinity (UPS), and pH using a multiparametric probe (model YSI Pro Plus); the sensor was placed ten centimeters above the seagrass canopy; rainfall data were obtained from Comisión Nacional del Agua (National Water Commission) (INEGI 2017). Additionally, samples of sediment within patches of seagrass beds were taken with a core of 4 cm in diameter and 15 cm in depth. The organic matter content and chlorophyll-*a* concentration were estimated, considering these values as an indirect measure of general productivity (Pinckney and Zingmark 1993).

Measurement of organic matter and chlorophyll a

Organic matter (OM) content analyses were carried out, following Walkley and Black (1934) methodology, such as is established in the Mexican Official Standard NOM-021-SEMARNAT-2000 AS-07 (DOF 2002). For the determination of chlorophyll, we extracted and measured the sediment from the first 2 cm of the cores, corresponding to the surface in contact with seawater. From each sample, 5 g of wet sediment was weighed and placed in 10-ml tubes with 90% acetone–water solution. All tubes were covered with aluminum foil and stored for 24 h at 4 °C in the dark. Later, we determined the concentration of Chl *a* with spectrophotometry, and we followed the methodology of Strickland and Parsons (1972).

Seagrass samples

We randomly selected two patches of *H. wrightii* (15.8 and 36.1 m^2 size) and collected the samples at low tide (depth: 0.4 to 0.75 m depending of the date). From each patch, five samples were taken at a distance of 1 m from each other. They were randomly collected approximately every three months completing during each sampling event 10 samples, from May 2016 to May 2017 [Dates: 15/05/2016 (spring), 12/07/2016 (summer), 23/11/2016 (Autumn), 24/01/2017 (winter), 07/05/2017 (spring)]. Thus, 50 samples were collected during the study period. We collected samples of *H. wrightii* and the sandy sediment by using a 19.5-cm-diameter core. The core was introduced 10 cm into the sediment to obtain the biomass of seagrasses (above and belowground parts). The samples were deposited in plastic bags with seawater. All of them were transported in an ice chest to the laboratory. The seagrass material was separated into aboveground (leaves) and belowground (rhizome and roots complex) components; the samples were dried at 60 °C for 48 h and then weighted to determine aboveground and belowground biomasses in dry weight (DW) separately. Values were expressed as g DW m^{-2}.

Taxonomic identification

We rinsed the seagrass samples, cleaned the sediment, and later poured the water through sieves with different mesh sizes (1.19, 0.54, 0.31, and 0.05 mm) for collecting the mollusks. After that, plants were placed in a tray with water and observed under a stereomicroscope (Nikon SMZ25) to collect the organisms that could be attached to the plant. The same procedure was performed with the sediment portion of the samples. All organisms were separated and fixed in 70% alcohol. The mollusks were identified at the lowest taxonomic level based on their morphological characteristics according to the available literature (Abbott 1954; Keen 1971; Brusca 1980; Kozloff 1987; Kerstitch and Bertsch 2007; Rosenberg 2009; Coan and Valentich-Scott 2012; Gurgo-Salice and Caceres 2020). The systematic arrangement within each major mollusk taxon (Gastropoda, Bivalvia, Scaphopoda) follows the criteria of WoRMS (2021) and MolluscaBase (2019).

Density and biomass of mollusks

For the estimation of the density of mollusks, we used the information of the organisms obtained from the core and extrapolated it to m^2 (area = 0.03 m^2). To estimate the biomass of mollusks on each sampling date, all specimens were weighted grouped (including the shell) using an Ohaus explorer analytic scale, with an accuracy of 0.0001 g. Before weighing the specimens, the excess water was removed with paper towels. The values were expressed as wet body weight in g (WW).

Trophic composition, diversity indices *and ecosystem health state*

The mollusks found in leaves and belowground components were considered together for all analyses. The mollusks were grouped according to their feeding habits from different references (Keen 1971; Rosenberg et al. 2009; Arapov et al. 2010; MolluscaBase 2019) as carnivorous, herbivorous, filter-feeders, detritivores, or parasites. The community structure of mollusks was analyzed using the species richness index (number of mollusks by taxa present in the sample). The diversity between mollusk taxa and seasonal sampling dates was analyzed with the Shannon–Wiener index. The diversity index of Simpson (1–λ) indicates the probability that two individuals randomly selected from a sample will belong to a different species. The value of this index ranges between 0 and 1, where 1 indicates the greater diversity in the sample. The Pielou index (J') was used to quantify the evenness component, and the nonparametric species estimator Chao 1 was used to predict the number of expected species of mollusks, and rarefaction curves were estimated (Chao et al. 2014).

We analyzed the index of trophic diversity (ITD) (Heip et al. 1998) using the functional (trophic) diversity of the mollusk assemblages at each season, which ranges from 0 to 1 (high and low trophic diversity, respectively), and was calculated according to the following equation: $\mathrm{ITD} = \Sigma\ \mathrm{qi}^2$, where qi is the relative contribution of the number of individuals of each trophic group (i) to the total number of individuals. For this study, the ITD was calculated as 1-ITD to have the highest trophic diversity with the greatest weight according to the modified version applied to mollusks (Antit et al. 2016). Pearson correlation analyses were performed for testing the relationship between the index of trophic diversity (expressed as 1-ITD) and ecological indices (species richness, Shannon–Wiener diversity, and evenness index).

The ecosystem health state (EHS) was estimated from the molluscan functional feeding groups based on the feeding evenness index (jFD) following the methodology of Gamito and Furtado (2009):

$$\mathrm{jFD} = \mathrm{H'FD}/\mathrm{Log}_2\, n$$

where H' is the Shannon–Wiener index (Shannon and Weaver 1963) and n is the number of feeding groups, in this case, five. The ecosystem health state (EHS) was determined from the ratio intervals following the method of Gamito et al. (2012): evenness values greater than 0.80 to 1 correspond to a "high" EHS; values between 0.80 and 0.60 indicate a "good" EHS; values of 0.40–0.60 indicate a "moderate" EHS; values 0.20–0.40 indicate a "poor" EHS, and evenness values less than or equal to 0.20 signaled a "bad" EHS.

Data analysis

Due to the small number of scaphopod species, both bivalves and scaphopod were combined to jointly make comparisons with the rest of the community (Cavalcante et al. 2019). We conducted Kruskal–Wallis tests ($\alpha < 0.05$) to determine seasonal differences in abiotic data, richness, abundance, and trophic guilds; a *G* test ($\alpha < 0.05$, software R, package DescTools27, Signorell et al. 2019) was used to determine seasonal differences in mollusk density and biomass, and the biomass of seagrasses.

Differences in the Shannon–Wiener diversity index were compared among groups, seasons, and trophic guilds using paired *t* tests (Hutcheson 1970). The species diversity indices, rarefaction curves, and *t* test were computed in the Past software package (Hammer et al. 2001). We used the rank abundance model to evaluate the patterns of diversity between seasons; this model helped to visualize the dominance of the mollusk community found during each season (Whittaker 1965). Spearman rank correlations (*r*) were calculated with a correlogram matrix to determine and visualize the relationships (direction, strength, and statistical significance 0.05) between the abundance and richness of groups of mollusks, trophic guild, the density of mollusks, and the biomass related to *H. wrightii* biomass. The relationships with *r* values < 0.5 were considered "weak", while those between 0.5 and

0.69 were "moderate", and r values ≥ 0.7 suggested a "strong" correlation (Taylor 1990). The correlation was performed using GraphPad Prism version 9.1.0 for Windows.

Results

Abiotic data

The temperature ($\chi^2 = 10.23$, df = 4, $p < 0.0366$), rainfall ($\chi^2 = 49$, df = 4, $p < 0.001$), organic matter ($\chi^2 = 28.85$, df = 4, $p < 0.001$), and chlorophyll a ($\chi^2 = 31.37$, df = 4, $p < 0.001$) in the study area showed significant differences between seasons (Table 1). The highest water temperature was reached in summer 2016 (27.35 °C) and the lowest in winter of 2017 (21.22 °C). The highest rainfall occurred during summer (52.6 mm), which represents the rainy month when hurricanes hit the area. Organic matter and chlorophyll a were lower in spring 2016 (0.17 g OM g^{-1}sed and 1.29 mg g DW^{-1}, respectively) and highest in winter 2017 (0.39 g and 3.05 mg g DW^{-1}, respectively). Salinity and pH did not show significant differences through the seasons in the study period ($p > 0.199$; $p > 0.681$, respectively, Table 1).

Species richness and functional groups

We collected 7284 specimens of mollusks associated with *H. wrightii,* 82.5% belonging to gastropods, 17.37% to bivalves, and 0.14% to scaphopods. A total of 89 species of mollusks were identified (Table 2, Fig. 1a–e supplementary material), distributed in 69 genera and 52 families. The class Gastropoda was the most abundant (61 species in 36 families), followed by Bivalvia (24 species in 14 families) and Scaphopoda (4 species in 2 families). The family Olividae (8 species) was the richest within Gastropoda, but Dialidae and Litiopidae contained the most abundant species. Lucinidae and Veneridae were the most abundant families belonging to Bivalvia, with four species each. The most abundant species of Gastropoda were *Diala* sp., *Alaba aladulensis*, *Alaba supralirata*, and for Bivalvia, the most abundant species were *Megapitaria squalida* and *Cavilinga prolongata*. In total, these species comprised 90% of the entire mollusk community in terms of abundance (Fig. 2). The absolute richness significantly varied between taxa ($\chi^2 = 12.5$, df = 2, $p < 0.001$).

Functional mollusk groups were defined according to feeding habits and divided into five trophic groups: carnivores, herbivores, filter-feeders, parasites, and detritivores. The carnivores exhibited the highest number of species (34), followed by filter-feeders (24) and herbivores (21); the parasitic and detritivore groups contained fewer species (5 each) (Table 4, Fig. 3). The trophic composition in terms of abundance showed herbivores as the most dominant (5547 individuals), followed by filter-feeders (1265 individuals) and carnivores (329 individuals), while parasitic and detritivore groups were the least abundant (20 and 123 individuals, respectively) (Fig. 3).

Mollusk abundance, density, biomass, and seagrass biomass

The total abundance of mollusks varied significantly throughout the seasons ($\chi^2 = 23.6$, df = 4, $p < 0.001$) and among taxa ($\chi^2 = 11.2$, df = 2, $p = 0.003$). The highest number of individuals was found during the summer of 2016 (2010 ind.; 27.6%) and the winter of 2017 (2030 ind.; 27.9%); in contrast, the lowest abundance was observed in the spring (273

Table 1 Seasonal variation of abiotic variables measured in the marine protected area of Bahía Balandra located in the southern region of the Baja California Peninsula (mean values ± standard error)

	Season	Temperature °C	Salinity UPS	pH	Rainfall mm	Organic matter (g OM g^{-1}sed)	Chlorophyll a mg g DW^{-1}
2016	Spring	24.58 ± 0.05	36.09 ± 0.06	8.04 ± 0.15	4.1 ± 1.2	0.16 ± 0.01	1.29 ± 0.02
	Summer	27.35 ± 0.13	36.51 ± 0.06	8.10 ± 0.32	52.6 ± 16.3	0.20 ± 0.02	1.63 ± 0.06
	Autumn	26.62 ± 0.08	36.12 ± 0.23	8.27 ± 0.07	5.4 ± 3.4	0.22 ± 0.02	2.20 ± 0.28
2017	Winter	21.22 ± 0.19	36.65 ± 0.07	8.33 ± 0.12	9.1 ± 5.2	0.38 ± 0.02	3.05 ± 0.08
	Spring	22.94 ± 0.11	36.72 ± 0.18	8.22 ± 0.23	1.2 ± 0.6	0.34 ± 0.02	2.05 ± 0.15

Table 2 Specific richness and trophic guilds of mollusks associated with *H. wrightii* in Bahía Balandra, southern Gulf of California. Listed by class, and alphabetical order of the family

Class	Family	Species	N	Trophic guild
Gastropoda	Aplysiidae	*Stylocheilus rickettsi*	6	Herbivore
	Bullidae	*Bulla punctulata*	2	Herbivore
	Cerithiopsiidae	*Seila assimilata*	3	Carnivore
	Columbellidae	*Anachis spadicea*	3	Detritivore
		Mitrella caulerpae	14	Carnivore
		Strombina maculosa	4	Detritivore
	Cylichnoidea	*Cylichnella defuncta*	50	Carnivore
	Cymatiidae	*Cymatium wiegmanni*	1	Carnivore
	Dialidae	*Diala* sp.	2278	Herbivore
	Drilliidae	*Globidrillia paucistriata*	2	Carnivore
	Epitoniidae	*Epitonium acapulcanum*	1	Carnivore
		Epitonium hindsii	4	Carnivore
		Epitonium willetti	2	Carnivore
		Opalia crystallina	1	Carnivore
	Eulimiidae	*Aclis* sp.	11	Parasite
	Fissurellidae	*Fissurella asperella*	4	Herbivore
	Granulinidae	*Granulina margaritula*	2	Carnivore
	Haminoeidae	*Aliculastrum exaratum*	4	Herbivore
		Haminoea cf. *vesicula*	11	Herbivore
	Litiopidae	*Alaba aladulensis*	1951	Herbivore
		Alaba supralirata	1193	Herbivore
	Littorinidae	*Echinolittorina albicarinata*	1	Herbivore
Gastropoda	Lottiidae	*Lottia* sp.	3	Herbivore
		Lottia digitalis	2	Herbivore
		Lottia fascicularis	14	Herbivore
		Lottia strongiana	3	Herbivore
	Mangeliidae	*Notocytharella phaethusa*	1	Carnivore
		Pyrgocythara danae	3	Carnivore
		Volvarina taeniolata	5	Carnivore
	Modulidae	*Modulus disculus*	22	Herbivore
	Nassariidae	*Nassarius tiarula*	41	Detritivore
		Tritia sp.	1	Detritivore
	Naticidae	*Polinices intemeratus*	11	Carnivore
		Polinices uber	1	Carnivore
	Olividae	*Oliva spicata*	11	Carnivore
		Oliva undatella	13	Carnivore

Table 2 (continued)

Class	Family	Species	N	Trophic guild
		Olivella biplicata	33	Carnivore
		Olivella dama	2	Carnivore
	Olividae	*Olivella fletcherae*	38	Carnivore
		Olivella gracilis	34	Carnivore
		Olivella sphoni	5	Carnivore
		Olivella steveni	5	Carnivore
	Omalogyridae	*Ammonicera* sp.	1	Herbivore
	Phasianellidae	*Eulithidium cyclostoma*	1	Herbivore
		Eulithidium substriatum	9	Herbivore
	Pisaniidae	*Gemophos gemmatus*	2	Carnivore
	Planaxidae	*Fossarus* sp.	7	Herbivore
	Pyramidellidae	*Odostomia* sp. 1	2	Parasite
		Odostomia sp. 2	1	Parasite
		Turbonilla sp. 1	3	Parasite
		Turbonilla sp. 2	3	Parasite
	Raphitomidae	*Microdaphne morrisoni*	3	Carnivore
	Retusidae	*Sulcoretusa paziana*	1	Carnivore
	Rissoidae	*Alvania cosmia*	25	Herbivore
	Scaliolidae	*Finella tenuisculpta*	74	Detritivore
	Siphonariidae	*Siphonaria* sp.	8	Herbivore
	Terebridae	*Terebra variegata*	14	Carnivore
	Tornatinidae	*Acteocina inculta*	36	Carnivore
		Acteocina infrequens	20	Carnivore
	Tornidae	*Solariorbis elegans*	2	Herbivore
	Triphoridae	*Metaxia convexa*	1	Carnivore
Bivalvia	Arcidae	*Anadara tuberculosa*	1	Filter-feeder
	Cardiidae	*Laevicardium clarionense*	9	Filter-feeder
		Laevicardium elenense	1	Filter-feeder
		Laevicardium substriatum	5	Filter-feeder
	Lucinidae	*Cavilinga prolongata*	102	Filter-feeder
		Divalinga eburnea	5	Filter-feeder
		Miltha xantusi	3	Filter-feeder
		Radiolucina cancellaris	3	Filter-feeder
	Mactridae	*Spisula williamsi*	2	Filter-feeder

Table 2 (continued)

Class	Family	Species	N	Trophic guild
Bivalvia	Margaritidae	*Pinctada mazatlanica**	1	Filter-feeder
	Mytilidae	*Modiolus americanus*	4	Filter-feeder
	Nuculanidae	*Bathyspinula calcar*	1	Filter-feeder
	Pharidae	*Siliqua lucida*	14	Filter-feeder
	Pteriidae	*Pteria sterna*	4	Filter-feeder
	Solecurtidae	*Tagelus politus*	2	Filter-feeder
	Tellinidae	*Eurytellina regia*	3	Filter-feeder
		Serratina brevirostris	7	Filter-feeder
		Strigilla serrata	2	Filter-feeder
	Thraciidae	*Cyathodonta pedroana*	2	Filter-feeder
	Thyasiridae	*Axinulus thackergeigeri*	43	Filter-feeder
	Veneridae	*Chione guatulcoensis*	8	Filter-feeder
		Chione undatella	18	Filter-feeder
		Leukoma grata	1	Filter-feeder
		Megapitaria squalida	1024	Filter-feeder
Scaphopoda	Dentaliidae	*Graptacme semistriata*	3	Carnivore
		Graptacme splendida	2	Carnivore
		Tesseracme quadrangularis	3	Carnivore
	Laevidentaliidae	*Laevidentalium edoardi*	2	Carnivore

*Considered as a priority protection species by Mexican Official Standard NOM-059-SEMARNAT-2010, modification 2019

N = number of individuals

ind.; 3.7%) and autumn 2016 (1223 ind.; 16.79%). Similarly, the gastropods reached its maximum value and decreased significantly during these seasons ($\chi^2 = 11.7$, df = 4, $p = 0.02$). Conversely, neither the abundance of bivalves and scaphopods varied between seasons (Bivalvia: $\chi^2 = 2.4$, df = 4, $p = 0.66$; nor Scaphopoda: $\chi^2{}_4 = 3.4$, df = 4, $p = 0.48$) (Fig. 2). Gastropod, bivalves, and scaphopod and total density of mollusks associated to *H. wrightii* significantly varied among seasons ($G_{\text{gastropod}} = 36{,}346$, df = 4, $p < 0.0001$; $G_{\text{biv-scaph}} = 4854$, df = 4, $p < 0.0001$; $G_{\text{total}} = 37{,}326$, df = 4, $p < 0.0001$). The gastropod density was generally higher than bivalves-scaphopods. Maximum values were recorded for gastropods during the summer of 2016, while it was recorded for bivalves-scaphopods in the spring of 2017 (Table 3). The total density of mollusks was higher in summer 2016 and winter 2017, while the lowest density was recorded during spring 2016 (Table 3). The gastropods *Alaba aladulensis, A. supralirata, and Diala* sp. as well as the bivalve *Megapitaria squalida* showed on average the highest densities throughout the study (Table 4).

The biomass of mollusks showed significant differences among seasons ($G = 42$, df = 4, $p < 0.001$), reaching its maximum value during the autumn of 2016 (57.86 ± 11.65 g WW m^{-2}), and its lowest value during the summer of 2016 (31.90 ± 12.98 g WW m^{-2}) (Table 3). The highest mean biomass values for *H. wrightii* were obtained in spring 2017 (aboveground: 35.50 ± 2.01 g DW m^{-2}, belowground: 139.98 ± 12.28 g DW m^{-2}, total: 175.48 ± 13.60 g DW m^{-2}) (Table 3). The aboveground biomass of *H. wrightii* did not show significant differences between seasons ($G = 4$, df = 4, $p = 0.3$); however, belowground and total biomass showed significant differences between seasons ($G = 10$, df = 4, $p = 0.02$; $G = 32$, df = 4, $p < 0.001$). The belowground and total biomass peaked in spring of 2017, 139.98, and 175.48 g DW m^{-2}, respectively, and the lowest values were recorded in Spring 2016 (Table 3).

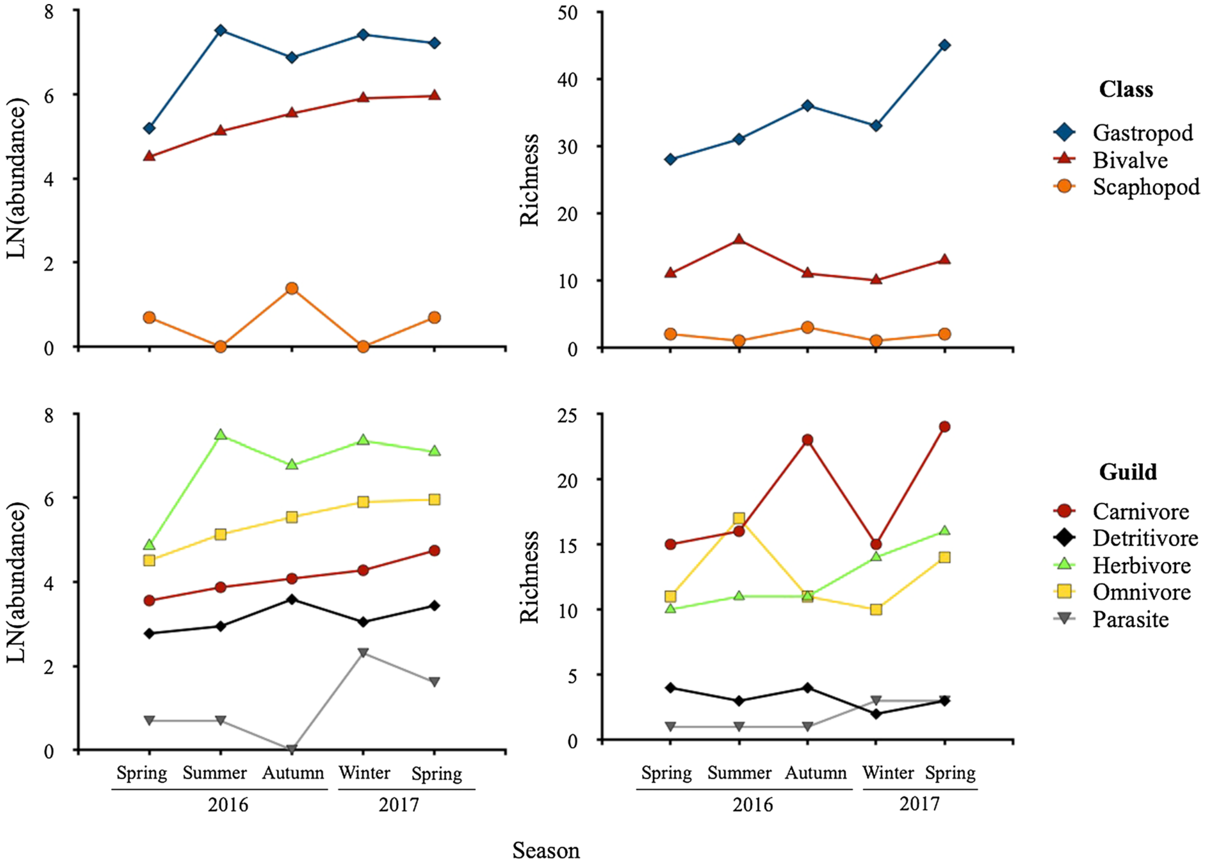


Fig. 2 Seasonal variation of mollusk taxa and trophic guilds in relation to abundance and number of species. Abundance values were transformed to natural logarithm (LN) in order to standardize the data variation

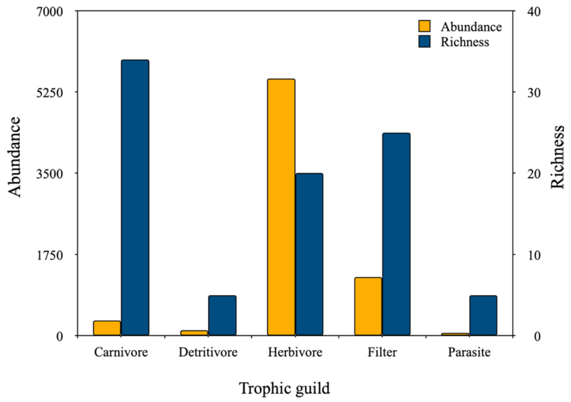


Fig. 3 Abundance (number of individuals) and richness (number of species) related to trophic structure of mollusks associated with *Halodule wrightii*

Diversity indices and ecosystem health state

The species richness according to the Chao1 estimator indicated that more than 87.8% of the available taxa were sampled; this means that most species of mollusks associated with *H. wrightii* were sampled during our study. Furthermore, with the sampling effort (50 samples), we obtained asymptotic rarefaction curves of alpha diversity in all taxa (Fig. 2a supplementary material).

Similarly, the rarefied and extrapolated diversity for each season were asymptotic, except during the spring of 2016 (Fig. 2b supplementary material). Likewise, the absolute richness varied significantly through trophic guilds ($\chi^2 = 20.2$, df = 4 $p < 0.001$). The lowest value of species richness was identified in spring 2016 (41 species) and the peak was reached in spring 2017 (60 species).

Table 3 Seasonal variation in density and biomass of mollusks and biomass of *H. wrightii* in the marine protected area of Bahía Balandra located in the southern region of the Baja California Peninsula (mean values ± standard error)

	Season	Density				Biomass		
		Gastropod Ind. m^{-2}	Bivalves-Scaphopod Ind. m^{-2}	All groups Ind. m^{-2}	*H. wrightii* Aboveground biomass g DW m^{-2}	*H. wrightii* Belowground biomass g DW m^{-2}	*Biomass H. wrightii* Total biomass g DW m^{-2}	Mollusk Biomass Total g FW m^{-2}
2016	Spring	607 ± 22.06	310 ± 24.15	917 ± 24.83	10.18 ± 0.62	44.55 ± 3.86	54.73 ± 4.29	43.44 ± 14.77
	Summer	6022 ± 613.1	560 ± 44.98	6582 ± 538.1	12.68 ± 1.74	56.88 ± 9.12	69.56 ± 10.78	31.90 ± 12.98
	Autumn	3213 ± 107.9	863 ± 56.6	4077 ± 118.2	25.31 ± 3.78	85.25 ± 10.88	110.56 ± 14.28	57.86 ± 11.65
2017	Winter	5580 ± 388.4	1230 ± 128.6	6810 ± 389.3	27.15 ± 2.89	93.90 ± 10.37	121.05 ± 12.14	34.11 ± 6.78
	Spring	4547 ± 120.4	1297 ± 93.63	5843 ± 143.4	35.50 ± 2.01	139.98 ± 12.28	175.48 ± 13.60	40.54 ± 16.91

Table 4 Density throughout the study period for those species of mollusks with the highest abundances at Bahía Balandra, southern Gulf of California (mean values ± standard error)

Class	Species	Density (ind. m^{-2})
Gastropoda	*Alaba aladulensis*	16,258 ± 1752
	Diala sp.	15,187 ± 6009
	Alaba supralirata	7953 ± 2375
	Finella tenuisculpta	493 ± 144
	Olivella gracilis	378 ± 40
	Cylichnella defuncta	333 ± 116
	Nassarius tiarula	273 ± 101
	Olivella fletcherae	267 ± 55
	Acteocina inculta	233 ± 111
	Olivella biplicata	220 ± 106
Bivalvia	*Megapitaria squalida*	6827 ± 1686
	Cavilinga prolongata	687 ± 129
	Axinulus thackergeigeri	478 ± 113

The community of gastropods was significantly more diverse ($H' = 1.6$) than the community of bivalves and scaphopods ($H' = 0.9$) ($t = 10.94$, df = 89, $p < 0.001$). Diversity measures also varied significantly across the seasons (Table 1 supplementary material). In the spring of 2016 and 2017, the community reached the maximum values of H' and λ diversity, as well the Q1 Hill number and Pielou's evenness (J'); in contrast, the lowest values of these indices were found during summer 2016 (Table 5). Differences in the dominance between the communities of gastropods against bivalves-scaphopods were found (t test = –21.1, df = 1352, $p < 0.001$). The higher dominance was found in spring 2016, while it diminished notably during autumn 2016 (Table 5, Fig. 4). Values of dominance were similar between communities (gastropods and bivalves-scaphopods) for most of the seasons, except during the autumn of 2016, when the dominance was lower (Fig. 4). The community of herbivores was more diverse ($H' = 1.12$) than all other trophic guilds, while the community of parasites had a lower diversity ($H' = 0.02$). The trophic diversity was significantly different among all groups ($p < 0.001$) (Table 2 supplementary material). The index of trophic diversity analysis (1-ITD) showed that the season with the lowest trophic diversity was spring 2016 (0.645) and the highest was the summer of 2016 (0.215). A significant and positive relationship was obtained between 1-ITD and the Shannon–Wiener diversity index ($R^2 = 0.9711$) as well as 1-ITD and evenness ($R^2 = 0.927$). A negative relationship was observed between species richness (as trophic species) and the index of trophic diversity ($R^2 = 0.765$). The EHS values in all seasons varied between 0.56 and 0.59, indicating that the ecosystem health in seagrass was moderate in Bahía Balandra.

The correlation analysis of density was strong and positive between gastropod and bivalves-scaphopods ($r = 0.79$); additionally, these groups were significantly related to total density (Fig. 5). A moderate positive correlation between mollusk total density and the biomass of *H. wrightii* was found (aboveground, $r = 0.55$; belowground, $r = 0.52$; and total, $r = 0.55$). The strongest positive relations were recorded between above-belowground biomasses with the total biomass of *H. wrightii*. There was a weak positive correlation between mollusk biomass with the density of mollusks and biomass of *H. wrightii* ($r < 0.5$)

Table 5 Summarized diversity alpha indices between mollusk taxa and across seasons associated with *Halodule wrightii*. Number of organisms (*N*), species richness (*S*), Shannon–Wiener diversity index (*H*´), Simpson index (λ), Pielou evenness index (*J*´)

		N	S	H´	1-λ	J´
Taxa	Gastropoda	6009	61	1.60	0.71	0.39
	Bivalvia-Scaphopoda	1275	28	0.93	0.34	0.28
2016	Spring	273	41	2.53	0.86	0.68
	Summer	2010	48	1.58	0.71	0.41
	Autumn	1223	50	1.77	0.67	0.45
2017	Winter	2030	44	1.74	0.74	0.46
	Spring	1748	60	2.09	0.81	0.51

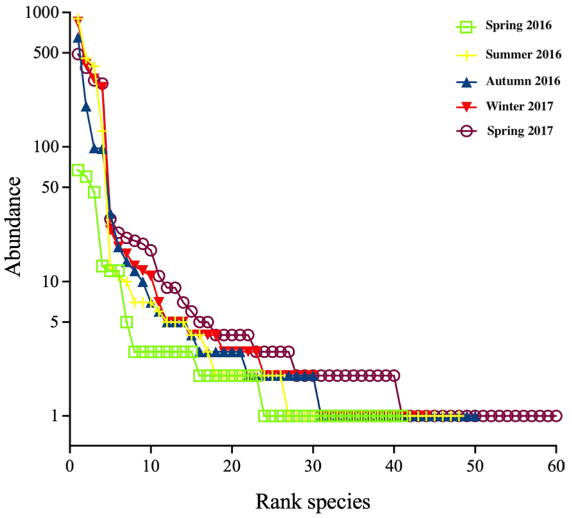


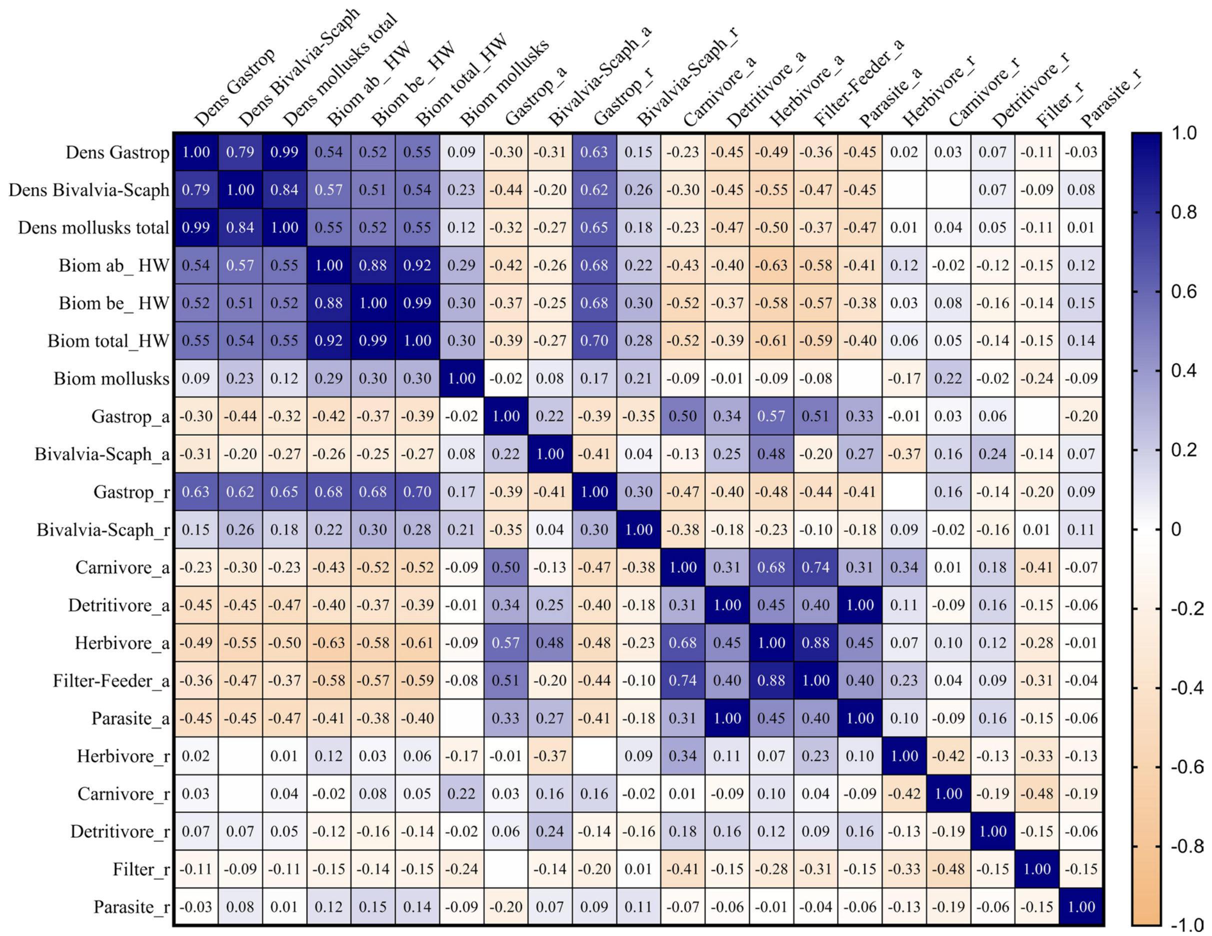
Fig. 4 Dominance in communities of mollusks (gastropods and bivalves-scaphopods) during the study period. The rank on the x-axis is the representation of the list of species arranged in ranges from highest to lowest abundance (number of individuals)

(Fig. 5). The gastropod richness presented a strong positive correlation with the biomass of *H. wrightii* ($r = 0.70$).

The abundance of gastropods indicated a moderate positive correlation with abundance of carnivores ($r = 0.50$), herbivores ($r = 0.57$), and filter-feeders ($r = 0.51$). Otherwise, there was a strong ($r \geq 0.7$) and positive correlation between the abundance of carnivores and herbivorous with the abundance of filter-feeders (Fig. 5). Parasite abundance was strongly correlated with detritivore abundance ($r = 1$) (Fig. 5).

Discussion

This study contributes with novel information on seasonal diversity and ecological functionality of mollusks associated with *Halodule wrightii* seagrass populations in a subtropical arid area. Seagrass beds may persist in a mosaic of various-sized vegetated patches surrounded by unvegetated sand or mud superimposing a high degree of habitat heterogeneity in a particular area (Orth 1992). One of the most notable features of seagrass beds is the high abundance and richness of resident infauna and epifauna invertebrates relative to those in adjacent, unvegetated habitats (Orth 1977, 1992; Heck and Orth 1980; Casares and Creed 2008). In addition, the abundance and diversity are important due to their role in the food web of the seagrass ecosystem through the different trophic guilds that form part of the interactions that contribute to maintaining the structure, function, and stability of the seagrass ecosystem. The presence of patches of the seagrass *H. wrightii* in Bahía Balandra increase the biodiversity and abundance of small mollusk species (≤ 25 mm) (7284 individuals and 89 species) in comparison with unvegetated areas and slightly larger species (678 individuals and 42 species) (Domínguez-Orozco 1996). The organisms were found attached to the surface of the seagrass leaves (e.g., Dialidae, Litiopidae, Margaritidae, Pteriidae), over the sand (e.g., Aplysiidae, Haminoeidae, Nassariidae, Olividae) within the sediment (e.g., Veneridae, Mytilidae, Thyasiridae), and attached to the roots of the seagrasses (e.g., Lucinidae) which suggests selectivity of habitat. Thus, the structural complexity of *H. wrightii* from roots to leaves provided a suitable habitat for their requirements such as food, protection from predators, reducing tidal currents and waves,



	Dens Gastrop	Dens Bivalvia-Scaph	Dens mollusks total	Biom ab_ HW	Biom be_ HW	Biom total_HW	Biom mollusks	Gastrop_a	Bivalvia-Scaph_a	Gastrop_r	Bivalvia-Scaph_r	Carnivore_a	Detritivore_a	Herbivore_a	Filter-Feeder_a	Parasite_a	Herbivore_r	Carnivore_r	Detritivore_r	Filter_r	Parasite_r
Dens Gastrop	1.00	0.79	0.99	0.54	0.52	0.55	0.09	-0.30	-0.31	0.63	0.15	-0.23	-0.45	-0.49	-0.36	-0.45	0.02	0.03	0.07	-0.11	-0.03
Dens Bivalvia-Scaph	0.79	1.00	0.84	0.57	0.51	0.54	0.23	-0.44	-0.20	0.62	0.26	-0.30	-0.45	-0.55	-0.47	-0.45			0.07	-0.09	0.08
Dens mollusks total	0.99	0.84	1.00	0.55	0.52	0.55	0.12	-0.32	-0.27	0.65	0.18	-0.23	-0.47	-0.50	-0.37	-0.47	0.01	0.04	0.05	-0.11	0.01
Biom ab_ HW	0.54	0.57	0.55	1.00	0.88	0.92	0.29	-0.42	-0.26	0.68	0.22	-0.43	-0.40	-0.63	-0.58	-0.41	0.12	-0.02	-0.12	-0.15	0.12
Biom be_ HW	0.52	0.51	0.52	0.88	1.00	0.99	0.30	-0.37	-0.25	0.68	0.30	-0.52	-0.37	-0.58	-0.57	-0.38	0.03	0.08	-0.16	-0.14	0.15
Biom total_HW	0.55	0.54	0.55	0.92	0.99	1.00	0.30	-0.39	-0.27	0.70	0.28	-0.52	-0.39	-0.61	-0.59	-0.40	0.06	0.05	-0.14	-0.15	0.14
Biom mollusks	0.09	0.23	0.12	0.29	0.30	0.30	1.00	-0.02	0.08	0.17	0.21	-0.09	-0.01	-0.09	-0.08		-0.17	0.22	-0.02	-0.24	-0.09
Gastrop_a	-0.30	-0.44	-0.32	-0.42	-0.37	-0.39	-0.02	1.00	0.22	-0.39	-0.35	0.50	0.34	0.57	0.51	0.33	-0.01	0.03	0.06		-0.20
Bivalvia-Scaph_a	-0.31	-0.20	-0.27	-0.26	-0.25	-0.27	0.08	0.22	1.00	-0.41	0.04	-0.13	0.25	0.48	-0.20	0.27	-0.37	0.16	0.24	-0.14	0.07
Gastrop_r	0.63	0.62	0.65	0.68	0.68	0.70	0.17	-0.39	-0.41	1.00	0.30	-0.47	-0.40	-0.48	-0.44	-0.41		0.16	-0.14	-0.20	0.09
Bivalvia-Scaph_r	0.15	0.26	0.18	0.22	0.30	0.28	0.21	-0.35	0.04	0.30	1.00	-0.38	-0.18	-0.23	-0.10	-0.18	0.09	-0.02	-0.16	0.01	0.11
Carnivore_a	-0.23	-0.30	-0.23	-0.43	-0.52	-0.52	-0.09	0.50	-0.13	-0.47	-0.38	1.00	0.31	0.68	0.74	0.31	0.34	0.01	0.18	-0.41	-0.07
Detritivore_a	-0.45	-0.45	-0.47	-0.40	-0.37	-0.39	-0.01	0.34	0.25	-0.40	-0.18	0.31	1.00	0.45	0.40	1.00	0.11	-0.09	0.16	-0.15	-0.06
Herbivore_a	-0.49	-0.55	-0.50	-0.63	-0.58	-0.61	-0.09	0.57	0.48	-0.48	-0.23	0.68	0.45	1.00	0.88	0.45	0.07	0.10	0.12	-0.28	-0.01
Filter-Feeder_a	-0.36	-0.47	-0.37	-0.58	-0.57	-0.59	-0.08	0.51	-0.20	-0.44	-0.10	0.74	0.40	0.88	1.00	0.40	0.23	0.04	0.09	-0.31	-0.04
Parasite_a	-0.45	-0.45	-0.47	-0.41	-0.38	-0.40		0.33	0.27	-0.41	-0.18	0.31	1.00	0.45	0.40	1.00	0.10	-0.09	0.16	-0.15	-0.06
Herbivore_r	0.02		0.01	0.12	0.03	0.06	-0.17	-0.01	-0.37		0.09	0.34	0.11	0.07	0.23	0.10	1.00	-0.42	-0.13	-0.33	-0.13
Carnivore_r	0.03		0.04	-0.02	0.08	0.05	0.22	0.03	0.16	0.16	-0.02	0.01	-0.09	0.10	0.04	-0.09	-0.42	1.00	-0.19	-0.48	-0.19
Detritivore_r	0.07	0.07	0.05	-0.12	-0.16	-0.14	-0.02	0.06	0.24	-0.14	-0.16	0.18	0.16	0.12	0.09	0.16	-0.13	-0.19	1.00	-0.15	-0.06
Filter_r	-0.11	-0.09	-0.11	-0.15	-0.14	-0.15	-0.24		-0.14	-0.20	0.01	-0.41	-0.15	-0.28	-0.31	-0.15	-0.33	-0.48	-0.15	1.00	-0.15
Parasite_r	-0.03	0.08	0.01	0.12	0.15	0.14	-0.09	-0.20	0.07	0.09	0.11	-0.07	-0.06	-0.01	-0.04	-0.06	-0.13	-0.19	-0.06	-0.15	1.00

Fig. 5 Heat map of the Pearson's correlation coefficients computed for the density and biomass of mollusks, *Halodule wrightii* biomass, abundance, richness, and trophic guild of mollusks. The scale palette expresses the direction and intensity of the relationship when significant ($P < 0.05$). The cells without color are non-statistically significant. *a* = abundance; *r* = richness; Gastrop = gastropods; Bivalvia-Scaph = bivalves-scaphopods; Dens = Density; Biom = biomass; ab = aboveground; bw = belowground; HW = *H. wrightii*

and enhanced the availability of oxygen for respiration and consequently improving the survival of the early stages of small mollusks.

Mollusk abundance, density, and seagrass biomass

In this study, we found a great abundance of small mollusks, which was higher in comparison with mollusk abundance in *H. wrightii* populations inhabiting close areas like the beach of la Concha in Baja California Sur (20 km away from our study area) (Corona 2018), or distant locations like with tropical rainy climate areas in Brazil (Barros and Rocha-Barreira 2013; Cavalcante et al. 2019). The comparison between our results with those reported in larger seagrass species indicated that the abundance in *Zostera marina* and *Zostera nolteii* in template climate was similar (Quintas et al. 2013). Conversely, in the seagrasses *Cymodocea nodosa* and *Posidonia oceanica* from subtropical desert areas the abundance was lower (Antit et al. 2016). The differences reported in these studies were related to the particularities of the plants, the area, and the sampling methods used. For instance, in this study, the sandy substrate was mostly composed of the remaining invertebrate shells and calcium carbonate, the samples were obtained in subtidal patches from 0.4 to 0.75 m depth in low tide (shallow waters) and the only contribution to fresh water comes from the rains (Table 1). In the study of Corona (2018), the substrate was sandy and rocky, and the samples were obtained in patches at a depth from 2 to 4 m; in addition, this was an area with sewage discharge. The gastropod abundance was higher than the bivalve one, which agrees with other studies in seagrasses (Arroyo et al. 2006; Rueda et al. 2008, 2009; Barros and Rocha-Barreira 2013; Urra et al. 2017; Cavalcante et al. 2019).

There was seasonality in abundance and density for gastropods, recording maximum values associated with the rainy seasons (Table 1), this was also reported by Barros et al. (2013) and Corona (2018). In Bahía Balandra during the periods of rain, there were high epiphytic algal abundances, which could be important for the herbivorous organisms since the epiphytes increase the structural complexity resulting in more niches and/or food resources supporting a wider variety of grazers (Heck and Valentine 2006). Four species of gastropods (*Diala* sp., *A. aladulensis*, *A. supralirata*, and *F. tenuisculpta*) were dominant during all sampling dates, showing the highest abundance and densities during the study period. These species were found mainly over the seagrass leaf surface close to their food sources (i.e., epiphytes). Cavalcante et al. (2019) reported a dominance of four mollusks species (*Eulithidium affine*, *Alaba incerta*, *Neritina virginea*, and *Smaragdia viridis*), while Corona (2018) reported only one species (*Barleeia* sp.). The species of the gastropod genus *Alaba* (shell length <5 mm) occur often in large numbers on algae and seagrasses in shallow water, with reports that the epiphytes could be a more suitable food source for microsnails due to their small size (Fong et al. 2018; Barnes 2019; Cavalcante et al. 2019; Barnes and Claassens 2020).

Temporal variation of abundance and density of bivalves did not show a defined seasonal pattern. Among bivalves, the families Lucinidae (*C. prolongata*, average 680 ind. m^{-2}) and Veneridae (*M. squalida*, average 6827 ind. m^{-2}) were the most abundant in our study (filter-feeders). The high occurrence of Lucinidae within seagrass populations has been previously reported (Johnson et al. 2002; Van der Heide et al. 2012; Barbier et al. 2017; Cavalcante et al. 2019), and appears to vary considerably depending on both the environmental conditions of the location and the seagrass species (Van der Heide et al. 2012). The greater abundance of lucinids in the *H. wrightii* seagrass could be directly related to the feeding habits of this family. Although species of Lucinidae can feed on particles (since they are filter-feeders), most of their nutrition is provided from symbioses with sulfide-oxidizing bacteria obtained from anoxic sediments (Taylor and Glover 2000a; Gros et al. 2003; Van der Heide et al. 2012).

The bivalve *M. squalida* represents one of the most important bivalve fisheries in Baja California Sur (López-Rocha et al. 2010). This species has been extracted from Bahía Balandra for many years, being an important fishing ground for the inhabitants or visitants of La Paz, Baja California Sur, Mexico. Adults of the species have been reported in high densities in non-vegetated areas in Bahía Balandra (Domínguez-Orozco 1996). In this study, most of the organisms of *M. squalida* found were seeds (<5 mm). A study performed with this species showed that individuals exhibit low vagility within short distances (Schweers et al. 2006), and subsequently move to other zones, suggesting that seagrass may be an important area for the reproduction.

During the study period, we found an increase in the density of bivalves (from spring 2016: 310 ind. m^{-2} to 1297 ind. m^{-2} in spring 2017) together with an increase in total seagrass biomass (from spring 2016: 54.73 g DW m^{-2} to 175.48 g DW m^{-2} in spring 2017). A moderate negative Spearman correlation between total seagrass biomass and density of filter-feeders was found. This may indicate that dense meadows may enhance the concentration of resources (e.g., deposition or settling) favoring food intake, but also may limit resources at high filter-feeder densities due to the lower turnover of the water and to the depletion of resources promoted by the active filtering of the organisms (González-Ortíz et al. 2014a). Moreover, high belowground biomass may also limit the density of infauna by acting as a mesh hampering the burrowing activity of infauna (González-Ortíz et al. 2014b). During the sampling dates, we did not find adult individuals of bivalves, although we observed a few of them within seagrass patches. In addition, most of the collected bivalves were small (1–30 mm) and were assumed as seeds. Corona (2018) also found only juveniles, which may indicate that *H. wrightii* is an important habitat for bivalve reproduction, metamorphosis, refuge, feeding, and as a zone of recruitment, which is crucial for organisms with a benthic-pelagic life cycle. Bivalves are benthic-pelagic in conditions where their populations are successfully regulated (Barbier et al. 2017).

Species richness, diversity indexes, trophic composition, and ecosystem health state

The mollusk species richness found in *H. wrightii* patches in Bahía Balandra (89 species) was higher than those reported for other *H. wrightii* meadows in Brazil with 31 species (Creed and Kinupp 2011) and 53 species (Cavalcante et al. 2019) in tropical climate, or 24 species in rainy tropics with a long dry season (Barros and Rocha-Barreira 2013), or even in some studies made with other species of seagrasses as *Zostera marina* (Arroyo et al. 2006; Cacabelos et al. 2008; Rueda and Salas 2008), but were lower compared with the richness found in larger seagrasses like *Posidonia oceanica* (Urra et al. 2017). In addition, the results here reported show a significant increase in the number of recorded species of mollusks inhabiting *Halodule wrightii* populations. The Spearman correlation indicated a high positive relationship between the richness of gastropods with the total biomass of seagrass; this means that the greater the seagrass biomass, the greater the richness of these groups. Of the species found, 19.1% were present in all seasons, which may indicate that these species are residents and probably may complete their life cycle there. Moreover, we found organisms of different sizes within seagrass communities, supporting the previous argument. The diversity index (H´) was higher during dry seasons, contrary to the findings of Barros and Rocha-Barreira (2013) for Brazil since they found the higher H´ in the rainy season.

Although, in this study, the organisms were grouped into five main trophic guilds (herbivores, carnivores, filter-feeders, parasites, detritivores), within these groups coexist a wide variety of feeding forms, depending on the structural characteristics of each organism and behavior (Kohn 1983). All trophic guilds found persisted during the study and most were found in the gastropod group, except for the filter-feeders. The most abundant trophic level found was gastropod herbivores (primary consumers: *Diala* sp., *A. supralirata*, *A. aladulensis, Stylocheilus ricketsii*), which are closely linked to the dynamics of productivity within *H. wrightii* communities in Bahía Balandra since this is an important mechanism of mobilizing carbon from primary producers and transferring it to higher trophic guilds (Valentine and Duffy 2006; Cavalcante et al. 2019).

The second group in abundance was the filter-feeders (bivalves, i.e., *M. squalida*) that can produce bioturbation in the sediment, modifying oxygen concentration, sediment porosity, stability, metal concentration, and pH, thereby making sediments suitable to other organisms (Ciutat et al. 2007). Moreover, fragmented and sparse seagrass meadows could offer protection and increase food availability (e.g., higher particles flux) for filter-feeders without reducing food availability within the canopy (González-Ortíz et al. 2014).

Of the species found, 47.19% were rare (carnivores and parasites mainly) since they occurred only in one or two seasons and abundance was low (from 1 to 2 individuals). Therefore, they may arrive at the seagrass populations at different times, probably due to their food preference or availability of prey, or that probably these species complete their life cycle in the area within a short time. One example was the gastropod ectoparasites (*Aclis* sp., *Odostomia* sp. and *Turbonilla* sp.) that feed on body fluids, mainly of bivalves, although also from other gastropods and polychaetes (Kohn 1983). This feeding group was found when the abundance of bivalves was high in the winter and spring of 2017, in comparison with Cavalcante et al. (2019), where the greater richness was represented by gastropods, mainly the family Pyramidellidae (parasites).

Species of the family Olividae were abundant in shallow waters since they have many adaptations for sand burrowing in sandy habitats, and the diet is mainly composed of small gastropods, bivalves, echinoids, and holothurians, as well as pieces of fish and shrimp (Olsson and Crovo 1968; Taylor and Glover 2000b). In this study, the species of this family occurred during all sampling dates. A significant relationship between the index of trophic diversity and diversity indices (Shannon–Wiener and evenness) was found, suggesting that the identity of each species was related to their trophic trait such as found by Antit et al. (2016) for molluscan in the Bay of Tunis (southern Mediterranean Sea). Finally, the structurally complex environments created by *H. wrightii* in Bahía Balandra increased the species diversity, providing more niches and different ways of exploiting environmental resources (Kerr and Packer 1997; Gingold et al. 2010).

In 2012, Bahía Balandra was declared a natural protected area with the purpose to maintain the integrity of the flora and fauna, the good state of conservation, and thus the environmental services provided by the natural ecosystems (CONANP 2016). However, when using the functional group diversity recorded to evaluate the ecosystem seagrass health of Bahía Balandra, it rendered a moderate health status. This result suggests that this area could be affected to some degree by either human activities (e.g., self-fishing, tourism) and/or natural events (e.g., El Niño and La Niña events and hurricanes). For instance during the period of this study, we observed an increase in tourism activities, such as a high number of visitants (CONANP 2019), boats in shallow water that caused physical damage on seagrass and sediment resuspension, and illegal harvesting of mollusks (mainly bivalves), which together have caused seagrass destruction and environmental degradation. Although this study did not evaluate directly the effect of natural events (e.g., El Niño and hurricane Newton 2016) on seagrass communities, it is known that these climatic phenomena may cause fluctuations in hydrodynamic conditions and precipitations, which increase turbidity causing changes in abiotic variables (i.e., temperature, salinity, and irradiance). Consequently, the structure and functioning of seagrass ecosystems are affected by these natural phenomena (Cabello et al. 2004; Wernberg et al. 2013; Rossi and Soares 2017; Coria-Monter et al. 2018; NOAA 2016). In addition, Pérez-Estrada et al. (2021) detected the loss of *circa* 70% of the area occupied by patches of *H. wrightii* in Bahía Balandra during 2015 to 2017 probably as a result of extreme climatological events (i.e., storms and hurricanes) and anthropogenic causes. The effects of tourism activities and natural phenomena need to be evaluated in the near future to better conservation of the seagrass ecosystem and their fauna associated.

Conclusions

The environmental conditions and the structural complexity of seagrass from roots to leaves provided a suitable habitat for the establishment of juvenile mollusks (< 2.5 cm) and consequently improved the survival of this early life stage, helping them to complete their life cycle until the adult phase. The seasonality in abundance and density differed between gastropods and bivalves-scaphopods. The most representative group in abundance was the herbivorous gastropods, and the species richness in this group had a strong correlation with the total biomass of *H. wrightii*. The second group in abundance was the filter-feeders that were related to the productivity of *H. wrightii*. The seagrass *H. wrightii* is an important habitat for the establishment of bivalves with commercial importance, like *M. squalida*. Conservation actions are typically focused on charismatic habitats and visible species, but more information and studies of fauna associated with seagrasses and small species inhabiting such populations are needed to promote sustainable use of marine and coastal resources and their conservation in the Gulf of California. Due to the bivalves importance for the conservation of seagrasses, we recommended regulations concerning the extraction of bivalves in the area. The ecosystem services that *H. wrightii* provided to mollusks can be summarized as 1. habitat to complete their life cycle, 2. a suitable area for reproduction, 3. a habitat with higher food diversity, 4. shelter from predators, 5. shelter from currents and waves, and 6. role in maintaining populations of commercially exploited species. The ecosystem health of seagrasses in Bahía Balandra was shown to be moderate, and therefore, we suggest continuing to develop studies to evaluate the impact of anthropogenic activities in Bahía Balandra on the seagrass and species diversity. Although the ecosystem seagrass health of Bahía Balandra resulted categorized as moderate, all the functional groups were present.

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Author's contribution CJPE, RRE, and FGBM were involved in conceptualization; CJPE, PGS, RRE, and MAML helped in data curation; CJPE, RVJ, and RRE contributed to formal analysis; FGBM and CJPE were involved in methodology; FGBM and RRE helped in supervision; CJPE, RRE, and RVJ contributed to writing—original draft; CJPE, RRE, FGBM, RVJ, EMB, PGS, and MAML contributed to writing—review & editing.

Data availability We will make the data available via GBIF.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval Collections were obtained under permits from Comisión Nacional de Áreas Naturales Protegidas: Permission F00-CONANP/AFPBALANDRA/236/2016.

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