

First Insights into the Vertical Patterns of Size Distribution, Abundance, and Spatial Aggregation of *Pseudechinus magellanicus* (Echinoidea) on a Wave-exposed Rocky Shore in San Jorge Gulf, Argentina

Damián Gaspar Gil^{1,2,*} and Héctor Eliseo Zaixso^{1,†}

¹Laboratorio de Bentos Costero Patagónico. Instituto de Desarrollo Costero (LBCP – IDC). Universidad Nacional de la Patagonia San Juan Bosco (UNPSJB). Ciudad Universitaria, Ruta Provincial 1 s/n. Comodoro Rivadavia (CP 9000), Chubut, Argentina. *Correspondence: E-mail: gil_damian@hotmail.com (Gil)

²Departamento de Biología y Ambiente. Facultad de Ciencias Naturales y Ciencias de la Salud. UNPSJB

† The author passed away on 29 Apr. 2015.

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ORCID:

Damián Gaspar Gil: <https://orcid.org/0000-0002-8084-2181>

The sea urchin *Pseudechinus magellanicus* is a dominant species in coastal habitats of southern Argentina and Chile. This study investigates its size distribution, abundance, and spatial arrangement in relation to coastal environmental gradients and habitat complexity along a depth gradient in central Patagonia (Argentina) during the austral spring. *P. magellanicus* exhibited a unimodal response to depth, with lower densities observed at intertidal levels and depths greater than 12 m. Size distribution showed depth-related patterns, with larger individuals prevalent at subtidal levels, intermediate sizes more common in intertidal and shallow depths, and recruits and juveniles most abundant at the infralittoral fringe and subtidal zones. A positive relationship between structural complexity and sea urchin densities was found, especially for smaller size classes. Conversely, larger individuals tended to inhabit areas with lower structural complexity and higher food availability. Sedimentation impacted the vertical distribution, particularly affecting recruits, juveniles, and young adults. Spatial arrangement analysis showed that aggregation is the predominant pattern along the coastal depth gradient. However, at depths of 3-5 m, where the kelp forest (*Macrocystis pyrifera*) dominates, recruits, juveniles, and intermediate-sized sea urchins displayed a less aggregated, more random distribution. These findings reveal the critical role of habitat complexity and depth in shaping the population dynamics of *P. magellanicus* and highlight the adaptability of this species to varying habitat conditions and its potential as an indicator of coastal ecosystem health.

Key word: Echinodermata, Patagonia, sea urchins, SW Atlantic Ocean

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BACKGROUND

Sea urchin populations vary greatly over time and space, causing significant changes in community structure due to intense competition, high herbivory pressure, and bioerosion from dominant species (Alcoverro and Mariani 2002; Levitan et al. 2014). Habitat structural complexity is considered a crucial factor influencing species distribution and abundance, with implications for higher organizational levels, such as providing refuge from predators and affecting resource availability and feeding rates (Hereu et al. 2005). Studies have shown positive correlations between structural complexity and sea urchin densities (Benedetti-Cecchi and Cinelli 1995; Cordeiro et al. 2014; Hereu et al. 2005). Field experiments have shown that structural complexity promotes the survival of sea urchin juveniles by reducing predation and enhancing recruitment (Hernández et al. 2008; Palleiro-Nayar et al. 2011; Scheibling and Hamm 1991).

The dwarf sea urchin *Pseudechinus magellanicus* is a dominant species in coastal habitats of southern Argentina and Chile (Brogger et al. 2013). Despite its ecological importance, the influence of biotic (e.g., predation, recruitment) and abiotic factors (e.g., density, size structure, spatial arrangement) remains scarcely studied (but see Ríos et al. 2003). In the central zone of the San Jorge Gulf, *P. magellanicus* is found in both the subtidal and intertidal regions, enabling the study of its vertical distribution (Gil 2015; Gil et al. 2021). The intertidal and shallow subtidal zones provide highly complex environments, ideal for examining environmental effects within microhabitats (Raffaelli and Hawkins 1996). The diversity and availability of microhabitats, combined with microclimatic variations resulting from interactions between topographical features (such as tidal pools and channels) and the structural complexity of various macroalgae groups (e.g., articulated corallines, kelps) (Zaixso et al. 2015), may contribute to environmental heterogeneity and likely influence the distribution and abundance of *P. magellanicus*.

Coastal benthic ecosystems are considered mosaics of environmental categories due to temporal and spatial variation of physical and biological factors (Archambault and Bourget 1996; Frascchetti et al. 2005). Baseline information on the influence of environmental heterogeneity along a coastal depth gradient on the density of adult, juvenile, and recruits of *P. magellanicus* is currently lacking. This information is particularly important for dominant species, especially in the context of

global climate change. Recruitment in benthic marine invertebrates varies in space and time, and is dependant on reproductive success, larval availability and transport, substrate selection for settlement, and early post-settlement mortality (Morgan et al. 2000; Pineda et al. 2009). Sea urchin larvae can settle in environments with high structural complexity, such as articulated coralline algae or foliose red algae, leading to active substrate selection by some species (Doll et al. 2022). Alternatively, recruits may settle indiscriminately in both intertidal and subtidal areas, with early mortality and migration influencing final distribution. In some species, sea urchin juveniles seek microhabitats with lower post-settlement mortality (Cameron and Schroeter 1980), while other studies suggest that post-settlement mortality alone determines recruit distribution and population density (Morgan et al. 2000).

The spatial arrangement of a species is a fundamental population feature, with aggregated dispersion being the most common pattern due to species traits, inter-individual relationships, and environmental variations (Krebs 1999). Sea urchins often exhibit aggregated dispersion due to factors such as reproductive and feeding aggregations (Levitan et al. 1992; Sun et al. 2021), environmental influences (Beddingfield and McClintock 2000), defense against predators (Bernstein et al. 1983), and protection for juveniles (Breen et al. 1985; Nishizaki and Ackerman 2007). It is expected that the spatial arrangement of *P. magellanicus* in coastal habitats will be influenced by habitat complexity and the availability of food and shelter in intertidal and subtidal environments. This field-based study aims to: (1) examine population parameters of *P. magellanicus* (e.g., size distribution and density) in relation to coastal environmental gradients and habitat complexity, and (2) determine spatial arrangement patterns among different size classes along a coastal depth gradient in San Jorge Gulf, Patagonia, Argentina.

MATERIALS AND METHODS

Study area and field sampling

Sampling was conducted in La Tranquera, a rocky shore located along the central coast of the San Jorge Gulf, Argentina (46°02'24.61"S; 67°35'52.61"W), from September to October of 2010. This timeframe was chosen to align with the austral spring, coinciding with significant spawning events typically observed between August and September (Gil et al. 2020), thus maximizing the chance of encountering recruits. The area consists of hard sedimentary bedrock with extensive shallow and deep tidepools, primarily located within the low mid-littoral zone and upper infralittoral fringe. The sampling area is subjected to a daily tidal cycle comprising of two

low tides and two high tides, with average and maximum fluctuations of around 4.2 and 6.1 meters, respectively. The annual variation in sea water temperature ranges from 6.1 to 13°C, while the salinity remains at approximately 34.5 psu (Verga et al. 2019).

Seven depth-related habitats/levels were predefined below the mean tide level, as no sea urchins had been observed above this level in preliminary surveys or previous research in the area (Cabezas et al. 2007; Gil et al. 2018; Verga et al. 2025). Within the intertidal zone, two shore levels were identified: the low midlittoral (LwMd, ranging between 1–2 m above Chart Datum) and the upper infralittoral shore zone (InfraL, situated between 0.2–1 m). In the subtidal zone, five coastal depth levels were defined: 3, 5, 9, 12, and 15 meters relative to MLW. Throughout the intertidal, shallow and deep tidepools are numerous and extensive. Intertidal platforms at LwMd are characterized by the presence of well-formed mussel matrix of *Perumytilus purpuratus*, occasionally combined with patches of the turf-forming coralline algae, *Corallina officinalis*. In the InfraL, the substrate is predominantly covered by turfs of *C. officinalis*/*C. elongata*, interspersed among dense mussel beds of *Aulacomya atra* (Zaixso et al. 2015). Tidepool bottoms vary in structural complexity, including rocky bottoms with crevices, loose rocks, shells, and debris that support abundant populations of *P. magellanicus*, often using these elements as cover (Gil and Zaixso 2024a). Subtidal habitats at 3 and 5 meters exhibited the highest densities of the kelp *Macrocystis pyrifera* in close association with other typical seaweeds such as *Aphanocladia robusta*, *C. elongata*, *Undaria pinnatifida*, and *Callophyllis variegata* (Zaixso et al. 2015). At depths of 9 and 12 meters, environments included channels and scattered large boulders or reefs, with isolated and sparse *M. pyrifera* individuals. These habitats displayed a contrasting influence of fine sediment, alternating between areas of deposition and bare rocky substrate. The 15-meter depth exclusively featured fine sediment bottoms. During sampling, the kelp forest was senescent, with few specimens and limited canopy development.

At each intertidal shore zone, 10–15 random benthic sampling units were taken, each comprising of a 15 × 15 (225 cm²) quadrat. For each sample, the following environmental variables were recorded: (1) presence and depth (± 0.1 cm) of small ponds or tidal pools, and (2) coarse sediment relative content, categorized into four ordinal levels: 0 (no sediment), 1 (scarce, < 1 mm deep), 2 (moderate, 1–3 mm), 3 (high, 3–5 mm), and 4 (very high, > 5 mm). Subsequently, all the biota of the sample, including sea urchins (if present), were carefully collected with a spatula and preserved in 5% saline formalin. In the subtidal area, four quadrats of 50 cm × 50 cm (2,500 cm²) were randomly collected per depth level through scuba diving. All samples, both intertidal and subtidal, were also photographed to aid structural complexity assessments (*e.g.*, presence of crevices, loose rocks, etc.) and seaweed abundance. Inundation levels were classified into five

ordinal categories: 0 (no inundation, exposed bedrock), 1 (low, 1–3 cm in tidal pools), 2 (moderate, 3–15 cm), 3 (high, 16–50 cm), and 4 (permanent, for subtidal depths).

Laboratory analysis

The samples preserved in 5% saline formalin were transported to the laboratory, where all sea urchins were separated, counted, and measured (test diameter) using a digital caliper (± 0.1 mm). Particular emphasis was placed on identifying recruits and juveniles of *P. magellanicus* during sample examination under a binocular stereomicroscope. Subsequently, the biological sample was divided into the following categories related to structural habitat complexity: (1) erect coralline algae (e.g., *Corallina* spp.), (2) small shell fragments or valves (length < 15 mm), (3) large shell fragments or valves (length > 15 mm), (4) small mussels (e.g., *P. purpuratus* and juveniles of other species), (5) large mussels (e.g., *A. atra*), (6) small rocks (< 5 cm²), (7) large rocks (> 5 cm²), and (8) kelp holdfasts (e.g., *M. pyrifera*). Once the different components were separated, the volume of each one was recorded by water displacement using a graduated cylinder (± 2 ml). The abundance of seaweeds present in the sample was also recorded through an ordinal scale of five categories; 0: absence, 1: scarce, 2: scarce-moderate, 3: moderate, and 4: high.

Structural complexity assessment

Structural complexity was assessed by computing a dimensionless index, which considered various factors influencing the physical complexity of the environment (Table 1). These factors included the relative abundance of: (1) articulated coralline algae (e.g., *Corallina* spp.) or other habitat-forming species, such as kelp (e.g., *M. pyrifera*); (2) mussels in two size ranges (e.g., *P. purpuratus* and *A. atra*); (3) inorganic biogenic elements in two size ranges (e.g., shell fragments); and (4) the existence of loose rocks and crevices or cavities. As the sampling units in the subtidal and intertidal zones varied in size, the volume data for each structural component were standardized to a similar area across depths (2,500 cm²) and used to define the contributions of different categories of structural complexity. To standardize the volume categorization of each structural component into scarce, moderate, and abundant categories, we used the third quartile (75%) as the threshold for the abundant category. This value was then halved to establish the threshold for the scarce to moderate abundance category. Each variable was assigned a distinct numerical value representing its structural complexity (SC) (see Table 1), based on its significance in habitat heterogeneity relative to the body size of *P. magellanicus*, a recognized small sea urchin species

(Gil and Zaixso 2024b). These SC values were summed for each sample, resulting in an integrated value for each sampling unit. The contribution of each structural component is detailed in table 1.

Table 1. Additive contribution values of different morphotypes for structural complexity (SC) calculation in each sample unit. SL: Shell length

Structural components	SC Values		
	Scarce	Moderate	Abundant
Articulated coralline algae	+2	+4	+6
Small mussels (SL < 20 mm)	+0	+1	+2
Large mussels (SL ≥ 20 mm)	+2	+4	+6
Small shells debris	+0	+1	+2
Large shells debris	+2	+3	+4
Kelp holdfast	+4	+6	+8
Tunicates	+2	+4	+6
Cavities or cracks ⁽¹⁾	+2	+4	+6
	Small ⁽²⁾	Large ⁽³⁾	
Presence of rocks	+2	+4	

⁽¹⁾ derived from *in situ* observations or photographs, ⁽²⁾ <40 mm; ⁽³⁾ ≥40 mm.

Sea urchin size distributions were analyzed by pooling individuals across coastal habitats due to sample size constraints. Habitats included the low mid-littoral (LwML), upper infralittoral (InfraL), subtidal kelp forest (3–5 m), and deeper subtidal zone (9–12 m). Subsequently, these distributions were compared between successive depths using a Kolmogorov-Smirnov two-sample test, with the significance level adjusted according to Bonferroni (Quinn and Keough 2002).

To analyze the vertical distribution of overall sea urchin density and its discrimination by size classes, three size categories were defined based on the diameters of *P. magellanicus*: (1) recruits and juveniles (TD ≤ 11 mm), (2) adults I, encompassing intermediate size classes (11 mm < TD ≤ 16 mm), and (3) adults II, comprising large size classes (TD > 16 mm). The upper limit of the recruit and juvenile size interval, set at 11 mm, approximately corresponds to the size of sexual maturity (Orler 1992). However, it is necessary to clarify that within this size category, the sampled sizes ranged only between 2 and 8 mm. The analyses considered the distribution across the four broad coastal habitats. Densities were expressed in ind.m⁻², except in multivariate analyses and Generalized Additive Models, where density values were standardized to an area of 2,500 cm².

The relationship between the densities of different size categories of *P. magellanicus* (recruits and juveniles, adults I, adults II) and a series of explanatory environmental variables was examined using a Canonical Correspondence Analysis (CCA). To standardize the data and facilitate the application of CCA and Generalized Additive Models, depth values for intertidal (heights above Chart Datum) and subtidal samples (depth below mean low water) were recalculated, with the mean tidal level as the reference point for the study area (depth 0 m). The explanatory variables used for

CCA were: (1) depth from mean tidal level (continuous), (2) availability of algae (ordinal), (3) sediment content (ordinal), (4) inundation levels (ordinal), and (5) structural complexity (ordinal). Following ter Braak (1995), ordinal variables with three or more categories were treated as continuous in ordination diagrams. In the CCA diagram, the projection of *P. magellanicus* size classes onto environmental variables vectors approximates their weighted means (ter Braak and Šmilauer 2002). Collinearity between explanatory variables was verified using a maximum variance inflation factor (VIF) criterion of 10.0. The significance of the first canonical axis was tested using unrestricted Monte Carlo permutations (9999 permutations).

Since sea urchin size class abundances can follow linear or unimodal models, Generalized Additive Models (GAM; Hastie and Tibshirani 1990) were used to assess their response to environmental variables. This analysis identified whether relationships were unimodal (with abundance maxima or optima) or monotonic. The complexity of the GAM model was controlled through a stepwise selection using the Akaike Information Criterion. GAM regressions and CCA analysis were performed using the CANOCO 4.5 software (ter Braak and Šmilauer 2002).

Spatial arrangement

The spatial arrangement of *P. magellanicus*, considering both overall data (pooled sizes) and discriminated by the three size categories of the sea urchin, in the four broad coastal environments, was estimated by computing the variance-to-mean dispersion index. The deviation from the Poisson distribution (a random distribution) was assessed through the utilization of a chi-square statistic. Additionally, the standardized Morisita index (I_p), Green index (I_g), and Lloyd patchiness index (Krebs 1999) were computed to examine whether the various size categories of *P. magellanicus* display an aggregated, uniform, or random distribution. These three indices were selected in order to have a consensus on the spatial disposition of *P. magellanicus* since the use of a single index can produce biased estimates (Krebs 1999; Rufino et al. 2018). The indices were computed utilizing the statistical package PASSaGE v2.0 (Rosenberg and Anderson 2011).

RESULTS

Vertical variation in size distribution and abundance

The test diameters of *P. magellanicus* ranged from 2.30 to 25.54 mm (mean: 17.36 ± 3.89 mm; $n = 326$). Size-frequency distributions along a depth gradient showed an increase in large size

classes from LwTL to 9-12 meters, with no sea urchins found at 15 meters (Fig. 1). Significant changes in size distribution were observed from the intertidal to subtidal levels (K-S test; $p < 0.005$), but no significant differences were found amongst subtidal levels (K-S test; $p = 0.10$) (Fig. 1). Recruits and juveniles were present in the InfraL and both subtidal levels, while LwML had less variability and lacked size classes smaller than 14 mm (Fig. 1). The smallest sizes were found in the infralittoral shore zone.

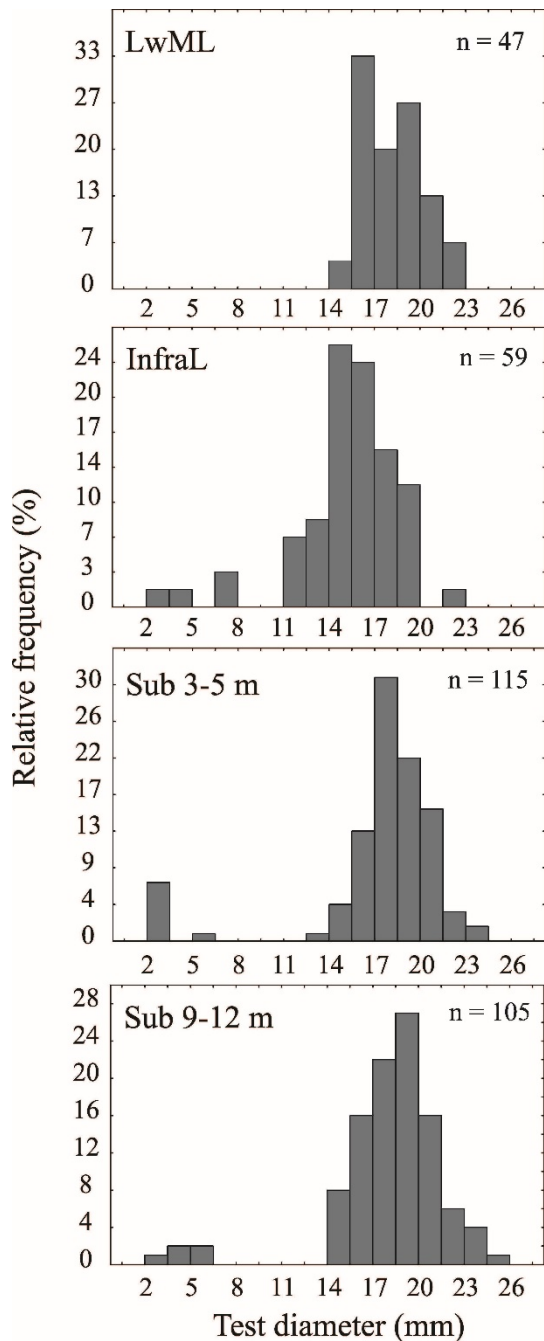


Fig. 1. Size-frequency distributions of *P. magellanicus* along a coastal depth gradient in the central area of the San Jorge Gulf.

Overall and size-class mean density of *P. magellanicus*, are indicated in figure 2. The highest overall abundance was found in the infralittoral shore zone (InfraL), with mean values

exceeding 100 ind.m⁻² (Fig. 2). The analysis by size class reveals that both recruits/juveniles and intermediate-size classes (adults I) reached mean densities of 7.7 ind.m⁻² and 56.2 ind.m⁻², respectively, in the infralittoral shore zone. Large size classes (adults II) showed a higher mean density at deeper levels, reaching nearly 50 ind.m⁻² (Fig. 2). The abundances of recruits/juveniles and intermediate-sized class (adults I) were highly correlated ($r = 0.78$; $p < 0.001$), while the abundance of larger sea urchins (adults II) showed no correlation with either of the other size classes ($p > 0.37$ in both cases).

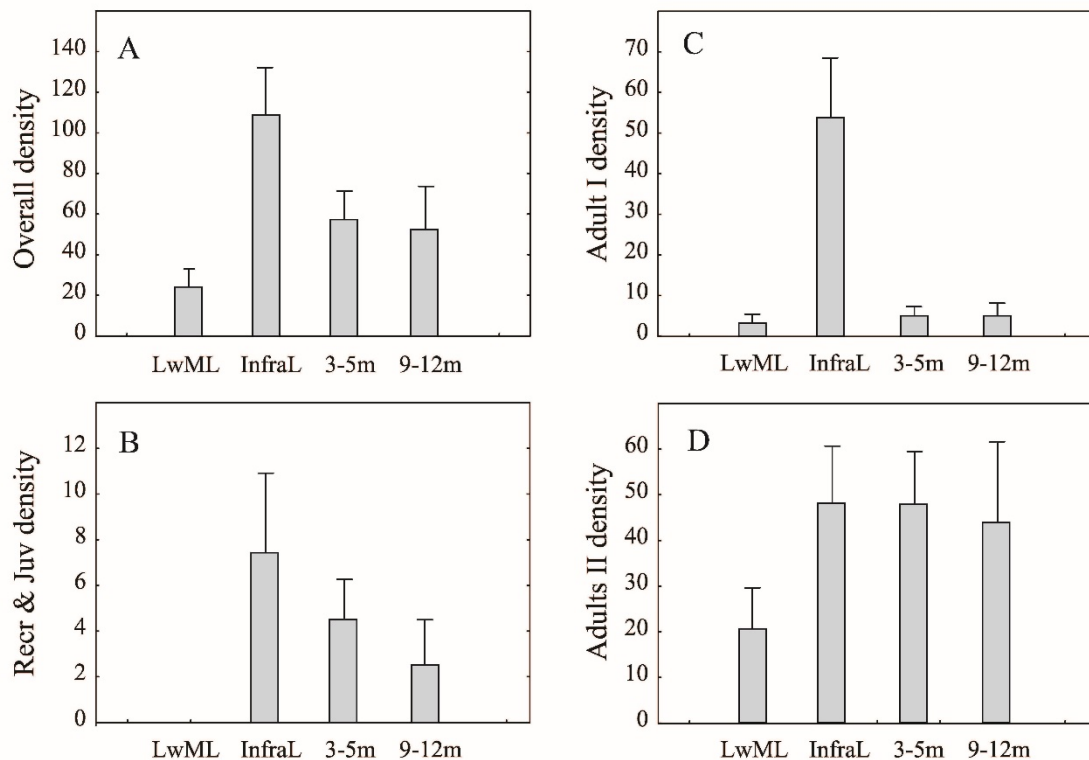


Fig. 2. Overall mean density (\pm SE; ind.m⁻²) (A) and discriminated by size classes (B–D) of *P. magellanicus* along a coastal depth gradient ($n = 8$ –28 sampling units per habitat).

Influence of environmental variables

The CCA illustrated the relationship between *P. magellanicus* size classes and environmental variables, which accounted for 75.1% of the total variation (Fig. 3, Table 2). Axis I, which explains 30.5% of total inertia, showed a positive correlation with water inundation ($r = 0.61$) and sediment content ($r = 0.53$), and a negative correlation with structural complexity ($r = -0.36$). Axis II was negatively correlated with seaweed availability ($r = -0.42$) and depth ($r = -0.17$). Depth positively correlated with water inundation, sediment content, and seaweed availability, and negatively with structural complexity (Fig. 3). Table S1 provides the variance inflation factor (VIF),

standard deviation (SD), and weighted means of each explanatory variable in the CCA, along with the results of cross-correlation analysis.

Table 2. Summary of Canonical Correspondence Analysis (CCA). Significance of the first canonical axis: $p < 0.001$ (Monte Carlo permutation)

CCA axes	I	II	III	IV	Total inertia
Eigenvalues	0.305	0.026	0.329	0.091	0.751
Size classes-environment correlations	0.695	0.467	0	0	
Cumulative percentage variance of					
Size classes data	40.6	44.1	87.9	100	
Size classes-environment relation	92.1	100	0	0	
Sum of all eigenvalues					0.751
Sum of all canonical eigenvalues					0.331

In the CCA biplot (Fig. 3), different size categories of *P. magellanicus* showed distinct ordinations. Recruits and juveniles were found in areas with high structural complexity, moderate inundation and sediment levels, abundant seaweeds, and depths deeper than average (mainly in the upper infralittoral shore zone and subtidal regions). Adults I were associated with high structural complexity, low sedimentation, low inundation, lower seaweed abundance, and shallower depths (e.g., LwMd and InfraL). Large sea urchins (adults II) were linked with deeper depths (subtidal habitats), higher sediment loads, permanent inundation, abundant seaweeds, and low structural complexity.

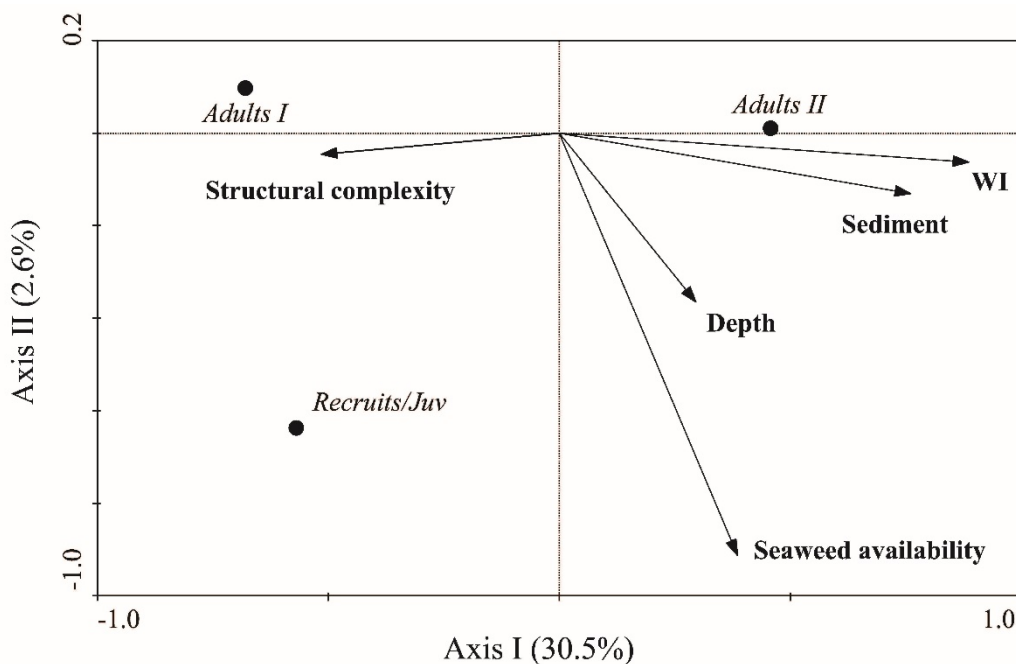


Fig. 3. Canonical Correspondence Analysis (CCA) biplot diagram. The circles represent *P. magellanicus* size classes. The arrows indicate explanatory variables. WI: water inundation.

The GAM modelling showed significant responses for structural complexity, depth, sediment content, water inundation, and seaweed abundance (Fig. 4; Table S2). The GAM curves for depth revealed a significant unimodal relationship only for the adult size categories (both classes). Large sea urchins (adults II) showed an optimum at 9 meters depth relative to the MTL, coinciding with the zone of maximum kelp forest development. Conversely, intermediate-sized sea urchins (adults I) exhibited an optimum at 4 meters from the MTL (InfraL). For recruits and juvenile sea urchins, the resulting GAM model was not significant compared to a null model, despite an apparent peak around 6 meters depth (beginning of *M. pyrifera* kelp forest) (Fig. 4).

The abundance of recruits/juveniles and adults I increased exponentially with higher structural complexity (Fig. 4). In contrast, larger sea urchins (adults II) showed a sharp density increase at lower complexity levels, maintaining high abundance thereafter. Different size classes responded differently to sediment: recruits/juveniles and adults I peaked in low sediment conditions and declined with increasing sediment, whereas larger sea urchins showed a peak abundance in moderate sediment environments and lower abundance in high sediment areas (Fig. 4).

Seaweed availability significantly impacted large-sized sea urchins, following a non-linear, asymptotic model with peak abundances in seaweed-rich areas (Fig. 4). Recruits/juveniles showed a similar but less pronounced pattern, while intermediate sea urchins (adults I) followed a unimodal model, peaking in areas with moderate macroalgae. However, the response curve for recruits and smaller individuals did not significantly differ from a null model (Supplementary Material 2).

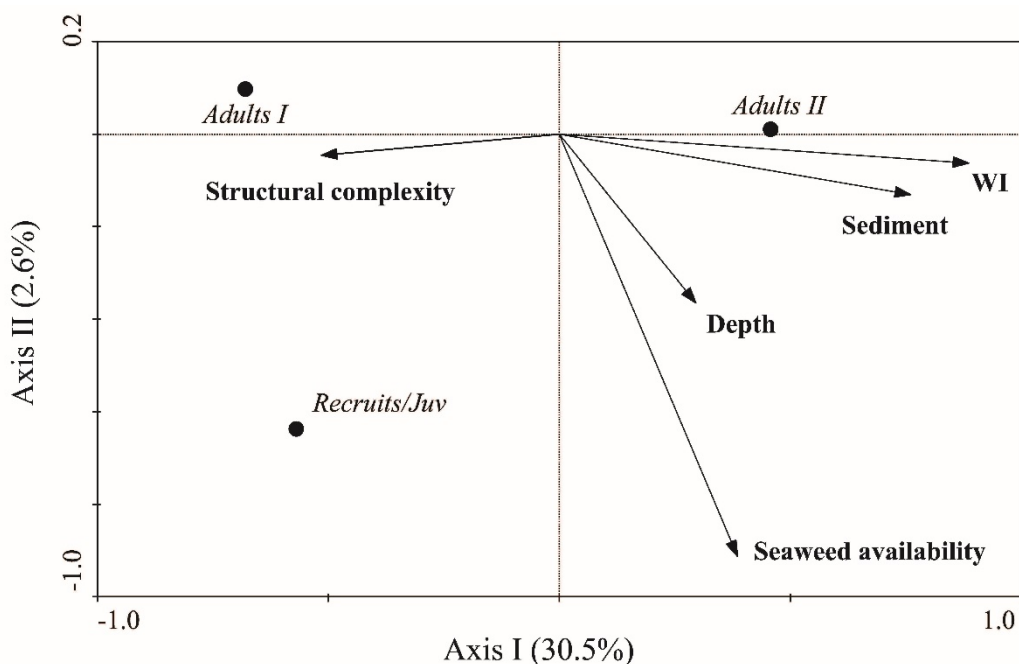


Fig. 4. Response curves for different size classes of *P. magellanicus* in relation to explanatory variables, modeled using Generalized Additive Models (GAM). RJ: Recruits and juveniles. See significances test in table S2.

Spatial aggregation

The spatial aggregation of *P. magellanicus* along a coastal depth gradient showed that aggregation is the most common distribution pattern (Table 3). However, disparities emerged among size classes: recruits and juveniles were highly aggregated in the upper infralittoral shore zone, showed high aggregation at 9–12 m depth, and tended towards randomness in the subtidal zone at 3–5 m depth (Table 3). The intermediate-size class (adults I) showed high aggregation in intertidal and random distribution in subtidal zones. Larger adults (adults II) were aggregated in all studied habitats (Table 3).

Table 3. Spatial aggregation indices for *P. magellanicus* and their interpretation at four coastal habitats in central Patagonia, Argentina

Size classes/Index	Coastal habitats			
	LwMd	InfraL	Sub 3–5 m	Sub 9–12 m
Pooled sizes				
p (Var-to-mean)	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$
Stand. Morisita	0.58 (Agg.)	0.53 (Agg.)	0.52 (Agg.)	0.57 (Agg.)
Green Index	0.88	1.60	0.80	2.29
Lloyd (patchiness) Index	5.26	2.34	1.39	2.22
Recruits and Juveniles				
p (Var-to-mean)		$p < 0.0001$	$p = 0.21$	$p < 0.005$
Stand. Morisita	--	0.66 (Agg.)	-0.10 (Random)	0.66 (Agg.)
Green Index	--	0.63	0.05	0.31
Lloyd (patchiness) Index	--	8.81	1.34	4.47
Adults I				
p (Var-to-mean)	$p < 0.0001$	$p < 0.0001$	$p = 0.051$	$p = 0.15$
Stand. Morisita	0.73 (Agg.)	0.56 (Agg.)	-0.24 (Random)	-0.11 (Random)
Green Index	0.35	1.80	0.14	0.07
Lloyd (patchiness) Index	13.68	4.08	1.80	1.35
Adults II				
p (Var-to-mean)	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$
I. Morisita Est.	0.59 (Agg.)	0.53 (Agg.)	0.52 (Agg.)	0.60 (Agg.)
I. Green	0.98	0.81	0.64	2.53
I. Lloyd	6.13	2.54	1.38	2.61

DISCUSSION

Environmental gradients and distribution of sea urchins

Our study reveals that *Pseudechinus magellanicus* exhibits a unimodal abundance pattern during spring along the coastal depth gradient in wave-exposed rocky shores of the central coast of San Jorge gulf, with peak densities in the low midlittoral to 12 meters. The species was absent at 15 meters, where sediment accumulation is high, but has been observed in deeper fine sediment bottoms (Fernández 2006). In the San Jorge Gulf, *P. magellanicus* seems to prefer rocky or coarse-grained substrates in shallow waters, selecting fine substrates only in sediment-resuspension-free deep waters. For other echinoid species, abundance decreases with depth due to light exposure, wave action, and sedimentation (Cordeiro et al. 2014). In our study, sedimentation influences the vertical distribution of *P. magellanicus*, impacting recruits, juveniles, and smaller adults the most, while minimally affecting larger individuals. The effects of sedimentation on rocky bottoms are complex but can lead to mortality due to burial and anoxia, and physical damage (Airoldi 2003). In northern Patagonian gulfs, the abundance of *P. magellanicus* decreases with higher fractions of very fine sands (Zaixso and Lizarralde 2000). Similarly, sediment presence can influence larval settlement and survival of *Evechinus chloroticus* (Phillips and Shima 2006; Walker 2007).

Sea urchins of different size are known to show different patterns of abundance based on their habitat (Domínguez et al. 2015). Larger *P. magellanicus* are abundant in low subtidal levels, particularly in kelp forests or at their interface with sandy bottoms. Intermediate-sized urchins mainly inhabit shallower waters from the midlittoral to upper infralittoral zones, while recruits and juveniles are mostly found in infralittoral tidepools and subtidal habitats. Similarly, smaller sea urchins were also found in intertidal rather than subtidal habitats in *Paracentrotus lividus*, likely due to stressful intertidal conditions, vertical migration of larger individuals, or selective predation (Domínguez et al. 2015; Ouréns et al. 2013). Early stages of *P. magellanicus* typically inhabit shelters or cryptic environments provided by coralline algae, while larger individuals are found in more exposed areas with lower structural complexity, possibly due to the scarcity of optimal shelters in subtidal zones. The absence of recruits and juveniles and the presence of smaller sizes at the upper limit of their distribution suggest limited larval settlement, irregular recruitment, and/or higher mortality from increased environmental stress. However, methodological constraints (e.g., narrow temporal sampling window, limited spatial coverage) may have also hindered the detection of recently recruited sea urchins at the upper limit. In contrast, the abundance of large adults in deep subtidal zones indicates high food availability and suggests migration to deeper waters. Kelp forests

at these depths provide trophic resources, enhancing nutritional conditions and promoting growth (Gil et al. 2021).

The number of recruits and juveniles in a population can be influenced by the interactions among three processes: substrate selection, larval availability, and early juvenile mortality (Cameron and Schroeter 1980; Morgan et al. 2000). Our study provides useful data on vertical variation during the austral spring. Primary spawning of *P. magellanicus* occurs in late winter (August to September) and minor spawning in summer (Gil et al. 2020), with a larval lifespan of 1–2 months (Kino and Kani 2009). Settlement is expected mainly in spring or early summer, with a secondary pulse in autumn. Our results document the vertical distribution shortly after the peak settlement or six months after a potential secondary pulse from summer spawning. Thus, the current distribution of recruits and juveniles could also be influenced by post-metamorphic events, including mortalities and migration. In some species of *Strongylocentrotus*, juveniles seek and migrate to microenvironments with lower mortality rates immediately after larval settlement (Cameron and Schroeter 1980). However, some authors argue that large-scale migration is not feasible, and that post-settlement mortality determines the distribution and contribution of recruits to populations (Morgan et al. 2000). In other species, high correlations have been found between juvenile and adult densities (Ouréns et al. 2014), and protective associations between juveniles and adults have been described (Breen et al. 1985; Nishizaki and Ackerman 2007). We showed that maximum densities of recruits and juveniles were not linked to adult sea urchin densities, which does not support the hypothesis of protection mechanisms by larger sea urchins. For *Strongylocentrotus franciscanus*, the likelihood of adults providing shelter to juveniles increased with sea urchin size and juvenile density, but remained generally low (Zhang et al. 2011). The presence of *P. magellanicus* recruits and juveniles in the lower infralittoral intertidal fringe and shallow rocky subtidal areas is linked to high structural complexity and conditions that support larval settlement. In contrast, their absence in higher intertidal levels may indicate high recruit mortality due to increased environmental stress. Long-term monitoring of plankton, larval settlement, and hydrographic characteristics could improve our understanding of *P. magellanicus* dispersion and settlement patterns.

Other mechanisms that could alter *P. magellanicus* densities include mortality from predation. In other coastal ecosystems, sea urchin populations are regulated by specialized predators, such as sea otters, lobsters and crabs, fish, and sea stars (e.g., Bonaviri et al. 2009; Clemente et al. 2013; Hereu et al. 2005). However, in Patagonian and southern Chilean coastal ecosystems, there is no evidence of a specialized predator regulating sea urchin populations (Barrales and Lobban 1975; Castilla 1985; Vásquez and Buschmann 1997). In our study area, predation on *P. magellanicus* has been recorded by king crabs *Lithodes santolla* (Vinuesa et al.

2013), the shrimp *Pleoticus muelleri* (Roux et al. 2009), the sea star *Cosmasterias lurida* (Tolosano, pers. comm.) and some coastal fishes (Marcinkevicius, pers. comm.). Predation during early settlement stages within articulated coralline algae assemblages could also occur, with polychaetes and crabs likely serving as primary predators. Further research on the predators of *P. magellanicus* is needed to better understand their ecological implications.

Influence of structural complexity

Our study revealed a positive relationship between habitat complexity and the abundance of recruits/juveniles and intermediate size classes of *P. magellanicus*, while larger size classes were more common in areas with lower structural complexity. Several studies (Benedetti-Cecchi and Cinelli 1995; Cordeiro et al. 2014; McClanahan and Shafir 1990) have shown positive associations between structural complexity and sea urchin densities. The habitats with higher structural complexity identified in our study—such as tide pools with loose shells, articulated coralline algae, and *M. pyrifera* holdfasts—offer physical features like crevices, holes, and protruding elements. These structures could provide more refuges, surfaces for larval settlement, and diverse niches, enhancing food diversity and availability. Circumstantial observations show that in the low infralittoral fringe, intermediate-sized sea urchins are anchored in crevices using their spines. Habitat structural complexity likely enhances the short-term survival of *P. lividus* juveniles (Hereu et al. 2005). Similarly, crevices have been shown to reduce predation and promote recruitment in *Strongylocentrotus purpuratus* (Scheibling and Hamm 1991), *S. franciscanus* (Palleiro-Nayar et al. 2011), *Centrostephanus rodgersii* (Andrew 1993), and *Diadema antillarum* (Hernández et al. 2008). Increased habitat complexity is likely to affect *P. magellanicus* through two main mechanisms: (1) mitigating physical stressors, such as wave action and light intensity, and (2) reducing mortality from predation. Although predation may contribute little to mortality, it cannot be ruled out, even in the absence of specialized predators.

Spatial aggregation

The spatial dispersion of *P. magellanicus* shows a prevalent pattern of contagious aggregation in natural populations. Vertical distribution variations were observed across size categories, with strong aggregation at intertidal levels and less aggregation, approaching a more random distribution, in subtidal kelp forests for recruits and small adults. Beyond the kelp forest zone, aggregation once more became more pronounced. These observations suggest that aggregation is common in intertidal zones due to environmental fragmentation, such as tide pools,

crevices, and mussel beds. Physical and biological heterogeneity are known to affect herbivore behavior, potentially causing aggregations (Andrew 1993). Conversely, reduced aggregation at depths of 3-5 meters may indicate a more homogeneous, less fragmented environment, with reduced stress. Future research should expand the temporal framework and explore the relationship between kelp forest condition (i.e., decaying or senesced algae) and demographic aspects of *P. magellanicus*. The 9-12 meters depth range, with increased sediment impact and fragmentation from channels and loose rocks, also exhibits spatial aggregation. Aggregations of *P. magellanicus* have been observed on detached *M. pyrifera* fronds on the seafloor (Tolosano, pers. comm.). Our results indicate a positive relationship between algae availability and adult *P. magellanicus* density, potentially contributing to feeding aggregations at this depth. Similar aggregation phenomena have been reported in other sea urchin species (Lauzon-Guay and Scheibling 2007; Rodríguez and Fariña 2001). Our findings are only based on observations during the austral spring on a wave-exposed rocky platform where kelp forests are present. The restricted temporal and spatial sampling in this study may not fully determine spatial variability or establish relationships between kelp forest occurrence and the density and spatial arrangement of this sea urchin. Future research should examine temporal and spatial changes in the aggregation patterns of *P. magellanicus* in relation to food availability and population density.

CONCLUSIONS

The sea urchin *Pseudechinus magellanicus* displayed clear patterns in size distribution, abundance, and spatial aggregation along a coastal depth gradient during the austral spring on the exposed coast of central Patagonia, Argentina. Population density followed a unimodal response to depth, with smaller and intermediate-sized individuals prevalent in intertidal and shallow waters, and larger individuals concentrated in deeper zones with lower structural complexity. The positive association between structural complexity and the densities of younger urchins highlights the importance of habitat features in shaping population dynamics, while factors such as food availability and sedimentation emerged as critical drivers of vertical distribution. Aggregation was the dominant spatial arrangement across the depth gradient, except where kelp forests prevailed, leading to a more random distribution of juveniles and intermediate-sized individuals.

These findings highlight the complex interplay between environmental variables and population structure in one of the most abundant sea urchins in Patagonian marine benthic ecosystems. By examining the depth-related distribution and habitat associations of *P. magellanicus*, this study establishes a baseline for future research on the temporal interactions

between this dominant species and its environment. Such insights are important for conservation strategies and management practices in coastal ecosystems, particularly in regions where environmental changes and human activities may affect habitat complexity and resource availability.

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Competing interests: DGG and HEZ declare that they have no conflict of interest.

Availability of data and materials: The data that support the findings of this study are available from the corresponding author, DGG, upon reasonable request.

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Supplementary materials

Table S1. Weighted means, standard deviation (SD) and variance inflation factor (VIF) of the explanatory variables in the CCA analysis, and cross-correlation analysis. (download)

Table S2. Generalized Additive Models (GAM) significance test relating the abundance of different size classes of *P. magellanicus* and a series of environmental predictors. (download)