Depth-related plasticity in the diet composition of *Pseudechinus magellanicus* (Echinoidea, Temnopleuridae) in nearshore environments off central Patagonia, Argentina

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Abstract *Pseudechinus magellanicus* is one of the most abundant sea urchins in southern South America, but many aspects of its feeding ecology in nearshore environments remain unknown. Here, we aimed to analyze the variability of the diet composition along a coastal depth gradient from intertidal tidepools to upper circalittoral zones and examine the relation between seaweed availability and the diet composition at intertidal tidepools. A total of 118 food items, including seaweeds and animal components, were identified. The diet composition showed a large variation between the different coastal habitats present along the depth gradient studied. In tidepools, articulate coralline seaweeds (*Corallina* spp.), mussel shell fragments and small crustaceans were frequent in the gut contents, suggesting that this species behaves like a general omnivore but can also act as a mussel bioeroder when consuming epizoic algae and microeuendolithic organisms. In intertidal tidepools, the species showed a negative preference toward typical species of late successional stages such as *Dictyota dichotoma*, *Adenocystis utricularis*, *Codium fragile* and *Chondria macrocarpa*. Sea urchins from kelp forests showed higher dietary diversity than those from intertidal and deeper subtidal habitats, but with prevalence of kelps. At upper circalittoral soft bottoms, diverse detrital items as benthic diatoms, cyanobacteria and drifted algae were observed in gut contents, usually associated with fine sediments, indicating that *P. magellanicus* captures drifted algae and behaves like a biofilm feeder. This trophic plasticity may allow this species to occupy contrasting habitats and may also contribute to explain its wide distribution in southern South America.

Keywords Benthos · Intertidal · Grazing · Echinodermata · Sea urchins

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Introduction

Ecological interactions of marine biological communities are crucial to understand their dynamics and

functioning (Bertness 1999). Marine grazers often have a strong control over the structure of macroalgal communities, especially in subtidal environments (Lubchenco 1978; Chapman and Johnson 1990; O'Connor et al. 2011). In particular, sea urchins are among the most important benthic grazers in both tropical and temperate ecosystems (Lawrence 1975; Harrold and Reed 1985; Bulleri et al. 1999; O'Leary et al. 2013). They can affect the abundance, settlement, distribution and composition of macroalgae and invertebrate assemblages and, as a result, may affect ecosystem productivity (Sammarco 1982; Uthicke et al. 2009). Moreover, sea urchin grazing on large kelp species can have ecological positive cascade effects on benthic detritivores (Yorke et al. 2019).

Regular sea urchins show plasticity in the hardness, size and structure of their dietary components, a fact that results in numerous omnivorous species (de Ridder and Lawrence 1982; Lawrence et al. 2013). They are known to capture, handle and ingest small invertebrates and seaweeds, including those chemically defended or heavily calcified (Larson et al. 1980; Bertness 1999). Some species exhibit sedentary habits and obtain most of their food from drifted algae, while others are scavengers or able to combine both feeding strategies (Lawrence et al. 2013). Scavengers may also show a tendency to carnivory (Wangensteen et al. 2011). Consequently, the high plasticity of feeding modes of sea urchins has allowed them to occupy diverse marine environments (Hughes et al. 2012). The diet composition of sea urchins is usually habitat dependent and may vary between different temporal (e.g., Harrold and Reed 1985; Kenner 1992) and spatial scales (e.g., between localities) (Endo et al. 2007; Kelly et al. 2007; Michel et al. 2016). It also varies due to changes in the availability and predictability of food resources or sea urchin feeding preferences (e.g., Harrold and Reed 1985; Lawrence et al. 2013).

In southern South America, the sea urchin *Pseudechinus magellanicus* (Philippi, 1857) is one of the most common species, occurring from Puerto Montt ($\sim$ 40°S) in the Pacific Ocean, including Juan Fernandez archipelago ($\sim$ 33°S) off the coast of Chile, to the outlet of the Río de la Plata River (35–36°S) in the Atlantic Ocean, including Falklands/ Malvinas and South Georgia Islands (Bernasconi 1953; Pawson 1966; Pierrat et al. 2012; Brogger et al. 2013). This species has a wide bathymetric range, from intertidal to 360 m depth (Larrain 1975), and is known to be especially abundant in nearshore habitats of San Jorge Gulf (SJG; 45.1–47°S) and southern region of Argentina and Chile (Ríos et al. 2003; Gil 2015). In the Argentine Sea, by means of a large-scale spatial approach, Penchaszadeh et al. (2004) described its trophic ecology, mainly focused in circalittoral mussel bank regions ($\sim$ 50 m) off Buenos Aires Province (37.4°S), and shallow waters of northern Patagonia (42–43°S) and the Beagle channel (55°S). In these environments, *P. magellanicus* behaves as an omnivorous and opportunistic species, showing a variable diet and the ability to feed from drifting elements (usually pieces of macroalgae) (Penchaszadeh et al. 2004). In kelp forests from Chile, *P. magellanicus* feeds primarily on drifting fronds and no active scraping over fixed plants has been observed (Pawson 1966; Castilla and Moreno 1982; Vásquez et al. 1984). However, its ecological role in Patagonian coastal ecosystems along a vertical (= depth) spatial scale has not yet been well explored.

The SJG has been recently studied in a multidisciplinary program focusing in marine ecosystem functioning and geology (St-Onge and Ferreyra 2018). This gulf is the largest semi-open basin in the SW Atlantic Ocean and one of the most productive marine regions in the Argentine Sea, showing high biodiversity levels (Fernández et al. 2005; Zaixso et al. 2015; Retana and Lewis 2017). Information regarding the principal benthic biotopes in the region has been previously described in Zaixso et al. (2015). In particular, *P. magellanicus* can be found from the intertidal zone to 100 m and is the most abundant sea urchin in nearshore and offshore benthic communities, being a dominant and functional key species (Roux et al. 1995; Gil 2015; Kaminsky et al. 2018). In the SJG, the species shows higher densities than northern Patagonia coastal populations, where it occurs only in subtidal areas (Zaixso and Lizarralde 2000; Epherra 2016). Despite its high abundance, there is limited information regarding its biological and ecological importance in subtidal and intertidal platforms (Gil 2015; Gil et al. 2020). Moreover, there are no studies examining its food preference or exploring the relation between seaweed availability and diet composition, especially in intertidal habitats. The wide coastal habitat heterogeneity/bathymetric range exhibited by *P. magellanicus* in the SJG provides an opportunity to explore its trophic role in coastal habitats.

Hence, the aim of the present study was to examine aspects of the feeding biology of *P. magellanicus* in nearshore habitats in the central coast of the SJG. In particular, we aimed to (1) analyze the variability of the diet composition of adult sea urchins along a coastal depth gradient from intertidal tidepools to upper circalittoral zones and (2) examine the relation between seaweed availability and diet composition at intertidal tidepools. New insights into the feeding ecology of this key species along a coastal depth gradient in Patagonia will be helpful to understand and propose further questions on its ecological role in benthic communities.

Materials and methods

Study area and field sampling

The study was performed in central Patagonia (Argentina), on a large exposed rocky shore of Playa La Tranquera (46°02′24.6′′S, 67°35′52.6′′ W), located in the central coast of the SJG (Fig. 1), during the end of June 2010 (early austral winter). The substrate consists of hardened sediment bedrock, with channels and crevices that slope gradually to about 10 m depth (below chart datum), where it grades to soft sediments

and scattered occurrence of some rocky reefs. A kelp bed of *Macrocystis pyrifera* extends from 3 to 9 m.

Four coastal habitats were identified along this coastal depth gradient: (1) intertidal low midlittoral tidepools (LMT; tidal heights of 1–2 m above mean low water) with biota dominated by *Corallina officinalis*, the mussel *Perumytilus purpuratus* and, to a lesser extent, the ribbed mussel *Aulacomya atra atra* at the tidepool edges; (2) infralittoral fringe tidepools (IFT; tidal heights of 0.3–1 m), which are exposed only during spring tides and the biota is dominated by turfs of *C. officinalis/C. elongata* and a high diversity of epiphyte species and Delesseriacea seaweeds and beds of *Aulacomya atra atra* (Zaixso et al. 2015); the invasive *Undaria pinnatifida* and a species of *Codium* usually identified as *Codium fragile* or *C. fragile* var *novae-zelandiae* (Boraso de Zaixso and Piriz 1975) can also occur along with some juvenile plants of *M. pyrifera*; (3) kelp forest of *M. pyrifera* (7 m depth), located in rocky subtidal platforms at around 7 m depth during low tides; and (4) upper circalittoral zone (12 m depth), located on platforms with a high sediment supply due to less agitation mode and characterized by the absence of seaweeds. Tides are macrotidal and show a semi-diurnal regime, with mean and maximum fluctuations of around 3.7 and 5.7 m, respectively. The coastal mean seawater temperature varies between 7.5 and 16.2 °C, whereas
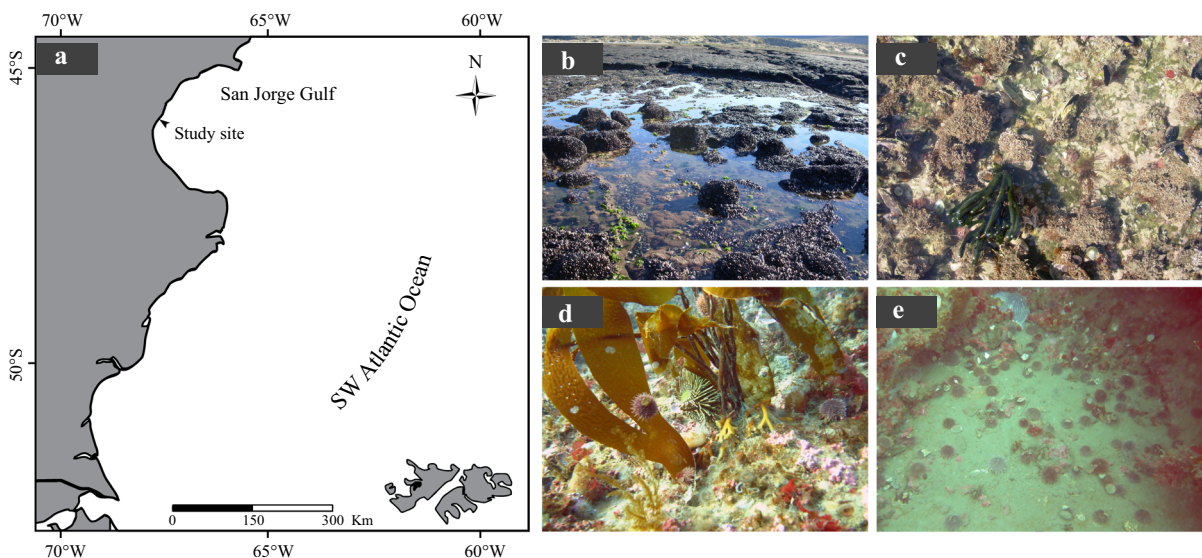
Fig. 1 **a** Location of the study area in Patagonia, Argentina, and coastal habitats used by *P. magellanicus* in San Jorge Gulf: **b** low midlittoral tidepools, **c**: infralittoral fringe tidepools, **d**: kelp forest of *M. pyrifera* (7 m depth), e: upper circalittoral zone (12 m depth)

salinity ranges between 34.4 and 34.7 (Verga et al. 2020).

To analyze the diet composition, a total of 60 adult sea urchins (test diameter > 14 mm; Orler 1992) were collected ($n = 15$ in each habitat) and immediately fixed in 5% saline formalin to prevent the digestion of food material. Each sea urchin collected was also inspected in situ for the presence of food items in their jaws and each food item recorded.

Sea urchins from subtidal levels were haphazardly collected by hand at each habitat by autonomous diving, and those from intertidal tidepools were retrieved from six random quadrat samples (225 cm^2 area) within each habitat (LMT and IFT). For each sample, all the biota was scraped from the substrate and fixed in formalin 5%. When necessary, additional sea urchins were collected out of the defined quadrats to reach the sample size in each intertidal habitat. Sea urchins from these samples were also used to examine the relationship between diet composition and relative abundance of macroalgae in intertidal habitats. The tidepools used in this study were similar in size (~ 40–50 m^2) and depth (~ 0.5–1 m).

Laboratory analysis

Once in the laboratory, the test diameter of each individual was measured (± 0.1 mm) and the digestive tract was removed, and all its contents were washed in a Petri dish and carefully examined under a stereoscope or light microscope. The dietary components were identified to the highest possible degree of taxonomic resolution. Some crustacean fragments could not be identified to species level, except for specimens that were complete or poorly digested within the stomach. In a few cases, fragments were identified by direct comparison of associated biota. Other non-living ingested items (e.g., mussel shell fragments, byssal threads, sediment) were also recorded because they may provide information on feeding behavior.

All seaweeds present in quadrat samples in LMT and IFT were identified, dried in an oven (60 °C) with air circulation for 48 h and weighed (± 0.0001 g).

Statistical analysis

The frequency of occurrence (FO) was expressed as the percentage of sea urchins in which a determined

food item was present in their gut (stomach and intestine). FO data were calculated for each food item separately and by pooling in higher taxa or main food type (e.g., macrofauna, Corallinacea rhodophytes, Laminariales).

For statistical analysis, epiphytic diatoms were grouped in a single category. Dietary diversity was estimated as the total number of different food items present in each individual. A one-way ANOVA was performed to test for differences in mean dietary diversity between habitats (fixed, four levels), followed by the REGW test for multiple mean comparison (Day and Quinn 1989). Prior to the ANOVA, the assumptions of homoscedasticity and normality in the distribution of residuals were verified using the Levene test and Shapiro–Wilk test, respectively (Quinn and Keough 2002).

To explore for differences in the diet composition of the sea urchin populations living in the four coastal habitats studied, food item data were arranged in a matrix of samples per species (food items) and then converted into a similarity matrix using the Sørensen qualitative index. Cluster analysis was performed in unweighted pairs with the arithmetic mean (UPGMA), and a non-metric multidimensional scaling (nMDS) was carried out on the similarity matrix. The quality of the nMDS ordination was evaluated by inspecting stress values (Clarke and Warwick 2001). Changes in the diet composition between coastal habitats were examined by performing a one-way analysis of similarity (ANOSIM), followed by post hoc comparisons (Clarke 1993; Clarke and Warwick 2001). To reduce an increase in the type I error in multiple comparisons, the level of significance was adjusted according to Bonferroni (Quinn and Keough 2002). Food items accounting for similarity within each habitat and those contributing to differences among habitats were analyzed using a percentage similarity analysis (SIMPER; Clarke and Warwick 2001).

The availability of seaweeds in LMT and IFT was estimated by calculating the relative abundance (RA%) of the most abundant seaweeds in the field as (B_a/B_t) *100, where B_a represents the dry weight of species a in the sample and B_t is the total seaweed weight in the sample. The relation between FO (%) in the diet and RA (%) of seaweeds was examined using bar plots at each intertidal level. Articulated coralline algae were excluded from the analysis because their RA% was greater than 95% in all the samples.

Results

Behavior and overall diet composition

Sea urchins had a test diameter ranging between 14 and 23.4 (mean: 17.1 ± 2.8 mm (SD), $n = 60$). During daylight surveys in low intertidal habitats, sea urchins were usually seen aggregated and hidden in cryptic microhabitats as tidepool bottoms under debris or remains of shells, under algae turfs or on beds of *Aulacomya atra atra*. In subtidal coastal habitats, cryptic behavior was less evident and sea urchins showed an extended distribution, occurring in different types of substrates or biogenic habitats, on holdfast, stipes and blades of senescent *M. pyrifera* and in crevices or low wave energy areas where detached seaweeds accumulated. In situ observation of sea urchins consuming biota was not common (8.3%), but remains of isopods (*Exosphaeroma* sp.), small crabs (*Halicarcinus planatus*), filamentous algae (e.g., *Chaetomorpha* sp.) or fragments of *C. officinalis/C. elongata* were seen in their mouth.

Nearly all the sea urchins analyzed (∼ 93%) showed food items in their digestive tract. Ingested items were often found aggregated in mucous-coated pellets and exhibiting an oval or spherical form with different colorations and textures depending on the main food source (e.g., algae, cyanobacteria or crushed mussel shells) and degree of packing. In some cases, pellets showing large invertebrate parts or fragments of articulated coralline algae were not completely formed.

A total of 118 different food items were identified: 5 taxa of Cyanobacteria, 28 Rhodophyta, 20 Phaeophyceae, 14 Chlorophyta, 20 Bacillariophyceae, 1 Dinophyceae, 1 Foraminifera, 1 Silicoflagellata and 28 food items corresponding to macrofaunal components (Table 1). The FO (%) for each food item, pooled by main type of food, revealed the presence of macrofauna in the diet of *P. magellanicus* in all the habitats studied, with a decrease in the kelp forest habitat. *Corallina* species were grazed more commonly in intertidal environments, while non-

Corallinaceae rhodophytes were better represented in guts from subtidal sea urchins. Feeding over laminarian species (mostly *M. pyrifera* and *U. pinnatifida*) was especially common in the kelp forest, while non-laminarian seaweeds were consumed in all the habitats studied, with a higher frequency in the infralittoral fringe and kelp forest. The presence of sediment and cyanobacteria increased toward areas of greater depth (Table 1).

Differences in diet diversity and composition between habitats

Diet diversity

The dietary diversity expressed as the number of different food items per sea urchin varied between 3 and 18 and significantly differed between the four coastal habitats studied (ANOVA, F = 4.27, $p < 0.005$). The sea urchins from the kelp forest (7 m) showed higher dietary diversity than those from the intertidal and deeper subtidal habitats (Fig. 2). The cumulative richness of food items in sea urchins from LMT was low compared to deeper habitats (Table 2).

Diet composition

The UPGMA detected three distinct groups of related samples and the nMDS discriminated mostly the diet composition of sea urchins from subtidal habitats (7 and 12 m) from that of those from intertidal habitats (LMT and IFT; group 3) (Fig. 3). A clear separation between samples from 7 m (kelp forest, group 1) and 12 m (group 3) was also observed, and dispersion within each habitat was similar (Fig. 3). Although samples from the intertidal tidepool were more interspersed, ANOSIM and post hoc comparisons found significant differences between all coastal habitats (R (global) = 0.62, $p < 0.001$).

The diet composition of sea urchins from LMT was highly similar to that of those from deeper habitats (Table 2). The most common food items in the sea urchins from LMT were *C. officinalis*, mussel shell fragments (*A. atra atra* and *M. edulis*) and the isopod *Exosphaeroma* sp. In IFT, the main food items were *Corallina* spp., shell fragments of *A. atra atra*, Myrionemataceae seaweeds and *Exosphaeroma* sp. In kelp forests (7 m), the diet was more diverse (Table 2) and represented by a high seaweed

Table 1 Frequency of occurrence (FO; %) of detailed dietary components of *P. magellanicus* during early austral winter in low midlittoral tidepools (LMT), infralittoral fringe tidepools (IFT), at 7 m depth (*M. pyrifera* kelp forest) and 12 m (mostly soft bottoms) in coastal habitats of San Jorge Gulf (Patagonia, Argentina)

Taxa/items	Coastal habitats			
	LMT	IFT	7 m	12 m
Bacillariophyceae				
Achnanthes sp.	0	15.4	0	0
Amphora sp.	15.4	0	7.1	7.7
Berkeleya sp.	0	7.7	0	7.7
Cocconeis sp.	46.2	7.7	7.1	7.7
Corethron pennatum	0	7.7	0	0
Grammatophora sp.	23.1	46.2	0	15.4
Gyrosigma/Pleurosigma complex	0	0	0	23.1
Haslea sp.	0	0	0	7.7
Licmophora sp.	0	0	7.1	15.4
Navicula sp.	0	0	0	15.4
Nitzschia sp.	0	0	0	7.7
Paralia sulcata	0	0	0	15.4
Pseudogomphonema sp.	0	15.4	0	0
Rhabdonema sp.	7.7	0	0	0
Rhoicosphenia sp.	0	15.4	0	0
Synedra sp.	7.7	0	0	0
Tabularia sp.	0	30.8	0	15.4
Trachyneis sp.	0	0	0	16.7
Unidentified centric diatom	0	0	7.1	15.4
Unidentified pennate diatom	23.1	30.8	21.4	25.0
Chlorophyta	38.5	38.5	78.6	38.5
Blidingia chadefaudii	0	0	7.1	0
Blidingia minima	0	0	14.3	0
Blidingia sp.	0	0	0	7.7
Bryopsis australis	0	0	7.1	15.4
Chaetomorpha linum	15.4	0	42.9	0
Cladophora sp.	0	7.7	14.3	23.1
Derbesia sp.	0	0	0	7.7
Rhizoclonium sp.	0	15.4	0	0
Ulothrix sp.	0	23.1	0	0
Ulva hookeriana	0	0	14.3	7.7
Ulva compressa	0	0	0	7.7
Ulva sp.	7.7	7.7	35.7	0
Urospora sp.	0	0	7.1	0
Unidentified epiphyte	15.4	0	7.1	7.7
Cyanobacteria	15.3	38.5	42.9	53.8
Chroococcales	0	15.4	0	0
Cyanophyceae indet	0	23.1	35.7	46.1
Hyella caespitosa	15.3	0	0	0
Microcoleus sp.	0	7.7	7.1	0
Oscillatoriales	0	15.4	0	15.3
Dinophyceae				
Prorocentrum micans	15.4	53.8	0	0

Table 1 continued

Taxa/items	Coastal habitats			
	LMT	IFT	7 m	12 m
Phaeophyceae				
Laminariales (pooled)	0	0	78.6	23.1
Laminariales indet	0	0	0	15.3
Macrocystis pyrifera	0	0	71.4	0
Undaria pinnatidida	0	0	7.1	7.7
Non-Laminariales (pooled)	53.8	61.5	78.6	15.3
Acinetospora crinita	0	0	35.7	0
Chordariaceae indet	7.6	15.4	0	0
Cladothele decaisnei	0	7.7	7.1	0
Colpomenia sinuosa	0	0	21.4	0
Cutleria multifida (Aglaozonia stage*)*	23.1	7.7	0	7.7
Dictyota dichotoma	7.7	23.1	7.1	7.7
Ectocarpaceae	0	7.7	0	0
Ectocarpus sp.	0	7.7	0	0
Feldmannia simplex	7.7	7.6	14.3	7.7
Hincksia granulosa	0	7.7	7.1	0
Myrionema sp.	0	7.7	0	0
Myrionemataceae	7.6	38.5	0	0
Petalonia fascia	0	0	14.3	0
Punctaria plantaginea	0	0	7.1	0
Ralfsia australis	0	0	0	7.7
Scytosiphon sp.	0	0	7.1	0
Sphacelaria sp.	7.7	0	0	0
Rhodophyta				
Corallinaceae (pooled)	92.3	100	42.8	38.4
Corallina elongata	0	0	42.8	0
Corallina officinalis	92.3	100	0	0
Encrusting Corallinaceae	0	0	21.4	38.4
Non-Corallinaceae (pooled)	61.6	76.9	92.9	92.3
Acrochaetiaceae indet	0	7.7	0	7.7
Anotrichium furcellatum	0	7.7	0	0
Antithamnion densum	0	0	0	23.1
Antithamnionella ternifolia	0	0	7.1	7.7
Aphanocladia robusta	0	23.1	21.4	7.7
Bostrychia intricata	7.7	0	0	7.7
Bostrychia sp.	23.1	0	7.1	0
Callithamnion sp	0	15.4	14.3	15.3
Catenella fusiformis	0	7.7	0	0
Ceramium tenuicorne	0	0	7.2	0
Ceramium virgatum	15.4	23.1	28.6	0
Delesseriaceae indet	15.4	23.1	28.6	53.8
Erythrotrichia sp.	0	15.4	7.1	0
Herposiphonia sulivanae	0	7.7	0	0
Heterosiphonia berkeleyi	0	0	64.3	0

Table 1 continued

Taxa/items	Coastal habitats			
	LMT	IFT	7 m	12 m
Lophurella hookeriana	7.7	7.7	0	0
Plocamium secundatum	0	0	0	7.7
Polysiphonia abcissa	0	0	0	7.7
Polysiphonia sp.	7.7	7.7	7.1	0
Porphyridium sp.?	0	0	0	30.8
Pyropia columbina	23.1	15.4	35.7	23.1
Rhabdonia coccinea	0	0	0	15.3
Rhodomelaceae indet	0	15.4	7.1	23.1
Schizoseris sp.	0	7.6	0	0
Streblocladia camptoclada	15.4	7.7	7.1	0
Other				
Foraminifera	23.1	23.1	64.3	46.1
Silicoflagellata	7.7	7.7	0	0
Macrofauna				
Ascideacea				
Didenmun sp.	0	0	0	15.4
Bryozoa				
Beania sp.	0	0	21.4	0
Bryozoa indet	0	0	21.4	15.4
Membranipora sp.	0	0	28.6	0
Crustacea				
Amphipoda indet	0	15.4	28.6	15.4
Copepoda indet	0	0	0	15.4
Crustacea indet	69.2	53.8	42.8	61.5
Decapoda (larvae indet.)	0	0	0	7.7
Exosphaeroma sp.	38.5	23.1	0	0
Halicarcinus planatus	0	15.4	0	0
Hydrozoa	7.7	7.7	14.3	38.5
Insecta				
Clunio brasiliensis (larvae)	15.4	0	0	0
Mollusca				
Aulacomya atra (recruit)	0	15.4	0	0
Mussel byssus	38.5	15.4	0	7.7
Lasaea sp.	0	0	0	30.8
Neolepton sp.	0	0	0	7.7
Pareuthria fuscata (recruit)	0	0	7.1	0
Perumytilus purpuratus (recruit)	0	7.7	0	0
Gastropoda (radula)	0	7.6	0	0
Shell fragments of *A. atra*	84.6	53.8	14.2	23.1
Shell fragments of *Mytilus platensis*	38.5	0	0	0
Nematoda				
Desmodorida indet,	0	0	0	7.7
Desmoscolex sp.	0	0	0	7.7
Nematoda indet	0	0	0	7.7

Table 1 continued

Taxa/items	Coastal habitats			
	LMT	IFT	7 m	12 m
Polychaeta				
Serpulidae indet	0	7.7	0	0
Polychaeta indet. 1	0	23.1	14.2	23.1
Polychaeta indet. 2	0	15.4	7.1	0
Porifera	38.5	15.4	7.1	84.6
Other elements				
Spines of *P. magellanicus*	0	0	7.1	38.5
Sediment	30.7	23.1	50.0	76.9
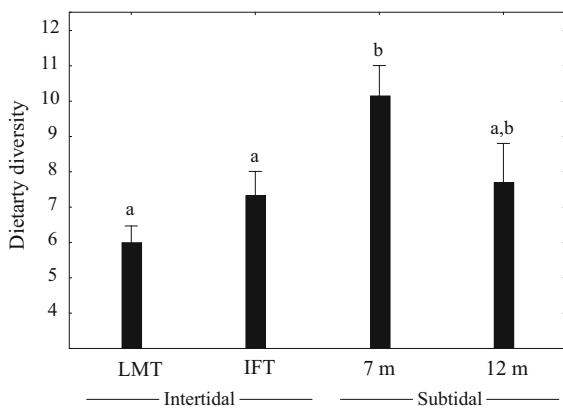
Fig. 2 Mean dietary diversity (± SE) in *P. magellanicus* in intertidal (LMT: low midlittoral tidepools; IFT: infralittoral fringe tidepools) and subtidal (kelp forest 7 m depth, upper circalittoral zone at 12 m depth) habitats. Different letters denote significant differences between means (REGW post hoc test)

component (*Macrocystis pyrifera*, *Heterosiphonia berkeleyi*, *Chaetomorpha linum*, *Corallina elongata*, *Pyropia columbina*, *Ulva* sp., *Acinetospora crinita*) and the encrusting bryozoan *Membranipora isabelleana*. At circalittoral bottoms, diverse detrital items as benthic diatoms, cyanobacteria and drifted algae

such as *Pyropia columbina*, *Antithamnion densum* and *Cladophora* sp. were observed in gut contents, usually associated with fine sediments. The contribution of each species (%) to the dissimilarity in the diet composition between successive depths is indicated in Table 3.

Seaweed availability and diet composition in the intertidal zone

In LMT (Fig. 4a), *P. magellanicus* consumed nearly all the abundant seaweeds available, with the exception of *Adenocystis utricularis* and *Cladophora* sp. In these tidepools, *Dictyota dichotoma* has a high relative abundance, but was less grazed than other seaweeds. In contrast, *Ceramium virgatum*, *Lophurella hookeriana*, *Streblocladia camptoclada* and *Chaetomorpha linum* showed high FO in the diet, but were less available in the field.

In the infralittoral fringe (Fig. 4b), the availability of non-Corallinaceae rhodophytes was higher. *Aphanocladia robusta*, *Cladophora* sp., *C. virgatum*, *Herposiphonia sulivanae*, *L. hookeriana* and *S. camptoclada* were eaten more often than their relative abundance in the field. Again, *D. dichotoma* was the

Table 2 Cumulative food item richness and intra-habitat similarity of food components of *P. magellanicus* along a coastal depth gradient in central Patagonia

	LMT	IFT	7 m	12 m
Total richness	30	51	52	48
Intra-habitat group similarity (%)	42.3	30.3	26.7	25.2
No. of taxa (85% intra-habitat similarity)	2	4	10	6
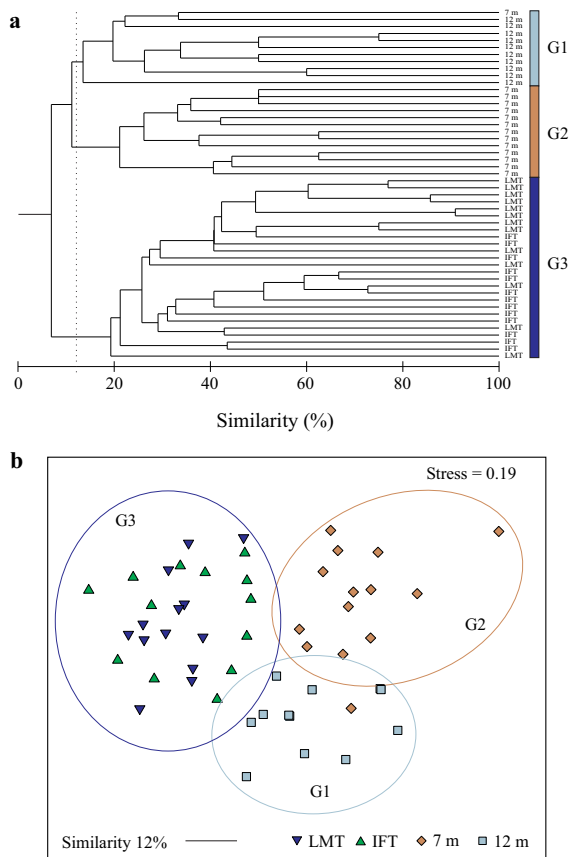
Fig. 3 Sorensen-based a) hierarchical clustering (UPGMA) and b) non-metric multidimensional scaling (nMDS) comparing dissimilarity in the diet composition between nearshore habitats: low midlittoral (LMT), infralittoral fringe tidepools (IFT), 7 m depth, kelp forest (7 m depth) and upper circalittoral zone (12 m depth)

most abundant seaweed, but only about 23% of sea urchins used it as food. On the other hand, *Codium fragile*, *Chondria macrocarpa* and *A. utricularis* were not grazed by *P. magellanicus* despite having relatively high abundances.

Discussion

In the Argentine Sea, in central Patagonia, *Pseudechinus magellanicus* is an omnivorous species, feeding on a high diversity of seaweeds, including heavily calcified ones, and small invertebrates. Both a high dietary plasticity and the prevalence of omnivory as the main feeding strategy have been reported in other functional key species of sea urchins as

Strongylocentrotus droebachiensis, *S. purpuratus*, *Psammechinus miliaris* (Kelly et al. 2007) and *Centrostephanus* (Vance and Schmitt 1979; Hill et al. 2003). In contrast, other sea urchin species as *Loxechinus albus* (Vásquez 2007) and *Heliocidaris erythrogramma* (Vanderklift et al. 2006) show a marked tendency to herbivory. In sea urchins, a mixed diet also ensures better body condition and gonadal growth (Briscoe and Sebens 1988; Nestler and Harris 1994; Meidel and Scheibling 1999). Regarding *P. magellanicus*, the omnivorous diet and field observations suggest that this species has diverse feeding methods: (1) passive grazing after capture of drifting seaweeds using their podia and pedicellaria, or by aggregating on detached seaweeds at low energy subtidal bottoms, (2) active grazing on living algae, (3) biofilm grazing in surface sediments, (4) rasping of mussel shells to consume epibionts and euendolithic organisms and (5) capture and ingestion (or scavenging) of motile and sessile invertebrates, each of which may have diverse and variable ecological significances. The high variability of food items found within each individual suggests that these behaviors can be flexible and that *P. magellanicus* may be able to alternate between different feeding techniques.

Penchaszadeh et al. (2004) determined that, in the broad spatial context of the Argentine Sea, the diet composition of *P. magellanicus* reflects the type of food available in the environment. Our study additionally showed a large variation between different coastal habitats along a short depth gradient. In general, the gut content of the sea urchins inhabiting intertidal tidepools had a diverse composition of food items, including mussel shell fragments, articulated coralline algae, filamentous and foliose seaweeds and small crustaceans typical of those tidepool habitats. The high occurrence of shell fragments and articulated coralline algae in these tidepool habitats suggests that *P. magellanicus* may play a role as a bioerosion agent in *Aulacomya atra atra* populations. The presence of shell-boring species as *Hyella caespitosa* (Cyanobacteria) and conchocelis phases of *Pyropia columbina*, together with mussel shell fragments, filamentous algae and benthic diatoms, denotes the consumption of microendolithic and epilithic species, and biofilms associated with hard substrates. Compared to other mytilids available in tidepools, shells of the ribbed mussel *A. atra* are known to harbor many epibionts due to the larger surface area provided by the ribbed

Table 3 SIMPER results of food items accounting for differences in the diet composition of *Pseudechinus magellanicus* between coastal habitats. LMT: low midlittoral tidepools, IFT: infralittoral fringe tidepools, 7 m: 7 m depth (kelp forest), 12 m: 12 m depth (soft bottoms)

(a) LMT vs IFT (mean dissimilarity = 67.2%)

Taxa/Food item	Relative frequency		Dis	Dis/SD	Cum.%
	IFT	LMT			
Prorocentrum sp.	0.54	0.15	5.21	0.95	7.75
Mussel shell fragments	0.54	0.85	4.58	0.81	14.57
Exosphaeroma sp.	0.23	0.38	3.98	0.82	20.49
Pyropia columbina	0.15	0.23	2.79	0.64	24.64
Ceramium virgatum	0.23	0.15	2.68	0.64	28.63
Myrionemataceae	0.31	0.08	2.65	0.68	32.58
Delesseriaceae	0.23	0.15	2.62	0.61	36.48
Cutleria multifida	0.08	0.23	2.51	0.57	40.22

(b) IFT vs 7 m (mean dissimilarity = 93.9%)

Taxa/Food item	Relative frequency		Dis	Dis/SD	Cum.%
	IFT	7 m			
C. officinalis	1	0	7.39	2.96	7.88
M. pyrifera	0	0.71	5.55	1.34	13.79
Heterosiphonia berkeleyi	0	0.64	4.5	1.2	18.58
Prorocentrum sp.	0.54	0	4.07	0.98	22.92
Mussel shell fragments	0.54	0.14	3.93	0.97	27.11
Pyropia columbina	0.15	0.36	2.97	0.77	30.28
Chaetomorpha linum	0	0.43	2.96	0.81	33.43
Cyanophyceae	0.23	0.36	2.91	0.79	36.53
Ulva sp.	0.08	0.36	2.79	0.73	39.5
C. elongata	0	0.43	2.66	0.82	42.34

(c) 7 m vs 12 m (mean dissimilarity = 88.4%)

Taxa/Food item	Relative frequency		Dis	Dis/SD	Cum.%
	12 m	7 m			
M. pyrifera	0	0.71	5.75	1.39	6.51
Heterosiphonia berkeleyi	0	0.64	4.67	1.23	11.78
Delesseriaceae	0.7	0.29	4.58	1.08	16.96
Cyanophyceae	0.6	0.36	4.13	0.97	21.64
Incrusting Corallinaceae	0.5	0.21	3.7	0.93	25.82
Pyropia columbina	0.3	0.36	3.32	0.84	29.57
Chaetomorpha linum	0	0.43	3.06	0.82	33.04
C. elongata	0	0.43	2.75	0.83	36.15
Ulva sp.	0	0.36	2.74	0.71	39.25

shell or limited shell cleaning mechanism (Thiesen 1972; Diez et al. 2016), a fact that might explain the high prevalence of shell fragments in the diet of *P. magellanicus*. Mussel recruits were also recorded in the gut contents, but they were not numerous (1–2 per sea urchin) or prevalent, although this could have been the result of the restricted temporal scope of our sampling. Other researchers have also observed scraping on mussel shells or ingestion of recruits in shallow subtidal and circalittoral population of *P. magellanicus* associated with blue mussel banks (Penchaszadeh et al. 2004) as well as in intertidal

a Low midlittoral tidepools

b Infralittoral fringe tidepools
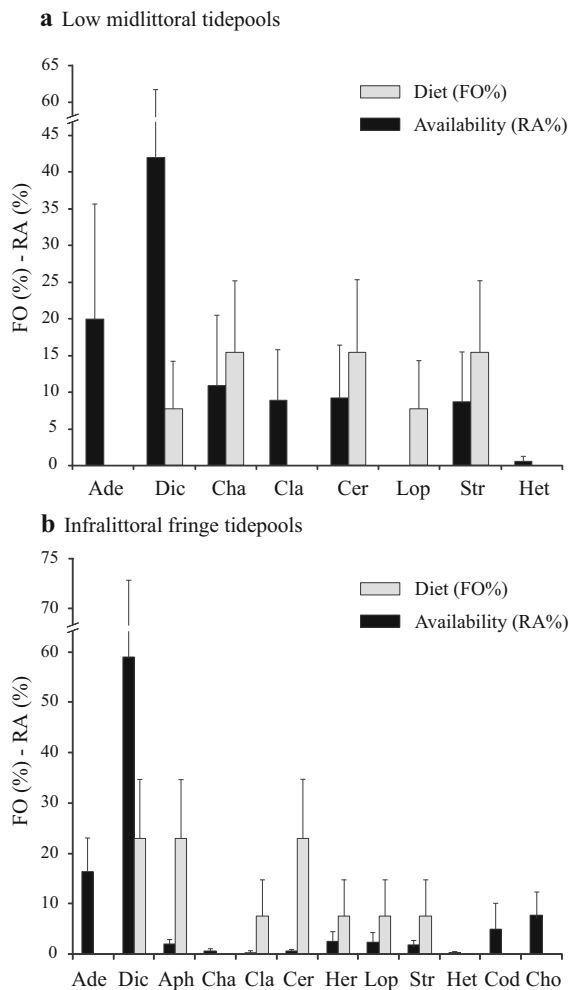
Fig. 4 Relation between frequency of occurrence (FO%) of seaweeds in the diet of *Pseudechinus magellanicus* and relative availability (RA%) in a) low midlittoral and b) infralittoral fringe tidepools. Error bars denote standard error of a sample mean for RA (%) and standard error in the binomial standard deviation for FO (%). Species abbreviations are represented by the first three letters of the genera: Ade, *Adenocystis*; Aph, *Aphanocladia*; Cha, *Chaetomorpha*; Cho, *Chondria*; Cla, *Cladophora*; Cer, *Ceramium*; Cod, *Codium*; Dic, *Dictyota*; Her, *Herposiphonia*; Het, *Heterosiphonia*; Lop, *Lophurella*; Str, *Streblocladia*

populations of *Tetrapygus niger* (Hidalgo et al. 2013). The role of *P. magellanicus* as a bioeroder needs further study, since this species constitutes one of the main grazers in low intertidal platforms and ribbed mussels show high levels of eroded shells (Gil 2015).

Macrofauna was found to be a prevalent food item of *P. magellanicus* in tidepool habitats. Although our study had a qualitative approach, the number of animal

prey in the content was sometimes high. The most common animal tissues recorded were isopods, fouling bryozoans, sponges, hydrozoans, crabs and polychaetes. The field observation of sea urchins with macrofauna leftovers in their jaws (e.g., *Exosphaeroma* spp. and *Halicarcinus planatus*) suggests that *P. magellanicus* is a scavenger or is able to catch and handle mobile living prey. The analysis of gut contents and in situ observations did not allow us to clearly discriminate between these feeding strategies, although a combination of both may occurred. Small keyhole limpets (*Fissurella radiosa*) in other studied areas have also been seen turned upside down and preyed on soft tissues (Damián Gil, pers. obs.). The potential capture of macrofauna could be facilitated during low tide or may occur when the potential prey seeks shelter under empty shells or debris in tidepool bottoms or in the bases of coralline algal turfs. Experimental evidence in other species indicates that sea urchins feeding on high-protein diets show higher growth rates and greater allocation to gonads than those feeding on algae-based lower nitrogen diets (Nestler and Harris 1994; Hammer et al. 2006). The ingestion by *P. magellanicus* of some animal food sources (especially microfauna) along with organic matter and sediment also suggests incidental ingestion of seaweeds or an opportunistic feeding behavior. However, it is important to note that the ingestion of animal soft tissues may be underestimated since they can be quickly digested and thus unnoticed.

In intertidal zones, turfs of articulated coralline algae (e.g., *Corallina* spp.) and associated filamentous and foliose algae are subject to high grazing levels. Previous studies in other sea urchin species have reported the ingestion of calcareous articulated seaweeds (Larson et al. 1980; Wright et al. 2005), but several studies have shown that these food items are usually negatively selected or not grazed due to their low caloric content or assimilation deficiencies (Paine and Vadas 1969; Littler and Littler 1980; Yatsuya and Nakahara 2004; Sonnenholzner et al. 2011). In particular, as a structural defense against herbivory, *C. officinalis* has incorporated calcium carbonate (calcite) into its tissues (Littler and Littler 1980); however, in the presence of high densities of sea urchins, this physical defense may not be enough to counteract the intense grazing by urchins (Wright et al. 2005). Consumption of coralline algae by *P. magellanicus* challenges the assumption of the optimal

foraging theory which maximizes the assimilation of energy per unit of time (Hughes 1980). However, the high prevalence and persistence of coralline algae in the diet of *P. magellanicus* may also denote a limiting condition of some other macroalgal food in the habitat or an accidental ingestion due to its association with other palatable epiphytic seaweeds. Lastly, consumption of carbonates from coralline algae in *P. magellanicus* may also respond to the requirement of calcium carbonate for its skeleton and complex dental apparatus, which is getting challenged by ocean acidification in sea urchins (Dupont and Thorndyke 2013).

The fact that *Pseudechinus magellanicus* usually grazes on the bases of the coralline turfs may weaken the stability of the algal mat, affect the associated community and promote indirect effects of ecological relevance (e.g., by affecting other species that rely on algal turfs as food or protection). Sea urchins are known to exert a strong control over the structure of macroalgae and invertebrate communities, by affecting their abundance, settlement, distribution and composition (Sammarco 1982; Uthicke et al. 2009). Moreover, herbivory-induced changes in algal communities may depend on the feeding preference of sea urchins as well as on the successional stage of the community (Lubchenco and Gaines 1981). The results of the present study suggest that *P. magellanicus* has a negative preference toward typical species of late successional stages such as *Dictyota dichotoma*, *Adenocystis utricularis*, *Codium fragile* and *Chondria macrocarpa*. In this respect, algal chemical defenses may also influence herbivore preference (Erickson et al. 2006). Dictyotalean seaweeds, particularly several species of *Dictyota*, produce a wide variety of complex mixtures of terpenoids, acetogenins and terpenoid–aromatic compounds, which are known to be antiherbivore defenses against fishes, sea urchins and amphipods (Amsler and Fairhead 2005). Chemical defense to invertebrate grazing has also been reported in *Adenocystis utricularis* (Amsler et al. 2005), *Codium fragile* (Lyons et al. 2007) and *Chondria* (Govenkar and Wahidulla 2000). Besides, these species may be difficult to graze within intertidal habitats due to their: (1) higher risk of dislodgment of an approaching sea urchin by wave-swept of large algae (e.g., *Codium*) or (2) the different microscale distribution between sea urchins and some species of seaweeds within tidepools (e.g., *Adenocystis* usually occurs on tops of *C. officinalis*, which is not easily accessible to the sea urchin in intertidal habitats). However, experimental research is needed to explore the incidence of grazing of *P. magellanicus* in Patagonian coralline turfs and associated seaweeds in low intertidal platforms. Lastly, it is interesting to note that we found no evidence of kelp remains (*M. pyrifera* or *U. pinnatifida*) in the guts from intertidal sea urchins. In intertidal habitats, *Undaria* is usually found only as young individuals during early autumn but, in the infralittoral fringe, a high wave-exposed area, it could develop a larger thallus (Victoria Alvarez pers. comm.). However, these larger *Undaria* individuals may be not easily accessible for sea urchins due to a high risk of being swept out by the strong waves.

In the kelp forest of *Macrocystis pyrifera*, the gut contents of *P. magellanicus* and field observations indicate a larger tendency to herbivory, with active and passive grazing of kelp and other seaweed species. Laminarian seaweeds are usually a typical food component in numerous species of sea urchins, possibly due to their high abundance, ease of detection, nutritional content, palatability and digestibility (Larson et al. 1980; Anderson and Velimirov 1982; Lauzon-Guay et al. 2006). In the northern hemisphere, grazing of kelp forests by high densities of purple sea urchins is known to affect their structure, prompting a shift from a foliose to a crustose algal-dominated state (barrens) (e.g., Scheibling et al. 1999; Gagnon et al. 2004; Wright et al. 2005). In central Argentine Patagonia, only two sea urchin species inhabit the kelp forest: *P. magellanicus* and *Arbacia dufresnii*, with the latter occurring at low densities in SJG (Epherra et al. 2015). These species seem not to regulate the populations of *M. pyrifera* (Barrales and Lobban 1975). A similar situation has been described in southern Chile, where sea urchins–algae interactions differ from known northern hemisphere patterns and sea urchin overgrazing is rare (Vásquez and Buschmann 1997). Inside the kelp forest, *P. magellanicus* has many food sources and may graze on a high diversity of understory seaweeds, on erect or detached plants of *M. pyrifera* and on drifting algae. Sea urchins may also prefer to feed on the less mobile lower parts of the *Macrocystis* fronds than on the highly mobile *Undaria* thalli, where they can suffer a whiplash effect, as reported for other brown algae like *Fucus* and *Lessonia* (Kiirikki 1996; Perreault et al.

2014; Westermeier et al. 2016). Aggregation on food sources is common in different species of sea urchins (Vadas et al. 1986; Rodríguez and Fariña 2001; Lauzon-Guay and Scheibling 2007). *P. magellanicus* has also been observed crowded on felled senescent kelp fronds during field samplings, especially during the senescence stage (Javier Tolosano, pers. comm.). Grazing over detached *M. pyrifera* by the sea urchins *Tetrapygus niger*, *Loxechinus albus* and *P. magellanicus* has also been observed in Chile (Castilla and Moreno 1982; Contreras and Castilla 1987).

Experimental manipulation of *P. magellanicus* in kelp forests in southern Chile indicates that sea urchins mostly use drift subtidal algae as food (Castilla 1985). Active grazing over kelp plants could vary between seasons of the year, showing different degrees of epibiosis. In this respect, our study was performed during winter, which is usually the period of maximum kelp loses (Barrales and Lobban 1975). Further studies on the contribution of drift algal fragments in the diet of this species and analyses of changes in its palatability at different times of the year are needed. Since *P. magellanicus* exhibits a wide range of feeding strategies, our limited data do not allow venturing about its trophic role in the forest. Possibly, the highly available biomass of other palatable understory seaweeds within the kelp forest may lessen its grazing on *M. pyrifera*. The presence of bryozoan epibionts, which varies throughout the year, may weaken the structural support of the algae and accelerate defoliation, increasing its weight or favoring its rupture, as seen in other kelp systems (Dixon et al. 1981; Scheibling et al. 1999). Under these circumstances, the kelp canopy descends closer to the bottom, which may ultimately facilitate its fragmentation and consumption by *P. magellanicus*. Grazing can also be promoted if animal tissues (e.g., *Membranipora*) are chosen as food. Additional studies on the temporal variations in active and passive grazing under different environmental circumstances and their relation to kelp annual population dynamics including time-integrated stable isotopes analysis should provide valuable insights into the role of kelp grazing in Patagonian coastal ecosystems.

In circalittoral habitats, *P. magellanicus* feeds on detrital items that may come from upper levels and are deposited on the substrate, due to a less agitated mode. The prevalence of sediments and decaying diatoms suggests that the species can feed on biofilms. This is particularly interesting since the species can be found at depths that are below the light compensation depth (100 m within SJG, but can reach 360 m depth) and this could explain the presence of *P. magellanicus* at such depths. The ingestion of diatoms from the sediment surface has been noted in other species of sea urchins, especially in circalittoral zones (Jacob et al. 2003; Michel et al. 2016). In addition, the finding of a relatively high prevalence of ingested *Pseudechinus* spines (> 35%) suggests the presence of cannibalism, scraping over dead sea urchins or ingestion of these along with sediments when scraping on biofilms. Nevertheless, so far, cannibalism has only been reported in laboratory conditions, mainly in response to food limitation or by competitive interference at high densities (Himmelman and Steele 1971; Richardson et al. 2011). The finding of macroalgae in gut contents in these areas devoid of seaweeds also highlights the importance of drift-capture behavior in the species described by Penchaszadeh et al. (2004).

Overall, these results indicate that the potential role of *P. magellanicus* in nearshore habitats of SJG in Patagonia is complex and variable at small (vertical) spatial scales. Since our study had no temporal/sites replication, further studies are needed in order to explore if the observed trophic plasticity may vary at a broader spatial scale or between seasons. Yet, our contribution provided new insights into the feeding ecology of this key species and relevant background information for food web studies. In the intertidal habitats, this species behaves mainly like a general omnivore, but can also act as a mussel bioeroder when consuming epizoic algae and microeuendolithic organisms, and may consume small invertebrates in tidepool cryptic habitats. Inside the *Macrocystis* forest, the macroalgal component in the diet is the most diverse but with prevalence of kelps. At circalittoral soft bottoms, *Pseudechinus* captures drifted algae and behaves like a biofilm feeder. These adaptive strategies regarding trophic plasticity, coupled with a high physiological tolerance, have ecological and evolutionary implications since they may allow the survival of the species during unfavorable times and the occupation of contrasting habitats and may also contribute to explain the wide distribution of this species in southern South America.

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Code availability Not applicable.

Data availability Available upon request.

Declarations

Conflicts of interest No potential conflict of interest was reported by the authors.

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