

Podding of *Paralomis granulosa* (Lithodidae) juveniles inhabiting kelp forests of the Cape Horn Archipelago (Chile)

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ABSTRACT

Subtidal observations along the Cape Horn Archipelago, Chile (CHA) in February 2017 revealed an unusually large aggregation (or pod) of juvenile false king crabs, *Paralomis granulosa* (Hombron and Jacquinot, 1846), in association with kelp forests (*Macrocystis pyrifera* and *Lessonia* spp.). This is the first study to report a dense aggregation of juveniles of this crab, which was observed at Wollaston Island (WI) (~ 10 m). *Paralomis granulosa* was present on half the transects at WI (N=10), with a density of 3.1 ± 9.9 ind. m^{-2} . Photographs from the podding event showed densities of *P. granulosa* ranging from 63 to 367 ind. $plant^{-1}$ (190 ± 133 ind. $plant^{-1}$). Juveniles (32.8 ± 7.3 mm carapace length) were recorded on kelp fronds, holdfasts, kelp stipes, and adjacent rocky bottom of this protected coast. This podding behavior resembles that of other juvenile king crabs in terms of homogeneity in size structure and may be a predator avoidance mechanism. These observations highlight three aspects of this kelp-animal relationship: (i) identification of a previously unknown ecosystem service provided by sub-Antarctic kelp forests to the associated benthic fauna; (ii) the ecological value of kelp as a bioengineering species; and (iii) pods being an important attribute for

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population assessments. Due to the importance of the CHA in the life cycle for this and other species, we suggest the archipelago be incorporated within the recently established Diego Ramírez Island-Drake Passage Marine Park.

KEYWORDS

Diego Ramírez Island-Drake Passage Marine Park, ecological recruitment, king crab ecology, seaweed-animal relationship, sub-Antarctic benthos

INTRODUCTION

Podding is a social aggregation of individuals of a certain age, sex, or size, as previously described for species of marine crustaceans, including the large Chilean king crab (*Lithodes santolla*) (Molina, 1782) (Cárdenas *et al.*, 2007). Podding can have various population effects on exploited lithodid crabs in the sub-Antarctic region due to: i) high parasite load (Roccatagliata and Lovrich, 1999; Cañete *et al.*, 2008; 2017); ii) biased stock assessments (Cárdenas *et al.*, 2007; Cañete *et al.*, 2017); iii) increased risk of predation (Morado *et al.*, 2014); and iv) reduction in optimal settling areas (Cañete *et al.*, 2008; Stevens, 2014).

A previous study described the podding of *L. santolla* around the holdfasts and stipes/sporophylls of giant kelp *Macrocystis pyrifera* (Linnaeus, 1771) C. Agardh, 1820 in a shallow, sandy-rocky embayment of the Magellan Strait, Chile (Cárdenas *et al.*, 2007). However, this behavior has not been reported in other sub-Antarctic king crab species, such as the false king crab *Paralomis granulosa* (Hombron and Jacquinot, 1846).

Despite the economic importance of *P. granulosa* and extensive investigation into its fishery (Hoggarth, 1993; Guzmán *et al.*, 2004; Wyngaard *et al.*, 2016; Almonacid *et al.*, 2018), limited research has been conducted on the early benthic stages and population dynamics of this species (Lovrich and Vinuesa, 1993; 1995; Lovrich, 1997; Tapella and Lovrich, 2006; Almonacid *et al.*, 2018). This lack of research is due in part to the difficult working conditions presented by the remote and restricted geographical range of this species (Lovrich and Tapella, 2014; Friedlander *et al.*, 2018).

The marine ecosystems of the Magellan Region in southern Chile are diverse and possess a unique biogeography; however, these ecosystems have been poorly studied to date (Rozzi *et al.*, 2006). Persistent unknowns about the ecology of the region include the importance of these cold, estuarine, shallow-water habitats as nurseries for commercially valuable species and the interconnectivity between deep and shallow water habitats (Friedlander *et al.*, 2018). Vast unfragmented habitats within the region are in relatively pristine condition, but efforts to maintain this healthy ecological state are challenged by a variety of anthropogenic activities such as benthic fisheries (Pollack *et al.*, 2008; Friedlander *et al.*, 2018; Almonacid *et al.*, 2018).

Our study represents the first observations of dense aggregation behavior by *P. granulosa* juveniles associated with two sub-Antarctic kelp forest species, *M. pyrifera* and *Lessonia* spp. in the Cape Horn Archipelago (CHA), southern Chile, during February 2017. This study brings attention to three aspects of this kelp-animal relationship: (i) the identification of previously unknown ecosystem services provided by sub-Antarctic kelp forests relative to associated benthic fauna in remote, pristine, high latitudes; (ii) the ecological value of kelp as a bioengineering species; and (iii) the importance of considering podding in stock-assessment surveys of king crabs.

MATERIALS AND METHODS

Cape Horn is the southernmost headland of the Tierra del Fuego Archipelago, marking the northern boundary of the Drake Passage, where three great oceans meet (Cunningham *et al.*, 2003). The Cape Horn National Park is the southernmost national

park in the world and was designated a UNESCO Biosphere Reserve in 2005 (Rozzi *et al.*, 2006; Cañete *et al.*, 2017; Friedlander *et al.*, 2018). This park encompasses the entirety of the CHA and is comprised of a series of islands and islets, including the large islands of Wollaston and Hermite. However, the recently established the Diego Ramírez Island-Drake Passage Marine Park does not include the islands and nearshore areas of the archipelago (Diario Oficial, República de Chile, 2019).

In February 2017, an expedition was conducted to the Magellan Region in the extreme south of Chile (Fig. 1a-c). The aim of this expedition, which included the Cape Horn and Diego Ramírez archipelagos, was to conduct a comprehensive, integrated assessment of these marine ecosystems using non-destructive sampling techniques (*e.g.*, visual surveys, video, and photography) (Friedlander *et al.*, 2018). A total of twelve sampling stations were surveyed across five islands (Grevy, Hermite, Herschel, Wollaston, Hornos).

Characterization of the benthos was conducted by scuba divers along two 25-m long transects at each sampling station except for one station at Hermite Island, where only one transect was surveyed. Transects were run parallel to the shoreline, with a target depth of 10 m, depending on the location of the kelp forest. For sessile and mobile invertebrates, including *P. granulosa*, the number of individuals was estimated 1-m on either side of the transect line (50 m²). Subtidal video and photography were conducted opportunistically at Wollaston, Hermite, and Grevy islands to document aggregations of *P. granulosa* (Fig. 1b, Suppl. material 1).

Photographic surveys were conducted to determine the abundance and size structure of *P. granulosa* juveniles in the one large pod observed at Wollaston Island (WI). Ten points were randomly assigned to each photograph, and the benthic cover beneath each point was recorded. Photographs (N = 7) were obtained with a Nikon D800 in an Aquatica housing and a Nikkor 10.5 mm lens.

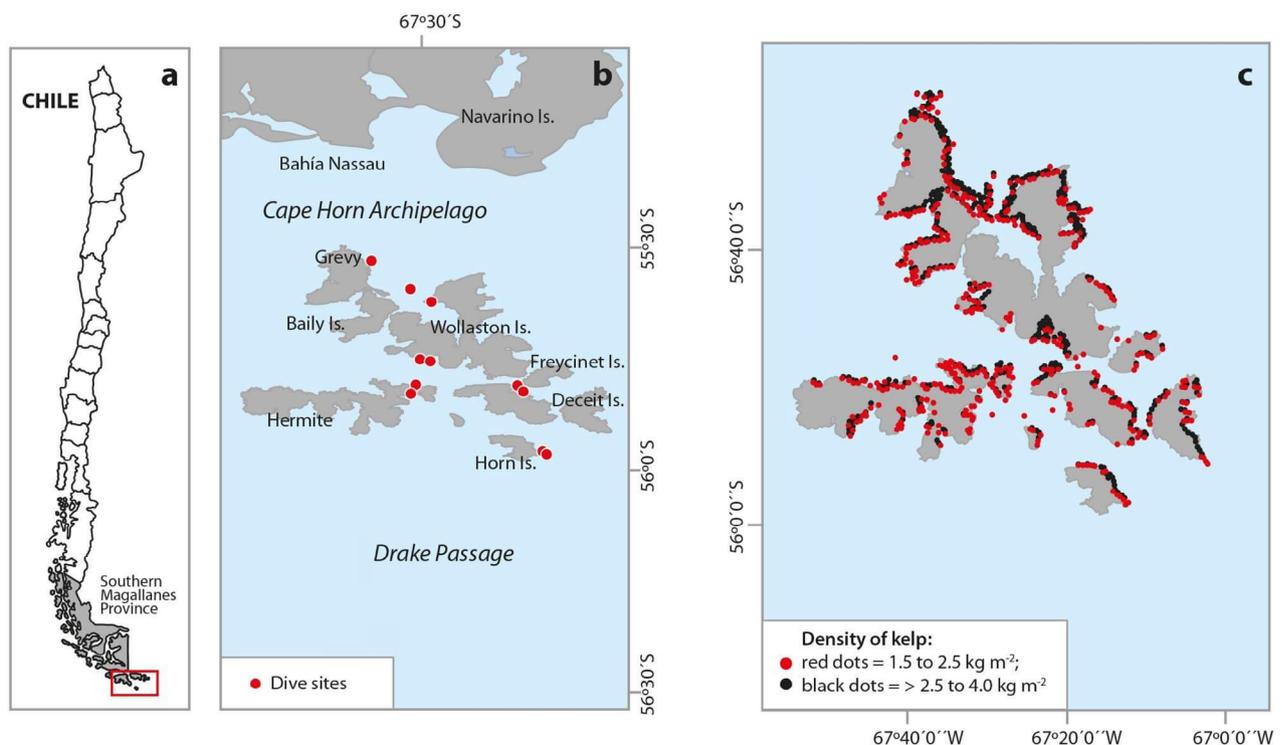


Figure 1. a) Location of Cape Horn Archipelago (CHA), southern Chile; b) sites at Wollaston Island where the photographic survey observed podding in the crustacean *Paralomis granulosa* around two species of sub Antarctic kelp forest (February 2017); red dots show diving sites; c) spatial distribution of abundance of the subtidal kelps *Macrocystis pyrifera* and *Lessonia* spp. around CHA (black dots are just high densities of red dots; 1.5 to 2.5 kg m⁻²; black dots just represent areas where the density of kelp was very high; > 2.5 kg m⁻²). Floating canopy of giant kelp was observed using the Landsat 8 Operational Land Imager (OLI) multispectral sensor. Kelp canopy biomass was $\sim 2.5 \pm 1.3$ kg m⁻². Densities of *M. pyrifera* were nearly three times higher than densities of *Lessonia* spp. (Friedlander *et al.*, 2018).

The *P. granulosa* podding event was used to estimate the abundance and size of juveniles, as well as their position on each section of the kelp plant. Abundance and size structure analyses were carried out using the Coral Point Count software with Excel extensions (CPCe 4.1, Kohler and Gill, 2006; Ferrari et al., 2018). A comparative sizing scale for the photographed *P. granulosa* juveniles was established by recording the diameters of fresh *M. pyrifera* stipes of plants stranded in the intertidal fringe of Navarino Island, Chile (Fig. 1b). A total of 30 stipes of equal number of plants were examined (mean diameter = 1.0 ± 0.2 cm; $N = 30$). Due to the presence of three species of the genus *Lessonia* in southern Chile (Searles, 1978; Santelices and Meneses, 2000; Rosenfeld et al., 2019), we identified all individuals of this genus as *Lessonia* spp. due to previous reports in the study area. Due to the high abundance of *P. granulosa* juveniles on some kelp plants, an area of 0.1 m^2 was established in the core of each photograph where all juveniles of *P. granulosa* were highlighted to determine their size. This also reduced errors relative to the angle of the photograph. The antero-posterior length of the carapace and the number of juveniles were determined for each photograph.

RESULTS

A total of twenty-three benthic transects ($1,150 \text{ m}^2$) were conducted at twelve different stations within the CHA (Tab. 1). *Paralomis granulosa* was present on

only seven (30.4 %) transects and at only five stations (41.7 %). The one transect at WI where podding of *P. granulosa* was observed had a density of 31.2 ind. m^{-2} . *Paralomis granulosa* was present on half of the transects conducted at WI ($N=10$), with an overall mean density at WI of $3.1 \pm 9.9 \text{ ind m}^{-2}$. Both transects conducted at Grevy Island had *P. granulosa* present, but the densities were low ($0.05 \pm 0.01 \text{ ind. m}^{-2}$). *Paralomis granulosa* was not recorded at any of the other islands surveyed during the expedition.

Photographs from the podding event at WI show densities of *P. granulosa* varying between 63 and 367 ind. plant^{-1} (mean abundance = $190 \pm 133 \text{ ind. plant}^{-1}$). Mean carapace length averaged $32.8 \pm 7.3 \text{ mm}$, with a coefficient of variation of 22.3 % (Fig. 2a–f). This dense aggregation extended along the south side of WI and was protected from the strong westerly winds. In this area, *P. granulosa* was observed in association with both *M. pyrifera* (Fig. 2a–c, e, f) and *Lessonia* spp. (Fig. 2d). Podding was denser on the single *Lessonia* plant photographed ($367 \text{ ind. plant}^{-1}$; $N = 1$) compared to *M. pyrifera* ($161 \pm 104 \text{ ind. plant}^{-1}$; $N = 6$). Combined, podding densities varied between 63 and $367 \text{ ind. plant}^{-1}$ (mean abundance = $190 \pm 123 \text{ ind. plant}^{-1}$). Juveniles were mainly recorded on kelp fronds and stipes and, to a lesser extent, on the rocky bottom and holdfasts (Tab. 2; Fig. 2a–d). Of note, some *P. granulosa* were found on the upper parts of *M. pyrifera*, reaching heights of 2 m above the bottom (Fig. 2c). Two adult king crabs (*Lithodes santolla*) were also recorded on the fronds (Fig. 2e, f).

Table 1. Densities of *Paralomis granulosa* at islands and stations in the Cape Horn Archipelago, southern Chile. Values are means per station with one standard deviation of the mean in parentheses. Station numbers shown in Fig. 1.

Island	Station	Depth (m)	Latitude	Longitude	Number/ m^2
Hornos	3	12	-55.961	-67.224	0
Hornos	4	8	-55.965	-67.214	0
Herschel	9	10	-55.812	-67.285	0
Herschel	10	15	-55.826	-67.270	0
Hermite	11	10	-55.810	-67.515	0
Hermite	12	12	-55.834	-67.522	0
Wollaston	13	9	-55.759	-67.485	15.60 (22.06)
Wollaston	14	9	-55.750	-67.479	0.01 (0.01)
Wollaston	15	9	-55.750	-67.508	0.07 (0.10)
Wollaston	16	15	-55.590	-67.525	0.02 (<0.01)
Wollaston	17	11	-55.625	-67.481	0
Grevy	18	11	-55.530	-67.606	0.05 (0.01)

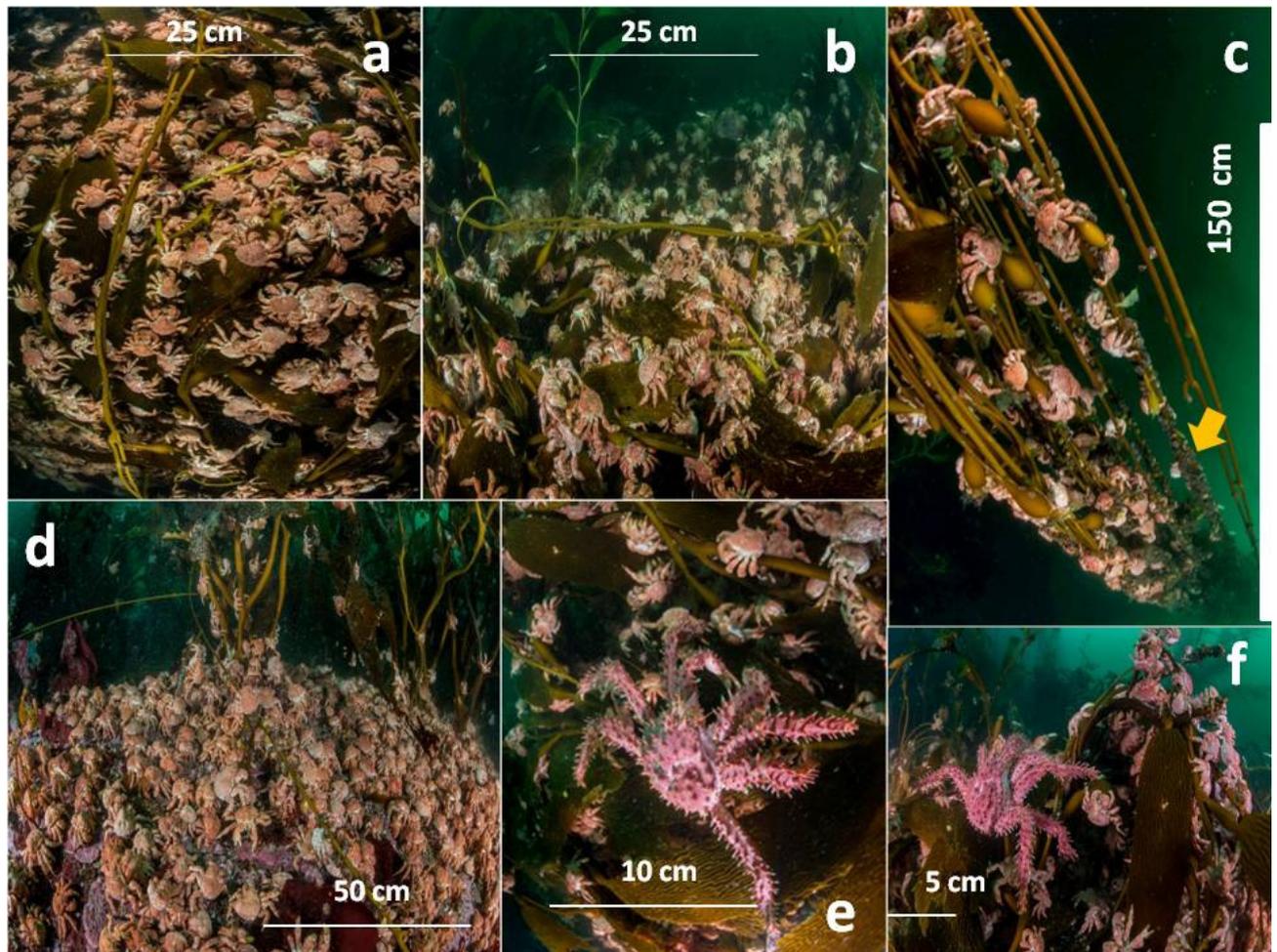


Figure 2. Podding of *Paralomis granulosa* (Lithodidae) juveniles on sub-Antarctic kelp: (a–c, e, f) *Macrocystis pyrifera*; (d) *Lessonia* spp. All photographs were taken at the Wollaston Island, Cape Horn Archipelago, south of Chile (February 2017); (c) yellow arrow shows fouled plant of *M. pyrifera* with the bivalve *Gaimardia trapesina*, a possible prey of *P. granulosa*; (e, f) large spiny crustaceans seen in each photo are adult king crab *Lithodes santolla*.

Table 2. Quantitative data regarding the relationship of two sub-Antarctic kelp species and recruits of the false king crab *Paralomis granulosa* during a survey at Wollaston Island, Cape Horn Archipelago, southern Chile (date: February 9, 2017; 10 m depth). All data were obtained from subtidal photography (N = 7 photos) on two kelp forest species. Some photographs of podding (columns 1–7) are showed in the Fig. 2a–e. Mp = *Macrocystis pyrifera*; Ls = *Lessonia* spp.; N = No; Y = Yes; * = values in parentheses indicate standard deviation.

Parameters	Photos recording the podding of <i>P. granulosa</i> recruits						
	1	2	3	4	5	6	7
Kelp taxa	Mp	Mp	Mp	Ls + rock	Mp	Mp	Mp
Total abundance of <i>P. granulosa</i> recruits/photo	234	335	85	367	139	109	63
Mean abundance of <i>P. granulosa</i> recruits/0.1 m ²	34	135	22	57	45	27	23
Mean size of <i>P. granulosa</i> juveniles (mm, cephalothoracic length) *	33.8 (32)	32.5 (32)	43.2 (5)	39.9 (32)	31.3 (20)	21.1 (15)	27.9 (8)
Position of juveniles along plant	Fronds	Fronds	Stipes	Stipes, holdfast and rock dominated by Corallinaceae algae	Fronds and stipes	Fronds	Fronds and stipes
<i>Lithodes santolla</i> adults	0	0	0	0	0	1	1
Presence of <i>Gaimardia trapesina</i> (Bivalvia)	N	N	Y	N	N	N	N

DISCUSSION

Kelp communities are considered one of the most diverse marine ecosystems on earth, providing abundant ecosystem services to humans (Dayton, 1985; Graham *et al.*, 2007; Smale *et al.*, 2013; Schiel and Foster, 2015). Kelp plants are ecosystem engineers that create complex habitats, which support a myriad of species with associated behaviors (Steneck and Johnson, 2014; Teagle *et al.*, 2017). The results of this study highlight the importance of plant/animal interactions during the early life of the sub-Antarctic Chilean false king crab *P. granulosa*, with massive podding of this species associated with kelp forests. Podding refers to structurally dense and socially organized groups of organisms in aggregations. In these pods, all individuals are similar in size and are in physical contact with one another (Stone *et al.*, 1993; Dew, 2010). Our observations are the first report of podding in the Chilean false king crab in sub-Antarctic kelp forests.

Kelp forests were the dominant nearshore ecosystem in the study area, with the giant kelp *M. pyrifera* being the most conspicuous component of this community. The brown seaweed *Lessonia* spp. forms dense understories within the *Macrocystis* canopy. Kelp canopy biomass was dense at the CHA with a mean canopy biomass density of $2.51 \pm 1.27 \text{ kg m}^{-2}$ (Friedlander *et al.*, 2018). Kelp extent was greater on the eastern and northern coasts of the CHA, likely due to being sheltered from the prevailing wind and swell that originate from the west (Fig. 1c). Podding was observed in the subtidal protected zone extended along the southwest coast of WI (Fig. 1b–c), where high densities of kelp were reported by Friedlander *et al.* (2018). Protected coasts (channels, embayments, and fjords) appear to favor podding in sub-Antarctic king crabs (Cárdenas *et al.*, 2007).

Podding behavior is probably a generalized characteristic of lithodids such as in *Paralithodes* J.F. Brandt, 1848 (Loher and Armstrong, 2000; Dew, 2010) and *L. santolla* (see Cárdenas *et al.*, 2007). This behavior has been well documented for other crustaceans of the family Majidae, including *Chionoecetes bairdi* Rathbun, 1924 (Stevens *et al.* 1994; Zhou and Shirley, 1997), *Chionoecetes opilio* O. Fabricius, 1788 (Comeau *et al.*, 1998), *Hyas lyratus*

Dana, 1851 (Stevens *et al.*, 1992), and *Maja squinado* (Herbst, 1788) (Sampedro and González-Gurriarán, 2004). Aggregations of *M. squinado* were reported by Carlisle (1957) to facilitate molting and mating, and Stevcic (1971) reported that such aggregations consisted primarily of females. Similar aggregations of mostly female *Loxorhynchus grandis* Stimpson, 1857 were reported by Hanauer (1988) and Culver (1991).

The term “podding” has been used for many species and behaviors, but there are important distinctions between different types of behavior. Podding has been used primarily to describe aggregations of juvenile or sub-adult king crabs of the genus *Paralithodes* (see Powell and Nickerson, 1965; Dew, 1990), and has been ascribed primarily to protection from predation for juveniles or to facilitate reproduction for subadults. Although the term was also applied to lyre crabs *H. lyratus* by Stevens *et al.* (1992), that behavior was an aggregation of mating individuals. Intense aggregations of hundreds of thousands of *C. bairdi*, consisting almost exclusively of females, was determined to be a mechanism for facilitating massive larval hatching (Stevens *et al.*, 2000), and are coordinated with onshore tidal current patterns (Stevens, 2003).

Although “mounds” (*sensu* Stevens *et al.*, 2000; Stevens, 2014) of crabs may look similar to pods, the structure, behavior, and characteristics of such aggregations differ greatly from that of king crab pods. All of these exist on a continuum of aggregative behavior ranging from: (1) loosely associated groupings of crabs at higher-than-average density ($>1/\text{m}^2$) but without contact; to (2) high density ($>10/\text{m}^2$) groups of crabs in contact in a single layer, to (3) extremely high density ($>100/\text{m}^2$) groups formed into a 3-dimensional stack, and (4) high densities of such stacks in a small area (as in *C. bairdi*). Possible explanations for podding behavior include: (i) protection during moulting, (ii) finding mates, (iii) aid in food capture, and (iv) protection against predation (Powell and Nickerson, 1965; Gardner, 1999). These prior studies further indicate that pods can vary in form and structure depending on the species, time of year, geographical area, as well as individual traits (*e.g.*, maturity stage, inter-moult stage). A protective function has also been suggested for juvenile aggregations of the spiny lobster *Jasus edwardsii* (Hutton, 1875) (Butler *et al.*, 1999).

Similarly, podding with high abundance of *L. santolla* juveniles was reported in protected channels, embayments, sounds, and fjords along the west Magellan Coast (Cañete *et al.*, 2017). High rates of infestation by the isopod *Eremitione tuberculata* on *L. santolla* were noted in these podding events. Similarly, aggregations of *P. granulosa* juveniles could favor the epibiosis by caprellid amphipods, which has been described around Navarino Island (Medina *et al.*, 2017).

Our observations in the study area indicate that podding of juveniles may be induced by high densities of epiphytic invertebrates on the stipes and fronds of *M. pyrifera*, which are prey for *P. granulosa*. For example, the bivalve *Gaimardia trapesina* (Lamarck, 1819) comprised 74.2 % of benthic taxa abundance at CHA, while the sea snail *Tegula atra* (Lesson, 1830) was also abundant in these kelp forests (Friedlander *et al.*, 2018). *Paralomis granulosa* juveniles likely feed on the small spat of this brooding bivalve based on their buccal appendage size and an abundance of this bivalve observed on the fronds and stipes of both kelp taxa (Fig. 2c). Prior research, however, does not report evidence of *G. trapesina* shell debris in the diet of *P. granulosa* juveniles, although molluscs were frequently observed in the diet of *P. granulosa* collected from the Beagle Channel off the Argentine coast (Comoglio and Amin, 1999).

The podding behavior shown by *P. granulosa* resembles that reported for the Alaskan red crab *Paralithodes camtschaticus* (Tilesius, 1815) (Zhou and Shirley, 1997) and Chilean king crab (*L. santolla*) in terms of size of juveniles, which ranged between 21- and 43-mm CL and may represent predation avoidance. Pods of *L. santolla* are comprised of individuals with a similar carapace length (< 50 mm; Cárdenas *et al.*, 2007; Cañete *et al.*, 2008; 2017) (Tab. 2). Another aspect of the podding of *P. granulosa* is the homogeneity in the size structure of individuals.

Podding in association with kelp forests may represent a key step in the life cycle of the false king crab and therefore likely provides an important benefit to maintaining the productivity of this valuable fisheries species. As a result, the life cycle of *P. granulosa* could be adversely affected by alterations to kelp communities in the Magellan Region, making the observations presented here of direct interest to

the management of both the crab fishery and the kelp harvesting industry (Cárdenas *et al.*, 2007; Almonacid *et al.*, 2018). We thus recommend protective measures be taken for the region, especially as they may be important for the sustainability of the fishery for the false king crab around the Beagle Channel and throughout the CHA.

Future research is needed to improve abundance estimates for the non-exploited phase of the false king crab population in southern Chile. Such estimates would be useful in determining the conservation status of *P. granulosa*, as well as for considering sustainability in fishery regulations (Subpesca, 2018). Given that the patchy nature of pod aggregations could introduce bias into population stock assessments, podding behavior needs to be included as a potentially crucial attribute of the population. It has been shown that highly predictable aggregations of some fisheries species can lead to hyperstable catch rates despite declining stock size (Erisman *et al.*, 2011; Alós *et al.*, 2019). Gaining better understanding of the spatial and temporal variability of pods requires long-term monitoring and efforts to protect *P. granulosa* juveniles and their associated habitats.

This study is one of many to highlight the importance of kelp forests for local biodiversity and ecosystem functioning (Santelices and Ojeda, 1984; Costanza *et al.*, 1997; Almanza *et al.*, 2012; Smale *et al.*, 2013; Rosenfeld *et al.*, 2014; Steneck and Johnson, 2014). This fact emphasizes the need for kelp forests to be given the highest conservation priority, particularly in sub-Antarctic habitats. Coldwater species that are large and have low fecundity and slow growth rates, such as king crabs, are at an elevated risk of overexploitation and extinction (Stevens, 2014; Kindsvater *et al.*, 2016). *Paralomis granulosa* juveniles with a carapace length < 50 mm are roughly 5 years of age (Lovrich and Vinuesa, 1995). Consequently, the protection of kelp forests, such as those observed along the CHA, are essential for effective marine conservation and the sustainability of sub-Antarctic fishing activities. The CHA lies at the southern end of South America, making the protection of this marine protected area of high priority to guarantee the connectivity of *P. granulosa* larvae and juveniles for Chilean and Argentinian exploited populations.

The fishing grounds of *P. granulosa* along the southern Chilean coast include three important protected areas (*i.e.*, Cape Horn Biosphere Reserve, Cape Horn National Park, and the recently established Diego Ramírez-Drake Passage Marine Park) (Diario Oficial de la República de Chile, 2018) (Cañete et al., 2017). However, only land biodiversity is included in the conservation goals of the Cape Horn Biosphere Reserve and Cape Horn National Park. Based on the present results, we suggest that the entire CHA be included within the recently established Diego Ramírez Island-Drake Passage Marine Park due to their importance during early life phase for valuable, sub-Antarctic benthic resources such as the false king crab (Vinuesa et al., 2013; Almonacid et al., 2018; this study).

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SUPPLEMENTARY MATERIAL

Video S1. Video on Cape Horn Archipelago produced by National Geographic, Pristine Seas Program: [youtube.com/watch?v=0liAgjzVP14](https://www.youtube.com/watch?v=0liAgjzVP14). In Spanish: “Cabo de Hornos: el mar del fin del mundo”. Duration: 44:40 minutes; at minute 35 the podding in *Paralomis granulosa* is shown.

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