Research Article

Biology, distribution, and abundance of *Allopetrolisthes punctatus* (Guérin, 1835) (Decapoda, Anomura, Porcellanidae), in the rocky subtidal of Chome, central Chile

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ABSTRACT. The porcellanid crabs are diverse and abundant species inhabiting the intertidal and subtidal rocky substrate. One particular species is *Allopetrolisthes punctatus*, a medium-sized crab, poorly studied but strikingly abundant in some places of Chile. Near Chome (central Chile) large aggregations have been reported by local fishermen. A direct population assessment with semi-autonomous scuba diving was performed to evaluate stock structure, distribution, and abundance. A monthly monitoring was established to analyze the temporal variability of biological traits during a one-year time period. Dense crab aggregations were observed over the naked unprotected rocky substrate, with corporal size and sexual proportion spatially segregated. *Allopetrolisthes punctatus* showed a relatively high fecundity (164-8,741 eggs) and uninterrupted yearly spawning, which seems to favor the quick and successful settlement for this species in Chome.

Keywords: Allopetrolisthes punctatus, Porcellanidae, stock structure, intertidal, subtidal, aggregations, settlement.

INTRODUCTION

Porcellanid crabs (Decapoda, Anomura, Porcellanidae) are the most common and abundant decapod crustaceans in rocky intertidal and subtidal habitats of the world oceans (Emparanza, 2007). Most of the species live scattered between protected places under boulders and crevices rocks. One species, however, is characterized by an atypical behavior and settlement strategy: Allopetrolisthes punctatus (Guérin, 1835) is a medium-size crab that lives in dense aggregations on a naked rocks in open-spaced unprotected zones, never occupied by other porcellanid species (Viviani et al., 2010). The species is distributed from the Bay of Ancon, Peru, to the northern area of the Arauco Gulf, Chile (Haig, 1960; Retamal, 1994). Information about its population and community aspects is scarce; several studies reported as a sparsely abundant decapod on holdfast of the macroalgae Lessonia nigrescens and Durvillea antarctica (Santelices et al., 1980; Cancino & Santelices, 1984) and over mussel matrices (Perumytilus purpuratus) (Prado & Castilla, 2006). In the rocky subtidal near to Coquimbo (northern Chile), large aggregations of have been described as hordes

The southernmost population of *A. punctatus* is found in the rocky subtidal near Chome, a small fishing cove in central Chile. Here, local fishermen reported a large aggregation that appears to develop a gregarious behavior similar to that observed in Coquimbo by Viviani *et al.* (2010). The present study aimed to provide the first quantitative measures of biological population traits for this species in Chome Cove with the purpose to identify endogenous factors that might have favored the successful settlement of this porcellanid crab in the study area.

MATERIALS AND METHODS

Study area and field work

The *A. punctatus* stock inhabiting the subtidal near Chome fishing cove, located between Turtle Islet and Las Chilcas (Fig. 1), was studied between November 2014 and February 2015. This area is dominated by plane hard bottoms, boulders, cracks, and a circuit of

concentrated on naked rocks, evidencing a unique settlement strategy within Porcellanidae (Viviani *et al.*, 2010).

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small islets with steep slopes. Since February 2015 until January 2016, a monthly sampling was maintained in the Alambre Islet sector. This place was chosen due to the continuous presence of individuals of both sexes and a wide size range (F. Santa Cruz, *pers. comm.*), which allowed us to evaluate the temporal stock dynamics.

At the beginning of the study period (November 2014), we identify the effective coverage area (ECA) with the presence of A. punctatus. A visual and filmed inspection of the bottom was performed by two scuba divers equipped with a surface-supplied compressed air system (Blatteau et al., 2015) in order to identify the ECA. The ECA covered the entire rocky surface, where places without A. punctatus were sandy bottoms. Considering the complex geography, difficult access for the boat and diver, and the large surface of the study area, the ECA was sampled weekly at six sites (Fig. 1). At each site, a net bag (locally called "chinguillo", a popular instrument used to extract different benthic resources) was filled by the diver, and a sample of 5 kg of porcellanid crabs was taken for biological analysis. For each specimen, the carapace length (CL, from the rostrum to abdomen, in mm), weight (in grams) and sex were measured. Ovigerous females were fixed in formalin (10%) for subsequent fecundity analysis.

Data analysis

Ovigerous females were classified in four egg development stages (S), based on the color and shape of the egg mass, and the ocular spot shape of the eggs (modified from Hernáez & Palma, 2003). According this, we used Stage I (S1) for yellow-orange eggs, uniform color, without visible ocular spot, Stage II (S2) for light brown eggs with punctiform ocular spot, Stage III (S3) for dark brown eggs with lenticular-shape ocular spot, and Stage IV (S4) for spawned females with few eggs and large brown setae in pleopods.

The carapace length-weight relationship for males and females was estimated using the power function W = acL^b, where W = weight and CL = carapace length (Rickter, 1973). Parameters *a* and *b* were estimated through a non-linear regression curve fixed by least squares. The type of weight increase was considered as isometric (b = 3), positively allometric (b > 3) and negatively allometric (b < 3) (Hartnoll, 1982). For parameter *b*, a probability density function was used to examine significant differences between the slopes of both sexes. Finally, a chi-square analysis was applied to compare sex ratios between months (Zar, 1999).

The fecundity was analyzed counting the eggs (independent of the embryonic developmental stage) carried by 36 ovigerous females of different sizes. The complete egg mass was weighed with a precision electronic scale (0.001 g). A single subsample of 0.5 g

was deposited in a Petri dish with water, and the eggs were counted using a Zeiss IV B stereoscope. The total egg number for each ovigerous female was estimated through the extrapolation of the egg number of the weighed subsample to the weight of the entire egg mass. The fecundity-length relationship was analyzed using the exponential function $F = a \exp^{(b*L)}$, where F = fecundity and CL= carapace length (Josileen, 2013).

Two methods were used to evaluate the stock abundance in each sampling site. First, we used an indirect approach based on the catch per unit effort (CPUE) estimation. CPUE was expressed as kg of crabs per minute of diving (kg min⁻¹). Second, we used a direct approach based on the crab density estimation: a one square meter quadrant was located by one diver on the bottom in each sampling site, and all individuals within the quadrant were collected in a net bag. The net bag content was weighed aboard the boat by a hanging weighing scale. Finally, depth (m), wave exposure (low, medium and high) and presence of macroalgae (low and high) were registered in each sampling site.

RESULTS

Size structure

The carapace length of males (n = 801) and females (n = 801)= 928) ranged from 5.0 to 41.6 mm and 9.3 to 41.3 mm respectively. Both sexes showed a bimodal size structure, with the first mode around 21 mm CL and the second mode around 31 mm CL (Fig. 2). Large-sized males (mode of 38 mm CL) were collected in Tortuga Islet, whereas virtually all sizes were equally represented in Las Ventanas, Alambre, Cullinto, and Lobo Negro sites. In Las Chilcas, a well-marked mode of around 30 mm CL was observed. Males were predominant in Tortuga Islet (78%) and in a lesser proportion in Las Ventanas (59%). In the islet circuit of Alambre, Cullinto, Lobo Negro and Las Chilcas, females predominated with 76%, 61%, 60% and 63% respectively (Fig. 3). The length-weight relationship was significantly different between sexes (P < 0.005), with positive allometric growth for males (b = 3.38) and negative allometric growth for females (b = 2.67) (Fig. 4).

Fecundity

The carapace length of ovigerous females ranged from 16.6 to 36.9 mm. The fecundity-length relationship was best represented by the exponential model with a fitness level up to 89%. Fecundity increased exponentially with female size. The smallest female (16.6 mm CL) carried 164 eggs while the largest one produced 8,741 eggs (Fig. 5).



Figure 1. Study area with the six sampling sites in Chome Cove, central Chile.



Figure 2. Size-frequency distribution of *Allopetrolisthes punctatus* from Chome Cove rocky subtidal.

Abundance

Highest CPUE values were estimated in Alambre Islet, with 25.6 kg min⁻¹. From this site, the CPUE show a decreasing pattern towards northern and southern of the study area boundary, reaching minimum values of 9.0 and 9.3 kg min⁻¹ in Tortuga Islet and Las Chilcas, respectively (Table 1). Direct evaluation values confirmed the high CPUE estimated in Alambre Islet, with the highest value of density of all sampling sites (26 kg m⁻²). The CPUE values were influenced by the topographic characteristics, wave exposure level, depth, and presence of patches of macroalgae at each site. These conditions affected also the swimming capacities of the diver during the catch process of the crabs; however, the estimates from both methods show very similar values (see Table 2 for more details).

Monthly monitoring

The monthly sex ratio showed a dominance of females throughout the year (ranging from 49.4 to 78.5%; Fig. 6) with a significantly higher proportion than males ($X^2 = 71.72$, P < 0.005). A high proportion of females



Figure 3. Size-frequency distribution of *Allopetrolisthes punctatus* males (black) and females (gray) from each sampling sites in Chome Cove, central Chile. Sexual proportion (male:female) and length mode (male-female) are indicated within each histogram.



Figure 4. The length-weight relationship for males and females of *Allopetrolisthes punctatus* from Chome Cove rocky subtidal, central Chile.

carrying eggs in Stage 1 were encountered during all months, and the percentage tended to increase towards winter (April and May) and remained around 50% during the rest of the year. Reproductive stage S2, S3, and S4 reached its highest values (up to 50%) during summer months, especially in February. Despite this summer peak, females in S4 were present throughout the year, except in July (Fig. 7). The monthly size structure showed a progression of the average size from 19



Figure 5. Fecundity-length relationship of *Allopetrolisthes punctatus* in Chome Cove rocky subtidal, central Chile.

mm in November 2014 to 22 mm in March 2015 and decreases to 18 mm in July 2015. After September 2015, average monthly size increased to a maximum of 23 mm in January 2016 (Fig. 8).

DISCUSSION

From some sporadic samplings performed during the year 2011 in San Vicente Bay (close to Chome fishing cove), huge aggregations of *A. punctatus* were for the

Table 1. Estimates of relative abundance (CPUE) and density (kg m⁻²) of *Allopetrolisthes punctatus* at the sampling sites in the rocky subtidal of Chome Cove, during November 2014. SD: standard deviation.

Site	$CPUE \pm SD$	Density $(k \alpha m^{-2})$
	(kg mm)	(kg m)
Tortuga Islet	9.0 ± 3.5	21.5
Las Ventanas	11.7 ± 4.5	20.5
Alambre Islet	25.6 ± 10.4	26.0
Cullinto Islet	11.6 ± 3.3	13.0
Lobo Negro	14.0 ± 4.2	19.0
Las Chilcas	9.3 ± 2.9	11.5

Table 2. Characteristics of each sampling site of Allopetrolisthes punctatus in the rocky subtidal of Chome Cove.

Site	Description	
Tortuga Islet	A site with the greatest water depth within the study area (10-13 m) and high wave exposure, causing considerable difficulties for the diver immersion.	
Las Ventanas	Site of great water depth (12 m), medium waves exposition that did not hinder diving activities. Aggregations of <i>A. punctatus</i> were more sparse and scattered	
Alambre Islet	A site with 2-3 m depth. Presence of vertical walls and low waves exposition that favored a fast extraction of specimens by the diver.	
Cullinto Islet	A site with high waves exposition and of greater water depth (9 m). Both factors complicated diving activities.	
Lobo Negro	A site with 5-6 m depth and low wave exposition. Aggregations of <i>A</i> . <i>punctatus</i> were less dense and more dispersed.	
Las Chilcas	A site with low wave exposure. Aggregations of <i>A. punctatus</i> in shallow water (2-3 m), but a high density of macroalgae meadows strongly hinders diving activities.	



Figure 6. The male-female proportion of *Allopetrolisthes punctatus* in Chome Cove, between November 2014 and January 2016.

first time observed. Since then, the coverage and visual density of the aggregations observed by the local fishermen have been increasing quickly (M. Retamal, *pers. comm.*). The present study provides the first evaluation of the population structure of these aggregations and we proceed to describe the main factors that have favored the successful settlement of the species near Chome.

Allopetrolisthes punctatus has been recorded as trophic item of bony fishes as Semicossyphus maculatus in northern Chile (Fuentes, 1981), cartilaginous fishes as Schroederichthys chilensis (Fariña & Ojeda, 1993), birds as the sea-side cinclodes Cinclodes nigrofumosus (Sabat et al., 2003) and sea-gull Larus dominicanus (observed by us, especially in places with high wave exposure where crabs are displaced towards the surface being captured by the birds), reptiles as the lizard Microlophus atacamensis in rocky subtidal off Atacama Desert (Farina et al., 2008), and mammals as the sea otter Lutra felina (Ebensperger & Botto-Magan, 1997; Medina-Vogel et al., 2004). Despite the presence of several of these predators in Chome Cove, they seem to



Figure 7. The proportion of sexual maturity stages (SMS) of female *Allopetrolisthes punctatus* in Chome Cove, between November 2014 and January 2016.

exert no significant predation pressure on *A. punctatus* population. This may be related to the fact that *A. punctatus* reduces predation by living in large aggregations and through active defense using the extraordinarily large-sized chelipeds (Viviani *et al.*, 2010).

The analyzed aggregations showed well-marked spatial sex segregation. Males dominated in Tortuga Islet, where they adhere to rocks under strong wave exposure conditions taking advantage of their large size and physical resistance (Table 2). The center of the study area (Cullinto and Alambre islets) showed crab individuals of all sizes and a higher proportion of females. Here, it was possible to obtain a large number of megalopae (not analyzed in this work), which were associated with the adult chelipeds, confirming similar observations reported by Viviani et al. (2010). The protected geographic Islet location and shallow water conditions observed in Cullinto and Alambre islets offer a suitable habitat for the settlement of megalopae. We hypothesize that both sites represent a breeding area for the A. punctatus population, where parental care of megalopae and juveniles occurs. The parental care is a relevant aspect of the Porcellanidae species settlement. Generally, the megalopae hide directly beneath conspecific adults, which is advantageous for the proper habitat selection and settlement success (Jensen, 1991).

Differential growth strategies were found between sexes. Males had a positive allometric growth with body weight increases faster than the CL, due to the development of the large, strong and heavy chelipeds,



Figure 8. Boxplot of monthly carapace length for combined sexes of *Allopetrolisthes punctatus* from Alambre Islet, central Chile, between November 2014 and January 2016.

essential for the territorial defense purposes. On the other hand, females showed a negative isometric growth, probably due to the reduction of their corporal development and the re-allocation of the energy toward reproduction processes. These differential lengthweight relationships indicate a sexual dimorphism for this species, which is common in many decapods including several species of porcellanid crabs (Miranda & Mantelatto, 2010; Baeza & Asorey, 2012).

The number of larval stages and the duration of the pelagic phase are key aspects of the survival and settlement success of decapods. A long duration enhances the risk of being eaten or transported out of suitable habitat (Anger, 2001, 2006). Among decapods, some groups have numerous and prolonged stages that can remain for months and years in the pelagic environment (Jeffs et al., 2005). Porcellanid crabs, however, present a relatively short larval development, with two pelagic stages (zoeas I and II) (Vela & González-Gordillo, 2016). Moreover, the duration of these two planktonic stages is relatively short ranging from 11 days in Petrolisthes unilobatus (Fujita et al., 2002) to 30 days in Pachycheles stevensii (Konishi, 1987). The congeneric species Allopetrolisthes angulosus completed the zoeal development on average in 23.2 days (Wehrtmann et al., 1996), while the zoeal development of Petrolisthes laevigatus, another porcellanid crab from Chile, lasted 39.7 and 21.5 days at 13 and 20°C, respectively (Mascetti & Wehrtmann, 1996). The few number of zoeal stages and the relatively short duration of the planktonic phase favors larval survival due to the reduced time of being exposed to predators in the planktonic environment. Furthermore, the megalopae settle among adult individuals (Viviani

et al., 2010; Retamal & Santa Cruz, in press), which probably increases their survival probabilities.

The monthly monitoring in Alambre Islet allowed evaluating the temporal variability of the population parameters of the *A. punctatus* in Chome Cove. With the exception of July, spawned females (S4) were found in all months, which suggests a continuous spawning throughout the year. Despite other porcellanid species in Chile show a seasonal reproduction pattern (*Petrolisthes laevigatus;* Lardies *et al.*, 2004), our results are consistent with those for *A. spinifrons*, where the proportion of females carrying embryos close to hatching remained similar throughout the year (Baeza *et al.*, 2001).

The smallest ovigerous females measured 16.6 mm CL, which differs from the 21.9 mm reported by Antezana et al. (1965) for A. punctatus, but is a relatively large size when compared to other porcellanid crab species: In A. angulosus the smallest ovigerous female measured 6.0 mm CL, in A. spinifrons 7.6 mm CL, in L. patagonicus 7.0 mm CL, in P. granulosus 4.7 mm CL, and in P. tuberculatus 8.8 mm (Hernáez & Palma, 2003). On the other hand, the maximum fecundity of 8,741 eggs of A. punctatus estimated in our analyzes was within the fecundity range of 540 and 16,380 eggs indicated by Antezana et al. (1965) for A. punctatus in Las Cruces (Valparaíso). The substantially higher maximum fecundity of females analyzed by Antezana et al. (1965) may be related to latitudinal differences (Hernáez, 2001). The fecundity results reveal that A. punctatus has a higher maximum fecundity compared to other porcellanid crab species, such as A. angulosus (1,301 eggs), A. spinifrons (5,661 eggs), Liopetrolisthes patagonicus (1,247 eggs), Petrolisthes granulosus (225 eggs), P. tuberculatus (537 eggs) and P. laevigatus (1,141 eggs) (Lardies & Wehrtmann, 1996; Baeza et al., 2001). These values indicate the high reproductive potential of A. punctatus among the porcellanids (Hernáez & Palma, 2003), being one of the largest species of the American Porcellanidae (Haig, 1960; Viviani et al., 2010).

The aggregations of *A. punctatus* have been described as real hordes of individuals on the rocky bottom (Viviani *et al.*, 2010). A similar situation was observed in Chome Cove, where along the entire study area (~3.5 km) dense aggregations were found, occupying unprotected rocky substrates. Both indirect and direct methods of abundance estimation used supported these observations. The CPUE showed values between 9.0 and 25.6 kg per min of diving, while densities varied between 11.5 and 26.0 kg m⁻². These values are much higher than those reported for other porcellanid species: *e.g., Petrolisthes angulosus*, the most abundant anomuran crab species in the rocky intertidal of northern Chile, has a density around 0.756

kg m⁻² (Emparanza, 2007). These high densities and the aggregation pattern observed on the naked rocky substrate of Chome confirm and validate the unique settlement strategy described among the porcellanids (Viviani *et al.*, 2010) and extend it to the southernmost stock described so far.

Finally, but not directly measured in the present study, we assume two exogenous factors as relevant for the settlement success of *A. punctatus*: i) the large amount of food available from the organic matter dumped by the fishing industry near Chome Cove, and ii) the high fishing pressure performed by local fishermen on other benthic species that exist in the area, allowed that an opportunist species and unexploited resource, such as *A. punctatus*, to use the empty substrate.

CONCLUSIONS

The following combination of factors may have contributed to the success of *A. punctatus* in the rocky intertidal of Chome Cove: 1) availability of rocky substrates, 2) optimal geographic conditions for settlement, 3) high fecundity, 4) continuous spawning throughout the year, 5) megalopae and juveniles protected by adults, 6) reduced number of zoeal stages, 7) relatively short planktonic phase, 8) availability of a large amount of food, and 9) the apparent absence of predators presence.

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