Revista Chilena de Historia Natural
62: 199-204, 1989

Galleries of the crabs *Acanthocyclus* under intertidal mussel beds: their effects on the use of primary substratum

Galerías de jaibas *Acanthocyclus* bajo mantos de mitílidos intermareales: sus efectos sobre el uso de sustrato primario

JUAN CARLOS CASTILLA, CAROLINA LUXORO* and SERGIO A. NAVARRETE

Estación Costera de Investigaciones Marinas, Las Cruces, Departamento de Ecología,
Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile

ABSTRACT

The mid rocky intertidal of Cachagua, like many other rocky sites in central Chile, is dominated by beds of the mussel *Perumytilus purpuratus.* Under these mussel beds the predatory crabs *Acanthocyclus gayi* and *A. hassleri* build separated blind-ending galleries whose floor is the rock and the roof is the mussel bed. Samples of 1 m^2 of *Perumytilus* beds (100% cover) showed that the surface area of crab galleries ranged between 17.4% and 34.7% of the total area, and that 80% of the crabs were *A. hassleri.* In 130 of the 157 galleries analyzed, one or two conspecific crabs were found. In the remainder, up to six crabs were found together. Comparisons between the floor of crab galleries and similar rocky areas under the mussel bed, but without galleries (controls), showed that both density and cover of *Balanus flosculus, Phymactis clematis* and bryozoans were significantly higher in galleries. Similarly, the total number of species was greater on the floor of the galleries than in the controls. Although from outward appearances the cover of *P. purpuratus* remained at 100%, crab galleries allowed more sessile species to occupy the mid intertidal fringe. This occurs because of the introduction of species typical of the lower intertidal, which would otherwise be excluded by mussels.

Key words: Rocky intertidal, crab predation, crab galleries.

RESUMEN

La zona intermareal rocosa intermedia de Cachagua, así como muchos otros sitios rocosos de Chile Central, está dominada por mantos del mitílido *Perumytilus purpuratus.* Bajo estos mantos las jaibas depredadoras *Acanthocyclus gayi* y *A. hassleri* construyen galerías cerradas no interconectadas entre ellas, que tienen como piso la roca y como techo mitílidos. Muestreos de 1 m^2 de mantos de *Perumytilus* (100% cobertura) mostraron que la superficie cubierta por galerías de jaibas fluctúa entre 17,4% y 34,7% del área total, y que el 80% de las jaibas corresponde a la especie *A. hassleri.* En 130 de las 157 galerías analizadas fueron encontradas una a dos jaibas conespecíficas. En el resto se encontró hasta un máximo de seis jaibas por galería. Comparaciones entre el piso de galerías de jaibas y áreas de roca similar bajo el manto de mitílidos, pero sin galerías (controles), mostraron que tanto la densidad como la cobertura de *Balanus flosculus, Phymactis clematis* y briozoos son significativamente más altas en las galerías. Asimismo, el número total de especies sésiles fue mayor en el piso de las galerías que en los controles. Aun cuando la cobertura externa aparente de *Perumytilus* permanece en 100%, las galerías de jaibas permiten que un mayor número de especies sésiles ocupen la franja intermareal intermedia. Esto ocurre a través de la invasión de especies típicas de la franja intermareal inferior, que de otra forma serían excluidas por los mitílidos.

Palabras claves: Intermareal rocoso, depredación por jaibas, galerías de jaibas.

INTRODUCTION

Intertidal mussel beds are conspicuous and important components of many rocky shores. Generally, mussel species are superior competitors for primary space, and their beds show complex community structures (Paine & Levin 1981, Suchaneck 1986). In the rocky shore of central Chile, beds of the mussel *Perumytilus purpuratus* (Lamarck 1819) are commonly found in the mid intertidal where the slope is 45° or less, in areas either sheltered or exposed to wave action (Castilla 1981). *Perumytilus purpuratus* is the dominant competitor at that intertidal level and, in the long term, is able to exclude other sessile species such as algae and barnacles (Castilla 1981, Paine *et al.* 1985).

The number of mussels per unit area

(*) Present Address: Istituto di Biología Marina; Via Alessandro Volta 6.56100 Pisa, Italia.

(Received 3 April 1989. Accepted 19 July 1989).

differs widely from one site to another because beds are formed by up to four or five layers of individuals. In those sites where the mussel beds are thicker, conspicuous mounds of mussels are observed, under which the predatory. Atelecyclidae crabs *Acanthocyclus gayi* Milne Edwards *et* Lucas 1844 and *A. hassleri* Rathbun 1898 build galleries.

Acanthocyclus gayi and *A. hassleri* recruit mostly in beds of *P. purpuratus*. They remain among or underneath the mussels until reaching 10 to 15 mm carapace width (CW). Above this size, the crabs that remain in the mussel bed build blind galleries which have the rock surface as floor and the mussel bed as roof[1]. Although such galleries are frequently found in the rocky intertidal of central Chile, particulary where the mussel beds are thicker, there are no studies focusing on (a) the effects they may exert over the use of primary substratum by sessile or mobile intertidal organisms, or (b) their influence on the stability or persistence of the mussel beds.

We study some aspects of the galleries built by *Acanthocyclus* spp. and mainly analyze the effects of these galleries on the utilization of primary substratum by sessile organisms, as well as on the densities of some mobile species that live underneath or among the mussels.

MATERIALS AND METHODS

The study was carried out from September to December 1981 in an exposed intertidal rocky site of ca. 50 m^2 in Cachagua (32°36'S, 71°25'W), central Chile. The mid intertidal of the study site was dominated by beds of the mussel *Perumytilus purpuratus*, which showed cover values near 100% over the entire area. The primary space (rock) of the upper intertidal (immediately above the mussel beds) was dominated by the barnacles *Chthamalus scabrosus* (Darwin 1854) and *Jehlius cirratus* (Darwin 1854). The same species were also found on the shells of *Perumytilus* in the middle zone. On the other hand, the lower intertidal was dominated in biomass by a belt of the brown alga *Lessonia nigrescens* Bory. The barnacles *Balanus flosculus* (Darwin 1854), *B. laevis* (Bruguiére 1789), *J. cirratus* and *C. scabrosus*, and the sea anemone *Phymactis clematis* (Drayton 1846) were typically found in the space between the *Perumytilus* belt and the *Lessonia* belt, and were often part of the *Lessonia* community of the lower fringe.

Samplings were performed at the middle intertidal in four 1 m x 1 m quadrats selected at random in different areas with 100% cover of *Perumytilus*. Inside these quadrats the mussels from the roof of the galleries were carefully removed, uncovering the crabs that occupied them. The crabs were identified, sexed, and measured (CW). Similarly, all sessile organisms settled on the floor of the galleries, as well as other mobile organisms, were identified, counted and measured. All crab galleries in the quadrats were sampled.

To determine the area occupied by each gallery, its maximum length and width were measured with a ruler (precision 1.0 mm), and to obtain an estimate of the mussel bed thickness, lateral walls of galleries were measured from the basal rock to the surface of the mussel matrix. A total of 157 crab galleries was analyzed (each gallery was considered as a replicate).

In areas with a 100% cover of *Perumytilus* adjacent to the quadrats, but without crab galleries (= controls), we removed mussels from the rock, leaving spaces similar to those occupied by galleries. All sessile and mobile organisms found on 40 such control areas were identified, counted and measured.

Cover of sessile organisms (% of total area), in crab galleries and controls, was estimated from individual measures taken as follows: a) rostro-carinal length of barnacles; b) maximum basal diameter of sea anemones; c) maximum length of mussels. Cover values were compared with one-way ANOVA after arc-sin transformation of data (Sokal & Rohlf 1981). Density values were expressed as number of individuals per 100 cm^2 surface and compared with one-way ANOVA after logarithmic transformation of data (Sokal & Rohl 1981).

RESULTS

Most galleries of *Acanthocyclus* spp. observed in the field were separate blind-ending units. Usually, (82.8%) only one or two large crabs (> 13 mm CW), always conspecific, were found inside each gallery. In the remaining ones, up to six crabs were found together (Fig. 1), but these did not exceed 13 mm CW. Sex ratios were, in all cases close to 1: 1 (Fig. 1). Eighty percent of the crabs found were *A. hassleri*. This species reached maximum adult sizes (36 mm CW) inside the galleries, whereas *A. gayi* did not exceed 19 mm CW in the same situation. No recruits of either species (crabs smaller than 3 mm CW at post-zoea stage) were found inside the galleries (Fig. 2).

The total area covered by crab galleries in 1 m^2 of *Perumytilus* bed ranged between 12.4% and 34.7%, and increased slightly with increasing thickness of the mussel bed (Table 1). The size of each gallery (maximum length in millimeters) increased with the size of the largest crab found in its interior (Fig. 3). The number of crabs per gallery also contributed significantly (P = 0.001, multiple regression R = 0.49) to account for the increase in the length of galleries.

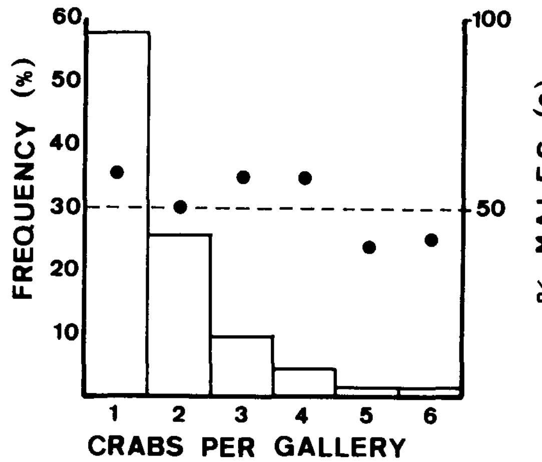

Fig. 1: Relative frequencies of crabs *Acantocyclus* spp, and percentage males found per gallery, under mussel beds of *P. purpuratus.*

Frecuencia relativa de jaibas *Acanthocyclus* spp. y porcentaje de machos encontrado por galería, bajo mantos de *P. purpuratus.*

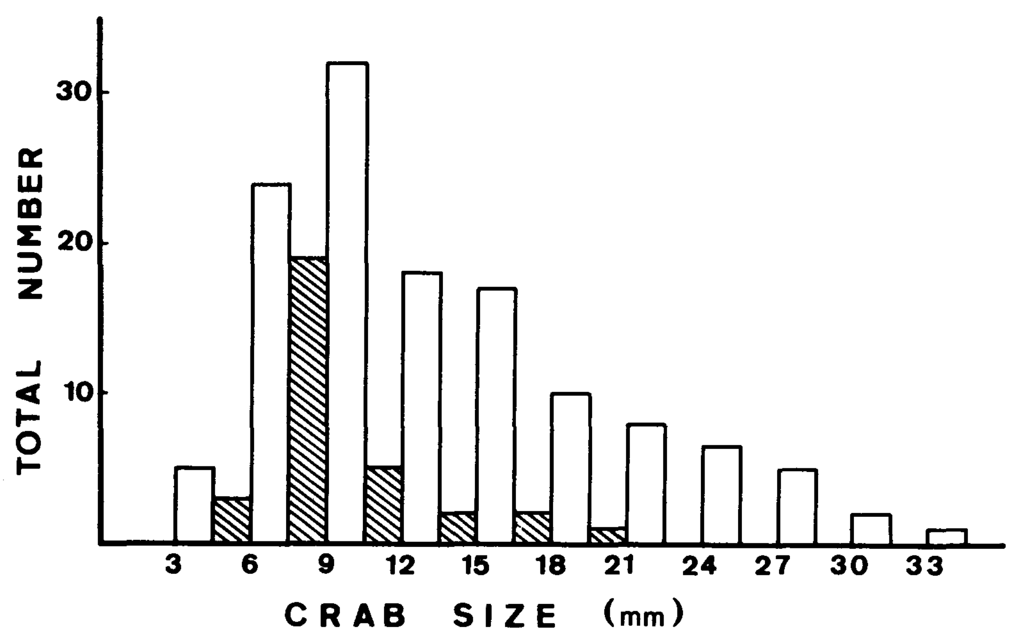

Fig. 2: Size-frequency distributions of *Acanthocylus gayi* (striped bars) and *A. hassleri* (open bars) inside galleries, under mussel beds of *P. purpuratus.*

Distribución de frecuencia de tamaño de jaibas *Acanthocylus gayi* (barras achuradas) y *A. hassleri* (barras claras) encontradas en el interior de galerías, bajo mantos de *P. purpuratus.*

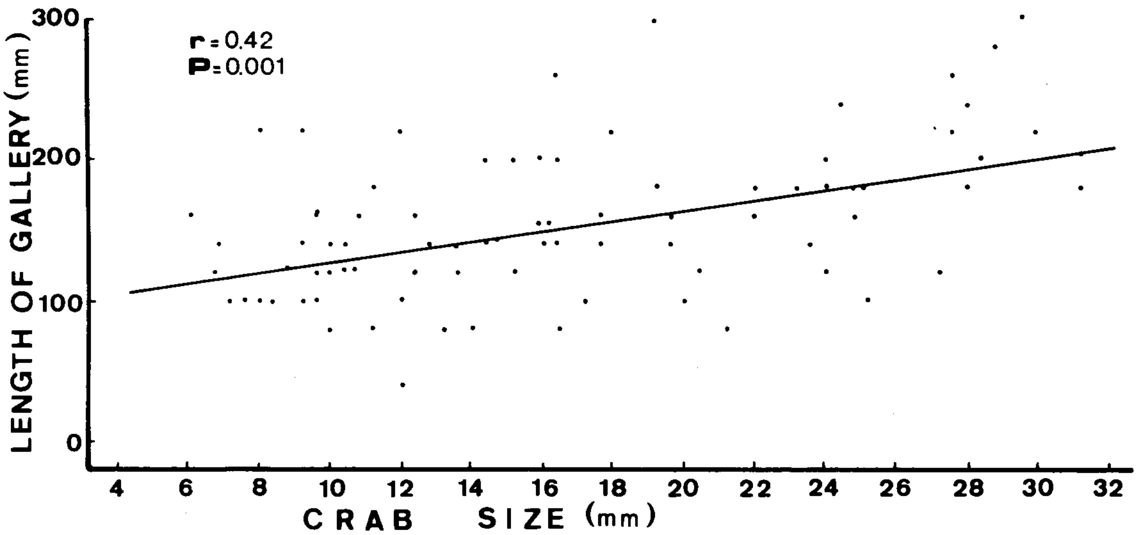

Fig. 3: Linear regression between the length of *Acanthocyclus* galleries and the size (CW) of the crabs that occupied them.

Regresión lineal entre el largo de las galerías de jaibas *Acanthocyclus* y el tamaño (CW) de las jaibas que las ocupaban.

TABLE 1

Area (primary substrate) occupied by galleries of *Acanthocyclus* spp. crabs under four 1 m^2 quadrats of *Perumytilus purpuratus* bed.

Area (sustrato primario) ocupada por galerías de jaibas *Acanthocyclus* spp. bajo cuatro cuadrantes de 1 m^2 de manto de *Perumytilus purpuratus*.

Area of galleries (cm^2)	% área galleries	Mussel bed thickness* (cm)	Nº of crabs in galleries
3474	34,74	3,43 ± 0,15 (n = 63)	105
2832	28,32	2,98 ± 0,09 (n = 35)	92
2049	20,49	2,42 ± 0,14 (n = 32)	38
1740	17,40	1,90 ± 0,08 (n = 27)	35

* : Mean ± S.E.

Figure 4 a and b shows the densities (ind/100 cm^2) and cover (%) of sessile species settled on the floor of the crab galleries, and those settled in the control areas. The number of sessile species was greater in galleries (n = 9) than in controls (n = 2). Moreover, the densities of *B. flosculus* and *P. clematis,* as well as the total density of organisms, were significantly higher inside galleries (one-way ANOVA results: P = 0.0001, P = 0.0485 and P = 0.0001, respectively). Similarly, the cover of *B. flosculus, P. clematis,* bryozoans, and the total cover of organisms were significantly higher in galleries than in controls (one-way ANOVA results: P = 0.0001, P = 0.0470, P = 0.0430 and P = 0.0001, respectively).

The mobile species *Chiton granosus* (Frembly 1827) and *Fissurella* sp. were found both in galleries and in controls. Their maximum sizes were 20.8 mm and 24.6 mm long respectively. Mean density of *C. granosus* was significantly lower (F = 22.36; d.f. = 1,144; P = 0.001) inside the galleries (0.01 ind/100 cm^2) than in the controls (0.3 ind/100 cm^2). Mean densities of *Fissurella* sp. were equally low (0.01 ind/100 cm^2) in galleries and in controls.

DISCUSSION

No individuals of *Acanthocyclus gayi* larger than 19 mm CW were found inside galleries, whereas individuals over 28 mm CW were frequently observed in crevices and in

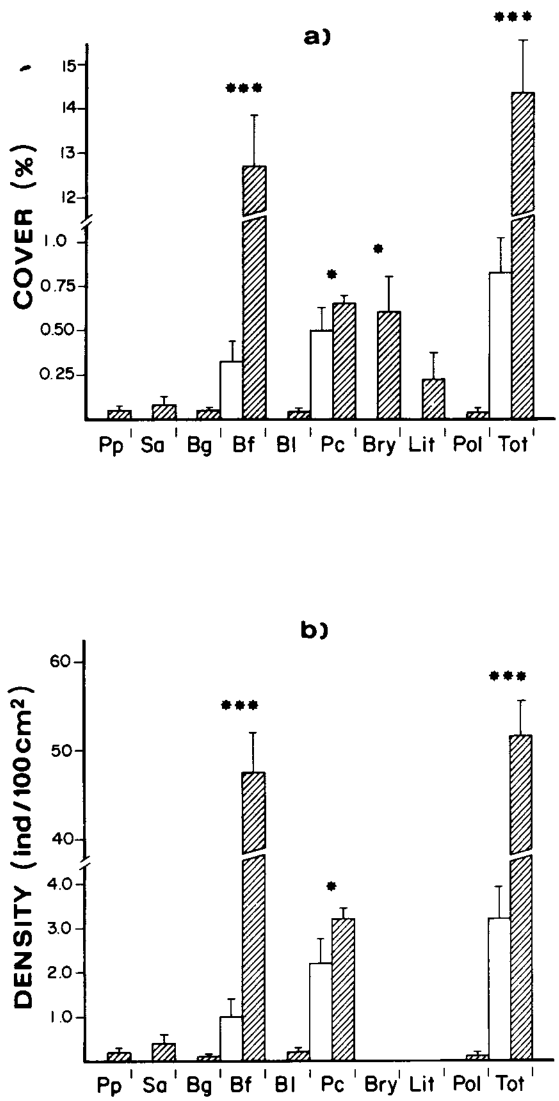

Fig. 4: a) Cover (%) and b) density (ind/100 cm^2) of sessile species on the floor of crab galleries (striped bars) and on the control areas under *P. purpuratus* beds (open bars). Pp: *Perumytilus purpuratus;* Sa: *Semimytilus algosus;* Bg: *Brachidontes granulata;* Bf: *Balanus flosculus;* Bl: *Balanus laevis;* Pc: *Phymactis clematis;* Bry: *Bryozoans;* Lit: lithothamnioid. Pol: *Phragmatopoma* sp.; Tot.: Total. Significant differences indicated by * : $P \leq 0.05$ and ***: $P \leq 0.001$.

a) Cobertura (%) y b) densidad ind/100 cm^2) de especies sésiles en el piso de las galerías de jaibas (barras achuradas) y en las áreas de control bajo el manto de *P. purpuratus* (barras claras). P.: *Perumytilus purpuratus;* Sa: *Semimytilus algosus;* Bg: *Brachidontes granulata;* Bf: *Balanus flosculus;* Bl: *Balanus laevis;* Pc: *Phymactis clematis;* Bry: *Bryozoans;* Lit: lithothamnioid. Pol: *Phragmatopoma* sp.; Tot: Total. Diferencias significativas indicadas por * : $P < 0.05$ y ***: $P < 0.001$.

Lessonia holdfasts (unpublished results). On the other hand, *A. hassleri* did reach maximum sizes inside galleries. This pattern of distribution has been previously reported in other localitities of central Chile, and has been explained as a result of interspecific interference competition, causing *A. hassleri* to exclude *A. gayi* from the thicker sectors of the mussel bed[1].

At this stage, it is difficult to establish whether crabs cause mounds to form *de novo* in the mussel bed or whether they take advantage of previously existing irregularities (i.e. crevices, fissures in the rock) to construct their galleries there. Our results strongly suggest that these species of Atelecyclidae settle among irregularities in the mussel bed, subsequently expanding them into mounds, hence the positive slope of the regression of gallery length on crab size. Indeed, *P. purpuratus* is an important component of the crabs' diet (Sotomayor & Zamorano 1985), and the two species are able to attack even the largest mussels in the beds (Navarrete & Castilla 1988).

The release of primary substratum (rock) produced by crab galleries under the mussel bed allows a greater packing of species in the mid intertidal as compared with controls, despite the external apparent cover of *P. purpuratus* remaining at 100%. It is worth noting that the invertebrate species that occupy this substratum (i.e., *B. flosculus, P. clematis*) are usually found in the lower intertidal. We did not find the typical species of the mid and high intertidal, such as *J. cirratus* and *C. scabrosus.* Settlement of these barnacle species occurs readily on middle intertidal rocks when the *Perumytilus* bed is removed (Castilla & Durán 1985). It is likely therefore that the filtering activity of the mussels and/or the abiotic conditions generated inside the galleries determine the type of species that can settle and live on the gallery floor. On the other hand, the low densities of *Chiton granosus* occurring inside the galleries may be attributed to the predatory activity of crabs, which frequently feed on this species.

1) NAVARRETE SA & JC CASTILLA (1988) Coexistencia y repartición de recursos en jaibas intermareales. Archivos de Biología y Medicina Experimentales (Chile) 21: R 316.

Finally, an interesting problem remains to be studied: the effect that these galleries and mounds exert on the stability or persistence of the mussel bed. Mounds may be strongly affected by the mechanical force of waves, because they are the weakest points in the mussel bed, and may facilitate the release of primary substratum in the middle intertidal.

ACKNOWLEDGEMENTS

Whe thank F. Jaksic and P. Marquet for helpful comments on an earlier draft. This work was generously supported by the Dirección de Investigación, Pontificia Universidad Católica de Chile, Research Project 018/88 to J.C. Castilla. S.A. Navarrete acknowledges support given by the Departamento de Ecología (Beca de Instructor), Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile. The paper was written during the sabbatical leave of J.C. Castilla at the Department of Zoology, U. of Washington. The support given by Fundación Andes and the Fulbright Commission are sincerely appreciated.

LITERATURE CITED

CASTILLA JC (1981) Perspectivas de investigación en estructura y dinámica de comunidades intermareales rocosas de Chile central. II. Depredadores de alto nivel trófico. Medio Ambiente (Chile) 5: 190-215.

CASTILLA JC & LR DURAN (1985) Human exclusion from the rocky intertidal zone of central Chile: the effects on *Concholepas concholepas* (Gastropoda) Oikos 45: 391-399.

NAVARRETE S.A. & JC CASTILLA (1988) Foraging activities of the Chilean intertidal crabs *Acanthocyclus gayi* Milne Edwards et Lucas and *A. hassleri* Rathbun. Journal of Experimental Marine Biology and Ecology 118: 115-136.

PAINE RT & SA LEVIN (1981) Intertidal landscapes: disturbance and the dynamics of pattern. Ecological Monographs 51: 145-178.

PAINE RT, JC CASTILLA & JM CANCINO (1985) Perturbation and recovery patterns of starfish – dominated intertidal assemblages in Chile, New Zealand and Washington State. American Naturalist 125: 679-691.

SOKAL RR & FJ ROHLF (1981) Biometry. WH Freeman & Company, San Francisco, California.

SOTOMAYOR JF & JH ZAMORANO (1985) Hábitos alimenticios de *Acanthocyclus gayi* Milne – Edwards & Lucas, 1844 y *A. hassleri* Rathbun, 1898 (Decápoda: Atelecyclidae), en el intermareal rocoso de Mehuín, Chile. Medio Ambiente (Chile) 7: 135-142.

SUCHANEK TH (1986) Mussels and their role in structuring rocky shore communities. In: Moore, PG & R Seed (eds) The ecology of rocky coasts: 70-96. Columbia University Press, New York, New York.