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Temporal and spatial patterns in the recruitment of *Balanus glandula* and *Balanus laevis* (Crustacea, Cirripedia) in Comodoro Rivadavia harbor (Chubut, Argentina)

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Abstract: The presence of *Balanus glandula* Darwin and *B. laevis* Bruguière is reported for the first time in Comodoro Rivadavia harbor (Province of Chubut, Argentina). Recruitment was studied during an annual period at three levels: upper and middle intertidal, and subtidal. Recruit density was around 30 times higher in *B. glandula* than in *B. laevis*. Both species had maximum recruitment during spring, but showed clear differences in vertical zonation. *B. glandula* recruited exclusively in the intertidal zone, whereas *B. laevis* was found mainly in subtidal samples, with a very low degree of overlapping. High variability in recruitment was observed at a scale of 20 m.

Key words: *Balanus*, recruitment, Comodoro Rivadavia harbor, Patagonia, Argentina.

The presence of a conspicuous barnacle belt is a characteristic feature of intertidal rocky shores throughout the world. Although intertidal barnacles have been described in southern Chile (Brattström, 1990) and Tierra del Fuego (Zaixso *et al.*, 1978), the Argentine coast from Santa Cruz to Buenos Aires Province lacked an intertidal zone of sessile balanomorphs until the decade of 1960 (Ringuelet *et al.*, 1962; Olivier *et al.*, 1966 a, 1966 b).

The occurrence of exotic species of *Balanus* was reported for the first time in Argentina for Mar del Plata harbor (Bastida, 1968). An invasion of *Balanus glandula* Darwin, 1854, a species native to the Pacific coast of North America (Pilsbry, 1916), was detected at the beginning of the 1970's within Mar del Plata harbor (Bastida *et al.*, 1980), as well as on natural rocky substrata (Penchaszadeh, 1973; Spivak & L'Hoste, 1976). Twenty years later, a thick belt of *Balanus glandula* has developed above the community of the mytilid *Brachidontes rodriguezi* at this locality (Vallarino & Elías, 1997).

Colonization of intertidal hard substrata by *Balanus glandula* continued southwards, being recorded later at Ingeniero White, in the Bahía Blanca estuary (Wagner *et al.*, 1993). It began to appear in San José Gulf between 1983 and 1984, and was detected in Nuevo Gulf in 1986 (Gómez Simes, 1993).

On the other hand, several native species of sessile barnacles have been recorded in the subtidal zone of Patagonia and Tierra del Fuego (Lahille, 1910). One of the most frequent species is *Balanus laevis* Bruguière, 1789, distributed from Cape Horn to the continental shelf off Mar del Plata in the Southwest Atlantic (Lahille, 1910; Pilsbry, 1916; Newman & Ross, 1976).

The aim of this study is to report for the first time the presence of *Balanus glandula* and *B. laevis* in Comodoro Rivadavia harbor, and to add information on their spatial and temporal recruitment patterns.

MATERIALS AND METHODS

Study area. Comodoro Rivadavia harbor is located at 45° 52' S, 67° 28' W (Fig. 1). It is composed of two kind of structures: an older section of vertical walls, and a new breakwater, which was built using natural rocks and man-made concrete blocks. Rocks were extracted from Cerro Dragón, located near Sarmiento (45° 35' S, 69° 04' W).

Comodoro Rivadavia has a tidal amplitude of 6.21 m and 4.34 m during spring and neap tides, respectively (Servicio de Hidrografía Naval, 1998). Since physical and chemical data of seawater within the harbor were not available,

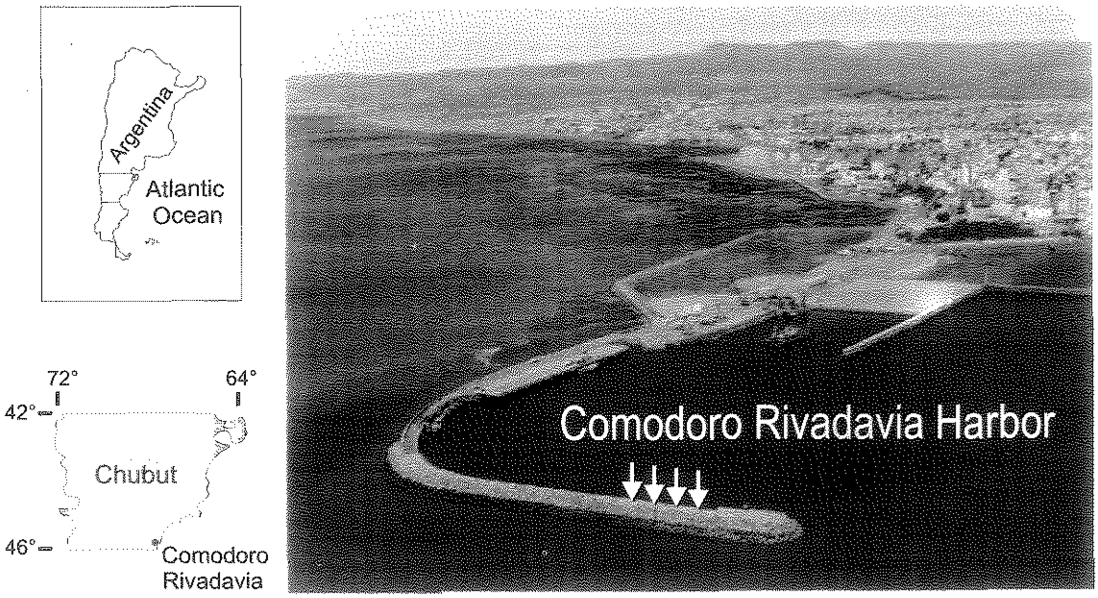

Fig. 1. Comodoro Rivadavia harbor. Arrows show the location of transects on the breakwater.

temperature and salinity were measured on individual samples collected at each season. Salinity varied between 33.4 and 33.8 psu and water temperature fluctuated between 9°C (August) and 16° C (February) during the study period.

Sampling and data processing. Stones with a roughly square shape (ca. 20 x 20 cm) were collected from the breakwater (Fig. 1), and glued to the substratum at similar orientations with epoxy putty at the beginning of each season. They were distributed along 4 transects perpendicular to the breakwater, at 3 different levels: upper intertidal, middle intertidal, and subtidal. The upper intertidal level was defined as the most elevated zone where macroscopic marine organisms could be found, and was dominated by a belt of green algae. Middle intertidal samples were glued 2-3 m below, in an area characterized macroscopically by the appearance of several invertebrate taxa, such as barnacles, molluscs and polychaetes. Stones could not be glued at the lower intertidal due to logistic problems. Subtidal samples were immersed around 4 m below mean low water level. Transects were separated by around 20 m. Stones remained immersed 84-100 days, during the following intervals: 19/12/97-29/03/98 (summer), 29/03/98-28/06/98 (autumn), 28/06/98-20/09/98 (winter), 20/09/98-20/12/98 (spring). A total of 48 samples (4 seasons x 3 levels x 4 replicates) were analyzed. Two additional stones were glued at each level, anticipating possible losses, but only one replicate was lost (spring, subtidal) throughout the study period.

Barnacles were identified and counted in the laboratory. All live individuals within a 10 x 10 cm quadrat in the center of the upper side of each stone were counted. Due to very high abundance, density of *B. glandula* in one spring replicate at the middle intertidal level was estimated taking a subsample of ten 1 cm^2 quadrats, covering 10 % of the surface.

Following Keough & Downes (1982), recruits were defined as all individuals surviving until collection of each replicate, thus involving a composite of juvenile stages representing one or more settlement events.

Data were analyzed by two-way ANOVAs (Sokal & Rohlf, 1981). Analyses were restricted to levels where recruitment occurred: upper and middle intertidal in *B. glandula*, and middle intertidal and subtidal in *B. laevis*. Homoscedasticity was achieved by means of logarithmic (*B. glandula*) or fourth root (*B. laevis*) transformations, and was verified by the Cochran's C test (Winer, 1971).

RESULTS

Taking into account all levels and seasons, recruitment was around 30 times higher in *B. glandula* than in *B. laevis*. *Balanus glandula* was found only in upper and middle intertidal levels, but was completely absent in subtidal samples. Recruitment in this species was an order of magnitude higher in the middle than in the upper intertidal level (P = 0.00005, Table 1). Differences in recruit density among seasons were also highly significant (P = 0.0003, Table 1), with a maximum in spring and almost total absence in winter (Fig. 2). The interaction between spatial and temporal factors was also highly significant (P = 0.0001, Table 1), since density values did not vary between levels in winter and autumn, but were much higher in the middle than in the upper intertidal in spring and summer (Fig. 2).

Balanus laevis recruited only in middle intertidal and subtidal levels, but was completely absent in upper intertidal samples. Seasonal and level differences in the density of *B. laevis* recruits were non significant (P = 0.26, Table 1). Like in *B. glandula*, however, a spring maximum was also observed in this species. Interaction between both factors was significant (P < 0.02, Table 1), because recruit density was higher in the subtidal than in the intertidal during spring and autumn, but the reverse trend occurred during winter and summer (Fig. 2).

High variability among replicates occurred in both species, particularly during spring (Fig. 2).

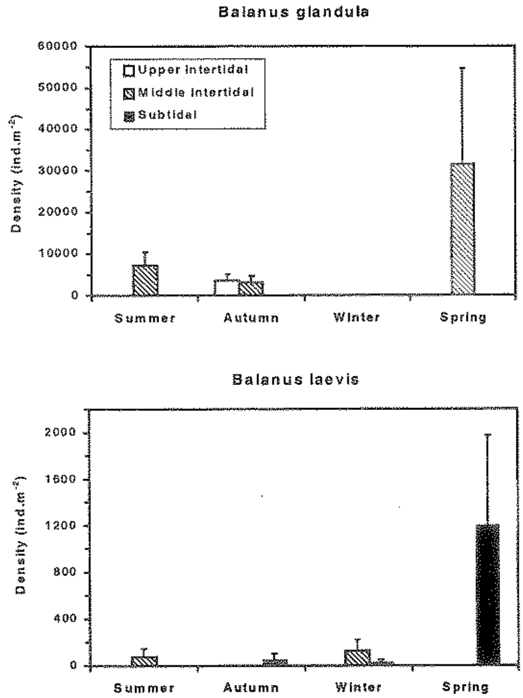

Fig. 2. Seasonal changes of mean density of *Balanus glandula* and *Balanus laevis* at different levels. Vertical bars represent one standard error. Density of *B. glandula* at middle intertidal level during winter (mean = 25, SE = 25) not visible due to scale.

Table 1: Two-way ANOVA of the density of *Balanus glandula* and *Balanus laevis* recruits in Comodoro Rivadavia harbor.

Source	Degrees of freedom	Mean square	F	P
		Balanus glandula		
Seasons	3	2.359	9.269	**0.0003**
Levels	1	6.252	24.560	**0.0005**
Interaction	3	2.644	10.386	**0.0001**
Error	24	0.255		

Log_{10} (x + 1) transformation, Cochran's C test: 0.351, P < 0.05

Source	Degrees of freedom	Mean square	F	P
		Balanus laevis		
Seasons	3	0.482	1.441	0.255
Levels	1	0.449	1.341	0.258
Interaction	3	1.249	3.731	**0.025**
Error	24	0.335		

Fourth root transformation, Cochran's C test: 0.421, P < 0.05

DISCUSSION

This study shows that *Balanus glandula* and *B. laevis* have a clearly contrasting zonation pattern in Comodoro Rivadavia harbor, the former recruiting exclusively on intertidal, and the latter mainly on subtidal substrata, with minimum overlapping. This pattern could have been caused by two different processes: a) Uniform larval settlement at both levels, followed by differential mortality during early stages of benthic life. No signs of massive recruit mortality were observed, however, at the level where a species failed to occur at the end of each season. b) Planktonic zonation of larvae. Grosberg (1982) showed in California that barnacle zonation was already determined before settlement, since 94 % of *B. glandula* cypris were found at the water surface, while those of another species of *Balanus* were deeper. Although vertical segregation of cypris in the water column seems to be the most probable explanation to the pattern found in this study, we still have no information on planktonic distribution of barnacle larval stages off the Province of Chubut.

Recruit density was an order of magnitude higher in *B. glandula* than in *B. laevis* (Fig. 2). Since its initial invasion in Mar del Plata (Penchaszadeh, 1973; Spivak & L'Hoste, 1976; Bastida, 1980), *B. glandula* has extended its range 8° of latitude southwards in 25 years. Its great ability to colonize intertidal hard substrata is favored by predator scarcity or absence at this level, and also because in Buenos Aires Province (37° - 41° S) larval release and settlement coincide with an increase in bare substratum after winter storms (Vallarino & Elías, 1997). The absence of an intertidal belt of barnacles in Santa Cruz Province (46° - 52° S) (Ringuelet *et al.*, 1962) may contribute to the future expansion of *B. glandula* further southwards.

The highest recruitment of *B. glandula* and *B. laevis* observed in spring, was probably simultaneous with a seasonal maximum of phytoplankton abundance in Patagonian coastal waters (i.e. San José Gulf, Charpy *et al.*, 1980 a, 1980 b), supplying abundant feeding for newly settled juveniles.

Seasonal changes in recruitment density of *B. laevis* were not significant. This was partly due to high variability among replicates, i.e. at a scale of 20 m (Fig. 2). Recruitment patchiness at scales of tens of meters seems to be a rather common feature in several intertidal species of barnacles (Caffey, 1985; Jenkins *et al.*, 2000).

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