

Patch recolonization by the tunicate *Pyura praeputialis* in the rocky intertidal of the Bay of Antofagasta, Chile: evidence for self-facilitation mechanisms

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ABSTRACT: Patch dynamics of intertidal *Pyura praeputialis* (Heller, 1878) were studied in experimentally cleared plots at 3 vertical levels (upper, mid and lower *P. praeputialis* levels) and 3 sites within the Bay of Antofagasta, Chile. The sites corresponded approximately to the northern limit (Las Conchillas), the center (El Way), and the southern limit (El Lenguado) of the species geographic distribution in Chile. Replicated 40 × 60 cm quadrats were photographed periodically to follow patch re-colonization. Patch recolonization (recolonized area) followed a sigmoid curve and could be fitted at most sites and levels by applying maximum likelihood techniques to the asymptotic model: $y = a / \{1 + \exp[-(x - b)/c]\}$ where Parameters *a* and *b* are asymptotic percentage cover and time for 50% recovery respectively, and Parameter *c* defines the shape of the curve (growing phase). Among sites, the highest asymptotic values and fastest recovery times were observed at El Way, in the center of the species distribution. Among levels, the highest asymptotic values were observed in the mid *P. praeputialis* level quadrats. The perimeter of the patches increased and subsequently decreased as a function of recolonized area. Recruitment observations showed the process of recolonization to be related to the perimeter of the patch to be colonized rather than to the area available. Further more, the recolonization patterns could be predicted using the patch perimeter scaled by a linear coefficient. We believe that the mechanism of recolonization is most probably related to the settlement of recruits to the border of previously settled individuals, possibly mediated by intraspecific self-facilitation mechanisms.

KEY WORDS: Patch recolonization · *Pyura praeputialis* · Tunicates · Border effects · Facilitation

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INTRODUCTION

Disturbances are essential to the functioning of ecological systems. Understanding the role of disturbances in the dynamics of natural populations has been one of the most challenging issues in ecology (Dayton 1971, Lubchenco & Menge 1978, Sousa 1984, Pickett & White 1985). Patch dynamics and the relative contribution of biological and physical factors are at

the center of this debate (Connell 1975, Sousa 1979, Pickett & White 1985). Post-disturbance population recovery patterns in sessile organisms such as terrestrial plants and marine algae have been studied for decades in the context of successional sequences (Dayton 1975, Connell & Slatyer 1977, Sousa 1979, Farrell 1989, 1991). Evidence for 3 successional models (facilitation, tolerance and inhibition) has been presented for natural systems, suggesting that the mechanisms underlying successional change may vary among communities (Connell & Slatyer 1977, Sousa 1979, Farrell 1991). The rate at which patches are created and occupied has

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been extensively used for population modeling (Levin & Paine 1974, Paine & Levin 1981, Wu & Levin 1994). By virtue of their immobile nature marine sessile organisms are ideal for population modeling. Moreover, due to their relatively high turnover rates they are especially suited for experimental manipulation aimed at elucidating the underlying mechanisms of recolonization. Experiments on beds of the mussel *Mytilus californianus* have shown that the mechanism of recolonization is related to patch size (Paine & Levin 1981). For this species the main patch-filling mechanism is related to the repositioning and growth of existent mussels; recolonization in the center of patches is rarely observed, suggesting intraspecific facilitation (self-facilitation) mechanisms for matrix recovery.

Pyura praeputialis (Heller, 1878) is a large tunicate species (up to 30 cm high) which, in Chile, is distributed exclusively along 60 to 70 km of coastline in and around the bay of Antofagasta (Clarke et al. 1999). This tunicate is a sessile, dominant species, capable of forming extensive beds of barrel-like individuals tightly cemented together in rocky intertidal and shallow subtidal zones (Paine & Suchanek 1983, Castilla 1998). Along its geographical range, *P. praeputialis* displays variations in terms of intertidal bed extension, percent cover, density, population biomass, and size structure (Castilla et al. 2000). In this paper, using experimental quadrats, we investigate the dynamics of patch recolonization by intertidal populations of the tunicate *P. praeputialis* in Chile after removal of adult individuals in order to elucidate the mechanisms that facilitate the persistence of tunicate beds. Our hypothesis is that the main patch-filling mechanisms are related to recruitment, and subsequent growth, of new individuals to the border zone of patches and is therefore more a function of patch perimeter than patch area.

MATERIALS AND METHODS

Intertidal system and study sites. The study was conducted from April 1997 to May 1999. Three localities, located inside the distributional limits of the species in Antofagasta, were selected to examine *Pyura praeputialis* recolonization dynamics (Fig. 1). The localities were selected to represent not only a latitudinal gradient but also a distributional gradient within the species range. Las Conchillas ($23^{\circ} 31' 40''$ S, $70^{\circ} 32' 01''$ W) is located near the northern limit of the species, distribution, El Way ($23^{\circ} 45' 02''$ S, $70^{\circ} 26' 43''$ W) is near the center of its distribution range, and Curva Lenguado ($23^{\circ} 46' 15''$ S, $70^{\circ} 28' 36''$ W) is close to its southern limit.

Storm-generated waves are common in this intertidal system, and during May 1997 we had the oppor-

tunity of monitoring *Pyura praeputialis* intertidal beds 2 d after a major storm (one of the heaviest in the whole year: Castilla pers. obs.). We measured storm-generated patches in the *P. praeputialis* beds, which were recognizable by the presence of live lithothamnoids (encrusting corallines) on the rocks. We measured the maximum length and width of all recently created patches at 6 sites located near El Way, and used these data to estimate patch-size frequency distribution.

Sampling and monitoring. At each of the experimental localities, replicate 40×60 cm quadrats were haphazardly chosen at 3 vertical levels, as described in Castilla et al. (2000): the upper, mid and lower vertical limits of *Pyura praeputialis*. All quadrats were photographed (except at Las Conchillas) and then cleared of all erect organisms with a chisel. Encrusting algae were not removed, since natural perturbations do not seem to remove these. Four replicate quadrats were removed from each intertidal level at Las Conchillas and Curva Lenguado; 3 'removal quadrats' were made at each level at El Way.

A monthly photographic monitoring of quadrats was started on April 1997 at El Way and Curva Lenguado and during May 1997 at Las Conchillas. During the second year, the sites were monitored once every third month. At El Way, the lower quadrats could not be photographed most of the time because of the unsuitable sea conditions; however, visual examination of the site revealed that no recruitment took place during the monitoring period.

Photographs were taken using a quadrat frame system (Witman 1985) especially adapted for intertidal

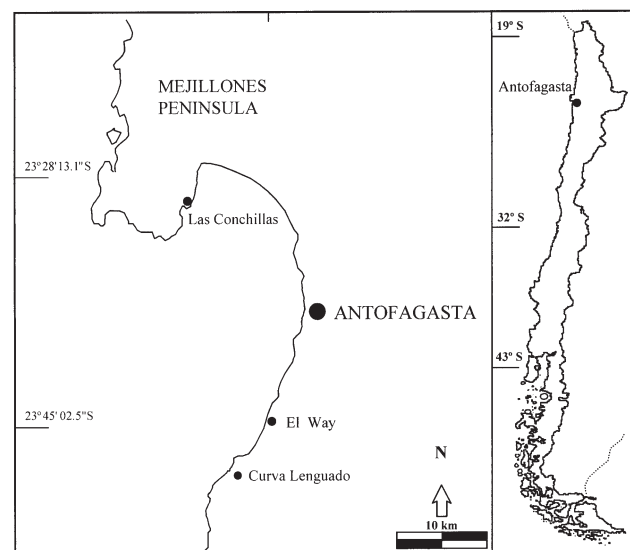


Fig. 1. Locations of study sites in Antofagasta Bay, Chile

photographs and a Nikonos IV camera with a 35 mm lens and one SB-105 submarine flash. On sunny days a reflective screen was used to prevent shadows. Quadrats were identified by labeled electric tape attached to the frame indicating locality, intertidal level, quadrat and date.

Data analysis. The quadrat slides were projected onto paper, and the area covered by *Pyura praeputialis* was drawn and painted black. These pictures were digitized with a Kodak DC 210 digital camera. The digital photographs were analyzed with the software Image Tools Version 1.28 with a pixel size of 0.3 mm² to obtain an estimate of the area occupied by *P. praeputialis* over time. To better understand the mechanisms contributing to the process of recolonization, we distinguished between peripheral and central growth. Peripheral growth or patch-closing is defined as the addition of new recruits and individual growth along the edges of the patch, i.e. a growing front. Central growth is the result of recruitment to bare space inside the patch and the subsequent growth of such recruits.

In order to compare re-population dynamics among sites and tidal levels, we fitted a simple asymptotic model of the form: $y = a/[1 + \exp[-(x - b)/c]]$, using maximum likelihood modeling techniques with the software package Table Curve (Jandel Scientific). This model enabled the use of the lowest number of parameters capable of fitting the most sites and levels.

We used data of the intertidal mid-level quadrats from the 3 sites as the basis for fitting a simplified recolonization model. Using the methods already described, we first estimated the extent of the area recolonized by *Pyura praeputialis* and the observed perimeter. Non-linear peak equations (unimodal positive functions) were then fitted to the data for the observed perimeter, using the area occupied by *P. praeputialis* as the independent variable to investigate the probable relationship between both variables. The observed perimeter was predicted from the area occupied by *P. praeputialis* using a logistic equation of the form: $y = 4an/(1 + n)^2$; with $n = \exp[-(x - b)/c]$. Finally, we used a simple approach to model recolonization, i.e. a discrete model in which the initial recolonized area was equal to zero ($A_{t=0} = 0$); adding the observed perimeter at $t-1$ (P_{t-1}) scaled with a linear coefficient (q) to obtained the predicted recolonized area at t ($A_{t=0} = 0$; $A_t = A_{t-1} + qP_{t-1}$; for $t > 0$). The linear coefficients were estimated by minimizing the sum-of-squares of the difference between the observed and predicted areas.

A preliminary-spatially explicit lattice model was used to explore theoretical recolonization patterns in 3 different situations (facilitation, independence and constant-rate recruitment). In the facilitation model a

few non-zero entries are uniformly distributed within the lattice, creating a sparse matrix for settlement, with 15% of usable cells ($0 < p \leq 1$; p uniformly distributed), but settled individuals increase the probability in the surrounding cells. In the independence model, probability of settlement is assigned randomly to the lattice cells, and it does not change with the presence of individuals; recruits can be assigned to empty or occupied cells. In the constant-rate model, a fixed number of recruits are randomly assigned to empty cells. In all 3 models, mortality is not modeled, and therefore once a cell has been occupied it remains occupied.

RESULTS

The size structure of the patches in the *Pyura praeputialis* beds generated during the May 1997 storm showed a primary mode between 2000 and 3000 cm² similar to that used for the removal quadrats (2400 cm²). A secondary mode of 7000 cm² was also observed; however this was much less important (ca 7%) than the primary mode (ca 25%) (Fig. 2).

Patterns of recolonization as a function of locality

At Curva Lenguado the most obvious differences were in the mean percent cover attained at the different vertical levels. The highest percent cover was attained at the mid-*Pyura praeputialis* (ca 80%) followed by the upper (ca 60%) and lower-*Pyura praeputialis* (ca 20%) levels (Fig. 3). At El Way, the pattern was similar to that at Curva Lenguado, with the highest percent cover in the mid level (ca 85%), followed by the upper level (ca 50%) (Fig. 3). At Las Conchillas, the pattern was less obvious. The maximum attained percent cover and recovery rates were much lower than at the other 2 sites. However, the higher percent cover was also observed at the mid-

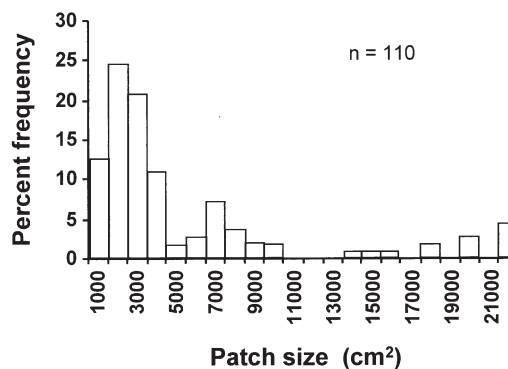


Fig. 2. Size of natural storm-generated intertidal open patches in *Pyura praeputialis* beds

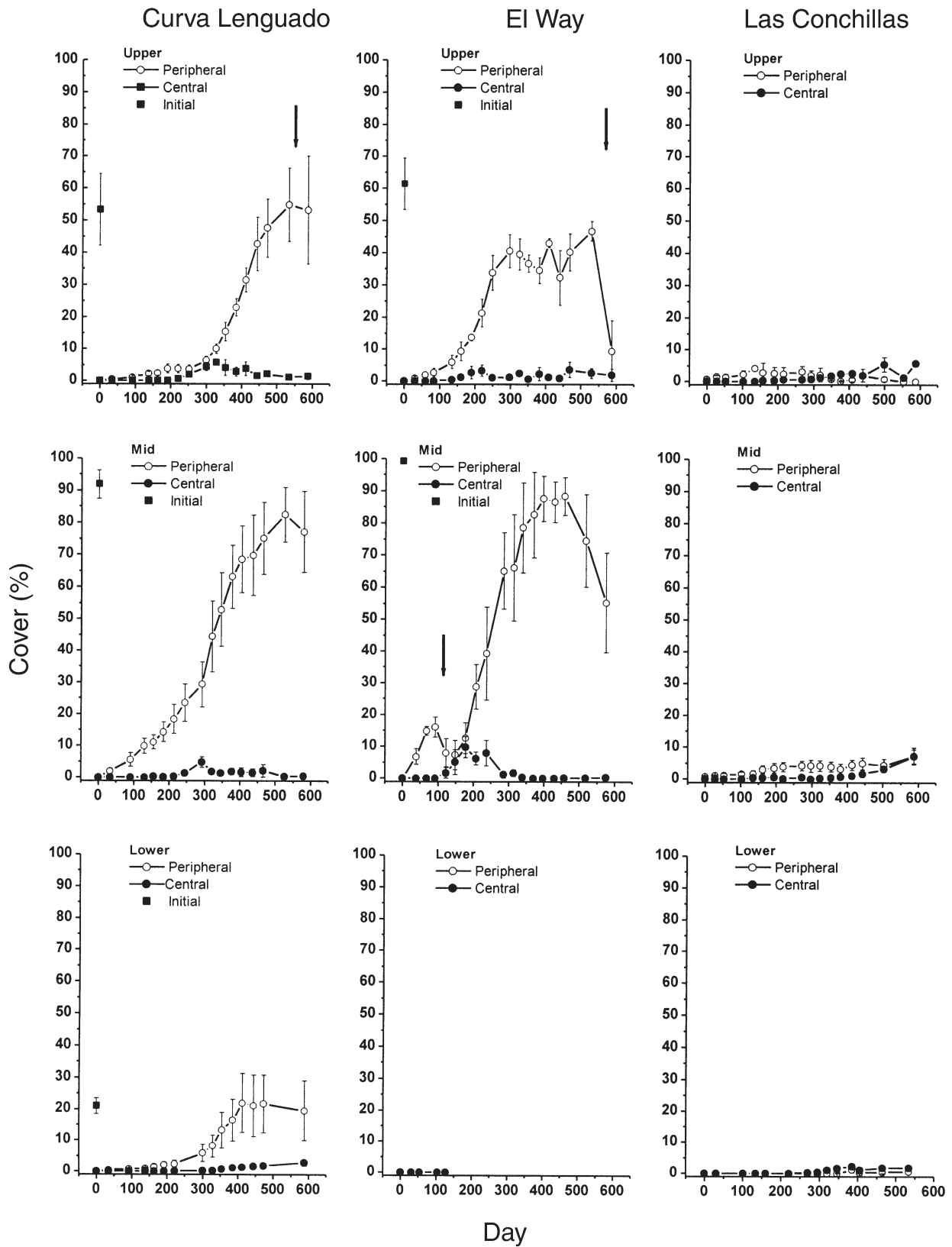


Fig. 3. *Pyura praeputialis*. Observed recolonization rates at the 3 study sites and the 3 intertidal *P. praeputialis*-levels (upper, mid, and lower intertidal). Arrows: intertidal perturbation caused by winter storm-waves

Pyura praeputialis level (ca 10%) followed by the upper (ca 5%) and lower-*Pyura praeputialis* (ca 2.5 %) levels (Fig. 3).

Patterns of recolonization as a function of vertical level

All 3 localities showed the highest initial percent cover in the middle of *Pyura praeputialis*' vertical distribution. This level also had the highest recolonization rate and attained the highest percent cover of all 3 levels (Fig. 3).

At the upper-*Pyura praeputialis* level, the localities not only attained different percent cover, but they did so at different rates. The highest percent cover was attained by Curva Lenguado, followed by El Way and Las Conchillas. Las Conchillas had a much lower percent cover than the other 2 sites. Curva Lenguado attained its maximum percent cover gradually. El Way had the highest recovery rate, but its dynamics seemed to fluctuate more around the maximum level than at Curva Lenguado (Fig. 3).

At the mid-*Pyura praeputialis* level, El Way and Curva Lenguado displayed similar dynamics, attaining comparable percent cover. El Way, however, had a shorter recovery time. Las Conchillas attained not only a lower percent cover but also at a much lower rate. Similar to the situation in the upper quadrats, fastest recovery was at El Way, which also showed the highest reduction in percent cover at the end of the sampling period. Curva Lenguado showed a gradual increase in percent cover and a little reduction at the end of the sampling period (Fig. 3).

For the lower-*Pyura praeputialis* level, the data is scarce and sketchy. Only Curva Lenguado could be properly evaluated, since it was the only locality for which both previous data and monitoring data existed. For El Way, more than 1 yr of data was lacking, and for Las Conchillas there was no previous data. Curva Lenguado seemed to attain maximum percent cover within 1 yr and fluctuated slightly around this value. Las Conchillas showed a much lower percent cover and little fluctuation around its maximum value (Fig. 3).

Recolonization mechanism

Most of the observed recruitment was due to peripheral growth. The relative contribution of central growth to total recruitment was negligible for most quadrats. Central recruitment appeared to be most important at all 3 *Pyura praeputialis*-levels in Las Conchillas, and marginally important at the mid level in El Way (Fig. 3).

Recolonization modeling

Patterns of recolonization can be best evaluated by analyzing the results obtained by fitting the asymptotic model: $y = a/[1 + \exp[-(x - b)/c]]$. Analyses of the model parameters allowed us to objectively compare site-by-level differences among quadrats. Asymptotic percent cover was estimated by Parameter a , and time for 50% recovery (50% of maximum cover) by Parameter b , whereas Parameter c defines the shape of the curve (growing phase). El Way and Curva Lenguado had higher asymptotic values than Las Conchillas, as evidenced by their parameter a (i.e. percent cover) values (Fig. 3, Table 1).

The turnover rate can partly be inferred from the value of Parameter b . Even though El Way and Curva Lenguado had similar asymptotic values for the upper and mid *Pyura praeputialis*-level quadrats, El Way had a shorter recovery time, as evidenced by the estimate for Parameter b (i.e. time for 50% recovery) (Fig. 3, Table 1). This is consistent with field observations, and could be regarded as further evidence of faster recolonization rates at El Way. The pattern was also consistent with our expectations within sites, with the mid-*Pyura praeputialis* level quadrats having the highest asymptotes and faster recolonization rates, followed by the upper and finally by the lower-*Pyura praeputialis* level quadrats (Fig. 3, Table 1). At Las Conchillas, the estimates for Parameters a and b in the mid quadrats, were not significantly different from 0, indicating that the dynamics at this particular site and level are not yet well defined. The results of adjusting the asymptotic model to the observed data could be considered as the primary step in describing the dynamics of *P. praeputialis* intertidal beds. The results should be considered as preliminary, and can serve as a starting point for further analyses.

Empirical model

The evolution of the patch perimeter was counterintuitive in the sense that initially it tended to increase rather than decrease, contrary to what would be expected for a regular shape decreasing in size. The reason, however, seemed obvious after analysis. Recruiting *Pyura praeputialis* are not perfect squares and do not recruit at regular intervals, and therefore the evolution of perimeter was far from an idealized, perfect rectangle decreasing in size. However, if the best function to describe the evolution of recolonization is an asymptotic logistic-like function, then the rate of change (slope of the function) should be quadratic or almost so (peak equation). Also, if recolonization is a function of the perimeter of the patch rather than of its area, a function

Table 1. *Pyura praeputialis*. Recolonization dynamics at different sites and vertical levels corresponding to upper, mid and lower distribution in intertidal beds. Parameter estimation uses the asymptotic model: $y = a / \{1 + \exp[-(x - b)/c]\}$. Parameter a = percent cover, b = time for 50% recovery, c = shape of the curve (growing phase) *: not significant. t -values correspond to hypotheses testing for values of the parameters being equal to zero

Tidal level	Parameter	Value	SE	t -value	95 % confidence limits	
Las Conchillas						
Upper	a	3.582	0.300	11.956	2.939	4.225
	b	54.485	27.553	1.977	-4.648	113.617
	c^*	44.527	27.375	1.627	-14.224	103.277
Middle	a^*	1035.789	73415.925	0.014	-156527.355	158598.933
	b^*	1876.548	20922.167	0.090	-43026.004	46779.099
	c	285.473	111.768	2.554	45.601	525.346
Lower	a	2.441	0.259	9.436	1.863	3.019
	b	323.626	10.527	30.742	300.111	347.140
	c^*	15.131	9.159	1.652	-5.328	35.591
El Way						
Upper	a	41.439	1.418	29.216	38.395	44.483
	b	200.378	7.768	25.794	183.706	217.050
	c	35.310	7.114	4.963	20.041	50.578
Middle	a	92.752	3.786	24.497	84.562	100.942
	b	238.634	9.386	25.425	218.332	258.936
	c	63.829	6.620	9.642	49.510	78.148
Curva Lenguado						
Upper	a	59.006	1.667	35.393	55.428	62.584
	b	389.061	5.188	74.998	377.928	400.195
	c	57.633	3.828	15.056	49.418	65.849
Middle	a	83.882	2.103	39.894	79.369	88.394
	b	302.803	6.140	49.314	289.625	315.981
	c	71.612	4.463	16.045	62.034	81.191
Lower	a	23.924	0.944	25.341	21.863	25.984
	b	341.775	5.783	59.105	329.155	354.395
	c	35.705	5.573	6.407	23.543	47.867

based on the evolution of the perimeter could be used to model recolonization dynamics. As expected, the observed perimeter could be predicted from the area occupied by *P. praeputialis* using a logistic equation of the form: $y = 4an / (1 + n)^2$; with $n = \exp[-(x - b)/c]$ (Fig. 4). The method used to model recolonization seems to have adequately reproduced the main characteristics of the *Pyura praeputialis* recolonization dynamics, as evidenced by the shape of the predicted curves for all 3 sites (Fig. 5). El Way showed the highest value for the coefficients used to scale perimeter ($q = 0.540$), followed by Curva Lenguado ($q = 0.439$), and Las Conchillas ($q = 0.154$).

DISCUSSION

The addition of new recruits to the intertidal *Pyura praeputialis* beds seems to be facilitated by the presence of conspecific adults. Most of the increase in percentage cover is attributable to the addition of recruits to the bases of attached individuals and their subsequent growth, along the borders of patches, as indicated by the high contribution of the borders to the

total increase in percentage cover observed. The relative contribution of central recruitment to total increase is difficult to assess, and could be even lower than estimated. Once a central recruit is established it immediately creates a border zone around itself. Therefore, further recruitment to its neighborhood could be considered border recruitment in the sense that it differs from recruitment to bare space. The relatively lower recruitment to the lower-*P. praeputialis* level might, in part, be explained by this mechanism. The lower-*P. praeputialis* level is characterized by the discontinuity of the *P. praeputialis* bed, and therefore at most has only 1 border along which the presence of adults could favor recolonization. The same is true for Las Conchillas where, because of the reduced densities observed prior to clearance, a reduced border effect was expected. Predation by the starfish *Heliaster helianthus* and *Stichaster striatus* could also be responsible for the lower recolonization rate in the lower *P. praeputialis* quadrats. Both predator species are frequently observed in the low intertidal zone preying mainly, but not exclusively, on sessile animals including *P. praeputialis* (Paine & Suchanek 1983).

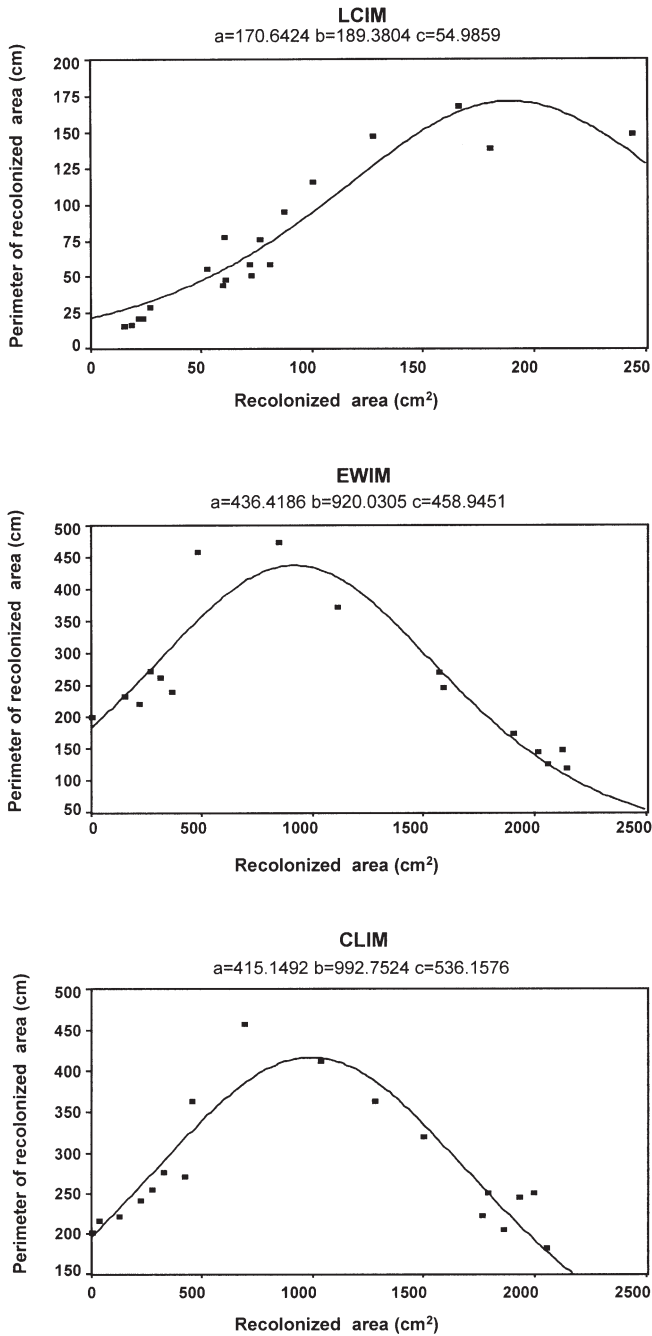


Fig. 4. *Pyura praeputialis*. Predicted perimeter of intertidal recolonized area using occupied area as predicting variable. Perimeter was estimated using the function: $y = 4an/(1 + n)^2$; $n = \exp[-(x - b)/c]$. LCIM: Las Conchillas mid; EWIM: El Way mid; CLIM: Curva Lenguado mid

The higher *Pyura praeputialis* recolonization rate at El Way together with a higher disturbance frequency (Fig. 3) indicates a higher turnover rate at this locality. Winter storms seem to disturb the platforms at El Way fairly regularly within intervals of close to 1 yr (Fig. 3, and Castilla pers. obs.). Moreover, the intertidal plat-

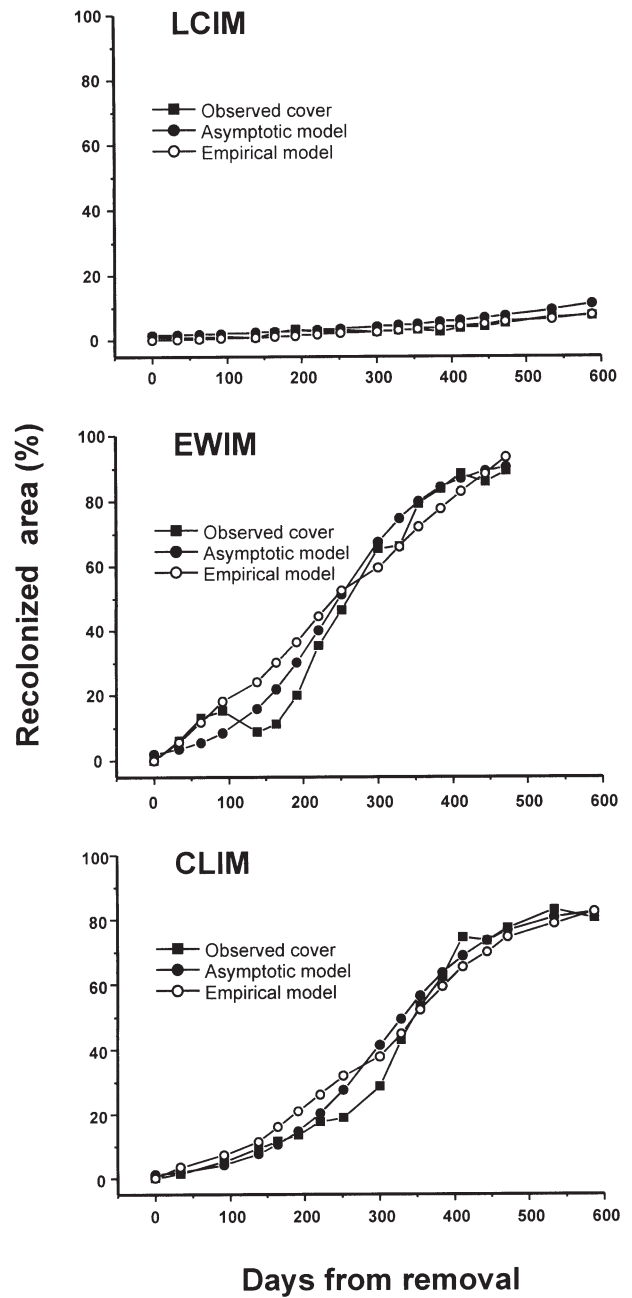


Fig. 5. *Pyura praeputialis*. Observed and model-predicted intertidal recolonization in mid-level quadrats. LCIM: Las Conchillas mid; EWIM: El Way mid; CLIM: Curva Lenguado mid

forms at El Way are constantly used as a foraging area by American oystercatchers *Haematopus palliatus pitanay* (see Pacheco & Castilla 2000, 2001), which prey on *P. praeputialis*, and generate multiple regions of instability in the tunicate beds, thus contributing to the higher instability of the platforms in this locality

during exposure to storm waves (Castilla pers. obs.). The higher *P. praeputialis* recruitment at El Way was expected for at least for 2 reasons: (1) the presence of extensive *P. praeputialis* intertidal beds, which would produce a higher availability of larvae; (2) a higher retention of larvae due to the substrate heterogeneity constituted by adult *P. praeputialis* and the reduced slope of the intertidal platforms. Thus, the higher turnover rate at El Way would be expected, as a result of increased disturbance and recruitment. In contrast, Las Conchillas showed the lowest recolonization rate of all 3 localities. Here probably because of the low recolonization rate, the quadrats did not seem to have attained an asymptotic level but to be still approaching it. This must also be considered a probable source of uncertainty in the estimation of parameters for the asymptotic model.

The observed recolonization rates can in part be explained by the differences in adult abundance between Las Conchillas and the other 2 localities (see Castilla et al. 2000 for information on density and biomass in these localities). As reported by Castilla et al. (2000), Las Conchillas has the lowest density and biomass of adults of all 3 localities. For species in which the time between larval release and settlement is relatively short (see Clarke et al. 1999 for information on *Pyura praeputialis*) we would expect the abundance of recruits, and therefore recolonization rate, to be related to the local abundance of adults.

The results from our empirical model strongly suggest that the main mechanism of *Pyura praeputialis* recolonization is related to self-facilitation. On the one hand, the perimeter alone (i.e. a linear function of the perimeter) seems capable of explaining the rate at which patches are colonized: this is in accordance with the actual observations that most recruitment was to the patch borders. On the other hand, a simple function by which the recolonized area is predicted from the area already occupied and the perimeter observed at $t-1$ (scaled by a linear coefficient) is capable of reproducing the general pattern of recolonization observed at all 3 sites.

Results from a preliminary, spatially explicit, lattice model, in which the probability of successful recruitment of a new settler increased in the proximity of previously settled individuals, not only reproduced the recolonization patterns observed in nature, but also revealed dynamics similar to those in the present study for intertidal populations of *Pyura praeputialis*, and differed from the pattern produced by a neutral and constant-rate model (Fig. 6). This confirms our findings and suggests possible mechanisms explaining the observed patterns. The increased recruitment near pre-settled *P. praeputialis* can be interpreted in at least 3 ways: (1) as a result of differential survival of individuals recruiting

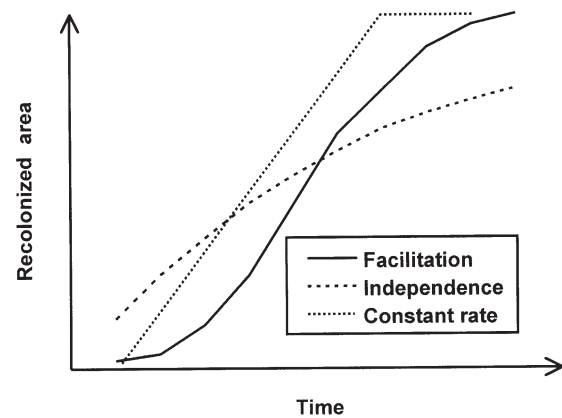


Fig. 6. *Pyura praeputialis*. Theoretical recolonization patterns in 3 different situations. Data from simulations using spatially-explicit lattice models. In the facilitation model, a few cells have a probability of settlement of $0 < p \leq 1$ (p uniformly distributed), but settled individuals increase the probability in their surrounding cells. In the independence model, probability of settlement is assigned randomly to the lattice cells and does not change with the presence of individuals; recruits can be assigned to empty or occupied cells. In the constant-rate model, a fixed number of recruits are randomly assigned to empty cells

in a random manner to the open patch; (2) as a result of differential recruitment to the patch border; (3) as a combination of both mechanisms.

Differential survival could result from changes in environmental conditions produced by previously settled individuals (Jones et al. 1994, 1997). Increased recruitment could result from microscale hydrodynamic changes produced by previously settled individuals that result in increased retention of recruits near the border (Eckman 1983, Grégoire et al. 1996), or could be a behavioral adaptation of larvae to settle near conspecific individuals, whereby the larvae actively seek sites in which conspecifics are already present (Jensen & Morse 1984, Burke 1986, Chabot & Bourget 1988, Minchinton 1997). The restricted distribution of this tunicate species is probably related to its recruitment pattern. Its low densities observed near the limit of its distribution and its short larval life-span could both contribute to further restraining the expansion of *Pyura praeputialis*' limits.

This study highlights the possibility of modeling, in simple ways, the colonization patterns observed in nature and the necessity of relating systematic field observations with analytic and theoretic background on the species studied.

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