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Recruitment variation in subtidal macrofouling assemblages of a Patagonian harbour (Argentina, south-western Atlantic)

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The recruitment of subtidal macrofouling organisms was studied in the Patagonian harbour of Comodoro Rivadavia (Argentina, 45°51′35″S 67°27′23″W). Changes in coverage and density were analysed in the central 100 cm² of upper and lower surfaces which were replaced monthly from January to December 2004. The fouling assemblage consisted of algae, spirorbid polychaetes, compound ascidians, hydrozoans, bryozoans and egg masses spawned by the small fish Helcogrammoides cunninghami. *Monthly changes in richness and diversity of taxa on upper and lower surfaces were significantly correlated with sea surface temperature. Fouling assemblage structure differed significantly between upper and lower surfaces. Filamentous algae were dominant on upper surfaces, while filter-feeding invertebrates were more abundant on the lower surfaces of the experimental panels. The density of the spirorbid* Romanchella scoresbyi *was two orders of magnitude higher on lower than on upper surfaces. Its recruitment began in late winter, reaching maximum values in spring.*

Keywords: recruitment, macrofouling, Comodoro Rivadavia harbour, Patagonia, Argentina

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INTRODUCTION

The supply of recruits from the plankton is usually a critical process that determines structure in benthic assemblages (Underwood & Denley, 1984; Underwood & Fairweather, 1989), since competitive interactions (Connell, 1961) and predation (Paine, 1971) may be key factors only in locations where recruitment is high (Gaines & Roughgarden, 1985). Several studies have analysed monthly recruitment patterns on artificial substrata immersed in harbours (e.g. Chalmer, 1982; Satheesh & Wesley, 2008), as this variation has important implications from both theoretical and applied points of view (Sutherland & Karlson, 1977; Dean & Hurd, 1980; Underwood & Anderson, 1994). Timing of panel immersion and the seasonal pattern of initial recruitment was found to influence the competitive outcome and succession of sessile organisms (Nandakumar, 1995, 1996). Orientation of substrata has also important effects, since epibiotic assemblages on upper and lower surfaces are often significantly different (Barnes, 1996; Glasby & Connell, 2001; Stark, 2008).

On the coast of Argentina (south-western Atlantic), the composition and temporal changes of fouling assemblages have been explored mainly in warm-temperate harbours of Buenos Aires Province (see e.g. Bastida, 1971; Bastida *et al*., 1974, 1980; Brankevich *et al*., 1988), but the available information on the macrofouling of cold-temperate Patagonian harbours is scarce (Bastida, 1973; Rico *et al*., 2005; Rico & López Gappa, 2006 and references therein; Schwindt *et al*., 2008). Therefore, the aims of this study are: (1) to identify the macrofouling taxa and describe their recruitment periods on artificial substrata in the Patagonian harbour of Comodoro Rivadavia; and (2) to compare the fouling assemblages which developed on upper and lower surfaces of experimental panels.

MATERIALS AND METHODS

Study area

Comodoro Rivadavia harbour (Figure 1; 45°51′35″S 67°27′23″W) was built between 1924 and 1929. A new breakwater was added in 1996 using natural rocks and man-made concrete blocks. Tidal amplitude during spring and neap tides are 6.21 and 4.34 m, respectively. Sea surface temperatures at Comodoro Rivadavia harbour were provided by Centro Argentino de Datos Oceanográficos (CEADO). The range of surface temperatures is around 15°C, with maximum and minimum values recorded during February (summer) and August (winter), respectively (Figure 2). Salinity shows minor variations, due to the absence of freshwater courses and the scarcity of precipitation in the area (Paruelo *et al*., 1998; Bertness *et al*., 2006). Oceanographic surveys in San Jorge Gulf confirm this pattern for the coastal zone, where the extreme values recorded between

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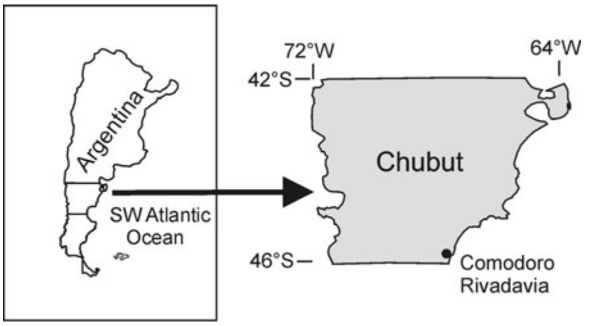

Fig. 1. Location of study area.

1999 and 2000 ranged between 33.07 and 33.80 psu (Fernández *et al.*, 2005).

Sampling

Artificial substrata were immersed in the harbour 4 m below mean low water and were never exposed during low tides. They consisted of 20 cm × 20 cm × 0.4 cm (400 cm^2) low-density polyethylene panels screwed to horizontal supporting structures of galvanized iron lying around 10 cm above the bottom. Panel surfaces were roughened to promote the settlement of sessile organisms. For the analysis of recruitment, we deployed 5 monthly replicates separated from each other by around 2 m. They were replaced at approximate monthly intervals from January 2004 to January 2005 (Table 1). During the collection of samples, each panel was placed in seawater within a zip-locked plastic bag to prevent the loss of organisms. Samples were then fixed in a solution of 4% formaldehyde in seawater and later preserved in 70% ethanol. To avoid any border effect, only the central 10 × 10 cm (100 cm^2) of the upper and lower surfaces was analysed. Thus, a total of 120 sampling units were examined (12 months × 5 replicates × 2 surfaces). Organisms were identified to the lowest taxonomic level possible without disturbing their spatial distribution on the panels. Specimens found outside the central 100 cm^2 were collected and used for taxonomic purposes. Coverage of each taxa was quantified by superposing a transparent plastic sheet with a grid of 100 regularly spaced points. The density of the small but very abundant spirorbid polychaete *Romanchella scoresbyi* was also quantified by counting the number of calcareous tubes in the central area.

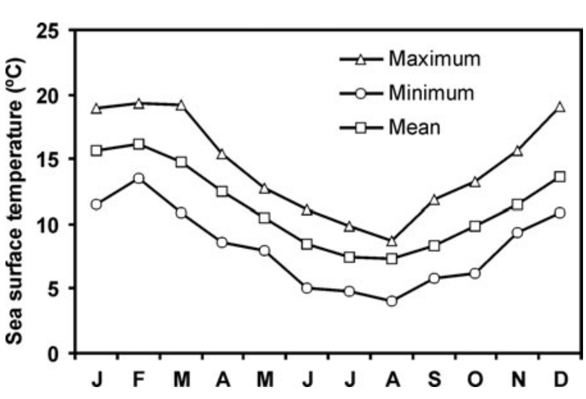

Fig. 2. Sea surface temperatures at Comodoro Rivadavia harbour.

Table 1. Sampling scheme for the study of recruitment at Comodoro Rivadavia harbour.

Date of immersion	Date of collection	Period of immersion
5 January 2004	10 February 2004	36
10 February 2004	8 March 2004	27
8 March 2004	7 April 2004	30
7 April 2004	5 May 2004	28
5 May 2004	9 June 2004	35
9 June 2004	6 July 2004	27
6 July 2004	4 August 2004	29
4 August 2004	3 September 2004	30
3 September 2004	4 October 2004	31
4 October 2004	3 November 2004	30
3 November 2004	3 December 2004	30
3 December 2004	4 January 2005	32

Data analysis

The basic data matrix was analysed with the PRIMER package (Clarke & Warwick, 2001). The DIVERSE routine was used to calculate richness and the Shannon–Wiener diversity index (log_e) of each sample. Coverage data were fourth-root transformed to reduce the influence of dominant taxa. A triangular similarity matrix was obtained applying the Czekanowski index (identified as the Bray–Curtis index in the PRIMER package, see Yoshioka, 2008). An ordination of samples was later produced by non-metric multidimensional scaling. The stress value indicates to which extent the bidimensional ordination is a satisfactory representation of the distances among samples in the similarity matrix. The hypothesis that the structure of assemblages developed on upper and lower surfaces differs significantly was tested by a one-way ANOSIM test (Clarke & Warwick, 2001). The SIMPER routine was then applied to obtain a list of taxa whose differences in coverage best discriminate between both surfaces.

Rank correlations between sea surface temperature and richness of taxa or Shannon–Wiener's diversity were calculated with the Spearman index (Sokal & Rohlf, 1981) using Statistica® 6.0.

RESULTS

The total number of taxa recruited during the whole study period was similar on upper and lower surfaces (10 to 11; Table 2). The fouling assemblage consisted of filamentous seaweeds, encrusting coralline algae, spirorbid polychaetes, compound ascidians, hydrozoans, cheilostome bryozoans and egg masses spawned by the small tripterygid fish *Helcogrammoides cunninghami* (Smitt) (Table 2). Monthly changes in number of taxa and Shannon–Wiener's diversity (Figure 3) were significantly correlated with sea surface temperature (Table 3) and followed a similar pattern on upper and lower surfaces, with the exception that a second peak in richness was observed on the lower surfaces during the autumn (April) (Figure 3).

Fouling assemblages on upper and lower surfaces were significantly different (Figure 4; one-way ANOSIM test, global $R = 0.2$, $P = 0.001$). The SIMPER routine (Table 4) showed that this difference was mainly due to the abundance of filamentous algae on upper surfaces, particularly the rodophyte *Polysiphonia* aff. *abscissa* J.D. Hooker & Harvey, the

Table 2. Coverage (mean ± SE, N = 5) on upper and lower surfaces.

	January	February	March	April	May	June	July	August	September	October	November	December
Upper surfaces												
Ceramium rubrum (Rh)	–	–	–	–	0.4 ± 0.4	–	–	–	–	–	–	0.2 ± 0.2
Encrusting coralline (Rh)	0.4 ± 0.4	–	–	–	–	–	–	–	–	–	–	–
Diatoms	26.4 ± 6.8	27.6 ± 9.1	22.2 ± 10.2	44.2 ± 8.5	62.8 ± 8.6	81.0 ± 10.0	83.6 ± 5.4	69.6 ± 9.9	57.4 ± 7.8	62.4 ± 14.9	60.0 ± 9.7	52.8 ± 4.4
Ectocarpus sp. (Ph)	–	8.6 ± 4.0	19.0 ± 2.9	15.6 ± 4.6	0.8 ± 0.8	–	–	5.6 ± 3.3	1.2 ± 1.0	2.0 ± 1.8	10.6 ± 3.4	5.0 ± 1.8
Polysiphonia aff. *abscissa* (Rh)	38.6 ± 8.1	19.6 ± 5.8	28.4 ± 5.6	14.2 ± 5.4	0.8 ± 0.4	–	0.2 ± 0.2	0.2 ± 0.2	1.0 ± 0.6	2.6 ± 1.3	10.4 ± 3.8	16.4 ± 6.2
Scytosiphon lomentaria (Ph)	–	–	–	–	5.8 ± 5.8	–	–	–	–	–	–	–
Ulva spp. (Ch)	4.6 ± 1.9	29.4 ± 13.1	12.4 ± 6.6	5.4 ± 2.3	5.6 ± 3.8	–	–	–	–	0.2 ± 0.2	8.2 ± 6.3	16.4 ± 5.4
Diplosoma longinquum (As)	–	0.2 ± 0.2	1.4 ± 1.0	1.2 ± 1.2	–	–	–	–	–	–	–	–
Helcogrammoides cunninghami (eggs) (Pi)	–	–	9.0 ± 4.2	–	–	–	–	–	–	–	–	–
Obelia sp. (Hy)	–	–	–	–	–	–	–	–	–	–	–	0.2 ± 0.2
Bare substratum	30.0 ± 12.1	14.6 ± 8.6	7.6 ± 2.8	19.4 ± 9.1	23.8 ± 6.5	19.0 ± 10.0	16.2 ± 5.5	24.6 ± 7.7	40.4 ± 8.2	32.8 ± 15.9	10.8 ± 6.6	9.0 ± 7.0
Lower surfaces												
Encrusting coralline (Rh)	0.2 ± 0.2	–	–	–	–	–	–	–	–	–	–	–
Diatoms	6.2 ± 2.9	20.0 ± 3.2	30.8 ± 4.6	48.6 ± 7.6	47.0 ± 12.1	10.8 ± 2.9	8.2 ± 4.9	6.6 ± 3.7	24.0 ± 7.4	35.0 ± 9.2	59.0 ± 4.8	57.0 ± 4.2
Ectocarpus sp. (Ph)	–	–	–	0.4 ± 0.2	1.0 ± 1.0	–	–	–	–	0.2 ± 0.2	0.2 ± 0.2	0.4 ± 0.4
Polysiphonia aff. *abscissa* (Rh)	0.6 ± 0.4	4.2 ± 2.5	1.4 ± 1.2	2.8 ± 1.8	–	–	–	–	0.2 ± 0.2	1.8 ± 0.5	2.2 ± 1.0	5.2 ± 1.4
Ulva spp. (Ch)	0.4 ± 0.4	0.2 ± 0.2	0.4 ± 0.2	–	–	–	–	–	–	–	0.2 ± 0.2	–
Sea anemones	–	0.2 ± 0.2	–	0.2 ± 0.2	–	–	–	–	–	–	–	–
Cryptosula pallasiana (Br)	1.0 ± 0.5	–	–	–	–	–	–	–	–	–	–	–
Diplosoma longinquum (As)	–	5.8 ± 2.3	0.2 ± 0.2	0.6 ± 0.4	0.8 ± 0.6	–	–	–	–	–	–	–
Helcogrammoides cunninghami (eggs) (Pi)	–	–	0.4 ± 0.2	–	–	–	–	–	–	–	–	–
Obelia sp. (Hy)	–	–	–	0.4 ± 0.2	–	–	–	–	–	–	–	0.8 ± 0.6
Romanchella scoresbyi (Po)	2.4 ± 0.7	–	–	0.2 ± 0.2	0.2 ± 0.2	–	–	0.2 ± 0.2	0.2 ± 0.2	0.2 ± 0.2	0.4 ± 0.2	0.6 ± 0.4
Bare substratum	89.2 ± 4.0	69.6 ± 3.2	66.8 ± 3.9	46.8 ± 7.9	51.0 ± 12.1	89.2 ± 2.9	91.8 ± 4.9	93.2 ± 3.7	75.6 ± 7.7	62.8 ± 9.2	38.0 ± 4.9	36.0 ± 5.5

Rh, Rhodophyta; Ph, Phaeophyta; Ch, Chlorophyta; As, ascidian; Pi, fish; Hy, hydrozoan; Br, bryozoan; Po, polychaete.

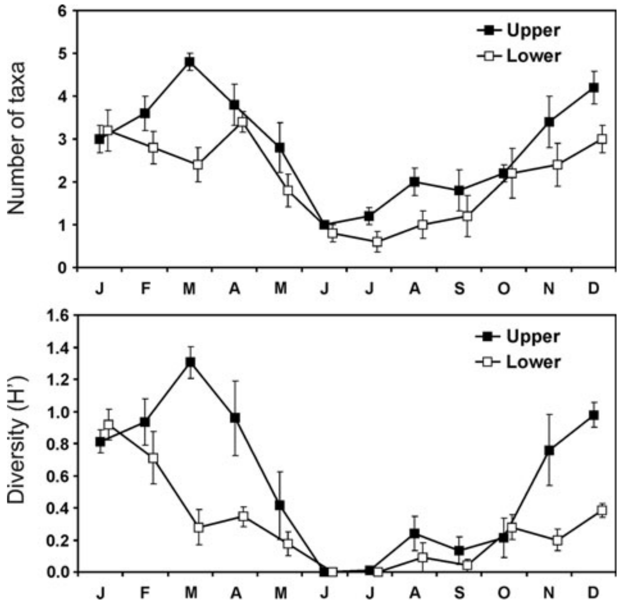

Fig. 3. Monthly changes in the number of taxa and Shannon–Wiener's diversity (mean ± SE, N = 5) of fouling assemblages on upper and lower surfaces.

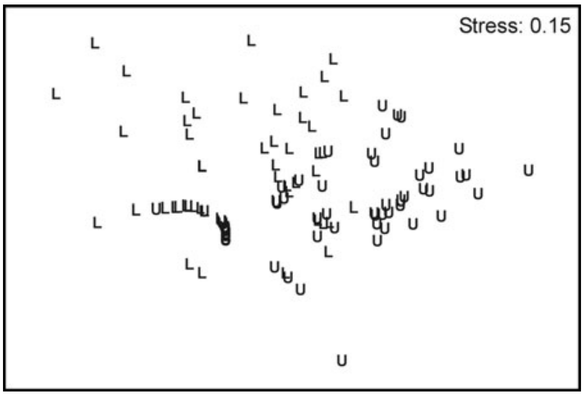

Fig. 4. Multidimensional scaling ordination based on fourth-root transformed coverage data of monthly assemblages on upper (U) (N = 60) and lower (L) (N = 55) surfaces. Five lower panels sampled from June to September were excluded from this analysis due to complete absence of macrobenthic organisms.

phaeophyte *Ectocarpus* sp., diatoms and chlorophytes belonging to the genus *Ulva* (formerly *Enteromorpha*, see Hayden *et al.*, 2003). On the other hand, filter-feeding invertebrates such as spirorbids and compound ascidians were more abundant on lower than on upper surfaces.

The density of the calcareous tubes of *Romanchella scoresbyi* (Harris) (Figure 5; recorded as *R. perrieri* (Caullery & Mesnil) and *Paralaeospira levinseni* (Caullery & Mesnil) in Rico & López Gappa, 2006) was 2 orders of magnitude higher on lower than on upper surfaces. Its recruitment on lower surfaces began on late winter (August), reaching maximum values in spring. A much smaller recruitment peak was observed during the autumn (April–May). *Romanchella scoresbyi* was almost absent on panels deployed during late summer (February–March) and early to mid-winter (June–July).

DISCUSSION

The present study shows that orientation of the experimental panels was a critical factor determining the composition and structure of the fouling assemblages which developed on them. Previous studies also found significant differences between fouling assemblages on upper and lower (Stark, 2008) or vertical and horizontal surfaces (Glasby & Connell, 2001). The identity of the dominant species and the competitive hierarchy were shown to be markedly different on sunlit or shaded surfaces of panels immersed in Tomioka Bay, Japan (Nandakumar, 1995). A widespread pattern observed on most shallow subtidal substrata is that upward-facing surfaces are monopolized by algae, whereas downward-facing surfaces are dominated by sessile invertebrates. Light and sedimentation interact in complex ways with surface orientation to maintain this pattern of habitat heterogeneity (Irving & Connell, 2002). In the first few months after settlement, mortality of coral larvae was highest on highly sedimented upper surfaces of experimental substrata (Babcock & Mundy, 1996). Preference for lower surfaces may also be due to active larval behaviour during settlement, since larvae of sponges and other invertebrates settle mainly on the undersurfaces of artificial substrata they were offered, regardless of which microhabitat they were placed in (Maldonado & Young, 1996). Bryozoans were almost entirely confined to the undersurfaces of rocks in encrusting communities from the Antarctic sublittoral, and the proportion of colonies occurring on the upper surfaces decreased in the deepest samples, where silt deposition apparently became a major influence (Barnes *et al.*, 1996). Acrylic panels immersed in Antarctica were dominated by

Table 3. Spearman rank correlations (R$_s$) between sea surface temperatures (°C) and richness of taxa/Shannon–Wiener's diversity on upper and lower surfaces.

	Rs	*P* value
Temperature-richness (upper surfaces)	0.804	0.002
Temperature-diversity (upper surfaces)	0.804	0.002
Temperature-richness (lower surfaces)	0.844	0.001
Temperature-diversity (lower surfaces)	0.862	0.003

Table 4. SIMPER analysis based on fourth-root transformed coverage data of fouling assemblages developed on upper and lower surfaces.

	Upper surfaces	**Lower surfaces**		
Taxa	**Average abundance**	**Average abundance**	**% contribution to dissimilarity**	**Cumulative % contribution**
Polysiphonia aff. *abscissa*	11.03	1.67	25.0	25.0
Ectocarpus sp.	5.70	0.20	18.2	43.2
Diatoms	54.17	32.11	17.9	61.2
Ulva spp.	6.85	0.11	17.0	78.2
Romanchella scoresbyi	0.00	0.40	6.5	84.7
Diplosoma longinquum	0.23	0.67	6.2	90.9

The list was truncated when cumulative percentage reached 90%. Average dissimilarity = 43.38.

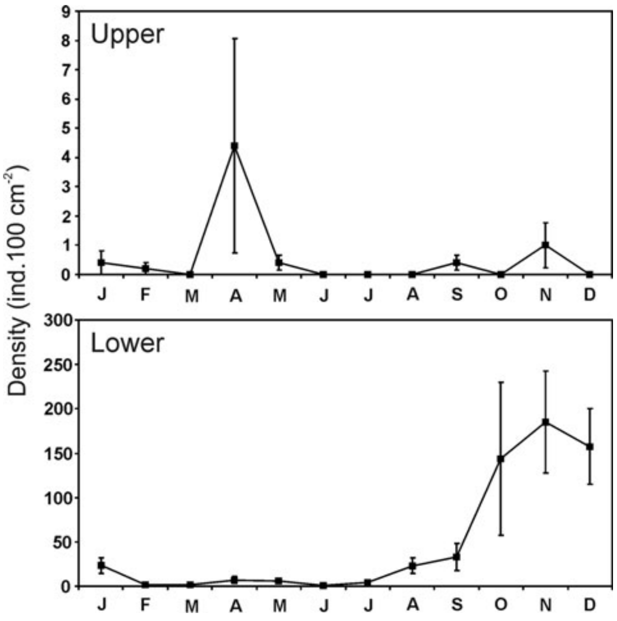

Fig. 5. Density (mean ± SE, N = 5) of the spirorbid polychaete *Romanchella scoresbyi* on upper and lower surfaces. Note the change of scale between both graphs.

encrusting bryozoans and spirorbid polychaetes (Bowden *et al.*, 2006). Recruitment rates of these taxa on upward-facing surfaces were comparable with that to downward-facing surfaces, but reduction in the number of recruits on upper surfaces suggested that post-settlement mortality may be important (Bowden, 2005).

The filter-feeding polychaete *Romanchella scoresbyi* was originally described from Tristan da Cunha (Harris, 1969) and later recorded for Marion Island and the Patagonian coast, where it was found on the fronds of the kelp *Macrocystis* (Knight-Jones & Knight-Jones, 1984). The biology of this species is almost completely unknown, except for the fact that up to 16 embryos can be incubated simultaneously in its tube (Harris, 1969). The existence of a bimodal recruitment in *R. scoresbyi* agrees with the temporal variability of the phytoplanktonic biomass of San Jorge Gulf, which shows the typical cycle of temperate water masses, with a main peak during spring and a secondary one during autumn (Cucchi Colleoni & Carreto, 2003; Fernández *et al.*, 2008).

The cheilostome *Cryptosula pallasiana* (Moll), a very common non-indigenous fouling bryozoan of worldwide distribution (Gordon & Mawatari, 1992), was already known from warm-temperate localities in the south-western Atlantic. It was found in Rio de Janeiro (Vieira *et al.*, 2008), Uruguay (see Scarabino, 2006) and the Argentine harbours of Mar del Plata, Quequén and Puerto Belgrano (Lichtschein de Bastida & Bastida, 1980), and had been recorded for the first time in Comodoro Rivadavia during a previous study (Rico & López Gappa, 2006).

The feeding habit of the small carnivorous fish *Helcogrammoides cunninghami* (=*Tripterygion cunninghami*) has been studied at the temperate coast of central Chile, where this species is a permanent resident of the intertidal zone. Its diet seems to be rather constant during ontogeny, as it consists mainly of amphipods (Muñoz & Ojeda, 1998).

This is the first record of the compound ascidian *Diplosoma longinquum* (Sluiter) for the Patagonian coast (see also Varela, 2007). It is not clear whether this species should be regarded as exotic, because it was previously recorded for the Antarctic Peninsula and near the Burdwood Bank, a relatively shallow area lying just south of the Malvinas/Falkland Islands (Kott, 1969, 1971).

During a preliminary study of the fouling assemblages of Comodoro Rivadavia harbour based on stones immersed during 84 to 100 days we found 31 taxa at the subtidal level (Rico & López Gappa, 2006). At least 29 sessile taxa have been identified in annual successions developed in this harbour (Rico, unpublished), a much higher figure than the 13 taxa found in the present study on surfaces replaced on a monthly basis (Table 2). This suggests that the length of the immersion period is a critical factor regulating biodiversity in this macrofouling assemblage, probably due to facilitation mechanisms by which pioneering species create suitable conditions for the settlement and establishment of later recruits (Connell & Slatyer, 1977).

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