

RECOVERY OF *DURVILLAEA ANTARCTICA* (DURVILLEALES) INSIDE AND OUTSIDE LAS CRUCES MARINE RESERVE, CHILE

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Abstract. We present the results for over two decades of monitoring on intertidal food-gatherers and the population of the low rocky shore dweller kelp *Durvillaea antarctica*, a short-distance disperser, inside and outside the no-take marine reserve, Estacion Costera de Investigaciones Marinas (ECIM), at Las Cruces, central Chile. It was hypothesized that protection of an initially extremely depleted population would recover by recolonizing first the no-take area and then adjacent non-protected (exploited) areas. We found that recovery of *D. antarctica* occurred slowly inside ECIM, with increase in density and biomass, of up to three orders of magnitude as compared to an adjacent non-protected area, which showed ~2-yr delay. These results suggest that the kelp population inside ECIM was likely regulated via intraspecific competition, which did not occur outside. Results showed no evidence for juvenile vs. adult density dependence other than a weak relationship for the central area of ECIM. These findings also suggest that the population recovery and cross-boundary seeding subsidies affected the population dynamics. Understanding these dynamics may enhance management and conservation policies. Our work highlights the critical value of baseline and long-term comparative studies in marine no-take protected and non-protected areas for understanding how population processes respond to human and conservation practices.

Key words: Chile; competition; conservation; cross-boundary seeding; *D. antarctica*; density dependence; food gatherers; marine reserve; population recovery.

INTRODUCTION

No-take Marine Protected Areas (MPAs) have gained worldwide recognition as a tool for biodiversity conservation and natural resource management. Benefits beyond their boundaries include their role as seeding grounds and improvements in fish extractions (Marríguez and Castilla 2001, Gell and Roberts 2003, Halpern 2003, Shears and Babcock 2003). Several objections have been risen to their value due to (1) the lack of baseline studies or information previous to MPAs establishment; (2) their small size, singularity, and lack of local/regional replication; (3) their limited value of inside (protected) vs. outside (non-protected) comparisons (Parnell et al. 2005, Sale et al. 2005). Conversely, not enough emphasis has been placed on MPAs role (1) in the recovery and persistence of overexploited populations, (2) as seeding grounds (spillover), (3) in improving our understanding of local ecological processes based on long-term data series.

In Chile, invertebrate and macroalgae extraction by intertidal food-gatherers and skin divers have been shown to significantly modify population and community structure of coastal systems (Moreno et al. 1984,

Castilla 1999). The Estacion Costera de Investigaciones Marinas (ECIM) reserve, at Las Cruces, central Chile, was established in 1982 as a protected research area, and since then it has been fenced to prevent human perturbations and harvesting. Since 1982, ECIM has served as a long-term experimental and observational system to (1) understand functional dynamics of rocky intertidal and shallow subtidal species (Castilla and Durán 1985, Oliva and Castilla 1986, Castilla and Bustamante 1989, Durán and Castilla 1989, Bustamante and Castilla 1990, Castilla 1999), (2) understand the role of human exploitation on rocky shores, (3) to assess how no-take MPA can act as a novel conservation and resource management tool (Castilla 1994, 2000, Fernandez and Castilla 2005).

Durvillaea antarctica, the bull-kelp, which has a short lived spore (~1–2 h [Buschmann et al. 1984]), inhabits exposed rocky intertidal and shallow subtidal sub-Antarctic and temperate southern hemisphere rocky shores (Hay 1977, Santelices et al. 1980). In Chile, the species is present throughout the Magellan region (~56–41° S), extending to ~32° S (~200 km north of ECIM). The stipe and dried fronds of *D. antarctica* have been exploited for human consumption in Chile initially by the Mapuches, prior to pre-Spanish settlement (Masuda 1986) and later on by modern intertidal subsistence food-gatherers and artisanal fishers. In the past seven years, landings of this kelp in Chile have been ~2600

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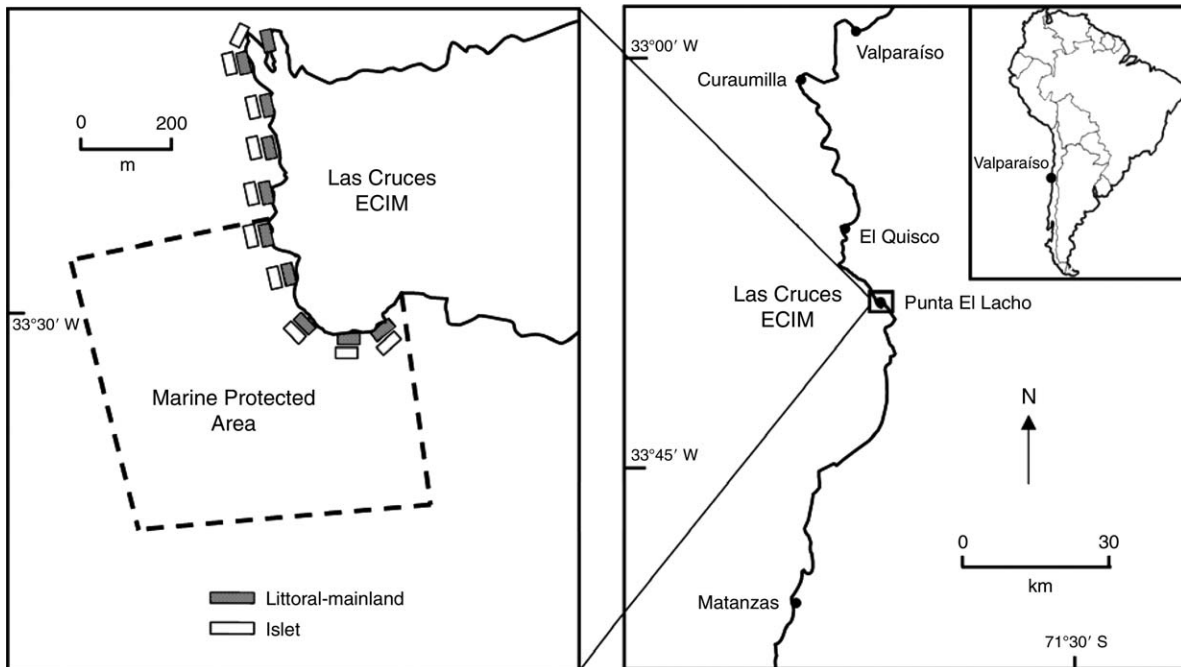


FIG. 1. Map of study region and schematic representation for monitored plots inside and outside Estacion Costera de Investigaciones Marinas (ECIM), at Las Cruces, central Chile.

(± 900) wet metric tons (Mg) per year; while in central Chile ($32\text{--}33^\circ$ S) landing is ~ 200 wet Mg/yr (SERNAP 2005). Here, we analyze data from 1980–2002 focusing on the number of food-gatherers impacting rocky shores, changes in *D. antarctica* density, size structure, biomass, and intraspecific competitive outcomes, inside and outside ECIM. Baseline studies (Castilla and Bustamante 1989, Bustamante and Castilla 1990) show that (1) at the establishment of ECIM (1982), the species had an extremely reduced local population due to heavy exploitation (< 1 plant per 100 m of coast), (2) complete protection of *D. antarctica* inside ECIM was effective during the first five years of the reserve operation, ECIM kelp density and biomass being significantly greater than non-protected areas (Castilla and Bustamante 1989). Based on the above, we hypothesized that the species recovery would (1) occur first inside the ECIM and that the process will expand later beyond ECIM boundaries, showing a time delay; (2) show a population recovery process with greater similarities in density, biomass, and size structure inside and outside ECIM for habitats with more difficult access for food-gatherers, i.e., small-islets detached from littoral-mainland habitats (Bustamante and Castilla 1990); (3) lead to density-dependent intraspecific competition regulation inside ECIM.

MATERIALS AND METHODS

Study site and habitats

The reserve ECIM, at Las Cruces ($33^\circ 30' \text{ S}$, $71^\circ 38' \text{ W}$; Fig. 1), is part of a research station of Catholic University of Chile. In December 1982, the rocky

littoral shore of ECIM (~ 0.6 km straight line; 0.5 ha of intertidal rocky shore; 4.4 ha of subtidal habitat) was fenced to stop human perturbations and resource extraction. The ECIM rocky shore is part of a high energy and wave-swept headland, formed by metamorphic gneiss with lamprophytic intrusions (Oliva and Castilla 1986). Similar rocky habitats are present to the south and north of ECIM (i.e., outside non-protected areas). The Las Cruces headland rocky habitats can be divided into (1) continuous and accessible blocks of rocky-intertidal–shallow-subtidal shores (0 to -0.5 m below low tide are littoral-mainland habitats), (2) less accessible islets, each less than $\sim 100 \text{ m}^2$, situated no more than 100 m from mainland (Castilla and Bustamante 1989).

Food-gatherers

Rocky intertidal and shallow subtidal food-gatherers manually extract eight to 10 species of invertebrates and *D. antarctica*, cutting the stipe of adult plants (Durán et al. 1987, Gelcich et al. 2006). *D. antarctica* knife-cut stipes can be easily identified (up to approximately one week) from plants detached by waves. Between January 1980 and November 1982, before the fencing of ECIM, food-gatherers were monitored along 1.5 km of rocky shore in Las Cruces headland during low tides. Following the fencing of ECIM (December 1982) the monitoring has continued inside ECIM, as well along ~ 1.5 km of rocky shore north of ECIM, with the exceptions of 1990, 1995, 1999, and 2001. Here, we use an intertidal food-gathering extracting effort based on

the annual mean number of extractors per 1.5 km of coast (1980–2002), monitored for 14–24 spring tides per year, recorded for eight to 12 months per year (~1–2 h observation per tide). During low tides, outside ECIM, food-gatherers walk along the shore, using the entire intertidal and do not select specific extracting sites. The species extracted have been occasionally identified, counted and measured (Durán et al. 1987). Occasional observations on *D. antarctica* extractors in littoral-mainland and islet at El Quisco (33°23' S, 71°41' W) and Matanzas (33°57' S, 71°52' W; Fig. 1) were done to evaluate the number and size of bull-kelp plants extracted. In 1999, capture per unit effort was measured (CPUE, number and size of plants extracted in 30 min by a group of five bull-kelp extractors).

Monitoring

D. antarctica populations were monitored at Las Cruces headland between January 1981 and May 2002 during spring low tides (tidal range, 0.02–0.33 m). This population is separated from other populations at least by 8–10 km. Littoral-mainland habitats were monitored before ECIM fencing in January 1981 and intermittently after fencing inside and outside until January 2002. *Durvillaea* population on islets were monitored inside and outside ECIM between March 1985 and January 2002.

Between 1981 and 1985, littoral-mainland and islet monitoring was done along a line of 500 m parallel to the low intertidal fringe: one inside ECIM (or before its fencing) and another outside (north) ECIM. Since 1986 monitoring inside and outside ECIM was modified. Two 500-m portions of rocky shore, inside and outside the reserve, were each divided into 50-m interspaced haphazardly selected plots and systematically sampled inside and outside the reserve (Fig. 1). The low intertidal area occupied by *Durvillaea* was calculated by multiplying the mean width of belts (ranging between 1.45 and 1.90 m), at 10–15 randomly chosen points, by the length of each 50-m plot. The mean density (no. plants/m²) and wet biomass (kg/m²) were determined per plot. Field measurements for individual plants were: (1) maximum holdfast diameter (cm), measured with calipers (precision 0.1 mm); (2) maximum holdfast diameter (cm) of knife-cut plants which were recorded separately; (3) total plant length (cm) from base of holdfast to tip of fronds. Only non-coalescent plants were included in the study (in this area coalescent plants are around 5% of the population [Castilla and Bustamante 1989]). Plants with holdfast equal or larger than 5 cm were considered as adults (Santelices et al. 1980; D. Schiel, *personal communication*). Wet mass (kg) of plants was determined using the allometric equation

$$M = 0.0021(\text{DH})^{2.2119}$$

where M is the individual wet mass (kg) and DH is the maximum holdfast diameter (cm; with $R^2 = 0.95$, $P < 0.001$; Castilla and Bustamante 1989). *Durvillaea* abun-

dance on the adjacent northern non-reserve area was evaluated through the estimation of the total average density and biomass per plot, at five interspaced 50-m plots from the reserve fence for the periods: 1986–1989, 1990–1993, 1994–1997, 1998–2002.

Statistical analysis

Data on plant abundance (density and biomass) were analysed using repeated-measures analysis of variance (Winer et al. 1991). The experimental design had three factors: (1) reserve site, a fixed factor, with two levels, protected and non-protected; (2) plots nested within site; and (3) time as the repeated measure with 16 levels (years). If there was a significant interaction, then the effect of reserve was examined using the SLICE procedure in PROC GLM (SAS Institute 2002). Data were $\log(x + 1)$ -transformed to meet assumptions of normality and homogeneity of variances (Levene's test, $\alpha = 0.05$). The temporal synchrony between site levels was examined by cross-correlation analysis. Size distribution of adult plants were compared using Kolmogorov-Smirnov test. *D. antarctica* density and biomass on the adjacent northern non-reserve site was analysed for the five interspaced 50-m plots, for four periods (four years each) using a χ^2 test for equal proportions, with $\alpha = 0.05$.

The regulation structure of *D. antarctica* was examined using the R function and assuming exclusively intraspecific competition. This function represents the relationship between the realized per capita rate of change, R , and previous population density, N_{t-n} , at a discrete time period. Following Berryman (1999), this rate can be estimated as $R = \ln(N_t/N_{t-1})$; where N_t is the density of population at time t and N_{t-1} at time $t - 1$. To estimate R -function parameters, we fitted a nonlinear model of the Ricker/Cook logistic model (Ricker 1954, Cook 1965): $R = a - bN_{t-1}^Q$, where a is the maximum per capita rate of change, Q is a coefficient of curvature, and b is the slope when $Q = 1$. The function is convex when $Q > 1$ (the slope of the function becomes steeper as density increases) and concave when $Q < 1$ (the slope of the function decreases with density). The term bN_{t-1}^Q represents the reduction in the maximum per capita rate of change due to intraspecific competition for fixed resources. Carrying capacity is reached at $R = 0$ (Berryman 1999). Density-dependent compensatory effects between plant recruits and adults were analyzed using the Ricker's (1975) stock-recruitment model:

$$\text{Rr} = S \times e^{a(1-\beta S)}$$

where Rr is the number of recruits (density); S is the size of the parental stock (density); a is the natural logarithm of the density-independent survival coefficient (dimensionless parameter); and β a density-dependent parameter with dimension $1/S$. Parameter estimations were performed by nonlinear convergence (Hooke-Jeeves pattern moves and quasi-Newton algorithm methods).

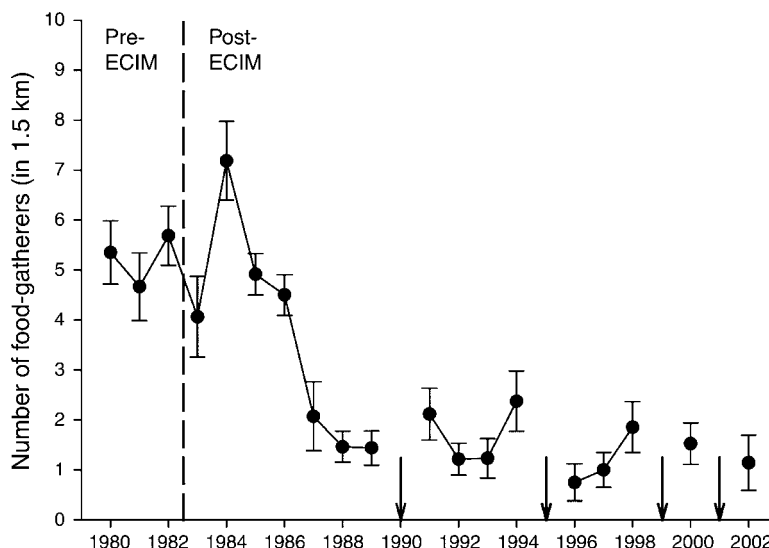


FIG. 2. Number of subsistence rocky intertidal food-gatherers along 1.5 km of coast at Punta El Lacho, Las Cruces, Chile (1980–2002, outside the ECIM reserve; mean \pm SE). Arrows indicate periods lacking monitoring.

RESULTS

Food-gatherers

No extraction of *D. antarctica* was detected inside the ECIM reserve and, when poaching events occurred, food-gatherers mainly targeted on gastropods (*Concholepas concholepas*, *Fissurella* spp.). Intertidal food-gatherers monitoring showed a large variability through time with high extraction occurring between 1980 and 1986 (Fig. 2). *Durvillaea* was extracted by 20–30% of the food-gatherers at Las Cruces, removing up to four to eight plants per low tidal excursion in littoral-mainland habitats. During the food-gathering monitoring outside ECIM (1983–2002) we recorded 174 knife-cut plants, mostly in littoral-mainland habitats, ranging from 0 to 19 plants cut per monitoring date (plant length, 212.3 ± 104.5 cm [mean \pm SD]; holdfast diameter, 12.5 ± 5.14 cm).

At El Quisco (Fig. 1), a *D. antarctica* extractor operating in mainland-littoral habitats, took 34 plants in 30 minutes (length, 315.2 ± 130.0 cm; holdfast diameter, 17.5 ± 6.1 cm). In 1999 at Matanzas (Fig. 1), five extractors took 558 plants during five hours (CPUE, 12.2 plants per 30 min per extractor; plant length 281.9 ± 118.8 cm; holdfast diameter, 15.9 ± 5.7 cm).

Littoral-mainland habitat

Inside and outside ECIM, total juvenile and adult densities first increased and then declined (Fig. 3). During the first seven years (1981–1988), total plant densities inside and outside ECIM were low and similar, <0.5 plants/m². Total plant density increased three orders of magnitude, first inside ECIM and later outside, ranging between 0.01 (1981–1986) and 2.4 plants/m² (1993; Fig. 3). Total plant density outside ECIM lagged behind ECIM by about two years (1989–1990, see Fig. 3). Nevertheless, the cross correlation is

not significant because the lag is only for two years of the 16. In 1993, both at ECIM and the outside reached their maximum densities: 2.0 and 2.4 plants/m², respectively. Thereafter, total densities similarly declined in ECIM and outside, reaching stable values of 0.5–0.6 plants/m² (1997–2002). Repeated-measures ANOVA shows significant of time \times site interactions (Table 1), and we compared the differential effects by years among treatments in each combination of site and time (Fig. 3).

In ECIM, between 1981 and 1986, the average total biomass increased slowly up to 0.3–0.4 kg/m² (1986), reaching its maximum in 1993 with ~ 2.4 kg/m² (Fig. 3). Thereafter (1998–2002), biomass declined to 0.2–0.7 kg/m². In the non-protected area, the average total biomass increased up to 0.3–0.4 kg/m² in about 10 years (Fig. 3). This total trend is explained by the biomass of the adult *D. antarctica* plants, but not for the juveniles (Fig. 3). Again, repeated-measures ANOVA shows significant time \times site interactions (Table 1) and, as with density, we compared significant effects by years among treatments in each combination of site and time (Fig. 3). During the ECIM pre-fencing period (1981–1982) and when the density of adult *D. antarctica* in Las Cruces was extremely low, holdfast diameter ranged between 5.2 and 6.6 cm (Figs. 3 and 4a). Following the fencing of ECIM, and with the greater density of adult plants, holdfast diameter expanded up to 40 cm. The holdfast diameter distributions were always larger and significantly different inside ECIM than outside (Kolmogorov-Smirnov tests, $P < 0.05$; Fig. 4a).

Islet habitat

Between 1985 and 1989, total plant density was low (less than 0.5 plants/m²) and similar at ECIM and outside (Fig. 5). Between 1990 and 1993, total juvenile and adult densities showed similar increases, with total

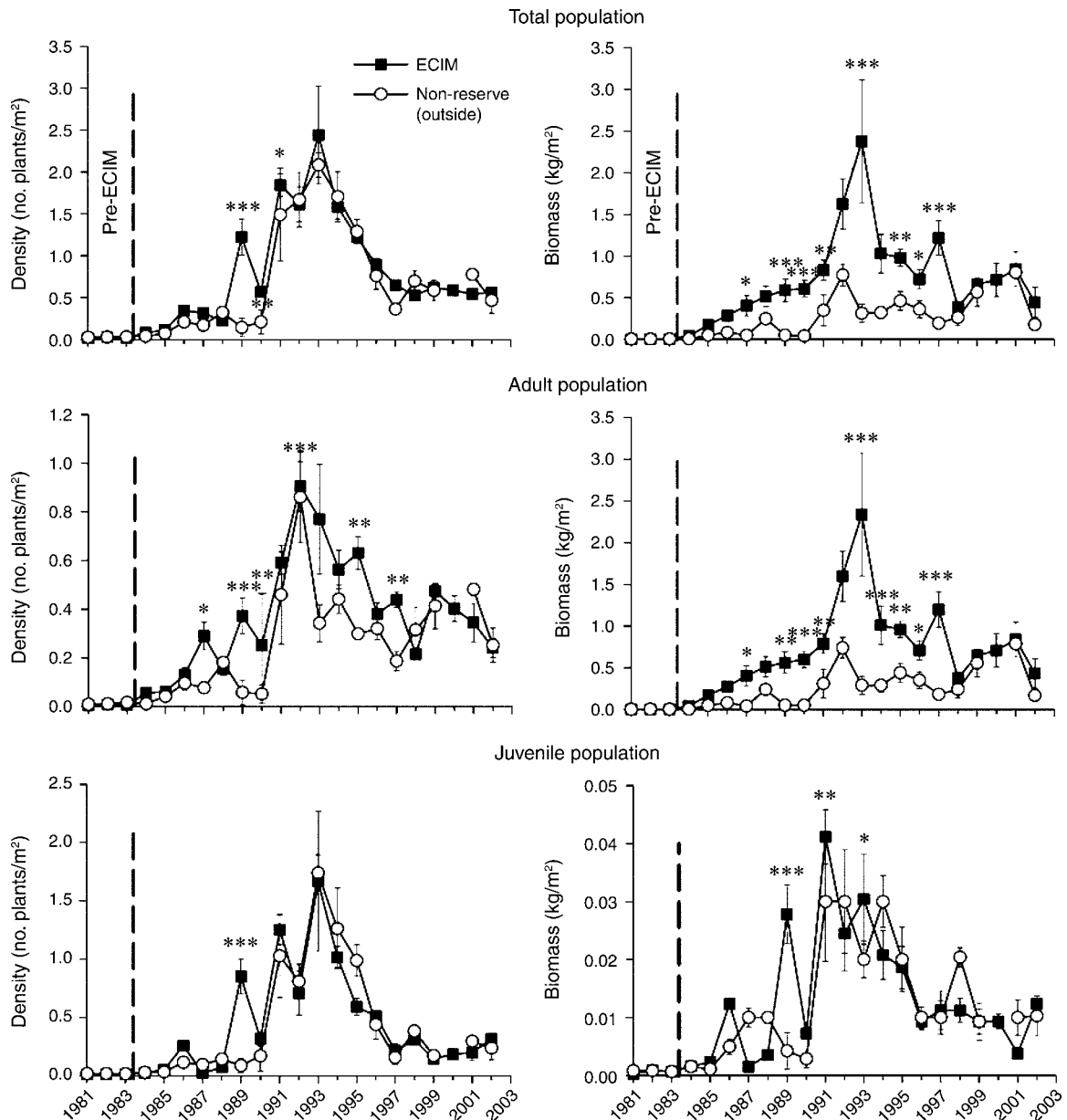


FIG. 3. *Durvillaea antarctica* populations in the littoral-mainland habitat. Density and biomass (mean \pm SE) for total, adult, and juvenile populations inside ECIM (black squares) and outside ECIM (open circles). Dashed lines separate pre- and post-fenced condition. Asterisks represent P values (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$) of site \times time effect shown by time for density and biomass (PROC GLM SLICED; SAS Institute 2002).

densities ranging between 0.5 and 2.9 plants/m², but with a time delay outside ECIM of about two years (1989–1990; Fig. 5). Cross correlation was not significant because the delay occurs in only two years. In 1993 in both areas, plants reached their maximum densities, 2.3–2.9 plants/m². Thereafter, total juvenile and adult densities declined in both areas, reaching stable values of \sim 0.5 plants/m² (Fig. 5). Repeated-measured ANOVA shows no significant effect of site, while the effect of time was significant. The interaction site \times time was not significant only for adults and juveniles (Table 2).

Between 1985 and 1988 at ECIM and outside, the total and adult biomass remained at 0.3–0.4 kg/m² (Fig. 5). In ECIM, total biomass rises and then falls with that of adult plant biomass, but not with juveniles, with a maximum biomass in 1993 (mean of 2.2 kg/m²; Fig. 5). Thereafter, biomass declined to 0.5–1.0 kg/m² (1998–2002). Outside, a time delay of about two years (1989–1990) was also observed for the increase in total and adult plant (not for juveniles) biomass while, in 1993, the maximum mean biomass was 1.3 kg/m² (Fig. 5). Cross correlation was not significant.

TABLE 1. Repeated-measures ANOVA on the effects of the Estacion Costera de Investigaciones Marinas (ECIM) protected area, site and time, for the density and biomass of *Durvillaea antarctica* in the littoral-mainland habitat.

Source of variation	df	Total			Adult			Juvenile		
		MS	F	P	MS	F	P	MS	F	P
Density										
Site	1	0.0641	2.78	0.1338	0.062	8.46	0.0196	0.0037	0.21	0.656
Error: plot(site)	8	0.0231			0.0073			0.0173		
Time	15	0.1667	34.96	<0.0001	0.0354	16.07	<0.0001	0.1322	29.37	<0.0001
Site × time	15	0.0173	3.64	<0.0001	0.0062	2.81	0.0009	0.0132	2.93	0.0006
Error	120	0.0048			0.0022			0.0045		
Biomass										
Site	1	0.72	69.95	<0.0001	0.734	73.38	<0.0001	<0.0001	0.07	0.7971
Error: plot(site)	8	0.0102			0.01			<0.0001		
Time	15	0.0591	9.39	<0.0001	0.0575	9.08	<0.0001	0.0002	11.9	<0.0001
Site × time	15	0.0219	3.47	<0.0001	0.0221	3.48	<0.0001	<0.0001	3.01	0.0004
Error	120	0.0063			0.0063			<0.0001		

Note: Data were $\log(x + 1)$ -transformed.

Between 1985 and 1987, the size structure of adult plants was not significantly different between ECIM and the outside (Kolmogorov-Smirnov test, $P > 0.05$; Fig. 4b). Thereafter, holdfast size distributions were larger and statistically different in ECIM when compared with the outside (Kolmogorov-Smirnov test, $P < 0.05$; Fig. 4b).

Spatial cross-boundary subsidies

Trends in density for the total population of *D. antarctica* over time (1986–2002, islet plus mainland habitats) are similar inside and outside the reserve plots (Fig. 6). The density increased two- to fourfold in inside and outside plots during the second, third, and fourth time periods analysed (Fig. 6). During the second period

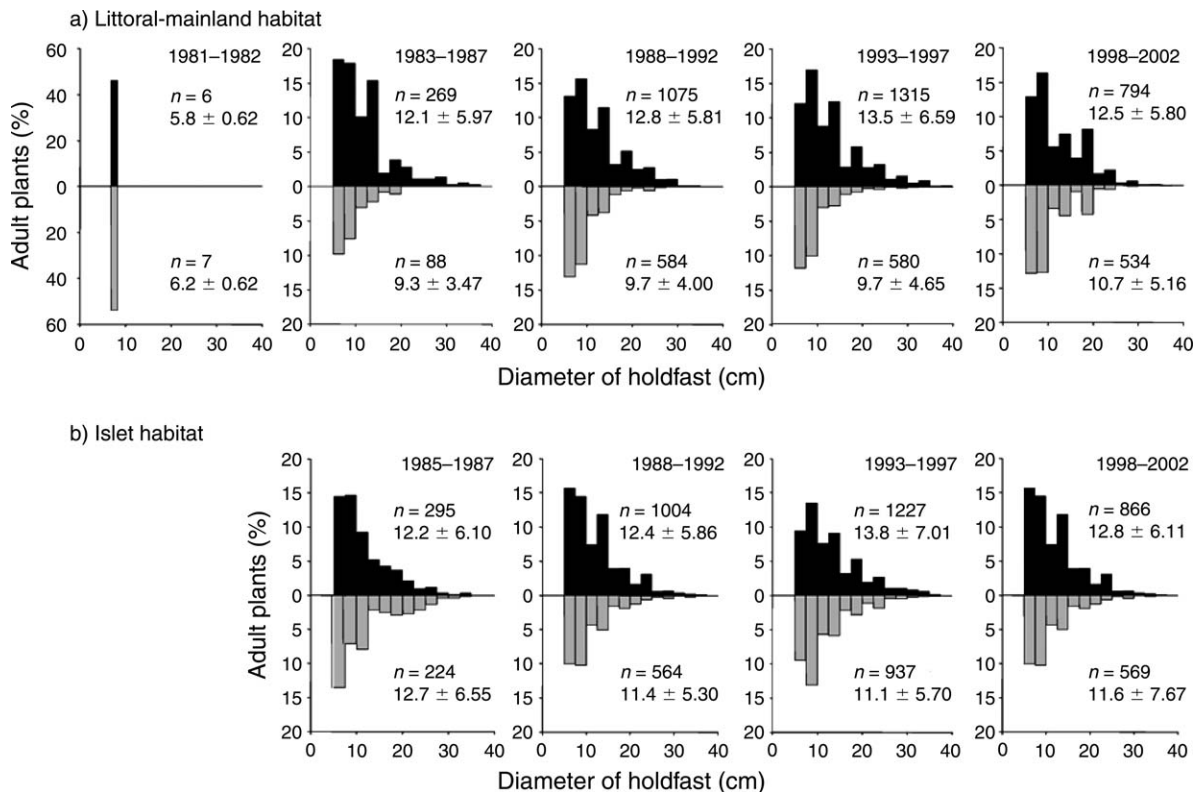


FIG. 4. *Durvillaea antarctica* (a) maximum holdfast diameter (cm) of adult plants in the littoral-mainland habitat inside ECIM (black bars) and outside ECIM (gray bars) (the 1981–1982 period corresponds to ECIM pre-fencing stage); and (b) diameter of adult holdfast plants in the islet habitat (bars as in panel a). Values reported in each panel indicate the number of plants (n) and mean \pm SD. Note the inverted axes.

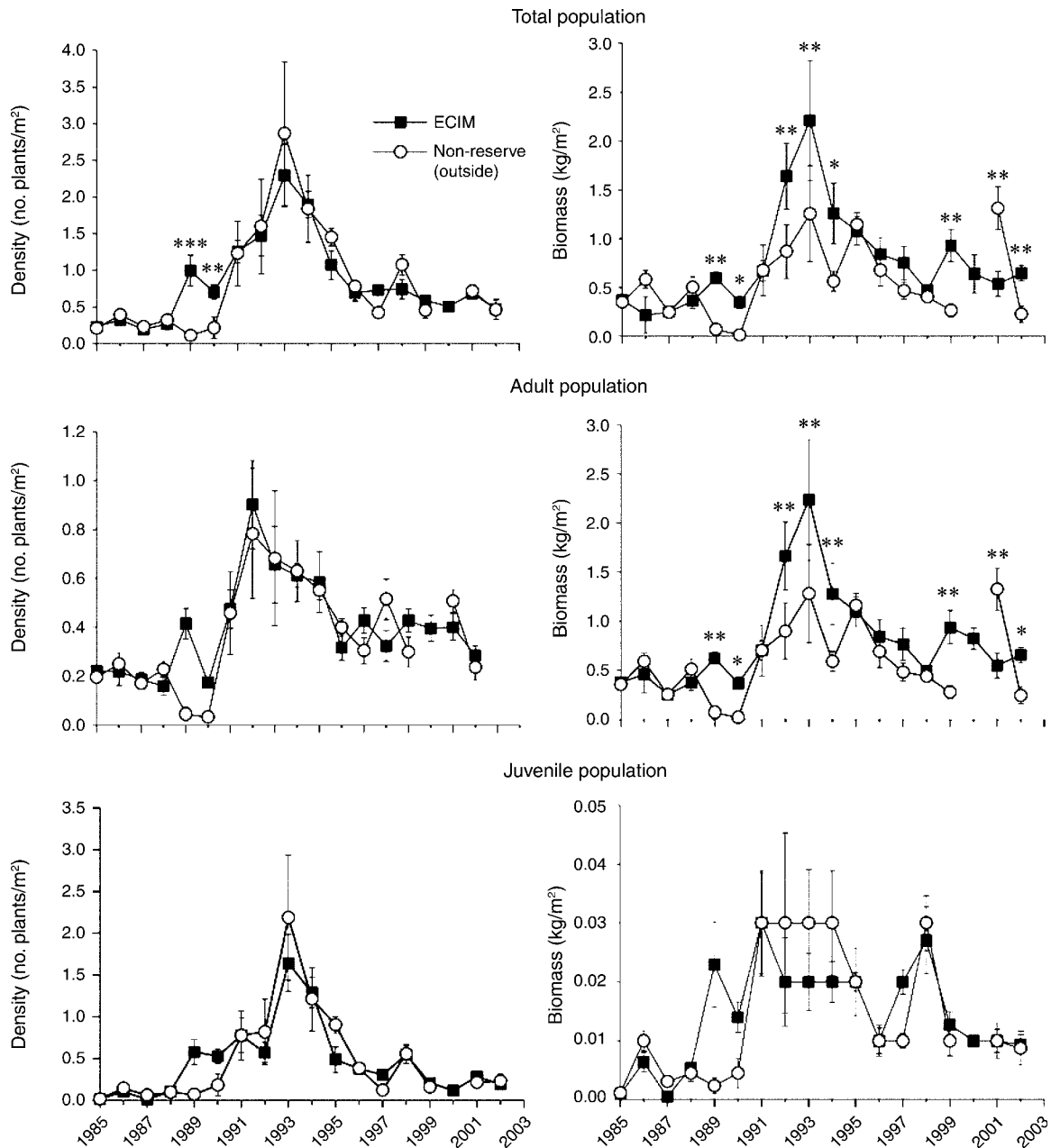


FIG. 5. *Durvillaea antarctica* populations in the islet habitat. Density and biomass (mean \pm SE) for total, adult, and juvenile populations inside ECIM (black squares) and outside ECIM (open circles). Asterisks represent *P* values (* *P* < 0.05; ** *P* < 0.01; *** *P* < 0.001) of site \times time effect shown by time for density and biomass (PROC GLM SLICED; SAS Institute 2002).

(1990–1993), the density was significantly greater in the outside plot closer to ECIM fence (50–100 m; $\chi^2_4 = 13.0777$, *P* = 0.0109) than in the plots further away. Trends in biomass are also similar inside and outside the reserve transect plots, but increases of two- to threefold in inside and outside reserve plots during the second, third, and fourth time periods observed (Fig. 6). The larger increases are observed for the plot inside the reserve and the first plot (50–100 m, closer to the fence) outside the reserve. Conversely, no significant differenc-

es in biomass among plots outside the reserve were found (Fig. 6), for any of the periods analyzed ($\chi^2_4 = 0.6671$, 6.0739, 0.1168, 0.1664; *P* = 0.9553, 0.1937, 0.9984, 0.9967, respectively).

Density-dependent compensatory effects

Inside ECIM, the fitting of the Ricker/Cook logistic model (Ricker 1954, Cook 1965) for *D. antarctica* population intraspecific regulation (1983–2002) was significant (*P* = 0.0391), although the variance explained

TABLE 2. Repeated-measures ANOVA on the effects of the Estacion Costera de Investigaciones Marinas (ECIM) protected area, site and time, for density and biomass of *Durvillaea antarctica* in the small-island habitat.

Source of variation	df	Total			Adult			Juvenile		
		MS	F	P	MS	F	P	MS	F	P
Density										
Site	1	0.0189	0.64	0.447	0.0063	0.53	0.4864	0.0058	0.28	0.6084
Error: plot(site)	8	0.0297			0.0118			0.0206		
Time	15	0.1569	20.19	<0.0001	0.0342	11.33	<0.0001	0.1279	19.25	<0.0001
Site × time	15	0.0172	2.21	0.0092	0.0048	1.6	0.0832	0.0104	1.56	0.0953
Error	120	0.0078			0.003			0.0066		
Biomass										
Site	1	0.1367	9.15	0.0282	0.1367	7.26	0.0273	<0.0001	0.32	0.5887
Error: plot(site)	8	0.0191			0.0188			<0.0001		
Time	15	0.0818	10.44	<0.0001	0.0808	10.34	<0.0001	0.0001	6.92	<0.0001
Site × time	15	0.0254	3.24	0.0002	0.0253	3.23	0.0002	<0.0001	1.12	0.35
Error	120	0.0078			0.0078			<0.0001		

Note: Data were $\log(x + 1)$ transformed.

was low ($R^2 = 0.4804$). Outside ECIM, the fitting was not significant ($P = 0.7477$, $R^2 = 0.2658$; Fig. 7). However, during the monitoring in ECIM littoral-mainland and islet habitats a lack of compensatory effect (Ricker 1975) between density of adult and juvenile plants was observed; either if site and habitat were combined or taken individually. In spite of this, a weak compensatory effect was observed for the 1987–2002 time series of mainland-littoral and islet habitats, at the centre of the ECIM reserve ($\beta = 0.8542$, $P = 0.1269$).

DISCUSSION

One of the hopes of no-take MPAs is that their existence would increase the inside density, size, and biomass of targeted species (Roberts 1995, Jennings 2001, Halpern and Warner 2002), and that spillover

would occur across their boundaries. Spillover has been demonstrated for fish and invertebrate species (e.g., Roberts 1995, McClanahan and Kaunda-Arara 1996, Kelly et al. 2002, Paddack and Estes 2000, Russ et al. 2003, Abesamis and Russ 2005). For sessile species, adult spillover cannot happen, thus population recovery of adjacent non-protected areas occurs through propagule dispersal from core MPA populations. This work demonstrates up to three orders of magnitude enhancements in density and biomass for the exploited bull-kelp *Durvillaea antarctica*, inside a no-take MPA (ECIM) and beyond the MPA boundaries. Before the fencing of ECIM, the rocky shore in and around the Las Cruces headland was heavily exploited by food-gatherers (Durán et al. 1987) and *D. antarctica* population was extremely reduced (<1 plant per 100 m of coast). The

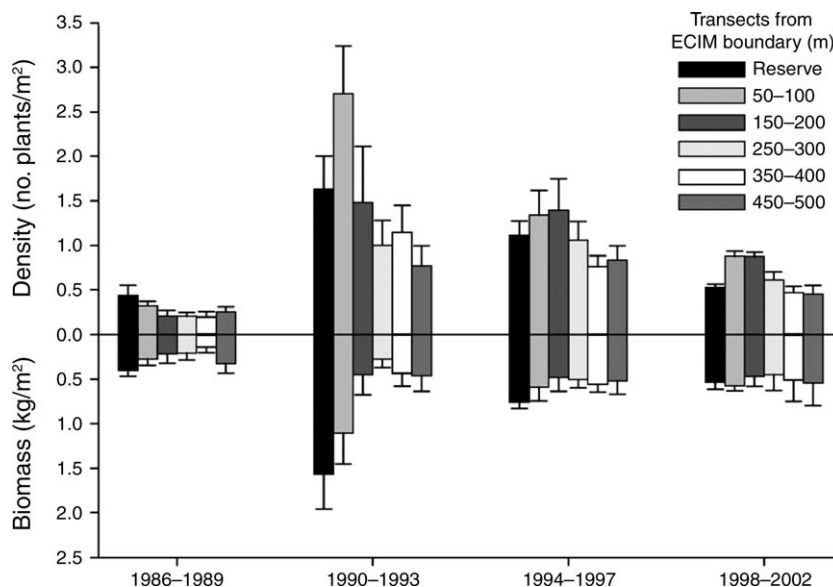


FIG. 6. Total population density and biomass (mean \pm SE) of *Durvillaea antarctica* from the islet plus littoral-mainland habitats at different distances (outside, non-protected) from the ECIM reserve fence during four time periods: 1986–1989, 1990–1993, 1994–1997, and 1998–2002. Note the inverted axis.

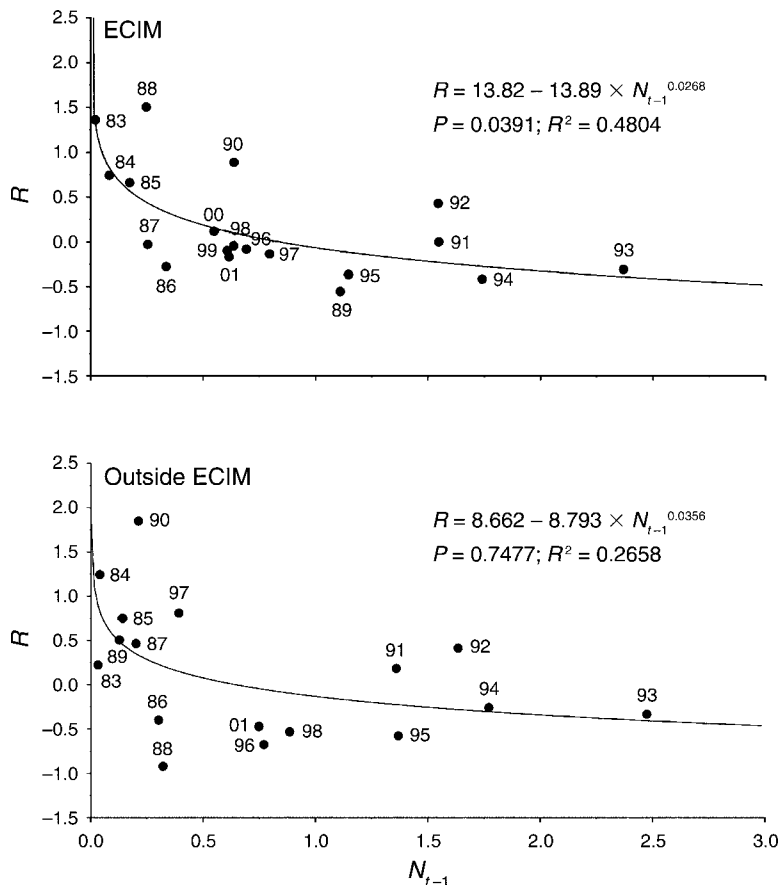


FIG. 7. Relationship between realized per capita rate of change and population density of *Durvillaea antarctica* inside and outside ECIM. The number over each point indicates the year (i.e., “88” indicates 1988).

number of intertidal food-gatherers operating at Las Cruces between 1980 and 1982 (pre-ECIM fencing) was of up to six food-gatherers per 1.5 km of coastline per low tide per year and continued at that level outside ECIM between 1983 and 1987. Unexpectedly, between 1988 and 2002, those numbers drastically dropped to around 30%. Part of the explanation may be linked to the increase of alternative employment in Chile. Previous to 1987, unemployment reached 19%, while between 1987 and 1997, it dropped to 6–10% (Soto 2004).

The recovery of *D. antarctica* adult population at Las Cruces headland initially took about five to seven years (Fig. 3) after the ECIM fencing and, as hypothesized, occurred first inside and later beyond ECIM boundaries in non-protected areas. We suggest that this slow population recovery was due to the extremely low kelp density at the initial stage. The plant population recovery on rocky shores outside ECIM, where intense kelp extraction occurred, lagged about two years (1989–1990) behind ECIM. This suggests cross-boundary seeding effect into non-protected areas due to recovery of a source population inside ECIM. During the ~10 last years of the monitoring, adult density ECIM stabilized at ~0.5 plants/m², which is similar to those

reported by Bustamante and Castilla (1990) for a *D. antarctica* population at Curaumilla (about 50 km north of ECIM), considered to be a site with difficult access for food-gatherers. *Durvillaea* biomass inside ECIM at its peak in 1993 was approximately five times greater than that reported for the early plant recovery at ECIM by Bustamante and Castilla (1990), indicating that reserve effects were operating. In the islet habitat, as hypothesized, there were no significant differences in adult plant density (1985–2002) between ECIM and the outside, although in approximately half of the monitored years, the biomass was significantly greater inside ECIM than outside. Adult size structures were more similar between ECIM and the outside for islet than for littoral-mainland habitats, but significantly greater for ECIM. This demonstrates that inside vs. outside as well as habitat accessibility to kelp extraction, as hypothesized, played a critical role in the population dynamics of this kelp. In 1993, we found in Las Cruces a single maximum *Durvillaea* recruitment peak of ~2–2.5 juveniles/m². These densities were two to five times lower than those found for austral summer-early autumn by Santelices et al. (1980) in central Chile (using 1-m² plots) and Westermeier et al. (1994) for southern

Chile (using a single plot similar in size to ours). Additionally, *Durvillaea* recruit densities in small patches (plots of 30 × 30 cm), around or next to adult plants, in mudstone platforms in South Island New Zealand, are at least one order of magnitude higher (Taylor and Schiel 2005). These differences in recruitment may be explained by habitat quality, differential mortality, density-dependent processes, and the fact that the *Durvillaea* population at Las Cruces is close to the northern limit of its distribution.

Our results preliminarily suggest that the *D. antarctica* population was regulated via intraspecific competition inside ECIM but not outside. At ECIM, the population tended toward an equilibrium rate following the closure of ECIM, a trend likely to be triggered following the 1993 density peak. However, inside ECIM, the trajectory of *R*-function points shows oscillatory trends (see sequences of years in Fig. 7), suggesting that the process of population regulation of *Durvillaea* might be due not only to intraspecific competition interactions (Berryman 1999).

Santelices et al. (1980) suggested a stock-recruitment relation (Ricker 1975) for *D. antarctica* at Los Molles, a locality about 200 km north from Las Cruces. Our results show a weak density-dependent relationship between adult and juvenile *Durvillaea* populations only for the central area of ECIM. A compensatory effect was observed if site and habitat were combined or for the two habitats separately. This could be due to (1) variability in local and seasonal recruitment and/or differential growth and mortality among sites (Westermeier et al. 1994, Taylor and Schiel 2005); (2) the size of the plots to evaluate plant density, since recruitment of *D. antarctica* appears to be patchy (Hay and South 1979, Taylor and Schiel 2005); or (3) competitive prevention for *Durvillaea* settlers by whiplash of the adult kelp frond (Santelices et al. 1980, Santelices and Ojeda 1984, Taylor and Schiel 2005).

Long-term data series have proven to be important to our understanding of changes in subtidal kelp-dominated ecosystems (e.g., for *Macrocystis pyrifera* [Tegner et al. 1997, Dayton et al. 1998]), where abiotic factors affect germination, growth, fecundity, and survivorship of adult plants. Particularly in East Pacific coastal zones, interannual oceanographic variability (El Niño/La Niña events, storms, nutrient depletion, hypoxia, see Grove et al. [2002]) tend to be intermixed with anthropogenic perturbations (i.e., overexploitation, pollution). Dayton et al. (1998) have argued that to differentiate between them “benchmark criteria of normal” are required. Nevertheless, benchmark criteria may be difficult to obtain, for instance, due to extreme overexploitation of a species, as is the case of *Durvillaea*. Here, for overexploited species, the only way to understand its natural history and dynamics may be to allow the populations to be recovered, for instance, inside a no-take MPA. In general, it is extremely difficult to plan ahead the logistics of MPAs, such as the selection of the right location, the right size, spatial replications, or the

establishment of MPAs networks (Castilla 2000, Gell and Roberts 2003, Sale et al. 2005). We argue that in facing these the consolidation of long-term data (decades) is crucial (Castilla 2000, McClanahan and Graham 2005, Russ et al. 2005). For instance, in the case of *D. antarctica* at Las Cruces, certainly we can not explain the single major recruitment event that occurred in 1993. This event is not linked to the 1993 cold La Niña conditions, which could have favored the recruitment for this sub-Antarctic kelp species, because our time series includes at least four La Niña conditions (data available online).⁴ Hence, we conclude that *D. antarctica* peak recruitment was most probably influenced by the demography of the population, via its density, adult plant size, and biomass.

In the world, there are thousand of MPAs, but long-term monitoring efforts of these sites are seldom reported in the mainstream literature (but see Jennings 2001, Russ and Alcala 2003, Shears and Babcock 2003, Micheli et al. 2004, McClanahan and Graham 2005). We suggest, however, that there is much that can be learned from these examples. This has been the case for the no-take ECIM area in Las Cruces, Chile, where the scientific information obtained inside ECIM and beyond its boundaries has informed national sustainable management plans. Findings done at ECIM have lead to the legal implementation in Chile of small-scale fishery co-management schemes and territorial users' rights for fisheries. This has resulted in the existence of several hundred management and exploitation areas for benthic resources (including *D. antarctica*) for small-scale artisanal fishers (Castilla and Defeo 2001, Gelcich et al. 2005, Castilla et al. 2006, Defeo and Castilla 2006).

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