Variation and persistence of the middle rocky intertidal community of central Chile, with and without human harvesting

L. R. Durán and J. C. Castilla *

Estación Costera de Investigaciones Marinas (ECIM), Departamento de Ecología, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile

Abstract

Humans are an important intertidal predator in central Chile. Following a five-year study we report on the effects of the exclusion of humans from the rocky intertidal at Las Cruces, central Chile. The middle intertidal of harvested and non-harvested areas diverged in species diversity and composition during the experiment. In harvested areas the middle intertidal rocky shore was dominated throughout the study by a monoculture of mussels, Perumytilus purpuratus. When humans were excluded, the middle intertidal community switched to one dominated by barnacles (predominantly Jehlius cirratus and Chthamalus scabrosus); this community has persisted for at least three years, despite the presence of forces e.g. mussel larvae, that have the potential to alter the community structure. Such changes were mediated by the muricid gastropod Concholepas concholepas, a key-stone predator. As a consequence of the above changes, the species diversity, H', (primary space occupiers) in the non-harvested area increased from $H' = 0$ at the beginning of the study in 1983 (when the middle intertidal community was dominated by mussels), to values ca $H' = 2$ toward the middle of the study in 1984 (which coincided with the maximum predatory impact of C. concholepas), and subsequently decreasing to ca $H' = 0.5$ at the end of the study in 1987 (when the middle intertida community was dominated by barnacles).

Introduction

The effect of humans, as top predators, on rocky intertidal communities has been the focus of recent studies, particularly in South Africa (Branch 1975, Siegfried et al. 1985,

* Please address all correspondence to J. C. Castilla, Department of Zoology, University of Washington, Seattle, Washington 98195, USA, until March 1990

Hockey and Bosman 1986) and Chile (Moreno et al. 1984, Castilla and Durán 1985, Oliva and Castilla 1986, Castilla 1986, Moreno 1986, Moreno et al. 1986, Castilla and Bustamante 1989), but also in Costa Rica (Ortega 1987) and Australia (Catterall and Poiner 1987). The intense human predation on the rocky intertidal community of central Chile (Durán et al. 1987) leads to a complete elimination of some species (a "press-perturbation" effect, sensu Bender et al. 1984). Predation by humans in this ecosystem is mainly directed at a carnivorous muricid gastropod, Concholepas concholepas, and at herbivorous key-hole limpets e.g. Fissurella crassa and F. limbata (Durán et al. 1987).

The effect on community structure of excluding critical predators that control the abundance of dominant competitors for primary space has been a recurrent subject in ecological literature (Paine 1966, 1971, 1974). Predation on sessile filter-feeders able to monopolize space almost invariably increases diversity of primary space users by preventing any monopoly, thereby creating free patches available for colonization by other sessile organisms (Paine 1977, Branch 1984, Castilla and Durán 1985).

Previous studies by Castilla and Durán (1985) and Oliva and Castilla (1986) illustrated the effects of a two-year exclusion of humans (1983 to 1984) from the rocky intertidal at Las Cruces, central Chile. The first effect was the increase of Concholepas concholepas (Castilla and Durán 1985), Fissurella crassa and F. limbata (Oliva and Castilla 1986) populations, followed by a dramatic decrease in the mean width of the Perumytilus purpuratus belt in the mid-intertidal zone. The reduction of P. purpuratus, a prey of C. concholepas, increased the availability of primary space, allowing for the settlement of macroalgae and barnacles and a subsequent increase in the species diversity of primary space users. The continuation of this experiment (Castilla and Durán 1985) together with the incorporation of an additional intertidal site now allows us to assess the community changes produced during a five-year period.

This study addressed the following questions: (1) Does species composition in the rocky intertidal of central Chile

Table 1. Physical characterization of the four non-harvested (A, B, B', C) and three harvested (D, E, F) sites. SE: semi-exposed; EX: exposed. Wave sweep frequency = mean number ($\pm$ SD) per 15 min

	Non-harvested				Harvested		
	A	B	B'	C	D	E	F
Exposure	SE	SE	SE	EX	SE	SE	SE
Orientation	W–SW	S–SW	S–SW	W–SW	W–SW	E–SE	W–SW
Slope	15°	10°	45°	40°	40°	45°	45°
Rock type	Granite	Granite	Granite	Granite	Granite	Granite	Granite
Wave sweep frequency							
High tide	55.7±6.4	58.8± 3.1	51.3±3.1	54.2±6.4	64.3±7.0	58.2±6.3	65.1±8.1
Low tide	5.0±4.0	8.0±11.2	4.4±4.9	42.8±6.8	6.2±4.0	5.8±5.2	4.8±3.1
Altitude over sea level (m)							
	1.2–1.8	1.4– 1.9	1.4–2.3	1.2–2.8	1.3–2.2	1.1–1.9	1.4–2.0

change when humans are withdrawn from the system for several years? If so, does this new species composition persist (Boesch 1974) over time, or is it a transient state? (2) Does species diversity of primary space occupiers change? If so, does this new species diversity persist through time?

Materials and methods

This work was carried out at Punta El Lacho, Las Cruces, central Chile (33°30'S, 71°38'W) between January 1983 and December 1987. In December 1982 the Pontificia Universidad Católica de Chile built the Estación Costera de Investigaciones Marinas (ECIM) at Punta El Lacho, Las Cruces. Since then the marine reserve of ECIM (500 linear m of rocky shore with an intertidal area of ca 4 152 m²) has been closed to tourists and fishermen, "mariscadores de orilla" (see Castilla and Durán 1985, Durán et al. 1987). This area of human exclusion (ECIM) is termed hereafter the non-harvested area.

Adjacent areas of the rocky shore with similar ecological and geological features (Oliva and Castilla 1986) and open to tourists and intertidal food gatherers or "mariscadores de orilla" were used as comparison areas, hereafter called harvested areas.

Four rocky platforms (sites) located in the *Perumytilus purpuratus* zone were selected in the non-harvested area: A = 3.6 m², B = 4.3 m², B' = 3.0 m² and C = 4.2 m²; and three in the harvested area: D = 4.0 m², E = 4.8 m², and F = 3.9 m². These sites, except Site B', are the same as those analyzed by Castilla and Durán (1985), and their denomination was maintained.

Wave exposure, orientation, slope, type of rock, frequency of wave sweeping at high and low tides, and height above sea level were determined for each site. Frequency of wave sweeps was observed on three different occasions. It was calculated as the mean number of wave sweeps in five sequential observations of 15 min every hour from 2 h before until 2 h after the high and low tide. Sites were classified as "exposed" or "semi-exposed" according to Castilla (1981).

Species composition of the intertidal community was determined by a point-intercept method: a 1 × 1 m string-grid quadrat with 162 regularly spaced intersection points was randomly located within each site. The fraction of points overlying a species was used as an estimate of its percentage cover. Each site was sampled 15 times during the five-year experiment. Throughout this paper we consider only those organisms occupying primary rock space. Angular transformations (Sokal and Rohlf 1981) were applied to percent cover data before calculating mean and standard error.

The Shannon-Wiener diversity index (Southwood 1978) was used for two reasons: (1) this index is sensitive to changes in the incidence of rare species (Peet 1974); and (2) it was employed in a previous study at the same sites (Castilla and Durán 1985) and so allows for valid comparisons.

Densities of *Concholepas concholepas*, *Fissurella crassa* and *F. limbata* were determined at each site by direct counts.

An earthquake occurred in central Chile while the study was in progress (March 3, 1985) resulting in a coastal uplift of about 40 to 60 cm (Castilla 1988). This earthquake is identified by an arrow in Figs. 1 to 4.

Results

Most sites were homogeneous for all physical parameters considered (Table 1). However, Site C differs from the others in wave exposure and in sweep frequency at low tide. Therefore, it is treated separately.

At the start of the experiment *Perumytilus purpuratus* was dominant at all sites (Fig. 1). This community persisted at the harvested sites, during the five years, with minimal encroachmente of macroalgae (Fig. 1a).

In the non-harvested area, *Perumytilus purpuratus* cover decreased from 95% in October 1983 to 0% in September 1985 (Fig. 1b), with a concomitant increase in cover of macroalgae and barnacles and the availability of bare rock space. Macroalgal cover peaked at 50% in September 1984 and subsequently decreased, stabilizing at ca 8% in Novem-
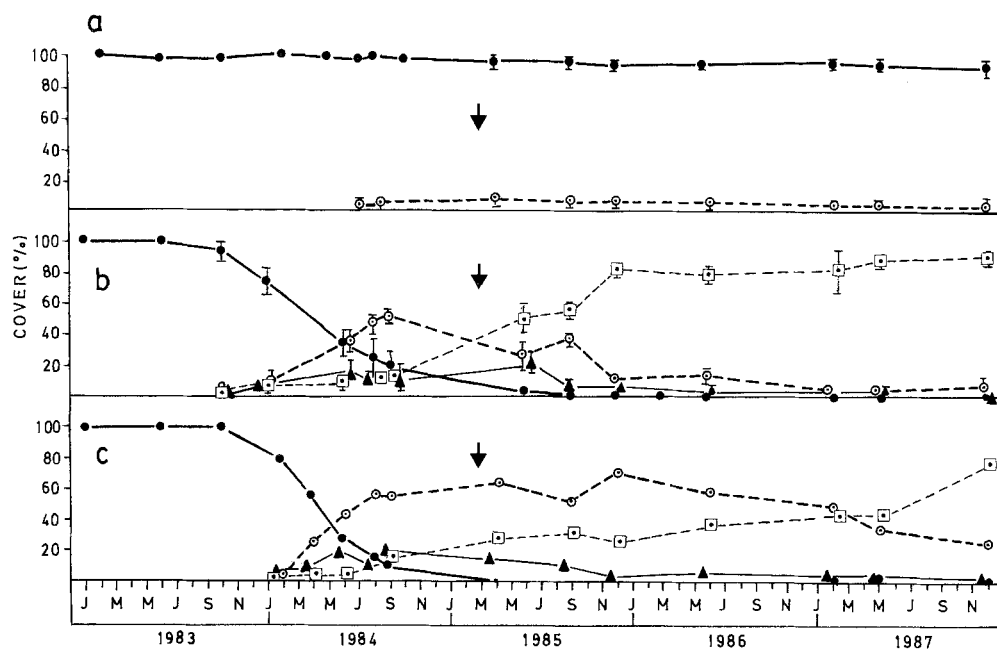
Fig. 1. Percent cover and SE (vertical lines) of *Perumytilus purpuratus* (●), macroalgae (○), barnacles (□) and bare rock (▲) in: (a) harvested area = Sites D, E, F; (b) non-harvested area = Sites A, B, B'; and (c) non-harvested area = Site C. Arrow indicates occurrence of March 1985 earthquake
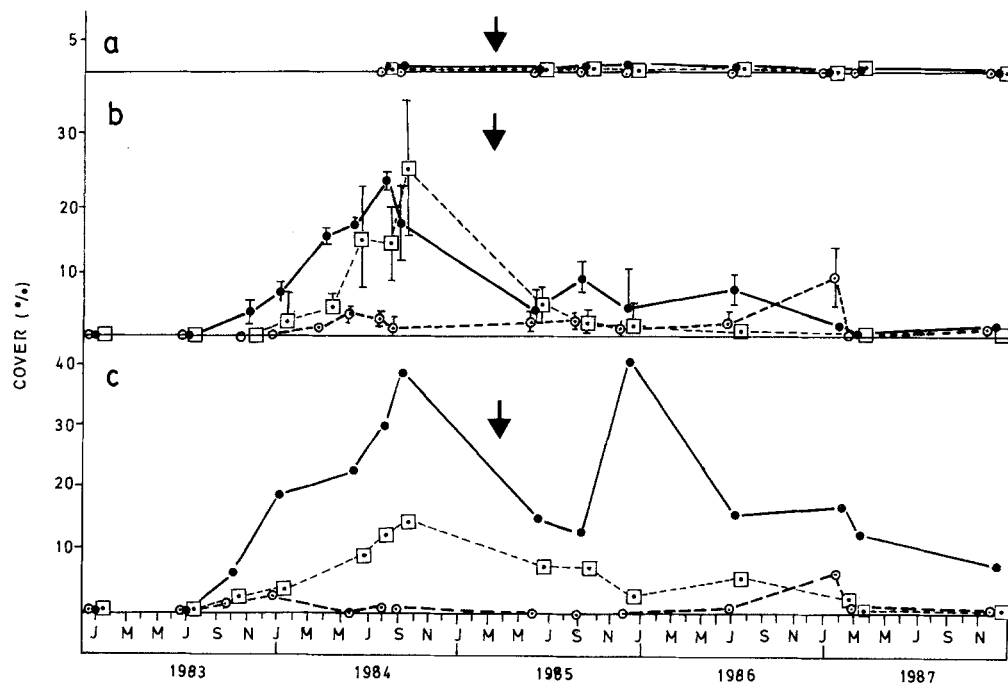

Fig. 2. Percent cover and SE (vertical lines) of Chlorophyceae (○), Phaeophyceae (□) and Rhodophyceae (●) in: (a) harvested area = Sites D, E, F; (b) non-harvested area = Sites A, B, B'; and (c) non-harvested are = Site C. Arrow indicates occurrence of March 1985 earthquake

ber 1985 (Fig. 1b). Availability of bare rock increased slowly, reaching a maximum of ca 20% in July 1985, which coincided with the decrease in cover of macroalgae. Between September and December 1985, barnacle cover increased to more than 80%. This high cover persisted until the end of the experiment (Fig. 1b).

At Site C there was also a dramatic reduction in the cover of *Perumytilus purpuratus*, which was eliminated by April 1985 (Fig. 1c). As mussel cover decreased there was a rapid increase in macroalgae. In contrast to the semi-exposed platforms, macroalgae cover persisted at over 50% for 30 mo. During the same period the percentage of bare

rock decreased to about 5% and barnacle cover gradually increased to over 40% in January 1987. Only in the last 9 mo of the experiment were barnacles more abundant than macroalgae, reaching 77.8% by December 1987 (Fig. 1c).

There were large differences in macroalgal cover among the sites (Fig. 2). The mean percentage cover of all algal divisions in the control sites, was extremely low throughout the study (Fig. 2a). In the non-harvested semi-exposed sites there was an initial increase in percentage cover of Rhodophyceae (November 1983) followed by Phaeophyceae (January 1984) and finally Chlorophyceae (June 1984) (Fig. 2b). Chlorophyceae maintained a mean cover of about 5% of the
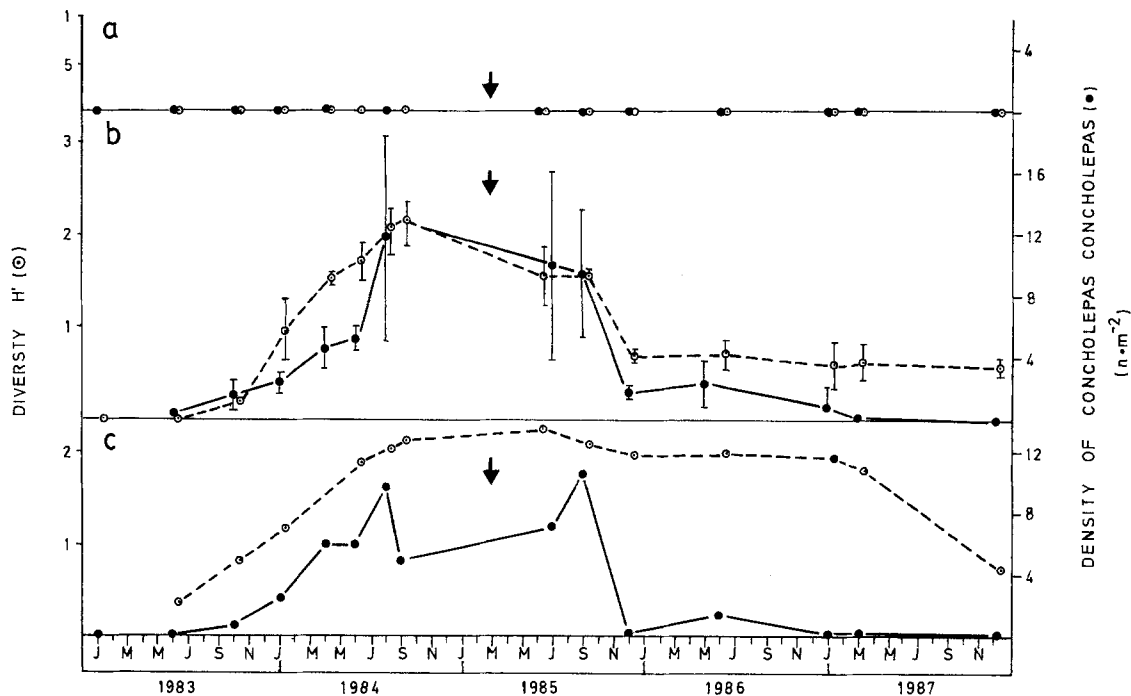
Fig. 3. *Concholepas concholepas.* Density (●) (±SE) and species diversity (○) (±SE) in: (a) harvested area = Sites D, E, F; (b) non-harvested area = Sites A, B, B'; and (c) non-harvested area = Site C. Arrow indicates occurrence of March 1985 earthquake

primary substratum, except in February 1987 (9.2±4.5%). Rhodophyceae and Phaeophyceae reached maximum cover in August to September 1984 (25.3±1.9% and 27.1±11.3%, respectively). Thereafter, the cover decreased to values close to 0% by March 1987 (Fig. 2b). Among the Chlorophyceae the main species was *Ulva lactuca rigida;* the main Rhodophyceae species were *Gelidium chilense, Centrosceras clavulatum, Corallina officinalis* var. *chilensis, Hildenbrandtia lecannellieri* and encrusting lithothamniod; and the main Phaeophyta species were *Adenocystis utricularis, Scytosiphon lomentaria, Ralfsia confusa* and *Colpomenia sinuosa.*

The situation at Site C was similar to the former, but with a greater cover of Rhodophyceae, which reached values of 39% in September 1984 and 43% in December 1985 (Fig. 2c). In March 1987, the cover of Rhodophyceae was 15%, decreasing to 9.8% in December 1987 (Fig. 2c).

Fig. 3 shows the variation in density of *Concholepas concholepas* and in species diversity (H') of the community with time. At all sites the diversity was initially close to 0. This situation persisted with time at harvested sites due to an almost total dominance of *Perumytilus purpuratus* (Fig. 3a), and persistent low density of *C. concholepas* due to intense human predation (Durán et al. 1987) (Fig. 3a).

At the three semi-exposed non-harvested sites, species diversity gradually increased, mainly due to the settlement of macroalgae, reaching a peak 21 mo after human exclusion (Fig. 3b). Over the next 15 mo diversity decreased, and had stabilized at ca 0.5, 35 mo from the start of the experiment. The variations in species diversity and density of *Concholepas concholepas* were closely coupled (Fig. 3b).

At Site C, *Concholepas concholepas* density increased prior to the increase in diversity (Fig. 3c), oscillated and then, after 35 mo, fell to very low levels from which it did not recover. Diversity remained constantly high $(H' \approx 2)$ for 14 mo after the *C. concholepas* population crash and then decreased steadily but did not stabilize (Fig. 3c).

The density of both key-hole limpet species was constantly low in the harvested sites (Fig. 4a). In the semi-exposed non-harvested sites, densities of both species peaked after 28 to 32 mo, ca 1 yr after the point of maximum species diversity (Fig. 4b). Thereafter, densities of both species decreased and then stabilized close to zero in the last 9 mo of the experiment (Fig. 4b).

Data on species diversity and densities of both key-hole limpets at Site C, are available from June 1985 only. The density of *Fissurella limbata* decreased drastically from 12 to 0 ind. m^{-2} between September and December 1985 (Fig. 4c). After an increase in density from December 1985 to January 1987, the density of *F. limbata* again decreased to zero by March 1987, and did not reappear during the study. *F. crassa* density remained relatively constant throughout the study period at ca 3 ind. m^{-2} (Fig. 4c).

Discussion

According to classical ecological theory, predation on a dominant competitor for primary space leads to increase species diversity in the community (e.g. Paine 1966, 1977, Branch 1984). The 21 mo study of Castilla and Durán (1985)
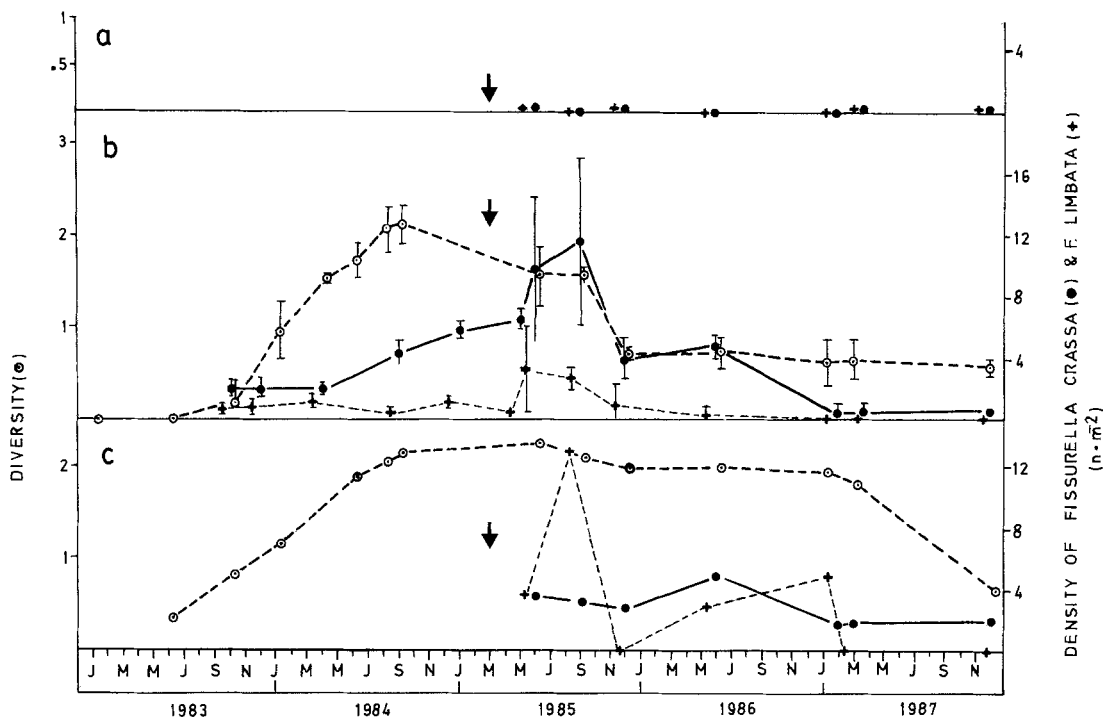
Fig. 4. Density of *Fissurella crassa* (●) and *F. limbata* (+) (±SE) and species diversity (○) (±SE) in: (a) harvested area = Sites D, E, F; (b) non-harvested area = Sites A, B, B'; and (c) non-harvested area = Site C. Arrow indicates occurrence of March 1985 earthquake

at the rocky intertidal community of Las Cruces supports this paradigm. At sites where human predators were excluded the key-stone muricid predator *Concholepas concholepas* increased in abundance dramatically, leading to a decrease in the cover of the competitively dominant mussel *Perumytilus purpuratus* and to an increase in species diversity, H', (primary space occupiers). Fig. 5 shows a schematic view of the changes in the non-harvested rocky intertidal community at Las Cruces during the five years of study. The first two schemes, 1982 and 1984, correspond to the results reported by Castilla and Durán (1985). Scheme 1982 shows the initial state with a predominance of *P. purpuratus* at the middle intertidal and a clear belt of *Lessonia nigrescens* at the lower intertidal. Scheme 1984 shows the same intertidal community ca 2 yr (September 1984) after the ECIM was enclosed. The lower intertidal continued to be dominated by *L. nigrescens* plants, while in the middle intertidal there appeared a transitional zone (b in Fig. 5) now covered with barnacles and algae. However, Zone c was still dominated by *P. purpuratus*. Scheme 1987 shows the state of the non-harvested rocky intertidal community approximately five years after the enclosing of ECIM. At this time the upper limit of *L. nigrescens* had moved lower (Castilla 1988) and *P. purpuratus* was virtually absent, except for small clumps. Although not represented in Fig. 5, the corresponding harvested rocky intertidal sites remained, during the five years of study, approximately, as pictured in Fig. 5, 1982

After five years and following a gradual and persistent decrease of *Concholepas concholepas* in non-harvested sites, the community became barnacle dominated and species di-

versity decreased. To date (August 1989) mussels have not recolonized the middle or lower intertidal fringes, and chthamaloid barnacles (*Jehlius cirratus* and *Chthamalus scabrosus*) intensively have been recruited onto available space, exhibiting a "weed-recruitment strategy" (Paine 1981, Castilla 1988).

At the harvested sites there was no predation of mussels by *Concholepas concholepas* throughout the study period. Consequently, these competitively dominant mussels, retained the primary space and species diversity remained low.

In the absence of predators, a mussel-dominated intertidal community has persisted for at least 60 mo; with predators present the community switched to one dominated by barnacles which has persisted (Boesch 1974) for 30 mo, in spite of, potential, structure-altering forces (e.g. predation by *Concholepas concholepas*, mussel larvae, algae spores; Fig. 3b). The barnacle "weed-recruitment strategy" has been the critical factor accounting for the persistency of this community (Castilla 1988). At this point in our study we feel that we do not have sufficient observations to support, or oppose, the existence of a middle intertidal stable barnacle community boundary point at ECMI (Lewontin 1969, Sutherland 1981). Also, 30 mo does not meet the Connell and Sousa (1983) time criterion for one complete turnover of all individuals of the community. Nevertheless, barnacles have persisted for many (5 to 6) minimal generation times (see Slobodkin 1961, Paine et al. 1985).

The March 3, 1985 earthquake caused an uplift of 40 to 60 cm of the central Chile shore (Anonymus 1985, Castilla 1988) which particularly affected the laminarian *Lessonia*
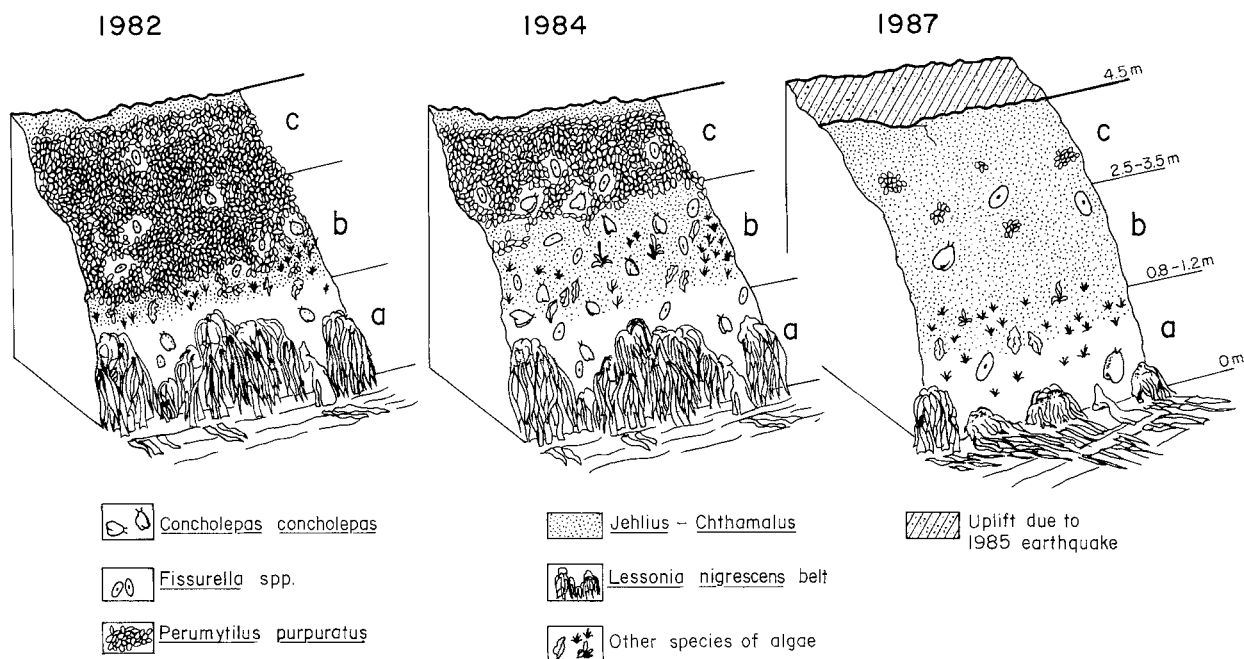
Fig. 5. Schematic view of non-harvested rocky intertidal at Las Cruces showing the three zones described in text. 1982: Initial state before ECIM enclosing; 1984: state ca 2 yr later; 1987: state ca 5 yr later, December

nigrescens (Zone a in Fig. 5). Its density and biomass were drastically reduced in the upper part of its pre-earthquake range (Castilla 1988); compare Zone a of Fig. 5 1982 and 1984 (pre-earthquake) and Fig. 5 1987 (post-earthquake). Castilla (1988) has documented that most of the upper border of the *L. nigrescens* belt was invaded by barnacles: *Jehlius cirratus* and *Chthmalus scabrosus*, which demonstrate their opportunistic colonization strategy (see Fig. 5 1987). At the middle intertidalzone, the change in relative level caused by the 1985 earthquake was most probably, responsible for the small reduction (5 to 10%) in cover of *Perumytilus purpuratus* at the harvested area (Fig. 1a). No settlement of this mussel has been observed to data (August 1989), either in primary space liberated by predation of *Concholepas concholepas*, or by the uplift.

At first glance, the ecological processes at the middle intertidal rocky shore of southern Chile seem to differ from those we found in central Chile. Hence, *Concholepas concholepas* removal experiments, carried out at Mehuin in southern Chile (Moreno et al. 1986), demonstrated a rapid recovery of *Perumytilus purpuratus* beds at the middle intertidal zone within less than two years of the initial manipulation. Plantigrade larvae of *P. purpuratus* recruit most intensively among the byssus threads of adult mussels (Ortiz and Castilla unpublished data, for other species see Seed 1976, Suchanek 1978, McGrath et al. 1988) and do not recruit on bare rock. Nevertheless, little is known about the intermediate factors (other than mussel byssus) that favor the establishment of *P. purpuratus* beds in Chile. Moreno et al. (1986) suggested that spaces between barnacles may facilitate establishment, and our observations in central Chile support that view (Navarrete and Castilla 1988). On the other hand, Bayne (1965) demonstrated that, for *Mytilus edulis*, filamen-

tous algae could act as one such intermediate factor. We believe that these factors are numerous (e.g. crevices with or without sand, crevices with or without filamentous algae, bare spaces among barnacles shells) and their availability will differ from one locality to another.

The decline in *Concholepas concholepas* populations in the non-harvested intertidal zone of ECIM after two to three years of the initial human exclusion may have multiple causes. The March 1985 earthquake generated a 40 to 60 cm uplift of the coast which had marked effects on the *Lessonia nigrescens* belt and it is known that their holdfasts and fronds provide shelter for *C. concholepas*. Furthermore, the effects of *C. concholepas* on the *Perumytilus purpuratus* beds during the initial two to three years (1983 to 1985) were devastating (Castilla and Durán 1985) and they were completely eliminated. *P. purpuratus* is one of the main prey of intertidal populations of *C. choncholepas*, and a food (mussel) shortage may have caused the decrease of *C. concholepas*, as occurs for example with predatory whelks (Fairweather 1988). However, *C. concholepas* also feeds on barnacles (Castilla 1981). Whether *C. concholepas* will return in the future to the middle intertidal and attack the barnacles beds remains to be seen.

During the five-year study at the harvested site macroalgae were rare (Fig. 1a). Mussels preempted the primary space (Schoener 1983). In contrast, primary space was liberated at the non-harvested sites and macroalgae showed a short-lived ability to monopolize it. The length of this transitory state varied with exposure: only a few months (1984) at the semi-exposed Sites A, B, B' (Fig. 1b), but nearly 3 yr at the exposed Site C (Fig. 1c). The role of grazers such as *Fissurella crassa* and *F. limbata* in the structure and dynamics of these transient algal communities is not well known.

Nonetheless, the reduction of algal cover (and dropping of diversity in 1985, see Fig. 1b) is tightly correlated with the increase in density of *F. crassa* (Fig. 4b) at the semi-exposed sites. Algal successions in rocky intertidal environments described by other authors (e.g. Hawkins 1981, Jara and Moreno 1984, Jernakoff 1985a, b) suggest a sequence in which Chlorophyceae represent a primary successional stage, gradually being replaced by Rhodophyceae and Phaeophyceae. In the present study, Rhodophyceae predominated throughout. Chlorophyceae occurred at low densities in the study sites. Among Rhodophyceae, calcareous forms (*Corallina* spp. lithothamnioid) predominated.

Finally, this study illustrates a clear case of "cascade effects" (Paine 1980) due to press-perturbation (sensu Bender et al. 1984). Hence, the exclusion of a top predator (humans) in the rocky intertidal resulted in an increase of a key-stone predator: *Concholepas concholepas,* and two species of herbivorous key-hole limpets. In turn, the increase of *C. concholepas* reduced the cover of *Perumytilus purpuratus,* a dominant competitor, favoring settlement of macroalgae in newly available primary space. This state is transient since macroalgae were subsequently eliminated from the system (most probably due to grazing by key-hole limpets). After five years, the community at the non-harvested area was dominated by barnacles. This may represent an alternative stable state to that of the mussel-dominated state that exists in numerous intertidal harvested areas in central Chile.

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