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Long-term changes in population density of *Fissurella picta* and *Fissurella limbata* (Gastropoda) in the marine reserve of Mehuín, Chile

Cambios a largo plazo en la densidad poblacional de *Fissurella picta* y *Fissurella limbata* (Gastropoda) en la reserva marina de Mehuín, Chile

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ABSTRACT

At the Marine Reserve in Mehuín, changes in density and distribution of key-hole limpets were detected during the first five years as consequence of human gatherers exclusion. However, later demographic changes could be explained by within-community ecological processes, not detected in presence of human gatherers. Competition for food, predation and recruitment, were explanatory hypothesis for such changes, and they were tested at the study site for two species: *Fissurella picta* and *Fissurella limbata*. At present, *F. limbata* does not occur at areas protected of the north winds, and F. picta shows a decreasing density in exposed areas. The competition hypothesis was tested at the exposed area through enclosure experiments. Predation over adult individuals was examined by means of a diet analysis for five predator species, from our data base of the Marine Reserve and other studies in that area and from other localities of the Chilean coast. Recruitment failure was studied on a long-term basis, using data on size structure accumulated in our data base. No inter or intraspecific competition was detected between the two species in the enclosure experiment, since neither species affected survivorship or biomass of the other. No evidence of an alternative to man predator of adults was found, but only a very low predation exerted by *Larus dominicanus, Sicyases sanguineus, Stichaster striatus* and *Rattus rattus*. A recruitment failure was detected for F. picta at the exposed area, and we detected the entry of individuals smaller than 30 mm during the last three years in the protected area. *F. limbata* recruited mainly in the exposed area. These results suggest us to evaluate the availability of suitable habitats that provide a refuge to predation and food requirements that warrant the survival of settlers.

Key words: key-hole limpets, long-term study, rocky intertidal, competition, predation, recruitment.

RESUMEN

En la Reserva Marina de Mehuín se detectaron aumentos en densidad y distribución de las lapas durante los primeros cinco años, debido a la exclusión de mariscadores. Sin embargo, cambios demográficos observados posteriormente podrían ser explicados por procesos ecológicos intracomunitarios no detectados en presencia de mariscadores de orilla. Competencia por alimento, depredación y reclutamiento constituyeron hipótesis explicativas de dichos cambios, que se analizaron en el área de estudio para *Fissurella picta* y *Fissurella limbata*, cuya abundancia y distribución espacial actuales muestran la ausencia de *F. limbata* en las áreas protegidas del oleaje y una disminución de la densidad de *F. picta* en las áreas expuestas. La hipótesis de competencia se puso a prueba a traves de experimentos de inclusión. La depredación se analizó considerando la dieta de cinco especies de depredadores de adultos, con información proveniente de nuestra base de datos de la RMM y de otros estudios del área y otras localidades de la costa chilena. Las fallas de reclutamiento fueron estudiadas en el largo plazo, usando nuestra base de datos. En los experimentos de inclusión no se detectó competencia inter o intraespecífica, ya que los individuos de ambas especies no se vieron afectados en su biomasa ni sobrevivencia. No se encontró evidencias de un depredador alternativo al hombre sobre adultos de ambas especies, sino sólo una leve depredación por *Larus dominicanus, Sicyases sanguineus, Stichaster striatus* y *Rattus rattus*. Se detectó fallas de reclutamiento para *F. picta* en el área expuesta, y en el área protegida se registró la entrada de individuos menores a 30 mm durante los últimos tres años; *F. limbata* presentó reclutamiento sólo en el área expuesta. Lo anterior sugiere evaluar la depredación sobre los reclutas y la disponibilidad de hábitat adecuados como refugio a la depredación y con alimento suficiente que garanticen una alta sobrevivencia de los recién asentados.

Palabras clave: lapas, estudio de largo plazo, intermareal rocoso, competencia, depredación, reclutamiento.

INTRODUCTION

In areas of Chile recently established as Marine Reserves, where previous selective exploitation by human gatherers has been precluded, the density and size of some commercially exploited mollusk species have initially increased and the abundance of their

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prey species decreased (Moreno et al. 1984, Castilla & Durán 1985, Oliva & Castilla 1986). Long-term studies, monitoring mollusk populations in protected coastal areas previously exploited by man, have been very scarce. However, at Dwesa Marine Reserve in South Africa, studies that begun 10 years after it was established showed that changes were not always consistent with an expected increase in size and abundance of exploited species (Dye 1988, 1989, Dye et al. 1994). This may be due to unreported ecological processes which generate long-term demographic changes in populations.

At the Marine Reserve of Mehuín (MRM), increase in size, number, and species richness of the key-hole limpets was reported four years after the Reserve was created (Godoy & Moreno 1989, Jara & Moreno 1984, Moreno et al. 1984). During the following years these species have shown density and spatial distribution fluctuations in two rocky sites at the MRM (personal observations) that cannot be explained as a consequence of human exclusion.

Competition, predation and environmental heterogeneity are important factors regulating the distribution and abundance of organisms in rocky intertidal communities (Branch & Moreno 1994, Connell 1983, Dayton 1971, Moreno et al. 1986, Oliva & Castilla 1986, Ortega 1985, Paine 1966, Schoener 1983, Sousa 1979, Sutherland 1974, Underwood 1978). When predation levels are low, or predators are excluded, competition between herbivorous prey species intensifies as resources become limiting (Paine 1966, Godoy & Moreno 1989, Lubchenco & Gaines 1981, Jara & Moreno 1984, Menge 1976, Moreno et al. 1984, Underwood 1979).

Some models of community regulation (Menge & Sutherland 1987) indicate that competition, predation or differential recruitment, or a combination of all, may produce the observed changes in abundance of saturated communities. In this study each factor was analyzed separately, to determine if community organization processes or remote origin factors can explain the density changes observed on two species of key-hole limpets at the MRM, *Fissurella picta* Gmelin, 1791 and *Fissurella limbata* Sowerby, 1835.

At the MRM, because it is a protected site, it is not possible to recolect specimens for dietary studies. Experiments concerning predation effects are also very difficult to perform due to the low density of some vertebrate predators (*Larus dominicanus* Lichtenstein and *Lutra felina* (Molina) 1782). Therefore we searched for information concerning predators of fissurellids, using bibliographic information and observations registered on our data base from the MRM in the long-term. On the other hand, some predictions from competition theory were analyzed by means of experimental manipulation in the field. Additionally, recruitment analysis involved mainly temporal and spatial series of observations, more than experimental work. Based on this, we analyzed the data base accumulated through the monitoring of the body size of *F. picta* and *F. limbata* in the MRM during 10 years.

MATERIALS AND METHODS

The Marine Reserve of Mehuín (MRM) (39° 24' S; 73° 13' W) is a coastal area of 6.000 m^2 of intertidal rocks, in Maiquillahue Bay, 70 Km NW of Valdivia (Figure 1). The Reserve was created in 1978, after which human gatherer activity was totally excluded.

Between 1978 and 1993, except for years 1988 and 1990 the population density and size of fissurellids was monitored both, in areas exposed (exposed site) and protected (protected site) to northern winds and wave action. Data from 1978 to 1982 were obtained from Moreno et al. (1984), and starting from 1983 to 1993 they were obtained following the linear transect methodology developed by Burnham et al. (1980). Only since 1984 data were obtained separately for "protected" and "exposed" habitats. Size data were obtained between 1985 and 1993 for *F. picta*, and between 1987 and 1993 for *F. limbata*, with the exception of 1988 to 1990.

At the MRM, the trophic impact of *Larus dominicanus* (data base) and *Rattus rattus* Linnaeus (Zamorano 1986) was studied

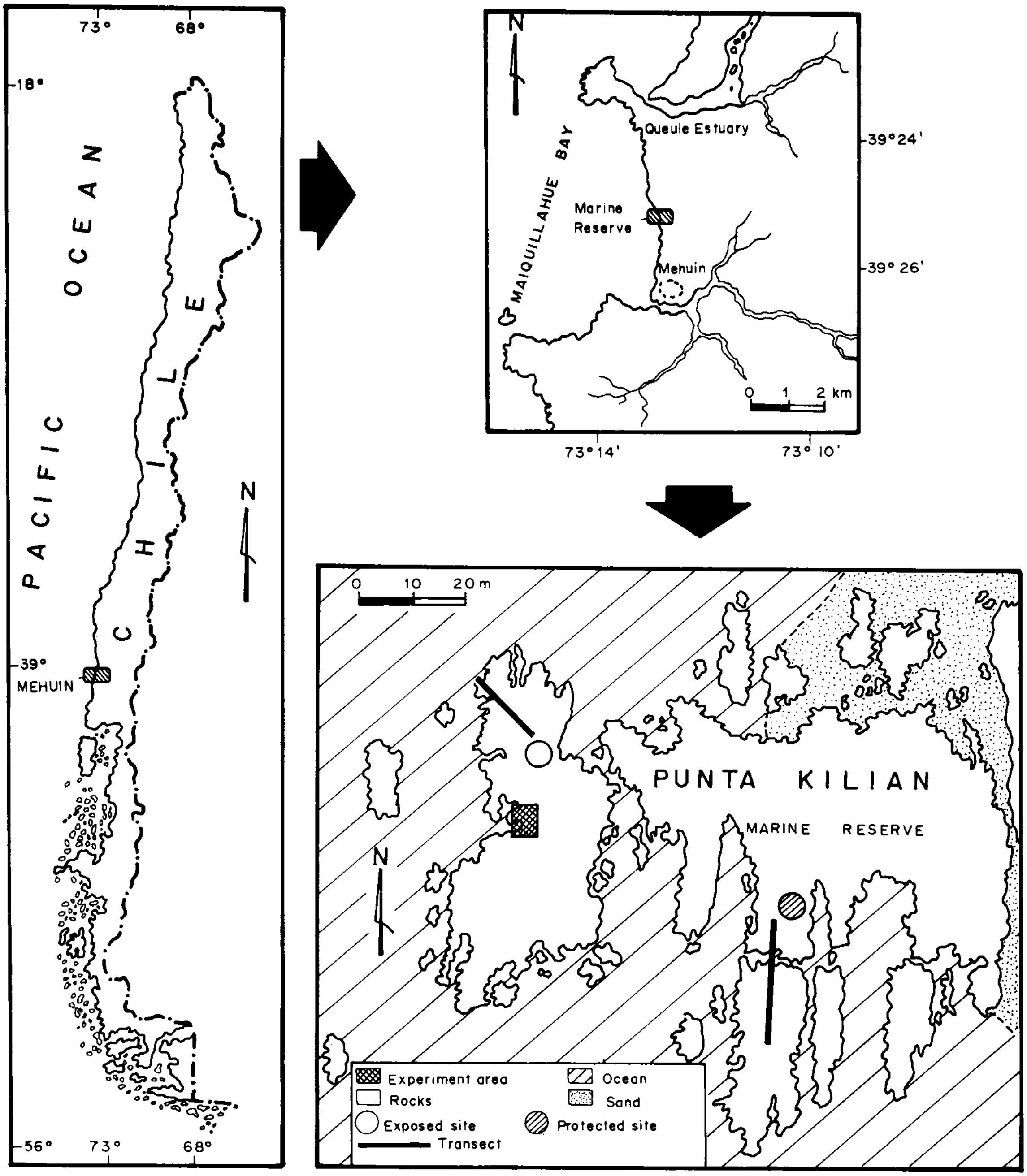

Fig. 1: Geographic location of the study site, Marine Reserve at Punta Kilian, Mehuín, Chile.
Localización geográfica del área de estudio, Reserva Marina de Punta Kilian, Mehuín, Chile.

analysing frequency occurrence data of the mollusk shells remaining at their foraging habitats. The predatory role of *Sicyases sanguineus* Muller y Troschel (Femenías 1994) and *Stichaster striatus* (Matus 1994) was evaluated through a gut content analysis. Also, information concerning frequency occurrence of key-hole limpets in the diet of these predators along the chilean coast was obtained from bibliographic references, including the other predator *(Lutra felina)*.

The field experiment was undertaken during the austral autumn-winter, throughout 132 days between April and August 1992. An experimental design to investigate intraspecific and interspecific competition was used (Underwood 1986). In an area of approximately 200 m^2, 25 stainless steel cages of 15 x 15 x 5 cm, with a mesh of 0.5 cm, were installed. Density of limpets inside the cages was 44.4 and 88.9 individuals per m^2 respectively, which was significantly greater than in the rocky intertidal (two per m^2). Fissurellids were enclosed in each cage, according with five randomly assigned treatments: five cages contained one individual of *F. picta* (T1). Another five contained one individual of *F. limbata* (T3). In other five, two individuals of *F. picta* (T2); in another five, two individuals of *F. limbata* (T4); and in the remaining five cages, a single individual of *F. picta* plus a single individual of *F. limbata* (T5). All other herbivores within each cage were previously removed by manual cleaning.

The specimens used corresponded to the most frequent sizes (total length: TL) with a mean of 47.4 mm (± 5.1 mm S.D.) for *F. picta* and 49.7 mm (± 7.7 mm S.D.) for *F. limbata*, whose mean weights were 13.7 g (± 3.0 g S.D.) and 18.5 g (± 4.8 g S.D.), respectively. Cages were checked and cleaned every fortnight, considering eventually the removal of small size gastropods that could have entered. Weight and shell length of survivors were measured monthly in the field using a balance OHAUS (± 0.1 g) and vernier calipers (± 0.1 mm), respectively. The final weight of the specimens from each treatment were compared using one way ANOVA considering pairs of treatments, after having verified data for normality and homocedasticity (Neter et al. 1985).

RESULTS

Analysis of density data for *F. picta* and *F. limbata* on the total area of the MRM, showed that *F. picta* increased gradually from less than one ind.m^{-2} in 1978 up to six ind.m^{-2} in 1983. Since then, densities decreased to two ind.m^{-2} in 1992. *F. limbata* was almost absent in 1978, but during 1979 a mean density of one ind.m^{-2} was recorded. Levels continued increasing until 1981 when a mean density of approximately two ind.m^{-2} was reached. Nevertheless, this value dropped in 1982 and remained almost constant at one ind.m^{-2} until 1991, after which the limpet disappeared from the monitoring areas, reappearing in 1993 (Figure 2).

However, when we analyze the density of both species between 1984 and 1993, according to the degree of exposition to wave action, they showed different tendencies; in the former, *F. picta* declined and increased in exposed and protected areas respectively, while *F. limbata* was always present in the low intertidal of the exposed rocky zone but it only appeared during three years at the protected area, although with mean densities lower than 0.5 ind.m^{-2} (Figure 3A and 3B).

Population size structure of both species during the total study period showed that the most frequent size range of the sampled population was 40 to 60 mm for *F. picta* (approx. 40%), and 50 to 75 mm for *F. limbata* (approx. 50 %), except in 1993 when most individuals of this species presented a size smaller than 50 mm (approx. 75%). Besides that, few specimens smaller than 30 mm were observed for either species, except in 1991 and 1993 when an increase of this size range was evident (Figure 4).

When we examined size structures of both species according to the degree of exposure to wave action, we found that *F. limbata* at the exposed area exhibited the pattern explained above (Figure 4), while at the

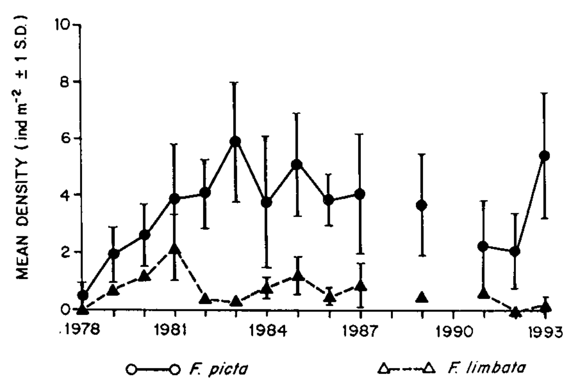

Fig. 2: Density (ind.m^{-2}) of *Fissurella picta* and *Fissurella limbata* at the Marine Reserve of Mehuín (MRM), Chile, during years 1978 to 1993.

Densidad (ind.m^{-2}) de *Fissurella picta* y *Fissurella limbata* en la Reserva Marina de Mehuín (RMM), Chile, durante los años 1978 a 1993.

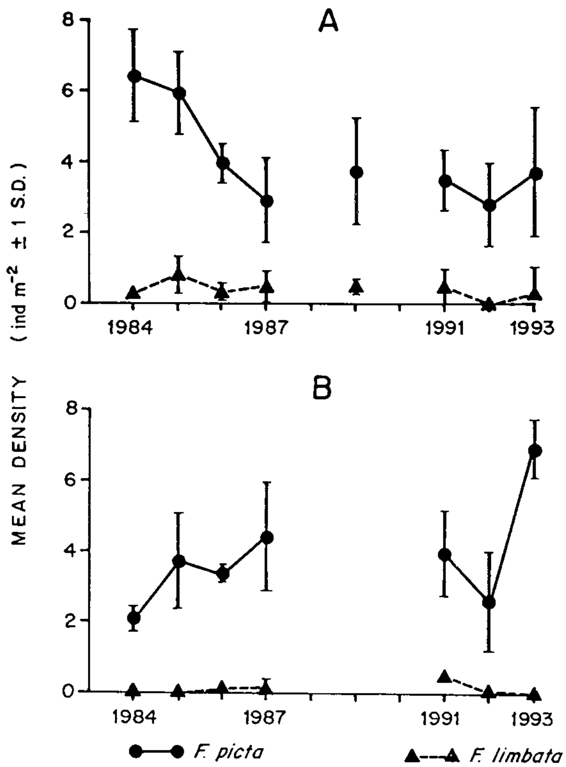

Fig. 3: Density (ind.m^{-2}) of *Fissurella* picta and *Fissurella limbata* at the rocky exposed (A) and protected (B) sites of the MRM, during 1984 to 1993.

Densidad (ind.m^{-2}) de *Fissurella picta* y *Fissurella limbata* en el frente rocoso expuesto (A) y protegido (B) de la RMM, durante 1984 a 1993.

protected area only a few larger individuals (60-70 mm) were found. Between 1986 and 1987, *F. picta* presented a similar size structure (60% of the specimens measured between 40 and 70 mm TL) in both areas, whereas from 1991 until 1993 sizes were smaller (60% of the specimens measured between 25 and 65 mm TL). In addition, the relative frequency of the individuals smaller than 30 mm was less than 15% at the exposed area during all the study period, whereas at the protected area they represented between 20 to 30% of the total measured specimens during 1991 to 1993 (Figure 5).

The frequency of occurrence of *Fissurella* spp. in the diet of the five predators (*L. dominicanus, L. felina, S. sanguineus, S. striatus* and *R. rattus*) was low, not only at the MRM but also at other localities of the Chilean coast. Excluding *L. felina*, the mean value was near 13 % for *L. dominicanus* and much smaller for the other three species (Figure 6).

Data on limpet consumption by *L. felina* based on information collected at the north-central zone of Chile (Castilla & Bahamondes 1979) showed that approximately 50% corresponds to four species of key-hole limpets (*F. crassa, F. limbata, F. latimarginata, F. maxima*). On the other hand, Rozzi & Torres-Mura (1990) (only 200 km south of MRM) did not report *Fissurella* as a food item of *Lutra* in the coast of Chiloé. Since at the MRM only one individual otter visits the area sporadically in some years, no information about its trophic activity is available. A similar situation was observed with *L. dominicanus* at the MRM, where it occurs at a very low density, even during its reproductive season (spring-summer).

In relation to the competition hypothesis, tested by means of an enclosure experiment, we observed no change in the weight of individuals. No mortality or cage loss occurred during the first half, but some cages were lost (10%) and mortality (near 20%) occurred in each treatment during the second part of the experiments. ANOVA results for the individual's final weight showed no significant difference between the five treatments. This indicated no change in survival or in biomass of the fissurellids during the experiment, regardless the number and composition of limpets in the cages (Table 1).

DISCUSSION

Competition, predation and recruitment failure are important regulating factors in the population dynamics of many limpets and other littoral organisms (Black 1979, Branch 1985, Branch & Moreno 1994, Connell 1983, Creese & Underwood 1982, Ortega 1985, Underwood 1979, Paine 1966). In reviewing competition in marine organisms, Branch (1984) found that interference was the predominant mode in the sea, occurring in 80% of the cases analyzed. Intraspecific competition has been shown to influence growth, survival, recruitment, body weight and reproductive output of limpets (Branch 1975, Creese 1980, Fletcher 1984, Ortega

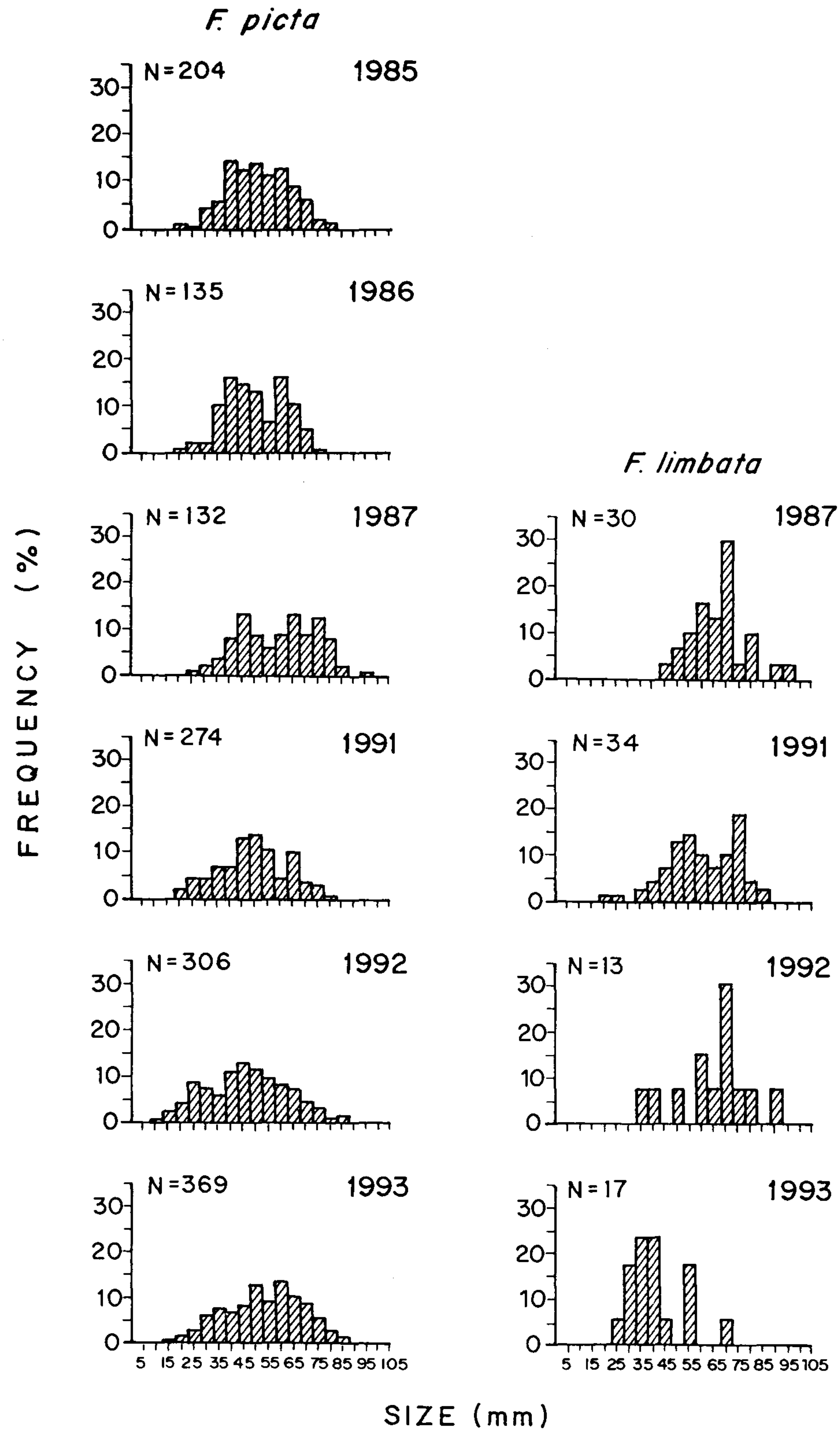

Fig. 4: Demograms of *Fissurella picta* and *Fissurella limbata* at the MRM, during spring (September - October) of 1985 to 1993.

Demogramas de *Fissurella picta* y *Fissurella limbata* en la RMM durante primavera (septiembre-octubre) de 1985 a 1993.

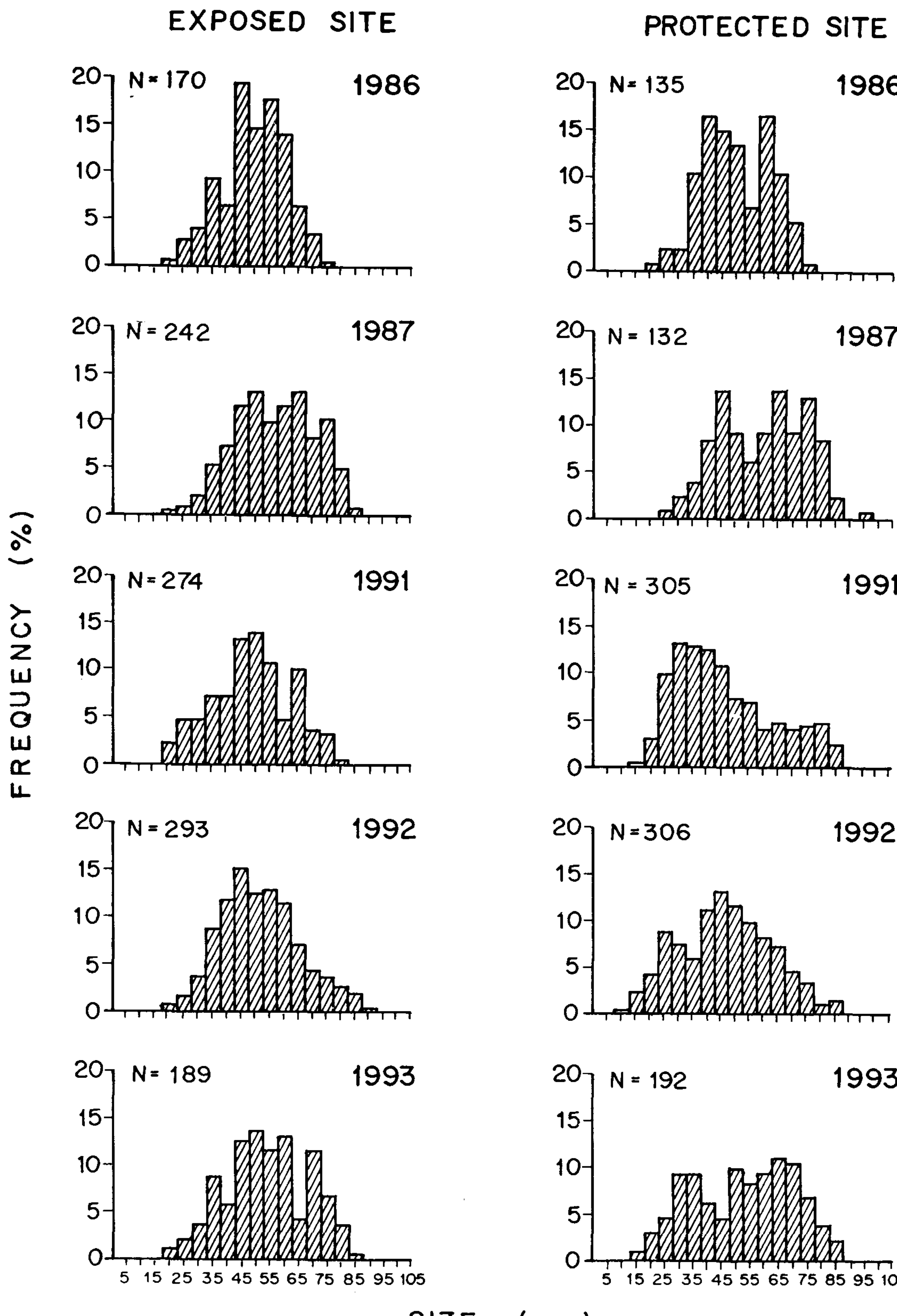

Fig. 5: Demograms of *Fissurella picta* in the exposed and protected sites at the MRM, during spring (September - October) of 1986 to 1993.

Demogramas de *Fissurella picta* en los frentes expuesto y protegido de la RMM durante primavera (septiembre-octubre) de 1986 a 1993.

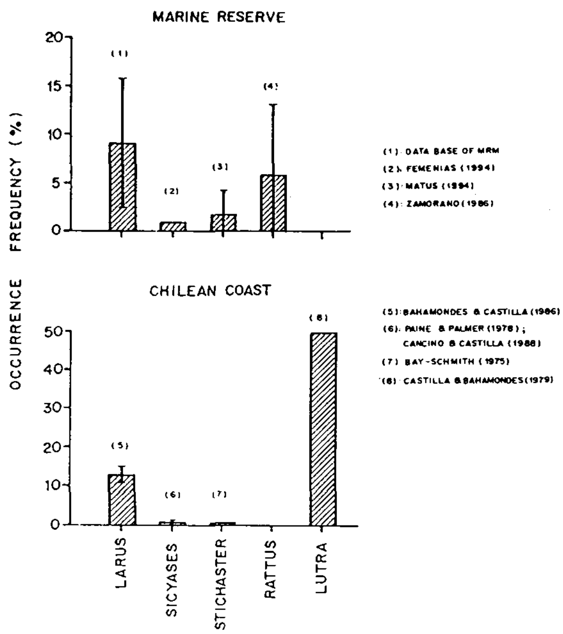

Fig. 6: Frequency of occurrence of key-hole limpets in the diet of *Larus dominicanus, Sicyases sanguineus, Stichaster striatus, Rattus rattus* and *Lutra felina* at the Marine Reserve of Mehuin and other localities of the Chilean coast.

Frecuencia de ocurrencia de las lapas en la dieta de *Larus dominicanus, Sicyases sanguineus, Stichaster striatus, Rattus rattus* y *Lutra felina* en la RMM y otras localidades de la costa chilena.

1985). Zonation patterns, habitat segregation and territoriality may be influenced by competition (Creese & Underwood 1982).

We hypothesize that within the Marine Reserve, habitat segregation and density fluctuations among fissurellids are the result of competitive interactions that lead to local extinction, and constrain the distribution of species to a specific microhabitat. The long-term observation of protected and exposed sites of coexisting *F. picta* and *F. limbata*, revealed the virtual local extinction of *F. limbata* in the former site, and in the second with a decrease of *F. picta* and permanence of *F. limbata* in the latter site. These kind of observations have been traditionally explained by interspecific competition (Giller 1984, Putman 1994). Nevertheless, the results of our experiment provide no evidence supporting this hypothesis. Thus, density changes of these intertidal herbivores must depend on other factors, including recruitment failure, survivorship of recruits,

TABLE 1

One way ANOVA of the final weight of *Fissurella picta* and *Fissurella limbata* in the (A) intraspecific and (B) interspecific competition experiments at the Marine Reserve of Mehuin, April to August 1992

ANDEVA de una vía para el peso final de *Fissurella picta* y *Fissurella limbata* en los experimentos de competencia (A) intraespecífica y (B) interespecífica en la Reserva Marina de Mehuin, entre abril y agosto de 1992

A) Intraspecific competition				
F. picta (T1 vs T2)				
Variation source	d. f.	S.S.	M.S.	F
Between samples	1	31.827	31.83	2.68 n.s.
Within samples	13	154.313	11.87	
Total	14	186.140		
F. limbata (T3 vs T4)				
Variation source	d. f.	S.S.	M.S.	F
Between samples	1	80.033	80.033	2.51 n.s.
Within samples	13	414.444	31.880	
Total	14	494.477		

$F_{0.05\,(1,13)} = 4.67$

B) Interspecific competition				
F. picta (T5 vs T1)				
Variation source	d. f.	S.S.	M.S.	F
Between samples	1	16.129	16.129	1.24 n.s.
Within samples	8	104.300	13.038	
Total	9	120.429		
F. limbata (T5 vs T3)				
Variation source	d. f.	S.S.	M.S.	F
Between samples	1	56.169	56.169	3.20 n.s.
Within samples	8	140.460	17.56	
Total	9	196.629		

$F_{0.05\,(1,8)} = 5.32$

or the presence of predators other than human gatherers.

The only alternative predators, of adult limpets, are the common sea-gull *(Larus dominicanus)*, which occasionally takes *Fissurella* spp., and the sea-otter *(Lutra felina)* observed rarely in the area (Lépez 1987, personal observations). Moreover, when examining predation exerted by these species plus other three predators over the total fissurellid populations at the MRM and other localities of the chilean coast, it is found that they do not constitute their principal food item. For *L. dominicanus, R. rattus* and *L. felina* the main item was *Concholepas concholepas* (data base of MRM; Bahamondes & Castilla 1986, Zamorano1986, Castilla & Bahamondes 1979), meanwhile for *S. sanguineus* and *S. striatus* most of their preys were primary substratum occupants, like barnacles and mytilids (Paine & Palmer 1978, Cancino & Castilla 1988, Femenías 1994, Bay-Schmith 1975, Matus 1994).

The first three predators occur in very low densities, with seasonal activity, sporadically, and at specific areas of the MRM, and thus their predatory action appears as minimal when compared with human gatherers predatory pressure (Jara & Moreno1984, Godoy & Moreno 1989, Moreno et al. 1984). For this reason, regardless of experimental proofs, we propose that predation would not be the regulating factor of the temporal and spatial distribution and density of adult limpets in this site.

On other hand, when examining the actual spatial distribution of *F. picta* at the MRM we observe that this species has monopolized the protected intertidal rocky shores, with effective recruitment, during the last three years, while it has diminished its density in exposed areas, showing a very low recruitment during the study period. Meanwhile, at the exposed area *F. limbata* has remained during all the study period, with individuals smaller than 30 mm in 1991 and in 1993 representing 23 % of the total amount of individuals found in the last year. These lead us to postulate that problems of recruitment for these species in specific habitats of the MRM are important in determining their present distribution and abundance. Furthermore, it is necessary to explain that size of settling specimens is between 0.5 and 1 mm (Vargas 1995) , and that the age of a *Fissurella* of northern Chile of 25 mm is one year (Bretos 1980). Consequently, time between settlement and what we call recruitment is at least one year or even more.

Possible factors generating problems in recruitment, range from large-scale oceanographic phenomena (e.g., ENSO) to stimulation of recruitment in the intertidal zone. The available information on recruitment in the area for *Concholepas concholepas* (Moreno et al. 1993) and *Phragmatopoma virgini* (J. Zamorano, personal communication) demonstrates that during 1992, when the "El Niño" phenomenon was present, recruitment for both species failed. Furthermore, the availability of *C. concholepas* larvae in Valdivian coastal waters was affected (Moreno et al. 1993). However, the analysis of the size structure of the populations of the two key-hole limpets in the Marine Reserve shows sizes smaller than 30 mm in *F. limbata* and *F. picta* only from 1991 to 1993 (e.g. Lépez & Moreno 1988, Moreno & Reyes 1988 and Reyes & Moreno 1990) indicating that recruitment occurred during 1991 and 1992, and suggesting that the process would be positively associated with "El Niño".

No specific research on the biology of Chilean Fissurellidae larvae has been conducted until now. Nevertheless, there are some studies related with the reproductive biology of these species. Bretos & Jiron (1980) and Bretos et al. (1983) detected, in different areas of the chilean coast, a parasitism problem in the gonads of *Fissurella*, which would affect its fecundity. On other hand Branch & Moreno (1994), have described the same phenomenon at the MRM. Besides this, as these key-hole limpets are Archeogastropods, they probably present a short-lived larvae in the coastal plankton, like *Haliotis* in Australia (Prince et al. 1988, Sheperd et al. 1992), and therefore it is worth to study these short larval cycles and their probable association with the decline of fecundity, and this with the recruitment variations of these species.

To account for our results, we need an hypothesis that incorporates aspects of community organization; where the characteristics of settlement habitat and post-settlement mortality factors are the most important for *Fissurella.* In a study about limpet recruitment at the MRM during 1993 (individuals smaller than 1.0 cm TL) (F. Navarrete, personal communication), we found that *F. picta* recruited in greater densities in crevices full of sea-water at the mid and low intertidal levels, in protected and semiprotected areas. In contrast, *F. limbata* showed a low number of recruits, all which were found in the same habitats as *F. picta*, but only in exposed areas. This evidence allow us to suggest that submerged crevices are important habitats for settlement for these two species, being also equally important their exposure to wave action.

Some recent observation on the settlement of unknown fissurellids species made in northern Chile (González et al. 1991) show recently metamorphosed individuals occurring on red algae in the low intertidal. During 1993, the hypothesis concerning the effect of algae and adult *F. picta* on limpet recruitment at the MRM was tested (Vargas 1995). She concluded that these factors were not important for the recruitment of these limpets. Nevertheless, although recruits were found both in presence and absence of adults, and in presence and absence of algae (mainly *Iridaea laminarioides*), they always occurred inside small crevices. This shows the importance of analyzing the factors that determine the movement of recruits in these habitats. Probably, crevices provide food and refuge to predation. In addition, if we consider that at the MRM some predators of small organisms appear in high density (*Stichaster striatus, Sicyases sanguineus, decapods* and recruits of *Concholepas concholepas*) (Matus 1994, Femenías 1994, Reyes & Moreno 1990, Moreno et al. 1993), the hypothesis of crevices as refuges to predation gains relevance. In spite of their abundance, there is surprisingly a lack of information concerning the diet of these small size predators. Therefore, in future studies, more attention must be paid on the consumers guild of post-settling gastropods. According with this, predation hypothesis can not be rejected until the closure of this gap in our ecological knowledge.

In exploited areas (off the MRM), the frequency of small fissurellids is higher than in the Marine Reserve, suggesting a demographic compensatory mechanism of key-hole limpets to human predation or to a decrease in density of the potential predators of their recruits. Humans have practically eliminated the natural alternative predators of these systems, so, no external control of the key-hole limpets can be measured. In this way, in the long-term, the community would reach a clear unbalance between the trophic levels and the initial goals of conservation of the natural processes would fail, probably due to the small size of the MRM (6 ha). So, conservation of the intertidal community needs to be accompanied by measures that tend to host a greatest number of high trophic level predators in the system.

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