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Effects of the 'El Niño' event on the recruitment of benthic invertebrates in Bahía Tortugas, Baja California Sur

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RESUMEN

Se realizó una evaluación de los efectos del Niño (1997-98) sobre el reclutamiento de invertebrados bentónicos y macroalgas en dos arrecifes rocosos de Bahía Tortugas, en la costa del Pacífico central de la península de Baja California. Para cuantificar el impacto de este evento, se midieron los cambios en densidad ocurridos en juveniles de abulón (*Haliotis fulgens* y *H. corrugata*), de macroalgas laminariales (*Macrocystis pyrifera* y *Eisenia arborea*), y en el asentamiento de postlarvas puerulus de langosta (*Panulirus interruptus*), antes, durante y después de El Niño.

El efecto del Niño tuvo un impacto diferente para cada especie: los bancos de "sargazo" fueron eliminados desde principios del otoño de 1997, recuperándose parcialmente un año después, y completamente hacia el invierno de 1999. La densidad de los juveniles de abulón de 1 año de edad mostró una drástica reducción en otoño de 1997, pero fue recuperándose lentamente de 1998 a 1999. Durante este último período, el grupo de 1 año de edad mostró una alta variación en su longitud de concha, lo cual sugiere un efecto indirecto de El Niño al alterar la base alimentaria de los juveniles de abulón. Por el contrario, la densidad en los asentamientos de puerulus y juveniles de langosta se estimuló positivamente durante El Niño, observándose los máximos asentamientos coincidentes con las máximas anomalías de temperatura y nivel medio del mar. Se concluye que la comunidad bentónica de esta región costera muestra una gran resistencia al cambio y que sus poblaciones están adaptadas para recobrar su condición normal uno y medio o dos años después de ocurrido el evento.

PALABRAS CLAVE: El Niño, langosta roja, sargazo, reclutamiento, Baja California.

ABSTRACT

An evaluation of the effects of El Niño (1997-98) on the recruitment of benthic invertebrates (abalone, spiny lobster, and kelp beds) was carried out in two reefs at Bahía Tortugas on the central Pacific coast of Baja California. Density changes of juvenile abalone (*Haliotis fulgens* and *H. corrugata),* kelp (*Macrocystis pyrifera* and *Eisenia arborea*), and puerulus settlement of spiny lobster (*Panulirus interruptus*), before and throughout El Niño, were used to measure the impact on the recruitment of benthic populations of the rocky sublittoral.

El Niño had a different effect on each species. Kelp beds were eliminated at an early stage in fall 1997, but recovered partially one year later and fully by winter 1999. Density of one-year-old abalone was reduced drastically in fall 1997. It slowly recovered throughout 1998 and 1999. During the latter period, this age group displayed high variability in length, suggesting an indirect effect of El Niño on the food supply of juvenile abalone. Density of puerulus spiny lobster settlement was positively stimulated during El Niño matching, without any time lag, the increase in mean sea level and surface temperature. We conclude that benthic communities on this part of the coast show high resilience, and their populations are adapted to recovering their structure and normal community conditions one and a half to two years after the El Niño event.

KEYWORDS: El Niño, spiny lobster, abalone, kelp, recruitment, Baja California.

INTRODUCTION

The occurrence of the El Niño event in 1997, the largest of the century, engaged the interest of the scientific community in much the same way as the one in 1983, the most severe of its kind up to that time. Where the fishing industry is important, the effects include a decrease of minor pelagic populations, such as sardine and northern anchovy (Kramer and Ahlstrom, 1968; Kramer, 1970), food reduction, temporary changes in the trophic structure of ecosystems (Guillén, 1983), incursion of tropical species into temperate zones, and changes in biodiversity. All these shifts may be deleterious for certain species. Nevertheless, they are episodic in nature, like the event itself, and their effect on the biotic community depends on the intensity and duration of the phenomenon.

El Niño in 1997 coincided with a project conducted by the authors in the area of Bahía Tortugas, B.C.S., giving us the opportunity to extend our observations on juvenile recruitment of benthic species such as abalone and spiny lob-

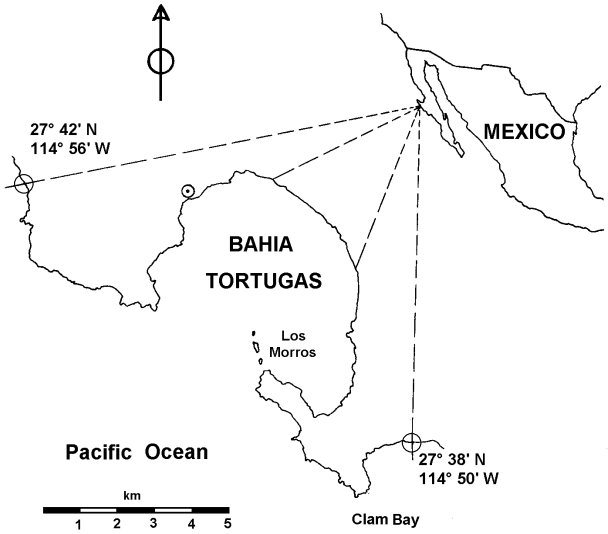

Fig. 1. Study area

ster, and to measure the effect of the event on these populations. We assumed that El Niño might have negative consequences on the recruitment and later abundance of these species, as well as on that of other constituents of the community. We extended our observations two additional years, and took into account other dominant species of the community. This article includes observations on changes noticed during and after El Niño in the recruitment of juvenile abalone (*Haliotis spp.*), spiny lobster (*Panulirus interruptus*), and two species of macro algae (*Macrocystis pyrifera* and *Eisenia arborea*), which coexist on the rocky coast marine community of Baja California.

MATERIALS AND METHODS

Study area

The study area is located on the western coast of the central portion of the Baja California peninsula near Bahía Tortugas, Mexico (Figure 1). Work was carried out at two sites on the rocky littoral, known as Los Morros (27°39'03" N, 114°52'27" W), at the mouth of the bay, and Clam Bay (27°37'11. 5" N, 114°50'38. 3" W), 10 km south of Bahía Tortugas (Figure 1). In the rocky reefs of this region, large kelp beds (*Macrocystis pyrifera*) are inhabited by benthic populations, such as abalone, lobster, snails, and macro algae that are commercially exploited.

Indicator species

The early developmental stages of abalone and spiny lobster were used as indicator species. In the case of the lobster, these were puerulus and juvenile stages (6 to 35 mm in cephalothorax length), and in abalone, juveniles 3 to 90 mm shell length. When El Niño appeared, observations were extended to macro algae (*Macrocystis pyrifera* and *Eisenia arborea*), as well as to other the dominant invertebrates in the community, such as turbo snails, sea cucumbers, urchins, and limpets. The data obtained for these other species, was inconclusive and only the macro algae were retained in the study.

Abalone

Population density of juvenile abalone was recorded at three depth levels: 6, 9, and 12 m in Los Morros bank, and 0.5, 3, and 5 m in Clam Bay. Seven underwater surveys were carried out in November 1996, April and November 1997, April 1998, January and July 1999, and January 2000. At each contour depth, three sampling stations were occupied, distributed in such a way as to represent the central portion and outer edges of each bank. In all, nine stations were sampled per bank. Transects were made at each station by reeling out a 15 m line and inspecting all the rocks found along its length within a 1-m swath on both sides of the line, thus covering a total area of 30 m^2 per station. The juvenile density observed on such a surface (equivalent to a 50-60 minute dive) was taken to represent a standard measure of juvenile recruitment for this species.

Lobster larvae settlement

We took advantage of a long-term monitoring program on puerulus larvae settlement carried out since 1993 in the area of rocky straits close to the mouth of the bay (Figure 1). A set of 6 collectors of puerulus larvae and juveniles of lobster had been installed there; verified monthly to collect newly settled juveniles and puerulus larvae (Guzmán del Próo *et al.,* 1996).

Other dominant species

Recruitment of the macro algae *Macrocystis pyrifera* and *Eisenia arborea* was documented along the central line of stations on Clam Bay and Los Morros banks, where the number of juveniles and adults were recorded in ten 1m^2 quadrants per station.

Kelp bed recovery

To complement our observations, the coastline was surveyed by air in January 1999 from Clam Bay to Punta Eugenia, at altitudes of 300 and 450 m (1000 and 1500 ft), taking photographs for a qualitative evaluation of the recovery of the giant kelp beds (*Macrocystis pyrifera*) along the shoreline.

DATA ANALYSIS

Abalone

Size frequencies of juvenile abalone were converted to age groups by means of the growth equation established for this species in Bahía Tortugas by Shepherd *et al.,* (1991). Development and strength of the cohorts of age groups 0, 1, 2, and 3 were tracked throughout the experiment. These data were used to calculate a temporal variability coefficient. Significant differences were detected (after normalizing the data) by means of a unifactorial ANOVA. Seasonal differences were determined by means of a multiple range test using the least significant difference (LSD) method.

An additional indicator of the effects of El Niño on abalone recruitment, the size variability coefficient, was calculated for age group 1, which includes organisms 20 to 29 mm in shell length. Data from juvenile *H. fulgens* at Clam Bay was used for this analysis, since they were the best represented of the two series. The coefficient of variation was considered to express the degree of heterogeneity in the size of recruits before and after El Niño.

Macro algae

Differences in the density of each bank were evaluated (after normalizing the data), through a bifactorial variance analysis to detect any species/seasonality interaction that might indicate a time lag in the recruitment of each species. Differences between the mean for each season, species, and interaction were obtained through a multiple (regression) test, using the LSD method.

Lobster

In order to correlate the lobster juveniles settlement with mean sea level and surface temperature, we accessed an oceanographical database (COADS) provided by NOAA and the University of Hawaii. The data from both series were normalized using natural logarithms to cross-correlate (Legendre and Legendre, 1998) mean sea level and settlement rate.

RESULTS

GENERAL OBSERVATIONS

Figure 2 shows temperature variations (thermal anomalies, from COADS) during the 1996-1998 period of observation, which includes the 1997 El Niño. The anomaly peaked at nearly +4 °C in October 1997, followed by a trough at -1.5 °C in October 1998. The increase in temperature in the

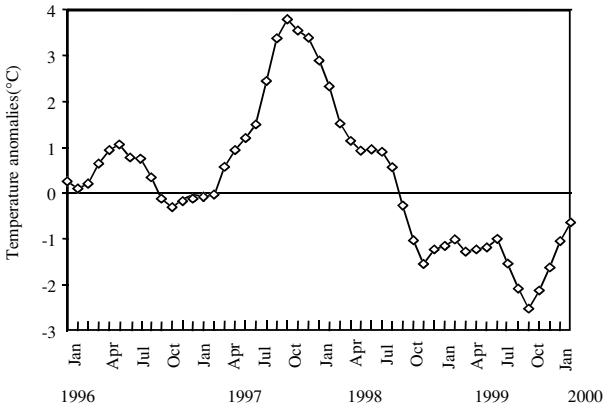

Fig. 2. Sea surface temperature anomalies. (From COADS / NOAA at 27° N,114 °W, January 1996 to January 2000.

Bahía Tortugas area showed maxima between August and November 1997. In September of that same year, we recorded 31 °C in the area; the most striking effects on the benthic biota took place during this same four-month period.

Autumn 1997

The most immediate effect was observed in the *Macrocystis* kelp bed community, which disappeared completely by November 1997; the near shore zone off Clam Bay and Los Morros were totally lacking of the characteristic forests, the bottom mostly barren. *Eisenia* was reduced to a few defoliated specimens, with only vestiges of the attachment organ (haptera) and thallus adhered to the rocks. Even articulated coralline algae were reduced in size, with bleaching of the thallus.

In November and December 1997, two months after the passage of Hurricane Nora, most of the sublittoral rocks off at Los Morros and Clam Bay seemed to have been overturned with large amounts of sediment moved about. Gastropod mollusks and urchins had an elevated mortality, as evidenced by an abundance of empty gastropod shells (mostly abalone and snail) and urchin skeletons on the bottom. Adult abalones were in poor condition, shown by some specimens that had a noticeable reduction in the size and volume of the muscle in relation to the shell length. This deficiency was clear when separating adult specimens from the rock: the shell was separated easily from the adductor muscle, which remained exposed, and adhering to the substrate.

Spring 1998

A new survey in April 1998 showed the sequels of the 1997 El Niño, slight recovery of flora and fauna were de-

tected; with mean surface temperature in April and May being 15.8 and 16.6 °C still 1 °C higher than normal for those months. Adult abalone remained in poor physiologic condition, characterized by flaccid muscles, reduced in size and vigor, most probably as a consequence of poor nourishment. Kelp beds (*Macrocystis*) were absent from the surface, while the earliest appearances of juvenile *Eisenia* were found on the bottom (10 to 15 cm high). In the Los Morros area in late April, the first two juvenile *Macrocystis* (30 cm in length) were found. The presence of 4 to 5 mm juvenile abalone at that time of the year suggests they were the result of spawning occurred in December 1997 or January 1998.

The effects of El Niño were reflected in the abundance of octopus from Punta Eugenia to Clam Bay. To take advantage of this abundance, the fishermen operating in Punta Eugenia area exploited this mollusk, reaching an unusual average catch per fisherman of 100–120 kg/day. By April 1998, the Fishermen Cooperative had collected 35 metric tons.

Summer 1998

In July 1998, young *Macrocystis* plants shoots more frequently observed. At station 2 off Los Morros, a 1-m long specimen was found, and some bare shoots reached the surface.

Winter 1998

Surveys in January 1999 indicated a partial recovery of the *Macrocystis* beds, emerging and once again covering large areas of the surface. An observation flight from Clam Bay to Punta Eugenia showed the banks of this species were present along the entire length of the coast. The near shore depths had recovered their normal appearance; the bottom, rocks, and sediments appeared undisturbed and the algae and fauna (both sessile and vagile) were also recovering. *Eisenia* and *Macrocystis* again became the dominant seascape element, although *Eisenia* was much more abundant than normal. Crustose and articulated coralline algae, which had evidenced a whitish coloring and rock denudation in November 1997, covered the rocks with new specimens, recovering their characteristic pinkish.

EFFECTS ON RECRUITMENT

Abalone recruitment

Figure 3 shows time variability in recruitment of juvenile abalone *Haliotis fulgens* and *H. corrugata* between fall 1996 and winter 1999 (pre- El Niño and post-El Niño conditions, is expressed in terms of density of age groups within a 270 m^2 area (9 stations x 30 m^2). Between fall 1996 and spring 1997, a decrease occurred in the 2- and 3-year-old age groups of these two species. Reduction was greatest in fall 1997, particularly off Los Morros bank, for both *H. fulgens* and *H. corrugata*. After the period of maximum temperature (28-31°C), recruitment of both species diminished sharply and their recovery was very slow. Off Clam Bay, the effect was more subdued. Recovery of recruitment levels that existed prior to El Niño 1997 began in spring 1998 with the presence of new 0+ and 1+ age groups and continued with similar densities through winter 1998 and summer 1999. During our final observations in winter 1999 (January 2000), densities of 10 to 15 individuals/270 m^2 were recorded for the 1+ age group of juvenile *H. fulgens* (Figure 3).

Figure 4a shows the changes in relative abundance of the 1-year-old juveniles (20-29 mm) of *H. fulgens* between fall 1996 (pre- El Niño) and winter 1999 (post-El Niño). The general pattern of relative abundance resembles a parabola, though the correlation is poor ($R^2 = 0.596$). During El Niño and continuing until spring 1998, there was a very distinct decrease of this age group. Starting in winter 1999, the trend is ascending. It must be noted that juvenile recruitment was never fully interrupted, since even the smallest sizes in the 0+ age group, between 3 and 18 mm, were always present, though in smaller proportions (Figure 3).

Figure 4b shows the size variability of 1-year-old recruits, expressed by the coefficient of variation for this size interval. The greatest size variability was recorded in fall 1997 and during the immediate subsequent seasons, and indirectly reflects the effects of El Niño on the growing conditions of recruits through its influence on the food base.

By applying the ANOVA to the data for observed density in each period, significant differences in density averages emerged in at least one season ($p=0.036$). The density recorded in fall 1996 (11 ab/270 m^2) differs significantly from those noted in fall 1997 (0.6 ab/270 m^2), spring 1998 (2 ab/270 m^2), and summer 1999 (1 ab/270 m^2). The density recorded in winter 1999 (7.6 ab/270 m^2), though smaller than the one noted in fall 1996, is not significantly different, according to a multiple regression test (LSD). This might be interpreted to mean that in winter 1999 (two years after El Niño), recruitment had recovered to levels near or similar to observed during non-El Niño years.

Macro algae recruitment

In fall 1997 both Macrocystis *pyrifera* and *Eisenia arborea* disappeared from the surface and bottom, leaving only vestiges of *Eisenia* thalli. In April-May 1998, *Eisenia* was the first to show signs of new recruitment. The sublit-

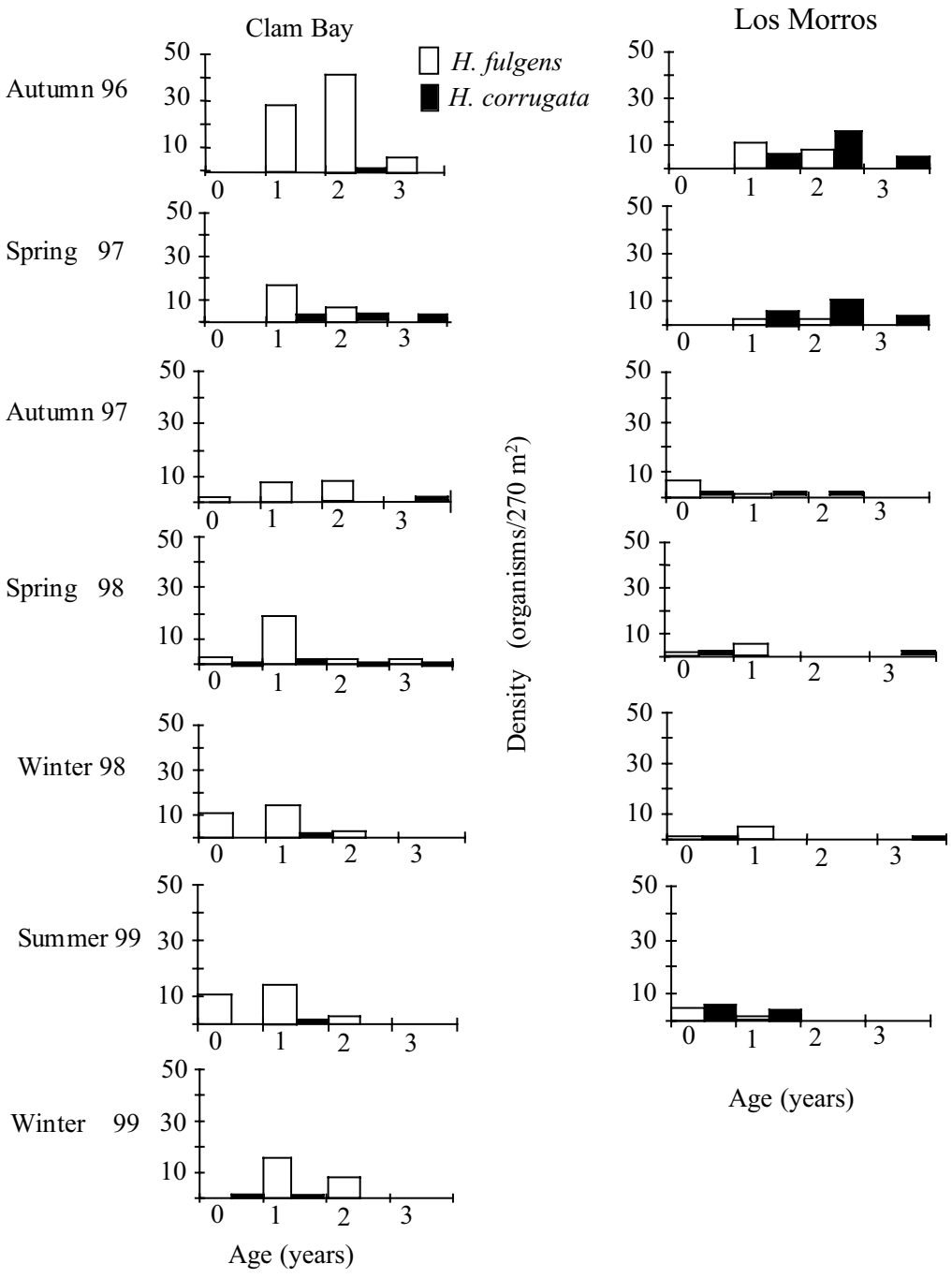

Fig. 3. Recruitment variability of the 0-3 age groups of juvenile abalone *Haliotis fulgens* and *H. corrugata*.

toral floor contained an abundant carpet of juvenile *Eisenia* plants with average densities of 2.5 (Los Morros) and 4.4 (Clam Bay) individuals/m^2 (Figures 5a and 5b). *Macrocystis pyrifera* recruitment also occurred during these months, but with very scarce juvenile densities, 0.0075 individuals/m^2. In January 1999, an observation flight showed the kelp beds emerging at the sea surface, but mainly located over the seaward reef. In summer 1999, juvenile recruitment of this species increased, on average, to 10 individuals/m^2 (Figure 5a). In winter 1999 there was a clear increase in adult average density to 1 individual/m^2 (Figure 5b), including shallow waters.

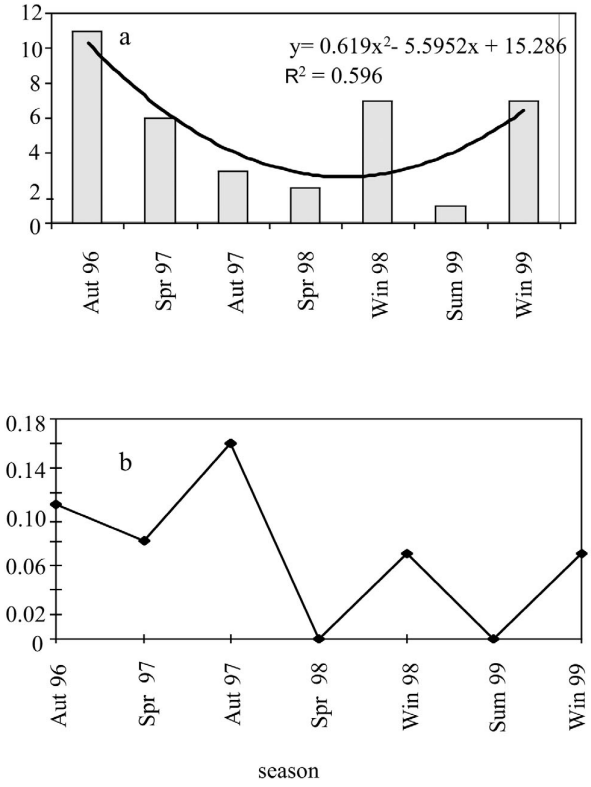

Fig. 4. a) Recruitment variability of one-year-old juvenile abalone (*Haliotis fulgens*). b) Coefficient variation of length shell of one-year-old juvenile abalone (20-29 mm length).

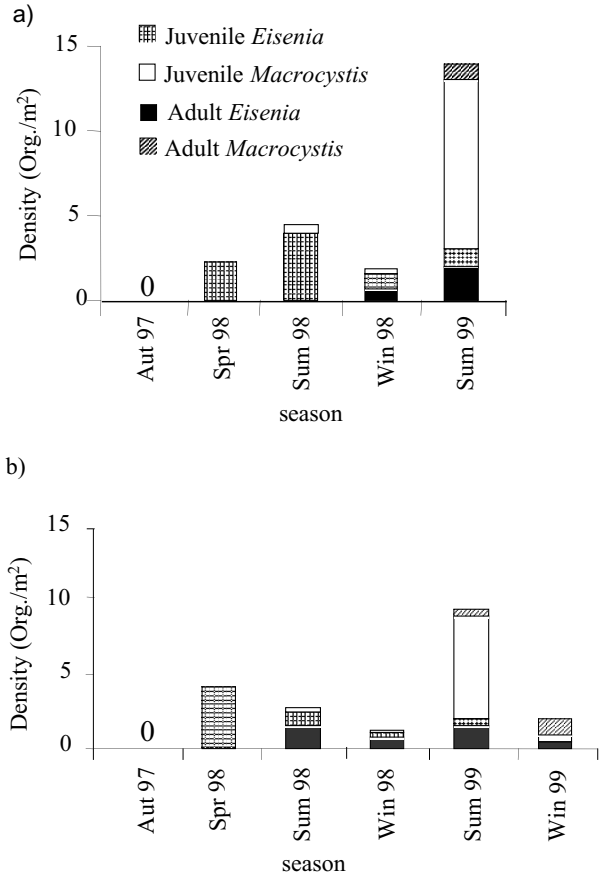

Fig. 5 Average density variation of juvenile and adult *Macrocystis pyrifera* and *Eisenia arborea* during and after El Niño. a) Los Morros; b) Clam Bay.

The ANOVA involving juvenile and adult plants showed that both seasonality and species/seasonality interaction were significantly different on both reefs beginning from summer 1998. Values were F=4.9 (p=0.01: seasonality) and F=4.75 (p=0.01: interaction) at Clam Bay; F=4.2 (p=0.01: seasonality) and F=3.0 (p=0.04: interaction), of Los Morros. Considering only seasonal effects, the multiple range test (LSD) showed the density of juvenile *Eisenia* at Los Morros was significantly different from zero from summer 1998 onwards ($p = 0.028$), increasing even more in summer 1999 (p=0.0008). At Clam Bay, density variability in *Eisenia* was significant since spring 1998 (p=0.046). This significant species/seasonality interaction confirms a lag in the density recovery of *Macrocystis* with respect to *Eisenia* . Both at Clam Bay and Los Morros, *Macrocystis pyrifera* density was not significantly different from zero until summer 1999, when a high recruitment of this species was recorded, whereas *Eisenia arborea* showed high recruitment on both reefs from spring 1998 on (Figure 6a, b).

Lobster recruitment

Figure 7 shows the full series of puerulus settlement rates between 1993 and December 1999 in the Tortugas area. Evidently, there was a period of abundant settlement during the months with the strongest El Niño effects and in those immediately following, with a peak in February 1998 (33.3 individuals/sampling unit). Altogether, these numbers provide evidence of vigorous recruitment during the El Niño year. Temperature anomalies recorded in the same year (Figure 2) show October to have had the maximum thermal anomaly (3.8 °C) and the maximum mean sea level anomaly (211mm) (Figure 7). Cross-correlation of settlement rate and mean sea level anomalies indicates no time lag between the maxima of both variables. This correlation was significant (a = 0.05) at a value of 0.3308 and no time lag between the two variables (Figure 8).

DISCUSSION

The period of observation of the El Niño effects on the benthic community of Bahía Tortugas, B.C.S., proved to be too short (1996-1999), limiting the scope of our conclusions, but the results indicate that species of the rocky coast community respond in various ways to this event. While the al-

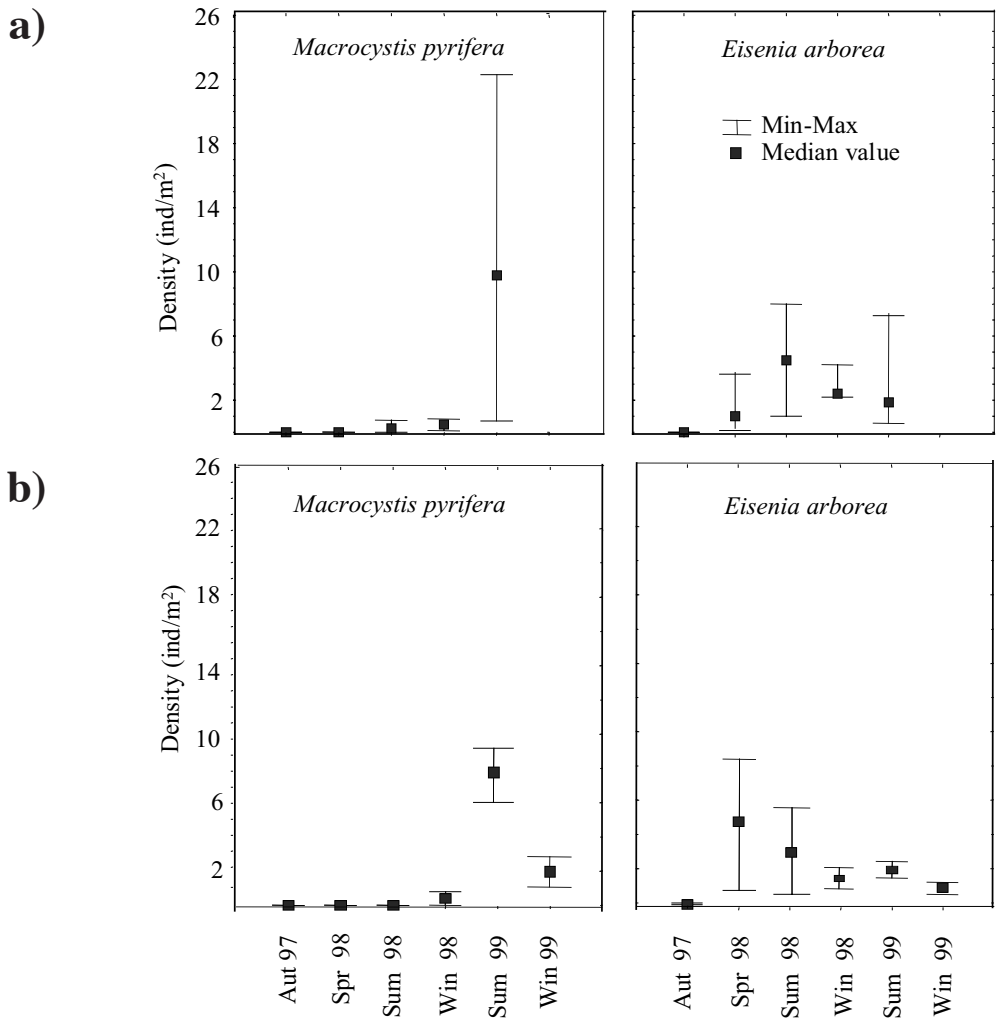

Fig. 6. Differential recruitment lag after El Niño in densities of *Macrocystis pyrifera* and *Eisenia arborea* a) Los Morros, b) Clam Bay.

gal community, particularly the *Macrocystis* and *Eisenia* beds, evidenced deleterious effects, including full disappearance, in other cases, such as abalone, the immediate effect was experienced by the entire population (both adults and juveniles), decreasing their density and affecting their physiologic condition, but never bringing a full disappearance. One year later these populations showed signs of recovery. In fact, the gathering of small (3 to 5 mm) abalone "seeds" during the maximum temperature months (November 1997) and the first months of 1998, suggests the continuation of larval settlement processes of these species and subsequent juvenile survival, thought at lesser rates.

The deleterious effect of El Niño on *Macrocystis* beds, leading to their disappearance, is a recurrent phenomenon, particularly in strong El Niños, but not so in weaker ones (Shepherd *et al.,* 1998). The kelp beds recover within a relatively short time, although it may take up to two years for them to attain their original density (Hernández-Carmona, 1987). Our aerial surveys indicate that one and a half years after the most intense phase moment of this event (fall 1997), the beds had recovered most of their surface cover.

The impact that algal disappearance may have on invertebrates, such as abalone, is still unclear. Some authors assert that the disappearance of *Macrocystis* beds affects the availability of food for abalone, and therefore decreases its population (Tegner and Dayton, 1987). Other authors, such as Shepherd *et al*. (1998), find a direct positive correlation between catches and thermal anomalies in the area of Isla Natividad, Baja California, with an 8-year time lag that they interpret as the time it takes adults to recruit to the fishery. On the basis of this correlation, these authors suggest El Niño has a positive effect on abalone recruitment in that area. The

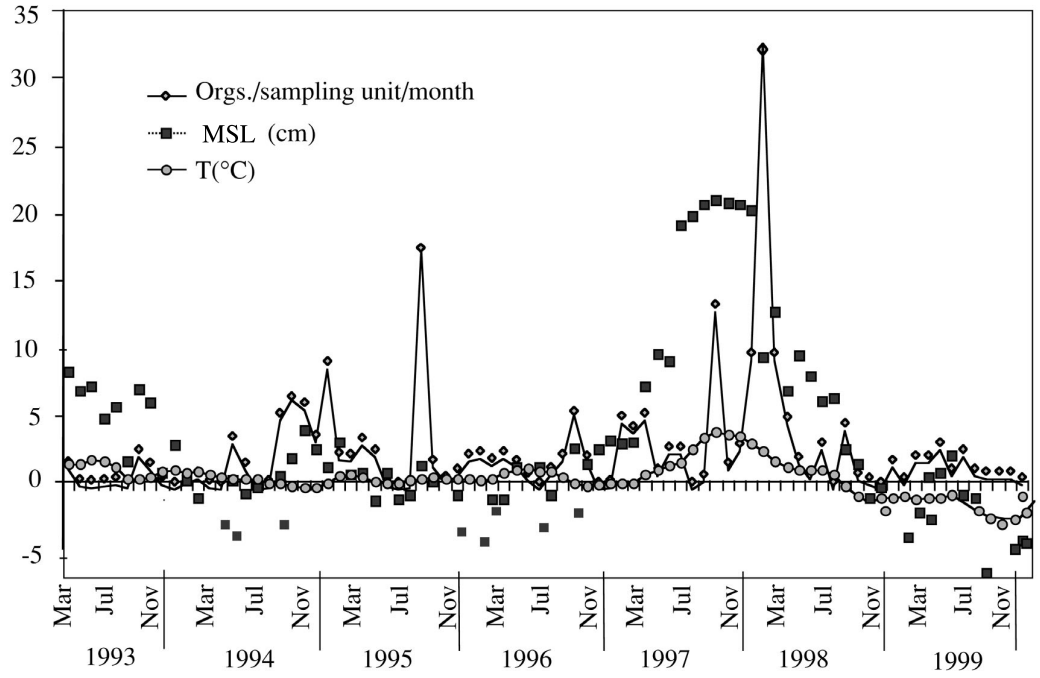

Fig. 7. Relationship between juvenile spiny lobster settlement, sea surface temperature and mean sea level anomalies.

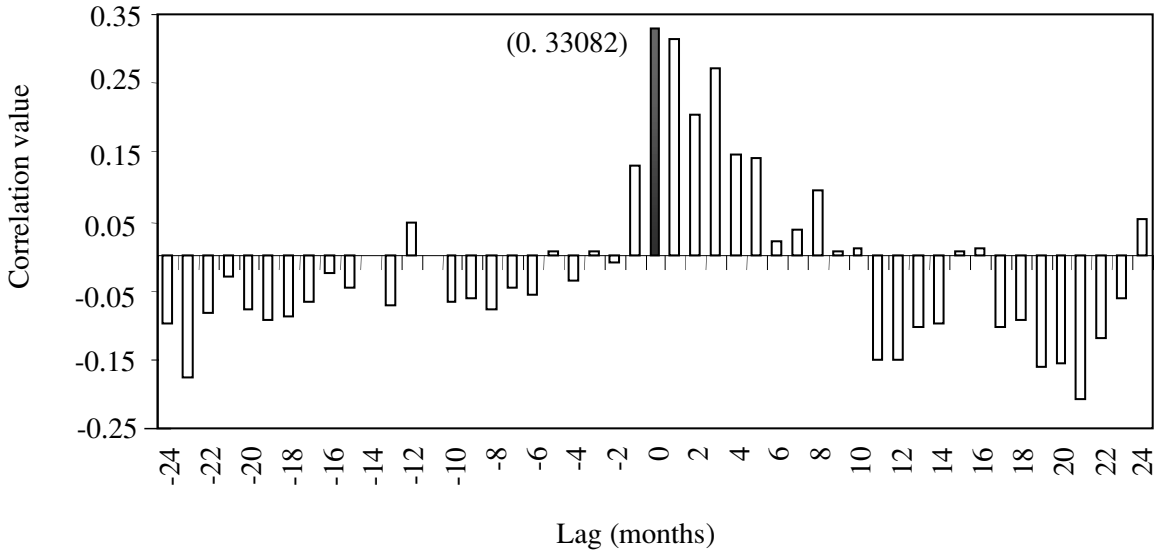

Fig. 8. Cross correlation between juvenile spiny lobster settlement rate and average sea level anomalies.

number of years it takes abalone to recruit is debatable, since growth studies in Baja California reveal they may attain catchable sizes (>140 mm) within 5 to 6 years (Doi *et al.,* 1977; Guzmán del Próo and Salas, 1983; Shepherd *et al.,* 1991;). Consequently, the 8 years mentioned by Shepherd *et al.* (1998) might not necessarily be years, but rather growth rings that have a different time scale. On the other hand, the same authors also mention that positive thermal anomalies of strong El Niños have a negative effect, while weak El Niños might be beneficial for recruitment. In other words, the effects of El Niño are still confusing. There would appear to be a synergetic effect, with greater or lesser impact, depending on the intensity of the event and the persistence of thermal anomalies.

Our data indicate an immediate direct effect on the adult population, diminishing its abundance and physiologic well-being, and a reduction of juveniles in the 1+, 2+ and 3+ age groups proved significant in the following months for both species (Figure 3). Nevertheless, the tracking of *H. fulgens* recruits, starting in summer 1999, and particularly that of the 1+ age group between April 1997 and January 2000, shows more plainly how recovery in this group follows a parabolic trend. It means that H. *fulgens* took almost three years to recover recruitment levels similar to those of 1996 (Figure 4). Nonetheless *H. corrugata* did not show signs of recovery (Figure 3). The effect of El Niño on the commercial catch of subsequent years is beyond the scope of this study, but, it is relevant that, despite its decline, recruitment was not interrupted during El Niño, and that even at the time of its maximum intensity, some juvenile cohorts, were able to survive its impact.

The effects of El Niño did not have the same deleterious impact on lobster as on other species, since the recruitment of juveniles and puerulus larvae of this species showed elevated densities. This correlation is not new. Several scholars have found significant correlations between lobster catch levels, mean sea level, and surface temperature (Phillips *et al*., 1994), factors that are in turn intimately associated with El Niño. They found, in the case of the Mexican lobster *Panulirus interruptus*, a significant correlation between commercial lobster catch and mean sea level with a four-year time lag. If we consider that it takes oceanic phyllosoma larvae from 7 to 10 months to metamorphose and return to coastal areas as puerulus (Johnson, 1960), the settlements observed between October 1997 and February 1998 showed correspond to individuals born in 1997. Thus, our observations lead us to propose that El Niño conditions might stimulate the reproductive mechanism and recruitment of this species and that, either through greater fertility or greater survival of the larval and juvenile stages, settlement abundance may reflect the vigorous recruitments stimulated by the El Niño event. This would be consistent with the observations of Pringle (1986), who asserts that there is a stronger pole ward flow of the Davidson Current during El Niño years, and mean sea level, and surface temperature increase, so that larval recruitment also tends to rise. Similar relations between lobster recruits and environmental variables have been observed by Phillips and Pearce (1991) for *Panulirus cygnus* in Australia. An alternative explanation would be that the disappearance of the kelp beds and the immediate mortality of sedentary populations of the benthic biota, particularly macro algae and invertebrates brought about by El Niño, left no refuge for puerulus and juveniles, whose habitat and shelter are marine grasses and algae. In consequence, puerulus and early juveniles would be more vulnerable and more easily attracted to the shelter of the artificial collector, which simulates marine grasses. As for adult lobster populations, which had high catch levels, the scarcity of the foods that make up their diet (mollusks and grasses; Díaz Arredondo, 1989) may have made them more susceptible to being caught, forcing them to go out in search of food and to be more easily attracted to the bait in the traps. If this latter hypothesis were correct, the abundance of lobster populations and puerulus settlements in El Niño years would be more of an apparent factor than a real one.

CONCLUSIONS

1. The 1997 El Niño had a different impacts on the benthic species of the rocky sub littoral of the study area. Whereas on some species the effects were negative, on others it appeared to be beneficial.

2. Populations of macro algae *Macrocystis pyrifera* and *Eisenia arborea* were negatively affected, from a decrease in their abundance during the fall and winter months of 1997 to full disappearance in the case of *Macrocystis,* and almost full disappearance of *Eisenia*. Once the strongest conditions El Niño ceased, from summer 1998 on, these species showed intense recruitment. *Eisenia* showed a quicken recovery than *Macrocystis*.

3. Adult abalone populations were severely diminished at an early stage (fall-winter 1997), and the physiologic condition of the survivors was seriously affected.

4. There was no interruption of juvenile recruitment of *H. fulgens* and *H. corrugata* during the early stage, but it, nevertheless, diminished in subsequent months, and the sizes of juveniles in the 1 age group became very heterogeneous, suggesting alteration of the food base.

5. Larval and juvenile recruitment of spiny lobster *Panulirus interruptus* apparently did not experience negative effects. On the contrary, settlements were some of the most vigorous recorded since 1993.

6. Altogether, the benthic community displayed great resilience and a capacity for speedy recovery. In the short term, the effects of the El Niño event affected the survival of benthic populations, particularly sedentary or low-vagility ones. Their recovery took place within a relatively short period, one and a half to two years after the occurrence of the event.

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