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CHANGES IN THE NATURAL DIET OF GREEN ABALONE *HALIOTIS FULGENS* DURING THE 1997 TO 1998 EL NIÑO EVENT IN BAJA CALIFORNIA SUR, MEXICO

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ABSTRACT A stomach content analysis was undertaken to determine the changes in the natural diet of the green abalone *Haliotis fulgens* as they relate to the 1997 to 1998 El Niño event at 2 sites along the central coast of the Baja California Peninsula. The index of relative importance of each identified food item was calculated, and Levin's index was used to determine the breadth of the diet. A total of 20 macroalgal species, 1 seagrass species, and 4 invertebrate species were observed from March 1997 to July 1998. The main constituents of the diet of *H. fulgens* before the 1997 to 1998 El Niño were *Macrocystis pyrifera*, *Phyllospadix torreyi,* and *Cystoseira osmundacea*. During and after, the principal items were *Sargassum* sp., *Spatoglossum howelli*, *Cystoseira osmundacea*, *Dictyota* sp., *Gelidium* sp., and *Phyllospadix torreyi*. Diet breadth of abalone diet was greater during and after El Niño 1997 to 1998 than before. Our results show that green abalone diet varies with the availability of the food source; therefore, El Niño events caused a major shift in diet related to changes in the local algal flora.

KEY WORDS: green abalone, *Haliotis fulgens*, stomach content, relative importance index, kelp forest, *Macrocystis pyrifera*, ENSO

INTRODUCTION

In Mexico, various species of abalone (*Haliotis* spp.) have been exploited since 1926 (Cox 1962), and the fishery is one of the most important in the region (Ponce-Díaz et al. 2000). In the Baja California Peninsula, 5 species are found: *Haliotis sorenseni* Bartsh, *Haliotis cracherodii* Leach, *Haliotis rufescens* Swainson, *Haliotis corrugata* Wood, and *Haliotis fulgens* Phillipi (Cox 1962). The latter 2 species account for more than 98% of the commercial catch (Searcy-Bernal et al. 2010).

Abalone is closely linked to kelp forest ecosystems that, besides furnishing habitat, provide their main source of food. In southern California, kelp canopies are very sensitive to oceanographic changes because kelp depend on the high nutrient concentrations in the water column. However, when the temperature of the water column increases, a decrease in nutrient concentrations occurs, which in turn has been correlated with marked reductions in giant kelp biomass (Hernández-Carmona et al. 2001). This reduction can lead to the disappearance of kelp forests during the more severe warm periods of an El Niño event (Ladah et al. 1999). Although the effects on kelp are relatively well understood, the impacts of these changes on grazers, such as abalone, are scarcely known. Changes in temperature affect abalone growth, fitness, and survival (Haaker et al. 1998, Rogers-Bennett et al. 2010, Vilchis et al. 2005), whereas temperature and storms affect the food supply of grazers (Tegner et al. 2001). Some negative effects of El Niño events on the recruitment of abalone (independent of their intensity) have been observed previously (Rodríguez-Valencia & Caballero-Alegria 2002). Since the main food of abalone is affected, it could also be predicted that the diet of green abalone would become restricted, but, to date, no study showing variations in the diet of abalone during El Niño events has yet been undertaken.

Stomach content analysis can be used to study trophic interactions and energy flows between communities, as well as to determine the nutritional requirements for purposes of aquaculture (Vadas 1985). There are several studies that assess the natural diet of abalone based on the analysis of stomach contents: *H. cracherodii* Leach (Leighton & Boolotian 1963), *Haliotis iris* Gmelin and *Haliotis australis* Gmelin (Poore 1972), *Haliotis midae* Linnaeus (Barkai & Griffiths 1986), and *Haliotis asinina* Linnaeus (Sawatpeera et al. 1998), adults (Serviere-Zaragoza et al. 1998), and juveniles of *H. fulgens* and *H. corrugata* (Guzmán del Próo et al. 2003b). In these studies, the stomach contents showed that abalone fed on whatever resources were available.

The most common food items found in the gut of adult green abalone at the southern extreme of its range in Baja California Mexico, where *Macrocystis pyrifera* (Linnaeus) C. Agardh is not present, were the macroalgae *Sargassum* sp., *Eisenia arborea* Areschoug, *Cryptopleura crispa* Kylin, and *Rhodymenia* sp., and the seagrass *Phyllospadix torreyi* Watson (Serviere-Zaragoza et al. 1998). Juvenile green abalones (10–100 mm in length) feed mainly on diatoms and some species of macroalgae (Guzmán del Próo et al. 2003b, Siqueiros-Beltrones et al. 2005). In the previous studies, spatial changes in the diet of *H. fulgen*s were highlighted, but no information on temporal changes was available. Based on the analysis of stomach contents, our objective was to determine the composition and temporal variation of the natural diet of adult *H. fulgens* during the 1997 to 1998 El Niño event.

MATERIALS AND METHODS

Study Area

Specimens of adult *H. fulgens* were obtained from 2 study sites: Chester Rock (27°51′30″ N, 115°03′30″ W) and Cardoncito (27° 41′30″ N, 114°56′45″ W) located along the central coast of

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the Baja California Peninsula (Fig. 1). Chester Rock has a mainly rocky substratum that forms small cliffs and platforms with sandy patches. It is influenced by the cold water of the California Current, and to, a lesser degree, by warm water from Bahía Sebastian Vizcaino. The mean annual temperature was 19.5°C (range, 16.5–21.7°C) (Hernández-Guerrero et al. 2001). Cardoncito is an exposed shore composed primarily of firm rock and boulders. It is strongly influenced by the California Current, with a mean annual temperature of 18.5°C (range, 15.2–20.5°C) (Hernández-Guerrero et al. 2001). Increases in temperature were observed in an adjacent area (Bahía Tortugas) that showed maximum anomalies of more than 3°C between August 1997 and January 1998. The kelp *Macrocystis*, which is usually common, disappeared during this period between Punta Eugenia and Bahía Tortugas (Ladah et al. 1999).

Sampling Design

Depending on the availability of adult *H. fulgens,* 6–17 specimens were collected randomly by divers using surface-supplied air (hookah) in the early morning at the 2 study sites, before (March and June 1997), during (August and November 1997), and after (April and July 1998) the El Niño event. Shell length and total body weight were measured, and the soft body parts were preserved in 10% formalin onsite.

The stomach content was recovered and washed with distilled water on a mesh sieve (700-µm size) and dried on absorbent paper in the laboratory; a measure of the displaced volume was taken as an indicator of the amount of food present. The different items were separated under a stereoscopic microscope and identified to the lowest taxonomic level permitted by the degree of digestion of the contents. The keys and the species descriptions of Joly (1967) and Abbot and Hollenberg (1976), as well as the complete macroalgae specimens collected from the benthic community at the same place and time of the samplings were used to guide the identifications.

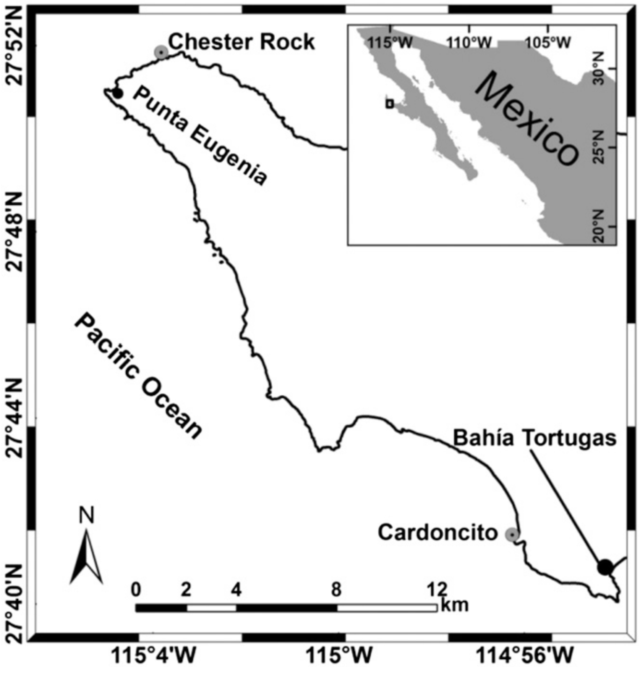

Figure 1. Location of the sampling sites on the central Pacific coast of the Baja California Peninsula, Mexico.

The relative abundance of each food component was estimated from a 1-mL sample of the stomach content. The sample was placed in a Petri dish previously marked with 30 points positioned at random. Then, the items found in or close to each point were collected and identified. Highly digested food fragments had a jellylike consistency so they could not be identified and were categorized as unidentified items, and were not considered in the later calculations.

Data Analysis

Randomized cumulative food item curves by site were constructed to determine whether the sample sizes were sufficient to describe the full diet (Preti et al. 2004). The order in which stomachs were analyzed was randomized 10 times, and the mean number of new prey items was accumulated consecutively and plotted against the number of stomachs examined. An asymptotic relationship between the number of stomachs analyzed and the number of new items observed was expected if the number of stomachs was sufficient to represent the diet (Preti et al. 2004).

The distribution of the displaced volume in the stomach failed normality and homoscedasticity tests, so the nonparametric Mann-Whitney *U*-test and nonparametric Kruskal-Wallis tests were used to detect differences between and within study sites between dates in each study site, respectively. An *a posteriori* nonparametric test of multiple comparisons was applied to determine the origin (Zar 2009) of significant differences within a study site. Spearman's rank correlation coefficient, r_s, was used (Zar 2009) to assess whether relations between length and weight of green abalone and displaced volume existed.

The index of relative importance (IRI (Pinkas et al. 1971)) of each food item was calculated using the percentage of frequency of occurrence (%F) and the numerical occurrence percentage (%N). %F was calculated as the number of stomachs containing prey of 1 taxon divided by the total number of stomachs containing food items multiplied by 100, whereas %N was the number of fragments of 1 taxon divided by the total number fragments identified multiplied by 100. The IRI was calculated as $\mathrm{IRI} = (\%\mathrm{F} \times \%\mathrm{N})$, expressed as percent. The values of IRI were calculated by grouping the items by phylum to assess the temporal variation in the main groups of the natural diet of *H. fulgens*.

Levin's index (B') was used to determine the breadth of the individual abalone diet (Krebs 2001), was calculated as $B = 1/\sum_{i=1}^{s} Pi^{-2^{-1}}$ and standardized with the expression $B' = (B - 1)/(S - 1)$, where S is the number of taxa present in the stomach. In this way, it takes values from 0–1. Low values (<0.6) indicate a diet dominated by a few items (specialist); high values (>0.6) indicate a varied diet (generalist). Because the data met the requirements of normality and homoscedasticity, 1-way ANOVA was used to detect differences between sites and within each site between dates, respectively, then Tukey's test was applied to detect the origin of the differences within a site (Zar 2009). Significance was set at $P < 0.05$. All statistical analyses were carried out using Statistica 6.0 (StatSoft, Tulsa, OK).

RESULTS

One hundred seventy-two *H. fulgens* adult specimens were collected (85 at Chester Rock and 87 at Cardoncito). Mean shell length and total wet weight (±SD) were 168.68 ± 15.86 mm and 666.50 ± 227.89 g, respectively. Of the 172 abalone analyzed, only 129 had identifiable fragments in their stomachs; further analyses used these animals only.

Volume displaced by fragments in the stomach of abalone from Chester Rock was 2.0 ± 1.8 mL (mean ± SD), which was less ($Z = -2.73$, $P < 0.01$) than the volume in stomachs of abalone from Cardoncito, with 3.3 ± 2.9) mL. No significant differences were found between sampling dates at Chester Rock ($H_{5,70} = 3.33$, $P = 0.65$; Fig. 2). At Cardoncito, higher values occurred in July 1998 ($H_{5,59} = 24.10$, $P < 0.01$; Fig. 2). Significant positive correlations were detected between volume of the stomach contents and length ($r_s = 0.25$, $P < 0.01$) and weight ($r_s = 0.29$, $P < 0.01$).

The randomized cumulative item curves for both sites indicated that sample size was large enough to represent adequately the diet of *H. fulgens* at Chester Rock and Cardoncito during the study period (Fig. 3)

Twenty-five food items were identified as part of the diet of *H. fulgens*: 20 species of macroalgae, 1 species of seagrass, and 4 metazoa. At Chester Rock, 20 food items were found, including 10 exclusive species, whereas at Cardoncito, 15 food items were identified, with 5 exclusive species (Table 1).

Food items in the diet of the green abalone showed differences between dates in their composition and IRI values. At Chester Rock from March to August 1997, *Macrocystis pyrifera, Cystoseira osmundacea* (Turner) C. Agard, and *P. torreyi* were the main constituents of the diet. From November to the end of the sampling period, *M. pyrifera* was not found, seagrass changed in importance from 83% to 2%, and *Gelidium* sp. increased its IRI from 1% in June 1997 to 32% in April 1998. The brown algae *C. osmundacea*, *Sargassum* sp., and *Spatoglossum howelli* Setchell & Gardner had higher IRI values during July 1998 than the rest of the sampling period (Table 1). At Cardoncito, *M. pyrifera* was the main component of the diet of *H. fulgens* during March and June 1997 (>80% of IRI). However, its importance decreased during August 1997 (to 30%), and *E. arborea* and *P. torreyi* were also present as important components. The kelp *M. pyrifera* was not present in the stomach contents since November 1997, when it was replaced by *Gelidium* sp. (>89% IRI). Besides *Gelidium* sp., the brown algae *Dictyota* sp., *Padina* sp., and an unidentified species were the main constituents of the diet of green abalone during April and July 1998 (Table 1).

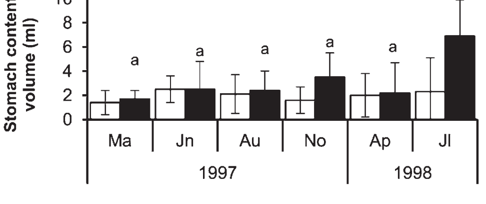

Figure 2. Displaced stomach content volume (mean and SD) of the *Haliotis fulgens* adults collected at Chester Rock and Cardoncito, Baja California Sur, Mexico. Ap, April; Au, August; Jl, July; Jn, June; Ma, March; No, November. Different letters indicate significant differences among dates at the same locality.

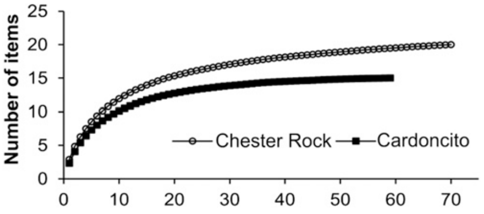

Figure 3. Randomized cumulative items curves for *Haliotis fulgens* stomachs at Chester Rock and Cardoncito, Baja California Sur, Mexico.

The IRI of the stomach contents of *H. fulgens* by phylum also changed between sites and between dates. At Chester Rock, brown algae were the main component during March (69%) and June 1997 (66%); by August 1997, their importance decreased, along with an increase in the consumption of red algae (46% and 35%, respectively). In November 1997, the seagrass was the main forage consumed by abalone (76%), and by April and July 1998, there was an increase in the importance of red and brown algae respectively (Fig. 4A). At Cardoncito from March to August 1997, the main group consumed by green abalone was the brown algae, representing more than 80% of the IRI, whereas this diet shifted to red algae (83%) in November 1997, and then to similar quantities of brown and red algae in April and July 1998 (Fig. 4B).

Levin's index at Chester Rock was $B' = 0.47 \pm 0.20$, and at Cardoncito was $B' = 0.41 \pm 0.22$; no significant differences between the sites were encountered ($F_{1,127} = 3.03$, $P = 0.08$). Significant differences were detected by date at Chester Rock and Cardoncito. The lowest values of Levin's index occurred in March and June 1997 at Chester Rock (Fig. 5), and were different from the higher values measured in August 1997, and April and July 1998 ($F_{5,64} = 2.28$, $P = 0.05$). At Cardoncito, Levin's index was lowest during June and November 1997, and higher values ($F_{5,53} = 2.55$, $P = 0.03$) occurred during April and July 1998 (Fig. 5).

DISCUSSION

Our results show that abalone sampled during the 1997 to 1998 El Niño (August and November 1997) had a distinctly different diet than before (March and June 1997) and after (April and July 1998). This shift was caused by changes in the availability of macroalgal species that abalone consume. The algal flora from Chester Rock to Bahia Asunción is typically of temperate affinity; it is characterized by *M. pyrifera* forests in association with *C. osmundacea*, *E. arborea*, and *Gelidium robustum* Gardner, Hollenberg & Abbot (Casas-Valdez et al. 2000). Before the 1997 to 1998 El Niño event, abalone fed mainly on *M. pyrifera*, which promotes greater growth rates and survival (Serviere-Zaragoza et al. 2001, Ponce-Díaz et al. 2004) than other available species. However, during the peak of the event, the warmer temperatures killed the *M. pyrifera* forest (Ladah et al. 1999), and changed the structure of macroalgal assemblages (Carreón-Palau et al. 2003), and this is reflected in the stomach contents of green abalone.

Macroalgal species observed near our localities during the 1997 to 1998 El Niño event are tolerant to warmer temperatures (Carreón-Palau et al. 2003), which is consistent with our findings,

TABLE 1.

Temporal variation of the index of relative importance of the diet components of *Haliotis fulgens* at Chester Rock and Cardoncito, Baja California Sur, Mexico.

	Chester Rock						Cardoncito					
	1997				1998		1997				1998	
	March	June	August	November	April	July	March	June	August	November	April	July
n =	6	11	13	16	16	17	15	13	15	15	14	15
Rhodophyta												
Gelidium sp.	—	0.7	17.6	13.5	32.4	17.0	4.3		4.1	89.0	52.1	33.8
Gracilaria sp.	—	—	0.1	—	0.6	—	—	—	—	0.5	0.9	0.4
Jania rosea	—	0.2	—	—	6.7	—	—	—	—	—	—	—
Hypnea sp.	—	—	2.4	—	0.1	0.7	—	—	—	—	—	4.5
Laurencia sp.	—	0.2	—	—	1.3	—	—	—	—	—	—	—
Plocamium cartilagineum	2.9	1.2	3.1	0.1	—	1.3	—	—	—	—	—	—
Prionitis sp.	—	—	0.1	0.2	2.0	—	—	—	—	—	—	—
Rhodymenia sp.	—	—	—	0.2	—	—	—	—	—	—	—	—
Red 1	—	2.4	—	—	—	—	—	—	—	—	—	—
Red 2	—	—	—	—	—	—	—	—	—	1.9	—	0.8
Ochrophyta: Phaeophyceae	—	—	—	—	—	—	—	—	—	—	—	—
Cystoseira osmundacea	20.8	0.7	11.0	2.3	5.9	20.3	—	6.5	—	—	—	1.9
Dictyota coriacea	—	—	—	—	—	—	—	—	—	0.7	1.7	1.2
Dictyota sp.	—	—	—	—	0.6	1.9	—	—	5.9	—	37.9	19.6
Eisenia arborea	—	—	—	—	—	—	1.4	2.1	37.3	1.4	—	—
Macrocystis pyrifera	39.3	75.2	38.6	—	—	—	86.3	90.3	30.2	—	—	—
Padina sp.	—	—	—	—	2.8	7.6	—	—	—	—	—	16.0
Sargassum sp.	—	—	—	0.1	—	22.6	—	—	—	—	0.1	0.3
Spatoglossum howelli	—	—	—	0.2	1.3	26.3	—	—	—	—	—	
Brown	—	—	—	—	—	—	7.7	—	—	—	—	21.2
Chlorophyta	—	—	—	—	—	—	—	—	—	—	—	—
Enteromorpha sp.	—	—	—	—	0.1	0.1	—	—	—	—	—	—
Magnoliophyta												
Phyllospadix torreyi	36.4	18.4	24.8	83.3	43.5	1.7	0.4		17.8	6.4	7.2	0.2
Metazoa												
Cerapus tubularis	—	0.2	—	0.1	0.6	0.1	—	—	—	—	—	—
Hydrozoa	0.6	0.2	2.4	0.1	2.2	0.4	—	0.9	4.7	—	0.1	0.1
Metandrocarpa sp.	—	—	—	—	—	—	—	0.2	—	—	—	—
Turbellaria	—	—	—	—	—	0.1	—	—	—	—	—	—

n, number of stomachs with identifiable stomach contents.

and include *C. osmundacea; Dictyota coriacea* (Holmes) I. K. Wang, H. S. Kim & W. J. Lee; *Jania rosea* (Lamark) Decaisne; and *Plocamium cartilagineum* (Linnaeus) Dixon; and species of *Hypnea, Padina, Sargassum,* and *Dictyota;* and the seagrass *P. torreyi*. The intensity of this event caused a shift in the main food groups of abalone (Fig. 4) from brown algae before the warm-water period to seagrass or red algae during and after it. Furthermore, a change in the green abalone diet breadth was observed, with less diet breadth before the El Niño event than during and after (Fig. 5). In general, the macroalgae that occurred in higher proportion in the stomach contents of *H. fulgens* during and after the warm-water period, such as *C. osmundacea*, *Sargassum* sp., *S. howelli*, *Dictyota* sp., *Padina* sp., *Gelidium* sp., and the seagrass *P. torreyi*, are considered of limited value as food for green abalone because, in laboratory studies, these species were scarcely consumed or resulted in limited growth rates (Uki et al. 1986, Leighton 2000). However, laboratory studies on the growth of *H. fulgens* juveniles from the Baja California Peninsula fed with *P. torreyi, E. arborea,* or *G. robustum* showed that these macroalgae were acceptable food that promotes similar growth rates, even though the growth rates were lower than those obtained with *M. pyrifera* (Serviere-Zaragoza et al. 2001). This result indicates that, although these species had a lower nutritional value than *M. pyrifera*, green abalone can use these resources effectively.

The differences in nutritional value of macroalgal species consumed by abalone may be related to differences in the chemical composition of each alga and the bioavailabity of elements (Nelson et al. 2002a). Although most elements are nutritionally important for growth, including carbohydrates and proteins, lipid components may be especially vital to abalone nutrition because they are needed for gonad maturation (Nelson et al. 2002a). Macroalgal lipid profiles differ between taxa, and vary geographically and seasonally. In particular, elevated temperatures induced changes in essential fatty acids (Nelson et al. 2002b), which may affect the nutritional quality of macroalgae for consumers. Along the Pacific coast of Baja California Peninsula, *M. pyrifera* and *E. arborea* nitrogen content decreases with increasing water temperatures (Hernández-Carmona et al. 2001, Sánchez-Barredo et al. 2011),

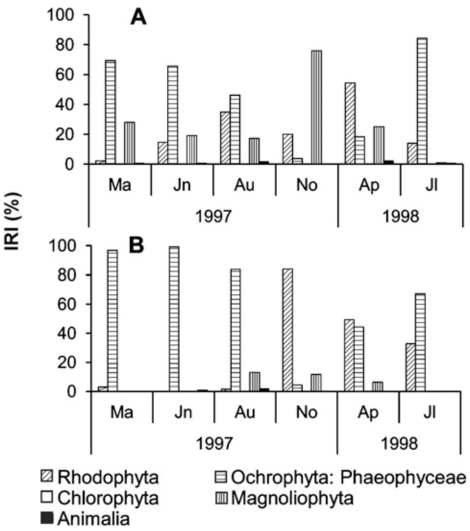

Figure 4. (A, B) Index of relative importance (IRI; mean and SD) of the main phyla in the stomach of *Haliotis fulgens* at Chester Rock (A) and Cardoncito (B), Baja California Sur, Mexico. Ap, April; Au, August; Jl, July; Jn, June; Ma, March; No, November.

indicating that the warmer water of El Niño events affects the quality of the available food, although *M. pyrifera*—their main food—was present. Therefore, the low recruitment and unhealthy conditions of the green abalone populations observed during El Niño events (Guzmán del Próo et al. 2003a), could be caused by the low nutritional quality of macroalgae together with the increase in the use of lipid reserves in green abalone during warm-water regimes (simulating El Niño 1997 to 1998 (Ponce-Díaz et al. 2004)).

Variations in the diet may also be related to the amount of food consumed. In our study, we did not find temporal changes in the volume of stomach contents of green abalone at Chester Rock and Cardoncito (Fig. 2), and the volume of stomach contents was related to the length and weight of the abalone.

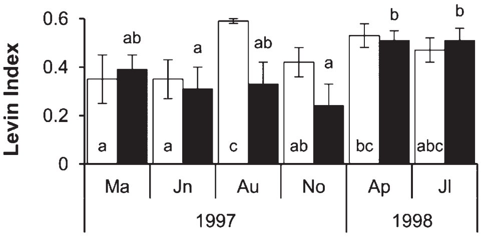

Figure 5. Levin's index (mean and SD) for the stomach contents of *Haliotis fulgens* at Chester Rock and Cardoncito, Baja California Sur, Mexico. Ap, April; Au, August; Jl, July; Jn, June; Ma, March; No, November. Different letters indicate significant differences among dates at the same locality.

Hence, the negative effects of El Niño events in the nutrition of green abalone were probably related more to the quality of the macroalgae than to changes in the quantity of food consumed by the organisms.

It can be concluded that the composition of *H. fulgens* diets had high temporal variability related to changes in the availability of the species, seen most dramatically during and after the 1997 to 1998 El Niño event. This change in the main constituents of abalone diet could be responsible, in part, for the poor condition of abalone during El Niño events.

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