

TOP-DOWN HERBIVORY AND BOTTOM-UP EL NIÑO EFFECTS ON GALÁPAGOS ROCKY-SHORE COMMUNITIES

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Abstract. We evaluated the effects of marine iguanas, sally lightfoot crabs, and fish on rocky-shore sessile organisms at two sites at Santa Cruz Island, Galápagos Islands, Ecuador, for 3–5 years during and after the 1997–1998 El Niño, using exclusion cages to separate the effects. Plots exposed to natural grazing were dominated either by encrusting algae or by red algal turf and articulated corallines. Algae fluctuated in response to El Niño in the following way. During an early phase, crustose *Gymnogongrus* and/or red algal turf were dominant. In the heart of El Niño, grazers had limited effects on algal cover but influenced algal sizes substantially. Most algae (particularly edible forms) were scarce or declined, although warm-water ephemeral species (notably *Giffordia mitchelliae*) flourished, increasing diversity and overgrowing crusts. Iguana mortalities were high, and crab densities low. When normal conditions returned, warm-water ephemerals declined, crab densities rose, and grazers had significant but site-specific effects on algae. At one site, any combination of grazers diminished most erect species, reducing diversity and restoring dominance of competitively inferior grazer-resistant crusts. At a second site, only the combined effect of all grazers had this effect. Laboratory experiments confirmed that crabs could control erect algae and promote crustose forms, and crustose *Gymnogongrus* developed into an erect form in the absence of crabs. Differences between sites and large-scale temporal changes associated with El Niño indicate that tropical shores are not all as constant in time and space as previously suggested. Mobile grazers did affect algal communities, but over the period of our observations far greater effects were attributable to intersite differences and temporal shifts in oceanographic conditions. El Niño events reduce nutrients, intensify wave action, and raise sea levels, affecting food availability for intertidal herbivores and their influence on benthic algae. Thus, the dramatic transformations of communities during El Niño presage the impacts of global climate change.

Key words: algae; bottom-up top-down effects; climate change; ENSO; Galápagos Islands; grazing; rocky shores.

INTRODUCTION

Two current focuses of ecology are the effects of global climate change and distinguishing the relative importance of bottom-up environmental effects versus the top-down influences of consumers (Menge and Branch 2001). The Galápagos Archipelago provides unique circumstances to explore both issues because it lies at the juncture of three major currents and is particularly susceptible to oceanographic shifts associated with El Niño. Its intertidal rocky shores are thermally stressed by the equatorial climate and herbivory appears intense. In this paper, we examine the impact of herbivory over periods of contrasting oceanographic conditions during and after the 1997–1998 El Niño, to examine (a) the magnitude of top-down effects of her-

bivory on community structure relative to (b) changes in bottom-up effects associated with oceanographic shifts.

The effectiveness of grazers can be restricted spatially and temporally by physical factors such as wave action and thermal stress (Dayton 1971, Cubitt 1984), habitat complexity or predation (Hockey and Branch 1994), or plant defenses (Lubchenco 1980). These processes act locally but can be affected by large-scale oceanographic conditions. Thus, changes in temperature, nutrient levels or propagule supply associated with patterns of ocean circulation can affect the settlement, growth and reproduction of algae and the activities of herbivores and, hence, interactions between them (Lubchenco and Gaines 1981). However, if grazing intensifies beyond a threshold, herbivores can decrease diversity, reducing the landscape to a few grazer-resistant species (Paine and Vadas 1969, Vance 1979, Menge et al. 1985, Hixon and Brostoff 1996).

Tropical intertidal systems contain a range of herbivore guilds, and there are few predictions as to how

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their plant assemblages are organized by the combined effects of numerous herbivores. The barren aspect of many tropical latitudes has been attributed to the presence of diverse consumers (Menge and Lubchenco 1981, Menge et al. 1986a, b, Brosnan 1992). In Panama, intertidal rocky shores are dominated by encrusting forms; sessile animals and macroalgae are scarce. Both fast-moving consumers (e.g., fish and crabs) and slow-moving consumers (e.g., limpets) are abundant and reduce diversity on open surfaces, maintaining a consistent community because their effects are important year-round (Menge and Lubchenco 1981, Lubchenco et al. 1984). In Hong Kong, the effect of consumers diminishes during summer because of reduced food availability and thermal stress (Williams 1993, 1994, Kennish et al. 1996). In Brazil, lush foliose algae and zoanthids cover the low intertidal, despite physical conditions there being comparable to those in Panama. The role of consumers is inconsistent and sometimes crabs and fish even enhance the growth of *Ulva*. Bare space is rare and competition between sessile forms often important (Sauer Machado et al. 1992, 1996).

Thus, there is conflicting evidence of the role of herbivory on tropical rocky shores. Generalizations have been based on a limited geographic coverage, and seldom integrate stochastic environmental changes and their possible modulation of herbivory (Brosnan 1992).

Rocky shores in Galápagos are characterized by a black, basaltic substratum of volcanic origin that reaches temperatures as high as 60°C. Thermal stress strongly affects community structure, but its influence differs at small scales related to intertidal height, wave exposure, and relief (Wellington 1984). In addition, three main currents converge on the archipelago, and can shift in position and intensity, resulting in fluctuating gradients of temperature and productivity. Even larger-scale disturbances are associated with El Niño–Southern Oscillation (ENSO) events, which occur at intervals of 3–7 yr and are characterized by unusually warm waters, a rise in sea level, greater wave action, and a depletion of nutrients that reduces primary productivity and ultimately affects all trophic levels (Cane 1983, Houvenaghel 1984, Glynn 1988, 1990, Laurie 1990, Bustamante et al. 2002). This dynamic environment creates an ideal scenario for the study of top-down influences of herbivores on plant assemblages against a background of environmental stochasticity that alters nutrient inputs and thus bottom-up effects.

Our work reports on a series of observations and experiments conducted on rocky intertidal shores in Galápagos, to examine the influence of fast-moving herbivores on algal assemblages and to compare community structure during and after El Niño. The experiments ran throughout the 1997–1998 ENSO event and for a year after its passage, and monitoring of control plots continued to February 2003.

Our goals were to assess the relative influences of herbivory by mobile species and temporal differences

between different phases of El Niño, and to test the generality of previous models accounting for the composition of tropical rocky-shore communities. To achieve this, we (1) quantified herbivores, (2) established whether differences existed in community composition among years, and (3) measured the effects of grazers on algae by field experiments excluding iguanas, crabs and fish, and by laboratory experiments with crabs.

MATERIALS AND METHODS

Study sites and conditions

The field experiments were replicated at two intertidal, south-facing, gently sloping, lava reefs in Academy Bay, Santa Cruz Island, Ecuador. Site 1 lay in front of the Charles Darwin Research Station Marine Laboratory on the outer, wave-exposed face of a lava bench forming an embayment (0°44′37″ S, 90°18′18″ W). Site 2 was located at La Ratónera, 200 m to the east in front of the meteorological station (0°44′46″ S, 90°18′09″ W). Site selection was based on (a) logistic accessibility, as the experiments had to be monitored regularly over a prolonged period, and (b) replication at sites that were sufficiently close by as to be regarded as physically comparable, but far enough apart to be independent. Both sites were subjectively rated as semi-exposed, but measurements with dynamometers (Palumbi 1984) revealed that Site 1 was slightly more exposed than Site 2 (experiencing maximum wave forces of 11.45 ± 2.32 N and 9.11 ± 2.84 N, respectively; ANOVA, $F_{1,42} = 18.19$, $P < 0.001$). Densities of iguanas and crabs and standing stocks of algae were measured at these two sites and at four sites at Punta Nuñez, the latter being selected to span the spectrum of algal availability during the El Niño (see Appendix A for map of sites). The tides in Galápagos are semidiurnal, spanning 1.8–2.5 m (Houvenaghel and Houvenaghel 1977). Our studies were confined to the two lower-most intertidal zones on the shore, which Wellington (1975) termed the midlittoral (0.5–1.5 m) and the infralittoral zones (0.25–0.5 m above chart datum).

The 1997–1998 ENSO began in March 1997, when sea surface temperature (SST) rose to 3–5°C warmer than normal from about May 1997 to May 1998 before declining precipitously, and from September 1998 conditions returned to being close to the long-term norm (see Appendix B for temperature records). Detailed studies of nutrient concentrations were independently undertaken at the time of our studies (Chavez et al. 1999), so we did not measure nutrients.

We began observations in June 1997, initiated our caging experiment in August 1997, and ran the caging experiment for a year in which sea temperatures reached their greatest departures from normal (termed the “El Niño period”), and the following year when temperatures were again normal (“post-El Niño”).

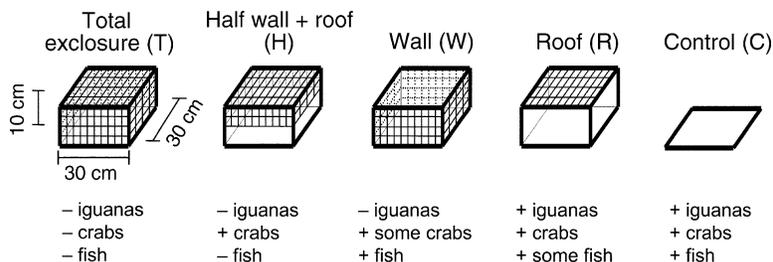


FIG. 1. Design of the experimental treatments to test the effects of grazers. The notation indicates grazers that were excluded (-) or could gain access (+). "Crabs" refers to *Grapsus grapsus*; "some" indicates that only a portion of that group of grazers would have gained access.

Monitoring of control sites continued for a further 4.5 yr of "normal" conditions.

Monitoring densities of consumers

Densities of marine iguanas and sally lightfoot crabs at Sites 1 and 2 were censused once every three months during low spring tides from August 1997 to September 1999 and again in July 2001, five instantaneous counts being made in areas of 40×5 m at 15-min intervals. Counts were made with binoculars at a distance of 100 m to avoid disturbing the animals. Fish were censused during high tide by snorkeling a 15×2 m transect parallel to the shore, at seven roughly equally spaced times between April 1998 and April 1999. Logistic constraints prevented replication within sites. Sedentary grazers (e.g., chitons, winkles, and limpets) were always scarce and were not a central focus of our study. To quantify their abundance, they were surveyed once in June 2001 in 10 1-m² quadrats in each of three shore heights at each site (0.5, 1.0, and 2.0 m above chart datum). The first two of these shore heights overlapped with the zone in which our experiments were done. We surveyed the uppermost zone in case there were species that could migrate down into the low shore during high tide. In calculating the sedentary herbivore abundance and biomass, we used only the data from the two lower zones. To approximate biomasses, densities were multiplied by the estimated wet masses of each species. Estimates for fish were obtained from Fishbase (*available online*),⁵ and averaged 91.05 g per herbivorous fish. For iguanas we used 883 g for small individuals and 1200 g for large individuals feeding in the intertidal zone (Wikelski et al. 1993). Direct measurements yielded values for *Grapsus grapsus* (mean 24 g), *Pachygrapsus transversus* (mean 0.8 g), and sedentary herbivores (4.8 g).

Crab diet

The diet of *G. grapsus* was determined for 30 individuals at each experimental site. Stomach volumes were measured by displacement and the stomach contents then extracted, spread on a slide, and compressed to a thickness of 0.5 mm before measuring the per-

centage of composition of all identifiable items and estimating the total volume. Gut fullness was calculated as [(volume of gut contents/volume of stomach) \times 100].

Selectivity of *G. grapsus* for different functional groups of algae was assessed by comparing their contribution to the diet with their contribution to the percentage of cover in control plots during weeks 2, 4, and 8 of the caging experiment (when diet was assessed). Selectivity was measured by the odds ratio, $O = p_1q_1/p_2q_2$, where p_1 = the percentage of diet contributed by a particular taxon, p_2 = the percentage of that taxon available in the environment, q_1 = the percentage of diet composed of all other taxa, and q_2 = the percentage of all other taxa available in the environment. Expressed as $\ln(O)$, this yields positive values for items that are selectively consumed relative to their abundance, and negative values for those selected against.

Densities of iguanas and crabs relative to algal standing stock

Densities of iguanas and the crab *G. grapsus* were assessed in August 1997 at Sites 1 and 2 and at four sites 100 m apart at Punta Nuñez, from instantaneous scans of five areas of 10 m² in each site. Ash-free dry mass (AFDM) of algae was determined from five 100-cm² samples per site, scraped to bedrock and ashed at 360°C for 12 h.

Caging experiment

The caging experiment was set up at Sites 1 and 2 in the low intertidal at heights that were equivalent at both sites, spanning 0.3–0.8 m above chart datum, and the positions of different treatments were randomly assigned within this height range. The cages and fences were designed to differentially exclude iguanas, *G. grapsus*, and fish to test their relative effects on algal composition and abundance. Each treatment plot was 30 \times 30 cm and was surrounded by an iron fence, totally or partially covered by stainless steel netting of mesh size 1.0 \times 1.0 cm (Fig. 1), with five randomly interspersed replicates per site. Pilot studies indicated that 96% of the diversity of the shore was incorporated in five replicate plots of this size. The total enclosure

⁵ (www.fishbase.org)

treatment (T) excluded all grazers larger than 1 cm. The half wall + roof (H) left a gap too small for iguanas and fish to enter but allowed crabs access; only crabs were ever seen in these plots. The wall treatment (W) effectively excluded iguanas, but fish and at least some crabs could enter it. The roof treatment (R) constituted a procedural control that theoretically allowed all grazers access while shading the plot like other roofed exclusion plots. All three types of mobile grazers were observed in the roof controls, and no significant differences were recorded between the responses of algae in them and in the controls (C) for four of the seven functional groups examined. In the remaining three, differences emerged in only two to four instances (out of 18 sets of observations). Thus, the roof is unlikely to have had serious shading effects. None of the treatments excluded the crab *Pachygrapsus transversus* (mean densities 10–20/m²) or small blennies, which could pass through the mesh. We assumed that their effect was similar in all treatments. No sedentary benthic grazers were ever recorded in any of the treatments.

The percentage of cover of the following functional groups of macroalgae and sessile invertebrates was scored every three months in quadrats with 400 intersecting grid points: algal crusts (*Gymnogongrus* and *Lithothamnium*), foliose greens (*Ulva* and *Enteromorpha*), filamentous greens (mostly *Chaetomorpha antennina*), red algal turf (intermingled species forming a dense turf <10 mm tall), filamentous brown algae (notably *Giffordia mitchelliae*), articulated corallines (mainly *Jania* spp.), the anemone *Isoactinia* sp., and the barnacle *Tetraclita milliporosa*. Frond lengths of *Ulva*, red algal turf, filamentous greens, and articulated corallines ($n = 5$ independent replicates per plot) were measured monthly initially and then once every three months for two years.

Aquarium experiments on the effects of crabs on algae

The effects of *G. grapsus* on algal communities were additionally determined in aquarium experiments. Twelve rocks (upper surface areas ~725 cm²) were prized from the low shore adjacent to Site 1, installed in separate cages (50 × 40 × 25 cm with a 2-mm mesh), and held in outdoor aquaria with a continuous supply of ambient seawater. Water depth was adjusted to simulate twice-a-day tides that left the upper half of each rock exposed for 2 h coincident with natural low tides. One crab was added to each of six cages; the remaining cages lacked crabs. The rock area per crab was equivalent to ~10 crabs/m², the highest density recorded in the field.

The upper surfaces of the rocks were monitored on days 0, 3, 6, 16, 27, and 33 to compare the changes in cover of encrusting versus erect forms. During the experiment, the normally crustose *Gymnogongrus* developed into an erect stage with upright knobby branches. Cover of the crustose and erect phases was estimated,

and the mean lengths of the upright branches measured ($n = 5$ independent replicates).

Univariate data analyses

For univariate analyses, the percentage of cover of sessile organisms was arcsine transformed for the purposes of ANOVA to meet assumptions of normality and equality of variance. There were no differences in the abundance of sessile organisms among treatments at the beginning of the experiment in August 1997 (two-way ANOVA with site as a random factor and treatment as a fixed factor; $P > 0.05$). Because the data for successive measures of each plot were not independent, a repeated-measures (RM) ANOVA (using SYSTAT 9; Systat Software, Port Richmond, California, USA) was used to test the effects of site, treatment, and temporal variation on algal abundance, with site and treatment (between subjects) as random and fixed factors, respectively. Time was analyzed as a within-subject effect. This model assessed the percentage of variation ascribable to each of the factors (and their interactions). Mauchly's tests were run for all RM ANOVAs. Adjusted degrees of freedom were applied to the F tests (using Greenhouse-Geisser and Huynh-Feldt corrections) for data sets that did not meet the sphericity assumptions (Kuehl 2000). Post-hoc contrasts, using Bonferroni/Dunn adjusted probabilities ($P < 0.005$ for significant differences) identified differences among the main effects of treatments on each sampling date. Successive measurements of frond lengths were independent because the chance of sampling fronds coming from the same plants or the same fronds on successive dates was remote. The data were also normal and had equal variances; so two-way ANOVA was applied to untransformed data for each site, with time and treatment as variables.

Diversity (Shannon-Weiner H'), species richness (Margalef's d), and evenness (Pielou's J') were based on percentage of cover of functional groups, using PRIMER version 5.2.2 (PRIMER-E, Roborough, UK). To test the effect of grazing, site, and time on these measures, repeated measures ANOVA was employed, using the procedure described for percentage of cover.

Differences between ENSO (from week 16 to week 40), post-ENSO (from week 52 to week 100), and normal (only controls, weeks 195 and 277) conditions were tested using ANOVA and post-hoc Bonferroni/Dunn adjusted probabilities contrasts. The results must be interpreted with caution, given the possibility of a type I error, as normality and homogeneity of variance were not always observed (Bartlett's and Cochran's C test). However, provided the design is balanced, ANOVA is not generally affected when these assumptions are not met (Day and Quinn 1989), and graphical inspection of the data (Quinn and Keough 2002) indicated that the heterogeneity of variance was not sufficient to compromise the ANOVAs.

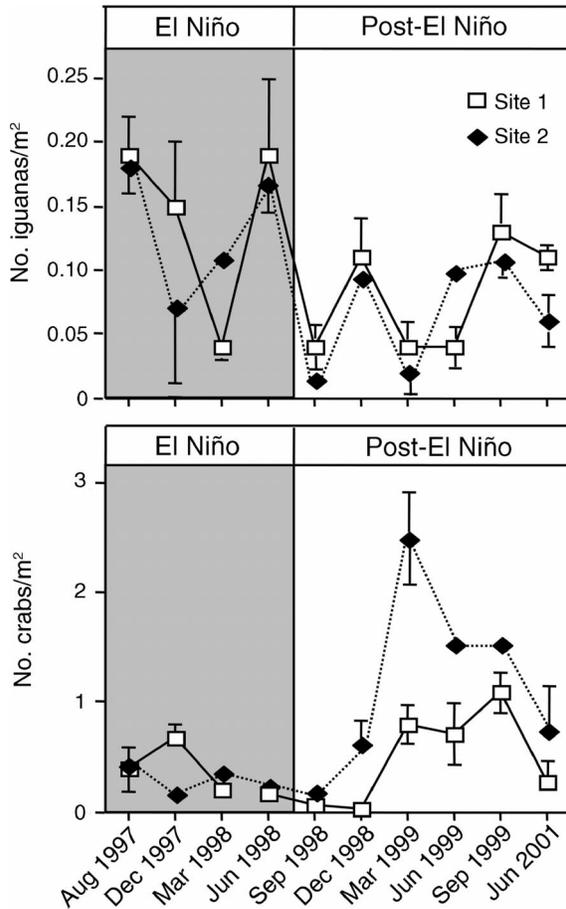


FIG. 2. Densities of marine iguanas *Amblyrhynchus cristatus* (upper panel) and sally lightfoot crabs *Grapsus grapsus* (lower panel) at Sites 1 and 2.

Multivariate analysis

Community structure within each treatment was analyzed by averaging the percentage of cover data for the five replicates of each treatment for each sampling date; the data were then double root transformed and analyzed by Bray Curtis similarity and nonmetric multidimensional scaling (MDS). Clusters recognized in the MDS were based on 80% similarity cutoff in the Bray Curtis similarity. SIMPER (similarity percentage) was used to calculate the contributions of each functional group to dissimilarities among clusters.

RESULTS

Consumers

On average, 0.10 ± 0.02 marine iguanas/m² were recorded at both sites (mean \pm SD). Densities fluctuated, but tended to decline until near the end of the observations (Fig. 2). Densities of *G. grapsus* foraging during low tide averaged 0.44 ± 0.10 individuals/m² at Site 1, and 0.84 ± 0.21 individuals/m² at Site 2. Both sites initially had similar densities of *G. grapsus* (0.4 individuals/m²), followed by a decline until September or December 1998. Substantial increases occurred after the El Niño period, mainly due to the appearance of juveniles, with numbers at Site 2 rising to double those at Site 1 (Fig. 2).

G. grapsus consumed mainly red algal turf and *Ulva*, but also erect thalli of *Gymnogongrus*, and small amounts of filamentous greens and articulated corallines (Fig. 3A). Differences between the sites reflected relative availability of algae. Filamentous brown algae were virtually absent from both diet and habitat at Site 2, and articulated corallines were near-absent at Site 1 (Fig. 3B). The selectivity indices (Fig. 3C) indicated a strong preference for red algal turf and *Ulva*. Erect thalli of *Gymnogongrus* were positively selected when present. The crabs displayed relatively neutral selectivity for articulated corallines and filamentous green

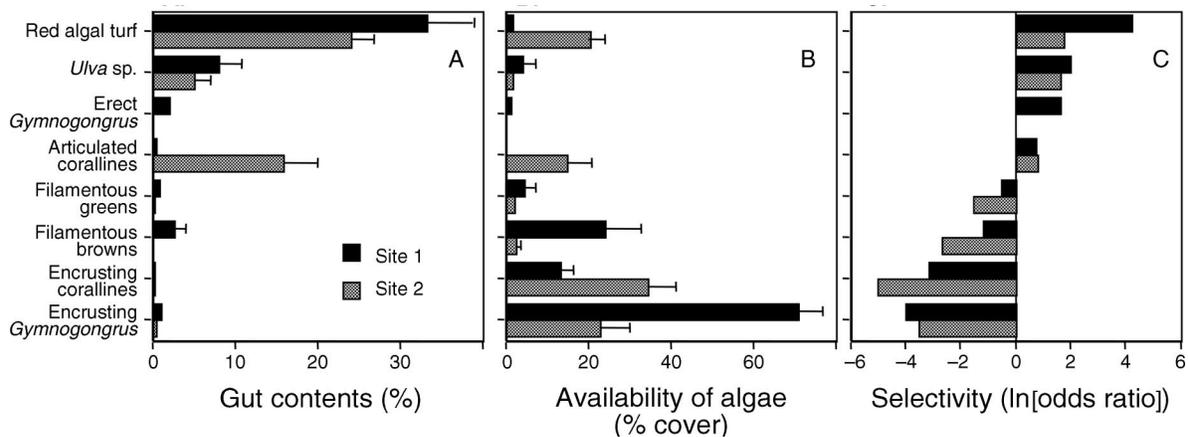


FIG. 3. (A) Percentage composition of gut contents of *Grapsus grapsus*, (B) availability of algal functional groups, and (C) selectivity indices indicating preference for particular functional groups (positive values) or avoidance of them (negative values). In (A) and (B), values are means, and error bars indicate SE.

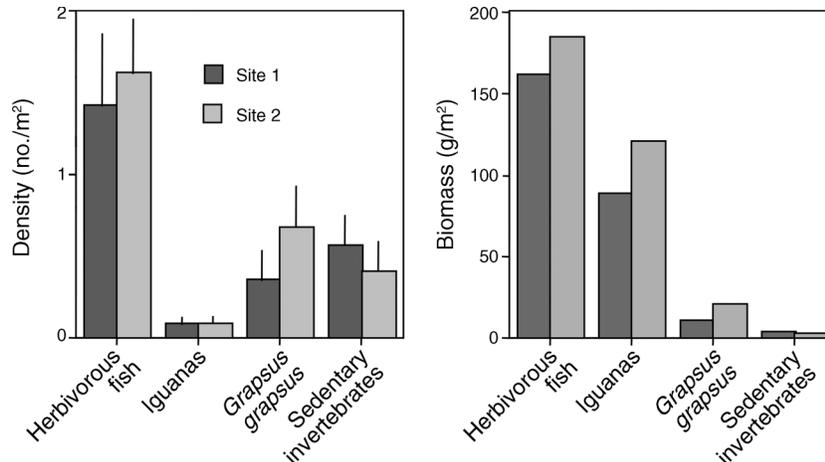


FIG. 4. Densities of herbivorous fish, iguanas, sally lightfoot crabs, and sedentary herbivores compared across times (mean + 95% CI), and approximate conversions to whole wet biomass (g/m²).

algae, and avoided filamentous brown algae, encrusting *Gymnogongrus* and encrusting corallines.

Nineteen fish species were recorded, including eight herbivores and three omnivores (see Appendix C for species list and densities). Numerically, fish were the most abundant mobile herbivores (collectively averaging 1.4 individuals/m²), with sally lightfoot crabs averaging 0.64 individuals/m² and iguanas 0.10 individuals/m² (Fig. 4)

Twenty-three species of sedentary benthic consumers occurred at the two sites, but none was ever abundant (see Appendix D for details of species and densities). Six species of herbivores occurred in the zones where we worked, but were sparse. Chitons and limpets were rare (0.012 individuals/m²). Sea urchins never grazed in the intertidal zone. Thus, sedentary herbivores were scarce (collectively <0.6 individuals/m²) but mobile consumers were abundant (totaling 2.14 individuals/m²). Biomass estimates emphasize the scarcity of slow-moving benthic herbivores (Fig. 4).

The densities of both crabs and iguanas (y , individuals/m²) were linearly related to algal standing stocks (x , g AFDM/cm²) when the two sites in Academy Bay and the four sites at Punta Nuñez were examined. (For iguanas, $y = 1.636x + 0.189$; $n = 6$, $r^2 = 0.986$; for crabs, $y = 6.848x + 0.496$; $n = 6$, $r^2 = 0.956$.) The gut fullness index for crabs was 83.3 ± 11.7 (mean \pm SE) for Site 1, and 50.0 ± 8.7 at Site 2, the differences being significant (t test; $t = 27.1$, $P < 0.001$), suggesting that food was more difficult to obtain at Site 2, despite algal biomass being higher there.

Natural changes in benthic community structure

Abundances of functional groups were initially comparable among treatments (ANOVA, $df_{4,40}$, $P > 0.05$ in all cases). Differences did exist between sites ($P < 0.001$), but there were no significant interactions between treatment and site ($P > 0.05$). Competition for

space appeared intense, unoccupied rock averaging only 0.9%. Site 1 was dominated by crustose *Gymnogongrus* (40–85% of cover) and red algal turf (initially 28%). Site 2 was at first dominated by red algal turf (approximately 75%). *Gymnogongrus* was scarce there at the start, but rose to 50–70%.

In the unmanipulated control plots, three types of temporal change occurred (Fig. 5). First, encrusting *Gymnogongrus*, *Ulva*, and *Enteromorpha* declined or were scarce during El Niño, and then became more abundant. Second, several groups were most abundant during the El Niño. *Giffordia mitchelliae* was absent initially but increased to 40–60% cover, replacing the previously dominant crustose *Gymnogongrus*, and then disappeared. At Site 2, red algal turf, *Chaetomorpha antennina*, and articulated corallines also peaked during the El Niño. The barnacle *Tetraclita milleporosa* declined from ~14% to <2% in the latter half of the study. Encrusting corallines covered 29% early in the El Niño, but declined to <3% and began to recover only three years after the El Niño. Third, erect *Gymnogongrus* and the anemone *Isoactinia* displayed no temporal trends (neither ever exceeding 3% cover).

The most obvious changes in cover occurred during the El Niño, when *G. mitchelliae* and *C. antennina* increased and crustose forms diminished. Once temperatures dropped, *Ulva* and *Enteromorpha* replaced *G. mitchelliae* and *C. antennina*, rising to cover ~48% of primary space; and encrusting *Gymnogongrus* recovered to become the eventual dominant. Bare space accounted for up to 20% during the El Niño but was almost nonexistent thereafter.

From week 76 onward, almost all of the functional groups changed scarcely at all in the control plots during the 4.5 yr of monitoring after El Niño passed.

Changes in community structure after herbivore manipulation

Temporal, site, and grazer effects significantly affected the abundance of all functional groups except

Lithothamnium (Fig. 5). Temporal differences usually had the greatest effect, accounting for 21–37% of the variability. Site effects were also substantial (16–32%), and grazer treatments less important (1–10%), but there were significant interactions in most cases (see Appendix E for details of statistical analyses).

Percentage of cover of encrusting *Gymnogongrus* differed significantly between El Niño and post-El Niño periods, increasing in the latter (Fig. 5A). At Site 1, only total exclusion of all grazers led to a decrease in this crust. At Site 2, both partial and total exclusions of grazers had this effect. Cover rose to 79% in the controls, but only 6–26% in all other treatments. Overall, encrusting *Gymnogongrus* declined or was held at low levels during the El Niño period (in all treatments) but increased thereafter, most obviously in treatments involving no exclusion or partial exclusion of grazers.

Ulva and *Enteromorpha* responded oppositely to *Gymnogongrus*, with abundance peaking inside the total exclusion treatments (Fig. 5B and C). Site and temporal differences were large, and grazing effects significant but of lesser magnitude. At both sites, total exclusion of grazers increased the cover of *Ulva* during the post-El Niño period from week 52 onward (Fig. 5B), and control plots had low values. *Enteromorpha* was only abundant at Site 1, where it responded negatively to grazing (Fig. 5C). In short, *Ulva* and *Enteromorpha* remained scarce in all treatments during the El Niño period, but thereafter increased in treatments where grazing was diminished or prevented.

No consistent grazing effect was observed for *Giffordia mitchelliae*, with opposite trends at the two sites (Fig. 5D). Most of its variation was explained by time (60%), with treatment, site and interactions between factors explaining no more than 7%. Its proliferation was thus clearly linked to El Niño.

Red algal turf was initially an important component, but progressively declined, and levels were significantly lower post-El Niño than during El Niño (Fig. 5E). Grazing had no effect ($P > 0.05$). Thus, cover of red algal turf was more abundant at Site 2 than Site 1, and more abundant during the El Niño than afterward, but was virtually unaffected by grazing.

Chaetomorpha antennina (Fig. 5F) did not differ among treatments or sites. Temporal effects dominated, with *Chaetomorpha* only being abundant during El Niño.

Articulated coralline algae were virtually absent from Site 1 (Fig. 5G). At Site 2, grazing had a small and marginally significant effect. Percentage of cover was initially small, but increased as the El Niño matured, particularly inside the treatments that provided partial protection against grazing (roof or half wall + roof), and declined post-El Niño. Grazing intensity was not correlated in any simple manner with percentage of cover, with the controls and total exclusion plots (highest and lowest intensities of grazing) often having the lowest cover. Encrusting corallines (Fig. 5H) de-

clined over time; but neither the main effects nor their interactions had any influence on abundance.

The effects of grazer treatments on all functional groups were clear when the data were contrasted between the El Niño and post-El Niño periods (Fig. 6), and most obvious (and significant) at whichever site supported the highest cover of each group. Four types of responses emerged. (1) Encrusting *Gymnogongrus* was promoted by grazing and suppressed during the El Niño. (2) *Chaetomorpha*, *Ulva*, and probably *Enteromorpha* were inhibited by grazing, with *Chaetomorpha* peaking during El Niño and the other two after its passage. (3) Red algal turf and articulate corallines yielded ambiguous results, with a suggestion of higher values at intermediate levels of grazing, at least at Site 2 where both were most abundant. El Niño promoted red algal turf but had no effect on articulated corallines. (4) Encrusting corallines and *G. mitchelliae* showed no consistent responses to grazing but both peaked during the El Niño.

Effects of grazers on algal size composition

Differences in frond length were initially nonexistent among treatment plots (ANOVA, $P > 0.25$ in all cases), but soon emerged and persisted for 8–52 wk (Fig. 7; for detailed data and ANOVA, see Appendix F).

Frond lengths of *Ulva* (Fig. 7A) were significantly affected by grazing ($P < 0.001$), being inversely related to grazing intensity most of the time at both sites. Red algal turf (Fig. 7B) showed similar clear-cut responses to grazing for the first 40 wk at Site 1 ($P < 0.001$) and for 16 wk at Site 2. *Chaetomorpha antennina* (Fig. 7C) showed striking effects of grazing up to weeks 40–52. Articulated corallines (Fig. 7D) showed no obvious patterns, although roofed treatments (roof and half wall + roof) had high values in weeks 4–28, similar to the pattern for percentage of cover (Fig. 5H).

Time and site always had significant effects, as did interactions between factors. The percentage of variation in the model significantly explained by grazing (0.2–9.9%) was always less than that attributable to time (21.0–59.9%) or site (0.3–32.3%). Without exception, the largest responses to grazing were linked to periods when each taxon was most abundant.

Algal diversity

There were initially no differences in any of the indices of diversity among treatments. By week 16, however, diversity, evenness, and richness had increased at both sites due to the addition of species such as *Giffordia mitchelliae* and *Chaetomorpha antennina*. After about weeks 40–52, all three indices progressively declined at both sites and in all treatments, mainly due to increased dominance by encrusting *Gymnogongrus* at Site 1 and by *Ulva* at Site 2, and because of declines in red algal turf, barnacles, and *Lithothamnium*.

Site 1 had less species richness than Site 2 (repeated-measures ANOVA, $P < 0.001$; see Appendix G for

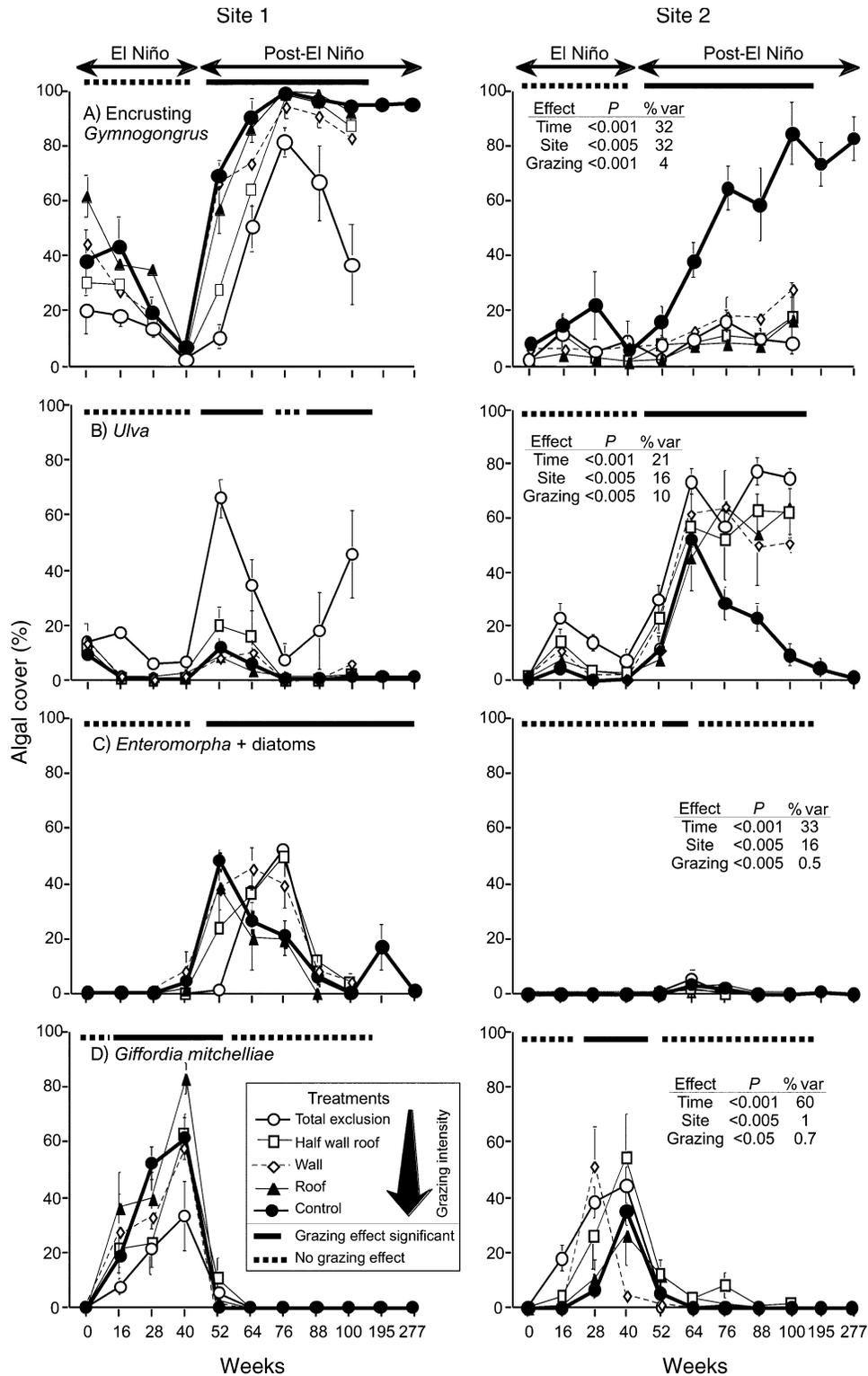


FIG. 5. Changes in algal cover (mean \pm SE) in experimental plots at Sites 1 and 2, August 1997–September 1999, and in control plots, August 1997–February 2003: (A) encrusting *Gymnogongrus* sp., (B) *Ulva* sp., (C) *Enteromorpha* and associated diatoms, (D) *Giffordia mitchelliae*, (E) red algal turf, (F) *Chaetomorpha antennina*, (G) articulated corallines, and (H) *Lithothamnium* sp. The significance of main effects and their contributions to percentage variance pooled across sites (% var) are shown on the right (see Appendix E for statistical analyses.) Solid horizontal bars indicate times when grazing effects were significant; dashed bars when they were not (post hoc contrasts; Bonferroni/Dunn adjusted to $P < 0.005$).

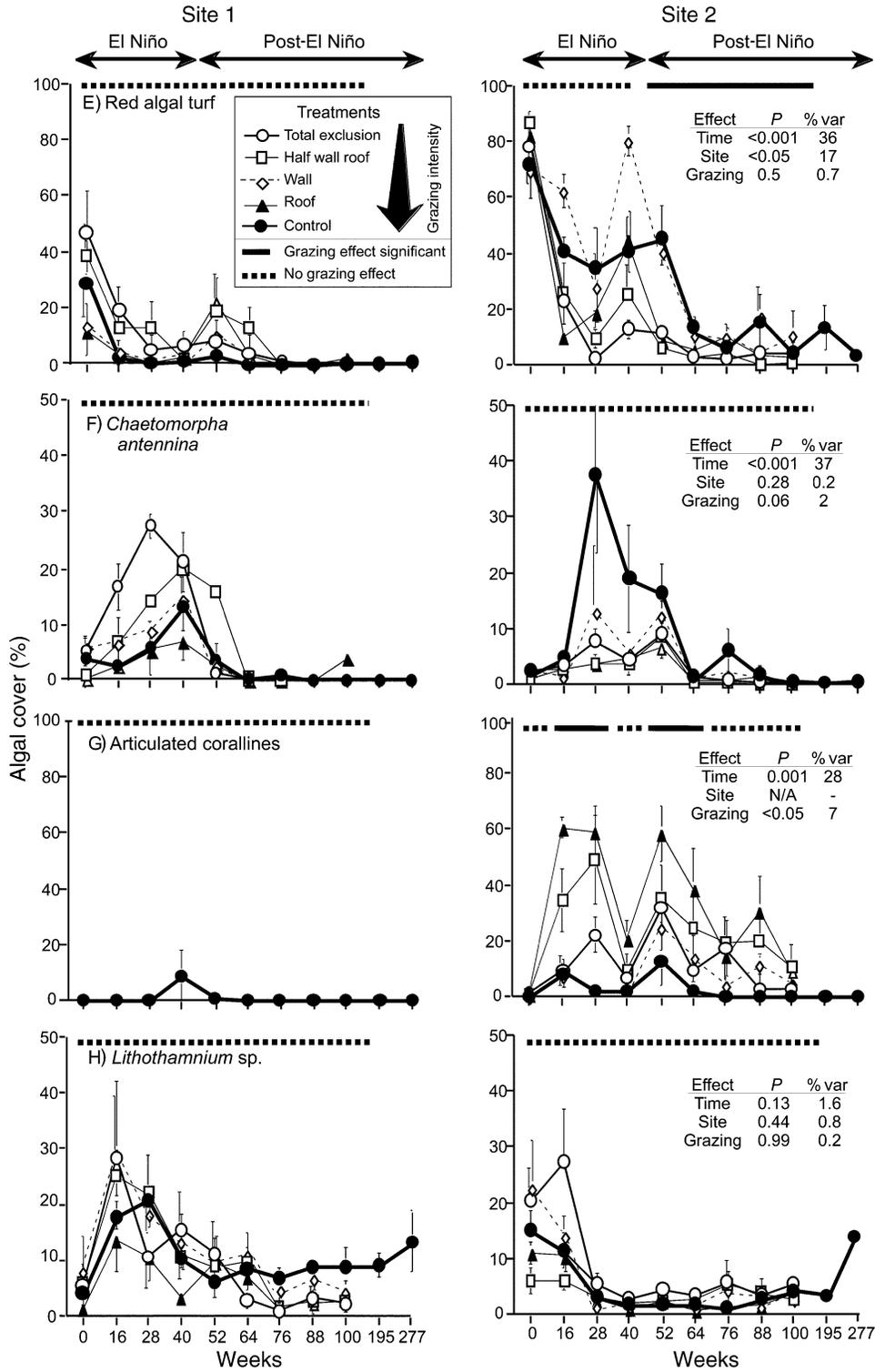


FIG. 5. Continued

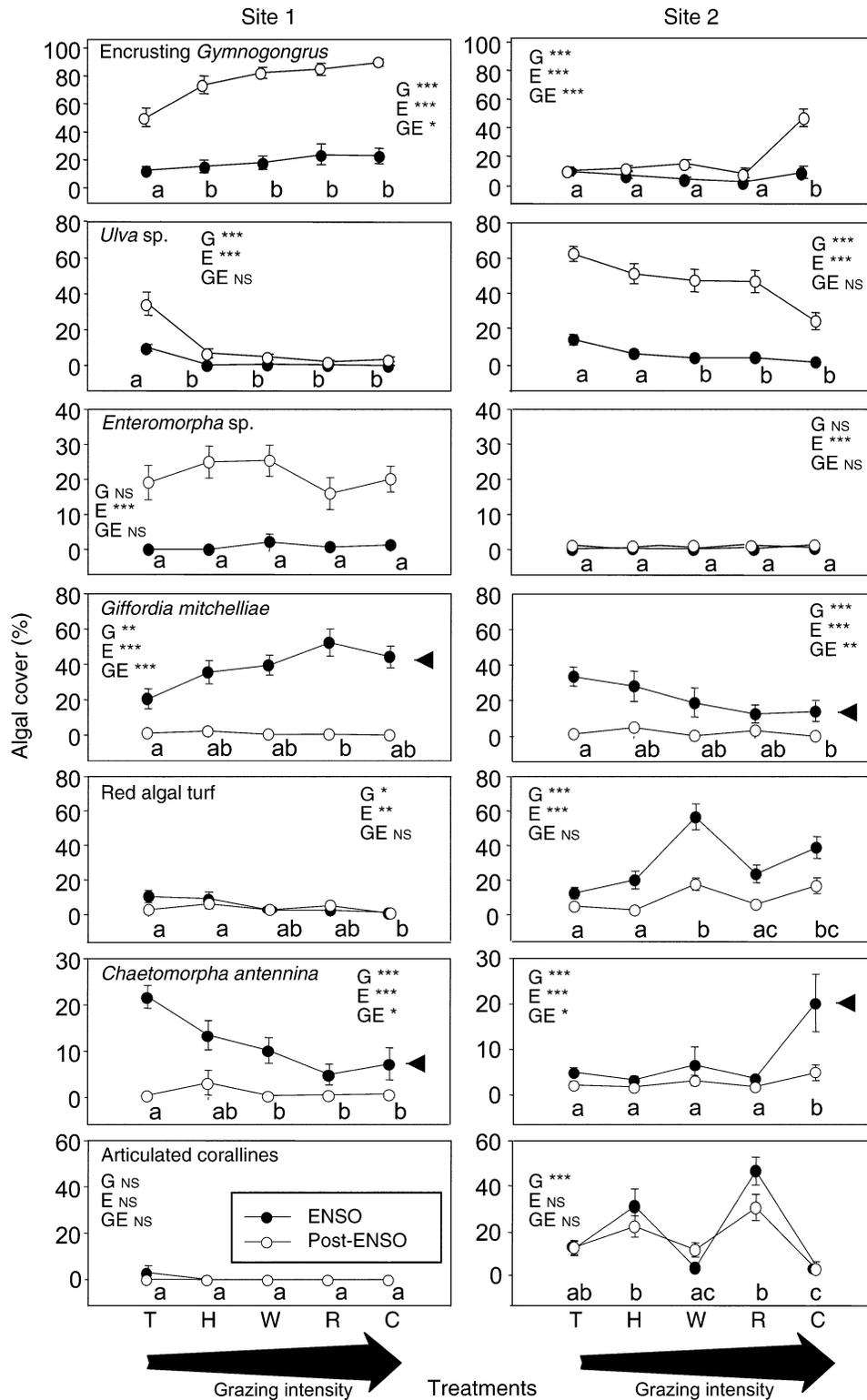


FIG. 6. Grazing effects (G) on the percent cover of algae comparing ENSO (December 1997–June 1998, solid circles) vs. post-ENSO (September 1998–September 1999, open circles) conditions (E), and the interaction between grazing and ENSO effects (GE) (ANOVA, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; NS, $P > 0.05$) at Sites 1 and 2. Letters on the x-axis represent different treatments (T, total enclosure; H, half wall + roof; W, wall; R, roof; and C, control). Within sites, treatments that share the same lowercase letter (just above the x-axis) were not significantly different (Bonferroni post hoc tests, $P > 0.05$). Where interactions are reported, arrows indicate the period when differences in grazing effect were found.

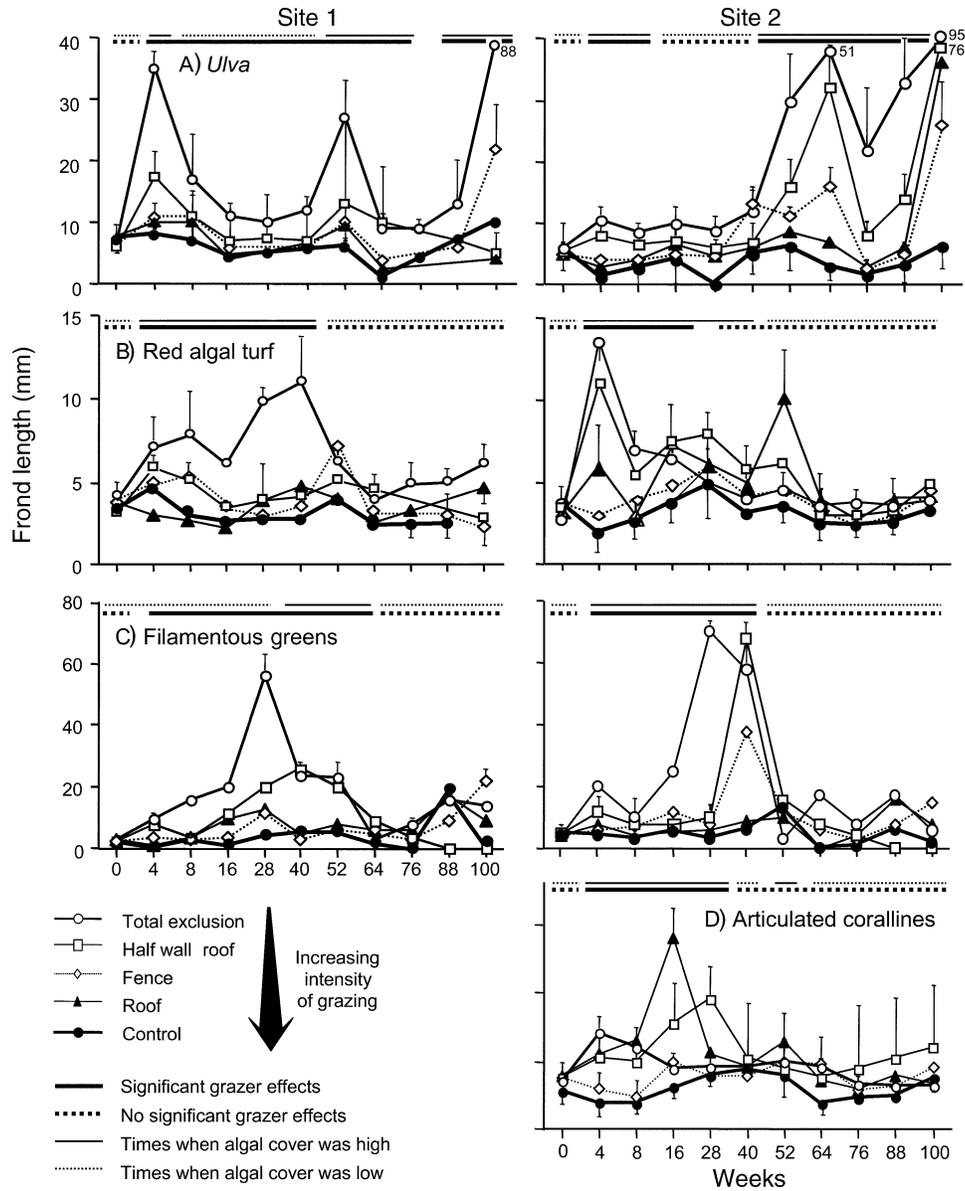


FIG. 7. Differences in the lengths (mean and SE) of algal fronds: (A) *Ulva* sp., (B) red algal turf, (C) filamentous green algae (mainly *Chaetomorpha antennina*), and (D) articulated corallines (which were absent from Site 1). Numbers next to data points indicate values for truncated portions of the graphs.

statistical analyses and Appendix H for temporal patterns of diversity between treatments); but diversity and evenness did not differ between sites ($P > 0.05$). Grazing affected all three diversity indices ($P < 0.001$). Total exclusion plots usually had high richness and diversity values compared to other treatments ($P < 0.005$; Fig. 8). The controls (which were most intensely grazed) yielded consistently low values, showed the greatest declines post-El Niño, and had the lowest final values.

Overall, contrast analyses showed that all three indices were significantly greater during the El Niño (particularly in total exclusion plots), and (in all but one

case) were significantly affected by grazing, being inversely related to grazing intensity (Fig. 8).

Multivariate analysis of community structure

Treatments were classified into Bray-Curtis hierarchical clusters and by MDS (see Appendices I and J), based on the mean percentage of cover of functional groups in each treatment on each date. There was a clear pattern dividing the samples into temporal clusters, rather than clusters based on treatments. For Site 1, seven clusters emerged, all distinguished by the time when samples were taken rather than by treatment. A similar predominantly temporal pattern occurred at Site

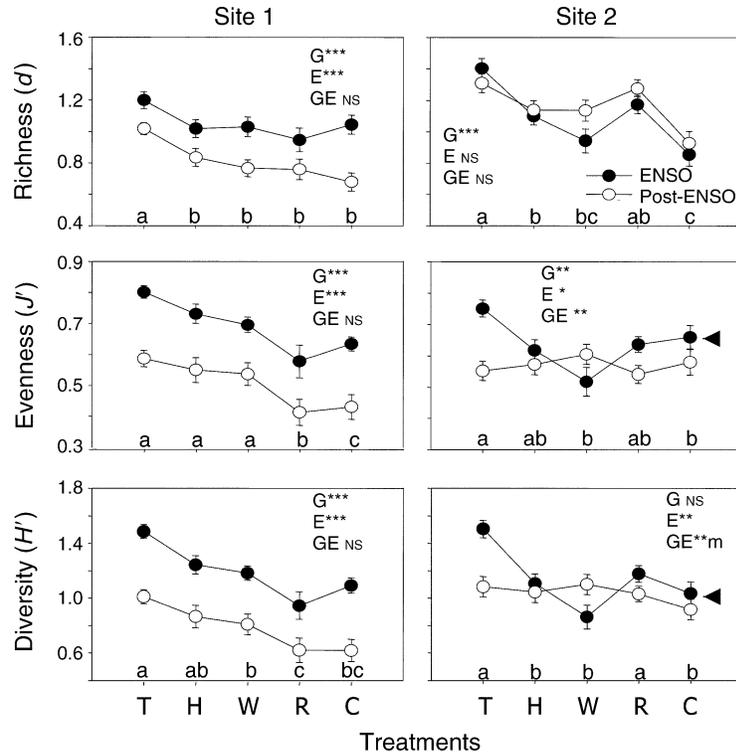


FIG. 8. Grazing effects (G) on species richness (Margalef's index d), evenness (Pielou's evenness index J') and diversity (Shannon-Wiener diversity index H') comparing ENSO (December 1997–June 1998, solid circles) vs. post-ENSO (September 1998–September 1999, open circles) conditions (E) and the interaction between grazing and ENSO effects (GE) (ANOVA, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; NS, $P > 0.05$). Diversity indexes were derived from percent cover of functional groups in experimental plots at Sites 1 and 2. Where interactions are reported, arrows indicate the period when differences in grazing effect were found. Letters on the x-axis represent different treatments (T, total enclosure; H, half wall + roof; W, wall; R, roof; and C, control). Within sites, treatments that share the same lowercase letter (just above the x-axis) were not significantly different (Bonferroni post hoc tests, $P > 0.05$).

2, where six clusters were identified. Clusters I to V comprised successive sampling times from weeks 0–100. The only case in which grazing treatments influenced the formation of clusters was the controls. At weeks 28 and 64, the controls did not cluster with other treatments for those dates, and the controls for weeks 76, 88, and 100 formed a separate group (cluster VI). Thus, the controls tended to separate out, but apart from this, grazing had no effect on the clustering of samples.

SIMPER identified the taxa characterizing and distinguishing clusters (Fig. 9). At both sites, there were three recognizable phases, between which there were significant differences in the abundance of almost all functional groups (post-hoc contrast analyses, $P < 0.001$ for all groups except articulated corallines, for which differences were not significant, $P > 0.05$). At Site 1, *Gymnogongrus* and red algal turf dominated the first phase (cluster I), corresponding to the early onset of El Niño, giving way in a second phase to a more diverse array and increasing domination by *G. mitchelliae* (clusters II–IV) during the mature stage of El Niño. Finally, in phase three, encrusting *Gymnogongrus* (initially with *Enteromorpha/Ulva*) became prevalent and diversity declined during post-El Niño con-

ditions (clusters V–VII). At Site 2, early domination by red algal turf in phase 1 (cluster I) gave way to a diversification and an expansion of *G. mitchelliae* in phase two (clusters II and III), whereas in phase three *Ulva/Enteromorpha* and encrusting *Gymnogongrus* dominated and diversity declined as ephemeral species diminished or disappeared (clusters IV–VI).

Aquarium experiments with crab grazing

Rocks held in aquaria developed different floras depending on whether they were exposed to crab grazing or not (Fig. 10). Initially, the rocks were covered by roughly equal proportions of encrusting and erect algae, with <5% bare space. Rocks exposed to *G. grapsus* (+crab) became progressively dominated by crustose algae (both *Gymnogongrus* and corallines). Erect algae (notably *Ulva*, filamentous greens and red algae) declined proportionally. In treatments lacking crabs (–crab), the opposite happened: erect algae increased and smothered crusts.

Gymnogongrus, the most important space occupier, initially almost solely comprised an encrusting phase, which occupied 32% of the rock surface. In the +crab treatment, this crust increased to 44% (Fig. 11A), but

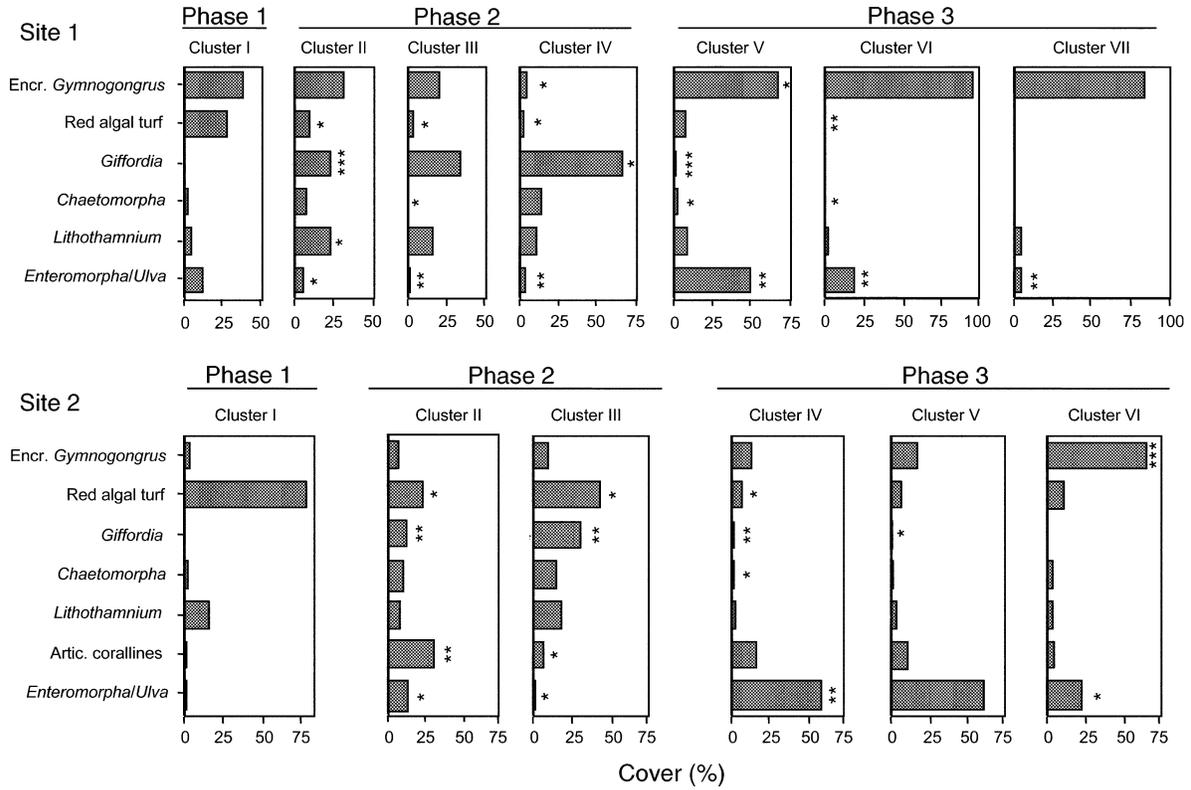


FIG. 9. Results of SIMPER (similarity percentage) analyses diagnosing functional groups characterizing clusters identified by Bray-Curtis similarity and MDS (multidimensional scaling); see Appendices I and J. See *Results: Multivariate analysis of community structure* for a definition of phases and clusters. Asterisks identify significant differences in abundance between successive clusters (* $P < 0.05$; ** $P < 0.001$; *** $P < 0.001$).

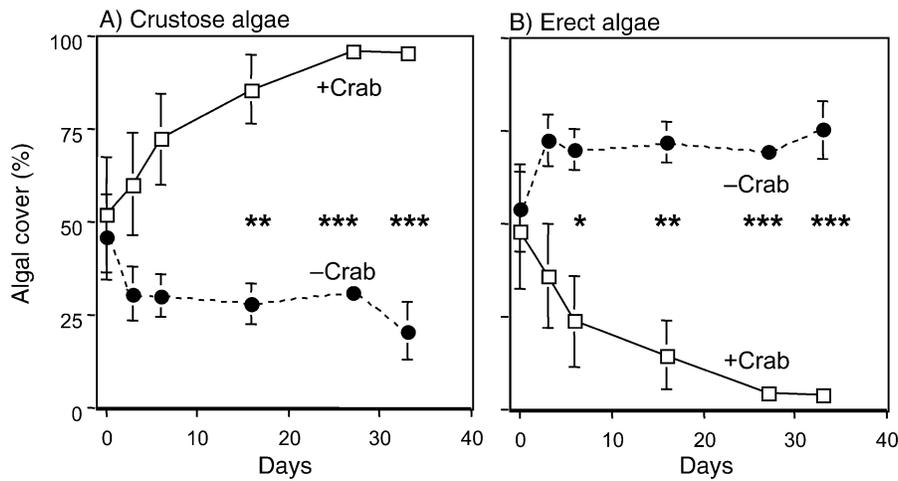


FIG. 10. Percentage cover of (A) crustose algae (corallines and *Gymnogongrus*) and (B) erect algae (filamentous red and green algae and foliose green algae) in aquaria that either contained or lacked a crab. Values shown are means \pm SE ($n = 6$ aquaria per treatment). Any differences between the sum of erect and crustose algae and 100% cover were contributed by bare rock. Asterisks indicate significant differences between treatments with vs. without a crab (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

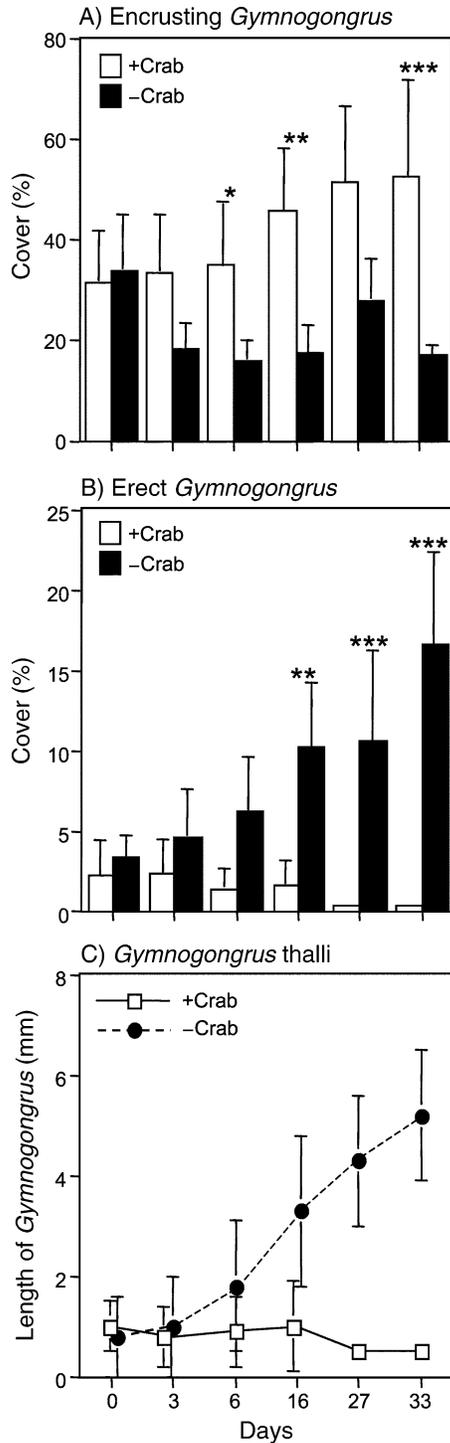


FIG. 11. Percent cover (mean + SE) for (A) encrusting *Gymnogongrus* sp., (B) erect thalli of *Gymnogongrus* sp., and (C) the length of thalli of erect *Gymnogongrus* sp. in aquaria that either held a single *Grapsus grapsus* or lacked a crab. Asterisks indicate significance of the crab effect (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

in the -crab treatment, it progressively transformed into an erect phase (Fig. 11B). Furthermore, thallus length of the erect phase increased fivefold in the -crab treatment, but remained stunted in the +crab treatment (Fig. 11C).

DISCUSSION

A central message emerging from the results is the interplay between (1) bottom-up forces, particularly related to changes in nutrients (Chavez et al. 1999), but also to other associated factors such as wave action and sea level during different phases of the El Niño cycle, and (2) top-down grazing effects. Moreover, differences between sites were greater than expected. Tropical intertidal rocky shores have previously been generalized as communities dominated by encrusting forms, in which temporal and spatial variation in sessile species is minimal (Garrity and Levings [1981] and Lubchenco et al. [1984] for the coast of Panama; Lubchenco and Gaines [1981] and Brosnan [1992] for a general review; Williams [1993] for the coast of Hong Kong). This apparent homogeneity has been attributed to the sustained combined effect of slow-moving benthic grazers coupled with mobile consumers, particularly fish, because they cover substantial ranges (Gaines and Lubchenco 1982, Lubchenco et al. 1984, Menge et al. 1985, Brosnan 1992). However, our study showed substantial temporal and spatial differences in composition and abundance. On average, 26.1% of the variance in abundance of functional groups was attributable to the main effect of time, 13.3% to site but only 4.8% to grazer treatment.

Differences between sites

There were several background differences between sites, including a high abundance of red algal turf at Site 2 and its scarcity at Site 1, and the presence of articulated coralline turf at Site 2 but not Site 1. Responses to grazers also differed between sites. Two possible causes are differences in wave action and thermal stress. Site 1 was more exposed to waves than Site 2, although the difference was not great. Intersite differences in thermal stress could have influenced the cover of erect algal species. We have no concrete evidence of thermal differences, however, and regard them as an unlikely explanation of differences in community structure between sites, as wave action (which will mitigate thermal stress) was less at Site 2 where erect algae were most common.

Grazing did seem to be more effective at Site 1, because each of the individual types of grazers affected algal cover there, whereas at Site 2 only the combined effects of all grazers influenced algal cover. Almost the same numbers of marine iguanas occurred at Sites 1 and 2, but smaller individuals visited Site 1 than Site 2. Juveniles are known to be more affected by waves than larger individuals and forage in more wave-protected areas or higher on the shore (Trillmich and Trill-

mich 1986, Wikelski and Trillmich, 1994). *G. grapsus* was more abundant at Site 2 than Site 1 during the post-El Niño period, but the gut fullness of crabs was greater at Site 1 than Site 2. These variations do not necessarily reflect differences in wave action, because both marine iguanas and *G. grapsus* feed during low tide when wave action has little effect (Kramer 1967, Buttemar and Dawson 1993).

In short, there were clear differences in community structure and dynamics between sites, but the causes remain uncertain although there are plausible explanations.

Temporal fluctuations in species composition

The clearest pattern was that all species underwent substantial changes in abundance over time. Abundance of all taxa except *Lithothamnium* was significantly different during versus after El Niño, apparently related to high temperatures, low nutrients, and strong wave action during El Niño (March 1997 to June 1998), followed by relative stability after the return of “normal” conditions (Chavez et al. 1999). These temporal differences explained more of the variance in the data than any other factor, and multivariate analysis divided the community into temporal clusters rather than clusters based on treatment.

At both sites, three phases existed (Fig. 9). Phase 1 was characterized by domination by encrusting *Gymnogongrus* and/or red algal turf. Phase 2 heralded ephemeral warm-water species, including *Giffordia mitchelliae*, which proliferated and aggressively overgrew encrusting algae. Red algal turf, *Enteromorpha* and *Ulva* (all preferred items in the diet of iguanas and sally lightfoot crabs) diminished or disappeared. *G. mitchelliae* seems characteristic of El Niño periods and has been linked to previous ENSO events (Laurie 1990). Phase 3 marked the exit of *G. mitchelliae*, with a return to encrusting *Gymnogongrus* as a clear dominant, initially together with *Ulva/Enteromorpha*.

Diversity indices were significantly higher during the El Niño because of the addition of warm-water ephemerals, but declined thereafter due to the disappearance of some taxa and increased domination by one group (Fig. 8). Both sites were eventually dominated by crusts (79–94% in control plots). No increases in warm-water ephemerals occurred at any time in the 4.5 yr during which control plots were monitored after the passage of El Niño, so their emergence during 1997–1998 was not just seasonal, but rather related to the anomalous oceanographic conditions (Chavez et al. 1999). The lack of any significant change in control plots between July 1999 (week 100) and February 2003 (week 277) implies stability over this period. Our data do not allow certainty on this point because sampling in the later years was infrequent, but they do show that inter-annual differences were small after the passage of El Niño. Previous tropical-shore studies have emphasized their inter-annual stability (Gaines and Lubchenco 1982,

Lubchenco et al. 1984, Menge et al. 1985, Brosnan 1992). Seasonal shifts of algal composition have been documented at Hong Kong, where crusts predominate in summer whereas filamentous and foliar algae proliferate in winter, profoundly altering food availability for herbivores (Kennish et al. 1996). Our results contrast with both of these perspectives because they reveal striking regime shifts between years, fueled by oceanographic anomalies and the bottom-up influences of El Niño. The magnitude of the interannual changes was greater than that previously recorded for any other tropical shores, and is an important reminder of the extent to which climate change may alter ecosystem structure and dynamics.

Our observations spanned both a year of El Niño and four years of “normal” conditions. El Niños recur at irregular intervals of five to 10 years. As a result, our work covered only a portion of the full cycle. This would probably have had the effect of overestimating the effect of time relative to herbivory. Temporal changes would have been greatest during El Niño, and community composition was relatively stable during the Post-El Niño period. The relative influence of herbivory might have increased had we run our experiments for an entire ENSO cycle. Indeed, the herbivory treatments were continuing to diverge at the end of the experiment. Nevertheless, our central conclusions remain robust: temporal changes were substantial and, at least over the period in which we operated, overshadowed the effects of herbivory.

Consequences of El Niño events

The shores of Galápagos do not have striking zonation patterns (Hedgepeth 1969, Wellington 1984), mainly due to the absence of obvious belts of algae, mussels or barnacles. In the past, dense mats of *Sargassum* and the endemic *Bifurcaria* (= *Blossevillea*) *galapagensis* formed a conspicuous band low on the shore (Houvenaghel and Houvenaghel 1977), but, after the 1982–1983 El Niño, these species disappeared and have not been observed since (G. Kendrick, *personal communication*; L. Vinuesa, *personal observation*). During the 1982–1983 El Niño, the endemic sea star *Heliaster cumingii* declined drastically (Hickman 1998). Its distribution was closely associated with the barnacle *Tetraclita milleporosa*, an important part of its diet (Wellington 1975, Hickman 1998). *T. milleporosa* declined during the 1982–1983 El Niño and, at our sites, during and after the 1997–1998 El Niño.

El Niño also seriously affects other marine communities in Galápagos. During the 1982–1983 ENSO, barnacles, gorgonians, giant scallops, ahermatypic corals, and fish declined drastically (Robinson 1985). Several species of birds failed to breed (Valle 1985), and corals were decimated by 97% (Glynn 1988, 1990). Laurie (1985, 1990) and Laurie and Brown (1990a) recorded 50% mortality of marine iguanas, and drastic reductions of red algal turfs and foliose green algae,

which are important constituents of the diet of marine iguanas and other intertidal grazers. The 1982–1983 El Niño also featured domination by *Giffordia mitchelliae*, never before recorded in the Archipelago (Laurie 1985).

Proliferation of *G. mitchelliae* (and concomitant reductions of edible species) has important implications, as the digestibility of *G. mitchelliae* is 21%, compared with 64% for foliar green algae and 78% for red algal turf. Its high terpenoid content probably reduces the digestive capabilities of iguanas and may have contributed to their declining condition and elevated mortality during El Niño (Laurie 1985, Laurie and Brown 1990b). Our data showed that *G. mitchelliae* was also avoided by *Grapsus grapsus*, although it is an important constituent of the diet of *Grapsus albolineatus* in Hong Kong (Kennish 1996). *G. mitchelliae* was among several species that increased their abundance or extended their range during the 1997–1998 El Niño, particularly species with affinities to the Indo Pacific and Panamic Province, which were probably transported southward by a warm tongue of water that extended to the whole eastern Pacific (Ruttenberg 2000).

The drastic changes in algal composition and edibility, accompanied by strong swells and extremely high sea levels, reduced food availability and restricted intertidal feeding opportunities. The correlation between algal biomass and densities of crabs and iguanas during El Niño also suggests they were aggregating where food was most available, implying that food was limiting at sites where algal stocks were low. All these factors would have contributed to the heightened mortality of marine iguanas (~50%) observed during 1982–1983 (Laurie 1990) and 1997–1998 (Romero and Wikelski 2001). After the 1997–1998 El Niño, *G. mitchelliae* disappeared, being replaced by encrusting *Gymnogongrus* and edible groups such as *Ulva*, *Enteromorpha*, and red algal turf. *G. grapsus* increased greatly, and marine iguanas recovered fast, reaching weights heavier than even those before the El Niño.

Types of consumers

Herbivorous fish, sally lightfoot crabs, and iguanas averaged densities of 1.4, 0.64, and 0.1 individuals/m², whereas slow-moving herbivores such as chitons, limpets, nerites, and urchins never exceeded 0.03 individuals/m². Their relative impacts on algae will be influenced by many factors, including biomass, rate of consumption, dietary preferences, duration of tidal foraging, mobility, and the edibility of different algae (Lubchenco and Gaines 1981). Most of these factors lie outside the scope of this investigation, but approximate conversions to wet biomass yielded estimations of 178.4, 89.4, 15.4, and 2.9 g/m² for herbivorous fish, iguanas, sally lightfoot crabs, and slow-moving grazers, respectively; providing a better perspective of their potential influence.

The barren aspect of Panamanian shores has been attributed to conspicuous slow-moving consumers (notably siphonariid and fissurellid limpets) that graze foliose algae down to grazer-resistant forms (Menge et al. 1986a, b). In Galápagos, and specifically at our experimental sites, slow-moving grazers were rare and their biomass low. In particular, the near absence of limpets at all intertidal rocky shores is striking. In short, sedentary intertidal grazers that exert an important influence on algae in other tropical areas are absent or scarce in Galápagos as a whole, and specifically at the two experimental sites.

Diets of consumers

Dietary preferences of consumers will also affect their influence on intertidal communities. With respect to iguanas, four generalities emerge from the considerable literature on their diets (Nagy and Shoemaker 1984, Laurie 1985, Wikelski et al. 1993, Wikelski and Hau 1995). First, iguanas consume most algae, especially foliar green algae. Second, they avoid certain species. For example, before the 1982–1983 El Niño, *Bifurcaria galapagensis* was abundant, but apparently never eaten by iguanas. Third, *Giffordia mitchelliae*, which rises to dominance during El Niño periods, appears to have negative effects on iguanas as described above. Fourth, low-growing algae are difficult for iguanas (and other herbivores) to graze. Consequently, crusts are rarely eaten (Wikelski and Hau 1995), and stand to benefit from the removal of superior competitors. Moreover, firmly attached erect algae such as red algal turf can be grazed down to a thin veneer, but are difficult to eliminate (Lubchenco et al. 1984, Menge et al. 1986b). Marine iguanas can completely remove weakly attached algae such as *Ulva* and *Enteromorpha*, but cannot graze on turfs <1 mm in height (Wikelski and Hau 1995). Our data showed that grazing reduced the height of red algal turf, but scarcely influenced its percentage cover.

Grapsus grapsus showed clear dietary preferences, with crusts and filamentous browns (notably *Giffordia mitchelliae*) being avoided. In contrast, *Grapsus albolineatus* preferentially feeds on filamentous algae, including *Giffordia* (= *Hinksia*) *mitchelliae* in Hong Kong (Kennish 1996, Kennish and Williams 1997).

Overall, grazers displayed four responses to algae. Encrusting forms were negatively selected because they are inaccessible; red algal turfs and foliar greens were positively selected; articulated corallines (and perhaps filamentous greens) were eaten in proportion to availability, and *Giffordia mitchelliae* was either avoided or had adverse effects because of its low digestibility.

Four corresponding responses to grazing existed among the algae. (1) Encrusting *Gymnogongrus* was enhanced by grazing, probably as an indirect response to grazer-induced reductions of foliar algae that would otherwise have overgrown them. The laboratory ex-

periments verified that by diminishing foliar and filamentous algae, crabs could enhance encrusting *Gymnogongrus* and encrusting corallines. In the field, encrusting and erect phases of *Gymnogongrus* are probably adapted to avoiding grazing and the threat of overgrowth by erect algae respectively (cf. Lubchenco and Cubitt 1980, Slocum 1980). (2) Some algae such as *Ulva*, *Enteromorpha*, and red algal turf were diminished by grazing. All these algae are preferentially consumed by iguanas and crabs. (3) Articulated corallines were scarcely affected by grazing and were eaten in proportion to availability. (4) *G. mitchelliae* was unaffected by grazing.

Changes in community structure due to herbivore manipulation

The effect of grazers fell into three phases. (1) During El Niño (March 1997 to June 1998), preferred food species were scarce, being replaced by *G. mitchelliae*. Heavy swells and high seas would additionally have hindered grazing. Densities of *G. grapsus* were low, and mortality of marine iguanas elevated (Romero and Wikelski 2001). (2) In the late stages of El Niño and its aftermath (July 1998 to March 1999), ephemeral algae (particularly *Ulva*) grew luxuriantly, reaching frond lengths of 80 mm and close to 75% coverage even in control plots exposed to all grazers. *Chaetomorpha antennina* achieved frond lengths of 100 mm and cover of *G. mitchelliae* rose substantially. Densities of mobile grazers such as iguanas and crabs were still low, and high primary production could have improved conditions for consumers and led to the greater body mass recorded for iguanas (Wikelski and Trillmich 1997). Sessile organisms competed for space, with ephemeral algae flourishing, crustose forms initially declining and barnacles diminishing to the lowest levels recorded. (3) After nutrient and temperature levels returned to normal (June 1999 onward), grazing effects of marine iguanas, crabs, and fish were pronounced and provoked changes in community structure, including a reduction of *Ulva* and *Chaetomorpha antennina*, and an increase in crustose forms.

The magnitude of responses to grazing was greatest when the cover of each functional group was high. This implies that during periods of low productivity, algae do not have the capacity to benefit from a reduction or elimination of grazing, and are probably limited by physicochemical conditions. Conversely, during periods of high productivity dramatically increased growth was recorded in grazer-exclusion plots. During the El Niño the bottom-up effects of nutrient limitation (Chavez et al. 1999) were prevalent, and rippled up the food chain to affect consumers, but when "normal" conditions returned, the top-down effects of herbivores on algal composition and sizes increased.

The effects of grazing differed between sites, being most obvious at Site 1 where the cumulative or individual effects of grazers reduced ephemeral species

such as *Ulva*, and indirectly promoted competitively inferior but grazer-resistant species such as crustose *Gymnogongrus*. At Site 2, edible foliar algae were more abundant, and only the combined effects of all grazers (in the control treatment) significantly reduced ephemerals and promoted crusts. However, not all crusts responded similarly; *Gymnogongrus* increased substantially, but *Lithothamnium* consistently decreased in abundance and never recovered fully. No grazing effect was detectable for *Lithothamnium*, although its highest levels of cover were associated with particular times (December 1997) and treatments (control and roof) in which the combined cover of red algal turf, *Gymnogongrus*, and ephemeral algae was lowest. Low competitive ability and slow growth may have retarded the recovery of *Lithothamnium*. Only three years after El Niño did its recovery begin.

Red algal turf declined from initially moderately high (Site 1) or very high levels of cover (Site 2) down to very low levels, but the intensity of grazing had little effect on its cover most of the time, in keeping with Hay's (1981) views than the colonial aggregations formed by turfs reduce herbivory. There were significant interactions between site and treatment. Grazing effects were undetectable at Site 1 where the cover of red algal turf was low. At Site 2, red algal turf was abundant, and increased in treatments with moderate to high intensities of grazing, perhaps benefiting from reductions of palatable, competitively superior species. Lewis (1986) reported a reduction of turf and crustose species in experimental plots that totally excluded grazers, and argued that turfs and crusts are adapted to intense grazing as they dominate areas that are heavily grazed.

Articulated corallines were virtually absent from Site 1. At Site 2, they were more common, and increased within roofed treatments (H, R) at all times. There are three possible explanations for this. One is that grapsid crabs (which would have entered these treatments) selectively removed competitively superior species such as *Ulva*. Second, articulated corallines may have been outcompeted in the total exclusion cages. Finally, intense grazing in the control may have diminished articulated corallines. The net effect was that these algae were most abundant at intermediate levels of grazing. Being heavily calcified, corallines represent a poor source of energy for grazers (Paine and Vadas 1969, Duffy and Hay 1990). Relative to their abundance, upright coralline algae were not an important part of the diet of *G. grapsus* or marine iguanas (Wikelski et al. 1993; L. Vinueza, unpublished data).

Effect of grazers on algal diversity

Grazers can potentially increase or decrease diversity. Some herbivores reduce the landscape to few grazer-resistant competitively inferior encrusting species. Examples include sea urchins (Paine and Vadas 1969, Vance 1979), parrotfish (Lewis 1986, Hixon and Bros-

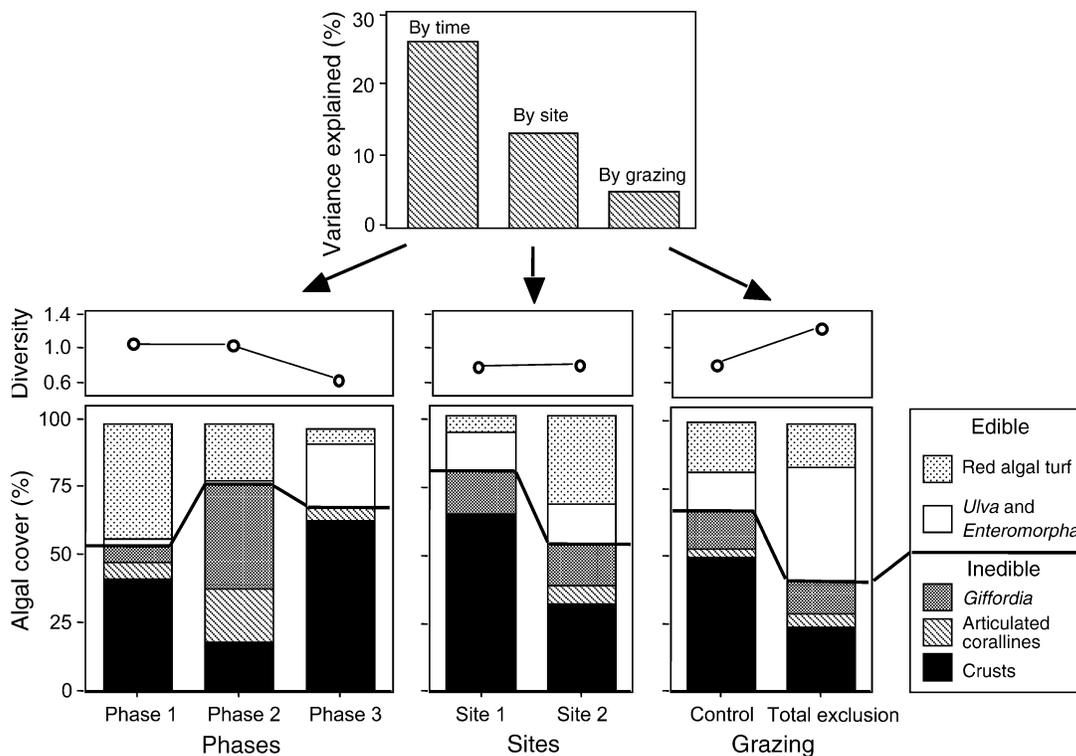


FIG. 12. Synthesis of the relative importance of temporal changes, differences between sites, and the effects of grazers in explaining variance in algal abundance. Changes in Shannon diversity (H') and the abundance of algae among phases are averaged across sites and are based on the percent cover reported for control plots. Differences between the sites are averaged across times and are also based on the percent cover of control plots. Effects of grazers are based on averages across both times and sites, and they compare control plots with total exclusion plots.

toff 1996), and the diverse guild of consumers present in Panama (Menge and Lubchenco 1981, Lubchenco et al. 1984).

We recorded differences in diversity between sites over time and among treatments (Fig. 8). First, Site 1 had lower species richness than Site 2. Second, substantial temporal fluctuations in diversity indices occurred in all treatments. Initially, diversity was intermediate (phase 1, week 0). During phase 2 (weeks 16–20), when temperatures were high and nutrient levels low, diversity increased due to the emergence of ephemerals such as *Giffordia mitchelliae* and *Chaetomorpha antennina*. In phase 3 (week 52 onward), decreases of several species and increased dominance by *Enteromorpha/Ulva* and/or *Gymnogongrus* were accompanied by colder temperatures and high levels of nutrients (Chavez et al. 1999). Thus, diversity declined when grazing probably became more intense, with crab densities rising sharply and the condition of iguanas improving.

Regional fluctuations of temperature and nutrients levels influenced diversity by addition or loss of ephemeral species. Superimposed on this, grazing treatment had a significant but relatively small effect, the clearest manifestation of which was to promote dominance by crustose *Gymnogongrus*, with associated

reduction in diversity, particularly post-El Niño, when algae were abundant and growth rates high.

Conclusions and broader implications

Our study provides new insight into the regulation of tropical intertidal communities, differing in several respects from previous descriptions (Gaines and Lubchenco 1982, Menge et al. 1985, Brosnan 1992). The near absence of sedentary grazers, significant differences between sites, and interannual variation related to the large-scale disturbances of El Niño show that factors additional to grazing have important effects in structuring Galápagos intertidal communities. Temporal and intersite differences were substantially greater than grazing effects, at least over the period of our study, reflecting the influences of large-scale oceanographic events (El Niño) and smaller-scale spatial effects on community structure. This echoes the conclusions of Sauer Machado et al. (1996) about tropical Brazilian shores, that although consumers do influence community structure, their effects are limited and variable. Fig. 12 summarizes the relative degrees to which variances in the data were explained by the main effects of time (27%), site (13%) and grazing (5%). There were, however, important interactions between time and treatment, with herbivores having less effect during

El Niño than after it. The bottom-up influence of El Niño and the top-down effects of herbivores thus changed in relative importance over time.

In short, the results emphasize the profound transformation that global climate change may bring to marine ecosystems, including shifts in composition, interactions, and productivity (Fields et al. 1993). The biota of Galápagos, having high endemism and being isolated and positioned at the juncture of contrasting oceanographic currents, is delicately poised and prone to extinction in the face of global changes. If El Niño conditions intensify or become more frequent, we can anticipate greater environmental stochasticity, higher temperatures, lower nutrient levels, reduced productivity and biomass, reductions in the densities of consumers, extinctions of cooler-water species, and probably long-term reductions in diversity.

These effects will have economic as well as ecological consequences, because many of the top consumers will be affected most, including fish that are harvested, and birds, iguanas, and sea lions that are charismatic attractions for the lucrative ecotourism trade.

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APPENDIX A

Map of the study sites (*Ecological Archives* M076-005-A1).

APPENDIX B

Figure showing the comparison of mean monthly sea surface temperatures in the Galápagos (*Ecological Archives* M076-005-A2).

APPENDIX C

Table showing mean abundances of fish/m² at the two study sites (*Ecological Archives* M076-005-A3).

APPENDIX D

Table showing relative abundance of slow moving invertebrates (no. individuals/m²) at the two study sites (*Ecological Archives* M076-005-A4).

APPENDIX E

Table showing the results of a repeated-measures ANOVA on the effect of treatment and site on the abundance of functional groups of algae (*Ecological Archives* M076-005-A5).

APPENDIX F

Table showing the results of an ANOVA on the effect of treatment, site, and time on algal frond lengths (mm) (*Ecological Archives* M076-005-A6).

APPENDIX G

Table showing the results of a repeated-measures ANOVA to test the effect of treatment and site on species richness, diversity, and evenness (*Ecological Archives* M076-005-A7).

APPENDIX H

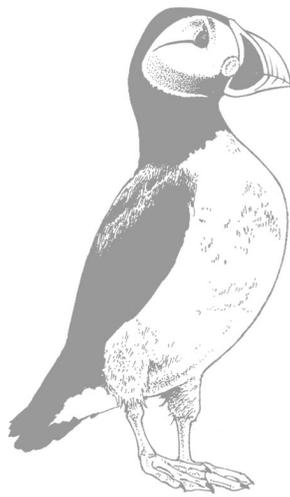
Figure showing temporal changes in species richness (Margalef's index d), evenness (Pielou's evenness index J'), and diversity (Shannon-Wiener diversity index H') (*Ecological Archives* M076-005-A8).

APPENDIX I

Dendrograms of Site 1 and Site 2 (*Ecological Archives* M076-005-A9).

APPENDIX J

Nonmetrical multidimensional scaling (nMDS) for Site 1 and Site 2 (*Ecological Archives* M076-005-A10).



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