Oceanographic and climatic variation drive top-down/bottom-up coupling in the Galápagos intertidal meta-ecosystem

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Oceanographic and climatic variation drive top-down/bottom-up coupling in the Galápagos intertidal meta-ecosystem

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Abstract. The impact of herbivores on primary producers in differing oceanographic regimes is a matter of intense ecological interest due to ongoing changes in their abundance, that of their predators, and anthropomorphic alteration of nutrient cycles and climatic patterns. Interactions between productivity and herbivory in marine habitats have been studied on temperate rocky shores, coral reefs, mangroves, and salt marshes, but less so at tropical latitudes. To determine how herbivore–alga dynamics varied with oceanographic regime, we used the comparative-experimental approach in rocky intertidal communities on the Galápagos Islands from January 2006 to January 2009. This setting was selected because strongly contrasting oceanographic conditions occurred within a range of ~181 km, with significant differences in temperature, nutrients, phytoplankton productivity, and intertidal communities, and in abundance of macro-herbivores, including marine iguanas. Experiments and measurements were conducted at two sites in each of three oceanographic regimes characterized by low, intermediate, and high bottom-up inputs. At sites of low inputs, macro-herbivores (fish, crabs, iguanas) had a consistent top-down effect, reducing algal abundance, and leaving a few grazer-resistant varieties. At sites of intermediate and high inputs, consumer impacts were stronger during La Niña (cool phase) than during El Niño (warm phase). At sites of high inputs, algal biomass was naturally relatively high and was dominated by the edible algae *Ulva* spp. Macro-grazers reduced algal biomass, but their primary effect was indirect, as articulated corallines displaced other species of algae in their absence. Prior results from the tropics had revealed dominant effects of top-down interactions and recruitment in structuring intertidal communities. Our results suggest that, when a broader oceanographic scenario is taken into account, the relative importance of top-down and bottom-up forces are context dependent, varying with oceanographic regime and climatic variability.

Key words: algae; bottom-up; climate; ENSO; Galápagos; herbivory; marine iguanas; oceanographic conditions; productivity; rocky shores; top-down; tropics.

Introduction

Changes in the strength of bottom-up (delivery of nutrients, particulates, and propagules) and top-down effects (impact of consumers) due to both natural climatic variation and human activities can have dramatic effects on the Earth's ecosystems. Consumer effects can be altered due to hunting, overfishing, and the introduction of exotic species (Jackson et al. 2001, Duffy 2003, Worm et al. 2006). The influence of bottom-up factors can be altered due to the modification of nutrient cycles by humans (Valiela et al. 1997, Vitousek

et al. 1997), large-scale environmental perturbations such as El Niño-Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO; Barber and Chavez 1983, Chavez et al. 1999), and human-induced climate change (Post and Pedersen 2008). Synergies between these factors can also be significant. For example, overfishing can be exacerbated by eutrophication, human-induced climate change, and large-scale perturbations such as ENSO, reducing the resilience of ecological systems and the ecological services they provide to humans (Smith et al. 1999, Worm et al. 2006, Worm and Lotze 2006, Diaz and Rosenberg 2008, Post et al. 2009). Therefore, it is important to understand the relative strength of top-down and bottom-up factors and how these vary with different environmental conditions.

In marine environments, bottom-up factors can be tightly coupled with top-down dynamics (e.g., Menge et al. 1997, 2003, 2004, Navarrete et al. 2005, Menge and Menge 2013). For herbivore–algal interactions, this seems partly explained by the shorter generation times and lower structural complexity usually associated with algae of higher nutritional value for marine grazers (i.e., with lower carbon to nitrogen ratios [C:N]). Examples include marine primary producers such as phytoplankton and ephemeral algae (e.g., *Ulva* spp., or red algal turf; Carpenter 1986). As a consequence, marine herbivores can remove three to four times more vegetation than their terrestrial counterparts (Cyr and Pace 1993, Shurin et al. 2006). For example, Poore et al. (2012) reported a 68% decline in primary producer abundance on marine systems due to grazers with 20% of those observations experiencing reductions >90%. In this context, the extirpations or population explosions of herbivores in the marine environment can cause dramatic changes in ecosystem structure and function. For example, declines of herbivorous fish and sea urchins led to phase shifts from coral- to algal-dominated communities in many parts of the Caribbean (Hughes 1994). Further, removal of sea urchin predators led to dramatic indirect changes such as the destruction of kelp forests due to urchin overgrazing (Estes and Palmisano 1974), or the transformation of salt marshes into mudflats by periwinkles due to the elimination of their predatory crabs (Silliman and Bertness 2002).

A 2006 meta-analysis of the role of herbivores in marine systems suggested that the impact of grazers on the abundance and type of primary producers could vary with latitude (Burkepile and Hay 2006). At higher latitudes, herbivores had strong top-down effects on the diversity of algae at sites of low productivity, but had little to no effect on species composition at sites of higher productivity (Burkepile and Hay 2006). At lower latitudes, in contrast, herbivores generally reduced algal biomass. Burkepile and Hay (2006) and other studies in the tropics (Diaz-Pulido and McCook 2003, Boyer et al. 2004) also demonstrated that herbivores could compensate for increased nutrient levels, facilitating grazing-resistant species of algae such as encrusting corallines and reducing total algal biomass, suggesting that top-down effects dominated over bottom-up effects. This analysis was consistent with the view that consumers have strong and consistent top-down effects on tropical marine ecosystems (Menge and Lubchenco 1981, Burkepile and Hay 2008). That is, tropical locations typically harbor a more diverse assemblage of herbivores, including slow-moving (chitons, limpets) and fast-moving consumers (e.g., fish, crabs, sea turtles, marine iguanas; Menge and Lubchenco 1981, Gaines and Lubchenco 1982, Vinueza et al. 2006). By this view, the diversity of tropical consumers, and especially the presence of fast-moving consumers, may enhance the efficiency of tropical grazers at consuming algae compared to their temperate counterparts (mostly slow,

mobile invertebrates such as limpets, chitons, sea urchins, and crustaceans). For example, community structure can differ strikingly between temperate and tropical rocky shores (Menge and Lubchenco 1981, Gaines and Lubchenco 1982, Vinueza et al. 2006). On most temperate rocky shores around the world, macrophytes form dense stands in the low intertidal zone (Witman and Dayton 2001). While grazers can be important in some temperate locations and with some types of algae, from this earlier research, they appeared to be inefficient at reducing algal biomass in low intertidal algal-dominated zones (Gaines and Lubchenco 1982, Schiel 2004).

This perspective of latitudinal variation in grazing was challenged by the more recent meta-analysis of Poore et al. (2012), who among other things, concluded that the evidence for latitudinal variation in grazing pressure was weak. In fact, their data suggest that the average impact of grazing in tropical intertidal habitats was weaker than in more poleward regions, the opposite pattern to that summarized in the previous paragraph.

The present study was motivated by three issues. First, increasingly, ecologists have focused on understanding the linkages between local-scale ecological dynamics of communities and large-scale environmental variation, including climate change. This focus has led to a new concept, the meta-ecosystem, defined as a set of local-scale ecosystems connected by the flow of materials, propagules, and energy (Loreau et al. 2003). In contrast to much previous research on species interactions, often done at single or few sites, and without documentation of relevant environmental variation, meta-ecosystem studies advance our ability to understand and explain the causes of variation in species interactions. Second, our knowledge base in herbivore–plant interactions is strongly skewed. Apart from coral reefs and mangroves, most investigations of herbivore–macrophyte interactions have been conducted in temperate regions (Burkepile and Hay 2006, Poore et al. 2012). Third, contradictory conclusions have been reached regarding the strength of grazing in tropical vs. temperate regions. As suggested by the Burkepile and Hay (2006) review, some have concluded that grazing is stronger in the tropics. In contrast, Poore et al. (2012) and Vinueza et al. (2006) suggested that herbivory was relatively weak in the tropics. However, for tropical intertidal habitats at least, these contradictory results are based on few empirical studies. Collectively, these issues stress the need for additional intertidal studies using consistent methodology specifically with respect to the factors underlying variability in grazing pressure caused by different environmental conditions (e.g., temperature, nutrient levels).

A model tropical ecosystem

The Galápagos Islands constitute an ideal model system to understand the role of a diverse assemblage of herbivores and the modulation of herbivory by con-

trasting oceanographic regimes in a tropical meta-ecosystem. Different sectors of the archipelago experience dramatic variation in environmental conditions occurring on seasonal, annual, and interannual temporal scales across spatial scales of meters to hundreds of kilometers. These differences are driven by local topography, winds, upwelling, and ocean circulation patterns that originate from different directions: the northeast (North Equatorial Counter Current), southeast (South Equatorial and Humboldt Currents), and west (Equatorial Undercurrent; Chavez et al. 1999, Banks 2002, Palacios 2004, Witman et al. 2010). Prior studies suggest that these differences in environmental conditions around the archipelago affect the abundance, size structure, composition, structure, and function of marine and terrestrial communities (Wikelski and Trillmich 1997, Edgar et al. 2004, Ruttenberg et al. 2005, Palacios et al. 2006, Witman et al. 2010). This scenario, with similar intertidal ecosystems occurring on islands spanning a wide range of oceanographic conditions, and varying in rates of input of ecological subsidies such as nutrients and phytoplankton from adjacent pelagic systems, fits the definition of a meta-ecosystem (Loreau et al. 2003).

In addition to these spatially contrasting climatic influences, the Galápagos Archipelago is located in a region strongly affected by El Niño-Southern Oscillation (ENSO), a large-scale oceanic–atmospheric perturbation (Barber and Chavez 1983, Chavez et al. 1999). During the warm ENSO phase (El Niño), trade winds weaken, altering upwelling patterns, and reducing or shutting down the nutrient pulses that drive primary production and sustain these unique ecosystems (Barber and Chavez 1983). The impact of reduced food availability cascades up to higher trophic levels, causing elevated mortality of marine iguanas and sea lions, breeding failure for sea birds, and other negative impacts on marine biota (Robinson 1985, Glynn 1988, Laurie 1989, Palacios et al. 2010). In the terrestrial realm, in contrast, species may benefit from increased rainfall (and thus, higher productivity) during El Niño (Grant et al. 2000, Holmgren et al. 2001). In both terrestrial and marine environments during the warm ENSO phase, however, invasive species usually increase diversity (Ruttenberg 2000, Castilla et al. 2005, Vinueza et al. 2006), while disease outbreaks become more likely (Robinson 1985, Harvell et al. 1999). During the cold ENSO phase (La Niña), impacts shift in the opposite direction. Strong trade winds lead to more productive waters and alleviation of food shortage thereby fostering the recovery of marine species, while in contrast, drought and low productivity prevail in the terrestrial realm (Glynn 1988, Holmgren et al. 2001, Grant and Grant 2002). Similar contrasting terrestrial vs. marine responses to ENSO cycles have also been observed elsewhere (e.g., Gulf of California; Polis et al. 1997).

Most of these insights on the influence of ENSO fluctuations come from detailed studies in terrestrial and open oceanic habitats. Apart from subtidal marine systems (coral reefs, Glynn 1988; rock walls, Witman and Smith 2003, Witman et al. 2010), and population studies of marine iguanas (Wikelski and Thom 2000, Wikelski and Carbone 2004) and sea birds (Valle and Coulter 1987), the responses of interface ecosystems such as the Galápagos rocky intertidal, and even tropical rocky shores in general remain poorly known. Therefore, understanding how primary producers in tropical coastal systems will respond to species extirpations and environmental perturbations such as those triggered by El Niño is of great interest, both fundamentally and for management and conservation.

The rocky intertidal region of the Galápagos Archipelago

Rocky shores are a conspicuous element of the marine realm in the Galápagos Islands (~1800 km of coastline; Snell et al. 1996) and harbor a diverse array of consumers, many of them endemic to the archipelago. These include the only sea-going lizard in the world, the herbivorous Galápagos marine iguana (*Amblyrhyncus cristatus*; Darwin 1859, Wikelski and Trillmich 1994). Species in these intertidal communities are highly sensitive to climate change (Vinueza et al. 2006, Edgar et al. 2008), environmental perturbations (Valle and Coulter 1987, Glynn 1988, Vinueza et al. 2006), pollution (Wikelski et al. 2001), introduced predators (Kruuk and Snell 1981), diseases (Bataille et al. 2009), and overfishing (Bustamante et al. 2002). Despite this knowledge, and some basic insights into the ecological impact of this diverse group of consumers (Vinueza et al. 2006), we have limited understanding of the modulation of top-down effects by variation in bottom-up effects for Galápagos marine life (but see Vinueza et al. 2006, Witman et al. 2010).

To understand the impact of macro-herbivory and the relative influence of different types of grazers within this diverse group of consumers, we selectively excluded different groups of macro-herbivores to create a gradient in grazing pressure on benthic marine macrophytes ranging from exclusion to presence of all macro-herbivores (mostly marine iguanas, sea turtles, fish, and crabs). To assess how grazing varied with different oceanographic regimes, we worked on three islands, each of them located in a different biogeographic region within the archipelago and characterized by distinct oceanographic conditions (Spalding et al. 2007). Our experiments started in January 2006 and ended in January 2009. During this period, a mild El Niño event and three cool-water events occurred, including one period that was similar in magnitude to the strong La Niña event of 1999–2000. We evaluated the hypothesis that the impact of consumers on the percent cover, size structure, and biomass of different groups of algae will vary with background oceanographic conditions and palatability of algae.

Based on theoretical models, empirical studies at higher latitudes, and a previous study in the Galápagos

rocky-shore communities during the 1997–1998 El Niño (Vinueza et al. 2006), we predicted that: (1) higher ocean temperatures and lower inputs of ecological subsidies (primarily nutrients) would intensify the impact of herbivores, while (2) colder temperatures and higher inputs of ecological subsidies would reduce their impact. (3) In the absence of consumers, the abundance of edible algae would increase at sites of low inputs, but, (4) at sites of higher inputs, communities would be dominated by competitively superior species of algae regardless of palatability. (5) We further predicted that seasonal changes in temperature in this tropical location would affect the impact of consumers, and (6) that these fluctuations would be sensitive to ENSO cycles, with enhanced consumer effects in El Niño conditions (due to reduced macroalgal productivity) and weakened consumer effects in La Niña conditions (due to increased macroalgal productivity that outstrips the ability of consumers to keep pace with macrophyte growth).

METHODS

Study sites

To span the range of oceanic conditions affecting the Galápagos, we chose three islands located in each of the three oceanographic regimes that influence the Archipelago (Figs. 1 and 2). Sites on each island were selected on the basis of ease of access, having relatively gently sloping benches, and having communities that were representative of the general shoreline in the area. Hereafter, we use "island" when used collectively, and "site" to refer to the sites nested within each island. We use the terms "low," "mid," and "high" productivity when we make comparisons among islands.

Each oceanographic regime differed in several ways (e.g., nutrient level, phytoplankton abundance, and productivity, salinity, temperature). Based on our prior work (Vinueza et al. 2006) and studies of ENSO impacts on plankton-based food webs (e.g., Chavez et al. 1999), key drivers underlying bottom-up variation are most likely nutrients (supports macroalgal and growth and productivity) and phytoplankton productivity (supports growth of sessile filter-feeding invertebrates). Macroalgae are generally the dominant sessile group in this system, so nutrients are likely the primary subsidy underlying bottom-up variation. Nutrient availability also underlies growth and productivity of microalgae (e.g., phytoplankton), but the sessile invertebrates that depend on this subsidy are generally scarce in this system. For simplicity, hereafter, we refer to each oceanographic regime as having low, mid, and high productivity, recognizing that we are referring primarily to macroalgae.

Isla Genovesa (low productivity; hereafter "Genovesa") is a small island located in the northeast corner of the archipelago (Fig. 1). This island is bathed by the tropical North Equatorial Countercurrent (NECC), and is characterized by waters of lower salinity and nutrient levels (Palacios 2004). The flora and fauna of this island have tropical affinities (i.e., reef-building corals and fish species of Panamic and Indo-Pacific origin), and a low level of endemism (Edgar et al. 2004). Here, marine organisms tend to be smaller than their counterparts at sites of mid and high productivity, an archipelago-wide pattern that has been observed in trees, whelks, damselfishes, and marine iguanas (Wikelski and Trillmich 1997, Ruttenberg et al. 2005; L. R. Vinueza, *unpublished data*). The intertidal zone is dominated by encrusting algae and has a low biomass of edible algae. The two study sites (GE1 And GE2) were located at Salvaje de Corazón, on the southwest part of the island, and were ~146 m apart (site GE1 at 89°58′29.06″ W, 0°18′42.14″ N, and site GE2 at 89°58′28.82″ W, 0°18′43.65″ N; Fig. 1A, B).

Isla Santa Cruz (intermediate or "mid" productivity; hereafter, "Santa Cruz") is located in the central part of the archipelago. Santa Cruz Island is mostly influenced by the South Equatorial (SEC) and Humboldt Currents, and harbors mixed assemblages of species from Panamic and Peruvian provinces (Edgar et al. 2004). Here, rocky intertidal communities are dominated by *Ulva* spp. and encrusting algae. Marine iguanas, *A. cristatus*, as well as whelks, *Thais melones*, are intermediate in size between the iguanas and whelks at Genovesa and those at the third site, Fernandina. Our two study sites (TB1 and TB2) were located 222 m apart on the south-central part of Santa Cruz, at Tortuga Bay Beach (TB1 at 90°20′18.92″ W, 0°45′53.61″ S, and TB2 at 90°20′28.50″ W, 0°46′2.35″ S; Fig. 1A, C).

Isla Fernandina (high productivity; hereafter "Fernandina") is located in the western part of the archipelago. Fernandina is strongly influenced by the Equatorial Undercurrent (EUC) that upwells cold nutrient-rich and highly saline waters to the shore, fueling high primary productivity, and sustaining the most abundant populations of several species of charismatic and endangered fauna of the Galápagos Archipelago (Palacios 2004, Palacios et al. 2006). These include the Galápagos Penguin, *Spheniscus mendiculus*, the Flightless Cormorant, *Phalacrocorax harrisi*, the marine iguana, *A. cristatus*, and several species of macroalgae, including the kelp *Eisenia galapagensis*, among others (Edgar et al. 2008). This area is also the most important fishing ground for local fishermen. The low intertidal zone is dominated by *Ulva* spp. and species of filamentous red algae, with dispersed patches of *Sargassum*, *Dictyota*, and encrusting algae. The middle and high intertidal zone are dominated by barnacles (scarce at both Genovesa and Santa Cruz), mussels (absent at Genovesa and Santa Cruz), and encrusting algae. At Fernandina, *Ulva* spp. and filamentous red algae have higher nutritional value than algae at sites of lower productivity (Rubenstein and Wikelski 2003). Our two study sites (PE1 and PE2) were located 406 m apart at Punta Espinosa, on the northeast corner of Fernandina (PE1 at 91°26′58.8″ W, 0°15′50.40″ S, and PE2 at 91°27′28.98″ W 0°15′43.06″ S; Fig. 1A, D).
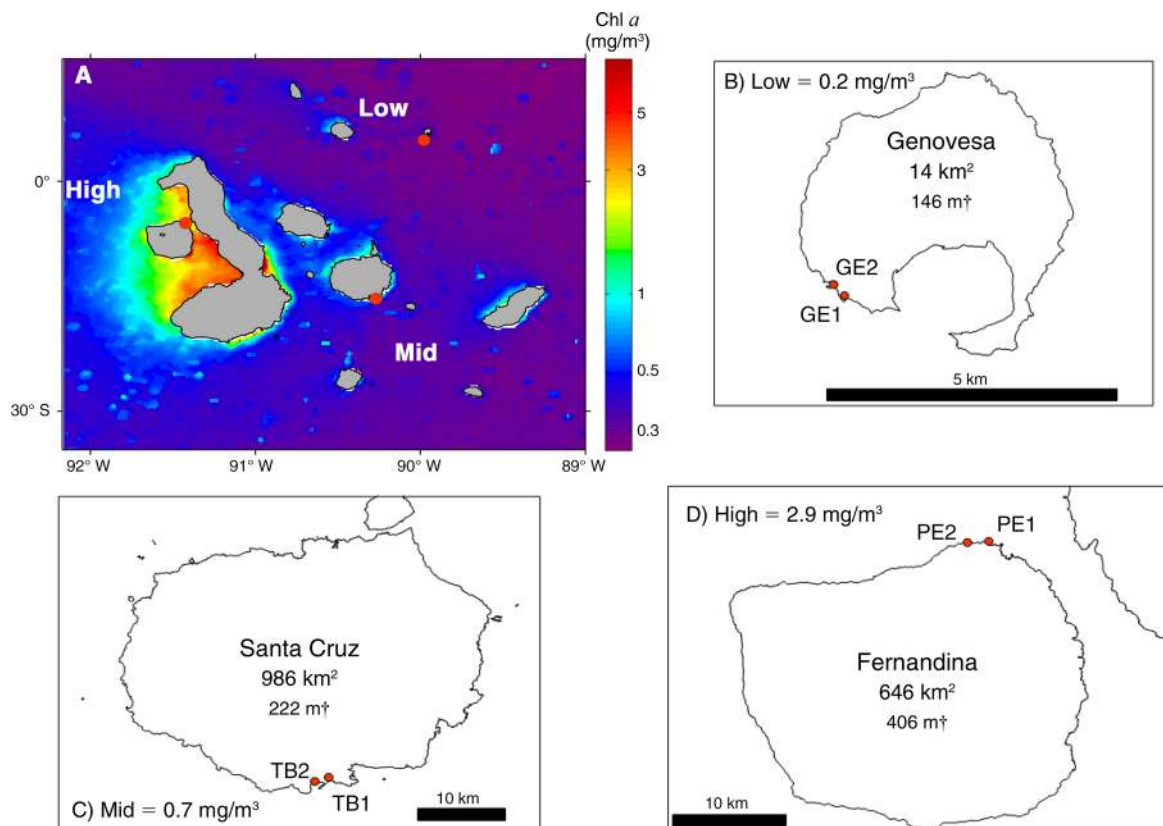
FIG. 1. (A) Map of the Galápagos Islands, Ecuador, showing average remotely sensed chlorophyll *a* (chl *a*) around the Galápagos Islands from sea-viewing wide field-of-view sensor (SeaWiFS) for the period from 4 September 1997 to 28 February 2009. (B–D) Close-ups of study site locations: GE1 and GE2 on Isla Genovesa, TB1 and TB2 at Tortuga bay Beach on Isla Santa Cruz, and PE1 and PE2 at Punta Espinosa on Isla Fernandina. Red dots indicate the locations of sites at each island, and the distance between sites on each island is indicated with a dagger (†).

Experimental design

We conducted manipulative experiments in the low intertidal zone (0 to +0.4 m above chart datum, with a total tidal amplitude of ~2 m). The low intertidal zone provides relatively benign environmental conditions for the growth of edible algae that are the primary food resources for "macro-grazers" (macro-herbivores) such as marine iguanas, sea turtles, fishes, and crabs (Menge and Lubchenco 1981, Vinueza et al. 2006). During spring low tides of <0.4 m, the low intertidal is usually exposed to land-based grazers such as marine iguanas and Sally Lightfoot crabs (*Grapsus grapsus*), while at high tide, it provides feeding grounds for a diverse group of fish, sea turtles, sea urchins, chitons, and other grazers of marine origin (Vinueza et al. 2006, Carrión-Cortez et al. 2010).

To test the effects of macro-grazers, we used cages made of stainless steel frames (30 × 30 × 10 cm) partially or totally enclosed with black vinyl-clad steel wire (OceanMesh; Hebei Ocean Wire Mesh, Hengshui, China) with mesh opening size of 2.5 cm. Three cage designs and an open control plot were established to create four herbivore treatments from no macro-

herbivores present (for brevity, referred to as "no grazing;" though we recognize that meso- and micro-grazers were present; see *Discussion*) to all macro-herbivores present ("high grazing"; Appendix A: Fig. A1). In addition to these treatments, prior experiments in this system (Vinueza et al. 2006) also included a partial cage (i.e., one with a roof) to control for the effect of shading by the mesh. We did not include this treatment in the present experiment because little to no difference was detected between cage controls and open control plots in the earlier study (Vinueza et al. 2006). The treatment −I−F−C (no iguanas, no fish no crabs; "no grazing") consisted of a cage covered on all sides by mesh that excluded all herbivores larger than 2.5 cm (primarily marine iguanas, fish, sea turtles, and crabs). Treatment −I−F+C ("low grazing") had a roof and a partial upper fence, allowing entry by Sally Lightfoot crabs, and on Genovesa, crabs and small marine iguanas (this was the only island on which small marine iguanas occurred as mature adults; i.e., <1 kg of body mass). Treatment −I+F−C ("intermediate grazing") had a complete fence but lacked a roof, allowing entry by fish, but excluding marine iguanas
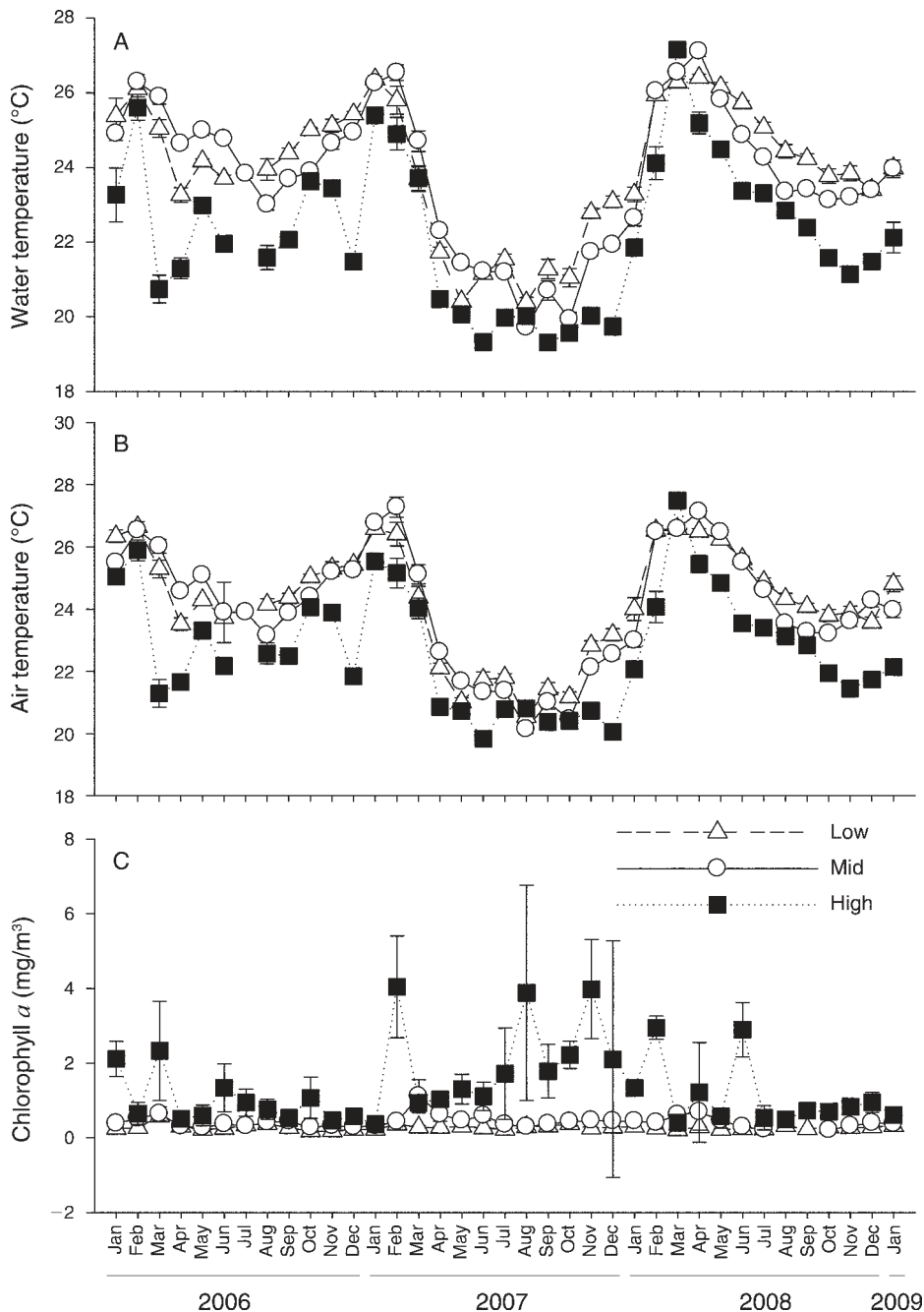
Fig. 2. Monthly (A) water and (B) air temperature measured in the low intertidal zone of the Galápagos rocky shores, averaged across two thermistors located at each site within each productivity level: low productivity at GE1 and GE2 on Genovesa Island, mid productivity at TB1 and TB2 on Santa Cruz Island, and high productivity at PE1 and PE2 on Fernandina Island. (C) Monthly average chlorophyll a derived from the satellite MODIS/Aqua with a radius of 15 km^2 around each position. Data are means ± SE.

and crabs. Treatment +I+F+C ("high grazing") was a plot marked at each corner by lag screws that allowed the access of all herbivores, including marine iguanas, sea turtles, fish, and crabs. Smaller organisms (<2.5 cm) such as isopods, copepods, limpets, newly recruited sea urchins, fish, and crabs had access to all these treatments. Repeated observations in the field at both

high and low tides were made to confirm that the exclusions performed as designed.

On each island, sites were close enough to experience similar physical conditions and biotic patterns, and far enough apart to be considered replicates. Although use of multiple islands within each oceanographic regime would have been ideal, resources available did not
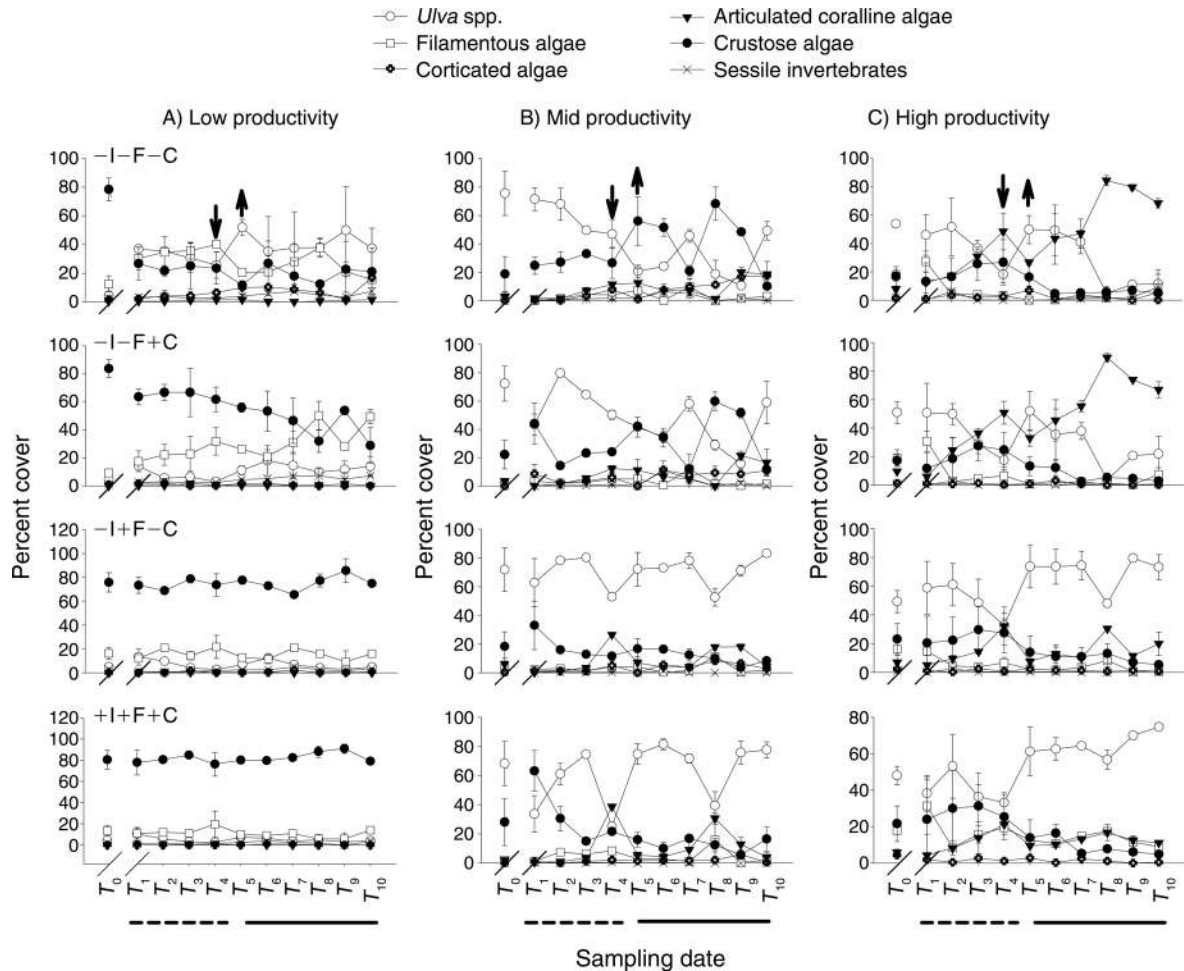
FIG. 3. Temporal patterns of space occupancy by sessile organisms from January 2006 (T_1) to January 2009 (T_{10}) as a function of background phytoplankton productivity level (columns [A] low, [B] mid, and [C] high productivity) and herbivory regime (four levels from −I−F−C [no I, iguana; no F, fish; no C, crabs; i.e., macro-herbivores] to −I−F+C [crabs only present, and small iguanas on Genovesa), to −I+F−C [fish only present] to +I+F+C [all herbivores included]). Symbols show mean percent cover ± SE ($n =$ 10) of six functional groups of sessile organisms. Values for January 2006 (T_0) show patterns before the onset of the experiment (see *Methods*). Dashed lines underline the warm phase; solid lines underline the cool phase. Downward-pointing arrow indicates the occurrence of an El Niño event, and the upward-pointing arrow indicates the onset of La Niña conditions. Between September 2008 (T_9) and January 2009 (T_{10}), six cages were lost, as follows: in low productivity, −I+F−C (1 replicate); in mid productivity, −I−F−C (2 replicates), −I−F+C (1); and in high productivity, −I−F−C (1), I−F+C (1), and −I+F−C (1).

permit use of more than one island per regime. At each site, experiments were arranged in a randomized block design with five blocks per site and four herbivore regimes per block. In January 2006, the percent cover of sessile organisms was recorded before the cages were fastened on the rock (Fig. 3). All biomass was then removed using a wire brush powered by a cordless drill until bare rock was exposed. Cages were bolted to the rock with stainless steel screws inserted into wall anchors in holes drilled in the rock. Thereafter, the percent cover of sessile species (i.e., algae, barnacles, and anemones) was monitored at intervals of three to four months, using both digital photography and point-intercept counts on a 100-point grid. At Genovesa (low productivity) and Fernandina (high productivity), cages were

cleaned of fouling organisms every 2–3 months. At one of the Santa Cruz (mid productivity) sites, *Ulva* spp. overgrew the cages several times. Due to its proximity to our field base (Charles Darwin Research Station), however, we were able to clean these cages at least once per month. Fernandina cages were sometimes lightly fouled with articulated corallines and small *Ulva* spp. fronds, but not enough to have a major impact on light or flow penetration. No algal overgrowth occurred at Genovesa sites. Sampling dates were assigned a code from T_0 to T_{10}: January 2006 was T_0; April 2006, T_1; August 2006, T_2; November 2006, T_3; February 2007, T_4; June 2007, T_5, September 2007, T_6, January 2008, T_7, May 2008, T_8, September 2008, T_9; and January 2009, T_{10}.

Response variables in the experiment included percent cover, species composition, algal frond length (all quantified during each visit), and algal biomass (final visit only). Percent cover of each algal species was classified into functional groups according to the classification scheme proposed by Steneck and Dethier (1994). Algal groups included crustose algae (*Gymnogongrus* spp., *Hildenbrandia* spp., and *Lithothamnium* spp.), green sheet-like algae (mainly *Ulva* spp.), filamentous algae (*Chaetomorpha antennina*, *Bryopsis* spp., *Cladophora* spp., *Ectocarpus* spp., *Polysiphonia* spp., *Ceramium* spp., *Centroceras* spp.), articulated corallines (*Jania* spp., *Corallina* spp., and *Amphiroa* spp.), and corticated algae (*Padina* spp., *Dictyota* spp., *Sargassum* spp., *Gelidium* spp., and *Kallymenia* spp.). The final group, sessile invertebrates, included sponges, barnacles, anemones, and ascidians.

We quantified algal frond length because (1) it provides an indirect measure of habitat complexity for meso-consumers, (2) different algal species have different stature, and therefore, potentially different light interception abilities, and (3) it also reflects algal biomass. Frond length was measured in each replicate and on each sampling date by averaging four randomly selected stands of each functional group of algae inside each replicate. In these measurements, we separated filamentous red and filamentous green algae. Biomass of sessile organisms was collected at the end of the experiment in January 2009 (T_{10}). Algae were sorted into functional groups and each sample was dried to constant mass for 48 h at 65°C, and dry mass was then measured.

Densities of iguanas, crabs, and sea turtles were quantified every three months with few exceptions following the same methodology described in Vinueza et al. 2006. Macro-grazers were counted with binoculars by scanning a specific area from 10 to 20 m within each study site. Five counts were performed every 10 minutes approximately for one hour. The average was then considered as the relative abundance for that particular sampling date. We were unable to quantify fish abundances at these sites due to the usually high wave action and logistical constraints. In general, fishes in the shallow subtidal included herbivorous, omnivorous, and carnivorous groups such as damselfish, parrotfish, and wrasses (L. Vinueza, *personal observations*).

Oceanographic measurements included temperature, chlorophyll *a* (a proxy for phytoplankton abundance), phytoplankton productivity, and wave force. Temperature was measured at 6-minute intervals at each site using HOBO Pro Water Temperature data loggers (±0.2°C accuracy; Onset Computer, Bourne, Massachusetts, USA). For each island, a position midway between the two sites was selected to obtain mean monthly values for chlorophyll *a* and phytoplankton productivity from January 2006 from NASA's MODIS/Aqua satellite. Chlorophyll *a* concentration values corresponded to the average value of all pixels within a radius of 15 km around each average position in the monthly images. Phytoplankton primary productivity was calculated from the MODIS data using chlorophyll *a*, temperature, and photosynthetically active radiation (PAR), and, due to a coarser spatial resolution of this product, values were extracted within a 30 km of radius around the average position for each site pair. The satellite that was sensing PAR stopped working in January 2008 and no data for primary productivity were available after that date. Maximum wave force was calculated using dynamometers (Bell and Denny 1994) attached to the cages by cable ties. Measurements were taken over a one-day period on each visit to each island, and thus, were not simultaneous among islands. Since wave action can vary on hourly to greater temporal scales, these estimates provide only a rough guide to the wave regime on each island.

Data analysis

All analyses were conducted using the SAS statistical analysis package (SAS Institute 2008). To test for differences in temperature (air and water), chlorophyll *a*, and phytoplankton productivity across oceanographic regimes we used a one-way analysis of variance (ANOVA), with post hoc linear contrasts to detect pairwise differences among regimes. Paired *t* tests were used to compare environmental conditions during the warm and cold phases of ENSO. In our analyses, sites were considered replicates ($n = 2$) because we were testing differences in productivity regime. Thus, data at the site level were averages of results in the $n = 5$ experimental units within each site.

Percent cover and frond length data were transformed (arcsine and log[$x + 1$], respectively) before analysis to normalize the data and homogenize variance. We used analysis of variance (ANOVA) to assess initial differences in percent cover of sessile organisms and frond length of algae with oceanographic regime and treatment as fixed explanatory factors. In analyses testing site effects, site was nested within island. We used nested repeated-measures analysis of variance (RM-ANOVA) to assess temporal trends in the interaction and strength of these factors on percent cover and algal frond length. The effect of macro-herbivory and oceanographic regime on percent cover and frond length averaged across April 2006 to January 2009 was analyzed using a two-way ANOVA.

Most interactions were significant, so we ran post hoc linear contrasts to test for the effect of macro-herbivore regime at each sampling period and island. To test differences in percent cover and frond length among climatic phases and macro-herbivore treatments, we used post hoc (Dunnett T3) multiple comparisons. To test for differences within macro-herbivore regimes between the El Niño (warm water) and La Niña (cold water) phases, we used paired *t* tests with Bonferroni corrections adjusted by the number of comparisons. Finally, we used a Kruskal-Wallis test to rank maximum

TABLE 1. Summary of average environmental parameters (mean ± SE) in each oceanographic regime.

Factor	Low productivity	Mid productivity	High productivity	F	P
Water temperature (°C)	24.0 ± 0.29	23.8 ± 0.32	22.7 ± 0.31	9.09	<0.0001
Air temperature (°C)	24.2 ± 0.29	24.1 ± 0.32	22.7 ± 0.31	7.39	0.001
Chlorophyll a (mg/m^3)	0.28 ± 0.01	0.42 ± 0.02	1.37 ± 0.17	55.94	<0.0001
Primary productivity (mg C·m^{-2}·d^{-1})	1297.4 ± 37.0	1675.3 ± 59.1	3305.0 ± 175.9	19.22	<0.0001

Note: The degrees of freedom in each case were 2, 109.

water speed, density of iguanas and crabs, and macro-herbivory treatments according to their dry biomass values in each oceanographic regime.

RESULTS

Oceanographic patterns during the experiment

Oceanographic patterns were as predicted and differed across all islands (Table 1, Fig. 2). Water and air temperatures were lowest at the high-productivity island and highest at the low-productivity island, while chlorophyll a and phytoplankton productivity showed the opposite pattern. In addition, wave action was higher at low-productivity sites followed by mid- and high-productivity sites (Kruskal-Wallis test; Appendix A: Fig. A2). Maximum water velocity ranged from 71.9 ± 5.2 m/s at GE1 (Genovesa site 1) to 42.8 ± 3.5 m/s at PE1 (Fernandina site 1).

Marine iguana density varied widely among islands and sites within islands. At low-productivity sites, densities were highest at GE1 (0.36 ± 0.002 individuals/m^2), while on GE2, densities were much lower (0.01 ± 0.001 individuals/m^2). At mid-productivity sites, densities were similar at both sites: 0.053 ± 0.029 individuals/m^2 at TB1, and 0.069 ± 0.017 individuals/m^2 at TB2. At high-productivity sites, densities were higher at PE1 (0.32 ± 0.003 individuals/m^2) than at PE2 (0.199 ± 0.004). Crab density was highest at the Genovesa (low productivity) sites (GE2 = 0.45 ± 0.281 individuals/m^2 and GE1 0.12 ± 0.081 individuals/m^2), but was substantially lower on Santa Cruz (mid) and Fernandina (high). At mid-productivity sites, crab density was 0.02 ± 0.003 individuals/m^2 at TB1, followed by TB2 at 0.0017 ± 0.004 individuals/m^2. Crabs were absent from high-productivity sites during our observations (PE1 and PE2).

Initial patterns of community structure

In January 2006 (T_0), before we started the experiment, abundance of all functional groups of sessile organisms did not vary among macro-herbivore treatments (data at T_0, Fig. 3; Appendix B: Table B1A). However, abundance of macroalgae differed among islands (data at T_0, Fig. 3; Appendix B: Table B1). Averaged across macro-herbivore treatments, at T_0, edible algae, including *Ulva* spp., filamentous red, and filamentous green algae, covered only 17.5% of primary substrate at the low-productivity island, but covered 74% and 68% of primary substrate at mid- and high-productivity islands, respectively (at T_0, Fig. 3). Crustose algae covered 79.6% ± 1.7% of primary substrate at low-productivity islands, but only 21.9% ± 4.2% and 19.7% ± 2.6% at mid- and high-productivity islands, respectively. Other functional groups were sparse. At maximum, corticated algae covered <3% of primary space, and articulated corallines covered 7.5%, both at the high-productivity island. Sessile invertebrates were most abundant at the low-productivity island (2.0% ± 0.4%).

At the onset of the experiment, initial frond length for all functional groups differed among islands ($P < 0.0001$; Fig. 4; Appendix B: Table B1B). Average frond length ranged from 0.01 cm for filamentous green algae at the low-productivity island to 1.72 cm for *Ulva* spp. at the mid-productivity island (Fig. 4).

Community response to herbivory and productivity

Overall response.—The abundance of most sessile organisms, averaged across the full time of the experiment was context dependent, varying with both macro-herbivore treatment (H) and productivity regime (P; Fig. 5, Appendix B: Table B2, see between subjects, P × H interactions). The only exception was sessile invertebrates, which were affected by both macro-herbivore and productivity regimes, but uniformly across both effects (Appendix B: Table B2A, see between subjects, P × H interaction, $P = 0.744$; H effect, $P = 0.005$; P effect, $P = 0.03$).

At the low-productivity island (Genovesa), macro-grazers had a major impact on relative abundances of sessile functional groups. Space occupancy shifted from dominance by crustose algae with high grazing (+I+F+C) to dominance by foliose algae, particularly *Ulva* spp. and filamentous algae, in treatments with no grazing (−I−F−C; Fig. 5A, B, E). These differences, and those for corticated algae, were not uniformly gradual, indicating that algal groups responded differentially to the composition of macro-herbivores within each treatment (Fig. 5). For example, abundance of *Ulva* spp. was greatest with no macro-grazers (−I−F−C), much less in low-grazing (crabs-only; −I−F+C) treatments, and even lower but similar at intermediate-grazing (fish-only; −I+F−C) and high-grazing (+I+F+C) treatments, suggesting that crabs (and small iguanas) alone (−I−F+C), fish alone (−I+F−C), and all herbivores (+I+F+C), had similar impacts on this alga (Fig. 5A). In contrast, all macro-herbivores (+I+F+C) and fish alone (−I+F−C) were sufficient to keep filamentous algae at similarly low abundance, while crabs (and small iguanas) alone (−I−F+C) had little effect on this group (Fig. 5B).
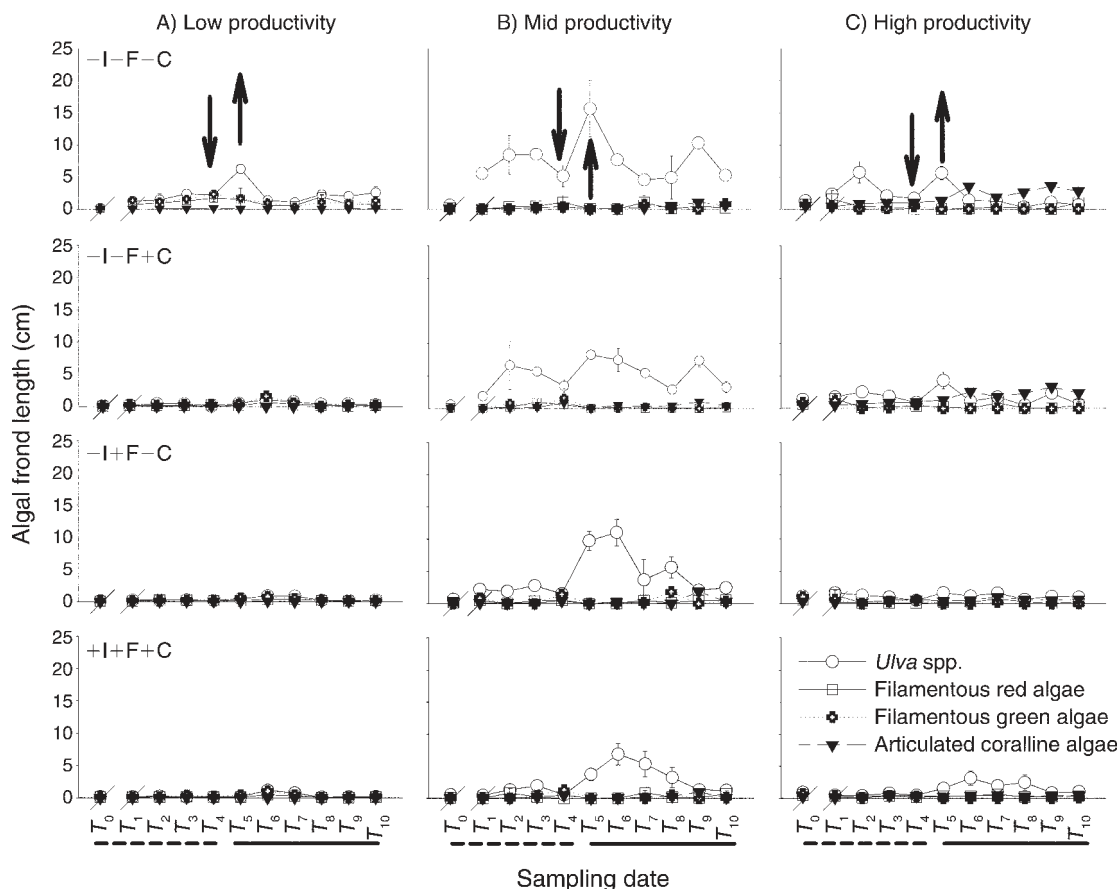
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FIG. 4. Temporal patterns of algal frond length from January 2006 (T_1) to January 2009 (T_{10}) as a function of background productivity (columns [A] low, [B] mid, and [C] high productivity) and herbivory regime (four levels from −I−F−C [no macro-herbivores] to +I+F+C [all herbivores included]). Symbols show mean ± SE frond length ($n = 10$) of four functional groups of algae. Dashed lines underline the warm phase; solid lines underline the cool phase. Downward-pointing arrow indicates the occurrence of an El Niño event, and the upward-pointing arrow indicates the onset of La Niña conditions. Values for T_0 show patterns before the onset of the experiment; see *Methods* and Fig. 3 legend for further details.

In strong contrast to the results from low-productivity sites, at the mid-productivity island (Santa Cruz), *Ulva* spp. was the dominant alga with high grazing (+I+F+C), with crustose algae occupying only ~20% cover (Fig. 5A). Reductions in macro-herbivory led to small declines in *Ulva* spp. cover, with increases in corticated and crustose algae occupying the space lost by the ulvoids with reduced macro-herbivory (Fig. 5C, E). Neither filamentous algae nor articulated coralline algae were affected by macro-grazers.

At the high-productivity island (Fernandina), *Ulva* spp. was also the dominant alga in high-grazing treatments (+I+F+C), with filamentous algae and articulated coralline algae each occupying ~10% of the space (Fig. 5A, B, D). Crustose algae and corticated algae were both relatively sparse. With no or low macro-herbivory (−I−F−C, −I−F+C), *Ulva* spp. abundance was lower and abundance of articulated corallines increased, becoming the dominant space occupier (Fig. 5A, D). Although both filamentous and corticated algae responded to macro-grazer manipulations, changes in

abundance were slight. Crustose algae did not respond to macro-grazing pressure variation at Fernandina, nor did sessile invertebrates, which were very sparse at all levels of grazing and productivity (Fig. 5F).

Temporal patterns

At the low-productivity island, with high macro-grazing (+I+F+C), abundance of crustose algae varied little through time (Fig. 3A). With reduced grazing, large changes in temporal pattern were observed, particularly in low- (−I−F+C) and no-grazer (−I−F−C) treatments. Ulvoids replaced crustose algae as the dominant almost immediately in no-grazer treatments. In low-grazing treatments, crustose algae slowly lost dominance until May 2008 (T_8), when filamentous algae was most abundant, which then shared dominance with crustose algae to the end of the experiment (Fig. 3A). As with high grazing (+I+F+C), dominance of crustose algae persisted in intermediate-grazing treatment (−I+F−C), suggesting that with low macroalgal produc-
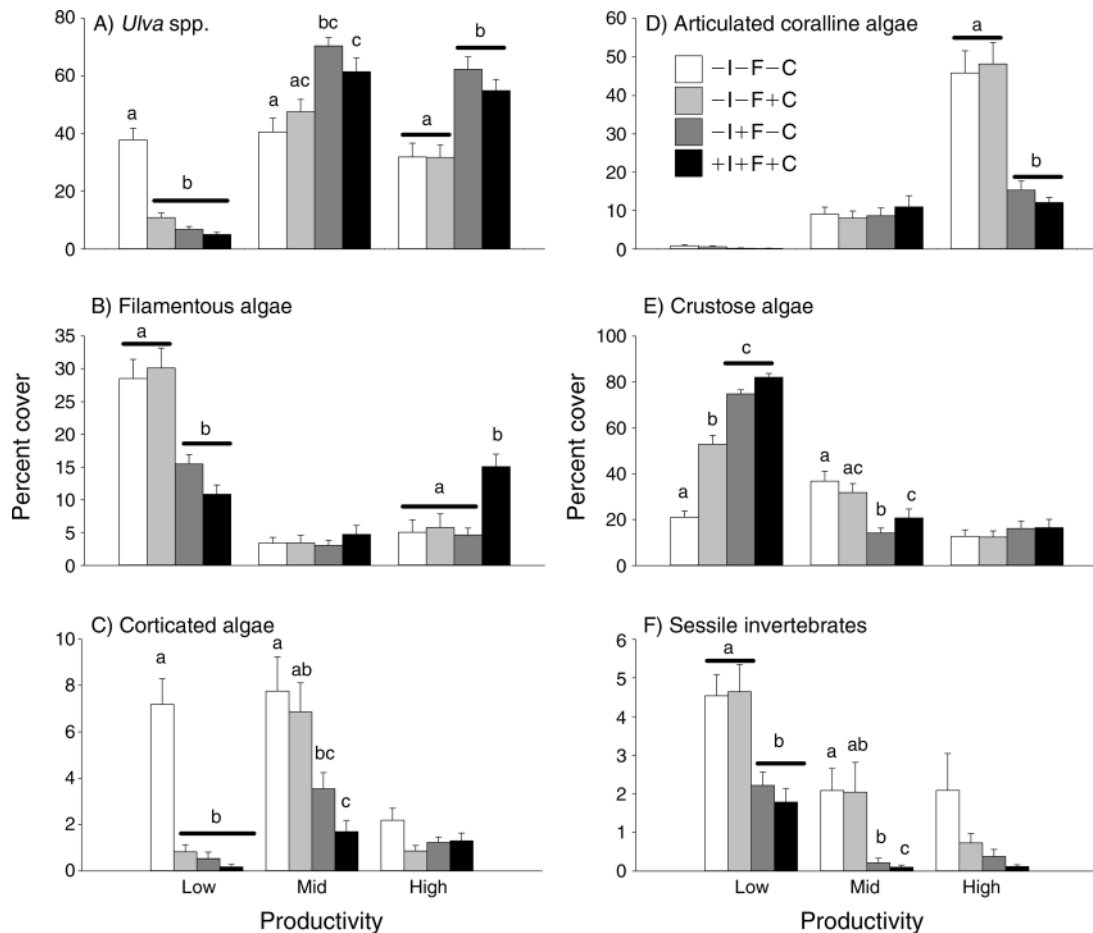
FIG. 5. Overall effects (from April 2006 [T_1] to January 2009 [T_{10}]) of background productivity and herbivory (four levels ranging from −I−F−C [no macro-herbivores;] to +I+F+C [all herbivores included]) on percent cover (mean ± SE) of sessile organisms: (A) Ulva spp., (B) filamentous algae, (C) corticated algae, (D) articulated coralline algae, (E) crustose algae, and (F) sessile invertebrates. Letters above bars indicate among-treatment differences within each location. Different letters indicate statistically different averages ($P < 0.05$), as determined by post hoc linear contrasts.

tivity, fish alone were sufficient to control foliose algae (Fig. 3A).

At the mid-productivity island, with high macro-grazing (+I+F+C), algal abundances fluctuated more widely, with major shifts occurring between ulvoids and crustose algae (Fig. 3B). Ulva spp. was dominant most of the time, however, with brief periods (T_4, T_8) where crustose algae were similar in abundance to Ulva spp. (Fig. 3B). With no- and low-grazing (−I−F−C and −I−F+C) treatments, the inverse fluctuations between crustose algae and Ulva spp. continued, but with periods of time where crustose algae was actually more abundant than Ulva spp. (e.g., Fig. 3B).

At the high-productivity island, with high macro-grazing (+I+F+C), abundance of several algal groups was relatively high during the first half of the experiment, but in the second half of the experiment Ulva spp. dominated, a pattern also seen in intermediate-grazing (−I+F−C) treatments (Fig. 3C). In contrast, in no- (−I−F−C) or low-grazing (−I−F+C) treatments,

articulated coralline algae became the dominant and had completely replaced Ulva spp. by the end of the experiment (Fig. 3C).

Response of algal size

Overall response.—Patterns of average frond length were also context dependent, varying among islands and with macro-grazing intensity (Fig. 6; Appendix B: Table B3). Frond length changes contrasted with those for percent cover, in which differing herbivory and productivity regimes led to both increases and decreases. With reduced grazing, algal length generally increased, while productivity regime effects varied with algal functional group. For example, for Ulva spp., reduced grazing led to increased frond length at all islands, but overall average response across grazing regimes varied unimodally with productivity regime, with greater lengths at the mid-productivity island (Fig. 6A). Filamentous red and green algae, in contrast, were longer with no grazers present
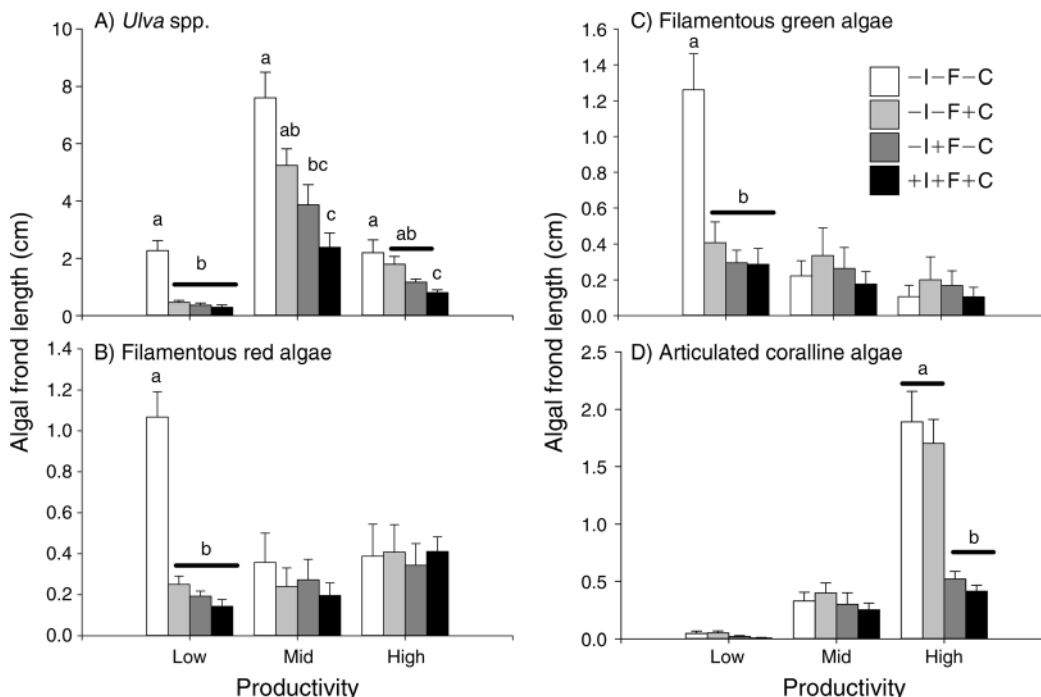
FIG. 6. Overall effects (from April 2006 [T_1] to January 2009 [T_{10}]) of background productivity and herbivory level (four levels) on algal frond length (mean ± SE) of (A) *Ulva* spp., (B) filamentous red algae, (C) filamentous green algae, and (D) articulated coralline algae. See Fig. 5 legend for further details.

(−I−F−C) only at the low-productivity island; otherwise, little difference in length occurred (Fig. 6B, C). Changes in articulated coralline length were as foreshadowed by results in change of cover. This group was almost absent at the low-productivity island, present and longer, but with no effect of macro-grazers at the mid-productivity island, and longest with high grazing at the high-productivity island (Fig. 6D). High- (+I+F+C) and intermediate-grazing (−I+F−C) treatments kept frond lengths less than half as long as with no- (−I−F−C) and low-grazing (−I−F+C; Fig. 6D) treatments.

Temporal change.—As suggested by Fig. 3, *Ulva* spp. frond length responded strongly to the manipulations through time, with articulated corallines responding next most strongly (Fig. 4; Appendix B: Table B3). At the low-productivity island, frond lengths changed little over time, except for a brief period (T_5) in no-grazing treatments (−I−F−C) when *Ulva* spp. was about three times longer than usual (Fig. 4A). At mid- and high-productivity islands, *Ulva* spp. was nearly always the longest alga, particularly with low or no grazing (Fig. 4B, C.). This height advantage varied greatly through time, especially at the mid-productivity island (Fig. 4B, C). After T_5 at the high-productivity island, articulated coralline frond length increased and persisted in no- (−I−F−C) or low-grazer (−I−F+C) treatments to the end of the experiment.

Patterns of space occupancy mediated by herbivory, productivity, and ENSO

During the first half of the experiment, a mild El Niño developed that lasted into February 2007 (T_4; Figs. 7A, B and 8C). Thereafter, conditions shifted to a rather strong La Niña (Figs. 7A, B and 8C). These contrasting conditions were reflected in both water temperature (Fig. 8A) and trends in sea surface chlorophyll *a* (Fig. 8B). Cooler waters typically characterize La Niña conditions, and during this time, water temperatures were also cooler (Fig. 8A). Chlorophyll *a* did not differ among islands or with ENSO phase, but tended to be higher during cool waters at the high-productivity island (Fig. 7D).

Percent cover and frond length patterns were often different between climatic phases (e.g., Figs. 3 and 4). Visually, the differences between the warm and cool phases of ENSO were often dramatic. For example, during the warm period at the mid-productivity island, ulvoids were almost absent (Appendix A: Fig. A3), while during the cool period, ulvoids turned the rocks green (Appendix A: Fig. A4).

To evaluate the effect of warm vs. cool water conditions (i.e., El Niño vs. La Niña) on community structure and its response to productivity regime and macro-herbivory, we reanalyzed our data including ENSO phase as a factor (Fig. 9; Appendix B: Table B4). As suggested by Fig. 3, ENSO phase interacted with macro-herbivory and productivity regime to
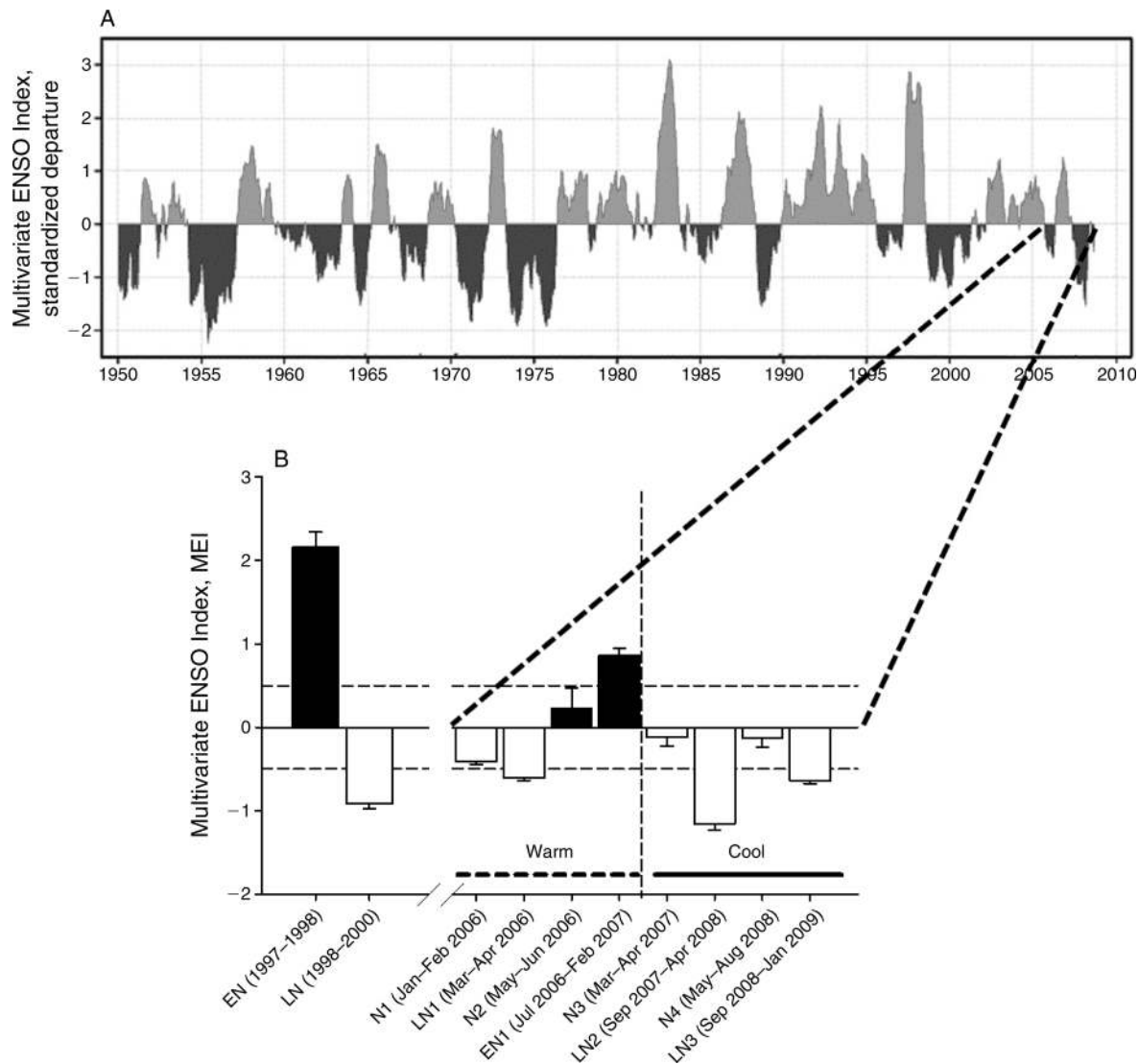
Fig. 7. (A) Long-term multivariate El Niño-Southern Oscillation (ENSO) index (MEI) time series from 1950 to 2010, showing warm (light gray) and cool (dark gray) conditions (Wolter and Timlin 1998). (B) MEI index during our study, 2006 to 2009, and during the strong El Niño (EN; left of the vertical dashed line) and La Niña (LN; right of the vertical dashed line) events in the late 1990s, comparing warm (MEI above +0.5, horizontal dashed line) and cool (MEI below −0.5, solid line) with normal (N) conditions.

influence patterns of abundance of most functional groups (Appendix B: Table B4A, see H × P × E interactions, $P = 0.005$ or less), except for corticated algae and sessile invertebrates ($P = 0.13$, $P = 0.72$, respectively). Variation in sessile invertebrates, however, was context dependent, varying with productivity regime and ENSO phase, and with ENSO phase and herbivore regime (Appendix B: Table B4A, see P × E interaction, $P = 0.001$, and E × H interaction, $P = 0.013$).

Low-productivity island.—At Genovesa during the ENSO warm phase, macro-herbivores reduced abundance of all groups except for articulated corallines, and crustose algae, which increased in abundance with increasing grazing pressure (Fig. 9A–F, top row).

During the cool phase, similar trends were seen with respect to herbivory regime (Fig. 9, top row). *Ulva* spp., filamentous algae, corticated algae, and sessile invertebrates tended to be more abundant in one or more treatments, likely as a result of relaxed grazing, higher growth rates for algae during the cool phase, or both. Decreases in crustose and filamentous algae in the no-grazing treatments were likely due to increases of other foliose algae and sessile invertebrates.

Mid-productivity island.—At Santa Cruz during the ENSO warm phase, differences among macro-herbivore regimes were modest, suggesting macro-herbivory was relatively weak during El Niño (Fig. 9A–F, middle row). During the cool phase, larger differences among macro-
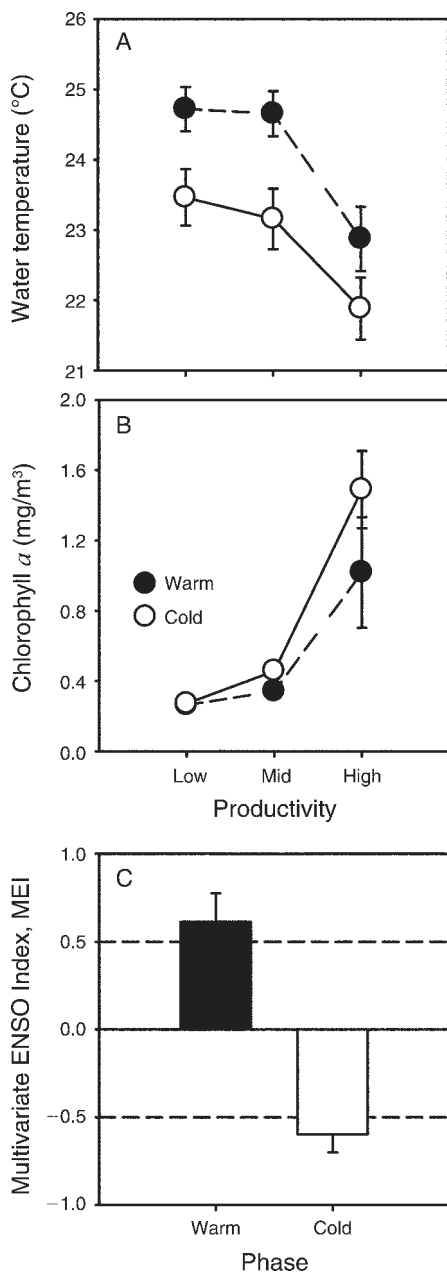
FIG. 8. (A) Average water temperature, (B) average chlorophyll a (mg/m^3), and (C) average multivariate El Niño index (MEI) during the warm (T_0 to T_4) and cold (T_5 to T_{10}) periods of the experiment.

algae, crustose algae, and sessile invertebrates, (Fig. 9C, E, F, middle).

High-productivity island.—At Fernandina during the warm phase, no differences among macro-grazing regimes were observed for any functional group (Fig. 9B, C, D, F, bottom row). During the cool phase, major changes relative to the warm phase occurred with *Ulva* spp., filamentous algae, and articulated corallines. During the cool phase, abundance of *Ulva* spp. was greater in intermediate- (−I+F−C) and high-grazing (+I+F+C) treatments (average cover = 67.7%) compared to the warm phase (45.2%; Fig. 9A, bottom). In no- and low-grazing treatments (−I−F−C and −I−F+C), the opposite pattern occurred: *Ulva* spp. was less abundant during the cool phase (28.2% vs. 37.4% during the warm phase; Fig. 9A, bottom), while articulated coralline algae was more abundant (Fig. 9D, bottom). Articulated coralline algae abundance with low grazing in the cool phase was more than twice that in the warm phase. Finally, compared to articulated corallines and *Ulva* spp., other groups were relatively sparse, and tended to be equal in abundance between phases or less abundant during the cool than during the warm phase (e.g., Fig. 9B, E, bottom).

Impact of ENSO phase on frond length

Frond length of *Ulva* spp., filamentous green algae- and articulated coralline algae also responded to changes in ENSO phase (Fig. 10; Appendix B: Table B4B, see two-way interactions for *Ulva* spp., P × E × H interactions for filamentous green and articulated coralline algae, $P = 0.022$ or less). During the warm phase, in all productivity regimes, frond length of *Ulva* spp. decreased with increasing macro-herbivory (Fig. 10A, left). Frond lengths were generally shorter at the low-productivity island, longer at the mid-productivity island, and intermediate at the high-productivity islands (Fig. 10A). During the cool phase, frond length in all productivity × macro-herbivore combinations tended to be greater than in comparable productivity × macro-herbivore combinations during the warm phase, and showed a similar pattern of variation among productivity regimes to that seen in the warm phase (Fig. 10A; Appendix B: Table B4B, see two-way interactions, $P = 0.005$ or less). These differences suggest that ulvoid growth was faster during the cool phase, or at least better able to survive both grazing and environmental stress effects.

Responses of frond length in the other groups were more variable. Patterns for filamentous red algae were similar in warm and cool phases, indicating that growth of this group was independent of ENSO conditions (Fig. 10B; Appendix B: Table B4B). Filamentous greens varied with all factors, doing somewhat better at the low-productivity island in the cool phase, but less well at mid- and high-productivity islands, with herbivory having effects only at the low-productivity island (Fig. 10C; Appendix B: Table B4B).
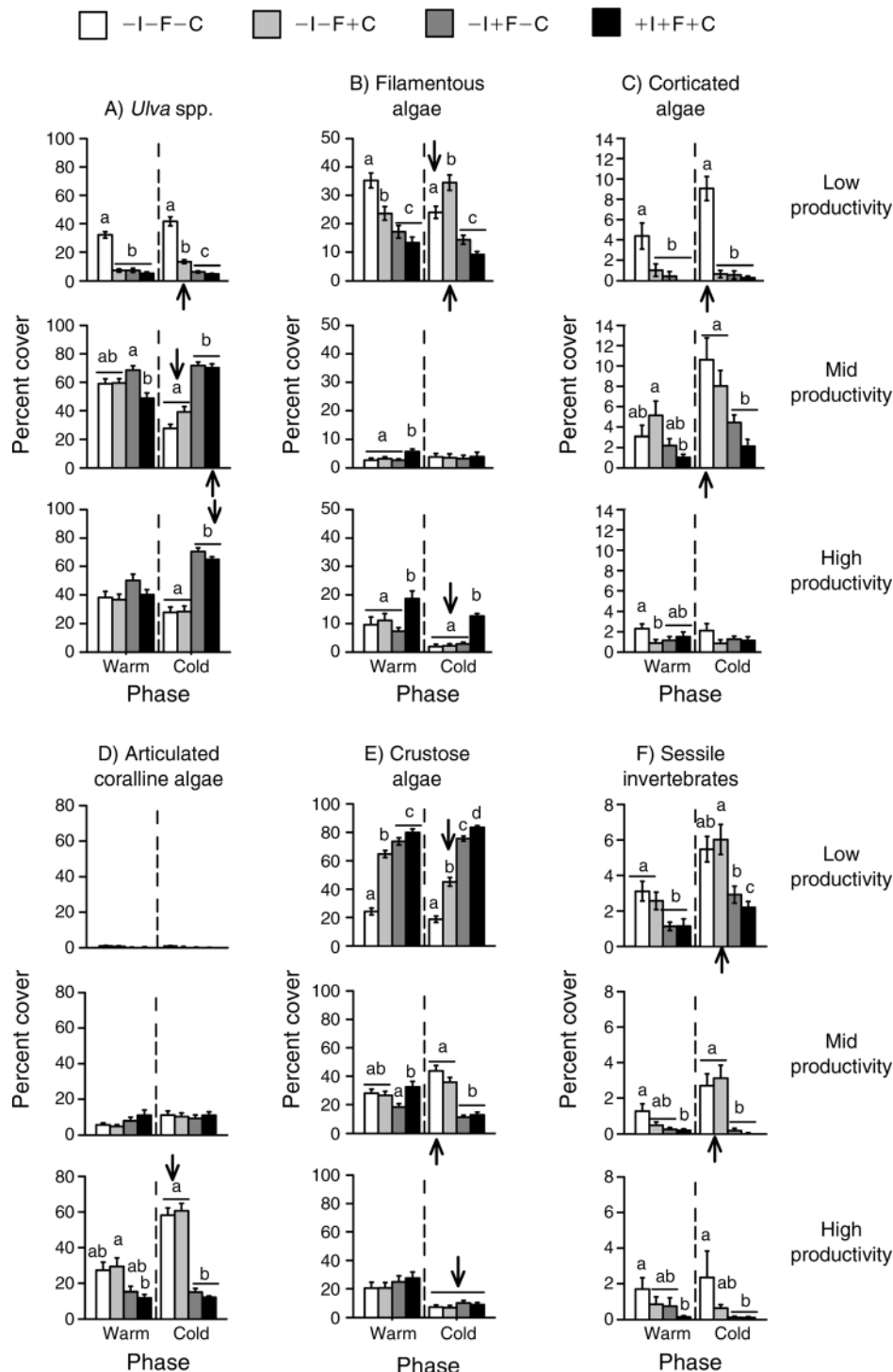
herbivore treatments were observed. *Ulva* spp. was notably more abundant in high-grazing (70.8%) and intermediate-grazing treatments (71.7%), but in contrast to the warm phase, was sparser in no- (−I−F−C) and low-grazing (−I−F+C) treatments. Average *Ulva* spp. abundance in these latter two treatments was 59.2% in the warm phase and 33.4% during the cool phase. Groups with greater cover at low herbivory in the cool phase relative to the warm phase included corticated

Fig. 9. Effects of productivity and herbivory on percent cover (mean ± SE) of functional groups of sessile organisms averaged over warm and cool phases of ENSO. Differences among herbivory levels within each phase were calculated using Dunnett's-T3 post hoc comparison. Bars with the same lower case letter above them correspond to herbivory regimes with no significant differences ($P > 0.05$) among them; short lines over some bars indicate that the lower case letter applies to pairs or trios of bars. Differences within the same herbivory regime at different phases were calculated using a paired t test with adjusted P values using the Bonferroni correction for multiple comparisons. Arrows represent significant changes ($P < 0.05$) in percent cover in the cool phase within the same herbivory regime with respect to the warm phase.
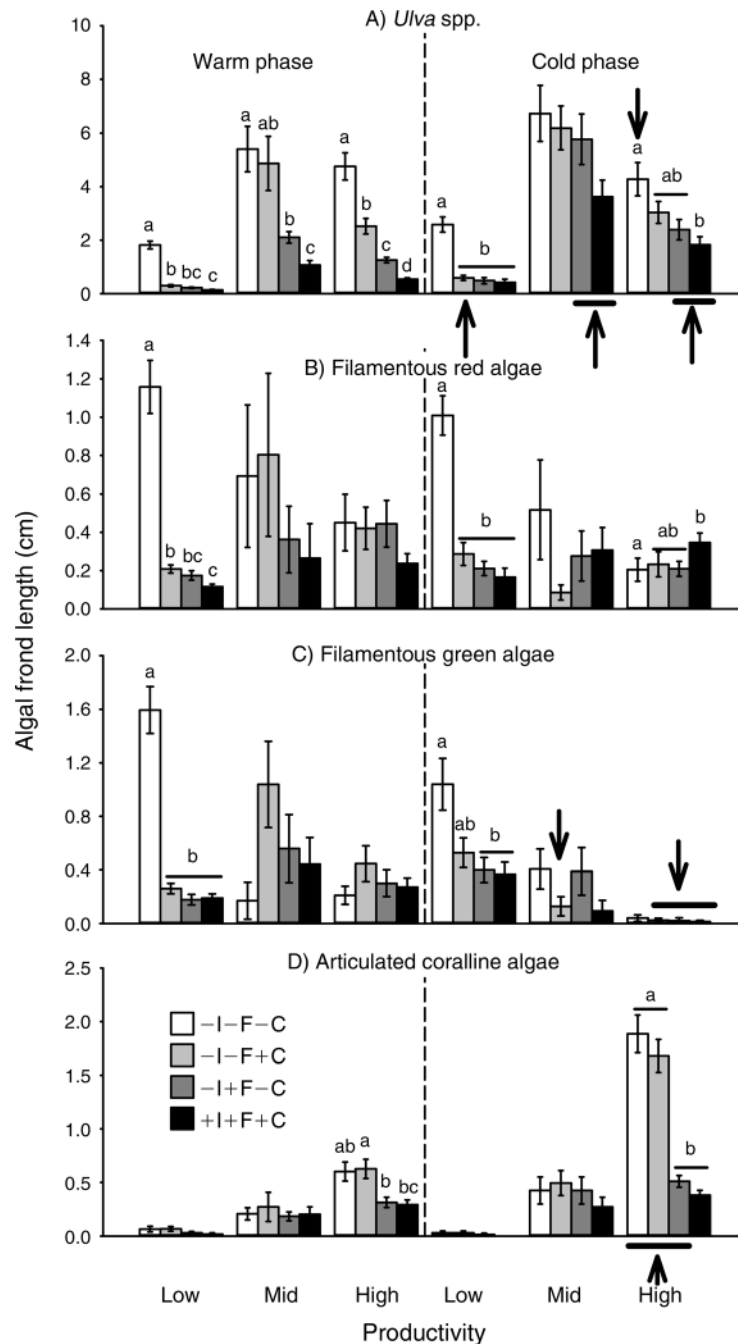
FIG. 10. Effects of productivity and herbivory regime on frond lengths (mean ± SE) of functional groups of algae averaged over warm and cool phases of ENSO. See Fig. 9 legend for further explanation.

The response of articulated coralline frond length was also context dependent. Macro-herbivory had no impact in either phase at low- and mid-productivity islands, but at the high-productivity island, frond length increased slightly with reduced grazing during the warm phase, an effect that was amplified during the cool phase (Fig. 10; Appendix B: Table B4B). In the cool phase, articulated coralline frond length in no- and low-grazing treatments

(−I−F−C and −I−F+C) was almost three times longer than during the warm phase (1.8 cm vs. 0.62 cm; Fig. 10D; Appendix B: Table B4B).

Biomass of primary producers

Total algal biomass was strikingly higher at the high-productivity island (Fig. 11F; Appendix B: Table B5). Comparing no-grazing (−I−F−C) treatments across
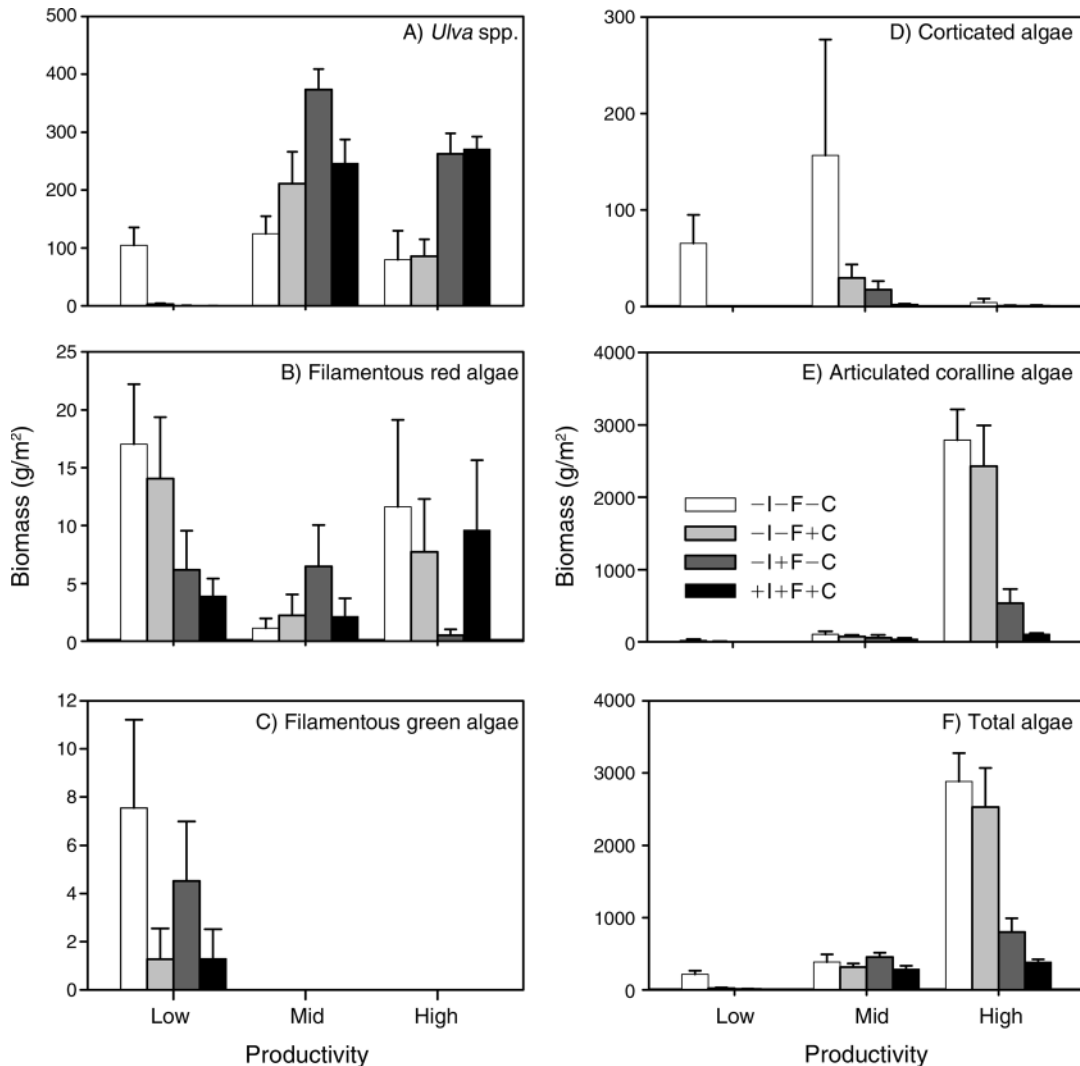
FIG. 11. Patterns of dry algal biomass (mean ± SE, $n = 10$) as a function of background productivity (low, mid, and high) and herbivory (four levels ranging from −I−F−C [no macro-herbivores;] to +I+F+C [all herbivores included]) intensity: (A) *Ulva* spp., (B) filamentous red algae, (C) filamentous green algae, (D) corticated algae, (E) articulated coralline algae, and (F) total algal biomass.

productivities, on average, treatments at the high-productivity island had accumulated 2.88 ± 0.39 kg/m² of dry algal biomass during the experiment vs. 0.39 ± 0.11and 0.21 ± 0.05 kg/m² of dry algal mass at mid- and low-productivity islands, respectively (Fig. 11F). A similar trend was seen in treatments with high grazing intensity (+I+F+C), which had 0.39 ± 0.03, 0.29 ± 0.05, and 0.01 ± 0.00 kg/m² of dry algal biomass at high-, mid-, and low-productivity islands, respectively (Fig. 11F). Algal biomass decreased gradually as herbivory intensity increased on low- ($\chi^2_3 = 18.8$, $P < 0.0001$) and high-productivity islands ($\chi^2_3 = 22.45$, $P < 0.0001$), whereas at the mid-productivity island, no differences were observed among macro-herbivory levels ($\chi^2_3 = 4.91$, $P = 0.1780$) (Fig. 11F; Appendix B: Table B5).

Ulva spp., and, particularly articulated corallines, were primary contributors to the disparity in algal dry mass among productivity and macro-herbivory levels (Fig. 11A, E; Appendix B: Table B5). Articulated corallines were minor components of biomass at the low-productivity island (9% and 18% of total biomass in no- and low-grazing treatments, none in stronger grazing treatments), contributed more at the mid-productivity island (27%, 23%, 12%, and 13% of total biomass in no-, low-, intermediate-, and high-grazing treatments, respectively). No differences in the rank of treatments with respect to median biomass of articulated corallines were observed on either low- or mid-productivity islands (Fig.11E; Appendix B: Table B5). In contrast, at the high-productivity island, articulated corallines represented 97%, 96%, 67%, and 27% of total

dry biomass in no-, low-, intermediate-, and high-grazing treatments, respectively, and differences among ranks were observed (Fig. 11F; Appendix B: Table B5).

For *Ulva* spp. at the low-productivity island, *Ulva* spp. represented 49%, 12%, 3%, and 1.2% of dry biomass in no-, low-, intermediate-, and high-grazing treatments, respectively, with differences among treatment rankings (Appendix B: Table B5). At the mid-productivity island, *Ulva* spp. biomass varied unimodally, representing 32%, 67%, 83%, and 68% of total biomass in no-, low-, intermediate-, and high-grazing treatments (Appendix B: Table B5). At the high-productivity island, *Ulva* spp. responded positively to high macro-herbivory intensity, representing 70%, 32%, 3.4%, and 2.8% of total biomass in high-, intermediate-, low-, and no-grazing treatments, respectively ($\chi^2_3 = 15.703$, $P < 0.0001$; Fig. 11A; Appendix B: Table B5). Other groups were either sparse and/or contributed minimally to biomass at most combinations of productivity and grazing regime (Fig. 11B, C, D; Appendix B: Table B5).

DISCUSSION

Our results suggest that top-down and bottom-up effects interact to shape primary producer communities on Galápagos Islands rocky-shore communities, and that the relative magnitudes of these effects are sensitive to seasonal changes and large-scale climatic variation. Thus, contrary to all null hypotheses, macro-consumers had an impact, and these effects varied with productivity, season, and large-scale perturbations with contrasting climate conditions. In the following two sections, we discuss our results in relation to our six specific predictions (see *Introduction*).

Top-down effects

At all islands, macro-consumers had important effects on percent cover, size structure, and biomass of algae, but the effects on the relative abundance of algae varied with oceanographic regime, being stronger at higher temperatures.

Consistent with prediction 1 (that macro-herbivory would be stronger at higher ocean temperatures and at lower levels of background primary production), at low-productivity islands, any group of macro-consumers had a consistent top-down effect on any upright form of algae, reducing both their frond length and percent cover (Figs. 3–6). For example, in no-grazer treatments (−I−F−C), several groups of upright macroalgae strongly increased in abundance. However, *Ulva* spp. became abundant only when all macro-herbivores were excluded. At mid- and high-productivity islands, in contrast, ulvoids were more abundant in the presence of consumers, which, combined with results at the low-productivity island, supports prediction 2 (that cooler water and higher primary productivity would reduce the impact of grazers). At all productivity levels, macro-herbivores decreased the size structure of algae. The

impact of macro-herbivores on size structure was more dramatic on the low-productivity island, reducing the frond length of all upright macroalgae, while differences in size structure among macro-herbivory levels for *Ulva* spp. were more gradual at the other two islands. Thus, predictions 1 and 2 were also met with respect to the impact of macro-herbivores on size structure of algae.

The impact of macro-herbivory on the biomass of algae was similar to that observed for percent cover on some functional groups of algae. Macro-herbivores had important top-down effects at Genovesa, the low-productivity island, reducing the biomass of edible algae. At mid- and high-productivity islands, biomass of edible algae (primarily *Ulva* spp.) was higher with macro-herbivores present. In no-macro-grazing (−I−F−C) or low-macro-grazing treatments (−I−F+C), articulated coralline algae, of lower nutritional value for herbivores, represented >80% of the total biomass. These results are consistent with predictions 1–4, that the interplay between ocean conditions and algal growth would generate strong top-down effects of macro-grazers in low-productivity regimes and weaken consumer impacts at mid- and high-productivity regimes. Changes that were not predicted were that species other than ulvoids would become competitively dominant in the absence of grazers at mid- and high-productivity islands. We address these unexpected results in the next section.

Seasonal differences and ENSO impact

At the low-productivity island, the effects of macro-consumers were consistent during both El Niño (warm water) and La Niña (cool water) conditions, reducing both frond length and percent cover of edible algae during both phases. At the mid-productivity island during the weak El Niño event (at T_4), the abundance of edible algae declined sharply in high-grazing treatments (+I+F+C), suggesting that the combined effect of all macro-herbivores had a stronger top-down effect at this time, consistent with prediction 1. After the warm phase ended, *Ulva* spp. cover declined in no- (−I−F−C) and low-herbivory treatments, and was gradually replaced by crustose algae.

At the mid-productivity island, this shift towards crustose algae under reduced grazing with the change from warmer to cooler water seems paradoxical. La Niña conditions are characterized by increased availability of nutrients (e.g., Chavez et al. 1999), so we expected that *Ulva* spp. and other foliose algae would maintain or increase their dominance in the absence of macro-herbivory. The mechanism of this shift towards increased cover by crustose algae with reduced herbivory may involve an interaction between algal length and wave disturbance. That is, although cover of *Ulva* spp. decreased with the onset of cool water (T_5; Fig. 3B top), *Ulva* spp. length increased at T_5 (Fig. 4B top). Thus, we hypothesize that the longer *Ulva* spp. blades during the cold phase increased wave-induced drag forces on this

relatively delicate alga, leading to biomass loss, thereby reducing its abundance on primary substrate with no and low herbivory from macro-grazers (−I−F−C and −I−F+C). Both cover and length of *Ulva* spp. underwent greater fluctuations after the onset of La Niña conditions (T_5 on). Such variation is consistent with an interaction between faster growth due to higher nutrients and a stronger loss of biomass due to wave-induced disturbance.

At the high-productivity island, as expected from prediction 2, initially no effect of macro-herbivory was apparent, but after the end of the warm phase (after T_4), ulvoids increased in abundance in intermediate- (−I+F−C) and high-grazing treatments (+I+F+C). At the same time, by the end of the experiment, articulated coralline percent cover had increased to 80% cover in no- and low-grazing treatments (−I−F−C and −I−F+C). This result also seems paradoxical. Other studies have suggested ulvoids are competitively dominant to turfy understory algae (e.g., Lubchenco 1978), leading to the expectation that ulvoids would dominate all other algae including articulated corallines in total exclusions. To the contrary, in this tropical Galápagos system, articulated corallines outcompeted all fleshy algae including *Ulva* spp.

The underlying mechanism of this unexpected result is unclear. One possibility is that high nutrients favor growth of all algae, and that as articulated corallines grow in length, they also increase the density of thalli. This could preempt *Ulva* spp. spores from settling on rock, and force attachment as epiphytes to the ends of articulated coralline fronds. Another implication of this result is that at the high-productivity island, macro-herbivores graze preferentially on articulated coralline algae. Calcium carbonate-containing corallines are typically the least favorite algal type for grazers, so this outcome clearly needs further exploration. In any event, as expected from prediction 4, in the absence of macro-consumers, communities were dominated by competitively superior species of algae. Our data are also in line with predictions 5 and 6, that these fluctuations would be sensitive to seasonal changes and ENSO cycles.

A previous study on Santa Cruz Island during the strong 1997–1998 El Niño-Southern Oscillation event yielded results different from what was observed during the warm phase in this study. During the 1997–1998 warm phase, less palatable and less nutritional brown filamentous algae became dominant (between 60% to 80% of primary space; Vinueza et al. 2006). This switch in community composition was associated with starvation and widespread mortality for marine iguanas, and a reduction in the abundance of Sally Lightfoot crabs. Thus, the system then was dominated by bottom-up processes and the influence of macro-grazers was minimal (Vinueza et al. 2006). However, during the cold (La Niña) phase following the 1997–1998 El Niño, the response of the system was similar to that observed during our study at low-productivity sites.

Role of consumers at different levels of productivity and phases

At the low-productivity island, densities of iguanas were high at Genovesa site 1 (GE1), while crabs were more abundant at Genovesa site 2 (GE2). Evidently, at these sites any combination of macro-grazers can reduce algae to a few grazing-resistant forms. This implies that on Genovesa, marine iguanas, crabs, or fish could have similar ecological roles by producing similar community effects on primary producers. This also suggests functional redundancy among these herbivore groups for the responses measured here.

At both mid- and high-productivity islands during the cool phase, macro-grazers facilitated the growth of the food they prefer during times of colder water (likely equal to higher nutrient inputs). Higher grazing intensity alleviated competition for light and space, eliminating competitively superior species of algae at times of high productivity. Furthermore, at these islands fish had ecological effects similar to the combined effect of all herbivores. This result is consistent with the prediction that primary producers sometimes tolerate grazing through faster growth rates fueled by higher nutrient levels (Wise and Abrahamson 2007).

Potential artifacts

Our study employed several approaches that could have introduced artifacts to the results. First, use of caging methods could affect the results in several ways. As noted in the *Methods*, we did not include a control cage in this study (e.g., a sideless cage or partial cage), because in our earlier study (Vinueza et al. 2006) in the same system, we saw little evidence that cages per se influenced results. For example, fouling could influence flow and light penetration to the substratum, but as noted earlier, in this study algal fouling was a problem at only one site on Santa Cruz. We cleaned these cages as often as possible, and do not believe that fouling had a direct influence on results. Cages could also limit the length of algae due to abrasion during high tide, but since the tallest algae on average measured 7 cm and the height of the cages was 10 cm, we do not think this is a problem either.

Second, our methods did not provide a test of the effects of smaller meso-grazers, which had free access to all treatments, and can have potentially strong effects (e.g., Poore et al. 2012). This suggests that, at least initially, meso-grazer effects were likely similar across treatments, but as the biomass of the algal mat increased and varied among treatments and islands, could differentially have attracted more meso-grazers to thicker mats. We have some evidence that differential colonization by some groups among treatments did occur; as algal frond length increased, meso-grazer (e.g., small crustaceans, gastropods) abundance also increased (L. Vinueza, *unpublished data*). Thus, it is possible that these high densities of meso-grazers led to significant grazing effects in no- and low-macro-grazer treatments.

We note, however, that this effect would make our conclusions more conservative; strong grazing effects were often observed in these treatments despite the uncontrolled potentially negative grazing effect of meso-grazers.

Third, on Genovesa, we observed that, to an extent, small iguanas were able to graze in −I−F+C cages, potentially compromising the orthogonality of this treatment compared to the other islands. This could have led to stronger effects of grazing in this treatment on the low-productivity island, thereby influencing our analysis. We suggest, however, that this possible artifact had a minimal impact on our conclusions. Inspection of Figs. 3–6 indicates that abundances and algal sizes in this treatment were not particularly anomalous, and indeed, generally ranked as we expected as the treatment with "low" grazing pressure.

Community theory implications

At the low-productivity island, low nutrient levels and higher temperatures probably resulted in slower growth rates of algae. Consistent with this inference, algae from Genovesa have a higher C:N ratio (Rubenstein and Wikelski 2003), indicative of nutrient limitation. Furthermore, marine iguanas at Genovesa and similar sites had higher rates of biomass intake per bite compared to islands with larger iguanas (Wikelski and Trillmich 1997), likely as a result of a higher metabolism and higher energy needs to meet their nutritional demands (Sanford 1999, Cebrian et al. 2009). The observed dominance of crustose algae under high grazing on the low-productivity island is in line with previous studies in coastal systems and with the relative dominance model that predicts the dominance of crustose coralline algae, typical of oligotrophic conditions and high herbivory intensity (Littler and Littler 1984).

We suggest that at the high-productivity island, the dominance of palatable species of algae for marine iguanas and other grazers with high-grazing (+I+F+C) treatments is due to faster growth and higher turnover rates. Characteristic of many aquatic primary producers, ulvoids seem to invest most of their energy in photosynthetic growth (e.g., Cyr and Pace 1993, Shurin et al. 2006). Under nutrient-rich conditions, such a strategy might help ephemeral species such as *Ulva* spp. to perform better with macro-herbivores present by compensating for the loss of tissue due to herbivory, and thereby becoming competitively dominant. This pattern has been observed between chitons and their major energy source, coralline algae (Littler et al. 1995), with red algal turf and herbivorous fish (Carpenter 1986), and between *Ulva* spp. and herbivorous fish on the coast of Brazil (Sauer Machado et al. 1996). Similarly, in tropical savannas of Africa, grasses at productive locations grew better in the presence of ungulate herbivores (Augustine and McNaughton 1998).

More complex forms of algae have tissues that are rich in carbon for structural support or invest more energy on morphological structures for defense, such as calcium carbonate, or to secondary compounds to deter consumers and fouling organisms (Hay et al. 1987). In our experiments, such algae only occurred in treatments of low-herbivory intensity, with mixed assemblages at low- and mid-productivity islands, and with articulated corallines dominating those plots at high-productivity islands. Our results at the latter, Fernandina, differed from theoretical models and previous studies that suggest that, with strong herbivory, fitness of palatable species will be reduced in favor of dominance of unpalatable and chemically better defended plants (Lubchenco 1978, Gough and Grace 1998).

Relation to other tropical rocky shores

Top-down effects at the low-productivity island and during warmer periods at the mid-productivity island appear similar to the effects of consumers on marine algae described at other tropical rocky shores in Hong Kong (Williams 1993) and Panama (Menge and Lubchenco 1981), but differ from results on rocky coasts in Brazil (Sauer Machado et al. 1996), Venezuela (Cruz-Motta 2007), and Peru (Hidalgo et al. 2008, Firstater et al. 2012). In these latter locations, ulvoid dominance in the presence of crabs, fish, and snails are more similar to what we observed at mid- and high-productivity islands. Both Brazil and Peru sites were influenced by upwelling and might be more productive than the study sites in Panama and Hong Kong, while a study in Venezuela suggested herbivory might not be important (Cruz-Motta 2007). In Panama, impacts of grazers were consistent year around (Menge and Lubchenco 1981), but in Hong Kong, winter months were milder, allowing macroalgae to escape herbivores, while during summer months thermal stress overrode the effects of herbivores (Williams 1993).

Temperate vs. tropical rocky shores

While macro-herbivores had an important effect at the high-productivity island, the biomass and types of algae present at temperate latitudes (Menge and Lubchenco 1981, Gaines and Lubchenco 1982) differ dramatically from the patterns observed in our study. Most temperate regions studied have algal zones dominated by perennial forms of brown and red algae (Witman and Dayton 2001) and are characterized by higher nutrient availability (Poore et al. 2012). In the Galápagos, sites on mid- and high-productivity islands tend to be dominated by ephemeral forms such as *Ulva* spp. in the presence of herbivores, while sites on low-productivity islands were dominated by encrusting algae. Differences in temperature and nutrient levels among tropical and temperate latitudes and in the types of consumers present at tropical vs. temperate locations might contribute to this pattern (Gaines and Lubchenco 1982). While herbivores can also be important structuring agents on temperate rocky coasts (e.g., able to remove up to 47% of primary producer abundance;

Poore et al. 2012), most are mollusks such as chitons, limpets, echinoderms such as sea urchins, or small crustaceans such as amphipods and isopods. These invertebrates tend to be relatively sluggish and slow moving, or to be small with limited foraging ranges (Menge and Lubchenco 1981). All such herbivores are less mobile than marine iguanas, sea turtles, fish, or shore crabs. While sea urchins are also present in the Galápagos intertidal, their distribution is restricted to the low intertidal or to permanent rock pools and crevices where they can seek relief from thermal stress and predation. At higher latitudes, the effects of consumers on the abundance and type of algae might be restricted spatially to sheltered shores (Nielsen 2001), to occur higher on the shore (Cubit 1984), predominate at sites of low productivity (Guerry et al. 2009), or decrease with increasing productivity (Worm et al. 2002, Worm and Lotze 2006). While herbivores might have overriding impacts on algae if their abundances are high, by selectively removing ephemeral species of algae these grazers can speed the succession pattern from ephemerals to more structurally complex and less palatable forms on temperate rocky shores (Lubchenco 1978).

A previous study on the role of macro-grazers on Santa Cruz Island (Fig. 1) was conducted during the 1997–1998 ENSO event (Vinueza et al. 2006). This previous investigation suggested that site differences were important (these earlier sites were not the same as those used in the present study), that ENSO had strong effects on variation in algal abundance and species composition, and that macro-herbivores played a minor role (Vinueza et al. 2006). During the warm (El Niño) phase, at both sites studied in this earlier investigation, any combination of macro-herbivores reduced the percent cover of *Ulva* spp. However, at site one, originally dominated by crustose algae, macro-herbivores reduced the biomass of all edible species of algae and facilitated the invasion of an algal species (*Giffordia mitchelliae*) that is unpalatable for marine iguanas. At site two, the cover of erect macroalgae was higher. Here, only the combined effect of all consumers reduced edible algae. At both sites, *G. mitchelliae* disappeared during the transition to the cold La Niña phase (Vinueza et al. 2006). This pattern was most similar to that observed at the low-productivity island during the present study.

Given the context provided by the earlier study, which was done within a single (mid) productivity regime that experienced dramatic climatic variation due to the 1997–1998 ENSO, we set out to determine the impacts of productivity by comparing identically designed and executed experiments done at locations of differing background productivity (i.e., using the comparative experimental approach; Menge et al. 1994). By conducting these experiments over three years, we also gained insight into temporal shifts in the productivity regimes associated with ENSO climatic variation. The new results provide a deeper understanding of the role of bottom-up influences on top-down effects, as well as

some novel outcomes that demand further investigation. Both sources of variation in bottom-up inputs (spatial and temporal) indicate that dramatic differences or shifts in algal functional group dominance occur, with a shift from dominance by grazer-resistant algal crusts with low nutrient inputs to dominance by palatable, fast-growing ephemeral species at higher nutrient inputs. In partial contrast to the earlier study, grazers had strong effects across all oceanographic conditions, with impacts on dominance, species composition, biomass, and algal size, but grazing strength varied with the bottom-up context, being stronger with low nutrients and weaker with high nutrients. Two surprises warranting further investigation were observed. First, with reduced grazing in the mid-productivity regime, crustose algae dominated, whereas most prior research suggested the expectation that crustose algae would decline and foliose algae would increase in abundance. Second, with reduced grazing in the high-productivity regime, articulated coralline algae dominated, whereas prior research led to the expectation that palatable fleshy algae such as ulvoids would dominate.

Conclusion

As noted in the *Introduction*, contrasting conclusions have been drawn about latitudinal variation in the strength of top-down effects. Some studies and meta-analyses conclude that top-down effects increase in strength with decreasing latitude (e.g., Menge and Lubchenco 1981, Pennings and Silliman 2005, Burkepile and Hay 2006, Freestone et al. 2011), while others concluded that there was no variation in top-down effects with latitude or that top-down effects were weaker in the tropics (e.g., Vinueza et al. 2006, Poore et al. 2012). Our experiments focusing on top-down effects of grazers and how these vary with oceanographic conditions and through time, all at the same tropical latitude, suggest that the context of bottom-up inputs may be an essential element lacking in many of these earlier analyses. In our system, top-down effects were strongest in low-productivity environments, and that the strength of such effects weakened as environments of greater productivity were considered. Further, important variation in top-down effects occurred through time, as the strength of bottom-up forces varied with different phases of ENSO. We therefore suggest that the oceanographic context, and how this varies through time, will be a critical element to include in future efforts to understand local- to large-scale variation in species interaction strength.

We believe that this study adds to the growing number of investigations of meta-ecosystem dynamics, defined as local ecosystems in a particular habitat that are connected through flows of materials and organisms (e.g., Loreau et al. 2003). Thus, in our case, each island was a local ecosystem, with biota interacting with oceanographic inputs such as nutrients. The different islands in the Galápagos Archipelago are connected by

the different currents summarized earlier (North Equatorial Counter Current, South Equatorial and Humboldt Currents, Equatorial Undercurrent), each of which generates different oceanographic regimes in the region of each of the three islands. We therefore assert that our system meets the definition of "meta-ecosystem." It is also the first meta-ecosystem-scale study to be carried out in a tropical rocky intertidal habitat, and provided results that are generally consistent with previous meta-ecosystem results: Bottom-up influences, often driven by variation in upwelling regime can be tightly coupled to top-down effects, with major consequences for community structure and dynamics (e.g., Bustamante et al. 1995, Menge et al. 1997, 2003, 2004, Navarrete et al. 2005, Witman et al. 2010, Menge and Menge 2013). Knowledge of the generality of, and constraints on, such conclusions would be greatly enhanced by further investigations at the meta-ecosystem scale.

Literature Cited

Augustine, D. J., and S. J. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: Herbivore selectivity and plant tolerance. Journal of Wildlife Management 62:1165–1183.

Banks, S. 2002. Ambiente fisico. Charles Darwin Foundation and the Galápagos National Park, Galápagos, Ecuador.

Barber, R. T., and F. P. Chavez. 1983. Biological consequences of El Niño. Science 222:1203–1210.

Bataille, A., A. A. Cunningham, V. Cedeno, A. Patino, A. Constantinou, L. D. Kramer, and S. J. Goodman. 2009. Natural colonization and adaptation of a mosquito species in Galapagos and its implications for disease threats to endemic wildlife. Proceedings of the National Academy of Sciences USA 106:10230–10235.

Bell, E. C., and M. W. Denny. 1994. Quantifying "wave exposure": a simple device for recording maximum water velocity and results of its use at several field sites. Journal of Experimental Marine Biology and Ecology 181:9–29.

Boyer, K. E., P. Fong, A. R. Armitage, and R. A. Cohen. 2004. Elevated nutrient content of tropical macroalgae increases rates of herbivory in coral, seagrass, and mangrove habitats. Coral Reefs 23:530–538.

Burkepile, D. E., and M. E. Hay. 2006. Herbivory vs. nutrient control of marine primary producers: context-dependent effects. Ecology 87:3128–3129.

Burkepile, D. E., and M. E. Hay. 2008. Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. Proceedings of the National Academy of Sciences USA 105:16201–16206.

Bustamante, R. H., et al. 1995. Gradients of intertidal primary productivity around the coast of South Africa and their relationships with consumer biomass. Oecologia 102:189–201.

Bustamante, R. H., G. M. Wellington, G. M. Branch, G. J. Edgar, P. Martinez, F. Rivera, and F. Smith. 2002. Outstanding marine features if the Galapagos Archipelago. Charles Darwin Foundation and World Wide Fund, Puerto Ayora, Galápagos, Ecuador.

Carpenter, R. C. 1986. Partitioning herbivory and its effects on coral-reef algal communities. Ecological Monographs 56:345–363.

Carrión-Cortez, J. A., P. Zárate, and J. A. Seminoff. 2010. Feeding ecology of the green sea turtle (Chelonia mydas) in the Galapagos Islands. Journal of the Marine Biological Association of the UK 90:1005–1013.

Castilla, J. C., et al. 2005. Down under the southeastern Pacific: marine non-indigenous species in Chile. Biological Invasions 7:213–232.

Cebrian, J., J. B. Shurin, E. T. Borer, B. J. Cardinale, J. T. Ngai, M. D. Smith, and W. F. Fagan. 2009. Producer nutritional quality controls ecosystem trophic structure. PLoS ONE 4:e4929.

Chavez, F., P. G. Strutton, G. E. Friederich, R. A. Feely, G. C. Feeldman, D. G. Foley, and M. J. McPhaden. 1999. Biological and chemical response of the equatorial Pacific Ocean to the 1997–1998 El Niño. Science 286:2126–2131.

Cruz-Motta, J. J. 2007. Spatial analyses of intertidal tropical assemblages associated with rocky shores in Venezuela. Ciencias Marina 33:133–148.

Cubit, J. D. 1984. Herbivory and the seasonal abundance of algae on a high intertidal rocky shore. Ecology 65:1904–1917.

Cyr, H., and M. L. Pace. 1993. Magnitude and patterns of herbivory in aquatic and terrestrial ecosystems. Nature 361:148–150.

Darwin, C. R. 1859. The origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. Random House, London, UK.

Diaz, R. J., and R. Rosenberg. 2008. Spreading dead zones and consequences for marine ecosystems. Science 321:926–929.

Diaz-Pulido, G., and L. J. McCook. 2003. Relative roles of herbivory and nutrients in the recruitment of coral-reef seaweeds. Ecology 84:2026–2033.

Duffy, J. E. 2003. Biodiversity loss, trophic skew and ecosystem functioning. Ecology Letters 6:680–687.

Edgar, G. J., S. Banks, R. Bensted-Smith, M. Calvopina, A. Chiriboga, L. E. Garske, S. Henderson, K. A. Miller, and S. Salazar. 2008. Conservation of threatened species in the Galapagos Marine Reserve through identification and protection of marine key biodiversity areas. Aquatic Conservation Marine and Freshwater Ecosystems 18:955–968.

Edgar, G. J., S. Banks, J. M. Farina, M. Calvopina, and C. Martinez. 2004. Regional biogeography of shallow reef fish and macro-invertebrate communities in the Galapagos Archipelago. Journal of Biogeography 31:1107–1124.

Estes, J. A., and J. F. Palmisano. 1974. Sea otters: their role in structuring nearshore communities. Science 185:1058–1060.

Firstater, F. N., F. J. Hidalgo, B. J. Lomovaksy, and O. O. Iribane. 2012. Grazing and nutrients effects on a high rocky intertidal region of the Peruvian central coast. Journal of Experimental Marine Biology 422:9–13.

Freestone, A. L., R. W. Osman, G. M. Ruiz, and M. E. Torchin. 2011. Stronger predation in the tropics shapes

species richness patterns in marine communities. Ecology 92:983–993.

Gaines, S. D., and J. Lubchenco. 1982. A unified approach to marine plant-herbivore interactions 2. Biogeography. Annual Review of Ecology and Systematics 13:111–138.

Glynn, P. W. 1988. El Niño Southern Oscillation 1982-1983: Nearshore population, community and ecosystem responses. Annual Review of Ecology and Systematics 19:309–345.

Gough, L., and J. B. Grace. 1998. Herbivore effects on plant species density at varying productivity levels. Ecology 79:1586–1594.

Grant, P. R., and B. R. Grant. 2002. Unpredictable evolution in a 30-year study of Darwin's finches. Science 296:707–711.

Grant, P. R., B. R. Grant, L. F. Keller, and K. Petren. 2000. Influence of the 1982–1983 El Niño on Galápagos marine life. Ecology 81:2442–2457.

Guerry, A. D., B. A. Menge, and R. A. Dunmore. 2009. Effects of consumers and enrichment on abundance and diversity of benthic algae in a rocky intertidal community. Journal of Experimental Marine Biology and Ecology 369:155–164.

Harvell, C. D., et al. 1999. Emerging marine diseases, climate links and anthropogenic factors. Science 285:1505–1510.

Hay, M. E., W. Fenical, and K. Gustafson. 1987. Chemical defense against diverse coral-reef herbivores. Ecology 68:1581–1591.

Hidalgo, F. J., F. N. Firstater, E. Fanjul, M. C. Bazterrica, B. J. Lomovasky, J. Tarazona, and O. O. Iribarne. 2008. Grazing effects of the periwinkle Echinolittorina peruviana at a central Peruvian high rocky intertidal. Helgoland Marine Research 62:S73–S83.

Holmgren, M., M. Scheffer, E. Ezcurra, J. R. Gutierrez, and G. M. J. Mohren. 2001. El Niño effects on the dynamics of terrestrial ecosystems. Trends in Ecology and Evolution 16:89–94.

Hughes, T. P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265:1547–1551.

Jackson, J. B. C., et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–638.

Kruuk, H., and H. Snell. 1981. Prey selection by feral dogs from a population of marine iguanas (Amblyrhynchus cristatus). Journal of Applied Ecology 18:197–204.

Laurie, W. A. 1989. Effects of the 1982–1983 El Niño–Southern Oscillation event on marine iguana (Amblyrhynchus cristatus, Bell, 1825) populations in the Galapagos Islands. Elsevier, New York, New York, USA.

Littler, M. M., and D. S. Littler. 1984. Relationships between macroalgal functional form groups and substrata stability in a sub-tropical rocky intertidal system. Journal of Experimental Marine Biology and Ecology 74:13–34.

Littler, M. M., D. S. Littler, and P. R. Taylor. 1995. Selective herbivore increases biomass of its prey: a chiton–coralline reef-building association. Ecology 76:1666–1681.

Loreau, M., N. Mouquet, and R. D. Holt. 2003. Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. Ecology Letters 6:673–679.

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. American Naturalist 64:1116–1123.

Menge, B. A., E. L. Berlow, C. A. Blanchette, S. A. Navarrete, and S. B. Yamada. 1994. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. Ecological Monographs 64:249–286.

Menge, B. A., C. Blanchette, P. Raimondi, S. D. Gaines, J. Lubchenco, D. Lohse, G. Hudson, M. Foley, and J. Pamplin. 2004. Species interactions strength: testing model predictions along an upwelling gradient. Ecological Monographs 74:663–684.

Menge, B. A., B. A. Daley, P. A. Wheeler, and P. T. Strub. 1997. Rocky intertidal oceanography: an association between community structure and nearshore phytoplankton concentration. Limnology and Oceanography 42:57–66.

Menge, B. A., and J. Lubchenco. 1981. Community organization in temperate and tropical rocky intertidal habitats: Prey refuges in relation to consumer pressure gradients. Ecological Monographs 51:429–450.

Menge, B. A., et al. 2003. Coastal oceanography sets the pace of rocky intertidal community dynamics. Proceedings of the National Academy of Sciences USA 100:12229–12234.

Menge, B. A., and D. N. L. Menge. 2013. Dynamics of coastal meta-ecosystems: the intermittent upwelling hypothesis and a test in rocky intertidal regions. Ecological Monographs 83:283–310.

Navarrete, S. A., B. R. Broitman, E. A. Wieters, and J. C. Castilla. 2005. Scales of benthic-pelagic coupling and the intensity of species interactions: from recruitment limitation to top down control. Proceedings of the National Academy of Sciences USA 102:18046–18051.

Nielsen, K. J. 2001. Bottom-up and top-down forces in tide pools: test of a food chain model in an intertidal community. Ecological Monographs 71:187–217.

Palacios, D. M. 2004. Seasonal patterns of sea-surface temperature and ocean color around the Galapagos: regional and local influences. Deep-Sea Research II 51:43–57.

Palacios, D. M., S. Bogard, D. Foley, and F. Schwing. 2006. Oceanographic characteristics of biological hot spots in the North Pacific: a remote-sensing perspective. Deep-Sea Research II: Topical Studies in Oceanography 53:250–269.

Palacios, D. M., S. K. Salazar, and F. H. Vargas. 2010. Galápagos marine invertebrates: responses to environmental variability and potential impacts of climate change. Pages 69–80 in I. Larrea and G. Di Carlo, editors. Climate change vulnerability assessment of the Galápagos Islands. WWF and Conservation International, Quito, Ecuador.

Pennings, S. C., and B. R. Silliman. 2005. Linking biogeography and community ecology: latitudinal variation in plant–herbivore interaction strength. Ecology 86:2310–2319.

Polis, G. A., S. D. Hurd, C. T. Jackson, and F. S. Pinero. 1997. El Niño effects on the dynamics and control of an island ecosystem in the Gulf of California. Ecology 78:1884–1897.

Poore, A. G. B., et al. 2012. Global patterns in the impact of marine herbivores on benthic primary producers. Ecology Letters 15:912–922.

Post, E., et al. 2009. Ecological dynamics across the Arctic associated with recent climate change. Science 325:1355–1358.

Post, E., and C. Pedersen. 2008. Opposing plant community responses to warming with and without herbivores. Proceedings of the National Academy of Sciences USA 105:12353–12358.

Robinson, G. 1985. Influence of the 1982–1983 El Niño on Galapagos marine life. Charles Darwin Foundation for the Galápagos Islands, Quito, Ecuador.

Rubenstein, D. R., and M. Wikelski. 2003. Seasonal changes in food quality: a proximate cue for reproductive timing in marine iguanas. Ecology 84:3013–3023.

Ruttenberg, B. I. 2000. An unusual pulse in recruitment of two reef fishes in the Galapagos Islands coincident with the 1997–1998 El Niño. Bulletin of Marine Science 67:869–874.

Ruttenberg, B. I., A. J. Haupt, A. I. Chiriboga, and R. R. Warner. 2005. Patterns, causes and consequences of regional variation in the ecology and life history of a reef fish. Oecologia 145:394–403.

Sanford, E. 1999. Regulation of keystone predation by small changes in ocean temperature. Science 283:2095–2097.

SAS Institute. 2008. SAS statistical analysis package. Version 9.2. SAS Institute, Cary, North Carolina, USA.

Sauer Machado, K. R. S., A. R. O. Chapman, and R. Coutinho. 1996. Consumer species have limited and variable roles in community organization on a tropical intertidal shore. Marine Ecology Progress Series 134:78–83.

Schiel, D. R. 2004. The structure and replenishment of rocky shore intertidal communities and biogeographic comparisons. Journal of Experimental Marine Biology and Ecology 300:309–342.

Shurin, J. B., D. S. Gruner, and H. Hillebrand. 2006. All wet or dried up Real differences between aquatic and terrestrial food webs. Proceedings of the Royal Society B 273:1–9.

Silliman, B. R., and M. D. Bertness. 2002. A trophic cascade regulates salt marsh primary production. Proceedings of the National Academy of Sciences USA 99:10500–10505.

Smith, V. H., G. D. Tilman, and J. C. Nekola. 1999. Eutrophication: impacts of excess nutrient inputs on freshwater, marine, and terrestrial ecosystems. Environmental Pollution 100:179–196.

Snell, H. M., P. A. Stone, and H. L. Snell. 1996. A summary of geographical characteristics of the Galapagos Islands. Journal of Biogeography 23:619–624.

Spalding, M. D., et al. 2007. Marine ecoregions of the world: A bioregionalization of coastal and shelf areas. BioScience 57:573–583.

Steneck, R. S., and M. N. Dethier. 1994. A functional group approach to the structure of algal-dominated communities. Oikos 69:476–498.

Valiela, I., J. McClelland, J. Hauxwell, P. J. Behr, D. Hersh, and K. Foreman. 1997. Macroalgal blooms in shallow estuaries: Controls and ecophysiological and ecosystem consequences. Limnology and Oceanography 42:1105–1118.

Valle, C. A., and M. C. Coulter. 1987. Present status of the flightless cormorant, Galapagos penguin, and flamingo populations in Galapagos after an El Niño year. Condor 891:276–281.

Vinueza, L. R., G. M. Branch, M. B. Branch, and R. H. Bustamante. 2006. Top-down herbivory and bottom-up El Niño effects on Galápagos rocky-shore communities. Ecological Monographs 76:111–131.

Vitousek, P. M., J. Lubchenco, J. M. Melillo, and H. A. Mooney. 1997. Human domination of earth's ecosystems. Science 277:494–499.

Wikelski, M., and C. Carbone. 2004. Environmental scaling of body size in island populations of Galapagos marine iguanas. University of California Press, Berkeley, California, USA.

Wikelski, M., L. M. Romero, and H. L. Snell. 2001. Marine iguanas oiled in the Galapagos. Science 292:437.

Wikelski, M., and C. Thom. 2000. Marine iguanas shrink to survive El Niño. Nature 403:37–38.

Wikelski, M., and F. Trillmich. 1994. Foraging strategies of the Galapagos marine iguana (Amblyrhynchus cristatus): Adapting behavioral rules to ontogenic size change. Behaviour 128:255–279.

Wikelski, M., and F. Trillmich. 1997. Body size and sexual size dimorphism in marine iguanas fluctuate as a result of opposing natural and sexual selection: an island comparison. Evolution 51:922–936.

Williams, G. A. 1993. Seasonal variation in algal species richness and abundance in the presence of molluscan herbivores on a tropical rocky shore. Journal of Experimental Marine Biology and Ecology 167:261–275.

Wise, M. J., and W. G. Abrahamson. 2007. Effects of resource availability on tolerance of herbivory: a review and assessment of three opposing models. American Naturalist 169:443–454.

Witman, J. D., M. Brandt, and F. Smith. 2010. Coupling between subtidal prey and consumers along a mesoscale upwelling gradient in the Galápagos Islands. Ecological Monographs 80:153–177.

Witman, J. D., and P. K. Dayton. 2001. Rocky subtidal communities. Pages 339–366 in M. D. Bertness, S. D. Gaines, and M. E. Hay, editors. Marine community ecology. Sinauer Press, Sunderland, Massachusetts, USA.

Witman, J. D., and F. Smith. 2003. Rapid community change at a tropical upwelling site in the Galapagos Marine Reserve. Biodiversity and Conservation 12:25–45.

Wolter, K., and M. S. Timlin. 1998. Measuring the strength of ENSO events: How does 1997/98 rank? Weather 53:315–324.

Worm, B., et al. 2006. Impacts of biodiversity loss on ocean ecosystem services. Science 314:787–790.

Worm, B., and H. K. Lotze. 2006. Effects of eutrophication, grazing, and algal blooms on rocky shores. Limnology and Oceanography 51:569–579.

Worm, B. H. K., H. H. Lotze, and U. Sommer. 2002. Consumer versus resource control of species diversity and ecosystem functioning. Nature 417:848–851.

SUPPLEMENTAL MATERIAL

Appendix A

Figures showing wave action, consumer densities, and landscape pictures showing the intertidal during the warm and cool phase (*Ecological Archives* M084-014-A1).

Appendix B

Tables showing analyses of variance and repeated-measures analyses of variance testing the effects of productivity, herbivore regime, and ENSO phase on percent cover and frond length through time and as an overall average, and Kruskal-Wallis tests of differences in biomass among different function groups among productivity and grazing regimes (*Ecological Archives* M084-014-A2).