

EL NIÑO EFFECTS ON THE DYNAMICS AND CONTROL OF AN ISLAND ECOSYSTEM IN THE GULF OF CALIFORNIA

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Abstract. The tremendous increase in precipitation associated with the 1992–1993 El Niño profoundly affected terrestrial communities on arid islands in the Midriff region of the Gulf of California. In 1992, winter precipitation was 5.4 times the historical mean, and winter precipitation over the entire El Niño was the highest two-year amount ever recorded. Increased precipitation led to an explosion of annual plant growth on the previously barren (0–4% cover) islands: plant cover increased 10–160 times over what it had been. With the resumption of arid conditions in 1994, live plant cover returned to the low levels seen before the onset of El Niño.

Insect abundance tracked this pulse in plant productivity and approximately doubled in 1992 and 1993 compared to 1991 levels. In 1994, the crash of annual plants caused insect densities to drop to the lowest levels recorded during the 5-yr study. El Niño also affected the composition of the insect assemblage. In the dry years 1990–1991, the assemblage was dominated by insects feeding on products originating in the ocean: detritivores/scavengers on shore drift of marine algae and carcasses, avian parasites, and detritivores of bird products. Herbivores were extremely rare. The heavy plant growth in 1992 stimulated large (40–190 times pre-El Niño levels) increases in herbivores.

The great increases in land plant biomass and insect abundance are indicative of an important change in the dynamics of this system. Previously, most material flowing through the food webs of these islands originated directly or indirectly in the ocean. In contrast, during this El Niño, most material originated via productivity by terrestrial plants. Thus, wet El Niños represent an agent that switches the system from one dependent primarily on allochthonous input to a system driven to a greater extent by in situ productivity. The influence of this pulse of terrestrial productivity extends beyond the El Niño years: the persistence and slow release of plant and detrital biomass reserves may also greatly affect dynamics for years after the El Niño event has passed. We suggest that large-scale climatic events such as El Niño may be long-lasting determinants of community dynamics rather than occasional disturbance events.

Key words: *arid ecosystems; climatic disturbance; community dynamics; desert arthropods and plants; El Niño–Southern Oscillation; food webs; Gulf of California; marine input; precipitation; pulse-reserve; terrestrial productivity.*

INTRODUCTION

Primary productivity is an important determinant of community dynamics and structure in ecosystems worldwide. It strongly affects the abundance of primary consumers, the presence and relative success of consumer populations at higher trophic positions, and the importance of consumer–resource interactions (Oksanen et al. 1981, Oksanen 1988, Hunter and Price 1992, Power 1992, DeAngelis et al. 1996, Persson et al. 1996). Primary productivity is influenced by many stochastically varying factors (e.g., nutrients, light, temperature, species composition), but it is also strongly altered by large-scale climatic disturbances. One of the most prominent disturbances is the cyclical El Niño–Southern Oscillation (ENSO) oceanographic/meteorological phenomenon. The Southern Oscillation refers to the pressure differential between the South Pacific

subtropical high-pressure region and the Indonesian equatorial low-pressure region. Occasionally, this pressure differential “flips”; in association with the relaxation of previously strong trade winds, this allows warm water from the western Pacific to move eastward to South America (Ramage 1986, Enfield 1987, Quinn 1987). This trans-Pacific movement and the subsequent spread of warm water far southward along the Peruvian coast is known as El Niño. El Niño occurs irregularly at intervals of 3–12 yr (Quinn 1987), and strongly affects marine ecosystems throughout the Pacific (Barber and Chavez 1983, Avaria and Muñoz 1987, Huyer et al. 1987, Torres Moya and Alvarez Borrego 1987, Wilkerson et al. 1987, Glynn 1988, Silva Cota and Alvarez Borrego 1988, Barry and Dayton 1991, Karl et al. 1995).

Through its effects on precipitation, ENSO exerts a tremendous impact on productivity and community dynamics in many terrestrial systems. The Southern Oscillation can bring drought to Australia and Indonesia

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(Quinn et al. 1978, Canby 1984, Nicholls 1991); concurrently, El Niños often bring large storms to the west coast of the Americas, greatly increasing precipitation (Markham and McLain 1977, Quinn and Neal 1983, Canby 1984, Cucalon 1987, Goldberg et al. 1987). Primary productivity on land is tightly correlated with precipitation (Rosenzweig 1968, Lieth 1973, Davidson 1977, Polis and Farley 1979, Noy-Meir 1981, 1985, Ludwig 1986, 1987, Polis 1991), and secondary productivity (consumer biomass) shows a high positive correlation with primary productivity and thus with precipitation (Davidson 1977, Orians and Solbrig 1977, Noy-Meir 1981, 1985, MacKay and MacKay 1984, Marsh 1986, Pianka 1986, Brown 1987, Vitt 1991). This is true at spatial scales across ecosystems (e.g., forests to deserts) and at temporal scales within ecosystems (e.g., "wet" vs. "dry" years).

The effects of ENSO on terrestrial productivity are particularly dramatic in arid regions, where many plants respond dramatically to pulses of precipitation. ENSO-related changes in terrestrial communities have been documented for the Atacama and Peruvian desert (Goldberg et al. 1987, Asa and Wallace 1990, Dillon and Rundel 1990, Meserve et al. 1993), the Chihuahuan desert (Brown and Heske 1990), the arid Australian interior (Canby 1984, Nicholls 1991), and the Galapagos Islands (Hamann 1985, Gibbs and Grant 1987, Trillmich 1991, Desender et al. 1992, Grant and Grant 1993).

Polis and Hurd (1995, 1996a, b) previously described an arid system of desert islands in the Midriff region of the Gulf of California, Baja California Norte, Mexico. Under normal arid conditions, this system is energetically driven by allochthonous input of marine biomass rather than by in situ primary productivity by terrestrial plants. Heavy El Niño precipitation could fundamentally affect the dynamics of this system by changing the energy base of the community; as such, it represents a potential switch in control from limitation by allochthonous productivity (dependent on the productivity of the surrounding waters and on such landscape variables as island perimeter/area ratio; Polis and Hurd 1996a) to limitation by autochthonous productivity (dependent on in situ characteristics such as plant species, soil quality, soil seed bank, and rain catchment). Here, we quantify the effects of the 1992 El Niño on terrestrial producers and primary consumers on these desert islands, and we delineate the immediate and longer-term effects of a change in the resource base. Elsewhere, we trace the direct and indirect effects of these changes up the food web to secondary consumers (G. A. Polis et al., *unpublished manuscript*).

MATERIALS AND METHODS

Study site

Field work was conducted from May–August in 1990–1994, October 1994, March 1994, and March

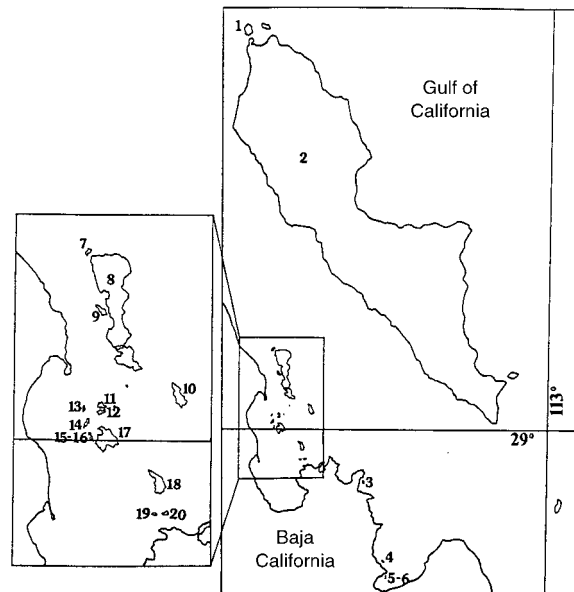


FIG. 1. A map of the Midriff area of the Gulf of California, showing the locations of the islands used in this study: (1) Mejia, (2) Angel de la Guarda, (3) Pescador, (4) Blanca, (5–6) Bahía Animas Norte and Bahía Animas Sur, (7) Coronadito, (8) Smith, (9) Mitlan, (10) Piojo, (11) Pata, (12) Bota, (13) Jorobado, (14) Flecha, (15–16) Llave and Cerraja, (17) Ventana, (18) Cabeza de Caballo, (19) Gemelos West, (20) Gemelos East.

1995. The research involved islands in the Midriff region of the Gulf of California, near Bahía de los Angeles (28°55' N latitude, 113°30' W longitude), Baja California Norte, Mexico (Fig. 1). The principal study site includes 16 islands between Bahía de los Angeles and Isla Angel de la Guarda, four islands at Bahía Animas (15 km ESE of Bahía de los Angeles), and the adjacent coast along the Baja California peninsula. This area is one of the driest in North America; mean annual precipitation at Bahía de los Angeles is only 59 mm (Reyes Coca et al. 1990). The study islands are within 20 km of the Baja California peninsula and lie in a region of the Gulf characterized by year-round upwelling due to tidal mixing and winds (Maluf 1983). Perimeter and area measurements of islands are from Due (1992).

Precipitation

Monthly precipitation data from 1954 to the present were collected at Bahía de los Angeles and provided to us by Ing. Isaac Orozco, Dr. Sergio Reyes Coca, and Ing. Ruben Roa Quiñónez of Centro de Investigación Científica y Educación Superior de Ensenada (CICESE) and Universidad Autónoma de Baja California, both in Ensenada, Mexico, and from Comisión Nacional del Agua, Mexicali, Mexico. This weather station is the only station in the area; all islands are within 40 km of this location and we assume that these weather data apply to our entire system. Precipitation in the Sonoran

Desert generally falls in two distinct periods: winter rains (December–March) and summer rains (late June–early September) (Shreve 1951, Crosswhite and Crosswhite 1982). The gentle, nontorrential, ground-penetrating winter rains are much more important for vegetation dynamics (Dice 1939, Crosswhite and Crosswhite 1982), especially in this area (Shreve 1951). Because rains in December affect ecosystem dynamics throughout the following year in a similar way to those from January to March, we use a December–November annual cycle rather than the artificial calendar year delineation. Results are reported for either annual (December–November) or winter (December–March) precipitation (e.g., 1991 annual precipitation is from December 1990 to November 1991; 1991 winter precipitation is from December 1990 to March 1991). This demarcation insures that winter rains and its effects on dynamics are not separated into two calendar years.

Plant surveys

The percentage of plant cover was determined by a combination of direct censuses and point-quarter estimates; due to variable surface conditions, no single method was effective for all islands for all years. For 1990–1991 (when there were almost no annual plants on most study islands), a very accurate estimate of cover was determined by counting the actual number and type of plants on the entire island, multiplying by an empirically determined size estimate for each plant type, and directly calculating the percentage of cover. In 1992, cover was estimated by transect. Straight transects were established, and at every fifth or tenth step, surface cover was assessed in the four 1-m² plots surrounding the point defined by that step. Transects were laid out to avoid cliffs and to sample microhabitats (e.g., alluvial plains, talus slopes) in their approximate proportions of total island area. Two observers independently assessed the percentage of surface cover of all plants, resolving conflicts prior to recording the data. In 1992, we surveyed 98 points on two islands, for a total of 392 individual 1-m² plots (196 ± 5.7 m² per island, mean \pm 1 SD). For three additional islands in 1992, cover was determined by visual estimates of the percentage of cover in each microhabitat, weighted to reflect the proportion of each microhabitat on the island. In 1993, the percentage of cover was determined using the point-quarter method, except that we distinguished between the percentage of total plant cover, drought-susceptible plants (Shreve 1951), drought-resistant plants (Shreve 1951), and rock. We surveyed 623 points on nine islands, totaling 2492 individual 1-m² plots (276.9 ± 150.1 m² per island). For 1994, we could not use the point-quarter method effectively because a large quantity of dead but still standing annual plants obscured visual estimates of living plant cover. Therefore, on one small island we directly counted the number of live plants, and on two islands we used counts along 50 m transects to estimate the number of

live plants. We then directly calculated the percentage of cover as in 1990–1991 for these three islands.

In March 1994, two small islands (Gemelos West, 0.02 km², and Coronadito, 0.07 km²) and two large islands (Ventana, 1.28 km², and Smith, 8.68 km²) were selected to estimate above-ground plant biomass by removal of annual plants. We chose different-sized islands because we observed that plant biomass was much greater on smaller islands, apparently from the fertilization effects of seabird guano. On each island, a 10 m \times 15 m area (10 m \times 10 m on Coronadito) was permanently marked into 1-m² grids. Beginning in May 1994 and repeating every six months, 15 randomly chosen grid plots were completely cleared of vegetation. Live vegetation was collected separately from dead vegetation. The vegetation was dried completely and then massed. The separation of live and dead material allows us to determine productivity during 1992–1993: the dead plant masses from May 1994 represent cumulative annual plant growth during the preceding two years (almost no annual plants existed on the islands prior to the 1992 rains). October 1994 clearings indicate that little biomass was lost to wind erosion during the intervening 6-mo time period, suggesting that the May 1994 data are a fair estimate of annual plant biomass from 1992–1993.

Insect trapping

The abundance of aerial insects was estimated using glue traps (Abepco, Orange, California) tied to *Opuntia* cactus (cholla). Each trap is a piece of cardboard with an 8.5 \times 12 cm glue area. The criterion for length of time trapped changed from 1990 to 1991. In 1990, traps were left for 15–19 d. By the end of this time, traps were no longer sticky; this suggests that in any comparison of arthropod abundance from year to year, the 1990 data will underestimate true values. In 1991, the following criteria were adopted: (1) traps left for <24 h were excluded since they do not encompass the full diel cycle; and (2) traps left for >120 h were excluded since beyond 5 d trap performance is compromised. To account for the loss of stickiness which affects traps after 5 d, 1990 insect trapping data presented in this paper were calculated using a trapping period of 5 d, i.e., we divided the total number of insects per trap by 5 d rather than by 15–19 d (this period is based on our tests of how long traps remain sticky in the field). This convention is, we believe, a much more accurate estimate of true insect abundance in 1990 than the calculations based on 15–19 d trapping periods; this also allows more accurate comparisons of 1990 insect abundance with other years. This is a conservative correction as it increases the estimated number of trapped insects in a dry period.

Our insect trap totals were as follows: 1990, an average of 7.9 ± 3.4 traps were placed on each of seven islands and the peninsula; 1991, 13.1 ± 4.8 traps on 13 islands and the peninsula; 1992, 10.1 ± 0.8 traps

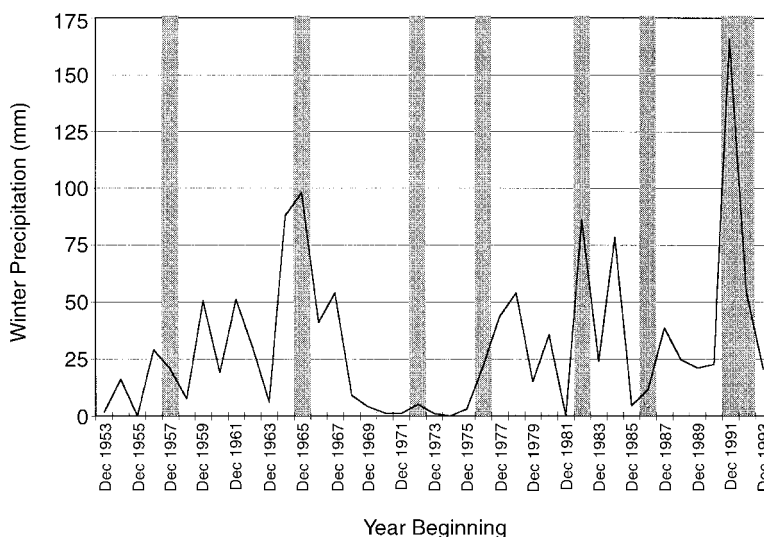


FIG. 2. El Niño and winter precipitation. Precipitation data are from Bahía de los Angeles, Baja California Norte, Mexico, 1954–1994. Winter precipitation is defined as December–March precipitation; “year beginning Dec 91” refers to precipitation from December 1991 to March 1992, and affecting producer dynamics in 1992. Grey areas indicate El Niño events.

on 17 islands and the peninsula; 1993, 10.2 ± 2.5 traps on 17 islands and the peninsula; 1994, 9.8 ± 0.5 traps on 13 islands and the peninsula.

Insect traps were placed on cacti located in the interiors of the islands. All insects trapped were scored for length in millimeters, allowing the calculation of arthropod availability in terms of both millimeters per trap per day (as a measure of the energy pool available to other consumers) and individuals per trap per day (as a measure of the abundance of a particular taxon, e.g., Hemiptera).

Marine input and terrestrial productivity estimation

To determine the relative importance of marine input (MI) and terrestrial productivity (TP) on the dynamics of these systems, Polis and Hurd (1996a) calculated the contribution from each source for each island. The annual contribution of biomass washed ashore per meter of shoreline was measured as $27\,930\text{ g}\cdot\text{m}^{-1}\cdot\text{yr}^{-1}$ (dry mass). With this value, the total MI biomass to an island was calculated as $\text{MI} = mP(10^3)$, where m = marine biomass input per meter per year ($27\,930\text{ g}\cdot\text{m}^{-1}\cdot\text{yr}^{-1}$), P = island perimeter in kilometers, and 10^3 converts kilometers to meters.

Annual terrestrial productivity (t) in grams of dry mass per square meter was determined for the islands using Lieth's (1978) equation relating terrestrial productivity to precipitation:

$$t = 3000(1 - e^{-0.000664N})$$

where N = annual precipitation in millimeters. Once the value of t is determined for a given annual precipitation level, total TP for each island is defined by the following formula: $\text{TP} = tA(10^6)$, where t = terrestrial productivity per square meter, A = island area in square

kilometers, and 10^6 converts square kilometers to square meters. (Our current research is designed to establish empirical values of TP based on sampling plant biomass. Our preliminary data suggest that Lieth's equation slightly overestimates primary productivity in dry years. Nevertheless, the values of TP used in this paper are fairly accurate and are useful in relative comparisons of TP among these islands, all of which experience similar climate and roughly similar vegetation.)

Once MI and TP are determined for each island, the ratio of MI/TP is used to calculate the relative importance of each source of energy and biomass. An island with $\text{MI}/\text{TP} = 1.0$ receives equal amounts biomass from MI and TP, while an island with $\text{MI}/\text{TP} = 0.5$ receives 33% of its overall biomass from MI and the remaining 67% from in situ TP. Because precipitation varied annually from 1990–1994, we have calculated the MI/TP ratio for each year. (Polis and Hurd [1996a] used mean annual precipitation to calculate the MI/TP ratios in an average year; they also used an empirically determined conversion factor for sterile rock area on each island, which is left out of this paper for simplicity.)

RESULTS

Precipitation

The study area is one of the driest places in North America, averaging 65 mm/yr of rainfall during the 41 yr over which data were collected (1953–1994). In 1990, the first year of this study, annual precipitation was 53% lower than the historical mean, and winter precipitation was 32% lower (Fig. 2); in 1991, they were 23% and 27% lower, respectively. The low precipitation in 1990–1991 was particularly significant

since it was a continuation of a dry period that began in 1986. Mean annual precipitation for 1986–1991 was 23% lower than the historical mean, and mean winter precipitation for the six years was 33% lower. This period was not broken by any extremely high-precipitation years; 1989 appears to have been a high-precipitation year, but this annual precipitation total is disproportionately inflated by heavy summer rains that year (precipitation from August–October of 1989 was 62 mm, or 60% of the annual total; the historical mean percentage of precipitation from August–October is only 34%). In terms of winter precipitation, none of the six years had particularly high values: the highest year, 1988, was only the 13th highest out of the 41-yr record. For winter precipitation, 1986–1991 is one of only two periods of extended drought in the 40-yr record (the other is the extreme 1969–1976 drought; see Fig. 2 below).

In contrast, winter precipitation for 1991–1992 was 165.5 mm, 5.4 times the mean winter precipitation, and the highest in 41 yr of recorded data (Fig. 2). Precipitation through spring, summer, and fall 1992 was normal, but in December 1992 heavier than average precipitation began again. Total winter rains for 1992–1993 were 54 mm, the sixth highest in 41 yr (1.8 times the mean winter precipitation). Combined, winter precipitation in 1992 and 1993 was the highest 2-yr period ever recorded.

The initiation of heavy rains in December 1991 coincided with the start of the 1991–1993 El Niño along the west coast of the Americas (Monastersky 1991), and the heavy rains in Bahia de los Angeles in early 1992 occurred at the same time that southern California was drenched by El Niño-related storms (Monastersky 1992). Furthermore, the resumption of heavy precipitation in December 1992 is consistent with the regained strength exhibited by this El Niño event (Monastersky 1993). It is quite probable that the heavy winter precipitation affecting 1992 and 1993 is directly related to the 1991–1993 El Niño event.

In 1994, precipitation returned to the dry regime seen in 1990–1991 that was characteristic of most years from 1954 to the present. Winter precipitation was only 20.5 mm (0.67 times the historical mean), and total precipitation from December 1993 to November 1994 was 30.5 mm (0.47 times the historical mean). These values are almost identical to the precipitation totals from 1990.

Vegetation

Plant growth and cover were extremely low on the islands in 1990 and 1991, most likely a result of the 1986–1991 period of scant winter rains. In fact, annual and drought-susceptible perennial vegetation were almost completely absent from most islands. This rendered small islands particularly barren, since many of them have very few drought-resistant perennials: Isla Gemelos West had only 24 individual plants (all pe-

TABLE 1. The percentage of live plant cover on six islands in Bahia de los Angeles, 1990–1994.

Island	Area (km ²)	Percentage live plant cover				
		1990	1991	1992	1993	1994
Gemelos West	0.020	0.3	0.3	48	17	4.9
Pata	0.136	3.8	3.8	40	18	ND
Islote de Vantana	3.2×10^{-4}	0.0	0.0	ND	17	1.4
Llave	0.022	1.0	1.0	27	31	ND
Cerraja	0.037	2.2	2.2	38	47	ND
Coronadito	0.072	0.8	0.8	40	20	0.8
Mean		1	1	39	25	2

rennials; no annuals) on the entire island in 1990 and 1991; Isla Llave had only 25 drought-resistant perennials and <100 *Atriplex barclayana* shrubs; Isla Calavera had only two perennials; and Islote de Ventana had no plants at all. Calculating the percentage of cover in these years from the known number of individual plants, cover in 1990 and 1991 ranged from 0% to 3.8% (Table 1).

In response to the heavy rains from December 1991 to March 1992, the plant communities were extremely productive during the 1992 growing season. Germination and growth of drought-susceptible perennials and a profusion of annuals caused both the total number of plants and the percentage of cover to increase dramatically. On Isla Gemelos West, absolute plant counts rose from 24 plants to an estimated $48\,000 \pm 9\,800$ individuals. Similarly, plant numbers on Isla Llave increased from <125 individuals in 1990–1991 to an estimated $200\,000 \pm 12\,000$ individuals in 1992. The percentage of cover for five islands shows the same trend: in 1992, plant coverage rose from 0–4% to 27–48% (Table 1). This increase in cover is even more dramatic when sterile rock-covered areas are excluded from analysis: plant cover, as a percentage of available growing surface, ranged from 54% to 89% (data not shown).

The increase in plant cover is almost entirely due to new drought-susceptible perennials and annuals. In 1993, the first year in which the percentage of cover was measured separately for drought-resistant or -susceptible plants, drought-susceptible cover represented 63–100% of total cover (>95% of cover on six of nine islands; data not shown).

Winter rains from December 1992 to February 1993 were heavy, but lighter than the previous year. Live plant cover in 1993 remained high, rising above 1992 levels on two of five islands and falling by about half on the other three (Table 1; we do not have 1992 cover data for Islote de Ventana). The percentage of cover in 1993 was still very high compared to levels observed in 1990–1991: on the five islands it was 5, 21, 25, 57, and 141 times greater in 1993 than in 1991 (Islote de Ventana had 0% cover in 1991 and 17% cover in 1993).

Live plant cover for 1994 taken on three islands (Gemelos West, Islote de Ventana, and Coronadito) re-

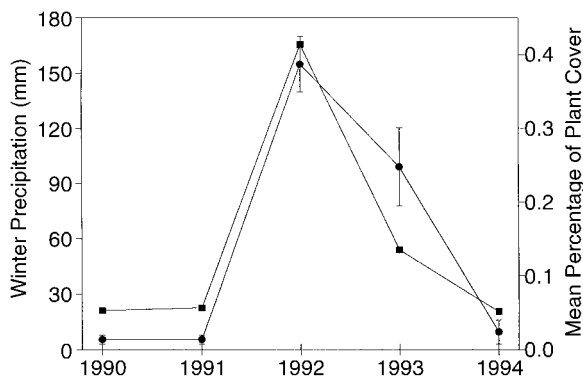


FIG. 3. Winter precipitation (■) and mean percent plant cover (●) from 1990–1994. Precipitation data are from Bahia de los Angeles. Plant cover data represent mean cover from several islands (see *Methods* and Table 2 for more information). Error bars indicate ± 1 SD for mean plant cover.

turned to preraifall levels (Table 1). Considerable detrital matter from the pulse of plant productivity remained on all islands, but live plant cover returned to the extremely low levels characteristic before 1992.

Considering the system as a whole, the mean percentage of plant cover on the islands tracked precipitation extremely well from 1990 to 1994 (Fig. 3). The spike in precipitation in 1992 was accompanied by a spike in plant cover, and the moderately high winter precipitation in 1993 supported reduced but still high levels of plant cover. A regression of plant cover as a function of winter precipitation (in millimeters) for the five years shows a significant relationship: percentage of plant cover = $-0.0087 + 0.0026(\text{winter precipitation})$; $N = 5$, $R^2 = 0.853$, $F = 17.45$, $df = 1, 3$, $P = 0.025$.

Annual plant growth was particularly prominent on small islands, a phenomenon most likely facilitated by enhanced nutrient availability from abundant seabird guano found on small islands. Drought-susceptible plant cover on larger islands consisted principally of relatively small, low-lying annual plants (e.g., *Muhlenbergia*, *Plantago*, *Camissonia*, *Nicotiana*; most <15 cm tall) or low drought-susceptible perennial *Atriplex barclayana* shrubs. Annuals (e.g., *Coreocarpus*, *Perityle*, *Amaranthus*, *Cryptantha*) on smaller islands were taller (most ≈ 30 –70 cm) and had much more dense foliage. Thus, the same percentage of cover of annual plants on small islands represented more biomass than on large islands. Plant removal data from four islands strongly supports this (Fig. 4). Biomass of annual plants per square meter is inversely and significantly related to island area. The largest island in the analysis, Smith (8.68 km²), had only 20.6 ± 14.9 g/m² of annual plant biomass (mean \pm SD), and Ventana (1.28 km²) had 85.7 ± 49.3 g/m²; in contrast, the two smallest islands, Coronadito (0.07 km²) and Gemelos West (0.02 km²), had 184.4 ± 120.8 and 190.5 ± 158.4 g/m² of biomass, respectively. Thus, in terms of biomass, small

islands supported much greater annual plant growth than did large islands during the El Niño.

In addition to the explosion of annual plant growth, perennial plants prospered during the wet El Niño period. In 1992, conspicuous leaf and flower production occurred on a number of important perennial species: e.g., elephant trees (*Bursera microphylla*), ocotillo (*Fouquieria splendens*), desert thorn (*Lycium* sp.), barrel cactus (*Ferocactus* spp.), and cardon (*Pachycereus pringlei*). Each had spectacular floral displays and fruit production. We also observed significant new growth on *Opuntia acanthocarpa* and *O. bigelovii* cholla (we surveyed hundreds of cacti on the islands and the peninsula). Unfortunately, this growth was before we tagged individual cacti with identification markers; thus in most cases we could not quantify growth for the same plants. However, we determined volume in each year for two distinct *Opuntia acanthocarpa* individuals on Isla Gemelos West. From 1991 to 1992, the volumes of each increased (55% and 51%). Growth continued in the second wet El Niño year: in 1993, volumes increased an additional 22% and 20%. For the entire El Niño period, these two cacti increased in volume by 89% and 81%. With the return of dry conditions in 1994, their volumes changed by -28% and -17% ; even after these declines, the two cacti were still 46–49% larger in 1994 than in 1991. These results, coupled with the qualitative observations of growth and flowering in a variety of perennials, suggest that the El Niño also greatly increased perennial plant biomass in this system.

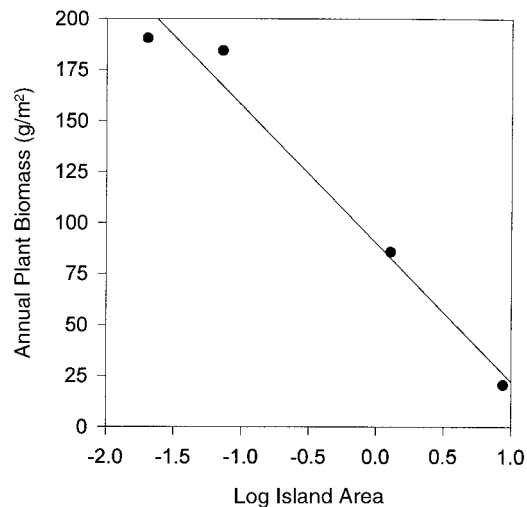


FIG. 4. Biomass of annual plants as a function of island area. Annual plant biomass (g/m²) present on four islands is negatively related to island area (annual plant biomass = $89.8 - 67.7(\log \text{ island area})$; $N = 4$, $R^2 = 0.973$, $P = 0.0136$). The two largest islands are Smith and Ventana; the two smallest islands were Coronadito and Gemelos West. Perennial plant biomass is not included.

TABLE 2. Aerial arthropod abundance and percentage change in abundance during 1990–1994.

Island	Aerial arthropods (mm-trap ⁻¹ .d ⁻¹)					Percentage change in arthropod abundance			
	1990	1991	1992	1993	1994	1990–1991	1991–1992	1992–1993	1993–1994
Bota		12.5	21.0	26.6	8.6		68	27	–68
Cabeza	13.8	6.1	6.7	15.7	4.3	–56	9	135	–73
Cerraja	19.9	9.4	19.7	50.8	5.4	–53	109	158	–89
Coronadito		8.9	33.8	42.0	6.7		282	24	–84
Flecha		10.2	130.2	35.8	2.3		1172	–72	–94
Gemelos E.	19.1	16.5	19.6	17.0	11.3	–14	19	–13	–34
Gemelos W.	30.2	20.6	19.9	61.4	2.9	–32	–3	208	–95
Jorobado		34.3	31.1	49.0	11.9		–9	57	–76
Mitlan		4.5	7.6	14.8	2.6		70	95	–83
Pata	6.8	3.4		15.7	2.0	–50			–87
Piojo	15.8	15.2	45.7	7.0	5.9	–4	201	–85	–16
Smith		3.7	15.1	5.0	1.6		308	–67	–68
Ventana	6.4	6.6	13.5	9.8	1.2	3	105	–27	–88
Animas N.			2.7	6.5				140	
Animas S.			3.8	9.0				136	
Blanca			6.8	11.2				64	
Pescador			13.0	6.6				–49	
Peninsula	2.9	3.4	4.3	7.0	3.4	18	27	62	–52
<i>N</i>	8	14	17	18	14	8	13	17	14
Mean	14.4	11.1	23.2	21.7	5.0	–23	181	47	–72
SD	8.9	8.5	30.0	18.0	3.5				
SEM	3.4	2.4	7.5	4.4	1.0				
Median	4.7	9.4	17.4	15.7	4.3	–23	70	57	–79

Aerial arthropods

In 1990–1991, the availability of aerial insects varied among islands by an order of magnitude, ranging from 2.9–30.2 mm-trap⁻¹.d⁻¹ in 1990 and from 3.4–34.3 mm-trap⁻¹.d⁻¹ in 1991. This variability is due to the influence of marine biomass input: trapped insects included large numbers of algivores, scavengers, detritivores, and seabird ectoparasites, with more insects trapped in areas receiving more marine input (Polis and Hurd 1996a).

The heavy rains of 1992 and 1993 stimulated important changes in the aerial insect fauna. Quantitatively, these rains led to more aerial insects on almost every island (Table 2). Mean availability trapped in 1992 on 17 islands was 23.2 mm-trap⁻¹.d⁻¹, 2.1 times the 1991 mean availability (11.1 mm-trap⁻¹.d⁻¹; 14 islands trapped). More insects were trapped in 1992 than in 1991 on 11 of 13 islands trapped in both years; two islands had slight decreases (–3% and –9%). The median increase from 1991–1992 was 70%.

In 1993, after the second winter of heavy rains, aerial insect availability remained high (mean of 21.7 mm-trap⁻¹.d⁻¹ on 18 islands, 2.0 times the mean abundance in 1991). Despite the small decrease in mean availability from 1992 to 1993 (–6.4%), the median change for the 17 islands was an increase of 57%.

In 1994, low precipitation and the consequent elimination of drought-susceptible plants led to a drastic decrease in aerial insects. Mean availability on the 14 islands trapped fell to 5.0 mm-trap⁻¹.d⁻¹. The median change in abundance from 1993 to 1994 was –72%,

and all 14 islands recorded their lowest aerial insect availability of the entire 5-yr period (1990–1994). The decrease in insect availability showed no geographic patterns, and was unrelated to either island area ($N = 13$, $R^2 = 0.041$, $P = 0.506$) or to aerial insect availability in the previous year ($N = 14$, $R^2 = 0.009$, $P = 0.742$).

Qualitatively, the insect assemblage likewise changed during the El Niño cycle: herbivores increased in 1992 and 1993 with the onset of rain. For example, 1992 was the first year in which large numbers of Coleoptera (e.g., *Ophryastes* curculionids) and Hemiptera (e.g., *Nysius* lygaeids) appeared. From 1992 to 1994, we recorded the taxonomic order of each insect captured on sticky traps; in 1990 and 1991, we discarded most traps before classifying all the insects. Isla Cerraja is the only island on which we have taxonomic information on the trapped insects from 1991, and the numbers of herbivorous Hemiptera trapped from 1991 to 1994 indicates a shift during the El Niño. In 1991, zero Hemiptera were trapped in a total of 32 traps per day; in 1992 and 1993, the number of Hemiptera trapped rose to 0.15 and 0.72 individuals-trap⁻¹.day⁻¹, respectively (4.8 and 23 Hemiptera trapped in 32 trap days); and in 1994, Hemiptera numbers fell to 0.05 individuals-trap⁻¹.d⁻¹ (1.6 Hemiptera per 32 trap days).

For the rest of the archipelago, we compare wet 1992–1993 to dry 1994 to determine if herbivorous taxa tracked changes in precipitation and plant growth. We again focus on herbivorous Hemiptera. The mean number of Hemiptera trapped on 16 islands in 1992

TABLE 3. Island physical characteristics, and marine input/terrestrial productivity ratios from 1990 to 1994.

Island name	Island area (km ²)	Perimeter (km)	P/A† ratio	Marine input/terrestrial productivity ratio				
				1990	1991	1992	1993	1994
Bota	0.093	1.43	15.4	7.2	4.4	1.2	3.6	7.2
Cabeza	0.704	3.96	5.6	2.6	1.6	0.4	1.3	2.6
Cerraja	0.037	0.96	25.9	12.0	7.3	2.1	6.0	12.0
Coronadito	0.072	1.09	15.2	7.0	4.3	1.2	3.5	7.0
Flecha	0.129	1.68	13.0	6.1	3.7	1.0	3.0	6.1
Gemelos E.	0.047	0.89	18.9	8.8	5.3	1.5	4.4	8.8
Gemelos W.	0.020	0.62	31.0	14.4	8.7	2.5	7.1	14.4
Jorobado	0.039	0.89	22.9	10.6	6.5	1.8	5.3	10.6
Llave	0.022	0.58	26.3	12.2	7.4	2.1	6.1	12.2
Mitlan	0.156	1.87	12.0	5.6	3.4	1.0	2.8	5.6
Pata	0.136	1.58	11.6	5.4	3.3	0.92	2.7	5.4
Piojo	0.533	3.25	6.1	2.8	1.7	0.48	1.4	2.8
Smith	8.684	19.81	2.3	1.1	0.64	0.18	0.53	1.1
Ventana	1.275	5.16	4.0	1.9	1.1	0.3	0.9	1.9
B. Animas N.	0.004	0.24	59.9	27.9	16.9	4.8	13.8	27.9
B. Animas S.	0.004	0.24	63.2	29.4	17.8	5.0	14.6	29.4
Blanca	0.029	0.66	22.8	10.6	6.4	1.8	5.3	10.6
Pescador	0.035	0.82	23.5	10.9	6.6	1.9	5.4	10.9
Angel	924.1	194.9	0.2	0.10	0.06	0.02	0.05	0.10
Mejia	3.032	7.74	2.6	1.2	0.72	0.20	0.59	1.2

† P = island perimeter; A = island area.

(3.04 individuals-trap⁻¹·d⁻¹) and 1993 (0.675 individuals-trap⁻¹·d⁻¹) were significantly greater (190 times and 42 times) than in 1994 (0.016 individuals-trap⁻¹·d⁻¹) (variances unequal; Wilcoxon nonparametric tests: 1992 vs. 1994, $Z = -3.24$, $P = 0.001$; 1993 vs. 1994, $Z = -2.981$, $P = 0.003$). The proportion of Hemiptera in the overall assemblage was likewise significantly greater in 1992 (5.9 times greater than 1994; paired t test: mean difference = 0.07, $df = 15$, $t = 2.40$, $P = 0.015$) and 1993 (2.2 times greater than 1994; mean difference = 0.03, $df = 15$, $t = 2.27$, $P = 0.019$). This increase in proportion indicates that during the El Niño, Hemiptera increased to a greater degree than did the rest of the assemblage. Analyses of "outbreak" traps—those capturing extremely high numbers of insects—also show that Hemiptera are more important during the El Niño than after. In 1992 and 1993, 19% and 10% of insects caught on traps with >20 insects/d were Hemiptera; but in 1994, they represented only 1%. When only the five most productive traps from each year are considered, the percentage of Hemiptera trapped falls from 32% in 1992 and 30% in 1993 to only 1% in 1994. These observations, along with the prominent increase in plant biomass, suggest that herbivores were a larger and more important component of the arthropod assemblage during the El Niño than during dry years.

Marine input/terrestrial productivity comparisons

Estimated annual terrestrial productivity (TP) changed greatly with the onset and departure of El Niño-related precipitation. Using Lieth's (1978) equation relating TP to precipitation, we estimate that primary productivity was only 60 g·m⁻²·yr⁻¹ in 1990 and

99 g·m⁻²·yr⁻¹ in 1991. The heavy El Niño precipitation of 1992 and 1993 greatly increased TP, estimated to be 352 g·m⁻²·yr⁻¹ in 1992 and 121 g·m⁻²·yr⁻¹ in 1993. TP again declined in 1994 to 60 g·m⁻²·yr⁻¹. Using these TP values, we can calculate the MI/TP ratio for each island in each year to assess the impact of El Niño on the energy base of the islands (Table 3). MI/TP ratios declined for all of the islands during the El Niño. The large increase in TP caused marked changes in the relative importance of allochthonous marine input (MI) compared to in situ productivity by land plants (Fig. 5). In 1990 only one island had MI/TP <1, and three other islands had MI/TP <2; in 1992, 8 of 20 islands had MI/TP ratios <1, and seven more islands had ratios <2. This dramatic change indicates that wet El Niños represent an agent that switches the system from one whose energy flow is primarily derived from allochthonous input to a system driven to a greater extent by in situ terrestrial productivity.

DISCUSSION

El Niño, switching controls, and variable community structure

The extremely heavy precipitation associated with the 1992–1993 El Niño exerted profound effects throughout the terrestrial food web on islands in the Gulf of California. Polis and Hurd (1995, 1996a, b) showed that during dry years (e.g., 1990–1991), secondary productivity and consumer dynamics on these islands were strongly influenced by allochthonous productivity arising in the surrounding productive marine ecosystem. This allochthonous productivity enters islands via shore drift of algae and carrion and active

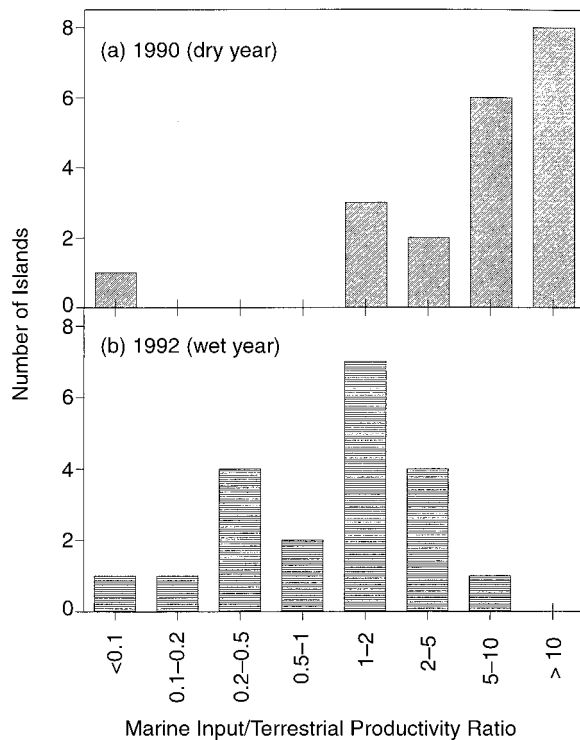


FIG. 5. Marine input/terrestrial productivity (MI/TP) ratios for islands in (a) 1990 (a dry year) and (b) 1992 (a wet year). In 1992, MI/TP ratios are distributed closer to zero, indicating that the relative importance of marine input declined from 1990.

transport into seabird nesting areas, and is converted into terrestrial biomass by detritivores and scavengers that eat marine detritus and bird products (Fig. 6a).

In contrast, with the onset of the 1992 El Niño, autochthonous terrestrial primary productivity increased; the impact of this in situ channel propagated throughout the food web to produce many effects on consumer populations. This increase de-emphasized the relative importance of marine-based energy. Mean percent plant cover on six islands rose from $\approx 1\%$ in 1990–1991 to 39% in 1992. The increase of annual plant biomass was particularly prominent on small islands, places where soils are high in nitrogen and phosphorus from deposition of seabird guano (D. W. Anderson and G. A. Polis, unpublished data). With the tremendous increase in plant cover, arthropod communities were no longer dependent solely on the input of marine detritus, and terrestrial plant communities contributed substantially to high consumer densities. This conclusion is supported by the shift in the relative composition of the arthropod assemblage away from detritivores and scavengers toward more herbivorous insects (Fig. 6b). Significant changes in the abundance of consumers at higher trophic positions (i.e., lizards, land birds, and predaceous arthropods) also took place (G. A. Polis et al., unpublished manuscript).

The switch in control from allochthonous marine input to in situ terrestrial productivity is likely further enhanced by a decrease in the absolute amount of allochthonous input from marine productivity. In other areas, the warm waters associated with El Niño often greatly decrease productivity at all levels throughout the marine food web (Barber and Chavez 1983, McGowan 1984, Glynn 1988, Barber and Kogelschatz 1990, Barry and Dayton 1991). Although we have no direct data on changes in marine productivity in our study area, we strongly suspect that there were significant decreases in productivity. For example, the death of many seabird hatchlings and the almost total failure of birds to fledge on our study islands, along with the death of many adult birds during the 1992 breeding season, were likely caused by a lack of food for foraging seabirds (D. W. Anderson, personal communication). This provided an immediate pulse of energy from seabird carcasses, but the depletion or elimination of resident seabirds on the islands and the failure to breed the following year led to a prolonged decline in energy transport via this conduit. Similar extreme seabird declines have occurred during prior El Niños as a result of declines in oceanic productivity (Anderson et al. 1982, Schreiber and Schreiber 1984, Duffy and Merlen 1986, Ainley et al. 1987, Tovar et al. 1987, Schreiber and Schreiber 1989, Duffy 1990, Bodkin and Jameson 1991, Wilson 1991). Thus it is likely that the relative decline in the importance of marine input was further exacerbated by an absolute decline in the amount of such input (but see Tershy et al. 1991).

Overall, climatic events such as El Niño can cause major changes in the dynamics and energetics of these desert island communities. El Niño has dramatic and immediate effects throughout the food web. But it also has subtle long-term effects: biomass from El Niño-derived terrestrial productivity persists for several years, and may greatly affect the dynamics of this community long after the El Niño has passed.

El Niño and pulse-reserve dynamics

Noy-Meir (1973, 1974) proposed the “pulse-reserve hypothesis” to explain the responses of populations to the extreme variation in productivity that generally characterizes deserts, and that we observe in our study system. He argues that plants and animals grow and establish reserves (e.g., seeds, tubers, tissue, fat, eggs) during good (wet) times; these reserves maintain individuals (and the population) during interim lean (dry) periods. Large quantities of detritus are also produced during good periods. Thus great stores of living tissue and detritus from productivity pulses form a reserve that is slowly used during long intervals of low productivity. The consensus is that such temporal “translocation” of organic matter and energy from good to bad times is central to the dynamics of desert communities (Noy-Meir 1973, 1974, Louw and Seely 1982, Polis 1991, Wiens 1991). Autecologically, it allows

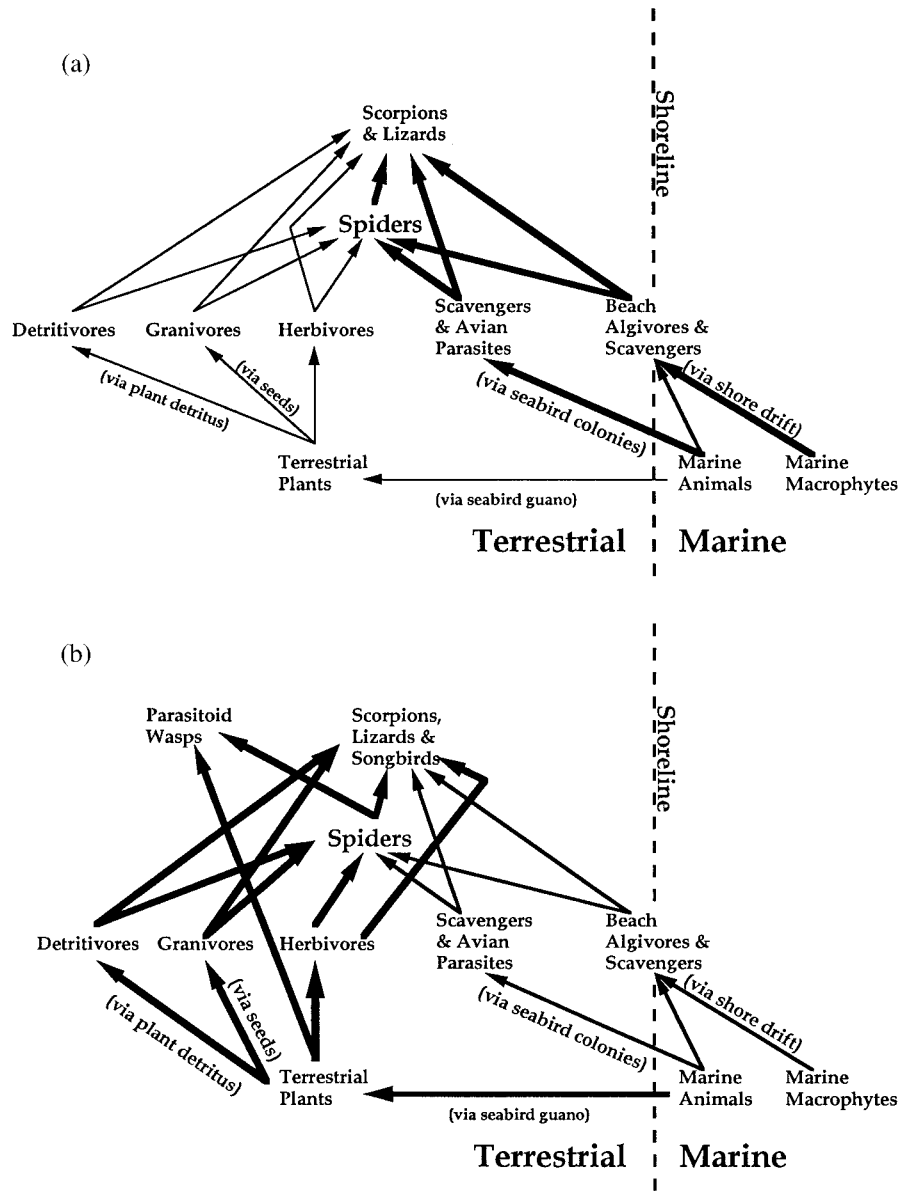


FIG. 6. Terrestrial food web of the islands. (a) In a normal dry year (e.g., 1990–1991, 1994), plant productivity is extremely low, herbivores are at low densities, and primary and secondary consumer populations are largely supported by allochthonous productivity from the sea or from land plant detritus remaining from a previous pulse of productivity during the last wet period. (b) In a wet year (e.g., 1992–1993), the amount and relative importance of in situ terrestrial productivity increases, herbivores increase, and allochthonous input becomes relatively and absolutely less important.

primary producers and consumers to persist during periods of little or no water availability and net primary productivity: perennial plants stay alive on their own reserves and annual plants remain as dormant seeds in the soil; primary consumers survive on stored living plant tissue, dormant seeds and/or detritus; and predators metabolize stored fat reserves and derive much of their energy from detritivores and granivores.

The effects of the 1992–1993 El Niño event may remain evident for some time on these islands. Although the annuals are dead, a tremendous amount of

seeds and detrital plant matter was deposited onto the islands (G. A. Polis et al., *unpublished data*). Increases in perennial plant biomass are still evident. Finally, populations of many consumers (e.g., predaceous arthropods and reptiles, granivorous rodents and ants) were elevated and remained so after the rains. Such changes in plant biomass (seeds, detritus, tissue) and consumer abundance will persist to varying degrees into the (dry) years that follow. For example, the great input of detritus has provided a base for a terrestrial detritivore web that has lasted several years (G. A. Polis

et al., unpublished data). Similarly, the large seed bank deposited in the soil should provide food for granivores for many years (see Inouye 1991, Polis 1991, Wiens 1991). Predators of detritivores and granivores should also benefit as the stored pulse of productivity is slowly released.

We suggest that productivity pulses and their reserves should exert profound changes on the structure and dynamics of populations, food webs, and communities on these desert islands for several years after the El Niño event. First, in the dry years that follow El Niño associated precipitation, bottom-up influences should elevate the numbers of granivores, detritivores, and perennial-plant herbivores relative to what is expected from contemporaneous primary productivity. Predator numbers should also remain elevated long after periods of high precipitation, because more detritivores and granivores are available as prey.

Second, consumer–resource dynamics should be affected (Polis et al. 1996). Storage of resources (detritus, seeds, prey) with gradual release to consumers should generally stabilize consumer–resource relationships. Storage by predators generally should depress resources because it allows predator persistence when prey are rare. The rate of release of reserves influences these dynamics. Reserves used slowly and regularly (e.g., detritus and seeds) will likely stabilize consumer populations and consumer–resource dynamics, compared to reserves released rapidly (e.g., leaves or fruit). This speculation may explain the observation that populations of desert detritivores and granivores are often much more stable than populations of desert herbivores (Louv and Seely 1982, Seely 1991).

Third, persistence of stored plant biomass would increase the relative importance of terrestrial productivity vs. marine input. We know that in 1990, 5 yr after the most recent heavy winter rains of 1984–1985, primary terrestrial productivity was insignificant relative to marine input (Polis and Hurd 1995, 1996a). The length of time that reserves from productivity pulses remain in the system is a key determinant of the trajectories that these terrestrial communities will take in future years. The importance of terrestrial productivity will decrease relative to marine input as a function of time from the last period of pulsed, El Niño-associated productivity.

Although the importance of these storage-related factors is most apparent in arid systems such as this one, we suggest that productivity pulses and subsequent storage and reserve effects are important in all seasonally fluctuating or otherwise variable habitats, from boreal forests and tropical savannas to marine pelagic and benthic systems (Polis et al. 1996). Note that Chesson and Huntley (1988, 1989) also model storage effects. Their use is somewhat different and refers to the effects of good years on recruitment that then alters competitive interactions for several years.

In general, the residence time of reserves and the

length of time before the next period of high productivity are key factors which influence many aspects of community dynamics through both good and bad time periods (Polis et al. 1996). Given a fixed amount of stored or detrital material, the residence time of these reserves will determine the rate of release and availability, thus determining the extent and duration of storage effects on the community. Interval length between pulses is also important, because it determines how frequently resource storage effects become relevant. In addition, interval length strongly affects how the community will respond to the pulse: long intervals between pulses of high productivity will reduce consumer abundance, consequently impeding resource suppression at the next productive period (this process underlies the evolution of masting by plants and synchronous reproduction in periodic insects; Janzen 1976). The effects of interval length become even more complex when the triggering event is aperiodic or only loosely periodic, as is the case with El Niño. In such cases, the community status may be far more dependent on how long it has been since the last triggering event than on any present-time variable.

El Niño: disturbance event?

The 40-yr record of winter precipitation for Bahia de los Angeles (Fig. 2) suggests an important relationship with El Niño. Four of the five years with the highest total precipitation are El Niño years, and three of the four highest winter precipitation totals occurred during El Niños. Not all El Niño events produce high precipitation: the strong El Niño event of 1972 (Quinn et al. 1987) coincided with one of the driest periods on record. But over the last four decades, years encompassing El Niño events were significantly more wet than non-El Niño years: mean winter precipitation (± 1 SD) during El Niño events is 57.9 ± 55.6 mm ($N = 8$), 2.4 times greater than non-El Niño years (24.1 ± 23.3 mm, $N = 33$; one-tailed t test: $df = 39$, $t = 2.71$, $P = 0.005$). Although some El Niños were dry (e.g., 1972), high-precipitation years associated with El Niños occurred every 7.8 ± 4.4 yr from 1954 to the present.

We do not know the biotic effects of earlier wet El Niños on our island communities, but it would not be surprising if similar biological effects occurred during these earlier El Niños. Depending on how long El Niño's effects remain evident in the system through the persistence of stored energetics reserves (e.g., detrital pools, seed banks, tissue reserves, and temporally subsidized consumers), El Niño may emerge as a strong, frequent, and long-lasting determinant of the community dynamics of this arid terrestrial system, rather than an occasional disturbance event.

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