



**Linking Marine and Terrestrial Food Webs: Allochthonous Input from the Ocean Supports High Secondary Productivity on Small Islands and Coastal Land Communities**

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LINKING MARINE AND TERRESTRIAL FOOD WEBS:  
ALLOCHTHONOUS INPUT FROM THE OCEAN SUPPORTS HIGH  
SECONDARY PRODUCTIVITY ON SMALL ISLANDS AND COASTAL  
LAND COMMUNITIES

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**Abstract.**—This study quantifies the flow of energy and biomass from a productive marine system to a relatively unproductive terrestrial system. Biomass from marine food webs (here, the Gulf of California) enters the terrestrial webs of islands and coastal areas through two conduits: (1) shore drift of algal wrack and carrion and (2) colonies of seabirds. Both conduits support dense assemblages of consumers: arthropods are 85–560 times more abundant in the supralittoral than inland and 2.2 times more abundant on islands with seabird colonies than those without. Marine input (MI), not terrestrial primary productivity (TP) by land plants, provides most energy and biomass for terrestrial communities on 16 of 19 study islands. The ratio of perimeter to area ( $P/A$ ) significantly predicts arthropod abundance on islands and is the major determinant of the relative importance of allochthonous flow; we expect  $P/A$  ratio to be important wherever transport of nutrients, detritus, and organisms among habitats occurs. Similar transport phenomena generally take place, often with significant impact, on coastal habitats and islands worldwide. Such input subsidizes a diverse array of terrestrial consumers; in many cases, subsidized consumers reach extraordinarily high densities and thus can depress their in situ resources. In general, we propose that such flow is often a key feature of the energetics, structure, and dynamics of populations, food webs, and communities whenever any two habitats, differing in productivity, are juxtaposed.

The ocean-land interface forms a major ecosystem, the coastal ecotone, that occupies about 8% of the earth's surface (Ray and Hayden 1992) along an estimated 594,000 km of coastline (Hammond 1990). Both the marine and terrestrial sides of this ecotone are relatively productive; about 25% of ocean productivity, two-thirds of humans and a disproportionate share of biotic diversity occur within it (Mann 1982; Barnes and Hughes 1988; Ray 1988; Ray and Hayden 1992). In this zone, aquatic and terrestrial habitats interact extensively and significantly—for example, altered thermal and climatic regimes on land and water, and decreased salinity and increased turbidity in coastal waters from land runoff (Mann and Lazier 1991; Garrison 1993). Interactions are not purely abiotic. Terrigenous input of nutrients and organic material is one major factor (along with upwelling and an enhanced light regime) that promotes high primary and secondary productivity in coastal waters, not only marine (Barnes and Hughes 1988; Mann and Lazier

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1991) but also freshwater (Westlake 1963; Vanni 1995). It is less clear how the often large input of material from these relatively productive aquatic systems into adjacent coastal lands affects productivity in the surrounding terrestrial area.

Productivity differences from water to land across the coastal ecotone may be great. In fact, waters along the littoral fringe are among the most productive habitats on the planet, with primary productivity as high as  $4,000 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$  for estuaries and reefs (Lieth 1978). Coastal areas contribute disproportionately to overall marine productivity: continental shelves represent 7.2% of marine surface area but contribute 16.9% of annual primary productivity, estuaries and reefs (0.55% of the area) contribute 7.3% of total primary productivity, and benthic macroalgal beds (0.028%) contribute an estimated 1.8% (Ryther 1962; Lieth 1978).

Terrestrial productivity varies from 3 to  $3,500 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$  dry mass (Lieth 1978). In several areas, tremendously productive coastal waters are juxtaposed with unproductive land habitats. This contrast is particularly evident in areas of great upwelling along arid coastlines, such as the Benguela current ecosystem and the hyperarid Namib Desert of western southern Africa, and the Peruvian current ecosystem and the hyperarid Atacama Desert of western South America (Schreiber 1968; Seely 1984; Payne et al. 1987; Duffy 1991). The juxtaposition of the Sonoran Desert of Mexico with the Gulf of California and the Pacific represents another extreme contrast between high- and low-productivity ecosystems.

This study quantifies the relative contribution of input from a highly productive marine system into a low-productivity land ecosystem. We analyze some biological effects of such input on the terrestrial organisms and food web on islands and coastal lands in the midriff region of the Gulf of California and Baja California. This region normally receives very little rainfall with great interannual variability (Crosswhite and Crosswhite 1982; Cody et al. 1983; Reyes-Coca et al. 1990), and it exhibits very low primary productivity. In contrast, productivity in gulf waters is extremely high. Marine phytoplankton productivity estimated by Zeitzschel (1969) in the central gulf east of the large island Angel de la Guarda is 4.5 times higher than estimated local terrestrial productivity (536 vs.  $115 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$  dry mass). Maluf (1983) documented year-round upwelling between Angel de la Guarda and the Baja California peninsula, our study area. This continuous upwelling may increase the difference between terrestrial and marine productivity by a factor of 10 (Ryther 1959; Dunbar 1975).

Such high levels of phytoplankton primary productivity support very large populations of invertebrates, fish, birds, and marine mammals in the midriff area west of Angel de la Guarda (Anderson et al. 1976; Odell 1981; Alvarez-Borrego 1983; Anderson 1983; Tershy 1992; Tershy et al. 1993). Large breeding colonies of gulls, pelicans, terns, petrels, boobies, egrets, and California sea lions occur. The local channel, Canal de Ballenas ("channel of the whales"), supports large resident and migratory populations of common and bottlenose dolphins and fin, blue, minke, and Bryde's whales (Tershy 1992; G. A. Polis and S. D. Hurd, personal observation). Carcasses of these animals wash ashore frequently and regularly.

Benthic macroalgae are also quite productive at our study site. Dense beds of littoral and sublittoral algae (*Sargassum*, *Gracilaria*, *Ulva*, *Codium*, *Colpomenia*, *Eucheuma*) grow offshore (Norris 1975; Zertuche-Gonzalez 1988; Barilotti and

Zertuche-Gonzalez 1990; Pacheco-Ruiz et al. 1992; G. A. Polis and S. D. Hurd, personal observation). These and other algae break up seasonally and wash ashore to form thick deposits in the supralittoral.

We describe two conduits by which marine productivity enters the terrestrial food web of islands and coastal areas: (1) shore drift of algae and carrion and (2) seabird colonies. Shore drift delivers a tremendous amount of allochthonous biomass to islands, far exceeding autochthonous terrestrial productivity on a per-square-meter basis. This drift fuels a food web based in the supralittoral but extending inland and helps explain the high numbers of many land animal species observed in coastal areas and on small islands (Due and Polis 1985; Grismer 1994; Polis and Hurd 1995a, 1995b). Utilizing estimates of terrestrial productivity and empirical values for input from shore drift, we contrast the relative contribution of each to the energy budgets of islands. On many small islands, the terrestrial system receives more biomass from marine drift than via in situ productivity of land plants.

Seabird colonies form the second conduit for marine productivity to enter land. Seabirds feed on marine prey and import energy and biomass into the terrestrial web through fish scraps, carcasses from chick and egg mortality, feathers, guano, and high densities of associated ectoparasites (Burger et al. 1978; Williams and Berruti 1978; Williams et al. 1978; Wilcox 1981; Duffy 1983, 1991; Hews 1990). Such allochthonous input increases the abundance of many consumer species and forms the base of a productive food web on some islands, especially smaller ones that lack mammalian and reptilian predators of nesting birds.

#### MATERIAL AND METHODS

Research was conducted on the midriff islands of the Gulf of California, Mexico, and adjacent mainland areas in the states of Baja California Norte and Sonora. Data in this article primarily were collected from May through August in 1990 (11 wk) and 1991 (9 wk) during approximately 4,500 person-hours of field time. Supplementary data were collected from 1992 to 1995.

##### *Study Site*

Bahía de los Angeles lies at 28°55' N latitude, 113°30' W longitude. The principal study site comprises 15 islands between Bahía de los Angeles and Isla Angel de la Guarda, Angel, and three small satellite islands, as well as the adjacent Baja California coast. These midriff islands are normally one of the driest areas of North America. Between 1954 and 1989, Bahía de los Angeles received an average of 59 mm of rainfall per year (Reyes-Coca et al. 1990) with high interannual variability (median annual precipitation of 43 mm/yr; in seven of 36 yr, precipitation was less than 10 mm; S. Reyes-Coca and I. Orozco, personal communication). Although most years are very dry, some years (e.g., 1985, 1992, 1995) receive heavy rains associated with El Niño events; in these years, terrestrial productivity is higher than during the mean or medium year (G. A. Polis and S. D. Hurd, unpublished data). Mean annual temperature is 20°–22°C (Crosswhite and Crosswhite 1982; Cody et al. 1983). Plant communities on both islands and

the adjacent peninsula are typical of the Sonoran Desert phytogeographical region (Shreve 1951). Most study islands are within 20 km of the Baja California peninsula (satellite islands are up to 40 km) and lie in a region characterized by year-round upwelling due to tidal mixing and winds (Maluf 1983).

Perimeter and area measurements of islands are from Due (1992). Topographical maps from the Secretaria de Programación y Presupuesto, Coordinación general del sistema nacional de información (SPP), were enlarged 1.5 times using a scanner and Apple Macintosh computer. Images were digitized using a HIPAD digitizing tablet (Houston Instruments) interfaced with Bioquant II (R & M Biometrics, 1984) software. This procedure was repeated in triplicate to ensure consistency; the mean of three trials is reported. Because various methods to determine island area yield slightly different results, these values may differ slightly from those previously published (Due 1992).

#### *Plant Cover Surveys*

Percentage plant and rock cover was estimated for islands using the point-quarter transect method. Straight transects were established, and at every fifth or tenth step, surface cover was assessed in the four 1-m<sup>2</sup> plots surrounding the point defined by that step. The transects were laid to avoid cliffs and to sample microhabitats (e.g., alluvial plains, talus slopes, guano flats) in their approximate proportions. Two observers independently assessed the cover of total plants, drought-susceptible plants (Shreve 1951), drought-resistant plants (Shreve 1951), and rock, resolving conflicts prior to recording the data. We surveyed 623 points on nine islands, totaling 2,492 individual 1-m<sup>2</sup> plots ( $276.9 \pm 150.1$  m<sup>2</sup> per island).

#### *Algal Drift Measurement*

Three sites were chosen to quantify algal drift deposited in the supralittoral zone. Each site is on the mainland, one in Bahía de los Angeles, the second (Don Juan Cove) 10 km E, and the third (La Unica) 15 km ESE past Punta Pescador. Similar beach topography and algal species occur around the islands. At each site, 10–12 transects were permanently marked in 10-m lengths (27 transects total). Each time the sites were visited, algal drift was collected, weighed, and disposed of inland so that it could not return to the transects. Sites were usually surveyed on different days in the same week; therefore, the survey dates in table 1 are presented by week. Plots were serially cleared throughout the year to obtain annual measures of drift. Algal drift was both dry and wet. If wet, dry mass was determined by desiccating measured amounts until dry, reweighing, and determining a factor to convert wet to dry mass.

Annual means were calculated by summing all algal biomass collected after the first clearing and dividing by the number of days between the first and last clearings. The clearings used for the first and last were those that yielded the overall time period closest to 2 yr for each site (site 1, July 6, 1992–July 19, 1994 = 743 d; site 2, June 10, 1992–June 14, 1994 = 734 d; site 3, July 1, 1992–June 9, 1994 = 708 d). Since drift is highly seasonal, this approach ensures that undue emphasis is not given to high summer values (i.e., it does not bias the data by including an extra summer in the calculations). At site 1, survey results from June 22, 1994,

were lost, so in the calculation of mean annual drift at site 1, the 40 d between the May 13, 1993, and June 22, 1993, surveys are subtracted from the calculation. All other blanks represent surveys not completed for logistical reasons. The days between such surveys are included in the calculations of mean annual drift, which yields a conservative measure of annual drift (drift reaching land between surveys would be consumed or lost to tidal action).

#### *Carcass Drift Measurement*

Carrion washed into the supralittoral was measured at the same sites along transects ranging from 630 to 1,800 m (4,230 m total). All carcasses were collected, identified, and permanently removed. Carcasses removed in the first survey are not included, since we cannot determine how much earlier these carcasses washed ashore (this exclusion eliminated from consideration a fresh 16.8-m fin whale carcass with an estimated mass of at least 25,000 kg). The average mass for both adults and juveniles for each species of bird and marine mammal was determined from the literature (Odell 1981; Gambell 1985; Bryden 1986; Dunning 1993; Johnsgard 1993).

#### *Insect Trapping*

The abundance of aerial insects (ants excluded) was estimated using glue traps (Abepco, Orange, Calif.) tied to *Opuntia* cactus (cholla). Each trap is a piece of cardboard with an  $8.5 \times 12$  cm glue area. In 1990, an average of  $7.9 \pm 3.4$  traps were placed on seven islands and the peninsula for an average of  $120 \pm 44$  trap-days per site (total trap-days = 962). In 1991, an average of  $13.4 \pm 4.9$  traps were placed on 15 islands and the peninsula with an average of  $55 \pm 21$  trap-days per site (total trap-days = 873). To determine insect abundance under specific conditions, we also placed traps in the supralittoral, in the interior, and within seabird colonies. Trapped insects were counted and measured to the nearest millimeter under a microscope. Cursorial arthropods (ants and spiders) were excluded from counts. The total length of insects on each trap was divided by the period of time the trap was active to determine the abundance of insects in millimeters per trap per day.

#### *Spider Density Surveys*

To determine spider density as a function of seabird colonies, five cardon cacti (*Pachycereus pringlei*) of similar size and branching pattern were surveyed both within and away from colonies. Spiders were censused to a height of 2 m; values are presented as spiders/m<sup>3</sup> of space available for web placement on the plant. For spider density as a function of coastal proximity, 100-m transect lines were laid immediately above the high-tide line and 100 m inland. The two sites had similar topography (talus slopes). Spiders were surveyed for each linear meter to a height of 2 m, and values are presented as spiders/m<sup>2</sup> of surface.

### RESULTS

#### *Terrestrial Productivity*

Productivity under the low-rainfall and high-temperature regime of these islands is extremely low, as evidenced by sparse plant communities. Isla Gemelos

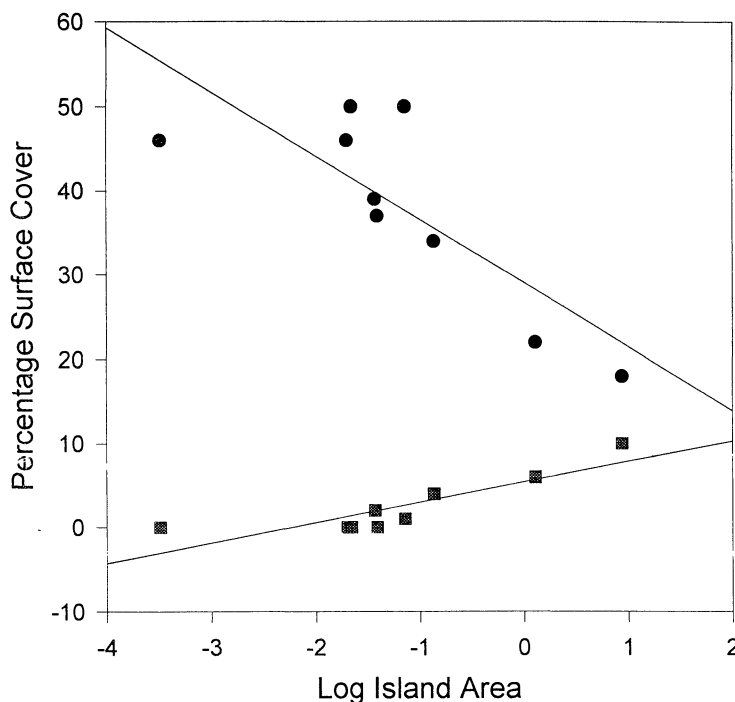


FIG. 1.—Rock cover (*circles*) and drought-resistant perennial cover (*squares*) as a function of island area. Percentage rock cover decreases with island area, while drought-resistant perennial plant cover increases with island area. Island terrestrial productivity estimates are reduced by the percentage of island surface covered with sterile rock.

West ( $0.02 \text{ km}^2$ ) supported only 24 perennial plant individuals and no annuals in either year, which comprised a percentage cover of less than 0.2%. Llave ( $0.022 \text{ km}^2$ ) had only 25 perennial plant individuals and a sparse scattering of *Atriplex barclayana*, with percentage cover of less than 1%. On Cerraja ( $0.037 \text{ km}^2$ ), total plants were too numerous to count because of many small *Mammillaria* cacti, but percentage cover in each year was estimated to be less than 5%. Islote de Ventana ( $3.25 \times 10^{-4} \text{ km}^2$ ), had no plants in either year. The cover of drought-resistant perennials on the nine islands surveyed ranged from 0% to 10% (fig. 1).

Cody et al. (1983) note that precipitation levels on gulf islands may be inferred by examining their plant communities. A comparison of the above percentage cover data for the islands with Shreve's (1951) historical data from the peninsula near Bahía de los Angeles (3%–12% cover in different microhabitats) suggests that precipitation conditions on the islands are as stringent, if not more so, than on the adjacent peninsula. We thus use precipitation records from Bahía de los Angeles to estimate the average annual primary productivity on the islands. Lieth (1978) relates primary productivity, in grams of dry mass per square meter per year, directly to precipitation by the formula

$$\text{productivity} = 3,000(1 - e^{-0.000664N}),$$

where  $N$  is annual precipitation in millimeters. For 59 mm of precipitation, we calculated an estimated terrestrial productivity of  $115 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$  dry mass. Total primary production for an island in the study site can be determined by multiplying this value by total island area. Total terrestrial productivity (TP) may be defined as

$$\text{TP} = tA(10^6),$$

where  $t$  is estimated terrestrial productivity in grams per square meter per year and  $A$  is island area in square kilometers ( $10^6$  converts  $\text{km}^2$  to  $\text{m}^2$ ).

Total plant production of each island is further reduced by areas of solid rock substrate, which lack any soil and are uninhabitable to plants. Each study island has high cover of barren rock (18%–50% on nine islands surveyed; fig 1). Rock cover is inversely related to island area, with larger islands having less barren rock surface:

$$\text{percentage rock cover} = 0.291 - 0.075(\log A)$$

$$(N = 9, R^2 = 0.637, p = 0.0099).$$

We adjust total terrestrial productivity (TP) for rocky areas that cannot support growth using the formula for percentage rock cover. Now  $A$  in the TP formula reflects the actual surface area available for plant growth:

$$\begin{aligned} \text{percentage of area available} &= 1 - [0.291 - 0.075(\log A)] \\ &= 0.709 + 0.075(\log A). \end{aligned}$$

The overall equation for total terrestrial productivity now becomes

$$\text{TP} = tA(0.709 + 0.075[\log A])(10^6).$$

#### *Marine Input through Algal and Vertebrate Drift*

Much marine productivity enters land via algae and carcasses deposited in the supralittoral directly above the highest high tide. From June 1992 to July 1994, we quantified algal drift along our shore transects (table 1). Removed mass is summed and divided by the total time to yield the average biomass deposited per year. This is a conservative and minimum estimate of actual algal drift because seaweed is lost between surveys (consumed, washed out with storms, eroded and dispersed by wind, or overwashed between surveys). The dry mass of algal drift arriving per linear meter of supralittoral ranges from 2.72 to 77.29  $\text{kg} \cdot \text{m}^{-1} \cdot \text{yr}^{-1}$  (table 1). This range has to do with breakup dates of different algal species. Much algae washes ashore in response to either storms or seasonal mortality and the breakup of algal beds. In the case of transect site 3, our sampling dates encompassed the seasonal breakup of dominant algae in both summers, which makes values for that site large. At the other sites, our sampling did not coincide with seasonal breakup; the values for these sites represent algal input from random breakup and one storm in 1994. These two sites thus underestimate marine drift.

Animal carcasses were counted and removed from longer shore transects. The



TABLE 1

SHORE DRIFT AT THREE MAINLAND SITES: ALGAL MASS (g) REMOVED PER METER OF SHORELINE IN 2 YR OF SERIAL CLEANING (TOP); MEAN DRIFT TOTAL PER METER OF SHORELINE PER YEAR (BOTTOM)

	DRY MASS REMOVED PER METER OF SHORELINE (g)			
	Bahía	Don Juan Dike	La Unica	Mean
Algal survey week:				
6/1/92	587	900	998	828
6/28/92	83	245	205	178
8/2/92	136	159	116	137
4/4/93	90	3,153	3,254	2,166
5/9/93	189	...	...	189
6/20/93	...	1,439	...	1,439
6/27/93	655	449	42,124	14,409
8/1/93	211	22	315	183
12/26/93	27	...	...	27
3/6/94	54	...	619	337
5/15/94	278	99	8,079	2,818
5/22/94	...	...	43,758	43,758
6/12/94	...	86	51,447	25,766
7/17/94	3,602	74	...	1,838
DRY MASS REMOVED PER METER OF SHORELINE PER YEAR (g)				
	Bahía	Don Juan Dike	La Unica	Mean
Drift type:				
Algae	2,720	2,810	77,290	
Carrion	530	340	110	
Total	3,250	3,150	77,400	
Average total drift per meter, all three sites (g · m <sup>-1</sup> · yr <sup>-1</sup> )				27,933

most common carcasses were pelicans (*Pelicanus occidentalis occidentalis*, 95 carcasses), with other seabirds (*Larus* spp.; *Sula leucogaster* and *Sula nebouxii*; *Aechmophorus occidentalis*, *Phalacrocorax auritus*, and *Phalacrocorax penicillatus*; *Sterna elegans* and *Sterna maxima*; and *Oceanodroma melania* and *Oceanodroma microsoma*) accounting for 67 carcasses. Marine animals contributed numerous carcasses: 84 fish (families Tetraodontidae, Balistidae, Serranidae, Carangidae, Dasyatidae, Rhinobatidae, and Alopiidae), 19 squid (*Dosidicus gigas*), and very numerous pelagic pteropods and crabs. By far the most biomass came from marine mammals: we collected and removed eight California sea lions (*Zalophus californianus*), one common dolphin (*Delphinus delphis*), and one bottlenose dolphin (*Tursiops truncatus*). When animal carcass numbers were converted to dry mass, the three sites received 110, 340, and 530 g · m<sup>-1</sup> · yr<sup>-1</sup>, respectively (table 1).

Combining algal and animal drift, we found that the dry mass input via drift ranges from 3.15 to 77.40 kg · m<sup>-1</sup> · yr<sup>-1</sup> (the mean is 27.93 kg · m<sup>-1</sup> · yr<sup>-1</sup>).

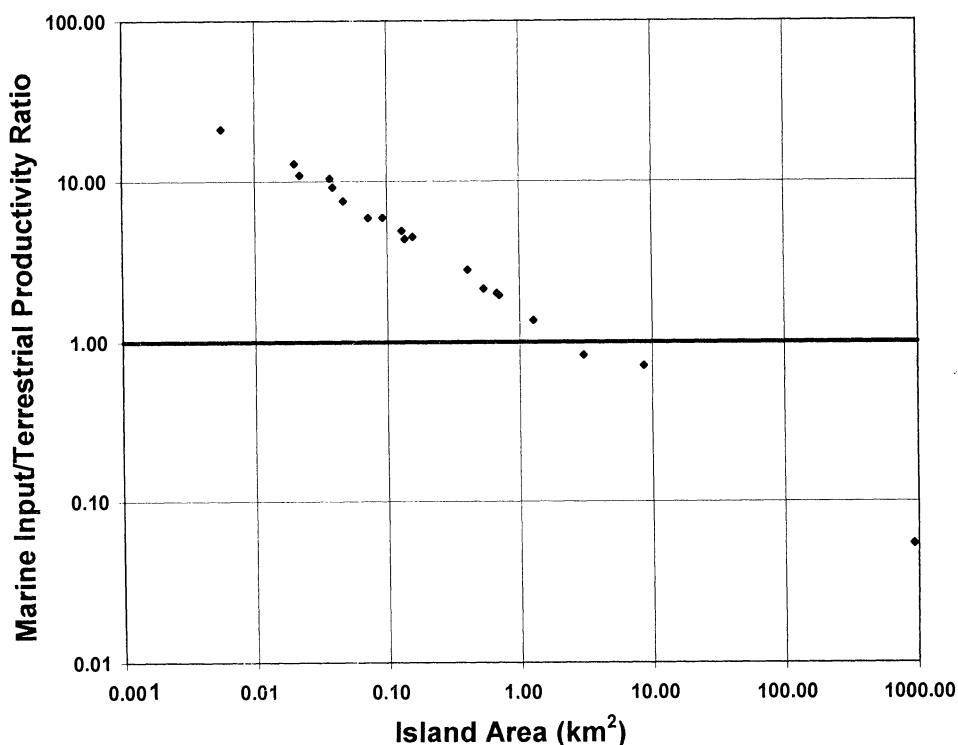


FIG. 2.—Graph indicating that marine input biomass (MI) exceeds terrestrial productivity (TP) biomass on 16 of 19 islands in the midriff area around Bahía de los Angeles. An MI/TP ratio of one would mean equal amounts of biomass enter the island through marine drift and primary productivity via photosynthesis by land plants.  $MI = mP(10^3)$  with  $m = 27,930 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ ;  $TP = tA(0.709 + 0.075[\log A])(10^6)$  with  $t = 98 \text{ g} \cdot \text{m}^{-1} \cdot \text{yr}^{-1}$ .

Given the mean deposited per meter of shoreline, the total biomass of marine input (MI) entering any island can be calculated as

$$MI = mP(10^3),$$

where  $m$  is shore drift in grams per meter per year and  $P$  is island perimeter in kilometers ( $10^3$  converts kilometers to meters).

#### *Comparison of Terrestrial Productivity to Marine Drift Input*

Using these equations, the  $P$  and  $A$  values for the islands (Due 1992), and data for terrestrial productivity and drift biomass, total biomass entering each island from TP and MI can be estimated, and the relative importance of MI to the energy budget of each island can be assessed:

$$\frac{MI}{TP} = \frac{mP}{tA(0.709 + 0.075[\log A])(10^3)}.$$

Figure 2 compares MI with TP for 19 study islands; 16 receive more biomass from marine input than from in situ terrestrial productivity. This phenomenon is

obviously size dependent: as island area increases, the relative importance of MI decreases. The amount of drift reaching an island is a function of the shoreline or perimeter of that island; terrestrial primary productivity is a function of island area. Since perimeter increases linearly while area increases as a squared function, the ratio of perimeter to area parabolically decreases with increasing island size. Small islands (thus with large  $P/A$ ) are greatly influenced by the large input of marine productivity, while large islands are less affected. Thus, although both small and large islands should receive, on the average, the same mass of drift per meter of shoreline, small islands receive much more marine biomass per unit area.

Figure 2 provides specific information on how marine drift influences islands of various sizes. Of the 16 islands receiving more biomass from MI than TP, Isla Ventana is the largest (1.28 km<sup>2</sup>), with an MI/TP ratio of 1.37. Of the three islands with MI/TP less than 1.0, two receive at least half as much biomass from drift as from terrestrial productivity; for example, the second largest island at our site, Isla Smith (8.68 km<sup>2</sup>), exhibits an MI/TP ratio of 0.71. Thus, even moderately large islands can receive an important influx of biomass from shore drift. Only Angel de la Guarda (the second largest island in the Gulf of California, with an area of 924 km<sup>2</sup>) is large enough to render MI insignificant compared to overall TP: its MI/TP ratio is 0.05, with total TP 20 times greater than what is received through marine drift. Thus algal detritus and beached carrion provide relatively large quantities of biomass to all but the largest islands. This input is relatively dominant on small islands and forms the base of one compartment of the food web of small islands and coastal areas.

#### *Marine Input through Seabird Breeding Colonies*

Marine-based organic material also enters islands via colonies of nesting seabirds. Colonies of cormorants, gulls, reddish egrets, boobies, osprey, petrels, pelicans, oystercatchers, and terns occur in various combinations on islands; in total, nine study islands support breeding colonies. Because of species-area relationships, smaller islands tend to lack predators of nesting seabirds and thus provide a refuge for bird colonies. Predators are often present on larger islands, and these islands generally lack seabird colonies. However, the stochastic nature of species-area relationships (especially predator presence) results in seabird colonies present on some larger (but more distant) islands but absent from some smaller (but nearer to the mainland) islands (Anderson 1983). Of the 10 smallest study islands, seven support colonies; of the 10 largest islands, only two have seabird colonies.

Seabirds contribute biomass to islands via fish scraps, the many carcasses left from chick mortality, and an array of parasites and scavengers that eat seabirds and their feathers, eggs, and guano. Chick mortality can provide significant biomass within seabird colonies. On Isla Raza in 1992, 68 Heerman's gull chick and nine elegant tern chick carcasses were counted in an area of only 100 m<sup>2</sup> (0.77 carcasses/m<sup>2</sup>). Thus, chick carcasses alone contribute an estimated 160 g/m<sup>2</sup> wet mass (19.9 g/m<sup>2</sup> dry mass [Crisp 1975], or 17% of estimated terrestrial productivity/m<sup>2</sup>) within colonies. In 1992 on Isla Pijo, 146 pelican chick carcasses were

counted in 1,628 m<sup>2</sup> of colony area in eight arroyos (0.09 carcasses/m<sup>2</sup>). Using a mean wet mass of 1.88 kg (derived from Schreiber 1976 and adjusted for subspecies using Johnsgard 1993), we calculate that this observation amounts to 170 g/m<sup>2</sup> wet mass of carcasses (estimated 21.1 g/m<sup>2</sup> dry mass [Crisp 1975], or 18% of estimated terrestrial productivity/m<sup>2</sup>) within the colony itself.

Piojo is a relatively large island (0.533 km<sup>2</sup>), and the importance of chick carcasses as a biomass input over the entire island is attenuated by large areas not used for nesting. The 1992 pelican breeding season started as a very productive one, but because of an El Niño-associated warming of the surface waters in Bahía de los Angeles prior to the fledgling period, it is estimated that pelican chicks suffered 100% mortality, which contributed an estimated 1,200 chick carcasses to the island (D. Anderson, personal communication). Over the entire island, this situation would contribute 4.2 g/m<sup>2</sup> wet mass (estimated 0.53 g/m<sup>2</sup> dry mass [Crisp 1975], or 0.5% of terrestrial productivity/m<sup>2</sup>).

Other forms of marine input via seabirds (guano, fish scraps, feathers, eggs, tissue to parasites) are likewise attenuated throughout larger islands, so that energy from this conduit should be locally significant within colonies, becoming less important with distance from colonies. However, as island area decreases, the percentage of the island used for nesting generally increases. In this study site, seabirds nest on islands as small as 0.039 km<sup>2</sup> (Jorabado) and 0.02 km<sup>2</sup> (Gemelos West). On islands this small, seabird nesting areas occupy most if not all of the island. On these smaller islands, seabird-imported marine energy is very important both locally and throughout the island and forms the base of a second food web compartment.

#### *Secondary Terrestrial Productivity Increases with Allochthonous Marine Input*

Marine input supports a great abundance of terrestrial and semiterrestrial arthropods that feed on drift in the interface between land and sea. Algae and carrion are converted into large numbers of a diverse set of detritivorous and scavenging Crustacea and insects in the supralittoral (see appendix); these primary consumers also support a large array of arthropod predators. This link between marine drift and arthropod consumers partially explains the tremendous secondary productivity of the supralittoral: our trappings show that arthropods are consistently far more abundant in the supralittoral than inland. For example, the mean number censused per 0.25 m<sup>2</sup> is 560 times greater in the supralittoral than 50 m inland, and insects captured on sticky traps placed directly on fresh algal wrack were 92 times greater than the number trapped on flowering plants 100 m inland (table 2). Supralittoral arthropods are the prey of many land predators, both vertebrate and invertebrate, and thus support a diverse terrestrial food web (see below).

Marine input from drift not only increases arthropod numbers in the supralittoral but also affects areas inland from the coast. Arthropods supported by marine drift will move and be blown inland to a certain extent along all coasts; however, on small islands, the close proximity of the interior to the edge elevates arthropod densities throughout the island. For example, on Coronadito, a very small island (0.072 km<sup>2</sup>), high densities of arthropods occur both in the supralittoral and in-

TABLE 2  
SECONDARY PRODUCTIVITY OF TERRESTRIAL AND SEMITERRESTRIAL ARTHROPODS

Autochthonous or Allochthonous Source	Prey Availability (Mean $\pm$ SD)	<i>t</i>	<i>p</i>
Supralittoral, insects on algae (8 traps)	53 $\pm$ 686 insects $\cdot$ trap <sup>-1</sup> $\cdot$ h <sup>-1</sup>	5.65	<.0005
Inland, insects on plants (8 traps)	.63 $\pm$ 2.0 insects $\cdot$ trap <sup>-1</sup> $\cdot$ h <sup>-1</sup>	...	...
Supralittoral, insect length on algae (8 traps)	175.8 $\pm$ 2.0 mm $\cdot$ trap <sup>-1</sup> $\cdot$ h <sup>-1</sup>	11.84	<.0005
Inland, insect length on plants (8 traps)	1.6 $\pm$ 2.5 mm $\cdot$ trap <sup>-1</sup> $\cdot$ h <sup>-1</sup>	...	...
Supralittoral, potential prey per .25 m <sup>2</sup> *	66.8 $\pm$ 72.3 arthropods	18.78	<.001
Inland, potential prey per .25 m <sup>2</sup> *	.12 $\pm$ .72 arthropods	...	...
Supralittoral, Isla Coronadito (5 traps)	21.1 $\pm$ 2.0 mm $\cdot$ trap <sup>-1</sup> $\cdot$ d <sup>-1</sup>	.145	.8870
Inland, Isla Coronadito (11 traps)	19.5 $\pm$ 3.2 mm $\cdot$ trap <sup>-1</sup> $\cdot$ d <sup>-1</sup>	...	...
Islands with seabird colonies (6 islands)	12.2 $\pm$ 1.7 mm $\cdot$ trap <sup>-1</sup> $\cdot$ d <sup>-1</sup>	3.464	.0025
Islands without seabird colonies (8 islands)	5.5 $\pm$ 1.4 mm $\cdot$ trap <sup>-1</sup> $\cdot$ d <sup>-1</sup>	...	...
Within seabird colonies <sup>+</sup>	12.3 $\pm$ 1.0 mm $\cdot$ trap <sup>-1</sup> $\cdot$ d <sup>-1</sup>	4.01	<.020
Away from seabird colonies <sup>+</sup>	4.5 $\pm$ 1.8 mm $\cdot$ trap <sup>-1</sup> $\cdot$ d <sup>-1</sup>	...	...
During seabird breeding season (12 traps)	455.0 $\pm$ 1.1 mm $\cdot$ trap <sup>-1</sup> $\cdot$ d <sup>-1</sup>	15.33	<.0005
Post-seabird breeding season (10 traps)	17.1 $\pm$ 1.2 mm $\cdot$ trap <sup>-1</sup> $\cdot$ d <sup>-1</sup>	...	...

NOTE.—Secondary productivity of terrestrial and semiterrestrial arthropods is greater on algal drift and in the supralittoral on the peninsula and large islands. On small islands such as Coronadito, arthropod density is high throughout the island. Arthropod abundance is also much higher on islands having seabird colonies, within seabird colonies, and during the seabird breeding season than at other places or times of the year.

\* Due and Polis 1985.

<sup>+</sup> Data from D. Hews (personal communication).

land, with no difference between the two (table 2). In general, when we measured arthropod availability in the interior of all islands by sticky trapping, abundance was directly and significantly related to  $P/A$  (fig. 3; 1990, mm  $\cdot$  trap<sup>-1</sup>  $\cdot$  d<sup>-1</sup> =  $2.0 + 0.21[P/A]$ ;  $N = 7$ ,  $R^2 = 0.76$ ,  $p = .011$ ; 1991, mm  $\cdot$  trap<sup>-1</sup>  $\cdot$  d<sup>-1</sup> =  $5.8 + 0.46[P/A]$ ;  $N = 15$ ,  $R^2 = 0.28$ ,  $p = .043$ ). As expected, as island area increases, fewer arthropods were trapped; the highest abundance of arthropods occurs on the smallest islands. These data suggest that allochthonous energy imported via drift allows small islands to support relatively more arthropods, whereas on large islands, marine influence becomes diluted over the entire island.

Seabird colonies also greatly increase arthropod prey availability by supporting several trophic categories of arthropods: ectoparasites feeding on birds (e.g., *Dasyhelea* spp. ["no-see-ums," Ceratopogonidae]; *Paraleucopsis mexicana* ["bobitos," Chamaemyiidae]; ticks and mites [esp. *Ornithodoros denmarki*; King et al. 1978]) and scavenging insects on bird tissue, fish scraps, and guano (e.g., darkling beetles, Tenebrionidae; skin beetles, Dermestidae; flesh flies, Sarcophagidae; bottle flies, Calliphoridae). Arthropod abundance is significantly higher on islands with seabird colonies compared to those without, within versus away from colonies, and during seabird nesting versus other seasons (table 2). The temporal pulse of arthropods during seabird breeding is remarkable. At this time, 99% of insects trapped were the ectoparasite *P. mexicana* (table 2), and more than 98% of prey identified in spider webs on seabird islands were *P. mexicana*.

In general, both conduits of marine input appear to influence significantly the

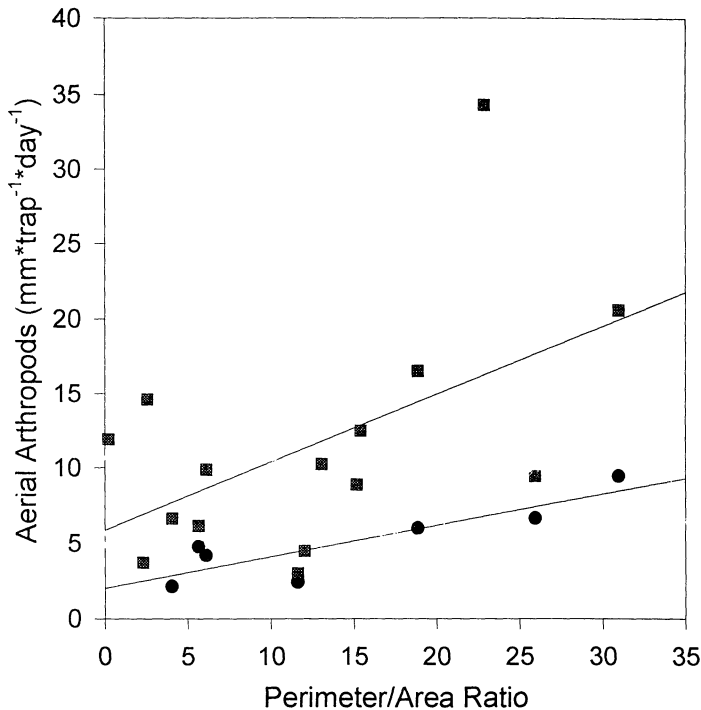


FIG. 3.—Graph indicating that in 1990 (*circles*) and 1991 (*squares*), arthropod density inland on plants increased with island perimeter/area ( $P/A$ ) ratio. Perimeter/area is a measure of the relative importance of marine input—higher  $P/A$  indicates greater input of marine biomass.

population dynamics of higher trophic levels of the terrestrial system. For example, spider densities are eight times greater within ( $14.3 \pm 1.5/\text{m}^3$ ,  $N = 5$ ) than away ( $1.8 \pm 1.5/\text{m}^3$ ,  $N = 5$ ;  $p < .0005$ ) from seabird colonies on the same island. Spiders also respond numerically to shore drift: densities are six times greater in the supralittoral ( $0.155 \pm 0.040/\text{m}^2$ ) than inland ( $0.025 \pm 0.017$ ;  $N = 100$ ,  $p = .003$ ). Similar trends occur among arthropodivorous lizards: they are highly significantly more abundant on islands with bird colonies compared to those without (three times), within compared to away from colonies (15 times), and within 100 m of the shore compared to inland areas (four times) (G. A. Polis and S. D. Hurd, unpublished data).

#### DISCUSSION

The allochthonous input of marine material makes the secondary productivity on small islands higher than that of large islands in the Gulf of California. This finding is counterintuitive to the general notion that larger, more elevated islands intercept more rain, support more plants, produce more topsoil, and are more productive than smaller ones (Lack 1954; Carlquist 1965). Our analysis of land

plants supports this contention: a strong positive relationship exists between island area and plant cover, with drought-resistant perennials more abundant on larger islands (fig. 1; plant cover =  $0.054 + 0.025 [\log A]$ ;  $N = 9$ ,  $R^2 = 0.737$ ,  $p = .0031$ ); moreover, smaller islands have more rock cover and thus less topsoil cover than larger islands (fig. 1). Nevertheless, smaller islands have more energy available to heterotrophs and greater heterotroph biomass per unit area.

These midriff islands are among the driest in the Gulf of California. This fact could suggest that this degree of dependence on marine input (MI) is peculiar to this region. However, even after incorporating the higher precipitation of other gulf islands into Lieth's (1978) equation for terrestrial primary productivity (TP), MI via shore drift is predicted to exert important effects on islands throughout the gulf. Of 68 gulf islands for which data on precipitation can be inferred from precipitation isohyets (Cody et al. 1983), and where island perimeter and area are known (Due 1992), 42 are predicted to have more MI than TP, and five others have MI/TP ratios of 0.50 to 1.00 (fig. 4; this analysis assumes similar supralittoral input as observed in the midriff area).

We expect that islands and coastal areas in many places experience conditions similar to our study area (low precipitation, low TP, relatively high MI): the Peruvian and north Chilean coast, the Patagonian coast of Argentina, the western coast of Australia, the north Arabian Sea, the Persian Gulf, the south coast of Saudi Arabia and the coast of Somalia, the Red Sea, the southeast Mediterranean, and the northwest and southwest coasts of Africa (Schreiber 1968). In several of these systems, adjacent marine productivity is quite high, and allochthonous input is expected to be great (e.g., islands off Baja California, Namibia, and Peru receive 5,000, 10,000, and 170,000 metric tons, respectively, of nitrogenous guano annually; Hutchinson 1950). Precipitation and TP are likewise low in some high-latitude areas, and we expect marine productivity to contribute much to terrestrial communities on certain subarctic (see, e.g., Hersteinsson and MacDonald 1982; Ryan and Watkins 1989; Zabel and Taggart 1989) and subantarctic (see, e.g., Burger et al. 1978; Williams and Berruti 1978; Williams et al. 1978) islands and coastal areas.

Islands elsewhere receive more precipitation and thus have greater TP than those in desert latitudes such as in the Gulf of California. Terrestrial productivity in nondesert ecosystems ranges as high as 35 times greater than on our study islands (Rodin et al. 1975; Lieth 1978). Even with this potentially higher TP, marine input can significantly influence subpolar, temperate, and tropical islands and coastal areas under either of two conditions.

The first condition is high nearshore production and input of marine plants. Although moderate macroalgal beds occur in the Gulf of California, kelp forests throughout temperate latitudes and some tropical areas exhibit extremely high biomass (MacFarlane 1952; Grua 1964; North 1971; Mann 1972, 1973; Estes et al. 1978). For example, the wet biomass of seaweed in Nova Scotia (1,481.5 kg/m shoreline;  $\approx 350$  kg dry mass; Mann 1972) is 13 times greater than the mean algal mass washing ashore yearly at our site. Marine angiosperms also can be extremely productive (Penfound 1956; Odum 1959; Ryther 1959; Zieman et al. 1979). Mangrove swamps (Odum and Heald 1975), salt marshes, and sublittoral

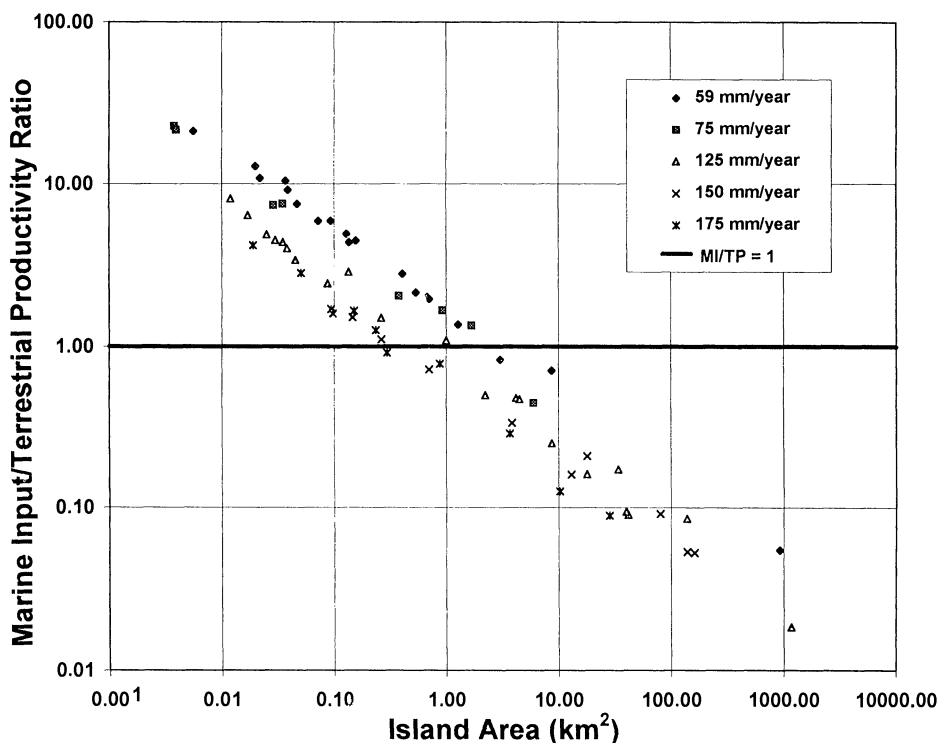


FIG. 4.—Ratio of marine input (MI) to total terrestrial productivity (TP) for 68 islands in the Gulf of California (including Bahía de los Angeles). Islands are marked differently based on their estimated annual precipitation (mm/yr). Despite the higher rainfall received by islands outside of the Bahía de los Angeles study site, 42 of 68 islands have more marine input than terrestrial productivity, and an additional five islands have at least half as much marine input as total terrestrial productivity. These calculations assume that other gulf islands receive similar amounts of detrital input in the supralittoral as coastal areas at our study site in the midriff area of the gulf. Rainfall is determined from Cody et al. (1983); perimeter and area data are from Due (1992).

grass beds (Westlake 1963) are among the most productive ecosystems in the world.

Much of this productivity enters the water column as dissolved organic matter from weathering fronds. However, much particulate detritus enters the supralittoral (Koop and Field 1980; Griffiths and Stenton-Dozey 1981; Stenton-Dozey and Griffiths 1983; Bally 1987; Kapraun and Searles 1990), littoral (Odum and Heald 1975; Zieman et al. 1979; Duggins et al. 1989; Bustamante 1994), surf zone (Robertson and Lenanton 1984), and even deep benthic zones (Menzies et al. 1967; Wolff 1976; Zieman et al. 1979; Vetter 1994). In these areas, detrital organic material and nutrients allow species throughout the food web to increase productivity or standing stock (Bosman et al. 1987; Duggins et al. 1989; Menge 1992; Vetter 1994). On beaches in the Benguela ecosystem, the detrital kelp input ranges from 1,200 to 2,179  $\text{kg} \cdot \text{m}^{-1} \cdot \text{yr}^{-1}$  (Koop and Field 1980; Stenton-Dozey



and Griffiths 1983), and the macrofaunal biomass from such "energy subsidy" is one to three orders of magnitude higher than on beaches lacking subsidies (Bally 1987). Most detrital algae in the supralittoral is converted into large and diverse populations of (semi-)terrestrial insects and Crustacea (Cheng 1976; Griffiths and Stenton-Dozey 1981; Koop and Lucas 1983; Due and Polis 1985; Brusca 1990) (see appendix).

Thus, productive marine plants would allow even productive small islands ( $<1 \text{ km}^2$ ) to receive more productivity from the ocean than from in situ production by their land plants. Overall, we suggest that coastal areas and small islands worldwide with high offshore plant productivity are strongly influenced by MI, regardless of the amount of terrestrial productivity (TP).

The second condition under which islands with favorable precipitation and temperature regimes may still be strongly affected by MI is when TP is reduced due to unfavorable substrates. Even where marine productivity is not high, MI can be significant if substrate conditions reduce or eliminate TP: unvegetated coral cays (Heatwole 1971; Heatwole et al. 1981a) and rock islands (Heatwole et al. 1981b; G. A. Polis and S. D. Hurd, personal observation), subpolar islands (Ryans and Watkins 1989), islands with little or no plant cover owing to volcanic activity (Howarth 1979; New and Thornton 1988; Thornton and New 1988; Rawlinson et al. 1990), or extreme guano deposition by seabirds (Hutchinson 1950; Duffy 1983, 1991; G. A. Polis and S. D. Hurd, personal observation). In these situations, potential TP based on favorable temperature and precipitation is not realized, which leads to an increased relative importance of allochthonous productivity imported from the ocean.

#### *The Importance of Seabirds*

Although much marine productivity enters islands through shore drift, most literature focuses on seabirds as a conduit for energy transfer (Heatwole 1971; Burger et al. 1978; Williams and Berruti 1978; Williams et al. 1978; Heatwole et al. 1981a, 1981b; Wilcox 1981; Duffy 1983, 1991; Edwards and Lubbock 1983; Hews 1990). Seabirds transport great quantities of nutrients and organic material to land via guano, food scraps, eggs, feathers, and the bodies of dead chicks and adults. They are also eaten by many predators—for example, foxes and cats (Williams 1978; Burger 1985; Zabel and Taggart 1989). Seabird parasites (Acari and Diptera) concentrated at colonies are a rich food source enabling spiders, scorpions, ants, and lizards to reach high densities, often one to two orders of magnitude greater than in other areas (Heatwole 1971; Wilcox 1981; Duffy 1983, 1991; Polis and Hurd 1995a, 1995b).

Seabirds feeding on fish and invertebrates concentrate and then transport great quantities of nutrients in their guano (e.g.,  $10^4$ – $10^5$  tons of marine P annually worldwide), which acts as a powerful fertilizer (Hutchinson 1950; Burger et al. 1978; Bosman et al. 1986). Allochthonous P and N in guano enhance land plant production in our system (G. A. Polis and S. D. Hurd, unpublished data) and other coastal and insular ecosystems worldwide (Hutchinson 1950; McColl and Burger 1976; Onuf et al. 1977; Burger et al. 1978; Ryan and Watkins 1989; Daugherty et al. 1990; Towns et al. 1990). Guano also increases algal and phytoplankton

production in the marine intertidal, estuarine, and nearshore waters (Hutchinson 1950; Bosman et al. 1986; Branch et al. 1987; Bosman and Hockey 1988) and lakes (Hutchinson 1950; Brinkhurst and Walsh 1967; Leentvaar 1967; McColl and Burger 1976), which thus potentially enhances input from these habitats to land.

Such fertilization reticulates throughout the food web, producing bottom-up effects beyond increased primary productivity: consumers grow faster, to larger sizes, and increase their population biomass and density. Overall, seabirds underlie complex food webs by supplying energy to many different channels (via detritivores, parasites, predators, and herbivores) (see references in the last paragraph and Williams et al. 1978; Siegfried 1981; Burger 1985).

Finally, colonies of seabirds and pinnipeds add carrion along the shores of the Gulf of California and elsewhere (Heatwole 1971; Heatwole et al. 1981a; Lord and Burger 1984a, 1984b; Zabel and Taggart 1989). Compared to macrophyte or land productivity, carrion often represents a minor food source (in our study, drift algae weighed 51 times more than carrion). However, carrion may be significant near bird or marine mammal colonies (McLachlan 1990). Carrion is eaten by many insects (Lord and Burger 1984a, 1984b; Brusca 1990) and vertebrates (Hersteinsson and MacDonald 1982; Zabel and Taggart 1989; G. A. Polis and S. D. Hurd, personal observation). Further, the production efficiency (mass gained by consumer/mass of food) of terrestrial poikilothermic consumers of flesh is about two times that of herbivores and five times that of detritivores (Brafield and Llewellyn 1982). Thus, a quantity of beached carrion converts to more secondary productivity than an equal mass of algal detritus.

#### *Perimeter/Area Ratios and Other Relevant Aspects of Landscape Ecology*

The identification of landscape ecology as a specific discipline is testimony to the recognition that multihabitat processes affect population and community dynamics. Landscape ecologists consider factors that affect exchange or flow rate among habitats. Flow rate is a function of habitat geometry interacting with organismal or nutrient characteristics—for example, the ratio of perimeter (edge) to area, frequency and spatial arrangement of adjacent habitats, boundary permeability, and vagility of nutrients or organisms as related to crossing boundaries (Forman and Godron 1986; Stamps et al. 1987; Turner 1989; Wiens 1989, 1992; Dunning et al. 1992; Hansen and di Castri 1992).

In particular,  $P/A$  ratio is a general and major determinant of the relative amount of input of allochthonous material and organisms from one essentially two-dimensional surface habitat to another. We illustrated the importance of  $P/A$  using shoreline to island area to predict the relative importance of marine input to terrestrial systems. The  $P/A$  value is likewise important for other habitats or patches—for instance, shoreline to lake area (Pieczynska 1975; Gasith and Hasler 1976), forest edge to interior (Wilcove et al. 1986; Andren and Angelstam 1988), size of reserve areas (Turner 1989), and territory size to boundary length (Stamps et al. 1987). For example, edge to area ratios determine input in both directions between lakes and riparian communities (Pieczynska 1975; Gasith and Hasler 1976). In a Polish lake, the deposition of  $7,440 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$  (dry mass) of organic matter produced an “edge effect” making the diversity and densities on the shore

greater than farther inland. Edge effects are likely universal, not only for marine and freshwater coastal ecotones worldwide but anytime two habitats that differ in productivity are juxtaposed (Polis et al. 1995).

The impact of one habitat on another is a function of  $P/A$  ratio. The  $P/A$  ratio is a function of size—larger islands or patches have less edge per unit area—but also of shape (e.g., compact vs. elongated) and the irregularity or folding of the edge. Thus islands or patches with equal areas may have quite different  $P/A$  ratios. Wetzel (1975) defines a variable, shoreline development ( $D_L$ ), to represent the irregularity of lakeshores independently of area by comparing the ratio of measured shoreline with the circumference of a circle of area equal to the lake's area:

$$D_L = L/[2(\pi A)^{1/2}],$$

where  $L$  is the measured perimeter of the lake and  $A$  is the lake area. Circular (e.g., crater) lakes have  $D_L$  approaching one;  $D_L$  of highly irregular (dendritic) lakes is much higher.

Using this relationship, we can decompose the  $P/A$  ratio into terms for both area and irregularity:

$$P/A = 3.5449 D_L/(A^{1/2}).$$

This approach does not render  $P/A$  determination any simpler— $P$  and  $A$  must still be measured directly to determine  $D_L$ . However, this restatement of  $P/A$  allows the consideration of both area and irregularity to compare islands. In our study, island areas range six orders of magnitude (0.0056–924.1 km<sup>2</sup>), while  $D_L$  values range by only a factor of two (1.003–1.87). Over such a broad range of sizes,  $D_L$  is a relatively much less important determinant of  $P/A$  as compared to area. However, islands or patches with a more limited range of areas (within one order of magnitude) should be strongly affected by differences in  $D_L$ . For example, a patch in which  $A = 4$  km<sup>2</sup> and  $D_L = 2.4$  would have the same  $P/A$  ratio as a patch in which  $A = 1$  km<sup>2</sup> and  $D_L = 1.2$ . Thus, over a narrow size range,  $D_L$  (irregularity) can contribute greatly to  $P/A$ .

#### *Subsidized Consumers*

In addition to increasing the abundance of primary consumers (detritivores and scavengers), the input of material from water to land allows dense populations of secondary consumers. Marine input via shore drift or seabirds supports, directly or indirectly, relatively high densities of predators on small islands and coastal areas worldwide: spiders (Spiller 1992; Polis and Hurd 1995a; 1995b), scorpions (see Due and Polis 1985 for references; Polis and Hurd 1995a), centipedes (Towns et al. 1990), ants (Duffy 1991), lizards (Towns 1975; Wilcox 1981; Hews 1990; Duffy 1991; Grismer 1994; Polis and Hurd 1995a, 1995b), tuataras (Daugherty et al. 1990; Towns et al. 1990), landbirds (Burger 1985; Zann et al. 1990), and carnivorous and omnivorous mammals (e.g., mice, coyotes, foxes, jackals, lions; Osborne and Sheppe 1971; Hersteinsson and MacDonald 1982; Zabel and Taggart 1989; Sheldon 1991; Navarrete and Castilla 1993; Oksanen et al. 1995; G. A. Polis and S. D. Hurd, unpublished data). For example, a diet of

living and dead birds and walrus carrion allows red foxes on the coast to be an order of magnitude more dense than inland (Zabel and Taggart 1989).

This beneficial reliance on allochthonous input is illustrated at our study sites by several species that forage or scavenge in the littoral and supralittoral (Polis and Hurd 1995a, 1995b; G. A. Polis and S. D. Hurd, unpublished data)—for example, many genera of spiders, scorpions, pseudoscorpions, centipedes (*Scolopendra* sp.), lizards (*Callisaurus*, *Uta* spp.), birds (Say's phoebe, *Sayornis saya*; ravens, *Corvus corax*; turkey vultures, *Cathartes aura*; roadrunners, *Geococcyx californianus*), and mammals (coyotes, *Canis latrans*; ring-tailed cat, *Bassariscus astutus*). For instance, coyotes were observed every night to eat carcasses washed ashore. Coyotes also consume marine invertebrates: during one night, coyotes excavated and ate 115 ghost crabs over a 1-km beach.

In many cases, marine energy acts to subsidize land consumers, which promotes a numerical response to densities impossible without such subsidy. In some cases, input allows populations to persist in low-productivity areas—for example, spiders, scorpions, centipedes, and lizards on some gulf islands with no or few land plants. Such subsidies contribute to the success of consumers in many (perhaps all) habitats and contribute significantly to food web dynamics of many communities (Polis and Hurd 1995b; Polis et al. 1995). Note that consumers feed on “normal terrestrial prey” in addition to marine foods. Elsewhere, we show that allochthonous subsidy of local consumers will often depress in situ resources to a greater extent than possible by consumers not so subsidized by cross-habitat input (Polis and Hurd 1995b; Polis et al. 1995; G. A. Polis and R. D. Holt, unpublished manuscript).

We believe that the transfer of energy and biomass is widespread along the boundaries of almost all systems and that the transfer is frequently significant to the maintenance of communities in varied circumstances and across several spatial scales worldwide (from patches to ecosystems). In many systems, input from other habitats is central to dynamics as in situ productivity is low or absent, and approximately 100% of organic materials, nutrients, and prey is imported: caves (Dourojeanni and Tovar 1974; Culver 1982; Howarth 1983), mountaintops (Mani 1968; Edwards 1987), polar snowfields (Teeri and Barrett 1975), new volcanic areas (Swan 1963; Howarth 1979; Ashmole and Ashmole 1986; Edwards 1987), marine aphotic zones and central oceanic gyres (Barnes and Hughes 1988), phytotelmata (Frank and Lounibos 1983; Pimm and Kitching 1987), and some barren deserts (see, e.g., Seely 1991) and islands (see above).

In these extreme systems, consumers depend totally on imported foods. However, regardless of in situ productivity, consumers in almost all systems benefit from foods produced in other habitats (Polis et al. 1995; G. A. Polis and R. D. Holt, unpublished manuscript). Such flow can be a major factor in the population dynamics of (subsidized) consumers and their in situ resources and greatly influence food web and community structure (Polis and Hurd 1995a, 1995b; Polis et al. 1995; G. A. Polis and R. D. Holt, unpublished manuscript).

#### CONCLUSION

We conclude by stressing the importance of analyzing more than just the focal habitat. Tremendous spatial heterogeneity exists, and natural systems are open:

nutrients, organic matter, and organisms move among habitats. Ecological dynamics are rarely contained within the boundaries of the area selected for study, and factors outside a focal system may exert substantial effects on the patterns and dynamics observed in the system. In many cases, between-habitat influences are relatively important as compared to internal, within-habitat effects. The dynamics of local populations are linked closely to those of neighboring populations through such spatially mediated interactions as source-sink (see, e.g., Holt 1985; Pulliam 1988) and metapopulation dynamics (see, e.g., Hanski and Gilpin 1991), supply-side ecology (see, e.g., Roughgarden et al. 1987), source-pool dispersal effects (see, e.g., Holt 1993), and the dynamics of discrete populations coupled by dispersal (Hastings 1993). Along with these processes, we stress that the flow of materials and organisms among habitats is often a key feature of population dynamics, energetics, and the structure of food webs and communities.

Aquatic ecologists have long recognized the interdependence of apparently separate habitats; many freshwater habitats are fueled by both autochthonous primary productivity and allochthonous material from the watershed (Schindler 1971; Hasler 1975; Pieczynska 1975; Gasith and Hasler 1976; Goulding 1980; Vannote et al. 1980; Mulholland 1981; Meyer and Tate 1983; Likens 1984; Welcomme 1985; Davies and Walker 1986; Naiman et al. 1987; Covich 1988; Ward 1988, 1989; Wetzel 1990). In fact, the terms *allochthonous* and *autochthonous* are usually restricted to the limnological literature. Likewise, limnologists recognize that the influence of such input to energy budgets and community structure depends on such landscape variables as the location of a body of water in a drainage, the nature of the surrounding lands, the size of the watershed, and the ratio of length of shore perimeter to water area (Schindler 1971; Pieczynska 1975; Vannote et al. 1980; Meyer and Tate 1983; Likens 1984; Ward 1988, 1989; Wetzel 1990; in fact, after writing this article, we discovered that all our "original" calculations of MI/TP as well as the decomposition of  $P/A$  into components of area and irregularity were previously derived by Gasith and Hasler [1976] to estimate the relative importance of allochthonous input to lakes). In contrast, these insights are only beginning to percolate into the worldview of marine (Bosman et al. 1986; Bosman and Hockey 1988; Duggins et al. 1989; Menge 1992; Vetter 1994) and terrestrial (Dial 1992; Polis and Hurd 1995a, 1995b) biologists. We hope that this article contributes to the recognition of the ubiquity and importance of the movement of nutrients, detritus, and organisms among habitats.

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## APPENDIX

### ARTHROPODS IN THE GULF OF CALIFORNIA SUPPORTED BY SHORE DRIFT OF ALGAE AND CARRION

The list is compiled from Brusca (1990) and G. A. Polis and S. D. Hurd (personal observation).

#### Scavengers, algivores, detritivores, and parasites:

- Talitrid amphipods (Talitroidea)
- Cirolanid isopods (Cirolanidae)
- Tyloid isopods (Tyliidae)
- Ligiid isopods (Ligiidae)
- Podurid collembola (Poduridae)
- Entomobryiid collembola (Entomobryiidae)
- Isotomid collembola (Isotomidae)
- Water boatmen bugs (Corixidae)
- Rove beetles (Staphylinidae)
- Darkling ground beetles (Tenebrionidae)
- Biting midges (Ceratopogonidae) (larvae)
- Midges (Chironomidae) (larvae)
- Seaweed flies (Coleopidae) (larvae)
- Sphaerocerid flies (Sphaeroceridae) (larvae)
- Tethinid flies (Tethinidae) (larvae)
- Beach flies (Canaceidae) (larvae)
- Shore flies (Ephydriidae)
- Anthomyiid flies (Anthomyiidae) (larvae)
- Ants (Formicidae) (opportunistic scavengers)
- Mites (three families)

#### Arthropod predators:

- Shore bugs (Saldidae)
- Tiger beetles (Cicindelidae)
- Ground beetles (Carabidae)
- Rove beetles (Staphylinidae)
- Hister beetles (Histeridae)
- Soft-winged flower beetles (Melyridae)
- Antlike flower beetles (Anthicidae)
- Robber flies (Asilidae)
- Long-headed flies (Dolichopodidae)
- Scorpions (Vaejovidae)
- Pseudoscorpions (four families)
- Jumping spiders (Salticidae)
- Wolf spiders (Lycosidae)
- Two-clawed hunting spiders (Clubionidae)

Arthropod predators (*continued*):

Desid spiders (Desidae)

Hackled-band weavers (Dictynidae)

Hunting spiders (Gnaphosidae)

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