

Nutrient exchanges between marine and terrestrial ecosystems: the case of the Galapagos sea lion *Zalophus wollebaecki*

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Summary

1. The movement of materials and organisms between ecosystems is a common process in nature.
2. In the present study we investigate the hypothesis that the transport of nutrients by low-mobility species and their effect on terrestrial ecosystems depends on habitat topography. Specifically, we hypothesized that the influence of a marine organism with low mobility on terrestrial environments would be spatially restricted.
3. To address this hypothesis we analysed the distribution (both geographical and local scales) of Galapagos sea lion colonies, and quantified the spatial extent of their influence on terrestrial ecosystems (soil and plants).
4. Our results showed that the influence of *Z. wollebaecki* on Galapagos terrestrial habitats is restricted to shorelines with low elevations, but that it is geographically ubiquitous across the Archipelago.
5. Our study demonstrated that *Z. wollebaecki* is an effective vector for the transport of marine nutrients to terrestrial ecosystems. Transported nutrients occur in high concentrations in the soils and are used by shoreline plants. These effects are spatially restricted to the areas where seals occur and the most parsimonious explanatory variable for these patterns is the islands' topography (or elevation).

Key-words: *Cryptocarpus*, isotopic enrichment, sea lion, *Sesuvium*, soil ammonia and nitrate, topography.

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Introduction

The movement of materials and organisms between ecosystems is a common process in nature (e.g. Likens & Borman 1975; Nakano & Murakami 2001). Cross-ecosystem exchanges can be categorized into three major groups: (1) transport of nutrients and materials by physical agents such as water or wind; (2) transport of nutrients and materials by biotic agents such as vertebrates; and (3) movement of prey and consumers

between habitats (Polis, Anderson & Holt 1997). Since Elton (1927), this process has been noted in both terrestrial and aquatic communities. However, a theoretical framework for it has only recently been generated, mainly based on food web theory (DeAngelis 1980; Polis *et al.* 1997; Huxel & McCann 1998; Fagan, Cantrell & Cosner 1999; Huxel, McCann & Polis 2002). In this framework it is recognized that nutrients and materials are transported from more to less productive ecosystems, and that these spatial subsidies depend on the permeability of adjacent habitats, or on specific characteristics of physical–biotic vectors. For example, in the case of physical transport, the flow, speed and volume of water and/or wind could determine the amount and kind of transported materials (Gosz 1991; Witman, Ellis & Anderson, in press). Mobility, behaviour and physiology are important characteristics

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that modify the impact of biotic vectors (Nystrom & Pehrsson 1988; Johnston & Bildstein 1990).

Most of the empirical approaches to these theoretical propositions have been tested in situations where differences between terrestrial and marine ecosystem productivity are large, such as desert islands located in areas with high marine productivity (Rose & Polis 1998). On these islands the perimeter–area ratio (P/A) is a major factor determining the extent of exchange caused by physical agents (i.e. marine input is more extensive and influential on small compared with large islands, Polis & Hurd 1995, 1996; Anderson & Wait 2001). In contrast, transport by biotic vectors (e.g. seabirds and seals) is far less dependent on the P/A ratio (i.e. Anderson & Polis 1999) but more dependent on habitat interface (i.e. marine–terrestrial) permeability (Polis & Hurd 1996).

Habitat interface permeability, defined as the degree to which the boundary between habitats deflects the movements of biotic and abiotic vectors (Wiens, Crawford & Gosz 1985), depends on topography (i.e. the coastline features and substrate elevation, Witman *et al.*, in press) as well as on the mobility of biotic vectors. Transport of nutrients by highly mobile vectors (e.g. seabirds) should be relatively independent of habitat topography when compared with transport by less mobile organisms (e.g. marine mammals, reptiles and flightless seabirds). For example, some topographic features, such as cliffs, act as barriers for the movement of low-mobility biotic vectors (seals and penguins), but attract other highly mobile organisms (e.g. seabirds). The mobility of biotic vectors also affects the spatial influence of nutrient transport. For example, two recent studies of low-mobility biotic agents (marine turtles and penguins) showed that the direct influence of transported marine nutrients is restricted to a local scale on nesting grounds and immediately adjacent areas (Erksine *et al.* 1998; Bouchard & Bjorndal 2000). In contrast, the impact of highly mobile animals (e.g. gulls) exerts a considerable spatial influence on their nesting places and may extend far beyond (Hutchinson 1950; Iason, Duck & Clutton-Brock 1986). Consequently, a direct relationship between mobility of biotic vectors and magnitude and spatial extent of nutrient transport in terrestrial habitats is expected.

Sea lions are conspicuous components of temperate and tropical coastal and island communities throughout the world (Nowak 1999). Because they spend long periods of time in coastal and shoreline habitats they could serve as important biotic vectors for the transport of food and nutrients across ecosystems. Transport by sea lions occurs primarily through defecation and secondarily via onshore mortality (Hutchinson 1950). Sea lion faeces could be an important source of nitrogen and phosphorus for terrestrial plants (Coker 1919). A large body of literature indicates that terrestrial plant growth and cover are limited by the availability of these macronutrients (DiTomasso & Aarsen 1989; Koerselman & Mueleman 1996). Therefore,

nutrient input by marine mammals' faeces is expected to increase primary productivity (Burger, Lindeboom & Williams 1978; DiTomasso & Aarsen 1989), but also, an excessive input may kill vegetation or alter composition of the plant community. Some studies have mentioned the alteration of island vegetation by seal manuring (Gillham 1961a,b; Smith 1978), but the factors determining their use of terrestrial habitats and the incidence and magnitude of marine nutrient transport by their defecation are virtually unknown. Because sea lions are low-mobility biotic vectors, they are excellent subjects for studying the influence of habitat permeability on biotic transport.

The Galápagos sea lion *Zalophus wollebaecki* (Silvertsen) is widely distributed throughout the Galápagos Archipelago (Limberger 1990). It occurs on gently sloping rocky shores and sandy beaches of almost all the central, west and south islands (Eibl-Eibesfeldt 1984). These islands range in area from 0.05 to 4500 km² and are located in a highly productive marine system (Houvenagel 1984). Low-productivity plant communities characterize the shorelines of these islands (McMullen 1999) because of their recent volcanic origin (Simkin 1984) and harsh climatological conditions (Colinvaux 1984). We predicted that marine-derived nutrients transported by sea lions would have significant effects on terrestrial plants (i.e. on their chemical composition and physiological-ecology).

In this study, we: (1) describe the distribution of breeding and non-breeding colonies of Galápagos sea lions at both regional (between islands) and local (within island) spatial scales; (2) analyse the spatial extent and magnitude of marine-derived nutrient transport to terrestrial ecosystems exerted by these marine mammals; and (3) place our findings in the context of the emerging theoretical framework for the process of nutrient exchange between marine and terrestrial ecosystems.

Materials and methods

STUDY SITE

The Galápagos Archipelago is composed of 18 large islands (area > 1 km²) and 108 small islands (area < 1 km², Snell, Stone & Snell 1996). Because of their volcanic origin these islands differ greatly in topography with mean elevations ranging from 10 to 1707 m above sea level (Yeakley & Weishampel 2000). The islands also differ in age with the oldest islands as old as 3.3 million years and the more recent islands around 0.7 million years. In the western side of the Archipelago, the larger and younger islands, Isabela and Fernandina, have very little vegetation whereas, in the eastern and central islands vegetation is more abundant (Perry 1984). On the central islands, plant community composition varies with altitude showing three distinct ecological zones (Johnson & Raven 1973). The littoral zone (0–50 m above sea level) comprises plants that

tolerate both dry and saline conditions (red, black and button mangroves, prickly pear and candelabra cactus, salt bush and common carpetweed). The arid lowlands (50–200 m above sea level) contain mid-size trees and bushes (Galápagos guaba, pisidia and pisonia). Trees (scalesia trees, catís claw, Galápagos miconia and tree fern) dominate the moist uplands (200–850 m above the sea level).

The islands are extremely arid compared with most tropical archipelagos and experience two distinct seasons each year (Colinvaux 1984): warm and cold. The warm season (typically January to May) is characterized by high sea-air temperatures and clear skies. Littoral and arid lowland regions experience a peak in plant growth during this period. In contrast, lower air and sea temperatures, overcast skies and little precipitation in the lowlands characterize the cold season (from June to December). There are no studies of terrestrial productivity in the Galápagos, but low levels of precipitation in the littoral region coupled with the volcanic origin of the soils are characteristic of low levels of primary productivity (Lieth 1978).

THE GALAPAGOS SEA LION

The genus *Zalophus* occurs as three isolated species: *Z. japonicus*, on the coasts of Japan and Korea, *Z. californianus*, on the Pacific coast of North America and *Z. wolfebaeki*, in the Galápagos Islands (Trillmich 1979). *Zalophus* is essentially a coastal animal, frequently hauling out on shore throughout the year and rarely found more than 16 km out to sea (Nowak 1999). On land *Zalophus* may walk slowly, move at a rapid gallop or stride over smooth surfaces using only the front flippers. In the Galápagos, *Zalophus* is basically diurnal, with peaks of activity in the morning and late afternoon (Eibl-Eibesfeldt 1984). The diet of *Zalophus* consists mainly of small pelagic fish and cephalopods (S. Salazar & R. Bustamante, unpublished data). In terms of behaviour these animals are highly gregarious even when empty space is available. They inhabit the islands in both their breeding and non-breeding seasons.

Eibl-Eibesfeldt (1984) reported that in the Galápagos, *Zalophus* might use sandy beaches for resting, but seldom, for breeding. Trillmich (1979), however, stated that the Galápagos sea lion prefers flat beaches, either sandy or rocky, where there is easy access to relatively calm waters, and where it can spend the hot hours around tide pools or in the shade of vegetation. There is local variation in the reproductive season but on central islands, peak pupping occurs during the warm season (January, H. Snell, personal communication in Eibl-Eibesfeldt 1984).

SEA LION SPATIAL DISTRIBUTION

To test the idea that topographic features determine the distribution of less mobile marine organisms in terrestrial environments, we analysed the distribution of the

Galápagos sea lion colonies at both regional and local scales (within 200 km² and 1 km², respectively, Waide *et al.* 1999).

The regional distribution of *Z. wolfebaeki* was recorded during three surveys covering 51 islands of the central, western and eastern archipelago (Fig. 1). These islands ranged in area from 0.004 to 4588 km², in perimeter from 0.2 to 634 km and in the P/A ratio from 0.138 to 113.6 (Table 1). In each survey, two observers recorded the presence and abundance of reproductive and non-reproductive colonies at each island, by disembarking from small inflatable or wooden-hulled dinghies. Reproductive colonies were recognized by the presence of pups. The differentiation between both kinds of colonies was important for the study because it is related to the individual permanence on the colonies. Non-breeding colonies are ephemeral whereas breeding colonies occur year round. This differentiation is also important because in spatial terms the reproductive colonies have less variable limits than non-reproductive colonies. The geographical position of each colony was registered by use of Global Positioning Systems (GPS) devices. Monitoring was conducted during daylight hours, using direct and indirect counting methods. The direct method consisted of recording all individuals occurring in the colonies and adjacent areas (e.g. shrubs, hills and coves). The indirect method was used in areas that were difficult to access. In this method observers used binoculars to count seals from a boat. The boat was never more than 50 m from the colonies and was driven at low speed (less than 8 knots) to ensure accurate counts. Colony positions and limits were downloaded from the GPS and, by the use of ArcView GIS (Geographic Information System) software (Environmental Systems Research Institute, Inc. 1996), geo-coded (added) onto a topographical geo-referenced map of the archipelago. In both direct and indirect methods the spatial extent of the reproductive colonies was calculated from the topographical map by establishing a buffer zone around the colony. To do this, a circle with a radius of 10 m surrounded the position of each colony on the map. The radius of 10 m is a conservative approximation that considers the natural home range of individual sea lions on land (Peterson & Bartholomew 1967). The spatial extent of the colonies on each island was calculated by the integration of the polygon defined by the overlapping circles.

To analyse the relationship between the spatial extent of sea lion colonies and the geographical characteristics of the islands, we used information on geographical variables available from several prior studies (Raven 1973; Connor & Simberloff 1978; Snell *et al.* 1996; Yeakley & Weishampel 2000; Rejmánek & Klinger 2002).

To explore in more detail the influence of topography on the distribution of sea lion colonies, a local-scale study was conducted on the Isles of Caamaño (0 45'21"S, 90 16'34"W) and Plazas Sur (0 34'56"S,

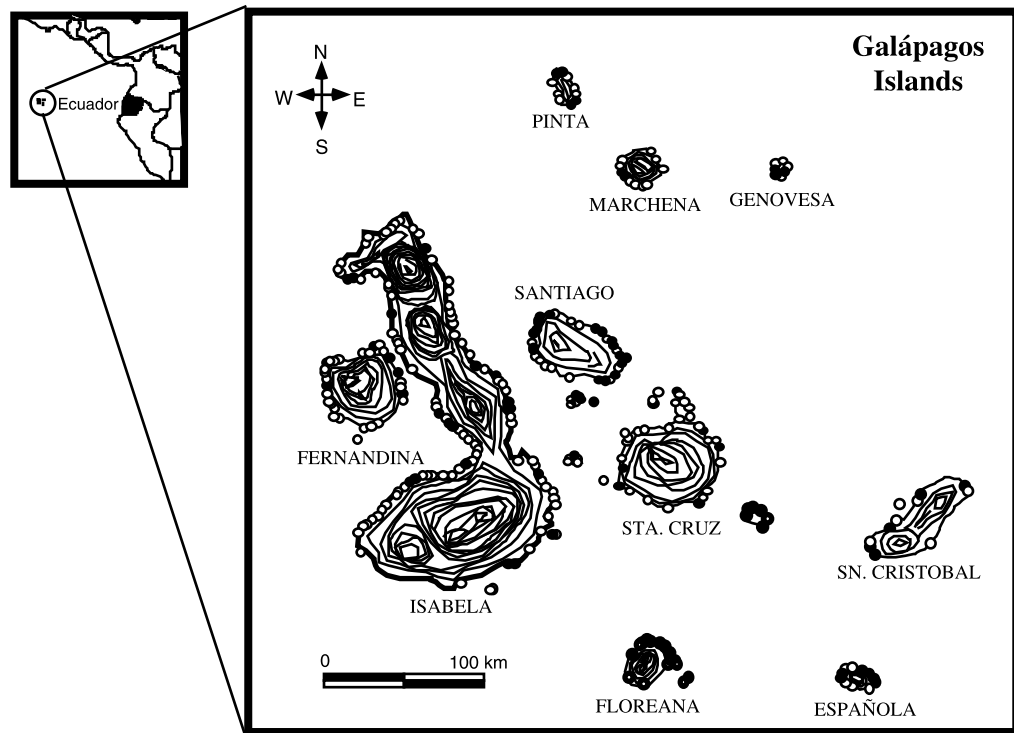


Fig. 1. Map of the Galápagos islands showing elevation curves (from the shore to inland each curve represent an increment of 50 m) of the islands and the distribution sea lions reproductive (●) and non-reproductive colonies (○).

90° 9'57"). Both isles are small and covered by littoral zone plant species (see above). Caamaño has an area of 0.045 km² and a perimeter of 0.77 km. Plazas Sur has an area of 0.12 km² and a perimeter of 2.3 km (Snell *et al.* 1996). In terms of topography, Caamaño is quite homogeneous with a maximum elevation of 5 m above the sea level, whereas Plazas Sur has a sloping north-south profile that increases from 0 to 15 m above the sea level. Sea lion colonies on these islands were surveyed using the direct monitoring and GIS methodologies explained above.

MARINE NUTRIENTS IN THE TERRESTRIAL ECOSYSTEM

The presence of marine-derived nutrients in terrestrial ecosystems was analysed at both regional and local scales.

To analyse the possible influence of marine-derived nutrients on plant communities on a regional scale around the archipelago, we collected plant tissue from seven randomly chosen islands ranging in area from 0.001 to 985 km². From each island, leaves of the most common plant species occurring in the colonies or adjacent to them (in cases where the colonies occurred just on rocky or sand substrates) were collected at the beginning of the 2001 and 2002 warm seasons (i.e. when peaks in both plant growth and sea lion pupping occur). These plant species collectively represented more than 80% of the community-biomass/ground cover of the island coastal and/or mainland sites. The material was transported in plastic bags to the Charles Darwin

Research Station on Santa Cruz Island. In the laboratory, plant material was oven-dried at 70 °C for 49 h and ground to fine powder. Treated samples were then submitted to the University of Arkansas Stable Isotope Laboratory for analysis of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotopes.

More detailed studies of plant isotopic composition and soil nutrient concentrations were conducted at the local spatial scale in January 2002. In these studies, we created a system of transects with evenly spaced sampling stations that formed a grid covering over 90% of each island (Fig. 2). A total of 54 stations was distributed on six plots on Caamaño (Fig. 2a) and 36 stations distributed within nine transects on Plazas Sur (Fig. 2b). To analyse the topography of the islands, the elevation of each station was measured using a digital altimeter with a precision of ± 1 m. Elevations were analysed using geo-statistical techniques detailed in the Statistical Analysis section. At each station, we collected plant tissues (leaves) and removed soil cores (0–10 cm depth). Plant tissues were treated and analysed for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotopes as described above. Soils were analysed according to procedures described in Mulder & Keall (2001). The procedure consisted of determining moisture content gravimetrically and using this value to calculate the nutrient concentration per gram of dry soil. For each station, 5 g of 2 mm sieved soil were extracted in 60 ml 2 M KCl for 24 h and filtered through Whatman GF/F glass fibre filters. Ammonia and nitrate content of the extracts were measured using Hach spectrophotometer techniques (Hach 1997). Considering their elevation and plant species composition, stations were grouped into six

Table 1. Island locations, main geographical features including the perimeter–area ratio (P/A) and the type of colony (NR = non-reproductive, R = reproductive) of *Z. wolfebaeckii*

Island	Latitude	Longitude	Perimeter (km)	Area (km ²)	P/A (km ⁻¹)	Colonies
Isla Baltra	0–25'30"S	90–16'30"W	27	26.20	1.03	NR
Isla Bartolome	0–16'51"S	90–32'48"W	6	1.25	4.82	R & NR
Isla Caamaño	0–45'21"S	90–16'34"W	0.7	0.05	15.56	R
Islote Champion	1–14'7"S	90–23'8"W	1.29	0.10	13.58	R & NR
Islote Corona del Diablo	1–12'43"S	90–25'14"W	0.5	0.00	113.64	NR
Islote Cousins	0–14'8.3"S	90–34'29.1"W	0.6	0.01	69.93	R
Islote Cuatro hermanos #2	0–50'41"S	90–47'54"W	2.42	0.30	7.96	NR
Islote Cuatro hermanos East	0–50'42"S	90–44'55"W	1.27	0.07	17.64	NR
Islote Cuatro hermanos South	0–51'30"S	90–46'30"W	4.46	0.73	6.11	NR
Islote Cuatro hermanos West	0–50'39"S	90–48'30"W	1.91	0.20	9.34	NR
Isla Daphne Mayor	0–25'11"S	90–22'12"W	2.36	0.33	7.15	NR
Isla Daphne Menor	0–23'30"S	90–20'56"W	1.24	0.08	15.58	NR
Isla Enderby	1–13'12.5"S	90–21'42"W	1.7	0.19	8.81	NR
Isla Española	1–22'30"S	89–40'30"W	40	60.48	0.66	R & NR
Isla Fernandina	0–22'0"S	91–31'20"W	102	642.48	0.16	R & NR
Isla Floreana	1–17'0"S	90–26'0"W	57	172.53	0.33	R & NR
Isla Genovesa	0–19'40"N	89–57'20"W	22	14.11	1.56	R & NR
Roca Gordon Este	0–33'48"S	90–8'22"W	0.4	0.03	13.79	NR
Isla Isabela	0–25'30"S	91–7"W	634	4588.12	0.14	R & NR
Isla Lobo	0–51'25.3"S	89–33'51.8"W	1.54	0.07	23.33	R
Isla Cowley	0–22'56"S	90–57'39"W	0.4	0.04	11.43	R
Islote Watson	1–20'41"S	90–18'31"W	0.86	0.03	28.20	NR
Isla Gardner	1–19'52"S	90–17'20"W	2	0.81	2.46	R
Islote Guy Fawkes (largest)	0–30'45"S	90–31'39"W	0.5	0.03	14.71	NR
Islote Guy Fawkes (2nd smallest)	0–29'48.5"S	90–30'46"W	0.2	0.01	16.67	NR
Islote Leon Dormido	0–46'26"S	89–31'0"W	0.97	0.05	19.36	NR
Isla Marchena	0–20'20"N	90–28'25"W	51	129.96	0.39	R & NR
Islote Mosquera	0–24'4"S	90–16'33"W	1.42	0.05	30.87	R
Isla Pinta	0–35'18"N	90–45'17"W	39	59.40	0.66	R & NR
Isla Pinzón	0–36'30"S	90–39'57"W	17	18.15	0.94	R & NR
Isla Plaza Norte	0–34'36"S	90–9'32"W	1.9	0.09	21.59	R & NR
Isla Plaza Sur	0–34'56.3"S	90–9'57.0"W	2.3	0.12	19.33	R
Isla Rabida	0–24'35"S	90–42'30"W	11	4.99	2.20	R & NR
Roca Sin Nombre	0–40'0"S	90–35'0"W	0.5	0.08	6.67	NR
Rocas Bainbridge #1	0–20'27"S	90–33'28"W	1.32	0.11	11.56	NR
Rocas Bainbridge #2	0–20'45"S	90–33'22.5"W	0.8	0.03	27.68	NR
Rocas Bainbridge #3	0–20'55"S	90–33'56"W	1.77	0.18	9.66	R
Rocas Bainbridge #4	0–21'24"S	90–33'48"W	0.93	0.03	27.03	NR
Rocas Bainbridge #5	0–21'45"S	90–33'56"W	0.9	0.04	22.11	NR
Rocas Bainbridge #6	0–21'56"S	90–34'11"W	0.8	0.04	17.84	NR
Rocas Bainbridge #7	0–22'23"S	90–34'20"W	0.42	0.01	52.76	NR
Roca Beagle North	0–24'40"S	90–37'40"W	0.6	0.01	84.15	NR
Roca Beagle South	0–24'57"S	90–37'46"W	1.39	0.09	15.92	R & NR
Roca Beagle West	0–24'52"S	90–37'53"W	0.71	0.04	16.51	R
Isla San Cristobal	0–48'30"S	89–25'0"W	162	558.09	0.29	R & NR
Isla Santa Cruz	0–37'0"S	90–21'0"W	176	985.55	0.18	R & NR
Isla Santa Fe	0–49'0"S	90–3'30"W	24	24.13	0.99	R & NR
Isla Santiago	0–15'30"S	90–43'30"W	146	584.65	0.25	R & NR
Isla Seymour Norte	0–23'30"S	90–17'0"W	4.9	1.84	2.66	R & NR
Sombrero Chino	0–22'2.5"S	90–34'55"W	1.8	0.21	8.61	R
Isla Tortuga	1–1'21.5"S	90–52'11.5"W	9.22	1.30	7.10	NR

plots of nine stations in Caamaño and nine transects with four sampling stations on each in Plazas Sur.

STATISTICAL ANALYSIS

The areas and P/A ratio of islands with different kinds of colonies (reproductive, non-reproductive and both) were contrasted using a one-way analysis of variance (ANOVA) model (Winer 1971). Colony category was considered the main fixed factor (with three levels) because

these levels represent all the possible combinations over which the study could be done (Underwood 1997).

Abundance patterns of reproductive and non-reproductive colonies were analysed using a one-way ANOVA model with the colony category (reproductive and non-reproductive) as a main fixed factor. To maintain a balanced ANOVA model, only islands with both kinds of colonies were considered for the analysis.

The relationship between the proportion of area (%) occupied by reproductive colonies and the geographical

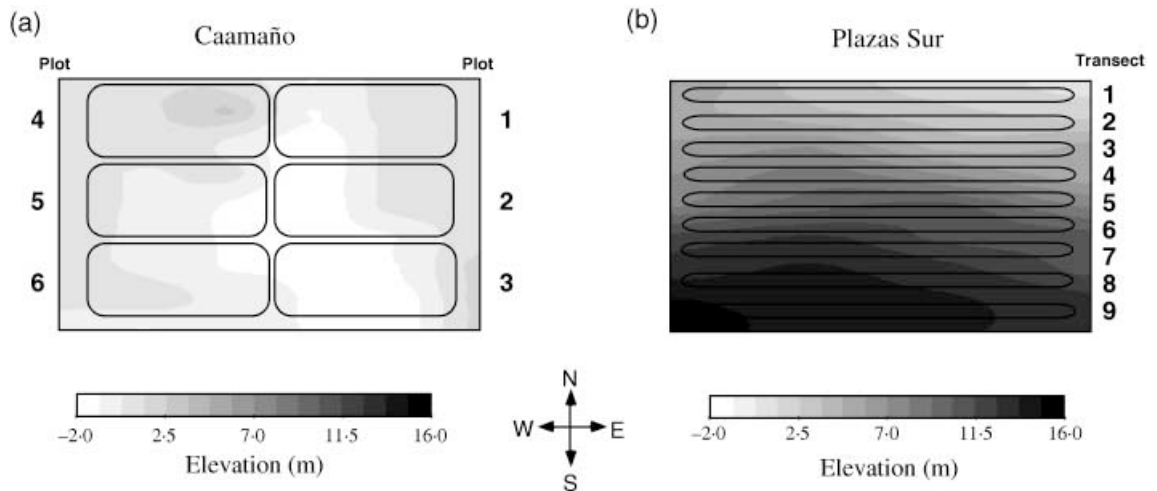


Fig. 2. Schemes showing the distribution of the sampling plots and transects in Camaño (a) and Plazas Sur (b) in relation with topography (elevation) of the islands.

characteristic of the islands (Area, Perimeter, P/A ratio and Elevation) was analysed using multiple stepwise regressions. After this, a simple regression analysis was performed using the significant variables identified in the previous step (Statsoft 2000). To maintain assumptions of the linear model, all the variables were log-transformed and the residuals were checked for normal distribution after each analysis.

The average values of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of the most common plant species sampled on the seven randomly chosen islands were contrasted by one-way ANOVA. In this analysis islands were considered as main random factors because no *a priori* hypotheses about them were stated, and their levels represented one of the several potential combinations over which the study could be done (Underwood 1997).

In all cases, a Tukey (HSD) multiple comparisons test (for single factors) was performed after the ANOVA (Day & Quinn 1989). Normality of the data was checked by graphical procedures, and when appropriate (i.e. for Area, P/A ratio and Abundance variables), the data were log-transformed. Results are reported using the original (i.e. non-transformed) variables. Homogeneity of variances and independence of the data were verified using Levene's and Durbin-Watson tests, respectively (Wilkinson, Blank & Gruber 1996).

The elevation patterns of Camaño and Plazas Sur were analysed using a geostatistical approach (Rossi *et al.* 1992). Contour maps were plotted by Kriging interpolation techniques (Spyglass Transform, version 3.0, Spyglass Inc., Savoy, IL), using the mean altitude of the stations distributed on each island sampling grid. Kriging is a geo-statistical tool in which, from a defined spatial grid with observed values, it is possible to predict (interpolate) non-observed values for a determined variable (Cressie 1991). The interpolation function was checked by analysing the variance homogeneity of the data in the interpolated matrix (Robertson 1987). To do this, the spatial pattern of variances was

also plotted in a contour map. For each case (i.e. beach) there were no significant differences in the spatial dispersion of interpolated variance.

Results

SPATIAL DISTRIBUTION OF SEA LION COLONIES AT THE REGIONAL SCALE

Sea lion colonies were recorded on the 51 islands surveyed (Table 1). Some islands have only reproductive or only non-reproductive colonies (10 and 23 islands, respectively), whereas others (18 islands) had both kinds of colonies. In terms of area, the islands with solely reproductive or non-reproductive colonies were significantly ($F = 31.63$, $P = 0.0001$) smaller (mean = 0.15 ± 0.07 and 1.3 ± 1.13 SE km², respectively) than the ones with both kinds of colonies (mean = 435.8 ± 253.8 SE km²). Consequently, the P/A ratio of the islands with only reproductive or non-reproductive colonies was significantly ($F = 27.23$, $P = 0.0001$) higher (20.76 ± 6.02 and 23.43 ± 5.53 SE, respectively) than on the ones with both kinds of colonies (3.74 ± 1.5 SE).

All the colonies occurred at shorelines with elevations lower than 20 m (Fig. 1). Within the 440 colonies, 72 were reproductive and 368 were non-reproductive. However, the opposite pattern was seen in terms of the number of individuals, with 5867 in the reproductive colonies and 2279 in the non-reproductive colonies out of a total of 8146 individuals. Owing to these two patterns, for each island the average number of individuals in reproductive colonies was higher than on the non-reproductive ones (Fig. 3). This difference becomes evident in the case of islands with both kinds of colonies where the reproductive colonies showed mean abundances (76.33 ± 16.73 SE individuals) that are significantly higher ($F = 50.44$, $P = 0.0001$) than the non-reproductive ones (11.53 ± 3.11 SE individuals).

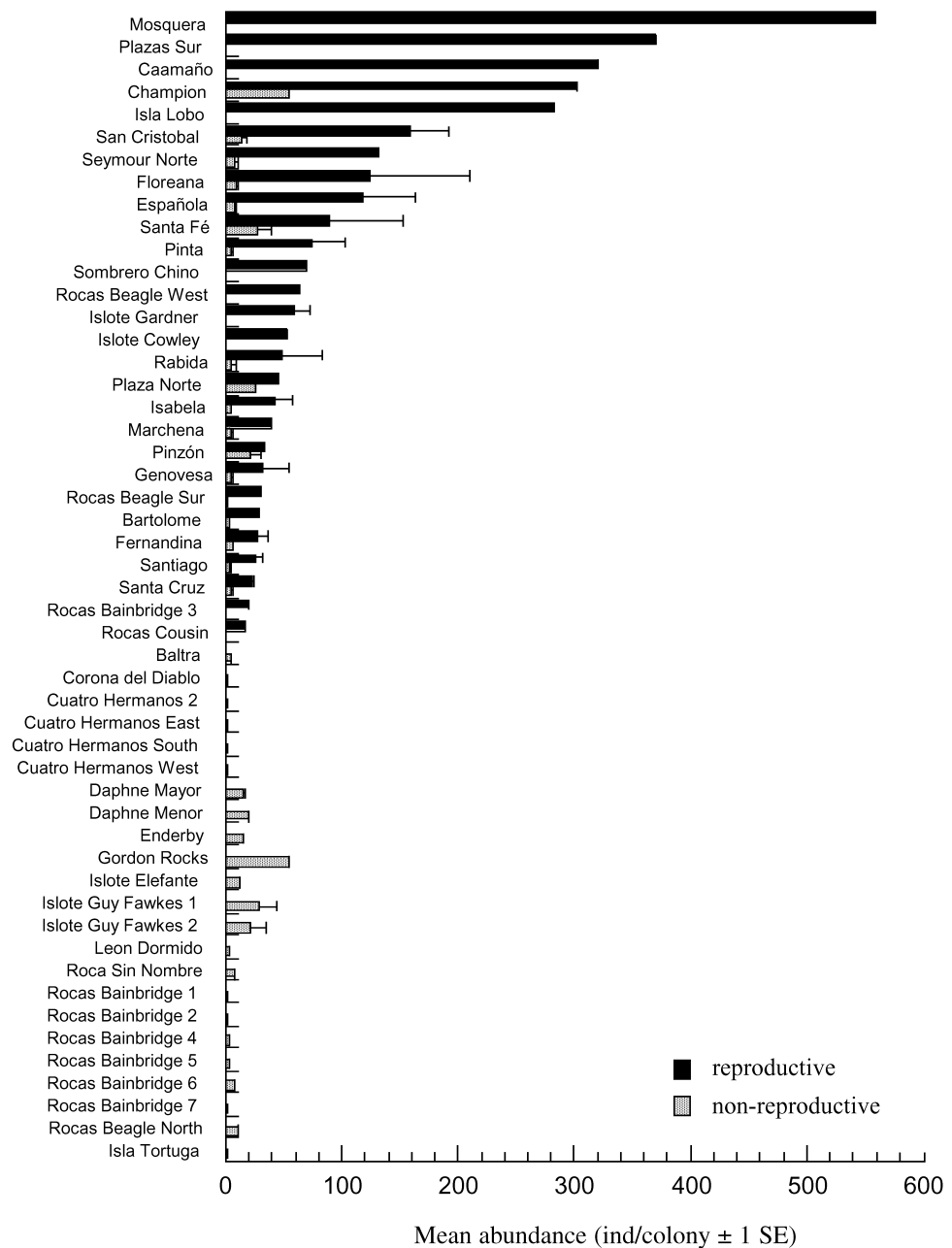


Fig. 3. Mean sea lion individual abundances on the reproductive and non-reproductive colonies recorded on the 51 islands surveyed.

The spatial extent of reproductive colonies ranged from 0.003 (Islote Cousins) to 0.08 km² (Isla Española) and the percentage of island occupation ranged from 0.0009 (Isla Isabela) to 56.81% (Isla Caamaño). The percentage of island occupation decreased significantly with area ($F = 454$, $P = 0.0001$), perimeter ($F = 255.5$, $P = 0.0001$) and elevation ($F = 132.6$, $P = 0.0001$). However, it increased significantly with the P/A ratio ($F = 403.0$, $P = 0.0001$) of the islands (Fig. 4). The stepwise multivariate regression analysis showed that the best explanatory variable for the percentage of island occupation was island area (adjusted $R^2 = 0.94$, $P = 0.0001$) followed by elevation (adjusted $R^2 = 0.95$, $P = 0.02$).

In the relationship between the percentage of island occupied and the P/A ratio (Fig. 5), two main groups of islands can be recognized. The first group contains big islands where the P/A ratio was always higher than the percentage of occupation and a second group of mainly small islands where in many cases the percentage of occupancy was higher than the P/A ratio. The most extreme example of the second group was Isla Caamaño, which had the highest value of island occupancy (Fig. 5). It is worth mentioning that some islands with similar geographical characteristics (P/A; i.e. Caamaño, Plazas Sur, Plazas Norte, Rocas Beagle West and Champion) showed completely different levels of island occupation.

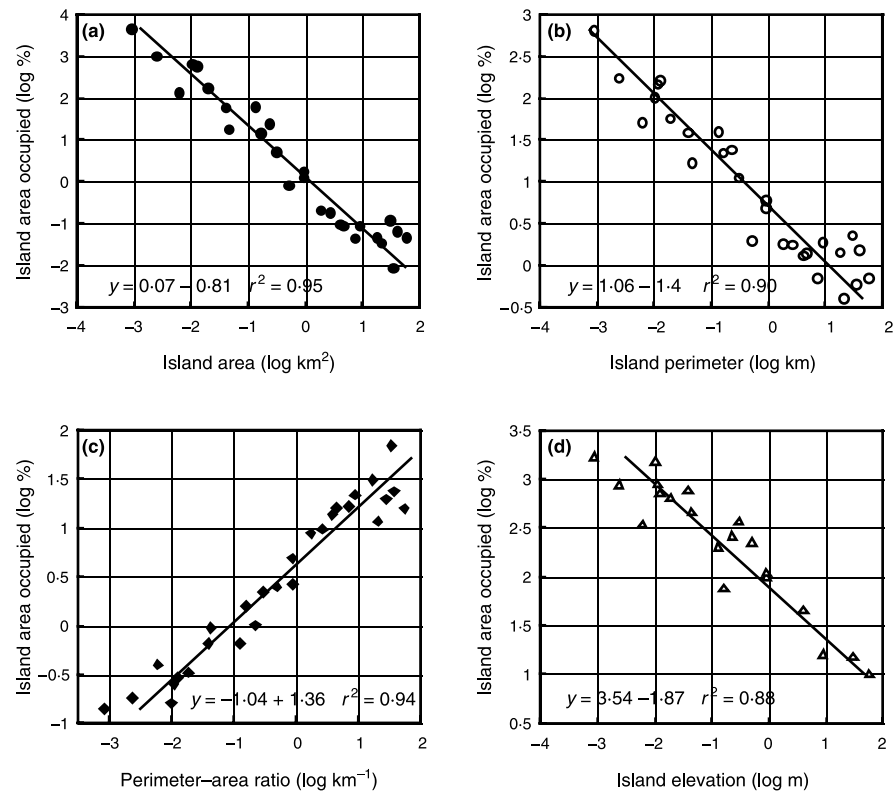


Fig. 4. Linear regression analysis between island area (a), island perimeter (b), perimeter-area ratio (c), island elevation (d) and the percentage of the islands areas occupied by the sea lions' reproductive colonies.

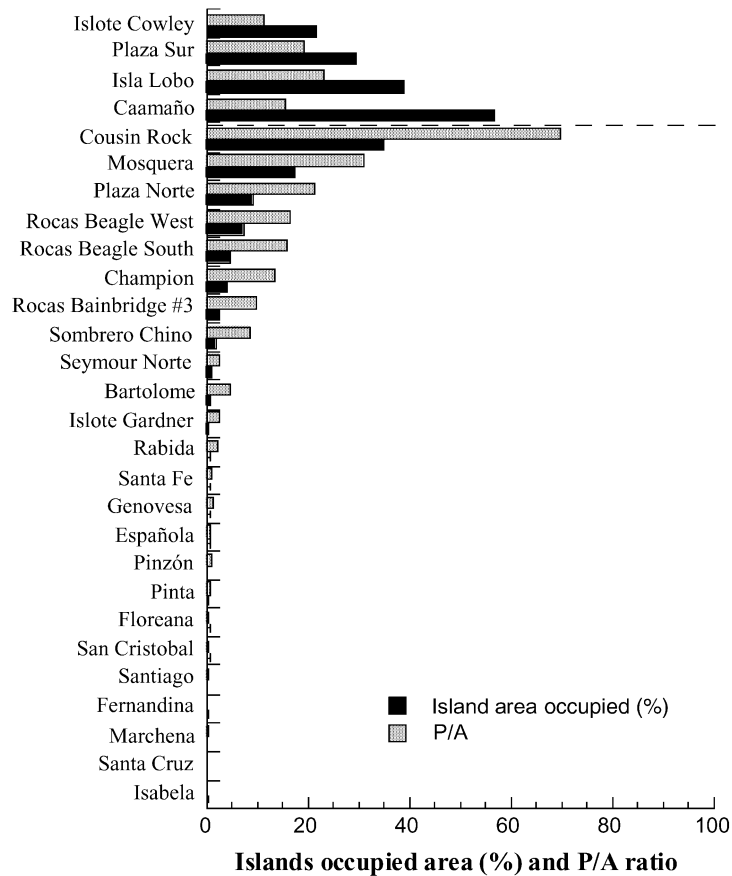


Fig. 5. Proportions (%) of the islands' areas occupied by the sea lions and the perimeter-area ratio of each island. Dashed line divides the two main groups of islands showing differences on the relation between both variables (see text for details).

SPATIAL DISTRIBUTION OF SEA LION
COLONIES AT THE LOCAL SCALE

At the local scale on Caamaño, one reproductive group with a total 321 individuals was recorded along the rocky shoreline. Major densities were on the west and east sides. Some sea lions usually walk across the middle of the island especially on the west side of the island. Mainly because of the high plant coverage (salt bushes), sea lions cannot walk through the east side of the island. At Plazas, one reproductive group composed by 370 individuals was recorded around the north-east shoreline. In this case no individuals were observed crossing or walking across the island.

MARINE NUTRIENTS IN THE TERRESTRIAL
ECOSYSTEM AT THE REGIONAL SCALE

At the regional scale, 10 different plant species were collected from the seven randomly selected islands (Fig. 6). The most common species (occurring on at least three islands) were *Cryptocarpus pyriformis* (Linnaeus), *Sesuvium edmonstonei* (Hook) and *Maytenus octogona* (L'Her). Isotopic analysis indicated that the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ averages of these species ranged from 0.1 to 29.9 and from -31.2 to -19.6 , respectively. High variability was observed in the isotopic averages of the

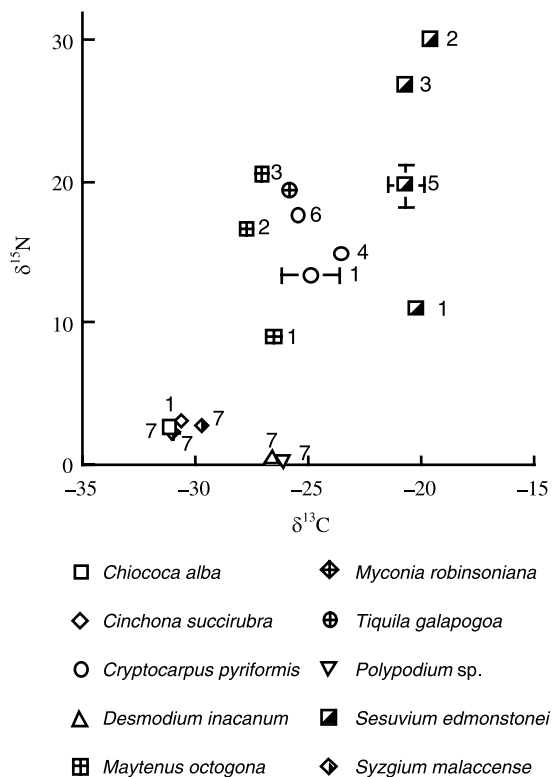


Fig. 6. Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopic signatures of plant species collected on seven randomly choose islands. 1 Isla Santa Cruz (elevation = 864 m), 2 Isla Plazas Sur (elevation = 16 m), 3 Cousin Rock (elevation = 20 m), 4 Isla Caamaño (elevation = 2 m), 5 Isla Champion (elevation = 46 m), 6 Isla Lobo (elevation = 2 m), 7 Isla Floreana (elevation = 640 m).

most common species occurring on each island. In spite of this, within each plant species the individuals from big and high-elevation islands showed lower levels of $\delta^{15}\text{N}$ than the ones from smaller and low-elevation islands. Low levels corresponded with values reported for plant communities taking up terrestrial nutrients, while high levels corresponded with ranges reported for plant communities influenced by marine nutrients (Anderson & Polis 1998). This trend was present and showed significant differences in *C. pyriformis* ($F = 179.4$, $P = 0.0001$), *M. octogona* ($F = 1395.9$, $P = 0.0001$) and *S. edmonstonei* ($F = 381.4$, $P = 0.0001$). In these cases, all the island averages were significantly different ($P < 0.0001$ for all the HSD *post hoc* comparisons).

In the case of carbon the main differences in $\delta^{13}\text{C}$ occurred between plant species and therefore low variability was observed within species. The lowest values corresponded to *C. alba* (-31.2 ± 0.14) and *M. robinsoniana* (-30.9 ± 0.4) from Floreana and Santa Cruz, respectively, while the highest values were observed for *S. edmonstonei* (-19.6 to -20.73) and *C. pyriformis* (-23.61 to -25.50) collected from several islands.

MARINE NUTRIENTS IN THE TERRESTRIAL
ECOSYSTEM AT THE LOCAL SCALE

The relationship between island topography (elevation) and differences in plant species isotopic signatures was also evident at a local scale. On Caamaño (Fig. 2a) the mean elevation was not higher than 2 m above sea level (ASL) and the central part of the island was 2 m below sea level. In Plazas Sur (Fig. 2b) the mean elevation was around 7 m ASL, with a sharp slope from the north side of the island (with elevations around 2 m ASL) to the southern side of the island (with elevations around 16 m ASL). On both islands, sea lions occurred in areas with lower elevations. On Caamaño sea lions usually occurred in the area located near the sampling stations 4, 5 and 6 (Fig. 2a), whereas on Plazas they were more common on the shoreline near the sampling transects 1, 2 and 3 (Fig. 2b).

Three plant species were collected from the sampling stations of Caamaño: *C. pyriformis*, *S. edmonstonei* and *Nolana galapagensis* (Christopher). Within these, *C. pyriformis* occurred at 45 out of 54 stations, while *S. edmonstonei* and *N. galapagensis* occurred at 11 and 1 stations, respectively. Mean isotopic values on *C. pyriformis* were 16.7 ± 2.4 SD for $\delta^{13}\text{C}$ and -21.9 ± 1.03 SD for $\delta^{15}\text{N}$. In the case of *S. edmonstonei* the averages were 15.11 ± 3.1 $\delta^{13}\text{C}$ and -23.27 ± 1.01 $\delta^{15}\text{N}$, and for *N. galapagensis* they were 14.3 ± 0.2 for $\delta^{15}\text{N}$ and -21.85 ± 0.6 for $\delta^{13}\text{C}$, respectively. Isotopic mean values of the plants occurring at the sampling stations ranged from 14.8 to 19.7 for $\delta^{15}\text{N}$ and from -23.6 to 24.7 for $\delta^{13}\text{C}$ (Fig. 7a). Significant differences were observed between $\delta^{15}\text{N}$ values ($F = 6.76$, $P = 0.0001$). The stations on the plots 4, 5 and 6 showed significantly higher values (on the range of marine-enriched plant species, Anderson & Polis 1998) of this variable than the ones on the plots

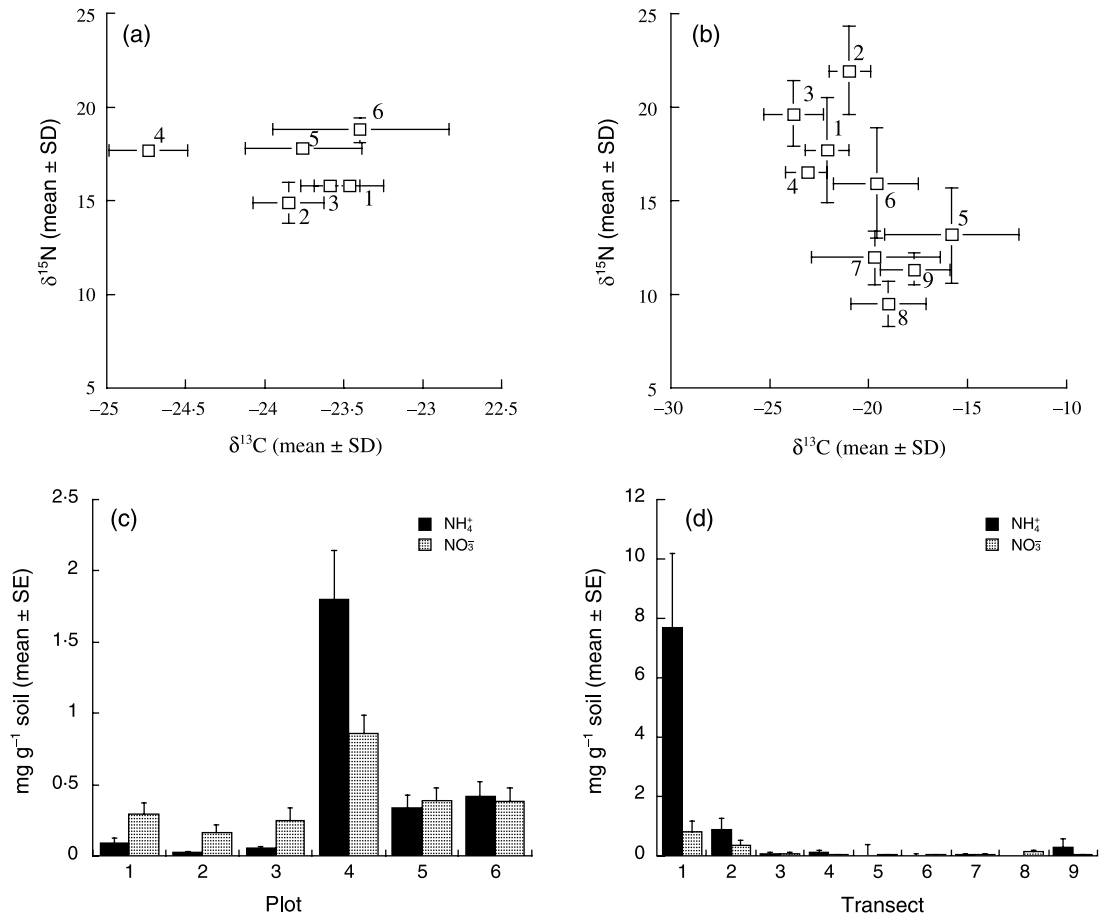


Fig. 7. Isotopic signatures of plants sampled on each plot in Caamaño (a) and Plazas Sur (b) (numbers indicate the corresponding sampling plot in Caamaño and sampling transect in Plazas Sur). Mean concentrations of ammonia and nitrate on the soil of the sampling plots of Caamaño (c) and sampling transects of Plazas Sur (d).

1, 2 and 3 (Fig. 7a). In the case of $\delta^{13}\text{C}$, there were no significant differences in the mean values of this variable at the different stations ($F = 1.65$, $P = 0.18$).

In Plazas Sur, seven plant species were collected from the sampling stations: *Castela galapageia* (Hook), *Languncularia racemosa* (Linnaeus), *Opuntia echios* (Howell), *Parkinsonia aculeate* (Linnaeus), *Scutia spicata* (Humboldt & Bonpland), *S. edmonstonei* and *Tiquila galapagoa* (Howell). The most common species were *S. edmonstonei* occurring on 30 stations and *T. galapagoa* occurring on 8 stations. Most of the other species were collected only from one station. Mean isotopic values of these species showed a high variability, ranging from 9.3 ± 0.8 (*T. galapagoa*) to 18.4 ± 6.3 (*S. edmonstonei*) in $\delta^{15}\text{N}$ and from 11.3 ± 0.3 (*O. echios*) to 26.1 ± 0.01 (*C. galapageia*) in $\delta^{13}\text{C}$. Mean isotopic values of the plants collected at each station also showed a high variability (Fig. 7b). In the case of $\delta^{15}\text{N}$, there were significant differences ($F = 4.82$, $P = 0.007$) mainly due to the high values observed on transects 2 and 3. In the case of $\delta^{13}\text{C}$, in spite of the high variability observed, there were no significant differences between the stations ($F = 0.42$, $P = 0.84$).

The islands also differed in terms of ammonia and nitrate content of the soils. For example, soil samples from Caamaño showed lower levels of both ammonia and nitrate than Plazas Sur (Fig. 7c,d). Ammonia concentrations in Caamaño ranged from 0.024 mg g^{-1} soil (plot 2) to 1.6 mg g^{-1} soil (plot 4). There were significant differences ($F = 12.1$, $P = 0.0001$) in mean ammonia concentrations, mainly due to the significantly higher levels recorded on stations 4, 5 and 6 (Fig. 7c). The same pattern of significant differences ($F = 26.7$, $P = 0.0001$) was observed for nitrate, but in this case only stations 4 and 6 showed significant higher concentrations. In Plazas Sur (Fig. 7d) ammonia concentrations ranged from 0.014 mg g^{-1} soil (transect 8) to 7.6 mg g^{-1} soil (transect 1). Mostly because of the high concentrations recorded on transects 1 and 2 there were significant differences between the stations ($F = 7.9$, $P = 0.0001$). Nitrate ranged from 0.012 mg g^{-1} soil (transect 9) to 0.803 mg g^{-1} soil (transect 1) and there were significant differences between the transect concentrations ($F = 4.72$, $P = 0.001$). Transect 1 showed significant higher concentrations of this nutrient than the other eight.

Discussion

THE INFLUENCE OF TOPOGRAPHY ON MOVEMENT OF NUTRIENTS ACROSS ECOSYSTEMS

We hypothesized that the influence of a marine organism with low mobility on terrestrial environments would be restricted spatially. This hypothesis is based on the general idea of a direct relationship between the mobility of marine organisms and the extent of their influence on terrestrial ecosystems. Highly mobile organisms could have a widespread influence on terrestrial ecosystems, whereas the influence of less mobile animals should be restricted to specific sites or areas. Several studies with marine birds (highly mobile on land) show that their influence on terrestrial systems (mainly islands and islets) is usually conspicuous and widespread (Gillham 1961a; Hodgdon & Pike 1969; Sobey & Kenworthy 1979; Anderson & Polis 1999). Some exceptions within this group are species with reduced mobility such as flightless cormorants and penguins. These birds have strong, but spatially restricted, influence on the terrestrial ecosystems (Erskine *et al.* 1998). Recently it has been proposed that, owing to their high nesting densities, flightless birds could have a strong indirect effect on the areas surrounding colonies through guano ammonia volatilization (Mizutani & Wada 1988; Mizutani, Kabaya & Wada 1991a,b; Myrcha & Tatur 1991; Tatur, Myrcha & Niegodysz 1997).

Zalophus wollebaecki colonies only occurred on shorelines with elevations lower than 20 m, but they were on all the islands surveyed. Consequently, the influence of this marine organism on Galápagos terrestrial habitats must be restricted to low-elevation shorelines but it is geographically ubiquitous across the Archipelago. As far as we know there is little information about the relationship between topography and the distribution pattern of sea lion colonies. Peterson & Bartholomew (1967) briefly described the distribution of the *Z. californianus* reproductive colonies on San Nicolas Islands, California. In this study, reproductive colonies (as well as the hauling groups) occurred mainly on flat areas on the shoreline. If the use of terrestrial ecosystems is related to the mobility of sea lions, it is possible to predict that many pinnipeds, with the exception of phocids, must use shorelines like *Z. wollebaecki*. Owing to their anatomical characteristics phocids are not very effective in land locomotion (Thewissen & Fish 1997) and as a consequence they should have a more restricted influence on terrestrial habitats. Smith (1978) and Norton *et al.* (1997) suggested that in New Zealand and on sub-Antarctic Marion Island, elephant seals, seals and fur seals, respectively, occur on flat areas of shorelines, similar to *Z. wollebaecki* in our study.

Marine vertebrates most commonly occur on land during their breeding seasons (see Erskine *et al.* 1998;

Bouchard & Bjorndal 2000; Helfield & Naiman 2001; Hutchinson 1950). This temporal aspect of their occurrence has not been explicitly considered in theoretical models describing the connections between marine and terrestrial food webs (Polis *et al.* 1996; Anderson & Wait 2001). Recently, Nakano & Murakami (2001) demonstrated that cross-ecosystem linkages are highly variable in time and space and proposed that to improve our knowledge of these processes, a more complete perspective of study is needed. In many cases the reproductive activities of marine mammals and birds are seasonal, and moreover could be significantly affected by unpredictable environmental perturbations, such as El Niño. Therefore, the magnitude of their effects may also be influenced by such perturbations to their breeding seasons. In our study, most individuals were in reproductive colonies, and the densities and spatial extent of reproductive colonies were higher than the non-reproductive ones (Fig. 3). In terms of seasonality, it is possible to find reproductive colonies of *Z. wollebaecki* in the Galápagos throughout the year, but peak abundance occurs in the warm season. Since our small-scale analysis (at Caamaño and Plazas Sur) was developed at the end of the cold season, it is possible that the high concentrations of nutrients in the soil resulted from the increasing abundance of the seals in their colonies and the low levels of precipitation. On the other hand, it is widely recognized that the first response of marine mammals and birds to the occurrence of perturbations, such as El Niño, is a decrease on their reproductive activities (e.g. Duffy 1990; Limberger 1990). For our study, during 1982–82 and 1997–98 El Niño events *Z. wollebaecki* migrate and decrease dramatically their densities at their colonies (S. Salazar & R. Bustamante, unpublished results). In consequence, it is likely that any effect of these organisms on the terrestrial system will be diminished during EL Niño events. Our research in the Galápagos continues to explore the effect of seasonal variations and also of the effects of possible unpredictable perturbations on the *Z. wollebaecki* colony distributions and their influence on terrestrial ecosystems.

In comparison with abiotic processes (Polis & Hurd 1996), the biotic transport of materials and nutrients from the sea to land (exerted by vectors such as marine birds and seals) must be more independent of the island area and perimeter. Anderson & Polis (1999) explicitly stated that in the case of highly mobile vectors, such as birds, a better explanatory variable for this case is island guano cover. In our study, we found that all the variables considered have a significant relationship with the percentage of island occupation. However, only two of these variables, Area and Elevation, have the high scores in the Multiple Stepwise Regression model. Considering that the percentage of island occupation was calculated by dividing the colony buffer area by island area, it is not surprising that this variable scales closely with island area. This situation also occurs in the study of Polis & Hurd (1996), where they

proposed that the relative importance of marine inputs (MI) vs. terrestrial productivity (TP), or MI/TP ratio, is negatively related to island area. These authors calculated TP as: $tA(0.709 + 0.075[\log A]) \times 10^6$, where t is an estimation of productivity based on the local amount of rainfall (Lieth 1978) and A is the island area. Owing to this, it is not surprising that in their study MI/TP scales negatively with island areas. The problem with the use of correlation and regression analysis to explore the possible relationships between some independent and dependent variables is not new in ecology (Huston 1997). In particular, for the Galápagos there has been much discussion on the search for the best variables to explain the patterns of plant diversity around the Archipelago (see Raven 1973; Connor & Simberloff 1978; Yeakley & Weishampel 2000). Rejmánek & Klinger (2002) recently stated that area is not always the best predictor of diversity patterns on islands and its importance is often attenuated by other factors such as habitat diversity or elevation (which in turn is a condition of habitat diversity). In our study the second better explanatory variable for the percentage of island occupation was island elevation. This variable, scaling negatively with island occupation, lends a strong support to our hypothesis that the use of terrestrial habitats by low-mobility marine organisms is mainly restricted by topography. Moreover, the differences on the island occupation between two islands with similar areas and perimeters such as Caamaño and Plazas Sur (mean occupations of 56.81% and 29.4%, respectively, see Fig. 5) can be related only by their elevation differences (2 and 16 m, respectively; see Fig. 2).

MARINE NUTRIENTS IN TERRESTRIAL ECOSYSTEMS

The isotopic analysis of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ has been widely used to describe the influence of marine-derived nutrients on terrestrial ecosystems (Mizutani & Wada 1988; Mizutani *et al.* 1991a,b; Anderson & Polis 1998; Erskine *et al.* 1998). In these studies the most conspicuous effect of the marine-derived nutrients on plants is the displacement of their $\delta^{15}\text{N}$ signatures from negative or small values (e.g. lower than 10 $\delta^{15}\text{N}$) to higher ones (e.g. closer or higher than 20) in what is called enrichment (Erskine *et al.* 1998).

In our study all the samples collected from Isla Santa Cruz, and Floreana showed signatures between 0 and 15 $\delta^{15}\text{N}$, while the samples collected from the other islands showed values between 15 and 30 $\delta^{15}\text{N}$. Clearly, the differences between these two main groups of samples are related to island area and elevation. The islands with big areas and high altitudes (Santa Cruz and Floreana) showed low values of $\delta^{15}\text{N}$, whereas the islands with small areas and low altitudes (Plazas Sur, Islote Cousins, Caamaño, Champion, Isla Lobo) showed the highest levels. This pattern of differences is evident in the comparison of $\delta^{15}\text{N}$ from the most common plants species on the islands (*C. pyriformis*, *M. octogona* and

S. edmonstonei). Islands' areas and their elevations are negatively correlated in the Galápagos (Rejmánek & Klinger 2002), and as a consequence it is impossible to isolate these factors to explain the observed variations on $\delta^{15}\text{N}$ in this study (but see the discussion about the results of our analysis at small scale). However, these results on the regional scale lend support to our hypothesis relating topography and the effect of marine vectors on terrestrial ecosystems. Wainright *et al.* (1998) found that because of the effect of marine bird colonies (murre, cormorants, kittiwakes, puffins, fulmars and auklets) living in an island system off the southern Bering Sea, Alaska, six plant species collected far from the colonies showed significantly lower values (around 11 $\delta^{15}\text{N}$) than ones collected from within the colonies (with values around 22 $\delta^{15}\text{N}$). The same kind of enrichment occurs in plants around penguin colonies on sub-Antarctic islands (Erskine *et al.* 1998).

In the case of carbon, the main differences in this isotope occur between C3, and C4-CAM plants, but also in relation to elevation (Lajtha & Marshall 1994). C3 species tend to have lower values (between -30 and -20 $\delta^{13}\text{C}$) than C4 and CAM species (between -20 and -10 $\delta^{13}\text{C}$), while a positive correlation has been described between $\delta^{13}\text{C}$ and altitude. Low-elevation plants present lower values of $\delta^{13}\text{C}$ than high-elevation plants. (Korner, Farquar & Roksandic 1988). In our study the differences observed corresponded with physiological traits of plants. *Sesuvium edmonstonei* uses CAM photosynthetic pathways while both *C. alba* and *C. succirubra* use C3 pathways (McMullen 1999). However a trend was also observed between $\delta^{13}\text{C}$ values and the mean elevation of the islands from where plants were collected. The species collected from Floreana (a high-elevation island) showed the lowest values while the species collected from Plazas Sur and Cousin Rock have the highest values for this isotope.

At small scale, Caamaño and Plazas showed similar geographical features and abundances in their sea lion colonies. However, these two islands had completely different patterns of topography (elevation). These patterns were reflected in the results of isotopic and soil nutrient concentration analysis. The isotopic analysis results from both islands were in concordance with the results obtained from the regional scale analysis. In Caamaño, all plant samples were in the range of marine influence (between 15 and 20 in $\delta^{15}\text{N}$) and their $\delta^{13}\text{C}$ values showed a restricted range of variation (between 25 and 23 in $\delta^{13}\text{C}$). The main differences on plant isotopic signatures from both sides of the island (east vs. west) were related with the almost continuous presence of sea lions that cross and walk around the east side. The reduced variability observed on the $\delta^{13}\text{C}$ isotopic signatures on this island were related with the low number of plant species observed (all the three species have CAM photosynthetic pathways) and with the low variability of island elevation. In Plazas, in concordance with the higher richness of collected plant species and higher variability in elevation, the isotopic $\delta^{13}\text{C}$

values showed a wider range of values. For both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopes there was a clear pattern of differences associated with stations elevation. All the stations with high elevations (i.e. from transect 6 above) showed higher values of $\delta^{13}\text{C}$ and lower values of $\delta^{15}\text{N}$ while the ones closest to the shoreline (specially transects 2 and 3) showed the opposite pattern.

Marine vertebrates can exert important effects on the chemistry of soils (Mizutani & Wada 1988). The presence of marine bird colonies is associated with increased concentrations of nitrogen compounds (NH_4^+ and NO_3^-). The arrival of gulls to their colonies in Scotland is associated with an increase on soil nitrogen from 5 mg g^{-1} soil to 250 mg g^{-1} soil (Iason *et al.* 1986). These increments are associated and depend on the bird species and their densities. In Baja California islands, Anderson & Polis (1999) reported that in average total nitrogen concentrations on the islands with bird species (cormorants, gulls, terns and herons) were around 2.2 mg g^{-1} soil while on islands without birds they were around 0.3 mg g^{-1} soil. The highest concentrations of nitrogen, ranging from 98 to 415 mg g^{-1} soil has been reported in penguin colonies (Moors, Speir & Lyon 1988; Tatur *et al.* 1997) and they could be related to low mobility, high densities or the fact that these birds, unlike other marine birds, usually and especially defecate when they rest on their colonies and not while they fly or swim (Hutchinson 1950). Analyses of soil nutrients concentrations associated with the occurrence of marine mammals on islands or on terrestrial systems are more scarce and mostly focused on Antarctic or subantarctic habitats. Erskine *et al.* (1998) shows that the soils from seal colonies on the subantarctic Macquarie Island have lower levels of ammonia and nitrite (around a 73% and 14%, respectively) than penguin colonies (around 86% and 18%, respectively). The concentrations of nitrogenous compounds on elephant seal colonies ranges between 1.9 and 4.9 mg g^{-1} soil for ammonia and between 0.1 and 0.9 mg g^{-1} soil for nitrate (Allen, Grimshaw & Holdgate 1976; Smith 1978).

For our study, normal concentrations of ammonia and nitrate on areas far from the influence of sea lions colonies in Galapagos range around 0.01 mg g^{-1} soil for ammonia and 0.04 mg g^{-1} soil for nitrate (H. Jagers personal communication). We found important increments on these variables associated with the presence of sea lions on some sampled areas of Caamaño and Plazas Sur (Fig. 7c,d). In Caamaño the plots on the east site of the island (and especially plot 4) showed the highest concentrations of both ammonia and nitrite. In Plazas Sur, transect 1 has the highest levels of both nutrients. This transect was the responsible for the differences of almost one order of magnitude of the nutrient concentrations occurring in both islands. The highest nutrient concentrations were associated with the presence of sea lions in these areas and also with the fact that transect 1 is part of the rocky shoreline with few plants on it. That explained why the plants on sta-

tion 1 did not show enriched $\delta^{15}\text{N}$ values. Apart from station 1, nutrient levels on both islands showed similar ranges with the highest significant values on the sampling stations with lower elevations (the east side of Caamaño and shoreline stations of Plazas Sur). The west side of Caamaño also has low elevations, but not high soil nutrient concentrations. As explained for the results of stable isotopes analysis, this pattern could be related with the fact that, owing to the high plant cover of this area, no seals can cross or walks around this side of the island. Soil nutrient concentrations are related to topography in both islands, giving support to our hypothesis.

Straddling the equator at 900 km west of the South American mainland, the Galápagos Archipelago boasts a unique and highly endemic fauna of sea mammals and seabirds (Harris 1984). These organisms, obtaining their food from a productive ocean and exerting their reproductive activities on the islands, are important vectors of marine nutrients (nitrogen and phosphorus) to terrestrial systems. Terrestrial plant growth and cover are usually limited by macronutrients and their interactions are highly affected by their availability (Tilman 1982). Sea lions and seabird colonies are completely segregated in the islands. Here we document the influence of one of these potential vectors and the use of transported nutrient by plants. Our study opens a new perspective for investigating how seabird-transported nutrients affect the terrestrial environments of the Galápagos and what the implications are of this transport for plant physiology and ecology.

In conclusion, our study demonstrated that the Galápagos sea lion *Z. wolfebaeckii* is an effective vector for the transport of marine nutrients to terrestrial ecosystems. These nutrients occurred in high concentrations in the soils and are used by shoreline plants. All these effects are spatially restricted to the areas where seals occur and, seals occur most frequently on islands with low elevation. As far as we know our study is the first report quantifying the magnitude of the effect of marine mammals on terrestrial habitats.

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