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Bárcena Volcano, 1952: a 60-year report on the repopulation of San Benedicto Island, Mexico, with a review of the ecological impacts of disastrous events

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Abstract. Long-term ecological studies are desirable, but rare. I here present data from a 60-year study on the repopulation of San Benedicto Island following a volcano eruption in 1952. Bárcena Volcano appeared on 1 August 1952 on San Benedicto Island, Revillagigedo Islands, Mexico. Within 20 min, the entire island was engulfed in a cloud of ash and pumice, which covered all the plants, killed an estimated 20 000 sea birds within hours and caused the subsequent extinction of an endemic race of rock wren (*Salpinctes obsoleta exsul*). The results of studies on revegetation and repopulation of the island for the first 10 years after the volcanic eruption were summarised by Brattstrom in 1963. This report extends the studies to 2012. The distribution of the land crab (*Aegecarcinus planatus*) has increased on the island. By 1971 the crab occurred only over the northern one-eighth of the island, but by 1978 it could be found on one-third of the island. No studies on its distribution have been made since then. Total sea bird populations steadily increased up to 1971 and then rapidly declined, though these changes in numbers are largely due to a fluctuation in the populations of the masked booby (*Sula dactylatra*). The changes in the booby population may have been due to reproductive and feeding success or to immigration and emigration. The decline in the shearwater (*Puffinus* ssp.) populations are largely due to erosion and destruction of their burrows; their numbers did not increase until 2000. The formation of a large lava delta created a new habitat, which permitted the establishment of a species of sea bird new to the island, the red-footed booby (*Sula sula*). Numerous non-resident waifs or stray birds have been observed on the island but most have not become established. The exception is the Laysan albatross (*Phoebastria immutabilis*), breeding at present in low (3–712) numbers. The original flora consisted of 10 species. The volcano caused four species to become extinct, two re-established themselves, and two species new to the island arrived. There have been marked erosional changes, and the accidental introduction of exotic plants may dramatically alter the vegetation of the island.

Additional keywords: ecological disasters, island ecology, Revillagigedo Islands, sea birds.

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Introduction

The Islas Revillagigedo consist of four volcanic oceanic islands (Socorro, Clarion, Roca Partida and San Benedicto) rising independently from the ocean floor (about 4 km deep) along the Clarion Fracture Zone, some 483 km west of Mexico and 354 km south of the tip of Baja California, Mexico (Fig. 1). San Benedicto, the youngest of the four islands, is 6.4 km long and 3.2 km wide and consists of several old coalescent and partially eroded volcanic cones. The boundary of the island has at least one discontinuous submerged Pleistocene erosion shelf.

On the morning of 1 August 1952, a new volcano, Bárcena, appeared in a large valley on the southern portion of San Benedicto Island (Fig. 2). The initial eruption of Bárcena occurred at 0745 hours, 1 August 1952 (Fig. 3). Within 20 min a dark cloud of ash had spread over the entire island. By 2 August, the pyroclastic volcanic cone had developed to a height of 335 m above sea level, but cone formation ceased during mid-September to early November. Activity resumed, and two domes of irregular blocks of lava formed in Bárcena crater during November and early December. On 8 December, lava issuing from the base of the volcano formed a delta, which extended nearly 0.8 km out to sea by the end of February 1953 (Fig. 4). Calculation (Richards 1959) indicated that 3200 m^2 of tephra and lava were produced during the eruption of Bárcena. No further activity except sulfataric steaming occurred after February 1953. The volcano had the highest index of explosiveness of any oceanic volcano in the eastern Pacific Ocean (Richards 1959). The entire island was quickly covered with a cloud of tephra, ash, and pumice, which killed an estimated 20 000 sea birds within hours. Thus, for the second time an island laboratory appeared for the study of the repopulation and revegetation of an island. Krakatau in 1883 was the first such laboratory, and the new island of Surtsey (1963) off the coast of Iceland was the third. Investigations on newer island volcanos as well as on old volcanic islands – Motmot Island, New Guinea, 1968; Deception Island, Antarctica, 1967; Ritter Island, 1888, New Guinea; Long Island, New Guinea, 1700s; Bogoslof Island, Bering Sea, 1976 (Ball and Glucksman 1975; Bassot and Ball 1972;

Diamond 1974; Fridriksson 1975; Simkin and Fiske 1983, 2003; Thornton 2000) – have contributed greatly to our understanding of extinction, survival, colonisation and repopulations of islands. The eruption of Bárcena differed from these other islands in that San Benedicto is a true oceanic island, the original biota of the island was a depauperate one and, unlike Krakatau and others where complete destruction of the biota occurred, only a portion of the terrestrial biota of San Benedicto was destroyed.

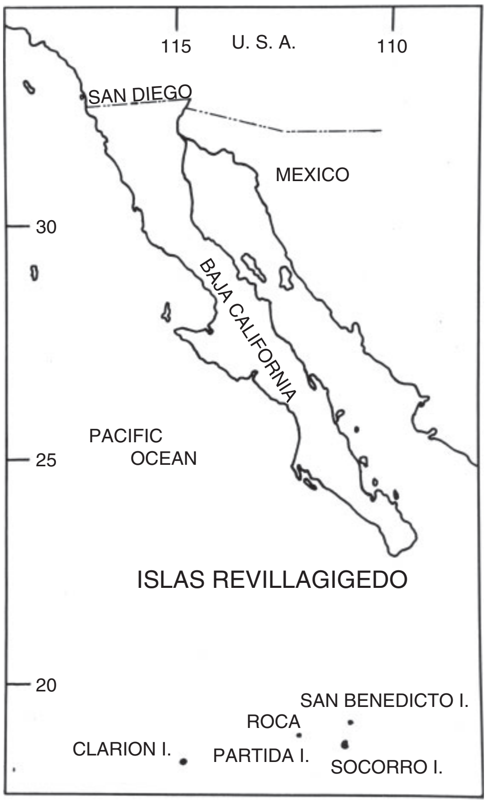

Fig. 1. Map showing location of the Islas Revillagigedo and San Benedicto Island.

Numerous scientific expeditions have visited San Benedicto Island (Richards and Brattstrom 1959). The most detailed collections and observations were obtained by the California Academy of Sciences in 1905 and 1925. The pre-Bárcena biota of San Benedicto included no terrestrial mammals, reptiles, amphibians or freshwater fish. However, ten species of plants (herbs and low shrubs), several species of sea birds (boobies, frigate birds, shearwaters and tropic birds) and an endemic race of rock wren (*Salpinctes obsoletus exsul*) did live on the island. The terrestrial invertebrate fauna was poorly known save for the land crab, *Aegecarcinus planatus.* The marine intertidal fauna was typical for a subtropical island of the eastern Pacific (Brattstrom, 1990). The marine fish fauna was poorly described (Richards and Brattstrom 1959; Brattstrom 1990).

The geological and biological aspects of Bárcena Volcano, its destructive effects and changes occurring after volcanic quiescence have been the basis of numerous long-term studies by a large team of scientists. Richards (1959, 1965, 1966) described the geology of San Benedicto Island, including a description of the origin of the volcano and subsequent erosional changes. The birds, reptiles and cactus (of the Islas Revillagigedo) have been described, as well as the initial effects of the volcanic eruption on the animals and plants (Brattstrom 1953, 1955, 1990; Brattstrom and Howell 1956). Brattstrom (1963) described the revegetation and repopulation of the island 10 years after the eruption. Long-term ecological studies are desirable but rare (Buden 2000; Collins 2001; Fryxell *et al.* 1998; Holmes and Sherry 2001; Marshall 1988; Shultz *et al.* 2012). This report summarises the results of studies by Brattstrom and others through 60 years of the history of Bárcena.

Fig. 2. San Benedicto Island before the eruption of Bárcena. Herrera Crater is to the right and the Ash Heap on the left. Bárcena now fills the valley to the left of the photograph. (Photography by G. D. Hanna in 1925.)

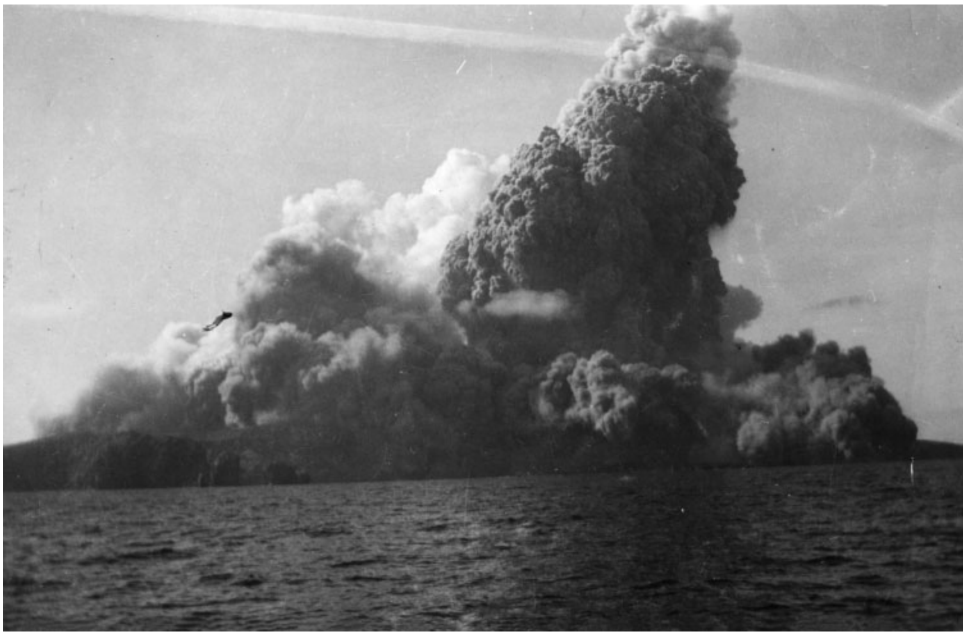

Fig. 3. San Benedicto Island approximately 15 min after initial eruption of Volcan Bárcena at 0745 hours, 1 August 1952. (Photograph by R. Petrie.)

Fig. 4. General view of San Benedicto Island from the south, with Bárcena and the Lava Delta in the centre and right foreground. (US Navy Photograph, 6 August 1954.)

Effect of Bárcena on the biota

The primary destructive force of Bárcena Volcano was the dense pumice dust, tephra and gas that covered the entire island, including a 0.5–1.0-m deposit of ash and pumice on the extreme north end of the island and on many of the small islets about the island. Many of the birds were killed when they refused to leave nests or were unable to fly due to the effects of the gas and dust (Cook *et al.* 1981; Pollack 1981; Hayward *et al.* 1982; Stolzenburg 2011). In November 1953, many skeletons of birds (some on nests with eggs) were exposed as ash was removed by erosion. Small numbers of the endemic rock wren survived the volcanic activity, as a few were seen by Lewis Wayne Walker in December 1952 (pers. comm.). However, none have been seen since December 1952 and they are assumed to be extinct. The eruption apparently destroyed all above-ground parts of all plants. There are early records (Townsend 1890; Kaeding 1905) of common ravens (*Corvus corax*) being common on San Benedicto and a predator of eggs and young of seabirds (Pitman and Ballance 2002). Brattstrom and Howell (1956) considered that the occasional ravens seen around the island were visitors or waifs from the population on Clarion Island far to the west. Only a few ravens have been seen about the islands in the 60 years since the eruption of Bárcena and none are known to breed there.

The intertidal regions of the island in 1953 were scoured by the large amounts of floating or partly submerged pumice and dust, and the water was extremely turbid. Repopulation, up to 1961, of these regions by marine algae, invertebrates and fish has been described by Brattstrom (1963). No subsequent marine studies have been done.

Materials and methods

Six trips were made to San Benedicto Island by ship (March 1953, November 1953, April 1955, November 1971, April 1978, and April 1981). I have spent over 915 h on one or more of the four islands of the Revillagigedo Archepelago, of which 270 were on or about San Benedicto. Between August 1952 and August 1961 many photoreconnaissance flights were made of the islands using planes of the United States Navy. Detailed low-altitude photographs, some being stereo pairs, taken on these flights clearly show plant and bird distribution. I was on two of these flights (October 1954, August 1961). Observations and photographs were also provided to me by many other investigators during 1952–2012. Each of my trips to the island consisted of landing north of the Lava Delta, traversing the delta, climbing the eastern slope of Bárceno and Herrara Craters, then north to the northern tip of the island (Fig. 4). The return trip descended to the eastern beach between the two larger craters. Erosion on the island made hiking extremely difficult and dangerous by 1978, so I was unable to reach the northern end of the island. Robert Pitman was able to do so in 1978, through 2000, and made population counts of birds (Pitman and Ballance 2002). Although it is possible to observe 80% of the island from the crest of Bárcena, Pitman's observations provided important data on canyons not visible from the volcano or ship. In 1981, the visit to the island was limited and erosion much more extensive. I was able to traverse the lava flow, and Drs Joe Jehl and Reid Moran ascended Herrera Crater and made population counts of birds and took photographs. On each of my trips the island was also circumnavigated by ship as close as safely possible, and the vertical cliffs were examined with binoculars. In this way, almost every portion of the island was observed.

Bird numbers (see Table 1; Jehl and Parkes 1982*a*; Pitman and Ballance 2002 for scientific names) were determined by actual count during the walk around the island and from counts as the ship circumnavigated the island. Since many of the birds were at sea during the day, these birds also had to be counted. On many trips we were in the vicinity of the island for several days doing geological and oceanographic work aboard ship. It soon became apparent after several early evening circumnavigation trips that most of the sea birds returned to the island from the south and south-east. Therefore, the ship was anchored in the late afternoon and evening to the north-east of the Lava Delta (Albatross Beach of Pitman and Ballance 2002) and actual counts of incoming birds were made on tally clickers as they approached the islands (often two or more observers would count, each doing one or more species). Counts made on 2–3 successive days did not vary significantly. These counts were supplemented by aerial photographs during 1952–61 and by photographs and observations made by others on other trips. I have not been on the island since 1981, other researchers (Pitman and Ballance 2002) did not necessarily circumnavigate the island nor make evening returning bird counts so their numbers are necessarily lower than mine. The number of burrowing shearwaters (*Puffinus* ssp.) was estimated from evening counts or the number of active burrows observed on the island (multiplied by two as a pair of birds share a single burrow). Shearwater distribution was plotted from the distribution of the burrows. While others made bird counts (Table 1) they may have not surveyed the island as well as Pitman or I. So counts made by Brattstrom and complete survey data in Pitman and Ballance (2002) are used. Only Brattstrom and Pitman surveys are similar.

Plant distribution was mapped by observation, photographs and Google maps (2013). Crab distribution up to 1978 was done by mapping active burrows and live crabs. Because of erosion, access and interests by others, no crab distribution data after 1978 are available.

Results

Repopulation of San Benedicto

Invertebrates, fish and marine algae

The repopulation studies of marine algae, invertebrates and fish by 1961 have been summarised elsewhere (Brattstrom 1963). Unfortunately, no subsequent studies have been made on these organisms.

Little has been done on the terrestrial invertebrates of San Benedicto Island before or after the eruption of Bárcena. Insects collected by the expeditions of the California Academy of Sciences and other expeditions have been described by numerous authors (see Richards and Brattstrom 1959 for a bibliography and Brattstrom 1990; Palacios-Vargas *et al.* 1982; Brattstrom 2015). None of these studies covered San Benedicto. In 1925, Hanna (1926) noted 'clouds of grasshoppers … ground beetles, carrion, and hippoboscid flies'. Flies were common on the island in 1953, and various entomologists collected many winged insects in 1953 and 1955. These insects are currently under study. In 1971, two species of grasshoppers, hippoboscid and muscid flies, ants, and honeybees were observed. Pitman (pers. comm.) saw the above plus two species of spiders in 1978. I saw only grasshoppers and two species of flies in 1981. However, time and terrain did not allow extensive collecting or population estimates of insects to be made on any of the trips.

Land crabs

Land crabs, *Aegecarcinus plantus*, are common on Clarion, Socorro and San Benedicto Islands. They live in holes and crevices, and migrate to the sea only to breed. Although the total population on San Benedicto prior to Bárcena is unknown, their distribution probably extended over the entire island associated with the wide distribution of plants (Fig. 5).

Undoubtedly, many crabs were killed when they and their burrows were covered with pumice, ash and dust. Toxic gases and dust also may have killed many by interfering with respiration. Some could possibly have survived in holes or crevices, at the northern end of the island, where the ash was only a few feet deep. Sea birds eat these crabs but it is unlikely that birds carried living crabs the long distance from Socorro to San Benedicto. Thus, repopulation of the island by land crabs probably resulted from the reproduction of those that survived the volcano or by recruitment of young crabs from the sea.

In March 1953, two live and several dead land crabs were observed on the north edge of the crater rim of Bárcena. The dead crabs had been torn apart, indicating that birds had dropped them there. In November 1953, land crabs were fairly common at the extreme northern end of the island (Fig. 5), but by 1955 crabs were found in only a small portion of the previous range. This reduction in the area occupied by the crabs may have been due to: (1) a depletion of food plants, (2) predation by the increasing bird population, and/or (3) destruction of burrows and crabs by ash reworked by wind and rain.

By 1971, land crab distribution had increased to include the northern one-eighth of the island (Fig. 5). In 1978, Robert Pitman (pers. comm.) observed land crabs all over the north end of the island as well as in the center of Herrara Crater, but in no other locations. Thus the crabs occurred on about one-third of the island by 1978 (Fig. 5). No other distribution data have been published by subsequent observers.

Birds

The most obvious inhabitants of San Benedicto Island are sea birds. Prior to the Bárcena eruption, eight seabird species and one passerine species were resident (Table 1).

Photographs taken during the expeditions of the California Academy of Sciences in 1905 (by Slevin) and 1925 (by Hanna) showed that most of the area on top of San Benedicto was occupied by birds. Frigate birds (*Fregata* ssp.) were the most common of the pre-Bárcena sea birds, making up 95% of the avifauna (Jehl and Parkes 1982*a*). Density estimates from photographs taken by Slevin and Hanna of San Benedico Island were 1–3 frigate birds per square metre in 1903 and 1–5 frigate birds per square metre in 1925. Hanna (pers. comm.), who was with me on the trip in November 1953, estimated that the sea bird population in November 1953 was only 1% of the 1925 population. Based on skeletal counts and Hanna's photographs and remarks, the pre-Bárcena sea bird population was estimated to be about 20 000 birds, most of which were killed by the volcano in the first minutes or hours after the initial explosion, as determined by skeletons buried by the ash, and later exposed by

Table 1. Seabirds observed on San Benedicto Island after the eruption of Bárcena Volcano with estimates of their numbers[A]
Asterisks indicate pre-Bárcena resident species

Species	Mar. 1953	Nov. 1953	Apr. 1955	Nov. 1971	Apr. 1978	Apr. 1981	Feb. 1988	Mar. 1988	Nov. 1990	Apr. 1992	Dec. 1999	Dec. 2000
Masked booby (*Sula dactrylatra*)*[D]	30	535	1067	11695	8568	3354	600	2500	300	800	3774	3976
Frigate bird (*Fregata* sp.)*[BD]	10	200	398	100	179	121	14	5	6	20		700
Shearwater (*Puffinus* sp.)*[CD]	600	?	1200	245+	2260	363			200	100		2000
Red-billed tropic bird (*Phaethon aethereus*)*[D]	39	3	39		5	1	70	300	150	120	30?	200
Brown booby (*Sula leucogaster*)*[D]	2	6	11	136	23	28			50	200	100	300
Blue-footed booby (*Sula nebouxi*)		3										
Red-footed booby (*Sula sula*)[D]		2		420	877	495	100	200	50		50	300
Red-tailed tropic bird (*Phaethon rubricauda*)							5	6	4	9	2	9
Laysan albatross (*Phoebastria immutabilis*)							14	17	4	2	18	25
Nasca booby (*Sula granti*)[E]							200	300	50	100		400
Total	681	747	2715	12596	11912	4362	1003	3328	814	1351	3974	7910

[A]1953–81 = Brattstrom original data; 1987–2000 data from Pitman and Ballance (2002): does not include incomplete or casual surveys reported in Pitman and Ballance (2002).
[B]Both greater (*Fregata minor*) and magnificent (*F. magnificens*) occur on the island and I did not always separate the species in my notes so the data are combined. See Jehl and Parkes (1982*a*) for discussions of the taxonomic status of these two and other species on the Revillagigedo Islands.
[C]Data for both species of shearwaters (*P. pacificus*, wedged tailed shearwater; *P. auriculatus*, Townsend shearwater) are combined until 1987. After 1987, all numbers are for *auriculatus* except 2 and 20 Townsend Shearwater seen in 1990 (Santaella and Sada 1991) and 1998 (Pitman and Ballance).
[D]Includes evening returning birds, 1977–81.
[E]Nasca booby not differentiated from masked booby until 1988 (Pitman and Jehl 1998).

erosion. Some skeletons of adult birds were found on or next to eggs and young (see photographs in Brattstrom and Howell 1956; Brattstrom 1963; also see Southern and Southern 1982).

The only resident passerine bird was the endemic race of rock wren, *Salpinctes obsoletus exsul.* As a result of the volcanic action this subspecies is now extinct.

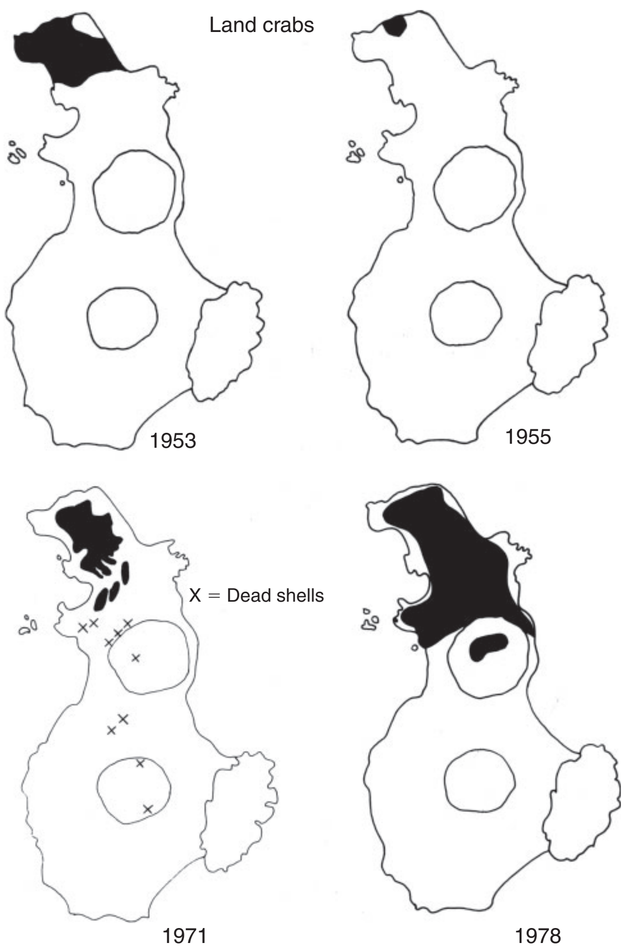

Fig. 5. Outline maps of San Benedicto Island showing distribution of land crabs.

The total number of birds of each species observed on the post-Bárcena trips by me and other researchers (see review in Pitman and Ballance 2002) is listed in Table 1. The total numbers of masked boobies occupying various regions of the island are given in Table 2. The area distributions of all species of birds on the island during the history of the investigations are shown in Fig. 6. While Table 1 gives bird numbers reported by a number of researchers, Figs 7 and 8 include Brattstrom's personal observations plus numbers from complete surveys reported only in Pitman and Ballance (2002) as only Brattstrom's and Pitman's survey techniques are similar.

After the eruption there was an increase in the numbers of sea birds and the area of the island occupied by them (Table 1, Fig. 6). In March 1953, birds occurred only on the bare vertical cliffs at the north end of the island. By November of that year, frigate birds were found in other regions at the north end of the island in areas where Bárcena ash had been removed (Figs 8, 9) and boobies were found in ash-covered areas not subject to winds. By 1955, the birds occupied much of the island in limited numbers. This was especially true of the shearwaters, which had begun to dig burrows in Bárcena ash on top of the volcano as well as in areas of their old centre of concentration called the Ash Heap. In addition, a few birds, mostly boobies, had begun to roost on the bare lava delta. By 1961, the number of birds roosting and nesting on the lava delta had risen to 7000, and by 1971 the population there had increased to 10 155. By 1981, the number of birds on the Lava Delta and the south end of the island was reduced and by 2000 no birds roosted or nested on the south end of the island, nor the Lava Delta. Erosion of Bárcena probably caused shearwaters to leave. Only by 1998–2000 did shearwaters start burrowing in northern parts of the island. Why birds left the Lava Delta is unknown. Laysan albatross started to roost and breed on the sandy area north of the Lava Delta (Albatross Beach) in 1987 (Podolsky 1990; Pitman and Ballance 2002).

Of the several species of birds on San Benedicto, the frigate birds were the most abundant before the eruption. After the eruption, the number of masked boobies far exceeded the number of frigate birds (Fig. 8). The low frigate bird population may be due to the absence of adequate sticks for nesting material, lack of food or a slow rate of reproduction. The other species of boobies also had low population numbers compared with the masked booby. One of the probable contributing factors

Table 2. Population estimates of masked boobies (*Sula dactylatra*) for various parts of San Benedicto Island

Part of island	Mar. 1953	Nov. 1953	Apr. 1955	Jan. 1956[A]	Aug. 1961[A]	Nov. 1971	Apr. 1978	Apr. 1981[A]	1998–2000[C]
North End	30	500	700	700	200	300	312	31	663
Herrera Crater	0	0	104	100	100	700	3170	1874	1980
Between Herrera and Bárcena	0	25	23	25	200	50	67	10	
Between Bárcena and Ash Heap	0	0	100	300	600	490	19	160	
Lava Delta	0	0	140	1000	7000	10 155	5000	560	
Totals	30	525	1067	2125	8100	11 695[B]	8568[B]	2635	mean: 2649

[A]Estimates from air (1961) and air photographs (1956, 1961).
[B]Includes evening returns, most of which went to Herrera Crater and the Lava Delta.
[C]Average of 3 years (Pitman and Ballance 2002).

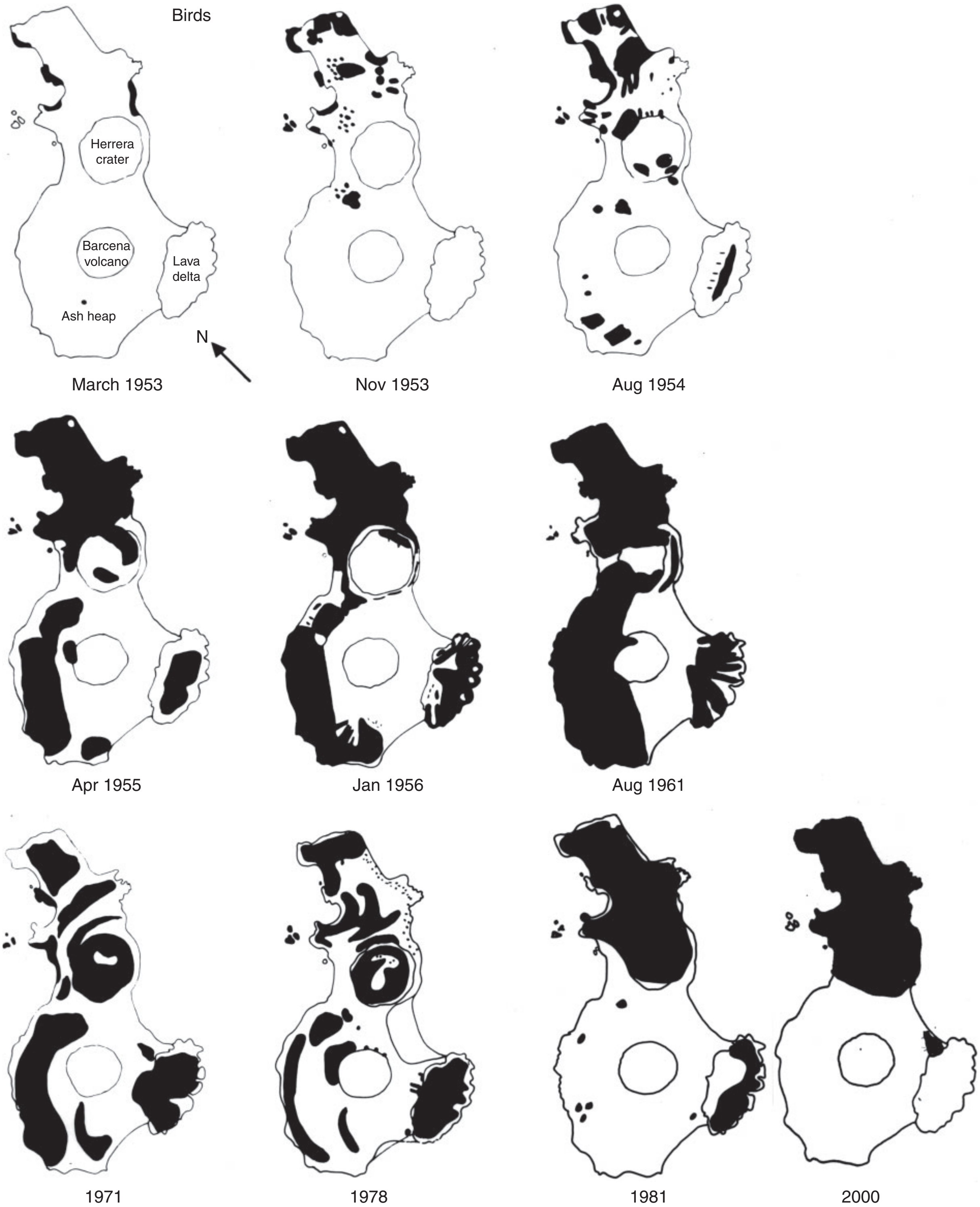

Fig. 6. Outline maps of San Benedicto Island showing distribution of roosting and nesting sea birds.

to the absence of red-footed boobies prior to the formation of the Lava Delta was the lack of shrubs on the island, which could provide protected nesting sites. Brattstrom and Howell (1956) noted that on Clarion Island, 364 km to the west, masked boobies nested on the ground while red-footed boobies built their stick nests in bushes or on cliffs. The lava delta on San Benedicto provided an equivalent habitat, and red-footed boobies were breeding there in 1971 (although two birds were seen there as early as November 1953). The rugged lava flow with its diverse topography provided both wind-protected areas for nesting and

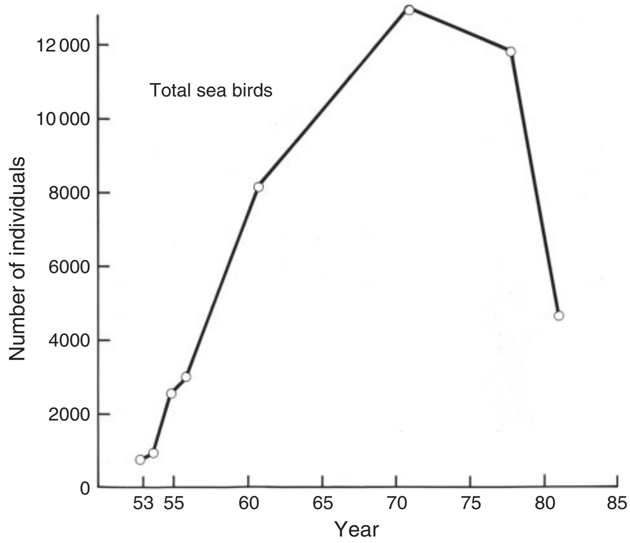

Fig. 7. Total number of sea birds present (nesting and roosting) on San Benedicto Island for several years. Only Brattstrom's original data and the complete surveys in Pitman and Ballance (2002) are used for this figure.

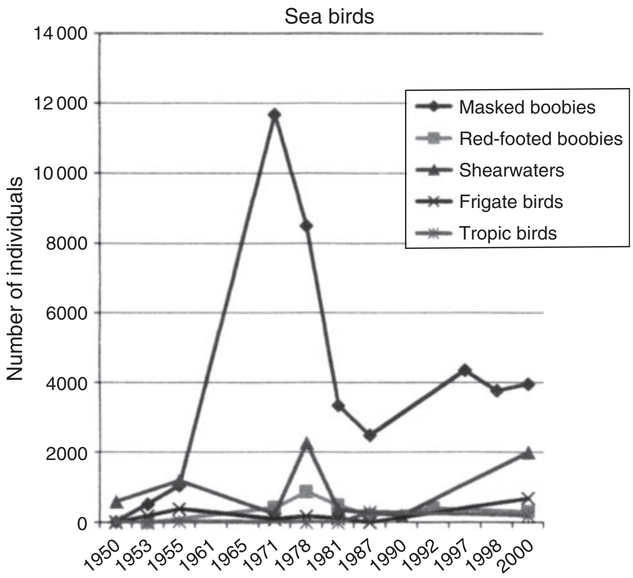

Fig. 8. Number of sea birds of different species present on San Benedicto Island for several dates following the eruption of Bárcena. Only Brattstrom's original data and the complete surveys in Pitman and Ballance (2002) are used for this figure.

allowed more nests in a limited area. Sometime in the late 1980s, all species of booby left the Lava Delta. While there were still several hundred Red-footed Boobies nesting on the Lava Delta in 1978, there were a larger number (400) nesting on the northern part of the island and a small number (67) in the valley between Bárcena and Herrera. Many of the red-footed boobies on the northern part of the island were on steep cliffs, while those in the valley were on the edges of the cliff-like gullies caused by the extensive erosion. Until 1955, most of the masked boobies occupied the north end of the island (Table 2); by 1961, most of them were nesting on the Lava Delta. Masked boobies had largely left the Lava Delta by 1978, and a large number occurred in Herrera Crater (Table 2). Brown boobies were found primarily on the northern part of the island. Frigate birds had left their main nesting area (Frigate Arroyo) in the north-central portion of the island (Fig. 9). The reasons for specific nest site selection and changing of nesting area from year to year is not clear (see Clark *et al.* 1983 and Duffy 1984, for a discussion).

While the shearwaters had begun to dig their burrows in the Ash Heap (by 1953) and on Bárcena (by 1955), the extensive erosion of the soft pumice volcano crater had destroyed almost all of their burrows by 1971. No shearwaters were seen, even during an early evening boat reconnaissance around the island when daytime-feeding shearwaters were expected to return to the island. The population estimate in Table 1 was based on the number of undestroyed burrows. Thermal winds on the island created large dust storms, contributing greatly to the elimination of shearwater burrows in 1971. By 1978, the hard crust of the Bárcena ash was mostly gone. The exposed softer material apparently made it easier for shearwaters to burrow and extensive burrows again appeared on Bárcena Crater, in Herrera Crater and in the central part of the island. By 1978 and 1981, there were a few burrows just above the Lava Delta where the original lava had extruded from the volcano. The extensive erosion seen in 1981 may have further damaged these burrows as few shearwaters were seen in the vicinity (Table 1). Shearwaters left the south part of the island in the late 1980s. Santaella and Sada (1991) report shearwaters on the north part of the island in November 1990. Pitman and Ballance (2002) also report shearwaters in the north part of the island in 1998 and 2000.

The total population of sea birds on San Benedicto increased steadily from 1953 to 1971 (Fig. 7), due almost entirely to the increase in the numbers of masked boobies (Fig. 8). By 1978, there was a decline in total sea birds and in the number of masked boobies. This decline was even more marked by 1981. By 1988 through to 2000, numbers of masked boobies had levelled off at 3000–4000. Shearwaters increased by 2000, and the sea birds maintained steady but low (under 500) population numbers (Figs 7, 8). A reduction in the total area of the island utilised by the sea birds also occurred with the decline in bird numbers (Fig. 6).

Non-resident waifs or stray birds have been observed in small numbers on San Benedicto (Table 1). Twenty-five species of birds (two from nearby Socorro) have been seen on San Benedicto after the eruption of the volcano (Brattstrom and Howell 1956; Howell and Webb 1990, 1992*a*, 1992*b*; Jehl and Parkes 1982*a*, 1982*b*, 1983; Pitman and Ballance 2002). These include: brown pelican (*Pelicanus occidentalis*), red-tailed tropic bird (*Phaethon rubricauda*), brown noddy (*Anous stolidus*), great blue heron (*Ardea herodias*), Sabines gull (*Kema sabini*), Socorro red-tailed hawk (*Buteo jamaiccensis socorroensis*), osprey (*Phandion haliaetus*), peregrine falcon (*Falcon peregrinus*), American kestrel (*Falco sparverius*), Socorro dove (*Zenaida grayson*), mourning dove (*Zenaida macroura*), short-eared owl (*Asio flammeus*), white-throated swift (*Aeronautes saxatalis*), barn swallow (*Hirundo rustica*), northern rough-winged swallow (*Stelgidopteryx serripennis*), violet-green swallow (*Tachycineta thalassina*), tree swallow (*Tachycineta bicolor*), barn swallow (*Hirundo restica*), northern mockingbird

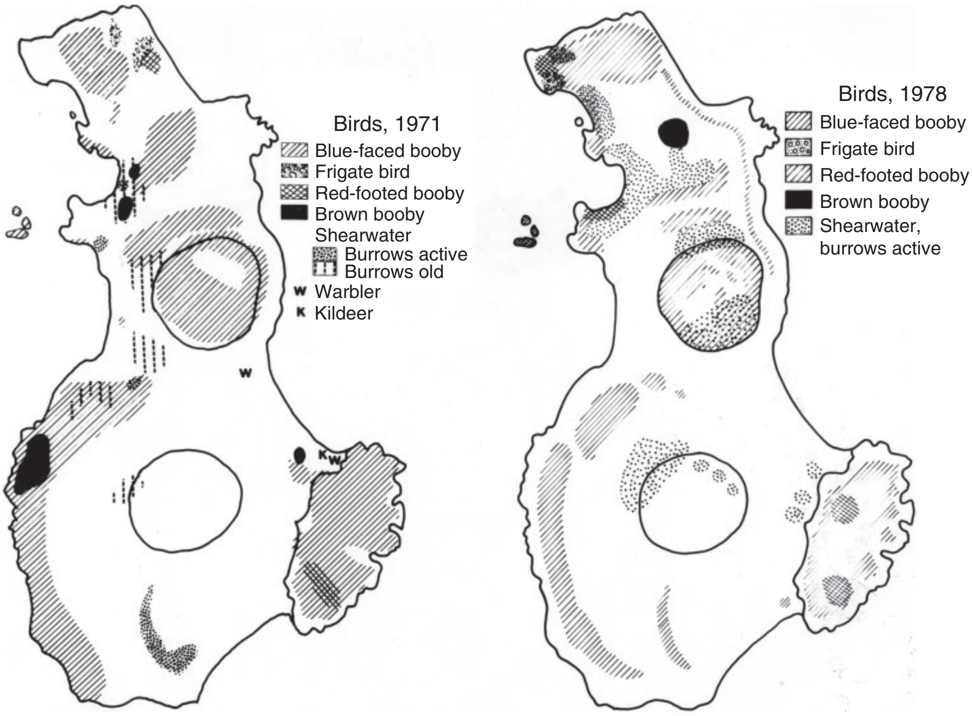

Fig. 9. Map of San Benedicto showing the distribution of birds on the island in November 1971 and April 1978.

(*Mimus polyglottos*), bay-breasted warbler (*Dendroica castanea*), killdeer (*Charadrius vociferous*), American redstart (*Setophaga ruticilla*), curlew sp. (*Numenious* sp.), yellow-rumped warbler (*Dendroica coronata*) and common raven (*Corvus corax*).

The barn swallows, redstart and warblers were probably lost birds or post-breeding migrants as they were seen only on November trips. The northern mockingbird has recently invaded Socorro Island and may have replaced the near-extinct Socorro mockingbird (*Mimoides grayson*) there (Jehl and Parkes 1982*a*). None of these birds have become established on the island, though the red-tailed tropic bird has been seen in prebreeding behavior on the island and may now be a coloniser (Pitman and Ballance 2002). The raven was reported on San Benedicto Island by Townsend (1890) and Kaeding (1905). Brattstrom and Howell (1956) considered the few ravens occasionally seen on San Benedicto as strays from Clarion.

Terrestrial plants

Photographs taken by Joseph R. Slevin in 1905 and G. Dallas Hanna in 1925 showed that San Benedicto was almost completely covered with low vegetation (Fig. 2). The upper slopes, the top of the Ash Heap and some of the steep rocky cliffs were devoid of vegetation. The angiosperm flora consisted of 10 species (Table 3), and the dominant plants were the two grasses, *Eragrostis diversifolia* and *Cenchrus myosuroides*, and the *Euphorbia* species.

The Bárcena ash fall covered the entire island with 0.6–335 m of ash. Photographs of the island, including those of the northern end, showed no plants visible in 1952 and early 1953 (Fig. 10). By November 1953, sufficient wind and water erosion had occurred to remove the Bárcena ash from the steeper slopes and gullies. It was at these locations that plants managed to sprout from old roots, underground stems or seeds (Zobel *et al.* 1992). No plants grew where there was any Bárcena ash; all were growing on pre-Bárcena 'soil'. Many dead stalks of pre-Bárcena plants seen in the eroded areas were being used by frigate birds for nests. By 1955, however, *Perityle* was growing in Bárcena ash in Herrera Crater – perhaps sufficient leaching of the ash had occurred in this area. The most common post-Bárcena plants in 1955 were *Euphorbia* and *Perityle.* On the 1957 trip, Richards (1959, 1965) noted fewer plants than on the 1955 trip. Erosion of Bárcena ash and the pre-Bárcena surface by rain and wind had apparently removed a large portion of the plants, which had resprouted and were well established in 1953 and 1955. By August 1961, the revegetation on the north end of the island had been greatly curtailed (Fig. 10); however, two new patches of plants were seen from the air. One consisted of a low group of grass-like plants covering an area of $\sim$9.2 m^2 at the southern end of the Ash Heap. It was impossible to determine whether these plants represented roots or seeds covered and dormant until 1961 or whether they represented a new invasion. All previous air photographs of this portion of the island were re-examined and all showed that the region concerned was covered with ash until at least 1957. This region was also an area of heavy burrowing activity by shearwaters which could have uncovered or brought to the surface the seeds or roots of plants. The most likely explanation is that these plants sprouted from seeds or old roots after the Bárcena ash had been removed by erosion and burrowing activity of birds between 1957 and 1961.

Table 3. The angiosperm flora of San Benedicto, Mexico, before and after the eruption of Bárcena Volcano
Asterisks indicate plant species considered to be new arrivals

Flora before Bárcena[A]	Occurs also on		Survived[D]	1971	1978	1981	1987–88
	Socorra	Clarion					
Eragrostis diversifolia[K]			×	×	×	×	×
Cenchrus myosuroides	×		×[B]				
Cyperus duripes	×	×	×	×	×	?	?
Aristolochia brevipes[L]	×		×				
Euphorbia anthonyi var.*[I]	×		×				
Perityle socorrensis	×	×	×		×*[F]	×	×[H]
Stenophyllus nesioticus[J]	×	?	×	×	×	×	×[H]
Ipomoea pes-caprae[C]	×	×		×*	×	×	×[H]
Teucrium affine var.[E]							
Erigeron crenatus[E]					×[G]		

[A]From Johnston (1931).
[B]Two individuals.
[C]Did not survive, but had reinvaded the island (beach north of Lava Delta) by August 1961. Present on beach south of Lava Delta in 1977, absent from there in 1978.
[D]Present 1953–56.
[E]Endemic to San Benedicto.
[F]Leafy branches found in red-footed booby nests. Probably brought in from Socorro. Present and established on North End of island according to Robert Pitman (pers. comm.).
[G]Robert Pitman, common worth-west side of Lava Delta, 1975, specimen Moran 25554, San Diego Natural History Museum.
[H]April 1987. Jeffrey A. Levin.
[I]*Chamaesyce anthonyi* of Levin and Moran (1989).
[J]*Bulbostylis nesiotica* of Levin and Moran (1989).
[K]*E. prolifer.*
[L]*islandica.*

Heavy erosion of the outer edges of the Lava Delta occurred between 1957 and 1971. Waves had carried large rocks shoreward, forming two large rock barriers north and south of the Lava Delta. Eroded pumice and ash from Bárcena filled in the area behind these rock barriers to form two large beaches. There are only two other beaches on the island (most of the perimeter of the island consists of vertical cliffs with no beaches or, at most, rocky ones that are awash at high tide with heavy seas. These two beaches (one east of the canyon between Bárcena and Herrera, the other south-east of the Ash Heap) are subjected to waves and seem unlikely places for the establishment of new immigrants to the island. The first invasion on the new beaches north and south of the Lava Delta had occurred by August 1961. From the air, clumps of beach morning glory (*Ipomoea pes-caprae*) were seen on the pumice beach just north of the Lava Delta. Since the beach did not exist prior to Bárcena, these plants did not resprout from old plants. This species is known for its ability to establish itself on oceanic islands. This patch persists to 2013 (Google Maps) and is where the Laysan albatross started roosting and breeding in 1987 and the beach was renamed Albatross Beach by Pitman and Ballance (2002).

By 1971, the vegetation of San Benedicto Island had not only recovered from the low level of 1961 but had extended over almost all of the northern end of the island (Fig. 10). However, three further species had become extinct during these 10 years (Table 3). The earlier arrival (the beach morning glory) now occurred on ~80% of the beach north of the Lava Delta. In addition, another species new to this portion of the island (*Perityle*) was found on the north beach in 1971. Dr Charles Hougue (pers. comm.) observed what appeared to be beach morning glory on the beach south of the Lava Delta in June 1977. This was the first record of plants on that beach.

By 1978, the entire northern end of the island and Herrera Crater, were covered by plants (*Eragrostis* and *Perityle*). The plants on the south and west portions of the Ash Heap still persisted (Fig. 10). On the beach north of the Lava Delta, *Ipomoea* and a single *Perityle* plant persisted (the latter in poor condition, probably due to salt spray and erosion of Bárcena). The morning glory had begun to invade the lava flow to a distance of ~4 m. No plants were seen on the south beach, thus the *Ipomoea* seen there in 1977 by Hogue had been eliminated. This may have been largely due to the beach being covered by pumice eroding from Bárcena. While erosion of the south beach continues with Bárcena ash filling it in, Google Maps of the island in 2013 show a small green patch, presumably of *Ipomoea,* persisting between erosion channels.

Euphorbia had apparently been eliminated from the island by 1971. However, leafy branches of this plant were observed in a red-footed booby nest on the Lava Delta although it was not growing there. Robert Pitman (pers. comm.) observed that this species was present and established on the north end of the island by 1978. While blue-faced boobies have bare nests, red-footed boobies and frigate birds use plant material to make their nests.

Euphorbia may have been brought in by these birds from nearby Socorro but could, of course, have sprouted from old roots or seeds.

Fig. 10. Outline maps of San Benedicto Island showing the distribution of plants. Plant distribution in 1925 is derived from photographs taken by G. D. Hanna (white areas on northern part of map are not covered by photographs; Lava Delta not present in 1925). No plants were present in March 1953.

There are now extensive nutrients (bird droppings) on the Lava Delta and it is slowly being covered by leached Bárcena ash eroding down from the east face of Bárcena. This area is thus ripe for the establishment of plants brought into this area by sea birds.

By 1981, the erosion of Bárcena had eliminated the small clump of *Perityle* that was seen on the south-west flank of the volcano in 1971 and 1978, and the area occupied by the grass south of the Ash Heap was more extensive (Fig. 10). Google

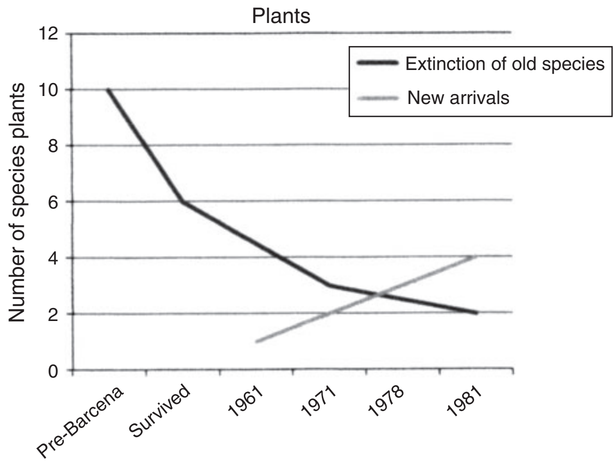

Fig. 11. Number of species of plants on San Benedicto at various dates.

Maps for 2012 and 2013 shows no plants on the south or southwest part of Bárcena. The morning glory on the beach north of the Lava Delta covered about 70% of the beach and had invaded the Lava Delta in many places (Fig. 10, Google Maps). The northern part of the island was almost entirely covered with plants except for a few ridges that were still covered with Bárcena ash (Fig. 10). *Perityle* also occurred on many of the vertical and near-vertical cliffs although it had been eliminated from the beach north of the Lava Delta.

Table 3 and Figs 10 and 11 summarise the changes in the terrestrial flora of San Benedicto Island. Of the 10 original species, six survived Bárcena, and four became extinct. Two of these re-established themselves and two new species arrived on the island, resulting in two of the original 10 species now considered to be extinct on the island. While *Perityle* never became extinct on the north end of the island, I consider the establishment of this species on the North Beach in 1971 as a new invasion of the island, since it never before occurred in this area and the beach did not even exist there until sometime before 1961.

Discussion

Brattstrom (1963) summarised 14 biological impacts and aftermaths of such destructive events as fires, volcanoes, deforestation, drought and radiation. These generalisations are expanded below and emended with ideas from McIntire (2004), Novak *et al.* (2011), Parker and Wiens (2005), Platt and Connell (2003), Turner (2010), Walker and del Moral (2003), and new studies on such disasters as:

Volcanos (Krakatau, San Benedicto, Parícutin, Surtsey, Mount Saint Helens and others) (Eggler 1948; Duellman 1954; Burt 1961; Thorarinsson 1964; Ball and Glucksman 1975; Ball and Johnson 1976; Hayward et al. 1982; Simkin and Fiske 1983; Andersen and MacMahon 1985, 1986; Wood and Del Moral 1987; Thornton *et al.* 1988, 1990; Compton *et al.* 1994; Bush *et al.* 1995; Thornton 2000; Whittaker *et al.* 1998; Lawrence and Ripple 2000; Bishop 2002; Winchester 2003; Dale *et al.* 2005*a*, 2005*b*; Lindig-Cisneros *et al.* 2006; O'Shea and Cook 2006; del Moral 2010; Munoz and Hewlett 2011; Pedersen *et al.* 2012).

Lava flows (Britten 1956; Drake and Mueller-Dombois 1993; Yamaguchi 1993; Thornton 2000).

Atomic blasts or radiation leaks (Platt and Mohrbracher 1959; Platt 1961; Shields and Wells 1962; Rickard and Beatley 1965; Turner and Gist 1965; Eden 2004; Planes *et al.* 2005).

Land slides (Flaccus 1959; Restrepo and Vitousek 2001; Velázquez and Gomez-Sal 2007).

Fires (Horton and Kraebel 1955; Sweeney 1956; Hjerpe *et al.* 2001; Schulte and Mladenoff 2005; Freeman *et al.* 2007).

Deforestation, logging, wind blow-downs, slash and burn (Rabor 1959; Bury 1983; Sakai 1988; Wilkie and Finn 1990; Rebertus *et al.* 1997; Carlton and Bazzaz 1998; Robinson 1998; Sinton *et al.* 2000; Kramer *et al.* 2001; Webb and Scanga 2001; Manolis *et al.* 2002; Penteriani *et al.* 2002; Brook *et al.* 2003; Schulte and Mladenoff 2005; Burris and Haney 2005; Wunderle *et al.* 2006; Rios-López and Aide 2007; Wardle *et al.* 2008; Brooks and Stouffer 2010; Pike *et al.* 2011; Belote *et al.* 2012).

Drought (Blair 1957; Tobin *et al.* 1999; Beard *et al.* 2005).

El Niño (=ENSO) (Gibbs *et al.* 1984, 1987; Hodder and Graybill 1985; Gibbs and Grant 1987; Curry and Stoleson 1988; Anderson 1989; Schreiber and Schreiber 1989; Cruz and Cruz 1990; Wilson 2005; Polis *et al.* 1997; Jaksic and Lazo 1999; Grant *et al.* 2000; Jehl *et al.* 2002; Fuller *et al.* 2004; Velarde *et al.* 2004; Charrette *et al.* 2006; Devney *et al.* 2009).

Hurricanes (Boucher *et al.* 1990; Dunning 1991; Roth 1992; Rivera-Milán 1995; Wunderle 1995; Faaborg and Arendt 1995; Latta *et al.* 1995; Asner and Goldstein 1997; Censky *et al.* 1998; Vandermeer *et al.* 1998; Frangi and Lugo 1998; Mabry *et al.* 1998; Hunter and Forkner 1999; Sullivan *et al.* 1999; Sherman *et al.* 2001; Walker *et al.* 2003; Boose *et al.* 2004; Ostertag *et al.* 2005; Pavelka and Behie 2005; Piou *et al.* 2006; Hawley 2006; Spiller and Schoener 2007; Watts and Byrd 2007; Knapp and Valeri 2008; Yaukey 2008; Vandecar 2011; McKnight 2012; Ramírez-Barajas *et al.* 2012; Plotkin *et al.* 2013).

Tsunamis (Wikramanayake *et al.* 2006).

Ski slopes (Titus and Landau 2003).

Earthquakes, seismic settlements (Gill *et al.* 2004; Lai *et al.* 2007).

Off-road vehicles (Brattstrom and Bondello 1983, 1997).

Mining, mining debris, dumps, waste sites (Wray *et al.* 1982; Manner *et al.* 1984; Skousen *et al.* 1990; Hopkins *et al.* 1997; Schreiber *et al.* 2001; Thompson and Thompson 2007; Baasch *et al.* 2010; Graves *et al.* 2010; Jorgenson et al. 2010; Stauffer *et al.* 2011).

Agriculture (Holl 1999; Knops and Tilman 2000; Martin *et al.* 2004).

Roads (Laurance 2004; Clark *et al.* 2010).

Moving sand dunes (Belsky and Amundson 1986).

Post-glacier melting (Tisdale *et al.* 1966).

Grazing (Day and Detling 1990; Sirotnak and Huntly 2000; Browning and Archer 2011).

Climate change (Kingsford 2011).

Oil spills (Belsky 1982; Wilson *et al.* 2004; Iverson and Esler 2010).

Winds, dust-bowls, Santa Anas, mistrals, siroccós.

Floods (McCarley 1959; Quanstrom 1966; Burger and Shisler 1980: Walker and Chapin 1986; Knopf and Sedgwick 1987; Friedman *et al.* 1996; Knutson and Klaas 1997; Seigel *et al.* 1998; Andersen *et al.* 2000; Benke *et al.* 2000; Tucker *et al.* 2001; Chamberlain and Leopold 2003; Jenkins and Boulton 2003).

Insect outbreaks (beetles, gypsy moths) (Logan *et al.* 2010; Koenig *et al.* 2011).

Disease outbreaks (Fonnesbeck and Dodd 2003; plus extensive literature on amphibian diseases).

Tornados (Prather and Smith 2003; McGlinn *et al.* 2010).

Wind turbines, transmission lines (Niemi and Hanowski 1984; Grodsky *et al.* 2011).

Meteors and asteroids (Fraser and Sues 1994; Officer and Page 1996).

These generalisations are as follows:

1. Repopulation or reinvasion is rapid. If there has been partial destruction (as in the case of San Benedicto), reproductive rates can usually allow for rapid intrinsic repopulation. If the area is surrounded by normal vegetation (as in instances of lava flow, atomic blast, fires, land slides) the reinvasion is rapid. If the area is in a location of high population density, repopulation from without (in the case of Krakatau) or reinvasion (in the case of atomic blasts, fires and land slides) will be rapid. If the site is distant from a source, reinvasion, but not necessarily intrinsic population growth, may be slow (San Benedicto).
2. Islands with complete or partial destruction appear to repopulate more slowly than terrestrial areas (lava flows, fires, Parícutin, atomic blasts) but this appears to be largely a matter of (a) amount of surviving intrinsic population, and (b) rate of chance dispersal to the island.
3. Species with good methods of dispersal invade areas faster than those with poor dispersal mechanisms, and species with high reproductive rates or with certain reproductive attributes (for instance, viviparity) repopulate faster than those without.
4. Reinvasion and repopulation may follow a pattern similar to the primary succession in the area (for example, primary soil-forming plants, Parícutin), or there may be peculiar jumps in the succession due to (a) chance survival of some forms, (b) population pressure outside the area, (c) peculiar dispersal patterns or mechanisms, or (d) special advantages given to certain species by the catastrophe (for instance, change in soil texture, type, moisture).
5. Species dominant in an area before the catastrophe may be dominant subsequently, or another species or group (or a species new to the area) may become dominant. Which obtains depends on, among other things, the limiting factors of the organism (that is, soil moisture, habitat availability, exposure, and so forth), number and type of surviving forms, and differences in dispersal or reproductive rates, or chance.
6. Weather and erosion factors, as well as competition, food, and behaviour may markedly alter the success of a species in its reinvasion or repopulation (Furness and Barrett 1991; McNab 1994).
7. The population size of a species may be reduced (due to limited survival, as on an oceanic island, or by isolation, as between lava flows). This may make the population ripe for genetic-drift mechanisms and hence lead to rapid evolution in such situations and areas.
8. The major effect of the catastrophe may not be the event itself. Even though the event be spectacular and destructive, the side effects or after-effects may be more critical to the survival of both individual and species (fires, hurricanes, absence of food, lack of water, change in erosion pattern, radiation after-effects) and to reinvasion and repopulation.
9. A major contributing effect of some of these events is the creation of new land (as in the cases of San Benedicto, Krakatau, and Hawaii) or the alteration of the physical or chemical character of the land (Parícutin, San Benedicto, fire, landslides, hurricanes or atomic blasts). Colonisation on new land may be fast and include exotics (Santos *et al.* 2011).
10. After the catastrophe, species may occupy new habitats or new types of habitats. The creation of new habitats often allows species not formerly present to become established in the area.
11. Organisms that have special powers of locomotion (insects, birds, large mammals) usually suffer heavy population losses by their ‘refusal’ to leave home areas or territories or by their confusion and inability to comprehend the event.
12. Unless a surviving animal has extended powers of flight (birds, insects), food supply may be one of the more critical limiting factors to animals.
13. Human factors related to the event (for example, planting and building, as in Parícutin and Hawai‘i) may increase the opportunity and decrease the time for reinvasion and repopulation.
14. The effect of the catastrophe depends upon its size and nature.
15. Changes in behaviour and ecology (especially feeding) may occur after the event.
16. Changes in soil chemistry (nutrients and antigrowth chemicals) may affect survival, recovery, and aid or deter new exotics (Green 1998; Shiels 2006; Meyer and Cowie 2010).
17. Postdisturbance management and restoration may be planned for the better but often the worse occurs (Chapman 1963; Jones and Kress 2012; Spear *et al.* 2012).
18. Weather, especially rainfall, temperature, seasonality events, or the event itself may affect physiology, reproduction, stress (in its short- and long-term effects) (Schreiber and Chovan 1986; Reichert *et al.* 2012).
19. Plants may survive the event, but die later due to the lack of water, nutrients, herbivore damage, and stress. Signals of stress (Christmann and Grill 2013) may affect plants that were unaffected by the event itself.
20. Some arrivals to the site may be soon after the event; others may not arrive until years or decades later (Denslow *et al.* 2009; Jones 2010*a*, 2010*b*).
21. The absence of pollinators will prevent some surviving species from reproducing and new species from becoming established.
22. After the event, animals may leave the area or move about the area in search of food, shelter, or reproductive sites. Some may return to the area, some may not.

23. The events or local weather events may make damaged plants more susceptible to insectivory, herbivory, and parasites, and they may not be able to produce protective chemical defences.
24. Some impacts of the event are immediate or short while others may last for centuries (Jones 2010*a*, 2010*b*).
25. The event may change recovery from previous disastrous events in the same area.
26. These events '… can negatively or positively affect social, economic and environmental assets' (of humans). 'Few cause major losses of human and homes, but when they do they make banner headlines in the world's media' (Gill *et al.* 2013).
27. Large islands will have more invaders earlier than small islands; but small continental sites will have new invaders more quickly than large sites. Edges will be invaded first unless the invader can fly.
28. The rate of extinction versus new arrivals may or may never come to equilibrium.
29. Exotic new invaders may do more damage than the event itself (Blackburn *et al.* 2004; Davis *et al.* 2008; Meyer and Cowie 2010).
30. Human visitors, even researchers and managers, to the area may have an impact on breeding birds or import exotic spores or seeds (Beale and Monaghan 2005).
31. If an endemic species occurs on the site (especially on an island), small post-event population numbers can lead to inbreeding aiding 'founders effect' evolutionary change or extinction (Frankham 1998).
32. Invaders or colonisers may bring in parasites or seeds, which may have beneficial or harmful effects on the native biota.
33. Aerial plankton (seeds, spores, insects, spiders), whether windborne or from the stratosphere, may bring early immigrants to the site (Edwards and Sugg 1993).
34. The topography of the area destroyed will impact the kind and rate of recovery (Cox and Cox 1977; Eason *et al.* 2012).
35. Survivors of the event may control revegetation and repopulation more than invaders (Plotkin *et al.* 2013).
36. Most impacts of these events are local. Some (hurricanes, fires, volcanic ash) may cover several States at most. Rarely are the impacts country- or world-wide (exceptions include volcanic ash in the stratosphere for years (Robock and Matson 1983), and speculation about world-wide effects of asteroids on dinosaurs, but not birds, mammals, crocodilians, snakes, lizards and amphibians).

The eruption on San Benedicto stands out in the following ways:

1. The island is far from sources of new invasions and thus reinvasion is slow, although nearby islands may be a source for some plants.
2. Frigate birds were more common on the island prior to the appearance of the volcano, but masked boobies became more numerous following its appearance.
3. Weather and erosion markedly affected the survival and repopulation of plants and may have been more destructive than the volcano itself.
4. Elimination of shearwater burrows by Bárcena and subsequent covers or erosion caused the major decline in shearwater numbers. Subsequent exposure and pre-Bárcena ash, then more erosion caused a rise and then a fall in shearwater numbers in 1978–81. Later (1988–2000) increases in shearwaters resulted from their finding new burrowing sites on the north part of the island.
5. New land and new landforms (Lava Delta and the barrier-protected beaches) aided in the establishment of a species of seabird new to the island and allowed for the establishment of new plant invaders (Stolzenburg 2011).
6. Tourism, fishermen and casual visitors slightly impact the island today, but provide a potential for the accidental introduction of exotics.

The question arises as to whether the increased sea bird population on San Benedicto is intrinsic or extrinsic. The reproductive strategies of tropical island sea birds are characterised by a seasonal or continuous breeding, large egg size, low clutch size, long fledging period, long postfledging feeding and low adult mortality (Dorward 1962; Diamond 1973; Nelson 1975; Dodson and Fitzgerald 1980; Schreiber and Burger 2003). This results in high survival of young and a long adult life at a slow, but stable reproductive rate consistent with food availability (low in tropical seas) and feeding strategies and energetics (Spendelow 1985), all conducive to a slow steady increase in the bird population (Hunt *et al.* 1986). This may be the reason for the steady population numbers of the frigate bird, tropic bird, and brown and red-footed booby populations on San Benedicto (Carmona *et al.* 1995). It cannot be the case for the rapid rise and subsequent decline seen in the masked booby populations (see discussion in Fontaine 2013). Little is known about interisland movements of sea birds in the eastern Pacific. Yet Anderson and Ricklefs (1987) show that masked boobies forage widely. At no time were there large populations of sea birds on the other islands of the Revillagigedo group, nor were anything but small populations of some of the Revillagigedo species ever observed on the Baja California peninsula, Alijos Rocks or Cedros Islands. The population increase of masked boobies on San Benedicto does seem to require some immigration of these boobies from elsewhere. However, the nearest potential sources of these birds would most likely be Clipperton Island, Cocos and the Galápagos (Mills 1998), both far south of the Revillagigedos (Ehrhardt 1971; Nelson 1968; Harris 1974; Anderson 1993).

With the subsequent decline in masked booby population numbers, the area occupied by sea birds also declined. The reason for the decline in the booby population has not been determined. Unexpectedly, there also was no breeding of boobies on Socorro in 1978 or 1981. There have always been no more than several hundred boobies nesting on the extensive lava flows and islets on and about that large island. Clarion Island to the west has never had more than several hundred sea birds. Roca Partida is so small that it provides room for only a few dozen birds. The general impression was that there were fewer fish (especially the surface fish upon which boobies feed) about the islands in 1978 than ever before. In 1978 and 1981, no flying fish were seen (they had always been numerous), and few fish or fish larvae came about the lights on the boat at night while at anchor. On previous trips flying fish (*Cypselurus*), half-beaks (*Hyporhamphus*), jacks (*Caranx*), larval fish and invertebrates were abundant about the boat at night. Further, in 1978 and 1981 there were few commercial tuna boats around the islands, and sport-fishing boats reported by radio that fish were rare. Intertidal and subtidal fish seemed abundant, but sea birds seldom feed on these fish (Brattstrom 1998). Evening fly-in counts suggest that sea birds fly long distances and fish at greater depths for food (Lewis 1973; Haney 1985; Anderson and Ricklefs 1987; Seki and Harrison 1989; Pitman and Ballance 1990; Anderson 1993; Spear *et al.* 1995; Le Corre 1997; Brattstrom 1998; Castillo-Guerrero and Mellink 2006). Perhaps there has been some oceanographic change, perhaps preceding or related to El Níño events, or the effect of numerous hurricanes that cross over the island each year (about one-third of all Eastern Pacific hurricanes recorded, 1851–2010, passed over the archipelago). Data from NOAA, which lowered the productivity about the islands, hence causing the decline in the masked booby population (Gibbs *et al.* 1984; Schreiber and Schreiber 1984; Halpern *et al.* 1983) in any event, masked booby populations levelled off and then increased slightly by 2002. Hurricane impacts (Duffy 1984) may have caused boobies to leave the Lava Delta. It is also possible that Brattstrom overestimated, and subsequent researchers underestimated (by not doing evening flying counts), this possible sampling error, combined with the seasonality of visits by researchers (Craig 1996; Douglas 1998; Norvell *et al.* 2003), and years of no visits by researchers (Bart and Earnst 2002; Thompson 2002), combined with El Níño and hurricane impacts may have affected the masked booby populations more than those of other species. Changes in shearwater populations (Fig. 8) are explained in part by erosion and exposure of burrow sites (Pitman and Ballance 2002).

Future of the island

There have been marked erosional changes on San Benedicto during the last 60 years. The soft volcanic pumice and ash has been extensively eroded so that the cone of Bárcena and other areas of ash are now heavily furrowed by erosion channels 40–50 m deep. The volcanic ash of the eastern side of the cone of Bárcena has washed down onto the lava flow and has filled in almost one-third of this delta. The guano deposits of the sea birds seem to have stabilised in the ash and, of course, added nutrients to both the land and the sea. This area should provide a suitable habitat for further plant growth.

The erosion from the cone has also formed the beaches north and south of the lava delta to such an extent that they have increased their size some 10-fold since 1961. Erosion of the outer fingers of the lava delta has destroyed the protective coves (an area previously heavily occupied by marine algae and fish). Lava boulders have been deposited as a barrier along the outer edge of both beaches, thus protecting them from subsequent marine erosion.

In 1971, a camping site of stranded fishermen was found north of the Lava Delta and in 1978 and 1981 there was a considerable amount of garbage (from fishing and sport boats) on the wave-swept beach east of Bárcena. In March 1988, Pitman and Ballance (2002) found much of the northern part of the island burned and exploded, presumably due to military ordinance on the island. Sport fishing boats inadvertently catch and drown unknown numbers of young boobies and frigate birds with their trolling gear (Pitman and Ballance 2002). Fishermen, sight-seeing visitors and scientists may accidentally bring outside organisms to the island. As yet, no rats, mice or cats have been introduced on the island. These animals could be disastrous for the seabird populations. The four islands of the Revillagigedos were designated in 1984 as a Biosphere Reserve for conservation purposes. It is hoped that the Mexican Government will restrict access to San Benedicto so that the casual introduction of plants and animals will not occur and this natural laboratory can be preserved and utilised for the ongoing study of repopulation and revegetation of such a unique island and event.

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