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Coral Cay Instability and Species-Turnover of Plants at Swain Reefs, Southern Great Barrier Reef, Australia[1]

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ABSTRACT

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The coral cays of the Swain Reefs are far removed (up to 200 km) from any mainland influence. There is a complex inter-relationship between species distribution, species-turnover, and coral cay instability. Factors promoting cay instability include: (1) seasonal variation in wind direction, (2) short term cyclonic influences, and (3) longer term changes in the direction of the dominant winds. The cyclonic influence appears to be a major cause of inter-cay variations in plant species distribution. This is shown by comparing the orientation and position of the cays in 1964 with their present morphology. Gannet Cay for example only has a very small percentage of the vegetated area common to both the 1964 and 1984 cay outlines. A total of 13 species of terrestrial vascular plants have been recorded from the cays. Four species were prevalent and persistent since 1967. There was local extinction and immigration of plants which resulted in considerable species-turnover. Patterns of extinction and immigration varied among islands. In general, immigration was more prevalent early in the study and extinction more prevalent later. Unstable islands tended to have higher rates of species-turnover than did more stable ones.

ADDITIONAL INDEX WORDS: *Cay instability, coastal plants, coral cays, distribution and zonation, Great Barrier Reef, Swain Reefs.*

INTRODUCTION

The cays within the Swain Reefs have received scant attention because of their relative inaccessibility until the last few decades The first detailed survey of the area was carried out by HMS Fly in company with the tender Bramble and reported on by JUKES (1847). More than 100 years passed until 1960 when a brief survey of the southeastern area located several uncharted cays (GILLETT and MCNEIL, 1962). This was followed by a visit by scientists from the Australian Museum (MCMICHAEL, 1963). Since 1967 several scientific parties have visited the area. LIMPUS and LYON (1981) reported on a visit to the area made in 1976. They were the first to record major variations in cay size, shape and vegetation cover.

The cays of the Swain Reefs are small and relatively remote from the Australian mainland. Furthermore, they are subject to periodic tropical cyclones, have undergone considerable erosion and redeposition of sand, and in some cases (*e.g.* Gannet) have moved rather great distances across the reef on which they are located.

The equilibrium theory of insular biogeography would predict that the small size and remoteness of these cays would (1) impose low species numbers upon them, (2) result in frequent local extinctions, and (3) restrict the flora to those species capable of frequent long-distance, over-water dispersal and of rapid reproduction once arrived. With frequent immigration and extinction, rapid species-turnover and hence observable changes in species composition of the floras would be expected.

The unstable conditions and the harshness of the physical environment would suggest that only salt-tolerant, drought resistant species able to withstand heat, wind, and shifting substrates would survive except ephemerally. Add to this the effect of trampling and guano deposition by dense breeding populations of sea birds and the destruction of vegetation by nesting sea turtles and one has the scenario of the cays of

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the Swain Reefs.

Seven vegetated cays were surveyed a number of times in order to detect temporal changes in species composition of the flora and to relate species-turnover to stability of the islands.

STUDY AREA

The Swain Reefs represent the most eastern and southern development of the Great Barrier Reef system. They cover an area of about 16,000 km^2, lying between 20°53'S and 22°24'S, and 151° 15'E and 152°48'E and extending from 110 km to 250 km offshore (Figure 1). Although the reef complex contains over 350 reefs, the number of coral cays is very small; six are vegetated and in addition there are several small sandbanks which dry at low water.

Inspection of black and white vertical aerial photographs taken in 1964 reveals that the Swain Reefs area is characterized by a moderately uniform distribution of cuspate, platform, elongate platform and lagoonal platform reefs (Figure 2) and by the absence of high density shelf-edge development which distinguishes it from the Pompey Reefs to the north. The majority of reefs (75%) are less than 3 km long. Their geomorphic development

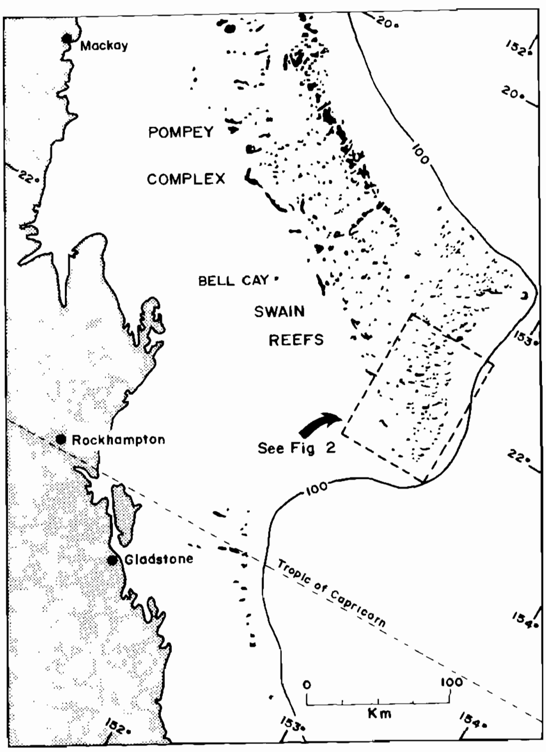


Figure 1. Location of the Swain Reefs.

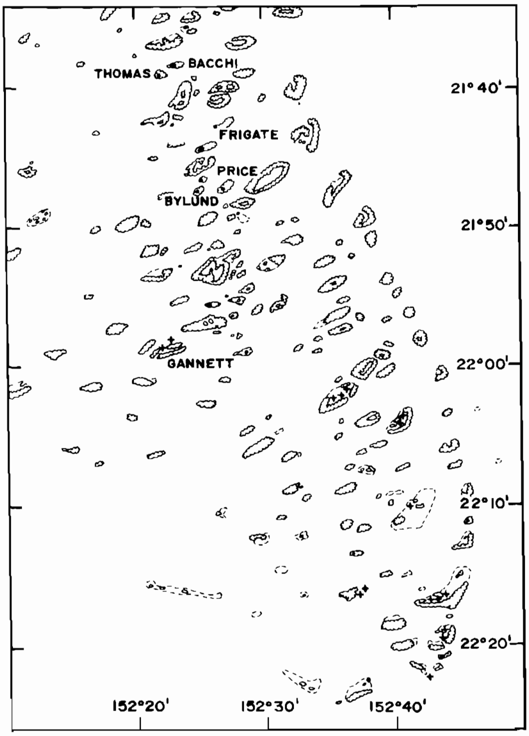


Figure 2. Details of the southern part of the Swain Reefs.

is controlled by the shape and variable surface relief in the underlying pre-Holocene reefal platforms (FLOOD, in prep.). Geophysical surveys and oil exploration drilling adjacent to the Swain Reefs (WILSON, 1967, 1969; ERICSON, 1976) have delineated the major structural features which reflect the underlying tectonic framework.

Six of the vegetated cays reported upon in this study are located towards the southeastern portion of the Swain Reefs. The seventh, Bell Cay, is located some 30 km to the west and is outside the Swain Reefs. Three of the cays are located on small elongate platform reefs whilst four are situated on the leeward side of elliptical-shaped platform reef (Figures 3, 4).

MATERIALS AND METHODS

Monitoring the Shape of the Cays

The shape of seven cays (Table 1) was monitored by examinining black and white aerial photographs taken in 1964 and again in 1984 (Plate 1) In addition, two field visits were made, in July 1983 and again in July 1985. During the latter visit the long

Table 1. Cay Dimensions.

Cay Name	GBRMPA Number	Measurements (m) 1985 Long Axis	Short Axis	Perimeter 1964[3]	1976[4]	1983	1984	1985	Area (1984) Vegetation	of Sand Cay
Bacchi	21-495	350 [277][5]	62 [95]	900	554	811	909	nd	2600	17200 m^2
Thomas	21-497	239 [129]	163 [104]	490	464	493	493	nd	4000[6]	16800 m^2
Frigate[1]	21-511	409 [465]	109 [277]	1070	912	1009	1036	1019	14400	42000 m^2
Price	21-518	374 [308]	117 [208]	900	769	818	818	845	10800	28400 m^2
Bylund	21-519	198 [371]	101 [185]	700	510	492	492	567	3400	28400 m^2
Gannet[2]	21-556	385 [325]	97 [161]	700	621	904	900	883	12500	27200 m^2
Bell	21-435	361 [nd]	145 [nd]	880	814	914	914	871	12000	43200 m^2

[1, 2] Called Gillett and Poulson respectively by GILLETT and McNEIL, 1962.
[3] Value obtained from 1964 vertical aerial photographs.
[4] Value is the estimated perimeter of the cay at low water in 1976 using the data of LIMPUS and LYON (1981) and the conversion factor established in 1985 for the ratio of the perimeter at low water and the perimeter at mean high water spring tide level.
[5] Values in brackets are the approximate measurements made in 1960 by GILLETT and McNEIL (1962).
[6] Very sparse vegetation, mostly dead.

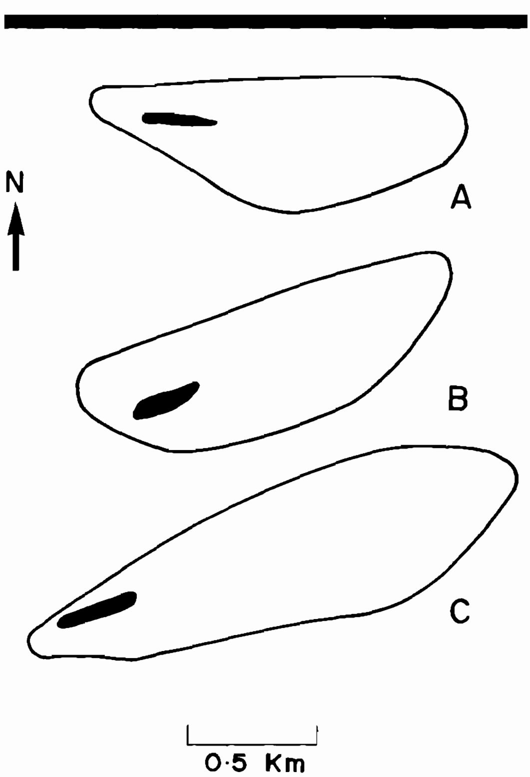


Figure 3. Elongate platform reefs with sand cays: A, Bacchi 21-495; B, Price 21-518; C, Frigate 21-511. (The numbers are official designation for the reefs, given by the Great Barrier Reef Marine Park Authority).

and short axes and the perimeters of the cays were measured using a trumeter. The perimeter measurement quoted in Table 1 was taken as the junction line of the beach and the reef flat. This position of measurement was different from that of LIMPUS and LYON (1981) who recorded the perimeter at the mean spring high tide level. This distance was recorded during the 1985 visits so that a conversion factor could be established for comparing the 1976 measurements with those obtained in 1985 and subsequent years.

In addition, previous positions of several cays are indicated by the occurrences of beachrock now separated from the cays. Six radiocarbon dates were obtained from *Tridacna maxima* clam shells which were embedded in the beachrock.

Monitoring the Vegetation of the Cays

The cays of the Swain Reefs have been visited at irregular intervals since 1967, with the visits for some cays becoming yearly beginning in 1980 and twice yearly beginning in 1984.

At each regular visit, a careful search for plants was made on each island and a floral list, believed to be complete, was compiled. Sketch maps were made and the island's dimensions measured. A short description of the physical characteristics and vegetation was written, the sea birds counted and their nesting areas sketched on the maps.

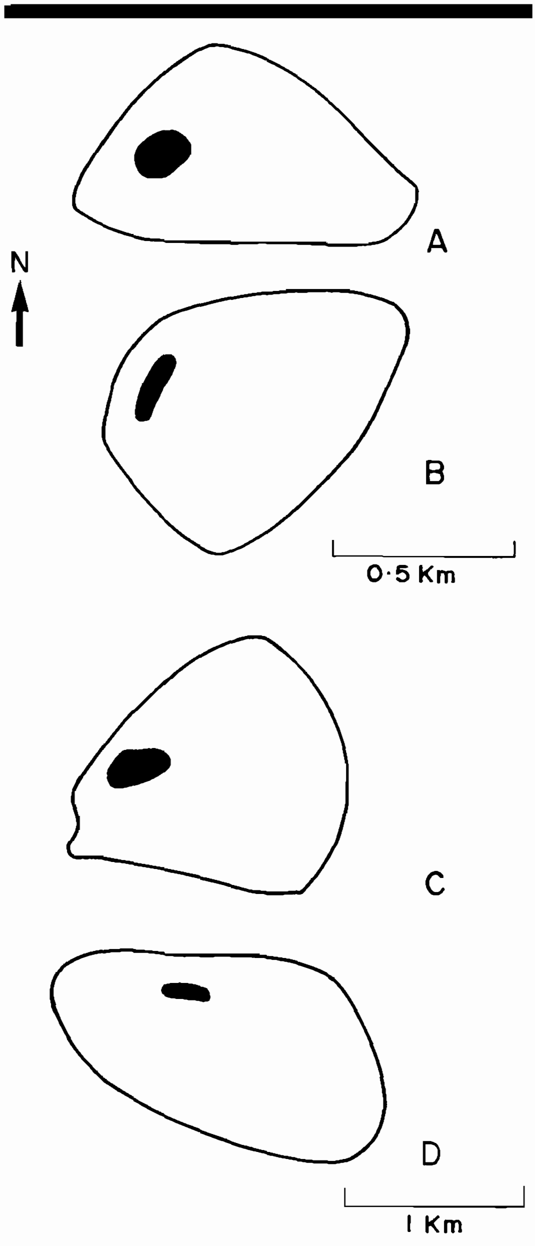


Figure 4. Elliptical-shaped platform reefs with cays; A, Thomas 21-497; B, Bylund 21-519; C, Gannet 21-566; D, Bell 21-435.

RESULTS

Cay Position and Shape Variability

The shape and orientation of a cay is controlled by the wave refraction pattern of its reef; accordingly, the shapes of individual cays closely mimic that of the reefs on which they lie. A generalized outline of the shape of each cay drawn from the vertical black and white aerial photographs taken in November 1984 is shown in Figures 5-8. Each diagram shows the distribution of beachrock where present, the trace of the junction of the sandy beach with the reef flat as observed at low water, and the trace of the high water spring tide mark which in most cases corresponds to the outer perimeter of the vegetated part of the cay.

All are sand cays composed of coarse sand and gravel-sized bioclastic sediment. The major skeletal components are coral, coralline algae, foraminiferans and molluscs. The sediments display varying degrees of sorting and rounding. In general, the

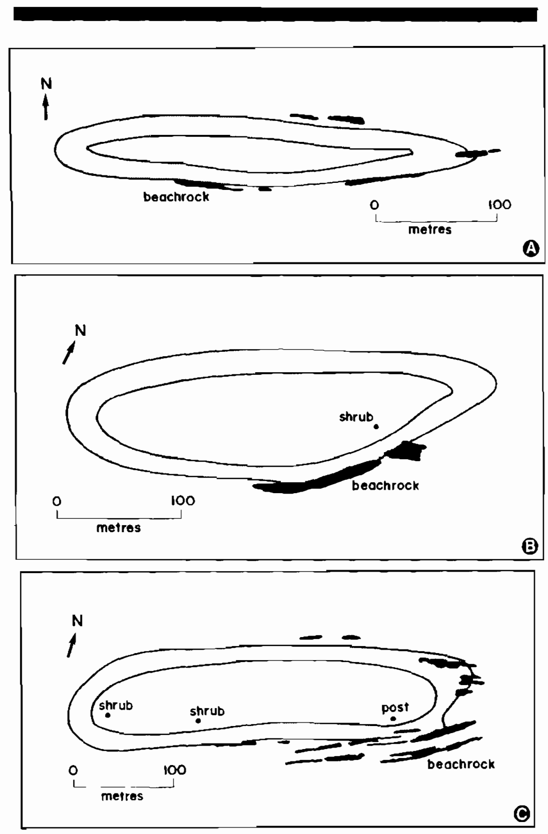
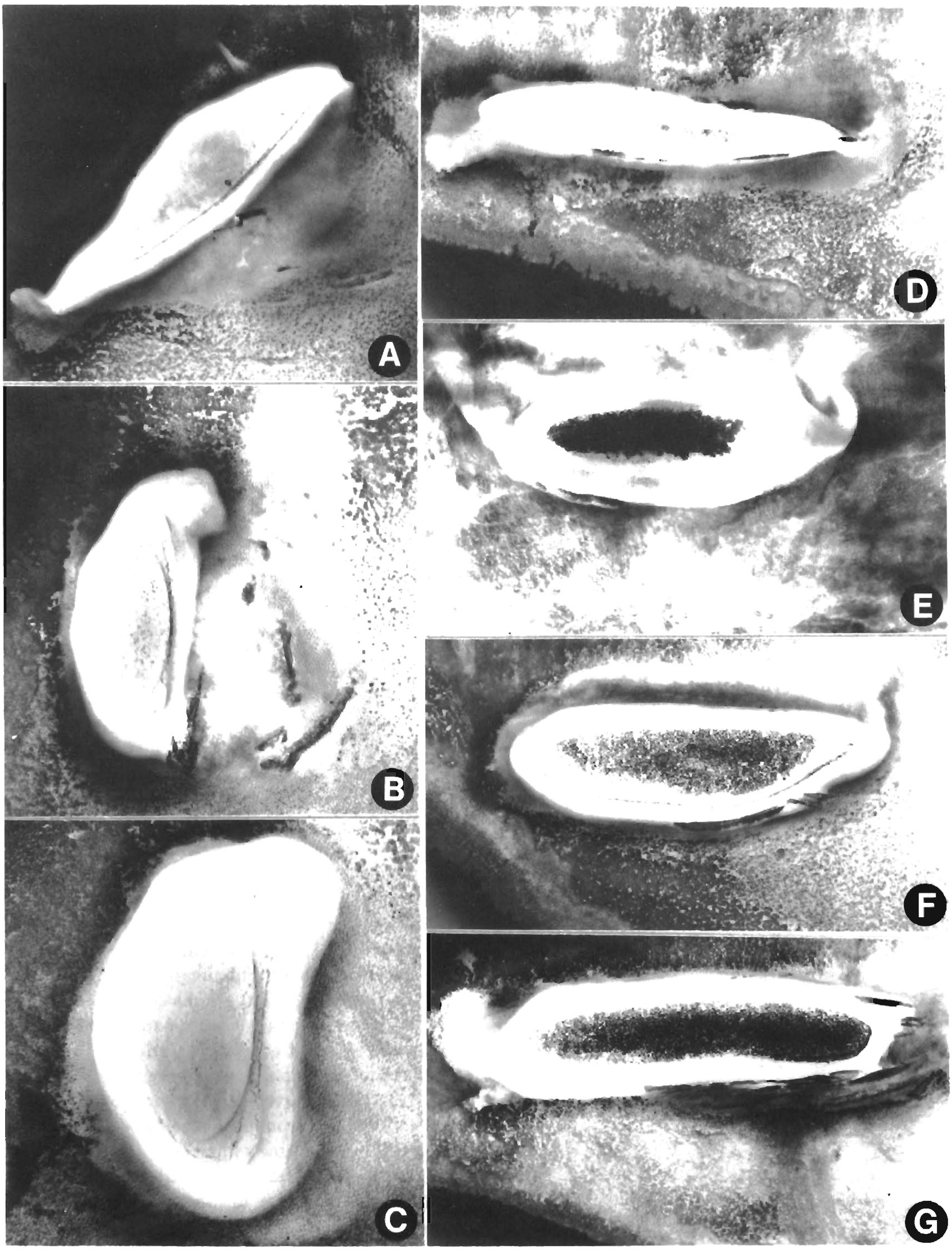


Figure 5. Detailed outline of the cays drawn from aerial photographs taken in November 1984: A, Bacchi; B, Price; C, Frigate.

Plate 1. (Facing page) Vertical aerial photographs (November 1984) of the vegetated cays of the Swain Reefs. See text-figures for scale and orientation of individual cays. A, Gannet; B, Bylund; C, Thomas; D, Bacchi; E, Bell; F, Price; G, Frigate.


A
B
C
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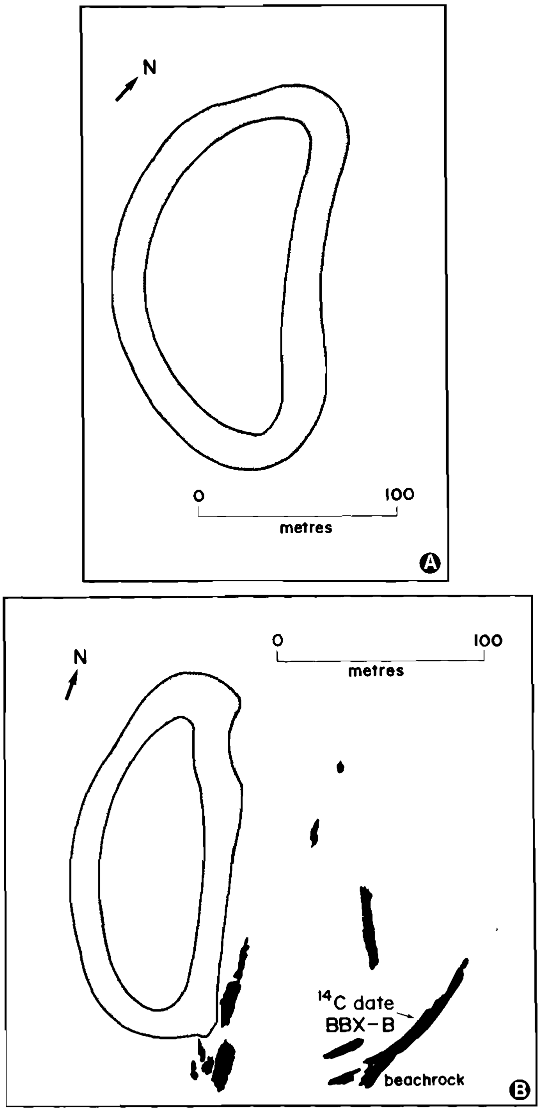

Figure 6. Detailed outline of the cays drawn from aerial photographs taken in November 1984. A, Thomas; B, Bylund.

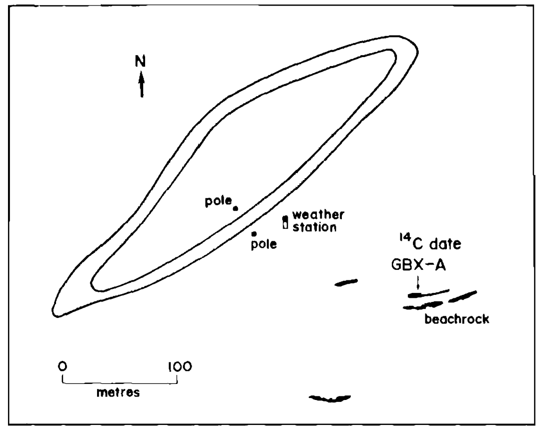

Figure 7. Detailed outline of Gannet Cay drawn from vertical aerial photograph taken in November 1984.

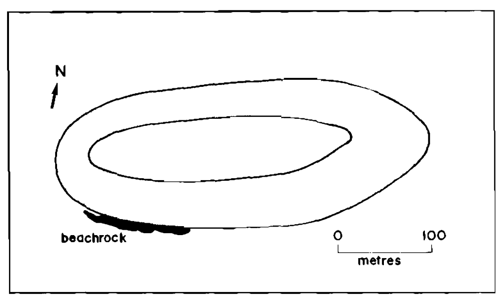

Figure 8. Detailed outline of Bell Cay drawn from vertical aerial photographs taken in November 1984.

windward sediments are coarser and better sorted than the leeward sediments.

There is considerable difficulty in reconciling all measurements quoted by GILLETT and McNEIL (1962) with the shape and dimensions of the cays as seen in the aerial photographs of 1964. Because they state that several measurements were approximate we feel justified in disregarding their data in the current discussion. The measurements of LIMPUS and LYON (1981) have been converted to provide an estimate of the perimeter of the cay as would have been measured at low water.

The overall trend shows little change in the perimeter of most cays between 1964 and 1983/85 except for Gannet Cay which has changed shape and increased its perimeter whereas Bylund Cay

Table 2. Radiocarbon ages of beachrock formation, Swain Reef[1].

Cay & Field No.	Beta Lab. No.	^{14}C age years BP	Conventional age BP ^{13}C adjusted	Reservoir Corrected ^{14}C age BP
Gannet, GBX-A	Beta 13946	1080±90	1510±90	1060±100
Bylund, BBX-B	Beta 13945	580±60	1010±60	560±70
Price, BAC-3	Beta 14526	840±70	1270±70	820±80
Bacchi, BAC-3	Beta 14527	690±80	1120±80	670±90
Frigate, FRI-11	Beta 14528	350±60	780±60	330±70
Bell	Beta 14529	100.0±0.7 modern	430±60	−20±70

[1] See Figures 6 and 7 for location of samples on Gannet and Bylund Cays; samples on Price, Bacchi and Bell Cays are from SW exposures of beachrock; sample from Frigate Cays is from outermost exposure on the SE.

has become smaller. It is these two cays which exhibit the largest degree of instability. Radiocarbon ages for *Tridacna maxima* clam shells which were collected from beachrock on the cays gave the following ages when corrected for environmental reservoir effects by substracting 450±35 yr from the ^{13}C corrected radiocarbon date (see Table 2).

These dates are maximum possible ages for the beachrock. They are of similar age as the date of 630±90 yr BP cited by MAXWELL (1969) for beachrock on Lavers (or Twin) Cays in the northern part of the Swain Reefs. They indicate that the cays have formed since one thousand years ago.

Plant Species Turnover

A total of 13 species of terrestrial vascular plants have been recorded from the cays of the Swain Reefs (Table 3). Only three species were present, at some time or other, on all of the vegetated cays; they were *Boerhavia diffusa* and the grasses, *Lepturus repens* and *Thuarea involuta*. One species occurred on five cays, one on four cays, one on three, two on two, and five species were found only on a single cay.

Table 3. Plants recorded from the Cays of the Swain Reers.

Taxon	Bell	Frigate	Gannet	Price	Bylund	Bacchi	Total (% of islands)
Nyctaginaceae							
Boerhavia diffusa	+	+	+	+	+	+	6 (100)
Chenopodiaceae							
Salsola kali	+						1 (17)
Amaranthacea							
Achyranthes aspera	+						1 (17)
Brassicaceae							
Coronopus integrifolius		+	+	+	+	+	5 (83)
Cakile edentula	+	+	+				3 (50)
Zygophyllaceae							
Tribulus cistoides	+						1 (17)
Tiliaceae							
Triumfetta procumbens		+				+	2 (33)
Cucurbitaceae							
Unidentified		+					1 (17)
Convolvulaceae							
Ipomea pes-caprae	+						1 (17)
Boraginaceae							
Argusia argentea	+	+	+	+			4 (67)
Poaceae							
Lepturus repens	+	+	+	+	+	+	6 (100)
Thuarea involuta	+	+	+	+	+	+	6 (100)
Arecaceae							
Cocos nucifera	+	+					2 (33)
Total (% of total Swains flora)	10 (77)	9 (69)	6 (40)	5 (39)	4 (31)	5 (39)	

Not all species necessarily present at any one time.

No island had at any time, or collectively over all surveys, all of the species known from the Swain Reefs. Bell Cay had the largest species list with a total of 10 of the 13 possible species (77%). Gillett Cay had nine species, and all others had less than half of the total possible species.

These figures do not give a very accurate picture of the flora of these cays. Most of the islands did not have, at any one time, all of the species listed for them. Rather there was considerable species turnover.

Only one island (Price) had exactly the same group of species at all surveys. The cays of the Swain Reefs are so small that species of plants are unlikely to have been overlooked during the intensive surveys carried out during the present study. Thus, the apparent species turnover is likely to be real and the error from incomplete surveys would be small.

Four species were prevalent (occur on many of the islands and account for a large biomass wherever they occur) and persistent (present at most surveys for a particular island). They can be considered as characteristic species. They obviously have the adaptative requisites for dispersing to remote islands, and once there, to survive and reproduce under the stringent, unstable conditions of small, ephemeral sand cays. The way these species cope with the insular environment and problems of dispersal are quite different. *Boerhavia* has a deep fleshy taproot and can reach deep water sources; it can maintain itself during periods when photosynthesis is reduced (persistent trampling off of shoots by seabirds); it also produces copious numbers of seeds that are sticky and dispersed by seabirds. *Coronopus* can grow in shifting sands of low organic content and produces large numbers of seeds even when very small. It is thus a good colonizer of new or disturbed habitat. The grasses reproduce vegetatively, *Thuarea* and *Lepturus* by sending out runners. They are thus able to colonize and consolidate unstable sands.

Argusia argentea is a good colonizer of remote islands, yet it occurred on only four of the cays, and where it did occur, it was represented by only one or a few individuals, none of which has yet reached reproductive maturity.

Of the remaining species, two were ephemeral and did not reproduce (*Cocos nucifera*, unidentified cucurbit), two were species characteristic of the more stable, interior parts of herbflats (*Tribulus cistoides, Achyranthes aspera*) and were found only on Bell Cay. One became established during the study (*Salsola kali*) and two were pioneering species that only occurred on one or two islands each (*Ipomea pes-caprae, Triumfetta procumbens*).

The first record of *Cakile* from the area was in 1972 when an ephemeral population of only a few plants was observed on Gannet Cay. The species had disappeared by the following visit (1979) and has not been present on that island since. Consequently, this occurrence represents an early dispersal to the region from the mainland or from the cays of the Capricorn group (perhaps via Bell Cay) but which did not take, and which did not serve as a base for colonization of other islands.

Cakile was well established on Bell Cay when the first floral survey was made there in 1981. It was growing luxuriantly, especially around the edges of the island, but was poorly represented in the interior of the herbflat, a status it still retains. Bell Cay is the second largest cay of the region and the one closest to the mainland and the Capricorn group of islands, the most likely sources of seed. It is not surprising therefore, that Bell was the first to be permanently colonized by this plant. Subsequently, *Cakile* reached Frigate Cay probably from Bell Cay. The species was first noted on Frigate as a single plant in July 1981. By the following year it had spread to become a patch about 10 metres in diameter on the southwestern part of the island. The plants appeared healthy and were flowering and fruiting. In 1983 the area covered by *Cakile* had increased and there were three patches of healthy plants on the eastern side of the island. It seems to be thriving and it is likely it will spread throughout the cays of the Swain area, much as it has in the Capricorn group (HEATWOLE, 1984). The colonization of the Swain Cays is probably just a part of its general northward progression along the Australian coast from its original introduction into the country near Melbourne sometime before 1863. It had reached the Capricornia region by 1958 and was in the Swains at least temporarily by 1972; unfortunately, its time of arrival on Bell Cay is unknown as it was well-established by 1981. There now follows an account of individual islands.

Bacchi Cay: The first record of the vegetation of this cay was on 1 November 1960, it being merely noted that it consisted mainly of coarse grass (GILLETT and McNEIL 1962). In November of 1976 a slightly more detailed description indicated that the vegetation had a cover of less than 25% and was of herbs and grasses (LIMPUS and LYON 1981).

On a visit in July 1979, the cay was sparsely vegetated. Only three species of plants were present. The most abundant one was *Triumfetta procumbens* with *Thuarea involuta* being the second most abundant species. *Lepturus repens* was represented only by two clumps. Total cover for all species combined was only about 10% and nowhere was the vegetation more than 15 cm tall.

The next visit was in 1982 and the situation had changed dramatically. *Triumfetta* had disappeared and *Thuarea and Leoturus* had become much more abundant. Two new species, *Boerhavia diffusa* and *Coronopus integrifolius* had become established (Table 4); both were thriving. The only change in the flora that occurred subsequently was that *Coronopus* was seasonally absent in January 1984.

Thomas Cay: In 1960 this cay had coarse grass present (GILLETT and MCNEIL 1962) and in 1976 had a cover of herbs of less than 25% (LIMPUS and LYON 1981). However, in July of 1980, 1982 and 1983 and both visits in 1984 and 1985, there were no plants present. Thus, it seems that Thomas Cay, though once vegetated, subsequently lost its plants and has been bare of vegetation for at least six years.

Table 4. Plants on Bacchi Cay.

Taxon	1979 July	1982 July	1983 July	1984 Jan.	1984 July	1985 Jan.	1985 July
Nyctaginaceae							
Boerhavia diffusa	-	X	X	X	X	X	X
Brassicaceae							
Coronopus integrifolius	-	X	X	-	X	X	X
Tiliaceae							
Triumfetta procumbens	X		-	-	-	-	-
Poaceae							
Lepturus repens	X*	X	X	X	X	X	X
Thuarea involuta	X	X	X	X	X	X	X
Total	3	4	4	3	4	4	4

*Two clumps only.

Frigate Cay: The only vegetation mentioned by GILLETT and MCNEIL (1962) at the time this cay was first described and named on 31 October 1960 was "coarse grass." An attempt was made subsequently to establish coconuts on the island by a fishing party aboard the M.V. Coralita in October 1975 and a sign to that effect was found on the island during the 1979 trip. They planted seven trees but only one still survived by November 1976 (LIMPUS and LYON, 1981) and none was left by the 1979 survey. The only other live coconut reported was in 1979 and it was one that was sprouting on the beach and only 30 cm high, obviously a new immigrant, not one of the intentionally planted ones. LIMPUS and LYON (1981) described the vegetation present in 1976 as "50-75% cover, with almost continuous herbs and grasses over central platform." That description would apply up to the present time, and the island is currently densely vegetated. The first floral survey was in 1979 and seven species were present, five of which were established and two of which were single individuals of transient species which were never present subsequently (Table 5). The cucurbitaceous plant perhaps resulted from a cucumber seed dropped on the beach from a visitor's lunch. Four of the established species remained permanently in residence throughout the study. The fifth declined and has not been seen since 1982 and is certainly locally extinct. Two new species immigrated. *Cakile edentula* occurred as a single plant for the first time in 1981 and has been there every year since. During the drier summer period (January) it was not in evidence on this island but may have been represented as seed in the soil. It has not spread beyond several small patches each of 1-3 m diameter. The second immigrant was the shrub/ *Argusia argentea*. The same individual plant has persisted since its first appearance in 1981.

Price Cay: In 1960 when it was first described "the conspicuous and main vegetation was . . . the same coarse grass as on the previous two cays" [*Thuarea involuta*] (GILLETT and MCNEIL, 1962). In 1976 it consisted of "25-50% cover of patches of herbs and grasses" (LIMPUS and LYON, 1981), a description that still fits rather well. The major change since then is the appearance of an *Argusia* shrub which was only about 30 cm high in 1982 but had grown to a height of 60 cm by the following year; it persists to the present. Since 1982 there has been no change in the floral list (5 species) of this island (Table 6). It appears to be rather stable and erosion has had little effect.

Bylund Cay: When the cay was first described in 1960, its vegetation "consisted only of the coarse grass *Thuarea involuta*" (GILLETT and MCNEIL, 1962). Several other species must have become established by 1976 as LIMPUS and LYON (1981) indicated that it had less than 25% cover of "scattered patches of herbs and grasses." That remained the case for the three surveys of the early 1980s in which the same two herbs and two grasses were present on most subsequent occasions. There was a seasonal disappearance of *Coronopus* during January 1984. Bylund appears to be a cay that became vegetated more than 20 years ago but has recently had a relatively stable flora of four species. Washover by sea water occurred several times prior to

Table 5. Plants on Frigate Cay[1].

Taxon	1979 July	1980 July	1981 July	1982 July	1983 July	1984 Jan.	1984 July	1985 Jan.	1985 July
Nyctaginaceae									
Boerhavia diffusa	X	X	X	X	X	X	X	X	X
Brassicaceae									
Coronapus integrifolius	X	X	X	X	X	X	X	X	X
Cakile edentula	-	-	X[2]	X	X	-	X	-	X
Boraginaceae									
Argusia argentea	-	-	X[2]	X[2]	X[2]	X[3]	X[3]	X[3]	X[3]
Tiliaceae									
Triumfetta procumbens	X	X	-	X	-	-	-	-	-
Cucurbitaceae									
Unidentified	X[2]	-	-	-	-	-	-	-	-
Poaceae									
Lepturus repens	X	X	X	X	X	X	X	X	X
Thuarea involuta	X	X	X	X	X	X	X	X	X
Arecaceae									
Cocos nucifera	X[3]	-	-	-	-	-	-	-	-
Total	7	5	6	7	6	5	6	5	6

[1]Data from 1981, P. Saenger and E. Yeoman.
[2]One plant only.
[3]Two plants only.

Table 6. Plants on Price Cay.

Taxon	1982	1983	1984	1984	1985	1985
Nyctaginaceae						
Boerhavia diffusa	X	X	X	X	X	X
Brassicaceae						
Coronopus integrifolius	X	X	X	X	?[1]	X
Boraginaceae						
Argusia argentea	X[2]	X[2]	X[2]	X[2]	X[2]	X[2]
Poaceae						
Lepturus repens	X	X	X	X	X	X
Thuarea involuta	X	X	X	X	X	X
Total	5	5	5	5	5(4)	5

[1]Neither presence nor absence recorded; probably present.
[2]One plant only.

Table 7. Plants on Bylund Cay[1].

Taxon	1960 Oct.	1980 July	1982 July	1983 July	1984 Jan.	1984 July	1985 Jan.	1985 July
Nyctaginaceae								
Boerhavia diffusa	-	X	X	X	X	X	X	X
Brassicaceae								
Coronopus integrifolius	-	X	X	X	-	X*	X*	X
Poaceae								
Lepturus repens	-	X	X	X	X	X	-	X
Thuarea involuta	X	X	X	X	X	X*	-	X
Total	1	4	4	4	3	2(4)	1(2)	4

[1]1960 data from GILLETT and MCNEILL (1962).
*Dead.

the January 1985 visit and several species had disappeared or were only present as dead individuals (Table 7). By the following July, all species had either re-immigrated or sprouted from seeds in the sand.

Gannet Cay: The first record of anyone visiting Gannet Cay was on 31 October 1960, when the Capre Expedition landed on it and provided a brief account (under the name of Poulson Cay) and a photograph (GILLETT and MCNEIL, 1962). The vegetation at that time "consisted mainly of the coarse grass, *Thuarea involuta*" and it was indicated that bridled terns nested in the shelter of "tussocks of grass." *Thurea* does not grow in tussocks so at least two different species of grass were present. From the photograph in GILLETT and MCNEIL (1962) it would appear that there were various other species as well.

In November, 1967, Gannet Cay was surveyed for its plants as part of the present study. At that time it was still rather heavily vegetated and five species of plants were present (Table 8), including the shrub *Argusia argentea* as well as low vegetation. In 1972 the vegetation had changed little, but the number of species reached a peak of six because of the temporary presence of *Cakile edentula*. It occurred on Gannet only at that time. By 1976 the vegetation had begun to decline and LIMPUS and LYON (1981) reported a cover of herbs and grasses of less than 25%; presumably shrubs had disap-

Table 8. Plants on Gannet Cay.

Taxon	1967 Nov.	1972 Oct.	1979 July	1980 July	1981[1] May July	1982 July	1983 July	1984 Jan.	1984 July	1985 Jan.	1985 July
Nyctaginaceae											
Boerhavia diffusa	X	X	X	X	-[2]	X	X	X	X	X	X
Brassicaceae											
Coronopus integrifolius	X	X	X	X	X	X	X	X	X	-	X
Cakile edentula	-	X	-	-	-	-	-	-	-	-	-
Boraginaceae											
Argusia argentea	X	X	-	-	-	-	-	-	-	-	-
Poaceae											
Lepturus repens	X	X	X	-	X	-	-	-	-	-	-
Thuarea involuta	X	X	X	X[3]	-	-	-	-	-	-	-
Total	5	6	4	3	2(3)	2	2	2	2	1	2

[1] Data supplied by Anne Veenstra for May and by Elizabeth Yeoman for July.
[2] Almost certainly present as roots in soil. Birds trample shoots and in 1980, 1982, and 1983 there were only a few small leaves appearing above the soil, but there were large storage roots below ground.
[3] Only one plant present.

Table 9. Plants on Bell Cay.

Taxon	1981 July	1982 July	1983 July	1984 Jan.	1984 July	1985 Jan.	1985 July
Nyctaginaceae							
Boerhavia diffusa	X	X	X	X	X	X	X
Chenopodiaceae							
Salsola kali	X[1]	X	-	X	X	X	X
Amaranthaceae							
Achyranthes aspera	X	X	X	X	X	-	-
Brassicaceae							
Cakile edentula	X	X	X	X	X	X	X
Zygophilaceae							
Tribulus cistoides	X	X	X	X	X	X	X
Convolvulaceae							
Ipomoea pes-caprae	-	X	X	X	X	X	X
Boraginaceae							
Argusia argentea	X[2]	X[3]	X[3]	X[3]	X[3]	X[3]	X[3]
Poaceae							
Lepturus repens	X	X	X	X	X	X	X
Thuarea involuta	X	X	X	X	X	X	X
Arecaceae							
Cocos nucifera	X[4]	-	-	-	-	-	-
Total	9	9	8	9	9	8	8

[1] Only one small patch of seedlings 5-7 cm high.
[2] Only three plants.
[1] Only two plants.
[1] One sprouting seedling just above high tide line.

peared by then as they reported that "none of these cays supported trees of shrubs" other than planted coconuts. In 1979 all the previously reported species of low plants, except *Cakile*, were still present even though much of the island was bare. The remaining vegetated parts were relatively lush and had 95% cover. However, thereafter the vegetation declined markedly and by 1980 there were only a few sparsely scattered plants of any species remaining in what had been vegetated patches, and one species, *Thuarea*, was represented by only individual. The number of species was reduced to three. *Thuarea* disappeared by the following year and has not reappeared since. From 1981 onwards, there has been only a few scattered plants, and these mainly as new shoots just barely protruding above the surface of the ground. At first glance, upon landing on the island, the cay appears completely devoid of vegetation and one has to search for the "vegetated" portion. In 1982 and 1983 only two species of plants remained, and they seemed to be in a precarious position. They were the only two species of plants that had been continuously resident. *Coronopus* was seen on every occasion but January 1985 and was probably present then as seeds in the sand. From 1982 onward it was represented primarily as small seedlings coming up from seed in the previously vegetated patches and only a few plants reached reproductive size. Unless conditions change this species may eventually disappear when the seed pool in the soil is exhausted. *Boerhavia diffusa* was probably continuously present since 1967 although it was not observed in 1981. From 1980 onwards this species only appeared as small shoots of several leaves above the soil. These came up, not from seeds, but from large storage roots left in the sand from more favorable times; the shoots never became large enough to flower and unless more favorable conditions for growth return this species will likely become locally extinct when the stored energy reserves of the roots are depleted.

Gannet Cay is thus a cay in decline. The number of species of plants has been reduced from 5-6 to 2 and those two are not likely to survive indefinitely under present conditions. The vegetation has altered from a rather heavy cover of low plants and a few shrubs to only sparsely distributed, small, usually non-reproductive shoots appearing temporarily above the soil.

The causes of this vegetative decline appear to be related principally to the mobility of the cay since 1976 (see Discussion).

Bell Cay: This cay was visited neither by the Gillett expedition nor by LIMPUS and LYON, and the 1981 visit of the present project constitutes the first floral survey and description of the vegetation for this island. Bell Cay has the greatest number of species (10) of any of the cays in the Swain Reefs, and it has several species not reported from any of the others. Six species were present at all seven visits; one was an unstablized transient, two immigrated and became established and one established species became extinct (Table 9).

One new immigrant was *Ipomoea pes-capre*. It was absent in 1981, but in 1982 there were four small plants on the southwestern corner of the island. In 1983 they had grown into a patch of rather large vines, with parts of the stems buried by sand and sending up new shoots and by 1985 they covered a considerable portion of the island.

The other probable immigrant was *Salsola kali*. It was first seen in 1981 as a small patch of very young plants, 5-7 cm high on the northeastern edge of the island. An intensive search was made for other individuals but none was found. The following year, there were many mature plants as well as additional seedlings scattered over a narrow strip of the western edge of the vegetated zone and extending for about one-third the length of the island. In 1983, the eastern edge of Bell Cay had been eroded away by waves and much of the vegetation had been lost, including *Salsola kali*: intensive searches for it were conducted, but no plants were found. However, it was probably represented as seeds in the soil for it was thriving again in 1984 in peripheral regions and persisted thereafter. It is probable that the few seedlings clumped together in 1981 represented a recent immigration, 1982 saw it spread along the eastern edge of the island, 1983 lost most through erosion but by 1984 it had reached peripheral areas of the island which were not subject to heavy erosion.

The coconut washed in and sprouted on the upper beach but never became established as it too was located on the eastern part of the island that subsequently eroded.

The *Argusia* shrubs were present all years but had a rather precarious existence. In 1981 there were three seedlings about 30 cm high; in 1982 there were only two left and they both had dead parts. Both remained in 1983 and had reached 50 cm in height but were partly buried by drifting sand; they persist to the present.

Achyranthes was the species that became extinct. It had declined to only a few individuals by 1984 and was not seen, despite intensive searches on later trips. As it occurred only on Bell, it is now extinct in the Swains.

Other Cays: The following additional cays have been examined and found to be bare of terrestrial plants: Laver Cays, 1984; Hixon Cay, 1967, 1983; Sunray Cay, 1983; Herald Prong No. 1 (Pop's Reef), 1983; Turban Cay, 1984; Tiny Cay and Riptide Cay, 1985.

DISCUSSION

Factors Promoting Cay Instability

It has been suggested (FLOOD, 1983) that the variability of shoreline positions on coral cays must indicate seasonal, and/or short term (cyclonic) or longer term climatic changes which are reflected in variations in the strength and direction of the wind-induced waves. Other potential variables which are of a more gradual nature such as changes in the net sediment supply or slight oscillations of sea level (either eustatic or geodetic) are not considered significant causes of the rapid reorientation and change in location of cays.

Formation and Maintenance of Coral Cays

Cays are morphologically coherent accumulations of bioclastic sediment resting on the reef tops. They may be vegetated or unvegetated. Wind-induced waves which break on the reef rim refract around the reef and reform as smaller waves which travel across the reef top. The pattern of refracted waves and diffracted waves tend to converge towards the leeward side of the reef top, and where the energy of the waves is least (the nodal point) sediment is deposited and builds the cay. Any change in the direction of the waves consequent upon a change in the wind direction will produce a change in the position of the nodal point and a reorientation of the leeward tail of the cay. The sensitivity of the orientation of the tail is such that when the wind is from the south-southeast the tail extends to the north-northwest whereas when the wind is from the east-southeast the tail is oriented west-northwest or sometimes even west-southwest depending on the orientation of the reef itself. The variable shape of the cays reflects changes in the wind-induced wave patterns. Erosion or accretion may occur depending on the balance of sediment movement onto or away from the cay and/or along a particular section of the beach in response to longshore drift.

Variations in the wind direction will influence the position of the nodal point of the pattern of wave refraction and diffraction. Consequently the alignment of the cay will alter accordingly. Cays are subjected to wind fluctuations on three time scales. The first is the annual cycle of seasonal fluctuations. This is clearly evident in the records from the weather station on Gannet Cay. Between February and August the east-southeasterly to southeasterly winds dominate, whereas variable northerly to northwesterly winds tend to occur between September and January. On some occasions where strong northwesterlies prevail for a short time the nodal point may move to the southwest or even to the southeast as has been documented (FLOOD, 1983). The overall seasonal wind pattern will produce a net migration of the cay towards the leeward part of the reef.

It is interesting to observe that the three cays on the elongate platform reefs (Bacchi, Frigate and Price) displayed a clockwise rotation of the long axis of the cay from 1964 to 1984 (Figure 9). The cays on the oval shaped reefs (Thomas, Bylund, Gannet and Bell) displayed the opposite trend, namely counter clockwise (Figure 10). This disparity in the sense of movement could possibly reflect the change in the dominant wind direction (FLOOD 1983) from SSE in the early 1960's to ESE in the late 1970's. Unfortunately the weather records within the Swain Reefs are only available after the automatic weather station was installed on Gannet Cay in 1973 (see Table 10).

The Gannet Cay records (Station 200831 Bureau of Meteorology) indicate that in 1974 the percentage of easterly winds decreased and the percentage of southeasterly winds increased. Such a change would increase the erosive power of the refracted waves reaching the cays on the oval-shaped reefs and account for their anticlockwise re-orientation. It did not, however, explain the clockwise re-orientation on the elongate reefs. In the latter case it is necessary for the energy of the diffracted waves to have increased. Although there is a consistent relationship between the shape of the reef and the movement of the cay, the precise nature of the relationship awaits clarification.

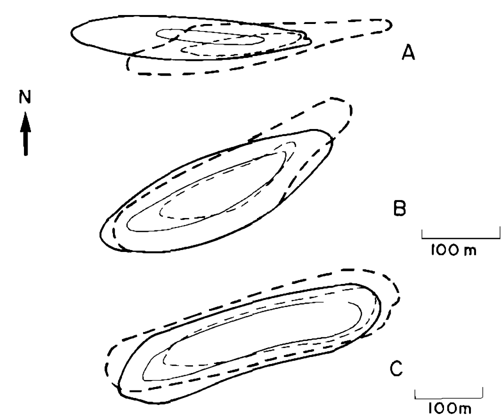

Figure 9. The vegetation boundary and LWM on the cay in July 1964 (dotted) and in November 1984 (solid). A, Bacchi; B, Price; C, Frigate (beachrock not shown).

The second time scale of accretion/erosion observed on the cays is associated with the occurrence of cyclones* during the period of December to April. On average, 14 cyclones occur per decade within the area bounded by 150-155°E and 20-25°S. The Swain Reefs area has been influenced by a major cyclone about once every four years (Emily, 1972; David, 1976; Simon, 1980). The effect of cyclones is generally unpredictable because it depends upon the path and intensity of the cyclone and the state of the tides. The net effect may be erosional if water levels are high (FLOOD and JELL, 1977) or constructional if water levels are low (FLOOD, 1980, 1981). Tropical cyclone David (January 1976) with a central pressure of 960 mb and wind gusts of up to 200 km/hr passed 20 km N of Gannet Cay and almost directly over Bylund Cay. The period of strongest winds coincided with the period of highest tides for the year (FLOOD and JELL, 1976). Heron Island, which was 150 km south of the eye of the cyclone, recorded storm surges exceeding 2 m above the level of mean high spring tides.

It is likely that this was the time when the cays

*The word cyclone is used in Australia to mean a severe tropical storm. It is equivalent to hurricane.

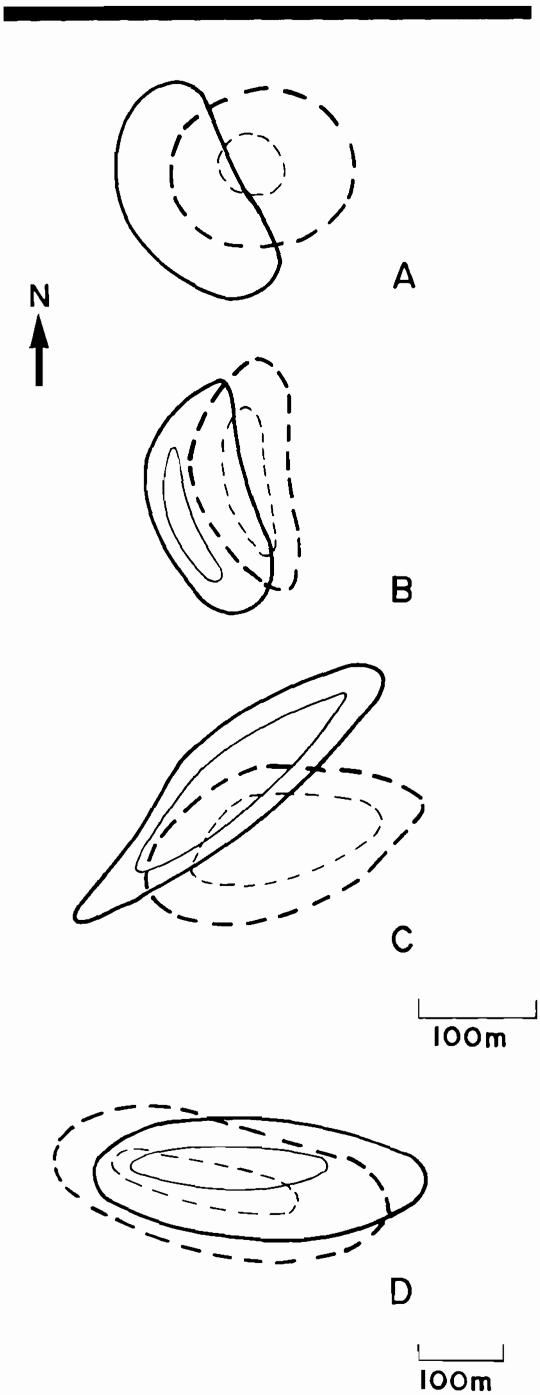

Figure 10. The vegetation boundary and LWM on the cay in July 1964 (dotted) and in November 1984 (solid). A, Thomas; B, Bylund; C, Gannet; D, Bell (beachrock not shown).

such as Gannet and Bylund experienced severe erosion and were moved towards the northwest of the reef top surface. The erosion was so severe that the foundations of the weather station which had been installed towards the centre of the cay in 1973 were undermined. By 1979 further erosion of the south-eastern beach necessitated the erection of a new weather station adjacent to the pre-existing one, but on the vegetated part of the cay.

In the period between visits to the cay in July 1979 and July 1980 the cay had moved and the newly installed weather station building was exposed on the beach. A further cyclone occurred during this period. It was cyclone Simon (February, 1980) with a central pressure of 960 mb. The cyclone was relatively slow-moving and mean winds greater than 100 km/hr and gusts of 170 km/hr were recorded continually over a three day period (24-27 February).

The magnitude of the change in the shape and location of Gannet Cay were mirrored in some other cays such as Bylund but changes to others were less marked. One possible explanation of this difference of behaviour during such an intense cyclonic event could be the exposed location of Gannet Reef compared to the other reefs.

In the WSW to ENE sector there exists almost 10 km of open water in front of Gannet Reef. This degree of exposure to southerly winds is sufficient for extremely large waves (>5 m amplitude) to build up under cyclonic influence. This could explain the extreme mobility exhibited by Gannet Cay.

A third time scale has been identified by studying the available meteorological records commencing in 1962 from Heron Island (FLOOD, in prep.). During the period 1962-1980 the wind records displayed a long term shift within a 45° arc from SSE to ESE. There appears to be a sudden change in the percent frequency of southerly winds about 1964 with an increase in the easterly winds. Such a change would mean that the nodal point would move from the northwest to the southwest. This pattern has been observed on several cays within the Capricorn Group (FLOOD 1983).

The six available radiocarbon dates for the age of beachrock formation suggests that the process of cay formation could have been in progress for not much more than one thousand years. This is in marked contrast to the much older beachrock dates reported from the Capricorn and Bunker Groups (CHIVAS *et al.*, 1986; MARSHALL and DAVIES, 1984) or from the cays in the central and northern Great Barrier Reef (HOPLEY, 1982; POLACH *et al.*, 1978)

Table 10. Frequency percent wind speed (knots) and direction, 1973-1981. Gannet Cay Weather Station (all readings combined).

Year	1-10	11-15	16-20	21-26	27-99	NNE	NE	ENE	E	ESE	SE	SSE	S	SSW	SW	WSW	W	WNW	NW	NNW	N
1981	52	18	20	7	3	3	5	2	22	21	9	12	6	3	2	2	3	2	3	3	3
1980	50	18	20	10	3	3	4	3	25	22	11	8	3	2	2	1	3	3	2	4	5
1979	41	22	18	13	5	4	5	4	29	23	10	7	2	1	1	1	2	1	2	3	4
1978	42	23	20	11	4	3	5	4	25	19	8	11	4	3	2	3	2	2	2	3	5
1977	33	25	24	13	5	3	54	4	29	25	10	8	2	2	1	1	1	2	1	3	3
1976	39	23	20	13	6	2	9	4	20	18	11	9	4	3	1	1	3	3	3	4	3
1975	34	23	22	13	7	3	5	4	24	25	14	8	2	1	-	1	2	1	2	3	4
1974	42	23	17	9	8	3	5	3	22	18	9	10	5	4	3	2	3	3	3	3	4
1973	31	30	27	10	1	2	5	7	44	16	2	-	1	2	-	-	2	3	6	6	6

where the process of cay formation and beachrock development has been in progress for at least several thousand years. Clearly the cays of the Swain Reefs are in a juvenile stage of development as is indicated by the radiocarbon dates and by the nature of the vegetation, especially the absence on most cays of anything other than herbs and grasses.

Factors Affecting Species-Turnover

The minimum number of immigrations, transients, and extinctions respectively during the study for the various islands are shown in Table 11. Including published information as well as that of the present study a minimum of nine immigrations and six extinctions occurred and there were four cases of transience. On the average about 10% of the species on these islands became extinct sometime between 1960 and 1985 and over a quarter of the total number of species immigrated. Transients were relatively unimportant; not only were they present briefly, but they accounted for less than 10% of the total flora on average. The above figures would seem to suggest that immigration is exceeding extinction on the Swain Cays generally and therefore the number of species would be expected to be building up. Such a summary masks several important trends. First of all, patterns of immigration and extinction varied greatly from island to island. Gannet and Thomas are clearly islands in decline, having lost most or all of their species. Bylund, by contrast is one on which 75% of its species immigrated before 1980 and despite washover and the killing of many individual plants, no species have been lost since. On Frigate and Bacchi immigration exceeded extinction by one species each, and on Bell extinction and immigration were balanced. Price had no species turnover at all. Clearly, no summary statement can apply to all cays. Secondly, there are temporal changes. Some of the reported immigrations and extinctions occurred before the regular surveys began in 1979. The highest turnover occurred from 1979 to 1982 and largely reflected immigration (9 events) rather than extinction (4 events). Since 1982 no immigration has occurred despite the fact that more islands were included in the surveys; all species-turnover during that time was caused by extinction. Thus, early in the study immigration exceeded extinction but later the reverse occurred.

Table 11. Minimum number of immigrations, transients, and extinctions reported for cays of the Swain Reefs, 1960-1985[1].

Cay	Immigrations	Transients[2]	Extinctions
Gannet	9 (0)	1 (17)	3 (50)
Frigate	2 (22)	2 (22)	1 (11)
Price	0 (0)	0 (0)	0 (0)
Bylund	3 (75)	0 (0)	0 (0)
Bell	2 (20)	1 (10)	1 (10)
Bacchi	2 (40)	0 (0)	1 (20)
Total events	9	4	6
$\overline{X}$ % of N	26	8	15
Total events 1982-85	0	0	2

[1]Seasonal disappearances or brief periods when species were not observed but were probably present as roots or seeds in the soil, are not counted as species-turnover.
[2]N = total number of species recorded for a given island.

If a long time intervenes between surveys of an island an underestimate of the turnover of species results. For example, a species present at the first survey may have become extinct and subsequently re-immigrated before the second survey, but would be tallied as continuously present. On the other hand, a species not present at either survey may have immigrated and then become extinct again between the surveys and not be recorded for the island at all.

The following formula can be used to calculate apparent species-turnover (I):

$$I = 100\,(E + H)\,/\,(C + D)$$

where E signifies the number of species immigrating between one survey and another, H the number of species present at the first survey and D the number present at the second one, or in general terms, I represents the percent of the total species pool of two surveys that either immigrated or became extinct.

HEATWOLE (1984) has shown that for the Bunker-Capricorn Islands of the southern Great Barrier Reef, I increased greatly as the interval between surveys decreased, and that an accurate assessment of actual turnover rates could not be achieved unless consecutive surveys were separated by only two years or less, a condition more amply fulfilled for most cays of the Swain Reefs during the latter part of the study (Table 12).

These relatively reliable estimates of turnover can be related to the degree of stability of the various cays. The diagram of Figures 9 and 10 showing movement of the cays over a 20-year interval was used as a means of ranking cay stability. Price Cay has shown less movement than any of the others and therefore was considered the most stable cay. The vegetated part of it has scarcely changed. Frigate Cay was the next most stable followed in

Table 12. Species-turnover of plants on cays of the Swain Reefs.

Cay	Intervals 1960-1980 I	I/yr	1967-1972 I	I/yr	1972-1979 I	I/yr	1979-1982 I	I/yr	1980-1982 I	I/yr	I for one-year intervals 1979-80	1980-81	1981-82	1982-83	1983-84	1984-85	$\overline{X}$
Gannet																	
including transients	-	-	9.1	1.8	20.0	2.9	-	-	-	-	0	16.7	20.0	0	0	0	6.1
excluding transients	-	-	0	0	11.1	1.6	-	-	-	-	0	16.7	20.0	0	0	0	6.1
Frigate																	
including transients	-	-	-	-	-	-	-	-	-	-	16.7	15.4	0	7.7	0	0	6.6
excluding transients	-	-	-	-	-	-	-	-	-	-	0	15.4	0	7.7	0	0	3.9
Price	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0
Bylund	60.0	3.0	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0
Bell																	
including transients	-	-	-	-	-	-	-	-	-	-	-	-	11.1	0	0	5.9	4.3
excluding transients	-	-	-	-	-	-	-	-	-	-	-	-	5.9	0	0	5.9	3.0
Bacchi	-	-	-	-	-	-	42.9	14.3	-	-	-	-	-	0	0	0	0

I = Species-turnover.

decreasing order by Bell, Bacchi, Bylund and Gannet, with Thomas being the least stable of all.

Because not all cays that had annual, or more frequent, surveys were surveyed over the same group of years, not all of the turnover rates in Table 11 are equivalent. Nevertheless, a rough ranking on this basis can be made. Price showed no species-turnover at all and should be ranked first. Among the other cays that were surveyed a number of times at short intervals, the one with the next lowest turnover rate was Bell, followed by Frigate. Bylund had no turnover between 1979 and 1985 (apparent temporary loss of species after washover was probably an artifact, with seeds still present in the soil), but a considerable turnover earlier, so should be ranked fourth.

Bacchi was not measured annually until after 1982, but during the three-year interval prior to that, had a high rate and probably should be ranked fifth, followed by Gannet which had a high turnover rate, and finally by Thomas which lost its entire flora.

Comparison of these two independent rankings reveal at least a rough, inverse relationship between insular stability and species-turnover:

DECREASING STABILITY:
Price → Frigate → Bell → Bacchi → Bylund → Gannet → Thomas
INCREASING TURNOVER:
Price → Bell → Frigate → Bylund → Bacchi → Gannet → Thomas

There is not a one-to-one correspondence in these series, but there is remarkable agreement, with only two species-pairs being inverted, Frigate-Bell and Bylund-Bacchi.

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