HATCHING, GROWTH, AND MORTALITY OF MAGNIFICENT FRIGATEBIRD CHICKS IN SOUTHERN BAJA CALIFORNIA

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ABSTRACT.—We studied growth and development of chicks of the Magnificent Frigatebird (*Fregata magnificens*) in 1985, 1986, and 1988 at a colony on Isla Santa Margarita, Baja California Sur, México. Hatching peaked at weeks 7, 12, 17.5, and 23.3 of the calendar year. Hatching frequencies around each peak were distributed normally. Growth was analyzed using Richards' model. Total length had the lowest growth rate and mass the highest. The asymptote for mass was reached before 150 days, as was the asymptote for culmen; the asymptotes for wing and wingspan were reached later. Chick mortality, recorded over a six-month period, was considered to be low (46%). During the same period there was 90% replacement and new occupation of nests, which resulted in temporal and spatial clustering of the clutches laid during the season. *Received 16 May 1994, accepted 1 Dec. 1994.*

Long-lived seabirds tend to have reduced clutch sizes and prolonged breeding seasons (Nelson 1979). The Magnificent Frigatebird (*Fregata magnificens*) represents an extreme case of this trend, having a clutch of one egg and a period of approximately 21 months from egg-laying to postfledging (Diamond 1972, 1973, 1975; Nelson 1975, 1979). Stonehouse and Stonehouse (1963) and Nelson (1967) hypothesized that females breed only biennially, whereas the males breed every year. From the eleventh week of chick's age males abandon both nest and colony (Moreno and Carmona 1988), so prefledging and postfledging feeding of the chick is fully assumed by the females. Frigatebird chicks are altricial and require about six months to fledge (Diamond 1973; Moreno and Carmona 1988). This prolonged care period produces a protracted reproductive season; in fact, Nelson (1967), Diamond (1972, 1973, 1975) and Kepler (1977) reported extended breeding in this frigatebird species with one to two annual peaks in laying in colonies located in tropical regions. Growth patterns in frigatebirds have received little attention, and the reports available (Diamond 1973, Nelson 1975) only present polynomial curves of actual data on mass, wing, and bill. In this paper, the timing of hatching, egg and chick mortality and chick growth are analyzed.

MATERIALS AND METHODS

We measured frigatebirds from May to October 1985, January to September 1986, and April to September 1988 at colony in the mangrove forest "Las Tijeras" at the southeast

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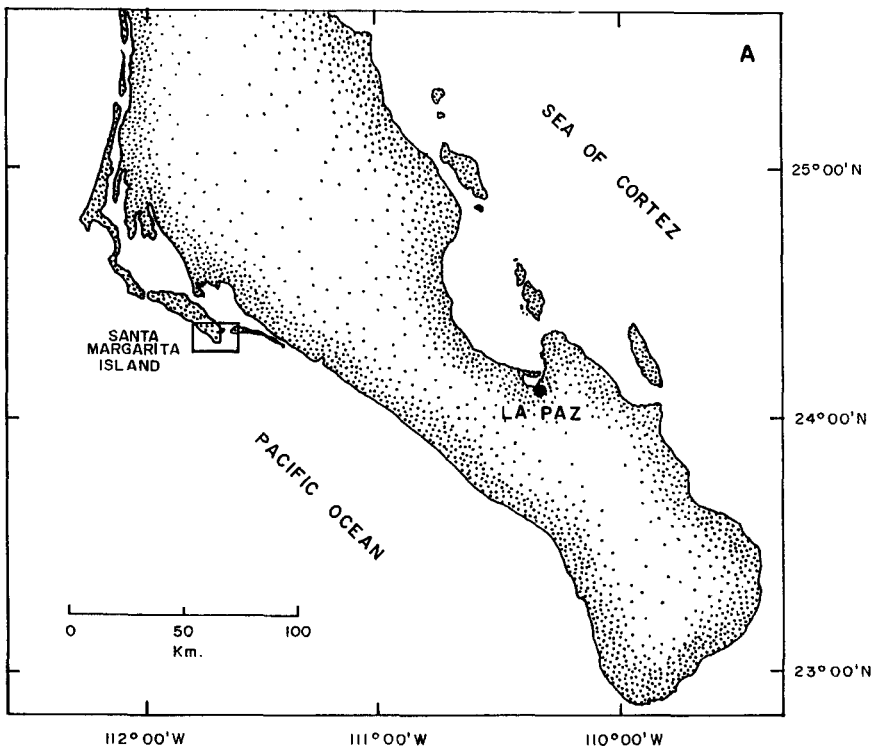
FIG. 1.   Location of the Magnificent Frigatebird colony at "Las Tijeras" on Isla Santa Margarita.

end of Isla Santa Margarita (24°25′N, 111°07′W) on the west coast of Baja California Sur, México (Fig. 1). The mangrove forest covered an area of 0.8 km^2 surrounding a tidal lagoon approximately 500 m long and 50 m wide. The mangrove species were red mangrove (*Rhizophora mangle*), black mangrove (*Avicennia germinans*), and white mangrove (*Laguncularia racemosa*). The canopy of the latter reached up to 5 m, covered about 22.8% of all mangrove areas, and was the preferred nesting substrate of the frigatebirds. Some nests were also built in red mangrove. The fragility of the mangrove branches presented a serious sampling problem, being a source of risk both for the chick to be captured and the researcher.

The hatching period was estimated by back calculation from a sample of 327 measurements of culmens taken randomly in the colony during three visits made in 1988 (April, June, and September). From the total sample, there were 35 data points on the size of culmens at hatching with their respective hatching dates, necessary for the back-calculation of hatching dates. The 327 back-calculated dates of hatching were grouped by weeks and analyzed for the presence of distinct modes by the Bhattacharya (1967) method. This is a statistical technique that separates into different gaussian (normal) components a polymodal frequency distribution.

For growth studies, we selected eight chicks in 1985 and 27 chicks in 1986. We measured the chicks every four days between hatching and fledging, which occurred at about five

months of age. We measured culmen, wing, wingspan, total length, with a measuring tape to the nearest 1 mm and culmen with vernier calipers to the nearest 0.1 mm. We measured mass with portable weight gauges. Precision was ± 1 g up to 100 g; ± 2 g from 101 to 300 g; ± 10 g from 501 to 1000 g and ± 50 g over 1000 g total mass.

We analyzed growth using Richards' sigmoid growth model (Richards 1959) and an iterative nonlinear regression technique (Marquardt 1963) and Statistical Graphics System 2.1. The curves derived from this model can be adequately interpreted from a biological point of view, i.e., by taking into account both physiological and ecological factors affecting growth.

The growth data collected in 1985 and 1986 were processed separately, and the resulting parameter estimates of asymptotic length (L) and mass (W), growth rate (K), and time to inflection of the curve (t_i) were tested for differences in slopes for the regressions (Student's t-test) and covariance analysis (F Fisher Test) for the homogeneity in the regression data (Steel and Torrie 1981). These showed there were no significant differences between years ($P < 0.001$ for the t-test with 70 degrees of freedom, and $P < 0.05$ for the F-test with 2, 70 degrees of freedom). Consequently, the two years' data sets were pooled.

To study chick and egg mortality, an area of approximately 300 m containing 90 active nests was selected in 1986. These nests were at a different location from the ones where growth studies had been conducted. The area was visited once a week over six months, and the number of new nests and their contents and those that had disappeared were recorded each time, taking extreme care to cause the least disturbance to the chicks.

RESULTS

Hatching.—The dates of hatching, as back-calculated from the 1988 data, were grouped by weeks, using the rationale that the standard error of the predicted curve for culmen length is about 3.5 days. The hatching dates showed four modes (Fig. 2A) that resulted in four distinct normal distributions, as tested with χ^2 tests of normality at a confidence level of 95%, with means at 7.05, 11.92, 17.45, and 23.33 weeks of the year, respectively, and standard deviations of 1.5, 1.45, 2.03 and 2.08 weeks, respectively (Fig. 2B). Moreover, a test of equality of the means was conducted, showing each peak as distinct from the other three, with their maxima separated by 5, 5.5 an 6 weeks, respectively.

Growth.—The pooled values for each parameter and structure (Table 1) were either identical to the 1986 values or extremely close (except for wing), which can be explained by the larger sample size in 1986. In all cases, the variance explained by the model (r^2) was very high. The average of data collected every four days (1985 and 1986), and the corresponding fitted curves, were characterized by a sudden variability of the means at about 100 days (Fig. 3). This variability, at least partially, can be attributed to sampling difficulties and to a decrease in sample size. The variability for mass gives, for example, a poorer fit to the model ($r = 0.96$). After 90 days, the handling of the chicks became rather laborious, and all individuals could not always be captured. The calculated curves were transformed to percentages of the asymptote of each mea-

surement. This puts the growth pattern of each structure in relative numbers so they can be compared to each other, and the growth pattern understood as a whole. Fig. 3B shows the following general characteristics (1) At hatching the size of wing, wingspan, and mass are relatively smaller but culmen and total length are relatively larger; (2) As expected, wing and wingspan growth are alike and their growth rates are similar to that of the culmen; (3) Total length had the lowest growth rate, and that of mass had the highest; and (4) The asymptote for mass (W) was reached before 150 days and the asymptote for culmen at 150 days. The structure that took longest to reach the asymptotic value was total length.

Mortality.—Chick mortality in the 90 original nests selected for monitoring, was 46% (Fig. 4). The highest mortality took place in April. As chicks died, new active nests appeared, sometimes built on top of abandoned ones. These new nests appeared mainly in March. After the last week of April, no new nests were observed. Mortality of chicks from new nests was only 30%, lower than that for the original group of 90 nests. The largest number of nests at one time was during the last week of March and first half of April.

DISCUSSION

The presence of four hatching peaks confirms the observation by Diamond (1973) that there were at least two laying peaks in Barbuda. The differences between Barbuda and Santa Margarita are probably due to differences in latitude and food availability, although the gross analysis made by Diamond may be another important reason for this difference.

Much usable space, occupied by young birds from the preceding breeding season, progressively became available by the start of the second laying period (about six weeks later than the first one). Once this second wave of reproduction was established, nesting space must have been near saturation (the highest peak recorded). This could explain why the third wave had a higher standard deviation (less synchronous) than the two preceding waves. The new pairs became established gradually as the males from the preceding groups abandoned the colony.

Nevertheless, the third batch had the higher number of chicks measured. The second and third laying groups were the main ones. If we consider there had been mortality of chicks from the three previous hatching waves (which makes the parents leave the nest), the fledglings from the first wave were already leaving, and the males from the second breeding group were abandoning their nests, the availability of space for nesting for the fourth group would have been at the same level as for the end of the second laying period. This could explain the similarity of the standard deviations between the third and fourth groups. The peak frequency
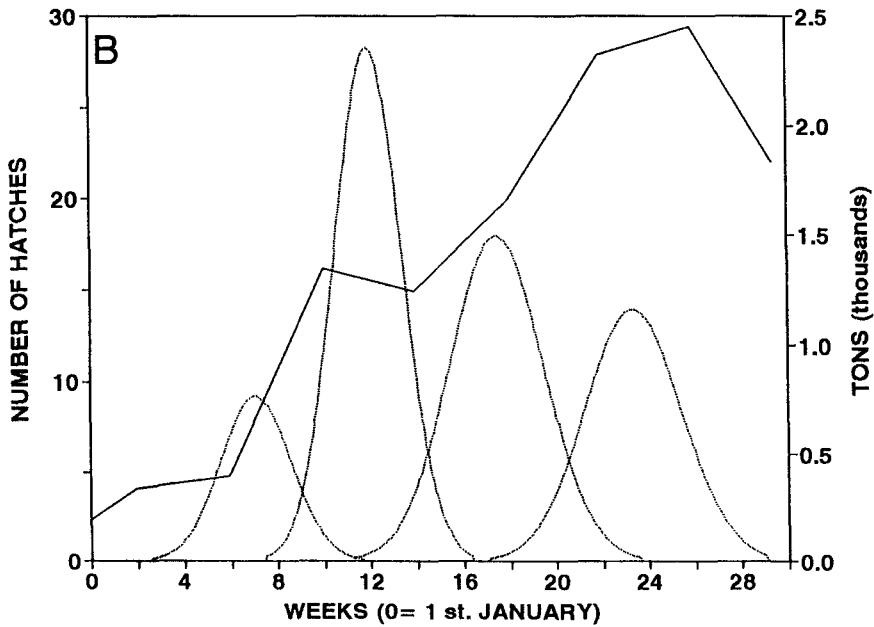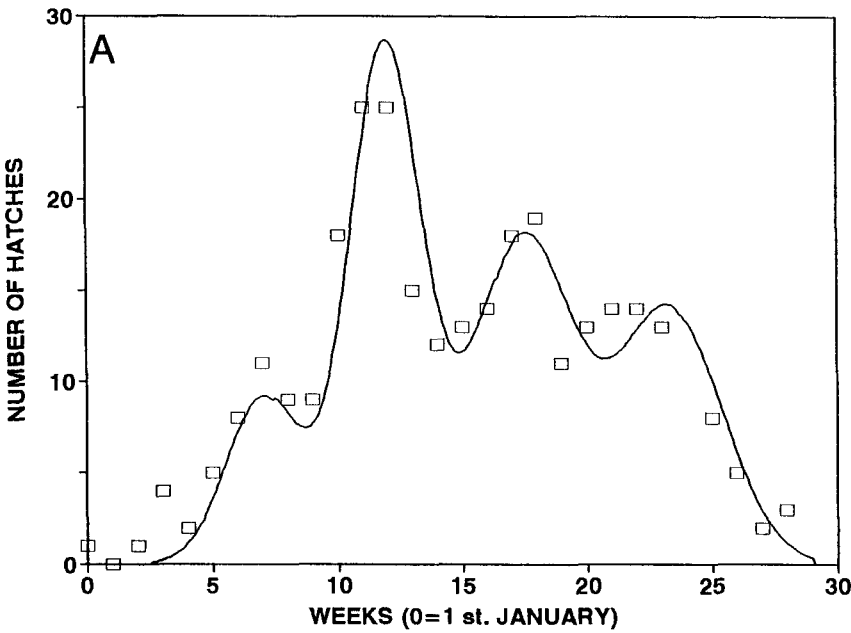
TABLE 1
PARAMETERS OF THE RICHARD'S CURVE[a]

Structure	Asymptote	K[a]	t_i[b] (days)	r^2[c]
Culmen	111.49	0.037	37.17	0.9864
Wing	1007.24	0.040	73.61	0.9910
Wing span	2077.50	0.041	70.11	0.9862
Total length	942.14	0.026	56.54	0.9877
Mass	1341.08	0.055	47.47	0.9609

[a] Pooled sample (1985 and 1986). Units of the asymptote in mm, except mass (g).
[b] Growth rate.
[c] t_i = Time to inflection of the curve.
[d] Variance explained by the regression model.

of only 15 also indicates that the breeding season was ending by that time.

The parents do not remain on the nest during all of the growth period. Chicks are left alone 50% of the daylight hours after the first six weeks (an age at which they are able to defend themselves and the space immediately contiguous to the nest). As the chick grows, parents gradually travel farther and for longer periods while searching for food. Finally, adult males abandon the nest at the eleventh week after hatching (Moreno and Carmona 1988). We have observed that the space defended by a six-week-old chick was smaller than the one defended by its parents. We can assume the pressure on the territory next to an established nest decreases, allowing new males to attempt to establish their courting territories in the area. By the time of the third and fourth laying periods, the males of the first and second periods have already left, again giving more usable space for the establishment of new nests.

The availability of prey may be another factor explaining the overall seasonality of Magnificent Frigatebird breeding in the area. The most abundant component of the chick's diet, observed from regurgitates, was the "sardine" type group (Moreno and Carmona 1988). Frigatebirds in this area fish by sight for surface fish comprising a group of four clupeid and one scombroid species. The commercial fishermen also fish by sight so "sardine" captures are a good indicator of abundance of available prey.

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FIG. 2. (A) Number of hatches per week, as backcalculated from culmen lengths (squares), and theoretical distribution of hatches adjusted for each peak (line). (B) Normal distributions based on data in figure 2A (light lines), and "sardine" captures for the year 1988 (heavy line), plotted as an indicator of the abundance of food.
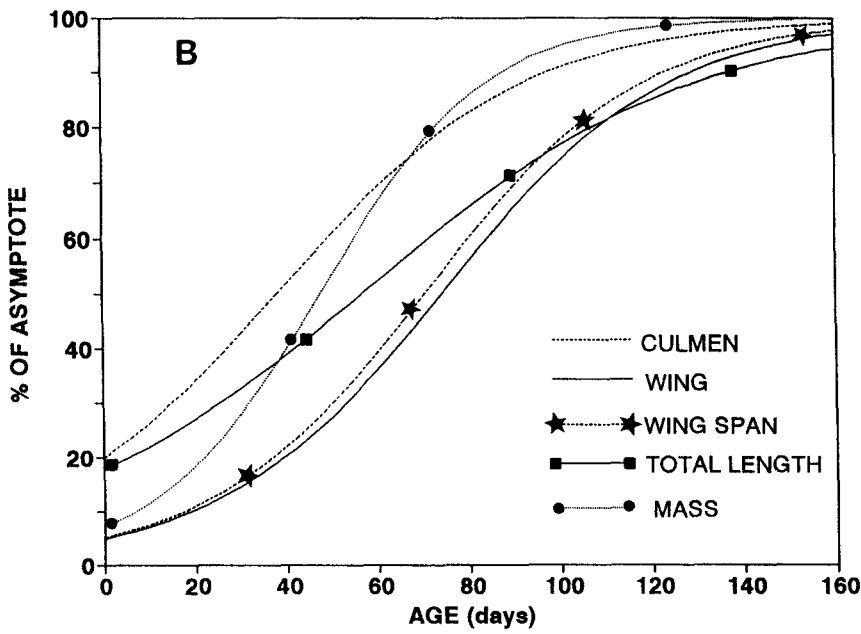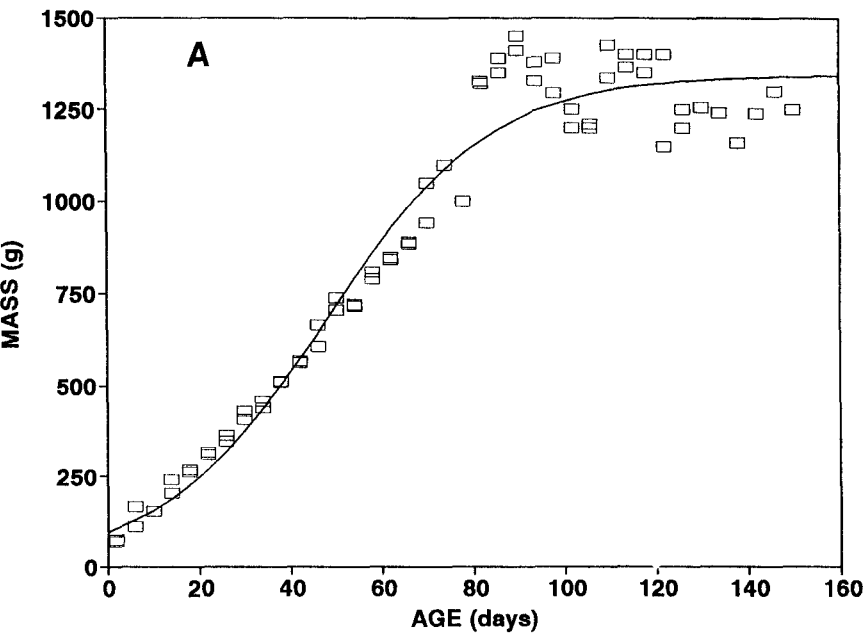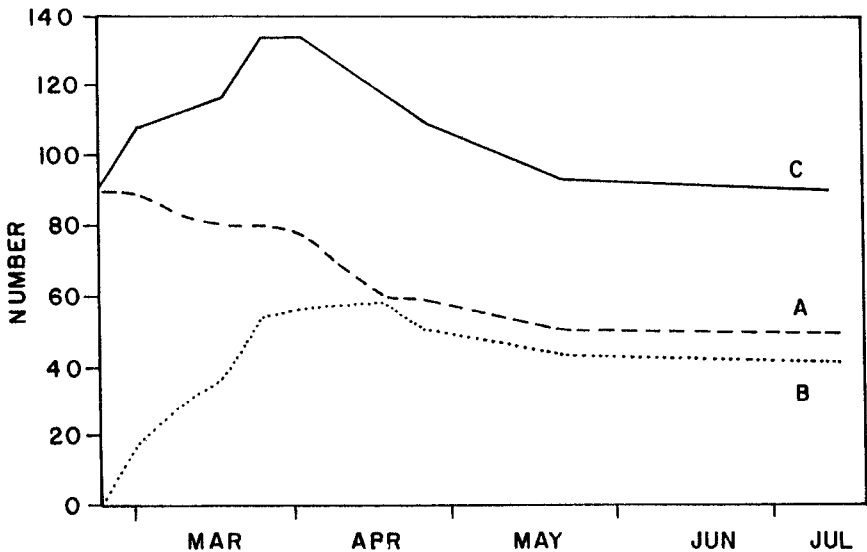
FIG. 4. Chick mortality and new nests of Magnificent Frigatebird. (A) Chick mortality, (B) "new" nestings, and (C) nests recorded = A + B.

It should be pointed out that the maximum number of chicks (from week 16 onward) was coincident with the highest captures of "sardine" by the commercial fishermen.

Putting together the data at hand, some personal observations on the behavior of females and fledglings in the colony, and some references from the literature, we tried to explain the occurrence of distinct hatching peaks with the implication of differential laying. Considering seven weeks of incubation (Diamond 1973, pers. obs.), plus 22 weeks of chicks' nest permanence (see growth), plus 26 weeks of females' post-fledging attendance (Trivelpiece and Ferraris 1987), we get a total of 55 weeks of females' care. Females with chicks hatched at weeks 7, 12, 17, and 23 (Fig. 2) could be in position of courtship at weeks 10, 15, 20, and 26 of the following year, respectively. In this way, the hypothesis of Diamond (1973) postulating biennial breeding for females is reduced to a little bit more than a year, increasing considerably the reproductive capacity of the colony.

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FIG. 3. Average data and calculated curve of the pooled sample (1985 and 1986) for: (A) mass and (B) curves calculated for each measurement, as percentages of their respective asymptotes.

Reville (1988) suggested that most of the nests that failed during the first half of the laying season will contain a new displaying male or courting pair soon afterwards. In our case, it has to be considered that 46% of eggs or chicks died at some stage of development, therefore, their parent females would have been available for entering the first or second laying periods of the next year.

The calculated curves presented here lie between the two sets of data of supposed males and females obtained by Diamond (1975) at Aldabra, although the curves proposed by Diamond did not have a statistical basis. In the present study, as well as in the one by Trivelpiece and Ferraris (1987), information was insufficient to determine sex and thus calculate separate curves. The highest deviations from the mean were at 100 days, which, as Diamond stated, is the age when sexual dimorphism becomes apparent.

At hatching the chick is altricial, requiring full time parental attendance. From the mass growth curve, using the results (*cif.* fig. 1) presented by Dunn (1976), we assume endothermy (in the sense used by that author) is acquired at about 3–4 weeks, which agrees with the reports of Diamond (1972). A prolonged phase of non-accelerated growth is apparent and is more conspicuous for mass, wing, and wingspan. This phase is much smaller and less evident for the culmen. In spite of the differences shown in the slow growing phases, the general growth pattern is harmonic in the sense that, at the end of the main growth period, all structures have acquired their adult characteristics at about the same time (except mass, which actually decreases after a maximum value).

At hatching, the culmen is proportionately larger than other structures. This might be related to a fast development necessary for the acquisition of thermoregulation (Dunn 1975) as well as defense and acquisition of energy reserves. It is supported by the observation that the parents gradually spend less time at the nest directly caring for the chicks, coming back mainly to feed them.

Although Reville (1988) suggested that the main cause of nesting failure in the Great Frigatebird is due to usurpation of nests by unpaired males, in our study the main cause of nesting failure was due to robbery of materials from nests with eggs or chicks not older than three weeks and not to usurpation of nests by males. For older chicks, the main factor causing mortality was wind. On several occasions, after periods of gusty winds, broken branches were found on which there were one or several nests or fallen chicks. Fallen chicks soon die, since they are incapable of moving around once they fall from the nest. Generally, they become entangled or break their wings. There was no observed predation during the study. It is interesting that the number of active nests at the end of six

months was also 90 which undoubtedly indicates a high degree of replacement of nesting pairs. This agrees very well both with the suggestion of Reville (1988) and the hypothesis of reproductive waves or batches.

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