

# THE BREEDING BIOLOGY OF THE EUROPEAN STORM-PETREL *HYDROBATES PELAGICUS* IN BRITTANY, FRANCE

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Cadiou B. 2001. The breeding biology of the European Storm-petrel *Hydrobates pelagicus* in Brittany, France. *Atlantic Seabirds* 3(4): 149-164 *In recent years (1996-1999), data have been collected on European Storm-petrel Hydrobates pelagicus colonies on the coast of Brittany, France, in order to investigate various breeding parameters, especially laying period, hatching success and breeding success. Data were obtained by regular examination of breeding sites and by estimating chick age at the time of ringing. Adults first returned to colonies in March or April. The laying period extended from the end of April to the beginning of August and showed high annual variability, with the date by which 50% of eggs had been laid ranging from mid May to early July. Annual variability in the timing of laying was probably due to variations in oceanographic conditions and food resources just before laying and had important implications for accurate censuses of breeding colonies. Data obtained from single visits at the same time in different years should be interpreted carefully, especially when using tape-playback methods only, as the proportion of attended nest sites may vary according to the interannual variation in the timing of laying. Estimates of hatching and breeding success were about 65% to 95% (over three years) and 0.53 (one year) respectively. The first chicks fledged in mid August, whereas the latest fledged in late October, or even sometimes November.*

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## INTRODUCTION

In the southern part of their European range along the Atlantic coast, European Storm-petrels *Hydrobates pelagicus* breed in Brittany, France; on at least sixteen islands and islets. The population estimate was about 500 apparently occupied sites (AOS) in 1997-1998 (Cadiou 1998), and 700 AOS in 1999, after a marked increase in the two largest colonies (B. Cadiou unpubl. data). Mainly due to the nocturnal habits and the underground breeding of the species, its biology still remains poorly known, with only a few published data for colonies in the north-east Atlantic (Davis 1957; Scott 1970; Bolton 1996) or elsewhere. The timing of laying has important implications for accurate censuses of breeding colonies and for the development of standardised census methods to obtain better estimates of breeding population size (Mainwood *et al.* 1997; Ratcliffe *et al.* 1998a, 1998b).

Since 1996, more accurate censuses of breeding colonies have been

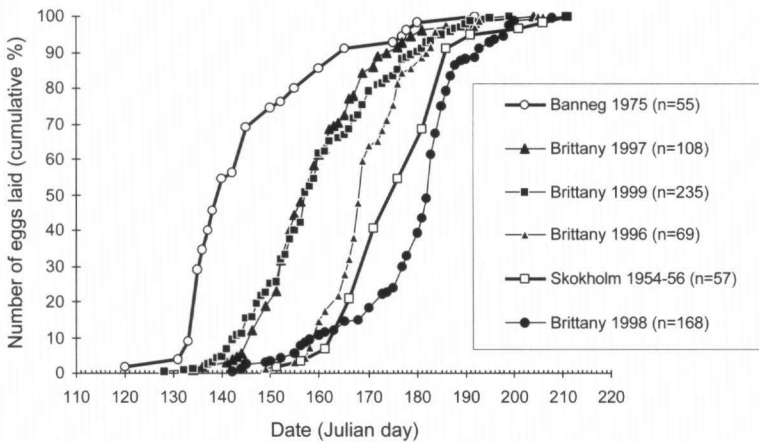


Figure 1. Laying period of European Storm-petrels in Brittany. Date in Julian days: 121 = 1 May, 152 = 1 June, 182 = 1 July and 213 = 1 August. Sample size in brackets.

Figuur 1. Legdatum van Stormvogeltjes in Bretagne. 121 = 1 mei, 152 = 1 juni, 182 = 1 juli, 213 = 1 augustus. Steekproefgrootte tussen haakjes.

made in Brittany and data on breeding biology have been collected simultaneously. The aim of this study is to investigate various breeding parameters that are poorly known in France and, indeed, in other parts of the breeding range, especially laying period, hatching success and breeding success. Before this study, the only available data on laying periods in Brittany came from a study conducted in 1975 on Banneg Island in the Molène archipelago (Henry & Monnat 1981). Laying ranged from early May to mid July, with 50% of laying around mid May (Fig. 1). Comparison with the data from Skokholm in Wales (Davis 1957) showed an earlier breeding period in Brittany (Fig. 1).

## METHODS

Most of the work was carried out in the Molène archipelago, and especially on three of the five colonies: Banneg Island (48°25'N, 05°0'W) and two neighbouring islets, Enez Kreiz and Roc'h Hir. About 600 AOS (85% of the regional population) were counted in 1999 in the archipelago. Data were also obtained from other smaller colonies in Brittany, which were visited less often

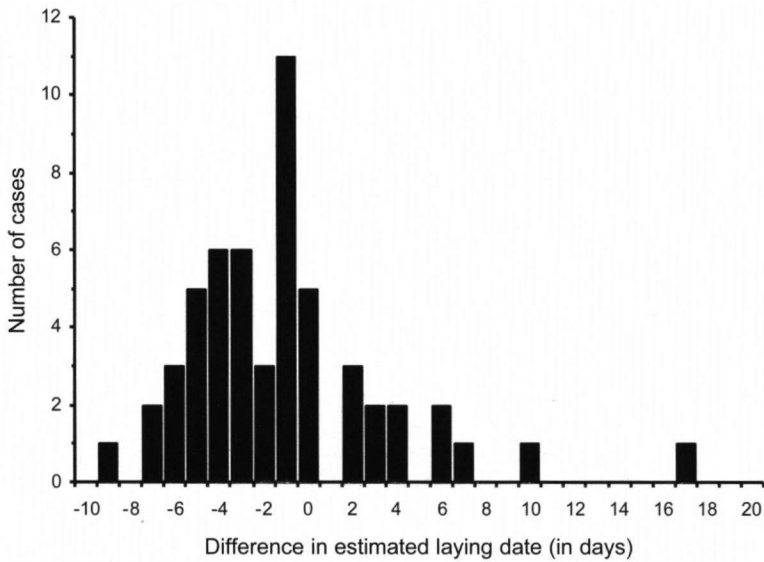


Figure 2. Accuracy of repeated ageing of European Storm-petrel chicks. The value on the x-axis is the difference between the estimated laying dates back-calculated from chick age determined on the second visit and age determined on the first visit in 1999 (or between third and second visit for the 3 chicks aged three times;  $n = 51$  chicks and 54 cases).

Figuur 2. Nauwkeurigheid van herhaalde leeftijdsbepalingen van stormvogelkuikentjes. Het getal op de x-as geeft het verschil aan tussen de geschatte legdatum berekend op basis van de kuikenleeftijd tijdens een tweede controle vergeleken met de schatting op basis van de eerste controle in 1999 (of tussen het derde en tweede nestbezoek bij kuikens waarvan de leeftijd drie maal werd bepaald;  $n = 51$  kuikens, 54 gevallen).

each year (especially Camaret islets and Sept-Iles archipelago). In the Molène archipelago, most of the petrels breed in old burrows of rabbits *Oryctolagus cuniculus*. The rabbit population became extinct in 1993 after a virulent myxomatosis epidemic. In all surveyed colonies, breeding sites were numbered and mapped.

Adults first returned to colonies in March or April. Early in the season, from the end of April, previously known sites were both regularly and randomly inspected in order to determine the beginning of the laying period. Intensive

census of the colonies was made after the peak of egg laying, mainly from July to September. All visits were conducted by day. Combinations of different methods were used for census: direct observation with a torch, direct investigation by hand and tape-playback method. Direct investigation by hand was made very carefully to limit disturbance and to avoid nest desertion, without taking out the adults, and by slipping the two longer fingers delicately under the bird to search for an egg or a chick. In most cases when using this technique, adults did not move away. For the playback method, a male purr call recorded on Banneg Island in 1989 by V. Bretagnolle was played for about 20 s, once or twice, using a standard tape recorder (Tamashi C-671). Occupied and attended nest sites refer, respectively, to sites with at least one proof of occupancy over the whole breeding season and to sites with at least one adult present at a given visit.

**Laying phenology** At the different colonies, all accessible chicks were ringed (except in 1996), and their age was estimated to the nearest five days using data on plumage development (Davis 1957). Other visible chicks were also aged in the same way. Estimation of the laying date was made by back-calculation, considering the chick's age and an average incubation period of 41 days (Davis 1957; Scott 1970). All sites with incubating birds or unhatched eggs on one day were as far as possible checked once again later in the season until hatching or failure was recorded.

There are at least three potential biases that can affect the estimate of the laying date from chick ageing. In the first place, the incubation duration is variable, ranging from 38 to 50 days, with a mean value of 41 days (Davis 1957; Scott 1970), used to back-calculate the laying date. Secondly, late laid eggs have lower hatching success (Scott 1970), and therefore all of them can not be taken into account. Thus, laying periods obtained from chick age are always partially truncated and slightly underestimated (see also Ratcliffe *et al.* 1998a). Thirdly, laying date may be overestimated for retarded chicks. But such chicks are generally easy to identify as they are lighter and smaller, sometimes unhealthy, and can be excluded from the analyses. The older the chick, the greater the effect of retarded or accelerated growth on the estimation of laying date. As discussed by Scott (1970), accuracy of ageing on plumage development can be very low in poor seasons, but in the present study, chick growth, based on weight and wing length at ringing, was very similar in 1997, 1998 and 1999 (B. Cadiou unpubl. data).

In 1999, 51 chicks were aged at least twice in the season within approximately 4 weeks, of which three were also aged a third time. The difference (mean  $\pm$  SE) in the estimate of the laying date between the second and the first observation, or between the third and the second one, was  $-1.1 \pm 0.6$

days (Fig. 2). The chick with 17 days of difference was assumed to be about 10 days old on 20 August, based on plumage features, but only 11-15 days old on 9 September, and unhealthy; the corpse was found on a subsequent visit on 27 September. Thus, with the exception of obviously retarded chicks, the difference for chicks aged twice in the season was generally less than 5 days (79.6% of the cases), and estimated laying dates for the older chicks were generally more advanced (negative values on Fig. 2). But the difference between these estimates and the true laying date remains unknown. For eight empty nests on the first visit, there was no discrepancy between the estimated laying dates and the field observations on subsequent visits (i.e. last day with empty nest and first day with an adult incubating an egg).

The terminology '50% (or 90%) of laying' refers below to the date, and not to the period, by which 50% (or 90%) of eggs had been laid in a given year.

**Breeding parameters** At the end of the season, some unhatched and abandoned eggs were measured to the nearest 0.1 mm using callipers. More regular visits were made to the small islet of Enez Kreiz to obtain data on hatching and breeding success (1997: 4, 5 July, 21 August and 24 September; 1998: 4 June, 23 July, 19 August and 23 September; 1999: 11, 22 June, 6, 20, 23 July, 18 August and 9, 27 September). Numbers of AOS on this islet increased from 61 in 1997, to 70-72 in 1998 and 122-125 in 1999. The increase from 1998 to 1999 was real and not a result of the more frequent visits to the islet or to changes in census methods. Out of these identified AOS, only the sites with breeders and chicks always easily visible or accessible, and found during the incubation or brooding period, were included in analyses of breeding parameters (i.e. 46, 55 and 94 nest sites for the three years respectively). Nests found late in the season at the chick stage were excluded to avoid an over-estimation of hatching and fledging success. Chicks come closer to the entrance of their burrows as they get older, and thus become more observable (pers. obs.). Breeding failure at the egg stage included all cases of broken, cracked, addled or desiccated eggs or intact unhatched eggs more than 50 days after initial observation. As breeding failure occurred at an unknown stage for some sites each year (nine in 1997, eight in 1998, eleven in 1999), two calculations were made for hatching and fledging success (number of chick fledged per egg hatched), assuming that all failures occurred before or after hatching respectively (i.e. at the egg stage or at the chick stage). Minimum (or maximum) hatching success = minimum (or maximum) number of eggs hatched / total number of eggs laid; minimum (or maximum) fledging success = total number of chicks fledged / maximum (or minimum) number of eggs hatched. This uncertainty has no influence on the calculation of overall breeding success (total number of chicks fledged / total number of eggs laid). Chicks were considered to be fledged if, based on ageing

by plumage features, they were potentially at least 50 days old on the date when the empty nest was recorded.

## RESULTS

**Laying period** In 1995, the few available data, for 9 chicks at one colony only, indicated a similar temporal pattern of laying to that in 1975. In 1996, more data were collected and the results indicated a delay in the laying period. Laying ranged from the end of May to the end of July, with 50% of laying around mid June (Fig. 1). This pattern of laying is closer to that recorded on Skokholm, Wales. In 1997, laying was more advanced than in the previous year and ranged from mid May to the end of July, with 50% of laying around early June. In 1998, a long delay in breeding was recorded. As in 1996, laying ranged from the end of May to the end of July, but 50% of laying was around early July (Fig. 1), i.e. 6 weeks later than in 1975. It appeared that a problem for the birds occurred in early June, with a temporary break in laying from 5 to 17 June. In 1999, the pattern of egg laying was very similar to that in 1997. Laying ranged from early May to mid July, with 50% of laying around early June. Field observations suggested that some eggs were probably laid during the first ten days of August, and perhaps even later. For example, on Banneg Island, one bird was found incubating an egg on 20 August 1999 and his partner on 9 September. Two weeks later, the egg was abandoned. Furthermore, from 1996 to 1999, the pattern of egg laying in Brittany appeared to be very similar between northern, western and southern colonies.

**Attendance patterns** A simple attendance model, assuming continuous attendance of one parent during the 41 days of the incubation period and the 7 first days of the chick's life (Ratcliffe *et al.* 1996), allows investigation of a potential effect of interannual variation in laying patterns on census results (Fig. 3). The results indicate that observers could sometimes easily underestimate a large change in breeding numbers using tape-playback methods in early July for example (Fig. 3). Depending on the year and the laying phenology, the theoretical proportion of nests attended can vary between about 90-95% and 60-65% or even less if the census is made a few days earlier or later in years with late or early breeding respectively (Fig. 3).

**Breeding parameters** A sample of 49 eggs was measured in 1999 in the Molène archipelago colonies. The mean size was  $27.9 \times 20.6$  mm ( $\pm$  SE:  $0.2 \times 0.1$ ; range:  $25.6\text{-}30.1 \times 18.3\text{-}22.3$  mm).

Data obtained from Enez Kreiz islet showed that hatching success ranged from 63.6% to 95.7% (Table 1); the uncertainty was due to some sites

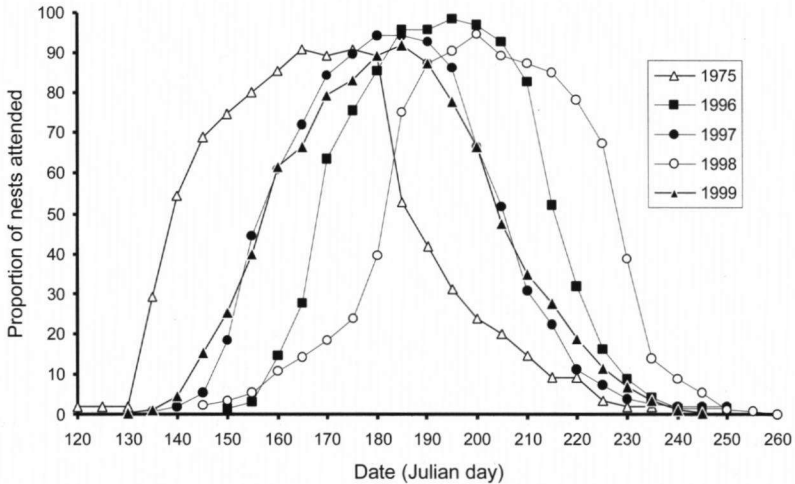


Figure 3. Theoretical proportion of European Storm-petrel nests attended by an adult. The curves are based on data from Fig. 2 and the model assumes a continuous attendance of one parent from laying to the seventh day of the chick's life (Ratcliffe et al. 1996). Date in Julian days: 121 = 1 May, 152 = 1 June, 182 = 1 July, 213 = 1 August and 244 = 1 September.

Figuur 3. Theoretische nestholtebezetting (%) door een volwassen vogel. De curves zijn gebaseerd op figuur 2 en op een model uitgaand van een voortdurende aanwezigheid van tenminste één ouder vanaf de eileg t/m de zevende levensdag van het kuiken (Ratcliffe et al. 1996). 121 = 1 mei, 152 = 1 juni, 182 = 1 juli, 213 = 1 augustus, 244 = 1 september.

where breeding failure may have occurred either at the egg stage or at the chick stage. In some instances, eggs disappeared between two successive visits, no remains, eggshells or corpses of dead chicks being found. More regular visits in 1999 allowed calculation of the minimum and maximum incubation period for these eggs: (last day of observation of the egg - first day of observation of the egg) and (first day with empty nest-site - first day of observation of the egg) respectively. For some eggs, already laid on the first visit, the minimum incubation period was equal to 0 because the corresponding nests were not checked again before the third visit and were empty by that time. The mean duration ( $\pm$  SE) was  $17.9 \pm 4.8$  days and  $39.5 \pm 4.7$  days respectively ( $n = 11$ ),

Table 1. Breeding parameters for European Storm-petrel in Brittany (data from Enez Kreiz islet, Molène archipelago). Sample size in brackets.

Tabel 1. Broedsucces van Stormvogeltjes in Bretagne (gegevens verzameld op Enez Kreiz eiland, Molène eilandengroep). Steekproefgrootte tussen haakjes.

Year	Sites <sup>a</sup>	Hatching success (%) <sup>b</sup>	Fledging success <sup>b,c</sup>	Breeding success <sup>d</sup>
1997	all	76.1-95.7 (46)	?	?
1998	all	63.6-80.0 (55)	?	?
1999	all	67.0-78.7 (94)	0.68-0.79 (74, 63)	0.53 (94)
	old	69.5-81.4 (59)	0.71-0.83 (48, 41)	0.58 (59)
	'new-old'	60.0-66.7 (15)	0.60-0.67 (10, 9)	0.40 (15)
	new	65.0-80.0 (20)	0.63-0.77 (16, 13)	0.50 (20)

<sup>a</sup>category of sites: old = sites with proof of occupancy at least in 1998 and 1999, 'new-old' = previously known sites but not occupied in 1998, new = sites unknown before 1999; <sup>b</sup>uncertainty for hatching and fledging success was due to some sites where breeding failure occurred either at the egg stage or at the chick stage (see Methods for the calculation of minimum and maximum values); <sup>c</sup>for hatched eggs only; <sup>d</sup>overall breeding success (young fledged per egg laid); ? = no precise data

indicating that breeding failure mainly occurred in the second part of the incubation period.

There was no between-year difference of hatching success for the minimum estimates ( $\chi^2_2 = 1.56$ , n.s.) but the difference was significant for the maximum estimates ( $\chi^2_2 = 6.81$ ,  $P < 0.05$ ), with a decrease from 1997 to 1998-1999 (Table 1). Precise data on fledging and breeding success were available only in 1999. Fledging success ranged between 0.68 and 0.79 for hatched eggs, and overall breeding success was 0.53 young fledged per egg laid (Table 1). Of the 13 nests where breeding failure occurred at the chick stage, the corpses were found in five cases (chick's age less than 1 week in four cases and less than 4 weeks in one case). In the eight remaining cases the chick disappeared between two subsequent visits; chick's age less than 3 weeks in one case, less than 4 weeks in six cases, and less than 6 weeks in one case. The value obtained for breeding success included an unknown number of older chicks depredated by Great Black-backed Gulls *Larus marinus*, before fledging when they left their burrows at night to exercise their wings or during the night of departure. At least two chicks were preyed upon on Enez Kreiz in 1999. The first one was 40-60 days old (feather remains were found nearby the entrance of the burrow), and the second one was 50-70 days old (the ring was found in a regurgitated gull pellet on the islet; the nest of this chick, found late, was not included in the study sample). The first chicks generally fledged around mid August, whereas



Table 2. Breeding parameters for European Storm-petrel in north-west Europe.  
 Tabel 2. Broedsucces van Stormvogeltjes in Noordwest-Europa.

Colony	Hatching Success (%)	Fledging success <sup>a</sup>	Breeding success <sup>b</sup>
Mousa, Shetland (Bolton 1996)	86	0.71	0.61
Skokholm, Wales (Davis 1957)	66	0.89	0.59
Skokholm, Wales (Davis 1970)	55-68	0.49-0.78	0.27-0.50
Enez Kreiz, Brittany (this study)	64-96	0.68-0.79	0.53
Biarritz, SW-France (Hémery 1980)	64	0.90-1.00	0.62
Benidorm, E-Spain (Minguez 1994)	70	0.90	0.63
Range	55-96	0.49-1.00	0.27-0.63

<sup>a</sup>for hatched eggs only; <sup>b</sup> overall breeding success

the latest fledged in late October, or even perhaps occasionally November in very late years (although no visits were conducted at this time of the year).

Given the marked increase in breeding numbers from 1997/98 to 1999, the potential effect of site history was also tested. There was no significant difference between new sites (discovered in 1999) and old sites (occupied at least in 1998), but 'new-old' sites (occupied before, but not in, 1998) showed the lowest estimates for each of the three breeding parameters (Table 1; hatching success:  $\chi^2_2 = 0.53$ , n.s., for minimum estimates and  $\chi^2_2 = 1.57$ , n.s., for maximum estimates, fledging success:  $\chi^2_2 = 1.25$ , n.s., for minimum estimates and  $\chi^2_2 = 0.68$ , n.s., for maximum estimates, breeding success  $\chi^2_2 = 1.60$ , n.s.).

## DISCUSSION

**Breeding parameters** Recorded egg sizes in this study were in the same range as those noted by others (Cramp & Simmons 1977, Scott 1970). Data from elsewhere in north-west Europe indicate greater variability in hatching success and fledging success than in overall breeding success (Table 2). The estimates obtained in Brittany accord well with other data (Table 2). Regular observations made in 1999 have shown that, after breeding failure, unattended and unhatched eggs may remain for some weeks in the nest sites (up to at least 7 weeks), but that corpses of young chicks disappear more rapidly. Scott (1970) showed that most of the failures after hatching occurred within 48 hours, and most of the eggs that subsequently disappeared in 1999 were incubated for at least 3 to 6 weeks (see Results). Thus, the higher estimates for hatching success are probably closer to the actual figures (maximum: 79-96% in Table 1), ranging

annually from about 75-80% to 90-95%. On Banneg and Roc'h Hir, and possibly on Enez Kreiz, there is a small population of shrews *Crocidura suaveolens*, and these small insectivorous mammals may perhaps eat and remove some dead young chicks (M. Pascal *pers. comm.*), further compounding the uncertainty about hatching success. The late breeding season in 1998 did not appear to have any impact on hatching success (Table 1).

Overall breeding success in 1998 seemed to be around 0.45 young per egg laid, but the data were far less accurate than in 1999. As a large increase in breeding numbers was recorded in 1999, potentially due to the recruitment of inexperienced birds, a global decrease in success could be expected (Scott 1970), but hatching success in 1999 was not lower than in the previous year (Table 1). Moreover, there was no significant difference in success between old sites (probably mainly reoccupied by experienced breeders) and new sites (Table 1), although the exact status of the breeders here was unknown. As hatching success tended to decrease from 1997 to 1998/99 (Table 1), a potential effect of disturbance due to intrusion in nest sites and the increasing number of visits cannot be excluded. There was no evidence of such an effect, which might be indicated by a high desertion rate, but it remained difficult to assess it in the absence of a sample of control nest sites receiving less disturbance. Another explanation of the higher hatching success in 1997 could be that only two main visits were conducted at an interval of 48 days, leading to an over-estimation as some sites with breeding failure would have not been detected. Due to the variability in incubation and rearing period duration (Davis 1957; Scott 1970), to the fact that all the nests taken into account were found during the incubation or brooding period, to the reduced numbers of visits on the study colony, and to the assumption that 'mortality rate is approximately even across each stage', the Mayfield method (Mayfield 1975) appeared not to be a feasible alternative approach to calculating the different breeding parameters.

**Potential effects of variation in laying date on census results** The attendance patterns based on estimated laying dates (Fig. 3) represent maxima as some breeders had already failed and deserted the colony and some eggs may have been left unattended, but non-breeders may also have responded to playback. On Mousa (Shetland), the observed proportion of nests attended peaked at 85-90% in late June (Ratcliffe *et al.* 1998a). Latitudinal extrapolation of the peak of laying, used in some studies to determine the optimum date for censusing colonies where there is no precise data on the breeding period (Mainwood *et al.* 1997; Gilbert *et al.* 1998), should be considered only as indicative. Nevertheless, early to mid July appears to be the recommended time for playback census at colonies, at least in Britain, Ireland and Brittany (Ratcliffe *et al.* 1998a; this study).

As chicks respond more frequently to playback than stated in Mainwood *et al.* (1997), especially when about 10 to 20 days old (pers. obs., but no quantitative data), the proportion of chicks heard during playback census could be an indicator of the laying phenology. Many responses of chicks would indicate that the peak of nest attendance by the adults, and thus the better census period, has been passed beyond. However, more precise data should be collected on response rate of European Storm-petrel chicks.

In conclusion, data obtained from single visits at the same time in different years should be interpreted carefully, especially when using tape-playback methods only, as the proportion of attended nest sites may be very different. It appears important to record, as much as possible, an adequate sample of nest contents and age of chicks when visiting European Storm-petrel colonies (using plumage features, Davis 1957, or tarsus length, M. Bolton *in* Ratcliffe *et al.* 1998a), in order to investigate the timing of breeding and discover any delays that could affect the results of the count. Inspecting nests in a study plot through the season would also be valuable.



*European Storm-petrel on Banneg island Stormvogeltje op Banneg-eiland (photo René-Pierre Bolan)*

**Laying period and observed variability** Despite the limitations of back-calculation of laying date from chick age (see Methods), the large sample sizes and consistency of methods in the current study indicate that the overall laying period extends from the end of April to early August and shows high interannual variability, with 50% of laying ranging over 6 weeks, from mid May to early July; 90% of laying appears to be less variable, ranging over 4 weeks, from mid June to mid July (Fig. 1). The situation between 1975 and 1996 is not known because very few chicks were ringed and aged. However, from samples of 17 and 22 chicks ringed and measured in August 1986 and 1990 respectively (J.-P. Cuillandre unpubl. data), it appears that the breeding period in both years occurred somewhere between that recorded in 1975 and 1997-1999 (Fig. 1), and seemed to be earlier in 1986 than in 1990.

The late 1998 breeding season in Brittany indicated a temporal pattern placed between the one recorded in Wales and the one recorded in northern Scotland (Davis 1957; Scott 1970; Ratcliffe *et al.* 1996; Mainwood *et al.* 1997). Such a great delay in a single colony seems not to have been recorded elsewhere for European Storm-petrels, and appears to be very uncommon for other seabirds, although one case of late breeding was reported for European Storm-petrels on Mousa (Ratcliffe *et al.* 1998b). Davis (1957) and Scott (1970), over seven breeding seasons on Skokholm, found that 50% of laying ranged over less than 10 days in an early year to other more typical periods. On Skokholm and Skomer, the Manx Shearwater *Puffinus puffinus* also exhibited a high constancy in laying (Brooke 1990), but one late season has been recorded on Rum, western Scotland (K. Thompson, pers. comm.).

**Factors influencing the timing of laying** Several factors can influence the duration of the breeding period in seabirds. Among European Storm-petrels, young, first-time breeders tend to breed later in the season than experienced breeders (Scott 1970), but population size in the Molène archipelago remained similar from 1997 to 1998, and the large increase in breeding numbers recorded in 1999 was not associated with a late breeding season (Fig. 1). Higher densities of breeders can induce an earlier breeding in seabirds (Danchin 1988; Harris & Wanless 1988), but in the present study all available data on laying, from different colonies and different areas within colonies, with different densities, were pooled together. Massive predation in consecutive years on eggs and chicks at some Black-legged Kittiwake *Rissa tridactyla* colonies in Brittany leads to a progressive delay in breeding from the end of April or early May (usual dates) to early June (J.-Y. Monnat & B. Cadiou unpubl. data). Predation by gulls, especially Great Black-backed Gulls, mainly on pre-breeding and breeding European Storm-petrels, has increased since the beginning of the 1990s in the Molène archipelago (Cuillandre *et al.* 1989; Cadiou 1998 and

unpubl. data), but an effect on laying date appears improbable. In alcid, the timing of laying appears quite constant from year to year within colonies. However, there are some occasional late years, apparently resulting from climatic conditions that may influence abundance and availability of food resources (Birkhead & Harris 1985; Harris & Wanless 1988). A potential link between food and late breeding was also suggested for the Black-legged Kittiwake (Coulson & Thomas 1985; Harris & Wanless 1997). A study of the Fork-tailed Storm-petrel *Oceanodroma furcata* in Alaska showed high between-year variability both in laying period, with a mean hatching date ranging over more than one month, and in chick growth (Boersma & Parrish 1998). The authors suggested that this was a direct response to environmental variability.

Thus, year-to-year variability in the timing of laying recorded in the present study on European Storm-petrels, and the temporary break recorded in June 1998 (Fig. 1), may be attributable to variations in oceanographic conditions and food resources at sea just before laying, when females have to store energetic reserves for egg production. The event that led to a delay in laying in 1998 should have been severe but confined to May-June only and not afterwards. It seems highly probable that other colonies, at least in the Celtic Sea, can exhibit similar year-to-year changes. Breeders originating from these different colonies may feed in adjacent areas of sea (Pollock *et al.* 1997) and encounter similar food conditions, and may thus respond in the same way to variation in food resources before egg laying.

Several studies have reported the broad spectrum of prey eaten by European Storm-petrels, especially zooplankton (Scott 1970; Cramp & Simmons 1977, d'Elbée & Hémery 1998), but it may be possible that during the pelagic phase of the breeding cycle, females feed mainly on a few prey species (for example ichthyoplankton), and become more sensitive to changes in their availability or abundance.

The El Niño Southern Oscillation (ENSO) climatic event has global and multifarious effects (Trenberth *et al.* 1998) and 1998 was the strongest ever recorded (Sydeman *et al.* 1999). It is tempting to propose a potential effect of El Niño on the laying period of European Storm-petrels. However, major ENSO events are generally associated in seabirds with effects over the whole breeding season and decreases in breeding numbers and breeding success (nest desertion, reduced productivity, etc.) or lower growth rate of chicks (Valle *et al.* 1987; Anderson *et al.* 1999; Sydeman *et al.* 1999). Clearly, no such effects were recorded in the present study (see Results; unpubl. data for chick growth). Other climatic events such as the North Atlantic Oscillation (NAO) or the Gulf Stream have direct effects on plankton communities (Fromentin & Planque 1996; Gerten & Adrian 2000), and, consequently, potentially on seabirds also (Hass 1999). However, the relationships between climate and plankton appears

difficult to generalise (Beaugrand *et al.* 2000). Indeed, annual changes in the abundance of plankton in the English Channel during 1979-1995 were correlated with the NAO index but variation in plankton abundance in the Celtic Sea and in the Bay of Biscay were not (Beaugrand *et al.* 2000). No published oceanographic data for Celtic Sea appear to exist for 1996-1999, and data on diet collected on Banneg Island from regurgitates of adults or chicks are not adequate to identify any change (J. d'Elbée comm. pers.).

Two questions remain; first, is the variability in laying period of European Storm-petrels a regular or occasional event and, secondly, whether it is a recent trend with a possible link to climate change. Only long-term studies on the laying phenology at different colonies, coupled with analyses of oceanographic and climatic data, will improve our knowledge. In this context, the European Storm-petrel might act as a potential indicator of changes in the marine environment.

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#### BROEDBIOLOGIE VAN STORMVOGELTJES *HYDROBATES PELAGICUS* IN BRETAGNE, FRANKRIJK

*De afgelopen jaren (1996-1999), zijn gegevens verzameld over de broedbiologie van Stormvogeltjes Hydrobates pelagicus in kolonies langs de Bretonse kust in Frankrijk. De belangrijkste onderzochte aspecten waren legdatum, uitkomstsucces en uitvliegsucces. De gegevens werden verzameld door regelmatige controles van bezette holen en door het schatten van de kuikenleeftijd tegen de tijd dat de vogels geringd konden worden. De broedvogels keerden in maart of april op de nestplaatsen terug. De periode van ei-leg strekte zich uit van eind april tot begin augustus (!) en het tijdstip verschilde van jaar tot jaar sterk (mediaan half mei tot begin juli). Deze jaarlijkse verschillen werden vermoedelijk veroorzaakt door oceanografische fluctuaties en schommelingen in het voedselaanbod kort voor de eileg. Het hoeft geen betoog dat dermate grote verschillen in het tijdstip van leggen (en de daarmee samenhangende aanwezigheid van broedvogels op de kolonie) belangrijke implicaties had voor de onderzoekers. Gegevens die gebaseerd worden op een enkel koloniebezoek moeten met grote terughoudendheid worden geïnterpreteerd, vooral wanneer alleen bandrecorders gebruikt worden om de populatie-omvang vast te stellen, omdat het percentage bezette nesten bij uitgestelde eileg buitengewoon laag kan zijn. Schattingen van het uitkomst- en uitvliegsucces bedroegen respectievelijk 65%-95% (over drie jaren) en 0.53 (één jaar). De eerste jongen vlogen half augustus uit, de laatste eind oktober of soms zelfs pas in november.*

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