

THE BREEDING DEMOGRAPHY AND EGG SIZE  
OF NORTH NORWEGIAN ATLANTIC PUFFINS  
*FRATERCULA ARCTICA* AND RAZORBILLS *ALCA*  
*TORDA* DURING 20 YEARS OF CLIMATIC  
VARIABILITY

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Barrett, R.T. 2001. The breeding demography and egg size of North Norwegian Atlantic Puffins *Fratercula arctica* and Razorbills *Alca torda* during 20 years of climatic variability. *Atlantic Seabirds* 3(3): 97-112. *The mean egg-laying dates of Atlantic Puffins Fratercula arctica and Razorbills Alca torda in north-eastern Norway varied between 13-30 May and 21 May-2 June respectively in the years 1980-1982 and 1988-2000. Atlantic Puffins laid on average 7 days before Razorbills, and the mean spread of laying dates each year was larger (22 days) for the former than the latter (19 days). There were significant correlations between egg-laying dates and air and sea temperatures in April and May, with lower temperatures resulting in delays in laying at a rate of 1-4 days °C<sup>-1</sup>. Late access to nesting sites due to snow and ice in burrows might explain some of the delay in egg-laying during cold springs. Such variation should be considered when planning field trips to monitor breeding populations. There was no inter-annual variation in the mean volumes of Atlantic Puffin eggs. Although Razorbill egg volume did vary between years, it was not influenced by either sea or air temperatures. This suggests that neither species adjusted egg size in order to advance laying dates.*

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INTRODUCTION

The censusing and monitoring of breeding populations of seabirds are often timed to coincide with certain stages of the breeding cycle of the species in question (Walsh *et al.* 1995). In Norway, counts of many species are recommended at specific times during the incubation period and/or early chick-rearing period (Lorentsen 1989). The success of any monitoring scheme thus depends on prior knowledge of the laying or hatching dates of the target species so that fieldwork may be timed to coincide with the recommended stage of the breeding cycle. Such knowledge is lacking in detail for nearly all Norwegian seabird species.

Mechanisms that determine the timing of breeding have long been a subject of discussion. Lack (1954) proposed that breeding was timed so that chicks hatched at the time of maximum food availability. However, the timing of breeding of females that lay single-egg clutches in temperate and high

latitudes has since been shown to be determined also by their food requirements during egg laying and incubation (Perrins 1970; Brooke 1978). On the Semidi Islands, Alaska, Hatch & Hatch (1990a) showed that eight of 11 seabird species bred as early as environmental conditions would allow, thereby supporting Perrins' (1970) hypothesis; the three exceptions were all puffin species whose sequence of laying accorded with Lack's (1954) predictions in that their breeding schedules converged at the chick-rearing period. Furthermore, there may be selection pressure for females to breed as early as possible because the breeding success of many species declines through the season (Perrins 1970).

Weather conditions may advance or delay breeding of seabirds by many days or weeks (Hornung & Harris 1976; Lloyd 1979; Murphy & Schauer 1994; Harris & Wanless 1988; Harris *et al.* 1998). In extreme cases, inclement weather or the late break-up of ice not only delays breeding but may also result in reduced egg size, chick growth or breeding success (Nettleship *et al.* 1984; Kilpi 1992; Gaston & Hipfner 1998).

The reduction in egg-size may be the result of a trade-off between egg volume and the timing of egg laying. The production of eggs is energetically costly and late laying birds may minimize the delay in breeding due to poor food availability by laying smaller eggs (Nettleship *et al.* 1984). Alternatively, a poor food supply early in the season may cause adults to either postpone laying until there is enough food to enable them to maintain continuous incubation (Brooke 1978) or even to defer breeding until a subsequent year (Hatch & Hatch 1990b).

Among the species included in the Norwegian Seabird Monitoring Programme (Lorentsen 1989, 1999) are Atlantic Puffins *Fratercula arctica* and Razorbills *Alca torda*. One of the colonies monitored is Hornøya, Finnmark, in the southwestern Barents Sea, where their population numbers and breeding success have been monitored annually since 1980. Here, both species are near the northern limits of their ranges and, because they both nest in burrows or cavities that are blocked by ice and snow in early spring, small variations in air temperature can be expected to have major consequences on their breeding demography (Belopol'skii 1957; Sealy 1975; Rodway *et al.* 1998).

Sea temperatures might influence food availability during the pre-laying period and so could be an ultimate factor controlling the timing of egg laying (Perrins 1970). Since 1980, there have been large fluctuations in sea temperatures off the Finnmark coast as a result of major inflows of warm Atlantic water into the Barents Sea in 1982/83, 1988/89 and 1998/99 (Loeng 1999; Loeng *et al.* 1992). This inflow of Atlantic water is a major determinant

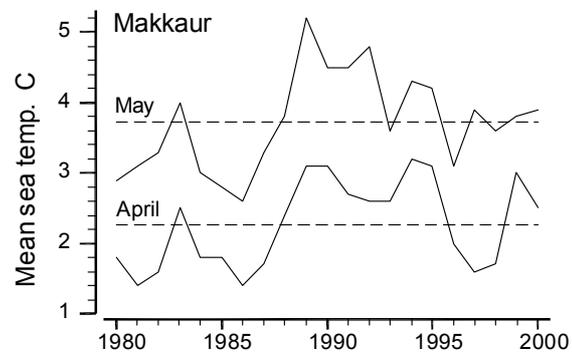
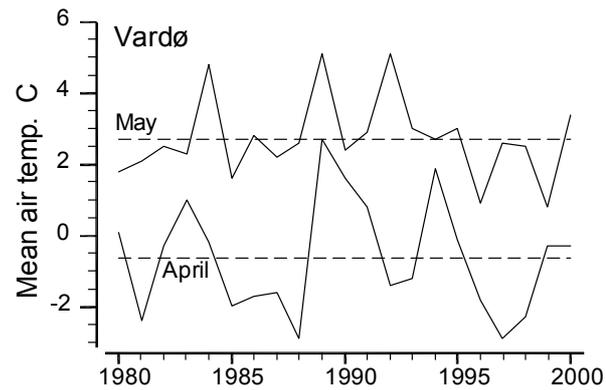


Figure 1. Variations in monthly mean air temperatures at Vardø and sea surface temperatures at Makkaur Lighthouse, East-Finnmark, in April and May 1980-2000. Dotted lines indicate the means for the period 1980-2000. Data from Norwegian Meteorological Institute.

Figuur 1. Variatie in gemiddelde maandelijkse luchttemperatuur in Vardø en zeevatertemperatuur bij Makkaur Lighthouse, Oost-Finnmarken, in april en mei 1980-2000. Data van Norwegian Meteorological Institute.

of ecological conditions at all trophic levels in the region, and its effects on seabirds breeding in the region have been described by Barrett and Krasnov (1996).

So while small changes in sea temperature may be one ultimate factor determining breeding demography, larger variations in air temperatures will have even greater short-term effects on the amount of snow and ice in and on the ground and so will affect access to breeding burrows and cavities on Hornøya. Mean monthly air temperatures during the pre-breeding period in April and May at the weather station in Vardø, c. 1 km from the colony, vary by as much as 5° C from year to year (Fig. 1). This results in large variations in snow cover on the island early in the breeding season (pers. obs.).

This aims of this study are: a) to document and discuss variations in the timing of breeding and egg size of the Atlantic Puffin and Razorbill over a 20 year period in north Norway, and b) to consider the possible effects of changes in sea and air temperature on these parameters.

#### METHODS

The study was carried out on Hornøya, a small (1000 x 700 m) island off the northeasternmost tip of Norway (70° 22'N, 31° 10'E) where a long-term study of colonial seabirds was initiated in 1980 (Barrett 1983, Barrett & Krasnov 1996). Approximately 5000 pairs of Atlantic Puffins and 500 pairs of Razorbills breed on the main cliff, which is otherwise dominated by c. 21 000 pairs of Black-legged Kittiwakes *Rissa tridactyla* (Furness & Barrett 1985; Barrett & Krasnov 1996).

In 1980-1982, c. 40-50 marked nests each of Atlantic Puffins and Razorbills were inspected once every 1-3 days during the late incubation and throughout the chick-rearing periods (Barrett 1985; Barrett *et al.* 1987). In and after 1988, the nests were checked once during the incubation period and twice during the chick-rearing period at a c. 10-20 day intervals.

In order to avoid possible interannual variations in breeding parameters due to changes in, for example, nest density, aspect, slope or distance from the cliff edge (Harris 1980; Hudson, 1982; Rodway *et al.* 1998), the same nests or, when abandoned, neighbouring nests were studied each year. Scattered along the whole breeding cliff, the total sample was considered representative of the colony.

All eggs were measured (length and breadth  $\pm 0.05$  mm) and their volumes were calculated using the equation  $v = klb^2$ , where  $v$  = volume in ml,  $k$  = 0.54 for Razorbill (Lloyd 1979) and 0.51 for Atlantic Puffin (Preston 1974),  $l$  = length in cm, and  $b$  = breadth in cm.

All chicks were weighed ( $\pm 2.5$  g) and their wings measured (maximum flattened chord, including down but excluding the small tuft at the end,  $\pm 2.5$  mm when downy and  $\pm 0.5$  mm after the eruption of the primaries or coverts) during the latter visits.

Hatching dates in 1980-1982 were determined directly during the frequent visits to the nests. In and after 1988, they were estimated using models relating wing length to age on the assumption that wing growth is less sensitive to nutrient variation than change in mass (Ricklefs & White 1975; Mauck & Grubb 1995). Despite considerable variations in chick diet during the study period (Barrett & Krasnov 1996), there was no suggestion of food shortages in any season that might have resulted in reduced somatic growth in chicks of either species (pers. obs.). The models relating wing length to age were based on data from chicks of known age, weighed and measured in two seasons in the early 1980s (Barrett 1985; Barrett *et al.* 1987), and the best model to fit each data set was determined using CurveExpert<sup>®</sup> 1.2 (<http://www.ebicom.net/~dhyams/cvxpt.htm>). In each case, quadratic regression equations were found to be the best fit, with regression coefficients of 99.6-99.9%. These equations were then used to calculate the hatching date of each chick whose wing length was known. If a chick was measured two or more times, the hatching date was calculated for each measurement and a mean of the values used. Differences in such multiple calculations were small (means  $0.7 \pm 0.7$  d for Razorbills and  $1.4 \pm 0.9$  d for Atlantic Puffins).

Once hatching dates were estimated, any obvious outlier at the end of a hatching period was removed from the data as they were assumed to be replacement eggs. These totalled four Atlantic Puffin eggs (in 1980, 1981, 1982 and 1998) and two Razorbill eggs (1994, 1995). Laying dates were back calculated from hatching dates using incubation periods of 39 days for the Atlantic Puffin (Ashcroft 1976) and 35 days for the Razorbill (Lloyd 1979), assuming no change over the duration of the study.

Minitab<sup>®</sup> Release 12 (<http://www.minitab.com>) software was used for all statistical analyses. Mean values are given  $\pm 1$  standard deviation.

## RESULTS

The estimates of the mean hatching dates of both species varied considerably and significantly from year to year, ranging from 21 June 1989–8 July 1981 for Atlantic Puffins ( $F_{15,570} = 16.0$ ,  $P < 0.001$ ) and 25 June 1989–7 July 1981 for Razorbills ( $F_{14,496} = 14.9$ ,  $P < 0.001$ ). There was a significant correlation between the mean hatching dates of both species each year ( $R^2 = 0.52$ ,  $P = 0.002$ ,  $n = 15$  yr). Accounting for the incubation periods, the ranges of mean laying

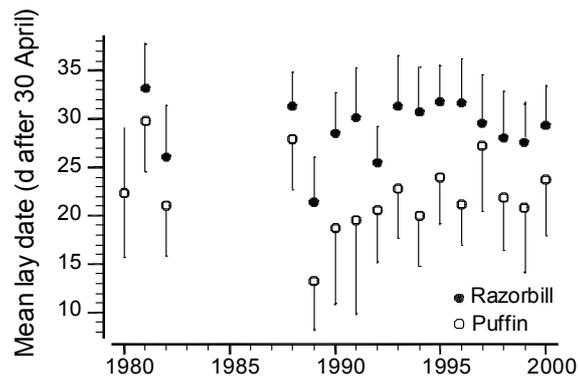


Figure 2. Mean laying dates of Atlantic Puffins and Razorbills at Hornøya, East Finnmark, 1980-2000. The dates are back-calculated from hatching dates with standard deviations (vertical lines) held constant.

Figuur 2. Gemiddelde eilegdata van Papegaaiduikers en Alken op Hornøya, Oost-Finnmarken, 1980-2000. De data zijn teruggerekend van de uitkomstdata, waarbij de standaarddeviaties (verticale lijnen) constant zijn gehouden.

dates were estimated at 13–30 May and 21 May–2 June respectively (Fig. 2). Atlantic Puffins laid on average 7 days before Razorbills (mean =  $6.9 \pm 2.8$  d, min = 3.2 (1997), max = 10.8 (1994),  $n = 15$ ).

The spread of laying within each year on Hornøya was greater for Atlantic Puffins (mean =  $22.1 \pm 4.8$  d,  $n = 16$  years) than for Razorbills ( $18.6 \pm 2.5$  d,  $n = 15$  years,  $t = 2.6$ ,  $P = 0.018$ ). The maximum variation in the mean laying dates between years for Atlantic Puffins (17 days) was also greater than that for Razorbills (12 days).

Mean sea temperatures in both April and May affected the hatching/laying dates of Atlantic Puffins with lower temperatures resulting in later laying ( $R^2 = 0.32$ ,  $P = 0.022$  (April),  $R^2 = 0.34$ ,  $P = 0.018$  (May; Fig. 3), whereas air temperatures had a similar but stronger influence in April ( $R^2 = 0.65$ ,  $P < 0.001$ ) but no influence in May ( $R^2 = 0.12$ ,  $P = 0.18$ ). While neither the mean air nor the mean sea temperatures in April influenced the laying dates of Razorbills, there were weak but significant effects of May temperatures, again with lower temperatures delaying egg laying ( $R^2 = 0.33$ ,  $P = 0.026$  (air),  $R^2 = 35\%$ ,  $P = 0.021$  (sea); Fig. 4).

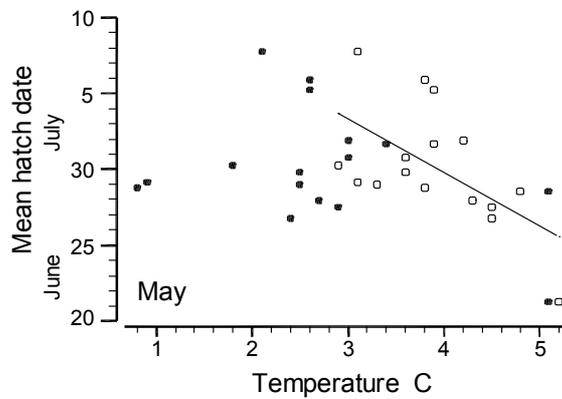
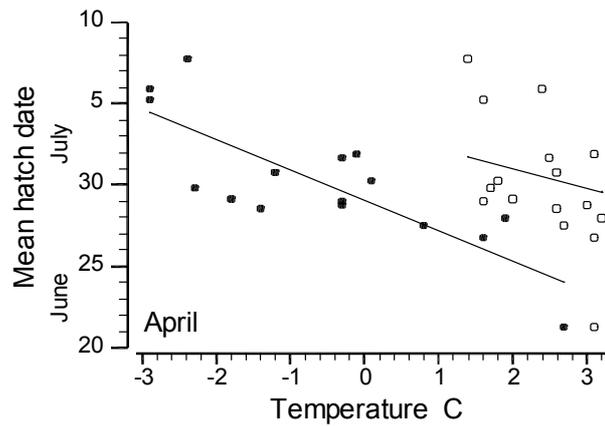


Figure 3. Correlations between mean hatching dates of Atlantic Puffin eggs and local air (solid symbols) and sea (open symbols) temperatures in East Finnmark in April and May 1980-2000. Equations for significant correlations are  $y = 29.1 - 1.85x$  (air, April),  $y = 38.7 - 3.54x$  (sea, April) and  $y = 43.9 - 3.53x$  (sea, May).

Figuur 3. Correlaties tussen gemiddelde uitkomstdata van eieren van de Papegaaiduiker en respectievelijk de luchttemperatuur (gesloten symbolen) en de zee temperatuur (open symbolen) in Oost-Finnmarken in april en mei 1980-2000. Vergelijkingen voor significante correlaties zijn  $y = 29.1 - 1.85x$  (lucht, april),  $y = 38.7 - 3.54x$  (zee, april) en  $y = 43.9 - 3.53x$  (zee, mei).

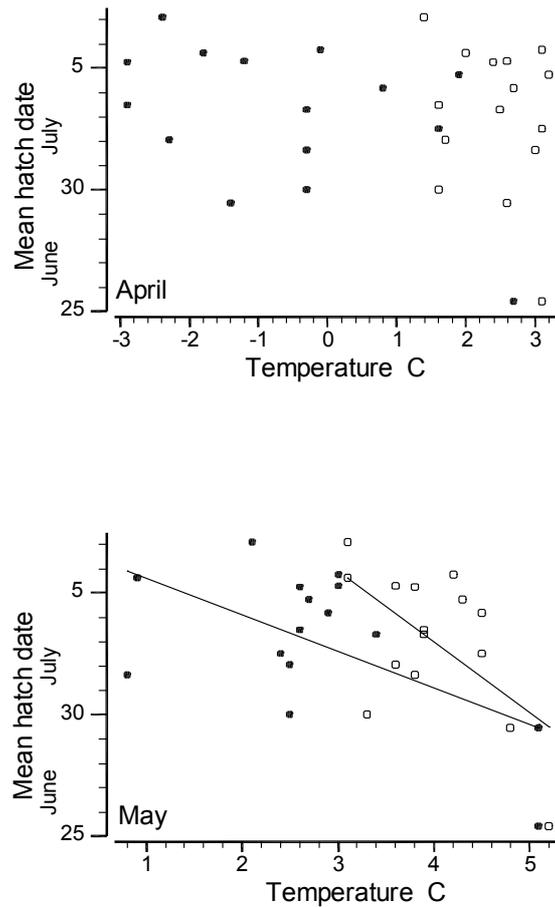


Figure 4. Correlations between mean hatching dates of Razorbill eggs and local air (solid symbols) and sea (open symbols) temperatures in East Finnmark in April and May 1980-2000. Equations for significant correlations are  $y = 37.1 - 1.47x$  (air, May) and  $y = 44.7 - 2.92x$  (sea, May).

Figuur 4. Correlaties tussen gemiddelde uitkomstdata van eieren van de Alk en respectievelijk de luchttemperatuur (gesloten symbolen) en de zee­temperatuur (open symbolen) in Oost-Finnmarken in april en mei 1980-2000. Vergelijkingen voor significante correlaties zijn  $y = 37.1 - 1.47x$  (lucht, mei) en  $y = 44.7 - 2.92x$  (zee, mei).

While the annual mean egg volumes of Atlantic Puffins did not vary among the 16 years for which data exist ( $F_{15,664} = 0.8$ ,  $P = 0.7$ , mean vol. =  $66.5 \pm 4.9$  ml,  $n = 680$ ), those of Razorbills varied within a range of  $97.6 \pm 8.7$  ml in 1999 to  $103.5 \pm 7.6$  ml in 1996 ( $F_{15,762} = 1.9$ ,  $P = 0.02$ ,  $n = 778$ ). While there was no continuous linear trend throughout the study period, there were suggestions of an increase in volume between 1988 and 1996 followed by a decrease (Fig. 5). Neither sea nor air temperatures in April or May had any effect on the volume of eggs laid by either species. Similarly laying date had no influence on egg volumes.

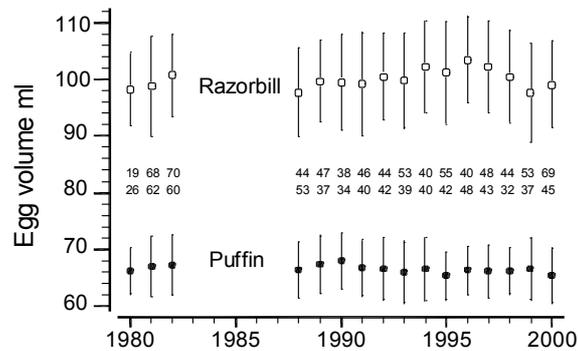


Figure 5. Mean egg volumes of Atlantic Puffins and Razorbills at Hornøya, East Finnmark, 1980-2000. Vertical lines represent standard deviations, and figures are sample sizes.

Figuur 5. Gemiddelde eivolumes van Papegaaiduiker en Alk op Hornøya, Oost-Finnmarken, 1980-2000. Verticale lijnen geven standaarddeviaties weer, getallen de steekproefgrootte.

## DISCUSSION

The consistency with which Atlantic Puffins on Hornøya laid eggs earlier than the Razorbills (Fig. 2) accords with Harris (1984) in that the former are among the earliest seabirds to lay. This may be explained both by the Atlantic Puffin's long incubation and chick-rearing periods and by the fact that they require less food (in absolute terms) than most other seabirds before breeding due to their

smaller size (Birkhead & Harris 1985). On Hornøya, the need to breed as early as possible is critical for species with long breeding seasons because of the short summers and the sometimes abrupt and early onset of autumn and winter.

As expected, both species laid eggs later than their conspecifics in boreal regions (Table 1) but as Birkhead & Harris (1985) point out, there is no clear latitudinal gradient in breeding demography. It is, for example, noticeable that Atlantic Puffins on the west coast of Britain and at Røst and Hornøya start laying at about the same time, whereas those on the Isle of May (east Scotland) lay earlier. Possibly, this might be related to where the adults spend the winter and when their pre-breeding moult occurs (Harris 1982; Harris & Birkhead 1985). At the north of their range, however, there appears to be a clear pattern, with Atlantic Puffins on Hornøya, Seven Islands and Novaya Zemlya laying successively later. The overall latitudinal pattern of Razorbill egg laying is also unclear with similar laying dates in Wales, Hornøya and Seven Islands, but later at Røst. These anomalies may be related to sea temperatures (Birkhead & Harris 1985) and to local hydrographical conditions (e.g. timing of upwellings) and hence feeding conditions around the individual colonies, as has been suggested to explain the similar lack of a simple relationship between latitude and laying dates among Common Guillemots *Uria aalge* in the eastern Pacific (Murphy & Schauer 1994).

The variations in the laying dates of first eggs by Atlantic Puffins at Hornøya agree well with the geographical pattern tabulated by Birkhead & Harris (1985). On the basis of few data points for five species, they suggest that the onset of laying in auks in general varies more in the Arctic than in boreal regions. This may be true for the Atlantic Puffin (and Black Guillemots *Cephus grylle*) where the spread in first egg dates seems to be greater in Arctic colonies (12-27 d) than in boreal ones (7-11 d). However, the spread among Razorbills and Common Guillemots seems to be similar in both Arctic and boreal regions, possibly the result of the more open aspect of Razorbills and Common Guillemot breeding sites. At Hornøya, in the four years (1981, 1988, 1992 and 1997) when Atlantic Puffins laid within five days of the Razorbills, the mean April air temperatures were at the lowest recorded during the study period. There was also a clear positive correlation between the interval between the mean laying dates of both species with both sea ( $R^2 = 0.38$ ,  $P = 0.014$ ,  $n = 14$ ) and air ( $R^2 = 47\%$ ,  $P = 0.005$ ,  $n = 13$ ) temperatures in April.

The response by Atlantic Puffins to the mean April air temperature was by far the strongest by either species to either air or sea temperature. This probably reflects the Atlantic Puffin's need to clear out burrows before nesting. As also found by Belopol'skii (1957) on colonies to the east of Hornøya, any ice or snow blocking a burrow would delay this process until the turf had warmed up, the ice had thawed and the burrow had dried out (Hornung & Harris 1976).

Table 1. Main egg laying periods of Atlantic Puffins and Razorbills in colonies in the north-east Atlantic. Dates in italics are estimated from hatching or fledging dates assuming incubation periods of 39 and 35 days for Atlantic Puffins and Razorbills respectively, and a fledging-period of 44 days for Atlantic Puffins at St. Kilda (Harris 1984). *n* = number of years for which data are available.

Tabel 1. Belangrijkste eilegperiode van Papegaaiduikers en Alken in kolonies in de oostelijke Atlantische Oceaan. Gecursiveerde data zijn afgeleid van uitkomst- en uitvliegdata, uitgaand van een broedduur van respectievelijk 39 en 35 dagen voor Papegaaiduikeer en Alk en een uitvliegduur van 44 dagen voor Papegaaiduikeer op St. Kilda (Harris 1984). *n* = aantal jaren waarvan data beschikbaar zijn.

<b>Atlantic Puffin</b>			
Locality	Period	n	Ref.
Skomer, Skokholm, Wales	2 - 22 May	2	1
Isle of May, E. Scotland	18 April-2 May	8	2
St. Kilda, W. Scotland	<i>8 May - 4 June</i>	18	3
Røst, N. Norway	<i>1-20 May</i>	19	4
Hornøya	<i>13-31 May</i>	15	5
Seven Islands, Murman	24 May-10 June	5	6
Novaya Zemlya	mid June-early July	2	7

<b>Razorbill</b>			
Locality	Period	n	Ref.
Isle of May, E. Scotland	10-30 May	7	8,9,10
St. Kilda, W. Scotland	9-13 May	6	11
Røst, N. Norway	<i>early June</i>	7	12
Hornøya	<i>21 May-3 June</i>	14	5
Seven Islands, Murman	<i>19 May-2 June</i>	6	6

References: 1. Ashcroft (1976), 2. Harris and Rothery (1985), 3. Harris *et al.* (1998), 4. Anker-Nilssen (1998), 5. This study, 6. Belopol'skii (1957), 7. Uspenski (1956), 8. Hudson (1982), 9. Plumb (1965), 10. Lloyd (1979), 11. Harris and Wanless (1989), 12. Ingold (1974).

Razorbill (and Common Guillemot) more open breeding sites are less susceptible to such blockage, might thaw more quickly due to their exposure and need less preparation. The laying dates of these species would thus be less affected by early air temperatures. The stronger response by Atlantic Puffins to temperature changes may be due not only to their earlier laying than Razorbills, but because they are smaller and therefore more susceptible to small changes in food availability caused by variations in sea temperatures early in the season.

The delay in egg-laying by Atlantic Puffins and Razorbills on Hornøya during cold springs corroborates several other studies on the same subject (summarized in Birkhead & Harris 1985). Harris & Wanless (1988) showed that a decrease of 1° C in mean sea surface temperatures off the Isle of May in March delayed Common Guillemot egg-laying by 5-6 days. Similarly, Hedgren (1979) found that a 1° C decline in spring air temperatures delayed the mean fledging date of Common Guillemots by 1 day in the Baltic, whereas Murphy & Schauer (1994) found that the same species in Alaska advanced their laying after a warm spring and hence early ice break-up. In this study, decreases in mean sea surface temperatures of 1° C in April or May delayed egg-laying in Atlantic Puffins and Razorbills by 1-4 days. A decrease in air temperatures by 1° C in April delayed Atlantic Puffins by 2 days, and in May delayed Razorbills by 1 day. Delays in breeding by Razorbills in colder weather have also been documented in Denmark, Murman and Wales (Paludan 1947; Belopol'skii 1957; Lloyd 1979). Harris *et al.* (1998) also refer to a link between early breeding and warm sea surface temperatures for several auks, including Atlantic Puffins but themselves documented the converse on St. Kilda, where breeding in the Atlantic Puffin occurred later in years when April sea temperatures were higher.

Hatch & Hatch (1990a) showed that seabird species breeding later in the season had a narrower range of laying dates and lower inter-season variability in egg-laying than those laying earlier. Such a strategy would be advantageous at high latitudes where marine production is strongly seasonal and limited to a short spring and summer period. While the spread of laying dates was indeed greater among those Atlantic Puffins that bred earlier than the Razorbills on Hornøya, there was no evidence of shorter laying periods in years of late laying in the Atlantic Puffin. For the Razorbill, the opposite seemed to be true, the correlation between length of laying period and mean laying date indicating a significantly greater spread of laying among Razorbills with later laying dates ( $R^2 = 0.31$ ,  $P = 0.03$ ,  $n = 14$ ).

That sea temperatures affected both species may be a response to changeable feeding conditions prior to egg-laying, even though it did not affect egg volumes. It has been shown, for example, that the pattern of the spawning migration and the spatial location of the Barents Sea capelin *Mallotus villosus* spawning grounds along the coast of North Norway in spring is generally determined by sea temperature conditions, with more fish spawning east of the North Cape in warm years (Ozhigin & Luka 1984). Capelin might also spawn in shallower water in warmer years (Stergiou 1991). This could result in capelin, a preferred prey species of all auks on Hornøya that remain in coastal waters for the whole summer (Furness & Barrett 1985, Barrett & Krasnov 1996), being more readily available during years of higher sea temperatures,

thereby facilitating an earlier breeding season. It is also possible, of course, that warmer seas produce warmer air temperatures (Fig. 1) resulting in less ice and snow on the cliff and thus earlier access to the burrows.

The lack of variation in egg volumes of either Atlantic Puffins or Razorbills on Hornøya in response to either temperatures or laying dates suggests that neither species made any attempt to reduce egg volume in order to advance egg laying as found by Nettleship *et al.* (1984). It also corroborates the studies of Birkhead & Nettleship (1987) and Gaston & Hipfner (1998), both of which failed to demonstrate any annual variation in egg volumes of guillemots despite variation in the laying periods.

Breeding populations of seabirds are generally monitored by annual counts of nests or birds at recommended periods of the breeding season, for example immediately before, during or soon after egg laying for Atlantic Puffins (Lorentsen 1989; Walsh *et al.* 1995). In the Norwegian monitoring programme, variations in the breeding demography of 12-17 days for Atlantic Puffins and Razorbills are large in relation to timing of c. 10-day monitoring field trips to remote colonies such as Hornøya. The chances of mistiming such trips may be reduced, however, by regarding sea and air temperatures prior to the field season. Although the actual monthly means are usually not available until after the field season, forecasts of temperature changes in the Barents Sea based on oceanographical measurements are published annually (Aure 1999). Knowing that increases in sea temperatures will advance the onset of breeding, these forecasts should be heeded when planning monitoring studies. Nevertheless, however well planned such a study may be, in order to avoid future problems in interpreting results arising from mistimed counts, observers should always assess and note the stage of the breeding season when counts are made.

Although this study did not provide any evidence of a long-term trend towards earlier egg laying in the Atlantic Puffin and the Razorbill that might be attributed to global climate change as has been documented for some European bird species (Crick *et al.* 1997; McCleery & Perrins 1998), its continuance will hopefully generate a sound baseline for future prediction of effects of climate change on northern seabirds (Brown 1991; Forchhammer *et al.* 1998).

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BROEDDEMOGRAFIE EN EIVOLUME VAN PAPEGAAIDUIKERS  
*FRATERCULA ARCTICA* EN ALKEN *ALCA TORDA* TIJDENS 20 JAAR  
VAN KLIMATOLOGISCHE VARIATIE

*Om het beste tijdstip van inventarisatiebezoeken aan kolonies met Papegaaiduiikers Fratercula arctica en Alken Alca torda in Noorwegen te bepalen is kennis nodig over de timing van de broedperiode en over de periode dat de jongen net uit het ei zijn gekropen. Op Hornøya in Noord-Noorwegen is hier in 1980-2000 een studie naar verricht. De gemiddelde eilegdata lagen in 1980-1982 en 1988-2000 tussen 13-30 mei voor Papegaaiduiiker en tussen 21 mei- 2juni voor Alk (figuur 2). Papegaaiduiikers legden gemiddeld 7 dagen eerder dan Alken. De gemiddelde spreiding in legdata was voor Papegaaiduiiker (22 dagen) ieder jaar groter dan voor Alk (19 dagen). Eilegdata en lucht- en zeetemperaturen in april en mei waren significant met elkaar gecorreleerd (figuur 3 & 4); lagere temperaturen hadden een vertraging in legdatum met 1-4 dagen °C<sup>-1</sup> tot gevolg. Ontoegankelijkheid van nestplaatsen als gevolg van sneeuw en ijs in holen (van Papegaaiduiiker) kan een deel van de verlate in eileg in koude voorjaren verklaren. Met de gevonden spreiding in eilegdata moet rekening gehouden worden bij de planning van inventarisatiebezoeken om broedpopulaties te monitoren. Bij eieren van de Papegaaiduiiker werd geen verschil in gemiddeld volume tussen de jaren gevonden (figuur 5). Hoewel het eivolume bij de Alk jaarlijks wel varieerde (figuur 5), werd het eivolume niet beïnvloed door lucht- of zeetemperatuur. Dit suggereert dat geen van beide soorten de eigroote aanpast om de eilegdatum te vervroegen.*

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THE DISTRIBUTION OF SPECTACLED PETRELS  
*PROCELLARIA CONSPICILLATA*  
IN THE SOUTH-EASTERN ATLANTIC

KEES (C.J.) CAMPHUYSEN<sup>1,2</sup>

Camphuysen C.J. 2001. The distribution of Spectacled Petrels *Procellaria conspicillata* in the south-eastern Atlantic. *Atlantic Seabirds* 3(3): 113-124. *At least 215 Spectacled Petrels Procellaria conspicillata were observed during systematic seabird surveys in the south-east Atlantic in January-March 2000 and 2001. These sightings provide a clearer picture of the pelagic distribution, relative abundance, habitat preferences, behaviour, and tendency to join vessels at sea of this rare seabird off Southern Africa. Spectacled Petrels were among the species that most readily associated with the research vessel, both during steaming and while the ship was stationary. Flocks of up to 18 individuals joined the ship. Nearby long-lining fishing vessels were also followed by this species. Most Spectacled Petrels occurred in an area where frontal edges of so-called Agulhas Rings provided enhanced feeding opportunities for a variety of seabirds. However, Spectacled Petrels were not seen to directly benefit from these conditions, which may have been caused by their predominantly nocturnal foraging habits.*

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INTRODUCTION

Spectacled Petrels *Procellaria conspicillata* are among the rarer seabirds in the world, only breeding at Inaccessible Island in the Tristan da Cunha group (37°18'S, 12°41'W; central South Atlantic), with an estimated population of 3000-4000 breeding pairs (Stattersfield & Capper 2000; Ryan & Moloney 2000). Murphy (1936) considered the *conspicillata* type "merely a phase that crops out from time to time in the Shoemaker [White-chinned Petrel *P. aequinoctialis*] population, and not a rare or dwindling species", but the Spectacled Petrel was described as a separate species in the late 1990s (Ryan 1998; Ryan 1999).

Very little information has so far been published on their pelagic distribution. Enticott & O'Connell (1985) summarised the available information and listed sightings of 80 individuals, suggesting that Spectacled Petrels dispersed throughout the South Atlantic between 25°S and 40°S latitude. Many birds have been recorded in Brazilian waters, where interactions with long-line fisheries are frequent (Olmos 1997; Neves & Olmos 1998; Ryan 1999). Camphuysen & Van der Meer (2000) reported sightings of 30 individuals off Southern Africa in February 2000, suggesting that the (summer) at sea

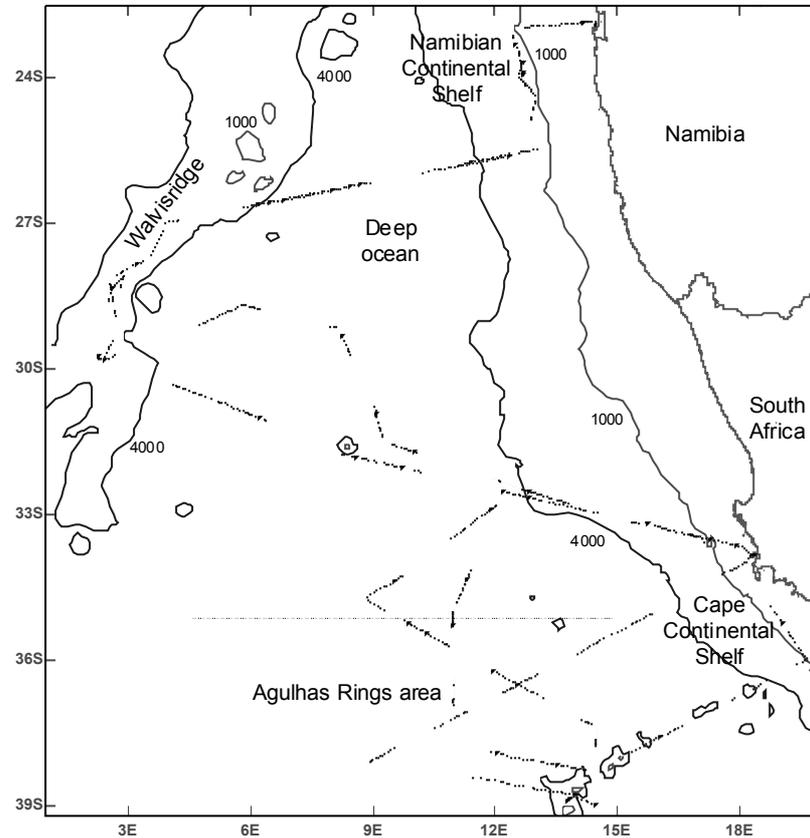


Figure 1. Study area and routes followed in 2000 and 2001. Solid lines represent transects. Subregions mentioned in this paper are indicated, as well as the 4000 and 1000m depth contours indicating Walvis Ridge, the continental shelf and various seamounts off Southern Africa.

Figuur 1. Onderzoeksgebied en afgelegde transecten in 2000 en 2001 (dikke lijnen). De in dit artikel genoemde deelgebieden zijn afgebeeld met daarnaast de 4000m en 1000m dieptelijnen, waarmee de Walvis Ridge, de shelfrand en verschillende onderzeese bergen zichtbaar worden gemaakt.

distribution of Spectacled and White-chinned Petrels was dissimilar, with the former being confined to deep ocean waters and the latter mainly to the shelf and shelf edge.

This paper reports the results of systematic seabird surveys between late January and mid February 2001 off Southern Africa between Walvis Bay

and Cape Town, covering the same area and therefore combined with data collected by Camphuysen & Van der Meer (2000) in the previous year. In addition to this, results are provided of systematic surveys within an adjacent sea area further to the south during mid-February-early March 2001. Additional notes include information on moult stage, (foraging) behaviour, habitat preferences and the tendency of Spectacled Petrels to associate with vessels.

#### MATERIAL AND METHODS

Systematic seabird surveys were conducted from 15 to 26 February 2000 and from 29 January to 11 February 2001 from Walvis Bay (Namibia) to Cape Town (South Africa) via Walvis Ridge (Fig. 1). Between 13 February and 3 March 2001, an area SW of Cape Town was worked in, between 32° and 39° S latitude and 18° and 8° E longitude.

Methods of observation were similar to those standardised for NW Europe, using a 300m wide transect, 10-minute periods of observation, and a snap-shot for flying birds (*cf.* Tasker *et al.* 1984). In 43 days, a total of 5771 km was surveyed, covering approximately 1700 km<sup>2</sup>. Seabirds associating with the vessel while stationary at Conductivity-Temperature-Depth (CTD) recording stations were counted one hour after arrival and listed separately ('additional birds on station'). Those that followed the ship during steaming were recorded as 'ship-associated during transects'.

Seabird counts were attached to the Netherlands Institute for Sea Research (NIOZ) Mixing of Agulhas Rings Experiment programme (MARE). This project was meant to determine the proportion of Agulhas current leakage that contributes to the northward branch of the oceans thermohaline circulation (THC). As part of that study, a selected Agulhas Ring (an eddy, a roughly circular water mass originating from the Indian Ocean travelling through the South Atlantic) was examined at different stages of its non-linear decay over a period of one year. The oceanographic research under MARE enabled studies of marine wildlife to investigate and interpret interactions with physical processes simultaneously. Agulhas Rings were characterised by relatively high surface salinity, their anti-clockwise rotating velocity, and could be traced down and followed best by altimetry from a satellite (Sea Surface Height Anomaly analysis from the Colorado Center for Astrodynamics Research). These data, in combination with continuous recordings of surface salinity (‰), surface temperature (°C), and water depth (m; analysed at 500m depth intervals), measured at 1-minute intervals and automatically recorded on board, were used to describe and classify habitats at sea in broad terms. Shifts in surface salinity within 10-minute counts of over 0.099‰ were categorised as steep gradients (5.6%,  $n = 550$  10-minute counts), shifts between 0.049 and 0.099‰ as medium

gradients (10.9%) and shifts <0.049% as (near-) stable situations (83.5%). Similarly, surface temperature shifts within 10-minute periods over more than 0.2°C were considered strong gradients (10.2%), between 0.1 and 0.2°C as medium gradients (22.7%), and shifts of less than 0.1°C as (near-) stable situations (67.1%). Observed numbers of petrels in each situation were compared with expectation based on the frequency of encountered gradients (G-test).

Foraging behaviour, feeding success and certain types of non-foraging behaviour (e.g. resting/sleeping, preening, courtship display) were recorded as standard practice during transect counts (Camphuysen & Garthe 2001). Specific differences in attraction of the research vessel were compared for the most numerous Procellariiform species and for the Spectacled Petrel, by calculating the total number of individuals seen, the proportion seen during steaming (not visibly attracted by the ship), the proportion recorded as ship-followers and the proportion assembling at stations only (excluding shelf and shelf edge data; 2001 only). Because Spectacled Petrels were so heavily attracted to the research vessel, it proved to be unwise to calculate densities. Results are therefore presented as numbers observed per km steamed ( $n \text{ km}^{-1}$ ).

On the basis of moult stage and individually characteristic head patterns, double counts could be avoided in 2000. In late February 2001, Spectacled Petrels became so numerous that this method did not work, so that only 'best professional judgement' could be used to separate newcomers from persistent or repeated attendants. In all cases, presented figures are either precise counts or estimates of a 'minimum number present'. Moulting stages were recorded as 'not moulting' (entire primary series intact) or 'moulting' (primary series interrupted by growing or missing feathers; no further details), whenever possible by an indication of the moult stage in three groups: start of moult (inner primaries missing or growing; P1-P4), progressed moult (central primaries missing or growing; P5-P7), or end of moult (outer primaries missing or growing; P8-10).

## RESULTS

During transect counts in February 2000, 30 Spectacled Petrels were observed, 13 of which were recorded as 'ship-associates'. The first three individuals were encountered in the Walvis Ridge area, at 29°50'S, 02°25'E, the others while the ship was on transit between Walvis Ridge and the Continental shelf off Cape Town. Most individuals (16) were encountered at approx 31°S, 9°E. In 2001, 96 Spectacled Petrels were recorded during transect counts, 61 of which as 'ship-associates', 5 as 'associated with nearby fishing vessel'. Additionally, 89 birds were recorded on stations, not following on subsequent transects. Of the

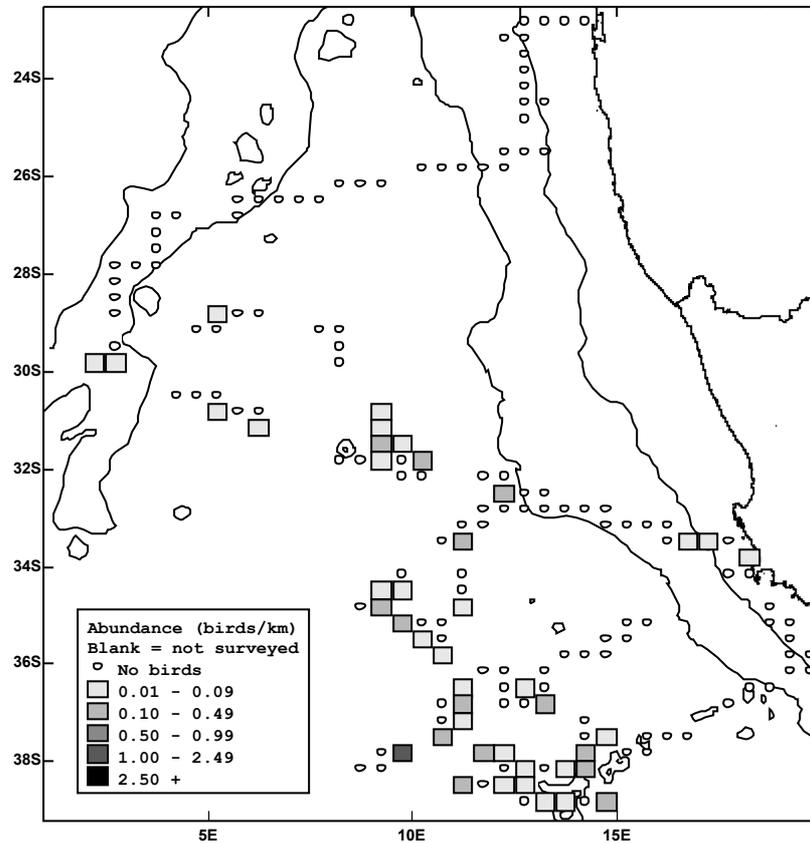


Figure 2. Distribution of Spectacled Petrels ( $n \text{ km}^{-1}$ ) based on systematic surveys off Southern Africa, January-March 2000 en 2001.

Figuur 2. Verspreiding van Gebilde Stormvogels ( $n \text{ km}^{-1}$ ) gebaseerd op systematische tellingen ten zuidwesten van Zuidelijk Afrika, januari-maart 2000 en 2001.

grand total, 215 individuals, most birds were seen either during transects, or assembling around the ship at stations, in the 'Agulhas Ring area' (35-39°S), well beyond the continental shelf (Table 1, Fig. 2).

Of 75 individuals that could be checked and recorded, 24 (32%) were actively moulting primaries, 51 were not moulting. Moulting stages included nine individuals that had just commenced, six with progressed moulting and five with nearly completed primary moulting.

Spectacled Petrels often joined the ship and were persistent ship-followers. Away from the continental shelf, 85.5% of all Spectacled Petrels ( $n =$

Table 1. Spectacled Petrels observed during transect counts and at stations in different parts of the study area (Fig. 1) in February 2000 and January-March 2001. Expectation was based on differences in observer effort (km steamed).

Tabel 1. Aantallen Gebrilde Stormvogels (Obs) tijdens transecttellingen en op stations in verschillende delen van het onderzoeksgebied. De verwachtingen (Exp) zijn gebaseerd op verschillen in waarnemingsinspanning (km steamed).

	km steamed	Obs	Exp
Continental shelf	1015	6	38
Walvis Ridge	529	5	20
Deep Ocean	2439	38	91
Agulhas Ring area	1788	166	67
	5771	215	215

197) were recorded in association with the research vessel (either during transect counts or while stationary), or with any nearby vessel, higher than any of the other common Procellariiform species observed away from the continental shelf (Table 2). Within the Agulhas Ring area, there was no obvious habitat preference of Spectacled Petrels when looking at surface temperature. However, Spectacled Petrels were seen in significantly higher numbers than expected during transects with moderate or steep surface salinity drops ( $G_{adj}$  11.2,  $df = 2$ ,  $P < 0.01$ ), with a non-significant tendency to become more abundant over water with relatively high salinity ( $>35.8\text{‰}$ ). Of all Spectacled Petrels recorded during transect counts, 80% were observed over water of at least 4500m depth (Fig. 3). Similarly, 92% of all Spectacled Petrels joining the ship on CTD-stations occurred in waters of at least 4500m depth (expected 65% based on number of stations per depth category). As in 2000, Spectacled Petrels were rather rare over the continental shelf in 2001 in comparison with the closely related and abundant White-chinned Petrels (Table 3). In areas defined as Open Ocean and 'influenced by' Agulhas Rings, both species occurred in appreciable numbers, with the latter at best being twice as numerous.

## DISCUSSION

The tendency to associate with a vessel was higher in Spectacled Petrels than in any of the other common Procellariiform species observed away from the continental shelf (Table 2), comparable only with notorious ship-followers as the White-chinned Petrel *Procellaria aequinoctialis* (79.7%,  $n = 232$ ), Black-browed Albatross *Thalassarche melanophrys* (70.5%,  $n = 362$ ), and Yellow-

Table 2. Tendency to associate with a vessel for the most numerous Procellariiform species observed over deep ocean waters beyond the continental shelf in 2001. Shown are total number observed, proportion seen during transect counts that did not follow the ship (% transect), proportion that followed the ship during transect counts (% assoc.), proportion seen in association with nearby fishing vessels (%trawler) and proportion seen assembling around the ship on stations (% station). Sorted by the apparent species-specific 'readiness' to join the ship.

Tabel 2. Soortspecifieke neiging tot associatie met schepen voor de meest talrijke stormvogelachtigen op open zee in 2001. Gegeven zijn het totaal aantal individuen en het percentage daarvan tijdens transecttellingen (niet volgend), achter het schip tijdens transecttellingen, bij een vissersschip, en tijdens het stilliggen op station. Aflopend gesorteerd naar het aandeel met schepen geassocieerde individuen.

	% transect	% assoc.	% trawler	% station	Total
Spectacled Petrel	14.5	33.0	2.8	49.7	179
<i>Procellaria conspicillata</i>					
White-chinned Petrel	20.3	34.9	8.6	36.2	232
<i>Procellaria aequinoctialis</i>					
Black-browed Mollymawk	29.6	30.4	15.2	24.9	362
<i>Thalassarche melanophris</i>					
Atlantic Yellow-nosed Mollymawk	30.0	24.0	18.0	28.0	50
<i>Thalassarche chlororhynchos</i>					
Great Shearwater	42.7	37.3	20.0	0	75
<i>Puffinus gravis</i>					
Wandering Albatross	43.5	39.1	0	17.4	23
<i>Diomedea exulans</i>					
Tasmanian Mollymawk	52.2	14.2	6.2	27.4	113
<i>Thalassarche cauta</i>					
Yellow-nosed Mollymawk	61.2	28.6	0	10.2	49
<i>Thalassarche chlor./carteri</i>					
Scopoli's/Cory's Shearwater	62.3	0.8	12.5	24.5	257
<i>Calonectris spp.</i>					
Indian Ocean Yellow-n Mollymawk	69.0	17.2	0	13.8	29
<i>Thalassarche carteri</i>					
Wilson's Storm-petrel	71.9	21.9	6.3	0	32
<i>Oceanites oceanicus</i>					
Cory's Shearwater	73.3	24.2	0	2.5	120
<i>Calonectris borealis</i>					
Great-winged Petrel	84.0	10.7	0.6	4.7	852
<i>Pterodroma macroptera</i>					
Scopoli's Shearwater	88.5	11.5	0	0	26
<i>Calonectris diomedea</i>					
Leach's Storm-petrel	97.8	2.2	0	0	723
<i>Oceanodroma leucorhoa</i>					
White-bellied Storm-petrel	100	0	0	0	14
<i>Fregetta grallaria</i>					

Table 3. Relative abundance of closely related White-chinned Petrels and Spectacled Petrels in different sea areas (Fig. 1) in 2000 and 2001 expressed as number of birds per km steamed and surveyed. Recorded water depth during surveys in either area is shown in parentheses.

Tabel 3. Verschillen in relatieve talrijkheid tussen de nauw verwante Witkinstormvogel en de Gebrilde Stormvogel in verschillende delen van het studiegebied (Fig. 1) in 2000 en 2001. Tussen haakjes is de tijdens tellingen geregistreerde waterdiepte in elk van de gebieden weergegeven.

		km steamed	White-chinned Petrel	$n \text{ km}^{-1}$	Spectacled Petrel	$n \text{ km}^{-1}$
Namibian Shelf (5 - 2000m)	2000	347	959	2.77	0	0
	2001	192	9	0.05	0	0
Walvis Ridge (1875 - 3675m)	2000	168	2	0.01	4	0.02
	2001	361	0	0	1	0.00
Deep Ocean (500 - 5200m)	2000	1174	69	0.06	26	0.02
	2001	1422	20	0.01	18	0.01
Agulhas Ring area (900 - 5500)	2001	1630	128	0.08	71	0.04
Cape Shelf (25 - 1980m)	2000	81	20	0.25	0	0
	2001	395	968	2.45	6	0.02

nosed Albatross *Thalassarche chlororhynchos* subsp. (70%,  $n = 50$ ). This tendency would bring them automatically in contact and potentially in conflict with long-line fisheries (Neves & Olmos 1998), even if such boats would not be overabundant in some of their preferred areas.

Off Southern Africa, White-chinned Petrel is one of the commonest seabirds throughout the year (Summerhayes *et al.* 1974; Ryan 1997), perhaps outnumbered only by the Sooty Shearwater *Puffinus griseus*. White-chinned Petrels regularly occur close inshore and are abundant at fishing vessels off Southern Africa's south and west coasts (Ryan & Moloney 1988). Sinclair (1978) reported three individuals visiting a deep-sea trawler in August 1977 in the midst of the 'common, aggressive and noisy' White-chinned Petrels, but otherwise, the Spectacled Petrel has been described as a scarce visitor to the west coast, primarily in winter (Ryan 1997). This picture is apparently changing as a result of recent pelagic trips off Southern Africa (P.G. Ryan *in litt.*). The data presented previously (Camphuysen & Van der Meer 2000), and certainly the sightings described in the present paper, confirm that just off the continental shelf of Southern Africa, Spectacled Petrels are relatively common summer visitors, occasionally visiting the shelf in that time of the year. The results point at spatial segregation of the two closely related species, White-chinned and Spectacled Petrels, with the former being comparatively numerous in inshore

*Spectacled Petrel in flight* Vliegende Brilstormvogel (photo C.J. Camphuysen)

*Resting Spectacled Petrels near stationary vessel* Rustende Brilstormvogels op een station van het schip (photo C.J. Camphuysen)

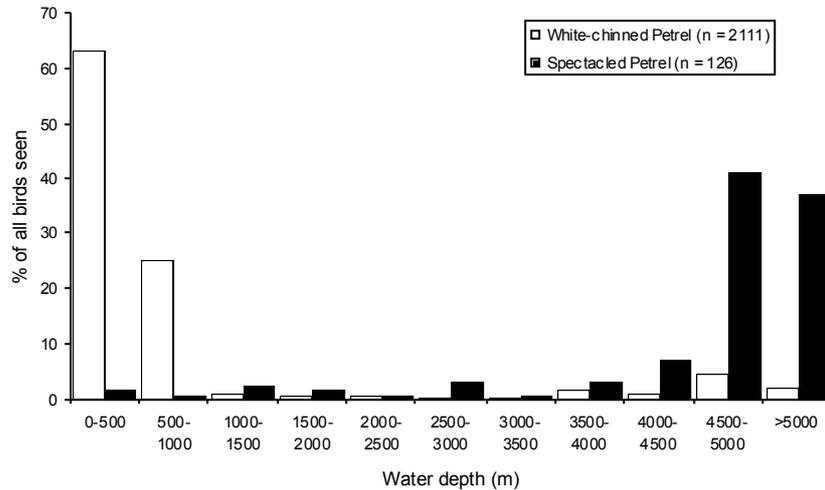


Figure 3. Fraction (%) of all recorded White-chinned and Spectacled Petrels during transect counts off Southern Africa in 2000 and 2001 in relation to water depth (m).

Figuur 3. Percentage (%) van geregistreerde Witkinstormvogels en Gebrilde Stormvogels tijdens transecttellingen voor de Zuid-Afrikaanse kust in 2000 en 2001 in relatie tot de waterdiepte (m).

waters, which is best illustrated by plotting the fraction observed of either species in different zones of water depth within the study area (Fig. 3).

The only other study that could be traced in which substantial numbers of Spectacled Petrels have been observed away from the breeding colony was conducted off Brazil and involved birds attending commercial bottom long-line fishing vessels (Olmos 1997). Spectacled Petrels were the commonest species in flocks of seabirds attending long-line fishing operations on the coastal shelf off southeastern Brazil during summer (Nov-Mar). In winter, the White-chinned Petrel (jointly with Yellow-nosed and Black-browed Albatrosses) were the commonest species, replacing Spectacled Petrels and suggesting a temporal segregation between the two taxa. More recent studies suggested that Spectacled Petrels are abundant off the shelf in winter (F. Olmos *in litt.*), indicating spatial segregation just as off southern Africa. Clearly, waters off southeastern Brazil are important feeding areas for some seabird populations nesting in the Tristan da Cunha and Gough group, including non-breeding Spectacled Petrels.

Very few Spectacled Petrels were actively foraging or feeding and in fact, most of the birds attracted to the stationary research vessel would

immediately alight and start preening or fall asleep. This suggests nocturnal foraging activities, or, as Fabio Olmos (*in litt.*) suggests, the associated birds simply wait for the ship to start fishing. In any case, a detailed analysis of hydrographical characteristics explaining their daytime distribution at sea is not likely to result into clear patterns for a bird so heavily attracted to any nearby vessel. Nevertheless, the relatively high numbers around the Agulhas Rings could be indicative of enriched foraging opportunities (albeit perhaps at night) for Spectacled Petrels in the general area of the rings. Most of the foraging activities of (mainly planktivorous) seabirds near Agulhas Rings was focussed at ring-edges, where the abrupt change in surface salinity and strong currents seemed to be attractive.

Ryan (1991) described Spectacled Petrels as highly localised ship-followers even in the Tristan archipelago itself (present at fishing vessels off their breeding station Inaccessible Island, absent off Nightingale island). It is therefore most likely that the Spectacled Petrels observed off Southern Africa in summer are non-breeders or immatures. If so, it is remarkable that the only two locations in the South Atlantic presently known to hold substantial numbers of Spectacled Petrels during the summer months are so wide apart: the coastal shelf off southeastern Brazil (Olmos 1997) and deep waters off the continental shelf of South Africa (this study).

#### ACKNOWLEDGEMENTS

Captains John Ellen and Hans de Groot and crew of RV *Pelagia* are thanked for their co-operation on board. Expedition leaders Gert-Jan Brummer and Kees Veth are thanked for hospitality during 'their' cruises and, together with Astrid van Veldhoven and Wilco Hazeleger for help with the interpretation of oceanographical data. Jaap van der Meer (2000) and Jonathan Barber (2001) are thanked as co-observers. Fabio Olmos and Peter Ryan kindly, constructively, and extremely quickly commented on an earlier draft of this paper.

#### DE VERSPREIDING VAN GEBRILDE STORMVOGELS IN DE ZUIDOOST-ATLANTISCHE OCEAAN

*In totaal tenminste 215 Gebrilde Stormvogels Procellaria conspicillata werden gezien tijdens systematische tellingen in het Zuidoost-Atlantische gebied in de maanden januari-maart, 2000 en 2001. Deze nieuwe waarnemingen geven een veel completer beeld van het voorkomen en de gebiedsvoorkeuren van deze zeldzame zeevogel in de zomer voor de kust van Zuidelijk Afrika, waar zij tot op heden als een schaarse wintergast te boek stond. Gebrilde Stormvogels werden enorm aangetrokken door het onderzoeksschip en daarom is het niet zinvol om verspreidingspatronen op basis van dichtheden ( $n$  per  $km^2$ ) uit te rekenen. In plaats daarvan is het aantal vogels per strekkende kilometer gegeven (figuur 2). Groepen Gebrilde Stormvogels verzamelden zich soms rond het stilliggende schip en er was geen andere zeevogel waarvan een zo groot aandeel werd genoteerd als 'schipvolger' (tabel 2). Ook een dichtbij langsvarende lijnvisser bleek door enkele Gebrilde Stormvogels te worden gevolgd. De meeste Gebrilde Stormvogels werden aangetroffen in een gebied waar de front-achtige randen van zogenaamde Agulhas-ringen (bellen warm, zout water uit de Indische Oceaan die in de Atlantische Oceaan terechtkomen en daar langzaam afkoelen op*

hun weg naar het noordwesten) kennelijk attractief zijn voor veel foeragerende zeevogels. Van de nacht-actieve Gebrilde Stormvogels werden overigens geen activiteiten waargenomen waaruit bleek dat zij inderdaad van deze situatie gebruik maakten. In vergelijking met de nauw verwante Witkinstormvogel *Procellaria aequinoctialis* was het voorkomen van Gebrilde Stormvogels veel meer beperkt tot de diepere delen van de oceaan. Op en langs de rand van het Continentale Plat was de Witkinstormvogel veel beter vertegenwoordigd (figuur 3, tabel 3). De gepresenteerde gegevens laten zien dat de diepere delen voor de kust van Zuid-Afrika na Brazilië vermoedelijk de meeste overzomerende Gebrilde Stormvogel huisvesten.

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UNUSUALLY LOW SUCCESS OF HERRING GULLS  
*LARUS ARGENTATUS* BREEDING ON THE NORTH  
SHORE OF THE GULF OF ST. LAWRENCE,  
QUEBEC, CANADA

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TITMAN<sup>1</sup> & NATHALIE BAYS<sup>1,4</sup>

Boyne A.W., Guillemette M., Titman R.D. & Bays N. 2001. Unusually low success of Herring Gulls *Larus argentatus* breeding on the North Shore of the Gulf of St. Lawrence, Quebec, Canada. *Atlantic Seabirds* 3(3): 125-136. *Herring Gulls Larus argentatus are the most numerous species of seabird in the Mingan Archipelago National Park Reserve (MANPR), however little is known about their nesting ecology or reproductive success. The number of active nests, nest density, clutch size, fate of eggs, number of successful nests, hatching success, and mean and median nest hatching dates were recorded in two study polygons on Île Nue, an island in the MANPR, 1994-1996. Clutch size was lower and mean hatching date was later on Île Nue than for typical Herring Gull colonies in all three years of the study. Hatching success was extremely low in 1995. In response, polygons with varying degrees of disturbance were set up to determine the effects of researcher disturbance and a clutch removal experiment was set up to determine whether there were sufficient food sources to allow gulls to produce replacement clutches. Low clutch size and hatching success could not be explained by researcher disturbance, predation, or competition for nest sites, leaving food-stress as the most likely explanation for the low reproductive success.*

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#### INTRODUCTION

In northern environments, Herring Gulls *Larus argentatus* form an important part of the coastal ecosystem. The Mingan Archipelago National Park Reserve, on the North Shore of the Gulf of St. Lawrence, Canada is an important seabird breeding area and, numerically, Herring Gulls *Larus argentatus smithsonianus* are the most important seabird species breeding in the Park. The number of Herring Gulls nesting in the Archipelago increased from 3772 breeding pairs in 1978 (Chapdelaine & Bourget 1981) to 9598 breeding pairs in 1990 (Grenier & Kavanagh 1993). The majority of the increase occurred on Île Nue, where the

Herring Gull colony increased from 1753 pairs in 1978 (Chapdelaine & Bourget 1981) to 6718 pairs in 1990 (Grenier & Kavanagh 1993), making it the largest colony in the Park. Factors that may have contributed to the increase in Herring Gulls on Île Nue include the increased protection that the colony received following the establishment of the National Park in 1984 (Grenier & Kavanagh 1993); increases in the availability of artificial food sources, such as fisheries' discards; increases in natural prey, such as capelin *Mallotus villosus*; and immigration from other colonies (Guillemette 1997).

Despite their abundance, little is known about the breeding biology of Herring Gulls in the Park. Parks Canada was concerned that the increase in the gull population may impact negatively upon the vegetation on Île Nue and other seabirds nesting in the Park (Grenier & Kavanagh 1993). In 1994 we initiated a three year study of the breeding biology of Herring Gulls nesting on Île Nue, and in 1996 we investigated whether food limitation or researcher

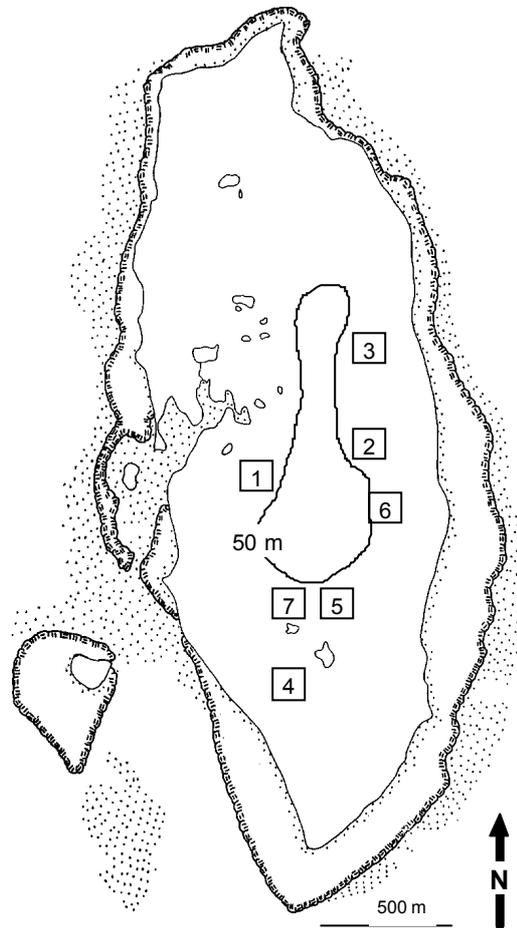


Figure 1. Île Nue showing seven study polygons; 1, 2 nesting polygons, 3 low disturbance, 4 moderate disturbance, 5 high disturbance and 6, 7 clutch removal polygons.

Figuur 1. Île Nue en de zeven studieplots met verstoringsexperimenten.

disturbance could explain the low clutch sizes observed in 1994 and 1995, and the low hatching success observed in 1995. In 1995, the majority of eggs disappeared during a short time period and no replacement clutches were observed. Polygons with varying degrees of disturbance were set up to determine the effects of researcher activities and a clutch removal experiment was set up as an indirect method of determining food abundance. We postulated that if human disturbance was the cause of low clutch size and hatching success, polygons with the most disturbance would have the lowest mean clutch size and hatching success, and if food availability was affecting the colony, the gulls would be unable to lay replacement clutches and clutch size would remain low regardless of disturbance rates.

This paper describes the nesting ecology of Herring Gulls on Île Nue and offers suggestions for what factors may be affecting their reproductive success in the pre-laying and incubation periods.

#### METHODS

Île Nue is located 4 km off shore in the easternmost section of the Mingan Archipelago National Park Reserve on the middle North Shore of the Gulf of St. Lawrence, Quebec, Canada (50°13'N, 64°08'W). Île Nue is 7 km in circumference and is dominated by shrub heath barren, lichen heath barren, and bog habitat. The most abundant plant species are fireweed *Epilobium angustifolium*, Labrador tea *Ledum groenlandicum*, and crowberry *Empetrum nigrum*. The largest colony of Herring Gulls in the Park nests on Île Nue, as well as smaller colonies of Arctic Terns *Sterna paradisaea*, Common Terns *S. hirundo*, Great Black-backed Gulls *L. marinus*, Black-legged Kittiwakes *Rissa tridactyla*, and Common Eiders *Somateria mollissima*.

**Nesting ecology, 1994-1996** Nesting ecology of the Herring Gull colony on Île Nue was followed 1994-1996 in two study polygons (referred to collectively as nesting polygons; Figure 1). The eastern polygon was 65 m x 65 m (area: 0.423 ha) and the western polygon was 120 m x 82.5 m x 81 m x 95.9 m (area: 0.909 ha). The western polygon was marked off during thick fog which explains the irregularities of its dimensions.

The polygons were visited approximately every three days from the time that eggs were first observed until the last egg hatched. During each visit new nests were marked with numbered stakes, and the number of eggs and chicks was recorded. Some eggs may have been laid and disappeared during the period between visits so the number of nests and eggs may be underestimated. From this we calculated the number of active nests (nests with at least one egg), nest density, mean clutch size, fate of eggs (hatched, dead/addled, or missing),

number of successful nests (nests that hatched at least one egg), hatching success (number of eggs hatched divided by the number of eggs laid), number of eggs hatched per nest, and mean and median nest hatching dates. We estimated date of hatching by assuming that it takes an egg three days to hatch once starting begins (small cracks but no hole) and one day after pipping begins (hole in shell). To minimise disturbance, visits to each polygon rarely exceeded 15 minutes.

**Researcher disturbance** In 1996, three additional polygons were set up to determine the effect of researcher disturbance; low, moderate, and high disturbance polygons (Figure 1). The high and low disturbance polygons were 75 m x 75 m (area: 0.562 ha). The boundaries of the moderate disturbance polygon were irregular and were not measured.

The low disturbance polygon was visited once during the incubation period and every three days after the median date of hatching to determine hatching success. This allowed us to collect nesting information with a minimum number of visits. The moderate disturbance polygon was visited approximately every three days starting when the first eggs were laid, which was similar to the number of visits to the nesting polygons, and the high disturbance polygon was visited approximately every two days from the time the first eggs were laid (Table 1). The same nesting parameters were measured in the three disturbance polygons as were measured in the nesting polygons.

**Clutch removal** Also in 1996, two study polygons (75 m x 75 m, area: 0.562 ha) were set up to explore the ability of Herring Gulls on Île Nue to replace lost clutches (Figure 1). On 8 June, approximately four weeks before the mean hatching date, 15 Herring Gull nests with 3-egg clutches were selected within the study polygons. This date coincided with the period in 1995 when most of the eggs disappeared, i.e. 6-14 June. A mixture of Malachite Green (18.75 g), petroleum jelly (250 g), and isopropyl alcohol (25 g) was applied to the top of the eggs in each clutch to mark the breasts of the incubating adults (Belant & Seamans 1993). This mixture was sufficient for the dye to last until the gulls re-nested, i.e. approximately 13 days. After at least one adult from each nest was marked by the dye, the eggs were removed from the nest. The length and width of each egg were measured to the nearest 0.1 mm with Vernier callipers, and volume was calculated using the formula,  $\text{volume} = \text{length} \times \text{width}^2 \times 0.476$  (Harris 1964).

We visited each polygon approximately every three days to look for replacement clutches. Herring Gulls often line their nests with breast feathers and we were able to identify replacement nests by locating green feathers. Herring Gulls tend to lay replacement clutches on their original territories

Table 1. Parameters describing nesting of Herring Gulls on Île Nue in the nesting polygons, 1994-96. Percentages are given in brackets. Parameters with similar letters are not significantly different (notation is only shown if there were significant differences;  $P < 0.05$ ).

Tabel 1. Broedresultaten van Zilvermeeuwen op Île Nue in de studieplots, 1994-96. Tussen haakjes zijn percentages weergegeven. Met een (overeenkomstige) letter aangeduide uitkomsten zijn niet significant verschillend.

Parameters	Year			Overall
	1994 <sup>1</sup>	1995	1996	
Active nests ( <i>n</i> )	100	73	83	256
Successful nests ( <i>n</i> )	82 (86.3)	12 (16.4)	69 (83.1)	163 (63.7)
Nest density (nests ha <sup>-1</sup> )	75	55	62	64
Eggs laid ( <i>n</i> )	204	135	178	517
Fate of eggs				
Hatched	157 (81.3)	19 (14.1)	140 (78.5)	316 (62.5)
Missing	33 (17.1)	115 (85.2)	32 (18.0)	180 (35.5)
Dead	3 (1.6)	1 (0.7)	6 (3.4)	10 (2.0)
Eggs hatched nest <sup>-1</sup>	1.65	0.26	1.69	1.26
Average clutch size	2.04	1.85	2.14	2.02
Date first nest hatched	20 June	21 June	20 June	-
Median hatching date	29 June	28 June	4 July	-
Mean hatching date	30 June <sup>a</sup>	28 June <sup>a</sup>	6 July <sup>b</sup>	-

<sup>1</sup>Unable to relocate 5 nests (total 11 eggs)

(Parsons 1976). We were confident determining which pair laid each replacement clutch because none of the pairs that we followed had territories bordering each other. When a new nest with green feathers was found, we measured distance to the original nest with a 25 m tape measure, and calculated the volume of each egg. We continued to follow replacement nests every three days to determine hatching date, which allowed us to estimate laying date (calculated by subtracting 30 days - the length of the incubation period - from the day the first egg hatched), length of refractory period (time between the removal of the original clutch and the initiation of the replacement clutch), mean clutch size and hatching success.

Wilcoxon signed ranks test was used to compare clutch size and paired *t*-tests were used to compare total clutch volume, egg volume, volume of the largest egg, and volume of the smallest egg for original and replacement clutches. Likelihood ratio chi squares ( $G^2$ ), comparing observed and expected frequencies were used to compare clutch size and hatching success in the nesting and disturbance polygons. The two nesting polygons were pooled before analysis as spatial differences were very small and our intention was mostly to look at temporal variation of breeding parameters. ANOVAs were used to

compare hatch dates (Zar 1984). Data were tested for normality and the level of significance was set at  $P < 0.05$  for all tests. Means are given  $\pm 1$  SD. SYSTAT was used for all statistical analyses (SYSTAT Inc. 1992).

## RESULTS

**Nesting ecology, 1994-1996** The overall mean clutch size in the two nesting polygons, 1994-1996, was 2.02 (Table 1). There was no significant difference in the frequency of 1-, 2-, and 3-egg clutches between years ( $G_4^2 = 7.378$ ,  $P = 0.117$ ). The mean hatching date for all nests, 1994-1996, was 2 July. Mean hatching date was significantly later in 1996 than either 1995 or 1994 ( $F_2 = 13.19$ ,  $P < 0.0001$ ; Table 1).

The number of successful nests differed between years ( $G_2^2 = 100.66$ ,  $P < 0.0001$ ). In 1994 and 1996 over 80% of nests were successful, whereas in 1995 less than 20% of nests were successful. Hatching success of eggs was also low in 1995. Most eggs in 1995 went missing; only one dead/addled egg was found (Table 1).

**Researcher disturbance** In 1996, mean clutch size in the nesting, and low, moderate, and high disturbance polygons was 2.20 eggs per nest. The frequency of 1-, 2-, and 3-egg clutches did not differ significantly between polygons ( $G_8^2 = 6.54$ ,  $P = 0.365$ ). The number of successful nests was high in all polygons, and hatching success was highest in the high disturbance polygon (Table 2). Mean hatching date in the nesting polygons was later than in the low, moderate, and high disturbance polygons ( $F_3 = 8.97$ ,  $P < 0.0001$ ; Table 2).

**Clutch removal** Fourteen pairs out of 15 laid replacement clutches, each on its original territory. In all cases it was possible to identify replacement nests by identifying green feathers in the nest bowls. It is possible but unlikely that a fifteenth pair laid a replacement clutch somewhere other than on its original territory and was thus not detected. Average clutch size for the 14 pairs was  $2.71 \pm 0.47$  (Table 3).

Replacement clutches had significantly fewer eggs than original clutches ( $Z = -2.12$ ,  $P = 0.034$ ). However, total volume of the 10 replacement clutches with three eggs and the volume of their original clutches did not differ significantly ( $t_9 = -1.7$ ,  $P = 0.12$ ). There were no significant differences in mean egg volume between original and replacement clutches ( $t_{13} = 1.155$ ,  $P = 0.269$ ), although the largest egg in each of the 14 replacement clutches was significantly smaller than the largest egg in their original clutches ( $t_{13} = -3.5$ ,  $P = 0.0038$ ). There was no significant difference between the smallest eggs ( $t_{13} = 0.24$ ,  $P = 0.81$ ) (Table 3).

Table 2. Parameters describing nesting of Herring Gulls in the nesting, low disturbance, moderate disturbance, and high disturbance polygons on Île Nue in 1996. Percentages are given in brackets. Parameters with similar letters are not significantly different (notation is only shown if there were significant differences;  $p < 0.05$ ).

Tabel 2. Broedresultaten van Zilvermeeuwen in studieplots met geringe, matige en zware verstoringen door onderzoekers op Île Nue in de studieplots, 1996. Percentages zijn tussen haakjes weergegeven. Met een (overeenkomstige) letter aangeduide uitkomsten verschillen niet significant.

Parameters	Polygon			
	Nesting <sup>1</sup>	Low disturbance	Moderate disturbance	High disturbance
Visits ( <i>n</i> )	12,13	6	13	16
Visits before mean hatching	4,6	1	7	8
Date of first visit	6,7 June	14 June	7 June	11 June
Active nests ( <i>n</i> )	83	43	54	44
Successful nests ( <i>n</i> )	73 (88.0)	43 (100.0)	49 (90.1)	43 (97.7)
Nest density (nests ha <sup>-1</sup> )	62	76	-	78
Number of eggs laid	178	101	125	99
Fate of eggs				
Hatched	140 (78.5)	92 (91.1)	107 (85.6)	92 (92.9)
Missing	32 (18.0)	2 (2.0)	8 (6.4)	0 (0.0)
Dead	6 (3.4)	7 (6.9)	10 (8.0)	7 (7.1)
Eggs hatched per nest	1.92	2.14	1.98	2.09
Average clutch size	2.14	2.35	2.31	2.20
Date first nest hatched	20 June	26 June	17 June	14 June
Median hatching date	4 July	27 June	1 July	3 July
Mean hatching date	6 July <sup>a</sup>	29 June <sup>b</sup>	30 June <sup>b</sup>	2 July <sup>b</sup>

<sup>1</sup> Two polygons were pooled together and collectively called the nesting polygons. In cases where there are two numbers in the same cell, the first number is from the eastern polygon and the second is from the western polygon (see Methods).

The mean distance between the location of the original nests and replacement nests was  $4.48 \pm 2.58$  m ( $n = 13$ ) and the mean refractory period was  $13.15 \pm 2.48$  days ( $n = 13$ ). One replacement nest disappeared before the distance between it and the original nest was measured.

Hatching success of replacement clutches was 74% which was similar to hatching success in the two nesting polygons (Table 1); all of the eggs hatched in 10 nests; the eggs in two 3-egg clutches did not hatch; a single egg did not hatch in another 3-egg clutch; and one 3-egg clutch disappeared.

*Table 3. Mean egg volume, clutch size, hatching date, and hatching success of original clutches and replacement clutches of 15 pairs of Herring Gulls included in a clutch removal experiment on Île Nue in 1996.*

*Tabel 3. Gemiddeld eivolume, legselgrootte, uitkomstdatum en uitkomstpercentage van eerste legsels en vervangende legsels bij 15 paren Zilvermeeuwen in het verwijderingsexperiment op Île Nue in 1996.*

Parameter	Clutch removal polygons	
	Original nests	Replacement nests
Volume of all eggs (ml)	78.39	76.12
Volume of largest eggs (ml)*	83.32	78.56
Volume of smallest eggs (ml)	73.24	73.87
Clutch size†	3	2.71
Hatching success (%)	Eggs removed	73.68
Hatching date	Eggs removed	21 July

\* The volume of the largest egg in original nests was significantly larger than the largest egg in replacement nests (paired t-test:  $t_{13} = -3.5$ ,  $P = 0.0038$ ).

† Clutch size of original nests was significantly larger than clutch size of replacement nests (paired t-test:  $t_{14} = 2.2$ ,  $P = 0.048$ ).

#### DISCUSSION

Mean hatch date was later and mean clutch size was lower on Île Nue, 1994-1996, than in other Herring Gull colonies in the Gulf of St. Lawrence. Mean hatching dates for Herring Gulls on Île Nue ranged from 28 June - 6 July, which is 2-3 weeks later than other colonies in the Gulf of St. Lawrence. The peak of hatching was 11-12 June in western Newfoundland (Howes & Montevecchi 1993), and the mean hatching date on the Gaspé Peninsula, Quebec, was 10 June (Guillemette 1994). In North America, *Larus* gulls tend to breed later at higher latitudes (see Ryder 1993, Pierotti & Annett 1995, Winkler 1996), and Île Nue is further north than other colonies studied in the Gulf of St. Lawrence. Furthermore, Herring Gulls on Île Nue rely on capelin during the breeding season (Boyne 1999), and capelin typically migrate inshore to spawn later along the North Shore of the Gulf of St. Lawrence than along the Gaspé Peninsula (Grégoire 1996) and Newfoundland (Carscadden 1982), possibly resulting in later clutch initiation on Île Nue. To maximise breeding success, seabirds synchronise the timing of nesting so that the hatching of young coincides with the period of greatest food availability (Lack 1968).

The average clutch size on Île Nue was never greater than 2.35 eggs per nest in any of the study polygons, and over the three breeding seasons the average clutch size in the two nesting polygons was only 2.02 eggs per nest. Mean clutch size at other colonies in the Gulf of St. Lawrence has been more than 20% higher: 2.55 - 2.76 in Kouchibouguac National Park, New Brunswick

(Martin & LaPierre 1986, Martin 1987); and 2.6 on the Gaspé Peninsula, Quebec (Guillemette 1994). Clutch sizes also tend to be higher in other colonies in eastern Canada and western Europe:  $2.8 \pm 0.4$ , in the Dutch Frisian Islands, the Netherlands (Bukacinska *et al.* 1996); 2.79 - 2.90 in Brittany, France (Pons & Migot 1995); 2.71 in Wales (Hiom *et al.* 1991);  $2.94 \pm 0.23$  in Georgian Bay, Ontario (Chudzik *et al.* 1994); and 2.52 - 2.77 on Boot Island, Nova Scotia (Macfarlane 1996). However, the mean clutch size at a Herring Gull colony thought to be food-stressed on Great Island, Newfoundland, was only 1.82 - 2.14 (Rodway & Regehr 1999), which is very similar to the mean clutch size observed on Île Nue. Food stress during the pre-laying period is known to cause low clutch sizes in Herring Gulls (Hiom *et al.* 1991).

The most striking difference among the three years of the study, was the low hatching success in 1995. In 1995 we were off the island during the period when the majority of eggs disappeared. We only found one unhatched egg so the fate of the majority of eggs was unknown. Robert & Ralph (1975) found that human disturbance affected hatching success in large gulls, however, the methodology in our study was similar in all three years and thus can not explain the low hatching success in 1995. In addition, hatching success in 1996 was highest in the high disturbance polygon, supporting the speculation that factors other than researcher disturbance affected hatching success. Researcher disturbance could not explain low clutch size either as there were no differences in mean clutch sizes among the five disturbance polygons.

As an indirect method of evaluating food availability we examined the ability of Herring Gulls to lay replacement clutches. In 1995, the majority of eggs laid in the nesting polygons disappeared during a short time period and no replacement clutches were observed. We hypothesised that the gulls could not lay replacement clutches in 1995 because food was limiting. This was not the case in 1996, as 14 of 15 pairs in the removal experiment laid replacement clutches after a refractory period of about 13 days. This time interval was similar to another study of Herring Gulls (Parsons 1976). Replacement clutches usually contain fewer and/or smaller eggs than first clutches (Paludan 1951; Parsons 1976), although in 1996, the clutch volume of 3-egg replacement clutches did not differ significantly from the volume of original clutches, and the mean clutch size of replacement clutches was higher than the mean clutch size in the nesting polygons. This result is puzzling and we underline two factors that probably led to favourable conditions for renesting: (1) we removed clutches from early layers, which tend to be older, more experienced birds (e.g. Reid 1988, Pyle *et al.* 1991), and we only removed 3-egg clutches which is an indication of parental quality (e.g. Pyle *et al.* 1991); and (2) food availability likely increased for at least the last few days of the refractory period; the period when females would have been acquiring the necessary body reserves to

produce a second clutch. Herring Gulls switched to feed mainly on capelin, an important food source for gulls in the Gulf of St. Lawrence (Boyne 1999; Cairns *et al.* 1991), around 18 June, likely in response to the pre-spawning migration of capelin to inshore waters (Boyne 1999). The arrival of capelin inshore would have increased food availability and quality because they migrate in large shoals and are of high nutritional value (Pierotti & Annett 1987).

Other potential factors affecting reproductive success on Île Nue include eggging, predation, and conspecific competition. Historically, eggging was a common practice on the North Shore of the Gulf of St. Lawrence (Blanchard 1994), but this practice has all but disappeared since the creation of the National Park Reserve. Moreover, it is difficult to believe that eggs were taken from both polygons since they were ca. 0.5 km apart and separated by a plateau. Mammalian predators can not explain the egg loss as only muskrats and small rodents are present on the island, however it is not possible to rule out avian predators although few, if any, avian predators are capable of removing such a large number of eggs from a gull colony. Mean nest density on Île Nue was low (ca. 64 nests/ ha), so competition for nesting territories or other density-dependant factors also can not explain low reproductive success.

Researcher disturbance, competition for nest sites, and eggging, cannot explain the low hatching success in 1995 or the low clutch sizes observed throughout the study. Although it is not possible to demonstrate that food is limiting the reproductive success of Herring Gulls on Île Nue, food-stress is known to cause low clutch sizes (Hiom *et al.* 1991), and increase predation on eggs of conspecifics (Parsons 1971; Robert & Ralph 1975). Although food-stress during the laying period did not prevent replacement clutches in 1996, the majority of chicks that were followed that year as part of another study, died of starvation (Boyne 1999). Years of poor capelin abundance along the North Shore, causing high Herring Gull chick mortality, have been noted in the past (Lewis 1934). The timing of capelin spawning in a given year may dictate at which stage of the breeding season food is limiting. Recently, cold surface water temperatures in the early 1990s delayed and even deterred capelin from spawning in eastern Newfoundland, causing breeding failure in Black-legged Kittiwakes and low reproductive success in Herring Gulls (Rodway & Regher 1999; Regher & Montevecchi 1997).

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ONGEWOON GERING BROEDSUCCES ONDER ZILVERMEEUWEN NESTELEND AAN DE  
NOORDKUST VAN DE GOLF VAN ST LAWRENCE, QUEBEC, CANADA

*Zilvermeeuwen* *Larus argentatus* behoren tot de talrijkste zeevogelsoorten in het Mingan Archipelago National Park Reserve (MANPR). Het aantal 'actieve' nesten, de nestdichtheid, legselgrootte, uitkomst- en uivliagsucces en de gemiddelde en mediane uitkomstdata werden onderzocht in twee studiegebieden op Île Nue, een eiland in MANPR, 1994-1996. In ieder jaar was de legselgrootte kleiner en de gemiddelde uitkomstdatum later dan karakteristiek voor de Zilvermeeuw. Het uitkomstsucces was extreem laag in 1995. Om uit te vinden wat er aan de hand was werden enkele experimenten opgezet, waarbij studieplots met verschillende gradaties van verstoring werden geconfronteerd terwijl elders een aantal legfels werd verwijderd om te bezien of de meeuwen gezien de beschikbare hoeveelheden voedsel in het gebied fysiek in staat waren om nieuwe legfels te produceren. Kleine legfels en een gering uitkomstsucces konden niet worden verklaard door de verstoring van onderzoekers. Predatie of competitie om nestgelegenheid waren vermoedelijk de factoren verantwoordelijk voor het geringe broedsucces.

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## ADOPTION IN THE COMMON GUILLEMOT *URIA AALGE*

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*Wilson L.J. & Birkhead T.R. 2001. Adoption in the Common Guillemot *Uria aalge*. *Atlantic Seabirds* 3(3): 137-140: On Skomer Island, Pembrokeshire, a pair of Common Guillemots *Uria aalge* with a newly hatched chick, was observed to adopt a second chick of the same age, which had been displaced from its natal site. Both chicks were successfully reared to fledging age. This is the second report of adoption for the Common Guillemot.*

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Guillemots *Uria* spp. breed in dense colonies on sea-cliffs and incubate their single egg on the cliff ledge, without construction of a nest. Birds often breed shoulder to shoulder, and this close proximity of breeding sites creates selection pressure for the development of parent-offspring recognition abilities. Parent-chick recognition is well developed in the Common Guillemot *Uria aalge*, and adults can recognize their chick's call even before the chick has emerged from the egg (Tschanz 1968).

Guillemot chicks are rarely left alone by their parents as they are vulnerable to chilling and are dependent on adults for the provision of warmth, food and protection from predators. However, adults occasionally desert their chicks temporarily during periods of food shortage or colony disturbance (Gaston & Nettleship 1981; Birkhead & Nettleship 1984). In addition, the close proximity of nest sites leads to the possibility that unattended chicks will intermingle with other chicks or accidentally fall to ledges below. When chicks are abandoned or displaced from their natal site, they usually seek shelter from adult strangers (Birkhead & Nettleship 1984). Alloparental care is unusual in seabirds and most species ignore each other's offspring or are aggressive towards them. The response of adult Common Guillemots to foreign chicks varies and has been found to depend on their own status. Birds brooding their own chick usually ignore or attack foreign chicks, while failed breeders, or birds whose own chicks have fledged, usually brood foreign chicks (Birkhead & Nettleship 1984).

Alloparental care, such as brooding another pair's chick, is not uncommon in guillemots. Birkhead & Nettleship (1984) found that 8% of Common Guillemot chicks that fledged successfully from a colony in Labrador

received some alloparental care. Common Guillemots have also been observed sheltering other pairs' chicks that had been temporarily deserted by their parents during a period of food shortage (Tschanz 1959, 1979; Birkhead & Nettleship 1984) and during colony disturbance (Tuck 1961). Wanless & Harris (1985) observed a chick being jointly raised (brooded and fed) by two pairs on two occasions.

Gaston *et al.* (1995) were the first to report the complete fostering (rather than temporary alloparental care or joint raising) of chicks in guillemots. They described four cases of adoption in Brunnich's Guillemots (*U. lomvia*): two pairs adopted and reared a chick to fledging age after they had lost their own egg, and two pairs adopted and reared a foreign chick in addition to their own chick. The first case of chick adoption in the Common Guillemot was recently reported by Harris *et al.* (2000). Here, we describe a further case of adoption in the Common Guillemot, which covered the entire period from hatching to fledging. Observations were made at Skomer Island, Pembrokeshire, Wales in 2000, where the colony was visited daily during the breeding season to monitor breeding success. Our observations were made using a 20-45x Nikon telescope and caused no disturbance to the breeding birds.

On 11 June at site A, an egg that had been incubated for 32 days was due to hatch, but was not present on 12 June. There were some eggshell remains on the ledge, indicating that the egg had hatched, but no chick was seen on the ledge. At site B, approximately 1.5m directly below site A, the resident pair's egg had been incubated for 31 days by 11 June, and was also due to hatch. Two newly hatched chicks were observed on this site on 12 June. We concluded that the chick at site A had hatched and fallen to site B, where the resident pair's chick had also just hatched. Both pairs involved were unmarked and were the sole occupiers of their ledge and daily monitoring of all other neighbouring sites indicated that no other individuals were involved. It is not unusual to observe young chicks falling from their natal site to ledges below and parents have been observed actively searching for lost chicks (Tschanz 1959; pers. obs.). Pair A were observed to show some searching behaviour, primarily directed to site B, which was within hearing range of the chick's call, but no attempt to retrieve the chick was observed and no interactions between the two pairs were observed.

The pair at site B brooded both chicks, and although no feeds were observed, the growth in size of both chicks clearly indicated that they were both being fed. No aggressive interactions between the two chicks were observed. It is not known if pair A was involved in brooding/feeding, but at least one member of pair A was present on its original site on most occasions. Both chicks reached fledging age but neither chick was seen departing from the colony. One chick had gone by 4 July and the other had gone by 8 July. Between 4 and 8 July, only one of the adults was ever seen at the site but it is unknown if

this was the male or female or if both parents visited the site. Even if both chicks departed successfully, their fledging strategy makes it unlikely that both survived. Guillemot chicks are semi-precocial, fledging at one quarter of adult body mass (Gaston & Jones 1998), and need to be accompanied by the male who continues to feed the chick at sea for up to a month (Varoujean *et al.* 1979; Scott 1990).

Our observations support existing evidence of alloparental care in guillemots. Adoption is an extreme case of alloparental care and we believe this report to be only the second to describe a case of adoption in the Common Guillemot. Previously, one case has been reported in the literature for the Common Guillemot (Harris *et al.* 2000) and four cases have been reported for the closely related Brunnich's Guillemot (Gaston *et al.* 1995). This evidence, although limited, indicates that guillemots are capable of adopting and rearing foreign chicks under natural conditions.

Gaston *et al.* (1995) suggested that chick age at adoption might be a factor in their acceptance, as all of the chicks in their study were less than 10 days old. In the case reported by Harris *et al.* (2000), the biological chick was 2 days old and the adopted chick was 8 days old at the time of adoption. In our case, both the biological and adopted chick involved were only 1 day old. Cross-fostering experiments with Brunnich's Guillemots show that the likelihood of adoption declines with the age of the chick. Chicks aged 1-5 days old had a 92% chance of being accepted by foster parents, but this declined to 36% at 6-13 days old (Lefevre *et al.* 1998). Lefevre *et al.* (1998) suggested that adult Brunnich's Guillemots probably learn their chick's call in the first few days after hatching and that it was possible that parents are unable to discriminate between their own chick and foreign chicks at a very early age. However, given the evidence of mutual recognition between parents and offspring in Common Guillemots demonstrated by Tschanz (1968), it seems unlikely that chick adoption in this species could occur due a pair being unable to recognize their own chick.

Gaston *et al.* (1995) considered that the four adoptions in Brunnich's Guillemots that they witnessed may not have been unusual and that adoption might in fact be a regular occurrence at that particular colony. However, with only two reports of adoption occurring in the Common Guillemot, it seems unlikely that this is a widespread behaviour. Certainly, any further information on its occurrence is likely to improve our understanding of this interesting phenomenon.

#### ADOPTIE BIJ DE ZEEKOET *URIA AALGE*

*Zeekoeten* *Uria aalge* broeden in dichtbezette kolonies op kliffen aan zee en bebroeden één enkel ei dat zo maar op de kale rotsen wordt gedeponeerd, zonder dat een nest wordt geconstrueerd.

*Zeekoetenouders en hun jongen zijn goed in staat om elkaar te herkennen en ouders kunnen nog voordat het kuiken uit het ei gekropen is het geluid van hun eigen jong onderscheiden van dat van de burens. Het is duidelijk dat de volle kolonies waarin Zeekoeten broeden om een dergelijk mechanisme vragen. Het enkele jong van een paar Zeekoeten wordt zeker kort na het uitkomen hoogst zelden door de ouders alleen gelaten, ter bescherming (tegen bijvoorbeeld meeuwen en Raven), maar ook ter voorkoming van afkoeling. Toch verlaten de ouders soms beiden het jong voor een korte periode en het komt dan nogal eens voor dat het kuiken tussen andere broedvogels en kuikens 'verdwaald' raakt, of dat een jong één of meer richels omlaag tuimelt. De op die manier feitelijk 'verweesde' kuikens zoeken instinctief bescherming bij andere adulte Zeekoeten. De reactie van die vogels wisselt en hangt in feite af van hun eigen status op de kolonie (broedvogel of bezoeker). Zeekoeten met een eigen kuiken of ei negeren zo'n verloren jong meestal of benaderen het agressief. Broedvogels waarvan het eigen jong de kolonie inmiddels heeft verlaten of waarvan het legsel verloren is gegaan bejegenen zo'n jong vaak wat vriendelijker en er zijn verschillende gevallen bekend van zeekoetenkuikens die door zo'n vreemde adulte vogel op zijn minst warm werd gehouden, maar in sommige gevallen ook werd gevoerd en tenslotte succesvol de kolonie kon verlaten. Ook komt het af en toe voor dat een individueel kuiken broedzorg en voedsel geniet van twee paren tegelijk, de eigen ouders en een stiefouderpaar. Volledige adoptie is echter zeldzaam, zowel bij de Zeekoet als bij de nauw verwante Dikbekzeekoet *Uria lomvia*. Harris et al. (2000) waren de eerste die zo'n geval voor de Zeekoet beschreven en in deze korte bijdrage wordt een tweede geval gedocumenteerd. Bij de Dikbekzeekoeten werden inmiddels vier gevallen gedocumenteerd en daarbij werd gesuggereerd dat adoptie misschien wel veel vaker voorkomt dan tot dusverre werd verondersteld. Dat er tot op heden slechts twee gevallen gevonden zijn bij de intensief bestudeerde Zeekoeten van de Britse Eilanden suggereert echter dat dit een zeldzaam verschijnsel is.*

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