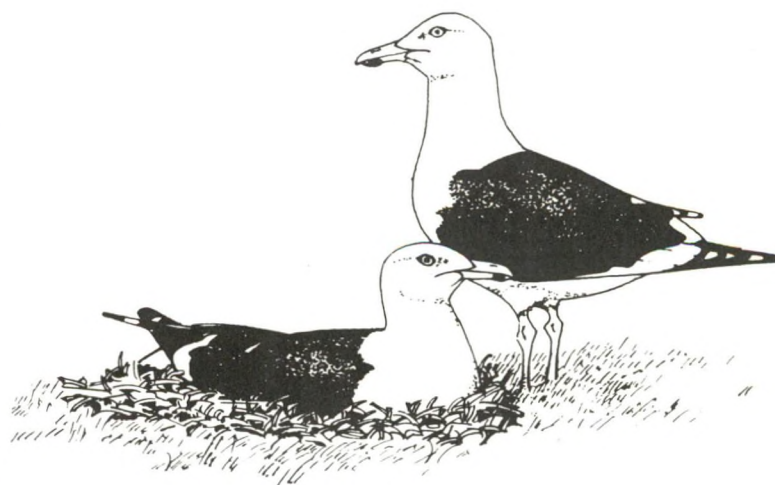


The relationship between food
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Black-backed Gulls *Larus fuscus*:
a pilot study

A.L. Spaans, M. Bukacińska, D. Bukaciński & N.D.van Swelm

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The relationship between food supply, reproductive parameters and population dynamics in Dutch Lesser Black-backed Gulls *Larus fuscus*: a pilot study

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PREFACE

In The Netherlands, over 100 species of birds breed in a narrow range along the coast, but only a few species can be indicated as seabirds, i.e. birds that obtain at least part of their food from the sea by travelling some distances over its surface. Of the eight gull species that presently breed in The Netherlands, the Lesser Black-backed Gull is the most marine species. Lesser Black-backed Gulls do not only feed on pelagic shoaling fish species but also rely to a great extent on fishery waste discarded by beamtrawlers. The species is therefore rather susceptible to changes in fishery practices.

In this pilot study, for eight colonies along the Dutch coast, data are presented of breeding parameters and diet. Furthermore, for one colony experimental evidence is given for the relationship between food supply, parental effort and chick survival.

By providing chicks with additional food in a colony where food was in short supply, it was shown that as a result of food shortages chicks not only die from starvation but also from an increased predation risk resulting from changes in the behaviour of both adults and chicks.

The comparative study was conducted (1) to assess the value of the parameters mentioned above and (2) to provide basic data on the breeding and feeding ecology of the species in view of future changes in local fishery activities.

Colonies differed in diet, egg sizes, chick growth and pre-fledging mass of chicks. Colonies in the northern Delta did worse throughout the breeding cycle, probably because they relied to a greater extent on terrestrial rather than marine food, in contrast to gulls in other colonies. For colonies where food is in very short supply during the chick stage, such as on Terschelling, recording chick masses is not sufficient to assess the local food situation, because in such a worse food situation only the strongest and most healthy chicks survive. It is therefore recommended to measure also the mean chick production per pair in monitoring programmes.

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1 INTRODUCTION

Many species of seabirds in the northern Atlantic region have increased dramatically in number during the present century (e.g. Fisher & Lockley 1954, Croxall *et al.* 1984). This population explosion has followed a numerical low at the end of the nineteenth and the beginning of the present century caused by large-scale eggging and extensive hunting practices at that time (e.g. Fisher & Lockley 1954, Croxall *et al.* 1984, Furness & Monaghan 1987). Recovery of numbers started almost immediately after conservation measures were taken, suggesting that human persecution was indeed determining population sizes prior to the numerical increase.

Fish and fish offal discarded by commercial fisheries form an important food supply for many species of seabirds and this supply has increased exponentially in the northern Atlantic region during the present century as a result of changing fishing practices (e.g. Hudson & Furness 1988, Furness *et al.* 1992, Camphuysen 1993). For many seabirds, present population levels are therefore probably higher than they would be without the large quantities of fishery waste that has become available for birds during the present century (e.g. Fisher & Lockley 1954, Croxall *et al.* 1984).

During the last few decades, however, the number of several species of seabirds stabilised or even decreased (reviewed in Croxall *et al.* 1984 and Brenninkmeijer & Stienen 1994). Food shortages, possibly through over-exploitation of local fish stocks, has often been mentioned as an important factor in this respect (e.g. Croxall *et al.* 1984, Croxall 1987, Furness & Monaghan 1987, Vader *et al.* 1990), although the causal relationship between fisheries effort and seabird population dynamics has never been proven (Bailey & Hislop 1978, Veen 1992).

Of the more than 100 bird species known to breed along the Dutch coast, only a minority obtain all or part of their food from the sea and only a few gull and tern species do so by travelling some distance over its surface. Population-wise the Sandwich Tern *Sterna sandvicensis* and the Lesser Black-backed Gull *L. fuscus* are most pronounced in this respect. Lesser Black-backed Gulls nesting on the Dutch coast do not only feed on pelagic shoaling species but also obtain a lot of food from commercial fishery vessels (The Netherlands: Noordhuis & Spaans 1992, this report, southern North Sea: Camphuysen 1993, 1994a, 1994b, in press). The species is therefore very susceptible to changes in fisheries activities (e.g. Croxall *et al.* 1984). For instance, population levels may go down when suggested plans to close inshore waters to beamtrawl fisheries off the coast of some of the Dutch Frisian Islands take effect (Bergman *et al.* 1991, Camphuysen 1994b).

During the last three-quarters of the twentieth century, gulls have been the subject of many ecological studies in The Netherlands, but until now relatively little attention has been paid to the Lesser Black-backed Gull. Exceptions are the food and population-dynamic studies conducted in the

mixed Lesser Black-backed and Herring Gull *Larus argentatus* colony near Wassenaar, north of The Hague, during the 1960s and 1980s, respectively (e.g. Croin Michielsen & Van der Meijden 1975, Wanders 1985, Bouman *et al.* 1991), a comparative study on the food ecology of Lesser Black-backed and Herring Gulls nesting on Terschelling in the 1980s (Noordhuis & Spaans 1992), a large-scale colour-ringing project in the Maasvlakte and Europoort colonies from 1990 onwards by N.D. van Swelm, and the recently started study on the feeding behaviour of Herring and Lesser Black-backed Gulls at sea by Camphuysen (1994a, 1994b, in press).

This report will try to fill some of the gaps still remaining. In Chapter 2, we will sketch the population development in The Netherlands during the present century. Chapter 3 describes egg sizes, adult condition at the end of the incubation period, chick growth and the diet of both adults and chicks for the main colonies along the Dutch coast. In Chapters 4 and 5, we present experimental evidence for the relationship between food supply, parental effort and chick survival in Lesser Black-backed Gulls nesting on Terschelling, where numbers stabilised in the early 1980s and reproductive output has been very low since the middle of the 1980s. In the general discussion (Chapter 6) we will compare the results of the two studies, and give recommendations for monitoring the impact of changes in fisheries activities and in the marine environment on Dutch Lesser Black-backed Gull numbers.

2 DISTRIBUTION AND POPULATION DYNAMICS OF THE LESSER BLACK-BACKED GULL IN THE NETHERLANDS DURING THE TWENTIETH CENTURY

Lesser Black-backed Gulls have nested along the Dutch coast since 1926, when three nests were found on Terschelling. During the following years the species also bred at four to five other colony sites along the coast, but in the late 1930s the total population still amounted to less than 20 pairs. In the late 1940s, there were at best 40-50 pairs and ten years later still less than 100 pairs, most of them on Terschelling. Since the middle of the 1960s, however, the population increased exponentially to approximately 9700 pairs in 1977, of which 8400 pairs nested on Terschelling (Teixeira 1979). This exponential increase in numbers of Lesser Black-backed Gulls was paralleled by a large increase in numbers of Herring Gulls and Common Gulls *L. canus* along the Dutch coast (Teixeira 1979), as well as a strong numerical increase in seabirds in the German coastal area (Vauk *et al.* 1989).

During the late 1970s and early 1980s, the population further increased to 20,000 pairs by the middle of the 1980s (Noordhuis & Spaans 1992). At that time, Lesser Black-backed Gulls had two main strongholds: Terschelling (maximum 13,500 pairs in 1984) and Wassenaar (maximum 2000 pairs in 1985-1987), with only a few small breeding colonies elsewhere along the coast (SOVON 1987, data Institute for Forestry and Nature Research).

Nevertheless, since the middle of the 1980s, the distribution of Lesser Black-backed Gulls has changed dramatically (Van Dijk 1992, 1993). The species has almost disappeared along the mainland coast after Red Foxes *Vulpes vulpes* became abundant in the dune area along this coast during the 1970s and 1980s (see Bouman *et al.* 1991 for a detailed description of the end of the colony in the dunes near Wassenaar, the largest Lesser Black-backed Gull colony along the mainland coast at that time). At present, Lesser Black-backed Gulls only nest in a few fenced-off spots in the dunes and on roofs of buildings in near-by towns, where the birds are safe from fox predation. The total number is, however, very low compared with the situation during the middle of the 1980s (Van Dijk 1993, Van Dijk *et al.* 1994).

Parallel to the numerical decrease along the mainland coast, the population of Lesser Black-backed Gulls has increased dramatically in numbers in the Wadden Sea and the Delta area (Van Dijk 1993). In 1992, almost 16,000 pairs of Lesser Black-backed Gulls nested in the Delta area, mainly on Schouwen and in the Maasvlakte and Europoort gulleries, while in that year the total Wadden Sea population was estimated at 18,000 pairs (erroneously given as 16,600 pairs in Dijkse 1993 and Van Dijk *et al.* 1994, SOVON pers. comm.). In 1993, the number of breeding pairs amounted to 19,000 in the Wadden Sea area (B.J. Koks pers. comm.) and between 11,000 and 15,000 pairs in the Delta area (Meininger *et al.* 1994, H.J.P.

Vercruysse pers. comm., N.D. van Swelm). The increase in the Wadden Sea area was most pronounced on Texel, Vlieland and Schiermonnikoog, with each having one thousand to a few thousands of breeding pairs at present. In contrast, numbers on Terschelling stabilised in the early 1980s and have remained at the established level since then. Nevertheless, Terschelling still has the largest Lesser Black-backed Gull colony in the country.

The opposite trends seen along the mainland coast and in the Delta and Wadden Sea area suggest that breeders moved actively from the mainland coast into the other areas during the late 1980s. For the Delta area, this is corroborated by several sightings of nesting colour-marked and metal-ringed Lesser Black-backed Gulls in the Maasvlakte and Europoort colonies during the early 1990s, that had bred in the Wassenaar dunes during the 1980s (R.M. Wanders pers. comm., N.D. van Swelm).

In 1992, the total Lesser Black-backed Gull population in The Netherlands amounted to over 34,000 breeding pairs (Van Dijk *et al.* 1994). A provisional reconstruction of the number of breeding pairs since 1926 is shown in Figure 1.

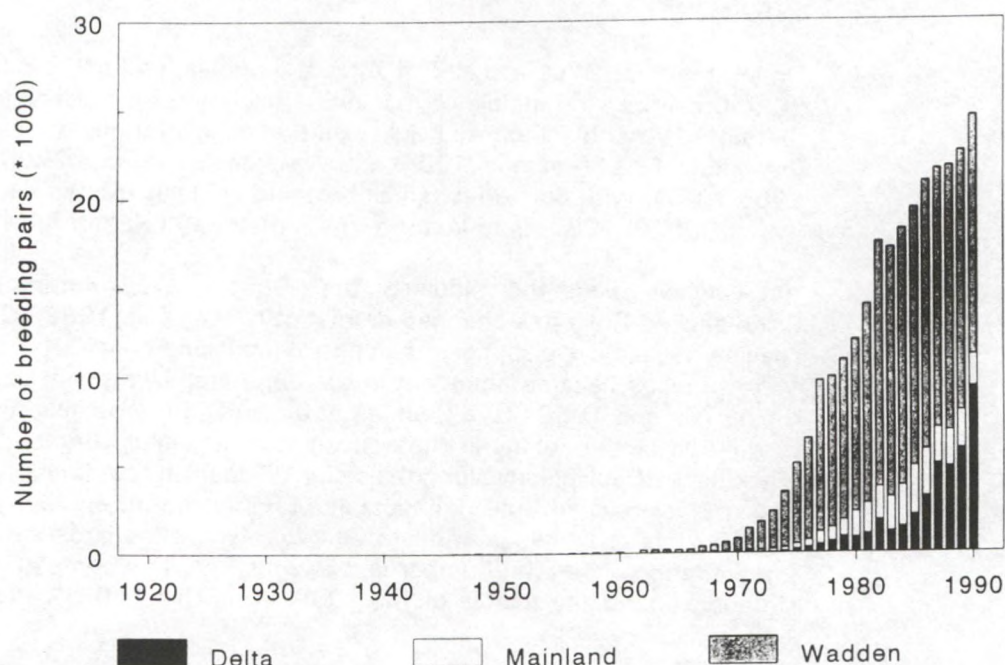


Figure 1. Provisional reconstruction of the number of breeding pairs of the Lesser Black-backed Gull in The Netherlands since 1926 (after Arts 1993).

Little is known about the reproductive output of the Lesser Black-backed Gulls in The Netherlands. In most colonies, it is characterised as good and rather good (Vlieland: H. Horn pers. comm., Texel: C.J. Camphuysen pers. comm., IJmuiden: F. Cottaar and C. Verbeek pers. comm., Maasvlakte and Europoort: N.D. van Swelm, Schouwen: H.J.P. Vercruysse pers. comm.). On

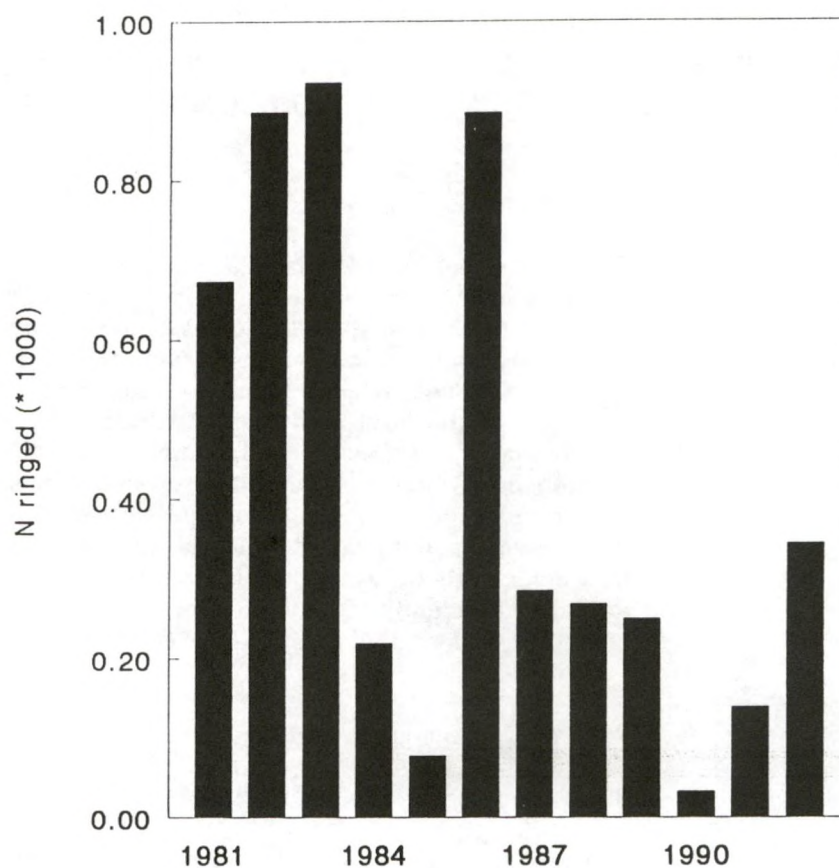


Figure 2. Number of Lesser Black-backed Gull chicks ringed during more or less standardised ringing activities on Terschelling since 1981 by the State Forestry Service, Terschelling (data H. Horn).

Terschelling, however, breeding success collapsed in the middle of the 1980s, and has remained very low since that time (Figure 2, State Forestry Service, Terschelling, A.L. Spaans), with the exception of 1986, a year in which small clupeids were rather abundant off the coast of Terschelling (Noordhuis & Spaans 1992). The data suggest that at present Lesser Black-backed Gulls nesting on Terschelling regularly suffer from food shortages.

3 COMPARATIVE STUDY OF BREEDING AND FEEDING BIOLOGY AT EIGHT COLONY SITES SCATTERED ALONG THE DUTCH COAST

3.1 Introduction

Since the late 1980s, Lesser Black-backed Gulls have only nested in large numbers in the Wadden Sea and Delta area, with small numbers nesting in-between (Chapter 2). All colonies in these areas but one have shown a progressive increase in numbers during the last 5-10 years, the exception being Terschelling, where numbers stabilised in the early 1980s and have remained at the level of the early 1980s since then. The present wide distribution of the species as a breeding bird along the Dutch coast and the differences in population growth between colonies, offer a unique opportunity to study geographical differences in diet and breeding parameters of the species, and to investigate the species' relationship to commercial trawlers off that coast. In this chapter, we will present data on egg measurements and the condition and diet of adults and chicks from eight colony sites along the coast from 1992 to 1993.

3.2 Study area and methods

3.2.1 Study area

In 1992 and 1993, we collected data on breeding parameters and food (1992 only) at eight colony sites (1992 seven sites) scattered along the Dutch coast (Figure 3). Three colonies were situated in the Delta area (Schouwen, Maasvlakte, Europoort), one on the mainland coast (IJmuiden) and four in the Wadden Sea area (Texel, Vlieland, Terschelling, Schiermonnikoog, the last one only in 1993).

The colony on Schouwen is situated in the dune area northwest of the village of Burgh-Haamstede, which is managed as a nature reserve by the State Forestry Service; whilst the colony sites at the Maasvlakte and Europoort cover industrial areas of the Port of Rotterdam harbour. The IJmuiden colony is located on the roof of a building near the harbour of that town. The four Wadden Sea colony sites are situated in dune areas (Texel through Terschelling) and in a saltmarsh (Schiermonnikoog). All four colony sites are managed as a nature reserve by either the State Forestry Service (Texel through Terschelling) or the Dutch Nature Conservation Society ('Vereniging Natuurmonumenten').

3.2.2 Data collection

Egg measurements Just before the first eggs would hatch in each colony, maximum egg length and egg width were measured to the nearest 0.1 or 0.05 mm, depending on the vernier callipers used, for

clutches of three eggs. Egg volume (V in cm^3) was calculated, using the formula: $V = 0.476 * \text{length} * \text{width}^2$ (Harris 1964).

Lesser Black-backed Gulls normally lay three eggs (according to their laying order in general indicated as the a-, b- and c-egg, respectively). By providing Lesser Black-backed Gulls with additional food during egg formation in an area where food was in short supply, Bolton (1991) showed that in a poor situation the ratio of the volume of the c- and a-egg is significantly smaller than normal.



Figure 3. Location of colony sites sampled in 1992-1993.

For most clutches we measured, we do not know in which sequence the eggs were laid. On average, the c-egg is the smallest of the three and the a- or b-egg the largest, with no significant size differences between these two eggs (Bolton 1991, own data). It seems therefore justified to use the ratio of the volume of the smallest and largest egg within a clutch as an index of the local food situation during the period of egg formation.

Condition of adults At four colony sites (1992: Maasvlakte- Europoort and Terschelling, 1993: Vlieland and Terschelling), we trapped adult Lesser Black-backed Gulls, using walk-in traps placed over the nest (Bub 1974) when at least one of the eggs was pipping, to obtain an estimate of the condition of breeding birds at the end of the incubation period. As a measure for condition we used the ratio of the cubic root of the body mass (g) and the maximum length of the wing chord (mm) of the bird. Birds were sexed on the basis of head-bill length, bill depth and body mass.

Chick growth and body mass of chicks before fledging Each year during the chick period, each colony was visited once or twice (Maasvlakte and Europoort in 1992 only, Schiermonnikoog in 1993 only, IJmuiden regularly) during one or more days to weigh as many chicks with feathered wings as possible to the nearest 1.0 g, using a Pesola spring balance, and to measure their wing length to the nearest 0.5 mm, using a ruler.

Based on masses and wing lengths of chicks of known age, we found that (1) the sigmoid growth curve of Lesser Black-backed Gull chicks levels off when the chick has a wing length of about 260 mm, corresponding with an age of approximately 30 days and (2) the curve approaches a straight line before that age (Terschelling: Bekhuis 1994, Weijers 1994, IJmuiden: F. Cottaar and C. Verbeek pers. comm., Maasvlakte and Europoort: N.D. van Swelm). Chicks of each colony were therefore divided into two groups (chicks with a wing length < 260 mm and those with a wing length > 260 mm, respectively). For each group of chicks with a wing length < 260 mm we calculated the daily mass increment (means $\pm$ SE) by means of linear regression. We preferred linear regression rather than logistic growth equations because growth curves of chicks of known age sometimes show large aberrations. In such cases, comparisons of logistic growth equations give poor results (Ricklefs 1968, Zach 1988). For each group of chicks with a wing length > 260 mm the arithmetical mean ($\pm$ SE) of the body mass was calculated.

Diet In 1992, at all study sites, pellets of adult Lesser Black-backed Gulls were collected within 0.75 m of nests of known identity and their contents analysed. We restricted the collection of pellets to an area of 0.75 m around nests to prevent the collection of pellets of Herring Gulls with which the Lesser Black-backed Gulls formed mixed colonies. Food boluses regurgitated that year by chicks during weighing and measuring were stored in 70% alcohol and sorted out and identified when the breeding season was over. Remains of most prey species were easily recognisable in pellets and regurgitations (Noordhuis 1987, Noordhuis & Spaans 1992).

Fish species were identified to the lowest feasible taxonomic level on the basis of otoliths (Schmidt 1968, Härkönen 1986) and characteristic bones (Noordhuis 1987). Moreover we also had a reference collection of identified otoliths and characteristic bones at our disposal for comparison. Otolith lengths and widths were converted into fish lengths (roundfish) and fish widths (flatfish, see Camphuysen 1994a) using the relationship between these parameters as established by the Netherlands Institute for Sea Research (NIOZ), Texel, for fish caught in the Wadden Sea area and surroundings.

3.2.3 Statistical analysis

Differences in egg measurements and condition of adults and chicks between colonies were analysed, using ANOVA and the Student's *t* test. Relationships between food types in pellets and regurgitations were tested using the Spearman rank correlation test (Siegel & Castellan 1988).

3.3 Results

3.3.1 Egg measurements

A summary of the egg measurements is shown in Table 1 and Figure 4. In 1992, individual egg sizes and total clutch volume were smallest at the three colony sites in the Delta area, with significant differences for total clutch volume between gulls nesting on Schouwen and those on Texel, Vlieland and Terschelling (Student's *t* test, $t = 2.06$, $P < 0.05$, $t = 3.33$, $P = 0.01$, $t = 2.94$, $P < 0.01$, respectively), between gulls nesting on the Maasvlakte and those on Vlieland (Student's *t* test, $t = 2.09$, $P < 0.05$), and between gulls nesting in Europoort and those in IJmuiden and on Texel, Vlieland and Terschelling (Student's *t* test, $t = 2.73$, $P = 0.01$, $t = 3.22$, $P < 0.01$, $t = 4.50$, $P < 0.001$, $t = 3.95$, $P < 0.001$, respectively).

In 1993, gulls nesting in Europoort had significantly smaller clutch volumes than those at any of the other colony sites (Student's *t* test, Schouwen: $t = 5.31$, $P < 0.001$, Maasvlakte: $t = 2.39$, $P < 0.05$, IJmuiden: $t = 4.99$, $P < 0.001$, Texel: $t = 6.16$, $P < 0.001$, Vlieland: $t = 5.94$, $P < 0.001$, Terschelling: $t = 4.94$, $P < 0.001$, Schiermonnikoog: $t = 2.22$, $P < 0.05$), while gulls nesting on the Maasvlakte had significantly smaller eggs than those on Schouwen, in IJmuiden, and on Texel, Vlieland and Terschelling ($t = 3.11$, $P < 0.01$, $t = 4.50$, $P < 0.001$, $t = 3.81$, $P < 0.001$, $t = 3.84$, $P < 0.001$, $t = 3.18$, $P < 0.01$, respectively). In contrast with the situation in 1992, the differences between the gulls nesting on Schouwen and those on the mainland and in the Wadden Sea area were not significant. Total clutch volume of gulls nesting on Schiermonnikoog was significantly smaller than of those nesting on Schouwen, in IJmuiden, on Texel, on Vlieland and on Terschelling (Student's *t* test, $t = 2.67$, $P < 0.01$, $t = 3.48$, $P = 0.001$, $t = 3.43$, $P = 0.001$, $t = 3.29$, $P = 0.001$, $t = 2.51$, $P < 0.05$).

Table 1. Measurements of eggs (means $\pm$ SD) in clutches of three eggs at eight colony sites along the Dutch coast in 1992 and 1993. N indicates number of clutches measured.

Colony, year	Length (mm)	Width (mm)	Volume (cm ³)	N
<i>Largest egg</i>				
Schouwen 1992	68.07 $\pm$ 2.7	47.63 $\pm$ 1.4	73.58 $\pm$ 5.4	100
Schouwen 1993	68.71 $\pm$ 2.5	47.65 $\pm$ 1.2	74.34 $\pm$ 4.8	100
Maasvlakte 1992	68.34 $\pm$ 2.5	47.89 $\pm$ 1.3	74.65 $\pm$ 4.7	30
Maasvlakte 1993	67.64 $\pm$ 2.4	47.51 $\pm$ 1.2	72.70 $\pm$ 4.1	49
Europoort 1992	67.58 $\pm$ 2.7	47.58 $\pm$ 1.3	72.90 $\pm$ 5.3	73
Europoort 1993	67.02 $\pm$ 2.9	46.80 $\pm$ 1.4	69.98 $\pm$ 5.5	42
IJmuiden 1992	69.30 $\pm$ 3.2	48.12 $\pm$ 1.7	76.54 $\pm$ 7.1	28
IJmuiden 1993	68.49 $\pm$ 2.6	48.63 $\pm$ 1.2	77.17 $\pm$ 5.3	17
Texel 1992	68.57 $\pm$ 3.0	47.92 $\pm$ 1.4	75.06 $\pm$ 6.0	131
Texel 1993	68.20 $\pm$ 2.6	47.98 $\pm$ 1.3	74.81 $\pm$ 5.3	162
Vlieland 1992	68.39 $\pm$ 2.8	48.23 $\pm$ 1.1	75.80 $\pm$ 5.2	89
Vlieland 1993	68.54 $\pm$ 2.3	47.91 $\pm$ 1.1	74.95 $\pm$ 4.8	93
Terschelling 1992	68.59 $\pm$ 2.7	48.04 $\pm$ 1.4	75.47 $\pm$ 6.0	101
Terschelling 1993	68.18 $\pm$ 3.1	47.89 $\pm$ 1.3	74.51 $\pm$ 5.6	100
Schiermonnikoog 1992	-	-	-	-
Schiermonnikoog 1993	67.07 $\pm$ 2.7	47.49 $\pm$ 1.6	72.13 $\pm$ 6.2	50
<i>Middle-sized egg</i>				
Schouwen 1992	66.84 $\pm$ 2.8	47.14 $\pm$ 1.3	70.77 $\pm$ 4.1	100
Schouwen 1993	67.60 $\pm$ 2.5	47.23 $\pm$ 1.2	71.86 $\pm$ 5.0	100
Maasvlakte 1992	67.32 $\pm$ 2.3	47.16 $\pm$ 1.6	71.36 $\pm$ 5.4	30
Maasvlakte 1993	66.46 $\pm$ 2.3	46.89 $\pm$ 1.2	69.62 $\pm$ 4.5	49
Europoort 1992	66.57 $\pm$ 2.8	46.99 $\pm$ 1.4	70.08 $\pm$ 5.8	73
Europoort 1993	65.61 $\pm$ 2.9	46.07 $\pm$ 1.4	66.43 $\pm$ 6.0	42
IJmuiden 1992	67.79 $\pm$ 3.8	47.69 $\pm$ 1.5	73.49 $\pm$ 6.6	28
IJmuiden 1993	68.07 $\pm$ 2.7	47.97 $\pm$ 1.2	74.64 $\pm$ 5.2	17
Texel 1992	67.44 $\pm$ 2.9	47.36 $\pm$ 1.4	72.10 $\pm$ 5.8	131
Texel 1993	67.07 $\pm$ 2.5	47.40 $\pm$ 1.3	71.82 $\pm$ 5.2	162
Vlieland 1992	67.49 $\pm$ 2.6	47.72 $\pm$ 1.2	73.23 $\pm$ 5.1	89
Vlieland 1993	67.37 $\pm$ 2.4	47.32 $\pm$ 1.2	71.89 $\pm$ 4.8	93
Terschelling 1992	67.71 $\pm$ 2.8	47.52 $\pm$ 1.4	72.80 $\pm$ 6.0	101
Terschelling 1993	67.39 $\pm$ 2.8	47.14 $\pm$ 1.3	71.38 $\pm$ 5.5	100
Schiermonnikoog 1992	-	-	-	-
Schiermonnikoog 1993	65.78 $\pm$ 2.6	46.99 $\pm$ 1.3	69.23 $\pm$ 5.4	50
<i>Smallest egg</i>				
Schouwen 1992	65.49 $\pm$ 2.7	45.99 $\pm$ 1.4	66.03 $\pm$ 5.4	100
Schouwen 1993	66.08 $\pm$ 2.4	46.04 $\pm$ 1.3	66.78 $\pm$ 5.1	100
Maasvlakte 1992	65.76 $\pm$ 2.4	45.62 $\pm$ 1.6	65.26 $\pm$ 5.5	30
Maasvlakte 1993	64.72 $\pm$ 2.3	45.37 $\pm$ 1.3	63.48 $\pm$ 4.5	49
Europoort 1992	64.87 $\pm$ 2.9	45.51 $\pm$ 1.8	64.06 $\pm$ 6.1	73
Europoort 1993	64.28 $\pm$ 2.7	45.02 $\pm$ 1.6	62.15 $\pm$ 5.9	42
IJmuiden 1992	66.91 $\pm$ 3.1	46.46 $\pm$ 2.3	69.03 $\pm$ 8.4	28
IJmuiden 1993	66.78 $\pm$ 3.4	46.86 $\pm$ 1.1	69.91 $\pm$ 5.8	17
Texel 1992	66.23 $\pm$ 2.8	46.29 $\pm$ 1.8	67.71 $\pm$ 6.7	131
Texel 1993	66.01 $\pm$ 2.5	46.39 $\pm$ 1.5	67.70 $\pm$ 5.0	162
Vlieland 1992	65.90 $\pm$ 2.7	46.67 $\pm$ 1.1	68.40 $\pm$ 4.8	89
Vlieland 1993	65.98 $\pm$ 2.2	46.36 $\pm$ 1.2	67.58 $\pm$ 4.6	93
Terschelling 1992	66.23 $\pm$ 2.8	46.69 $\pm$ 1.5	68.87 $\pm$ 6.2	101
Terschelling 1993	65.82 $\pm$ 2.9	46.26 $\pm$ 1.4	67.17 $\pm$ 5.7	100
Schiermonnikoog 1992	-	-	-	-
Schiermonnikoog 1993	64.61 $\pm$ 2.3	45.85 $\pm$ 1.5	64.78 $\pm$ 5.5	50

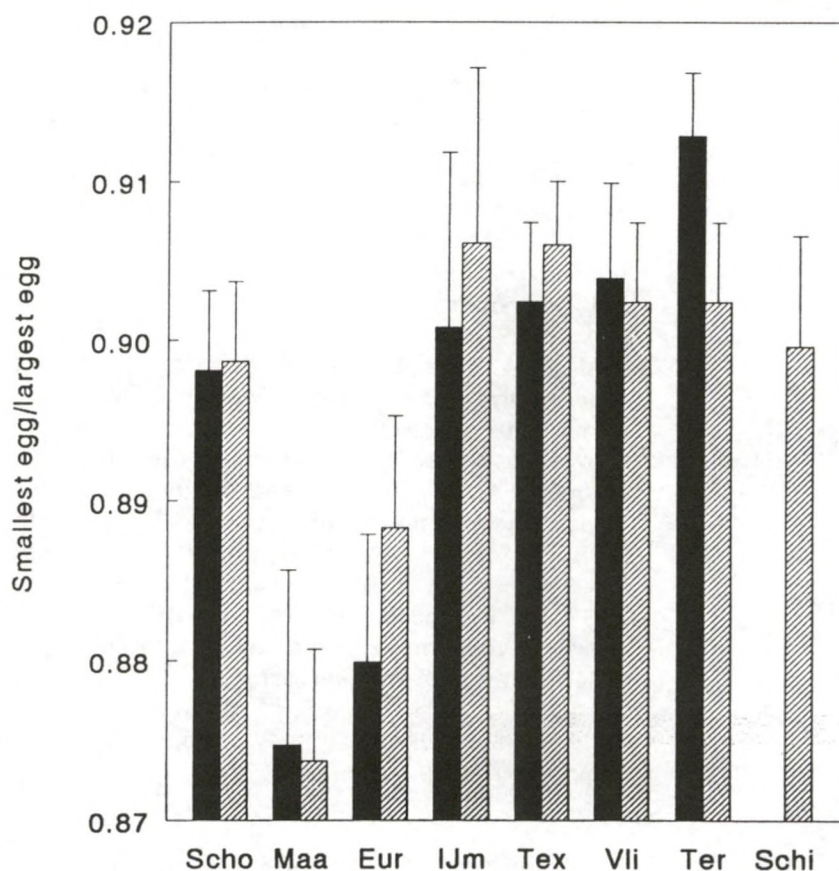


Figure 4. Average volume ($\pm$ SE) of the smallest egg as a proportion of that of the largest egg in the same clutch for eight colonies in 1992 (black bars) and 1993 (hatched bars). Scho = Schouwen, Maa = Maasvlakte, Eur = Europoort, IJm = IJmuiden, Tex = Texel, Vli = Vlieland, Ter = Terschelling, Schi = Schiermonnikoog (for numbers of clutches measured each year, see Table 1).

For none of the colonies studied in both years, was the difference in total clutch volume between the two years significant. The same held for individual egg sizes.

In both 1992 and 1993, the ratio of the volume of the smallest and largest egg within a clutch was smallest for Lesser Black-backed Gulls nesting on the Maasvlakte and in Europoort (1992: 0.875 and 0.880, respectively; 1993: 0.874 and 0.888, respectively). In 1992, there were significant differences between gulls nesting at these colony sites and those on Schouwen, Texel, Vlieland and Terschelling (Student's *t* test, Maasvlakte: $t = 2.25$, $P < 0.05$, $t = 2.41$, $P < 0.05$, $t = 2.58$, $P < 0.05$, $t = 3.86$, $P < 0.001$, Europoort: $t = 2.00$, $P < 0.05$, $t = 2.56$, $P < 0.05$, $t = 2.52$, $P < 0.05$, $t = 3.70$, $P < 0.001$). In 1993, the volume ratio of gulls nesting on the Maasvlakte was significantly smaller than at any of the other colony sites but Europoort (Student's *t* test, Schouwen: $t = 2.99$, $P < 0.01$,

IJmuiden: $t = 2.34$, $P < 0.05$, Texel: $t = 4.02$, $P < 0.001$, Vlieland: $t = 3.50$, $P = 0.001$, Terschelling: $t = 3.13$, $P < 0.01$, Schiermonnikoog: $t = 2.60$, $P < 0.05$), whilst for gulls nesting in Europoort only the difference between those on Texel was significant. In 1992, gulls nesting on Schouwen significantly differed in this respect from those nesting on Terschelling (Student's t test, $t = 2.28$, $P < 0.05$). For none of the colonies studied in both 1992 and 1993, was the difference in volume ratio between the two years significant.

3.3.2 Condition of adults

In all, 104 Lesser Black-backed Gulls were trapped on nests with pipping eggs. Analysis of variance showed that the condition of these birds differed significantly between sexes (Figure 5, ANOVA, $F = 5.98$, $P = 0.02$). Males showed a higher condition index than females in the Maasvlakte and Europoort colony in 1992 and on Terschelling in 1993 (Student's t test, Maasvlakte-Europoort 1992: $t = 2.13$, $P < 0.05$, Terschelling 1993: $t = 2.48$, $P < 0.05$). No significant difference between sexes was found for gulls nesting on Terschelling in 1992 and those breeding on Vlieland in 1993. On Terschelling in 1992, however, the trend was different from that in any of the other colonies (higher condition index for females than for males rather than the reverse).

Body condition did not differ significantly between years and colony sites (Figure 5, ANOVA).

3.3.3 Chick growth and body mass of chicks before fledging

In 1992, there were no significant differences in mass increment in relation to wing length (Figure 6). Chick growth was lowest for Lesser Black-backed Gulls in Europoort and highest for those on the Maasvlakte, but even these extremes in growth rate were not significantly different from each other. In contrast, the average mass of chicks before fledging (all chicks with a wing length > 260 mm) sometimes showed large differences between colony sites (Figure 7). Thus, the average mass of chicks grown up on the Maasvlakte was significantly lower than that of chicks in any of the other colonies (Student's t test, Schouwen: $t = 3.42$, $P < 0.01$, Europoort: $t = 2.29$, $P < 0.05$, IJmuiden: $t = 3.63$, $P = 0.001$, Texel: $t = 4.85$, $P < 0.001$, Vlieland: $t = 4.28$, $P < 0.001$, Terschelling: $t = 4.77$, $P < 0.001$), whilst the chicks on Texel were also significantly heavier than those in Europoort ($t = 2.88$, $P < 0.01$) and on Terschelling ($t = 2.55$, $P < 0.05$).

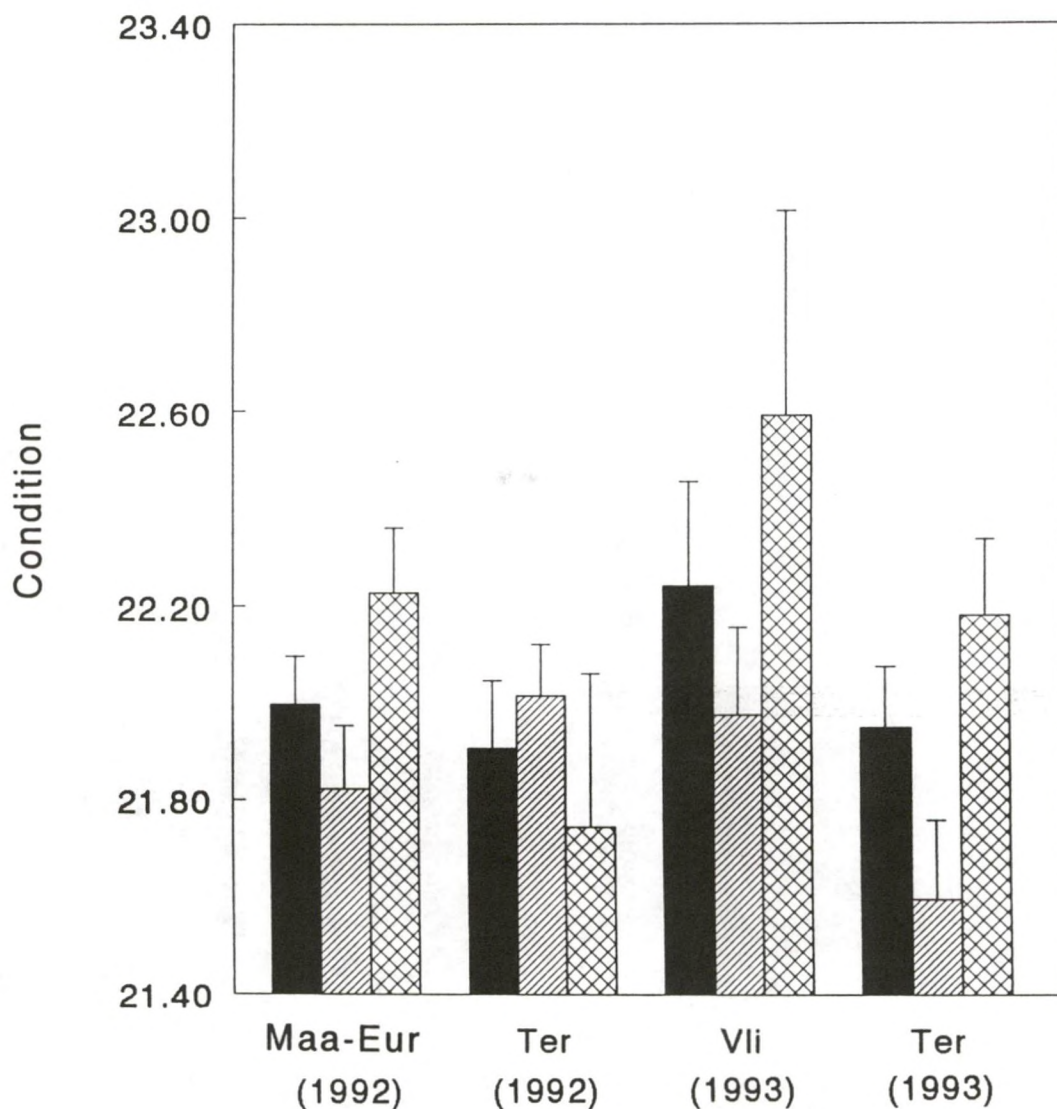


Figure 5. Average (and SE) condition index (cubic root of mass (g) * 100 * wing length (mm)⁻¹) of adult Lesser Black-backed Gulls just before hatching of the eggs at three colony sites in 1992-1993 (black bars: sexes combined, hatched bars: females, cross-hatched bars: males; for abbreviations of colony sites, see Figure 4). Numbers of birds handled: Maasvlakte-Europoort, 1992: 21 females and 16 males; Terschelling, 1992: 15 females and 10 males; Vlieland, 1993: 6 females and 8 males; Terschelling, 1993: 11 females and 17 males.

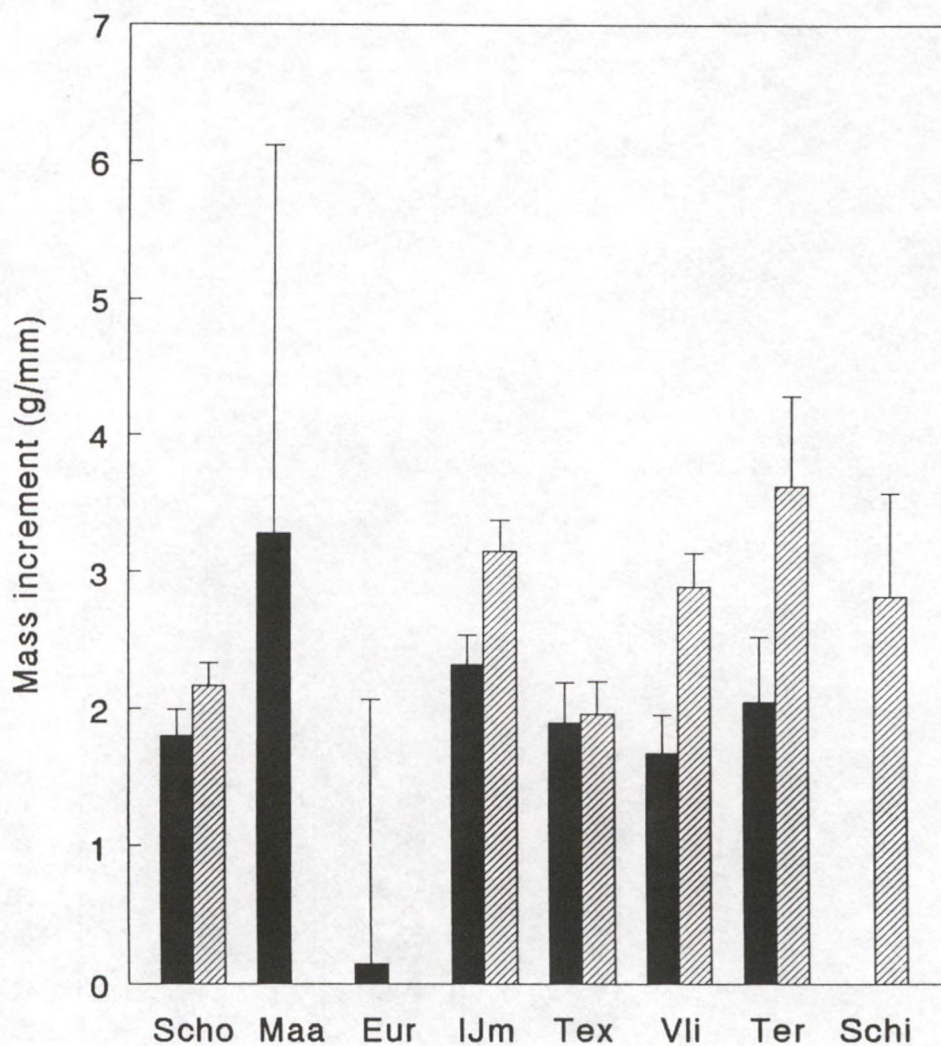


Figure 6. Mass increment (g for each mm increase of wing length up to 260 mm) of Lesser Black-backed Gull chicks at eight colony sites in 1992 (black bars) and 1993 (hatched bars). Bars indicate SE. For abbreviations of colony sites, see Figure 4. Numbers of chicks handled: Schouwen, 1992: 81, 1993: 84; Maasvlakte, 1992: 8; Europoort, 1992: 13; IJmuiden, 1992: 26, 1993: 25; Texel, 1992: 51, 1993: 57; Vlieland, 1992: 60, 1993: 41; Terschelling, 1992: 45, 1993: 25; Schiermonnikoog, 1993: 26.

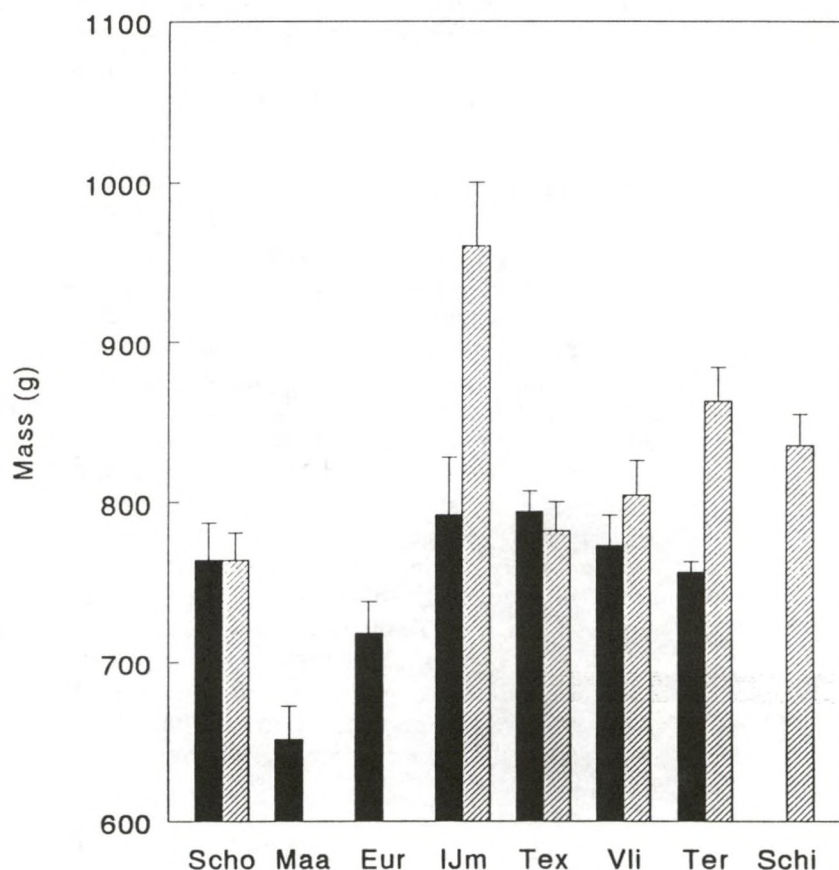


Figure 7. Average mass (g) of Lesser Black-backed Gull chicks with a wing length > 260 mm at eight colony sites in 1992 (black bars) and 1993 (hatched bars). Bars indicate SE. For abbreviations of colony sites, see Figure 4. Numbers of birds handled: Schouwen, 1992: 24, 1993: 38; Maasvlakte, 1992: 15; Europoort, 1992: 20; IJmuiden, 1992: 10, 1993: 2; Texel, 1992: 72, 1993: 58; Vlieland, 1992: 47, 1993: 25; Terschelling, 1992: 5, 1993: 32; Schiermonnikoog, 1993: 34.

In 1993, mass increment of chicks significantly fell behind on both Schouwen and Texel compared with that of chicks in IJmuiden, on Vlieland and on Terschelling (Figure 6, Student's t test, Schouwen-IJmuiden: $t = 2.92$, $P < 0.01$, Schouwen-Vlieland: $t = 2.15$, $P < 0.05$, Schouwen-Terschelling: $t = 2.38$, $P < 0.05$, Texel-IJmuiden: $t = 3.09$, $P < 0.01$, Texel-Vlieland: $t = 2.42$, $P < 0.05$, Texel-Terschelling: $t = 2.60$, $P < 0.05$). This was reflected in the mass of chicks before fledging. Chicks born on Schouwen were significantly leaner than those in IJmuiden, on Terschelling and on Schiermonnikoog, respectively (Student's t test, $t = 2.62$, $P < 0.05$, $t = 3.73$, $P < 0.001$, $t = 2.94$, $P < 0.01$, respectively), those on Texel were significantly leaner than those on Terschelling ($t = 2.80$, $P < 0.01$).

Mass increment in relation to wing length tended to be larger in 1993 than in 1992, with significant differences between years for IJmuiden and Vlieland (Student's t test, $t = 2.69$ and $t = 3.25$, respectively, both $P < 0.01$). Likewise, several colonies showed larger pre-fledging masses in 1993 than in 1992, but only for Terschelling was the difference between the two years significant (Student's t test, $t = 4.83$, $P < 0.001$).

3.3.4 Diet

Pellets adults In 1992, 1559 pellets were collected around nests of Lesser Black-backed Gulls at seven colony sites. Total number of pellets collected at each site ranged from 23 (Vlieland) to 743 (Terschelling). A summary of the frequency of occurrences of indigestible food remains in the pellets is given in Table 2. Marine fish, marine invertebrates (predominantly swimming crabs *Liocarcinus holsatus*) and terrestrial invertebrates (mainly earthworms *Lumbricus* spp. and leather-jackets *Tipula* spp., see Noordhuis & Spaans 1992) were most frequently encountered in the pellets (40%, 17% and 50%, respectively). Pellet composition differed markedly between colony sites. Marine fish were found in 13% (Europoort) to 94% of the pellets (Texel). Marine invertebrates were encountered in 2% (Europoort) to 42% (Schouwen) of the pellets. The proportion of terrestrial invertebrates ranged from 8% (Texel) to 84% (Europoort). Garbage, invertebrates from tidal flats (molluscs, shore crabs *Carcinus maenas*, brown shrimps *Crangon crangon*), terrestrial vertebrates (mammals and birds) and freshwater fish were only rarely present in more than 10% of the pellets (garbage: Maasvlakte 13%, IJmuiden 52%, invertebrates tidal flats: Terschelling 14%).

We found that the proportion of pellets with marine fish and marine invertebrates was positively correlated (Spearman rank correlation test, $R_0 = 12.5$, $P = < 0.05$), and that each of these proportions and the proportion of pellets with terrestrial invertebrates were negatively correlated ($R_0 = 110$, $P < 0.005$ and $R_0 = 104.5$, $P < 0.025$, respectively). No relationship was found between any of the other food types shown in Table 2.

Based on the food remains found in the pellets, marine elements predominated in the food of adult Lesser Black-backed Gulls on Schouwen, Texel, Vlieland and Terschelling (but the least in gulls from Terschelling), and terrestrial invertebrates in that of gulls from the Maasvlakte and Europoort. The birds from IJmuiden were intermediate in their food choice and were also marked by their strong tendency to scavenge for garbage.

Table 2. Proportion (%) of Lesser Black-backed Gull pellets (N = 1559) with a certain type of food in 1992 (Sch = Schouwen, Maa = Maasvlakte, Eur = Europoort, IJm = IJmuiden, Tex = Texel, Vli = Vlieland, Ter = Terschelling).

Food type ¹	Colony site						
	Sch	Maa	Eur	IJm	Tex	Vli	Ter
Marine fish	77	26	13	34	94	91	63
Marine invertebrates	42	4	2	21	27	26	27
Tidal invertebrates	0	1	0	3	6	4	14
Terrestrial vertebrates	0	0	6	3	4	0	1
Freshwater fish	0	1	+	0	2	0	+
Terrestrial invertebrates	21	63	84	45	8	22	30
Garbage	9	2	13	52	8	4	1
N pellets	43	163	506	29	52	23	743

¹ + = < 0.5%.

Table 3. Proportion (%) of Lesser Black-backed Gull pellets with marine fish (N = 688) comprising a certain species or species group in 1992 (Sch = Schouwen, Maa = Maasvlakte, Eur = Europoort, IJm = IJmuiden, Tex = Texel, Vli = Vlieland, Ter = Terschelling).

Species (group)	Colony site						
	Sch	Maa	Eur	IJm	Tex	Vli	Ter
Clupeidae	3	7	0	0	2	0	2
Gadidae	79	43	29	30	82	52	49
<i>Trachurus trachurus</i>	21	7	2	10	27	29	8
<i>Ammodytes tobianus</i>	0	0	0	0	0	0	1
Callionymidae ¹ , Agonidae ²	12	2	5	0	4	5	3
<i>Eutrigla gurnardus</i>	9	17	2	10	41	29	14
Flatfish	24	55	40	10	39	10	49
Species indet.	6	12	35	50	2	5	8
N pellets	33	42	65	10	49	21	468

¹Dragonet *Callionymus lyra* (23 fishes), ²Hook-nose *Agonus cataphractus* (1 fish).

Species or species groups of marine fish identified are summarised in Table 3. Gadids and flatfish were most frequently encountered (56% and 50%, respectively, of all pellets with marine fish, followed by Grey Gurnard *Eutrigla gurnardus* (17%) and Scad *Trachurus trachurus* (11%). Other species (groups) were encountered less frequently.

Half of the 16 clupeid otoliths found were from Herring *Clupea harengus*; the other half of the clupeids could not be identified to the species level. Among the 489 gadids found in the pellets, the Whiting *Merlangius merlangius* (76.3% of all gadids found) was most abundant, followed by the Bib *Gadus luscus* (10.4%). Cod *Gadus morhua* (3.5%) and Poor-cod *Gadus minutus* (2.2%) were found less frequently; 7.6% of the gadids could not be identified to the species level. Among the 73 flatfish identified to the species level, the Dab *Limanda limanda* (79%) was most abundant, the remaining 21% being made up by Flounder *Platichthys flesus*, Plaice *Pleuronectes platessa* and Sole *Solea solea*; 88.5% of the flatfish otoliths could not be identified to the species level with certainty.

The length of gadids consumed ranged from (10) 17 to 34 cm (median 25 cm, $N = 359$) for the Whiting, from 12 to 30 cm (median 22 cm, $N = 42$) for the the Bib, from 13 to 18 cm (median 17 cm, $N = 9$) for the Poor-cod and from 21 to 29 cm (median 26 cm, $N = 7$) for the Cod. For the Scad the length ranged from 21 to 33 cm (median 27 cm, $N = 25$). The width of the Bib consumed ranged from 5 to 9 cm (median 7 cm, $N = 40$). The width of the Plaice amounted to 4 and 5 cm ($N = 2$).

Species (group) composition also varied markedly between colonies. Thus, frequency of Gadidae ranged from 29% (Europoort) to 82% (Texel) and that of flatfish from 10% (IJmuiden and Vlieland) to 55% (Maasvlakte). Ranges for other species (groups) were Grey Gurnard from 2% (Europoort) to 41% (Texel) and Scad from 2% (Europoort) to 29% (Vlieland). Other species groups showed a frequency of less than 10%, with the exception of the Callionymidae and Agonidae (Schouwen 12%).

There were also marked differences in the proportion of Whiting, Bib and Poor-Cod between colonies. In the Wadden Sea area, 65.8% (Texel) to 86.0% (Terschelling) of the gadids were Whiting. In the Delta area, the proportion of Whiting amounted to 53.2% (Maasvlakte-Europoort) and 54.2% (Schouwen). The Bib and the Poor-cod, on the contrary, reached their highest proportion in the Delta area (Bib: Maasvlakte-Europoort and Schouwen 29.8% and 31.3%, respectively, against 4.3% to 10.5% on Terschelling and Texel, respectively; Poor-cod: Maasvlakte-Europoort and Schouwen 2.1% and 10.4%, respectively, against 0% on Vlieland to 1.3% on Texel and Terschelling, respectively).

We found no relationship between any of the species (groups) given in Table 3, except for the proportion of pellets with gadids and unidentified species (correlation negative, Spearman rank correlation test, $R_0 = 108$, $P < 0.01$) and between each of these proportions and Scad (correlation positive, $R_0 = 12$, $P < 0.05$ and correlation negative, $R_0 = 98$, $P < 0.05$, respectively).

Chick regurgitations In 1992, 132 regurgitations (2-32 at each of the seven colony sites sampled) of Lesser Black-backed Gull chicks were collected during handling of the chicks (Table 4). Marine fish were again the most frequent food type found, ranging from 75% in regurgitations of chicks handled in Europoort to 100% of those sampled on the Maasvlakte, Texel and on Vlieland, respectively. All other food types were less frequently encountered, and reached only a few times the 10% level (marine invertebrates: IJmuiden 13%, Schouwen 25%; terrestrial vertebrates: Terschelling 10%, Europoort 33%; terrestrial invertebrates: Vlieland 13%, Europoort 17%; garbage: Europoort 17%). Tidal invertebrates, seeds of *Zostera spec.* and corn *Zea mays* were encountered each at one colony site only (Europoort one regurgitation, Vlieland three regurgitations, IJmuiden one regurgitation, respectively).

Table 4. Proportion (%) of Lesser Black-backed Gull chick regurgitations (N = 132) with a certain type of food in 1992 (Sch = Schouwen, Maa = Maasvlakte, Eur = Europoort, IJm = IJmuiden, Tex = Texel, Vli = Vlieland, Ter = Terschelling).

Food type	Colony site						
	Sch	Maa	Eur	IJm	Tex	Vli	Ter
Marine fish	94	100	75	92	100	100	94
Marine invertebrates	25	0	8	13	0	9	0
Tidal invertebrates	0	0	8	0	0	0	0
Terrestrial vertebrates	1	0	33	0	0	3	10
Terrestrial invertebrates	6	0	17	4	0	13	3
<i>Zostera</i> seeds	0	0	0	0	0	9	0
Corn	0	0	0	4	0	0	0
Garbage	0	0	17	0	0	3	3
N regurgitations	16	2	12	24	15	32	31

We found no relationship between any of the marine food types, nor between these food types and any of the foods of terrestrial origin. The proportion of regurgitations with terrestrial vertebrates and that with terrestrial invertebrates, those with terrestrial vertebrates and garbage, and those with terrestrial invertebrates and garbage, were nevertheless positively correlated, although in the last case the relationship did not quite reach the significance level (Spearman rank correlation test, $R_0 = 15.50$, $P < 0.05$, $R_0 = 6.50$, $P < 0.05$, and $R_0 = 17$, $P < 0.1$, respectively).

In general, chick diet did not differ much between colonies. Most food fed to the chicks was of marine origin. However, Lesser Black-backed Gulls nesting in Europoort, also relied to a significant extent on terrestrial foods (33% of the regurgitations with terrestrial vertebrates, 17% with terrestrial invertebrates and 17% with garbage).

Table 5. Proportion (%) of Lesser Black-backed Gull chick regurgitations with marine fish (N = 122) comprising a certain species or species group in 1992 (Sch = Schouwen, Maa = Maasvlakte, Eur = Europoort, IJm = IJmuiden, Tex = Texel, Vli = Vlieland, Ter = Terschelling).

Species	Colony site						
	Sch	Maa	Eur	IJm	Tex	Vli	Ter
Clupeidae	20	100	43	50	7	13	38
Gadidae	40	0	29	0	27	28	14
<i>Trachurus trachurus</i> ¹ , <i>Scomber scombrus</i> ²	0	0	0	5	0	3	0
<i>Zoarcetes viviparis</i>	0	0	0	5	0	0	0
Ammodytidae	7	0	0	9	0	3	0
Callionymidae ³ , Agonidae ⁴	13	0	0	0	0	0	7
Gobiidae	20	0	0	0	0	0	0
<i>Eutrigla gurnardus</i>	0	0	0	9	27	25	3
Flatfish	73	0	14	14	47	44	48
Species indet.	7	0	29	18	13	13	10
N regurgitations	15	2	7	22	15	32	29

¹1 fish, ²1 fish, ³Dragonet (2 fishes), ⁴Hook-nose (2 fishes).

Species or species groups of marine fish found in the regurgitations are summarised in Table 5. On average, clupeids (29%), gadids (20%), Grey Gurnards (12%) and flatfish (42%) were the most frequent groups of marine fish fed to the chicks.

Among the 26 gadids found in the regurgitated food boluses, the Whiting was again most abundant (50% of all gadids found, 100% of all gadids identified to the species level, no identification to the species level possible for remaining gadids). Of the 20 clupeids which could be identified to the species level 18 (90%) were Sprat and 2 (10%) were Herring; for 41 clupeids an identification to the species level was not feasible. Among the 69 flatfish found, Flounder and Dab were most abundant (17% and 13%, respectively, of all flatfish found; 40% and 30%, respectively, of all flatfish identified to the species level). Plaice, Solenette *Buglossidium luteum* (each 3% of all flatfish found and 10% of all flatfish identified to the species

level), Sole (3% and 7%, respectively) and Lemon Sole *Microstomus kitt* (2% and 3%, respectively) were encountered less frequently.

The length of the fish found ranged from 10 to 27 cm (median 19 cm, $N = 16$) for the Whiting and from 20 to 21 cm (median 20 cm, $N = 4$) for the Grey Gurnard. The width of the flatfish consumed ranged from 2 to 6 cm (median 5 cm, $N = 12$) for the Flounder, from 6 to 8 cm (median 6 cm, $N = 8$) for the Bib and from 3 to 9 cm (median 4 cm, $N = 3$) for the Plaice.

The proportion of gadids was irregularly distributed along the coast, ranging from 0% on the Maasvlakte and in IJmuiden, respectively, to 40% on Schouwen. Clupeids, however, were most frequently found along the mainland coast and in the northern Delta area (43-100%, elsewhere 7-38%), whilst flatfish were encountered most frequently in the Wadden Sea and southern Delta area (44-73%, elsewhere 0-14%). Other species (groups) showed no clear trend. Grey Gurnard was most frequently found on Texel and Vlieland (27% and 25%, respectively, elsewhere 0-9%).

No relationship was found between the occurrence of any of the species (groups) of fish in the regurgitations, except for a negative relationship between the proportion of regurgitations with flatfish and that with clupeids (Spearman rank correlation test, $R_0 = 118.50$, $P < 0.01$), reflecting the geographical distribution of these fish groups in the diet of the chicks (see above). The proportion of pellets with Grey Gurnards and the proportion of regurgitations with that fish species were positively correlated (Spearman rank correlation test, $R_0 = 14$, $P < 0.05$).

3.4 Discussion

From 1992 to 1993, we measured egg size, adult condition at the end of the incubation period and chick growth of Lesser Black-backed Gulls at eight colony sites located between Schouwen and Schiermonnikoog, thus covering almost the entire Dutch North Sea coast. The aim of this comparative study was to investigate (1) whether these breeding parameters differ between colonies and (2) if so, whether these differences can be related to local differences in diet. Although colony sites were well-distributed along the coast, the mainland coast was less well represented because recently numbers fell in that area after Red Foxes increased dramatically in numbers there. The only colony we could easily sample along the mainland coast was one on the roof of a building near the harbour of IJmuiden, where gulls nested safe from fox predation.

In 1992, clutch volumes of three-egg clutches were smallest at the three colony sites in the Delta area. In the following year, the clutch volume was smallest for gulls nesting in Europoort, directly followed by those breeding on the Maasvlakte and on Schiermonnikoog. In 1993, clutch volume was largest in IJmuiden.

In both years, the ratio between the smallest and largest egg within a clutch was smallest for Lesser Black-backed Gulls nesting on the Maasvlakte and

in Europoort. In 1992, gulls nesting on Schouwen showed a higher ratio than the gulls at the two other Delta colonies, but nevertheless the ratio was smaller than for those at the other colony sites.

For the Maasvlakte and Europoort the ratio between the volume of the c- and a-egg varied between 0.874 (Maasvlakte, 1993) and 0.888 (Europoort, 1993), for the other colonies between 0.898 (Schouwen, 1992) and 0.913 (Terschelling, 1992). The low values for the Maasvlakte and Europoort correspond well with the ratio (0.868) given by Bolton (1991) for gulls nesting in an area where food was in short supply, while the values for the other colonies reach the range for situations where this was not the case (0.914-0.928).

The condition index of adults at the end of the incubation period varied with sex (highest for males in two of the four cases) and years (in 1993, lower for females on Terschelling than in 1992). We found, however, no differences between colony sites and years for either of the sexes.

Mass increment and pre-fledging mass of chicks varied markedly between colony sites. In 1992, no differences in mass increment of young up to a wing length of 260 mm (when chicks are approximately 30 days old) were found between colony sites. In 1993, however, chick mass increment was significantly lower on Schouwen and Texel than in IJmuiden, on Vlieland and on Terschelling (no data available for the Maasvlakte and Europoort).

In both years, we also found significant differences in pre-fledging mass. In 1992, pre-fledging masses were significantly lower on the Maasvlakte than in any of the other colonies studied this year, whilst those on Texel were significantly higher than on Terschelling and in Europoort. In 1993, pre-fledging masses on Schouwen were significantly lower than in IJmuiden, on Terschelling and on Schiermonnikoog, whilst those on Texel were significantly lower than on Terschelling (again no data available for the Maasvlakte and Europoort).

In 1993, on average, chicks grew better and reached a higher pre-fledging weight than the year before (mass increment significant for IJmuiden and Vlieland, pre-fledging mass for Terschelling).

Summarising, the data show that significant differences in breeding parameters existed between colony sites and years. Gulls nesting on the Maasvlakte and in Europoort did relatively worse during both the egg (1992 and 1993) and chick stage (only data available for 1992), whilst those in IJmuiden and on Schiermonnikoog did relatively best (for Schiermonnikoog, however, only data available for 1993, when chick growth and pre-fledging masses on Vlieland and Terschelling showed high values as well). Gulls nesting on Schouwen had a rather low egg volume ratio in 1992 (in-between those from the Maasvlakte and Europoort on the one hand and the remaining colonies on the other). In 1993, Terschelling chicks reached significantly higher pre-fledging masses than in 1992.

Thus, our data suggest that in both years food was in short supply during the entire breeding season for Lesser Black-backed Gulls nesting in the northern Delta area (Maasvlakte and Europoort) and in part of the breeding season for those nesting on Schouwen (egg stage 1992) and Terschelling (chick stage 1992).

The food data we presented indicate that Lesser Black-backed Gulls nesting along the Dutch coast feed predominantly at sea, with the exception of those on the Maasvlakte and in Europoort. Pellets and regurgitations collected in the last two colonies showed that these gulls also regularly feed on land. Of the seven colonies sampled in 1992, the Maasvlakte and Europoort had the lowest proportion of pellets and regurgitations with marine foods, in particular fish, and the highest proportion with terrestrial foods. We suggest that gulls which feed regularly on land are at a disadvantage compared with gulls which do so almost exclusively at sea. The composition of pellets and regurgitations in 1992 do not give any clues about the possible causes of the rather low egg volume index on Schouwen and the relatively low pre-fledging mass on Terschelling in this year. The data presented in this Chapter suggest, however, that for some colony sites marked differences in food availability may occur between years and different stages of the breeding cycle. The worse situation on Terschelling in 1992 will be further discussed in Chapter 5.

Our data show that clupeids, gadids and flatfish form a significant portion of the diet of Lesser Black-backed Gulls nesting along the Dutch coast. Fish length of consumed gadids in this study ranged from 10 to 34 cm and fish width of flatfish from 2 to 9 cm. Fish of these sizes are under natural circumstances not available for plunge-diving gulls such as the Lesser Black-backed Gull (e.g. Muus 1966). The gulls must therefore have obtained the fish as discards at beamtrawlers off the Dutch coast. This is corroborated by observations at research vessels and a commercial trawler in the southern North Sea by Camphuysen (1993, 1994a, 1994b, in press). Camphuysen showed that during the breeding season (April-August) Lesser Black-backed Gulls are the dominating scavengers at trawlers in the southern North Sea. Moreover, fish species and sizes taken at trawlers by the gulls were similar to the species and sizes we found in our diet study. Thus, the median length of consumed Whiting in discard experiments at the southern North Sea was 23 cm (range 9-31 cm), whilst the median width of discarded flatfish that was consumed by Lesser Black-backed Gulls was 6 cm (range 3-9 cm, Camphuysen 1994b). The two studies indicate that Lesser Black-backed Gulls nesting on the Dutch coast rely to a great extent on fish discarded by beamtrawlers off that coast.

4 EXPERIMENTAL EVIDENCE FOR THE RELATIONSHIP BETWEEN FOOD SUPPLY, PARENTAL EFFORT AND CHICK SURVIVAL IN LESSER BLACK-BACKED GULLS NESTING ON TERSCHELLING: THE SITUATION IN A YEAR WHEN FOOD IS IN SHORT SUPPLY

4.1 INTRODUCTION

In recent times, the numbers of several populations of Lesser Black-backed Gulls of the subspecies *fuscus* and *graellsii* have stabilised or decreased (e.g. Finland: Hario 1989, northern and central Norway: Bevanger & Thingstad 1990, Strann & Vader 1992, Great Britain: Gibbons *et al.* 1993, The Netherlands (locally): SOVON 1987, pers. comm.). The numerical decrease is often paralleled by a decline in reproductive success attributed to a lack of local food supplies (e.g. Hario 1990, Strann & Vader 1992, Gibbons *et al.* 1993, A.L. Spaans).

Food availability can affect reproductive output in both a direct way and an indirect way. Fluctuations in prey abundance and differences in individual foraging efficiency can directly influence the amount or quality of the food that adult birds can provide their offspring with (Winkler 1985, Pierotti & Annett 1987). When food is in short supply at the time of the formation of the eggs, food availability can indirectly affect the reproductive output. This is owing to the fact that females with a nutritive and therefore energetic deficit will either produce a lower number of eggs, eggs of smaller size, or do not breed that year (Drent & Daan 1980, Martin 1987).

The relationship between food availability and reproductive success has been experimentally studied in the field, but with different results (Harris 1978, Wehle 1983, Blaucher & Robertson 1987, Hussell & Quinney 1987, Hiom *et al.* 1991, Navarro 1991, Van Klinken 1992). Compared with control gulls, both Hiom *et al.* (1991) and Van Klinken (1992) found an increase in egg size, but not in the mean date of egg-laying, in Lesser Black-backed and Herring Gulls, respectively, that were provided with additional food. Van Klinken (1992), who continued the provision of additional food after the eggs had hatched, also established an increase in chick survival, but found no effect on chick growth.

There is a lack of experimental studies which deal with the direct (through starvation) and indirect effect (through changes in the behaviour of adults or chicks) of local food shortage on fledging success in colonial nesting seabirds. In this chapter, we will show how adult and chick behaviour affect chick survival and chick growth in a colony of Lesser Black-backed Gulls when food is in short supply. We predict that in this situation the provision of additional food to chicks will positively affect mass increment, skeleton growth and feather development of chicks, and will reduce chick mortality rate. We also predict that adult gulls will improve synchronization of their parental efforts and the equatability of their parental care, and that chicks will roam about less in the territory and so will reduce the risk of predation

by other gulls.

4.2 Study area and methods

4.2.1 Study area

The study was carried out in the mixed Herring and Lesser Black-backed Gull colony in the 4400-ha Boschplaat nature reserve on the eastern side of the West Frisian Island of Terschelling (53°25' N 05°28' E) from April to July 1992. The Boschplaat consists primarily of a series of low, undulating dune complexes surrounded by salt marshes which are intersected by large tidal creeks (for a more detailed description of the area we refer to Spaans 1971 and Spaans *et al.* 1987). Lesser Black-backed Gulls have nested in the reserve since 1926 (SOVON 1987). In 1992, 11,500 pairs of Lesser Black-backed Gulls and 13,800 pairs of Herring Gulls bred in the reserve (Van Dijk *et al.* 1994). Lesser Black-backed Gulls bred predominantly in the dips of the dunes and in the salt-marshes, Herring Gulls mainly on the crests of the dunes.

4.2.2 Data collection

We studied 56 pairs of Lesser Black-backed Gulls distributed over two study plots, which were 150-200 m apart. Each nest was marked with a numbered stick as soon as the first egg was found in the nest. The contents of each nest were checked at least once every two days. Eggs were individually marked *a*, *b*, and *c*, according to their laying order. We measured the length and width of each egg with a vernier callipers to the nearest 0.1 mm. Egg volume (*V*) was calculated using the formula $V = 0.476 \times \text{length} \times \text{width}^2$ (Harris 1964). A few days before the eggs hatched we surrounded all territories with a 0.5-0.8 m high fence to prevent young leaving the area before fledging. At the same time, we put a wooden shelter (0.6 * 0.4 * 0.2 m) near each nest, irrespective of the presence of natural hiding possibilities in the territory, to protect all chicks as much as possible against predators and bad weather conditions (Burness & Morris 1992).

Chicks were individually marked with small coloured rings just after hatching. We weighed chicks to the nearest 1.0 g, using spring balances, and measured their tarsus lengths to the nearest 0.1 mm, using a vernier callipers, on each day until day 20 and once every two days during the rest of the chick stage. Wing length was measured to the nearest 1.0 mm, using a ruler, from the 8th day onwards.

From the day the gulls arrived in the colony we monitored their behaviour once every two days for 3-4 hours (with a total of 150 observation hours for each pair). Parameters studied included (a) the proportion of time male and female were present alone at their territory, the partners were present simultaneously and the pair was absent, (b) the frequency and the duration of their foraging trips, (c) the frequency of chick feeding, and (d) the period of time the chicks were wandering in the territory, calling, and hiding in

natural or artificial shelters. For an analysis of the data we distinguished 4 stages in the breeding cycle: (a) the period before egg-laying, (b) the incubation period, (c) the early chick stage (chicks younger than 7 days), and (d) the older chick stage (chicks older than 7 days).

4.2.3 Experimental design

Before the eggs had hatched, we randomly divided the nests into a control group and two experimental groups (group 1 and 2, respectively). At the end of our daily visits to the colony, the chicks of the experimental groups were provided with additional food (sprat *Sprattus sprattus* and juvenile herring *Clupea harengus*) from the day of hatching of the first egg in the nest until the youngest chick was either 6 days old (group 1) or able to fly (group 2). During the first week after hatching, chicks received on average $46 \text{ g fish} \cdot \text{chick}^{-1} \cdot \text{day}^{-1}$, during the next two weeks on average $76 \text{ g fish} \cdot \text{chick}^{-1} \cdot \text{day}^{-1}$ and during the rest of the chick stage on average $150 \text{ g fish} \cdot \text{chick}^{-1} \cdot \text{day}^{-1}$ (i.e. each day 200%, 100% and 50%, respectively, of the estimated amount of fish, chicks require daily, Spaans unpublished data, cf. also Spaans 1971 for data on daily food requirements of chicks in Herring Gulls).

To establish a possible relationship between the behaviour of adults and their reproductive output, we divided the gulls into three groups (irrespective of the birds belonging to the control group or to the two experimental groups): (1) unsuccessful pairs (all eggs or chicks lost), (2) less successful pairs (only one chick reaching fledging age) and successful pairs (2 or 3 young reaching fledging age).

4.2.4 Statistical analysis

Statistical tests used to analyse our data included Student's t test, Mann-Whitney U test, Kruskal-Wallis test and ANOVA for independent samples, and Wilcoxon signed-ranks test and Friedman two-way non-parametric analysis of variance for related samples. Normality of distribution was tested using the χ^2 -test (Zar 1984, Siegel & Castellan 1988). To adjust the significance levels to the number of tests performed we used a sequential Bonferroni test (Rice 1989). We compared the daily increment of mass (between day 5 and 30, when the growth curve of individual chicks approached a straight line) and wing and tarsus lengths (between day 10 and 30 and between day 5 and 22, respectively) by means of linear regression, using the F test (Zuk 1989). We preferred linear regression between day 5 and 30 rather than a logistic growth curve from hatching to fledging, because growth curves of control chicks sometimes showed large aberrations. A comparison of logistic growth curves gives poor results in this situation (Ricklefs 1968, Zach 1988). Level of significance was set at $P < 0.05$ in all statistical tests.

4.3 Results

4.3.1 Breeding parameters

A summary of the breeding data for the three groups of breeding pairs is shown in Table 6. There were no differences in median laying date, clutch and egg sizes, or hatching success between the three groups. There were, however, significant differences in fledging success between control pairs and experimental pairs of group 2 (Table 6). The latter not only showed a higher proportion of pairs with fledged young ($\chi^2 = 6.75$, $P < 0.01$), but also had a higher number of fledged young*pair⁻¹ (Mann-Whitney *U*-test, $z = 2.85$, Bonf. adj., $P < 0.02$). Experimental pairs of group 1 showed intermediate values for these parameters (Table 6).

Table 6. Egg biometry and breeding parameters (for clutch size, egg sizes and young*pair⁻¹ means $\pm$ SD are given) for control and experimental pairs (group 1, pairs whose chicks were provided with additional food during the first week after hatching; group 2, pairs whose chicks were provided with additional food until fledging) successfully hatching eggs on Terschelling in 1992.

Parameter ¹	Control pairs	Experimental pairs	
		Group 1	Group 2
Median date of laying	10 May	12 May	12 May
Clutch size	2.92 $\pm$ 0.32	2.88 $\pm$ 0.34	2.94 $\pm$ 0.25
Egg length (mm)	67.27 $\pm$ 2.52	67.58 $\pm$ 2.54	67.79 $\pm$ 2.15
Egg width (mm)	46.88 $\pm$ 1.42	47.24 $\pm$ 1.30	47.88 $\pm$ 1.53
Egg volume (cm ³)	70.35 $\pm$ 5.80	71.91 $\pm$ 5.60	74.14 $\pm$ 5.96
Clutch volume (cm ³)	209.3 $\pm$ 16.5	207.8 $\pm$ 34.2	212.6 $\pm$ 35.3
Hatchlings*pair ⁻¹	2.69 $\pm$ 0.47	2.75 $\pm$ 0.45	2.75 $\pm$ 0.45
Chicks*pair ⁻¹ after one week	1.37 $\pm$ 1.30	2.00 $\pm$ 0.88	2.06 $\pm$ 0.99
% nests with chicks after one week	62.5	92.9	87.5
Fledglings*pair ⁻¹	0.85 $\pm$ 0.92	1.31 $\pm$ 1.08	1.88 $\pm$ 1.02
% nests with fledglings	56.0	66.7	87.5
<i>N</i> pairs	26	16	14

¹Differences among groups only significant for % nests with chicks after one week ($\chi^2 = 5.99$, $P < 0.05$), fledglings*pair⁻¹ (Kruskal-Wallis test, $H = 8.90$, $P < 0.01$) and % nests with fledglings ($\chi^2 = 5.97$, $P < 0.05$).

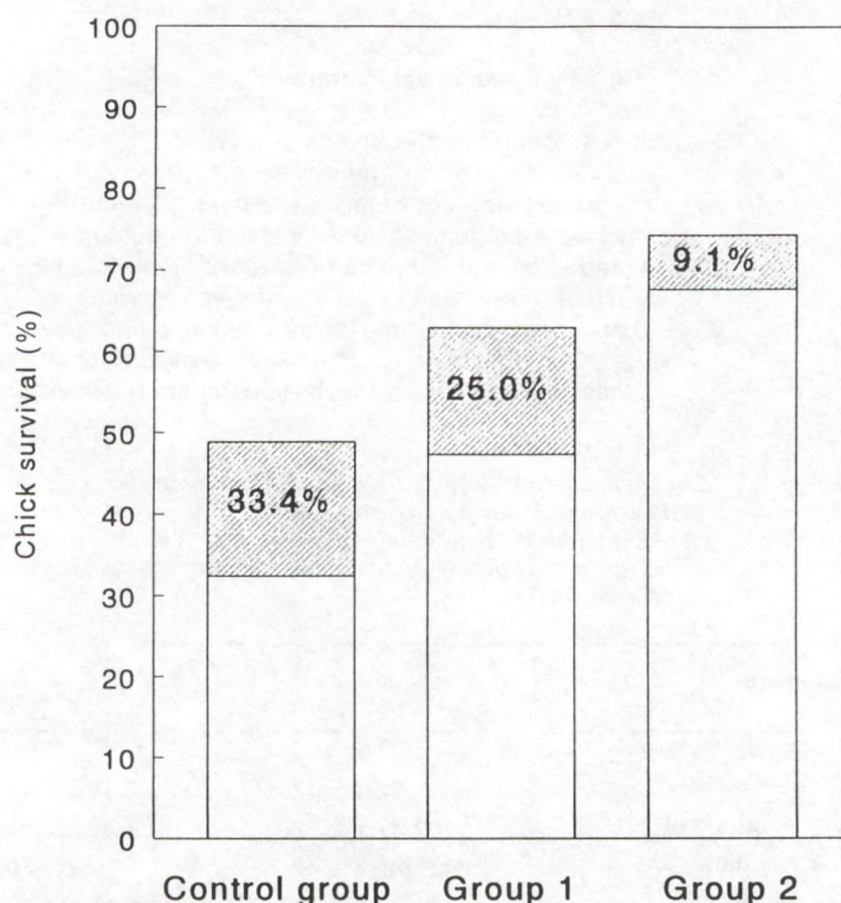


Figure 8. Chick survival in control (left bar) and experimental pairs (central bar: pairs whose chicks were only provided with additional food during the first week after hatching, right bar: pairs whose chicks were provided with additional food until fledging) on Terschelling in 1992. Open bars, proportion of chicks surviving the first week after hatching that fledged; hatched bars, proportion of chicks surviving the first week after hatching that died before fledging.

In the two groups of experimental pairs a significantly higher proportion of chicks survived the first week after hatching than in the control group (group 1 and 2, $\chi^2 = 4.47$ and 4.20 , respectively, $P < 0.05$). No difference was found, in this respect, between the two experimental groups. After the young had reached the age of one week, chick survival in experimental pairs of group 1 was no different from that in control pairs. In group 2, however, chick survival was significantly higher than in each of the other two groups ($\chi^2 = 5.76$ and 5.80 , respectively, $P < 0.05$, Figure 8).

Egg and chick predation by Herring Gulls was the main factor affecting the reproductive output in the study plots (60% of all failures, Bukaciński *et al.* in prep.). Starvation of chicks occurred much less frequently and only took place in the control group and in the experimental group 1 after we had stopped the provision of additional food.

4.3.2 Parental attendance

The proportion of time males and females spent alone at the territory changed considerably during the breeding cycle (Friedman two-way non-parametric analysis of variance, $\chi^2 = 22.7$, $P < 0.0001$ in males and $\chi^2 = 18.3$, $P < 0.001$ in females). Both sexes spent the least time solitarily at the territory during the pre-laying period (males 13.8%, females 9.7%) and most time during the chick stage (males 41.9%, females 32.6%). Overall, males spent more time alone at the territory than females (Wilcoxon signed-ranks test, $z = 2.96$, $P < 0.01$), and the difference increased when chicks became older. When chicks were one week old, territory attendance remained more or less stable during the rest of the chick stage in the males, whilst it decreased in the females.

Partners were present simultaneously at the territory for the longest period of time (63%) before the eggs were laid, and for the least time (7.5%) after the chicks had reached the age of one week. During the pre-laying period, the territory was also left unguarded by the pair for the longest period of time (20%). Partners left the territory unguarded for the shortest period of time during the incubation period (1.8%) and during the first week after the eggs had hatched (1%).

There were, however, clear differences in territory attendance between control and experimental pairs. In pairs that were provided with additional food (groups 1 and 2) the difference in attendance between sexes was highest during incubation (Table 7, Wilcoxon signed-ranks test, $z = 2.75$, $P < 0.01$ for group 1, $z = 2.11$, $P < 0.05$ for group 2). The difference decreased after the eggs had hatched. For pairs of group 1 the difference increased again as soon as we stopped the provision of additional food (Wilcoxon signed-ranks test, $z = 2.14$, $P < 0.05$ for the older chick stage), resulting in a decrease in the proportion of time females spent solitarily at the territory (Table 7). In control pairs, however, the difference in territory attendance between the sexes increased after the eggs had hatched and remained significantly high during the entire chick stage, with males spending twice as long at the territory as females stayed (Table 7, Wilcoxon signed-ranks test, $z = 1.98$ and $z = 2.04$ for the early and late chick stage, respectively, both $P < 0.05$). The proportion of time that females of group 1 spent alone at the territory after we stopped the provision of additional food was significantly lower than that of females of group 2 (Mann-Whitney U test, $z = 2.29$, $P < 0.05$).

There were also differences among groups in the simultaneous presence and absence of partners at the territory (Figure 9). During the chick stage, partners of the experimental groups were present simultaneously at the territory for longer periods of time than partners of the control pairs (Kruskal-Wallis test, $H = 13.45$, $P < 0.001$). The former also left the territory unguarded for shorter periods of time (Kruskal-Wallis test, $H = 7.12$, $P < 0.05$). When we finished the provision of additional food to chicks in group 1, the parents of these chicks were together at the territory for shorter periods of time than those of group 2, which were provided with additional food until fledging (Mann-Whitney U test, $z = 4.15$, Bonf. adj.,

$P < 0.02$), whilst the reverse was true for the proportion of time the territory was left unguarded (Mann-Whitney U test, $z = 4.62$, Bonf. adj., $P < 0.02$).

Table 7. *Proportion of time (%) that females and males of control and experimental pairs (group 1, pairs whose chicks were only provided with additional food during the first week after hatching; group 2, pairs whose chicks were provided with additional food until fledging) were present at the territory solitarily (excluding pairs which failed to hatch eggs) on Terschelling in 1992.*

Stage of breeding cycle	Female		Male
<i>Pre-egg period</i>			
Control pairs	11.3 ± 20.7		16.3 ± 30.9
Experimental pairs, group 1	10.5 ± 18.2		12.3 ± 22.5
Experimental pairs, group 2	7.7 ± 16.6		13.2 ± 23.9
<i>Egg stage</i>			
Control pairs	25.5 ± 36.6		27.4 ± 40.5 **
Experimental pairs, group 1	21.5 ± 36.9	**	51.1 ± 45.2
Experimental pairs, group 2	24.9 ± 37.6	*	40.4 ± 42.9
<i>1st week after hatching</i>			
Control pairs	29.7 ± 38.6	*	51.8 ± 40.8
Experimental pairs, group 1	35.4 ± 36.8		36.3 ± 37.5
Experimental pairs, group 2	32.1 ± 34.6		39.7 ± 39.3
<i>Older chicks</i>			
Control pairs	28.2 ± 37.7	*	44.6 ± 38.4
Experimental pairs, group 1	26.8 ± 37.4	*	40.2 ± 41.2
	*		
Experimental pairs, group 2	36.2 ± 39.2		41.3 ± 38.8

Differences between groups and sexes are indicated with asterisks (Mann-Whitney U test for differences between groups, Wilcoxon signed-ranks test for differences between sexes, $P < 0.05$ (*) and < 0.01 (**), respectively).

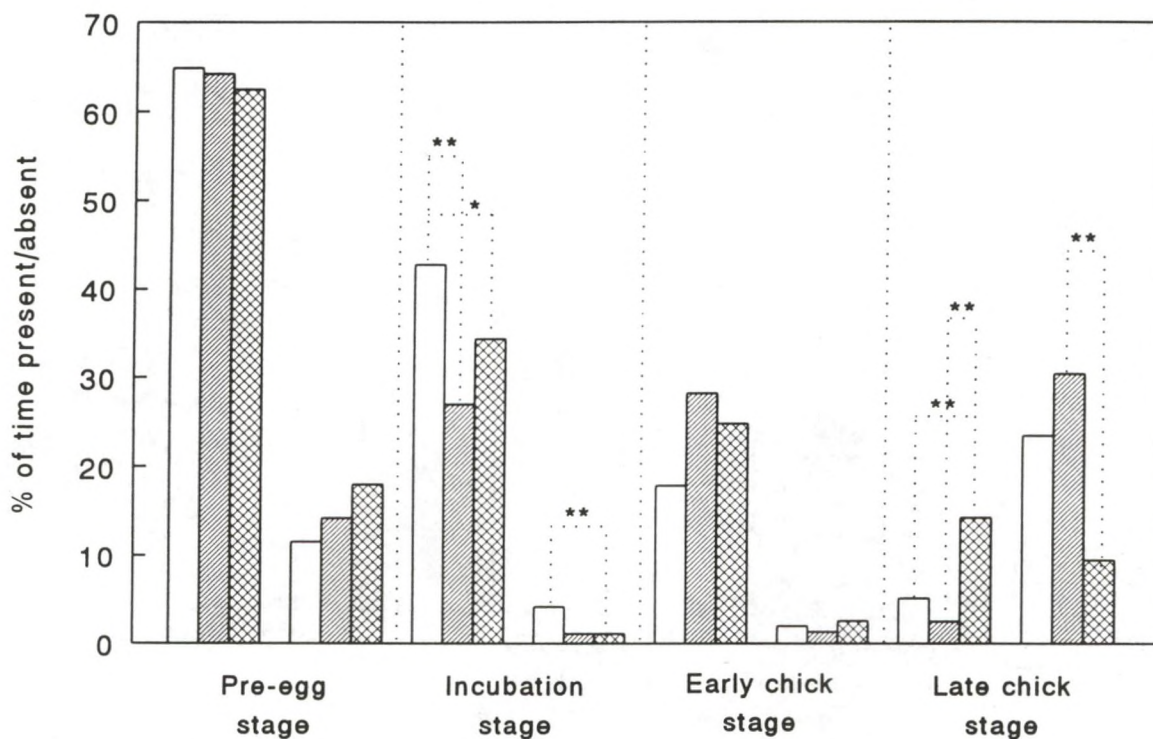


Figure 9. Proportion of time (%) that (a) partners of pairs were present simultaneously at the territory (left bars) and (b) the territory was left unguarded (right bars) on Terschelling in 1992 (both a and b excluding pairs which failed to hatch eggs). Open bars, control pairs; hatched bars, pairs whose chicks were only provided with additional food during the first week after hatching; cross-hatched bars, pairs whose chicks were provided with additional food until fledging. Mann-Whitney U test, Bonf. adj., $P < 0.05$ (*) and < 0.02 (**), respectively.

Figure 10 shows the relationship between territory attendance and reproductive output, irrespective of the experimental design. Overall, males and females of unsuccessful pairs remained alone at the territory for shorter periods of time than males and females of pairs that raised either one chick to fledging (Mann-Whitney U test, $z = 2.33$ and $z = 2.23$ for males and females, respectively, Bonf. adj., both $P < 0.02$) or two or three young (Mann-Whitney U test, $z = 2.93$, Bonf. adj., $P < 0.02$ for males). Males and females of unsuccessful pairs also spent longer periods of time together at the territory than those of the two other groups (Mann-Whitney U test, $z = 2.63$, Bonf. adj., $P < 0.02$ for pairs raising one fledgling and $z = 2.26$, Bonf. adj., $P < 0.05$ for pairs with two or three fledglings). Unsuccessful pairs also left the territory unguarded for longer periods of time than the other pairs (Mann-Whitney U test, $z = 2.54$ and $z = 2.60$ for less successful and successful pairs, respectively, Bonf. adj., both $P < 0.02$).

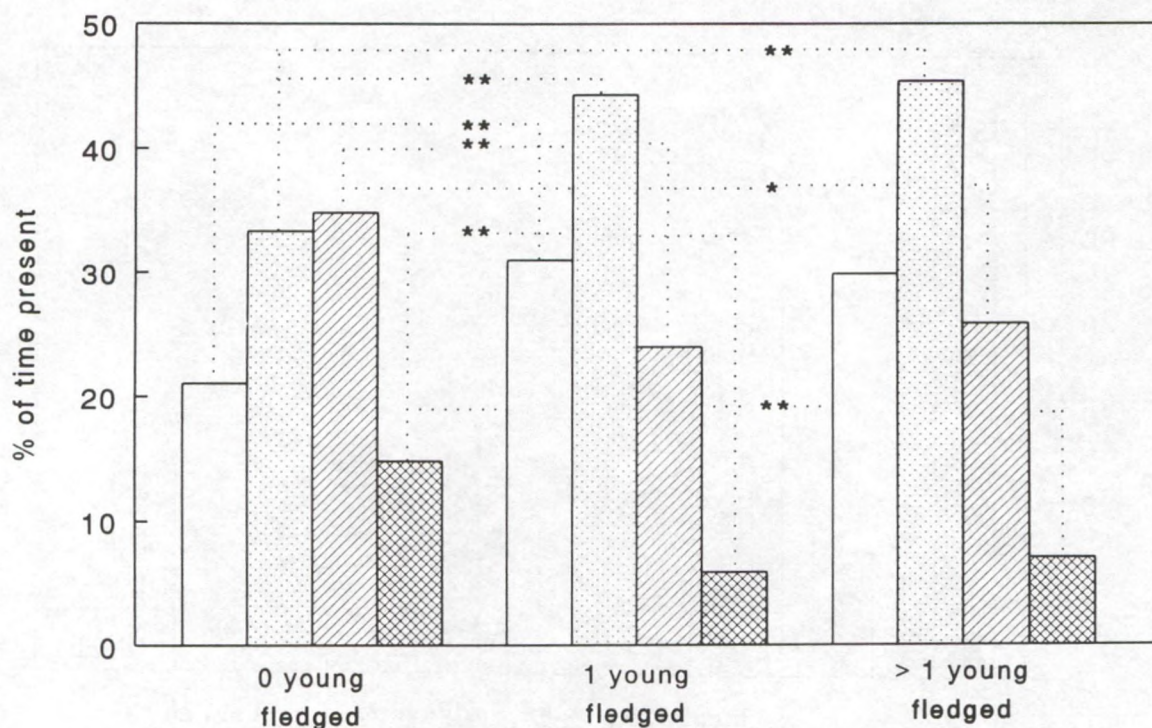


Figure 10. Territory attendance (data lumped for whole breeding season) in relation to reproductive success on Terschelling in 1992. Open bars, only female present; stippled bars, only male present; hatched bars, female and male simultaneously present; cross-hatched bars, territory left unguarded. Mann-Whitney U test, Bonf. adj., $P < 0.05$ (*) and < 0.02 (**), respectively.

In all three groups, a difference in territory attendance between sexes was present, with males spending longer periods of time alone at the territory than females (Figure 10).

4.3.3 Frequency and length of feeding trips

The number of feeding trips*observation period⁻¹ of three hours, varied considerably during the breeding season (Friedman two-way non-parametric analysis of variance, $\chi_r^2 = 13.9$ and $\chi_r^2 = 15.1$ for males and females, respectively, both $P < 0.05$). Trip frequency was highest before egg-laying and around hatching (ranging from 0.72 to 1.21 departures*observation period⁻¹ for individual males and 0.87 to 1.15 departures*observation period⁻¹ for individual females), with no significant differences among control and experimental groups.

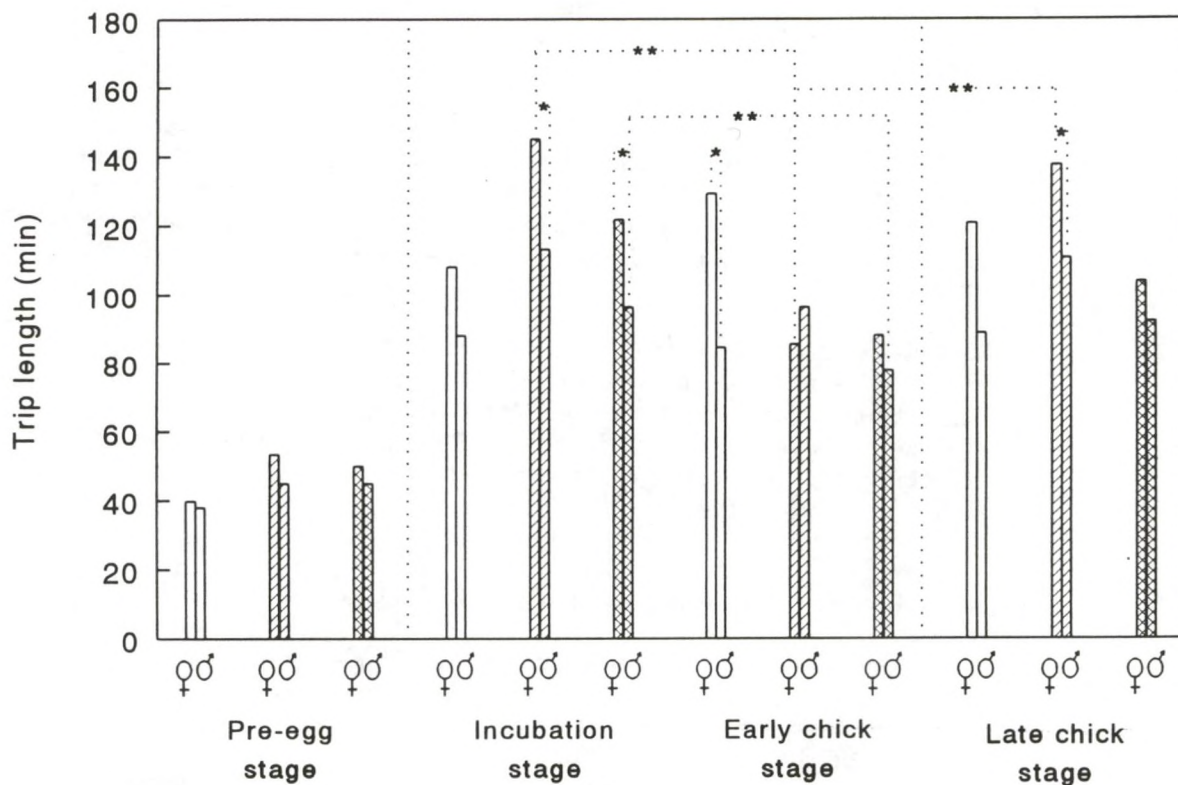


Figure 11. Average length (min) of feeding trips (excluding pairs that failed to hatch eggs) on Terschelling in 1992. Open bars: control pairs, hatched bars: pairs whose chicks were only provided with additional food during the first week after hatching, cross-hatched bars: pairs whose chicks were provided with additional food until fledging (early chick stage: first week after hatching, late chick stage: from second week after hatching until fledging). Wilcoxon signed-ranks test, $P < 0.05$ (*) and < 0.01 (**), respectively.

There were, however, significant differences between groups in the duration of the feeding trips during the season, and the differences in trip length between males and females also varied between groups.

In the control pairs, the mean length of feeding trips remained more or less stable in males and increased slightly (but not significantly) in females during the egg and chick stage. During all three stages of the egg and chick period, females remained on the feeding grounds for longer periods of time than males (Figure 11, Wilcoxon signed-ranks test, $z = 2.17$, $P < 0.05$ for early chick stage).

In contrast, the mean length of feeding trips of females from group 1 decreased dramatically, shortly after hatching (Wilcoxon signed-ranks test, $z = 2.78$, Bonf. adj., $P < 0.01$), but increased again after one week, when additional food was no longer provided (Wilcoxon signed-ranks test, $z = 2.48$, Bonf. adj., $P < 0.01$). Likewise, the difference in mean trip length

between mates, which had decreased considerably during the first week after hatching (Figure 11), became distinct again after week 1 (Wilcoxon signed-ranks test, $z = 2.25$, $P < 0.05$). No trend was discernible in the mean length of feeding trips in males from group 1.

In the pairs from group 2, the mean trip length decreased dramatically for males after hatching of the eggs (Wilcoxon signed-ranks test, $z = 2.75$, Bonf. adj., $P < 0.01$). This was paralleled by a strong decline in the difference in trip length between partners, which still differed significantly during the incubation period (Wilcoxon signed-ranks test, $z = 2.36$, $P < 0.05$).

Irrespective of the treatment, unsuccessful pairs remained on the feeding grounds on average, for longer periods of time than pairs that were successful in raising young (Kruskal-Wallis test, $H = 11.01$, $P < 0.01$ for the egg stage, $H = 5.50$ and 5.98 , both $P < 0.05$, for the two periods of the chick stage, respectively). No differences were found between groups in the frequency of trips.

4.3.4 Rate of chick-feeding and behaviour of chicks

We found considerable differences in the frequency of chick-feeding (Kruskal-Wallis test, $H = 12.56$, $P < 0.001$) and in the behaviour of the offspring (Kruskal-Wallis test, $H = 21.9$, $P < 0.001$) in relation to the food situation of the chicks. For broods of control pairs, the frequency of chick-feeding did not change during the chick stage and was significantly lower than for broods of pairs from group 2 (Table 8, Mann-Whitney U test, $z = 2.24$ and 3.02 , Bonf. adj., both $P < 0.05$, for the two periods of the chick stage, respectively), despite the fact that in the experimental pairs the frequency decreased significantly as the offspring became older (Wilcoxon signed-ranks test, $z = 2.40$, $P < 0.02$).

For broods of pairs from group 1, the frequency of chick-feeding resembled that for broods of group 2 during the first week after hatching and was significantly higher than that for broods of control pairs (Mann-Whitney U test, $z = 3.29$, Bonf. adj., $P < 0.02$). When we stopped providing the chicks from group 1 with additional food, the frequency decreased dramatically (Wilcoxon signed-ranks test, $z = 2.61$, $P < 0.01$). The frequency was significantly lower than that for chicks of the same age of pairs from group 2 (Mann-Whitney U test, $z = 4.09$, Bonf. adj., $P < 0.02$), but did not differ significantly from that for chicks of the same age of control pairs.

Table 8. Mean number of feedings $\cdot h^{-1}$ ($\pm$ SD) and proportion of time (% , means $\pm$ SD) that chicks hid in shelters (group 1, pairs whose chicks were provided with additional food during the first week after hatching; group 2, pairs whose chicks were provided with additional food until fledging) on Terschelling in 1992.

Age of chicks	Control pairs	Experimental pairs	
		Group 1	Group 2
Feeding frequency ¹			
0-7 days	0.28 $\pm$ 0.4 **	0.53 $\pm$ 0.4 ***	0.50 $\pm$ 0.4 **
> 7 days	0.23 $\pm$ 0.3	0.13 $\pm$ 0.3 *	0.35 $\pm$ 0.4
% of time chicks hid in shelter ¹			
0-7 days	44.7 $\pm$ 40.0 *	77.5 $\pm$ 30.0 **	85.1 $\pm$ 25.0
> 7 days	62.2 $\pm$ 39.9	61.7 $\pm$ 43.0 **	80.60 $\pm$ 33.0

The differences in feeding conditions between groups of chicks were reflected in the behaviour of the young. Offspring from control pairs spent a shorter period of time hidden in natural and artificial shelters than chicks from pairs of the experimental groups (Mann-Whitney U test, $z = 3.18$, Bonf. adj., $P < 0.05$, and $z = 3.98$, Bonf. adj., $P < 0.02$, for chicks of group 1 and 2, respectively). When the provision of food was stopped after one week for the broods from group 1, the chicks left their shelters frequently, roaming about in the territory. As a result, the chicks hid for a shorter period of time in their shelters than those of the same age from group 2, which were additionally fed until fledging (Table 8, Mann-Whitney U test, $z = 2.58$, Bonf. adj., $P < 0.05$).

Irrespective of the treatment, unsuccessful pairs fed their chicks on average less frequently (0.14 feedings $\cdot h^{-1}$) than pairs that produced either one fledgling (0.22 feedings $\cdot h^{-1}$) or two or three fledglings (0.36 feedings $\cdot h^{-1}$), the difference between unsuccessful pairs and successful reproducing pairs being significant (Kruskal-Wallis test, $H = 16.95$, $P < 0.001$).

4.3.5 Chick growth and body mass of chicks before fledging

Control and experimental pairs showed significant differences in growth parameters (average daily increase in mass between day 5 and day 30: $F = 30.53$, $P < 0.001$, asymptotic mass: Kruskal-Wallis test, $H = 7.12$, $P < 0.05$, age at which asymptotic mass was reached: ANOVA, $F = 16.33$, $P < 0.001$, average daily increase in wing length between day 10 and day 30: $F = 10.54$, $P < 0.005$).

Chicks of pairs from group 2 showed a faster daily increase in mass (Figure 12, upper graph) and wing length (Figure 12, lower graph) than both young of pairs from group 1 (mass: $F = 58.75$, $P < 0.001$, wing length: $F = 19.81$, $P < 0.005$) and those of control pairs (mass: $F = 17.29$, $P < 0.001$, wing length: $F = 9.58$, $P < 0.005$). Chicks of pairs from group 1 increased in mass more slowly than chicks of control pairs (Figure 12, upper graph, $F = 8.33$, $P < 0.001$). No difference was found between the two groups for the increase in wing length.

In both groups, chicks reached a lower asymptotic mass and did so at a later time than young of pairs from group 2 (Table 9, asymptotic mass: Mann-Whitney U test, control group and group 1, $z = 2.60$ and 2.24 , respectively, Bonf. adj., both $P < 0.05$; time: Student's t test, control group and group 1, $t = 4.57$ and 5.22 , respectively, Bonf. adj., both $P < 0.05$).

Table 9. Comparison of asymptotic level of daily mass increment (g) and day after hatching that this level was reached (means $\pm$ SD) between control and experimental broods (group 1, broods whose chicks were only provided with additional food during the first week after hatching; group 2, broods whose chicks were provided with additional food until fledging) on Terschelling in 1992.

Parameter ¹	Control pairs	Experimental pairs	
		Group 1	Group 2
Asymptotic level		*	
daily mass increment	712.0 $\pm$ 52.6	718.0 $\pm$ 84.0	* 822.0 $\pm$ 92.0
Day level reached	35.6 $\pm$ 1.5	35.4 $\pm$ 2.5	* 31.9 $\pm$ 1.9
		*	

¹Significant differences between groups indicated with asterisks (Mann-Whitney U test for differences in asymptotic mass level, Student's t test for differences in age (days after hatching) at which this level was reached, $P < 0.05$ (*)).

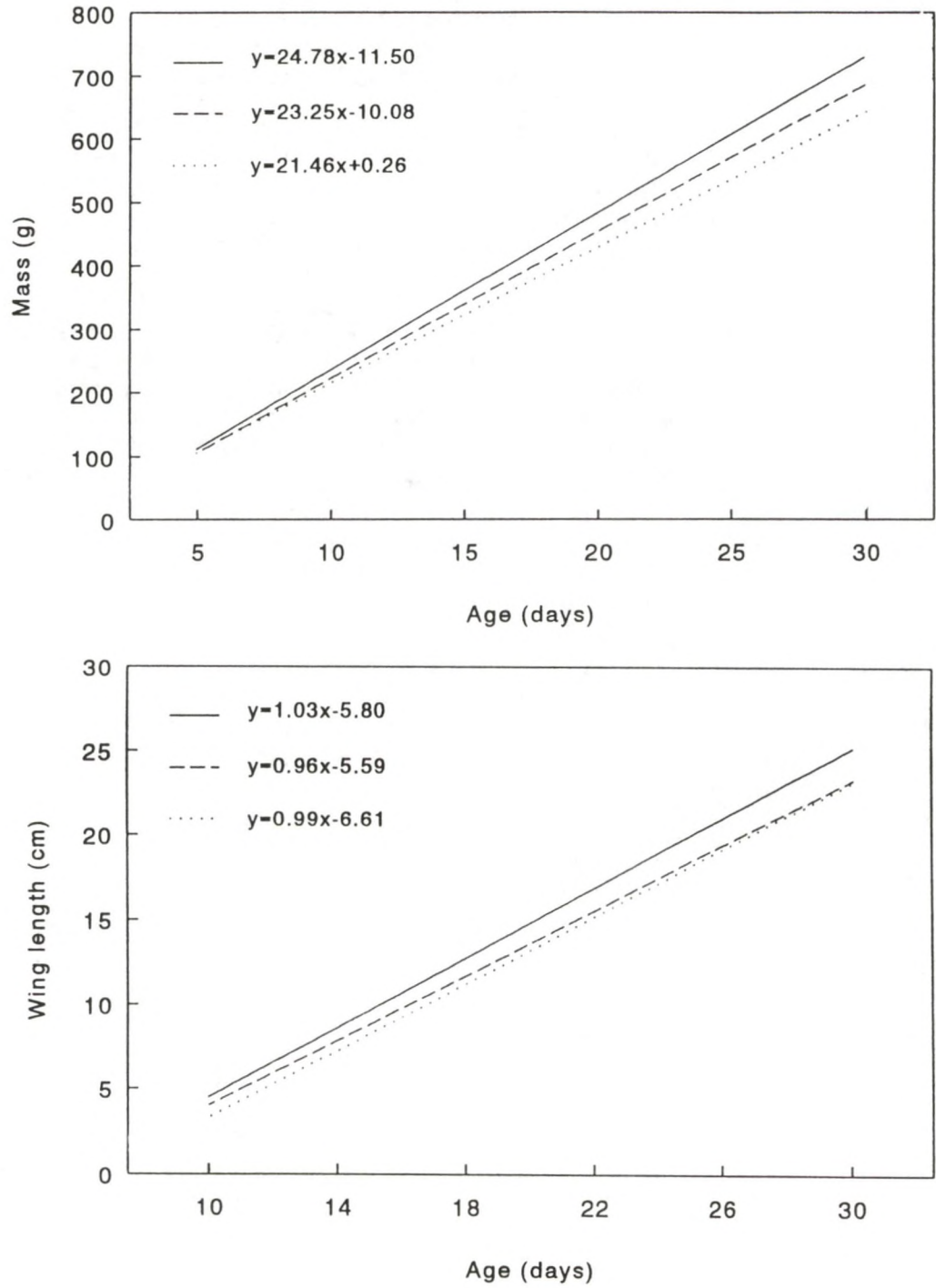


Figure 12. Linear regression lines of daily mass increment between day 5 and day 30 (upper graph) and daily increase in wing length between day 10 and day 30 (lower graph) on Terschelling in 1992. Dashed lines, control pairs; stippled lines, chicks which were only provided with additional food during the first week after hatching; solid lines, chicks which were provided with additional food until fledging.

No differences were found in the daily increase in tarsus length between day 5 and day 22. There was, however, a tendency, in particular during the first 10 days after hatching, for a faster increase in tarsus length in chicks of experimental pairs.

In 1992, we also fenced territories of Lesser Black-backed Gulls in the Maasvlakte-Europoort colonies and provided the chicks in these territories with wooden shelters, exactly as we did on Terschelling. We did, however, not provide the chicks with additional food. Chicks were regularly weighed and measured (Figure 13). No significant differences in the daily mass increment (21.68 g , $N = 23$), asymptotic mass ($683.4 \pm 144.3 \text{ (SD)}$, $N = 5$), age at which this mass was reached ($35.0 \pm 1.73 \text{ days}$, $N = 5$) and the daily increase in wing length (0.83 cm , $N = 14$) were found between these chicks and the chicks of the control pairs on Terschelling. Because several chicks prematurely may have escaped from the fenced territories at the Maasvlakte-Europoort colony sites, we cannot provide data about the reproductive output of the gulls studied at these two colony sites.

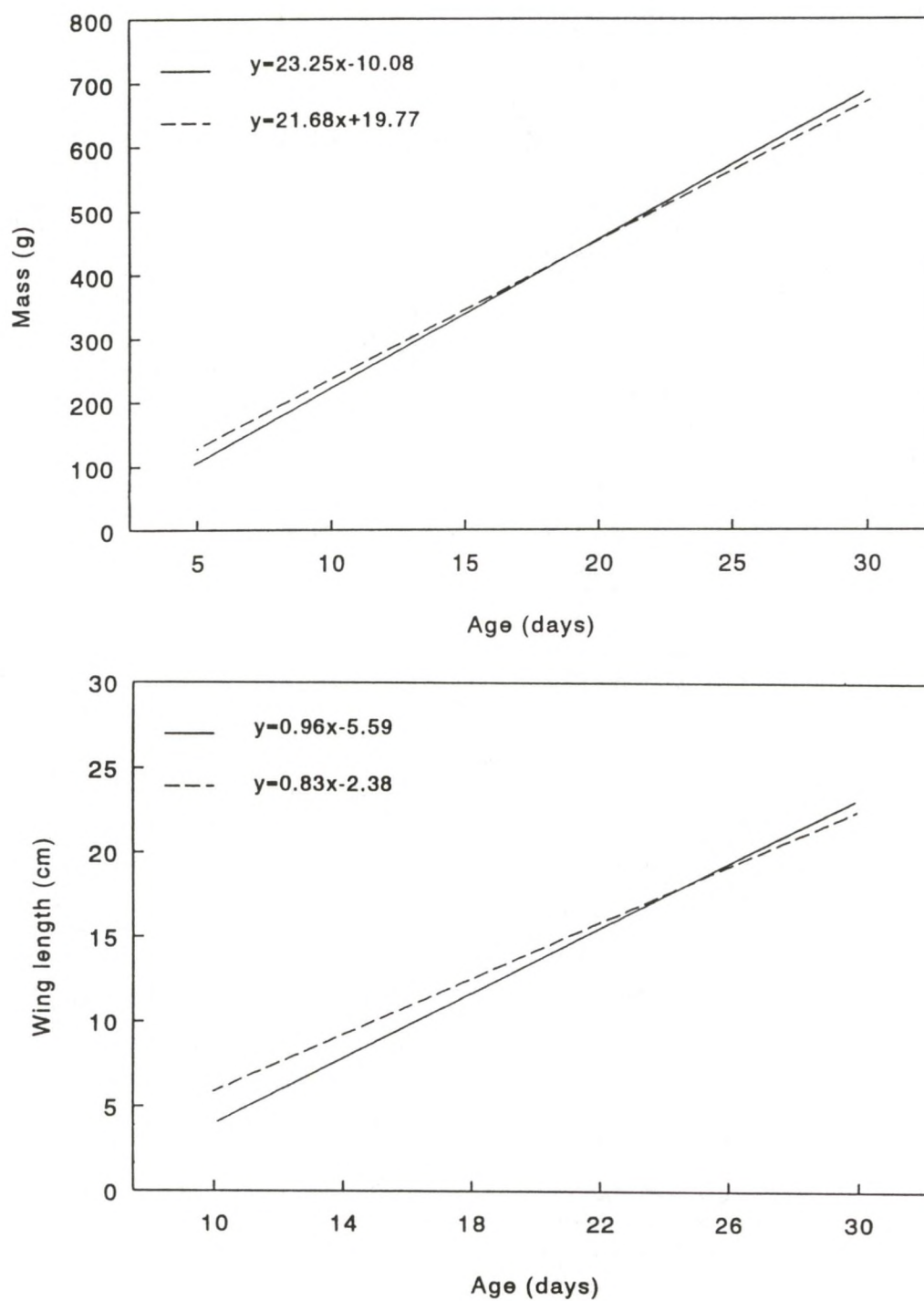


Figure 13. Linear regression lines of daily mass increment between day 5 and day 30 (upper graph) and daily increase in wing length between day 10 and day 30 (lower graph) in 1992. Solid lines, chicks of control pairs from Terschelling; dashed lines, chicks of pairs from the Maasvlakte-Europoort colonies.

4.4 DISCUSSION

4.4.1 Reproductive output

Lesser Black-backed Gulls nesting on Terschelling did not differ markedly in egg and clutch sizes and the number of eggs hatched pair^{-1} from those in other colonies of the species (e.g. Paludan 1951, Harris 1964, Chapter 3). The proportion of control pairs that raised at least one young to fledging age and the number of fledglings pair^{-1} were, however, very low compared with the reproductive output in other colonies, although similar low values have been found for the species in Finland (Hario 1985, 1989) and northern Norway (Strann & Vader 1992). Reproductive success on Terschelling collapsed during the middle of the 1980s and has been low ever since then (State Forestry Service, Terschelling, pers. comm.).

4.4.2 Mortality factors

Heavy predation of eggs and in particular chicks, by Herring Gulls, appeared to be the main factor affecting the present reproductive success on Terschelling. It is therefore remarkable that reproductive success did not improve after the local number of Herring Gulls, and therefore probably the predation pressure by the species, has decreased dramatically since the middle of the 1980s (Spaans *et al.* 1987, Noordhuis & Spaans 1992, State Forestry Service, Terschelling), suggesting that other factors may also play a role.

The present study shows that at present, food is in short supply on Terschelling during the chick stage. Local food shortages to Lesser Black-backed Gulls (this study) and also Herring Gulls (Spaans *et al.* 1987, Noordhuis & Spaans 1992) may even be the primary underlying factor for the present low reproductive success of the Lesser Black-backed Gulls, since local food shortages markedly increase the predatory behaviour in Herring Gulls (Paludan 1951, Harris 1964, Kadlec & Drury 1968, Spaans *et al.* 1987, Uttley *et al.* 1989). Many Herring Gulls specialise in feeding on only a few kinds of foods (McCleery & Sibly 1986). During periods of food deficiency, the gulls may become opportunistic predators of chicks of conspecifics and other gull species with which they form mixed breeding colonies (Parsons 1971, own observations). A summary of the relationships between food shortage and reproductive output is shown in Figure 14.

Whether chick predation by other gulls has also played a role at the Maasvlakte-Europoort colony sites in 1992 is unknown. Our data on chick growth and pre-fledging masses show, however, that the food condition for the chicks in these colonies was far from optimal that year, and confirmed the results we obtained from these colony sites in the comparative study we conducted during the same year (Chapter 3).

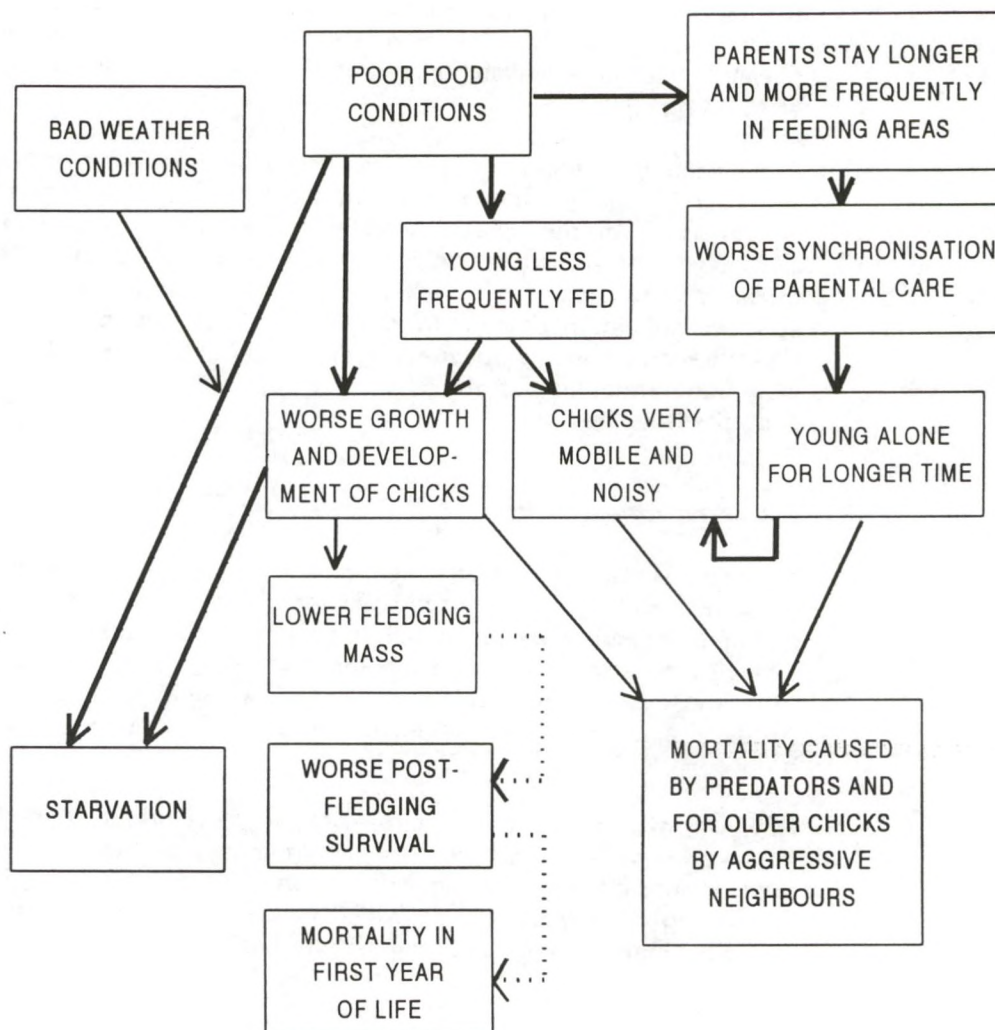


Figure 14. Relationships between food supply and chick and post-fledging survival when food is in short supply. Broken lines, data taken from literature.

4.4.3 The early chick stage

The impact of food on fledging success changed with the age of the chicks. During the first week after hatching, food affected chick survival mainly indirectly. Chicks for which food was not in short supply (chicks of group 1 during the first week after hatching, chicks of group 2) were quieter and remained more hidden in shelters than chicks that suffered from food shortages (control chicks, chicks of group 1 after the first week after hatching). Roaming about crying in the territory for longer periods of time, the latter were more susceptible to predation by robbing gulls than the former (own observations). Well-nourished chicks also grew faster than chicks for which food was in short supply, and so shortened the period that

the chicks were most susceptible to predation, by 1-3 days (based on their tarsus lengths 85% of all Lesser Black-backed Gull chicks found in pellets of Herring Gulls were taken during the first 8 days after hatching, Bukaciński *et al.*, in prep.).

Better feeding conditions of the chicks also resulted in a higher synchronisation and in more equitability of the parental duties, and therefore in an enhancement of the chicks' chances of survival (Burger 1987, Morris 1987). The better feeding conditions resulted in a shortening of the lengths of the feeding trips of the adults, and consequently in the necessity of a strict co-ordination of parental duties. This also allowed partners to be present simultaneously at the territory for longer periods of time, resulting in a better guarding of the chicks in a period that young were most susceptible to predation.

4.4.4 The late chick stage

Food also played a significant role after the first week after hatching. When the provision of additional food was stopped after the first week after hatching (experimental group 1), chick survival, chick growth and the behavioural patterns of chicks and adults of this group differed significantly from those of broods which were provided with additional food until fledging, and were not significantly different from those of the control broods.

However, after the first week after hatching, the effect of food provision acted more directly, and was mainly reflected in the growth rate and fledging masses of the young, rather than in differences in predation rates by robbing adult gulls. Chicks which were provided with additional food increased faster in mass and wing length than chicks of control broods. The former also reached a higher mass at fledging and reached it at an earlier age than the latter. The lower fledging mass of chicks for which food was in short supply will probably result in a lower post-fledging mass, poorer condition and a higher mortality during the first winter.

After the first week after hatching, the behaviour patterns of adults and young were still related to the feeding conditions of the chicks, and in this way affected the survival of the chicks. For adults of chicks for which food was in short supply, feeding trips lasted longer, the frequency of feeding was lower, and the inequality of parental care between the partners of a pair was more distinct than for adults whose chicks were provided with additional food. The former also left their chicks unguarded for longer periods of time than the latter, and undernourished chicks roaming about for longer periods of time in the territory were more likely to be killed by neighbours defending their territories than chicks for which food was not in short supply. Consequently, after the first week of hatching, young suffering from food shortages are susceptible to both starvation (lower feeding rates, slower growth rates) and killing by neighbours defending their territories.

4.5 Conclusion

Our research showed strong direct and indirect effects of food abundance on growth and survival of young Lesser Black-backed Gulls. An effect of food abundance on these breeding parameters was also found recently by Harris (1978) for the Atlantic Puffin *Fratercula arctica*, by Quinney *et al.* (1986) for Tree Swallows *Tachycineta bicolor* and by Smith & Arcese (1991) for Song Sparrows *Melospiza melodia*. No positive effect of the provision of additional food was found by Wehle (1983) for Tufted *F. cirrhata* and Horned Puffins *F. corniculata*, by Ricklefs *et al.* (1987) on Leach's Storm Petrel *Oceanodroma leucorhoa* and by Navarro (1991) for the Cape Gannet *Sula capensis*. These authors emphasise, however, that in their study areas food was abundant for the species involved. Likewise, in 1993, when clupeids, an important type of food for young Lesser Black-backed Gulls (Chapter 3), was much more abundant off Terschelling than in 1992 (Chapter 5), no differences in growth and fledging survival were found between experimental and control pairs (Chapter 5).

Summarising, the Terschelling data show that local food shortages affect fledging success in colonial nesting seabirds both directly (through slower growth and development of feathers of chicks) and indirectly (through changes in the behaviour of adults and chicks, resulting in a higher predation risk in the early chick stage and a higher chance of being attacked by neighbours defending their territories in the late chick stage).

5 EXPERIMENTAL EVIDENCE FOR THE RELATIONSHIP BETWEEN FOOD SUPPLY AND CHICK SURVIVAL IN LESSER BLACK-BACKED GULLS NESTING ON TERSCHELLING: THE SITUATION IN A YEAR WHEN FOOD IS NOT IN SHORT SUPPLY

5.1 Introduction

During the early 1980s, the number of Lesser Black-backed Gulls nesting on Terschelling stabilised at approximately 13,000 pairs, whilst the reproductive success collapsed in the middle of that decade and has remained low ever since then (Chapter 2). Egg and in particular chick predation by Herring Gulls is the main cause for the present low reproductive output for that colony site. Fledging success was, however, found to be higher in years that clupeids, one of the main foods of Lesser Black-backed Gull chicks on Terschelling (Chapter 3), were more abundant off Terschelling than in years when this was not the case. This suggests that during the chick stage food may be in short supply for Lesser Black-backed Gulls nesting on this island.

In 1992, we studied experimentally the relationship between food supply, parental care and chick survival to test the hypothesis that food was indeed in short supply at that moment (Chapter 4). By providing chicks with additional food we proved that in that year control pairs had difficulties in supplying their chicks with food. Chicks which were provided with additional food until fledging grew faster, reached a higher fledging mass, and reached this mass a few days earlier than control chicks. The former also showed a significantly higher survival rate until fledging than the latter. The study revealed that food affected chick survival not only directly through a slower growth and development of the feathers than normal, but also indirectly through changes in the behavioural patterns of adults and chicks, resulting in a higher predation risk during the early chick stage and a higher chance of being attacked by neighbours defending their territories during the late chick stage.

In 1993, we repeated the study to investigate whether the results found in 1992 were typical for that colony site. However, we restricted the study to observations on mass increment and on reproductive success. No observations were made on the behaviour of chicks and adults that year.

5.2 Study area and methods

We conducted the study at the same two study plots as in 1992. For details on data collection and experimental design we refer to Chapter 4. We followed the same procedures as in 1992 to make the studies in the two years as comparable as possible. In 1993, clutches were randomly divided into a control group and only one experimental group. Chicks of the latter were provided with the same amount of additional food (sprat) until fledging as in 1992. So in 1993, we skipped the experimental group whose

chicks were only provided with additional food during the first week after hatching. For statistical tests used, we also refer to Chapter 4. Level of significance was set at $P < 0.05$ in all statistical tests.

5.3 Results

5.3.1 Breeding parameters

Breeding success for control and experimental pairs is summarised in Table 10. In total, we marked 111 nests (69 clutches of three eggs, 27 clutches of two eggs and 15 nests of one egg). Fifty-four per cent of the eggs found disappeared before hatching, incomplete clutches even before full incubation started. As in other years predation by Herring Gulls was the main cause of egg loss. Ten eggs did not hatch because the eggs were infertile or showed an early embryonic mortality. Of the 118 eggs that hatched only 47 young (39.8%) fledged. Again predation by other gulls, in particular of the small chicks, was the main mortality factor.

As a result of the high predation rate, only 25 experimental and 21 control broods were left over for the chick-feeding experiment. The 46 nests were distributed over two different habitats: (1) open areas with low vegetation (height mainly a few cm) and (2) tall vegetation (height a few dm) surrounding the open areas. Of the 21 control nests 6 were situated in the open areas and 15 in the tall vegetation. For the experimental nests these numbers were 14 and 11, respectively. The difference between control and experimental broods was not significant. So, we lumped the data for the two habitats for the calculation of reproductive output (Table 10).

Hatching success was 70% ($N = 63$) for the control group and 77% ($N = 75$) for the experimental group (difference not significant). Of the 44 control chicks 34% fledged, of the 58 experimental chicks 52% did so (difference not significant). Nevertheless, the difference in the total reproductive success (control group 24%, $N = 63$, experimental group 40%, $N = 75$) appeared to be just significant ($\chi^2 = 4.02$, $0.02 < P < 0.05$). As a result, the average production*pair⁻¹ amounted to 0.71 fledged young*pair⁻¹ for the control group and 1.20 fledged young*pair⁻¹ for the experimental group.

*Table 10. Clutch size, hatching success, fledging success and average reproductive output*pair⁻¹ on Terschelling in 1993 (control = used in feeding experiment as control group, experimental = chicks provided with additional food until fledging, others = eggs (partially) preyed upon before hatching, c/2 and c/1 = clutches which started full incubation incompletely).*

Clutch size	<i>N</i> nests	<i>N</i> eggs	<i>N</i> hatched	<i>N</i> fledged	Fledged *pair ⁻¹
c/3					
Control	21	63	44 (70%)	15 (34%)	0.71
Experimental	25	75	58 (77%)	30 (52%)	1.20
Others	23	69	2 (3%)	0 (0%)	0
c/2	27	54	13 (24%)	2 (15%)	0.07
c/1	15	15	1 (7%)	0 (0%)	0
Total	111	276	118 (42.8%)	47 (39.8%)	0.42

5.3.2 Chick growth and body mass of chicks before fledging

In 1993, control and experimental pairs showed no significant differences in daily mass increment between day 5 and day 30 (Figure 15, upper graph), asymptotic mass, day at which this mass was reached (Table 11) and daily increase in wing length between day 10 and 30 (Figure 15, lower graph).

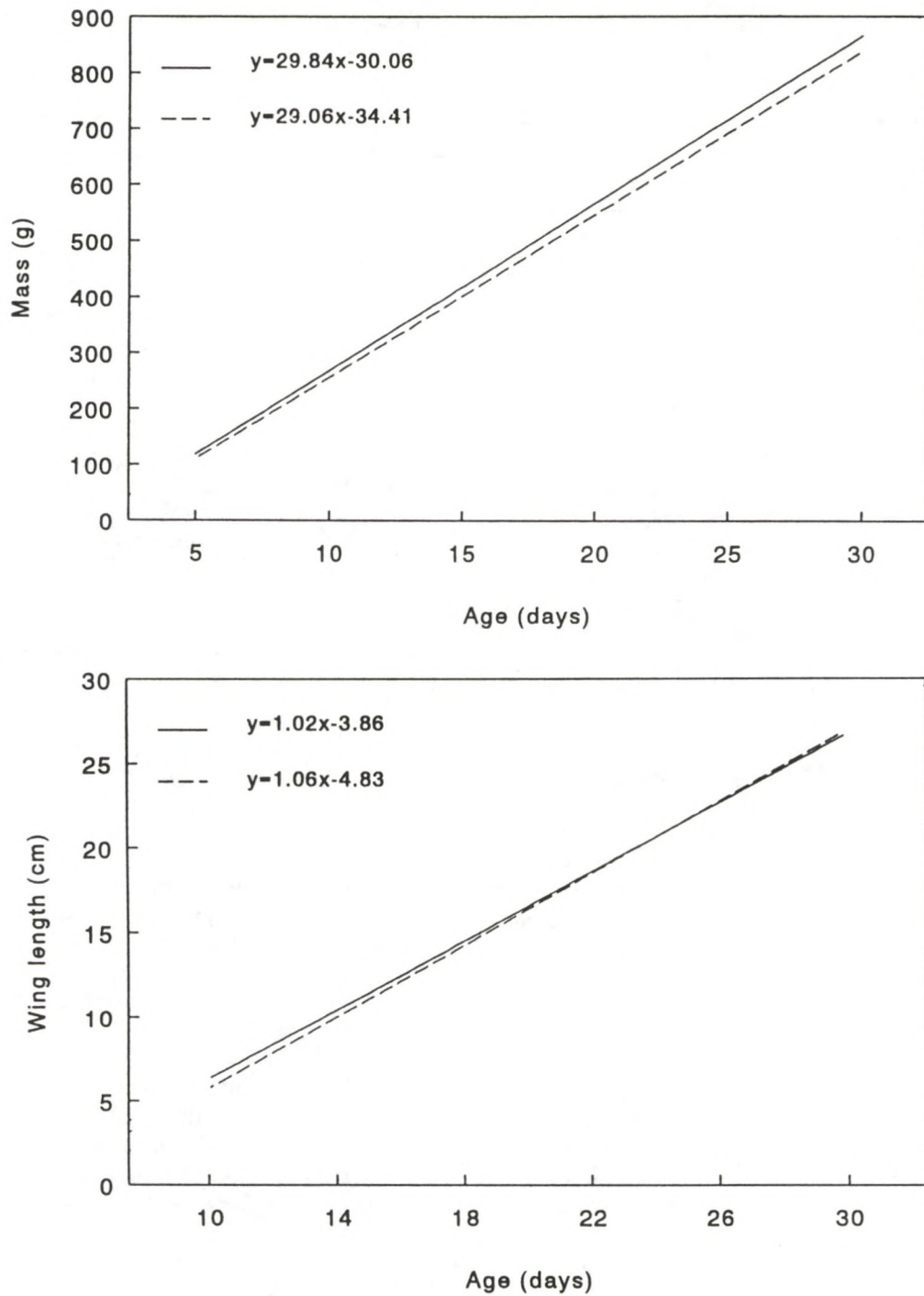


Figure 15. Linear regression lines of daily mass increment between day 5 and day 30 (upper graph) and daily increase in wing length between day 10 and 30 (lower graph) on Terschelling in 1993. Solid lines, control pairs, dashed lines, experimental pairs.

Table 11. Comparison of asymptotic level of daily mass increment (g) and day after hatching that this level was reached (means $\pm$ SD) between control and experimental broods on Terschelling in 1993.

Parameter	Control pairs	Experimental pairs
Asymptotic level		
daily mass increment	799.3 $\pm$ 130.5	816.1 $\pm$ 105.9
Day level reached	31.0 $\pm$ 2.6	30.3 $\pm$ 2.6

In 1993, chicks increased faster in mass and wing length and reached the asymptotic mass at an earlier age than in 1992 (control pairs: daily mass increment $F = 103.38$, $P < 0.001$, daily increase in wing length $F = 44.30$, $P < 0.001$, age at which asymptotic mass was reached Student's t test, $t = 4.06$, $P < 0.01$; experimental pairs: daily mass increment $F = 81.82$, $P < 0.001$, daily increase in wing length $F = 55.76$, $P < 0.001$, age at which asymptotic mass was reached Student's t test, $t = 2.15$, $P < 0.05$). There were, however, no differences in pre-fledging masses between the two years in either group of chicks.

5.4 DISCUSSION

In 1993, we found no significant differences in fledging success, daily increase of mass and wing length of chicks, and fledging mass of young between control and experimental broods. Neither did we find a significant difference in hatching success between these groups. The direction of the trend in hatching and fledging success was, however, identical (in experimental pairs larger than in control pairs), so that on average the reproductive output in experimental pairs was higher than in control pairs, although the difference was only barely significant.

In 1993, the average number of fledged young*pair⁻¹ was lower than in 1992, because egg and chick predation was much higher in 1993 than in 1992. Daily mass increment and daily increase of wing length, however, was much higher in 1993 than in 1992 (Figure 16). For the mass at fledging, no differences between the two years were found.

The lack of differences between control and experimental pairs in 1993 suggests that in this year food was more abundant in the period of chick rearing than in 1992 (Chapter 4). This is corroborated by the feeding frequency of Sandwich Tern *Sterna sandvicensis* chicks on the isle of Griend, situated between Terschelling and the main land of the province of Friesland, in 1992-1993 (Table 12). In 1993, Sandwich Terns provided their chicks with 80% more fish than in 1992 and almost twice as many

clupeids, a main food item in the Lesser Black-backed Gull chick diet (Noordhuis & Spaans 1992, Chapter 3), as in 1992. From these data we conclude that at present small clupeids play a central role in the reproductive output of Lesser Black-backed Gulls nesting on Terschelling.

Table 12. Number of fish (means chick⁻¹ * day⁻¹) supplied to Sandwich Tern chicks on the isle of Griend in 1992-1993 (data taken from Brenninkmeijer & Stienen 1994).

Year	N total	N clupeids	N <i>Ammodytes</i> spp.	N others
1992	5.2	2.4	2.7	< 0.1
1993 ¹	8.9	4.5	4.3	< 0.1
1993 ²	8.5	4.9	3.6	< 0.1

¹subcolony 6, ²subcolony 8.

6 GENERAL DISCUSSION

Lesser Black-backed Gulls have increased dramatically in number (1994 over 34,000 breeding pairs), since the species colonised The Netherlands in 1926. The species is presently well-distributed along the coasts of the Delta area and the Wadden Sea islands, with only small numbers of gulls nesting in-between (Van Dijk *et al.* 1994). At many colony sites, the numbers of breeding pairs are still increasing. Nevertheless, on Terschelling, the oldest and since the beginning the largest colony in the country, the number of breeding pairs stabilised in the early 1980s and have remained at that level since then. Reproductive output collapsed in the middle 1980s, and has remained low up till now, except in 1986, a year when small clupeids were relatively abundant off the coast. This observation suggests that at present food in most years is limited for Lesser Black-backed Gulls nesting on Terschelling.

In 1992 and 1993, we provided additional food to chicks from the day the first chick in a nest was born until the chicks were 7 days old (in 1992 only) or had reached the fledging stage (1992, 1993) to test this hypothesis. In 1992, chick survival and chick growth were much higher in chicks that were provided with additional food until fledging than in those that were not additionally fed. Differences in chick survival were related to both a higher chick mortality through starvation and a higher predation of chicks by Herring Gulls in control chicks than in experimental chicks.

Control chicks ran a higher predation risk, because they grew slower, hid less in natural and artificial shelters, and roamed about crying for longer periods of time than chicks which were provided with additional food. The behaviour patterns of the parents of control chicks also differed from those of experimental chicks. Feeding trips of control pairs lasted longer than those of experimental pairs. As a result, control pairs were present simultaneously at the territory for shorter periods of time and absent simultaneously for longer periods of time than pairs whose chicks were provided with additional food. Moreover, females of the former were present alone at the territory for shorter periods of time than the latter. All differences mentioned resulted in a larger chick predation in control pairs than in experimental pairs. As soon as the provision of additional food to chicks of experimental pairs was stopped, adults and chicks reacted as control pairs did, indicating that food supply was indeed the causal factor in this respect.

On Terschelling, many Lesser Black-backed Gull chicks are robbed by Herring Gulls, even in years in which small clupeids are more abundant. In contrast to Lesser Black-backed Gulls, Herring Gulls nesting on the island feed mainly in the tidal area of the Wadden Sea and on land (Noordhuis & Spaans 1992). Only a small proportion feeds at the North Sea. Here, adult Herring gulls are mainly confined to a small strip of water along the coast. On average, Lesser Black-backed Gulls feed at much greater distances of the colonies (Bekhuis 1994, Camphuysen in press). Herring Gulls can therefore take much less profit of the greater abundance of clupeids at sea

in such years than Lesser Black-backed Gulls. This may explain why Herring Gulls continue robbing chicks of both Lesser Black-backed Gulls and conspecifics in such years. The data on chick predation by Herring Gulls indicate that at present also for this species the local food situation is far from optimal.

The comparative study on food conducted in 1992-1993 showed that Lesser Black-backed Gulls nesting along the Dutch coast predominantly feed at the North Sea. For Terschelling, this is corroborated by observations of the flight directions of breeding birds to and from the colony (Noordhuis & Spaans 1992, Bekhuis 1994, M. Bukacińska and D. Bukaciński).

Gulls nesting in the northern Delta area, however, also fed to a great extent on land, as indicated by the high proportion of pellets and regurgitations with terrestrial organisms and garbage. These colony sites were also characterised by smaller egg sizes, slowly growing chicks and a lower pre-fledging condition of the chicks. The small average volume of the smallest egg compared to the volume of the largest egg in the same clutch indicates that gulls nesting in these colonies suffered from food shortages. If so, it is obvious that terrestrial foods are inferior to marine fish and were a second choice for the gulls.

Both in 1992 and 1993, Lesser Black-backed Gulls nesting on Terschelling laid eggs of normal sizes, while chick growth of young, randomly sampled outside the enclosures, reached average values compared to chicks of flourishing colonies. In 1992, however, pre-fledging masses were rather low, compared with neighbouring colonies and the situation in 1993. Thus, the comparative study does not fully support the conclusion of the experimental study that food was a limiting factor during the chick stage in 1992.

The comparative study, however, did not include observations on reproductive success. In 1992, outside the enclosures, reproductive success was very low, reflecting the very high predation rate of, in particular, lean, starving chicks by Herring Gulls. Within the enclosures, however, the predation risk for chicks of control pairs was much lower than outside the enclosures, because all chicks had artificial shelters which protected them against bad weather condition and predators. As a result, within the enclosures control pairs had relatively more lean and slow growing chicks than outside these areas.

The results of the comparative and experimental studies show that for colonies where food is in very short supply during the chick stage and chick predation by other gulls is very high, recording of only chick growth and pre-fledging masses is insufficient to assess the local food situation. It is therefore recommended to measure also the reproductive output in future monitoring programmes.

Gadids, flatfish and clupeids formed the main marine fish species groups found in the pellets and regurgitations along the coast of The Netherlands, although large differences between colonies existed. Noordhuis & Spaans

(1992) came to the same conclusion based on data from Terschelling from the middle of the 1980s. In pellets, gadids and flatfish predominated. In the regurgitations, half of the foods consisted of clupeids, emphasising the importance of this species group for young Lesser Black-backed Gulls. Flatfish and gadids are mainly caught by the gulls as discards (Noordhuis & Spaans 1992, Camphuysen 1994b, this paper) and are important during the entire breeding season.

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The experimental studies on Terschelling were conducted by Patricia Bekhuis (1993), Monika Bukacińska (1992), Dariusz Bukaciński (1992) and Dirk Janssens (1993). In 1992, deep-frozen fish for the experiment was provided by the Netherlands Institute for Sea Research, Texel. The fish was transported to Terschelling by the 'Phoca' of NBLF. The Nature Museum of Terschelling placed a refrigerator at our disposal to keep the fish deep-frozen. The State Forestry Service was very helpful in transporting material to the study area. The Biological Station 'Schellingerland' provided accommodation during our stay on the island. Miriam Hall corrected the English text. Allix Brenninkmeijer, Kees Camphuijsen, Fred Cottaar, Mardik Leopold, Erik Stienen, Kees Verbeek and Harry Vercuijsse provided useful comments on an earlier draft of this report.

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SAMENVATTING

De kleine mantelmeeuw is een van de weinige broedvogels langs onze kust die het grootste deel van zijn voedsel uit de Noordzee op enige afstand van de kust haalt. De soort is daardoor gevoelig voor veranderingen in het mariene milieu, met name voor eventuele veranderingen in de commerciële boomkorvisserij. De soort is wijd verspreid langs onze kust en daardoor een goede soort om geografische verschillen in voedsel en broedbiologische parameters te onderzoeken.

In 1992 en 1993 zijn met hulp van vrijwilligers in acht (1992 zeven) kolonies gegevens over eigrootte, conditie van de oudervogels vlak voor het uitkomen van de eieren (vier kolonies), groei van de kuikens en voedsel (alleen 1992) verzameld. Daarnaast is op Terschelling door middel van een bijvoerproef onderzocht in hoeverre het slechte broedsucces aldaar sinds de jaren tachtig het gevolg is van voedselschaarste.

De kleine mantelmeeuw heeft zich in 1926 in ons land gevestigd (Terschelling drie paren). De soort is eerst langzaam, vanaf de jaren zestig exponentieel, toegenomen tot ruim 34.000 paren in 1992. In het begin van de jaren tachtig is op Terschelling het aantal broedparen gestabiliseerd. Sinds het midden van deze decade is ook het reproductiesucces sterk gedaald. Alleen in jaren met veel haringachtigen voor de kust, is het succes iets hoger dan in andere jaren.

Langs de kust van het vasteland van Noord- en Zuid-Holland is de soort sinds de jaren tachtig sterk in aantal achteruitgegaan (invloed van de vos). In het Deltagebied en in het Waddengebied is de soort sindsdien sterk in aantal toegenomen (deels door verhuizing van vogels van het vasteland: kleurringwaarnemingen).

Het voedsel is gedurende het gehele broedseizoen voor het grootste deel afkomstig uit de Noordzee (braakballen vooral kabeljauwachtigen en platvissen die door de commerciële boomkorvisserij als discards over boord zijn gegooid, braaksels jongen ook veel haringachtigen). De broedvogels uit het noordelijke Deltagebied (Maasvlakte and Europoort) foerageren ook veel op het land (vogels, zoogdieren, regenwormen, emelten, afval van vuilstortplaatsen).

De vogels uit deze twee kolonies hebben ook de kleinste eieren, terwijl de jongen het slechts groeien en de laagste uitvlieggewichten hebben. Verondersteld wordt dat zeevoedsel de eerste keus is van de meeuwen en vogels in staat stelt grotere eieren en betere jongen voort te brengen dan wanneer zij op het land foerageren.

In 1992 werd op Terschelling experimenteel vastgesteld dat de soort in dat jaar ter plekke te maken had met een ernstig voedseltekort. Zowel controle als experimentele nesten waren ingegaasd en voorzien van extra schuilmogelijkheden. Jongen die dagelijks werden bijgevoerd, hadden niet alleen een

hoger broedsucces dan kuikens van controle paren, maar zij groeiden ook sneller, hadden een hoger uitvlieggewicht en bereikten dat gewicht eerder dan vogels die niet bijgevoerd werden.

Vogels die alleen de eerste week werden bijgevoerd, ontwikkelden zich gedurende die week als de vogels die tot aan het uitvliegen werden bijgevoerd, en als de controle proef zodra het bijvoeren werd stopgezet. Dit bewijst dat een voedseltekort inderdaad de causale factor is. De hoge mortaliteit onder de controle groep was niet alleen een gevolg van verhonger, maar vooral van een grotere predatie van de kuikens door zilvermeeuwen. De grotere kans op predatie hing samen met de slechte lichamelijke conditie van de kuikens en met gedragsverschillen bij kuikens en ouders die roof door zilvermeeuwen bevorderden.

De groei van ingegaasde kuikens op de Maasvlakte en in Europoort was identiek aan die van de kuikens van de controle groep op Terschelling.

In 1993 werd de proef op Terschelling op beperkte schaal herhaald. Er werden toen geen verschillen gevonden tussen kuikens uit de controle en de experimentele groep. Verondersteld wordt dat dit is terug te voeren met een talrijker voorkomen van haringachtigen in 1993 voor de kust van Terschelling.

Het is opvallend, dat in 1992 de slechte voedselsituatie voor de kust van Terschelling niet kon worden opgemaakt uit de kuikengroei van vogels die buiten de perken opgroeiden. Dit kwam doordat bij de vergelijking tussen de kolonies geen aandacht kon worden besteed aan het reproductiesucces. Uit het verschil in kuikensterfte en groei van de kuikens in en buiten de exclusures wordt geconcludeerd dat zwakke en langzaam groeiende kuikens door predatie niet het einde van het kuikenstadium haalden (de ingegaasde kuikens waren doordat zij de beschikking hadden over extra schuilmogelijkheden voor een groot deel tegen roof gevrijwaard). Het is dus zaak bij monitoring-programma's in broedkolonies van zeevogels die tot doel hebben de kwaliteit van de voedselgebieden van deze vogels te meten, ook het reproductiesucces in de vergelijking te betrekken.

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