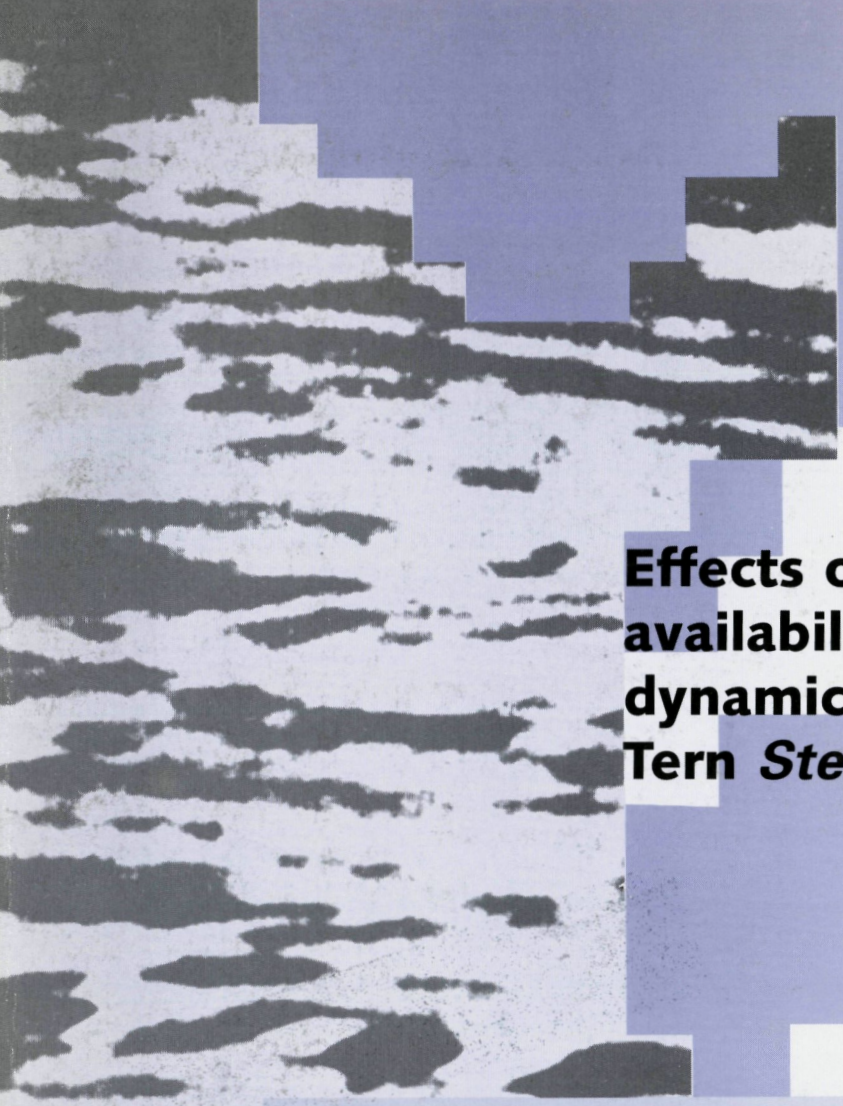

Effects of changing food availability on population dynamics of the Sandwich Tern *Sterna sandvicensis*

Beleidsgericht
ecologisch onderzoek
van de
Noordzee/Waddenzee

BEON

IBN-DLO
RIVO-DLO
RWS-RIKZ

B

IZWO
Instituut voor Zeewetenschappelijk Onderzoek (vzw)
Institute for Marine Scientific Research
VICTORIALAAN 3 - B - 8400 OOSTENDE BELGIUM
Tel. +32-(0)59 - 32 10 45 — Fax: +32-(0)59 - 32 11 86

Effects of changing food availability on population dynamics of the Sandwich Tern *Sterna sandvicensis*

662

E.W.M. Stienen (IBN-DLO)
A. Brenninkmeijer (IBN-DLO)

april 1998

BEON Rapport nr. 98-3

BEON project IBN 95 H 24

ISSN 0924-6576

CONTENTS

SUMMARY 5

1 INTRODUCTION 7

1.1 Target of the study 8
1.2 Theme 9
1.3 Relationships with other studies 9
1.4 Ecology of the Sandwich Tern 10
1.5 Ecology of prey fishes 11

2 MATERIALS AND METHODS 14

2.1 Research on Griend 14
2.2 Sampling prey fish availability 15
2.3 Statistics 16

3 RESULTS 17

3.1 Formation and composition of the population 17
3.2 Population dynamics 19
3.3 Emi- and immigration 24
3.4 Effect of chick condition on post-fledging survival 29
3.5 Food brought to the colony 31
3.6 Prey fish availability 38
3.7 Food provisioning in relation to prey fish availability 45
3.8 Prey fish availability influencing the terns' foraging behaviour 48

4 DISCUSSION 51

4.1 Composition of the population 51
4.2 Survival 51
4.3 Emigration to other colonies 53
4.4 Food supply in relation to food availability 54
4.5 Food availability influencing the distribution of the terns 55
4.6 Changing food situation affecting population dynamics 56

5 RECOMMENDATIONS 63

6 ACKNOWLEDGEMENTS 64

CONCLUSIONS 65

REFERENCES 66

SUMMARY

During the 20th century the numbers of nesting Sandwich Terns *Sterna sandvicensis* in The Netherlands have fluctuated heavily. After the collapse in the 1960s the number of breeding pairs increased only slowly and stabilised at a low level. Earlier studies showed that population trends may be related to changes in food availability. Since the Sandwich Tern is a highly specialised piscivorous seabird, which feeds almost exclusively on four species of fish (herring, sprat, sandeel and greater sandeel), the Sandwich Tern is probably highly vulnerable to changes in the availability of its prey species. To determine the key factors influencing population size the Institute for Forestry and Nature research (IBN-DLO), in co-operation with the Netherlands Institute for Fisheries Research (RIVO-DLO) and the National Institute of Coastal and Marine Management (RIKZ), started a study on the population dynamics of the species in 1995. The study was conducted on Griend, the largest Sandwich Tern colony in western Europe. The target of this study was twofold, namely:

(1) To assess to what extent emigration to other colonies takes place.
(2) To come to a better understanding of the importance of food availability during the breeding season for chick and post-fledging survival, and ultimately for population dynamics.

In 1992-1997, the provisioning of food to the chicks fluctuated strongly from year to year. Parallel with these changes the condition of the breeding adults and parental effort changed. These parameters can be regarded as indicative for the food situation in the local foraging areas. Changes in adult condition, the amount of food supplied to the chicks (in particular herring) and parental effort coincided with a parallel change in the number of breeding pairs. In years in which these parameters indicated a scarcity of food, the number of breeding pairs was accordingly low. In 1995, a sampling programme was started to investigate whether the assumed fluctuations in food availability as measured in the colony on Griend, were reflected by changes in food abundance in the local foraging areas. Isaac's Kidd Middwater Trawl net catches indicated that food availability decreased from 1995-1997. Although a parallel decrease was seen in the terns population size, the fish catches did not reflect other changes in the colony on Griend. The used sampling method was probably not suitable to detect changes in the amount of food available for the terns. However, the fish sampling programme made clear that fish availability was greatly influenced by water clarity. In relatively clear water the fish was present at greater depths, thus beyond the reach of foraging terns. Sandeels were evenly distributed over the five sampling locations, but herring availability increased towards the northern positions. At sampling points where herring availability was high, the number of foraging terns were accordingly high.

Along with the changes in the number of breeding pairs, the age composition of the population on Griend showed large fluctuations. In 1995, the proportion

of older birds was relatively high, whereas in 1996 and in 1997 a large proportion of young birds nested on Griend. These changes were related to a high local survival rate of 3- and 4-year old birds in 1996 and 1997.

A considerable part of both the population nesting on Griend and the Danish population consists of birds immigrated from other colonies. However, site fidelity of the terns on Griend was much higher than in Denmark. The majority of the emigrating terns settled in colonies less than 200 km away from their original colony.

1 INTRODUCTION

There are several known cases of piscivorous seabirds, which as a result of the collapse of their prey fish, were not able to raise any young or drastically decreased in numbers during a series of years (Heubeck 1988, Monaghan *et al.* 1989, Vader *et al.* 1990, Bailey 1991, Suddaby & Ratcliffe 1997). As a reason for the collapse of the prey fish population one often pointed towards the commercial fishery, although a causal relationship with fishery could never be proved. The fact that the collapse of only one species of prey fish can result in a decreased reproduction rate in some seabird species demonstrates the sensibility of these animals for fluctuations in their food availability.

Throughout the 20th century, the Dutch population of Sandwich Terns *Sterna sandvicensis* has shown large fluctuations in the number of breeding pairs. Three times human intervention (through shooting of adult birds, egging and poisoning with organochlorines) caused severe population collapses (figure 1). After the collapse in the 1960s, the population recovered only slowly and stabilised at a level about one third of the former.

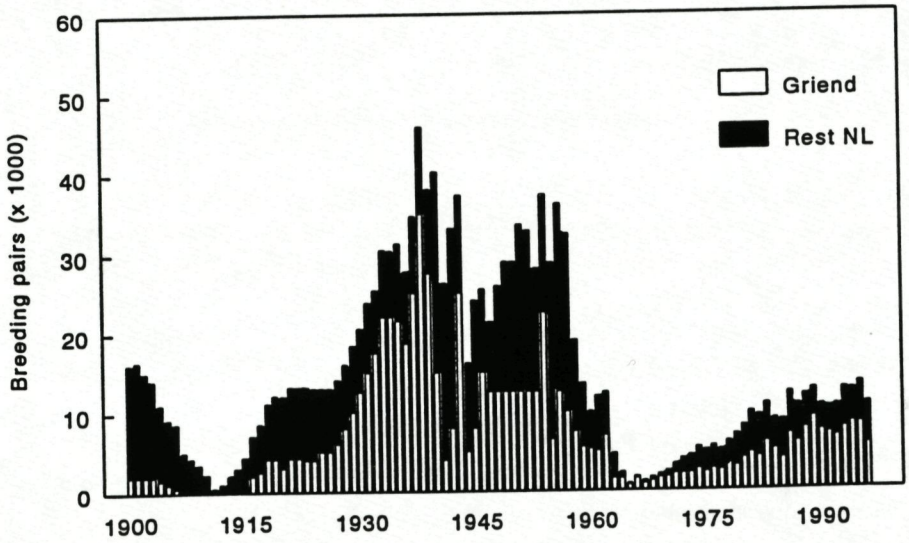

Figure 1. Reconstruction of the population size of the Sandwich Tern during the twentieth century (Brenninkmeijer & Stienen 1992, completed with own data).

The central question in this respect is: **What is the reason for the slow recovery and why did the number of breeding Sandwich Terns stabilise at such a low level?**

The stabilisation of the number of breeding pairs at a low level can have a number of potential causes. In the breeding areas habitat loss (both breeding and foraging habitat), pollution, decreased prey fish abundance, decreased fish availability (e.g. through changes in water clarity), shifts in the foraging areas and emigration to other colonies may play an important role. In the wintering areas tern catching (especially of juvenile birds) and increased commercial fishery can be mentioned as potential threats to the population. The influence of water clarity on the foraging success of terns and a possible shift in foraging areas have been studied in 1992-1993 by the Institute of Forestry and Nature Research (IBN-DLO) (Stienen & Brenninkmeijer 1994). The effects of contamination of eggs and chicks of terns (in particular Common Terns) have been studied in 1992-1993 by the National Institute of Coastal and Marine Management (RIKZ) in association with the Universities of Utrecht and Wageningen (Bosveld *et al.* 1993). Emigration to other breeding colonies has been studied within the framework of the present project in 1996 by the IBN-DLO (Brenninkmeijer & Stienen 1997).

Factors such as contamination, emigration and habitat loss do not seem to affect the Dutch population of Sandwich Terns in recent years. A number of other aspects, such as food availability and mortality in the wintering areas have been insufficiently studied and will be examined within the framework of this project by means of a co-operation between the IBN-DLO, the RIKZ and the Netherlands Institute for Fisheries Research (RIVO-DLO).

1.1 Target of the study

The aim of this study is tripartite, namely:

(1) To assess mortality rates in the African wintering quarters
(2) To assess to what extent emigration to other colonies takes place
(3) To come to a better understanding of the importance of food availability during the breeding season to population dynamics, chick and post-fledging survival. In this respect the following questions can be distinguished:

* Is there a relationship between prey fish availability in the foraging areas and food supply in the colony?
* To what extent does food availability in the local foraging areas affect growth, condition and survival of the chicks?
* What is the influence of growth rate and condition of the chicks on post-fledging survival?
* Which population dynamic parameters are influenced by food availability?

The final aim is to build a model on population dynamics of the Sandwich Tern with special attention for effects of food availability and human stress-factors.

Since data on mortality rates in the African wintering quarters became available just before finishing this report, these results will be presented elsewhere.

1.2 Theme

This study will lead to a better understanding of the importance of local food availability to the occurrence of the Sandwich Tern. Both natural and man-induced fluctuations in food availability can either directly (through the number of fledged chicks) or indirectly (through post-fledging survival) influence the number of Sandwich Terns nesting in The Netherlands. By means of this research it must become clear to what extent the abundance of prey fish, as well as the temporal and spatial distribution of the fish influences population dynamics of the Sandwich Tern. The study contributes to the following questions of policy set by BEON:

- What is the importance of certain habitats for the Sandwich Tern (main point Habitat Disturbance)
- What are the short- and long-term negative effects of commercial fishery in the North Sea and the Wadden Sea (main point Effects of Fishery).

1.3 Relationships with other studies

The quality of various water systems gives cause for concern in many countries. In the "Derde Nota Waterhuishouding" of the Dutch Ministry of Transport, Public Health and Water Management, the Sandwich Tern has been chosen as a species of which the population size may be indicative for the quality of the marine environment. In order to develop a model on population dynamics of this species (BEON*ECOLMOD), the IBN-DLO performed a literature study on the ecology of the Sandwich Tern (Brenninkmeijer & Stienen 1992), a study on the relationships between water clarity and foraging success of terns (Stienen & Brenninkmeijer 1994), and a study on the influence of kleptoparasitism on food supply and reproductive output of the Sandwich Tern (Geschiere 1993, Stienen & Brenninkmeijer 1994). The IBN-DLO has further performed studies on the effects of weather and tide on food provisioning to the chicks (Brenninkmeijer & Stienen 1994) and on growth and survival of chicks (1992-1994). In 1994, co-workers of the IBN-DLO, the RIKZ and Vereniging Natuurmonumenten together with volunteers of the Dutch Seabird Group, performed a pilot study on the influence of food availability on the foraging behaviour of the Sandwich Tern.

These studies showed, that in 1992 and 1993 the amount food supplied to

the chicks was low compared with the period 1966-1970 and compared with colonies abroad. Furthermore, they revealed that food supply and species composition of the food can vary greatly between years, leading to large year to year variations in growth rate and pre-fledging condition of the chicks. The aim of the present study is to assess the influence of pre-fledging condition on post-fledging survival. These results are necessary for a complete picture of the population dynamics of the Sandwich Tern. For further development of a model on population dynamics, supplementary data on emi- and immigration are necessary. Research in the foraging areas of the Sandwich Tern have to contribute to our knowledge of the effects local food availability on the number of nesting Sandwich Terns.

1.4 Ecology of the Sandwich Tern

The colonial breeding Sandwich Tern nests at sites with no or only a scarce vegetation (mainly islands) lying within 15 km from the foraging areas. The breeding colonies are very dense (2-10 nests per m^2) and the inter nest distance in the centre of the colony is about 25 cm, within pecking distance from each other. In Europe, Sandwich Terns prefer to nest in association with Black-headed Gulls *Larus ridibundus* and sometimes in association with other tern species. The majority of the eggs are laid between late April and late May. Per nest one, two or seldom three eggs are laid. It takes about 25 days of incubating before the eggs hatch. Both parents take part in incubating the eggs and feeding the young. Approximately 28 days after hatching the chicks are able to fly. In The Netherlands, the reproductive output is on average 0.7 chick per pair (Veen 1977, Brenninkmeijer & Stienen 1992).

In The Netherlands there are three important colonies, namely Griend (5600 pairs in 1996), De Hooge Platen (2800 pairs in 1996) and Hompelvoet/Markenje (1800 pairs in 1996). In 1996, 2 new colonies were established in the Dutch Wadden Sea (Rottum and on Schiermonnikoog), which both increased to 800-1000 pairs in 1997. During the past decade Griend comprised the largest Dutch colony (5000-8000 breeding pairs). Also on northwestern European scale Griend is the largest colony (10-16% of the total northwestern European population). Apparently, breeding conditions on Griend are extremely favourable. The island is flooded during most winters, which contributes to the maintenance of the scarce vegetation and the washing away of sources of infectious diseases. Furthermore, there are no land predators or human disturbances, factors which can adversely influence breeding success. A third factor of importance is the presence of a suitable foraging area at a short distance from the colony. The foraging area ranges from Griend to a few kilometres to the north of Vlieland and Terschelling (Veen 1977, 1994, Brenninkmeijer & Stienen 1992, 1994).

Sandwich Terns are specialised piscivorous seabirds. In the southern North Sea they feed almost exclusively on small Clupeidae (herring *Clupea harengus* and sprat *Sprattus sprattus*) and on Ammodytidae/Hyperoplidae (sandeel

Ammodytes tobianus and greater sandeel *Hyperoplus lanceolatus*). Also the food provisioned to the young consists mainly of these four species of prey fish. For each prey offered to their young, a parent has to make a foraging flight of approximately 20 km and normally brings only one fish at a time to the colony (Veen 1977, Brenninkmeijer & Stienen 1992, 1994). The specialised piscivorous character of the Sandwich Tern makes this species highly vulnerable for changes in food availability.

1.5 Ecology of prey fishes

Herring The North Sea herring is part of the species *Clupea harengus*. Within the North Sea, one can distinguish several races. At present time only the autumn spawners are important for the Dutch Sandwich Terns. Before the closing of the Zuiderzee (now Lake IJsselmeer 1932), the so called Zuiderzee herring was also important for the Sandwich Tern. The present spawning areas important for the Dutch sandwich Terns are situated in the western and northwestern parts of the North Sea and in the English Channel. They are situated in such a way that the prevailing currents normally take the freshly hatched larvae to the shallow, nutritious waters of the eastern North Sea, which serve as a 'nursery'. After they have used up their yolksac reserves, the larvae depend on the production of plankton in the neighbourhood of their place of birth. At the onset of the winter period, the larvae have reached a length of 15 mm. In November-March, most larvae of the western part of the North Sea drift towards the shallow coastal waters of the eastern North Sea and the Skagerrak/Kattegat. Larvae born in the English Channel form an exception to this rule. They hatch in December-January, when the production of plankton has nearly ceased. These larvae have a larger yolk-sac to their disposal, which makes it possible for them to survive the first weeks of their life. For these larvae the distance to the nurseries in the southern North Sea is relatively short (Corten 1996).

Half year old herring larvea with a mean length of 42mm and born in the western central North Sea enter the Wadden Sea from half February till half April. From half March until half May smaller larvae (32 mm) born in the English Channel ("Downs herring") drift into the Wadden Sea (Corten & Van de Kamp 1976). When the larvae reach the coastal area in early spring, they soon reach the metamorphose phase. When they reach a length of 5 cm, they change into small herrings (so-called 'bliekjes'). In June the larvae from the western part of the central North Sea will be of a suitable length to serve as food for the Sandwich Tern chicks. The 0.5 year old herring from the English Channel, however, are too small to feed to the Sandwich Tern chicks. They can, however, serve as food for adults and fledglings in July.

Of the 1.5 year old herring the smallest individuals winter in the Wadden Sea. Unpublished data from herring larvae surveys performed by the RIVO-DLO in the period 1979-1987 show, that these herring migrate from the Wadden Sea to the North Sea in March-April. By half April they all have left the Wadden

Sea.

Herring born in the central and northern parts of the North Sea grows at a faster rate than herring born in the southern North Sea. In the Skagerrak/Kattegat, but not in the North Sea, the growth rate during the first two years depends on the size of the population (Corten 1996). Since 1925 the growth rate of herring shows a steady increase and as a consequence the herring reaches maturity at a lower age. In the period 1925-1965 the mean length at a certain age showed a steady increase and is on a high level since (Burd 1984, unpublished data from RIVO-DLO).

The herring stock in the North Sea has shown large fluctuations throughout the 20th century. In 1975, the stock size of the total North Sea was reduced to 80 000 tons, 2% of the size just after World War II. In 1977, the EU proclaimed a ban on the fishery of herring in the North Sea. The herring stock increased again, but very slowly. Only the herring in the English Channel clearly recovered after 1978. In 1981, a limited fishery of this part of the stock size was allowed again. In 1981-1986, the recruitment of young herring gradually increased, resulting in an increase of the stock size. Since 1989 the spawning stock size decreased again and in 1995 the threshold of the so called 'minimum biological acceptable level' of 800 000 tons was reached. However, the population changes of the total North Sea do not reflect the situation in the separate populations. The herring in the English Channel, for example, produced a series of strong year classes since 1978, while in the same period the recruitment of other stock components was far beneath the normal level (Corten 1990, 1996).

The commercial fishery is not the only factor which may affect the abundance of herring. Also natural changes in the ecosystem can have large effects on stock size. For example, the reason for the low recruitment in the period 1972-1979 is assumed to be a disturbed circulation of water masses. As a result of the decelerated currents the larvae did not reach the nursery areas in time. There are also some clues for natural processes gradually changing the abundance of herring. These processes influence the relative importance of the separate spawning areas and the distribution of herring during both winter and summer (Corten 1990).

Sprat The North sea stock consists of spring and autumn spawners. Maturity is reached when 2 year old (10 cm). Due to the high natural mortality rates sprat older than 4 years (15 cm) is seldom found. The most important stocks are found in the eastern part of the North Sea, but in the 1970's a lot of sprat was caught in the western North Sea. This coincided with a reduced inflow of ocean water into the North Sea. It seems that the North Sea sprat consists of different local spawning groups, which can adapt fast to changing hydrographic circumstances. In winter sprat has a more inshore distribution in the eastern North Sea and in the Wadden Sea.

Young sprat with a length of 3-6 cm migrates into the western part of the Dutch Wadden Sea in July-August. From then on the numbers increase,

reaching a maximum in October, when sprats measure 6-8 cm. In January, the young sprat migrate to the coastal areas and stay there together with the adult sprat (9-12 cm). Adult sprat leave the coastal waters in May, probably to spawn offshore. The young sprat, still present in the coastal waters, grow further to a length of 10 cm in August and also leave the coastal areas (Fonds 1978).

Sandeel Although sandeel in terms of biomass is the most important species in the North Sea, our knowledge on the biology of this species is poor. Sandeel escape through the meshes of most fishing gear, but are caught in high numbers in particular by Danish fisherman (Macer 1966). There are some indications that sandeels, in contrast to other smelt species, are buried in the sediment at night and swim near the surface during daylight (Macer 1966, Appenzeller & Leggett 1995), thus probably they are only available for foraging Sandwich Terns some time after sunrise until a few hours before sunset.

Catches of sandeel in the western part of the Dutch Wadden Sea in 1963 and 1964 show that this species is mainly found in the coastal areas of the Wadden Sea and to a lesser extent in the Wadden Sea itself. The numbers increase during spring and decrease again in autumn, suggesting that sandeels winter offshore. Only the smaller individuals (up to 12 cm) probably winter in the Wadden Sea (Fonds 1978).

Greater sandeel Greater sandeels are predominantly caught in the coastal areas of the Wadden Sea and only a minority is caught in the Wadden Sea itself. Young greater sandeel (6-8 cm) appear in the Wadden Sea in autumn. The numbers of one-ringers (i.e. 1-year old and 9-12 cm) in the Wadden Sea increase in May-June and reached its maximum in August. Older individuals are mainly caught in the period April-June. This predator fish probably follows its favourite prey species, young herring and sprat (Fonds 1978). During the past years, greater sandeel has probably been an unimportant prey species for the Sandwich Tern on Griend. Catches using an Isaac's Kidd Midwater Trawl net in the period 1995-1997 show that the abundance of this species was extremely low (paragraph 3.6).

2 MATERIALS EN METHODS

2.1 Research on Griend

Ring recoveries During the courtship period in 1995-1997, the codes on the metal rings were read from a hide, using a binocular or a telescope. Reading of the rings took place at open spots in the colony and at the beaches of Griend, where large groups gathered for courtship display and roosting in the late afternoon. Almost all rings were read in the three hours before sunset and most of the readings referred to displaying birds. Some additional rings were recovered by catching the birds on their nests.

Exchange with other colonies We used the ring recoveries to calculate the proportion of foreign birds in the population on Griend. The Dutch ringing centre provided us the number of chicks and adults actually ringed for all European countries in the period 1960-1995. Of each country we reconstructed the number of breeding pairs in this period (for a detailed description see Brenninkmeijer & Stienen 1997). Per country and year a conversion factor was obtained by dividing the number of ringed chicks and adults, respectively by the number of breeding pairs and fledglings. Using these conversion factors all recoveries (both read with a telescope and caught on the nest) on Griend in 1995 and 1996 were analysed. Birds recovered in 1997 were excluded from the calculations since not all ringing details of this year are yet received.

In order to calculate the degree of emigration, some assumptions about survival rates of young and adults had to be made. We assumed that (1) 80% of the chicks actually fledged; (2) first-year survival was 50%; (3) subsequent annual survival was 90%. Using these assumptions, we calculated the number of ringed individuals still alive in a certain year. The degree of emigration was calculated by dividing the number of individuals seen on Griend (corrected for the chance of recovery) by the number of birds thought to be alive (for a detailed description of this method see Brenninkmeijer & Stienen 1997).

Food brought to the colony Food supply was observed from a hide using a binocular or by bare eye. The hide was placed at a few metres distance of a courtship area or a colony. Prey length was estimated using the adult's bill as a reference (mean bill length = 54.6 mm, N = 93). Estimating prey size (in quarters of a bill length) was calibrated per observer by holding fishes of different species and length in front of a stuffed tern's bill at comparable distance. Calibration greatly increased the accuracy of the estimates and the largest error of an experienced observer was 0.25 bill lengths. Both for herring/sprat and for sandeel/greater sandeel an allometric equation relating fish length to mass was obtained, using least square analysis on fish found in the colony and caught in the Wadden Sea (figure 2).

Each year, a few days before hatching 75-100 nests were enclosed with 50 cm high wire netting to avoid the chicks from walking away. Within these

enclosures approximately 20 chicks of known age were colour-dyed for individual recognition. We followed the same chicks every day as much as possible. Observations on food provisioning to the chicks were made during the complete course of the daylight period (4:30h - 22:30h).

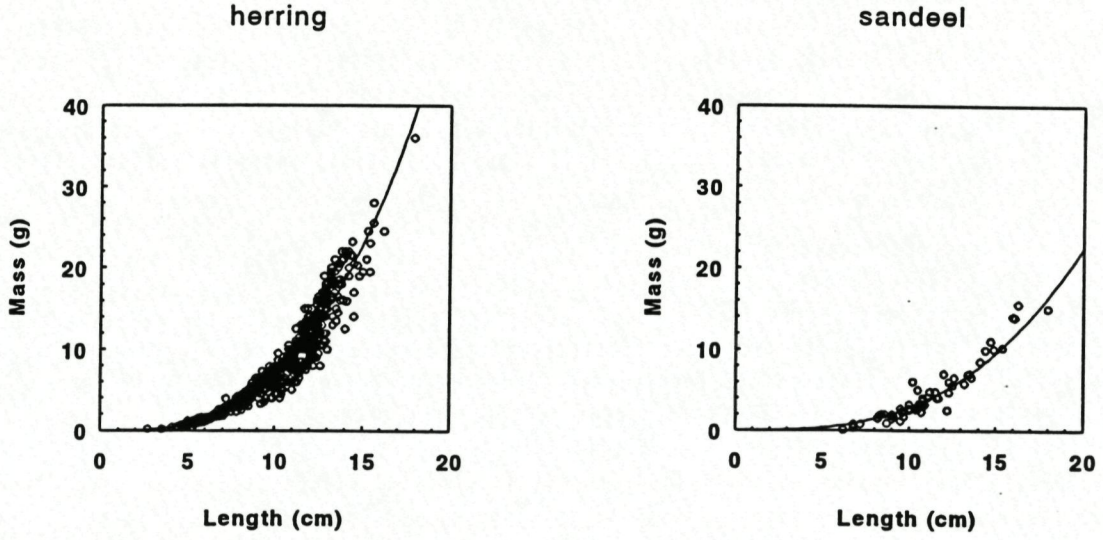

*Figure 2. Length-mass relationship in herring and sandeel. Herring: Mass = 0.00682 * length$^{2.996}$, N = 825, R^2 = 0.94; Sandeel: Mass = 0.00296 * length$^{2.982}$, N = 73, R^2 = 0.97.*

Growth and condition of chicks Within 3 days from hatching as many chicks as possible were ringed using stainless steal rings. The age of the chicks was estimated using the size of the yolksac, the size of the total head (i.e. head and bill) and the plumage as a reference. Every 3 days we tried to retrap the chicks to measure growth (body mass, head size and the maximal wing chord). When non-ringed chicks were caught, they were ringed and biometrics were taken. As a measurement for the chick's condition we used the relative deviation of measured body mass from expected body mass at a certain head size (chapter 3.4).

2.2 Sampling prey fish availability

In each of the years of 1995-1997, during 3 periods of 5 days, several hauls of approximately 30 minutes were performed at 5 fixed locations near the Vliestroom (Vliestroom, Westmeep, Stortemelk, Vliesloot and Oosterom). The five locations covered most of the foraging area of the Sandwich Terns breeding on Griend (Stienen & Brenninkmeijer 1994). Unfortunately, it was not possible to sample in the shallow coastal waters north of Vlieland and Terschelling. We used an Isaac's Kidd Midwater Trawl net (IKMT-net) with a

mesh size of 6 mm. This net samples only the upper 2 m of the water layer, in accordance with the diving depth of terns (Borodulina 1960, Dunn 1972). During each haul, the water clarity (using a Secchi-disk) and water temperature was measured. The 3 sampling periods corresponded with the courtship period, the early chick stage (chicks less than 1 week old) and the late chick stage (in the week before fledging) of the terns. In order to compare the fish samples with the fish brought to the colony we used only herring/sprat measuring 5-12 cm and sandeel/greater sandeel measuring 6-17 cm in the analyses. Average numbers instead of cumulative numbers were used, since cumulative numbers can give a skewed picture. When for example a shoal of fish is caught this can have an unrealistic large effect on the cumulative numbers, while by using average numbers this effect will be less pronounced. As the numbers of the fish were not normally distributed the numbers were Ln-transformed.

2.3 Statistics

For data processing and all tests other than regression analyses, SPSS-PC+ was used. Regression analyses were performed with Genstat.

3 RESULTS

3.1 Formation and composition of the population

Ring sightings on Griend show, that in all 3 study years the first 2-year-old terns were seen relatively late in the season: 9-26 days later than the first recovered bird (figure 3). Obviously, young inexperienced birds settle late in the season. The same, but less obviously, holds for 3-year-old terns. This picture can be greatly biased by the number of chicks ringed in the subsequent years. Therefore we corrected the ring sightings for ringing effort and expressed them in relative numbers (figure 3). After correction for the ringing effort, it becomes obvious that the proportion of young birds (2-3 years old) increased during the course of the season, whereas the proportion of older birds decreased (figure 3). In 1995 and in 1996, the increase in the proportion of young birds was clear, but in 1997 it was less obvious. In the beginning of the season in 1996 and in 1997, the pattern shows large alterations. This is probably due to the small sample sizes. After day 125 the pattern was fairly smooth in all three years. Strikingly, the proportion of the 1991-cohort was small in all three years. The proportion of 1990-birds sharply decreased from 1995 onwards. Both in 1996 and in 1997, the proportion of birds younger than 4 years (almost 75% at the end of the season) was much higher than in 1995 (less than 40% at the end of the season). Of course these relative proportions can be biased by the number of year classes present in a certain year, but in chapter 3.2 it will be shown that also local survival differed greatly between observational years and cohorts.

Conclusions

* *Older birds (> 3 year old) start their courtship activities earlier in the season than younger birds.*
* *The age composition of the population greatly varied between years*

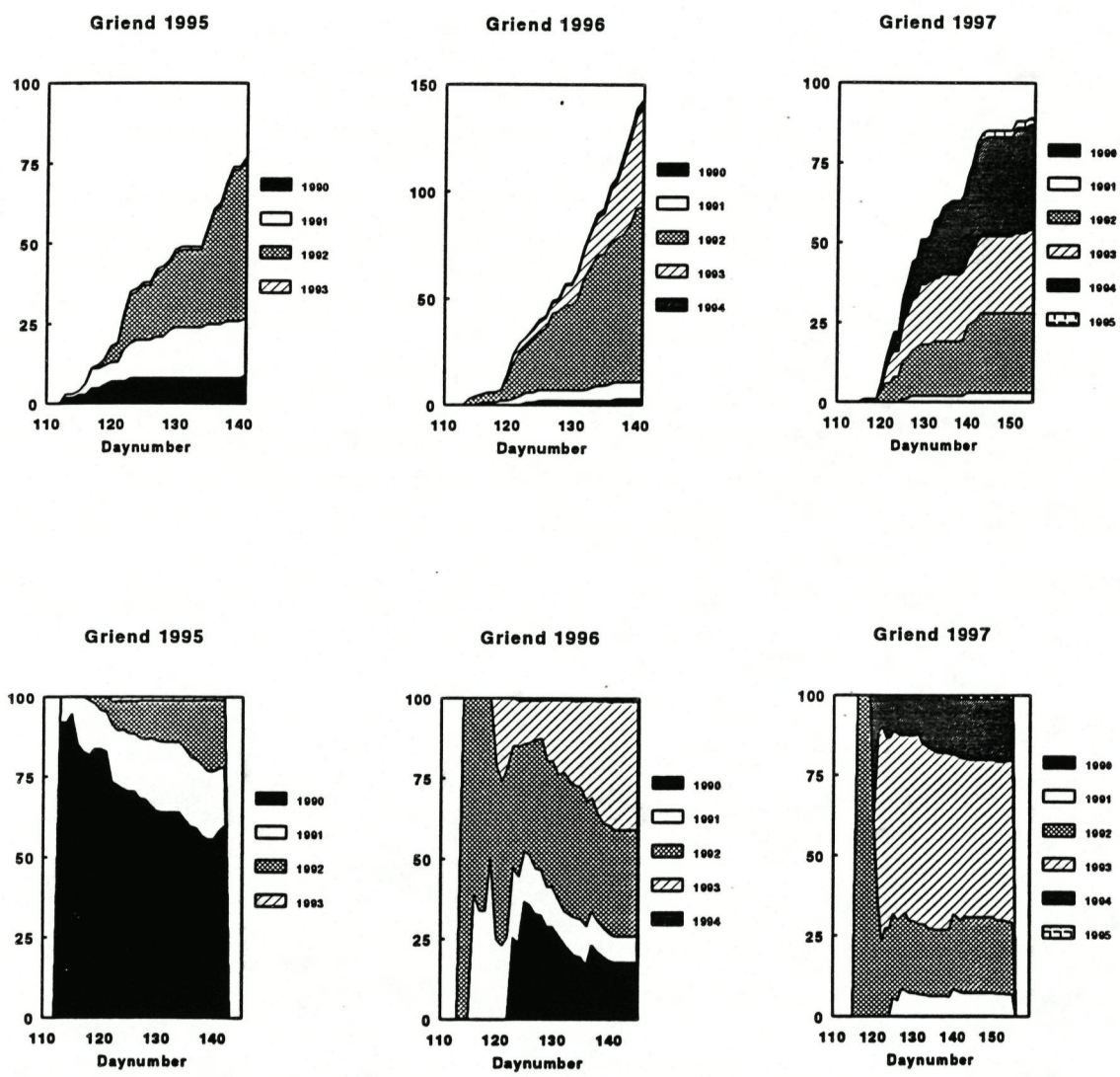

Figure 3. Cumulative number of recovered birds per cohort during the courtship period (upper panel) and the relative abundance of each cohort after correction for ringing effort (lower panel). Day number = day since January 1st.

3.2 Population dynamics

Each year we ringed a number of adult birds at the nest. As a result of mortality, emigration and fluctuations in the number of breeding pairs, not all ringed adults will return to Griend in the subsequent year. This means that in order to obtain the number of ringed adult terns in a certain year present in the following year, corrections for the above-mentioned parameters have to be developed. Yearly mortality rates of adult Sandwich Terns vary between 10-17% (DiConstanzo 1980, Brenninkmeijer & Stienen 1992). For convenience, adult mortality was set at 15% in the following calculations. Emigration of adult terns to other colonies is hard to assess, but is probably low. Brenninkmeijer & Stienen (1997) showed that in 1966-1996 not one adult tern ringed on Griend was recovered in Denmark and also emigration of Danish terns to Griend was low (< 1%). Therefore we will not account for emigration of adult terns from Griend. Finally, a correction has to be made for yearly fluctuations in the number of breeding pairs. For convenience we assume, that a reduction in the number of breeding pairs of e.g. 25% resulted in an equal percentage of adult birds ringed in the previous year that did not return to the colony. Using the number of ringed adult terns and the mentioned conversion-factors, one can calculate the number of adults ringed in year *x*, expected in year *x+1* (table 1). However, from these individuals only a minor part will actually be seen. The quotient of the number seen and the number expected forms the 'chance of recovery' of a ringed bird.

Local survival of each cohort was calculated using the following equation:

$$LS = 100 * \left(\frac{Nspot}{CR} * 100 \right) \Big/ Nring$$

Where LS = local survival, Nspot = number of ringed birds spotted, Nring = number of birds ringed, CR = chance of recovery from table 1.

Yearly difference in age composition of the ringed pulli may have biased local survival rates. In some years, nearly all ringed pulli were close to fledging, while in other years a high proportion of freshly hatched chicks was ringed. Since the chances of surviving until fledging greatly differ between freshly hatched and almost fledged chicks, this probably results in unrealistic local survival rates. In order to exclude such differences in age composition at ringing, in a second analysis only chicks older than 18 days (i.e. chicks with a total head, thus head and bill together, measuring more than 65 mm) were included in the calculations. An additional calculation was done leaving out all chicks with a total head measuring less than 70 mm (i.e. being approximately 21 days old).
Table 2 shows that local survival differs greatly between cohorts and between

years of observation. We consider survival rates of chicks with a head measuring more than 65 mm as the most accurate. Using a more strict selection (head > 70 mm) in most cases leads to the same results, but sample sizes are small in some cases.

Table 1. Calculation of the chance of recovery on Griend in 1995-1997 (for methods see text). The average percentage spotted (printed bold) is used as the chance of recovery for that year. BP = number of breeding pairs.

Parameter	Year of ringing					
	1992	1993	1994	1995	1996	Total
Griend 1995:						
N adults ringed	30	58	73	82	111	
N expected 15% annual mort.	18	42	62			122
N expected reduction BP	18	42	61			121
N spotted	4	11	11			26
% spotted	22.2	26.2	18.0			**21.5**
Griend 1996:						
N expected 15% mort.	16	36	53	70		
N expected reduction BP	13	26	36	48		123
N spotted	1	8	4	5		18
% spotted	7.7	30.5	11.2	10.5		**14.6**
Griend 1997:						
N expected 15% mort.	13	30	45	59	94	
N expected reduction BP	10	20	27	36	84	177
N spotted	2	3	2	5	7	19
% spotted	19.8	15.1	7.4	13.8	8.3	**10.7**

Table 2. Local survival on Griend of chicks ringed in 1990-1995. The number of spotted individuals is shown between brackets.

	Year of ringing					
	1990	1991	1992	1993	1994	1995
Griend 1995:						
All chicks	31.0 (10)	10.1 (19)	11.7 (56)	0.5 (1)		
Total head > 65 mm	31.0 (10)	15.9 (15)	17.3 (27)	0 (0)		
Total head > 70 mm	31.8 (10)	13.7 (9)	17.6 (18)	0 (0)		
Griend 1996:						
All chicks	13.7 (3)	6.3 (8)	26.5 (86)	34.7 (52)	1.0 (5)	
Total head > 65mm	13.7 (3)	10.9 (7)	42.5 (45)	45.4 (34)	0.7 (1)	
Total head > 70mm	14.1 (3)	4.5 (2)	45.9 (32)	42.0 (25)	0 (0)	
Griend 1997:						
All chicks	0 (0)	4.3 (4)	11.3 (27)	27.3 (30)	9.0 (33)	0.9 (3)
Total head > 65mm	0 (0)	8.5 (4)	11.6 (9)	29.1 (16)	13.3 (14)	2.2 (3)
Total head > 70mm	0 (0)	9.2 (3)	11.8 (6)	22.9 (10)	15.1 (10)	2.2 (2)

The survival rates presented in table 2 are difficult to interpret. Therefore we calculated the deviation from the expected survival (figure 4). Brenninkmeijer & Stienen (1992) estimated that survival is about 48% during the first year and 80-90% in the subsequent years. For convenience we used a survival of 50% for the first year and 85% for the subsequent years to calculate expected survival.

In all three study years, local survival (of chicks with a total head > 65 mm) during the first and second year was much lower than expected (figure 4). The latter is not surprising, since all first-year and most second-year terns stay in the wintering quarters during summer. In 1995 and in 1997, local survival of 3 years old birds was 19-23% lower than expected. In 1996, however, local survival of 3 years old birds was almost 10% higher than expected. In 1995, local survival of almost all year classes was lower than expected. Only the survival of 5 years old birds was about 5% higher than expected. In 1996, survival of 3 and 4 years birds was approximately 10% higher than expected, while that of older birds was much lower than expected. In 1997, survival of 3 years old birds was lower than expected, while that of 4 years old birds was slightly lower than expected. In this year survival of the older birds (5-7 year) was 10-20% lower than expected.

When different cohorts are considered and when we concentrate only on the survival of birds older than 3 years (only from the 4th year onwards all terns have returned to the breeding grounds) large differences between cohorts can be seen (figure 4). Most striking is the low survival of the 1991 cohort. In all 3 years of observation, local survival of this cohort was 14-15% below expected survival. Throughout the 3 study years, the 1990 cohort shows a sharp decline in local survival, which is also the case for the 1992 cohort from 1996 to 1997.

Conclusions

* *Local survival greatly differed between years and between cohorts. In general local survival of the 1990-cohort was low.*
* *All first-year and most second-year terns stay in the wintering quarters during summer. As a consequence local survival of these year classes was low.*
* *In 1995 local survival rates of terns older than 4 years was high, whereas in 1996-1997 survival rates of older birds was much lower than expected.*

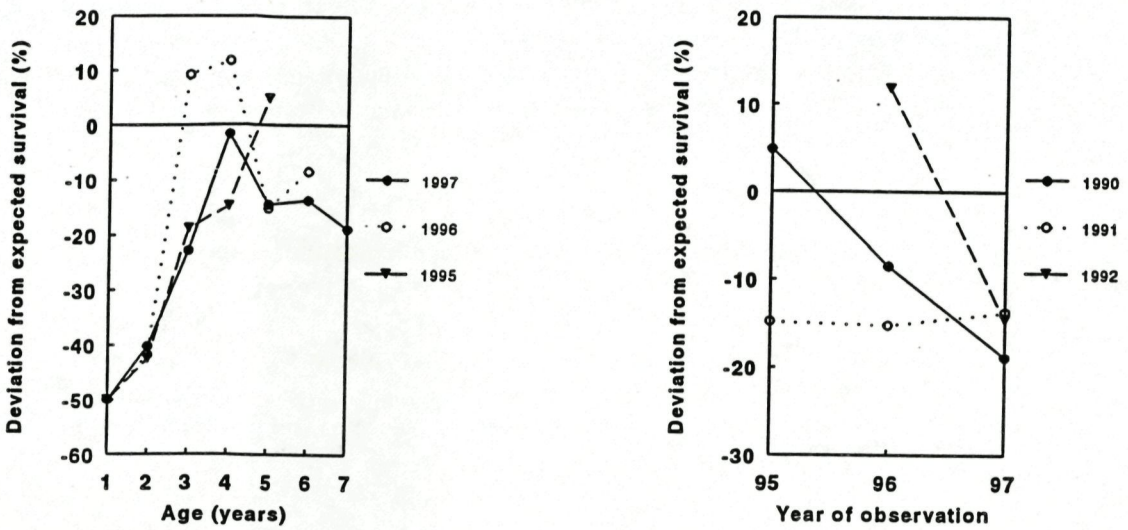

Figure 4. Deviations of local survival rates from expected survival of different age classes (left panel) and of the 1990, 1991 and 1992 cohort (right panel).

3.3 Emi- and immigration

The results of the readings of rings on Griend show that 28-31% of the terns ringed as a chick originated from colonies other than Griend (table 3). Most foreign birds originated from the United Kingdom & Ireland, other colonies in the Netherlands, Denmark, Belgium and Sweden. About 18% of the terns ringed as an adult originated from foreign countries, mainly Belgium and the United Kingdom & Ireland.

However, these results may be greatly biased by ringing effort. When, for example, in country 'A' all chicks were ringed every year, a recovered bird from this country stands for only 1 bird. When in country 'B' with the same population size only 1% of the chicks was ringed every year, for each recovered bird from country 'B' there are 9 non-ringed birds. For this reason the results were corrected for ringing effort in the subsequent countries and years. Figure 5 shows the composition of the population on Griend (results of 1995 and 1996 combined) after correction for ringing effort. Almost 75% of the population consists of birds born on Griend. From the terns born in foreign colonies, 14.3% originates from other Dutch colonies, 7.4% from the United Kingdom & Ireland and almost 3% from Denmark. Of birds ringed as adults, the proportion which originates from Griend itself is 94%. Of the remaining 6% most birds were ringed in colonies in the United kingdom & Ireland (5.0%). The high proportion of adults ringed in Belgium stands for only 0.6% of the population on Griend after correction for ringing effort.

For comparison data from Denmark were analysed in the same way. The

Danish picture differs greatly from that of Griend (figure 5). Only 18.4% of the birds ringed as a chick was found nesting in the colony of birth. Another 74.2% originated from other colonies in Denmark or adjacent countries (East-Germany and Sweden) and 7.4% originated from foreign countries such as the United Kingdom & Ireland (3.2%), The Netherlands (2.0%) and West-Germany (1.9%). As on Griend, the proportion of birds ringed as an adult which returned to their former breeding colony in Denmark (36.7%) was much larger than that of birds ringed as a chick (18.4%). Another 52.2% of the adult ringed birds originated from other colonies in Denmark or adjacent countries and 11.1% originated from foreign countries.

Conclusions

* *Both the population on Griend and in Denmark hold a significant proportion of terns that have migrated from other colonies.*
* *Danish Sandwich Terns show a lower site fidelity than the terns on Griend.*
* *Once established in a colony terns are less inclined to migrate to other colonies than first year breeders.*

Table 3. Colony of origin (% of total) of ringed Sandwich Terns recovered on Griend (without correction for ringing effort). See table 4 for the number of recoveries.

Country	Pulli		Adults	
	1995	1996	1995	1996
Griend	68.5	71.6	81.8	81.8
Other Dutch colonies	6.9	2.3	0.0	0.0
United kingdom & Ireland	13.8	15.1	3.0	9.1
Denmark	3.8	2.8	3.0	0.0
Belgium	3.1	4.6	12.1	9.1
Sweden	2.3	1.8	0.0	0.0
West-Germany	0.0	0.5	0.0	0.0
East-Germany	0.8	0.5	0.0	0.0
Estonia	0.8	0.9	0.0	0.0

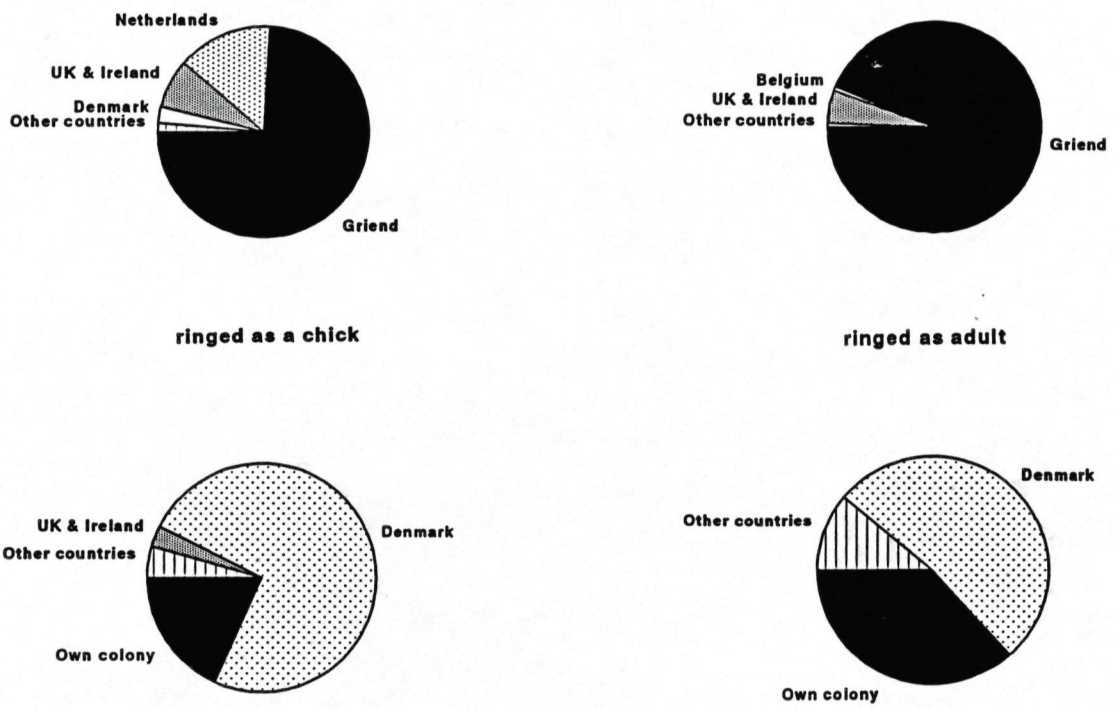

Figure 5. The composition of the population on Griend (1995 and 1996 combined, upper graphs) and in Denmark (1960-1983, lower graphs) after correction for ringing effort.

Table 4 shows the proportion of the original populations (corrected for ringing effort) that emigrated yearly to Griend. It seems that the proportion of immigrants was much higher in 1996. A relatively high proportion (4.9-6.7%) of the chicks born in Dutch colonies outside Griend bred on Griend in later years. The proportion of Belgium (3.0-6.1%) and English (1.3-3.5%) chicks that emigrated to Griend is also relatively large, while that for the other countries was less than 2%. The calculation of emigration rate for adults is less reliable because in some countries no adults were ringed at all in the past decades (which explains some zeros in table 3). Nevertheless, the high proportion of adult birds from Belgium that was recovered on Griend (17.4-13.0%) is remarkable.

Table 4. Proportion of the original population that settled on Griend. The results are corrected for ringing effort in the various countries and the involved years. Numbers of recoveries between brackets.

Country	Pulli				Adults			
	1995		1996		1995		1996	
Griend	29.2	(42)	55.4	(98)	92.7	(27)	58.4	(18)
Other Dutch colonies	6.7	(9)	4.9	(5)	0.0	(0)	0.0	(0)
United kingdom & Ireland	1.3	(18)	3.5	(32)	0.7	(1)	2.2	(2)
Denmark	1.0	(5)	1.6	(5)	0.8	(1)	0.0	(0)
Belgium	3.0	(3)	6.1	(6)	17.4	(4)	13.0	(6)
Sweden	0.8	(2)	1.7	(3)	0.0	(0)	0.0	(0)
West-Germany	0.0	(0)	1.1	(1)	0.0	(0)	0.0	(0)
East-Germany	0.2	(1)	0.4	(1)	0.0	(0)	0.0	(0)
Estonia	?	(1)	?	(2)	0.0	(0)	0.0	(0)

Emigration is strongly related to the distance from the original colony (figure 7). The majority of Dutch and Danish migrants settled in colonies at less than 200 km away from their original colony. Danish adults settled close to the colony of origin. Approximately 80% of the adult migrants settled at less than 150 km away from their original breeding site. Danish migrants ringed as chicks settled somewhat further away form the colony of origin, with just over 80% settled at less than 200 km distance of their colony of birth. Dutch migrants ringed as a chick moved much further away (approximately 80% settled at less than 350 km distance of their colony of birth). The same picture arises when we looked at the migrating distance of birds recovered on Griend (figure 7). Most birds recovered on Griend originated from colonies less than 200 km away from the colony of origin. Again, the migrating distance of birds ringed as adults was smaller than that of birds ringed as chicks.

Conclusions

* *A relatively large proportion of the Dutch, Belgium and English terns migrate to Griend.*
* *Most migrants settle in colonies less than 200 km from their original colony.*
* *First year breeders settle further away from their colony of origin than experienced breeders.*

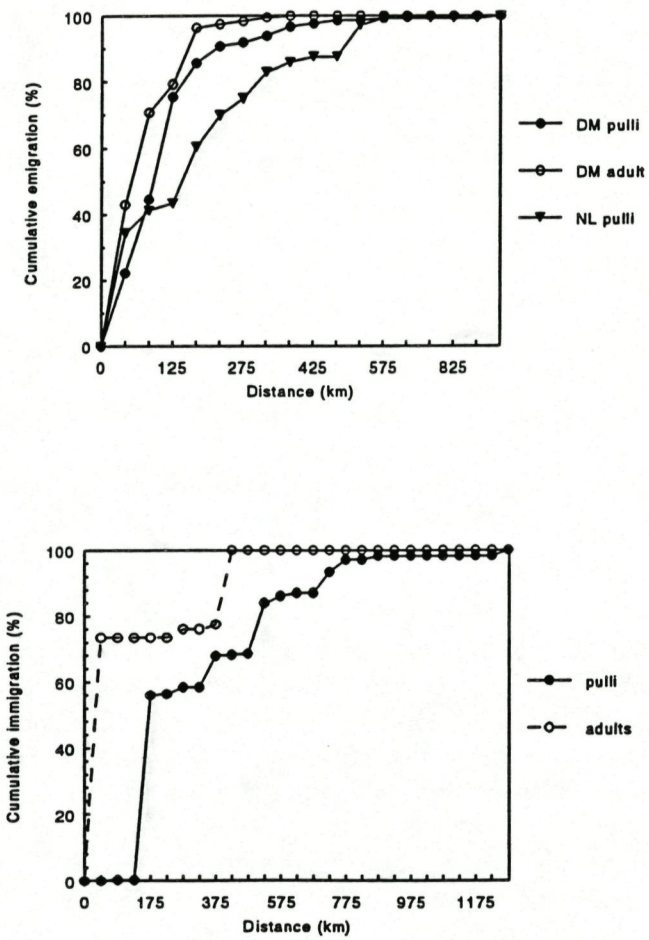

Figure 7. Cumulative proportion of emigrated terns from Denmark and the Netherlands (upper panel) and of immigrated terns on Griend (lower panel) in relation to the distance to the colony of origin. DM pulli = ringed as pulli in Denmark, DM adult = ringed as adults in Denmark and NL pulli = ringed in The Netherlands as pulli.

3.4 Effect of chick condition on post-fledging survival

An analysis of variance shows that the body mass of the chicks ringed in 1990-1995 was related to the size of the head (ANCOVA, $F_{1, 8426} = 100713$, $p < 0.001$), the year of ringing ($F_{5,8422} = 42.4$, $p < 0.001$) and whether they returned in later years ($F_{1, 8426} = 16.4$, $p < 0.001$). In other words, corrected for the size of the chicks and yearly influences, returned chicks were heavier than chicks that did not return. The latter suggests, that chicks in 'good condition' have a higher chance to survive until first breeding. However, the analysis included ringed chicks in all age classes. It is therefore, still questionable whether the conclusion holds for chicks that actually did fledge. For this reason, in further analysis we included only chicks presumed to have fledged. As in chapter 3.1 we used 2 selection criterion for being fledged, namely either chicks with a total head length of more than 65 mm or chicks with a total head length measuring more than 70 mm. As a measurement for chick condition the difference between measured body mass (M in g) and expected body mass (M_{exp} in g) at a certain size of the head was used. For M_{exp} we used the average body mass at a certain head size of all chicks measured on Griend in the period 1992-1995 (figure 8). Condition indexes (CI in %) were calculated according to the formula:

$$CI = \frac{M - M_{exp}}{M_{exp}} * 100\%$$

A chick with a body mass higher than the mean body mass (at a certain head size) is believed to be in good condition.

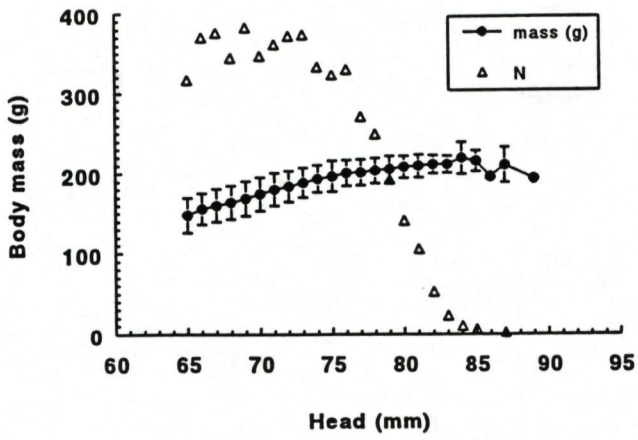

Figure 8. Average body mass ± SD of chicks in relation to head size (i.e. head and bill), Griend 1992-1995.

The average condition-index of chicks with a head larger than 65 mm and not seen on Griend in later years (Ci^{not} = 0.4%, N = 3827) was lower than that of chicks which did return to the island (Ci^{return} = 3.3%, N = 164) (Students' t-test, t = 3.53, $p < 0.001$). When we omitted chicks with a head measuring less than 70 mm from the analysis the difference between the 2 groups still exists (Ci^{not} = 0.3%, N = 2543 and Ci^{return} = 2.6%, N = 113) (Students' t-test, t = 2.73, p = 0.006). The chance of returning to the breeding grounds increases with the condition of the chick (logistic regression analyses, head > 65 mm: deviance = 12.25, $p < 0.001$; head > 70 mm: deviance = 6.80, $p < 0.01$) (figure 9).

Conclusions

* *The results strongly suggest that pre-fledging condition influences recruitment. Chicks in low pre-fledging condition have a lower chance to return to their colony of birth.*

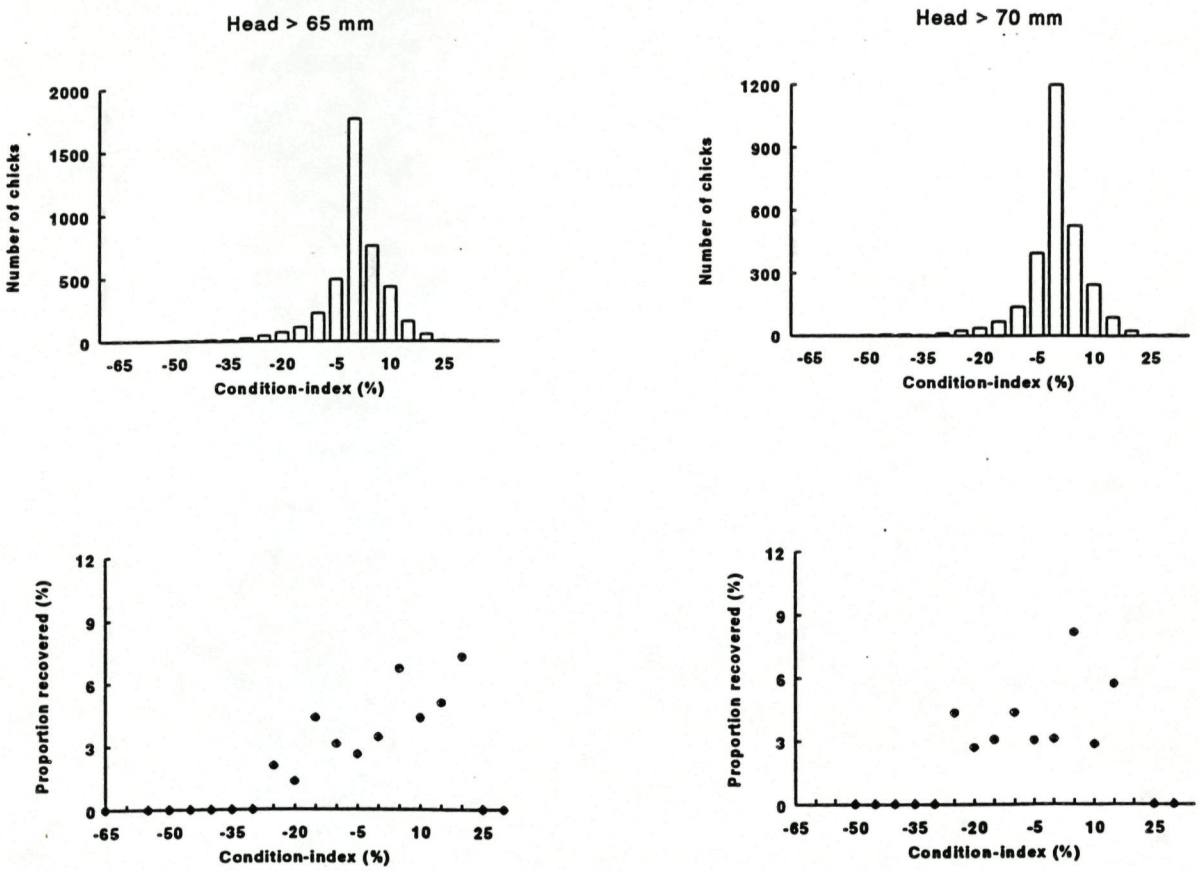

Figure 9. Frequency distribution of the condition of chicks ringed on Griend in 1990-1995 (upper left figure: head > 65 mm; upper right figure: head > 70 mm) and the proportion of recovered birds in relation to their condition (lower left figure: head > 65 mm; lower right figure: head > 70 mm). Condition index is divided into categories (CI -65 = -69 to -65, CI -60 = -64 to -60 etc.).

3.5 Food brought to the colony

Composition of the food In all observation years , the food brought to the colony consisted mainly of Clupeidae and Ammodytidae/Hyperoplidae, less than 1% consisted of other species (mainly goby *Gobius* spp., cod *Gadus morhua* and whiting *Merlangius merlangus*). Unless otherwise stated, we further use 'herring' when referring to Clupeidae and 'sandeel' when referring to Ammodytidae/Hyperoplidae. Furthermore, species other than herring and sandeel were omitted from the analyses since they amounted less then 1% of the food brought to the colony.

The proportion of the prey species showed large variation throughout and within years (figure 10). In 1995, food supplied to the partners during the courtship period almost exclusively consisted of sandeel. Only from 30 April (day 120) onwards herring was brought to the colony. After day 120, the proportion of herring gradually increased and amounted to about 60% at the onset of the chick rearing period (day 140). During the chick rearing period, the proportion of herring fluctuated around 60%. In 1996, a completely different picture was found (figure 10). At the beginning of the courtship period the proportion of herring was relatively high and amounted to about 65%. After day 115 the proportion of herring gradually decreased to about 25% at the time that the first eggs hatched (day 140). During the first 3 weeks of the chick rearing period the proportion of herring was low and fluctuated around 25%. In the week before fledging the proportion of herring increased to about 50%. In 1997, except from two peaks (possibly due to the small sample size), the proportion of herring was slightly lower than 50% during the entire courtship period. At the onset of the chick rearing period the proportion of herring sharply increased and amounted to more than 80% of the food supply later in the season. Only in the last week before fledging, the proportion of herring decreased to less than 60% for a few days, but after that it increased again to about 80%.

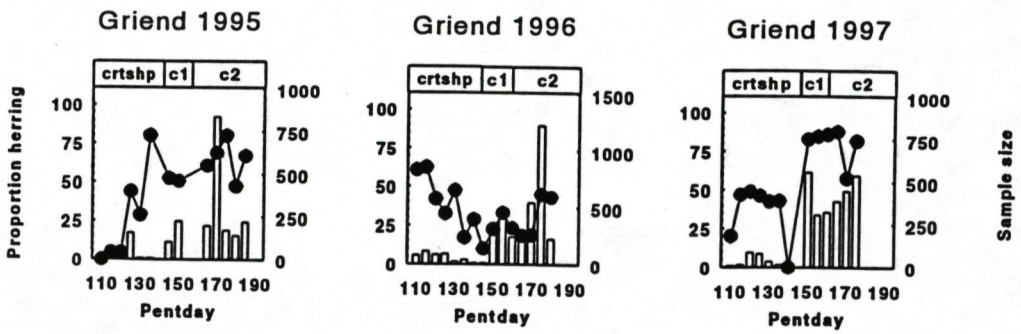

Figure 10. Proportion of herring brought to the colony in 1995-1997 (Pentday = day since Jan 1st: 140 = 140-144, 145 = 145-149 etc.). Bars denote sample size. Below the X-axis the periods of courtship (crtshp), period with young chicks (c1) and period with older chicks (c2) are indicated.

Prey size The size of the preys varied within and between seasons (figure 11). In general it can be seen, that fish (both herring and sandeel) supplied to chicks less than 1 week old were smaller than those brought to the colony during courtship and those supplied to older chicks. However, some exceptions can be seen. In 1997, the size of the herring supplied during the courtship period was relatively small and did not differ from the herring supplied during the first week of the chick rearing period. Both in 1996 and in 1997, the herring offered to larger chicks was comparable to that offered to the smaller chicks. In fact, the herring was relatively small in size in all 3 periods in 1997.

Conclusions

* *The proportion of herring in the food brought to the colony greatly varied within and between years.*
* *In general fish (both herring and sandeel) supplied to chicks less than 1 week old were smaller than those brought to the colony during courtship and those supplied to older chicks.*

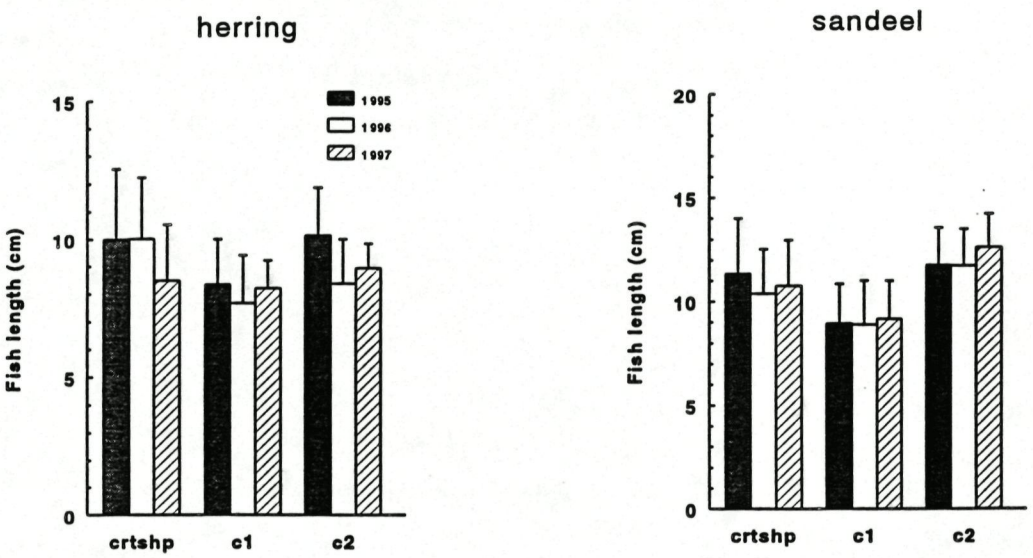

Figure 11. Mean length (± SD) of fish brought to the colony during courtship (crtshp) and the chick period (c1 = first week after hatching, c2 = older chicks; herring left graph, sandeel right graph).

Amount of food supplied to the chicks In 1995, food supply was measured only for chicks of more than 2 weeks old. In that year, parents offered their chicks approximately 10 fishes per day (figure 12). The numbers of fish supplied to the chicks during the first two weeks of the chick rearing period in 1996 was relatively low (approximately 7 fishes per chick per day); after that period fish supply increased to about 13 fishes per chick per day (figure 12). In 1997, the food supply fluctuated around 9 fishes per chick per day during the entire chick rearing period, somewhat lower than the supply in the previous years. A multiple regression approach analysing the food supplied to the chicks yielded a significant effect of age ($F_{1,824} = 164.9$, $p < 0.05$). Including year into the model significantly improved the explained deviance ($R^2 = 17.3$, $F_{2,822} = 3.47$, $p < 0.05$). The model predicts that food supply was lowest in 1995 and highest in 1997. In 1996 food supply did not differ significantly from 1997.

Mass supplied to the chicks From an energetic point of view food supplied to the chicks should be expressed in weight rather than in numbers. In order to distinguish this from food supply we will further call it mass supplied to the chicks. In 1995, the older chicks were offered approximately 60 grams of fish each day (figure 13). In 1996, the mass supplied gradually increased from less than 20 grams per day during the first days after hatching to 60-70 grams just before fledging. In 1997, the chicks were offered 20-30 grams of fish during the first days after hatching, after which the supplied mass increased to 40-50 grams in the week before fledging. A regression approach yielded a significant effect of age on mass supply ($F_{1,825} = 639.4$, $p < 0.05$). Including year significantly improved the model ($R^2 = 44.9$, $F_{1,823} = 15.4$, $p < 0.05$). The mass supply recorded in 1995 was significantly higher than in 1996 and in 1997. Although in 1996 mass supply was on average lower than in 1997, this difference was not significant.

Conclusions

* *Food supplied to the chicks was lowest in 1995 and highest in 1997. In 1996 food supply was extremely low during the first two weeks, but greatly improved afterwards.*
* *In terms of biomass, food supplied to the chicks increased with the age of the chicks. Mass supply was highest in 1995.*

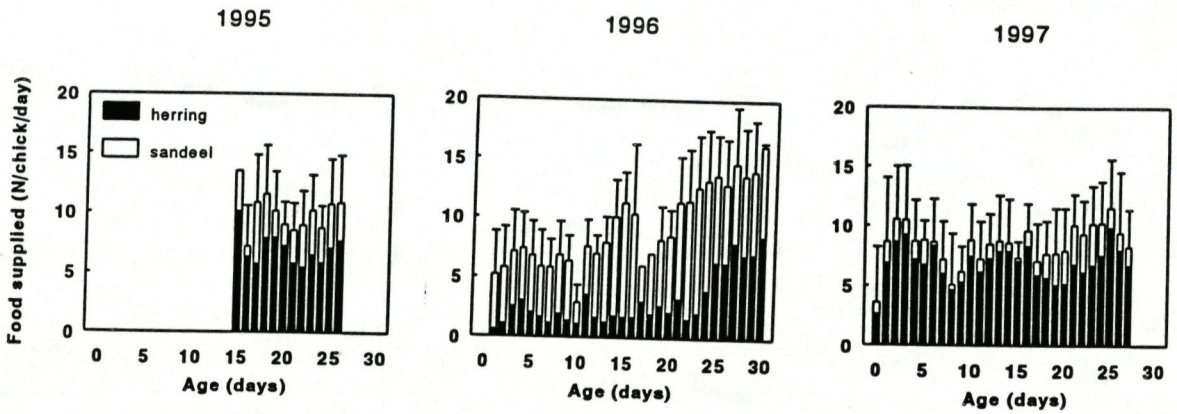

Figure 12. Mean number of fish supplied to the chicks (± SD) in relation to the age of the chicks.

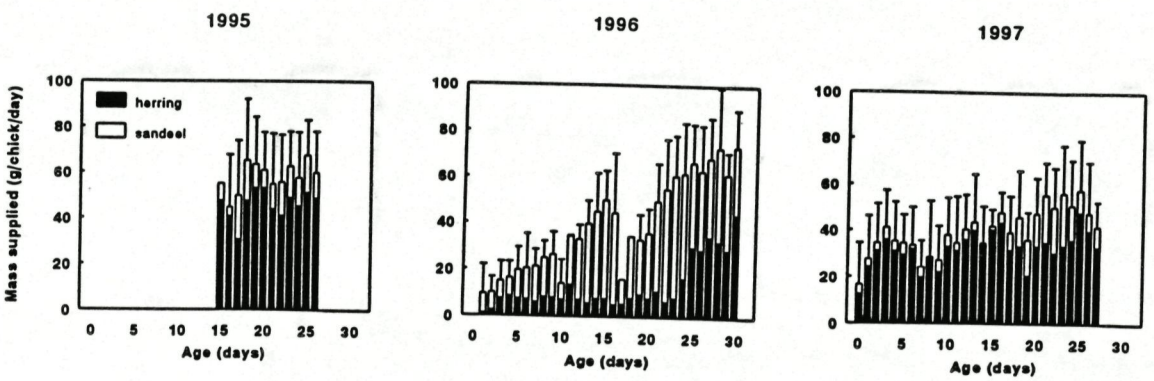

Figure 13. Mean mass supplied to the chicks (± SD) in relation to the age of the chicks.

Parental effort In order to relate the amount of food brought to the colony to the situation in the foraging areas, it is more realistic to express the food supplied per parent instead of per chick. The reason for this is, that when the chicks are somewhat older, both parents may go out foraging at the same time, and thus increase the amount of food supplied to their chicks. In that case, the food situation in the foraging areas can be suboptimal, while the food or mass supplied to the chicks is still fairly high due to increased parental effort.

Parental effort varied both within and between years. In all three study years the chicks were almost never left alone during the first 2 weeks after hatching (figure 14). More than 90% of the time (apart from some exceptions) 1 parent stayed with the young and brooded the chick most of the time. After approximately 2 weeks the chicks are thermo-stable and need no brooding anymore (Klaassen *et al.* 1992). At that time they can be left alone from an energetic point of view. In the older chicks parental effort was highly variable between years. In 1995, even older chicks were almost never alone (on average less than 20% of the time). In 1996, chicks of 15 days old were left alone for approximately 10%. After that the parents rapidly increased their foraging effort and during the last week before fledging the chicks were left alone for more than 75% of the time. In 1997, the same increase was noted, but only up to 30-40% of the time.

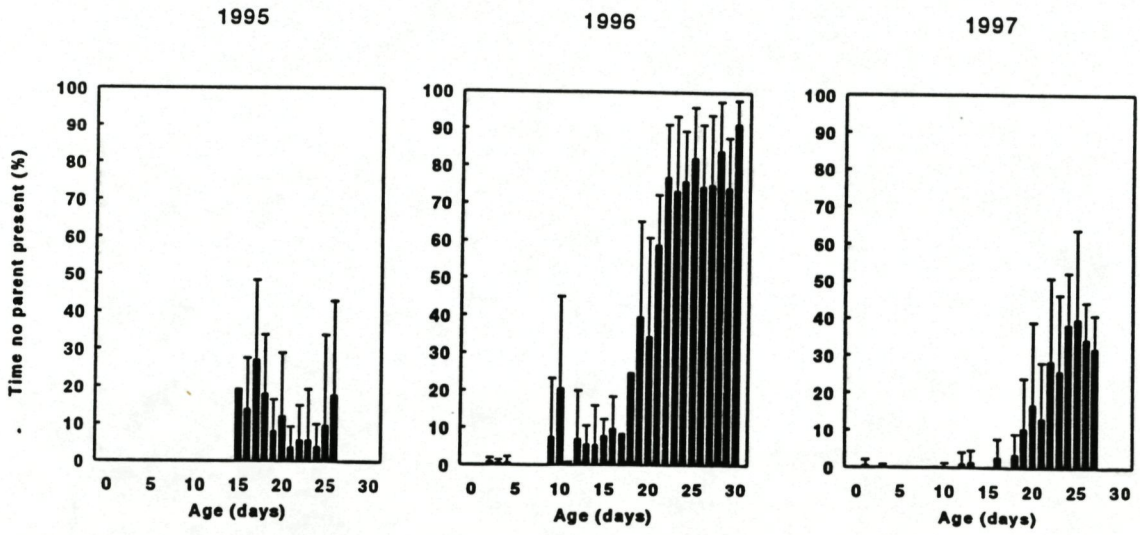

Figure 14. Mean proportion of the daylight period (± SD) that the chicks were left alone at the nest.

Food or mass supplied to the chicks was corrected for parental effort using the following equation:

$$\text{cor. supplied} = \%\,1\,\text{parent} * \text{supply} + \left(\frac{\%\text{no parent} * \text{supply}}{2}\right)$$

Where cor. supplied = corrected food or mass supplied, % 1 parent = percentage of time that 1 parent was present at the nest and % no parent = percentage of time that no parent was present at the nest.

Corrected food supply Taking parental effort into account leads to a completely different picture of the amount of food supplied to the chicks (figure 15). In all three study years, the corrected amount of food supplied was rather constant during the course of the chick-rearing period, compared with the highly variable amount of food supplied when no correction for parental effort was applied (compare figure 12). In 1995, 1996 and 1997 respectively the corrected amount of food supplied fluctuated around 9, 7 and 9 fishes per chick per day. A multiple regression approach still revealed a significant effect of age ($F_{1, 778} = 7.44$, $p < 0.05$), but the explained variance did not significantly differ from 0 ($t_{1, 778} = 1.92$, $p > 0.05$). Including year into the model significantly improved the explained deviance ($R^2 = 8.6$, $F_{2,776} = 32.8$, $p < 0.05$). The model showed that in 1996 the corrected amount of food supplied to the chicks was significantly lower than in 1995 and 1997. The corrected amount of food supplied in 1995 did not differ from that in 1997.

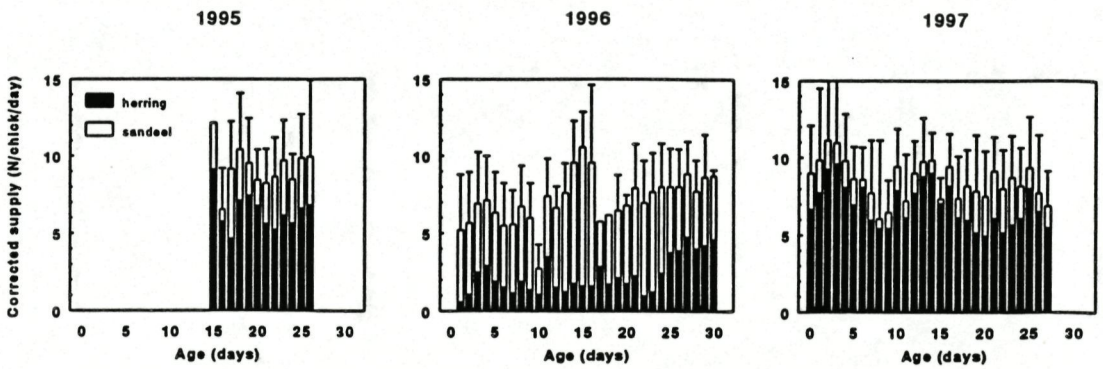

Figure 15. Mean amount of food supplied to the chicks (± SD) corrected for parental effort.

Corrected mass supply Corrected mass supplied to the chicks was somewhat less than 60 grams of fish per chick per day in 1995. In 1996, corrected mass supply increased from less than 20 grams after hatching to 35-40 grams in the 2 weeks before fledging. In 1997, corrected mass supply fluctuated around 40 grams during the entire chick-rearing period. Multiple regression revealed a significant effect of age ($F_{1,778} = 283.7$, $p < 0.05$) and an additional significant effect of year ($R^2 = 0.41$, $F_{2,776} = 133.0$, $p < 0.05$).

Conclusions

* *Corrected for parental effort the amount of food supplied to the chicks was rather constant throughout the chick-rearing period.*
* *Corrected food supply both expressed in numbers and in gram fish was lowest in 1996 and did not differ between 1995 and 1997.*

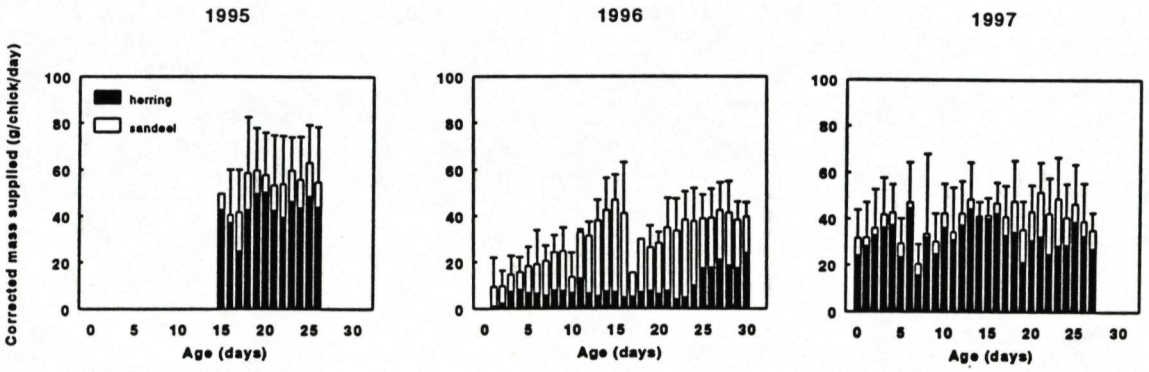

Figure 16. Mean amount of mass supplied to the chicks (± SD) corrected for parental effort.

3.6 Prey fish availability

Fish length The length distribution of the fish caught by the Isaac's Kidd Midwater Trawl net (IKMT-net) greatly differs from that caught by the terns (figure 17). The herring caught in the net was much smaller than the fish caught by the terns. To the contrary, the sandeel caught in the net was somewhat larger than that caught by the terns. This difference is partly caused by the catching efficiency of the net. For example, most sandeels smaller than 9 cm are able to escape through the meshes (Gerrit van de Kamp). Another reason for this difference is that the terns select certain length classes. In order to be able to compare the length distribution in the IKMT-samples with that found in the colony, only herring measuring 5-12 cm and sandeel measuring 6-17 cm were included in the analysis. In that case the difference in length between the fish samples and the fish brought to the colony still exist (chapter 3.7). In order to further reduce this difference, the catches were expressed in weight and ln-transformed into a availability-index. Note that this availability-index does not reflect fish abundance but merely the amount of fish available for the Sandwich Terns (i.e. fish of the appropriate size in the upper 2 meter of the layer). The availability-index is further simply called fish availability.

Fish availability Greater sandeel was only caught in small numbers in 1995 (less than 1% of the total amount of fish available for the terns) and they were not present at all in the fish samples in 1996 and 1997 (table 5). The proportion of herring ranged from 21% in 1995 to 38% in 1996. Sprat amounted to 18-19% of the total abundance in 1995 and in 1996, while its proportion was 31% in 1997. The proportion of sandeel decreased from 60% in 1995 to 38% in 1997.

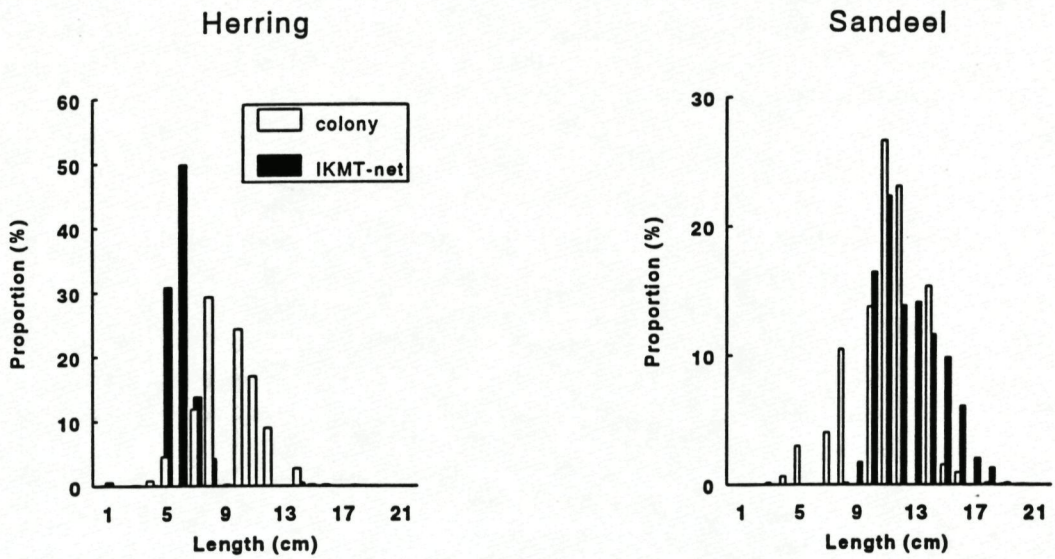

Figure 17. Length distribution of herring and sandeel caught in the IKMT-net compared with that brought to the colony.

Table 5. Species composition in the IKMT-samples. Each figure represents the mean proportion (± SE) per year (N = 38, 40, and 33 hauls containing fish in 1995, 1996 and 1997 respectively).

Species	1995	1996	1997
herring	21.2 ± 5.1	38.1 ± 6.0	31.0 ± 6.5
sprat	17.7 ± 4.4	18.5 ± 3.9	30.8 ± 6.8
sandeel	60.3 ± 6.9	43.4 ± 6.4	38.2 ± 6.73
greater sandeel	0.8 ± 0.6	0	0

Within and between years variation in fish availability The availability of both herring and sandeel decreased during the study period (figure 18), although only sandeel availability in 1995 significantly differs from 1996 and 1997 (Scheffé-test, $F = 7.87$, $p < 0.05$). Herring availability was on average lowest during the courtship period and relatively high during the chick-rearing period, although the difference was not significantly (Scheffé-test; n.s.) (figure 19). Sandeel availability decreased throughout the season (Scheffé-test: courtship > early chick stage & late chick stage, $F_{2,261} = 20.57$, $p < 0.05$). Total availability gradually decreased throughout the season, although no

significant changes between the various periods could be found (Scheffé-test; n.s). Subdividing the various years into the period of courtship, the early chick stage and the older chick stage makes the picture much more complex (figure 20). In 1995, most herring was caught during the early chick stage (although the values are not significantly different). In the following year, herring availability shows no changes during the breeding period. In 1997, it was lowest during the early chick stage and highest in the week before fledging (although the difference is not significant). Sandeel availability shows a decrease within 1995 and 1996 (Scheffé-test: courtship period > late chick stage both in 1995 and in 1996, courtship period > early chick stage in 1995, $F = {}_{8, 255}$, $p < 0.05$). In 1997, sandeel availability was low just after hatching, after which it increased. The changes, however, were not significant (Scheffé-test; n.s.).

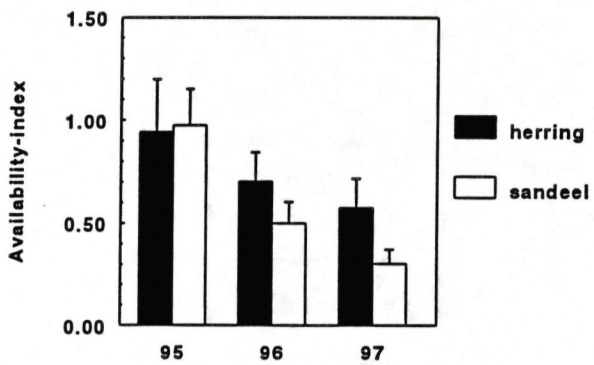

Figure 18. Prey fish availability (± SE) in 1995-1997.

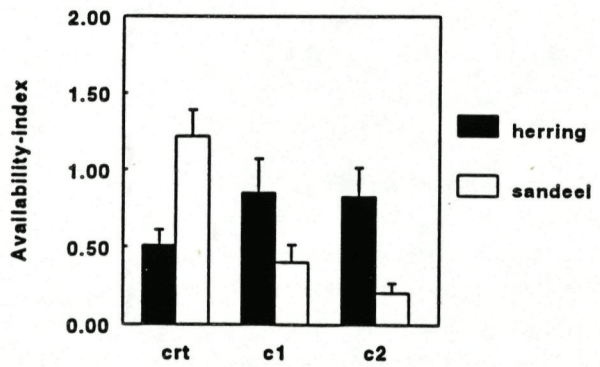

Figure 19. Prey fish availability (± SE) during the courtship period (crt) and the periods with small chicks (ch 1) and large chicks (ch 2).

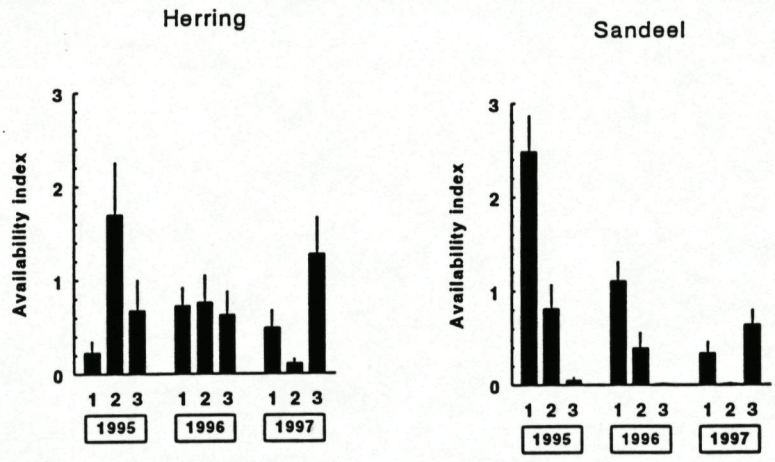

Figure 20. Prey fish availability (± SE) in the period 1995-1997 subdivided for the period of courtship (1), the small chicks stage (2) and the large chicks stage (3).

Distribution of the prey fish Sandeels were evenly distributed over the five sampling locations (figure 21). The availability of herring, however, highly depended on the location of the sampling point (although not always significantly). Especially in the Vliesloot herring availability was high (Scheffé-test: Vliesloot > than all other sampling sites, $F_{4, 259} = 26.9$, $p < 0.05$). In the Stortemelk and the Oosterom herring availability seems higher than in the Vliestroom and the Westmeep (but not significantly).

Effects of tide Tidal rhythm did not influence the availability of sandeel. Herring availability, however, appeared to depend on tide (figure 22). During high and low water periods the catches of herring were low, but they did not significantly differ from that during ebbing and flooding.

Effects of windspeed Using a Scheffé-test, no significant influence of windspeed could be found, although most herring were caught at 7 Bft (figure 23). The latter is due to logistic problems. During strong winds it was only possible to fish in sheltered areas. This happens to be the Vliesloot (VL 22) were herring was most abundant.

Effects of water clarity In contrast to windspeed, the clarity of the water had a large effect on both herring and sandeel availability (figure 24). The clearer the water the less fish was present. Although not caught in the IKMT-net (sampling the upper 2 meter of the water layer) fish was abundant in clear waters, but at higher depths. Using an echo sounder in 1997 showed that the depth were the fish was abundant increased with the clarity of the water.

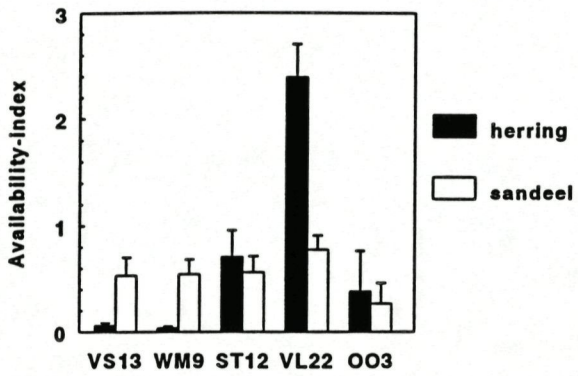

Figure 21. Distribution of the fish (mean availabilty ± SE) over the 5 sampling sites (VS13 = Vliestroom, WM9 = Westmeep, ST12 = Stortemelk, VL22 = Vliesloot, OO3 = Oosterom).

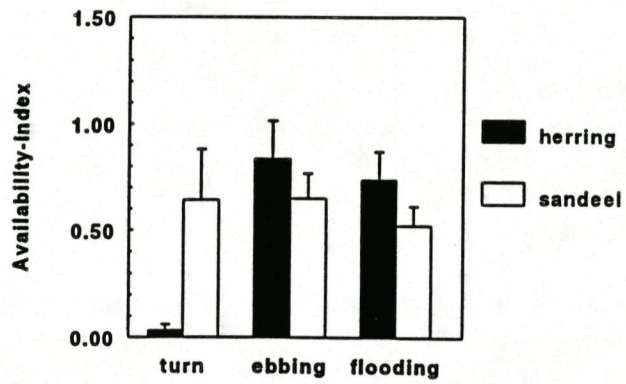

Figure 22. Prey fish availability (± SE) in relation to tide.

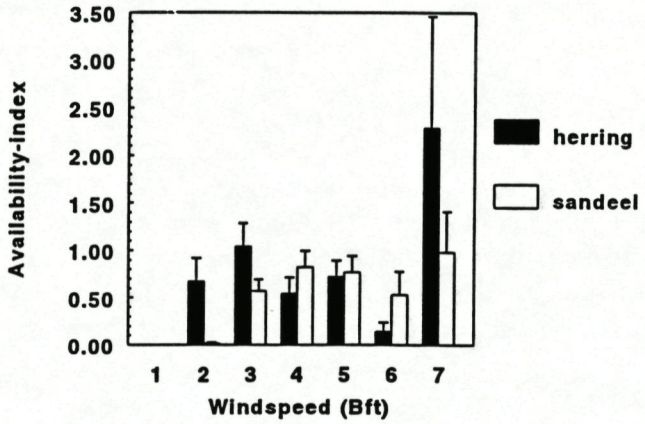

Figure 23. Prey fish availability (± SE) in relation to windspeed (Bft).

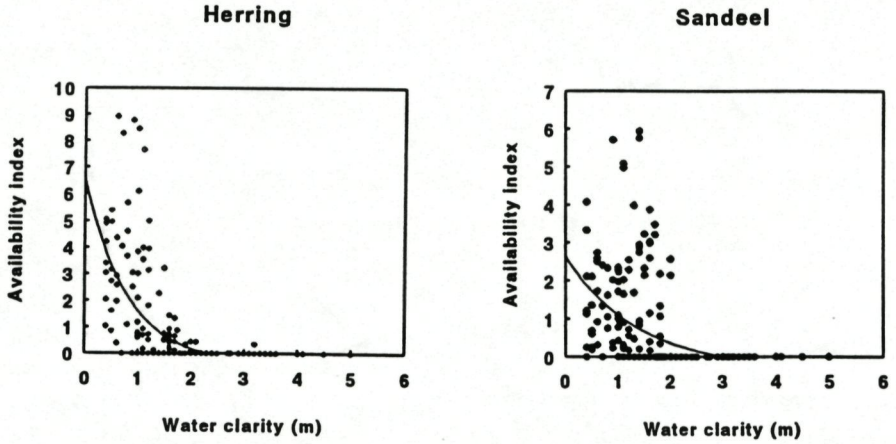

Figure 24. Prey fish availability in relation to water clarity (herring: $Y = -0.411 + 6.937 * 0.2911^X$, $R^2 = 39.8$; sandeel: $Y = -0.327 + 2.953 * 0.482^X$, $R^2 = 18.2$).

To examine the influence of all various parameters (location, year, period, tide, windspeed and water clarity) a stepwise regression approach was used (table 6). We started with a completely empty model. For convenience, apart from the year*period interaction term no other interaction terms were used. Sampling location, water clarity and period significantly contributed to explain herring availability. Sandeel availability depended on water clarity, period, year and year*period. The latter indicates that the same seasonal trend was found in all years.

Conclusions

* Prey fish availability varied within and between years.
* Sandeels were evenly distributed over the foraging area of the terns, whereas herring was most abundant at the northern sampling locations.
* Fish availability was strongly related to water clarity. In clear waters fish was abundant at greater depths, thus beyond the reach of the foraging terns.

Table 6. Multiple regression analysis on fish availability. Predictors which were dropped from the model are not shown. R^2 = 35.3 and 36.0 for herring and sandeel respectively (N = 264).

Parameter	*df*	F	P
Herring			
Sampling location	4	28.8	< 0.001
Water clarity	1	24.3	< 0.001
Period	2	4.87	0.008
Sandeel			
Water clarity	1	56.9	< 0.001
Period	2	15.6	< 0.001
Year	2	9.3	< 0.001
Year*period	1	46.2	< 0.001

3.7 Food provisioning to the colony in relation to prey fish availability

Fish length The average fish length in the IKMT-samples did not match the fish length provisioned by the terns. The average length of the herring caught in the IKMT-net (after selection for length classes caught by the terns) was in all stages of the breeding period much smaller than that of herring provisioned by the terns. In contrast, the length of the sandeel caught in the IKMT-net was slightly smaller than that of sandeel caught by the terns. However, the seasonal pattern in fish length in the samples is comparable with that found in the food supplied by the terns. In both herring and sandeel the average length in the samples shows a minimum at the onset of the chick-rearing period, comparable with the general pattern found in the colony. Even when the data are subdivided over the three years, the within-year patterns in herring length, but not in sandeel, are more or less comparable with the patterns found in the colony (figure 25). In 1995, relatively large herring were offered during the courtship period. Comparable with the situation in the IKMT-samples, the length of the herring provisioned by the terns decreased just after hatching and increased towards fledging. In 1996, relatively large herring were offered during the courtship period and smaller herring during chick-rearing period. In 1997, relatively small herring were brought to the colony during the courtship period, with only a slight increase at the end of the chick-rearing period (sample size at the onset of the chick-rearing period was too small). These patterns in herring length can also be found in the IKMT-samples. Sandeel sample sizes were often too small to asses reliable mean values. In all study years the same seasonal pattern was found in sandeel length supplied by the terns. Relatively large sandeels were offered to the partners during the courtship period, decreasing in size during the onset of the chick-rearing period and increasing again at the end of the chick-rearing period. Only for 1995 the seasonal pattern in sandeel length in the IKMT-samples (as far as available) was comparable with that found in the colony. In contrast to the sandeels supplied by the terns the length of the sandeels in the IKMT-samples (as far as available) did not change within the season in 1996 and in 1997. Also most inter-year changes in fish length were not confirmed by the IKMT-catches. Only the pattern in herring length during the courtship period (relatively small herring in 1997) and the late chick stage (relatively small herring in 1996) is more or less comparable between colony-samples and IKMT-samples.

Fish availability Neither inter-year differences nor within-year differences in herring and sandeel availability are reflected in the food brought to the colony by the terns (figure 26). For example, an increase in herring availability in the IKMT-samples at the end of the 1997 chick-rearing period was accompanied by a decrease in the herring supplied to the chicks.

Species composition In 1995, the mass-proportion of sandeel in the colony follows the sandeel availability in the IKMT-samples fairly well (figure 27). A high proportion of sandeel during the courtship period and a decrease during

the chick rearing period. In 1996, the proportion of sandeel in the IKMT-samples followed the same pattern as in 1995 (relatively high during courtship, lower during the early chick phase and almost none just before fledging). However, in this year an opposite pattern can be found in the food brought to the colony (a low proportion of sandeel during the early courtship period increasing to 50-75%). In 1997, the pattern in sandeel proportion found in the colony again matches the IKMT-samples fairly well (relatively high proportions during courtship, a sharp decline when the chicks hatched and an increase just before fledging).

The proportion of herring in the food brought to the colony parallels herring availability in the foraging areas fairly well (figure 28). In 1996, for example, herring availability was generally low throughout the season and the proportion of herring in the tern's food was accordingly low. Also the low herring availability during the courtship period in 1995 was accompanied by a extreme low proportion of herring in the colony. These parallels can be explained form the fact that Sandwich Terns prefer herring above sandeel. When herring becomes available the proportion in the tern's diet increases, whether sandeel is available or not. This would also explain why no relationship could be found between the proportion of herring available in the foraging area and that found in the colony.

Conclusions

* *Seasonal patterns in herring length as found in the IKMT-samples do parallel those found on Griend.*
* *The proportion of herring in the diet of the terns seems to depend on herring availability in the foraging areas. In general, however, changes in fish availability are not reflected in the amount of fish brought to the colony at Griend.*

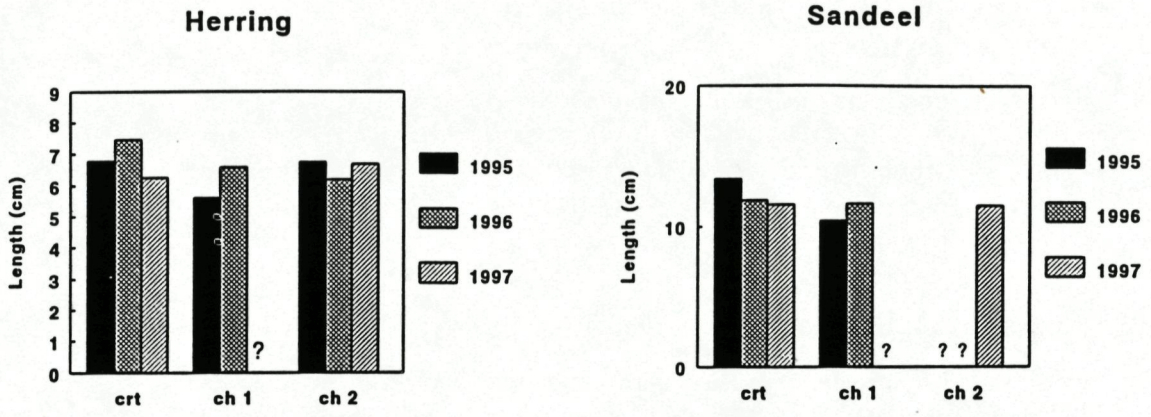

Figure 25. Average fish length during the courtship period (crt), the early chick stage (ch1) and the late chick stage (ch2), respectively, in the IKMT-samples during 1995-1997. ? = sample size too small.

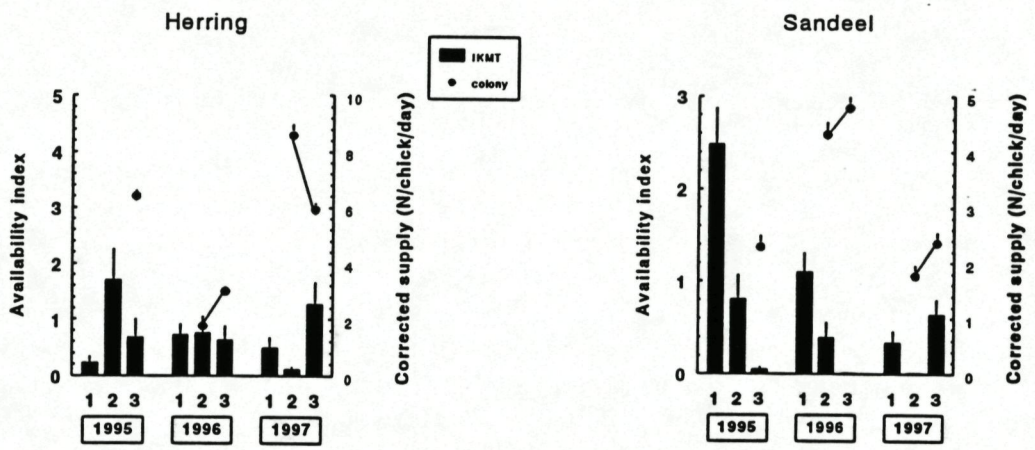

Figure 26. Changes in fish availability (± SE, left axis) compared with changes in the chicks food provisioning (i.e mean corrected food supply ± SE, right axis).

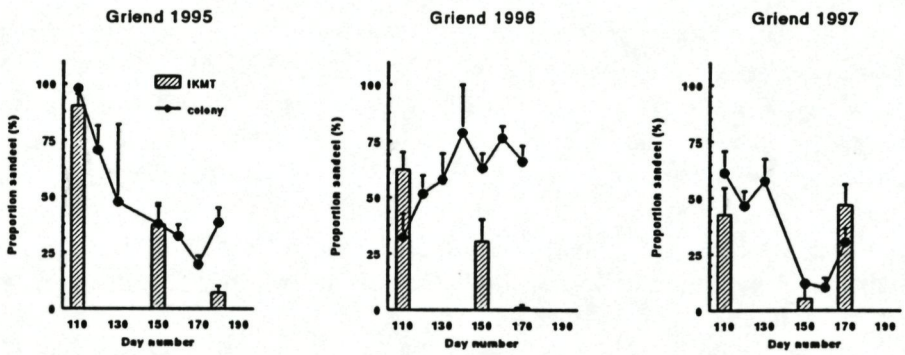

Figure 27. Changes in the proportion of sandeel in the foraging areas compared with changes in the mass-proportion as found on Griend. Bars denote SE. Day number 110 = 110-119, 120 = 120 - 129 etc.

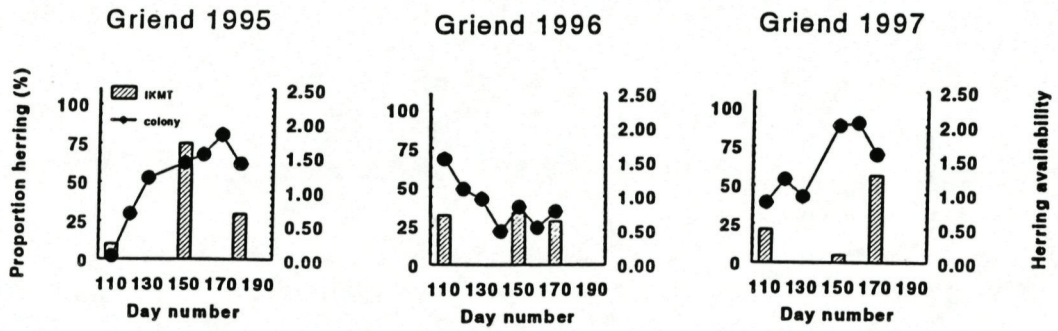

Figure 28. Changes in herring availability compared with changes in the proportion of herring in the tern's diet. Day number 110 = 110-114, 115 = 115 - 119 etc.

3.8 Prey fish availability influencing the terns' foraging behaviour

During each haul with the IKMT-net the number of foraging terns was counted in a 90° angle up to 1 km from the ship. Within the three study years the average number of foraging terns dropped from more than 3 in 1995 to about 1 in 1997 (figure 29) (Scheffé-test: 1995 > 1997: $F = 4.68$, $p < 0.05$). This drop parallels the decrease in fish availability as found in the IKMT-samples (compare figure 18). The same, but less obvious, parallel was found between the number of foraging terns (figure 30) and herring availability within the breeding cycle (compare figure 19). Most foraging terns were counted during the early chick stage (Scheffé-test: early chick > courtship, $F = 4.22$, $p < 0.05$), followed by a slight decrease during the late chick stage (although not significantly). However, it is questionable whether these are truly causal parallels. We believe that the number of foraging terns were merely a reflection of the birds present on Griend rather than a result of changing fish availability. For example, in 1995-1997 the number of breeding pairs on Griend decreased from 8600, via 5600 to 5000 which parallels the decrease in the number of terns foraging around Griend. The same holds for the pattern found within the breeding cycle. During the courtship period the numbers of terns on Griend were relatively low as all terns had not yet arrived. When the first chicks had hatched, the number of terns present on Griend were highest. Afterwards, the numbers decreased again as some of the parents lost their chicks and left Griend. For this reason the number of foraging terns is probably, merely an indication of the birds present on Griend rather than a result of changing fish availability.

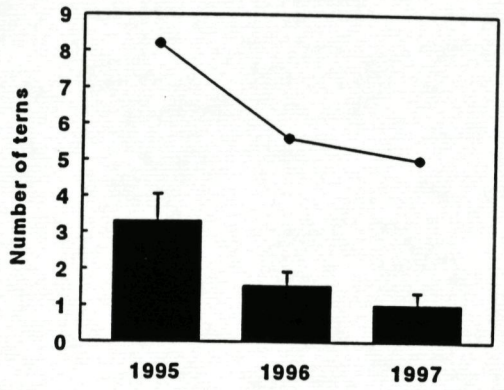

Figure 29. Mean number of foraging Sandwich Terns (± SE) counted in a 90° angle up to 1 km from the ship (bars) in relation to the number of breeding pairs on Griend (line x 1000).

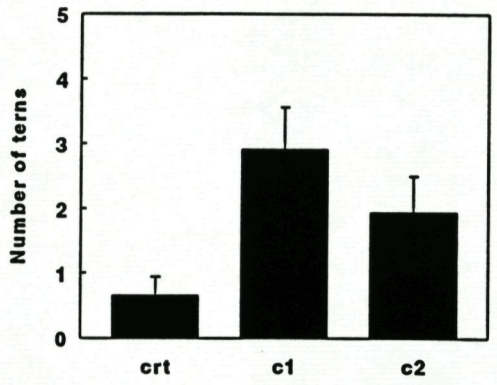

Figure 30. Number of foraging terns (± SE) counted in a 90° angle up to 1 km from the ship during the breeding cycle. Crt = courtship period, c1 = small chick stage and c2 = large chick stage.

In order to find out whether the numbers of foraging terns around Griend are actually influenced by fish availability one can either investigate whether the distribution of the terns is in accordance with the distribution of the fish or if abiotic parameters like tide and water clarity have the same effects on prey fish availability as on the presence of the terns. As was shown in chapter 3.6 most fish (especially herring) was available in the Vliesloot and in the Stortemelk. Likewise, the numbers of foraging terns were relatively high in these areas (although not significantly different from other areas). In the Vliestroom, however, the numbers of foraging terns were also high whereas the availability of fish was relatively low in the Vliestroom (figure 31). This is probably an effect of the Vliestroom being used as the main flyway of the terns to the foraging areas. Whenever a tern flying to the foraging areas encounters a fish in the Vliestroom it will try its luck. The striking influence of water clarity on fish availability, however, was not reflected in the number of foraging terns (figure 32). Also the relatively high abundance of prey fish during ebbing and flooding compared with the low and high water period was

not reflected in the number of foraging terns (figure 33). Actually the numbers of foraging terns were highest around the turning of the tide (Scheffé-test: turning > ebbing, $F = 5.43$, $p < 0.05$).

Conclusions

* Between and within year differences in the number of foraging terns were related to the number of terns present on Griend
* Most terns were counted in the Vliestroom and the Stortemelk, where herring availability was accordingly high.
* the strong effect of water clarity on fish availability was not reflected in the number of foraging terns

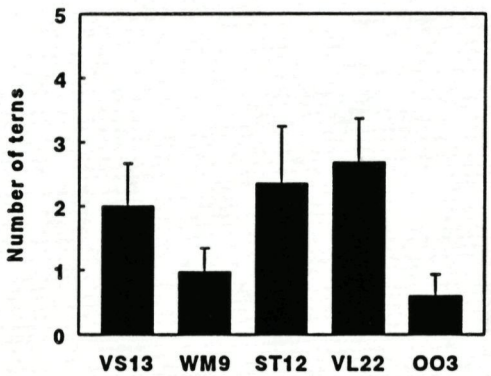

Figure 31. The number of foraging terns in a 90° angle up to 1km from the ship (± SE) at the 5 sampling locations (VS13 = Vliestroom, WM9 = Westmeep, ST12 = Stortemelk, VL22 = Vliesloot, OO3 = Oosterom).

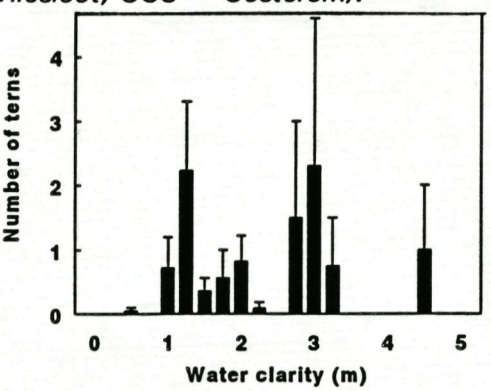

Figure 32. The number of terns foraging within 100 m from the ship (± SE) in relation water clarity.

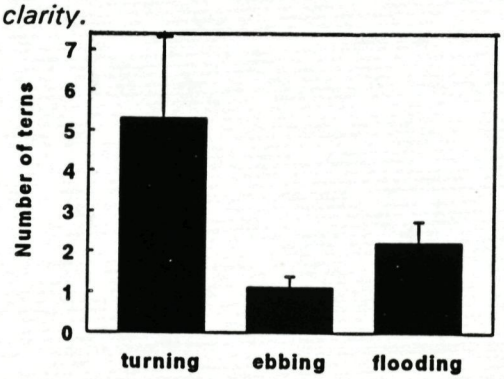

Figure 33. The number of foraging terns (90° angle up to 1km from the ship) in relation to tide. Bars denote SE.

4 DISCUSSION

4.1 Composition of the population

The observed changes in the age-composition in the population on Griend are for a large extent based on ring readings before egg laying. It is therefore not guaranteed that all terns of which the rings were read actually nested on Griend. However, almost all rings were read during courtship display making it likely that those birds started nesting on Griend. Besides, we caught some of the birds seen during courtship display on their nest later on in the season.

Veen (1977) found that colonies established later in the season consisted mainly of young, inexperienced birds. We showed that young birds not only nest later on in the season, but also start courtship activities later in the season than older birds do. Apparently most young birds arrived in the breeding colonies late in the season, resulting in a delayed courtship period and consequently a delayed incubation period. Another possibility is that young birds, although they arrive in the surrounding of the breeding areas at the same time as the older birds, may have to find a partner first, while the older, experienced birds may be already paired at arrival and thus can start producing eggs sooner. Both in 1995 and in 1996, the increase in the proportion of young birds during the course of the season was obvious. In 1997, however, this pattern was less pronounced if even discernible. The capricious character of the age composition of the population at the beginning of the courtship period in 1996 and 997 is probably a result of the small sample size. During the course of the season the sample size grows and the curve becomes less irregular.

4.2 Survival

Local survival Local survival of the 2-year old birds on Griend was considerably lower than expected from mortality rates, showing that most 2-year old birds do not return to the breeding grounds, but stay in the African winter quarters for the summer. Local survival of birds older than 2 years greatly differed between cohorts and years. In broad outlines, one can conclude that local survival of birds older than 4 years was low in 1996 and in 1997, whereas that of 4 year old birds was relatively high in those years. In 1995 the opposite was seen, local survival of young birds (3 and 4 year old) was relatively low, while that of older birds was relatively high. These changes were also reflected within the 1990 and 1992 cohorts. Survival of these cohorts sharply declined throughout the three years of observation. However, this was not the case for the 1991 cohort, of which survival was generally low throughout the years. The latter could be related to the bad weather conditions at the end of the 1991 breeding season (Brenninkmeijer & Klaassen 1991). This caused a high chick mortality and the chicks which did not die probably were in poor condition and as a consequence had a low post-

fledging survival.

In years with a relatively low number of breeding pairs (1996 and 1997) in particular the older, experienced birds did not return to the breed. It is highly unlikely that all these birds (more than 6000 individuals) died. Suggesting that they must either have skipped breeding or have emigrated to other colonies. In contrast to this, Brenninkmeijer & Stienen (1997) found that especially young, inexperienced birds emigrate to other colonies. It remains unclear why in the case of Griend in particular the older birds did not return.

Apart from the above results it is impossible to deduce firm conclusions on population dynamics of the Sandwich Tern from this study. It is for example somewhat premature to speak of young (3 and 4 year old) and old birds (5 to 7 year old) since members of this species can become older than 25 years. In order to draw firm conclusion further research must be done, using this method of reading rings in the colony with practically no disturbance for the birds.

Post fledging survival Analyses revealed that pre-fledging condition is related to post-fledging survival. The better the condition of a chick just before fledging, the higher are its chances to survive until first breeding. This relationship is very strong when pre-fledging condition was expressed as the condition of chicks older than 18 days. However, when the analyses is done for chicks older than 21 days the relationship becomes weaker. In fact one could conclude from figure 9b, that chicks with a body mass less than 30% beneath the average body mass do not return at all. Possibly these chicks died in the last week before fledging and did not fledge at all. The remaining part of the chicks (condition > 30%) have an equal chance of returning, regardless their condition. This would imply that no relationship between chick condition and survival exist at all. However, the sample size is low and in order to draw firm conclusions further research on this subject is needed. Perhaps an even better method to study the relationship between fledging condition and post-fledging survival may be to compare the pre-fledging condition of birds found dead after fledging with the pre-fledging condition of chicks which actually returned to the breeding grounds. To conclude, the results strongly suggest that condition just before fledging affects the chance to survive until first breeding. It is extremely important to improve our knowledge on such relationships since they can have serious consequences for a model on population dynamics. For example, it is possible that in years with relatively high reproductive output the condition of the fledglings is low. In spite of the high breeding success, such years may be of minor importance for the population, since a large part of the fledged chicks will die before reaching maturity. This would also imply that monitoring breeding success alone should be not sufficient. A good monitoring program should also include condition measurements as well.

4.3 Emigration to other colonies

Emi- and immigration do frequently occur in Sandwich Terns. Both in Denmark and on Griend a considerable part of the population consists of birds which originate from other colonies. Emigration can be the result of the disappearance of breeding grounds (e.g. through succession of the vegetation, disturbance or utilisation for (agri)cultural purposes), forcing the terns to move to a new breeding site. Especially in Denmark, where during the past decades a lot of small colonies were established and disappeared again in a relatively short time, this is probably the main reason for the low site fidelity of the Danish terns. Griend, on the other hand, forms an important and reliable breeding site for Sandwich Tern at least since the 19th century (Brenninkmeijer & Stienen 1992). Terns which nested or were born on Griend could always find back their former site in next years. This may be the reason for the high site fidelity of the terns on Griend.

When terns emigrate to other breeding sites, the chance that they will settle near their former colony is high. This explains that the population on Griend comprises a high proportion of birds ringed in other Dutch colonies and in Belgium. Terns from Belgium originate from the colony at the harbour of Zeebrugge. This colony increased from 1 pair in 1988 to 1650 pairs in 1993 (Veen *et al.* 1997). From 1994 onwards, the population declined and in 1995 only 250 pairs bred in Zeebrugge. Probably a part of the terns which originated from this colony emigrated to the adjacent colonies Hompelvoet and the Hooge Platen in the Dutch Delta area. But another significant part emigrated to Griend. No less than 13-17% of the adult birds from the Zeebrugge colony were found on Griend. The proportion of chicks born in Zeebrugge and found later on Griend was much lower (3-6% of the Zeebrugge population), probably since most of them did not yet return to breed. It is conceivable that the proportion of Belgium birds ringed as a chick will increase on Griend in the following years, unless the breeding site in Belgium will be restored.

Emigration of Danish birds shows a gradually increase with distance from the colony of origin, whereas the curves of the Dutch birds show a less smooth increase. This can be explained from the large distance between Griend and the most nearby colonies at the isle of Hompelvoet and the Hooge Platen. Emigrating terns from Griend can not find a suitable place to nest in between the Delta Area and Griend. In Denmark, however, there are a lot of (mostly small and short lasting) colonies at a short distance from each other, thus explaining the smooth curves.

Emi- and immigration rates are of indispensable value for a model on population dynamics. Earlier calculations showed, that the Dutch population is not able to maintain itself considering the present reproduction and survival rates (Brenninkmeijer & Stienen 1992, Van Boven & Schobben 1993). Immigration of Sandwich Terns from other parts of Europe could explain the discrepancy between the reality (a more or less stable population) and the output of the models. Brenninkmeijer & Stienen (1992) calculated that in the

period 1970-1973 the net import must have been 12% in order to explain the increase of the population in that period. At present time the population is more or less stable, thus less import is needed. Our calculations show that at present time 1.0-1.6% of the Danish population (ringed as a chicks) emigrates to Griend (data 1995 and 1996). Brenninkmeijer & Stienen (1997) calculated that in the period 1966-1996 0.4% of the Danish population emigrated to Griend, while in the period 1971-1996 0.8% of the population on Griend emigrated to Denmark. As the number of breeding pairs in Denmark and on Griend were comparable, one would not expect a large net import of Danish terns on Griend. For adults we show that 0-0.8% of the Danish population emigrates to Griend. Brenninkmeijer & Stienen (1997) computed that 0.3% of the adult Danish birds emigrated to Griend (1971-1996). They further show that in the period 1966-1991 no adult ringed tern from Griend was recovered in Denmark. This suggests that there is a small net import of Danish adult birds on Griend, but by far not enough to explain the above-mentioned discrepancy between reality and the model. This means that either the assumptions on reproductive output or adult mortality used in earlier models (Brenninkmeijer & Stienen 1992, Van Boven & Schobben 1993) were inaccurate (1), or the calculations presented in the present report are not completely reliable (2) or the net import from European colonies other than Denmark is large (3). Option 3 seems not likely considering that less than 5% of other European populations emigrate to Griend (this report). The other two possibilities can not be excluded. Earlier models rested on ring recoveries, and these could be biased by ring loss caused by abrasion of the rings (Hatch & Nisbet 1983, Bailey *et al.* 1987, Nisbet & Hatch 1988) and by the small sample sizes. The present calculations on emi- and immigration also rest on assumptions on mortality rates and small sample sizes. Probably the presented emi- and immigration rates are too low (in particular for terns ringed as a chick) as can be concluded from the unrealistic low proportion of terns ringed on Griend and recovered on Griend in later years (table 4 of this report and Brenninkmeijer & Stienen 1997). To conclude, the present data do not point towards a large influx of foreign terns into The Netherlands, The present data, however, are based on small sample sizes and a lot of assumptions. Nevertheless, the results show that emigration to other colonies does frequently occur and that there can be considerable differences in migration rates between different colonies.

A remarkable difference was found in the emigration rate of terns ringed as a chick and terns ringed as an adult. This suggests that terns once established in a colony are less inclined to give up their familiar breeding site. While on the other hand, the chances to settle in an unknown colony are much higher for young, inexperienced birds.

4.4 Food supply in relation to food availability

Fish length In general, the fish provisioned to the chicks in the first week after hatching was smaller than those fed during the courtship period and in

the late chick stage. It is conceivable that this is a result of the impossibility for small chicks to swallow large fish and that therefore the parents selectively forage on small fish. However, the IKMT-samples showed, that the length of the fish on offer (both herring and sandeel) was in general also relatively small during the early chick phase. Although the length distribution of the sampled fish (especially herring) was not in accordance with that measured in the colony, it seems that the timing of the breeding season is such, that at the time that the chicks hatch the availability of small fish is highest. In other words, the provisioning of small fish to freshly hatched chicks is not only a matter of selective foraging by the parents but is also the result of a higher abundance of small fish at this stage of the chick-rearing period. The decrease in the length of the fish on offer, however, was only found when using the averages of the three years of investigation. Within-year and annual changes in fish length found in the IKMT-samples were not always reflected in the food provisioned to the chicks. This can have several reasons, but probably the most obvious reason is that the IKMT-samples were too small to detect such differences. Furthermore, the samples did probably not reflect the genuine fish availability for sandwich Terns since (1) the IKMT-net caught selectively (in particular for sandeel) and (2) sampling took place at only a few sites within the foraging area of the terns (only at sites where the water was of sufficient depth for the ship). Terns, on the other hand, were often seen foraging along the edges of the gullies and in the shallow waters northwest of Vlieland and Terschelling, where sampling was impossible.

Fish availability and species composition Differences in prey fish abundance were not reflected in the food supplied by the terns. Even when all fishery data are lumped in yearly categories the apparent decrease in fish availability (both herring and sandeel) throughout the years was not reflected in the amount of fish brought to the colony. In 1997, food provisioning in the colony was relatively high, whilst the availability of the fish was relatively low according to the IKMT-samples. Also the species composition found in the IKMT-samples do not match that found in the colony in all years. In 1995 and in 1997 the species composition as found in the colony followed that in the IKMT-samples fairly well, but in 1996 large differences exist. On the other hand, the proportion of herring in the food brought to the colony do reflect herring availability in the foraging areas fairly well. These findings suggest that the used sampling methods are not suitable to measure all aspects of food availability for terns.

4.5 Food availability influencing the distribution of the terns

In the Westmeep and in the Oosterom, fish availability was low and only few foraging terns were encountered in these areas. Most foraging terns were encountered in the Vliesloot, the Stortemelk and the Vliestroom, although no significant differences could be proved. In these areas, but in the Vliestroom, fish abundance (in particular herring) was accordingly high (although not always significantly higher). However, most terns were seen flying further to

the north, where sampling of prey fish was not possible due to the shallowness of the water. Probably the abundance of herring was relatively high in these waters, as could be concluded from the relatively high numbers of terns returning from these areas holding herring in their bill (own observation; 62% of all terns carrying herring, N = 52). Also the fish samples show, that most herring was available in the waters north of Vlieland and Terschelling. This implies that further to the north herring abundance may be even higher. This means that Sandwich Terns have to make longer foraging trips to get hold of herring. This was also found in a study were radio transmitters were used to track the foraging terns on Griend (Raaijmakers *et al.* 1993). There are some clues that herring born in the western part of the central North Sea did not occur in the fish samples. This herring would be of appropriate size for the chicks. It is possible that the terns therefore have to make relative long foraging flights to get hold of the 1.5 year old herring present in the North Sea.

The availability of both herring and sandeel highly depended on water clarity. In waters with a high visibility no fish was caught in the IKMT-net. By means of acoustic equipment the presence of fish in these clear waters could be demonstrated, although at greater depths. Since terns catch their fish in the upper 2 m of the water layer (Borodulina 1960, Dunn 1972), in clear waters the fish is, although present, not available for foraging terns. It is therefore conceivable that clear waters are not attractive for foraging terns. However, no relationship between water clarity and the number of foraging terns was found. Even in waters with a visibility of 5 m foraging terns were encountered. The reason for this is not clear. Possibly, the terns do actually spot the fish in clear water and subsequently dive at the fish, but do not succeed in their efforts since the fish is beyond their reach. Unfortunately, we do not have sufficient data on the terns' foraging success in relation to water clarity.

4.6 Changing food situation affecting population dynamics

Although changing food availability could not always be proved by fishery data, it is clear that in the course of the three years food availability has changed considerably. Not only food supply to the colony but also the composition of the food and parental effort showed large annual changes. Parallel with these changes the composition of the population altered significantly. This suggests that population changes may have been induced by changes in food availability. In 1995, 8200 pairs nested on Griend; in 1996, the number of breeding pairs was reduced to 5600 pairs and this was further reduced to 5000 pairs in 1997. We already showed that in particular older birds failed to return to Griend in 1996. Although it can not be excluded that the birds which did not return to Griend actually died, it is more likely that they either emigrated to other colonies or skipped breeding. In 1996, we have no indications that they moved to other Dutch colonies (no recoveries and no increases of the same order in other Dutch colonies), so they probably skipped breeding or nested abroad. In 1997, the colonies on Schiermonikoog and

Rottum (established in 1996) increased in numbers and together held 1800-2300 breeding pairs. Probably a large part of these birds originated from Griend. However, this can not completely explain the loss of 3200 breeding pairs on Griend compared with 1995. This means that at least a part of the birds must have skipped breeding or must have emigrated elsewhere. Skipping one or more breeding seasons is not unknown in seabirds. For example in Shetland, where the number of breeding Arctic Terns was extremely low during a series of years (Heubeck 1988, Phillips *et al.* 1996, Suddaby & Ratcliffe 1997). The collapse of the population coincided with the collapse of the local sandeel stock. Also in other seabirds such a relationship between food availability or food abundance and the number of breeding seabirds was found (Furness 1989, Vader *et al.* 1990, Bailey 1991, Anker-Nillsen & Barrett 1991, Phillips *et al.* 1996). This suggests that food availability could also be a key-factor in the regulation of the number of nesting Sandwich Terns breeding on Griend. In fact there are some clues that such a relationship exists for Sandwich Terns. Brenninkmeijer & Stienen (1994) found that the number of breeding pairs in The Netherlands was related to the abundance of young herring in the North Sea. On a local scale, however, such relationship was never demonstrated. The short term character of this study makes it impossible to detect such relationships. Fortunately we have data of 6 years (1992-1997) at our disposal on a series a series of parameters which may be indicative for the local food situation around Griend, namely:

- clutch size
- adult condition
- food supplied to the chicks
- parental effort
- reproductive output

For each of these parameters we discuss their indicative value for the local food situation and look for a possible relationship with the number of Sandwich Terns breeding on Griend

Clutch size In several Sterninae clutch size is related to food availability or quality of the food (Boecker 1967, Lemmetyinen 1973). However, Monaghan *et al.* (1992) found that clutch size was only slightly reduced in a poor food situation. Clutch size in terns is however also related to the age of the birds (Hays 1978, Nisbet *et al.* 1984). Considering the changes in age composition of the population on Griend, this could also have influenced clutch size. Therefore the indicative value of clutch size as a parameter for food availability is questionable.

In 1992-1997, clutch size varied from 1.4 eggs per nest in 1996 to 1.8 eggs per nest in 1992. The number of breeding pairs on Griend showed no correlation with clutch size (figure 33).

Adult condition A second clue for a changing food availability, acting somewhat later in the season, is the condition of the adult birds. In a year with low food availability, when the birds can not find sufficient food, one

would expect that their condition is also low. In fact, Monaghan *et al.* (1992) argued that not clutch size but rather adult condition and nest desertion could be an important indicator of food availability. We defined adult condition as the relative deviation from the expected body mass in the same way as was done for chicks (chapter 3.4). In the period 1992-1996 adult condition follows fluctuations in the number of breeding pairs exactly (figure 33). In 1997, however, adult condition was relatively high and did not fit into this relationship.

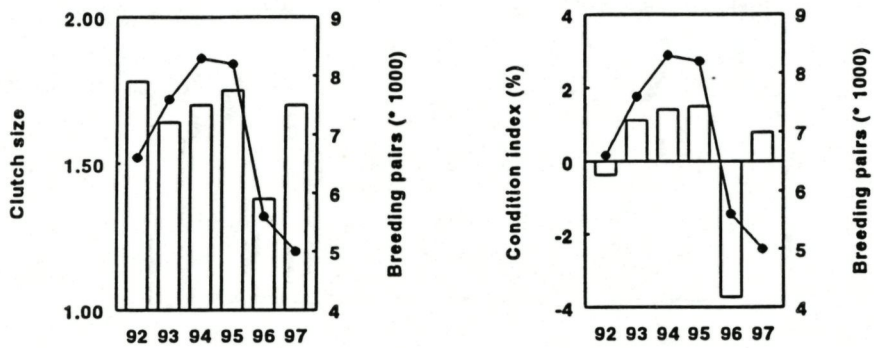

Figure 33. The number of breeding pairs on Griend in 1992-1997 (right axis) compared with clutch size (left graph) and adult condition (right graph).

Food provisioning In 1992-1996, the number of herring brought to the chicks (after correction for parental effort) followed the number of breeding pairs on Griend exactly (figure 34). In years with relatively few breeding pairs the amount of herring supplied to the chicks was low, suggesting that herring availability in the foraging areas was accordingly low. However, in 1997 the number of breeding pairs was extremely low, while the amount of herring supplied to the chicks was relatively high. The amount of sandeel supplied to the chicks shows no parallels with the number of breeding pairs. The total amount of fish supplied was highest in 1994 and 1995, when the number of breeding pairs was accordingly high. In 1992 and in 1996, when the number of breeding pairs were low the total amount of fish supplied was also low. Again 1997 does not fit in. Although the total amount supplied was fairly high in 1997, the number of breeding pairs was the lowest since 1992.

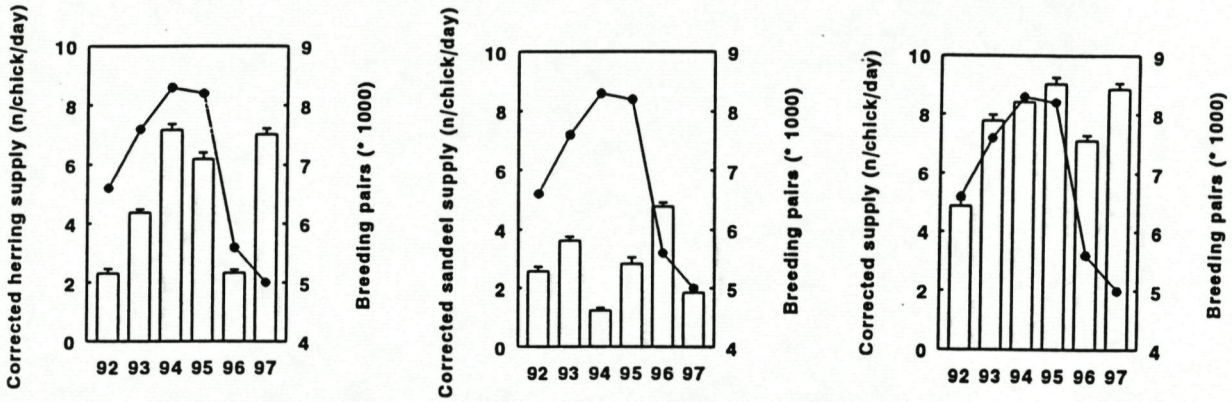

Figure 34. Amount of fish supplied to the chicks (corrected for parental effort) in relation to the number of breeding pairs on Griend. Bars denote SE.

Parental effort Parental effort may also be indicative for the food situation. During the chick rearing period parents can compensate for low food availability by foraging both at the same time. During early development tern chicks can not do without brooding (Klaassen *et al.* 1994), thus one parent has to stay at the nest. Older chicks were left alone 10-71% of the time (figure 35). In the period 1992-1996, the number of breeding pairs was negatively correlated with parental effort. In 1997, however, the number of breeding pairs was low while the parents left their chick alone for only 20% of the time.

Reproductive output Finally reproductive output may be indicative for the food situation. However, reproductive output is hard to asses and also depends on other factors like weather conditions, the rate of kleptoparasitism and the subcolony were the measurements are performed. Except for 1992, we accurately measured breeding success in the same subcolony in which the amount of food supplied was measured. The reproductive output in these subcolonies followed the observed population trend fairly well (figure 35).

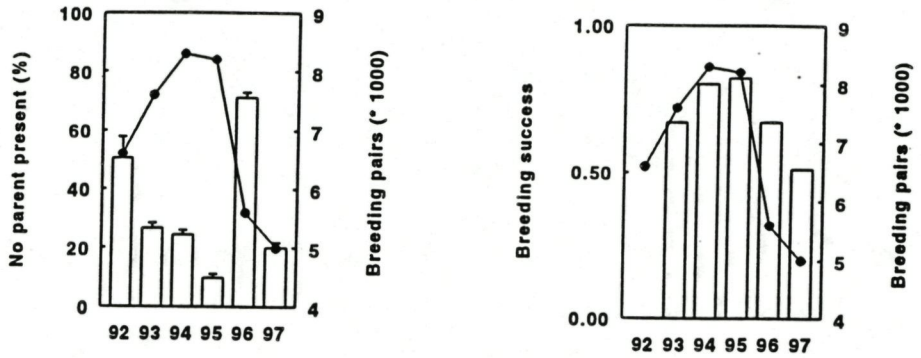

Figure 35. Fluctuations in nest attendance and reproductive output compared with the observed population trend.

When the above-mentioned indicators of food availability are ranked into 3 classes (good, intermediate and bad), a clear picture arises (table 7). In the two years with the highest number of breeding pairs (1994 and 1995) all parameters indicated that the food situation was either good or fairly well. On the other hand, in years with a low number of breeding pairs (1992 and 1996) most parameters indicated a bad food situation. In 1993, both the number of breeding pairs and other parameters indicative for the food situation had an intermediate position. Only the results found in 1997 do not fit in. Most parameters indicate that the food situation around Griend was not so bad at all in 1997, whereas the number of breeding pairs was low. However, in this year the colonies on Schiermonnikoog and Rottum sharply increased in numbers. Probably these terns all originated from Griend, which is the most nearby colony. We hypothise that as a result of the bad food situation in 1996 a part of the population on Griend moved to Schiermonnikoog and Rottum in 1997. This would imply that the entire Wadden sea population has to be considered instead of the population on Griend. If we correlate the parameters for the local food situation as measured on Griend with the number of Sandwich Terns breeding in the entire Wadden Sea strong relationships exists (figure 36). In particular adult condition, the corrected amount of herring supplied and parental effort predicts the number of breeding pairs in the Wadden Sea extremely well. Apparently, the local food availability strongly influences the number of nesting Sandwich Terns in the Wadden Sea.

Table 7. Indicators of the local food situation ranked over 1992-1997. The two lowest values were ranked as -, the two intermediate values as ± and the two highest values as +.

Parameter	1992	1993	1994	1995	1996	1997
Breeding pairs	6600	7600	8300	8200	5600	5000
Clutch size	+	-	±	+	-	±
Adult condition	-	±	+	+	-	±
Corrected herring supplied	-	±	+	±	-	+
Corrected fish supplied	-	±	±	+	-	+
Nest attendance	-	±	±	+	-	+
Breeding success	?	±	+	+	±	-

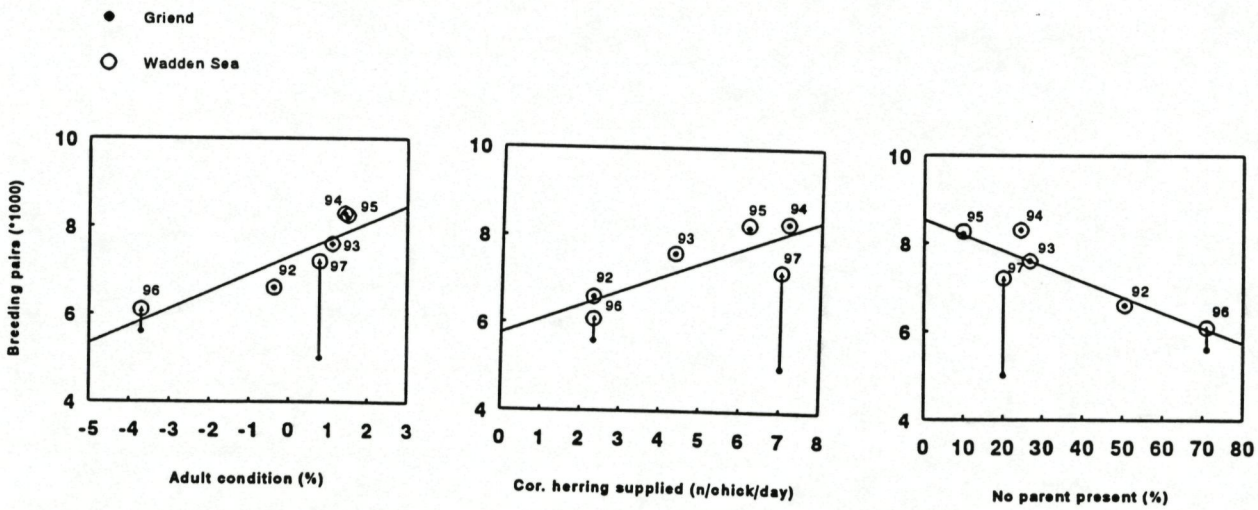

Figure 36. Relationship between adult condition, the corrected amount of herring supplied to the chicks and parental effort, respectively, and the number of Sandwich Terns breeding on Griend and in the entire Wadden Sea in 1992-1997.

One question left unanswered is whether the above-mentioned indicators of food availability actually reflect the food situation in the local foraging areas. Unfortunately, until now the fish sampling programme could not clarify this. Nevertheless, we believe that the sampling should be continued. In the first place, the sampling programme can give us valuable information on the spatial distribution of the prey fish and the influence of abiotic factors like weather, tide and water clarity on the distribution of the fish. Moreover the complex migration patterns of the fish can only be understood by means of a long lasting monitoring program. Assessing food abundance, however, is extremely difficult because fish is not randomly distributed, and can occur in large shoals. To answer the question of how food availability influences the birds

decisions further research is needed. Probably only birds in good condition decide to start the strenuous breeding season, which should explain the lower condition of the adult birds in years with low food-availability indices. The mechanism behind this is completely unclear and is probably very complicated.

Summarising the results strongly suggest that food availability and in particular the availability of herring in the local feeding areas around Griend has an effect on number of breeding Sandwich Terns. In years that several parameters indicate a low food availability the numbers of breeding pairs were accordingly low. In such years the older, experienced birds do not return to nest on Griend, while the young birds start breeding in spite of the sub-optimal food situation. In years with low food availability the condition of the adult birds is low, food provisioning to the chicks is low and as an attempt to compensate for this, the parents increase their effort. It seems that further growth of the population is limited by food availability.

5 RECOMMENDATIONS

The central question in this report is: what factors affect the population size of Sandwich Terns. To answer this question a detailed knowledge is needed on factors influencing population dynamics. The present study filled some important gaps in our knowledge. Yet, our knowledge is still insufficient to answer all questions on how the size of the population is regulated. Because of the short-term character of this study natural variation in the studied parameters can have disproportional large influences. Moreover, only a minor part of the life of a Sandwich Tern is covered by this research, since birds of this species can become more than 25 years old.

Important hiati in our knowledge include:

- information on birds older than 7 years;
- exact estimates of survival rates;
- the fate of the birds which did not return to Griend;
- decisions of the birds with respect to breeding;
- our knowledge on distribution and behaviour of the prey fish

Some of these questions are relatively easy to answer. For example, reading rings in the new colonies on Schiermonnikoog and Rottumeroog could make clear whether or not these birds originate from Griend. Other questions can only be clarified by means of long-term studies.

6 ACKNOWLEDGEMENTS

The study on Griend would have been impossible without the help of Peter Boerkamp, Aswin Bouwmeester, Nico van den Brink, Wilma Dijkman, Gijs Doeglas, Mories Driessen, Einar Flensted-Jenssen, Jan de Jong, Jan van de Kamp, Marcel Kersten, Marcel Klaassen, Chris Klok, Johan Krol, Noël van Rens, Joost Roelse, Hans Schekkerman, Thea Smit, Piet van Tienen and Jan Veen. We thank Dirk van Holk for his punctional provisioning of our food. Jan van Dijk, Dirk Kuiper, the crew of the Krukel and the RP-Harlingen transported researchers and equipment to and from Griend. The company of the photographers Martijn de Jonge and Jan van der Kam was always very pleasant. Discussions with Rudi Drent, Arie Spaans and Jan Veen were very stimulating for this project. The manuscript greatly benefited from comments by Henk Baptist, Gerrit van de Kamp, Dick de Jong and Arie Spaans.

Gerrit van de Kamp (RIVO-DLO) performed the sampling of the prey fish. We thank him, Ad Corten and Henk Heessen for their pleasant co-operation. Hans van den Bergh, John Habraken and Chris Winters were of indispensable value in counting terns in the foraging areas.

CONCLUSIONS

- The number of Sandwich Terns nesting in the Dutch Wadden Sea are strongly correlated with various parameters indicative for food availability as measured on Griend. Years with low numbers of breeding pairs were paralleled by a poor condition of the breeding adults, a limited provisioning of food (in particular herring) to the chicks and an increased parental effort. This suggests that further growth of the population is limited by food abundance.

- Sampling of prey fish availability in 1995-1997 did not confirm the changing food situation. The used sampling method is probably not suitable to detect such changes.

- The age composition of the population on Griend was related to the population size. In 1996-1997, when the numbers of breeding pairs were low, the population on Griend consisted of relatively high numbers of young birds, whereas in 1995 (high number of breeding pairs) the proportion of older birds was relatively large.

- The results strongly suggest that post-fledging survival is affected by the pre-fledging condition of the chicks. The better the pre-fledging condition of the chicks the higher were the chances to return to Griend.

- Prey fish availability was strongly influenced by water clarity. In relatively clear water fish was present at greater depths, but beyond the reach of the foraging terns.

- Sandeels were evenly distributed over the foraging area of the terns. The availability of herring, however, was highest in the gullies around Vlieland and Terschelling, suggesting that Sandwich Terns have to make longer foraging flights to get hold of herring.

- The highest number of foraging terns were encountered in the gullies around Vlieland, where herring availability was accordingly high. However, other factors influencing prey fish availability (such as water clarity and tide) did not affect the number of foraging terns.

- Emigration is a common phenomenon in Sandwich Terns. Both on Griend and in Denmark, a considerable part of the population consisted of foreign birds. However, site fidelity of the terns on Griend was much higher than that of the Danish birds.

- Emigration is strongly related to the distance from the original colony. The vast majority of the migrating terns settled down at less than 200 km away from their former colony. Terns ringed as adults settled closer to their former colony than birds ringed as a chick.

REFERENCES

Anker-Nillsen, T. & A.T. Barrett 1991. Status of seabirds in northern Norway. British Birds 84: 329-341.

Appenzeller, A.R. & W.C. Leggett. An evaluation of light-mediated vertical migration of fish based on hydroacoustic analysis of the vertical movements of rainbow smelt (*Osmerus mordax*). Canadian Journal of Fishery and Aquatic Science 52: 504-511.

Bailey, E.E., G.E. Woolfende & W.B. Robertson 1987. Abrasion of and loss of bands from Dry Tortugas Sooty Terns. Journal of Field Ornithology 58: 413-424.

Bailey, R.S. 1991. The interaction between sandeels and seabirds - a case history at Shetland. International Council for the Exploration of the Sea (ICES) 165: 1-12.

Boecker, M. 1967. Vergleichende Untersuchungen zur Nahrungs- und Nistökologie der Flußseeschwalbe (Sterna hirundo L.) und der Küstenseeschwalbe (Sterna paradisaea Pont.). Bonner Zoologische Beitrage 18: 15-126.

Borodulina, T.L. 1960. Biology and economic importance of gulls and terns of southern-USSR water bodies. Akad. Nauk SSSR. Trudy Inst. Morf. Zhiv. 32: 1-132.

Bosveld, A.T.C., J. Gradener, M. van Kampen, A.J. Murk, E.H.G. Evers & M. van den Berg 1993. Occurrence and effects of PCBs, PCDDs and PCDFs in hatchlings of the Common Tern (Sterna hirundo). Chemosphere 27: 419-427.

Boven, R.M. van & J.H.M. Schobben 1993. Risico-analyse voor een indicator-soort van het zeemilieu: de populatiedynamica van de Grote Stern in Nederland. RWS-rapport DGW-93.006. Rijksinstituut voor Kust en Zee, Den Haag.

Brenninkmeijer, A. & M. Klaassen 1991. Griend, vogels en bewaking 1991. Intern rapport. Rijksintituut voor Natuurbeheer, Arnhem.

Brenninkmeijer, A. & E.W.M. Stienen 1992. Ecologisch profiel van de Grote Stern (Sterna sandvicensis). RIN-rapport 92/18. Instituut voor Bos- en Natuuronderzoek (IBN-DLO), Arnhem.

Brenninkmeijer, A. & E.W.M. Stienen 1994. Pilot study on the influence of feeding conditions at the North Sea on the breeding results of the Sandwich Tern Sterna sandvicensis. IBN Research Report 94/10. Instituut voor Bos- en

Natuuronderzoek (IBN-DLO), Wageningen.

Brenninkmeijer, A.W.M. & E.W.M. Stienen 1997. Migratie van de Grote Stern Sterna sandvicensis in Denemarken en Nederland. IBN-rapport 302. Instituut voor Bos- en Natuuronderzoek (IBN-DLO), Wageningen.

Burd, A.C. 1984. Density dependant growth in North Sea herring. International Council for Exploration of the Sea. 1984/H:4.

Corten,A. 1990. Long-term trends in pelagic fish stocks of the North Sea and adjacent waters and their possible connection to hydrographic changes. Netherlands Journal of Sea Research 25: 227-235.

Corten, A. 1996. Ecoprofiel haring. Rapport CO59/95. Rijksinstituut voor Visserijonderzoek (RIVO-DLO), IJmuiden.

Corten, A. & G. van de Kamp 1979. Abundance of herring larvae in the Dutch Wadden Sae as a possible indication of recruitment strength. International Council for Exploration of the Sea. C.M. 1979/H:26.

DiConstanzo, J. 1980. Population dynamics of a Common Tern colony. Journal of Field Ornithology 51: 229-243.

Dunn, E.K. 1972. Studies on terns, with particular reference to feeding ecology. Ph.D. thesis Durham University, Durham.

Fonds, M. 1978. The seasonal distribution of some fish species in the western Dutch Wadden Sea. In: N. Dankers, W.J. Wolff & J.J. Zijlstra (eds.), Fishes and fisheries of the Wadden Sea. Stichting Veth tot steun aan Waddenonderzoek, Leiden.

Furness, R.W. 1989. Declining seabirds populations. Journal of Zoology 219: 177-180.

Geschiere, C.E. 1993. Kapers op de kust. Het effect van enkele abiotische en biotische variabelen op het kleptoparasitisme door de kokmeeuw Larus ridibundus op de grote stern Sterna sandvicensis en de gevolgen hiervan op de reproduktie van de grote stern op Griend. Intern rapport, Instituut voor Bos- en Natuurbeheer (IBN-DLO), Arnhem.

Hays, H. 1978. Timing and breeding success in three- to seven-year-old Common Terns. Ibis 120: 127-128.

Hatch, J.J. & I.C.T. Nisbet 1983. Band wear and band loss in Common Terns, Journal of Field Ornithology 54: 1-16.

Heubeck, M. 1988. Shetland's seabirds in dire straits. BTO News 158: 1-2.

Klaassen, M., B. Habbekotté, P. Schinkelshoek, E.W.M. Stienen & P. van

Tienen 1994. Influence of growth rate retardation on time budgets and energetics of Arctic Tern Sterna paradisaea and Common Tern S. hirundo chicks. Ibis 136: 197-204.

Lemmetyinen, R. 1973. Clutch size and timing of breeding in the Arctic Tern in the Finnish archipelago. Ornis Fennica 50: 18-28.

Macer, C.T. 1966. Sand eels (*Ammodytidae*) in the south-western North Sea; their biology and fishery. Fishery investigations Series II. Ministry of agriculture, fishery and food, London.

Monaghan, P., J.D. Uttley, M.D. Burns, C. Thaine & J. Blackwood 1989. The relationship between food supply, reproductive effort and breeding success in Arctic Terns Sterna paradisaea. Journal of Animal Ecology 58: 261-274.

Monaghan, P., J.D. Uttley & M.D. Burns 1992. Effect of changes in food availability on reproductive effort in Arctic Terns *Sterna paradisaea*. Ardea 80: 71-81.

Nisbet, I.C.T., J.M. Winchell & A.E. Heise 1984. Influence of age on the breeding biology of Common Terns. Colonial Waterbirds 7: 117-126.

Nisbet, I.C.T & J.J. Hatch 1988. Durability of incoloy bands on Common Terns. Colonial Waterbirds 11: 113-114.

Phillips, R.A., R.W.G. Caldow & R.W. Furness 1996. The influence of food availability on the breeding effort and reproductive success of Arctic Skuas Stercorarius parasiticus. Ibis 138: 410-419.

Raaijmakers, M.H.J.E., P.W.M. van Beers & J.M.P.M. Habraken 1993. Telemetrische bepaling van de foerageerplaatsen en foerageerroutes van de op Griend broedende grote sterns Sterna sandvicensis. Doctoraalverslag K.U. Nijmegen, Vakgroep Dieroecologie, Instituut voor Bos- en Natuuronderzoek, Wageningen.

Stienen, E.W.M. & A. Brenninkmeijer 1994. Voedselecologie van de Grote Stern (Sterna sandvicensis): onderzoek ter ondersteuning van een populatie-dynamisch model. IBN-rapport 120. Instituut voor Bos- en Natuuronderzoek (IBN-DLO), Wageningen.

Suddaby, D. & N. Ratcliffe 1997. The effect of fluctuating food availability on breeding Arctic Terns (*Sterna paradisaea*). Auk 114: 524-530.

Vader, W., T. Anker-Nilssen, V. Bakken, R.T. Barrett & K.-B. Strann 1990. Regional and temporal differences in breeding success and population development of fisheating seabirds in Norway after collapses of herring and capelin stocks. Transactions 19th IUGB Congress (Trondheim 1989): 143-150.

Veen, J. 1977. Functional and causal aspects of nest distribution in colonies of the Sandwich Tern (Sterna s. sandvicensis Lath.). Behaviour Supplement 20: 1-193.

Veen, J. 1994. De broedvogelbevolking van Griend. De Levende Natuur 95: 112-118.

Veen, J., E.W.M. Stienen, A. Brenninkmeijer, H. Offringa, P. Meire & J. van Wayenberge 1997. Ecologische randvoorwaarden voor de aanleg van een broedplaats voor sterns in de voorhaven van Zeebrugge. Rapport IN 97/15. Instituut voor Natuurbehoud, Brussel.

Reeds verschenen BEON rapporten:

BEON rapport nr.	1.	BEON Meerjarenplan 1988-1993.	1987
BEON rapport nr.	2.	BEON Jaarwerkplan 1988.	1988
BEON rapport nr.	3.	BEON Modellering.	1988
BEON rapport nr.	4.	BEON meerjaren Uitvoeringsprogramma 1988-1993.	1989
BEON rapport nr.	5.	BEON Jaarwerkplan 1989.	1989
BEON rapport nr.	6.	Findings of the BEON Workshop in preparation for the Third North Sea Conference.	1989
BEON rapport nr.	7.	Beleidspresentatie BEON 23 juni 1989 Den Haag.	1989
BEON rapport nr.	8.	Effects of Beamtrawl Fishery on the Bottom Fauna in the North Sea.	1990
BEON rapport nr.	9.	BEON Jaarwerkplan 1990.	1990
BEON rapport nr.	10.	BEON Voortgangsrapport 1988-1989.	1990
BEON rapport nr.	11.	Beleidspresentatie BEON 31 mei 1990 Den Haag.	1990
BEON rapport nr.	12.	Beleidspresentatie BEON 20 juni 1991 Den Haag.	1991
BEON rapport nr.	13.	Effects of Beamtrawl Fishery on the Bottom Fauna in the North Sea. II. The 1990 - studies.	1990
BEON rapport nr.	13 A.	BEON Jaarwerkplan 1991.	1991
BEON rapport nr.	14.	BEON Jaarwerkplan 1992.	1992
BEON rapport nr.	15.	Beleidspresentatie BEON 19 juni 1992 Den Haag.	1992
BEON rapport nr.	16.	Effect of Beamtrawl Fishery on the Bottom Fauna in the North Sea. III. The 1991 - studies.	1992
BEON rapport nr.	17.	Beleidspresentatie BEON 12 december 1991.	1992
BEON rapport nr.	18.	Trace Element Geochemistry at the Sediment Water Interface in the North Sea and the Western Wadden Sea.	1993
BEON rapport nr.	19.	Effecten van met benzo(a)pyreen verontreinigd sediment op de Helmkrab (Corystes cassivelaunus). Rapportage Project BEONADD I/II.I	1993
BEON rapport nr.	20.	Scavenging seabirds behind fishing vessels in the Northeast Atlantic. (With emphasis on the Southern North Sea).	1993
BEON rapport nr.	21	Brug tussen Beleid en Onderzoek (Rapportage over het eerste BEON Meerjarenprogramma 1988-1992).	1993
BEON rapport nr.	93-1	Naar een duurzame ontwikkeling van de Noordzee. (Tweede Meerjarenprogramma BEON1993-1997).	1993
BEON rapport nr.	93-2	The appearance of scars on the shell of Arctica Islandica L. (Mollusca, Bivalvia) and their relation to bottom trawl fishery.	1993
BEON rapport nr.	93-3	BEON Jaarwerkplan 1993.	1993
BEON rapport nr.	93-4	BEON Beleidspresentatie "Zee en Wadvogels. "Voorkomen en invloeden daarop" d.d. 10 december 1993.	1993

1994

BEON rapport nr. 94-1	Effecten van verschuivingen van nutriëntenconcentraties op biota in de Nederlandse kustwateren. Philippart, C.J.M. & E.G. de Groodt, A.G. Brinkman, R.G. Jak, M.C.Th. Scholten (IBN 93 E 02).
BEON rapport nr. 94-2	Vervalt; zie 96-3
BEON rapport nr. 94-3	Jaarwerkplan 1994.
BEON rapport nr. 94-4	Jaarverslag 1993: Algenonderzoek in mesocosms en modelleringlering. Riegman, R. (NIOZ 93 E 01).
BEON rapport nr. 94-5	Impact of anthropogenic activities on the productivity of the western Wadden Sea ecosystem. Veer, H.W. van der. (NIOZ 93 E 02).
BEON rapport nr. 94-6.1	Bentic nutriënt generation in the ERSEM ecosystem model of the North Sea. Ruardij, P. and W. van Raaphorst. (NIOZ 93 E 03)
BEON rapport nr. 94-6.2	The EcoWasp model and it's environment. Smit, J.P.C., A.G. Brinkman, E.G.M. Embsen, P. Ruardij, and W. van Raaphorst. (NIOZ 93 E 03)
BEON rapport nr. 94-7	Risico-analyse Mariene Systemen (RAM*2 project) Eindrapport van de RAM-Auditgroep.
BEON rapport nr. 94-8	Comparison of models describing species composition of marine phytoplankton Michielsen, H & Berg, A. van den & Joordens, J., et al.(project MANS-FYFY, WL 93 E 01).
BEON rapport nr. 94-9	Verslag BEON Workshop Risico-analyse, d.d. 27 april 1994, Den Haag.
BEON rapport nr. 94-10	BEON Beleidspresentatie "Microverontreinigingen: effecten en trends", d.d. 21 juni 1994.
BEON rapport nr. 94-11	De epi- en endofauna van de Nederlandse, Duitse en Deense kustzone: een analyse van 20 jaar bijvangsgegevens. Buijs, J., J.A. Craeymeersch, P. van Leeuwen, A.D. Rijnsdorp. (BEONADD IV/V)
BEON rapport nr. 94-12	De inductie van cytochroom P450 1 A in platvis door blootstelling aan polyaromatische koolwaterstoffen in de Noordzee. INP-programma 1991- 1992. Boon, J.P., H.M. Sleiderink, M.L. Eggens, A.D. Vethaak (NIOZ 93 M 05)
BEON rapport nr. 94-13	Directe effecten van de visserij met de 12m en 4m boomkorren op het bodemleven in de Nederlandse sector van de Noordzee. Bergman, M.J.N. en J.W. van Santbrink. (NIOZ 93 V 07)
BEON rapport nr. 94-14	Scavenging seabirds at beamtrawlers in the southern North Sea, distribution, relative abundance, behaviour, prey selection, feeding efficiency, kleptoparastism and the possible effects of the establishment of protected areas'. Camphuysen, C.J. (BEONADD IV/V)
BEON rapport nr. 94-15	The relationship between food supply, reproductive parameters and population dynamics in Dutch Lesser Black-backed Gulls Larus fuscus: a pilot study. Spaans, A.L., M. BukaciÑska, D. BukaciÑska. (BEONADD IV/V)
BEON rapport nr. 94-16	Pilot study on the influence of feeding conditions at the North Sea on the breeding results of the Sandwich Tern Sterna sandvicensis. Brenninkmeijer, A. & E.W. M. Stienen. (BEONADD IV/V)
BEON rapport nr. 94-17	BEON-studie naar de effecten van de teruglopende nutriëntenbelasting van de Nederlandse kustzone. Boddeke, R. en P. Hagel. (RIVO 93 E 03)

1995

BEON rapport nr. 95-1	Effecten van de scheþdiervisserij op het bodemleven in de Voordelta. Van der Land, M.A. (RIVO 94 V 06).
BEON rapport nr. 95-2	Jaarwerkplan 1995.
BEON rapport nr. 95-3	Trends in het voorkomen van vissen en epibenthische evertebraten in de Noordzee: Een vergelijking van datasets. Van der Veer, H.W., J.A. Craeymeersch, J. Van der Meer, A.D. Rijnsdorp, J.IJ. Witte. (NIOZ 93 A 04)
BEON rapport nr. 95-4	De ontwikkeling van een in vitro assay voor de bepaling van de invloed van biotransformatie op de bioaccumulatie van lipofiele organohalogeen verbindingen in mariene toppredatoren. I. Validatie van de assay met PCBS en de eerste resultaten met Toxafeen. Boon, J.P., van Schanke, A., Roex, E., de Boer, J., Wester, P. (NIOZ 94 M 01)
BEON rapport nr. 95-5	BEON beleidspresentatie "Ontwikkelingen in het beleid", d.d. 9 december 1994.

BEON rapport nr. 95-6 BEON beleidspresentatie "Modellering: de stand van zaken en het belang voor beleid en beheer", d.d. 31 maart 1995.

BEON rapport nr. 95-7 Wetenschappelijke discussie. De visserij-intensiviteit van de Nederlandse boomkorvisserij op de Noordzee mede in het licht van de milieu effecten en gesloten gebieden.

BEON rapport nr. 95-8 Antropogene eutrofiëring en natuurlijke variaties. Consequenties voor de produktiviteit van de Noordzee. INP-MOORING/PELAGIC FOOD WEB/STED/ STRAECOS. Van Raaphorst, W., F.C. van Duyl, H. Ridderinkhof, R. Riegman, P. Ruardy. (NIOZ 94 E 01)

BEON rapport nr. 95-9 Effecten van antropogene aktiviteiten op de produktiviteit van het ecosysteem in de Westelijke Waddenzee. Van der Veer, H.W., J.J. Beukema, G.C. Cadée, J. Hegeman, B. Mom, W. Van Raaphorst, J. IJ.. Witte (NIOZ 93 E 02)

BEON rapport nr. 95-11 Biomarkers of Toxic effects chemoreceprion: effects of contaminated dredge spoil on chemoreception acuity in whelks.Ten Hallers-Tjabbes, C. and C.V. Fisher. (NIOZ 93 M 05)

BEON rapport nr. 95-12 Habitatkarakteristieken van de Nederlandse kustzone. Wintermans, C. et al. (IBN 94 H 02)

BEON rapport nr. 95-13 BEON Tweejaarverslag 1993-1994. Onderzoek en beleid kiezen samenhet ruime sop; PB-BEON; augustus 1995.

BEON rapport nr. 95-14 Toxische algen tussen Noordwijk- en Terschelling-raai. Peperzak, L. et al. (RIKZ 94 E 05; RKZ-040).

BEON rapport nr. 95-15 Korte en lange termijn veranderingen in macrofauna veroorzaakt door verschillende vormen bodemvisserij. Bergman, M. et al. (NIOZ 94 V 01).

BEON rapport nr. 95-16 Intercallibratie en toepassing Noordzee-modellen (MANS-FYFY) fase 2. (WL 94 E 04).

1996

BEON rapport nr. 96-1 De ontwikkeling van een in-vitro assay voor de bpaling van de invloed van biotransformatie op de bioaccumulatie en de mutageniteit van lipofiele organohalogeenverbindingen in mariene toppredatoren. II. Toxafeen. Boon, J.P., H.M. Sleiderink, J. De Boer, P. Wester, H.J. Klamer, B. Govers.(NIOZ 95 M 03).

BEON rapport nr. 96-2 Spisula subtruncata als voedselbron voor Zeeëenden in Nederland. Leopold, M.F. (IBN 95 V 29).

BEON rapport nr. 96-3 BENTOX. Toxische effecten van verontreinigde sedimenten voor marien benthos. 1e fase: Verkennend onderzoek met 'natuurlijk' verontreinigde sedimenten , 2e fase: Benzo(a)pyreen en fluoranteen, 3e fase: BaP concentratiereeks. Kaag, N.H.B.M., J.P. Boon, K. Booij, C.V. Fischer, E.M. Foekema, M.T.J. Hillebrand, H. Hummel, H. Kralt, M.C. Th. Scholten, B.M.H. Timmermans, A.P.M.A. Vonck, M. de Vries, E. van Weerlee. (TNO 93 M 04,TNO 94 M 06, TNO 95 M 16).

BEON rapport nr. 96-4 Algenbegrazing: Een nadere analyse van de invloed van toxicanten op het ontstaan van eutrofiëringsproblemen. Jak, R.G., Michielsen, B.F. (TNO 95 E 07).

BEON rapport nr. 96-5 Habitatkartering en beschrijving Nederlandse kustwateren (IBN 95 H 36)

BEON rapport nr. 96-6 Onderzoek naar de invloed van fluctuaties in de lokale voedselbeschikbaarheid op de populatiedynamiek van de grote stern Sterna sandvicensis: tussentijdse resultaten. Stienen, E.W.M. & A. Brenninkmeijer. (IBN 95 H 24).

BEON rapport nr. 96-7 Resultaten BEON Workshop NW4.

BEON rapport nr. 96-8 Thema bijeenkomst Boomkorvisserij.

BEON rapport nr. 96-9 Jaarwerkplan 1996.

BEON rapport nr. 96-10 SCREMOTOX (WL 95 M 21).

BEON rapport nr. 96-11 Effecten van de schelpdiervisserij op het bodemleven in de Voordelta: De schelpdierbestanden in de Voordelta in 1995. Van der Land, M.A. (RIVO 95 V 30).

BEON rapport nr. 96-12 Verslag van de BEON workshop ter voorbereiding van de Nederlandse inbreng van de tussenconferentie van Noordzee- en Visserijministers (IMM 97).

BEON rapport nr. 96-13 BEON thema bijeenkomst polycyclische aromatische koolwaterstoffen (PAK's). 22 februari 1996 Den Haag.

BEON rapport nr. 96-14 Evaluatierapport BEON 1996. Tussentijdse evaluatie Tweede Meerjarenprogramma BEON 1993-1997. Rapport naar aanleiding van de BEON evaluatieworkshop d.d. 2 februari 1996, Den Haag.

BEON rapport nr. 96-15 Onderzoek naar mogelijkheden tot vermindering van discard produktie door technische aanpassing van boomkornetten (NIOZ 95 V 05). Fonds, M. & W. Blom

BEON rapport nr. 96-16 INP-Mooring 94-96: Antropogene eutrofiëring en natuurlijke variaties in de open Noordzee: metingen op een verankeringsstation in de Oestergronden (NIOZ 95 E 01)

1997

BEON rapport nr. 97-1 Fluctuaties in de lokale voedselbeschikbaar in relatie tot de populatiedynamiek van de Grote Stern Sterna sandvicensis: resultaten 1995-1996 (IBN 95 H 24). Stienen, E.W.M. en A. Brenninkmeijer.

BEON rapport nr. 97-2 Vervallen.

BEON rapport nr. 97-3 Jaarwerkplan 1997.

BEON rapport nr. 97-4 De betekenis van het zout- en silicaatgehalte in Nederlandse kustwateren voor het zeegrasareaal. Kamermans, P., M.A. Hemminga, D. de Jong, K.S. Dijkema. (NIOO 96 EH 07).

BEON rapport nr. 97-5 GiftigeAlgen en de Reductie van de Nutriëntenbelasting (BEON-GARdeN) Competitie tussen algen. Jaarverslag 1996. Riegman, R., K. Peeters, H. Los.(NIOZ 95 E 02).

BEON rapport nr. 97-6 In vitro biotransformatie van organohalogeenverbidingen in zeezoogdieren en vogels. Mogelijke gevolgen voor bioaccumulatie en genotoxiciteit. III: Gebromeerde vlamvertragers (Polybroom difenylethers & polybroom bifenylen). Boon, J.P., M.J. Greve, J.B. Bouma, M.K. de Boer, W.E. Lewi, H.J.C. Klamer, D. Pastor, P. Wester, J. de Boer (NIOZ 95 M 03).

BEON rapport nr. 97-7 The impact of marine eutrophication on phytoplankton, zooplankton and benthic suspension feeders. Stratification in mesocosms, a pilot experiment (Escaravage, V, L.P.M.J. Wetsteyn, T.C. Prins, A.J. Pouwer, A. de Kruyff, M. Vink-Lievaart, C.M. van der Voorn, J.C.H. Peeters &A.C. Smaal (RIKZ 96 E 01).

1998

BEON rapport nr. 98-1 In vitro biotransformatie van organohalogeenverbindingen in zeezoogdieren en vogels. Mogelijke gevolgen voor bioaccumulatie en genotoxiciteit. IV. Polychloor terfenylen (PCT's). Boon, J.P. D.E.C. Smith, W.E. Lewis, H.J.C. Klamer, D. Pastor, P. G. Wester, J. de Boer (NIOZ 95 M 03)

BEON rapport nr. 98-2 De verspreiding van (epi) benthische macrotauna op het NCP in relatie met de microverspreiding van de boomkorvisserij vanaf 1993. Bergman, M.J.N., J. Buys, J. Craeymeersch, G.J. Piet, A.D. Rijnsdorp, J.W. van Santbrink. (NIOZ 96 V 26)

Informatie BEON:

PROGRAMMA BUREAU BEON
p/a Directoraat-Generaal Rijkswaterstaat
Rijks Instituut voor Kust en Zee
Kortenaerkade 1
2518 AX Den Haag
Postbus 20907
2500 EX Den Haag
070- 3114258/3114259/3114260
Telefax: 070- 3114321

e-mail: beon@rikz.rws.minvenw.nl.