Institute for Forestry and Nature Research

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CONTENTS

PREFACE

The Dutch breeding population of terns forms an important part of the total European population. Of all four tern species breeding in the Netherlands, the Sandwich Tern is the most specialised piscivorous bird. During the breeding season, Sandwich Terns feed mainly on marine fish, such as herring, sprat, sandeel and lesser sandeel. The species is therefore extremely vulnerable to changes in the availability of these prey species. The Dutch breeding population of the Sandwich Tern has shown large fluctuations in numbers. During the twentieth century, three major collapses of the population were caused by human interactions such as egging, shooting of adult terns, and pollution with organochlorine pesticides. After the collapse in 1965 the population has increased relatively slowly and seems to stabilise at a much lower level than previous to the collapse.

In this pilot study, data are presented on the diet of the Sandwich Terns breeding on Griend. A comparison is made with results obtained in earlier studies in the same colony. The results suggest that food availability was low in 1992 and 1993. A detailed description of relationships between food supply to the chicks, windspeed and age of chicks is given.

A radio-tracking programme showed that the terns mainly feed in the Wadden Sea and to a lesser extent at the North Sea. It seems as if there is a little shift in foraging area compared with 1970.

Analysis of data on the abundance of young herring in the North Sea suggests a relationship between the number of herring and the number of breeding Sandwich Terns, but not between the number of herring and breeding success.

It is argued that the stabilisation of the number of breeding pairs since the 1980s is related to a low food availability.

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Head Department of Animal Ecology

1 GENERAL INTRODUCTION

During the last decades, several studies revealed a decline in breeding success and population size of seabirds, such as Puffins *Fratercula arctica*, Kittiwakes *Rissa tridactyla*, Little Auks *Alle alle*, Brünnich's Guillemots *Uria lomvia*, Arctic Terns *Sterna paradisaea*, and Scandinavian Lesser Black-backed Gulls *Larus fuscus fuscus* (Anker-Nilssen & Barrett 1991, Danchin 1992, Monaghan *et al.* 1992). These declines in breeding success and population size often coincided with the collapse of local fish populations, such as the Atlanto-Scandian herring *Clupea harengus* in the late 1960s (Anker-Nilssen & Barett 1991), the Barents Sea capelin *Mallotus villotus* in 1985 (e.g. Jakobsson 1985, Hamre 1988, Klaassen 1989, Vader *et al.* 1990), Bering Sea prey fish (Springer *et al.* 1986) and the Shetland sandeel *Ammodytes marinus* in the early 1980s (e.g. Furness 1982, Ewins 1985, Harris & Ruddiford 1989, Monaghan *et al.* 1989, Harris & Wanless 1990, Bailey 1991, Hamer *et al.* 1991, Danchin 1992, Monaghan *et al.* 1992, Hamer *et al.* 1993). Although these declines are often believed to have been caused by overfishing (Jakobsson 1985), this has never been proved with hard causal links (Bailey & Hislop 1978, Knijn *et al.* 1993). In fact, Bailey (1991) showed that the seabird breeding failures at Shetland were not only caused by sandeel fishery but also by natural factors acting on the early life history of the sandeel.

However, the fishing industry can influence seabirds in many ways. Scavenging seabirds may benefit directly from fishing activities, whilst in contrast, many diving seabirds can be caught in fishing nets (Furness 1978, Bergman 1982, Furness *et al.* 1988, Vader *et al.* 1990, Camphuysen 1990, 1993, Howes & Montevecchi 1993, Camphuysen 1994). Fishery pressure can also change ecosystems. For example, in the case of whitefish fishing, fish-eating seabirds can profit of the fishery pressure, as food competitors of the seabirds are removed (Macer 1966, Furness 1978, Furness *et al.* 1988). In fishing of small pelagic schooling fish, pelagic foraging birds may suffer, because their prey fish are removed. Or they will benefit, when as a result of the decline (most likely by overfishing) of one species (e.g. herring in the late 1960s), the stocksize of another species (sandeel) increases. According to Hopkins (1990), this is because sandeel larvae sometimes form an important part of the diet of herring. Sandeels are the staple diet of many breeding seabirds in the North-east Atlantic (i.e. over 80% of all food taken by seabirds at Shetland in 1981), therefor this shift benefited most seabirds (Bailey & Hislop 1978, Furness 1978, Hislop & Harris 1985, Furness 1990). In the late 1970s and the early 1980s the availability of sandeels declined and a number of surface-feeding seabirds, such as Arctic Tern and Kittiwake, did not fledge any chicks, whereas Fulmar *Fulmarus glacialis*, Arctic Skua *Stercorarius parasiticus*, Great Skua *Catharacta skua*, Razorbill *Alca torda*, Puffin and Black Guillemot *Cepphus grylle* suffered a serious reduction in breeding success due to food shortage (Martin 1989, Monaghan *et al.* 1989, Bailey 1991, Hamer *et al.* 1991, Uttley 1992, Hamer *et al.* 1993). Other surface-feeders, such as Herring Gulls *Larus argentatus*, Great Black-backed Gulls *L. marinus* and Great Skuas, switched to preying upon chicks of other seabirds (Hamer *et al.* 1991, Danchin 1992). Great Skuas showed an increased foraging time at sea, resulting in a decrease in breeding success, owing to severe predation of the unguarded chicks (Hamer *et al.* 1991). Puffins and Gannets switched to feeding their chicks a mixture of species such as whiting *Merlangius merlangus,* rockling *Ciliata/Gaidropsarus* spp. and other small gadoids (Puffins in 1987 and 1988) and herring and mackerel *Scomber scrombrus* (Gannets) (Martin 1989). In Norway, the collapse of the Atlanto-Scandian herring stock in the late 1960s affected the breeding success of the Puffin, whose chicks virtually all starved to death in most years after the herring crash of 1969, leading to a strong decrease in the breeding population. In 1985 the Barents Sea capelin stock crashed, which had a negative effect on the number of breeding pairs of the Common Guillemot (Vader *et al.* 1990).

Sandwich Terns *Sterna sandvicensis* are highly specialised piscivorous birds. In The Netherlands, as elsewhere in western Europe, the prey items delivered to chicks consist mainly of high calorific fish such as herring, sprat *Sprattus*, sandeel *Ammodytes tobianus* and greater sandeel *A. lanceolatus* (Dircksen 1932, Rooth 1965, Veen 1977, Brenninkmeijer & Stienen 1992). Therefore they are extremely vulnerable to changes in the availability of these prey fish. During the twentieth century the number of breeding Sandwich Terns in The Netherlands have shown large fluctuations (Fig. 1). In the early part of the century, numbers were low, caused by large scale egg-collecting and adult-tern-shooting, for tern feathers were much wanted in the ladies' fashionable hats. As a result of the protection of this species, numbers gradually increased from 1908 onwards. In World War II egging again caused a drop in numbers. After World War II the population increased up to about 35,000 pairs in the 1950s. At the end of the 1950s, numbers dropped markedly and the number of breeding pairs were reduced to 875 in 1965. This decrease was due to pollution of the Dutch coastal waters by organochlorine pesticides. When the pollution stopped, the population increased again, but the large numbers from the period previous to this have never been reached since then. Compared to previous population recoveries, the recovery after the pollution in the 1960s has been slow, and at present the population appears to have stabilised at only about 11,000 breeding pairs since the 1980s, about one third of the population in the 1930s and the 1950s. The observed population on Griend shows the same fluctuations during the twentieth century as described for the whole Dutch population. (Brouwer *et al.* 1950, Veen 1977, Veen & Van de Kam 1988, Brenninkmeijer & Stienen 1992).

This leads to the main subject of this report: 'What is the cause of the slow recovery of the Sandwich Tern after the decline in the 1960s and why is there a stabilisation in breeding pairs at such a low level?'. Although this could be due to many factors, we concentrated on the food situation during chick rearing. In 1992, a pilot study was started to investigate the feeding conditions of breeding Sandwich Terns. This study consisted mainly of the following three items, which will be dealt with in three chapters in this report:

(1) What is the species composition and what is the length distribution of prey-items delivered to the chicks of Sandwich Terns on Griend, the main colony in The Netherlands, and have there been noticeable shifts compared with the late 1960s and early 1970s (chapter 2)?

(2) Where do the adult terns catch the fish, and are there any shifts in this respect compared with the late 1960s and early 1970s (chapter 3)?

(3) Is there a relationship between fish availability and the population size and breeding success of the Sandwich Tern (chapter 4)?

Study area

The study was conducted on Griend, a little uninhabitated island in the centre of the Dutch Wadden Sea (53°15'N, 5°15'W, fig. 1). What is left of Griend are the remains of a much larger island (of around 800 ha), which was inhabited by man until at least the end of the eighteenth century (Brouwer *et al.* 1950, Veen & Van de Kam 1988, Janssen *et al.* 1994). Nowadays, on average, about 75% of the Dutch (and about 15% of the European) Sandwich Tern population nest on Griend (Brenninkmeijer & Stienen 1992, Veen 1994). As the island appeared to be vanishing into the sea as a result of constant attacks by western winds and winter storm floods, a large reconstruction was carried out in 1987 and 1988 to rescue the most important Dutch breeding ground of terns. A 2500 m long and 50-100 m wide sand dike was built, to the west and north of the old island, thus doubling the size of Griend from 16 ha to 35 ha (Veen & Van de Kam 1988, Essink & Bosch 1993, Piersma *et al.* 1993). Due to the natural process of erosion and accretion, the potential breeding area was enlarged to about 57 ha in 1993 (Brenninkmeijer & Stienen 1994).

Statistics

All statistical analyses were carried out with the statistical packet of SPSS/PC+ version 4.0. For linear regression method and Scheffé-test we used a significance level of 0.05. For multiple regression method we used the standard SPSS significance level of 0.1.

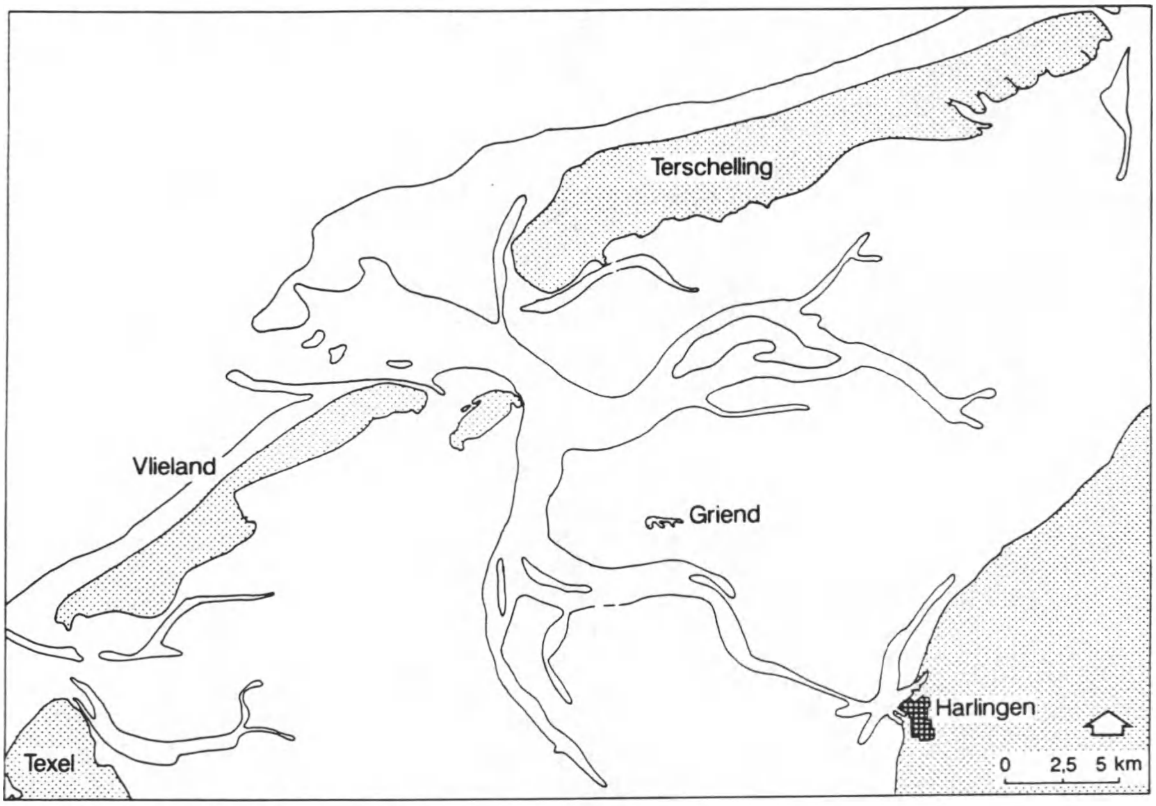


Figure 1. Griend and surroundings in 1992.

2 DIET

2.1 Introduction

The diet composition of Sandwich Tern chicks on Griend in the late 1960s and the beginning of the 1970s is well documented by Veen (1977). He found that 96-98% of the prey items fed to the chicks were herring, sprat, sandeel and greater sandeel. In his work, he further described the distribution of the length classes of the delivered food items. Through his work we were able to compare the food situation in 1992 and 1993 with the situation in the late 1960s and the early 1970s. Changes in food provisioning, species composition and length distribution of the the food between the periods 1969-1970 and 1992-1993 could possibly explain some aspects of the stabilisation of the growth of the Dutch breeding population (chapter 1). Through a comparison with foreign colonies we try to explain something about the slow recovery rate of the Dutch breeding population after the population crash in 1965. In order to make a proper analysis of the food supply to the chicks, first a detailed knowledge of abiotic (windspeed) and biotic (age of the chicks) influences is necessary.

2.2 Methods

In this report the following units in the nest distribution pattern of the Sandwich Tern have been distinguished:

(1) colony (consisting of a number of synchronously laid eggs which are clearly seperated in space from other colonies).
(2) island population (consisting of all the colonies in that year).

From hatching until fledging the feeding behaviour of 5 to 20 chicks per observed colony was studied. In 1992, in one colony (first eggs hatched during the last few days of May) and in 1993, in two colonies (colony 6, where the first eggs hatched during the last few days of May and colony 8, where the first eggs hatched at the end of June) chicks were observed daily from approximately 4.30 h to 22.30 h with binoculars (up to 10 times magnification) as well as with the naked eye from a small observational hide, placed within a few metres from the colonies under study. To recognize individuals, chicks were ringed and colour-marked just after hatching. To prevent chicks from walking away from the colony, a group of synchronously laid clutches (in 1992 200 nests, in 1993 75 nests per colony) were fenced in. The enclosures had no adverse effects on the behaviour of chicks, parents or areal predators (Brenninkmeijer & Stienen 1994). Whenever possible, the same chicks were studied each day. Food delivered to chicks was classified into four different classes: *eaten* (eaten by chick), *robbed* (stolen by Black-headed Gull *Larus ridibundus*), *lost* (when it was certain that it had not been eaten by the chick, but uncertain whether a parent or a Black-headed Gull had eaten the prey) and *other* (eaten by parent or stolen by another Sandwich Tern). Prey items were divided into three distinguishable groups: herring/sprat (henceforth called clupeids), sandeel/greater sandeel (henceforth called ammodytidae) and other prey items (cod *Gadus morhua*, flounder *Platichtys flesus*, eelpout *Zoarces viviparus*, squid *Loligo forbesi* and *Gobius sp.*). Fish length was estimated in quarters of the adult bill length (average bill length 54.6 mm, s.d. = 2.3 mm, N = 93). The estimation of fish length was experimentally calibrated between the different observators by placing a large number of fish of various length into the bill of a stuffed Sandwich Tern. Practising highly improved the estimation accuracy. Windspeed was measured every hour, using the standards of the KNMI. For the analysis the mean daily windspeed is used.

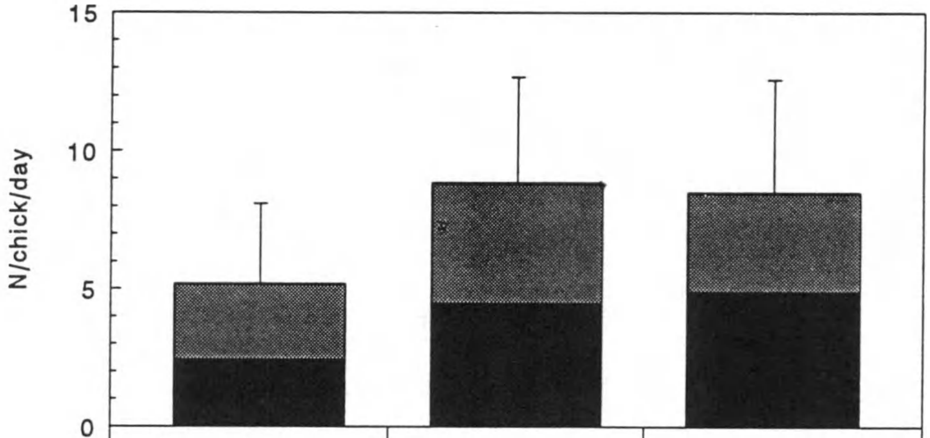
2.3 Results

2.3.1 Variation between colonies

Because clupeids and ammodytidae comprised 99.2-99.7% of the total diet in 1992-1993 (Fig. 2), other prey items are excluded in the rest of this report. The proportion of clupeids in the various colonies ranged from 46.8 to 57.8%, that of ammodytidae from 42.0 to 52.4%. In 1992, the number of prey supplied daily to the chicks was, on average, lower than in the two colonies in 1993 (1992: 5.19 prey items per chick per day, 1993: 8.85 and 8.51 prey items per chick per day in colony 6 and 8, respectively, Scheffé-test, $F = 63.6$, $P < 0.05$).

However, in 1992, the mean length of ammodytidae brought to the chicks was much larger than in 1993 (1992: 11.28 ± 1.72 cm, 1993: 9.81 ± 2.16 cm in colony 6 and 10.14 ± 1.95 cm in colony 8) (Scheffé-test, 1992 > 1993 (colony 6), $F = 58.6$, $P < 0.05$; 1992 >1993 (colony 8), $F = 58.6$, $P < 0.05$). In colony 8 the terns brought in larger ammodytidae than those in colony 6 (Scheffé-test, $F = 58.6$, $P < 0.05$). The length of the supplied clupeids was the same in all three colonies (Scheffé-test, n.s.). Using the length-mass relationship of clupeids and ammodytidae given by Veen (1977), the total weight of fish per chick was approximately 34 g/day in 1992, 45 g/day in colony 6 in 1993 and 45 g/day in colony 8 in 1993. Thus when expressed in mass, the daily amount of fish supplied to the chicks was relatively low in 1992.

However, not all the food supplied was actually eaten by the chicks. In 1992, 77.4% of the food items supplied were eaten by the chicks, 15.2% were robbed by Black-headed Gulls, and 7.4% fell in one of the two other categories (Fig. 3). In 1993, the proportion of prey eaten was 67.3% in colony 6 and 76.5% in colony 8, while the proportion of robbed fish was 18.6% and 14.4%, respectively. These proportions were roughly the same for clupeids and ammodytidae.



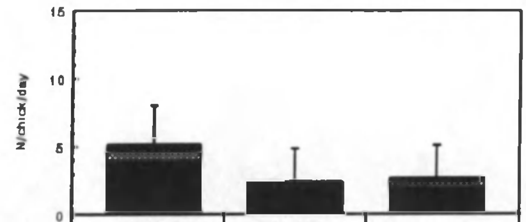
	1992	1993 (6)	1993 (8)
other	0.04	0.03	0.04
sandeel	2.72	4.34	3.57
herring	2.43	4.48	4.9

Figure 2. *Mean number of prey items delivered to the chicks (N/chick/day) in 1992 and 1993 (colony numbers between parentheses). Plotted s.d. is the standard deviation of the total number of prey items delivered.*

The robbed fish were larger than the fish eaten (clupeids as well as ammodytidae) when we look on average (Fig. 4) (Scheffé-test, clupeids 1992, robbed eaten, $F = 11.5$, $P < 0.05$; clupeids 1993 (colony 8), robbed eaten, $F = 15.1$, $P < 0.05$; ammodytidae 1992, robbed eaten, $F = 8.4$, $P < 0.05$; ammodytidae 1993 (colony 6), robbed eaten, $F = 8.6$, $P < 0.05$; ammodytidae 1993 (colony 8), robbed eaten, $F = 28.2$, $P < 0.05$). Only in colony 6 (1993) were the robbed clupeids as large as those eaten by the chick (Scheffé-test, n.s.). Further analysis of data (Stienen & Brenninkmeijer 1994) showed that this result was not only due to the fact that robbing as well as the length of the fish showed a positive relationship with the age of the chicks. When corrected for age the Black-headed Gulls still preferred relatively large prey-items.

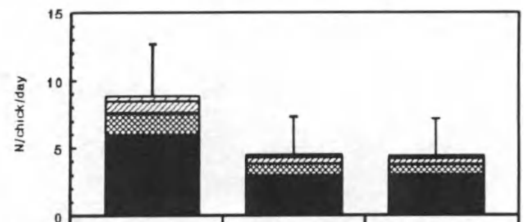
Based upon the mean number of clupeids and ammodytidea eaten by daily by a chicks, the daily mass eaten by a chick (according to the length-mass relationship of Veen 1977) was approximately 24 g/day in 1992, 29 g/day in colony 6 in 1993 and 32 g/day in colony 8 in 1993.

1992



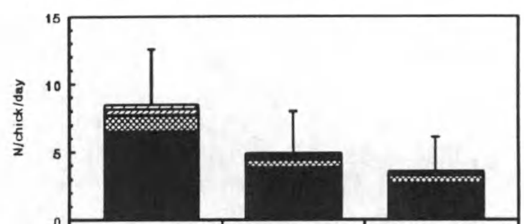
	total	herring	sandeel
rest	0.12	0.08	0.04
lost	0.26	0.13	0.13
robbed	0.78	0.3	0.47
eaten	3.98	1.91	2.07

1993 (6)



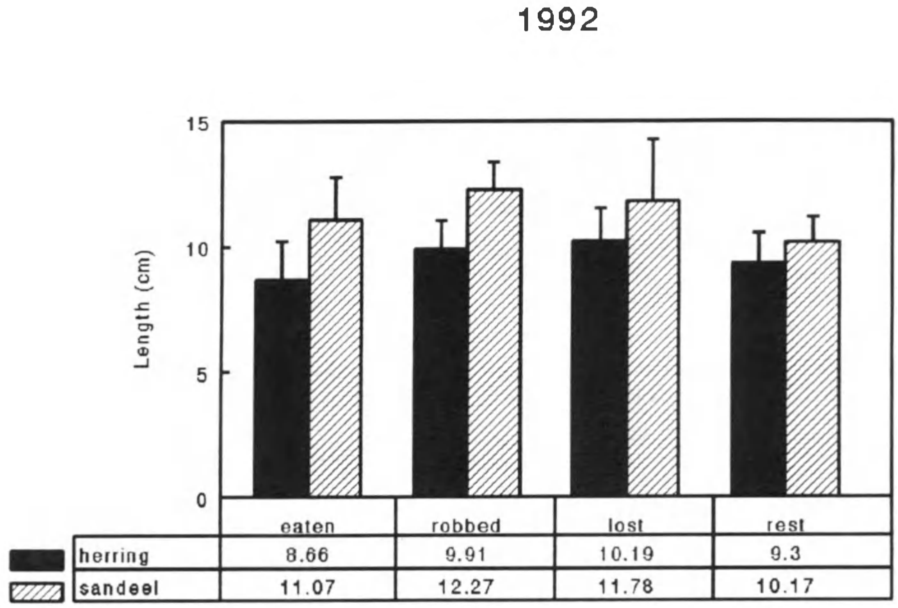
	total	herring	sandeel
rest	0.38	0.21	0.16
lost	0.87	0.46	0.41
robbed	1.64	0.88	0.76
eaten	5.94	2.93	3

1993 (8)



	total	herring	sandeel
rest	0.37	0.2	0.17
lost	0.4	0.23	0.18
robbed	1.22	0.63	0.59
eaten	6.49	3.84	2.65

Figure 3. *Fate of delivered prey items in 1992 and 1993 (colony numbers between parentheses). Plotted s.d. is the standard deviation of the total number of fish delivered.*



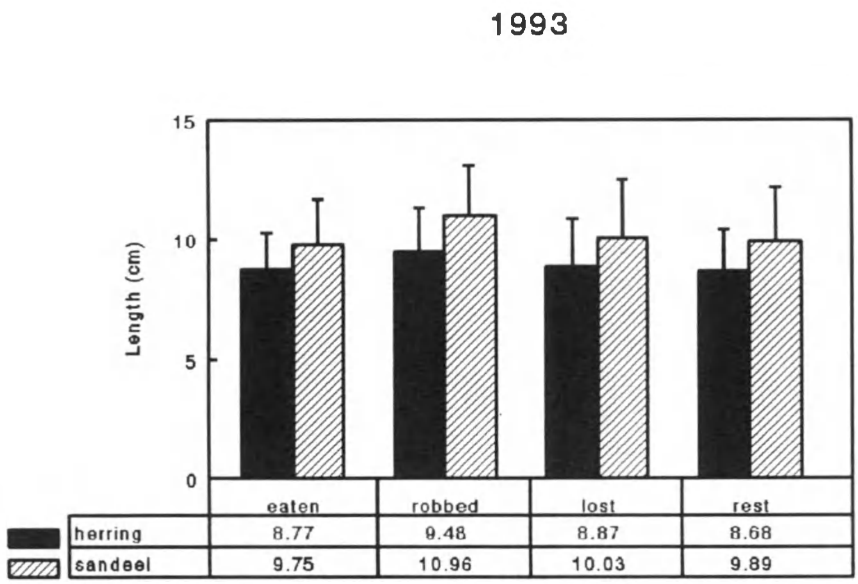


Figure 4. Mean length of clupeids and ammodytidae delivered to chicks in 1992 and 1993 for different fates of prey.

2.3.2 Relationship between age and diet

As the number and the length of the fish supplied, and the number of the fish robbed show a relationship with both windspeed and the age of the chicks, we used a multiple regression method to analyse the data. First, we describe the figures regardless of windspeed and further down in chapter 2.3.3 we describe the statistic results of the multiple regression.

In 1992, the number of fish supplied was almost the same for each age (about 5 fish/chick/day, Fig. 5). In 1993, the number of fish supplied increased from day 1 to day 3. The relatively large number of fish supplied at day 0 were probably due to the small N (only one chick). From day 4 to day 20 the food supply was almost stable at about 7-8 fish/chick/day in both colony 6 and 8. After day 20, there was an increase to about 10 fish/chick/day in colony 8, but no increase could be seen in colony 6. The proportions of clupeids and ammodytidae supplied, fluctuated during chick-rearing (Fig. 5).

If we focus on the fate of the delivered prey items (Fig. 6), a difference between 1992 and 1993 can be seen. In 1992, robbing by Black-headed Gulls was very severe after about 12 days (less than 50% of the fish supplied were eaten by chicks). In 1993, robbing also became evident when the chicks were about 12 days old, but in that year the robbing was less severe (over 70% of the fish supplied were eaten by the chicks).

In 1993, the mean length of the clupeids supplied, increased during the first 6 days from about 7 to 9 cm (Fig. 7). The length of the ammodytidae supplied, increased from about 7 cm at hatching of the chicks to about 11 cm when the chicks were 20 days old.

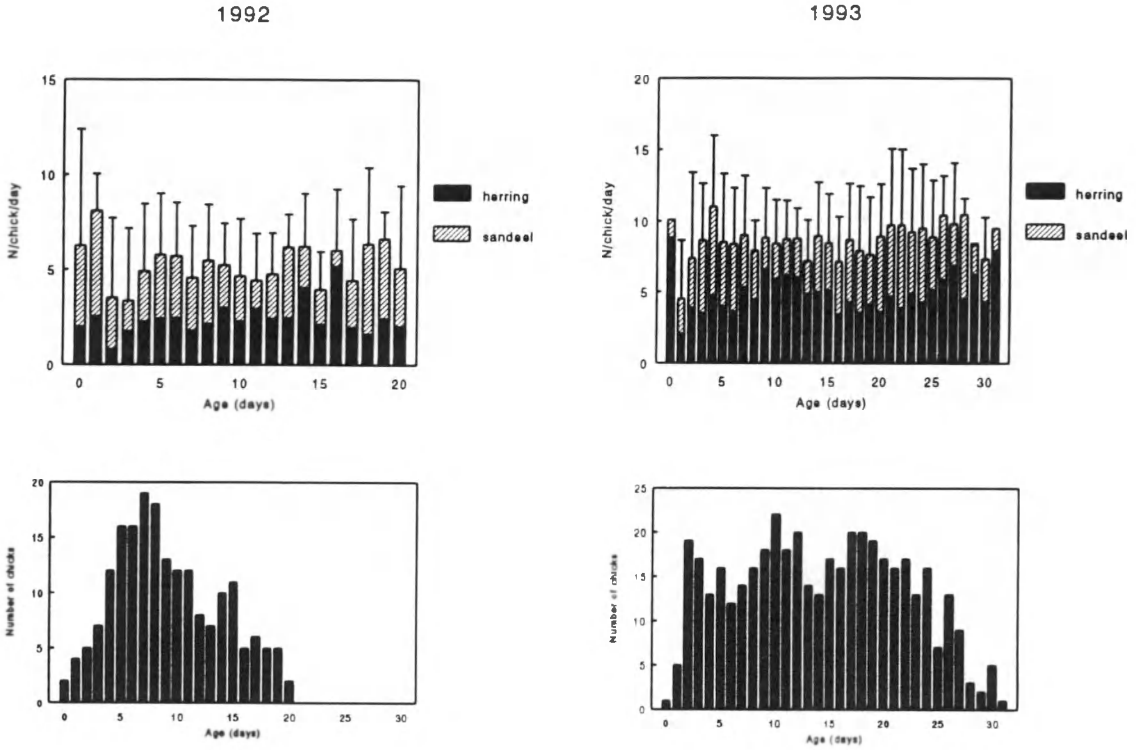


Figure 5. *Relationship between the age of the chicks and number of clupeids and ammodytidae supplied in 1992 and 1993 (upper graphs). The plotted s.d. is the standard deviation of the total number of fish delivered. Number of chicks per age followed (lower graphs).*

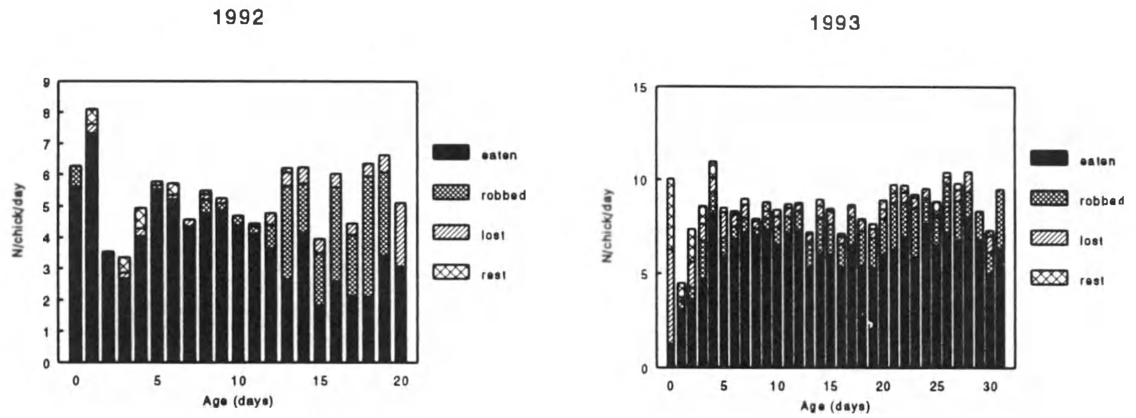


Figure 6. *Fates of the fish supplied in relation to the age of the chicks in 1992 and 1993 (for number of chicks see Fig. 5).*

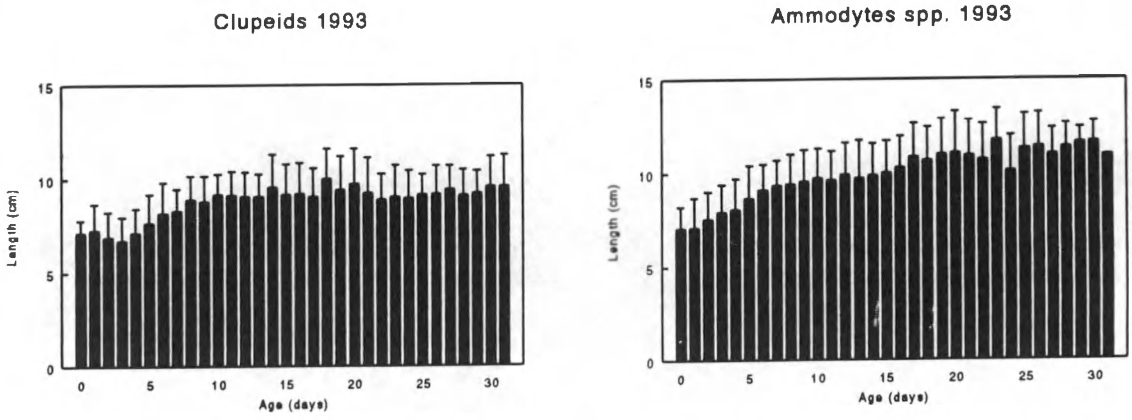


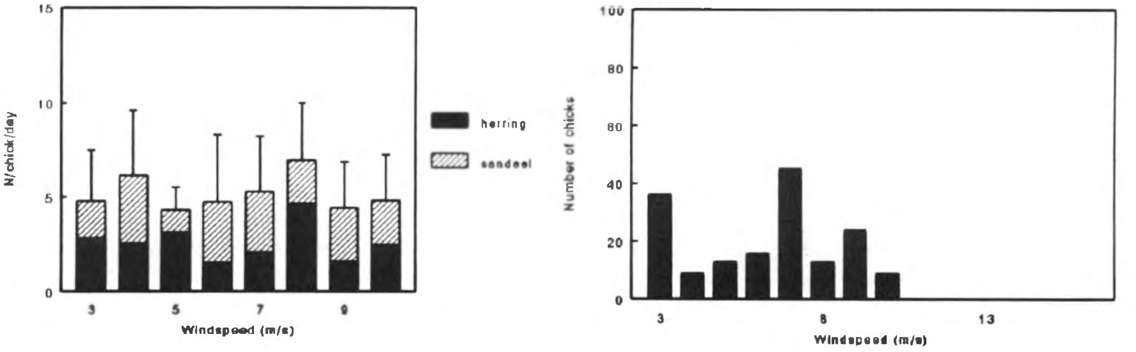
Figure 7. *Length of the fish supplied in relation to the age of the chicks in 1993 (for number of chicks see Fig. 5).*

2.3.3 Relationship between windspeed and diet

As in chapter 2.3.3, we first describe the figures and further down we give the results of the multiple regression on age and windspeed.

Without correction for effects of age the figures show no relationship between the number of clupeids and ammodytidae supplied and windspeed (Fig. 8). Also the proportions of clupeids and ammodytidae (Fig. 8) and the proportion of robbed fish (Fig. 9) seem to have no relationship with windspeed, although with windspeeds higher than 13 m/s the proportion of robbed fish increased to about 50% (Fig. 9), but this is based on only a few data (Fig. 8). However, the length of the clupeids and ammodytidae supplied seem to decrease when windspeed exceeded 12 m/s (Fig. 10).

1992



1993

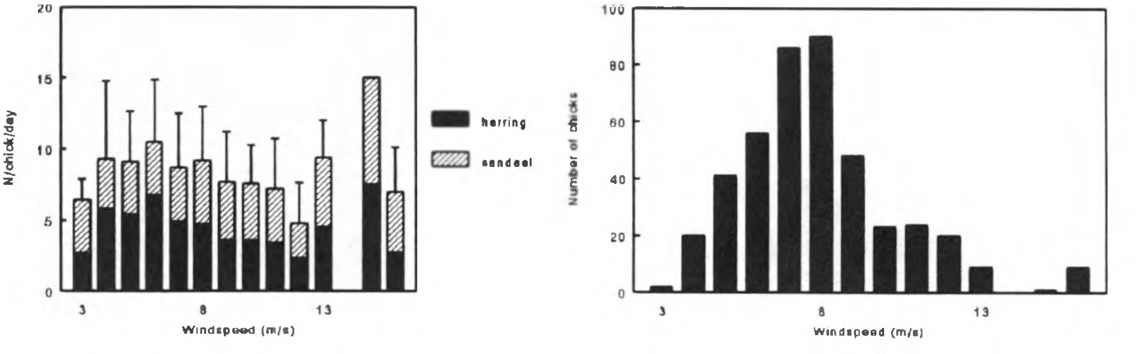


Figure 8. Relationship between windspeed and the number of clupeids and ammodytidae supplied per chick per day in 1992 and 1993 (upper graph). The plotted s.d. is the standard deviation of the total number of fish delivered. Number of chicks per windspeed followed (lower graphs).

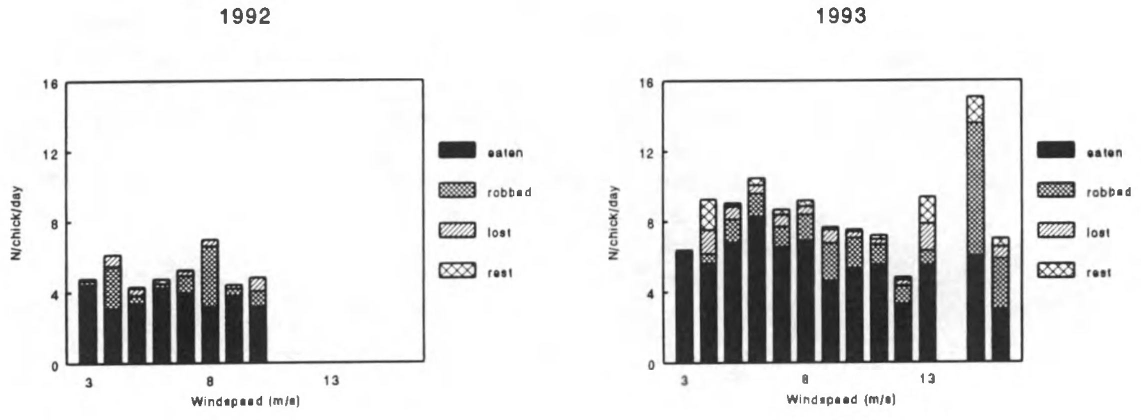


Figure 9. *Fates of the fish supplied per chick per day in relation to windspeed in 1992 and 1993 (for number of chicks see Fig. 8).*

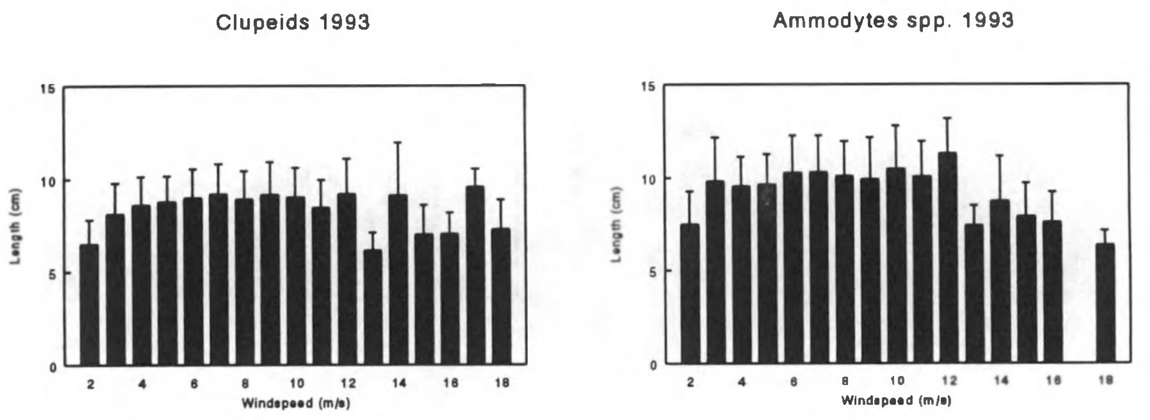


Figure 10. *Length of the fish supplied in relation to windspeed in 1992 and 1993 (for number of chicks see Fig. 8).*

Statistics on age and windspeed

Since fish supply, robbery by gulls and fish length can have relationships with both age and windspeed, we used a multiple regression method to correct for any interactions between these parameters. All regression analyses were carried out in two steps. In the first step we checked for colony differences (1993). In the second step year-effects were checked, regardless of colony effects. Note that the backward regression was carried out with a significance level of 0.10.

The supply of fish in 1993 showed a positive relationship with age and a negative relationship with windspeed (Table 1). There was no colony effect for this parameter. Between years there was again a positive effect of age, a negative effect of windspeed and also a positive effect of year on the supply of fish. The clupeids supplied again showed a negative relationship with windspeed, but no relationship with the age of the chicks nor with the colony (Table 2). Between years, the clupeids supplied again showed a negative effect of windspeed, but also a positive effect of age and year. The supply of ammodytidae showed a positive effect of age and a negative effect of colony within 1993 and a positive effect of age and year between 1992 and 1993 (Table 3). Wind had no effect on the number of ammodytidae supplied.

In 1993, the number of robbed fish per chick per day showed a positive relationship with age and windspeed and a negative effect for colony (Table 4). Corrected for age and windspeed, robbing in colony 6 was higher than in colony 8. Between years there was again a positive effect of age and windspeed on robbing and no effect of year. Checking robbing separately for clupeids and ammodytidae, a negative relationship between number of robbed clupeids and the colony (1993) was shown (Table 5). But there was no effect of age and windspeed. Between years there was a positive effect of year and also of age on the number of robbed clupeids. Number of robbed ammodytidae showed positive relationships with age and wind, without any effect of colony or year (Table 6).

In 1993, the length of the clupeids supplied showed a positive logarithmic relationship with age and a negative relationship with colony, but no relationship with windpeed. The length of ammodytidae showed a positive logarithmic relationship with age, but no effect of colony or windspeed (Table 7).

Summarizing, the statistic analysis shows that (1) parents provided more and larger preys to chicks when growing up, (2) with increasing windspeed the food provisioning to the chicks was reduced, caused by a reduced supply of clupeids and a higher chance of robbing, (3) fish supply was higher in 1993 than in 1992 and (4) robbing (expressed in number of robbed fish) was equal in both years (5) late breeding in 1993 resulted in an increased supply of ammoditidae (which were also larger) and less robbing.

Table 1. Multiple regression analysis of the total number of fish supplied to the chicks. For all significant parameters the T-value (T), the significance of T (Sign. T) and the partial regression coefficient (B) after removal of the non-significant parameters, are listed. D.F.: degrees of freedom of the residual; Windspeed^2: quadratic function of windspeed.

Parameter	T	Sign. T	B
In 1993 (D.F. = 426)			
Constant	15.3	< 0.05	10.55
Age	2.2	< 0.005	0.06
Windspeed	-4.5	< 0.005	-0.34
Windspeed^2	1.4	n.s.	
Colony	-1.0	n.s.	
Between years (D.F. = 591)			
Constant	-10.4	< 0.005	-338.73
Year	10.6	< 0.005	3.75
Age	2.7	< 0.005	0.06
Windspeed	-4.2	< 0.005	-0.26

Table 2. Multiple regression analysis of the number of clupeids supplied to the chicks. For all significant parameters the T-value (T), the significance of T (Sign. T) and the partial regression coefficient (B) after removal of the non-significant parameters, are listed. D.F.: degrees of freedom of the residual; Windspeed^2: quadratic function of windspeed.

Parameter	T	Sign. T	B
In 1993 (D.F. = 427)			
Constant	16.2	< 0.005	7.53
Windspeed	-6.3	< 0.005	-0.36
Age	1.5	n.s.	
Colony	1.3	n.s.	
Between years (D.F. = 591)			
Constant	-9.5	< 0.005	-234.25
Year	9.7	< 0.005	2.59
Age	2.1	< 0.05	0.03
Windspeed	-6.5	< 0.005	-0.31
Windspeed^2	0.3	n.s.	

Table 3. Multiple regression analysis of the number of ammodytidae supplied to the chicks. For all significant parameters the T-value (T), the significance of T (Sign. T) and the partial regression coefficient (B) after removal of the non-significant parameters, are listed. D.F.: degrees of freedom of the residual; Windspeed^2: quadratic function of windspeed.

Parameter	T	Sign. T	B
In 1993 (D.F. = 427)			
Constant	6.2	< 0.005	6.22
Age	1.7	< 0.1	0.03
Colony	-3.0	< 0.005	-0.38
Windspeed	0.3	n.s.	
Windspeed^2	0.2	n.s.	
Between years (D.F. = 592)			
Constant	-4.9	< 0.005	-110.61
Year	5.0	< 0.005	1.23
Age	1.7	< 0.1	0.03
Windspeed	1.0	n.s.	
Windspeed^2	0.8	n.s.	

Table 4. Multiple regression analysis of the number of fish robbed by gulls. For all significant parameters the T-value (T), the significance of T (Sign. T) and the partial regression coefficient (B) after removal of the non-significant parameters, are listed. D.F.: degrees of freedom of the residual; Windspeed^2: quadratic function of windspeed.

Parameter	T	Sign. T	B
In 1993 (D.F. = 425)			
Constant	2.5	< 0.05	1.49
Age	5.3	< 0.005	0.05
Windspeed	2.5	< 0.005	0.07
Colony	-2.7	< 0.05	-0.20
Between years (D.F. = 590)			
Constant	-1.2	> 0.05	-338.73
Age	7.5	< 0.005	0.06
Windspeed	3.2	< 0.005	-0.26
Year	1.0	n.s.	

Table 5. *Multiple regression analysis of the number of clupeids robbed by gulls. For all significant parameters the T-value (T), the significance of T (Sign. T) and the partial regression coefficient (B) after removal of the non-significant parameters, are listed. D.F.: degrees of freedom of the residual; Windspeed^2: quadratic function of windspeed.*

Parameter	T	Sign. T	B
In 1993 (D.F. = 427)			
Constant	4.4	< 0.005	1.61
Colony	-2.4	< 0.05	-0.12
Age	1.5	n.s.	
Windspeed	0.5	n.s	
Windspeed^2	0.6	n.s.	
Between years (D.F. = 592)			
Constant	-3.2	< 0.005	-28.75
Year	3.2	< 0.005	0.31
Age	2.8	< 0.05	0.02
Windspeed	0.9	n.s.	
Windspeed^2	1.0	n.s.	

Table 6. *Multiple regression analysis of the number of ammodytidae robbed by gulls. For all significant parameters the T-value (T), the significance of T (Sign. T) and the partial regression coefficient (B) after removal of the non-significant parameters, are listed. D.F.: degrees of freedom of the residual; Windspeed^2: quadratic function of windspeed.*

Parameter	T	Sign. T	B
In 1993 (D.F. = 426)			
Constant	-2.5	> 0.05	-0.46
Age	6.4	< 0.005	0.04
Windspeed	3.3	< 0.005	0.07
Colony	-1.5	n.s.	
Between years (D.F. = 592)			
Constant	-2.6	< 0.05	-0.40
Age	7.2	< 0.005	0.05
Windspeed	2.9	< 0.005	0.05
Year	-1.3	n.s.	

Table 7. *Multiple regression analysis of the length of the clupeids and ammodytidae supplied to chicks in 1993. For all significant parameters the T-value (T), the significance of T (Sign. T) and the partial regression coefficient (B) after removal of the non-significant parameters, are listed. D.F.: degrees of freedom of the residual; Log age: logarithmic function of age.*

Parameter	T	Sign. T	B
Clupeids (D.F. = 1746)			
Constant	26.6	< 0.005	7.43
Age	-6.6	< 0.005	-0.08
Log age	13.7	< 0.005	4.09
Colony	-6.8	< 0.005	-0.25
Windspeed	-0.3	n.s.	
Ammodytidae (D.F. = 1452)			
Constant	42.4	< 0.005	6.47
Log age	24.2	< 0.005	3.29
Age	1.6	n.s.	
Windspeed	-0.1	n.s.	
Colony	0.9	n.s.	

2.4 Conclusions

The proportions of clupeids and ammodytidae supplied to the chicks are within the ranges found by Veen (1977) for the period 1966-1970. In his study, the proportion of ammodytidae fed to the chicks ranged from 30.8 to 64.3%, while the proportion of clupeids ranged from 34.0 to 66.5%.

Likewise, the proportion of fish taken by Black-headed Gulls is not different between the two periods (17.8% in 1966 and 14.4-18.6% in 1992-1993) (not tested). This is surprising because there is a large difference in the number of breeding gulls (700, 21,000 and 16,000 in 1966, 1992 and 1993 respectively) and the gull/tern-ratio (0.5, 3.2 and 2.1 in 1966, 1992 and 1993 respectively). It is possible that the density of black-headed gulls near the observed tern colony is of importance. In 1992 and in colony 6 in 1993 the observed colony was situated in the middle of a dense gull colony, while colony 8 (1993) was surrounded by only a few breeding gulls. Indeed robbing was highest in the two colonies situated in a dense gull colony (note that the chicks were only followed upto day 20 in 1992, which loweres the mean robbing proportion). But probably the robbing behaviour is even more complex (see further down). The high proportion of robbed fish in 1967-1970 (up to 37.5%) found by Veen (1977), can not be compared with our result because of a difference in observation methods (Veen made no individual protocols in these years, which can cause an overestimation of the more conspicuous robbing events).

There is, however, a great difference in the number of fish fed to the chicks in the two periods. Unfortunately Veen was not able to follow the chicks after they were 5 days old. But when we compare the first five days of the chick stage, terns fed a smaller number of fish to the chicks in 1992-1993 than in 1966. Especially in 1992 (4 fish/day/chick), but also the 1993 (8 fish/day/chick) numbers were small compared with 15 fish/day/chick in 1966. Also compared with other colonies the food deliverance was extremely low in 1992 and somewhat less in 1993. In literature the number of prey items brougth to the chicks ranges from 7-15 per day (Pearson 1968, Isenmann 1975, Campredon 1978). On average the adult terns brought daily 34-45 g food to the chicks. This is low compared with 42 g (Pearson 1968), 65 g (Campredon 1978) and 125 g (just before fledging) (Isenmann 1975) in other colonies. This indicates that the food availability at the foraging grounds of the adult terns was low, especially in 1992. Low food availability is one possible cause of the low number of breeding Sandwich Terns in the 1980s and 1990s compared with the 1950s. It can influence survival both directly (lower breeding success, which seems not to be the case) and indirectly (through a higher mortality of slowly grown juveniles, but for Sandwich Terns nothing is known in this respect) and can limit directly the number of breeding birds (chapter 4).

The low supply of fish in 1992 parallels the results found for chick growth and reproductive output of Lesser Black-backed Gulls on Terschelling (Spaans *et al.* 1994, Bukaciński *et al.* 1995). In 1992, but not in 1993, an additional food supply to Lesser Black-backed Gull chicks resulted in a higher chick survival and a faster growth rate of these young, compared with chicks of control pairs.

Many authors showed a clear relationship between food availability (or density of prey items at the foraging grounds) and the number of breeding pairs (Monaghan *et al.* 1989, Vader *et al.* 1990, Bailey 1991, Anker-Nilssen & Barrett 1991, see also chapter 4). Indeed the population size on Griend in 1992 (6600) was the lowest since 1986. The increase in number of breeding pairs to 7600 in 1993 (when food supply was higher) also supports the idea that food availability was low in 1992. A low food availability does not necessarily mean that the number of prey fish is low. It can also be caused by increased water turbidity (reduced sight during foraging, Stienen & Brenninkmeijer 1994) or a change in feeding areas (longer feeding trips). The results in chapter 3 show that the foraging area has changed somewhat. In 1993 the terns foraged mainly in the Wadden Sea, while in the 1970s the foraging areas were mainly located in the North Sea. Thus the flight distance to the foraging areas has changed in advantage of the terns. Increased turbidity of the water could be a possible cause, but unfortunately there are no long-term measurements of turbidity at the local feeding ground of the terns. Some authors report an increased eutrophication of the Wadden Sea during the last two decades, but this does not explicitly mean an increased turbidity (De Veen 1971, Cadée 1984, 1986). Data on number of young clupeids and ammodytidae at the local feeding areas are not available. So without additional research, nothing can be said about the causal aspects of low food availability.

Terns seem to try to compensate for a low food supply by bringing in longer fish. The majority of the clupeids delivered to the chicks in 1992-1993 were between 8 and 10 cm long, whereas in 1967-1970 most clupeids were 4-5 cm. Almost 50% of the delivered clupeids in 1967-1970 were less than 5 cm, whilst in 1992-1993 almost none (less than 1%) were smaller than 5 cm. This held even for clupeids supplied to chicks from 0 to 1 day old. The lengths of supplied ammodytidae, however, were almost the same in both periods. One could argue that there might have been a change in growth rate of young clupeids. In the 1970s, according to Cadée (1984, 1986) and Gerlach (1987), there was an increase in the phytoplankton primary production. In the 1970s, one- and two-ringers of clupeids were larger than in 1953 (De Veen 1971). But this increase in growth rate was probably due to a decrease in number of young herring (A. Corten pers. comm.) and not as suggested by De Veen (1971) a result of increased phytoplankton production. At present the growth rate of herring is the same as previous to the 1970s (A. Corten pers. comm.), so this increase in growth rate can not explain the increase in length of the fish brought to the chicks. Furthermore, the results of 1992-1993 also suggest that a lower food supply is compensated for by bringing in larger fish. In 1992 (a year with a low fish availability), the mean length of ammodytidae consumed was 11.0 cm, whereas in 1993 (a higher fish availability) this mean length was 9.8 cm. In 1992, the median length of the clupeids and ammodytidae supplied was also longer than in 1993 (note that the chicks were only followed up to day 20 in 1992 and until fledging in 1993). Another explanation for the increase in the mean length of ammodytidae could be a density effect. It is quite possible that the growth rate of young ammodytidae increases in years with low number of this species. But unfortunately no data on the abundance of young ammodytidae are available.

In accordance to the findings of Veen (1997) we found that Black-headed Gulls prefered relatively large preys. Even when corrected for any influence of age, robbed preys were larger than eaten ones (Stienen & Brenninkmeijer 1994). Still this relationship is very complex as robbing increases with the length of the fish when the chicks grow up (most gull eggs hatch a few days before tern eggs do). Also a learning process of the gulls plays an important role in this respect. In the first days after hatching of the eggs the gulls pay almost no attention to the delivered preys and act rather clumsy when they try to rob one. But when the chicks grow up some gulls change into professional robbers (pers. obs.). In this respect it is also noteworthy to point out a difference with the findings of Veen (1997). In the 1970s the food pirates consisted of mainly non-breeding gulls, while in 1992-1993 almost all pirates were nearby breeding gulls. It was very clear that robbing of these breeding gulls was influenced by the demand of their chicks. When food supply to the chicks was low (with high tide or stormy weather), the gull chicks spent a lot of time on begging for food. This seemed to stimulate the robbing intension of the adult gulls (pers. obs.). The same could be the case with the development of the chicks. With the growing food demand of the growing gull chicks, the adult gull who is present at the nest is more eager to steal a fish from a nearby Sandwich Tern. But it is quite possible that the causal aspects of the robbing behaviour of Black-headed Gulls are even more complicated. Annual fluctuations in the food availability of gulls, timing of tern breeding and the breeding density of the gulls around the tern colony could also influence the robbing behaviour.

The increasing demand for food during the development of the chicks was mainly compensated for by bringing in larger preys, especially larger ammodytidae. However, the supply of clupeids and ammodytidae also increased with the development of the chicks, although (in 1993) the supply of clupeids was not significantly correlated to the age of the chicks. The increase in the number of fish supplied when chicks reached the age of about 20 days in colony 8 in 1993 was caused by the fact that from that age onwards two parents often went out fishing, leaving the chicks alone. In colony 6 both parents also went out fishing together around day 20, but figure 5 does not reflect this, probably caused by relatively strong winds in the 10 days before fledging, which reduced the number of delivered prey items. The fact that both parents were foraging at the same time could again be an indication that food supply was not sufficient. Leaving the chick alone in an early stage of life can be fatal for the chicks, because of the high thermoregulatory costs for non-brooded chicks at that time of the chick stage (Klaassen *et al.* 1994). But even for older chicks it is risky to be left unattended, not only because of higher thermoregulatory costs (which can be compensated for by a higher food supply), but also because of severe aggressive attacks by neighbouring Sandwich Terns and Black-headed Gulls.

Strong winds reduce food intake in two ways. The number of supplied clupeids decreases and furthermore the number of robbed ammodytidae increases with increasing windspeed. The increase of robbing parallels the findings of Veen (1977) and Gorke (1990). Veen (1977) also found that with strong winds robbing of larger ammodytidae in particular, increased. Strong winds reduce the fishing success of adult terns (Dunn 1973, Taylor 1983) and can change the spatial distribution of fish (Birkhead 1976, Safina & Burger 1988, Frank & Becker 1992), resulting in a lower supply to the chicks. Reduced fish supply in periods with strong winds has also been found by Veen (1977) for Sandwich Terns and by Stienen & Van Tienen (1991), Frank (1992) and Frank & Becker (1992) for Common Terns. In contrast to the findings of Veen (1977), we found a reduced supply of clupeids with increased windspeed, but no reduced supply of ammodytidae. It is possible that ammodytidae are mainly caught in the Wadden Sea in the shelter of the islands Vlieland and Terschelling, while clupeids are mainly caught in windy areas, such as the tidal inlet between Vlieland and Terschelling (chapter 3). Bearing this in mind, it is interesting that with the development of the chicks there is a clear increase in the ammodytidae supply. But when windspeed also increases with the development of the chicks the supply of ammodytidae is not reduced, whereas the robbing of this fish species increases. Apparently it is not possible for the terns to switch over to clupeids, which are less vulnerable to robbing, with strong winds.

A short period of strong wind has, however, almost no effect on the breeding success of Sandwich Terns, but when lasting more than 4 days it can cause a high mortality rate (Dircksen 1932, Veen 1977, Brenninkmeijer & Stienen 1992).

Late breeding in 1993 increased the numbers and the length of the supplied ammoditidae. It is possible that the conditions for foraging upon these preys are more favourable later on in the breeding season. Also robbing by Black-headed Gulls was less severe later on in the season. However, breeding later on in the season can have negative effects also. As the gull chicks are larger later on in the season, they are capable of swallowing freshly hatched tern chicks. Indeed in the first days after hatching chick predation was relatively large in colony 8 (pers. obs.). But the latter can also be caused by the inexperience of late breeders, as Veen (1977) found out that late breeding Sandwich Terns were mainly first year breeders. There is another negative aspect of late breeding, which plays no important role on Griend but can have great influence in other colonies. Black-headed Gulls act as a natural buffer against ground predators and are very effective in dislodging predators. Thus in this respect terns profit from breeding in the middle of or nearby a colony of Black-headed Gulls (Veen 1977). Late in the season most gull chicks have (almost) fledged and there are only solitary breeding gulls or relatively small colonies left. But as there are no ground predators and little active avian predators (except for Black-headed Gulls and in some years Common Gulls and Herring Gulls) on Griend, late breeding on Griend can also have positive effects because of an increased food supply and a reduced chance of robbing.

Summarizing, we conclude that (1) the food intake of the chicks is influenced by windspeed both directly (reduced fishing success) and indirectly (increased robbing), (2) food supply (number of fish supplied as well as the length of the fish supplied) increases with increasing age of the chicks, (3) food supply in 1992 was very low compared with the late 1960s and early 1970s and with foreign colonies, (4) the terns can compensate for a lower supply to some extent by delivering larger preys and (5) low food availability possibly limits the growth of the Sandwich Tern population.

3 RADIO-TRACKING

3.1 Introduction

This chapter deals with a pilot study on tracking radio-tagged adult Sandwich Terns. In 1991-1993, the study was conducted to obtain more information about the terns' feeding grounds, especially where exactly the adult terns catch their fish and if there are any shifts in this respect compared with the findings of Veen (1977) in the 1970s.

3.2 Methods

In 1991, four transmitters, developed for Common Terns by the German Institut für Vogelforschung 'Vogelwarte Helgoland' in Wilhelmshaven, were attached to the back of Sandwich Terns, by glueing a plastered round transmitter on the back with UHU-sofortfest 2-components epoxy-glue (dry in approximately 5 minutes). The area for the transmitter was made free of feathers by cutting and then made grease-free with acetone (Becker *et al.* 1991). We preferred glueing the transmitter rather than the use of a harness, because glueing affects the bird's behaviour less than a harness (Kenward 1987, Giroux 1990, Hill & Talent 1990, Becker *et al.* 1991). The TW-2 type transmitters (from Biotrack, Wareham, U.K.) had a frequency of around 165 MHz, impulse-frequencies of 50-90 per minute, measured 18x16x13 mm, contained two antennas of 23.8 and 13.8 cm length and weighed approximately 8 g (about 3% of the Sandwich Tern body weight). Klaassen *et al.* (1992) showed that transmitters, weighing less than 5% of a Common Tern's body mass, did not affect the daily energy expenditure of these terns. The range of the transmitters was about 8 to 9 km. The transmitters had a theoretical battery-life of more than 4 weeks.

As the yagi-antenna was not posted high enough on our radio-tracking post on Griend in 1991 (only 6 m) to have a good reception of the signal, we had great difficulties in following the transmittered birds, in particular when they stayed on the ground and after they had crossed the northern sand dunes of Griend for a foraging trip. From one nest the eggs were robbed, from another the chicks were predated and from the third and fourth nest the chicks walked away from the original site after a few days. After one week of irregular attendance-responses the observations were stopped. We concluded that it was very important to keep the chicks together on the same spot. Otherwise it would be impossible to study their feeding behaviour for more than the first few days.

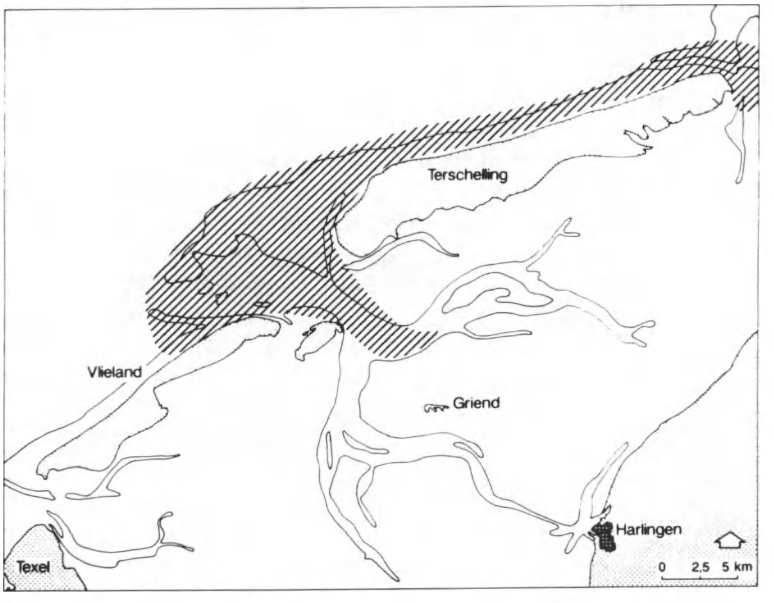
We also needed to gain more height for the antenna on Griend to improve the receiving of the signal. Furthermore we decided to expand the amount of receiving stations around the feeding area of the Sandwich Tern. As we noted that 95% of the Sandwich Terns flew away in northern to western direction, and arrived at the colony from that same direction, resembling the sight observations made by Veen (1977), we decided that for future attempts high radio-tagging posts should be stationed on the northern and northwestern islands of Terschelling and Vlieland (Fig. 11). In order to improve the reception, in 1992, various types of radio-transmitters were tested by fixing them to the ferry from Harlingen to Terschelling, which passes the isle of Griend six time per day. The 450 MHz VHF-transmitters, developed by the IBN-DLO institute in Arnhem, proved to be better than the German ones, as the former had a stronger receiving signal and a longer range (at least 12 km). To keep the tern chicks 'grounded', we fenced in a number of nests (Brenninkmeijer & Stienen 1995). Unfortunately, technical and logistical problems made it impossible to do further experiments with transmitters on birds that year.

In 1993, the transmitters were further developed at the IBN-DLO and at the end of May and in the beginning of June eigth unmodulated pulsating transmitters (power +7dBm, frequencies between 450.071 and 450.489 MHz on the 70 cm band), were glued on eight adult Sandwich Terns, in the same way as described for 1991. These transmitters were cylinder-shaped, measured 37x13.5x13.5 mm, had one antenna of 12 cm, and weighed about 10.1 g (4% of the mean body weight). An eight-element vertical polarized yagi-antenna (profit 10.2 dB, 3 dB 43° opening angle) was attached to a Yaesu-FT290MK2 receiver. As we used a converter, which translated the received signal from the 2 m band to the 70 cm band, the length of the antenna could be limited compared with the 1991 antennas. Tern positions were radio-tagged every 10 minutes by taking the middle of the range of the best reception. It should be noted that the accuracy of these positions was rather low, because often the loudest perception covered a range between 60° and 180°, and when the bird was close to the observation post, even 360° round. A foraging route has been roughly drawn by connecting every synchronously radio-tagged position of a tern from the moment of leaving the colony until returning again with or without a fish. Simultaneously, the time of begining and ending of a trip, as well as identification and length estimation of the fish supplied, were observed from a hide in the colony. As in chapter 2, herring and sprat are referred to as clupeids, and sandeel and greater sandeel as ammodytidae. The foraging speed has been estimated by dividing the distance of the foraging route (from leaving the nest till returning to the colony) by the time needed to cover this distance (Raaijmakers *et al.* 1993).

3.3 Results

Foraging area

According to the sight observations made by Veen (1977), terns foraged between 1965 and 1972 mainly at the North Sea from the eastern part of Ameland, through the entire coast of Terschelling to the middle of the coast of Vlieland (Fig. 11). In 1993, however, terns foraged more in the south-western part of the North Sea coast adjacent to the Frisian Islands, from the northern part of Texel, along the entire coast of Vlieland and to the middle of the coast of Terschelling (Raaijmakers *et al.* 1993). In 1993, also the Wadden Sea, in particular the area directly south of Vlieland and Terschelling, was used as a foraging area. In both periods, however, terns foraged mainly in the 'Zeegat van Terschelling', the 'Vliestroom' and the 'Stortemelk' (Fig. 11). Although we were well able to follow foraging terns, we actually saw a tern returning to the colony with fish and were able to locate the exact spot where a Sandwich Tern caught a fish (Fig. 11) only four time. Terns with chicks foraged mainly around Terschelling, whereas the terns that lost their clutch, predominantly foraged around Vlieland (up to Texel) (Raaijmakers *et al.* 1993).



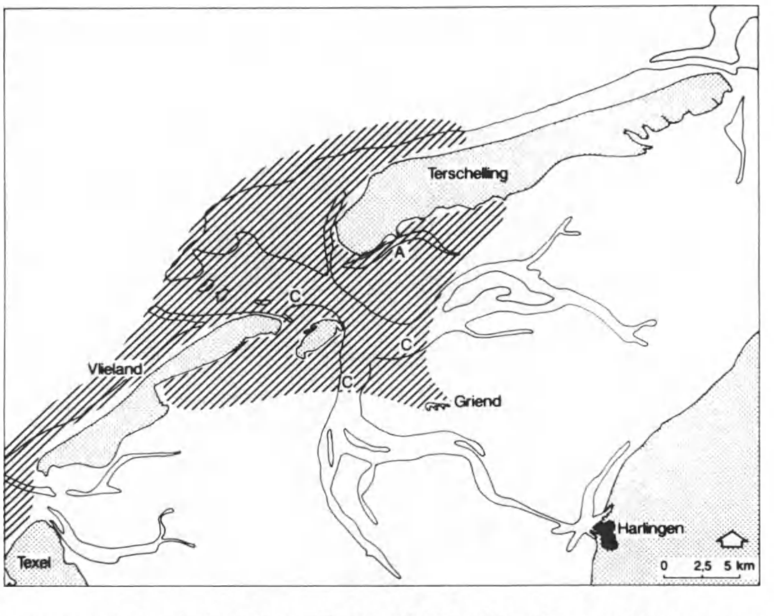


Figure 11. Foraging areas of Sandwich Terns in the 1970s (based on sight observations conducted by Veen 1977) (upper graph) and in 1993 (based on radio-tracking, after Raaijmakers et al. 1993) (lower graph). Letters indicate the spots where clupeids (C) and ammodytidae (A) were caught by the terns.

Foraging speed

The mean foraging speed (as defined in methods) of two radio-tagged Sandwich Terns was 24.4 km per hour. This is a very rough estimate, taking into account the low accuracy of radio-tagged positions. But the actual speed during foraging is probably somewhat lower because we made no correction for flying speed to and from the foraging grounds nor from one fishing spot to another.

Behaviour

The first four adult birds were caught on their nests with walk-in-traps, while incubating pipping eggs. Birds were released after approximately 35 minutes. The birds revealed, however, atypical behaviour after that, by not returning to their nest until 3.0 0.8 days after catching. One bird did not return at all. Moreover, all three remaining pairs with radio-tagged terns delivered fewer fish (4.79 fish/day/chick) to their chicks than the untagged control pairs (8.64 fish/day/chick, Student t-test, s.d. = 4.4, $P < 0.05$) (for more details see Raaijmakers *et al.* 1993). The radio-tagged parents did not fledge any chicks. The next 4 terns we trapped were therefore treated in a different way. In the first place the handling time of glueing was shortened to an average of 18 minutes. Furthermore another two terns were tagged with dummy transmitters. In order to investigate the influence of the treatment, a plaster (weighing 0.5 g) without transmitter was attached on the back of one bird. And to investigate the influence of the shape of the transmitter, a flat round dummy containing three Dutch quarter-coins (weighing 9.9 g) was attached on another tern. Two dummy-tagged terns and one radio-tagged bird returned to their nests after 2.7 ± 2.1 days. The other three radio-tagged terns did not return at all, as their eggs were robbed very soon after they were caught. The fate of the chicks of the three returning tagged terns is unknown, because the chicks walked away after three to four days. And in these few days too little information had been gathered for conclusions to be drawn on transmitter shape and weight, as well as on adult fishing capacity (Raaijmakers *et al.* 1993).

3.4 Conclusions

Foraging area

It is remarkable that all four places where fish were caught by the terns, were located in the Wadden Sea, along the gullies. The ammodytidae were caught in the Schuitendiep. Especially when weather conditions, such as a high windspeed, make foraging difficult on open waters, the Schuitendiep which is situated in the shelter of the island of Terschelling, seems a good place for foraging. This could explain why the delivery of clupeids dropped with increasing windspeed, whereas the delivery of ammodytidae did not decrease (chapter 2). Probably Sandwich Terns forage near the borders of these gullies where fish swim from the depths of the gullies to the surface. The fish can also be driven to the surface of these gullies by predatory fish such as mackerel (Veen 1977). If the few results are representative for other terns, they suggest that there is a slight shift of foraging area towards the south-west compared with the results of Veen (1977). At present the terns forage mainly in the Wadden Sea. In spite of these findings we do not expect that a shift in foraging area is a possible cause of the stabilisation of the number of breeding pairs since the 1980s. In fact this shift could well be favourable for the terns as this shortens the foraging distance.

Foraging speed
According to Pearson (1968) the average foraging speed of 24.4 km per hour is about half the maximum speed Sandwich Terns can reach.

Behaviour
In contrast to Common Terns (Klaassen *et al.* 1992) and Razorbills (Wanless *et al.* 1988), most radio-tagged Sandwich Terns did not behave normally. All terns delivered fewer fish to their chicks than their untagged partners. In contrast to Guillemots, where transmittered birds also stayed away longer and returned more often without prey (Wanless *et al.* 1988), this did reduce the terns' breeding success dramatically. Therefore, one has to be very carefull when radio-tagging Sandwich Terns. Still, it should be possible to obtain better telemetric results with this species, but then a number of changes have to be made. In the first place experiments should be done with smaller and flatter transmitters, as this might enlarge the freedom of locomotion of the birds, especially when plunge diving. Another step in improving the locomotion of the birds is to attach the transmitters to the rump instead of between the shoulders, as has been done with sandpipers (Warnock & Warnock 1993). Furthermore the birds have to be transmittered as fast as possible, resulting in a preferable release within 15 minutes after catching. Finally, the accuracy of the receivers has to be improved to obtain more reliable results on foraging routes and foraging speed.

4 BREEDING PARAMETERS AND FISHERY

4.1 Introduction

In this chapter we will discuss the relationship between the number of prey fish and some of the Sandwich Tern breeding parameters, such as breeding success and population size. It is widely known that population size and breeding success of seabirds are highly dependent on their prey fish availability. Thus the guano production of Cape Gannets and the estimated biomass of the adult pilchard stock (the main food of this species) are highly correlated (Furness & Monaghan 1987). The collapse of fish populations often coincides with the decline of seabird populations and low breeding success (e.g. Furness 1982, Ewins 1985, Jakobsson 1985, Springer *et al.* 1986, Hamre 1988, Harris & Ruddiford 1989, Klaassen 1989, Monaghan *et al.* 1989, Harris & Wanless 1990, Vader *et al.* 1990, Bailey 1991, Danchin 1992, Monaghan *et al.* 1992). A causal relationship with fishery investment has never been proven, although many authors mention overfishing as a possible cause for the collapse of seabirds breeding populations (see also chapter 1). It is very probable that the highly specialised Sandwich Tern is very sensitive to changes in fish availability. The main question in this chapter is whether there is a relationship between the population size of the Sandwich Tern and the estimated number of prey fish, in particular young herring, the only species for which data are available.

4.2 Methods

Prey fish abundance was obtained from North Sea herring fishery data gathered between 1916 and 1992. There is too little information on sprat, sandeel and greater sandeel for a proper analysis. We used only data on the estimated number of young herring (one-ringers and two-ringers), as there is no relationship between spawning stock size and number of recruits within herring (N. Dankers & C.J. Camphuysen, pers. comm.). At the time they become one year old the length of young herring is about 9 cm and when two year old they match about 18 cm (Wheeler 1969). So the length of these age-classes coincides with the length of herring delivered to the chicks (chapter 2). For 1916-1972 data on the abundance of two-ringers of herring (Burd 1978) were used and for 1962-1991 we obtained data on the abundance of one-ringers (Corten 1990, Knijn *et al.* 1993).

4.3 Results

From 1916 to 1972 there was a positive relationship between the estimated number of two-ringers of herring in the total North Sea (Burd 1978) and the total Dutch breeding population of Sandwich Terns (linear regression $r^2 = 0.37$, $P = 0.01$) (Fig. 12). The population on Griend (where 30-75% of the total Dutch population nested in this period) showed the same relationship with the estimated number of two-ringers of herring in this period (linear regression, r^2 = 0.39, $P < 0.01$). As the number of breeding pairs in this period were strongly influenced by human interactions other than fisheries, the years with human influences should preferably be left out of the analysis. In the beginning of the century large scale shooting of adult terns and egging strongly reduced the number of breeding pairs. From 1912 onwards, many tern breeding areas were guarded during the breeding season, and in 1914 a law against egging and shooting of terns became operative, resulting in a marked increase in the number of breeding pairs. In the last two years of World War II egging again reduced the number of breeding pairs, but not as severely as in the beginning of the century (Veen & Van de Kam 1988, Brenninkmeijer & Stienen 1992). In the 1960s the population collapsed again. This collapse was due to the pollution of the Dutch coastal zone with organochlorine pesticides (Koeman 1971, Veen 1977, Brenninkmeijer & Stienen 1992). In fact the number of breeding pairs in the three periods just mentioned were far below the expected numbers, according to the relationship between the number of two-ringers in these periods (Fig. 12). Only egging during World War II did not reduce the number of breeding pairs as markedly as in the two other periods, although the 1944 and 1945 numbers were smaller than the expected numbers. In a second analysis we left out the periods 1900-1920 and 1960-1972 from the calculations, in order to correct for human influences. Thus linear regression again showed a positive relationship between young herring and the number of breeding pairs (r^2 = 0.38, P = 0.01 for the total Dutch population; r^2 = 0.35, P = 0.01 for the population on Griend). In the period 1962-1991, the number of Dutch breeding pairs and the number of herring one-ringers in the total North Sea given by Knijn *et al.* (1993) showed a positive correlation (linear regression, r^2 = 0.15, P = 0.03) (Fig. 13). The number of breeding pairs on Griend (about 75% of the total Dutch population in this period) also showed a positive relationship between the recruitment of herring (linear regression r^2 = 0.20, P = 0.01). Corrected for human influences (see above) the relationship becomes very strong (r^2 = 0.76, $P < 0.01$ for the Dutch population; r^2 = 0.72, $P < 0.01$ for the population on Griend). The slope of the corrected regression line is almost the same in the period 1921-1959 (not tested) (slope 0.011 for the total Dutch population; slope 0.009 for Griend) as in the period 1973-1991 (slope 0.020 for the total Dutch population; 0.015 for Griend). The only information on young herring, somewhat more focused on the Dutch situation, is given by Corten (1990), who gives the number of herring one-ringers in the Southern North Sea in the period 1967-1985. These numbers show a strong relationship with the number of breeding pairs in The Netherlands and at Griend (r^2 = 0.40, $P < 0.01$ for the total Dutch population; r^2 = 0.34, P = 0.01 for the population on Griend) (Fig. 14). Leaving out the period of pollution makes the relationship even stronger (r^2 = 0.62, $P < 0.01$ for the total Dutch population; r^2 = 0.51, $P < 0.01$ for the population on Griend).

No significant relationship was found between the data of Knijn *et. al.* (1993) or Corten (1990) (linear regression; n.s.) and the breeding success of the Sandwich Terns in 1964-1991.

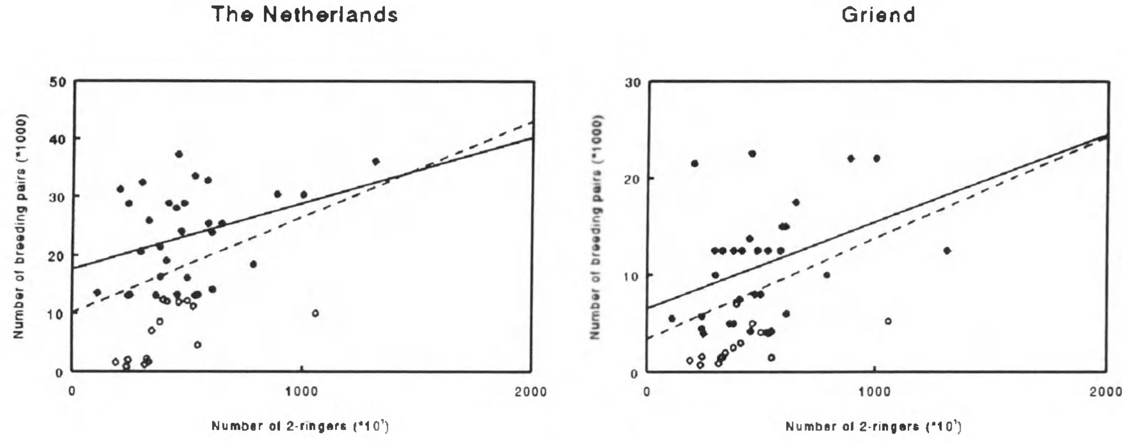


Figure 12. *Relationship between number of two-ringers of herring in the total North Sea (Knijn et al. 1993) and number of breeding pairs of the Sandwich Tern. Closed circles and solid line: years without human interaction. Open circles: years with human interaction. Broken line: regression without correction for human interactions.*

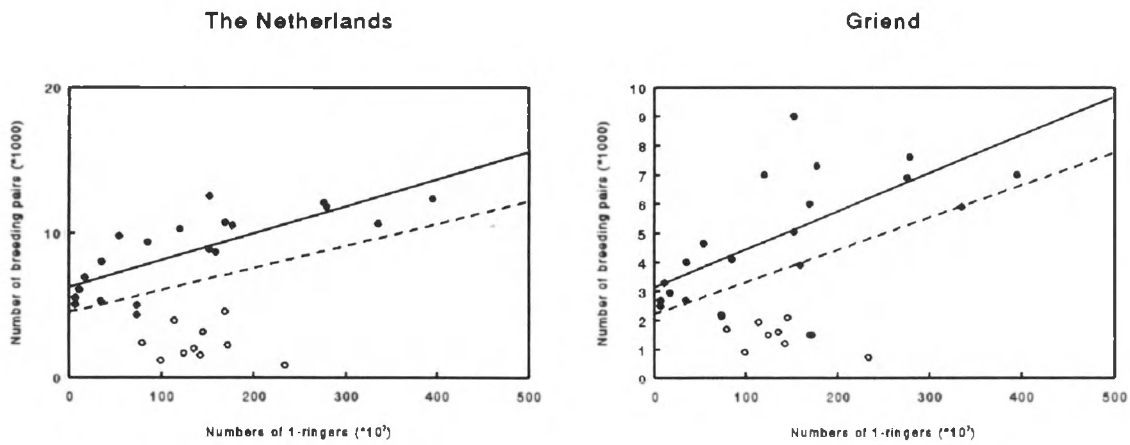


Figure 13. *Relationship between number of one-ringers of herring in the total North Sea (Burd 1978) and number of breeding pairs of the Sandwich Tern. Closed circles and solid line: years without human interaction. Open circles: years with human interaction. Broken line: regression without correction for human interactions.*

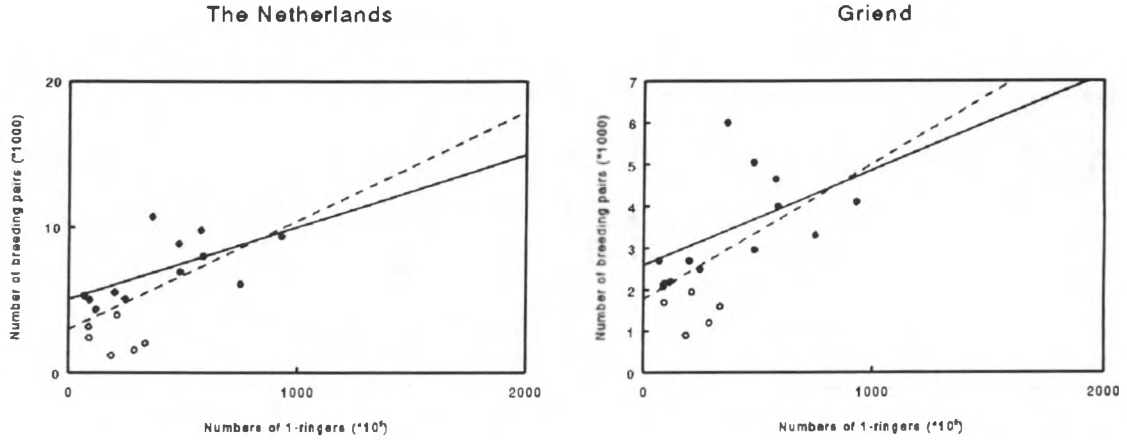


Figure 14. Relationship between number of one-ringers of herring in the southern North Sea (Corten 1990) and number of breeding pairs of the Sandwich Tern. Closed circles and solid line: years without human interaction. Open circles: years with human interaction. Broken line: regression without correction for human interactions.

4.4 Conclusions

Although the relationships between the number of young herring and the number of breeding pairs (in particular of the total Dutch population) suggest a causal relationship between the food supply in the North Sea and the breeding population of Sandwich Terns, the causal aspects of the relationship should be interpreted with caution. Firstly, the foraging areas of the terns are restricted to the direct surroundings of the breeding areas. As shown in chapter 3 the foraging areas of the Sandwich Terns breeding on Griend are located within a distance of approximately 20 km from the colony. Apparently these Sandwich Terns depend on very local food situations. Therefore, the suggestion that the yearly number of breeding pairs are regulated by the number of young herring only holds if the data of the total North Sea also reflect the local food situation. The dependence of seabirds on local food situations is made quite clear by the collapse of the sandeel population around the Shetland Islands in the 1980s (Ewins 1985, Furness 1989, Martin 1989, Bailey 1991, Hamer *et al.* 1991, 1993). Another reason for taking great care in interpreting the relationship found is that the fishery data only reflect young herring, while approximately 50% of the food supply to the chicks consist of ammodytidae and the other 50% of the food supply consists of either herring and/or sprat. In order to find supporting evidence for a possible causal relationship between the number of fish and the number of breeding pairs a long monitoring programme of the local food situation is necessary.

There are two reasons which support the suggestion that the number of Sandwich Terns are regulated by the number of young herring. In the first place the fact that years with strong human influences do not reflect this relationship. And in the second place this relationship also holds for other seabirds in The Netherlands such as the Lesser Black-backed Gull (Spaans *et al.* 1994). Nevertheless, it is very precipitous to conclude that the number of Sandwich Terns are regulated by the number of young herring. It is interesting that the breeding success of the Sandwich Terns does not show a relationship with the abundance of young herring in the North Sea. The mean breeding success of the Sandwich Tern on Griend in the period 1961-1991 was 0.7 fledged young per pair and shows little annual variation (Brenninkmeijer & Stienen 1992). Years with a low breeding success always coincided with years with a period of heavy storms. This suggests that a low food abundance limits the total number of fledged young (low number of breeding pairs) and not the number of fledged young per pair. The better the food situation the more adults decide to breed. This phenomenon is widely known among birds. Many bird populations consist of a relatively large pool of floaters which every year again decide to breed or not to breed (Smith & Arcese 1989, Newton 1991, Aebischer & Wanless 1992). It is possible that only terns which are able to work hard enough to cope with the actual feeding situation decide to breed.

Concluding we could say that the results in this study suggest a relationship between the abundance of young herring and the number of breeding Sandwich Terns, which confirms the findings in chapter 2 that food is in short for further growth of the population. But in order to draw firm conclusions about such relationship, research on fish abundance of all four prey species at the local feeding grounds of the terns is needed.

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SAMENVATTING

Van alle vogels die langs de Nederlandse kust broeden is de grote stern de meest gespecialiseerde viseter. De soort foerageert tijdens het broedseizoen voornamelijk op pelagisch zwemmende vissen, met name haring, sprot, zandspiering en smelt. Daardoor is deze soort extreem gevoelig voor veranderingen in het mariene milieu.

Het populatieverloop van de grote stern in Nederland kent grote fluctuaties gedurende de twintigste eeuw. Door menselijk ingrijpen is de soort tot drie keer toe sterk in aantal afgenomen. In het begin van deze eeuw waren de aantallen zeer laag door het op grote schaal rapen van eieren en door massale jacht op adulte vogels bestemd voor de dames-hoedenindustrie. Na beschermingsmaatregelen herstelde de soort zich tot 45.000 paren in 1938. Tijdens de Tweede Wereldoorlog is door het rapen van eieren het aantal gedaald tot 16.000 paren in 1944. Daarna heeft de soort zich weer hersteld tot 36.000 paren in de jaren vijftig. Vergiftiging met gechloreerde koolwaterstoffen was de oorzaak van de enorme achteruitgang aan het einde van de jaren vijftig en in het begin van de jaren zestig, met als dieptepunt 1965, toen er nog slechts 875 paren in Nederland broedden. Na deze laatste ineenstorting heeft de soort zich slechts langzaam hersteld en het aantal broedparen is sinds de jaren tachtig gestabiliseerd op ongeveer 11.000 paren, ongeveer een derde van de populatie van de jaren dertig en vijftig.

De centrale vraag in dit rapport is: "Wat is de oorzaak is van het langzame herstel na de laatste ineenstorting en waardoor wordt een verdere toename van deze soort beperkt?". Hoewel dit bepaald kan worden door vele factoren, wordt in dit rapport de nadruk gelegd op het voedselaanbod tijdens de broedperiode van de grote stern. In drie hoofdstukken worden de volgende punten behandeld:

(1) Hebben er veranderingen plaatsgevonden in de aantallen, de lengte en de samenstelling van het voedsel in de broedkolonie op Griend in vergelijking met de periode 1969-1974 en zijn er aanwijzingen dat de aanvoer van voedsel naar de kuikens een beperkende factor vormt?

(2) Waar halen de adulte sterns de vis bestemd voor hun jongen vandaan, en hebben er veranderingen van het foerageergebied plaatsgehad in vergelijking met de jaren zeventig?

(3) Bestaat er een relatie tussen de aanwezigheid van vis en het aantal broedparen van de grote stern of met het broedsucces van deze soort?

De samenstelling van het voedsel bleek in 1992-1993 niet veranderd ten opzichte van 1969-1974. Het aantal prooien dat per dag naar een kuiken werd gebracht, was in 1992-1993 echter wel aanzienlijk kleiner dan in 1969-1974. Vooral in 1992 was de aanvoer zeer laag. Zelfs wanneer rekening wordt gehouden met de geconstateerde toename van de lengte

van de aangevoerde prooien ten opzichte van 1969-1974 en vergeleken met buitenlandse kolonies, was de aanvoer in 1992 laag. De hoeveelheid voedsel die door de kuikens dagelijks werd gegeten, werd zowel direct (door een verlaagde aanvoer als gevolg van een laag foerageersucces op zee) als indirect (door een toegenomen kleptoparasitisme door kokmeeuwen) beïnvloed door de windsnelheid. De lage aanvoer van voedsel kan een oorzaak zijn van de stabilisatie van het aantal broedparen op een lager niveau dan voorheen.

Uit de telemetrische gegevens blijkt dat het foerageergebied van de sterns in grote lijnen hetzelfde is als in 1970, hoewel er een lichte verschuiving richting Waddenzee te zien is.

Er is een duidelijk verband gevonden tussen het aantal jonge haringen in de Noordzee en het aantal broedparen van de grote stern. Het broedsucces van de grote stern vertoont hiermee echter geen verband. Hoewel de gegevens van jonge haringen de totale Noordzee omvatten en dus niet noodzakelijkerwijs representatief zijn voor de plaatselijke voedselsituatie en deze vissoort bovendien maar een beperkt deel vormt van het totale voedselpakket van de grote stern, lijkt het erop dat het populatieverloop inderdaad sterk samenhangt met de aanwezigheid van deze prooivissen.

SUMMARY

Of all gulls and terns breeding along the the Dutch coast the Sandwich Tern is the most specialised piscivorous bird. During the breeding season terns feed mainly on pelagic fish as herring, sprat, sandeel, and lesser sandeel. This makes the species extremely vulnerable to changes in the marine ecosystem.

During the twentieth century, the number of breeding Sandwich Terns in the Netherlands has shown large fluctuations. In the beginning of this century, numbers were low, because of large-scale egg-collecting and shooting of adults. As a result of the protection following the slaughter for the lady's hat fashion, numbers gradually increased up to 45,000 pairs in 1938. In World War II, egging again caused a drop in numbers. After World War II, the population increased up to 36,000 pairs in the 1950s. At the end of that decade, numbers dropped markedly and the number of breeding pairs were reduced to 875 in 1965. This decrease was due to a pollution of the Dutch coastal waters by organochlorine pesticides. After the pollution stopped, the population increased in numbers again, but the large numbers from the period previous to the pollution have never been reached since then. Compared to previous population recoveries, the recovery after the pollution in the 1960s was slow, and since the 1980s the population seems to stabilise at approximately 11,000 breeding pairs, almost one third of the population during the 1930s and the 1950s.

This leads to the main subject of this report: 'What is the reason of the slow recovery of the Sandwich Tern after the numerical decline in the 1960s and why is there a stabilisation of breeding pairs at such a low level?'. Although this could be due to many factors, we have focussed our study on the food situation during the chick rearing period. The study deals with three items:

(1) What is the species composition and what is the length distribution of prey items delivered to the chicks of Sandwich Terns on Griend, the main colony in The Netherlands, and have there been remarkable shifts compared with the late 1960s and early 1970s (chapter 2)?

(2) Where do the terns feed, and are there any shifts in this respect compared with the late 1960s and early 1970s (chapter 3)?

(3) Is there a relationship between fish availability and either population size or breeding success of the Sandwich Tern (chapter 4)?

The species composition of the fish delivered to the chicks in 1992-1993 was identical to that in 1969-1974. The number of fish brougth to the chicks, however differed markedly from that in 1969-1974. In both years (most pronounced in 1992) the food supply was low compared with 1969-1974, and also compared with foreign colonies. The amount of food actually eaten by the chicks was strongly influenced by windspeed. An increasing windspeed did not only lower the supply of food (resulting from

a lower foraging success) but also increased kleptoparasitism by Black-headed Gulls. The low food supply in recent times might be a possible explanation for the stabilisation of the number of breeding pairs since the early 1980s.

Experiments with radio-tagged adults revealed that the foraging area of the terns is not markedly different from that in 1970, although there a little shift towards the Wadden Sea.

Analyses of data on the abundance of young herring in the North Sea and the number of breeding Sandwich Terns revealed a positive relationship between these two parameters. However, the number of fledged young showed no relationship with the abundance of young herring. Although the data set on young herring refers to the total North Sea and do not necessarily show the local abundance of this species, the results suggest that the breeding population of the Sandwich Tern at Griend is regulated by the availability of food.

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