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ON THE FEEDING ECOLOGY OF THE HERRING GULL *LARUS ARGENTATUS* PONT. IN THE NORTHERN PART OF THE NETHERLANDS

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CONTENTS

1. INTRODUCTION

1.1. AIM OF THE STUDY

During the twentieth century, several species of *Larus* gulls have increased considerably in number in both the northern and southern hemispheres. The Herring Gull *Larus argentatus* is one of these species. The increase in the Herring Gull population has been documented by several authors, but quantitative data not restricted to a few colonies are scarce. They are known from the Netherlands (Mörzer Bruyns 1958, unpublished reports of the former State Institute for Nature Conservation Research), Germany (Goethe 1956, 1964), Finland (G. Bergman, pers. comm.), the New England region of The United States (Kadlec & Drury 1968), and the north shore of the Gulf of St. Lawrence, Canada (review in Kadlec & Drury 1968). It is clear that there has also been an increase in Ireland (Kennedy, Ruttledge & Scroope 1954), Scotland, the Orkney Islands, Fair Isle, and the Shetland Islands (Baxter & Rintoul 1953), England and Wales (Parslow 1967), Denmark (Salomonsen 1963), the Scandinavian countries (Salomonsen, in Blaedel 1963) and the Great Lakes, North America (Kadlec & Drury 1968). During the same period the species colonized Iceland, Bear Island, and Spitsbergen (see Voous 1960) and extended its North American breeding area southwards (Kadlec & Drury 1968). In Ireland (Kennedy, Ruttledge & Scroope 1954), England (Parslow 1967), and Sweden (Lindroth 1946, Olsson 1958) the species has also shown an extension of the breeding area from the coast to inland areas.

This increase followed a period of drastic persecution in the nineteenth and the beginning of the twentieth centuries, during which the breeding population in most countries decreased to a very low point. Therefore, it is often postulated that the increase of the Herring Gull (and other gull species) is no more than a return to the normal population level, resulting from protective measures. It is also frequently claimed, however, that the increase was made possible by the large quantity of extra food supplied indirectly by man as a result of the current intensification of commercial fishery (resulting in more discarded fish and offal) and the increasing quantity of garbage produced in countries with a high level of prosperity. Supporters of this view point to the fact that the utilization of refuse dumps and other sources of human waste by Herring Gulls only dates from the past few decades. There are very few quantitative data available supporting either of these hypotheses. The present paper is intended as a contribution to the filling up of some of the gaps in our knowledge concerning the role of the increased food supply.

1.2. STUDY AREA

I restricted my study to the Herring Gulls breeding on the Dutch Frisian Islands. During the study I lived on the island of Terschelling, and therefore most of the information on the feeding ecology of the species was gathered

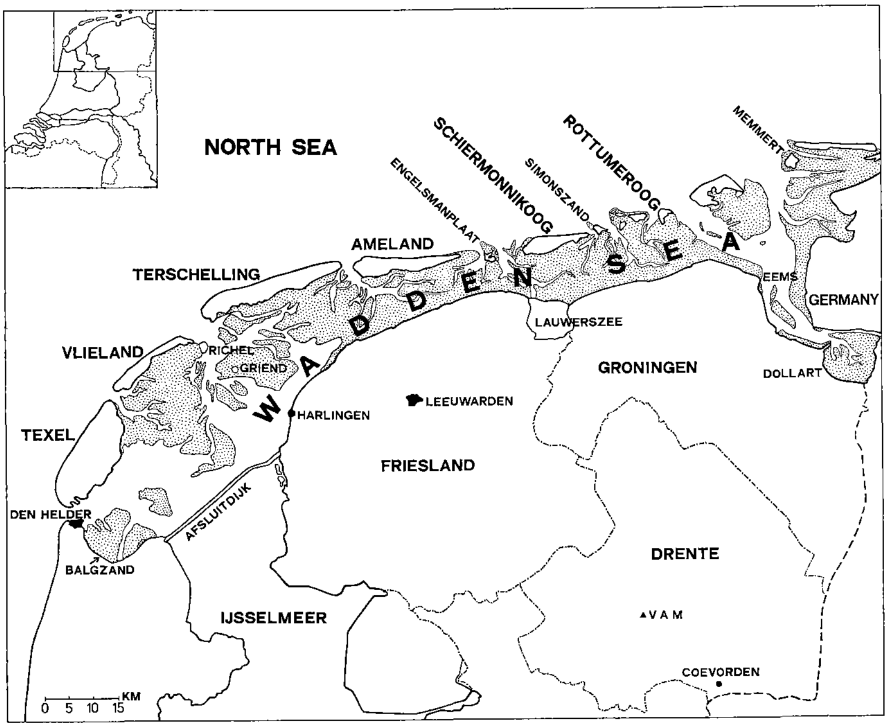

Fig. 1. Map of the northern part of The Netherlands. Stippled areas = tidal mudflats in the Wadden Sea.

there and on the neighbouring island of Vlieland, which was rather easy to reach from Terschelling. Throughout the year, however, the distribution area of the breeding population of the Frisian Islands includes a large part of the mainland. Therefore, the study was extended to the whole northern part of The Netherlands. Figure 1 shows this area and the locations of many of the places mentioned in the text.

During the past few years the Dutch Frisian Islands have harboured about 12,500 breeding pairs of the Herring Gull, of which about 6,000 pairs nested in the dunes and on the salt marshes of the nature reserve, the Boschplaat, situated in the eastern part of Terschelling. The colony on Vlieland is much smaller. During the study, the number of breeding birds there fluctuated between 1,400 and 1,900 pairs. This colony is situated in the dunes and polders in the western part of the island, which is maintained as a nature reserve.

Most of the study was carried out in 1966–1969, but some data collected in the preceding years have been included.

1.3. OUTLINE OF THE PAPER

The best way to tackle problems like the present one is to make the study as wide as possible. If this is not done, the risk of interpreting the observations incorrectly will be increased. Therefore, various aspects of the biology of the species were studied.

A study of this kind is hardly possible without some knowledge of the distribution of the population in the course of the year. The distribution area of the Herring Gull population of the Dutch Frisian Islands, determined on the basis of the recoveries of gulls ringed on these islands, is discussed in Chapter 3. Chapter 4 presents the fluctuations in the number of Herring Gulls in the different parts of the distribution area of the population, as well as an estimate of the total numbers of gulls in these areas. The results of the food analyses are given in Chapter 5. Since the possibility could not be ruled out that the growth-rate of a chick has an effect on both its pre-fledging and post-fledging survival, attention was also given to the growth of the young and to some factors influencing the variations in growth-rate (Chapter 6). In Chapter 7, I have tried to answer the question of whether food plays a role in the regulation of numbers of the Herring Gull population of the Dutch Frisian Islands and could therefore be responsible for its increase during this century.

1.4. ACKNOWLEDGEMENTS

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I also wish to thank all those who assisted me during the study in many other ways: Mr. G. J. M. Visser and the members of the International Biological Programme team on Terschelling, who were always ready to provide all the technical and practical help needed; Mrs. C. Jansen and Messrs. G. P. M. Jansen and F. van der Plas, who assisted me in the breeding seasons of 1967 and 1968, and the bird wardens of the State Forestry Service on Terschelling and Vlieland, for their help and hospitality in the field.

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Last but not least I must thank my wife, who assisted me in the field and with the preparation of the manuscript and has always been a great inspiration.

2. ANNUAL CYCLE OF THE HERRING GULL

This chapter comprises a brief review of the annual cycle of the species in the Wadden Sea area, based mainly on our observations in 1966–1969.

The ringing data indicate that the Herring Gulls of the Frisian Islands show no seasonal migration. Most of the gulls are recovered within a radius of 100 km from the ringing locality, much less frequently from greater distances.

The first gulls*) usually appear at the breeding sites in February and sometimes even at the end of January, but most of them do not return until March or April. During the pre-egg stage they are only to be found in the colony during daytime around high tide. When the tide goes out the gulls leave the colony to forage on the exposed mudflats of the Wadden Sea. They do not spend the night in the colony before the eggs have been laid, but even during the first week of incubation the eggs are often deserted (see Drent 1967).

The Herring Gull has only one brood per year. If a clutch is lost, replacement laying starts in about 12 days (Paludan 1951). The clutch generally consists of three eggs. Two- and one-egg clutches are, according to Paludan (1951), usually three-egg clutches with one or two eggs lost. Four-egg clutches occur only sporadically (Gross 1940, Paludan 1951).

The eggs are laid at intervals of 48 hours (Paludan 1951, Drent 1967). The two sexes take about equal shares in incubation (for review see Drent 1967).

The first eggs on the Frisian Islands are laid in the first week of May, exceptionally in the last few days of April. Laying culminates around the 18th of May. After the 1st of June fresh eggs can still be found but these are almost certainly replacement clutches.

The incubation period lasts about four weeks (for exact details, see Paludan 1951, Drent 1967), which means that most of the eggs hatch in June.

The adult birds, which until hatching begins forage only during low tide, no longer show this tidal rhythm after the eggs have hatched, when they begin to forage throughout the day and probably also on nights that are not too dark.

The chicks fledge in about six weeks, so most of the new generation is on the wing early in August. According to our observations of recognizable individuals, most of the young birds stay in the vicinity of the gullery for a few weeks, some of them returning occasionally to the old territories. In this period they are still fed regularly by the parents. Toward the end of August the breeding places are deserted except for a few late hatchers.

After the breeding season the population disperses in all directions over the northern part of The Netherlands, a large proportion (fluctuating between

*) Throughout the paper the word "gull" refers to the Herring Gull unless otherwise stated.

at least 32% and 77–82%; see 4.3.4) taking its food from human sources (refuse dumps, fish and meat processing factories, harbours, and towns and villages).

3. DISTRIBUTION OF THE HERRING GULLS OF THE DUTCH FRISIAN ISLANDS, BASED ON RINGING RESULTS

3.1. INTRODUCTION

In northwestern Europe the Herring Gull is not truly migratory (Drost & Schilling 1940, Eykman et al. 1949, Salomonsen 1953, Goethe 1956, Harris 1964a, Ingolfsson 1967). Only the populations from Scandinavia and Finland seem to show true migratory movements to some extent (Olsson 1958).

To obtain an impression of the dispersal pattern of the population of the Dutch Frisian Islands, I analysed the recoveries of gulls ringed as chicks on these islands.

3.2. METHODS

Unless otherwise mentioned I included only birds ringed in the 1950s and 1960s (and recovered up to 1 January 1969), because before 1950 the gulls moved further from the breeding sites than they did afterwards (see 3.3), and I was interested mainly in the present situation. Other exclusions concern:

1) Recoveries for which the month of recovery was not known, and those for the month of July not indicating whether the recovery was made in the first or second half of the month.
2) Recoveries of birds that must have been dead for a considerable period when found ("long dead", "decaying", "remnants", and "only leg or ring found").
3) Recoveries made in the ringing colony before 1 September in the year of ringing. Most of these birds had probably died before fledging.
4) Recoveries made south of 50° N, of gulls ringed on Terschelling from 1950 onward. These recoveries lie outside the dispersal area of the birds ringed on the other Frisian Islands in the same period, and probably concern misidentified Lesser Black-backed Gulls *Larus fuscus* (cf. Harris 1964a). During the last twenty years, numbers varying from some tens to several hundreds of pairs of the latter species, which is migratory, have nested among the Herring Gulls on the island of Terschelling, but on the other islands this did not occur or concerned only a few pairs.

The recoveries are mapped for each island separately (Figs. 2–6) and have been divided into six age-groups. Although Herring Gulls can reach sexual maturity by the end of the third year, most of them do not start breeding until the end of the fourth or even the fifth year (see 3.4). In general, therefore, the adult birds are subdivided into three age-groups: 4, 5, and over 5 years.

The year is divided into the following periods:
1) 16 July – 31 October (dispersal period),
2) 1 November – 31 January (winter season),
3) 1 February - 30 April (return of breeding birds to colony),
4) 1 May – 15 July (breeding season).

This division of the year is based on the seasonal fluctuations in the numbers of gulls on the Frisian Islands and on the mainland (see 4.2.1.2 and 4.3.2.2). Although according to these counts October is actually a winter month, I have included it in the dispersal period for the analysis of the ringing data, because in the 1950s and the beginning of the 1960s intensive measures were taken to control the Herring Gull in The Netherlands (Mörzer Bruyns 1958, unpublished reports of the State Institute for Nature Conservation Research), resulting in many replacement clutches late in the season, by which most of the young fledged 1 to 1½ months later than normal.

3.3. DISPERSAL AND WINTERING AREA

It is evident from Figures 2–6 that after the breeding season the gulls disperse in all directions, at least if the North Sea area (where there is almost no chance of recoveries) is not taken into consideration. The distribution of the autumn and winter recoveries is more or less random around the ringing localities. Only the gulls of Texel moved in their first year in a predominantly southern direction.

It is evident that most of the gulls remained within a distance of 100 km of the place where they hatched and that only a very small percentage went further than 150 km (see also Table 1).

As a result of this dispersal pattern over a relatively short distance, the gulls from each island have a more or less distinct distribution area. These areas have been called local dispersion zones by Poulding (1955). In the northern part of The Netherlands, however, there is considerable overlapping between the various areas.

Most of the recoveries from distances of more than 100 km from the ringing sites are located within a zone of 100 km from the coast. It is hardly likely that living conditions at greater distances from the coast are as limited as the occurrence of the Herring Gull would seem to suggest (cf. also Drost 1955, 1958). Therefore, some other factor must be responsible for the accumulation of recoveries in the coastal area. On the mainland, the occurrence of the Herring Gull is limited mainly to refuse dumps, cities, and villages. The utilization of these food sources by gulls is relatively recent (the last 40 years).

Figs. 2–6. Recoveries of Herring Gulls ringed as chicks on the Dutch Frisian Islands from 1950 onward, and recovered up to 1 January 1969. To give an impression of the distances involved, concentric circles have been drawn at 50 km intervals from the ringing locality, which is indicated by an arrow.

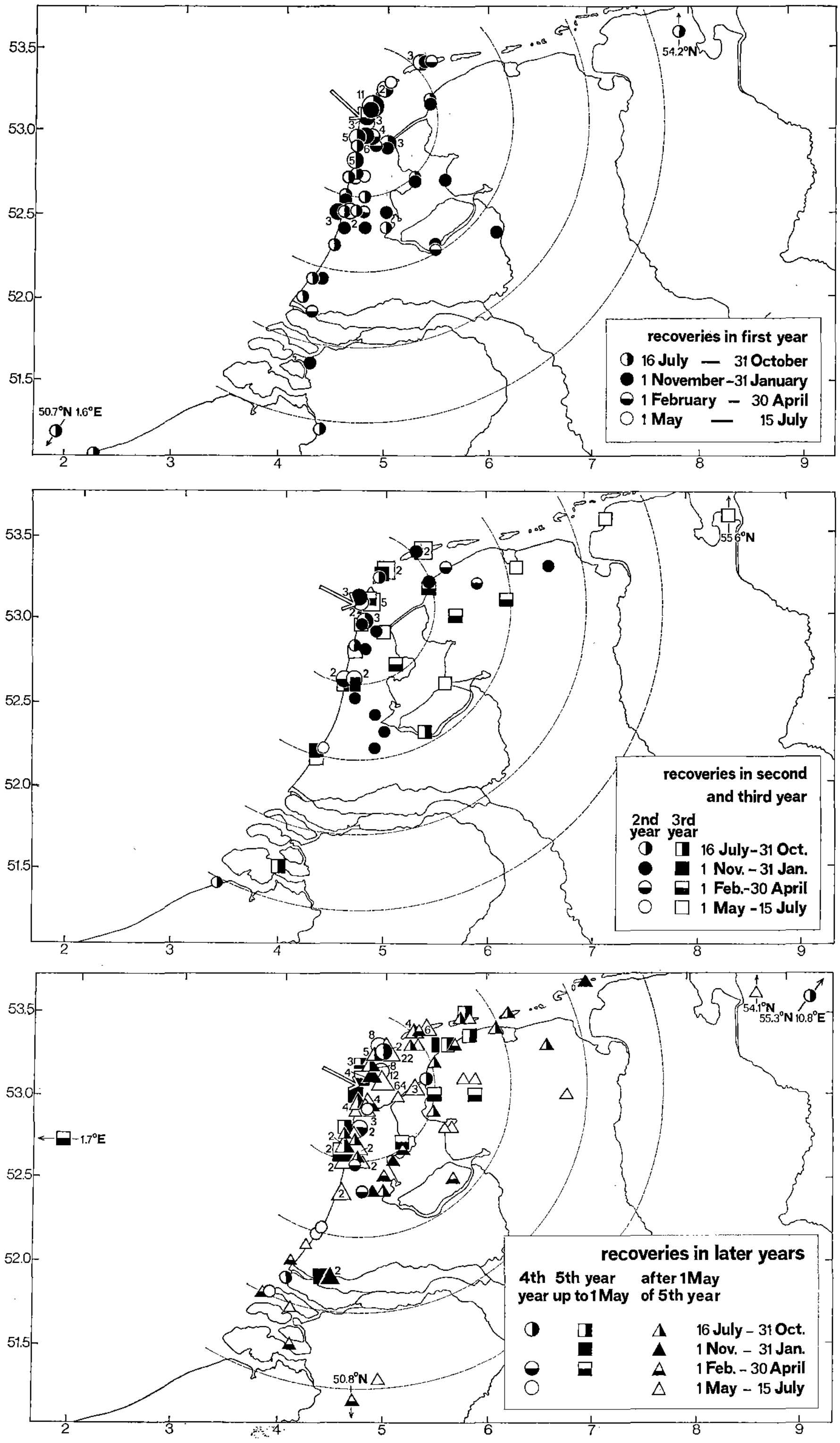
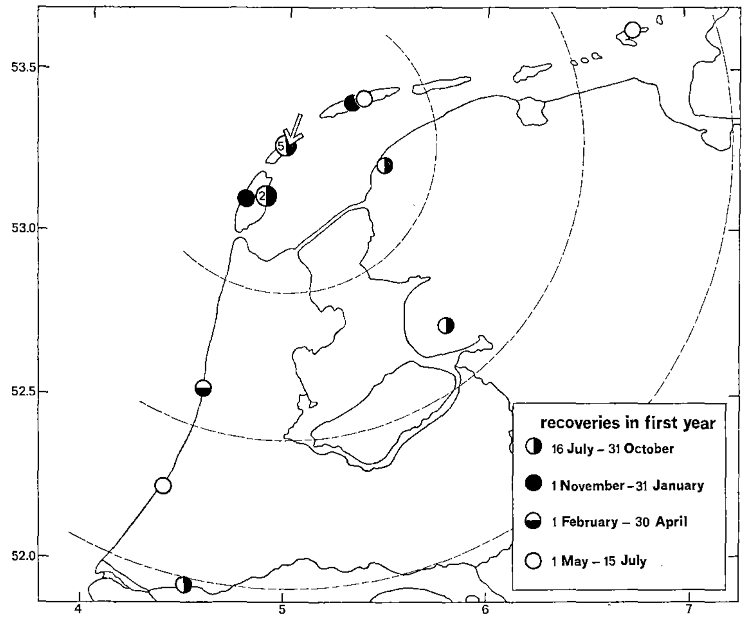


Fig. 2. Recoveries of Herring Gulls ringed as chicks on Texel.



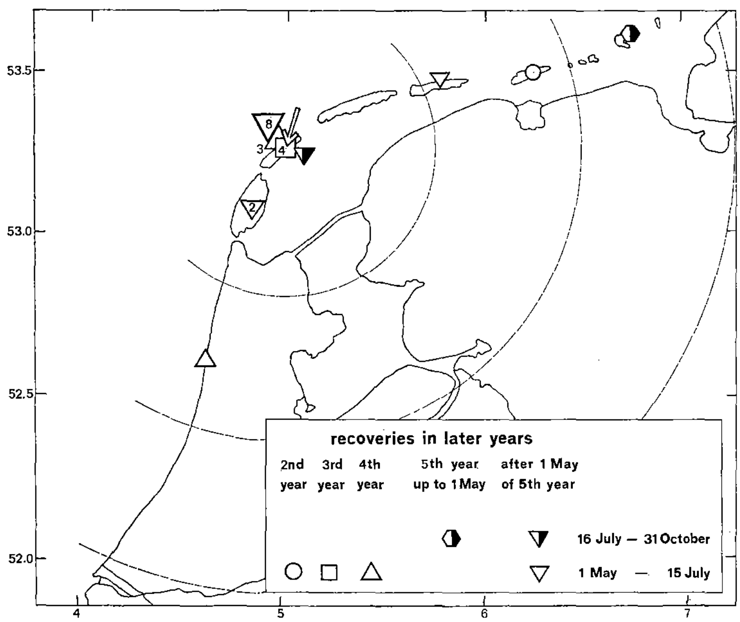


Fig. 3. Recoveries of Herring Gulls ringed as chicks on Vlieland.

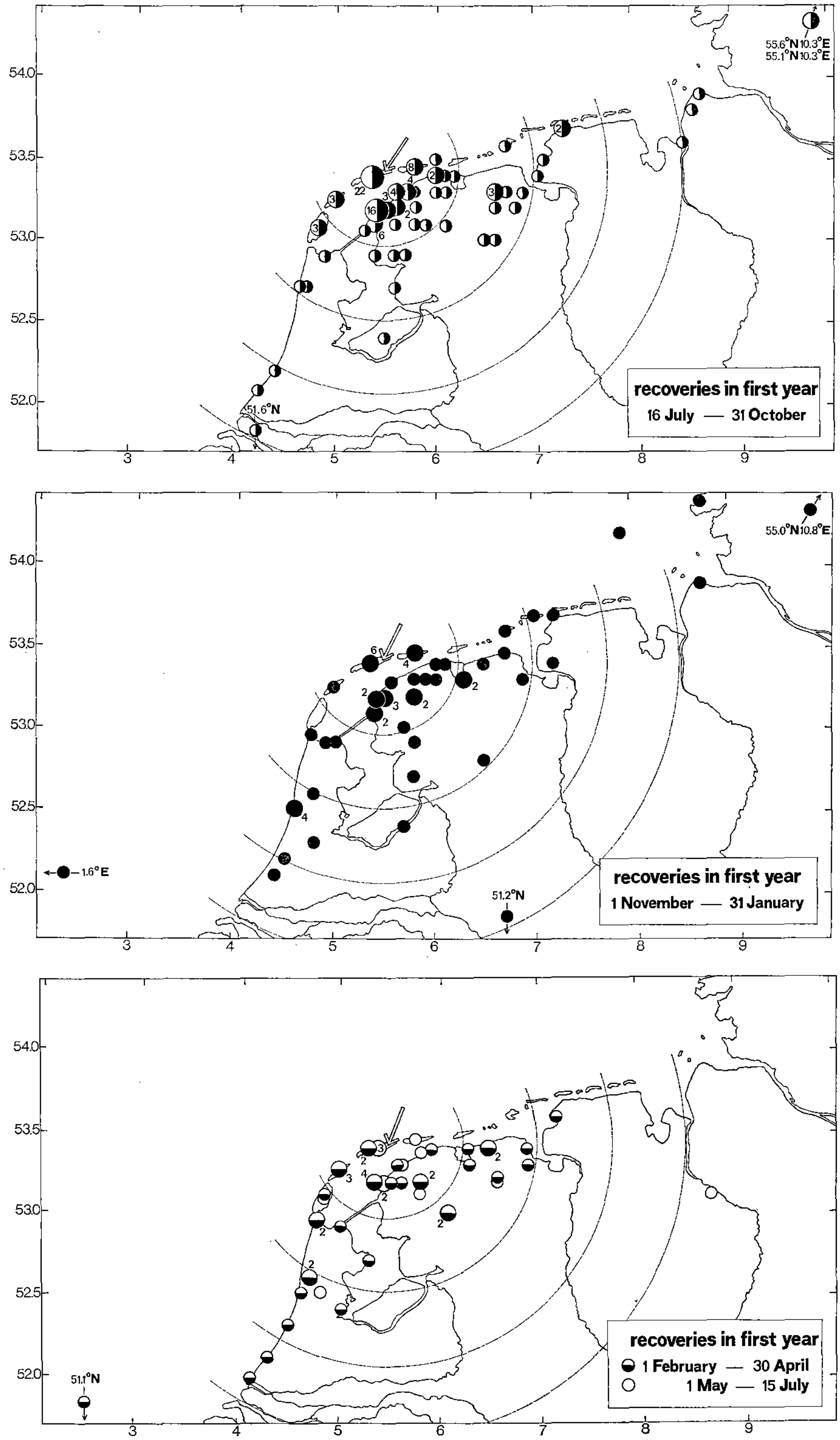


Fig. 4a. Recoveries of Herring Gulls ringed as chicks on Terschelling.

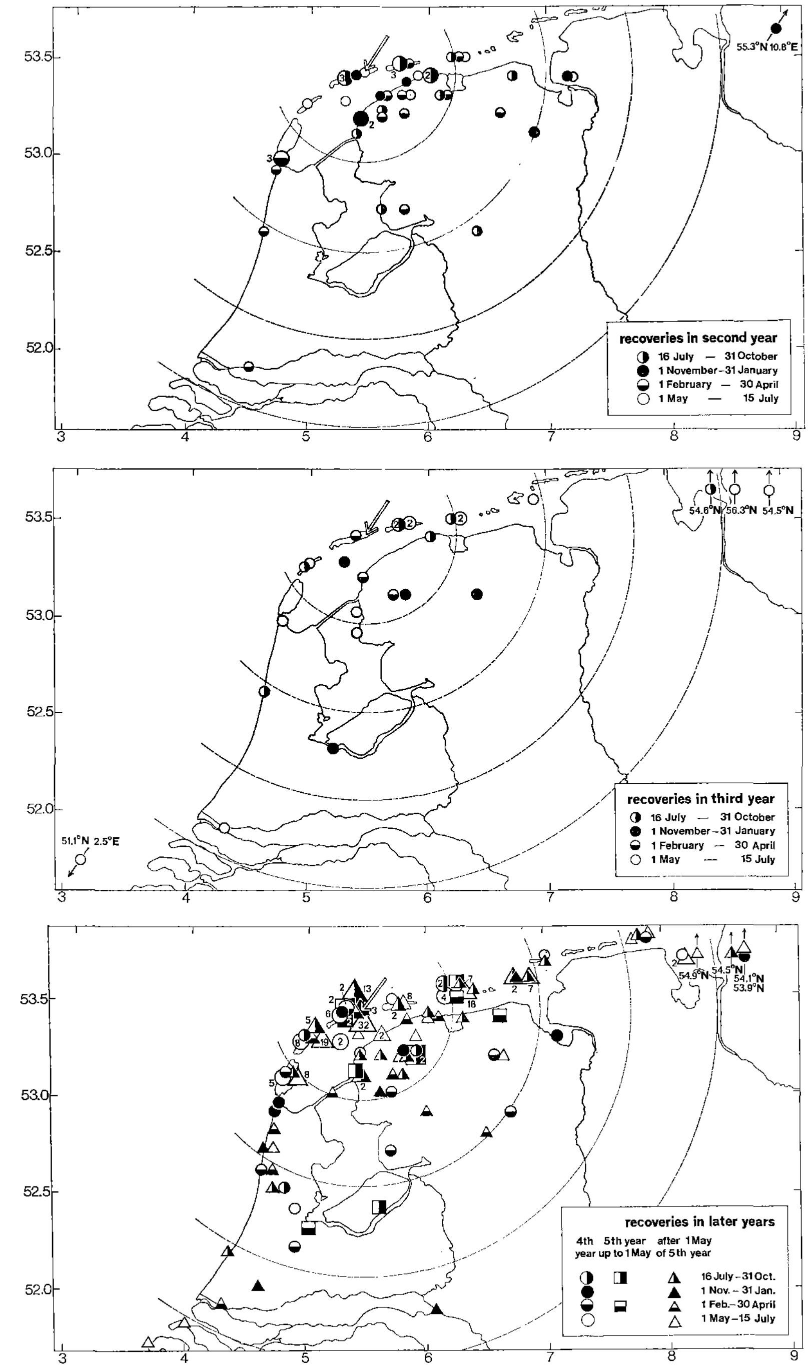


Fig. 4b. Recoveries of Herring Gulls ringed as chicks on Terschelling.

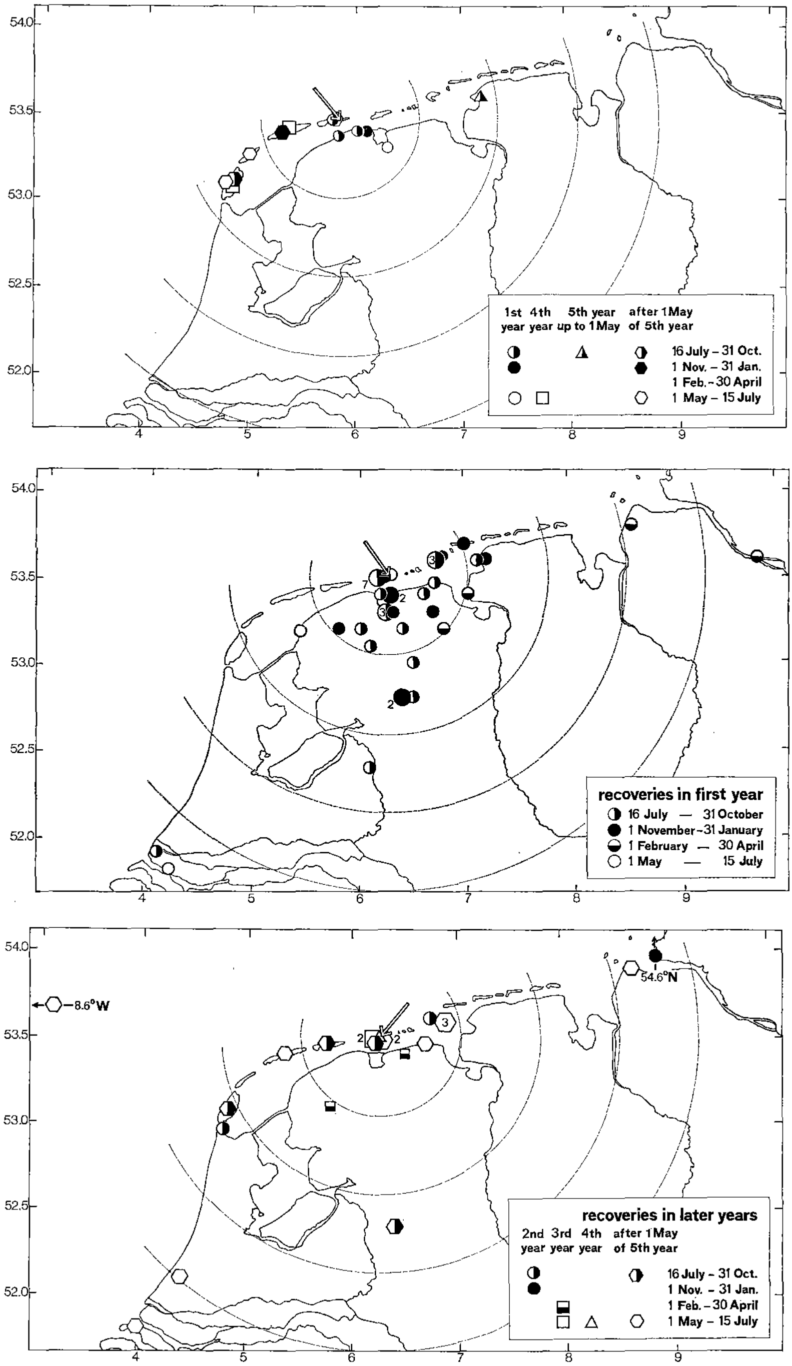


Fig. 5. Recoveries of Herring Gulls ringed as chicks on Ameland (top) and Schiermonnikoog (centre and bottom).

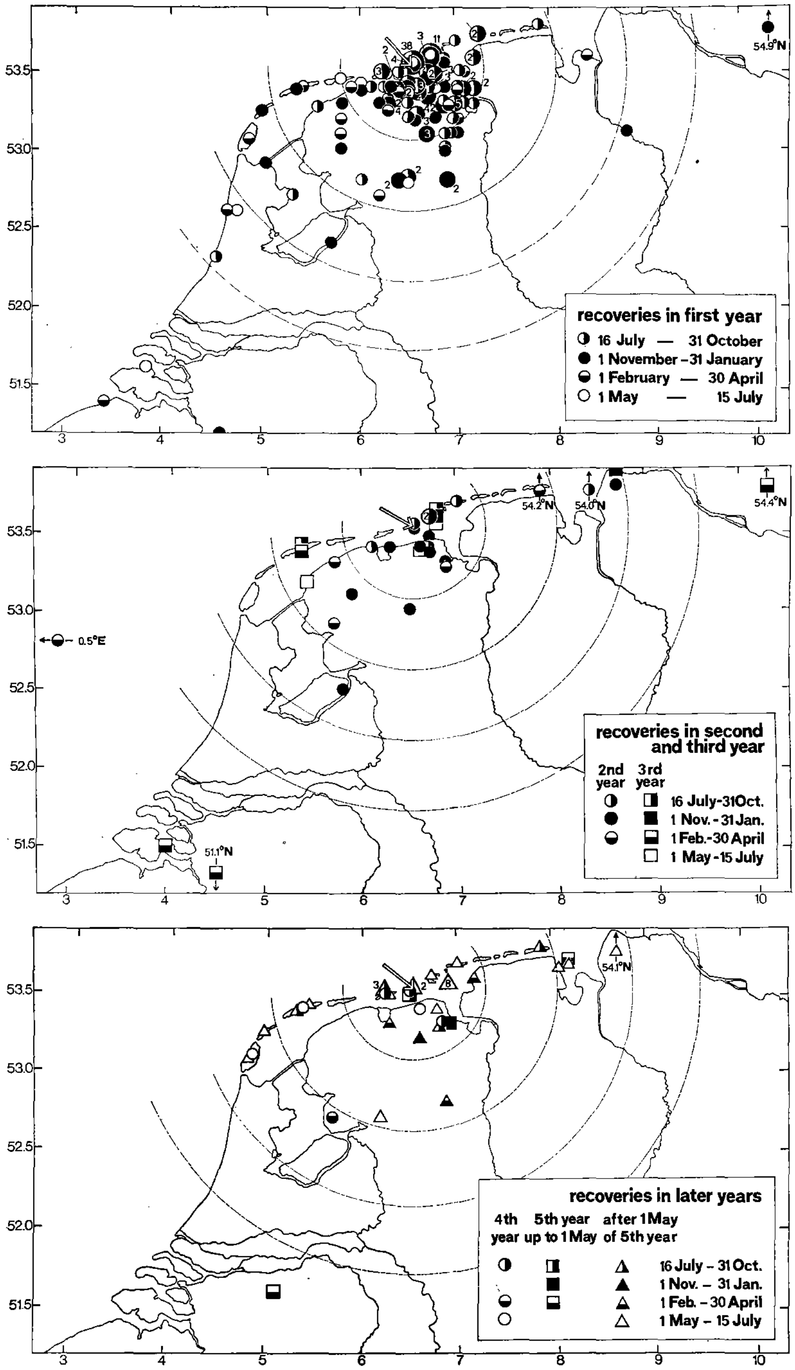


Fig. 6. Recoveries of Herring Gulls ringed as chicks on Rottumeroog.

Previously, the species probably occurred only in the Wadden Sea and Zuiderzee (now IJsselmeer) area, and along the coast and in the coastal waters of the North Sea. These birds probably roosted exclusively on the North and Wadden Seas and on the IJsselmeer. As far as we know, most if not all of the gulls foraging on the mainland of the northern part of the country still do so, at least during the winter period (see 4.3.3.2). The greatest distances I observed between roosting area and foraging area for individual birds amounted to 50-100 km. This means that in the northern part of The Netherlands the diameter of the area in which, according to the ringing data, the gulls are found in large numbers corresponds roughly with the maximum observed size of the 24-hour range of individual birds. I suggest that the gulls' traditional use of the original roosting areas is one of the factors that may have determined the extent to which the population of the Dutch Frisian Islands could penetrate the hinterland in any numbers (however, see also the discussion of Smith 1959 for the situation in North America).

Due to the predominantly S–N direction of the coast from Belgium to Texel and the predominantly W–E direction from Terschelling to Rottumeroog (the change in direction occurring in the neighbourhood of Vlieland), the gulls show a dispersal in roughly the western (or southern) and eastern directions. Goethe (1956) suggested that the dispersal in these directions might be a result of the shifts occurring when there are heavy gales along the coast (for a detailed discussion of this gull "migration", see Tinbergen 1952), but this is not likely. In the first place, the winds in the Wadden Sea area during late summer and autumn blow predominantly from the West and the South. These winds induce a "migration" along the coast in a western (or southern) direction, which is the result of the gulls' preference for flying into the wind. This would mean that recoveries could be expected mainly from places to the West and South. Indeed, the Dutch ringing data show a slight predominance of recoveries from a southwestern direction, but the German data (Drost & Schilling 1940, Goethe 1956) show slightly more recoveries from an eastern direction. In the second place, adjacent colonies sometimes show differences in the direction from which recoveries are reported: for some colonies more birds are reported from the West, for others more from the East. This picture would be impossible if the dispersal of the Herring Gulls was determitned by a "migration" under the influence of the wind. In my opinion, these differences are to be attributed to the location of the colonies with regard to favourable feeding areas (cf. Olsson 1958, and also Fordham 1968 for the related Dominican Gull *Larus dominicanus* of the southern hemisphere).

According to some authors (Drost & Schilling 1940, Gross 1940, Eykman et al. 1949, Woodbury & Knight 1951, Goethe 1956, Hofslund 1959, Smith 1959), the Herring Gull shows a tendency toward greater dispersal in the first autumn and winter than in subsequent years. But data of other authors

Table 1. Distances from ringing locality in November–January of Herring Gulls ringed as chicks on the Dutch Frisian Islands from 1950 onward and recovered up to 1 January 1969

Year-class	Distances from ringing locality (in km)										Total	
	0–50		51–100		101–150		151–200		> 200			
1st	84	(57%)	36	(24%)	16	(11%)	4	(3%)	7	(5%)	147	(100%)
2nd	18	(56%)	7	(20%)	5	(20%)	1	(2%)	1	(2%)	32	(100%)
3rd	5		1		3		—		—		9	
4th	2		2		1		—		1		6	
5th	3	(50%)	1	(23%)	1	(13%)	—	(10%)	—	(3%)	5	(100%)
6th and older	10		4		2		3		—		19	
Total	122	(56%)	51	(23%)	28	(13%)	8	(4%)	9	(4%)	218	(100%)

Table 2. Distances from ringing locality in November–January of Herring Gulls ringed as chicks on the Dutch Frisian Islands before 1950 and recovered up to 1 January 1969

Year-class	Distances from ringing locality (in km)										Total	
	0–50		51–100		101–150		151–200		> 200			
1st	39	(55%)	9	(13%)	5	(7%)	2	(3%)	16	(23%)	71	(100%)
2nd	3	(38%)	4	(31%)	1	(15%)	—		2	(15%)	10	(100%)
3rd	2		—		1		—		—		3	
4th	—		—		2		—		—		2	
5th	1	(45%)	—	(20%)	—	(25%)	—		1	(10%)	2	(100%)
6th and older	8		4		3		—		1		16	
Total	53	(51%)	17	(16%)	12	(12%)	2	(2%)	20	(19%)	104	(100%)

(Paludan 1953, Harris 1964a) indicate that this does not hold everywhere, which is confirmed by our data (Table 1). However, comparison of the various year-classes is not entirely justified (this also holds for the literature cited), since not all the gulls return to their original colony to breed; furthermore, they do not return to the breeding grounds at all during their first summer, and only some of them do so in their second. Consequently, dispersal does not start for all ages from the same place. However, so few sub-adult and adult birds are ringed at the breeding colonies that a better comparison cannot be made.

The data mentioned above differ appreciably from the ringing results for The Netherlands (through 1941) given by Eykman et al. (1949). Of the 399 first-year gulls recovered between September and April, 138 (34.6%) came from other countries; for the 108 second- and third-year birds this number was 21 (19.4%), and for the 95 fourth-year and older birds 12 (12.6%). The differences between the three age-groups are significant (χ^2 test, $P<0.001$). In the first decades of the present century, thus, relatively more Herring Gulls were recovered from other countries in their first autumn and winter than in the same seasons at later ages. Table 2 shows that the data from the Dutch Frisian Islands point in the same direction, although the difference in the number of recoveries at more than 150 km from the ringing locality between first-year and older birds is not significant (χ^2test, $P>0.05$).

In connection with these data, I made a comparison (Table 3), for the first-year, sub-adult, and adult gulls, of the recoveries in the months of November–January of birds ringed before and after 1950. The birds in their first year show a significant difference (χ^2 test, $0.001<P<0.005$). For the sub-adult and adult gulls, the null hypothesis of no difference could not be rejected (Fisher's Exact Probability test, for both cases, $P \gg 0.05$). It may be concluded from this that in former years only the first-year birds were recovered further from the breeding grounds than at present. The difference between then and now could, of course, be due to a difference in the chance of recovery. Since many of the recoveries in other countries concern birds that had been shot, such a difference would depend mainly on differences in hunting intensity, but it hardly seems likely that hunting would have decreased so strongly in these countries since 1950. I therefore assume that during the last twenty years the first-year gulls actually have not moved as far away from their birthplaces as in the preceding period.

Because it is not likely that the sudden change in the migratory habit of these birds has a genetic basis, a change in the environmental conditions must be responsible for this phenomenon. During the 1950s and early 1960s, intensive control of the Herring Gull was applied in The Netherlands. In some years on the Frisian Islands alone, 2,000 to 3,000 breeding birds were killed, and reproduction was restricted as much as possible (Mörzer Bruyns 1958, unpublished reports of the State Institute for Nature Conservation Research). As a result of this decimation, the food situation after the breeding season

Table 3. Distances from ringing locality in November–January of Herring Gulls ringed as chicks on the Dutch Frisian Islands and recovered up to 1 January 1969, in relation to period of ringing

Distances from ringing locality (in km)	Year-class					
	1st		2nd + 3rd		4th and older	
	Ringed before 1950	Ringed after 1949	Ringed before 1950	Ringed after 1949	Ringed before 1950	Ringed after 1949
0– 50	39 (55%)	84 (57%)	5 (38%)	23 (56%)	9 (45%)	15 (50%)
51–100	9 (13%)	36 (24%)	4 (31%)	8 (20%)	4 (20%)	7 (23%)
101–150	5 (7%)	16 (11%)	2 (15%)	8 (20%)	5 (25%)	4 (13%)
151–200	2 (3%)	4 (3%)		1 (2%)		3 (10%)
> 200	16 (23%)	7 (5%)	2 (15%)	1 (2%)	2 (10%)	1 (3%)
Total number of recoveries	71	147	13	41	20	30

was relatively more favourable in those years than it had been before. It is conceivable that the few surviving young birds found so much food in the Wadden Sea area and its vicinity that the migratory tendency was weakened. The examples given by Olsson (1958) indicate that Herring Gulls tend to stay in places where feeding conditions are favourable, and move further away when conditions are unfavourable (cf. also Fordham 1968 for the Dominican Gull).

Gull control was terminated in The Netherlands in 1966. Although there are too few data covering recent years to permit the drawing of conclusions, I have the impression that at present the young birds are once again being recovered at greater distances from the colony than during the two decades before 1967.

3.4. AGE OF FIRST BREEDING

Most bird species start breeding when about one year old. The Herring Gull, however, shows what is often called a deferred maturity; the first gulls do not start breeding before the end of their third year. According to Drost, Focke & Freytag (1961), however, most of the gulls breed for the first time at the age of four or five years.

Our data point in the same direction. The recoveries for the period between May 1st and July 15th in the Fifties and Sixties pertain mainly to birds killed in the breeding colonies during the Herring Gull control program. In view of the control method applied (the placement near the nest of poisoned eggs) it seems likely that most of the birds killed in this way were indeed breeding birds. If all gulls start breeding at the same age (e.g. at the end of their third year), the number of recoveries should decrease in each successive year, other factors being equal. Of the gulls ringed as chicks on the Dutch Frisian Islands from 1950 onward, 39 were recovered between May 1st and July 15th of their third year, 62 in the same period of the fourth year, and 112 in the same period of the fifth year. These data show that in the Dutch Wadden Sea area, too, most of the gulls do not start breeding until they are four or five years old.

3.5. ATTACHMENT OF BREEDING GULLS TO COLONY OF ORIGIN

Many bird species return to their native area to breed. To a rather high degree this also holds for the Herring Gull (Gross 1940, Eykman et al. 1949, Drost 1953, 1958, Tinbergen 1953, Goethe 1956, Olsson 1958, Drost, Focke & Freytag 1961).

Table 4. Location of recoveries between 1 May and 15 July, in relation to ringing locality, of fourth-year and older Herring Gulls ringed as chicks on the Dutch Frisian Islands from 1950 onward and recovered up to 16 July 1968

Ringing locality	Location of recovery											
	Belgium and Ireland	western part of The Netherlands	Texel	Vlieland	Terschelling	Ameland	Schiermonnikoog	Rottumeroog	northeastern part of The Netherlands	German Frisian Islands	other parts of Germany and Denmark	Total number of recoveries
Texel	1	20	[76]	30	6	1			9		1	144
Vlieland		1	2	[11]		1						15
Terschelling		4	13	27	[38]	9	22		10	13	2	138
Ameland			2	1	1	[1]						5
Schiermonnikoog	1	2			1		[3]		1	3	1	12
Rottumeroog			2	1	2		1	[2]	3	10	2	23

Table 4 shows the data for gulls ringed as chicks on the Dutch Frisian Islands from 1950 onward and recovered between May 1st and July 15th from their fourth year onward. It is evident from these results that a proportion of the gulls returned to their native colonies to breed. However, relatively many birds joined other, usually nearby, colonies. During the Fifties and early Sixties, intensive control measures were applied on the Dutch Frisian Islands in the breeding season of the Herring Gull. In all probability, the relatively strong dispersal of the gulls was promoted by the intensive control measures taken during this period. During the Thirties and Fourties the species was controlled less intensively than in the Fifties, but nevertheless regularly, so that only the recoveries dating from before 1930 offer a reliable basis for comparison. Unfortunately, there are too few recoveries from this period to permit analysis.

3.6. SEASONAL FLUCTUATIONS IN NUMBER OF RECOVERIES

Figure 7 shows the seasonal distributions of the recoveries in relation to the age of the birds recovered. To make direct comparison possible between the unequal periods of the year, the number of recoveries per 100 days is indicated on the ordinate. It is evident from Figure 7 that there are apprecia-ble differences in the distribution of the recoveries between the various age-classes. For first-year gulls there is a distinct peak in September–October

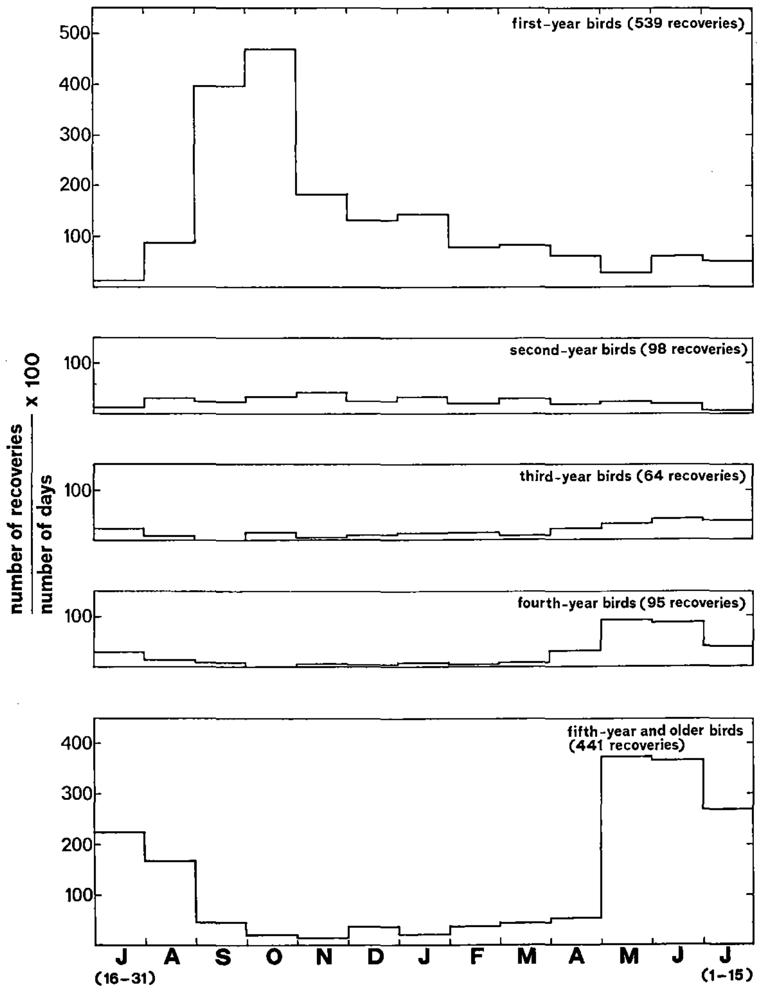


Fig. 7. Seasonal distributions of the recoveries of Herring Gulls ringed as chicks on the Dutch Frisian Islands from 1950 onward and recovered up to 1 January 1969, in relation to age.

(end of the dispersal period). For second- and third-year birds the recoveries are distributed rather evenly over the year, possibly with a slight increase in May–July (breeding season) of the third year. From their fourth year onward most gulls are recovered during the breeding season.

The recoveries include not only dead and sick birds but also intentionally captured live birds. But there are no indications that the latter source of recoveries influences the seasonal fluctuations, and Figure 7 may therefore be taken as giving an approximation of the distribution of the mortality over the year.

Harris (1964a) found the same preponderance of recoveries of young Herring Gulls in late summer and autumn in England, and it seems to occur in many bird species shortly after the breeding season. Woodbury & Knight (1951) found, however, that in the Western Gull *Larus occidentalis* and the Glaucous-winged Gull *Larus glaucescens* of the western coast of North America, the highest mortality of first-year birds was delayed until the late autumn and winter months. This indicates that the high mortality of juvenile birds shortly after the breeding season, found in most species, is primarily related to bad environmental conditions.

It is not probable that the mortality of first-year gulls in The Netherlands in late summer and early autumn is the result of predation. Natural predators are almost entirely lacking in this country, and human interference outside the breeding season is also very limited there. The peak in recoveries of first-year gulls coincides with an increase in the number of gulls brought by the public to laboratories and institutes. In many cases these birds are underweight and ill, and often die shortly afterwards (C. Swennen, pers. comm.). Although the possibility cannot be ruled out that disease is the primary cause of death in such cases, this does not seem very likely to me. Since the peak in mortality coincides with the end of the dispersal period, I suggest that the high mortality is the result of a high feeding pressure during the dispersal period as a result of an increased number of gulls. Because of their inexperience and their lack of familiarity with the local situations in the dispersal area, it is obvious that the first-year gulls especially suffer from this feeding pressure.

A preponderance of recoveries of adult gulls in the breeding season was also observed in Britain by Harris (1964a). To my knowledge, no intensive control measures have been taken against adult gulls in the British Isles. Therefore, the preponderance of recoveries of adult gulls during the breeding season in The Netherlands is probably not due primarily to the intensive control program during the breeding season in the Fifties and early Sixties, although it may have amplified this tendency. There is some evidence that in other bird species breeding also increases the mortality of the parents (see Lack 1968).

4. NUMBERS OF GULLS PRESENT IN THE DIFFERENT PARTS OF THE DISTRIBUTION AREA

4.1. INTRODUCTION

The ringing data indicate that not only during but also after the breeding season a large part of the population stays within a relatively small area. This made it possible to use counts to determine the distribution over the dispersal area throughout the year quantitatively.

From the combined results of the various counts the share of refuse in the total food supply could be estimated. Outside the breeding season this approach to the food problem is preferable to such conventional methods as analyses of stomach contents, pellets, and faeces, because in this period the gulls do not return to a central place and it is therefore almost impossible to take a random sample of the population. (The same of course holds during the breeding season for the non-breeding gulls remaining outside the gulleries.)

For practical reasons I limited the area to be investigated to the Dutch Wadden Sea area and the mainland of the provinces of Friesland, Groningen, and Drente. Since these areas comprise the most important part of the dispersal area of the Herring Gulls of the Dutch Frisian Islands, it may be assumed that the results hold approximately for the entire population of these islands.

4.2. POPULATION IN THE WADDEN SEA AREA

4.2.1. Periodical counts of gulls present on Terschelling and Vlieland

In the Wadden Sea area the daily activity pattern of the Herring Gull is determined almost entirely by the rhythm of the tides. Twice a day a large part of the bottom of the Wadden Sea emerges at low tide. The exposed mudflats, together with the North Sea beaches, form the most important source of food for the Herring Gulls in this area.

When the incoming tide drives the birds from the flats and beaches they shift to areas above the high-water level, where they wait in groups for the next low-water period. Since almost all the birds follow this pattern, counts made at these places around high tide give a good picture of the numbers present in the area.

To obtain an impression of the numerical variations in the Wadden Sea area, counts were made regularly around high tide, from September 1966 to October 1968, of the birds present on Terschelling and Vlieland.

4.2.1.1. Methods

The time available for counts during the high-water period is quite short, because the highest number of resting birds is only present for a few hours.

In practice, however, it could be lengthened somewhat by choosing places for the beginning and end of the observation round, where resting and foraging areas were close together.

At each count all areas were visited in which gulls could be expected to be present in appreciable numbers. On Terschelling these areas included the Noordsvaarder, the North Sea beach, the Boschplaat (including its gulleries), the polders, the harbour and its vicinity, and the refuse dump with some nearby pools in the dunes. In 1967–1968 I found a resting place near the refuse dump, occupied at peak times by several hundreds of birds, which had been overlooked during the 1966–1967 season. In the autumn of 1966 no counts were made on the mudflat side of the Boschplaat, but observations in later years showed that no appreciable numbers were present there at that time of the year. Since it was found in 1966–1967 that the numbers present on the western part of the Noordsvaarder were low (which was confirmed by checks made in 1967–1968), only the eastern part of this sandflat was included in subsequent seasons.

On Vlieland, counts were made in the following areas: the Vliehors, the North Sea beach, the harbour and its surroundings, the refuse dump, the Wadden Sea along the southern side of the island, the Kroonspolders, and the few small meadows and the breeding colonies in the dunes. Because the Vliehors is used for military exercises, the westernmost parts of this sandflat could not be included in the counts, but as far as is known no appreciable numbers were present there.

On Vlieland, all the counts could be made during one high-tide period. On Terschelling, where the distances are greater and several large areas could only be covered by foot, usually two but sometimes even three or four high-tide periods were required to complete the counts. Although I have no exact data on the extent to which birds changed their resting places, I feel justified in concluding from the stable location of these places and the rather constant numbers found there on successive days that not many birds were missed or counted more than once. In Figure 8, for these multi-day counts the middle day is taken as date of counting.

4.2.1.2. Seasonal variations

It is evident from Figure 8 that the number of gulls on Terschelling decreased sharply in August–September. This trend holds for all three years. Although no data are available for August of 1966, it can be estimated from the number of breeding birds (roughly 12,000) and reproductive success (low due to gull control, but at least a few thousand young fledged) that the number of Herring Gulls at the end of that breeding season must have amounted to at least 15,000, quite apart from the number of non-breeding gulls for which no data are available.

In 1967 and 1968 there were again at least 12,000 breeding birds, and

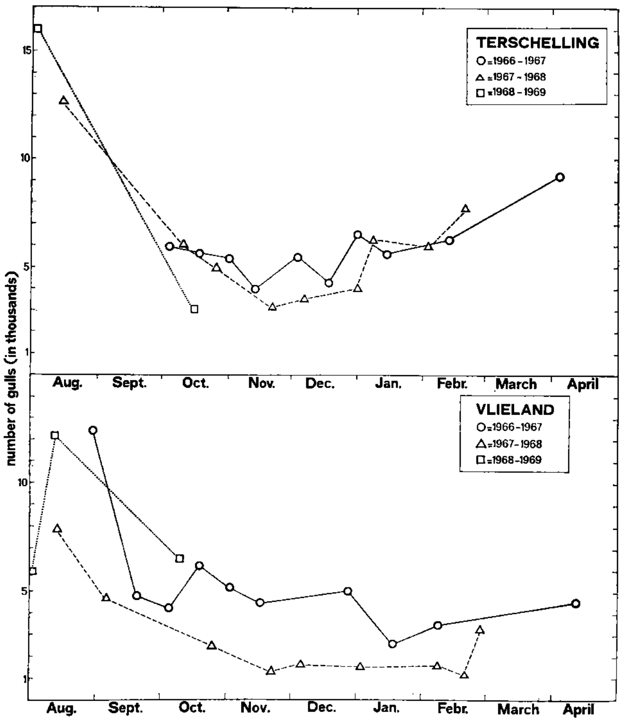


Fig. 8. Seasonal changes in the numbers of Herring Gulls present during high tide on Terschelling and Vlieland in 1966–1968. The second census for August 1968 for Vlieland is taken from Odink (1969).

as a result of the termination of gull control measures, almost 10,000 young fledged. This means that at the end of the breeding season in both years there were at least 20,000 to 25,000 birds. But on the 1st and 3rd of August in 1968, only 16,133 gulls were counted, and on the 15th and 16th of August in 1967 only 12,713. This means that a decrease must have already started in July; it must be kept in mind that the majority of the young cannot fly before the end of July, so that this first departure must have consisted mainly of non-breeding gulls or birds having lost their eggs or young (cf. also 4.3.2.2).

In both 1966 and 1967, there was a further numerical reduction during October and November. In both these years the lowest numbers were reached in November and December and an increase occurred shortly after the end of the year. The duration of this increase is not known. The data collected in 1967, in which year I counted 9,283 Herring Gulls on the island in April and estimated that in May the total breeding population included about 12,000 birds, suggest that in the middle of April not all the birds had returned to the gulleries yet, but these data are misleading because in April I underestimated the number in the colony, so that the total number given for this month is too low (but see also 4.3.2.2).

The results obtained on Vlieland differ to some extent from the Terschelling data (Fig. 8). In all three years higher numbers were counted in August than could have been expected from the numbers of breeding birds and fledged young.

On the 30th of August in 1966, 12,605 gulls were counted. In that year about 1,600 pairs bred on Vlieland and, due to gull control, not more than 1,000 young fledged, so that at the end of the breeding season a population, including the non-breeding gulls (estimated at not more than a few thousand), of at most 6,000 birds was to be expected. This means that at the end of August at least 6,000 birds must have come from elsewhere to the island.

In 1967, the number of breeding pairs amounted to about 1,400 and not more than 2,000 young fledged. The number of non-breeding gulls probably did not amount to more than one to two thousand, so that on the 14th of August, when 7,895 gulls were counted, at least one to two thousand birds from elsewhere must have been present.

In 1968, about 1,900 pairs bred (D. Buitenhuis, pers. comm.), and at most 3,000 young fledged. With an estimated couple of thousand non-breeding gulls, the expected population at the end of the breeding season would be maximally 9,000 birds. On the 2nd of August, 5,928 Herring Gulls were counted, thus about one-third less than expected. But on the 12th of August, according to Odink (1969), the counts showed at least 12,240 Herring Gulls, which means an increase of more than 6,000 birds after the beginning of August. The observations made in this year suggest that a decrease did occur after the breeding season but was soon offset by an influx of birds from elsewhere. The ringing data show that the greater part of the population does not disperse more than 100 km from the ringing locality. Since Terschelling is the only place within a radius of 100 km from Vlieland with a breeding population of more than 1,500 pairs (about 6,000 pairs in each of the three years of the study), I assume that these birds originated mainly from there.

But in all years the increase was followed in August–September by a sharp decrease, comparable with the situation on Terschelling. In 1967 (as in 1966 and 1967 on Terschelling) the numbers continued to drop in October and November. In 1966, this decrease did not occur and up to the end of December the numbers fluctuated between 4,189 and 6,208, a sharp decrease falling in January. In both 1966 and 1967 in the autumn months the highest number was found on the North Sea beach, so that these birds must have been entirely responsible for the differences between these years. The feeding area of these gulls is restricted to the littoral and sublittoral zones on the beach, where the most important preys are Mussels *Mytilus edulis* and Starfish *Asterias rubens* on the stone groynes. It is possible that the food situation on the beach was more favourable in the autumn of 1966 than in the next year; this would explain the differences, but I have no data on this point.

In 1967, as on Terschelling, a slow numerical increase started in January. In 1968, in contrast to Terschelling, the numbers remained low until an increase started in the last week of February.

4.2.1.3. Fluctuations in the winter

The months of December and January show strong fluctuations in the numbers of gulls present, probably due mainly to weather conditions. On Terschelling on the 3rd and 4th of December in 1966, after three days of a westerly storm, the counts showed 5,540 Herring Gulls as against 4,040 and 4,329 on 13th and 14th November and 18th–20th December, respectively.

During short periods of light frost, too, the numbers were higher than usual. For example, at the end of December in 1966 on Terschelling the counts showed 6,603 Herring Gulls as against 4,329 two weeks earlier and 5,652 two weeks later. On Vlieland, 5,105 Herring Gulls were counted at the end of December 1966 as against 2,576 about two weeks later. Large numbers of Herring Gulls were also seen on the other Frisian Islands at the end of December (see 4.2.2.2).

In 1968 I observed an increase of this kind twice. On Vlieland, 1,520 Herring Gulls were counted on the 3rd of January, and the next day the temperature dropped slightly below freezing. Two days later, 2,640 Herring Gulls were counted on just the beach and the mudflat side of the island (no counts were made on the rest of the island at that time). During the same week an increase was also observed on Terschelling, where I counted 4,064 Herring Gulls on 1st and 2nd January and exactly a week later 6,290. In all likelihood the increase under storm conditions is to be attributed to birds that under normal conditions forage on the North Sea. According to data collected by Swennen (pers. comm.), foraging Herring Gulls are seen on the North Sea up to 20 km from the coast. Being independent of the tidal rhythm, these birds normally do not fly to the islands during rising tide and therefore cannot be observed from the coast. In rough weather they cannot rest at sea, however, and then probably do come to the islands (cf. also Goethe 1939 and Tinbergen 1952).

In western Europe, periods of frost usually coincide with easterly winds. Under these conditions the numbers of Herring Gulls found at the refuse dumps on the mainland reach their lowest winter levels (4.3.2.2). It therefore seems probable that the high numbers on the islands during freezing weather are related to the low numbers seen at the dumps on the mainland.

The changes in the numbers of Herring Gulls in the Wadden Sea area can be briefly described as follows. Immediately after the breeding season there is a marked dispersal leading to a sharp drop in the numbers of gulls on the islands (although locally this dispersal may cause a temporary increase). The lowest numbers are reached between November and February. Under the influence of the weather, however, the numbers can fluctuate greatly. In winter the highest numbers are found under storm conditions and during light frost. Shortly after the end of the year there is a gradual increase to the breeding season level.

4.2.2. Simultaneous counts throughout the area

To obtain an impression of the total population in the Wadden Sea area, a few more or less simultaneous counts were made over almost the entire region.

4.2.2.1. Methods

These counts were made around high tide (see 4.2.1.1). The Herring Gulls on the large islands were counted partly from the ground and partly from a small aeroplane, all those on the small islands and the open water of the Wadden Sea from an aeroplane.

The aeroplane always carried two observers, to permit observations on both sides. Over the Wadden Sea, the width of the strip in which individual birds could still be seen amounted to roughly 0.5 to 1 km, but large concentrations were discernible at greater distances, and the choice of the route makes it unlikely that any large groups were missed.

Because of military exercises, large parts of the area were closed to civil aviation on weekdays and our observations therefore had to be confined to the weekends. In addition, flights had to be limited to days with good weather and on which high tide occurred in the middle of the day. As a result, a more or less simultaneous count of roughly the entire area could only be performed on two occasions. Together with the data from the end of August 1963 (Rooth 1966), therefore, we could draw on three simultaneous counts.

4.2.2.2. Results

The results of these counts are shown in Table 5. Rather unexpectedly, they show more or less similar total numbers. The numbers counted in December of 1966 on Terschelling and Vlieland are among the highest of that winter. Therefore, the winter census approximates roughly the maximum number present in the Wadden Sea area during that winter.

In the winter of 1966–1967 – on the basis of the numerical changes on Terschelling and Vlieland (see 4.2.1.2) I included in this period only the months of November through January – on Terschelling and Vlieland the lowest numbers counted were 4,040 and 2,576, respectively, totalling 6,616 Herring Gulls. The highest numbers reached in that winter were 6,603 and 5,200, respectively, totalling 11,803 birds. If we assume that the census of

Table 5. Numbers of Herring Gulls in the Dutch Wadden Sea area (counts made more or less simultaneously)

	23–8–1963 (Rooth 1966)	27–12–1966/4–1–1967 [1]	10/17–8–1967
Texel	1,700	6,160	11,935
Vlieland	4,750	5,105	7,895
Richel	2,000	(—) [3]	306
Griend	100	(41)	20
Terschelling	12,000	6,603	12,713
Ameland	3,000	12,598	1,381
Engelsmanplaat	3,000	(341)	1,345
Schiermonnikoog	2,850	3,250	1,789
Simonszand to Rottumeroog	3,000 [4]	≧ 776	820
Wadden Sea (open water)		187	67
Den Helder [2]	900 (Den Helder, Balgzand, Afsluitdijk)	321	
Balgzand		15	
Afsluitdijk			
coast of Friesland [2]		p.m.	≧ 270
Lauwerszee	73	75	
coast of Groningen [2]	p.m. [5]	790	
Dollart	15	(—)	
Total	33,388	36,262	38,541

[1]) Data between parentheses concern counts made on 17 and 18 December. These areas were not visited during the census at the end of the month.
[2]) Numbers for these areas concern only birds at high-tide refuge areas (not gulls in towns, at dumps, etc.).
[3]) — = no birds present.
[4]) plus 500 *L. argentatus* and *L. marinus* mixed.
[5]) 1,250 *L. argentatus* and *L. marinus* mixed.

December 1966 gives a picture of the normal distribution of the population over the Wadden Sea area, 32% of the entire population is found during high tide on Terschelling and Vlieland. This means for the entire population of the Wadden Sea area a "minimal" figure of $^{100}/_{32} \times 6{,}616 = 21{,}000$ and a "maximum" of $^{100}/_{32} \times 11{,}803 = 37{,}000$.

During the winter of 1967–1968 the lowest numbers seen on the two islands were 3,200 and 1,269, respectively or a total of 4,469, and the highest were respectively 6,290 and at least 2,640, totalling at least 8,930. For the entire population this means a "minimum" of 14,000 and a "maximum" of at least 28,000 gulls.

4.3. POPULATION ON THE MAINLAND OF THE PROVINCES OF FRIESLAND, GRONINGEN, AND DRENTE

4.3.1. Introduction

According to the ringing results, the distribution area of the population of the Frisian Islands reaches as far as the mainland of the northern part of The Netherlands throughout the year. The occurrence of the Herring Gull is almost entirely limited, however, to harbours, cities, villages, and refuse dumps, which made it possible to determine the changes in the number of gulls as well as the size of the population in this area rather accurately.

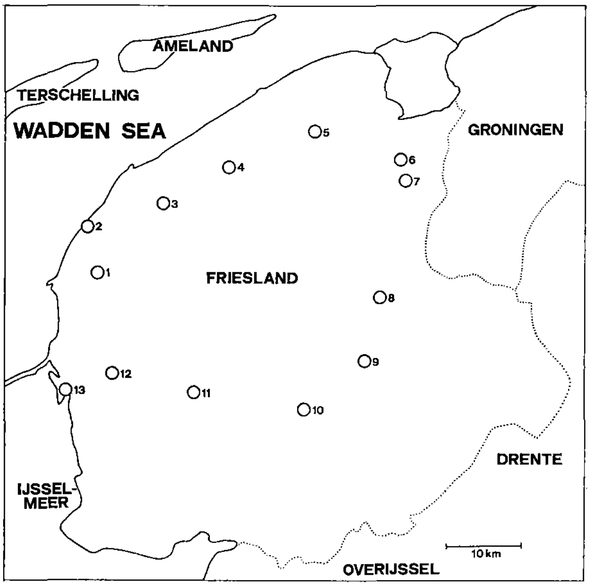


Fig. 9. Locations of the 13 refuse dumps in the province of Friesland at which counts were made regularly during 1967–1969. The dumps have been numbered in the sequence in which they were visited; numbering corresponds to that in Table 6.

4.3.2. Periodical counts of gulls present at thirteen refuse dumps in the province of Friesland

To obtain an impression of the fluctuations in the number of gulls on the mainland, I made counts regularly at 13 refuse dumps in Friesland from August 1967 through January 1969 (Fig. 9). Because the refuse dumps in this province form the most important source of food for the Herring Gull, it may reasonably be assumed that the fluctuations in the number of birds on the mainland as a whole correspond fairly closely to those observed at the dumps.

4.3.2.1. Methods

The counts at the refuse dumps were made in the sequence shown in Figure 9. In the beginning it took me more than 9 hours to make a complete count, but this could soon be reduced to between 5 and 7 hours. As a result, even in the winter months, when the numbers were not complete until 9.30 to 10 o'clock in the morning and the first gulls began to depart for the roosting areas at 3 or 4 o'clock in the afternoon, the counts could be made at all the dumps in one day.

The birds spent only a small part of the available time in active foraging,

Table 6. Fluctuations in the numbers of Herring Gulls at 13 refuse dumps on the mainland of the province of Friesland

Dump nr.[1]	Municipality	Date 1967			1968													1969
		17-8	6-10	10-11	12-1	2-2	23-2	15-3	5-4	3-5	28-5	1-7	26-7	16-8	13-9	11-10	15-11	17-1
1	Franekeradeel	1	25	40	(13)[2]	10	38	14	3	0	2	0	2	13	9	50	23	22
2	Barradeel	92	262	218	150	207	160	79	138	10	9	8	76	290	153	282	120	267
3	Het Bildt and Leeuwarderadeel	308	295	300	300	750	300	320	400	35	110	41	100	250	130	330	190	450
4	Ferwerderadeel	325	360	590	350	700	180	400	340	200	180	55	230	550	220	700	140	780
5	Dokkum	150	350	500	240	790	180	200	600	145	70	24	150	230	50	440	250	350
6	Kollumerland	44	60	120	(39)	40	1	140	10	20	0	2	70	60	100	80	130	170
7	Achtkarspelen	70	46	200	(86)	340	10	90	50	13	35	26	30	140	36	200	220	304
8	Smallingerland	(367)150	(530)230	860	360	890	310	670	750	140	140	33	70	350	250	470	400	600
9	Opsterland	10	90	217	115	400	180	230	300	28	4	3	50	68	20	130	110	0
10	Heerenveen	(368) 30	(532)200	620	(435)	980	390	1,100	400	55	40	11	70	145	140	380	530	640
11	Sneek and Wymbritseradeel	140	95	330	(93)	40	40	190	150	3	0	28	35	150	45	100	40	25
12	Bolsward	25	70	55	(93)	230	170	190	100	4	15	18	30	40	39	75	140	100
13	Wonseradeel	62	120	87	(45)	100	85	40	50	23	15	14	45	210	105	200	40	120
	Total	1,407 (1,962)	2,203 (2,835)	4,137	1,515 (2,319)	5,477	2,044	3,663	3,291	676	620	263	958	2,496	1,297	3,437	2,333	3,828

[1]) Numbering as in Fig. 9.
[2]) The corrected numbers of gulls are given between parentheses.

passing most of the day on the farmlands in the immediate vicinity of the refuse dumps, digesting what they had eaten and waiting for the arrival of the full garbage trucks or for periods when they could forage undisturbed. Gulls were also almost always found on nearby lakes and waterways (drinking, bathing). Consequently, there were usually relatively few birds actually present at the dumps. In the fields the gulls formed easily observed groups and therefore their numbers could generally be counted accurately.

The data from the counts are given in Table 6 and Figure 10. The numbers for the refuse dumps in Smallingerland and Heerenveen in August and October of 1967 are underestimated because of observational difficulties, and have been corrected to make comparison with the other results possible. The corrections are based on the ratio found during the other winter months between the numbers of birds at these two dumps and the total numbers counted. A similar calculation was made for the 12th of January 1968, when some of the dumps were made inaccessible by a heavy snowfall. The corrected numbers, which are shown between parentheses in Table 6, were used for Figures 10 and 11.

4.3.2.2. Seasonal variations

It can be seen from Figure 10 that the lowest numbers were found during the breeding season. Immediately thereafter there was an increase, and the winter level was reached as early as October. Wide fluctuations occurred between October and April. During April there was a rapid decrease to the low summer level.

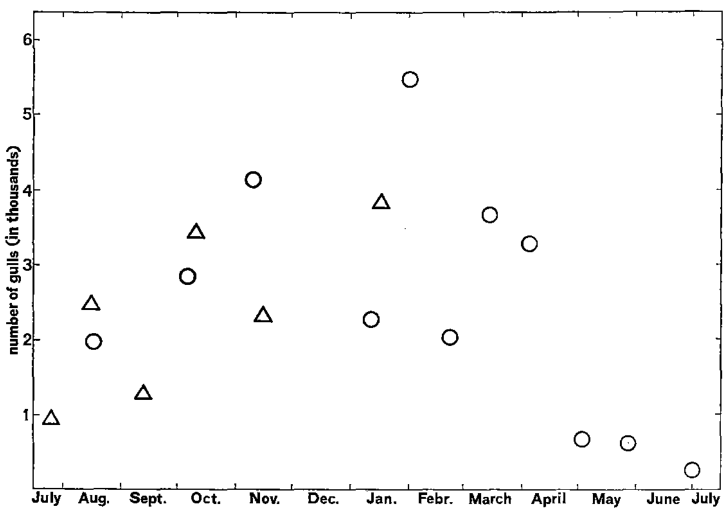


Fig. 10. Seasonal variations in the total number of Herring Gulls present at 13 refuse dumps in the province of Friesland during 1967–1968 (circles) and 1968–1969 (triangles).

The gulls seen at the dumps between May and the middle of July included both adult and sub-adult but few first-year birds. Some of the adults visiting the dumps in the breeding season are breeding birds from the islands, as could be determined experimentally (5.3.3.5).

The increase in the latter half of July was probably due to non-breeding gulls or unsuccessful breeders. In any case it was not caused by an exodus of parents and their young from the gulleries, since on the 26th of July 1968 only 4 young were counted at the dumps. In August of both years, however, I saw young at all but one dump.

It is noteworthy that an appreciable decrease was not noticeable until April, whereas on the Frisian Islands an increase, albeit small, started as early as January (4.2.1.2).

4.3.2.3. Fluctuations in the winter

All 13 refuse dumps included in this study are situated at a short distance from the coast, the longest distance amounting to about 40 km. Depending on wind force and direction, this means a flight of only 0.6 to 1.3 hours for a Herring Gull (for data on flight-speed, see Table 7 and Meinertzhagen 1955). An attempt was therefore made to find out whether the numerical fluctuations observed at the dumps in the winter period show any relationship with the feeding conditions on the mudflats of the Wadden Sea.

Table 7. Flight-speed of Herring Gulls going to roost

Date	Wind		Flight-speed [1]) (km/h)		Number of counts
	Direction (degrees) [2])	Speed (km/h)	average	min.–max.	
21–12–1968	120	14.4	33.3	31.2–38.3	9
11–01–1969	308	18.3	50.2	45.0–53.7	4
25–01–1969	10	17.5	61.7	51.4–72.0	8
8–02–1969	84	71.3	32.5	29.8–35.0	5

[1]) The measurements were made on the Texel beach over a distance of 400 m (21 December) and 200 m (other dates) by two observers using walkie-talkies and a stopwatch.

[2]) Counting clock-wise: 0° = flying with a following wind, 180° = flying directly into the wind, and so on.

In the winter months the food on the flats consists mainly of Cockles *Cardium edule* (5.4), whose distribution is limited to the lower parts of the flats. Feeding possibilities for gulls therefore depend both on the area of exposed Cockle beds and the duration of exposure. Both factors, however, are closely related to each other. According to Kristensen (1957), Cockle density starts to decrease at places exposed for 6 to 8 hours per tide under normal conditions and is very low at places exposed for more than 8 hours.

Thus, there are only limited feeding possibilities for gulls on the parts of the flats exposed for more than 6 hours per tide, which includes almost all the areas lying above 0 cm NAP (Dutch Ordnance Level). To simplify matters, I have assumed that the Cockle beds become accessible to the gulls when the water falls below this level. It is clear that in this case the area of exposed Cockle beds and the duration of exposure will increase the longer the water remains below 0 cm NAP. Therefore, the length of the latter period may be taken as a measure of the feeding possibilities for the gulls on the flats. The length of this period during the low-water interval falling mainly within the period of daylight is shown in Table 8 under X_1, according to the situation at Harlingen. These data were put at my disposal by the Rijkswaterstaat at The Hague.

Table 8. Number of Herring Gulls at 13 refuse dumps in the province of Friesland during October–April in relation to environmental conditions in the Wadden Sea

Date	Number of gulls (N)	Time of low tide [1]) (hrs G.M.T.)	X_1 [2])	X_2 [2])	Highest water-level during previous high tide (cm above/ below NAP) [1])	Wind during previous night [1]) (at 00, 03, and 06 hrs G.M.T.) Direction	Force (Beaufort scale)
23–02–1968	2,044	11.31	9.8	3.5	+ 18	ENE	5
12–01–1968	2,319	14.05	7.6	0.5	+ 69	N-NE'N	4
15–11–1968	2,333	11.48	13.0	1.5	— 9	E'S-ESE	6
6–10–1967	2,835	06.34	4.7	5.3	+ 157	W	4–6
5–04–1968	3,291	08.47	5.6	5.6	+ 93	WSW-W	1–3
11–10–1968	3,437	07.24	5.7	5.8	+ 90	W-W'N	4
15–03–1968	3,663	17.54	4.5	4.7	+ 100	S'W-SW'W	5–7
17–01–1969	3,828	16.03	5.7	2.6	+ 103	S'W-SSW	5–6
10–11–1967	4,137	10.53	4.1	3.5	+ 150	NW	5–6
2–02–1968	5,477	07.47	3.5	6.1	+ 177	SW-W	5–6

[1]) High and low tide refer to Harlingen, wind direction and wind force to West-Terschelling.

[2]) X_1 = duration of period that water-level remained below 0 cm NAP during low tide (in hours), X_2 = duration of overlapping between high-water period and period of census (in hours).

Because foraging on the flats is limited to a rather short period around low tide, it is possible that during the day some of the gulls shift from the mudflats to the dumps during the period of high tide. This possibility must be taken into consideration, because I was not always able to choose the day of the counts in such a way that the periods of high and low water always fell at about the same time of the day.

Since the interval between two successive low-water periods is well over 12 hours and the maximum length of the foraging period 6 hours (see above), we can put the duration of the high-water resting period for the gulls at 6 to 7 hours. For the sake of simplicity, I took a time of 6.5 hours (3.25 hours before and 3.25 hours after high tide).

The refuse dumps were visited in a fixed sequence. In the winters of both 1967–1968 and 1968–1969, there was no significant correlation between this sequence and the average number of gulls at the dumps (Spearman's rank correlation test, $P >> 0.1$). The dumps with "many" and "few" gulls were therefore distributed more or less randomly over the day. If the assumption that during high tide some of the birds shift from the mudflats to the dumps is correct, it is clear that the effect on the numbers counted would become stronger the more the high-water period overlaps the counting period. This overlapping period was taken as index for the effect of the tidal rhythm on the numbers, and is shown in Table 8 under X_2.

The relationship between the number of gulls at the dumps (N) and X_1 and X_2 was analysed by means of a multiple regression analysis, taking as model $N_i = a + bX_{1i} + cX_{2i} + e_i$ $(i = 1, \ldots, k)$, in which a, b, and c are unknown constants and e_i $(i = 1, \ldots, k)$ a normally distributed random variable with zero expectation and unknown variance; the e_i are assumed to be stochastically independent.

This model is based on the assumption that the relation between the dependent variable N and the independent variables X_1 and X_2 is linear. This is only an approximation. Application of the more suitable partial rank correlation analysis (Kendall 1948) would have been advisable, but was not attractive in this case involving more than four observations (see Moran 1951).

The estimations of the regression coefficients and the calculated T values (which under the null hypothesis $b = 0$ or $c = 0$, respectively, follow a Student distribution) are:

$$a = +4{,}579$$
$$b = -234, \; T = -2.09 \; (0.025 < P < 0.05)$$
$$c = +0.02, \; T = +0.39 \; (P > 0.25).$$

On the basis of these results, only the null hypothesis $b = 0$ is rejected. Therefore, the tidal rhythm may be assumed to have no demonstrable influence on the number of gulls present at the dumps. But the period in which the water remains below 0 cm NAP during the low-water period (and therefore the area of the Cockle beds exposed and the length of exposure of these beds) has a negative effect on the number of gulls at the dumps. The larger the area of exposed Cockle beds and the longer the duration of exposure (and thus the greater the feeding possibilities for gulls on the mudflats) the smaller the numbers at the dumps (see also Fig. 11).

Although the data from the winter of 1968–1969 are limited, the numbers of gulls at the dumps seem to have been a little higher in that winter than in the preceding one (Fig. 11).

As already mentioned, the dumps were visited in a fixed sequence, the first six always before 13.15 hrs, the others after 12.15 hrs. Because there is a positive correlation between the numbers at the two groups of dumps (Spearman's rank correlation test, $P < 0.025$), I assume that the gulls resorting from the flats to the dumps do so early in the day (thus in many cases

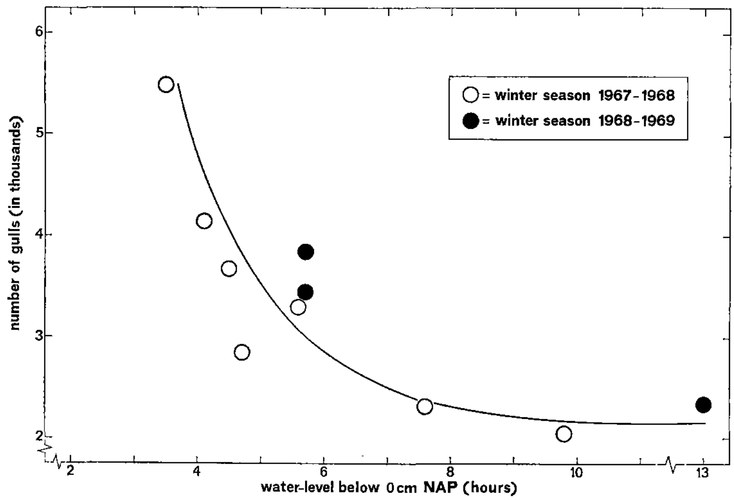


Fig. 11. Number of Herring Gulls present at 13 refuse dumps in the province of Friesland during October–April, in relation to the duration of the period that the water-level in the Wadden Sea remained below 0 cm NAP during low tide. (Line drawn by eye.)

long before the flats are exposed) and not in the course of the day. This raises the question of what stimuli are responsible for whether or not the gulls go to the flats early in the day to forage.

I first investigated the relation with the foraging conditions during the preceding low-water period; a correlation proved to be absent ($P >> 0.05$). This makes it necessary to determine what factors influence the length of the period during which the Cockle beds are exposed. The main factor here is the level reached by the preceding high tide, and secondly the rate at which the water flows through the tidal inlets in either direction. Per observation day, there is a distinct negative correlation ($P < 0.005$) between the level of the preceding high tide and the length of the period during which the water-level remains below 0 cm NAP (see Table 8). Since in 8 out of the 10 cases this high tide occurred during the night, the high-tide level could indeed serve as a stimulus, for instance through the covering of a part of the high-tide refuge areas. The rate at which the water flows through the tidal inlets is strongly influenced by the direction and force of the wind. With strong westerly winds the water enters the Wadden Sea more rapidly at flood tide and flows out of it with more difficulty. As a result, water accumulates in the Wadden Sea. Strong easterly winds have the opposite effect. It can be seen from Table 8 that the water-level during westerly winds indeed remained only briefly below 0 cm NAP, and that the long periods accompanied easterly winds. It is therefore also possible that the gulls make up their mind in the later part of the night, making allowance for direction and force of the wind.

It must be kept in mind that these birds are mainly local breeding birds, which can be assumed to be familiar with and to make use of local conditions.

4.3.2.4. Numerical differences between dumps

It can be seen from Table 6 that the numbers of gulls vary widely from dump to dump. The differences between the dumps are highly significant (Friedman's test, $P \ll 0.001$; incomplete counts omitted). From the fixed course of the flights from the roosting areas to the dumps and back it may be concluded that the dumps are visited by the same gulls over a long period.

It is obvious to assume that the occurrence is primarily determined by the available amount of food, although the attractiveness of a dump is also determined by the openness of the surrounding country, the character of the local vegetation, and the presence of suitable resting places and sufficient water (see Drury 1964).

It is not probable, however, that the differences in the numbers of gulls between the 13 dumps were caused by differences in the landscape, since in this respect the dumps differed little. Only those of Achtkarspelen, Opsterland, Heerenveen, and Bolsward were surrounded by trees, and since the birds at these dumps were not noticeably more shy than those at the other dumps this factor may be assumed to have had little influence on the numbers present.

No data are available concerning the amount of refuse brought to the various dumps, and I therefore took as measure the number of inhabitants of the respective municipalities (data obtained from the Centraal Bureau voor de Statistiek 1968). Because the effect can be expected to be maximal when the highest numbers of birds are present, I used the winter data only for the correlation calculations.

The correlation between the number of inhabitants and the number of gulls (average of 1967–1968 and 1968–1969 figures) is not significant (Spearman's rank correlation test, $P = 0.17$). The municipalities of Sneek/Wymbritseradeel and Wonseradeel, however, dump part of their refuse into an incinerator, leaving a smaller quantity for the gulls than would be expected from the number of inhabitants. It is therefore justifiable to leave these municipalities out of consideration, and then the correlation becomes almost significant ($P = 0.06$). I consider this to be an indication that the available amount of food indeed influences the distribution of the gulls (cf. also 4.3.3.3), and assume that this distribution is determined by competition for food during the dispersal period (August–September).

It is striking that the differences in numbers between the dumps are also seen in the months of May, June, and July, when the numbers of gulls at the dumps are low and therefore the amount of intraspecific competition is small. It seems likely that in April proportionally equal numbers of gulls depart from all dumps for the breeding sites. The attachment of the remaining gulls to the same dumps for long periods can uphold the same ratio between the dumps as in winter.

4.3.3. Census covering all refuse dumps in the three provinces

To obtain a basis for an estimate of the share taken by the dumps in the total food-supply of the winter population in the northern part of The Netherlands, I performed counts at all the dumps in the three northern provinces, with only a few exceptions, between the 12th and 23rd of December 1967.

4.3.3.1. Methods

The three provinces have a total of 104 dumps used for the disposal of garbage (Fig. 12) To facilitate this study, information about the location of the dumps was obtained from the municipal authorities in advance. Thanks to the exact description of the local situation provided by these authorities, the census went very smoothly.

The gulls were counted in the same way as applied for the periodical counts in Friesland (4.3.2.1). However, near the compost works of the Vuilafvoermaatschappij N.V. (VAM) in Drente, where the refuse of almost 1 million

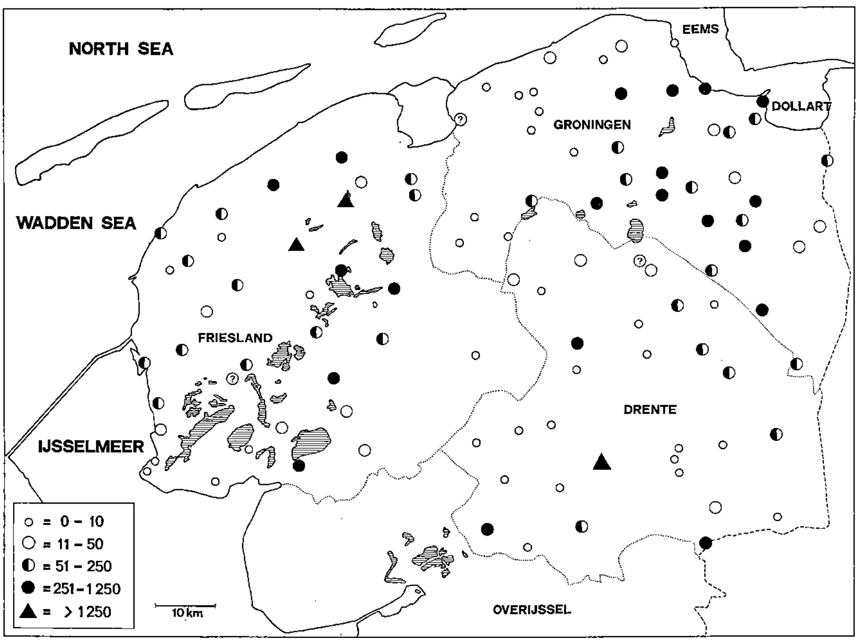


Fig. 12. Locations of the refuse dumps in the provinces of Friesland, Groningen, and Drente, and the numbers of Herring Gulls counted there during the census of December 1967.

people is processed and more than 8,000 Herring Gulls were present, the gulls were counted during the departure of the birds for the roosting areas. The birds could be counted with great accuracy because they departed through a narrow corridor over a period of about two hours.

4.3.3.2. Size of total population

A total of 26,097 Herring Gulls was counted at these dumps (Fig. 12). It must be kept in mind, however, that the census concerned one particular moment, and that in reality the numbers fluctuate strongly during the seven winter months due to fluctuations in the feeding conditions in the Wadden Sea (4.3.2.3). However, combination of the December census with the periodical counts made in that winter, makes it possible to indicate roughly the outer limits within which the number of gulls probably fluctuated (Table 9).

As measure for the feeding conditions on the mudflats I took, as for the periodical counts (4.3.2.3), the length of the period during which the

Table 9. Estimated outer fluctuations of the numbers of Herring Gulls at the mainland refuse dumps of the provinces of Friesland, Groningen, and Drente during the winter of 1967–1968, based on the December 1967 census and on the regularly made counts at 13 dumps in Friesland during that winter

Dates (December 1967 census)	Duration of period that water-level in the Wadden Sea at Harlingen remained below 0 cm NAP during low tide (in hours)	Dumps assumed to be under the influence of foraging conditions in the Wadden Sea			
		Numbers counted	Calculated outer limits for winter period: lowest value	highest value I [1]	highest value II [2]
12	5.3	1,500	1,035	2,833	3,983
13	6.6	1,542	1,259	3,447	4,846
14	6.7	1,294	1,067	2,923	4,109
15	4.9	3,995	2,536	6,946	9,765
16	2.1	1,829	475 [2]–668 [1]	1,829	1,829
17	5.0	287	187	511	719
19	4.6	361	208	569	800
20	6.0	2,099	1,599	4,380	6,157
21	6.7	1,100	907	2,484	3,493
22	4.6	1,525	878	2,404	3,379
23	4.3	858	434	1,190	1,673
Total number of gulls at the dumps assumed to be under the influence of foraging conditions in the Wadden Sea		16,390	10,585–10,778	29,516	40,753
To be added number of gulls at the dumps assumed not to be under the influence of foraging conditions in the Wadden Sea		9,707	9,707	9,707	9,707
Grand total		26,097	20,292–20,485	39,223	50,460

[1]) and [2]) denote $n_{max.} = n_{2.1} = n_{3.5} = 5{,}477$ and $n_{max.} = n_{2.1} = 7{,}700$, respectively (see text).

water-level at Harlingen remained below the level of 0 cm NAP during the low-water period. Figure 11 gives the number (n_t) that would have been present during this length of time in the winter of 1967–1968 at the 13 dumps in Friesland at which periodical counts were made. If we indicate the lowest number at these dumps in the given winter as $n_{min.}$ and the highest number as $n_{max.}$, the fractions min./n_t and max./n_t give the factors with which the numbers counted on the various days in December 1967 must be multiplied to find the outer limits of the fluctuations in that winter.

From Figure 11 it is evident that $n_{min.}$ would amount to about 2,000. The upper limit is harder to define. During the periodical counts the lowest value found for the time during which the water-level remained below 0 cm NAP was 3.5 hours (see Table 8, for 2–2–1968). But during the December census a much lower value was found, i.e. 2.1 hours (see Table 9, for 16–12–1967). It is not known under what conditions the numbers at the dumps reach the maximum. I have therefore given two values for the upper limit; for the first, it was assumed that the highest number found during the periodical counts (5,477) was also the maximum, and for the second value it was assumed that the increase between 3.5 and 2.1 hours occurred according to the relation found in Figure 11. In this case the $n_{max.}$ amounted to 7,700. The true value probably lay somewhere between the two.

The distance inland to which the influence of the feeding conditions on the mudflats of the Wadden Sea extended is not known either. I have assumed that this influence extended into the whole area from which the gulls went to roost on the Wadden Sea. No special study was performed to localize the places where the gulls roosted. On the basis of the incidental data collected during the census, however, I can give a rough indication of the sites. The majority of the population of Friesland may be assumed to roost on the Wadden Sea, since during the census gulls were seen in the afternoon flying in the direction of the sea from deep in the provincial mainland. In eastern Groningen and northern Drente the gulls flew in the afternoon in the direction of the Eems-Dollart area and returned from there in the early morning, so I assume that this population roosted in that estuary. Lastly, in southwestern Drente (VAM) we saw the birds flying in westerly direction in the afternoon – as was also the case in the winter of 1968–1969. These birds probably roosted on the IJsselmeer. On the basis of these observations I have assumed that the influence of the fluctuating feeding conditions on the mudflats of the Wadden Sea on the number of birds at the dumps extended through Friesland and Groningen, and the upper part of Drente. The borderline has been taken just above the word "Drente" in Figure 12.

From Table 9 it can be seen that the number of Herring Gulls feeding at the more than 100 refuse dumps on the mainland of these three provinces in the winter of 1967–1968 can be put at 20,000 to 39,000–50,000.

4.3.3.3. Numerical differences between dumps

We have seen (4.3.2.4) that for the dumps at which periodical counts were made there is a positive (although not significant) correlation between the number of gulls and the number of inhabitants of the relevant municipalities. It is obviously of interest to know whether such a correlation was also present during the December 1967 census.

Because the water-level in the Wadden Sea (and therefore the numbers of gulls at the dumps; see 4.3.2.3) fluctuated rather strongly during the census period, the numbers had to be corrected to make the data refer to the same situation on the mudflats. For this, I took the situation in which the water-level at Harlingen remained below 0 cm NAP for five hours per low-water period. The method used for these calculations is analogous to that described in 4.3.3.2.

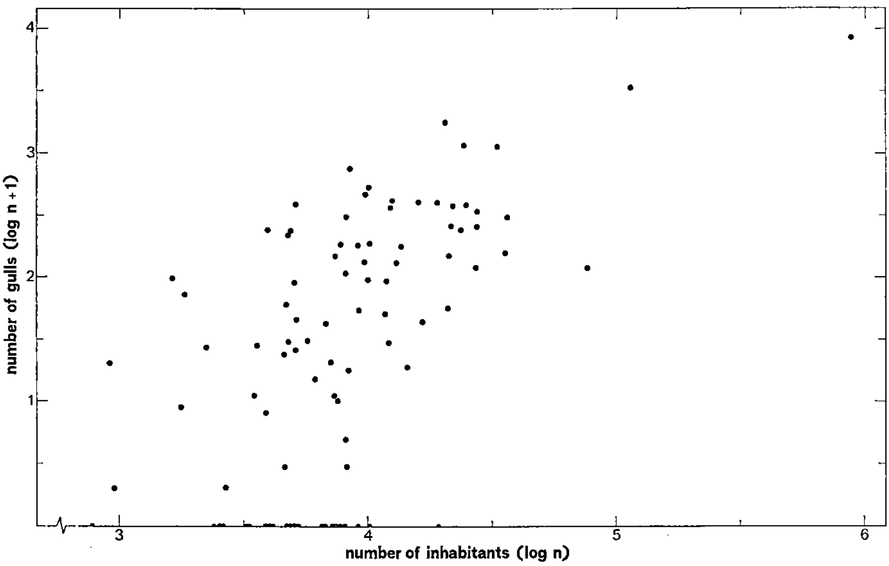


Fig. 13. Numbers of Herring Gulls at the refuse dumps of the provinces of Friesland, Groningen, and Drente during the census of December 1967, in relation to the number of inhabitants of the corresponding municipalities on 1 January 1968. Because the foraging conditions on the mudflats in the Wadden Sea fluctuated widely during the census period, the gull counts were corrected to have the data refer to the same foraging situation.

The relation between the number of inhabitants on 1 January 1968 (data taken from the Centraal Bureau voor de Statistiek 1968) and the number of gulls (corrected values) is shown in Figure 13. The data from municipalities using a communal as well as a local dump were consistently combined, since the distribution of refuse over the two was not known.

Figure 13 shows that there is a positive correlation between the number of inhabitants and the number of gulls (Spearman's rank correlation test, $P << 0.0001$). This demonstrates a distinct influence of the available amount of food on the distribution of the gulls over the dumps.

Table 10 shows that the dumps at which no gulls were seen were not distributed evenly over the area of the study. For municipalities with up to 5,000 inhabitants as well as for those with 5,000 to 10,000, the difference between the coastal provinces of Friesland and Groningen on the one hand and Drente (further inland) on the other, is significant (Fisher's Exact Probability test, $P = 0.019$ and $P = 0.007$, respectively). The number of gulls per 100 inhabitants (because the number of inhabitants has an influence on the number of gulls, it is preferable to compare the data in this way) at the remaining dumps is slightly lower in Drente than in Friesland and Groningen, although the difference is not significant (Wilcoxon test, $0.1 < P < 0.2$).

Table 10. Distribution of the refuse dumps over the provinces of Friesland, Groningen, and Drente, according to the presence or absence of Herring Gulls during the December 1967 census

	Size of municipalities (number of inhabitants)								
	< 5,000			5–10,000			> 10,000		
	(1) [1]	(2) [1]	(3) [1]	(1)	(2)	(3)	(1)	(2)	(3)
Gulls present	5	9	3	10	9	3	12	11	8
Gulls absent	2	2	7	1	2	6	2	0	0
Total [2]	7	11	10	11	11	9	14	11	8

[1]) 1 = Friesland, 2 = Groningen, 3 = Drente.
[2]) Since it was necessary to pool the data for a number of dumps, the total number in this Table is slightly lower than the number included in the study.

The difference between the two coastal provinces and Drente can be connected with both the distance from the dumps to the coast and differences in landscape. Friesland and Groningen comprise mainly low-lying pastures and arable fields (in general, an open landscape with many stretches of water), whereas Drente is composed mainly of high-lying sandy soils partially covered by moors and woods (less open and less water). However, without a special study on this point, the separate influence of these factors cannot be evaluated.

4.3.3.4. Other gull species

In addition to Herring Gulls, Great Black-backed Gulls *Larus marinus*, Common Gulls *Larus canus*, and Black-headed Gulls *Larus ridibundus* were seen, but since their numbers were not counted, only the order of magnitude can be given. Only some tens of the Great Black-backed Gull were seen. There were more Common Gulls, but not more than a few hundred in total. The Black-headed Gull was the most numerous of the three species, with 1,000 to 2,000 individuals.

These numbers are clearly much lower than those of the Herring Gull. Although in The Netherlands the four species are not equally numerous in the winter (Commissie voor de Nederlandse Avifauna 1962), these differences cannot account for the ratio seen at the dumps. They depend largely on differences in the feeding ecology of these species, the Great Black-backed Gull foraging more at sea, the Common and Black-headed Gulls more on farmland than the Herring Gull. The Black-headed Gull also occurs more frequently in cities and villages than the Herring Gull. Differences in feeding ecology between the four species are also found on the IJsselmeer (Swennen 1970) and the Wadden Sea (Swennen, in prep.).

In the western part of The Netherlands, however, the Black-headed Gull is numerous at refuse dumps. This also holds during the breeding season in the northern part of the country, e.g. at the VAM compost works in Drente (F. R. Fabriek, pers. comm.). Thus, the species does not avoid refuse dumps as much as the winter distribution in the northern part of the country might suggest. The small numbers at the northern dumps in the winter must have another cause. I think this must be the large numbers of Herring Gulls feeding at these dumps, which are not only appreciably larger than those in the breeding season (cf. the periodical counts in Friesland, 4.3.2.2) but also much greater than the numbers present in the winter at the dumps in the western part of the country, due to the greater number of breeding birds (over 12,000 pairs on the Frisian Islands as against a few thousand pairs along the coast of the western provinces of the country). The data suggest a strong interspecific competition, resulting in a departure of the Black-headed Gulls when the Herring Gull becomes more numerous.

4.3.4. Size of total winter population on the mainland

As already mentioned, the occurrence of the Herring Gull on the mainland is limited almost entirely to harbours, cities, villages, and refuse dumps, of which the last form the most important source of food. The census of December 1967 therefore offers a sound basis for an estimate of the total winter population of this area (Table 11). At that time a total of 26,097

Table 11. Size of the Herring Gull population on the mainland of the provinces of Friesland, Groningen, and Drente during the winter of 1967–1968

		Counted or estimated numbers	Fluctuations during the winter (calculated values) min.	max.
Refuse dumps	(December 1967)	26,097	over 20,000	39,000–50,000
Cities and villages	(Winter 1967–68)	2,000	over 3,000	8,000–12,000
Factories	(December 1967)	at least 1,000		
Harbours	(Winter 1967–68)	1,000		
Farmlands	(December 1967)	1,200		
Total		32,000	24,000	47,000–62,000

Herring Gulls was counted at the dumps, but under the influence of the fluctuating feeding conditions on the mudflats of the Wadden Sea the number fluctuated during the winter between 20,000 and at least 39,000 (4.3.3.2).

The Herring Gulls in cities and villages have never been counted comprehensively. According to the data of the Centraal Bureau voor de Statistiek (1968), more than 80% of the 129 municipalities on the mainland of Friesland, Groningen, and Drente have a rural character. In this area there are only two large and 12 small urban agglomerations. In the built-up area of most of the rural municipalities the number of gulls in the winter probably amounted to less than 10, giving a rough total figure of not more than 1,000 birds. According to incidental counts, in the small cities the numbers must have amounted to some tens, making a total for these 12 cities of about 500 gulls. Appreciable numbers occur only in the two large cities, which together have a few hundred birds. For all towns together, therefore, we arrive at a figure of about 2,000 Herring Gulls.

During the December 1967 census, concentrations of Herring Gulls were also seen around factories in Harlingen (800 birds) and Coevorden (100 birds). In Harlingen the gulls were feeding on the waste of a shellfish cannery and on the unprocessed sheepkins on the grounds of a leather factory. In Coevorden the birds scavenged mainly on the sewage of a poultry slaughterhouse. No special study was made of the numbers present at such places, but around some other factories only smaller numbers were seen during the census, giving a total of about 1,000 birds. However, higher numbers may have been present at such places in other parts of the area investigated. The total number was therefore probably higher than the 1,000 counted, but I think it could not have been more than a few thousand higher.

The species is a common winter bird in the eight fishing harbours on the coasts of Friesland and Groningen. According to incidental counts made in the winter of 1967–1968, the number in the Harlingen harbour varies between several tens and a few hundreds of Herring Gulls. Most of the harbours are, however, much smaller than that of Harlingen. The total for all the harbours was probably about 1,000 birds.

During the December 1967 census, a distance of about 2,000 km was covered outside the built-up area. The width of the strip in which we could identify the different gull species from the car was about 200 m, so we could view a total surface of about $2,000 \times {}^1/_5 = 400$ km^2, or about 5% of the total area of the three provinces. In this strip about 60 Herring Gulls were observed, not including birds obviously going to or coming from their roosting areas. The total number for the three provinces thus amounted to about 1,200 Herring Gulls.

According to these estimates, at least 5,200 Herring Gulls fed on the mainland of the three provinces in the winter of 1967–1968 in addition to the dump scavengers. This figure is a combination of partial counts and rough estimates, and it is therefore impossible to give exact outer limits of the range in which the numbers fluctuated in these areas under the influence of the feeding conditions on the mudflats of the Wadden Sea. For the sake of simplicity I have assumed that the counted and estimated numbers represent the average situation and that the fluctuations in the numbers of gulls corresponded to those observed for the dumps. In the same way as shown in 4.3.3.2, we find as lowest value 2,000/3,395 ($n_{min.}/n_{aver.}$) × at least 5,200 = over 3,000 gulls and as highest value 5,477 to 7,700/3,395 ($n_{max.}/n_{aver.}$) × 5,200 = at least 8,000 to 12,000 birds.

For the total population on the mainland in the winter of 1967–1968 we therefore arrive at a value fluctuating between 24,000 and 47,000–62,000, depending on the feeding conditions in the Wadden Sea area (Table 11).

Combination of the counts made in the Wadden Sea area and on the mainland in the winter of 1967–1968 shows that the size of the total population in the northern part of The Netherlands at that season may be put at minimally 52,000 (at least 28,000 in the Wadden Sea area plus 24,000 on the mainland) and maximally 61,000–76,000 (14,000 in the Wadden Sea area plus 47,000–62,000 on the mainland). This means that at least 32% (24,000/76,000 × 100%) of the total winter population foraged constantly on the mainland, feeding almost exclusively on garbage and other human waste, whereas during less favourable foraging conditions in the Wadden Sea, where the gulls' diet consists mainly of natural food (5.4), the percentage of gulls on the mainland increased to maximally 77% (47,000/61,000 × 100%) – 82% (62,000/76,000 × 100%).

5. FOOD

5.1. FORAGING RHYTHM

In the Wadden Sea area Herring Gulls are found primarily in the littoral and sublittoral zones, their activities being determined, outside the breeding season, almost exclusively by the rhythm of the tides (see also Blösch 1966, Fig. 1, and Drent 1967, Figs. 7–9). As soon as the eggs have hatched, this rhythm is disturbed; the birds now forage throughout the day and probably also on nights that are not too dark. During the first two to three weeks the parents go on foraging flights alternately, so one parent is almost always present in the territory during the period in which the young are most vulnerable to predators. Later, they forage simultaneously, so that the young are left unprotected in the gullery. This is probably related to the increasing food requirements of the growing chicks, which reach the maximum level at the age of about three to four weeks (5.6.3). Shortly after the young are able to fly, the Herring Gull in the Wadden Sea area again becomes a predominantly tidal bird.

Outside the breeding season, however, the refuse dumps on the mainland also form an important source of food (4.3.4). Like most land birds, the gulls that forage on the mainland have a diurnal rhythm, feeding during the day and roosting at night. This probably also holds for the gulls foraging in the coastal waters of the North Sea, independent of the tides.

5.2. METHODS

a. Sampling. The data on diet are mainly based on analyses of pellets, faeces, and lumps of food sometimes regurgitated by chicks when handled. Supplementary data were obtained from examination of the contents of oesophagus and stomach of adult birds and chicks, and by direct observations of the feeding of the young.

Considerable attention has been given in the literature to the advantages and limitations of various methods of food analysis (e.g. Kluyver 1933, Hartley 1948, van Koersveld 1951, Ashmole & Ashmole 1967); I will therefore confine myself here to a few remarks concerning the methods applied in this study.

Pellets and faeces. The indigestible components of the food are partially vomited as pellets and partially evacuated with the faeces. Since the colour and shape of the hard components generally make them easily identifiable with the naked eye, the examination of pellets and faeces offers a simple method to obtain information about the diet. However, because the proportion of indigestible material is not the same for all kinds of food, this method does not indicate the ratio in which the prey species occur in the diet; its main usefulness is for the study of differences between areas or changes in the composition of the diet.

Direct observations of the feeding of the young. The food regurgitated by the adult gulls for the chicks is usually only slightly or not at all digested, and can therefore be recognized easily from a blind (we used 7 × 50 binoculars). However, it is sometimes eaten up so rapidly by the chicks that there is a possibility of a bias favouring the most easily recognizable food. In addition, on Terschelling and Vlieland the undulating terrain and the high vegetation often made it impossible to see what was being fed, and therefore the method was not entirely satisfactory.

Between two foraging flights the adults usually regurgitated several times. What the chicks did not consume, the parent bird ingested again and regurgitated it again later. For this reason, observations between two foraging flights have consistently been taken as one observation of the parent in question.

Regurgitations of the chicks. The food regurgitated by the chicks (the same of course holding for the stomach contents) is often in a more advanced state of digestion than that regurgitated by the parents, but it is possible to examine it more closely, whereas other characteristics beside the visual can be used. For instance, bread, cheese, boiled potatoes, smoked foods, and even rather well digested fish could be easily identified by their distinctive smell. However, the kneading of the food in the gizzard often made further identification of the fish difficult, since the regurgitated material was analysed in the field and, after examination, refed to the chicks to avoid an influence on weight increase of the young in question. When the fish was not at least partially intact, it was usually not possible to do more than identify the family, using as characteristics the colour of the skin and flesh, and the shape of the bones. The Mackerel *Scomber scombrus* was the only species that could be recognized in this way (from the isabeline colour of the flesh and the characteristic pattern on the skin). In the other cases the species could only be identified when the otoliths were present. Because of their high degree of species-specificity, the otoliths are useful in food analysis (see e.g. Maag 1917, Lumsden & Haddow 1946, van Dobben 1952, Geiger 1957, Vauk & Gräfe 1961, Martini 1964, 1966, Löhmer & Vauk 1969, 1970). The identification of the collected otoliths was based on Frost (1925, 1926, 1930), Chaine & Duvergier (1934, 1935, 1936, 1937) and Schmidt (1968), while I also had at my disposal a small reference collection of otoliths of the common local species.

Another problem associated with the analysis of regurgitations and stomach contents is the question of which parts are to be considered as food. When the quantity of hard and indigestible material is small, the components can remain in the gizzard for some days. To avoid a bias favouring food leaving clearly recognizable residual material in the stomach, only digestible components were considered as food unless otherwise indicated.

b. Assessment. The simplest and therefore the most frequently used method to express the results of food analysis is to give the number of times each type of food is found. This method was also used in the present study. The advantage of the method is that differences between series of observations can be analysed by simple statistics, albeit with the necessary caution (cf. also King & Ikehara 1956). However, it has the objectionable aspect that it gives only an approximation of the occurrence of the various types of food and not of the true composition of the food, for it is possible that a given type of food may be present in each regurgitation but with respect to weight or volume may only represent a small part of the total food-supply. This of course does not mean that the food in question is not important for the birds, since it may contain components that the birds require in small amounts to remain healthy. In 1967 and 1968, I frequently weighed the regurgitations of the chicks as well, to study the influence of a bias due to frequently occurring food contributing little to the birds' food-supply.

To obtain an impression of the proportions in which certain species of fish occurred in the diet, I compared the numbers of otoliths of each species found. This of course pertained only to the species in which the size of the otoliths gave roughly the same chance of being observed.

5.3. DIET DURING THE BREEDING SEASON

5.3.1. Stomach contents of adult gulls

In 1961 we had an opportunity to investigate the stomach contents of 37 Herring Gulls poisoned in the second half of May during a gull control program in the breeding colony on Vlieland. Because only a few of the stomachs contained digestible food components, the indigestible components were also taken into consideration when the quantity of this material was so large that it could safely be assumed to have derived from the last foraging flight. The results, shown in Table 12, indicate that during the second half of May, when most breeding birds have eggs, the food consists mainly of prey species from the littoral and sublittoral zones.

Table 12. Occurrence of various types of food in stomachs of Herring Gulls poisoned during a gull control program at the nesting sites on Vlieland in the second half of May 1961

Types of food	Males	Females	Total
Marine fish	2	2	4
Marine invertebrates	10	16	26
Macropipus holsatus	2	—	2
Carcinus maenas	3	4	7
Mytilus edulis	7	13	20
Asterias rubens	3(4?)	(1?)	3(5?)
Material without food value	2 [1])	3 [2])	5
Full stomachs	12	18	30
Empty stomachs	1	6	7

[1]) Some dead specimens of *Hydrobia ulvae* and a tube of *Lanice conchilega.*
[2]) Vegetable matter (grass, moss, and *Ulva lactuca*).

It is also evident from Table 12 that there are probably no appreciable differences in the choice of food between the sexes (Fisher's Exact Probability test, for all types of food, $P>0.05$). Harris & Jones (1969) too did not find an intersexual difference in this respect for Herring Gulls on the coast of Wales, nor did Ingolfsson (1969) for those on Iceland. For Herring Gulls in the Barents Sea, however, Belopol'skii (1961) found a difference in diet between both sexes (males more fish and predatory behaviour; females more littoral invertebrates, insects, and berries of *Empetrum nigrum*), but he did not indicate whether the differences, which were not large, are statistically significant. Since the occurrences of the various types of food are given as percentages of the number of scores for all types of food together, without mention of this total number (= 100%), it is also not possible to determine this from his data.

5.3.2. Pellets and faeces

Over a period of four years, we examined more than 27,000 pellets and faeces in the Terschelling and Vlieland colonies. All this material was relatively fresh, because we restricted ourselves to pellets and faeces that had not yet fallen apart due to the effect of weather.

The material was examined in the field, which made it possible to investigate a large number of pellets and faeces in a relatively short time, but doubtful cases were examined in the laboratory. Nevertheless, some of the material could not be identified.

The colony on Terschelling was sampled in 6 more or less fixed places and the one on Vlieland in 7 places. In the Terschelling colony the sampling places were located in that part of the gullery where there were no breeding pairs of the Lesser Black-backed Gull. Although an attempt was made to include all the places at each sampling, this was not always possible. The sampling results are shown in Tables 13 and 14.

a. The most frequent prey species.

The great majority of the pellets and faeces consisted of remains of Starfish *Asterias rubens*, Mussels *Mytilus edulis*, Cockles *Cardium edule*, Sand Gapers *Mya arenaria* (on Vlieland, however, almost absent), crabs (mainly *Carcinus maenas*), Shrimps *Crangon crangon*, and fish, thus demonstrating once again the importance of the littoral and sublittoral zones of the Wadden and North Seas as feeding areas. These results are in agreement with earlier data from the Dutch (Rooth 1957) and German Wadden Sea areas (review in Goethe 1956; also Ehlert 1957, 1961, Vauk & Löhmer 1969), albeit with appreciable quantitative differences.

Figure 14 gives a picture of the variations in the occurrence of these seven prey species. It is evident that on both islands the share taken by *Cardium*, *Mya*, and *Asterias* was sharply reduced in the course of the spring months, the two mollusc species even disappearing almost completely from the samples. In 1966 the share taken by *Cardium* increased slightly in the late summer on Terschelling. The share of *Asterias* increased in the course of the summer on Vlieland in 1964 and 1966, but this increase was not seen on Terschelling.

The share of crab and fish showed a distinct increase on both islands in the spring and early summer. Fish reached the highest values in the period from May to July, after which there was a slow decrease. On Vlieland, the increase of *Asterias* in the course of the summers of 1964 and 1966 was accompanied by a decrease of crabs, but on Terschelling in 1966 the percentage of the latter remained constant at a high level into September.

Mytilus showed an irregular course on both islands and *Crangon* showed only fluctuations around a low level.

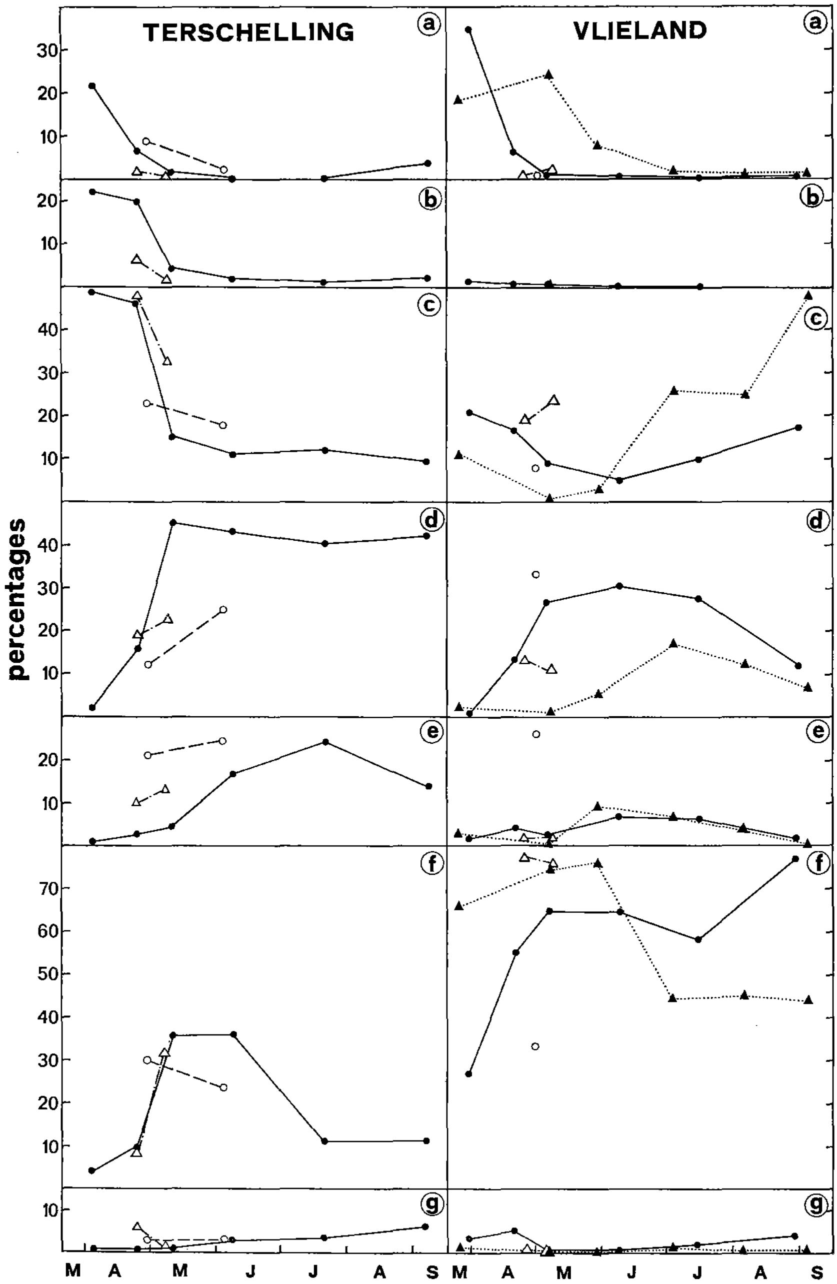


Fig. 14. Seasonal fluctuations in the occurrence of *Cardium edule* (a), *Mya arenaria* (b), *Asterias rubens* (c), crabs (d), fish (e), *Mytilus edulis* (f), and *Crangon crangon* (g) in pellets and faeces of Herring Gulls from Terschelling and Vlieland during the breeding seasons of 1964 (solid triangles), 1966 (dots), 1967 (open triangles), and 1968 (circles).

Table 13. Occurrence of various types of food in pellets and faeces of Herring Gulls collected in the breeding colony on Terschelling

Types of food	1966						1967		1968	
	3/4-IV	24/25-IV	10/12-V	7/9-VI	20/22-VII	6/8-IX	24/25-IV	5/11-V	30-IV	3/4-VI
Marine fish	7	33	57	189	198	100	51	80	238	181
Marine invertebrates										
Polychaetes:										
Nereis spp.		2	17	4		1	10	4	1	
Crustaceans:										
Corophium volutator										4
Crangon crangon	12	11	20	36	29	47	28	9	33	26
Macropipus holsatus } *Carcinus maenas* }	29	219	679	492	327	308	95	146	133	188
Spec. indet.		5	5	11	4	3	1	1		
Molluscs:										
Mytilus edulis	60	125	539	417	92	84	41	205	339	184
Cardium edule	299	84	11			22	8	1	97	17
Macoma balthica	4	2	1	13	6	3	2	9	7	
Mya arenaria	304	269	57	19	8	13	28	11		
Hydrobia ulvae		1	5			1			3	
Spec. indet.	4		2	9	5			1		2
Echinoderms:										
Asterias rubens	687	635	224	122	95	65	239	209	263	136
Psammechinus miliaris		1								
Terrestrial animals										
Mammals			8	4	4	10	2		24	74
Birds						3	1			1
Eggs					36					5
Insects			3	11	2	2		1		6
Vegetable matter	16		1			7	4			5
Garbage	5	6	6	2	7	80	12	6	47	3
Sand and mud	38	201	105	73	39	18	22	39	29	27
Unidentifiable material	23	31	82	56	92	86	33	31	14	12
Number of pellets and faeces investigated	1,408	1,363	1,506	1,148	821	742	500	648	1,135	767

Table 14. Occurrence of various types of food in pellets and faeces of Herring Gulls collected in the breeding colony on Vlieland

Types of food	1964						1966						1967		1968
	26-III	5/8-V	27/31-V	1/6-VII	5/6-VIII	3-IX	30-III	20-IV	5-V	8-VI	15-VII	29-VIII	26-IV	8-V	1-V
Marine fish	28	28	80	77	45	6	20	51	39	102	81	33	9	10	63
Marine invertebrates															
Polychaetes:															
Nereis spp.		1						3	23	2		1			
Crustaceans:															
Crangon crangon	12	4	3	21	6	1	33	60	4	16	23	64	1	5	
Macropipus holsatus } *Carcinus maenas*	19	25	47	187	128	72	3	159	436	445	360	178	48	61	82
Spec. indet.								37	2	7					
Molluscs:															
Mytilus edulis	667	1,965	691	482	457	462	256	679	1,065	943	743	1,140	285	413	81
Cardium edule	188	657	75	20	8	9	332	79	18	7		8	2	10	3
Macoma balthica		5	1				7		4	13		1	1	3	1
Mya arenaria		1					9	8	1		1				
Littorina littorea	1	1					89								
Hydrobia ulvae						1				7					
Spec. indet.							1	1		2		6			
Echinoderms:															
Asterias rubens	113	17	26	283	257	507	200	211	149	76	131	247	72	130	20
Terrestrial animals															
Mammals												2			
Birds					1					11	1				
Eggs			1							1					
Insects				1		2			1	5		1			
Molluscs					1										
Vegetable matter			1	54	135	9			2	2	45	4			1
Garbage	13	2	5	9	27	20	2		4	4	14	20		4	1
Sand and mud							17	32	50	56	21	1	5	2	5
Unidentifiable material	8	54	69	65	49	40	10	24	24	80	49	12	9	15	15
Number of pellets and faeces investigated	1,016	2,665	915	1,104	1,025	1,063	949	1,231	1,644	1,477	1,284	1,486	372	545	246

The differences between Terschelling and Vlieland are mainly to be attributed to differences in local conditions. The North Sea coast of Vlieland is protected by about 60 stone groynes carrying a thick cover of small Mussels (Swennen & Spaans 1960), and where many young *Asterias* live in the summer. The Terschelling beach does not have such groynes. On Vlieland many groynes are situated only a few hundred metres from the centre of the gullery, and in the spring and summer, there is literally an exodus of Herring Gulls to the groynes with the falling tide.

The groynes are probably responsible for the high percentages of Mussels in the pellets and faeces on Vlieland, and this also holds for the increase of *Asterias* on this island during the course of the summer. The differences in the occurrence of most other marine prey species are in all probability closely related to the differences in the occurrence of *Mytilus* and *Asterias*. The almost total absence of *Mya* in the pellets and faeces on Vlieland, however, probably has a different basis. Since *Mya* lives burrowed a few decimetres deep in the substrate, it can only be taken by the gulls when it has been exposed by currents (cf. Goethe 1937, Meijering 1954). The most likely explanation for the difference between Terschelling and Vlieland is that, possibly due to hydrographic differences, this situation occurs more often in the flats off Terschelling than in the flats off Vlieland.

The variations in the occurrence of *Cardium*, *Mya*, and crab during the spring agree with the findings of Meijering (1954) in 1949 and 1950 on Spiekeroog and of Ehlert (1957) in 1957 on Mellum (both being East Frisian Islands). However, in the spring of 1959 there was no decrease of *Cardium* on Mellum, and the percentages fluctuated throughout the breeding season at a high level, those of crab around a low level (Ehlert 1961). The share of crab decreased during the late summer on both Spiekeroog and Vlieland. On the former island, it was replaced in 1949 by *Cardium*, in 1950 by *Mytilus* in August and by *Littorina littorea* later in the autumn. On Spiekeroog the pattern of *Macoma balthica* and *Mytilus* (both of which were rare on Mellum) was more or less the same as that of the other molluscs. The pattern shown by *Mytilus* on Spiekeroog was therefore quite different from that seen on Terschelling and Vlieland. On the latter islands *Macoma* was rarely found in the pellets and faeces. In June and July Meijering found a small peak for fish and Starfish, two types of food he otherwise hardly ever saw. This latter also holds for Ehlert's observations. There was thus also a difference between Spiekeroog and Terschelling–Vlieland for the pattern shown by the Starfish.

The increase of crab in the spring is related to the return of *Carcinus maenas* (the species to which most of the crab remains belonged) from the channels and tidal inlets to the sublittoral and littoral zones. There is probably a causal relationship between this increase and the decrease in the share taken by molluscs during this period. It is not likely that the variations are primarily related to the chicks' special food demands, as Goethe (1956) believed. On Terschelling and Vlieland crabs are not an important food for the chicks (5.3.3). Furthermore, the crab increase does not always occur in the same month, and it occurs to an appreciable degree before the first chicks have hatched (mostly the beginning of June). The spring decrease of Starfish may also be related to the increase in the share of crabs during this period, but since the former inhabit slightly deeper water in the summer than in the winter their lesser accessibility may also play a role here.

In my opinion, the summer decrease of crab is also related to the occurrence of alternative prey species. On Vlieland this decrease was accompanied by an increase of *Asterias*, on Spiekeroog by an increase of *Cardium* and *Mytilus* (at least early in the season). As already mentioned, the increase of *Asterias* on Vlieland can be traced to the high numbers of young specimens on the groynes there. On Spiekeroog the increase of *Cardium* and *Mytilus* began in the course of July–August. This coincides roughly with the time in which the young Cockles and Mussels in the Dutch Wadden Sea reach the size taken by the Herring Gull (before that they are evidently too small). Unfortunately, nothing is known about the size of the Cockles taken by the gulls on Spiekeroog, but the *Mytilus* specimens were qualified as small.

Nothing can be said concerning the question of whether the changes in the occurrence of fish are to be attributed, like that of crab, to differences in accessibility, because too little is known about the kind of fish species taken in the course of the year.

The variations in the occurrence of Mussels on Terschelling and Vlieland are difficult to explain, and no distinct pattern can be distinguished.

On the basis of the foregoing data, I am of opinion that the changes in the composition of the pellets and faeces are to be attributed primarily to changes in the abundance, accessibility, and attractiveness (in the broadest sense) of the various prey species. This is in agreement with the views of Leege (1917) and Meijering (1954). Leege stated that many variations in the diet can be traced to a transient shortage of certain types of food resulting from season, weather, and water currents. According to Meijering, various factors are responsible for the changes in the composition of the food, but he considered the abundance of the prey species in any given month to be the most important factor.

b. The less frequent components of the food

Marine organisms. *Littorina littorea* was not found on Terschelling during routine sampling, but we saw this species elsewhere in the colony several times each year in the months of March and April. The *Nereis* remnants found in the pellets and faeces in April and May all belonged to *Nereis virens*. Later in the season, remains of other *Nereis* species were found on a few occasions (exact identification was not possible). The occurrence of *Nereis virens* is limited to the period in which this worm swarms, as was also found by Löhmer & Vauk (1970) for the Herring Gulls on Heligoland. In this period, however, the species may be taken by large numbers of gulls. On 12 April 1967, for instance, at high tide in the middle of the western part of the Wadden Sea, Swennen (pers. comm.) observed more than 3,300 Herring Gulls catching *Nereis virens*. From Terschelling a few days later I myself twice observed a group of about 1,000 Herring Gulls over the Wadden Sea whose foraging behaviour indicated that they too were taking *Nereis*.

Non-marine food. Remains of non-marine animals were found in relatively large numbers only incidentally. The mammals found were almost exclusively juvenile Rabbits *Oryctolagus cuniculus*. The difference in occurrence of mammalian remnants between Terschelling and Vlieland, could be related to the small numbers of Rabbits on the latter island. After the myxomatosis epidemic in 1956, the Rabbit population decreased drastically in number. Since then, stringent control has kept the number to a level considerably below that of the Terschelling population. Other mammals found on Terschelling (these data concern larger parts of the colony than the routine sampling areas) included the Mole *Talpa europaea* (found each year in a few pellets and faeces), Wood Mouse *Apodemus sylvaticus*, Common Shrew *Sorex araneus*, either Common or Short-tailed Vole *Microtus arvalis* or *agrestis*, and Northern Vole *Microtus oeconomus*, all incidental prey species. On Vlieland no remains of other mammals were found.

The occurrence of Mole, Northern Vole, and Common or Short-tailed Vole on Terschelling is interesting, because these species do not belong to the fauna of the island (van Wijngaarden 1964). The nearest places where the Mole and Northern Vole occur lie on the mainland of the province of Friesland, for the latter species at least 40 km from the colony (for a discussion of the occurrence of the Northern Vole in Friesland, see van Wijngaarden 1967). Remains of mammals originating from the mainland have also been found in pellets of Herring Gulls of the East Frisian Islands (Goethe 1939, Vauk & Löhmer 1969), but the distances between these islands and the mainland are considerably smaller than in our case. Bergman (1939), Focke (1959), and Drury (1964) also reported long distances travelled by foraging Herring Gulls during the breeding season (25–35 km, 35 km, and 25 miles, respectively; see also 5.3.3.5).

The remains of birds found in pellets and faeces on Vlieland belonged, with the exception of one adult Song Trush *Turdus philomelos*, to Eider *Somateria mollissima* chicks. In former years, we also found remains of Shelduck *Tadorna tadorna* chicks. According to direct observations, on Vlieland chicks of both species of ducks are regularly taken by Herring Gulls (see also van Dobben 1934, Mörzer Bruyns 1958, Spaans 1959). On Terschelling, in addition to Eider ducklings we found Pintail *Anas acuta* (probably found as carrion), Oystercatcher *Haematopus ostralegus* (chick), Black-tailed Godwit *Limosa limosa* (chick or juvenile), Herring Gull (chicks), House Sparrow *Passer domesticus* (adult), and Starling *Sturnus vulgaris* (these data concern larger parts of the colony than the routine sampling areas). Remains of chicks of conspecifics were regularly found. Starlings were found each year between June and August, when large groups of predominantly young birds forage on the Boschplaat (the remnants in the pellets concerned first-year animals almost exclusively). The other species were all found only once.

The egg-shell remnants observed in the 36 pellets and faeces on Terschelling in July of 1966 during routine sampling all derived from Herring Gull eggs. All remnants were recognizable from the blue colouring matter added to the oil suspension used to spray the eggs as part of the control program. Most of the eggs had probably been taken from abandoned nests. On Vlieland, we occasionally found pellets consisting of remains of Eider eggs.

Remains of insects were seldom found during routine sampling. Table 15 shows the species found in pellets and faeces on Terschelling and Vlieland (these data too were also obtained outside the routine sampling). *Phyllopertha horticola* and *Philopedon plagiatum* were the most frequently found species. In some years, both also occurred frequently in the food taken by Herring Gulls on the East Frisian Islands (Goethe 1956).

Table 15. Insects found in pellets and faeces of Herring Gulls on Terschelling (T) and Vlieland (V)

Coleoptera	Lepidoptera
Carabidae	Microlepidoptera spec. indet. (T)
? *Calathus* spec. (V)	Diptera
Platynus marginatus L. (T)	Bibionidae
Amara familiaris Duft. (T)	*Dilophus* spec. (T)
Amara spec. (V)	Hymenoptera
Scarabaeidae	Formicidae
Phyllopertha horticola L. (T)	*Tetramorium caespitum* L. (T)
Anomala aenea De G. (T)	Spec. indet. (V)
Elateridae	
Lacon murinus L. (T, V)	
Corymbites tessellatus L. (V)	
C. aeneus L. (V)	
Tenebrionidae	
Olocrates gibbus F. (T)	
Curculionidae	
Brachyrrhinus ovatus L. (T, V)	
Philopedon plagiatum Schall. (T, V)	
Apion spec. (V)	

On Terschelling we also found, although only a few times and outside the routine sampling, the Natterjack *Bufo calamita* (Amphibia), but only in one case part of the regurgitated animal was digested. On both islands we also found the Roach *Rutilus rutilus*, a few times; this fresh-water species does not occur on either island and was probably taken by the gulls on Texel or the Frisian mainland.

The vegetable matter mentioned in the Tables 13 and 14 comprises remains of grains, seeds of Gramineae and Cyperaceae, and berries of *Empetrum* *nigrum*, as well as material without nutritional value such as straw and other dry parts of plants.

Remains of garbage were found regularly but in relatively small amounts during routine sampling. In September 1966 and in April 1968, however, rather high scores were reached on Terschelling. On both islands the remains of garbage consisted mainly of wrapping papers, which had contained butter or margarine, and meat bones.

The analyses of stomach contents and pellets and faeces show that during the occupation of the breeding colony the food of the Herring Gulls on the Dutch Frisian Islands consists mainly of invertebrates from the littoral and sublittoral zones, at least when the food of the chicks, which consists mainly of fish (5.3.3), is not taken into account.

A similar preponderance of marine invertebrates in the food of the Herring Gull is found on the East Frisian Islands (Leege 1917, Goethe 1937, Meijering 1954, Goethe 1956, Ehlert 1957, 1961, Vauk & Löhmer 1969) and in Iceland (Ingolfsson 1967). On Heligoland, however, where the littoral zone is not much extended, in the breeding season the main food is fish, probably mainly deriving from commercial fishery (Löhmer & Vauk 1969, 1970).

The Herring Gulls of Wales are mainly scavengers existing for the most part on fish-waste and garbage, although they also feed to a large extent on arable land (Harris 1965). The gulls of Walney Island on the west coast of England eat mainly fish, invertebrates from the littoral and sublittoral zones, and garbage (Brown 1967a), as do the Danish gulls (Spärck 1951). In Finland, where the littoral zone is virtually absent, the food consists mainly of garbage and fish-waste (Bergman 1939, Bergman, Fabricius & von Haartman 1940, Nordberg 1950, Lemmetyinen 1963). In East Murman, Russia, in some years fish are most important, in other years littoral invertebrates predominate, and in still others terrestrial animals and berries are as frequently eaten as fish (Belopol'skii 1961). The inland-nesting population of Kalmytskaya, however, feeds mainly on rodents (Minoranskii 1963). In a colony along the Adriatic coast of Yugoslavia, Spitzenberger (1961) found predominantly the remains of insects in the food of Herring Gulls.

Although the Herring Gulls of some colonies in the New England region of The United States feed predominantly on natural food, the main foods of the species found in this region are garbage, sewage, fish-waste, and pig food (Drury 1964, Drury & Nisbet 1969). In Newfoundland, the food consists mainly of fish, littoral invertebrates, and garbage and other human refuse (Threlfall 1968). Along the Gulf of St. Lawrence gulls were found to eat mainly insects, crustaceans, and fish (Mills 1957). In the Canadian arctic Smith (1966) found that in areas where lemming populations were high, these rodents were the only food taken. In areas where lemmings were not abundant, Smith found small crustaceans exclusively.

The feeding habits of the Herring Gull in the various parts of its distribution area illustrate the omnivorous character of this species. Recently, Harris (1965) has given a review of the animals known to be eaten by Herring Gulls.

5.3.3. Food fed to chicks

5.3.3.1. Direct observations

In 1966, on Terschelling, I attempted to make observations from a blind to collect data on the food regurgitated by the adult gulls for the chicks. This method did not prove entirely adequate (5.2), and therefore it was not used in following years. The 1966 results and occasional observations from 1967 and 1968 are given in Table 16. According to Table 16, marine fish were brought most frequently (53%). Marine invertebrates were seen much less frequently (22%). Other kinds of food were seen only three times (5%),

Table 16. Occurrence of various types of food regurgitated by adult Herring Gulls for their chicks on Terschelling (observations from a blind)

Types of food	1966	1967	1968	Total
Marine fish	31	2	1	34 (53%)
Marine invertebrates	10	1	3	14 (22%)
Crangon crangon	2		1	3 (5%)
Macropipus holsatus } *Carcinus maenas*	4	1	2	7 (11%)
Mytilus edulis	1		1	2 (3%)
Mya arenaria (pieces of siphons)	3			3 (5%)
Asterias rubens	3			3 (5%)
Terrestrial animals		1		1 (2%)
Larus argentatus (chick)		1		1 (2%)
Garbage	1	1		2 (3%)
Unidentifiable material	12		4	16 (25%)
Number of regurgitations	53	4	7	64
Number of broods studied	13	2	4	19

Table 17. Occurrence of various types of food in the diet of Herring Gull chicks on Vlieland in 1964

Types of food	Food regurgitated for chicks by adults; observations from a blind (10 broods)	Food regurgitated by chicks (5 broods)	Total (13 broods)
Marine fish	31	4	35
Marine invertebrates	34	2	36
Arenicola marina	8		8
Crangon crangon	2		2
Macropipus holsatus } *Carcinus maenas*	11	1	12
Mytilus edulis	5		5
Cardium edule (flesh only)	7	1	8
Asterias rubens	8	1	9
Garbage	2		2
Unidentifiable material	19		19
Number of feeds	68	6	74

once a gull chick and twice garbage. In 16 cases (25%) the exact nature of the food could not be identified. Since garbage is less easily recognized from a blind than other types of food, its occurrence may have been underestimated, but most of the unidentifiable components derived from marine organisms.

Previously, in 1964, direct observations were made from a blind on Vlieland. These observations included 68 feedings at 10 broods, the age of the young ranging between just hatched to 15 days. The results are shown in Table 17.

It is evident from these data that just as on Terschelling the food consisted mainly of marine organisms, although the proportion of marine invertebrates on Vlieland was rather high (34 out of 68 as against 14 out of 64 regurgitations for Terschelling). The proportion of fish, to the contrary, differed little (31 out of 68 as against 34 out of 64 regurgitations). Garbage was seen in 2 out of 68 cases (on Terschelling in 2 out of 64). The proportion of unidentifiable food was roughly the same for the two islands (19 out of 68 as against 16 out of 64 cases).

Because the food could not be identified in a rather large number of cases, the results of the blind observations provide only an indication of the proportions in which the various types of food occur.

5.3.3.2. Regurgitations

Between 1966 and 1969, we examined on Terschelling 264 regurgitations vomited by chicks during weighing, ringing, and checking of the ringed birds (Table 18). Food regurgitated by other chicks of the same brood at the same time (and in most cases probably originally supplied by the same parent) was considered as one regurgitation. More regurgitations were examined from some broods than from others. Since this could have led, due to possible food specialization of the adult birds, to a certain bias, I have given both the number of regurgitations and the number of broods in which a given type of food was found. Since it was not known to which brood all the chicks belonged, the brood data concern a slightly smaller number of regurgitations than the total number examined. Since the regurgitations sometimes consist of more than one type of food, the values for the groups of food types are often smaller than the sum of the separate components.

It is evident from the data in Table 18 that marine fish were found most often in the regurgitations (in about three-fourths of all regurgitations and in more than four-fifths of all broods), followed by garbage (in about one-fourth of all cases) and marine invertebrates (in about one-sixth of the regurgitations and about one-fifth of the broods). Except for garbage, non-marine food was almost entirely absent.

The annual variations in the occurrence of fish and marine invertebrates as a group are not statistically significant, in contrast to the occurrence of garbage (χ^2 test, $0.025<P<0.05$). The occurrence of garbage was, however,

Table 18. Occurrence of various types of food in regurgitations of Herring Gull chicks on Terschelling (Part of the data concern chicks from nests with artificial brood-size)

Types of food	Regurgitations					Broods				
	1966	1967	1968	1969	Total	1966	1967	1968	1969	Total
Marine fish	52	67	67	10	196 (74.2%)	24	40	50	5	119 (82.6%)
Marine invertebrates	11	9	20	2	42 (15.9%)	6	7	14	2	29 (20.1%)
Sphaeroma rugicauda		1			1 (0.4%)		1			1 (0.7%)
Crangon crangon	6	5	3		14 (5.3%)	3	4	3		10 (6.9%)
Macropipus holsatus } *Carcinus maenas*	1	2	3	1	7 (2.7%)	1	2	3	1	7 (4.9%)
Mytilus edulis (length of shells < 10 mm)			8		8 (3.0%)			3		3 (2.1%)
Mytilus edulis (flesh only)			1		1 (0.4%)			1		1 (0.7%)
Cardium edule (flesh only)			5	1	6 (2.3%)			4	1	5 (3.5%)
Mya arenaria (pieces of siphons)	3	2	5	1	11 (4.2%)	1	1	3	1	6 (4.2%)
Asterias rubens	2	2	5		9 (3.4%)	2	2	5		9 (6.3%)
Terrestrial animals	2	2	1		5 (1.9%)	1	2	1		4 (2.8%)
Sturnus vulgaris	1				1 (0.4%)					
Insecta	1	2	1		4 (1.5%)	1	2	1		4 (2.8%)
Vegetable matter	4	2	3		9 (3.4%)	3	1	3		7 (4.9%)
Empetrum nigrum (berries)	1				1 (0.4%)	1				1 (0.7%)
Straw, leaves, and petals [1])	3	2	2		7 (2.7%)	2	1	2		5 (3.5%)
Unidentifiable			1		1 (0.4%)			1		1 (0.7%)
Garbage	9	30	22	2	63 (23.9%)	4	19	13	1	37 (25.7%)
Unidentifiable material	2	6			8 (3.0%)	2	2			4 (2.8%)
Number of regurgitations investigated	67	92	92	13	264	28	48	61	7	144

[1]) Presumably mainly swallowed by accident with other food.

strongly influenced by the size of the brood (5.3.3.5), which was artificially changed in the study area in connexion with other problems investigated between 1966 and 1968.

The chicks of some broods were handled much more often than others. Consequently, the data in Table 18 were not randomly collected and may therefore give a biassed picture of the occurrence of certain types of food. To investigate this point, the regurgitations in Table 18 which were collected randomly and derived from broods whose size had not been influenced by us, are shown separately in Table 19. The similarity between Tables 18 and 19 is so great that it may be assumed that no bias was introduced by the way the data in Table 18 were collected.

Table 19. Occurrence of various types of food in randomly sampled regurgitations of Herring Gull chicks from nests of natural brood-size on Terschelling

Types of food	1966	1967	1968	1969	Total
Marine fish	14	4	10	10	38 (72%)
Marine invertebrates	3	1	4	2	10 (19%)
Crangon crangon	2	1			3 (6%)
Macropipus holsatus } *Carcinus maenas*				1	1 (2%)
Mytilus edulis (length of shells $<$ 10 mm)			4		4 (8%)
Cardium edule (flesh only)				1	1 (2%)
Mya arenaria (pieces of siphons)	1		2	1	4 (8%)
Terrestrial animals	1				1 (2%)
Sturnus vulgaris	1				1 (2%)
Vegetable matter (leaf from a tree) [1]	1				1 (2%)
Garbage	3	2	6	2	13 (25%)
Number of regurgitations investigated	19	5	16	13	53

[1]) Presumably swallowed by accident with other food.

As already mentioned (5.2), the evaluation based on the frequency of occurrence of a given type of food can give an incorrect picture of the actual composition of the diet, because the quantities involved are not indicated. Therefore, in 1967 and 1968 we determined both frequency of occurrence and quantity in 95 regurgitations (total weight 2,524 g). These data concern part of the regurgitations shown in Table 18. In many cases it was not possible to isolate the various components in regurgitations with more than one type of food for separate weighing. In these cases the proportion of each such component was estimated on the basis of the size or the number of specimens of the prey in question.

More than two-thirds of the total quantity (1,741 out of 2,524 g) comprised regurgitations (68 in total) with only one type of food. In addition, the individual components of 10 regurgitations (186 g) containing more than one type of food could be weighed exactly. Thus the remaining quantity, in which the share taken by the various components could only be estimated, amounted to less than one-fourth of the total weight.

The results are shown in Table 20, in which the numbers between paren-

Table 20. Composition of the regurgitations of Herring Gull chicks on Terschelling, according to the weight (g) of the different types of food (The frequency of occurrence is given between parentheses)

Types of food	1967	1968	Total	Percentages
Marine fish	1,117 (44)	594 (24)	1,711 (68)	67.8 (72)
Marine invertebrates	95 (8)	147 (9)	242 (17)	9.6 (18)
Sphaeroma rugicauda	+[1](1)		+ (1)	(1)
Crangon crangon	12 (5)	3 (2)	15 (7)	0.6 (7)
Macropipus holsatus } *Carcinus maenas*	10 (2)	7 (1)	17 (3)	0.7 (3)
Mytilus edulis (length of shells < 10 mm)		1 (3)	1 (3)	< 0.1 (3)
Cardium edule (flesh only)		101 (2)	101 (2)	4.0 (2)
Mya arenaria (pieces of siphons)	63 (2)	7 (1)	70 (3)	2.8 (3)
Asterias rubens	10 (1)	28 (3)	38 (4)	1.5 (4)
Terrestrial animals	+ (2)		+ (2)	(2)
Insects	+ (2)		+ (2)	(2)
Vegetable matter (leaves and petals) [2]	+ (2)	+ (1)	+ (3)	(3)
Garbage	285 (22)	239 (8)	524 (30)	20.8 (32)
Unidentifiable material	47 (4)		47 (4)	1.9 (4)
Total	1,544 (62)	980 (33)	2,524 (95)	

[1]) + = negligible quantities.
[2]) Presumably swallowed by accident with other food.

theses indicate the number of times the food in question occurred in the regurgitations. Comparison of the frequency with which fish, marine invertebrates (as group), and garbage occurred (the other food groups occurred only sporadically) with the frequency of these groups in Table 18, shows that there are no great differences between the two. We may therefore assume that the regurgitations we weighed represented a random sample as far as the nature of the food was concerned.

It is evident from Table 20 that according to weight about two-thirds of the food consisted of fish, about one-tenth of marine invertebrates, about one-fifth of garbage, and less than one-fiftieth of other types of food. There proves to be a rather good agreement between the occurrence of food types and the food composition according to weight, although the former leads to a slight bias favouring marine invertebrates and garbage.

Our data agree with those collected on Terschelling in 1955 and 1956 (Rooth 1957). In 1955, of about 100 regurgitations 90 contained fish, 5 Starfish, and 5 Shrimps. In 1956, of about 40 regurgitations 35 contained fish, 3 Starfish, 2 Shrimps, and 2 crabs.

On Vlieland only a few regurgitations were collected. They are included in Table 17.

5.3.3.3. Stomach contents

Some of the invertebrates belonging to the diet of the Herring Gull, e.g. Mussels and crabs, have a hard shell. When a chick's gullet is full of these, their presence is easily palpable. During the course of the study I noticed on several occasions that chicks handled in this situation did not regurgitate, which suggested that the tendency to regurgitate might be influenced by the nature of the food, leading to a bias in the relevant data favouring soft food (fish and garbage). To investigate this point, I examined the stomach contents of 38 chicks during the last ten days of June 1969, as a supplement to the regurgitation observations. The age of these birds varied between 1 day and more than 3 weeks, but 33 of the 38 were less than 10 days old. The stomachs were examined immediately after the birds were killed. The results are shown in Table 21.

Table 21. Occurrence of various types of food in stomachs of Herring Gull chicks from Terschelling, 22–29 June 1969

Types of food	Occurrence
Marine fish	28 (88%)
Marine invertebrates	4 (13%)
Crangon crangon	1 (3%)
Macropipus holsatus } *Carcinus maenas* }	3 (9%)
Mya arenaria (pieces of siphons)	1 (3%)
Coleoptera	4 (13%)
Vegetable matter (straw) [1]	10 (31%)
Garbage	2 (6%)
Full stomachs	32
Empty stomachs	6

[1]) Presumably mainly swallowed by accident with other food. The straws were sometimes clustered, forming the beginning of a pellet.

Six stomachs contained only indigestible remains of food; these cases are given in Table 21 as empty. Of the other 32 stomachs, fish was found in 88%, marine invertebrates in 13%, beetles in 13%, garbage in 6%, and vegetable matter in 31%. The last percentage is remarkably high, but this material consisted entirely of straw and other dry vegetable matter which I assume was not eaten deliberately but taken together with food (however, see also Goethe 1937). In some cases this material showed the early stage of the formation of a pellet containing a few fish-bones and otoliths.

Comparison of the data in Table 21 with the regurgitation data of 1969 (Table 18) shows that there is hardly any dietary difference between the two. Consequently, there is no reason to assume that the regurgitation analyses give a biassed picture of the diet.

In 1960 and 1961, I had the opportunity to examine the stomach contents of 29 chicks killed by gull control measures on Vlieland. These birds varied in age from a few days to almost 6 weeks. Most of them were examined directly after they were killed, and only a few several hours later. The results are shown in Table 22.

Table 22. Occurrence of various types of food in stomachs of Herring Gull chicks killed on Vlieland

Types of food	July 1960	August 1960	July 1961	Total
Marine fish	6 [1]	2	1	9 (53%)
Marine invertebrates	3	4	1	8 (47%)
Jassa falcata	1			1 (6%)
Crangon crangon		1	1	2 (12%)
Carcinus maenas		1	1	2 (12%)
Mytilus edulis	3	2		5 (29%)
Cardium edule (flesh only)			1	1 (6%)
Asterias rubens	2	3		5 (29%)
Garbage	1	2		3 (18%)
Full stomachs	8	7	2	17
Empty stomachs	10	0	2	12

[1]) Two originating from siblings killed simultaneously.

The stomachs of 3 chicks contained no food remains at all, and 9 showed only indigestible material. The other 17 contained mainly marine organisms. The data indicate that a greater share was taken by marine invertebrates on Vlieland (8 out of 17 full stomachs) than on Terschelling (4 out of 32), and the proportion of fish (9 out of 17) was lower than on Terschelling (28 out of 32). The first result agrees with that of the direct observations. The differences between Terschelling and Vlieland possibly reflect a higher intensity of fishing by man off Terschelling as compared to Vlieland.

Summarizing the foregoing: it may be stated that the various results indicate that the food of the chicks on Terschelling during the period of the study was predominantly marine in origin. The main component was fish. Invertebrates were seen much less frequently, and also according to weight they did not account for a large proportion of the food-supply. Non-marine food other than garbage was rare. There was no great variation in the diet from one year to the other, except for the proportion of garbage. On Vlieland, marine invertebrates were taken more frequently and fish possibly less frequently than on Terschelling.

On the East Frisian Islands the food of the chicks is also reported to consist mainly of fish and marine invertebrates (Goethe 1937, Meijering 1954, Goethe 1956, Focke 1959, Ehlert 1961), but a larger proportion seems to be formed of invertebrates from the littoral and sublittoral zones than is the case for the Dutch Frisian Islands, and a smaller proportion is made up of garbage.

Otterlind (1948) found that off the NW coast of Skåne, Sweden, fish, mainly deriving from commercial fishery, took first place in the food of the chicks, followed by waste meat from refuse dumps on the mainland. Although shell fragments of molluscs were found in most stomachs investigated, this does not mean that molluscs were a common food, since Otterlind remarks that some of this material could have been taken up together with other food.

In Finland, Bergman (1939) found that small chicks were mainly fed with fish, at least partially deriving from commercial fishery. On the East Murman coast the food consists mainly of fish and molluscs (Belopol'skii 1961).

In the New England region of The United States, there is a strong specialization on Herring and Mackerel, refuse taken at fish piers, and garbage from dumps, when adults are feeding young (Drury 1964). In Newfoundland, on the contrary, many chicks seem to be fed with Mussels (Threlfall 1968).

Thus, in some regions fish, fish-waste, and garbage and other human refuse are the most prominent constituents of the food of the chicks, in others marine invertebrates are most important. We shall return to the large proportion of marine invertebrates in the food of the chicks on the East Frisian Islands in the discussion on chick growth in relation to food (6.6).

5.3.3.4. Species of fish identified

From the blind it was generally not possible to identify exactly the fish species regurgitated by the parents for their young. I shall therefore only mention that on Terschelling, of the 34 times that fish was regurgitated it consisted in 22 cases of round-fish (with certainty: Clupeidae, Gadidae, and *Scomber scombrus*) and in 5 of flat-fish. In 7 cases identification was impossible. On Vlieland, of 31 cases round-fish (with certainty: Clupeidae, Gadidae, Ammodytidae, and *Scomber scombrus*) was found 19 times, flat-fish (with certainty: *Solea solea*) 3 times, and unidentifiable fish 10 times.

Table 23 shows the occurrence of the various families of fish found in regurgitations and stomachs on Terschelling (the Vlieland data were not informative on this point). Table 24 gives a picture of the composition according to the weight of the various families of fish. There is rather good agreement between the percentages in the two Tables. The data indicate that the fish in the diet of the chicks were mainly Clupeidae, Gadidae, and flat-fish. A preponderance of one or more of these groups of fish in the food of the chicks has also been found on the East Frisian Islands (Leege 1917, Goethe 1956, Ehlert 1961), in the Barents Sea (Belopol'skii 1961), and in the New England region of The United States (Drury 1964).

Clupeidae. The regurgitations and stomachs contained otoliths of both Sprat *Sprattus sprattus* and young Herring *Clupea harengus*. The length of 34 otoliths lay between 1.1 and 1.9 mm, corresponding to a fish length of about 8 to 14 cm (Schmidt 1968). Both species are common along the Dutch coast during the summer months, albeit with strong fluctuations. Otoliths of Sprat were found 55 times, of young Herring 4 times. This ratio does not reflect the occurrence of these species in the western part of the Wadden Sea area (Swennen, pers. comm.). The difference may be due to ecological dissimilarities as a result of which young Herrings largely escape predation by Herring Gulls, but the birds may also catch Sprat selectively Experimental work with captive gulls showed that Herring Gulls prefer fatty

Table 23. Occurrence of various families of fish in regurgitations (1966–1969) and stomach contents (1969) of Herring Gull chicks on Terschelling

Families of fish	1966	1967	1968	1969	Total
Clupeidae	14	21	18	8	61 (27%)
Anguillidae		1		1	2 (<1%)
Gadidae	3+2? [1]	9+2?	7+1?	4	23+5? (13%)
Ammodytidae	2	2	4	6	14 (6%)
Callionymidae	1		1		2 (<1%)
Scombridae	1		4		5 (2%)
Triglidae		1			1 (<1%)
Pleuronectidae and Soleidae	5+2?	9+1?	12+3?	4+2?	30+8? (17%)
Fish with gray flesh [2]	1	6	9	7	23 (10%)
Fish with white flesh [3]	2	5	7	2	16 (7%)
Unidentifiable fish	23	12	8	4	47 (21%)
Number of regurgitations and stomachs with fish	52	67	68	37	224

[1]) ? = identification uncertain.
[2]) Mainly Clupeidae or Ammodytidae.
[3]) Mainly Gadidae or flat-fish.

Table 24. Composition of fish in food regurgitated by Herring Gull chicks on Terschelling, according to the weight (g) of the various families of fish found (The frequency of occurrence is given between parentheses)

Families of fish	1967	1968	Total	Percentages
Clupeidae	463 (15)	113 (5)	576 (20)	33.7 (29)
Anguillidae	22 (1)		22 (1)	1.3 (1)
Gadidae	220 (7)	168 (4)	388 (11)	22.7 (16)
	57? [1] (3)	29? (1)	86? (4)	5.0 (6)
Ammodytidae	5 (1)	22 (2)	27 (3)	1.6 (4)
Scombridae		67 (1)	67 (1)	3.9 (1)
Triglidae	29 (1)		29 (1)	1.7 (1)
Pleuronectidae and Soleidae	136 (6)	106 (3)	242 (9)	14.1 (13)
	14? (1)	9? (2)	23? (3)	1.3 (4)
Fish with gray flesh [2]	64 (3)	25 (2)	89 (5)	5.2 (7)
Fish with white flesh [3]	29 (2)	21 (3)	50 (5)	2.9 (7)
Unidentifiable fish	78 (7)	34 (2)	112 (9)	6.5 (13)
Total quantity and number of regurgitations	1,117 (44)	594 (24)	1,711 (68)	

[1]) ? = identification uncertain.
[2]) Mainly Clupeidae or Ammodytidae.
[3]) Mainly Gadidae or flat-fish.

fish (de Vries & Swennen, unpublished). Sprat not only has a higher proportion of dry material but also more fat than young Herring, as can be seen by drying the fish in an oven: fat drips from Sprat but not from Herring.

Gadidae. In the regurgitations and stomach contents I found otoliths of Whiting *Odontogadus merlangus* 9 times and of Haddock *Melanogrammus aeglefinus* once, but a better picture of the ratio of the various Gadidae species (and other large fish) is obtained from the heads found everywhere in the colony in the period during which chicks are present (see below).

Ammoditydae. I could only identify the Greater Sand Eel *Hyperoplus lanceolatus* with certainty, although one of the two (or both) native *Ammodytes* species was also present in the material. All three species are common along the Dutch coast (Nijssen 1968). The otoliths of 8 specimens had a length of 2.1 to 3.1 (4.5) mm, which corresponds to a fish length of about 15 to 20 (28) cm (Schmidt 1968).

Flat-fish. I was unable to identify all the otoliths of flat-fish with certainty. Once, an intact Sole *Solea solea* was regurgitated. On the basis of the otoliths found, I could only identify the Plaice *Pleuronectes platessa* with certainty. The length of 11 otoliths (various species) ranged between 1.4 and 3.6 mm, corresponding to a fish length of about 5 to 15 cm (Schmidt 1968).

Other species. A Common Eel *Anguilla anguilla* was found twice, a Common Dragonet *Callionymus lyra* twice, a Mackerel *Scomber scombrus* five times, and once a gurnard *Trigla* sp. Occasionally we found unidentifiable fish remnants not belonging to any of the species mentioned.

In the rearing period heads of rather large fish, picked to the bones, can be found everywhere in the colony. Small fish can usually be swallowed without much difficulty, even by small chicks, but large fish are usually ripped to pieces, especially when the chicks are very young, the head and bones left lying on the ground. Later in the season it is usual to find only heads. The heads almost always still contain the otoliths, so that species identification of the fish fed to the young is rather simple. Table 25 shows the data collected on Terschelling in 1966–1968.

Table 25. Occurrence of various species of fish in the food of Herring Gull chicks on Terschelling, based on the number of clean-picked heads with otoliths found in the breeding colony

	1966		1967		1968		Total
	June	July	June	July	June	July	
Gadidae							
Odontogadus merlangus	33	65	26	27	18	10	179
Trisopterus luscus			1	1			2
Melanogrammus aeglefinus					9	2	11
Gadus morhua	3	10	17	2	5	1 [1]	38
Carangidae							
Trachurus trachurus		4		1		4	9
Triglidae							
Trigla spec.					1	1	2
Pleuronectidae							
Limanda limanda		1					1
Pleuronectes platessa	1	1			2		4
Unidentifiable flat-fish		5	1			2	8
Total	37	86	45	31	35	20	254

[1] Found on 1 August.

G a d i d a e. It is evident from Table 25 that a little over 90% of the heads derive from Gadidae, the only group of large fish fed to the chicks in any numbers. The ratio of Whiting, Bib *Trisopterus luscus*, Haddock, and Cod *Gadus morhua* corresponds roughly to the occurrence of these species in June and July in the coastal waters of the North Sea (Swennen, pers. comm.). The occurrence of Haddock in 1968 is interesting because at present this species is rarely caught on the Dutch coast due to overfishing. But in the autumn of 1968, in contrast to other years, large numbers of Haddock were brought to Den Helder by commercial fishing boats (Swennen, pers. comm.), which makes it probable that there were more young Haddock off the Dutch coast in 1968 than in other years.

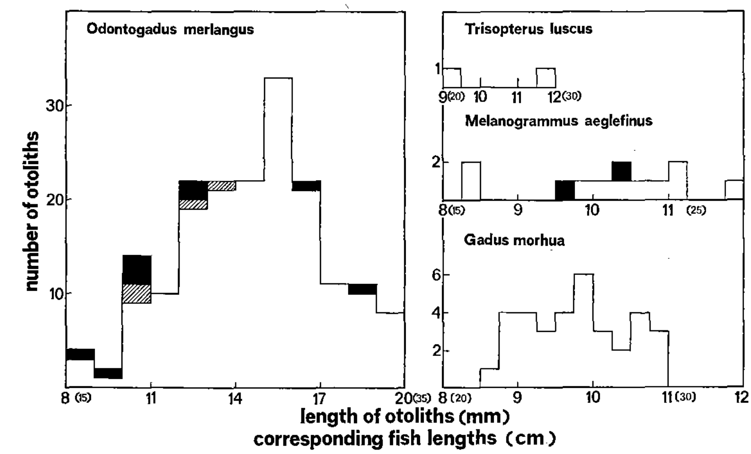


Fig. 15. Frequency distributions of the lengths of otoliths (between parentheses, corresponding fish lengths according to Werner 1963) of Gadidae spp. in the food of Herring Gull chicks on Terschelling in 1966–1969, based on clean-picked heads (blank) and partially intact fish (hatched) found in the colony, and regurgitations and stomach contents (black).

Figure 15 shows the frequency distributions of the lengths of the otoliths found in the heads, as well as those found in regurgitations and stomach contents and in partially intact fish found in the colony. The length of the corresponding fish taken from the data provided by Werner (1963) is also plotted. As can be seen, the length of the fish ranged from about 15 to 35 cm, with the greatest number lying between 20 and 30 cm.

F l a t - f i s h. In addition to Plaice, the Dab *Limanda limanda* was identified. The length of the 13 otoliths amounted to 4.3–5.8 (6.8) mm, corresponding to a fish length of about 19–28 (33) cm (Schmidt 1968).

O t h e r s p e c i e s. The length of the otoliths of the 9 Horse-mackerels *Trachurus trachurus* amounted to 8.1–10.1 mm, which according to Schmidt (1968) corresponds to a fish length of about 24–30 cm.

The fish lengths of the Gadidae and flat-fish found in the food of the chicks on Terschelling agree very well with those observed by Löhmer & Vauk (1969) in the food of summering Herring Gulls on Heligoland.

The fish found in the food of the young fall into three groups according to their vertical distribution. The first group comprises the pelagic species such as Sprat, Herring, the three species of sand eels, Mackerel, and Horse-mackerel, all of which live in schools and can occur very close to the surface. Because plunge-diving enables the Herring Gull to take prey to a depth of several decimetres, I assume that the pelagic species can be caught easily by the Herring Gull in this way.

The second group includes the bottom-fish such as Common Eel, Common Dragonet, gurnard, and the smaller flat-fish (<5–10 cm), which can occur in such shallow water that we may assume that they can also be caught by plunge-diving.

The third group comprises the various species of Gadidae – except the smaller animals (<5–10 cm) with more pelagic habits – and the larger flat-fish – except the Flounder *Pleuronectes flesus*, which belongs more to the preceding group. The members of this group also live close to or on the bottom of the sea but in deeper water than the preceding group and therefore cannot be taken by the gulls under normal circumstances.

Figure 15 shows that the Gadidae found in the food of the young were longer than 15 cm, which leads me to assume that they were all obtained directly or indirectly through commercial fishery. Although during the summer there is ordinarily no special fishing for Whiting, Haddock, or Cod (the Bib has no importance as a table fish) in the northern coastal waters, all four species occur in the nets of the coastal fishing boats trawling for Shrimps and flat-fish. Since the gutting and storage necessary for Whiting, Haddock, and Cod make it unprofitable to keep them, they are usually thrown overboard. The air-bladder of the Gadidae, however, is often ruptured due to the rapidity with which the nets are hauled in, and the species of this family form an easy prey for the gulls when thrown back into the water.

Although the smallest flat-fish found in the food can be caught by the gulls by plunge-diving, I assume that most of the flat-fish taken by the birds derive from commercial fishery. Firstly, most of them were longer than 5–10 cm and therefore must have lived at depths beyond the reach of the gulls; and secondly, I found no otoliths of the Flounder with certainty, although this species occurs more frequently in shallow water than do the Plaice and Dab. To simplify matters, I have assumed for the following calculations that all the flat-fish were taken through commercial fishery, which may have entailed a slight over-estimate.

In Table 26 an attempt has been made to estimate the share taken by commercial fishery in the food-supply of the young. With respect to the frequency of occurrence, Table 26 is based on the data in Tables 18 and 23,

Table 26. Estimated contribution of commercial fishery to the diet of Herring Gull chicks on Terschelling in 1966–1969 (Frequency of occurrence is given for all years; composition of food, according to the weight of food items, only for 1967 and 1968 (data between parentheses); all data are given in percentages and based on data from Tables 18, 20, 23, and 24)

	1966	1967	1968	1969	1966–1969 combined
Gadidae	9.6	16.4 (24.8)	11.8 (33.2)	10.8	12.5 (27.7)
Flat-fish	13.5	14.9 (13.4)	22.1 (19.4)	16.2	17.0 (15.4)
Fish with white flesh	3.8	7.5 (2.6)	10.3 (3.5)	5.4	7.1 (2.9)
Total (a)	26.9	38.8 (40.8)	44.2 (56.1)	32.4	36.6 (46.0)
Marine fish (b)	77.6	72.8 (72.3)	72.8 (60.6)	76.9	74.2 (67.8)
Total contribution of commercial fishery to diet (a x b)	20.9	28.2 (29.5)	32.2 (34.0)	24.9	27.2 (31.2)

and with respect to the weights, on those in Tables 20 and 24. The percentages of the Gadidae, flat-fish (both including the uncertain identifications), and white-fleshed fish (mainly Gadidae and flat-fish) were calculated from the data in Tables 23 and 24 (for instance, occurrence Gadidae 1966 from Table 23 amounts to $(3 + 2) / 52 \times 100\% = 9.6\%$. The total of the three components (a) gives the percentage of fish deriving from fishery. Tables 18 and 20 give the percentage of fish in the total diet (b). Thus, a × b gives the share of commercial fishery in the total food-supply.

According to Table 26, the occurrence of fish from commercial fishery showed little fluctuations in 1966–1969 (21–32%). On a weight basis, this share was 30% in 1967 and 34% in 1968. When the share taken by garbage (Tables 18 and 20) is included, the human contribution to the food-supply in the different years amounted to 34–61% on the basis of frequency of occurrence and to 48–58% on a weight basis.

5.3.3.5. Feeding of garbage in relation to brood-size

On Terschelling, the chicks' food was composed predominantly of fish. Garbage was found in only one-fourth of all regurgitations (5.3.3.2). There is, however, a positive correlation between the size of the brood and the occurrence of garbage in the chicks' food (Fig. 16). The increase was significant in 1967 and 1968 (test for trend in an ordered K × 2 table, $P = 0.001$ and $P = 0.038$, respectively) and in 1966 almost significant ($P = 0.068$).

Throughout the chick stage the young are dependent for their food-supply on the parents. The total food requirement of a brood of young gulls is directly proportional to the number of chicks (since young Herring Gulls are semi-precocial, there is no decreasing heat loss and therefore no change in the energy requirements with increasing brood-size as in altricial and semi-altricial young; cf. Royama 1966 and Mertens 1969 for the Great Tit *Parus major*). We shall see (6.6) that chicks which regurgitated garbage as well

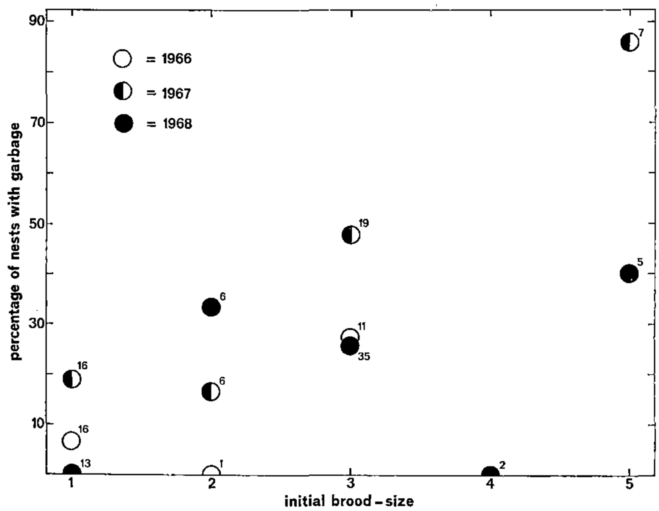


Fig. 16. Occurrence of garbage in the regurgitations of Herring Gull chicks on Terschelling, in relation to initial brood-size. The numbers of broods studied are shown beside the symbols.

as natural food (including fish from commercial fishery) grew faster than otherwise comparable chicks regurgitating only natural food. This means that in terms of energy the parents bringing garbage as well as natural food supply their broods with more food than the parents bringing only natural food. It therefore seems probable that the positive correlation between brood-size and the occurrence of garbage in the diet must be explained as a reaction on the part of the parents to satisfy the increasing food requirements of the broods with increasing brood-size. The data indicate that even parents with a brood of 3 chicks were not always able to satisfy completely the food requirements of their young under natural conditions.

If, in terms of energy, the gulls feeding their young on garbage supply more food and therefore can satisfy the food requirements of the young more easily than gulls supplying only natural food, the question arises of why the parents of small broods supplied so little garbage. The most probable answer, in my opinion, is that the availability of garbage on Terschelling is limited. Although some breeding birds foraged on the dumps of the nearby island of Ameland and the Frisian mainland (as revealed from Ameland- and Friesland-marked butter wrappings found in the gullery on Terschelling, and from recoveries of marked wrappings we threw out on the Leeuwarden dump, about 35 km from this gullery; see also 5.3.2), most of the garbage was probably obtained on Terschelling itself.

If the assumption of the limited availability of garbage on Terschelling is correct, gulls can only obtain such food at the expense of others. Under these circumstances, fights can be expected to occur repeatedly. It is suggested that because of their inability to satisfy completely the food requirements of their chicks in a natural way, the gulls with the largest broods have the greatest need to acquire garbage and will therefore be dominant in such fights over food.

5.3.3.6. Digestion

The food of the Herring Gull includes hard indigestible components later regurgitated as pellets or evacuated with the faeces. The chicks are able to produce pellets at very early ages. A 3 to 4-day old chick to which I had fed small Mussels produced a pellet of shell fragments about the size of a marble. Goethe (1937) reported the production of a pellet by a 2-day old chick.

The pellets of adult gulls regularly contain fish-bones, which means that not all or none of the bones are digested by these birds. This does not hold for the chicks, as I found during the feeding of gull chicks in captivity. In 1968, my 25 chicks consumed during the first 6 weeks not only about 150 kg Sprat, young Herring, and Ammodytidae species, all of which have rather soft bones, but also 64 kg Gadidae species, Horse-mackerel, and flat-fish, which have hard bones. But I never saw a single bone of any of these fish again, or even the very hard otoliths. Since the floor of the gull run was covered with sand, any pellets would certainly have been observed. When these birds were 3 to 4 months old they did regurgitate the bones of Horse-mackerel. Evidently, the Herring Gull can completely digest fish-bones when young, but later cannot do so or only partially.

Van Dobben (1952) made similar observations in the Cormorant *Phalacrocorax carbo*. Young birds fed fish for several weeks in captivity never regurgitated the bones. Free adult birds, to the contrary, regurgitated most of the bones, which were not noticeably affected by digestive juices.

It seems reasonable to assume that the gastric juice of young birds have a lower pH than those of adults. Vonk, Brink & Postma (1946) indeed found in young Chickens a lower pH (2.77) than in older chicks and adults (3.08). As far as I know, this is the only species for which data on the pH of the digestive juices of both young and old birds are available. In his young Cormorants, van Dobben found very low pH values (0.9–2.9) 30 minutes after the chicks had been fed with fish, and he says that "it would be surprising if fish-bones escaped digestion in such an acid milieu". At the end of the digestive process a higher pH (4.6) was found, however. I know of no data on the pH values of the digestive juices of adult Cormorants.

This phenomenon has not only a causal but also a functional aspect. Both the Herring Gull and the Cormorant digest the bones of fish only in the period during which the skeleton of the bird is developing, but some species such as the Grey Heron *Ardea cinerea* still digest the bones at older ages as well (Lowe 1954).

Since there are indications that young Herring Gulls fed on Shore Crabs (whose external skeleton is not digested) do not grow as fast as chicks supplied with fish (6.6), it is possible that the substances released by the digestion of fish-bones are used by the chicks for skeletal growth.

The shells of molluscs are also not digested by the chicks. Crabs and molluscs form a large proportion of the food of the adult gulls, but the chicks' food is composed mainly of fish. It therefore seems possible that the large share taken by fish in the diet of the latter may be also functional in this respect.

5.3.4. Differences in diet between adults and chicks

In the Dutch Wadden Sea area the food of the young consists for the most part of fish but that of the adults mainly of marine invertebrates (molluscs, crabs, and Starfish). Although the data on the food of the chicks (based mainly on regurgitations and stomach contents) and of the adults (based mainly on pellets and faeces, and therefore leading to a bias favouring marine invertebrates with a high proportion of indigestible material) are only directly comparable to a certain extent, it is nevertheless clear that there is a distinct difference between the food of these two groups, a phenomenon already brought forward by Goethe (1937), Meijering (1954), and Ehlert (1961). It is doubtful, however, whether in the period when there are young, the adults actually make a distinction between their own food and that of the chicks, as claimed by Ehlert (1961).

When no chicks are present, the adults feed primarily during the period of low tide, and rest during high tide. But as soon as the chicks have hatched this tidal rhythm is disturbed and the parents forage throughout the day. Because the intertidal zone is not accessible when under deep water, the shift from marine invertebrates to fish found in our study may be partially explained by the breaking of the gulls' tidal rhythm. In the German Wadden Sea area, however, the shift is mainly from molluscs to Shore Crabs (which under natural conditions are only to be captured during the low-water period), and therefore other factors must also play a role here.

According to Meijering (1954), the chicks require soft food when they are small, and Goethe (1956) states that molluscs are not a suitable food for the young. In 1964, as early as the second week, my captive chicks regularly consumed large quantities of small Mussels (of the same size as observed, albeit seldom, in the food of the chicks in the colony), which the chicks cracked normally in the gizzard, the remains being regurgitated or evacuated with the faeces in the normal way. Consequently, any unsuitability of molluscs as food for chicks must pertain to the first week of life.

Although the older chicks are able to cope with molluscs, I seldom found Mussels and never Cockles (at least in the shell) in the food of the chicks on Terschelling and Vlieland. Evidently, the parents continue to supply fish much longer than is physiologically necessary. This might of course be traceable to a kind of tradition concerning the foraging area or the methods used, but there is no certainty on this point.

The quantity of food that the parents can carry at one time is limited and usually is consumed by the larger chicks at one feeding. In view of the indications that the parents are not always able to satisfy completely the food requirements of the chicks (5.3.3.5), it may be of importance that the parents bring food with the highest possible nutritional value and as low as possible a proportion of indigestible material. Fish forms such a type of food. Marine invertebrates, to the contrary, have a large quantity of indigestible material representing useless ballast to be transported by the parents. It therefore seems likely that chicks fed exclusively with marine invertebrates receive less food than those receiving fish.

Lastly, there is still another possible explanation of the feeding of the chicks with fish throughout the chick stage. The shells of molluscs, the exoskeletons of crabs, and the calcareous plates and spines of Starfish, unlike the bones of fish, are not digested (5.3.3.6) but regurgitated or evacuated with the faeces. I have postulated in that section that during the digestion of fishbones substances might be freed that are of importance for the building of the skeleton, whose development does not terminate until the sixth week (see Maschlanka 1954).

I performed some preliminary experiments to test these hypotheses, but the results are too meagre to permit the drawing of conclusions.

5.3.5. Effect of predatory behaviour of the Herring Gull on other species of birds

It is striking that so few remains of birds were found in the pellets and faeces, since on the Frisian Islands the Herring Gull has the reputation of being a formidable robber of eggs and chicks of ducks, waders, and terns (see e.g. van Dobben 1934, Mörzer Bruyns 1958). This might be an indication that in recent years there has been a sharp reduction in the predation by the Herring Gull on the Frisian Islands, but this is hardly likely since direct observations showed that the robbing of young birds still continues on a large scale. It is more probable that the predatory individuals are mainly young birds and others that for some reason do not breed, so that they seldom or never visit the colony, as a result of which part of the predation goes unobserved in the investigation of pellets and faeces collected in the colony. It is also possible, however, that the presence of the observer in the field alarms the parents of the other bird species, so that their young are more exposed to predation by Herring Gulls than under normal circumstances. I am unable to judge which of these two factors is more important on the Frisian Islands.

Because of its predation on eggs and young, the Herring Gull is everywhere considered to be harmful for other bird species. Control of Herring Gulls was practised in The Netherlands for several decades, but was terminated in 1966. It is still continued in other countries, however.

The bad reputation of the Herring Gull is based primarily on observations of robbing of eggs and young and seldom on the influence of this predation on the populations of species affected. I shall therefore include here a few data on the population fluctuations of the Eider, Shelduck, and Avocet *Recurvirostra avosetta* on the island of Vlieland, three species so heavily predated by the Herring Gulls on this island that at the end of the Fifties the object of control was still to clear the island of Herring Gulls altogether (Mörzer Bruyns 1958). A review of the fluctuations in the numbers of breeding birds of these species has appeared elsewhere (Spaans & Swennen 1968), and it will suffice here to give a rough idea of the patterns.

Since the beginning of the present century, the Eider has been a breeding bird on Vlieland. Initially, the population increased so slowly that in 1925 the number of breeding pairs was estimated to be only about ten. After 1925 there was a rapid increase, and in 1959 there were about 3,500 pairs, in spite of the large numbers of eggs and chicks taken annually by the gulls, which during the same period also increased in number (Mörzer Bruyns 1958).

The Shelduck also belongs to the species of which the gulls take a heavy toll on Vlieland, and with a few exceptions (see below) almost no offspring reached the fledging stage for several decades (unpub. annual reports of State Forestry Service, Vlieland). Despite this predation, the population has fluctuated since the Twenties between 50 and 150 pairs. But during the Sixties, higher water-levels in the polders in the western part of the island (maintained as a nature reserve) led many ducks to stay with their young in these polders, where they were much less vulnerable to predation by gulls than on the tidal mudflats. As a result, appreciably more chicks fledged than previously. In 1963 we estimated the number of large ducklings at a few hundred, and in 1965 at about 1,000. But in later years these favourable breeding seasons failed to result in an increase in the number of breeding pairs. The high breeding success seems to have had no noticeable effect on the breeding population. The absence of any increase in the number of breeding pairs after the favourable years suggests that a level of about 150 pairs is the upper limit under present conditions. It is not known, however, what factors determine this limit.

The breeding population of the Avocet has fluctuated, except for a few sharp drops, between 40 and 85 pairs since the end of the Twenties (before that the species had not bred on Vlieland for many years), and the annual production of young birds has been low.

Apparently, the population fluctuations of these three species on Vlieland have not been influenced noticeably by the heavy toll of the new generation taken annually by the Herring Gull. The number of breeding pairs of the Eider even increased in the face of this predation. These results can only be explained by the assumption that the populations of these species on Vlieland are not closed but open, the gulls' predation being compensated for by immigration of birds from other places. The situation may of course be quite different elsewhere, but the situation on Vlieland shows that even large-scale local predation needs not necessarily lead to the disappearance of the prey species. Consequently, it is a mistake to depreciate and therefore control the Herring Gull (and this of course also holds for many other animal species) solely on the basis of its habit of robbing eggs and young.

5.4. DIET IN AUTUMN AND WINTER

In the autumn and winter in the Wadden Sea area the species is primarily a bird of the tidal mudflats and the sublittoral zone, the periods of foraging and resting being determined entirely by the rhythm of the tides (5.1). On the basis of the pellets and faeces found at the high-tide refuge areas, an impression could be obtained of the nature of the diet of these gulls during this period of the year. Because other gull species (mainly Great Black-backed and Common Gulls) were regularly seen among the Herring Gulls, an exact analysis of the material was not made, and we only noted the main prey species. On Terschelling, these were Cockles and sometimes Starfish. On the mudflat side of the island of Vlieland Cockles again predominated markedly, but on the North Sea coast Mussels (influence of the local stone groynes; cf. 5.3.2). On both islands few crab and fish remains were found, in agreement with the pellet and faeces data from the colony in the early spring (see 5.3.2). On the North Sea beach of Terschelling, I also found tough yellowish faeces lacking identifiable components; according to our observations in captive gulls, these were probably faeces of gulls that had eaten fat or other offal. In general, the data suggest that in the autumn and winter the diet in the Wadden Sea area consists primarily of Cockles.

A few words must be said about the share taken by commercial fishery on the Wadden Sea and along the North Sea coast in the food-supply of the Herring Gulls. It is striking that the pellets and faeces show little influence of fishery, whereas the gulls are seen so frequently, sometimes in large flocks, following the fishing boats on the Wadden Sea and the North Sea. I attribute this phenomenon to a bias in the observations. The gulls living exclusively or partially on what fishery offers are much less dependent on the tides and therefore show a much less pronounced tidal rhythm. But it is difficult to obtain quantitative data on the numbers that live on fishery. Not all the birds rest and forage at the same time, and therefore the composition of the flocks following the boats changes continually. The other birds are meanwhile digesting their meals, bobbing on the water or resting on exposed flats, indistinguishable from gulls that forage for natural food. However, when the whole fishing-fleet is at sea the total number may be put at several thousands.

Under certain circumstances large numbers of marine organisms are washed up on the North Sea beaches of the Frisian Islands, which attract not only Great Black-backed and Common Gulls but also thousands of Herring Gulls. The nature of this food is highly variable. Sometimes the beach is full of Starfish, at other times mainly of molluscs (predominantly *Mactra corallina, Donax vittatus, Angulus fabula,* and *Ensis* spp.) lying piled in high banks reaching a height of several decimetres locally. But such situations occur only a few times each winter. Ordinarily, the quantity of washed-up material is limited and of little importance as a source of food for the gulls.

On the North Sea the occurrence of Herring Gulls is restricted to a narrow strip along the coast. According to observations made by Swennen (pers. comm.), the species forages only as far out as 20 km from the coast. Presumably, the food of these gulls consists of self-caught fish but also, probably to an important extent, of fish obtained from commercial fishery and offal discarded by fishing boats and other ships. The share of these components in the diet is not known.

On the mainland of the northern provinces, the occurrence of the Herring Gulls is restricted almost entirely to places where refuse is present, such as refuse dumps, factory sites, cities, villages, and harbours (4.3.4).

As has already been mentioned, it is difficult to distinguish which part of the population on the North Sea and the Wadden Sea obtains its food through man and which part forages naturally. The foraging possibilities vary widely for both bodies of water (cf. 4.2.1.3 and 4.3.2.3). Under less favourable foraging conditions, a proportion of the gulls from the Wadden Sea (and possibly also from the North Sea) shifts to the mainland. As a result of these shifts, the numbers on the mainland fluctuate widely. According to our estimates (4.3.4), in the autumn and winter of 1967–1968 at least 32% of the total population in the northern part of The Netherlands was constantly feeding on the mainland, whereas during less favourable foraging conditions on the Wadden Sea (and North Sea?) the percentage of gulls on the mainland increased to maximally 77–82%. Since on the mainland the Herring Gulls fed almost exclusively on garbage and other human waste, the percentages mentioned give a rough idea of the proportion of the winter population that lived constantly or partially on food supplied indirectly by man.

Recently published data on the food and distribution of Herring Gulls outside the breeding season in other regions (Kadlec & Drury 1968, Drury & Nisbet 1969, Löhmer & Vauk 1970) suggest that the high proportion of garbage and other human waste in the diet of the gulls in that season is not a local phenomenon (see also Fordham 1968 for the related Dominican Gull).

5.5. FOOD INTAKE OF FULL-GROWN GULLS

Little is known about the daily food requirements of Herring Gulls. It therefore seems worth-while to include my data on this point here.

In general, it is not possible to observe individual foraging Herring Gulls in the field for any length of time. Usually, one loses track of them too soon, either because the foraging area is too large or because the birds forage too close together. I have therefore supplemented my data from the field on food intake with observations on captive birds.

5.5.1. Field data

These data were collected on Vlieland in the summer of 1961. The food consisted of *Cardium edule*.

5.5.1.1. Study area and methods

The data are derived from gulls foraging on a Cockle bed south of the village of Oost-Vlieland. At low tide the bed was over 1,400 m long and at its widest about 140 m wide, lying with the nearest point about 100 m from the coast. A deep channel lay on both sides of the bed, reducing human disturbances to a minimum.

The greater part of the bank was covered with algae (*Enteromorpha* spp. and *Ulva lactuca),* some patches remaining covered with a thin layer of water at low tide.

The observation post was situated on the dike running along the mudflat side of the island. The birds were observed with a 40 × 60 telescope, at distances varying from 100 to 300 m.

During the period of the study the infauna of the bed was investigated quantitatively several times.

5.5.1.2. Foraging aspects

On the bed, only Cockles from the year-classes 1961 (first-year Cockles) and 1960 (second-year Cockles) were abundant. Both groups were eaten by the gulls, but not in the same proportion by all individuals (Table 29).

Table 27 shows the mean shell lengths of the Cockles in the substrate and

Table 27. Mean shell length (in mm) of *Cardium edule* sampled in the substrate and taken by Herring Gulls near Vlieland in the summer of 1961 (The number of shells measured is given in parentheses)

Observation date	Substrate		Taken by Herring Gulls [1]	
	year-class 1961	year-class 1960	year-class 1961	year-class 1960
19 July		20.8 (19)		
14 August	9.9 (199)	21.5 (119)	10.2 (119)	20.6 (17)
9 September	12.6 (275)	23.8 (91)		

[1]) Based on regurgitated shells.

of those taken by gulls. The results suggest that the birds made no selection according to size within a given year-class of Cockles.

The gulls started feeding shortly before the bed emerged. Paddling against the outgoing tide, they continually ducked their heads under water and regularly brought up a Cockle.

While foraging on the exposed flats, the gulls generally did not walk much. Second-year Cockles were taken from the mud with jerky movements of the bill, first-year Cockles were washed out by treading (cf. Goethe 1956, Tinbergen 1962). The Cockles were swallowed with intact shell.

The shells are cracked in the gizzard, the small fragments being evacuated with the faeces, the large ones regurgitated as pellets. Because the shells of first-year Cockles, unlike those of the older ones, are thin and brittle, the remains of the former tend to be evacuated more often with the faeces and less often as pellets than the latter (Table 28).

Table 28. Number of pellets and defaecations produced per hour by Herring Gulls after eating *Cardium edule* of different year-classes; Vlieland, summer 1961 (Total observation time (in hours) is given between parentheses)

Year-class	Pellets	Defaecations
1960	1.5 (12.5)	5.8 (11.3)
1961	0.5 (5.9)	15.2 (5.9)

The gulls foraged throughout the period of low tide (possibly with somewhat less intensity towards the end of the period). The total foraging activity (i.e. all actions necessary to obtain and swallow the Cockles) occupied only part of the total low-tide period (Table 29, column 4). The gulls rested intermittently a little higher up on the flats. In these intervals of rest the shells were cracked. At the end of a resting period, a pellet was often regurgitated. I have never seen a Herring Gull do so during active foraging.

5.5.1.3. Intake of Cockles

Table 29 shows the food intake of individual gulls that could be observed for at least 30 minutes. Numbers 1–4 and 10 consumed second-year Cockles almost exclusively. If the first-year Cockles consumed by number 1 and 3 are each equated with one second-year Cockle, the consumption of these five gulls averages 50 (38–65) second-year Cockles per hour. The food intake of the three gulls consuming only first-year Cockles (numbers 5, 7, and 8) averages 365 (296–412) Cockles per hour. The intake of numbers 6 and 9, which consumed Cockles of both year-classes, averaged 27 second-year and 137 first-year Cockles per hour.

During the period o fthe study, the Cockle bed was usually exposed for $4^1/_2$ to $5^1/_2$ hours per low-tide period. If we take 5 hours as the average duration, the intake of food amounts to 248 (190-325) second-year or 1,825

Table 29. Consumption of *Cardium edule* by Herring Gulls in the field; Vlieland, summer 1961

Bird nr.	Date	Length of observation period (min)	Time spent in foraging (%)	Consumption: Number of Cockles, total (1)[1]	(2)[2]	per hour (1)[1]	(2)[2]	Volume of meat (ml) per hour
1	3–8	108	14.6	67	6	37	4	20.4
2	3–8	87	15.3	58	—	40	—	22.0
3	7–8	125	10.5	131	14	64	7	36.0
4	9–8	133	10.3	132	2	60	1	33.6
5	23–8	97	43.4	—	625	—	387	27.9
6	24–8	30	14.2	5	108	10	216	22.4
7	25–8	95	39.5	—	468	—	296	22.8
8	28–8	37	33.5	—	254	—	412	34.8
9	29–8	53	18.5	38	50	43	57	33.4
10	1–9	76	8.4	56	—	44	—	30.1

[1] (1) = Cockles from year-class 1960.
[2] (2) = Cockles from year-class 1961.

(1,480-2,060) first-year Cockles. Since the gulls started feeding before the bed emerged, the total consumption was somewhat higher. On the basis of some incidental observations, the extra number may be put at some tens of second-year Cockles; the maximum number I observed was 46, and this number has been adopted for present purposes. The total consumption per low-tide period thus amounts to about 294 second-year or 2,165 first-year Cockles (1 second-year Cockle being put, on the basis of the average intake per hour, equal to 7.4 first-year Cockles).

The gulls continue to forage during nocturnal low-tide periods, but no quantitative data on the intake in these periods are available. From the behaviour of the birds on light nights, I suppose there is no difference between the intake on such nights and that during the day, but the intake may be lower on dark nights. This would give an average intake estimated to about 588 second-year or 4,330 first-year Cockles per gull per 24 hours.

On some days the volume of meat of Cockles taken from the substrate was determined by measurements of the water displacement of previously wiped specimens. Data for other days were obtained by interpolation.

The last column in Table 29 shows the intake of Cockle meat, which averaged 28.3 (20.4–36.0) ml per hour. During the period in which the Cockle bed was exposed, the intake therefore amounted to $5 \times 28.3 = 142$ ml, plus 25 ml during the period preceding exposure (46 second-year Cockles; see before). This amounts, per 24 hours, to $2 \times 167 = 334$ ml.

5.5.2. Experimental data

In the autumn and winter of 1967 and 1968 I determined for a number of types of food the quantity consumed daily by full-grown Herring Gulls in captivity.

5.5.2.1. Material and methods

The gulls were all first-year birds taken from the gullery as one day-old chicks and raised in captivity. They were kept in outdoor cages measuring 8.0 × 3.5 × 0.85 m (winter 1967–1968) and 4.0 × 3.5 × 1.7 m (autumn 1968) and were provided with fresh water daily.

After the chick stage the diet consisted of bread, canned dog and cat food, fish, and meat waste. During the experiments, the birds received Horse-mackerel, Sprat and young Herring (mixed) or bread. The Horse-mackerels were large fish (about 250 g), which were cut into pieces before use. Sprat and young Herring arrived mixed and frozen in lots of a few kilograms and were therefore fed together, but to obtain an idea of the ratio between the two species a sample containing about 25 fish was taken from each batch, tallied and weighed. On the basis of these data, the quantity of each species fed to the birds was calculated. Sprat and young Herring averaged 8 g in weight and were fed whole. Bread was broken into pieces.

Food was supplied ad lib. during the experiments. It was offered in the morning and supplemented later in the day when necessary. At the end of the afternoon the remaining food was removed and weighed. On the basis of the dry weight of fresh and left-over food, a correction was applied to adjust for any change in the weight of the food due to drying or water absorption.

The gulls were weighed at the beginning and end of the experimental periods. Weighing was done before food was given, to permit comparison of data.

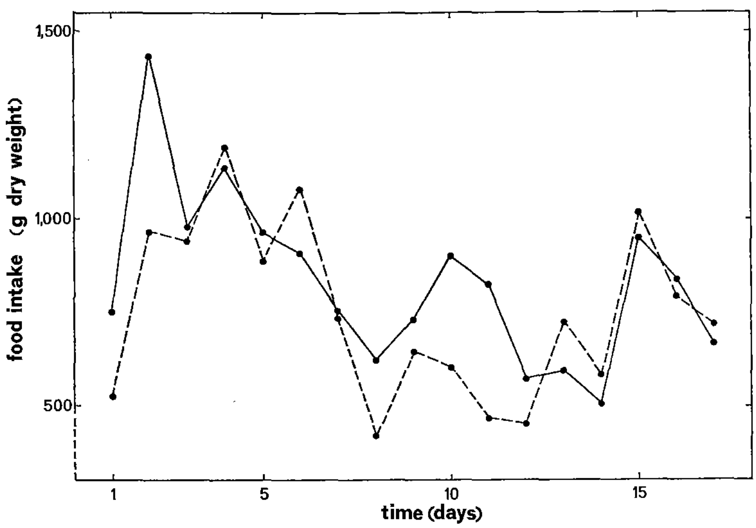


Fig. 17. Fluctuations in the daily food intake of two groups of full-grown captive Herring Gulls (—— = 14 birds; - - - = 11 birds).

Table 30. Daily food intake of first-year Herring Gulls in captivity

Types of food	Date	Number of days	Number of gulls	Number of meals	Mean bird weight (g) at beginning and end of observation period	Food intake (g)				Remarks
						Total		Per bird per day		
						fresh	dry	fresh	dry	
Horse-mackerel	19-09/23-09-1968	4	14	56	1,163–1,232	20,316	6,391	363	114	
	19-09/22-09-1968	3	11	33	1,130–1,175	12,129	3,816	368	116	
Sprat and young Herring (mixed)	28-09/15-10-1968	17	14	238	1,151–1,279	47,387	14,112	199	59	} onset moult of body feathers
	28-09/15-10-1968	17	11	187	1,130–1,315	42,880	12,747	229	68	
Bread	31-10/03-11-1967	3	5	15	960–933	1,205		80		
	6-11/12-11-1967	6	5	30	974–957	3,042	2,010	101	67	
	3-12/10-12-1967	7	4	28	1,000–953	1,793	1,170	64	42	
	22-09/28-09-1968	6	11	66	1,175–1,130	6,503	4,229	99	64	
	23-09/28-09-1968	5	14	70	1,232–1,151	3,353	2,161	48	31	

5.5.2.2. Daily intake

Figure 17 gives a picture of the variations in the daily consumption during a diet of Sprat and young Herring (the longest series of observations available).It is clear that there is a wide fluctuation from day to day in the amount of food consumed.

The data on the mean daily intake are shown in Table 30, from which it can be seen that the mean food consumption calculated over a couple of days or longer can also show considerable variation. It is evident, however, that the body weight of the gulls changed also during the experiments. According to Figure 18, there is a distinct relation between mean food intake and mean weight changes during the experiments. The data in Figure 18 suggest that in captivity a gull requires 100 to 200 g of food per day, dependent on the nature of the food, to maintain a constant weight. The intake of the various types of food could of course be compared more accurately if the food consumption was expressed in the quantity of calories taken, but unfortunately I was not in the position to determine these values.

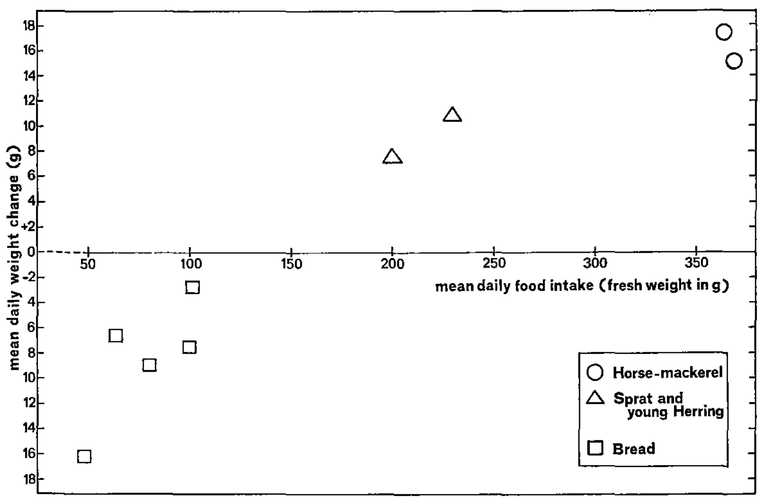


Fig. 18. Relation between mean daily food intake and mean daily weight change of full-grown captive Herring Gulls (based on data from Table 30).

The variation in intake was much smaller within one type of food than between various types of food. Obviously, not all types of food are equally liked. Taste probably plays an important role here. Preference tests with captive Herring Gulls (de Vries & Swennen, unpublished) have shown that this species can distinguish between and shows preferences among a substantial series of prey species, with a pronounced preference for fatty fish.

The food intake of wild gulls is certainly higher than that of our captive birds, which did not have to search for their food and did not fly much in

Table 31. Daily food intake of some fish-eating bird species

Species	Body weight [1] (g)	Mean daily food intake (g)	(% of body weight)	Remarks	References
Podicipitidae					
Podiceps cristatus	ca. 1,000	ca. 260	ca. 26	hungry bird in captivity	Heinroth & Heinroth (1928)
	ca. 1,000	ca. 200	ca. 20	estimation for wild birds	Heinroth & Heinroth (1928)
	740	157	21	captivity	Knopfli (1956)
Phalacrocoracidae					
Phalacrocorax carbo	ca. 2,500	nearly 500	ca. 20	Herring; zoo	Madsen & Spärck (1950)
	ca. 2,000	400	ca. 20	estimation for wild birds	van Dobben (1952)
Ardeidae					
Ardea cinerea	ca. 1,650	340	ca. 21	trout; captivity	Lowe (1954)
	ca. 1,650	501	ca. 30	captivity	Creutz (1958)
Ciconiidae					
Mycteria americana	2,115	340 (346 kcal)	16	captivity	Kahl (1964)
	2,500	520	21	estimation for wild birds	Kahl (1964)
Plataleidae					
Platalea leucorodia	1,960	ca. 500	ca. 26	freshwater fish; captivity	Koenig (1952)
Anatidae					
Mergus merganser americanus	1,160	447	39	captivity	White (1957)
	1,203	385	32		
	ca. 1,200→1,050	310	ca. 26–30		
Laridae					
Larus argentatus	1,163→1,232	363	29–31	Horse-mackerel; captivity	this paper
	1,130→1,175	368	31–33		
	1,151→1,279	199	16–17	Sprat and young Herring; captivity	this paper
	1,130→1,315	229	17–20		
Alcidae					
Uria aalge	ca. 1,050	ca. 60	ca. 6	Herring and sand eel; estimation for wild birds in East Murman	Belopol'skii (1961)
Uria lomvia	ca. 1,000	ca. 100	ca. 10	estimation for wild birds in Novaya Zemlya	Uspenskii (1956), in Belopol'skii (1961)

[1] Where not mentioned by authors, values given here are approximate mean values taken from handbooks.

their cages. Since flying takes considerable energy (cf. Pearson 1950, Lasiewski 1963, LeFebvre 1964, Tucker 1968), the most important factor in the difference between the intake of wild and captive gulls is probably the energy required by the former for flying back and forth from the resting places to the foraging areas. Without more data on the energy expenditure of resting and flying gulls it is impossible, however, to estimate the factor by which the data on captive birds must be multiplied to obtain an approximation of the situation in wild birds.

The literature contains few data on the quantity of the daily food intake. Bruns (1963) mentions a figure of 1 kg fish per day. Since he does not state how he arrived at this figure, I assume that it represents a guess intended to indicate the harmfulness of the Herring Gull for the German economy. In view of our observations on this species and those of other observers on other fish-eating species (Table 31), Bruns's figure seems too high.

Kruuk (1964, Table 1) reports that an adult male Herring Gull in captivity consumed 60 whole eggs as well as half or less of 6 eggs of the Black-headed Gull *Larus ridibundus* in 5 days (but not successive days). This amounts to slightly more than 12 eggs per day. According to Schönwetter (1963), the mean weight of a fresh egg of a Black-headed Gull is 37.5 g and the mean weight of the egg-shell 2.2 g, the content thus amounting to 35.3 g. The daily intake of this Herring Gull was therefore more than 12 × 35.3 = over 424 g of egg contents.

Harris (1965) reports that maximum daily intakes of a captive adult Herring Gull weighing about 800 g and using only one type of food throughout the test periods were 429 g fish, 557 g Starfish, 330 g shell-fish flesh, 169 g bird flesh, and 160 g bread. These intakes agree with our maximum mean daily intakes (413 g Horse-mackerel, 129 g bread).

For purposes of comparison, I have given in Table 31 the daily food intake of a number of fish-eating species of birds. To permit mutual comparison, the intake is expressed as a percentage of the birds' body weight. As was to be expected, there is an appreciable variation in intake, but most of the values lie between one-sixth and one-third of the body weight. Our data on the Herring Gull all lie within this variation.

5.6. FOOD INTAKE OF CHICKS

To my knowledge, there are no data in the literature concerning the quantity of food required by young Herring Gulls during the chick stage. It is difficult to collect accurate data on this point in the field, since it is necessary to know not only the frequency with which the young are fed but also the amount of food taken per feeding. Because the latter can vary from a few grams to more than 100 (the highest weight I obtained for a regurgitation of a chick was 111 g), a very large series of observations would be required for an accurate estimate of this factor. In addition, an estimate made from a blind is extremely inaccurate, and the amount of time required for a more precise estimate (based, for example, on the chicks' weight before and after feeding) is too great to permit the collection of sufficient data.

The best approach to the problem therefore seemed to be to determine the intake on birds in captivity. I did this in 1968 for two groups of chicks. The first group consisted of 14 chicks hatched in the first half of June, the second of 11 hatched in the second half of June.

5.6.1. Methods

Shortly after hatching, the chicks were brought from the gullery to indoor cages. For the first few days they were kept warm with a lamp and a hot-water bottle. In this period drinking-water was supplied regularly, and the chicks spent a few hours of each day in the open. After a little less than a week they were transferred to outdoor runs, which were provided with shelters, perches, and containers with water, which was refreshed daily.

Because in the field the chicks' food consists primarily of fish (5.3.3), it was decided to feed the chicks exclusively with fish. During the first few days, however, I added small amounts of bread, cheese, and meat. The fish were fed intact, i.e. with the intestines.

The birds were fed only during the day. The first few days food was offered with tweezers, but the chicks soon started to take the fish from the containers independently. The containers were refilled several times a day, after an attempt had been made to feed left-over fish by hand. To make this left-over fish more attractive, it was moistened; in addition, small fish were broken in half.

The quantity of food consumed was determined by subtracting the weight of the left-over food from the amount originally offered. Initially, however, the small fish were counted and the weight of the amount consumed was determined by multiplying the number by the average weight.

Wild chicks fledge at about 6 weeks of age. On this basis, the growth stage was considered to terminate on the 42nd day. The birds were raised and fed as a group, but since they had hatched on different days, only the daily intake of the group as a whole is known.

5.6.2. Growth of the chicks

The weight curves are not the same for the two groups of chicks (Fig. 25). The second group had a lag of about two to three days as compared to the first group. Up to the 30th (32nd to 33rd) day there was little difference with respect to the growth of wild chicks, but after that a difference appeared. In some of the captive chicks the weight continued to increase into the last week, whereas in wild chicks it remains around a given level from the 30th day onward (see Fig. 22). Evidently, at the end of the chick stage the parent gulls do not bring enough food to the chicks to permit the increase seen in the laboratory. The food intake of the captive chicks must therefore have been slightly higher than is normal in wild chicks.

5.6.3. Intake

The daily food intake of the two groups of chicks is shown in Figure 19. The curves based on dry weight begin to level off around the 30th day, after which the total intake varies more or less around a given value for some time. The youngest chicks are then 20 days old, the oldest 30 days. It follows from this that the intake of individual birds reaches the maximal value as early as the fourth week. This is several days before the chicks cease to gain weight in the wild and even some weeks before the growth of the skeleton and plumage has been completed (for data on skeletal growth, see Maschlanka 1954).

Table 32 shows the total amounts consumed by the chicks during the first six weeks. These were, for the first group, 9.2 kg fresh weight (2.5 kg dry weight) per chick, and for the second group 8.4 kg fresh weight (2.4 kg dry weight) per chick. It follows from these data that for a brood of three chicks, roughly 25 to 27.5 kg fish is required for the entire chick stage.

Table 32. Total food intake (g fresh (dry) weight/bird) of young Herring Gulls in captivity during chick stage

Types of food	Group of 14 chicks	Group of 11 chicks
Sprat	4,590 (1,483)	5,585 (1,804)
Herring	1,162 (280)	359 (86)
Ammodytidae spp.	248 (55)	99 (22)
Gadidae spp.	1,574 (326)	1,488 (308)
Horse-mackerel	1,065 (269)	660 (167)
Flat-fish	156 (30)	141 (27)
Various species mixed	403 (101)	34 (7)
Other food [1])	3 (2)	4 (3)
Total weight	9,200 (2,546)	8,370 (2,424)

[1]) Other food consisted of meat, cheese, and bread.

The largest mean daily intake was 333 g fresh weight per bird for the first group and 323 g for the second. For a brood of three this comes to about 1 kg fish per day in the period of maximum food intake (last 2 to 3 weeks of the chick stage).

We fed our chicks a mixture of fatty, moderately fatty, and lean species of fish. This combination probably also occurs among wild birds, unless the parents specialize in particular prey species. Since the caloric value of fat is more than twice that of protein, it is evident that parents supplying only lean fish to their chicks will have to bring larger quantities as compared to parents

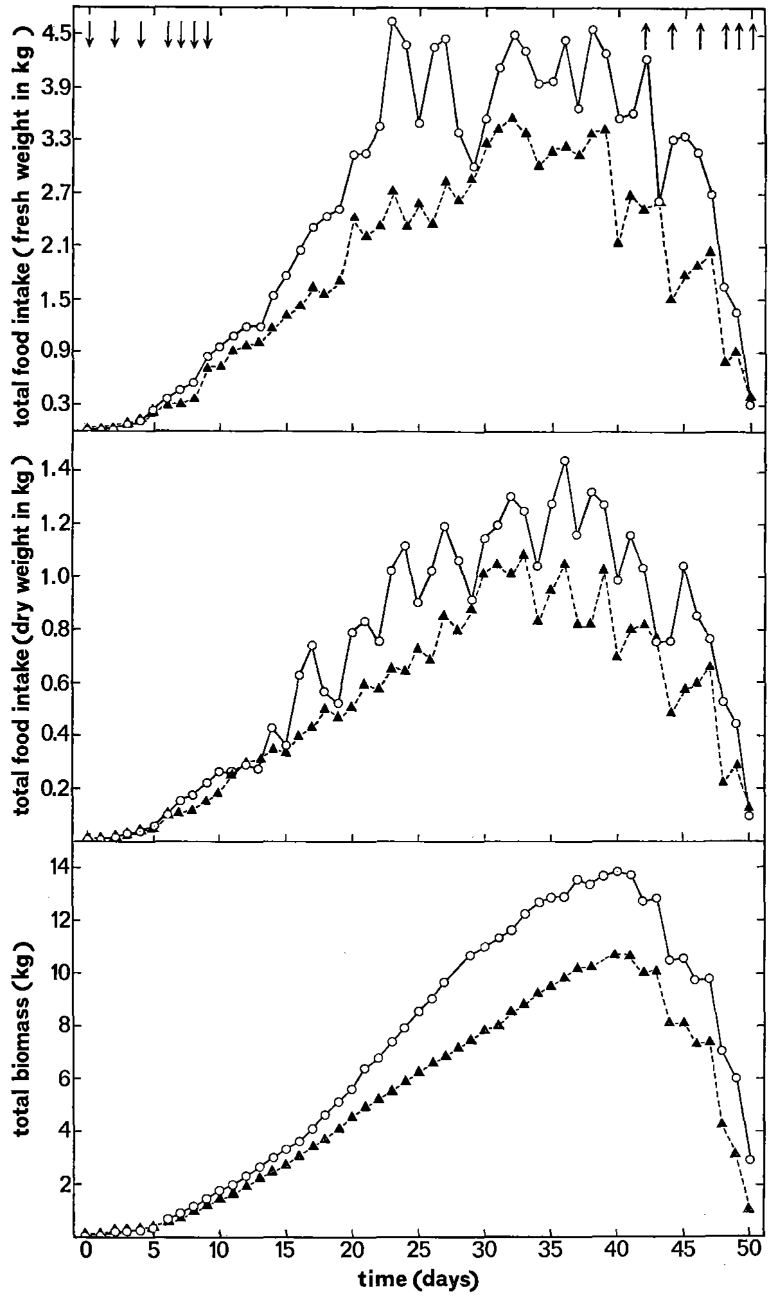


Fig. 19. Changes in the daily food intake and biomass during the chick stage for two groups of captive Herring Gull chicks. Circles: 14 chicks; solid triangles: 11 chicks. Because the chicks hatched on different days, the total observation period is somewhat longer than the individual chick stage, which is taken here as 6 weeks. Days on which chicks were added or removed are indicated by arrows.

bringing only fatty fish to obtain the same daily weight increase.

Although we now have a rough picture of the daily food intake of young and full-grown Herring Gulls, I think that in view of the uncertainties about the exact composition of the food of the entire population throughout the year, it would be premature to offer an estimate of the secondary production of the species in the Wadden Sea.

5.7. OBSERVATIONS ON STARVING GULLS IN CAPTIVITY

In the autumn and winter the feeding possibilities on the mudflats fluctuate widely. When weather conditions deteriorate, part of the population shifts to refuse dumps on the mainland (4.3.2.3). The quantity of food that can be taken on the flats in bad weather in evidently too small to feed the entire population of the Wadden Sea area. The utilization of the refuse dumps by the gulls is of recent date, however, and the food-supply must formerly have had a rather irregular character, as is still the case for the gulls foraging in the coastal waters of the North Sea. Unfavourable conditions can persist for several days in the autumn and winter. But this does not mean that gulls resorting to dumps under these conditions would otherwise succumb. For one thing, it is conceivable that Herring Gulls are able to fast for several successive days without harmful effects. In 1968 an attempt was made to obtain some information on this point with gulls in captivity.

5.7.1. Material and methods

Gulls and experimental conditions were the same as mentioned in 5.5.2.1, except that no food was supplied during the experiments. Sufficient water was available for drinking and bathing. The gulls were weighed early in the morning daily throughout the experiments.

5.7.2. Results

In January of 1968, I withheld food from 6 gulls that had been fed in excess for several days on canned dog food. After 3 days of starvation, food was again offered in excess.

Figure 20 shows the weight changes in these birds, which lost 97 to 105 g (average 100 g) per bird during the 3 days of fasting. The loss of weight was highest on the first day, and may be assumed to have included faeces deriving from food ingested on the preceding days. It can be seen from Figure 20 that within 2 to 3 days the gulls were able to compensate completely for the loss of weight.

In November of 1968, 23 gulls were fed in excess before fasting for 8 days. The weight changes of these birds are shown in Figure 21, from which it is again evident that the weight loss was highest on the first day and then

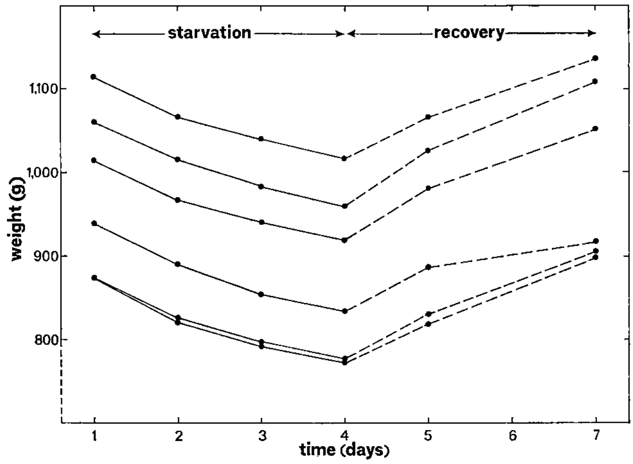


Fig. 20. Weight changes of 6 captive Herring Gulls during a starvation period of 3 days and a subsequent recovery period of 3 days.

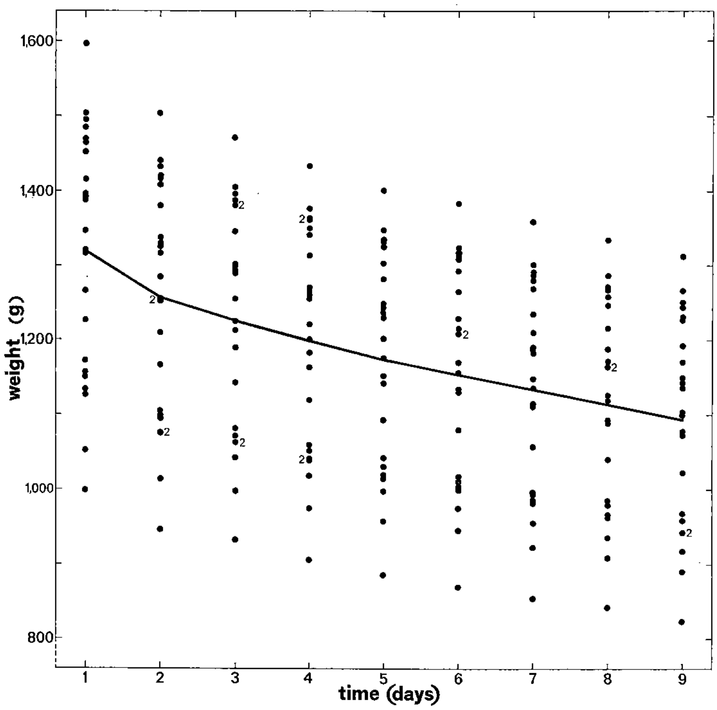


Fig. 21. Weight changes of 23 captive Herring Gulls during an 8-day starvation period. (Line drawn through mean values.)

decreased, remaining constant after the fourth day (average 20.25 g per gull per day). It seems likely that from the fourth day on, the loss of weight was due entirely to the consumption of reserves and the resulting defecation. After 8 days of starvation the birds did not appear to be on the verge of succumbing.

These data make it probable that well-fed Herring Gulls are able to withstand more than a week of fasting. However, and this seems to me to be equally important, the gulls seem able to restore the lost weight within a few days, and this quickly puts them in shape to withstand another period of starvation. The species seems to be well adapted to an irregular food-supply and to brief periods of bad weather (and therefore of unsuccessful feeding), without the availability of garbage. The shift from the mudflats to the dumps, when bad weather does not last for more than a week, does not seem to be as important as one is led to think at first, unless the ability to react to predators or the resistance against pathogenic parasites is reduced during a period of starvation. It is of course possible that the physical condition of the birds does suffer from longer periods of bad weather.

6. GROWTH IN CHICKS

6.1. INTRODUCTION

From data collected by various authors it is clear that there is a wide variety in the pattern of weight increase in young birds of the same species. This chapter deals with a study performed to determine the extent to which the variation in growth-rate of young Herring Gulls on Terschelling is related to date of hatching, brood-size, and diet. The influence of this variation on fledging weight is discussed.

6.2. METHODS

The growth curve of young Herring Gulls has, like that of most bird species, a sigmoid shape (Fig. 22; see also Peters & Müller 1951, Maschlanka 1954, Harris 1964b). During the first few days after hatching, weight increases very slowly. Around day 4 (the day of hatching is put at day 0), the weight of the young suddenly begins to increase rapidly. The point of inflection of the growth curve lies at about day 17–18. Around day 30 the curve levels off, after which the weight varies more or less around a given value.

Thus, the greatest increase in weight occurs between day 4 and day 30 (for the sake of convenience the fact that the length of this period varies slightly from individual to individual is not taken into consideration). For the sake of simplicity, the sigmoid-shaped curve is approximated by a straight line between day 4 and day 30, as seems justified from Figure 22. Hence, if the young are numbered 1, 2, ... , n, and the age of the chicks in days is

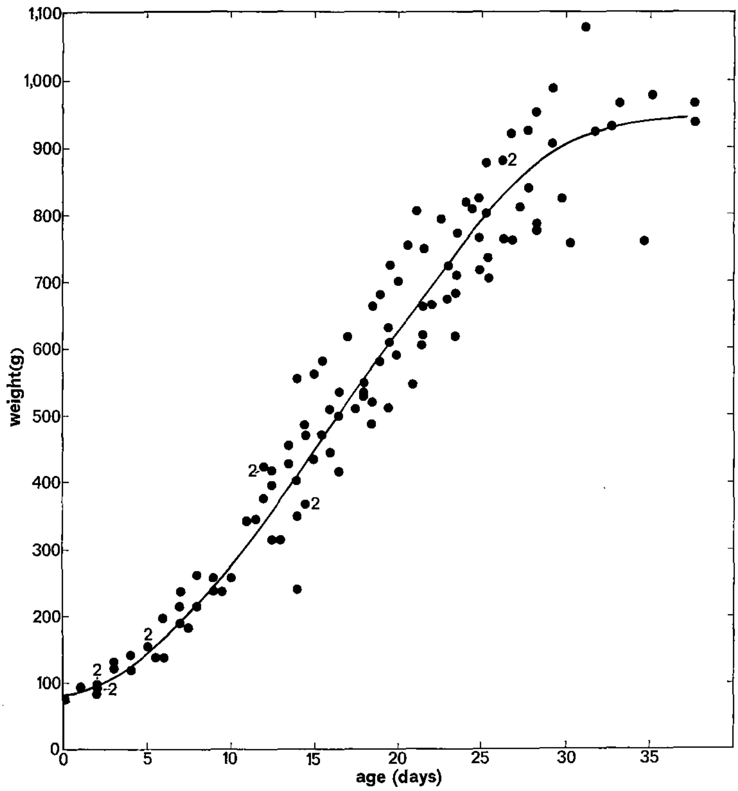


Fig. 22. Growth curve of Herring Gull chicks, based on 117 weights for 16 chicks from artificial broods of one young; Terschelling, 1966.

indicated by i, the weight of chick j on day i, $y_{i,j}$, between day 4 and day 30 equals a + b.i + $e_{i,j}$; a and b are unknown parameters, to be estimated from the sample (a to be interpreted as the hypothetical weight at day 0 and b as the daily weight increase during the time interval involved). We assume that $e_{i,j}$ is a realization of a random variable with normal distribution function, expectation zero, and a variance proportional to i, in other words proportional to age (this last being based on the fact that the weights of older chicks show a wider variation than those of younger chicks). Furthermore, it is assumed that all random variables are mutually independent. This means in practice that it is assumed that each captured chick is randomly chosen from a large population of chicks.

On the basis of the observations, the so-called weighted least squares estimates were calculated with the IBM 360-50 computer of the Centraal Rekeninstituut of the University of Leiden. Hypotheses concerning a and b were tested by means of the well-known F-test. The general theory underlying this method of estimation and the F-test is described in Scheffé (1959).

6.3. GROWTH-RATE IN RELATION TO DATE OF HATCHING

Although there is a considerable degree of synchronism in the breeding season, there is nevertheless a rather large interval between the dates on which the first and the last chicks hatch. On Terschelling the first chicks appear at the end of April or beginning of May, the bulk following during the second and the beginning of the third ten-day period in June. The last chicks, probably all deriving from replacement clutches, hatch around the middle of July. On the basis of this pattern, the chicks were divided into four groups:

1. an early group,
2. a mid-early group (hatched in the first half of the peak period),
3. a mid-late group (hatched in the second half of the peak period),
4. a late group.

Table 33. Regression equations for the weight increase between day 4 and day 30 of Herring Gull chicks on Terschelling, in relation to hatching period and brood-size (see also Fig. 23)

Year	Hatching period	Brood-size 1 [1]	2	3
1966	mid-early	y=34.48x—23.83 (19)[2]		y=31.40x+ 0.74 (44)
1966	mid-late	y=31.40x— 3.74 (63)		y=28.40x+ 5.93 (43)
1966	late	y=28.32x—22.63 (17)		
1967	early	y=32.75x— 1.08 (23)	y=32.84x—21.34 (9)	y=35.66x—20.30 (72)
1967	mid-early	y=31.38x+18.04 (24)	y=34.07x— 9.54 (4)	y=29.60x+ 3.11 (61)
1967	mid-late	y=31.15x—60.47 (32)	y=29.26x—18.05 (7)	y=26.95x+ 1.56 (31)
1967	late	y=25.64x+ 9.83 (16)		y=25.50x+ 6.84 (12)
1968	early	y=35.84x—10.28 (14)		y=32.33x—19.03 (35)
1968	early [3]			y=29.34x—11.65 (46)
1968	mid-late	y=36.34x—52.94 (14)		y=32.48x—22.23 (26)
1968	mid-late [4]			y=34.30x—36.87 (34)

[1]) Broods with one chick were mainly made artificially.
[2]) y = weight in grams; x = age in days; between parentheses: number of weights recorded.
[3]) Fostered by mid-late parents.
[4]) Fostered by early parents.

Growth of the chicks was investigated for each group separately. Figure 23 shows the calculated growth curves between day 4 and day 30 (see also Table 33). It is evident from Figure 23 and Table 33 that in 1966 and 1967 the daily weight increase became smaller the later in the season the chicks had hatched, although the differences between the various hatching groups are not significant for all cases (1966: b/1, $P<0.001$; b/3, $0.05<P<0.10$; 1967: b/1, $P<0.001$; b/2, $0.10<P<0.25$; b/3, $P<0.001$). In 1968 there was no difference between early and mid-late chicks (b/1, $0.10<P<0.25$; b/3, $P>0.975$). Thus, in some years the early chicks grow faster than the later chicks. This seasonal variation could be the result of differences in:

1. quality and/or size of the chicks,
2. quality of the parents,
3. environmental conditions.

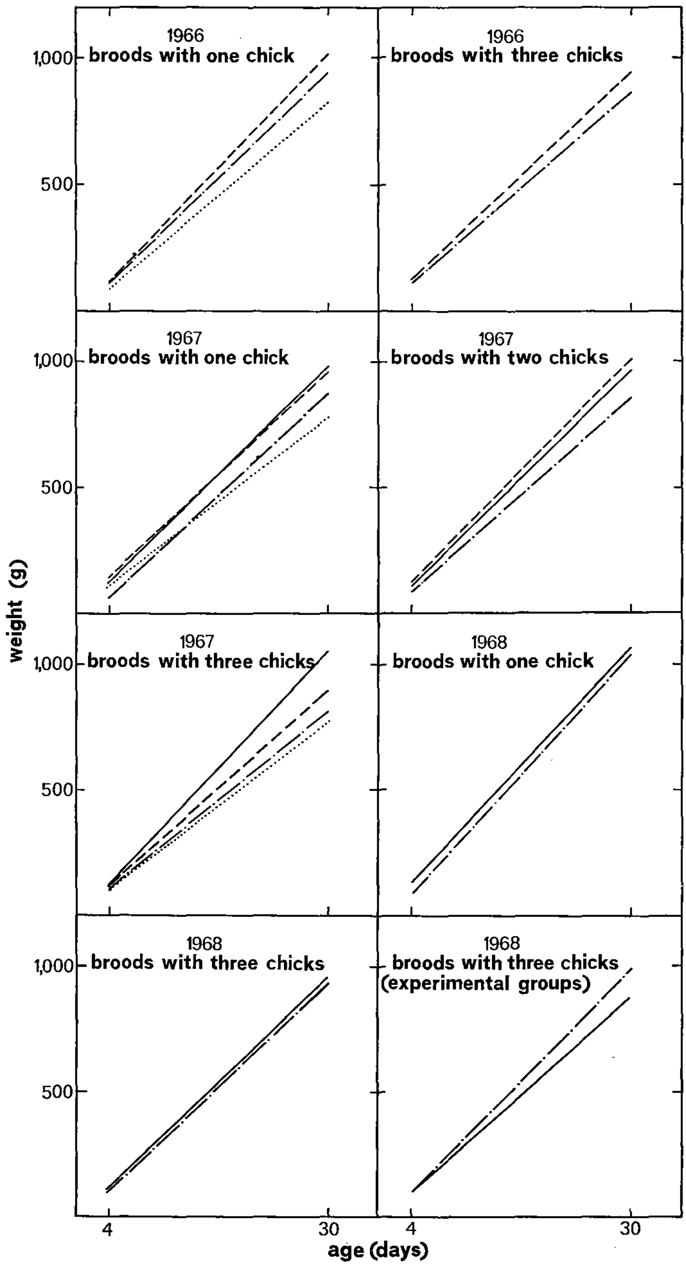


Fig. 23. Growth-rates between day 4 and day 30 of Herring Gull chicks on Terschelling, in relation to seasonal time of hatching and brood-size (—— = early chicks; - - - = mid-early chicks; —·— = mid-late chicks; . . . = late chicks). (See also Table 33.)

I have no data on the quality of the chicks, but it is conceivable that the growth-rate of Herring Gull chicks is related to their size at hatching. In hens, chicks from larger eggs grow faster than those from smaller eggs (Skoglund, Seegar & Ringrose 1952, Godfrey, Williams & Marshall 1953). In 1969 we measured and weighed the chicks in part of the gullery shortly after hatching. Although there was considerable variation in measurements and weights, which was related to the size of the eggs, no trend could be distinguished during the course of the season. Because the growth of the chicks was not followed any further in that year, no conclusions on this point can be drawn from these data.

In 1968 we attempted to find out something about the quality of the parents by comparing the growth of chicks in early and mid-late b/3 with that of chicks in b/3 from the same hatching group raised by parents from the other group, which gave 4 groups of chicks and parents according to the following scheme:

		chicks	
		early	mid-late
parents	early	control group 1	experimental group 2
	mid-late	experimental group 1	control group 2

The two experimental situations were obtained by transferring eggs of early parents, a few days before hatching, to nests of mid-late parents that had just started incubating, their eggs being put in the nests of the early parents. As a result of this exchange, the early parents incubated on the average for about six weeks, the others about two weeks, i.e. either about two weeks longer or two weeks shorter than normally. The results showed no observable influence on the percentage of eggs hatched or the behaviour of the parents (cf. Paludan 1951).

The growth results of the two experimental groups are also shown in Figure 23 and Table 33, from which it can be seen that the early chicks raised by the mid-late parents (experimental group 1) grew less fast than the corresponding control group ($0.01<P<0.025$), whereas the mid-late chicks raised by early parents (experimental group 2) grew slightly faster than the control group. The difference was not significant, however ($P>0.75$). But it must be kept in mind that in 1968, unlike the other two breeding seasons, the control mid-late young grew as fast as the control early chicks. It is reasonable to assume that the differences between the experimental and control groups are to be attributed to the quantity or quality of the food supplied by the parents to the chicks.

Although these experiments show that differences in quality between parents in relation to date of laying do indeed exist, it remains a question whether these differences account for the differences in growth-rate in relation to date of hatching observed in 1966 and 1967. In both years, we did find a difference in growth-rate for both large and small broods, and it therefore seems unlikely that the quantity of food the parents can supply to the chicks is responsible for the variation in relation to hatching date. There are indications that a difference in growth-rate in relation to date of hatching also occurs for the Lapwing *Vanellus vanellus* (Rayfield 1958) and the Little Ringed Plover *Charadrius dubius* (Walters 1961), two species in which the offspring are not fed by the parents but find their own food. In these cases environmental conditions doubtless play the most important role.

Since the reduction in the growth-rate of the young Herring Gulls in the course of the season occurred in both b/1 and b/3, it is unlikely that in these cases the available food supply exercises an influence. Although the possibility of an influence of the quality of the food cannot be ruled out, it does not seem very likely to me. However, another possible explanation might be an influence of the weather. It is difficult for young chicks to protect themselves against extreme temperatures and rain. Our captive chicks showed a strong urge to drink water, even in the first few days after hatching. We obtained the impression that when the gulls were unable to drink an adequate amount of water they showed less appetite for food than normal. In the dry dunes, rain and dew drops form the only source of water apart from the fluid in the regurgitated food from the parents. Unfortunately, I have no data on the daily amount of water available to the chicks, but it is conceivable that this amount diminishes in the course of the season due to increasing temperatures. It is also possible that the amount of water the chicks require tends to increase as the season progresses, due to their increased evaporation. Finally, the temperature might have an influence on the feeding behaviour of the adult gulls. Fordham (1964) states that in the Dominican Gull "there is a tendency for older chicks at least to be fed more often on cold days than very hot days".

6.4. GROWTH-RATE IN RELATION TO BROOD-SIZE

Figure 23 and Table 33 indicate that in addition to the hatching date, the brood-size also influences the growth-rate. In several cases the daily weight increase of chicks in b/1 was greater than that of chicks in b/3 from the same hatching group. The differences between b/1 and b/3 are significant in two cases (1967, mid-late; 1968, early; $P<0.05$) and in three cases almost significant (1966, mid-late; 1967, early and mid-early; $0.05<P<0.10$). In three cases the differences are clearly not significant (1966, mid-early; 1967, late; 1968, mid-late; $P>0.25$).

Since the chicks are dependent on the parents for their food throughout the chick stage, it is likely that the differences between the one- and three-chick broods reflect the inability of some parents with three chicks to satisfy entirely their progeny's food requirements.

A difference in growth-rate between chicks in b/1 and larger broods was also found by Vermeer (1963, 1970) for the Glaucous-winged Gull *Larus glaucescens* on Mandarte Island, Canada, and for the California *Larus californicus* and Ring-billed *Larus delawarensis* Gull in Alberta.

Harris (1964b), who studied the growth of young Herring Gulls and Lesser Black-backed Gulls on the island of Skomer (Wales), came to the conclusion (but without statistical analysis of his data) that "the curves (of the Herring Gull chicks) are all similar, flatten out at different levels about ten days before fledging, first the b/3 . . . , then b/2 . . . , then . . . b/1". His Figure 8 gives the impression, however, that the growth-rate also drops from b/1 to b/3. His young Lesser Black-backed Gulls in b/1, however, seem to have grown as fast as those in b/2.

Fordham (1964) found that in New Zealand in the Dominican Gull "chicks from all broods grew at approximately the same rate, although the heaviest chicks from the two- and three-chick broods grew slightly faster than the single chicks". However, the size of the sample on which his data are based was very small.

6.5. SUPERNORMAL BROODS

Clutches with more than three eggs occur only sporadically. Therefore, the formation of artificially supernormal broods offers the only means to determine whether the growth-rate of chicks in broods with more than three chicks undergoes a further decrease. In 1967, I added to six nests with pipping eggs or newly hatched chicks, two eggs or chicks of the same age taken from other nests. The nests were situated in a dune area with a circumference of 300 m and surrounded by wire netting over 50 cm high to prevent the chicks from leaving the vicinity of the nest before fledging (this occurred repeatedly in the rest of the colony).

During the first ten days, five of the thirty chicks (all from different nests) died, leaving us one b/5 and five b/4. This mortality was slightly higher than in b/3 and, apart from one case of strangling in the fence, is probably to be attributed to the parents' inability to give all five chicks adequate protection against unfavourable weather conditions (cf. Harris & Plumb 1965).

The growth of the chicks from the supernormal broods is shown in Figure 24. The weight increase was less regular than that of chicks from normal broods. In a few cases there was a distinct negative relation between the weight changes of two chicks within a single brood. In nest 311, the weight of the lightest chick suddenly dropped for unknown reasons, starting on day 31; after this day one of the other chicks, which had maintained the same weight for 14 days, suddenly showed a sharp increase. Nest 314 showed a similar case. These two cases make it likely that there was a sharp competition for food among the chicks in the supernormal broods, as a result of which one or more chicks received less than they could maximally have eaten.

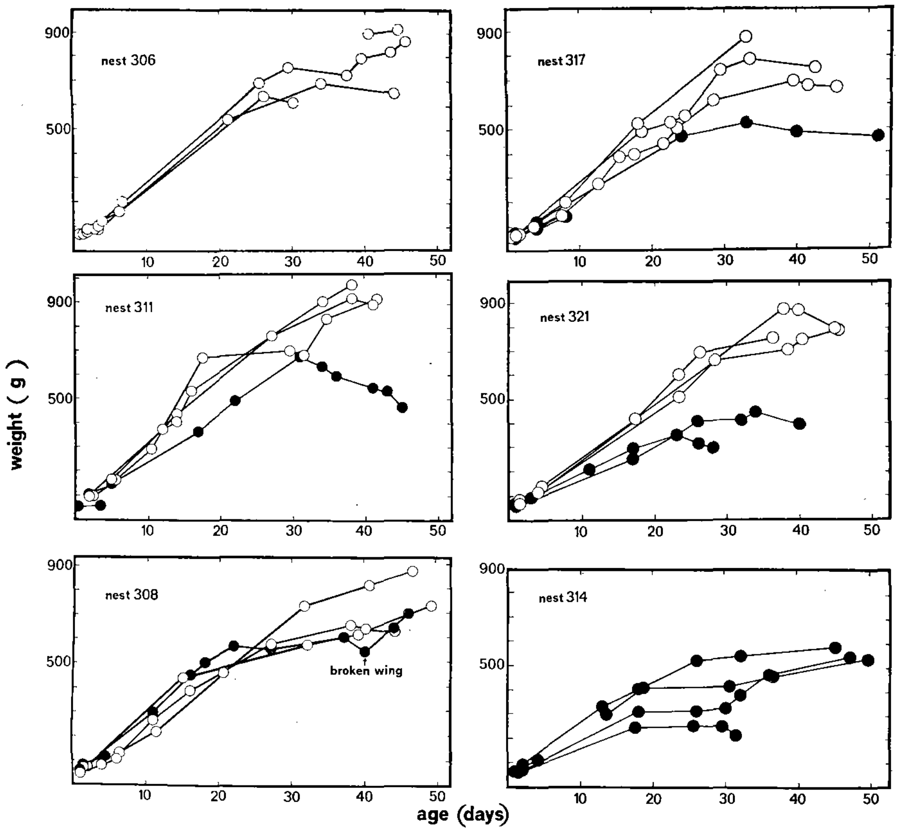


Fig. 24. Growth curves for 6 supernormal Herring Gull broods (solid circles = data from chicks known to have died during or shortly after the chick stage); Terschelling, 1967.

Or the 25 birds over ten days of age, only 18 (72%) reached a weight of 600 g or higher; all of the 22 chicks in b/3 and 22 in b/1 investigated in 1967 reached this weight. This too indicates that the parents of the supernormal broods were not able to satisfy the food requirements of the chicks completely.

The 7 birds that did not become heavier than 600 g were all found dead during the chick stage or shortly after fledging, whereas this occurred in only 2 of the 18 chicks weighing more than 600 g. Furthermore, one of these two birds had a broken wing, which prevented it from leaving the fenced area. This bird was probably deserted by the parents when the other chicks of this brood fledged.

At least 15 chicks could still be caught with the hand after the sixth week (the age when normally they can fly). These birds could not fly and were evidently somewhat retarded in development. Although there is probably less predation of large chicks than of small ones, it does occur. Elsewhere in the colony, in various years several large chicks were eaten by Hedgehogs *Erinaceus europaeus*, and had probably been killed by them. Rooth (1956) states that large chicks are taken by the Marsh Harrier *Circus aeruginosus*. Prolongation of the chick stage increases the chance of predation. Rapid growth of the chicks therefore clearly has survival value.

The data concerning the supernormal broods make it probable that at present the Herring Gulls in the Dutch Wadden Sea area are not able to raise more than three healthy chicks (the maximum number in the natural situation), notwithstanding a large share of the food supplied to the chick becomes available to the gulls by human activities. It is interesting that on the island of Skomer (Wales) the chicks from supernormal broods of Lesser Black-backed Gulls, whose food comes mainly from natural sources, developed normally and reached the same fledging weights as chicks from b/1 and b/2 (Harris & Plumb 1965).

6.6. GROWTH-RATE IN RELATION TO FOOD

On Terschelling, only one-fourth of the regurgitations of the young was made up of garbage (5.3.3.2). The percentage of gulls feeding their chicks with garbage increased with brood-size, however (5.3.3.5). We have considered this to be a reaction of the parents, to cope with the greater food demands of the large broods, and have postulated that gulls can supply more food (measured in calories) if they shift partially from marine food to garbage. The weight increase of the chicks for which we know the nature of the food supplied offers a means to check this hypothesis. Since both the date of hatching and brood-size influence growth-rate, we compared only data of chicks from the same hatching period and brood-size (Table 34).

It can be seen from Table 34 that in 1966 and 1967, in four out of five cases the chicks fed additionally with garbage grew faster than chicks receiving no garbage, although the difference for early b/3 in 1967 is not quite significant (1966: mid-late b/1, $P<0.001$; mid-early b/3, $0.025<P<0.05$; 1967: early b/3, $0.05<P<0.10$; mid-early b/3, $P<0.005$). The difference in mid-late b/3 in 1966 is significant at the 0.001 level. The six weights of chicks fed with garbage all refer to the beginning of the chick stage, however, so that the calculated growth curve for these birds cannot be considered very reliable.

The results indicate that chicks from broods fed on garbage as well as other food grew faster than chicks in otherwise comparable broods but not supplied with garbage. The greater weight increase of the former must be attributed to a greater intake of calories. This means that gulls are able to cope at least partially with increased food demands by supplying garbage in addition to natural food.

Table 34. Regression equations for the weight increase between day 4 and day 30 of Herring Gull chicks of the same hatching period and brood-size on Terschelling, in relation to the occurrence of garbage in the diet

Year	Brood-size	Hatching period	Occurrence of garbage in diet: With	Occurrence of garbage in diet: Without
1966	1	mid-late	y=34.33x+ 0.08 (15) [1]	y=29.04x—10.38 (22)
1966	3	mid-early	y=33.71x+38.22 (5)	y=28.27x+42.14 (19)
1966	3	mid-late	y=22.92x— 5.04 (6)	y=25.65x+44.10 (24)
1967	3	early	y=38.04x—41.01 (47)	y=29.82x+15.23 (12)
1967	3	mid-early	y=32.23x— 6.86 (26)	y=23.59x+31.64 (15)

[1]) y = weight in grams; x = age in days; between parentheses: number of weights recorded.

In the field we gained the impression that chicks whose diet, as judged from the large accumulations of remains of crabs in the territories, consisted to a considerable extent of *Macropipus holsatus* and *Carcinus maenas*, showed a slower growth-rate than other chicks, but our data on this point are not sufficiently numerous to permit statistical analysis. It is interesting in this connexion to refer to observations on growth and diet of young gulls on the island of Memmert (Goethe 1937).

Goethe gives the weight increase of 7 chicks deriving from 4 nests during the first 16 days after hatching, which, he notes, was slower than Heinroth & Heinroth (1928) mentioned for captive chicks. Goethe ascribes this difference to the fact that the chicks of Heinroth & Heinroth developed " unter günstigen, gleichmässigen Ernährungsbedingungen". The data collected by Heinroth & Heinroth are not only in agreement with those of later authors for gulls in captivity (e.g. Peters & Müller 1951, Maschlanka 1954, and our data) but also with findings of various authors in wild birds (e.g. Belopol'skii 1961, Harris 1964b, and our data). It is therefore probable that Goethe's data differ more strongly from the "normal" picture than those of Heinroth & Heinroth. I assume that there may have been some connexion between the diet of the chicks on Memmert (mainly Shore Crabs) and the slow growth-rate (compare in this connexion also 5.3.3.6).

6.7. COMPENSATORY GROWTH AND POSSIBLE EFFECT OF GROWTH-RATE ON FLEDGING WEIGHT AND POST-FLEDGING SURVIVAL

In the preceding sections we have seen that there can be considerable variation in the weight increase occurring between day 4 and day 30 in relation to the date of hatching, brood-size, and diet. Various data indicate that the chicks can compensate for any retardation undergone in this period by weight increases after day 30 (when normally the growth curve begins to level off). In 1967, we observed this in chicks from the supernormal broods (nests 311 and 314, see Fig. 24) and in 1967 and 1968 in young raised in captivity. Figure 25 gives the weight curves of two groups of captive chicks raised as far as possible under identical circumstances. From Figure 25 it can

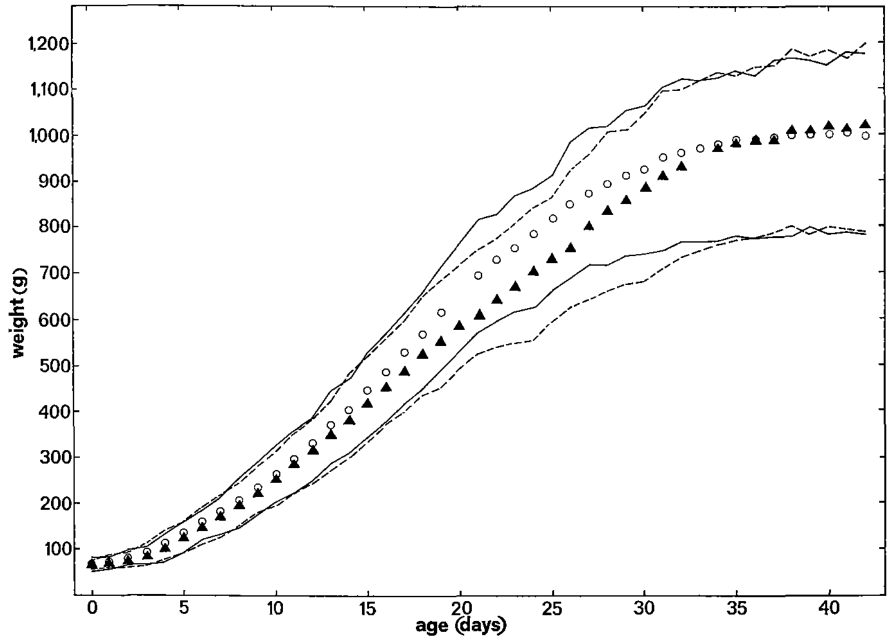


Fig. 25. Growth (mean and range of weight) of two groups of captive Herring Gulls (O and —— = 14 chicks hatched 1–10 June 1968; ▲ and - - - = 11 chicks hatched 18–27 June 1968).

be seen that one of the two groups (for otherwise unknown reasons) clearly had a somewhat slower growth-rate than the other but finally nevertheless reached a slightly higher fledging weight. Figure 26 shows that in extreme cases growth can continue beyond the age of nearly two months. In the first few weeks the growth-rate of these chicks was strongly retarded, but it increased suddenly when they were transferred from indoor cages to outdoor runs and a preparation containing vitamins and calcium was added to the diet of gutted fish. The phenomenon of compensatory growth has long been known for cattle and other domestic animals, both mammals and birds (Wilson & Osbourn 1960).

Thus, the termination of the growth-phase is not connected with a particular age. The animals are physiologically capable of continuing growth after the age at which it ceases under normal conditions. But this does not always occur, as is clearly shown by the weight curves of some of the chicks from supernormal broods (compare also the growth curves of undernourished chicks in Maschlanka 1954). The chicks from the supernormal broods 311 and 314 did not recover until one of the other chicks in the nest decreased in weight, i.e. when relatively more food became available to the other chicks. Our captive chicks always had more food available than they could consume.

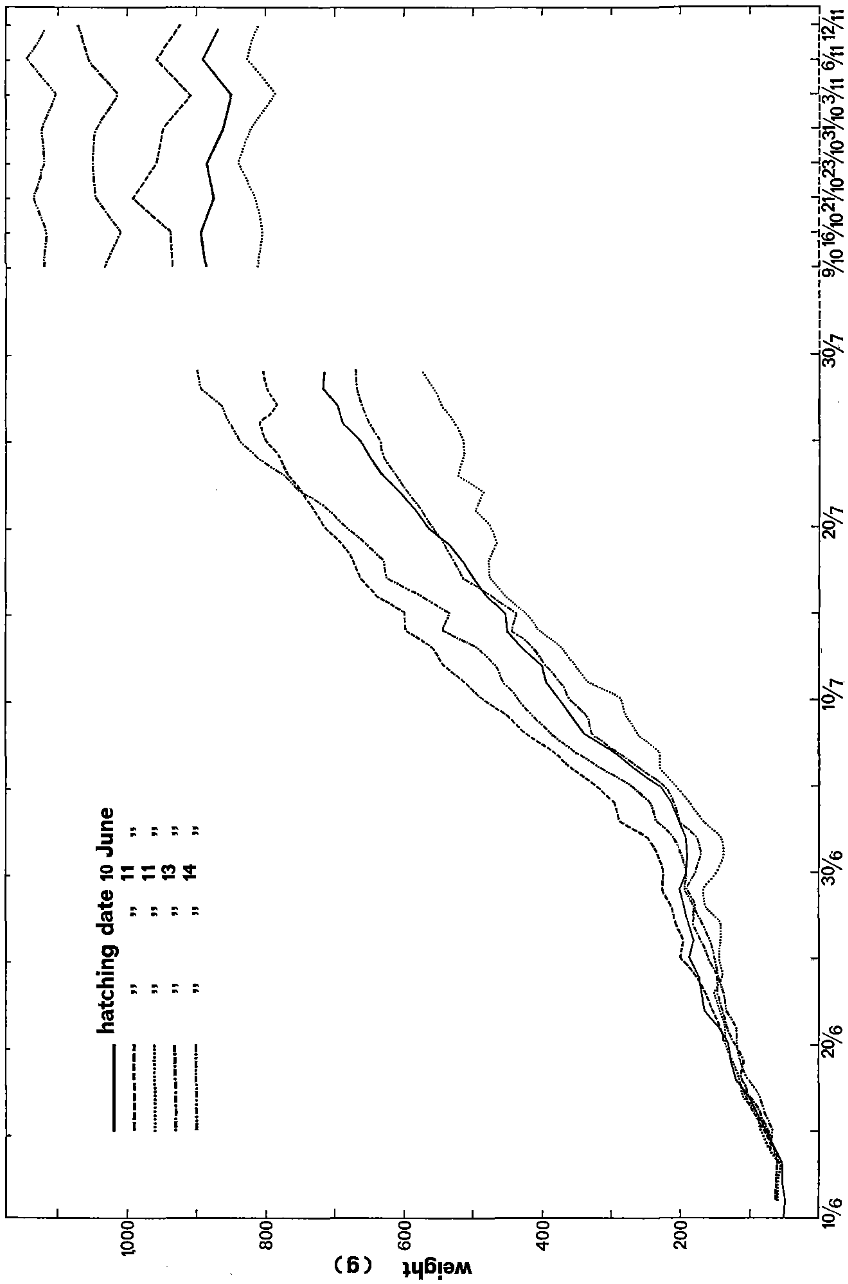


Fig. 26. Compensatory growth in 5 captive Herring Gull chicks.

These data make it probable that compensatory growth occurs only when the food situation improves.

The differences in growth-rate observed in the colony on Terschelling in relation to date of hatching, brood-size, and diet are presumably related, as we suggested, to differences in the amount of food brought by the parents or that the chicks would consume. When conditions are otherwise unchanged, there is no reason to assume that the food situation in the colony becomes more favourable as the chicks become older, so that compensatory growth does not occur. I therefore assume that the differences in growth-rate can be traced later in the fledging weights of the chicks. It is not known whether these differences influence the survival-rate of the chicks in the post-fledging period. Unfortunately, we have too few recoveries of ringed gulls whose hatching date, brood-size, and diet are known, to answer this question. Lack, Gibb & Owen (1957) and Perrins (1965) found, however, that the post-fledging survival of young tits (Paridae) was greater the heavier the birds were just before fledging. Just what determines the greater survival-rate of the heavier birds is not known, but Lack (1966) assumed that the extra weight of heavier birds consists mainly of subcutaneous fat. It could also be possible, however, that the heavy birds are somewhat larger than the light birds, and that the differences in size account for the differences in weight. In that case the differences in survival-rate might be due to an advantage of the larger individuals in competition for food or other requirements.

7. DISCUSSION

According to the ringing results, most Herring Gulls return to their native or neighbouring colonies to breed; only a few seem to settle at greater distances from their hatching places (3.5). Consequently, exchanges between the various countries of northwestern Europe only occur on a small scale. This means that the breeding population of the Dutch Wadden Sea area may be considered as a more or less closed unit, its size being determined mainly by local conditions.

At present, it is rather generally accepted that the size of animal populations is regulated by density-dependent factors, although there is no concensus of opinion concerning the way in which this regulation occurs. According to Lack (1954,1966), in wild birds the numbers are regulated by food shortages. Wynne-Edwards (1962) claims, however, that food forms only an ultimate factor, and postulates that as a result of group-selection animals have developed specially-timed communal behaviour patterns (called epideictic displays by him), which through a feed-back mechanism regulate the size of the breeding population, thus preventing overpopulation and a resulting exhaustion of the food supply.

During the early spring Herring Gulls do indeed show various communal behaviour patterns, such as roosting, visits to the breeding colony, and the so-called "panic flights", which could function as epideictic displays. But it is difficult to understand how this behaviour could "elicit the required response from the breeding stock (in order to) produce the quota of recruits that current economic conditions dictate", to quote Wynne-Edwards's own words (see also Brown 1967b), and how this type of selection must have been evolved (see also the discussion on these subjects in Lack 1966). It seems more likely that selection occurs at the individual level.

A different way in which the size of the breeding population might be regulated is territoriality. The presence of non-breeding adults in the breeding season has been shown to exist for German (Drost, Focke & Freytag 1961) and New England (Kadlec & Drury 1968) Herring Gulls and has been assumed for the Dutch ones. It was observed during the gull control program in The Netherlands over the last four decades that territories falling vacant in the colony in the course of the breeding season were quickly re-occupied by other gulls (van Dobben, Kluyver, pers. comm.). During our study in the gullery on Terschelling, however, it appeared that even in an undisturbed situation new gulls continue to settle within the colony till late in the season. It therefore remains a question whether the birds that settled in the course of the breeding season during the gull control program were late-arriving gulls or birds that would otherwise not have bred. But even if the latter were true, it remains a question whether the exclusion of these gulls from the breeding process by other gulls has a regulating effect on the size of the total population. Kadlec & Drury (1968) suggest that in Massachusetts the segment of the adult population that does not breed represents gulls with lessened motivation, which have been shown to produce few, if any, young to fledging age.

Lack (1954, 1966) came to the conclusion, on good grounds, that starvation, in particular outside the breeding season, is the most important density-dependent factor in most wild birds. It therefore seems useful to evaluate this factor with respect to the Herring Gulls of the Dutch Frisian Islands.

The Herring Gull is an omnivorous bird. In the northern part of The Netherlands its diet includes many kinds of marine organisms (from small crustaceans to large fish), terrestrial animals (mainly Rabbits, eggs and young of birds, and insects), carrion and refuse, grains, and the berries of *Empetrum nigrum* (Chapter 5). With the mudflats of the food-rich Wadden Sea and the beaches and coastal waters of the North Sea in the immediate vicinity of the breeding places, as well as the more than 100 refuse dumps on the mainland of the three northernmost provinces, all within reach for the greater part of the winter population, it does not seem probable at first sight that food is the limiting factor in this situation. We shall therefore take a closer look at the situation in the northern part of The Netherlands on the basis of the results of the present study.

During the study period the food of the young consisted for the greater part of fish. About one-fifth to one-third of the total food-supply was estimated to originate from commercial fishery (5.3.3.4). Garbage was observed in about one-fourth of the cases, so that on the average about 50% of the food of the young can be considered to have derived from human activities. There was a positive correlation between brood-size and percentage of gulls supplying their young with garbage in addition to natural food (the latter also included fish from commercial fishery) (5.3.3.5). We have seen that chicks fed with natural food plus garbage grew faster in several cases than those fed solely on natural food. This means that, measured in terms of energy, the parents bringing natural food as well as garbage to their offspring provided them with more food on the average than was the case for parents bringing only natural food. This finding makes it probable that the increase of the percentage of gulls supplying garbage to their chicks as brood-size increases, represents a reaction of the parents in an attempt to satisfy the higher food requirements of the increasing number of young. It therefore seems probable that parents with large broods find it difficult to resort solely to natural sources for satisfying the increased food demands. It seems likely that, at least in this part of its distribution area, the Herring Gull cannot raise more than 3 chicks. The observations on growth-rate of chicks from supernormal broods point in the same direction (6.5). This is in agreement with the hypothesis of Lack (1954, 1966) that in bird species in which the young are fed by the parents, clutch-size is adapted to the maximum number of young that the parents can raise.

We found, except for the supernormal broods, no definite cases of death in which starvation could have been the primary cause. Likewise, Harris (1964b) observed no sign of starvation on Skomer Island, Wales. Paynter (1949), however, stated in a study on chick mortality of the Herring Gull on Kent Island, Canada, that two siblings apparently died of starvation.

The absence of starvation on Terschelling, however, does not mean that the feeding of the chicks was always adequate. The observed retarded growth-rates of the young, which at least partially could be related to sub-optimal feeding, point in the opposite direction. It has been argued that differences in growth-rate may be reflected in the fledging weights of the young birds and therefore possibly in their post-fledging survival (6.7). This brings us to a closer examination of the situation outside the breeding season.

Immediately after the breeding season the gulls show a non-directional dispersal over relatively limited distances (3.3). To some extent this dispersal might be related to the food supply. During the breeding season the gulls' food comes mainly from the mudflats and the sea. During autumn and winter several prey species are more difficult or impossible to obtain because they migrate to deeper water. In addition, weather conditions often make the food supply in autumn and winter inaccessible. With a decreasing food supply in the vicinity of the breeding area, it would seem favourable to disperse over a larger area after breeding has been completed. Whether, in this situation, food is a proximate or an ultimate factor, remains an open question (however, see Drost 1955). Probably, food plays a proximate role in the distances of movements involved, as indicated by the ringing data before and after 1950 (3.3).

The largest part of the population remains within 100 km of the breeding sites. There, the occurrence is limited to the mudflats of the Wadden Sea, where during the winter the food consists mainly of Cockles (5.4); to the coastal waters and beaches of the North Sea, where the food probably consists mainly of marine organisms living near the surface of the sea, offal and refuse from fishery and ships, and material washed up on the beaches; and to refuse dumps and other sources of human waste on the mainland.

The distribution of the gulls over the refuse dumps shows a positive correlation with the numbers of inhabitants of the municipalities in question (4.3.3.3), which indicates that the quantity of food at these dumps has an influence on the distribution of the birds over the dumps. This distributional pattern must be the result of intraspecific competition. During the winter, the number of gulls at these dumps shows marked fluctuations (4.3.2.3) related to the feeding conditions on the Wadden Sea. Because even a slight deterioration of these conditions is reflected in the number of gulls at the dumps, I am of opinion that the food situation in the Wadden Sea cannot support a larger winter population than is found there at present. Interestingly enough, the gulls only shift to the dumps temporarily. It is possible that this indicates a preference of the gulls for natural food over garbage, but this does not seem likely to me. There is always a group of gulls at the dumps, even under most favourable feeding conditions in the Wadden Sea (see righthand part of the curve in Figure 11). Furthermore, the increase in the number of gulls at the dumps in late summer and early autumn starts at the end of the breeding season, which does not suggest that dumps are a second choice. It is therefore more likely that the food supply at the dumps cannot support a larger population over a more prolonged period. This means that outside the breeding season the number of gulls in the Wadden Sea area and on the mainland represents the maximum population. This in turn implies that birds added to the population above this number after the breeding season, as a result of reproduction and limited immigration, will either have to migrate (or to continue their migration) or die of starvation. As shown by the recoveries of gulls ringed before and after 1950 (3.3), movements over great distances are only involved to a certain extent, although they seem to increase when the food situation is unfavourable at the beginning of the dispersal period.

The mortality of old and young gulls is not identically distributed over the year (3.6). Recoveries of sub-adult birds are equally distributed over the year;

the adults have the highest mortality in the breeding season, and the first-year gulls show a peak in autumn. Conditions in late summer and early autumn are evidently unfavourable for the latter. The peak in mortality of the young coincides with the end of the dispersal period. It has been suggested (3.6) that this high mortality is the result of a food shortage during the dispersal period, when feeding pressure is high as a result of an increased number of gulls.

If our evaluation of the role of food outside the breeding season as regulating factor is correct, the termination of control in 1966, which led to an appreciable increase in the number of young fledged (4.2.1.2), can be expected to have no great influence on the size of the breeding population, at least provided that all other factors remain more or less equal. Furthermore, it must be taken into consideration that there may be a decrease in the Herring Gull population if the municipal authorities in the three northern provinces decide to build incinerators for garbage disposal, as may be expected in view of the problems associated with pollution now urgently requiring solution in this overpopulated country.

We must now attempt to answer the question of the extent to which the protective measures taken during the first decades of this century and the increased quantity of food supplied indirectly by man, are responsible for the increase of the Herring Gull population in this century.

During the nineteenth century, the Herring Gull suffered seriously from human persecution, which resulted in a very low breeding population. In 1906, Leege (1907) estimated the total number of breeding Herring Gulls on the Dutch Frisian Islands at maximally 1,500 to 2,500 pairs, mainly on the almost uninhabited island of Rottumeroog. On most of the inhabited islands, Leege found only a few breeding pairs. During these years, all eggs found by the inhabitants of these islands were collected for food (see also van Dobben 1934). The Herring Gull has therefore undoubtedly benefited from the protective measures taken in the beginning of the twentieth century, as a result of which the species has been able to breed undisturbed and to raise more offspring.

The utilization by gulls of refuse dumps and other places with human waste on the mainland dates from the end of the 1920s or the beginning of the 1930s, i.e. from the period during which the gull population showed a rapid increase.

We have seen that chicks from broods fed on garbage as well as other food grew faster than chicks in otherwise comparable broods not supplied with garbage (6.6). We believe that the difference in growth-rate must have led to a higher fledging weight of the former (see 6.7). We suggest that during the dispersal period, when feeding pressure is high, a higher fledging weight may lead to a higher post-fledging survival. This is one way in which the increased amount of garbage available to the Herring Gulls could have led to a higher population level.

The gull population reaches its largest numbers immediately after the breeding season, whereas the natural food situation is worst in the winter. Therefore, another positive effect of garbage and other human waste on the population level might be expected outside the breeding season. During the winter of 1967–1968, at least 32% of the total population of the northern part of The Netherlands fed constantly on garbage and other human waste; corresponding to the feeding conditions on the mudflats in the Wadden Sea, this figure could increase to at least 77% (4.3.4). Thus, during the winter refuse dumps and other places with human waste play a large role in the food-supply of the population of the northern part of The Netherlands. It seems likely that on this basis the population could increase to a higher level than would otherwise have been possible.

It is beyond doubt that the protective measures taken in the beginning of the present century are responsible for the population increase seen in recent times. I suggest, however, that the amount of food made indirectly available by human activities has determined the level to which the numbers could increase.

8. SUMMARY

This paper deals with the feeding ecology of the Herring Gull in the northern part of The Netherlands (Fig. 1). Most of the data were collected in 1966–1969. The aim of the study was to obtain quantitative data on the share of garbage and other offal, supplied indirectly by man, in the diet of this species, as a contribution toward the discussion of the causes of the population increase shown by the species during the present century.

Chapter 2 gives a short review of the annual cycle of the species in the Wadden Sea area. The first gulls usually arrive at the breeding places in February, but are sometimes already present at the end of January. The first eggs are laid at the end of April or the beginning of May. The first young are ready to fly by the middle of July. At the end of August, most of the gulls have left the breeding colonies.

An analysis of recoveries of Herring Gulls ringed as chicks on the Dutch Frisian Islands (Chapter 3) indicates that like most northwestern European populations the gulls in the Wadden Sea area do not show a seasonal migration but disperse non-directionally over a limited area (Figs. 2–6, Tables 1 and 2). The majority of the population remains within 100 km of the ringing locality. During the first half of the present century more Herring Gulls travelled further from the ringing locality than after 1949, but the difference was significant only for the first-year gulls (Table 3). These differences are attributed to the intensive control of the Herring Gull in The Netherlands in the 1950s and early 1960s, resulting in a high mortality of the adult gulls during the breeding season and a low production of young. This in turn led to a smaller population and a relatively more favourable food situation at the beginning of the dispersal period than would normally have been the case. It is suggested that the migration tendency of part of the population was weakened as result of this situation.

Most of the Herring Gulls of the Dutch Frisian Islands do not start to breed before the end of their fourth or fifth year. There was a tendency, although not a very pronounced one, to return to the colony of origin to breed; quite a number of gulls, however, settled in nearby colonies (Table 4). This dispersion is attributed to the disturbances at the nesting sites resulting from the intensive control measures.

Most of the mortality among first-year gulls occurs in September and October, i.e. at the end of the dispersal period (Fig. 7). Second-year and third-year gulls show a more or less constant mortality throughout the year. Fourth-year and older birds die mainly

during the breeding season (May–July). The latter pattern does not seem to be a result of the control program.

Since most of the population spends the entire year within a limited area, it was possible to determine the distribution of the gulls outside the breeding season by counts (Chapter 4). Counts made regularly around high tide on Terschelling and Vlieland in 1966–1968 (Fig. 8) show that on the Frisian Islands the numbers drop rapidly after the breeding season. On Vlieland, the decrease was followed by a temporary increase, probably due to the dispersing gulls of the Terschelling colony, which accounts for about half of the breeding population of the Frisian Islands. On Terschelling the numbers were lowest during November and December, on Vlieland in January (1966–1967) and during November–February (1967–1968), after which the numbers increased gradually. The numbers on both islands showed appreciable fluctuations during the winter, probably under the influence of weather conditions.

More or less simultaneous counts made in the Dutch Wadden Sea area give total numbers of 33,000–39,000 Herring Gulls (Table 5). The estimated minimum and maximum numbers in the winter of 1966–1967 were 21,000 and 37,000, respectively, and in the winter of 1967–1968 14,000 and at least 28,000.

In 1967–1969, counts were made regularly at 13 refuse dumps on the mainland of the province of Friesland (Figs. 9 and 10, Table 6). There, the lowest values were obtained during the breeding season. The numbers increased from the end of the breeding season onward; the winter level was reached as early as October, and the numbers remained high until April. During the winter months the numbers at the dumps showed marked fluctuations. There appeared to be a negative correlation between the feeding conditions on the mudflats of the Wadden Sea and the numbers of gulls at the dumps (Fig. 11, Table 8).

In December 1967, a census was taken of the gulls at almost all of the 104 refuse dumps in the three northern provinces (Fig. 12), i.e. covering the main dispersal area on the mainland. The total shown by this census was 26,097 Herring Gulls, but as a result of the varying feeding conditions on the Wadden Sea this value must have fluctuated during the winter of 1967–1968 between 20,000 and at least 39,000 gulls (Table 9).

There proved to be a positive correlation between the number of inhabitants of the relevant municipalities and the number of gulls at the dumps (Fig. 13), which indicates that the distribution of the gulls over the refuse dumps is closely related to the quantity of food locally available. It is suggested that this distribution is brought about by intraspecific competition during the dispersal period.

Few gulls of other species were observed at the refuse dumps during the census. This is partially related to differences in the feeding ecology of the various species. But in parts of The Netherlands where Herring Gulls were scarce, Black-headed Gulls did occur in large numbers at refuse dumps during winter. The same held for some of the dumps in the northern provinces during the breeding season. It is therefore suggested that in the northern part of the country in winter a high proportion of the Black-headed Gulls retreats from the dumps as result of interspecific competition.

The total number of Herring Gulls on the mainland of the provinces of Friesland, Groningen, and Drente must have fluctuated during the winter of 1967–1968 between 24,000 and at least 47,000 (Table 11).

Results of food analyses, based on examination of pellets, faeces, regurgitated food, and stomach contents, are given in Chapter 5.

The food of full-grown Herring Gulls visiting the breeding colonies on Terschelling and Vlieland consisted mainly of marine invertebrates from the littoral and sublittoral zones (Tables 12–14). During the breeding season no difference in diet was observed between the sexes (Table 12). Examination of more than 27,000 pellets and faeces showed marked changes in the composition of pellets and faeces in the course of the season (Fig. 14). These seasonal variations are attributed mainly to changes in abundance, accessibility, and attractiveness of the various prey species.

The food of chicks consisted mainly of fish (Tables 16–22), with a preponderance of Clupeidae, Gadidae, and flat-fish (Tables 23 and 24). Most or all of the Gadidae and flat-fish derived from discards of commercial fishery. This source was estimated to provide about one-fifth to one-third of the total food-supply (Table 26). Garbage provided about one-fourth of the total food-supply. Thus, on the average about 50% of the food was obtained through man.

A positive correlation was found between brood-size and the percentage of gulls feeding garbage to their chicks in addition to natural food (including fish from commercial fishery) (Fig. 16). It is suggested that this represents a reaction of the parents to the increasing food requirements of the larger broods.

The chicks completely digest fish bones, but juveniles, like the adults, regurgitate them.

Some possible explanations of the differences in diet between chicks and adults are discussed.

On the basis of the fluctuations in the breeding population of the Eider, Shelduck, and Avocet on Vlieland during the last four decades it is concluded that the Herring Gull cannot be considered harmful to these species in spite of the heavy toll of eggs and young birds taken by the gulls annually. It seems likely that the results of predation are counterbalanced by immigration.

Outside the breeding season, a large proportion of the Herring Gull population feeds at refuse dumps and other places with human waste on the northern mainland of The Netherlands. For the winter of 1967–1968 this part of the population is estimated, on the basis of various counts made in the Wadden Sea area and on the mainland, to amount to at least 32% of the total winter population when foraging conditions on the Wadden Sea were favourable. When these conditions were unfavourable, this percentage increased to at least 77%.

Some data on the food intake of full-grown gulls (Tables 29 and 30, Figs. 17 and 18) and chicks (Table 32, Fig. 19) are given. The intake of wild gulls foraging on Cockles is estimated to average 294 Cockles over one year old or 2,165 Cockles a few months old, i.e. 167 ml Cockle flesh, per low-water period. Full-grown gulls in captivity showed the following mean daily intakes (fresh weight): 363, and 368 g Horse-mackerel; 199, and 229 g Sprat and young Herring; and 48 to 101 g bread. There was a distinct relationship between the mean quantity consumed daily and the mean changes in body weight (Fig. 18).

The total food (fish) intake of two groups of chicks in captivity during the first 6 weeks (chick stage) amounted to 9.2 kg fresh weight (2.5 kg dry weight) and 8.4 kg fresh weight (2.4 kg dry weight), respectively, per chick.

Full-grown Herring Gulls in captivity proved to be able to fast for 8 consecutive days without untoward consequences (Fig. 21), and to recover rapidly from the effects of starvation (Fig. 20). It is suggested that the Herring Gull is adapted to an irregular food-supply.

Chapter 6 deals with the growth of chicks. In 1966 and 1967, but not in 1968, the growth-rate decreased from early-hatched to late-hatched chicks (Fig. 23, Table 33). Since this holds both for broods with one young and for broods with 3 young, the differences were suggested to be caused by weather conditions.

In several cases chicks of b/1 grew faster than chicks of b/3 (Fig. 23, Table 33). The weight increase of chicks in supernormal broods was irregular (Fig. 24). Several chicks grew very slowly and reached a much lower maximum weight than did chicks of normal broods. Chicks that did not reach a body weight of 600 g all died during or shortly after the chick stage. According to the present findings, in the Wadden Sea area the Herring Gull does not seem to be able to raise more than three young, which is the maximum natural brood-size found.

Chicks fed on garbage in addition to natural food generally grew faster than otherwise comparable birds in broods fed only on natural food (Table 34).

Undernourished chicks show compensatory growth only under improved food conditions. Presumably in wild gulls the variations in growth-rate result in differences in fledging weights. The possible influence of fledging weight on post-fledging survival is discussed.

The possible role of the extra food supplied indirectly by man on the regulation of the number of gulls is discussed in Chapter 7. On the basis of the data obtained during the present study, it seems probable that the northern part of The Netherlands has a greater winter population than it would have without garbage supplied by man. It seems likely that this extra food determined the level to which the population could increase.

9. REFERENCES

Ashmole, N. P. & M. J. Ashmole. 1967. Comparative feeding ecology of sea-birds of a tropical oceanic island. Bull. Peabody Mus. nat. Hist. 24.

Baxter, E. V. & L. J. Rintoul. 1953. The birds of Scotland. Vol. 2. Edinburgh & London, Oliver & Boyd.

Belopol'skii, L. O. 1961. Ecology of sea colony birds of the Barents Sea. Jerusalem (translated from the 1957 Russian edition by the Israel Program for Scientific Translations).

Bergman, G. 1939. Untersuchungen über die Nistvogelfauna in einem Schärengebiet westlich von Helsingfors. Acta Zool. Fenn. 23: 1–134.

Bergman, G., E. Fabricius & L. von Haartman. 1940. En preliminär undersökning över silltrutens, *Larus f. fuscus* L., och gråtrutens, *Larus a. argentatus* Pontopp., näringsbiologi, särskilt ur jaktvårdssynpunkt. Orn. Fenn. 17: 33–41.

Blaedel, N. 1963. Nordens fugle i farver. Band 7. Copenhagen, Munksgaard.

Blösch, M. 1966. Die Aktivität der Salzdrüsen. Vogelwarte 23: 225–231.

Brown, R. G. B. 1967a. Species isolation between the Herring Gull *Larus argentatus* and Lesser Black-backed Gull *L. fuscus*. Ibis 109: 310–317.

——— 1967b. Breeding success and population growth in a colony of Herring and Lesser Black-backed Gulls *Larus argentatus* and *L. fuscus*. Ibis 109: 502–515.

Bruns, H. 1963. Angewandte Ornithologie als staatliche Aufgabe. Angewandte Orn. 1: 104–111.

Centraal Bureau voor de Statistiek. 1968. Bevolking der gemeenten van Nederland op 1 januari 1968. 's-Gravenhage, Staatsuitgeverij.

Chaine, J. & J. Duvergier. 1934–1937. Recherches sur les otolithes des poissons. Actes Soc. Linn. Bordeaux 86: 5–254; 87: 5–242; 88: 5–246; 89: 5–252.

Commissie voor de Nederlandse Avifauna. 1962. Avifauna van Nederland. Ardea 50: 1–103.

Creutz, G. 1958. Zur Biologie des Graureihers. Falke 5: 208–213.

Dobben, W. H. van. 1934. Bijdrage tot het meeuwen-vraagstuk. Org. Club Ned. Vogelk. 7: 63–78.

——— 1952. The food of the Cormorant in the Netherlands. Ardea 40: 1–63.

Drent, R. H. 1967. Functional aspects of incubation in the Herring Gull (*Larus argentatus* Pont.). Thesis, Univ. Groningen.

Drost, R. 1953. Über die Heimattreue deutscher Seevögel. J. Orn. 94: 181–193.

——— 1955. Wo verbleiben im Binnenland frei aufgezogene Nordsee-Silbermöwen? Vogelwarte 18: 85–93.

——— 1958. Über die Ansiedlung von jung ins Binnenland verfrachteten Silbermöwen (*Larus argentatus*). Vogelwarte 19: 169–173.

Drost, R., E. Focke & G. Freytag. 1961. Entwicklung und Aufbau einer Population der Silbermöwe, *Larus argentatus argentatus*. J. Orn. 102: 404–429.

Drost, R. & L. Schilling. 1940. Ueber den Lebensraum deutscher Silbermöwen, *Larus a. argentatus* Pontopp., auf Grund von Beringungsergebnissen. Vogelzug 11: 1–22.

Drury, W. H. Jr. 1964. Results of a study of Herring Gull populations and movements in southeastern New England. Colloque: Le problème des oiseaux sur les aérodromes (Nice, 1963), p. 207–217. Paris, Inst. Nat. Rech. Agron.

Drury, W. H. & I. C. T. Nisbet. 1969. Strategy of management of a natural population: the Herring Gull in New England. Proc. World Conf. Bird Hazards to Aircraft (Kingston, Ontario, 1969), p. 441–454.

Ehlert, W. 1957. Zur Ernährung der Silbermöwe (*Larus argentatus* Pont.) in der Vorbrutzeit. Orn. Mitt. 9: 201–203.

——— 1961. Weitere Untersuchungen über die Nahrungswelt der Silbermöwe (*Larus argentatus*) auf Mellum. Vogelwarte 21: 48–50.

Eykman, C., P. A. Hens, F. C. van Heurn, C. G. B. ten Kate, J. G. van Marle, M. J. Tekke & Tsj. Gs. de Vries. 1949. De Nederlandsche vogels. Deel 3. Wageningen, Wageningsche Boek- en Handelsdrukkerij.

Focke, E. 1959. Zur Ernährung der Silbermöwe (*Larus argentatus*). Vogelwarte 20: 86–88.

Fordham, R. A. 1964. Breeding biology of the Southern Black-backed Gull II: Incubation and the chick stage. Notornis 11: 110–126.

——— 1968. Dispersion and dispersal of the Dominican Gull in Wellington, New Zealand. Proc. N.Z. Ecol. Soc. 15: 40–50.

Frost, G. A. 1925, 1926, 1930. A comparative study of the otoliths of the neopterygean fishes. Ann. Mag. Nat. Hist. (9) 15: 152–163; (9) 18: 483–490; (10) 5: 231–239.

Geiger, W. 1957. Die Nahrung der Haubentaucher (*Podiceps cristatus*) des Bielersees. Orn. Beob. 54: 97–133.

Godfrey, G. F., C. Williams & C. E. Marshall. 1953. Relative influence of egg-size, age at sexual maturity and mature body weight on growth to 12 weeks. Poult. Sci. 32: 496–500.

Goethe, F. 1937. Beobachtungen und Untersuchungen zur Biologie der Silbermöwe (*Larus a. argentatus* Pontopp.) auf der Vogelinsel Memmertsand. J. Orn. 85: 1–119.

——— 1939. Die Vogelinsel Mellum. Abh. Geb. Vogelkde 4. Berlin, Friedländer.

——— 1956. Die Silbermöwe. Neue Brehm-Bücherei 182. Wittenberg Lutherstadt, A. Ziemsen Verlag.

——— 1964. Lenkung der Möwenbestande an der deutschen Nordseeküste mit Hilfe der Einschläferung erwachsener Möwen durch Glukochloralose-*a*. Int. Rat Vogelschutz, Deutsche Sektion 4: 53–57.

Gross, A. O. 1940. The migration of Kent Island Herring Gulls. Bird-Banding 11: 129–155.

Harris, M. P. 1964a. Recoveries of ringed Herring Gulls. Bird Study 11: 183–191.

——— 1964b. Aspects of the breeding biology of the gulls *Larus argentatus, L. fuscus* and *L. marinus*. Ibis 106: 432–456.

——— 1965. The food of some *Larus* gulls. Ibis 107: 43–53.

Harris, M. P. & P. H. Jones. 1969. Sexual differences in measurements of Herring and Lesser Black-backed Gulls. Br. Birds 62: 129–133.

Harris, M. P. & W. J. Plumb. 1965. Experiments on the ability of Herring Gulls *Larus argentatus* and Lesser Black-backed Gulls *L. fuscus* to raise larger than normal broods. Ibis 107: 256–257.

Hartley, P. H. T. 1948. The assessment of the food of birds. Ibis 90: 361–381.

Heinroth, O. & M. Heinroth. 1928. Die Vögel Mitteleuropas. Band 3. Berlin, Bermühler.

Hofslund, P. B. 1959. Fall migration of Herring Gulls from Knife Island, Minnesota. Bird-Banding 30: 104–114.

Ingolfsson, A. 1967. The feeding ecology of five species of large gulls (*Larus*) in Iceland. Unpub. Thesis, Univ. Michigan.

——— 1969. Sexual dimorphism of large gulls (*Larus* spp.). Auk 86: 732–737.

Kadlec, J. A. & W. H. Drury. 1968. Structure of the New England Herring Gull population. Ecology 49: 644–676.

Kahl, M. P. 1964. Food ecology of the Wood Stork (*Mycteria americana*) in Florida. Ecol. Monogr. 34: 97–117.

Kendall, M. G. 1948. Rank correlation methods. London, Griffin.

Kennedy, P. G., R. F. Ruttledge & C. F. Scroope. 1954. The birds of Ireland. Edinburgh & London, Oliver & Boyd.

King, J. E. & I. I. Ikehara. 1956. Comparative study of food of Bigeye and Yellowfin Tuna in the Central Pacific. U.S. Fish and Wildlife Serv., Fish. Bull. 57: 61–85.

Kluyver, H. N. 1933. Bijdrage tot de biologie en de ecologie van den Spreeuw (*Sturnus vulgaris vulgaris* L.) gedurende zijn voortplantingstijd. Versl. Meded. Plantenziektenk. Dienst 69.

Knopfli, W. 1956. Die Vögel der Schweiz. Liefg. 19. Bern, Eidg. Dep. des Innern.

Koenig, O. 1952. Ökologie und Verhalten der Vögel des Neusiedlersee-Schilfgürtels. J. Orn. 93: 207–289.

Koersveld, E. van. 1951. Difficulties in stomach analysis. Proc. Int. Orn. Cong. 10: 592–594.

Kristensen, I. 1957. Differences in density and growth in a cockle population in the Dutch Wadden Sea. Archs. Néerl. Zool. 12: 351—453.

Kruuk, H. 1964. Predators and anti-predator behaviour of the Black-headed Gull (*Larus ridibundus* L.). Behaviour Suppl. 11.

Lack, D. 1954. The natural regulation of animal numbers. Oxford, Clarendon Press.

——— 1966. Population studies of birds. Oxford, Clarendon Press.

——— 1968. Ecological adaptations for breeding in birds. London, Methuen.

Lack, D., J. Gibb & D. F. Owen. 1957. Survival in relation to brood-size in tits. Proc. zool. Soc. Lond. 128: 313–326.

Lasiewski, R. C. 1963. Oxygen consumption of torpid, resting, active and flying hummingbirds. Physiol. Zool. 36: 122–140.

Leege, O. 1907. Ein Besuch bei den Brutvögeln der holländischen Nordseeinseln. Orn. Monatschr. 32: 334–353; 357–379; 389–398; 419–432.

——— 1917. Die Nahrung der Silbermöwen an der ostfriesischen Küste. Orn. Monatsber. 42: 110–116; 123–134.

LeFebvre, E. A. 1964. The use of D_2O^{18} for measuring energy metabolism in *Columba livia* at rest and in flight. Auk 81: 403–416.

Lemmetyinen, R. 1963. Lokkien esiintymisestä ja ravinnosta gullkronan selän koillisosassa. Suomen Riista 16: 69–82.

Lindroth, S. 1946. Ett bidrag till frågan om gråtrutens (*Larus argentatus* Pontopp.) ställning som marin relikt i våra insjöar. Vår Fågelvärld 5: 97–114.

Löhmer, K. & G. Vauk. 1969. Nahrungsökologische Untersuchungen an übersommernden Silbermöwen (*Larus argentatus*) auf Helgoland im August/September 1967. Bonn. zool. Beitr. 20: 110–124.

——— 1970. Ein weiterer Beitrag zur Ernährung Helgoländer Silbermöwen (*Larus argentatus*). Vogelwarte 25: 242–245.

Lowe, F. A. 1954. The Heron. London, Collins.

Lumsden, W. H. R. & A. J. Haddow. 1946. The food of the Shag (*Phalacrocorax aristotelis*) in the Clyde sea area. J. Anim. Ecol. 15: 35–42.

Maag, A. 1917. Haubentaucherabschuss auf dem Zürichsee. Schweiz. Fischerei-Z. 25: 72–74.

Madsen, F. J. & R. Spärck. 1950. On the feeding habits of the Southern Cormorant (*Phalacrocorax carbo sinensis* Shaw) in Denmark. Dan. Rev. Game Biol. 1: 45–75.

Martini, E. 1964. Otolithen in Gewöllen der Raubseeschwalbe (*Hydroprogne caspia*). Bonn. zool. Beitr. 15: 59–71.

——— 1966. Otolithen in Gewöllen der Westmöwe (*Larus occidentalis*). Bonn. zool. Beitr. 17: 202–227.

Maschlanka, H. 1954. Proportionsmessungen an Silbermöwen. Zool. Jb. (Physiologie) 65: 209–218.

Meinertzhagen, R. 1955. The speed and altitude of bird flight (with notes on other animals). Ibis 97: 81–117.

Mertens, J. A. L. 1969. The influence of brood size on the energy metabolism and water loss of nestling Great Tits *Parus major major*. Ibis 111: 11–16.

Meijering, M. P. D. 1954. Zur Frage der Variationen in der Ernährung der Silbermöwe, *Larus argentatus* Pont. Ardea 42: 163–175.

Mills, D. H. 1957. Herring Gulls and Common Terns as possible predators of lobster larvae. J. Fish Res. Bd. Canada. (Reference not seen).

Minoranskii, V. A. 1963. Nesting of the Herring Gull (*L. argentatus*) in Lake Manych-Gudilo. N.D.V.S. Biol. Nauki 3: 51–53. (Reference not seen).

Moran, P. A. P. 1951. Partial and multiple rank correlation. Biometrika 38: 26–32.

Mörzer Bruyns, M. F. 1958. Gulls which are a menace to other species. Bull. Intern. Comm. Bird Preserv. 7: 103–107.

Nijssen, H. 1968. Zeevissen. Wetensch. Meded. 65, tweede druk. Hoogwoud, Bureau K.N.N.V.

Nordberg, S. 1950. Researches on the bird fauna of the marine zone in the Åland Archipelago. Acta Zool. Fenn. 63: 5–62.

Odink, J. 1969. Wadvogeltelling 12 augustus. In: Wadvogels op Vlieland. Amsterdam, Vogelwerkgroep C.J.N.

Olsson, V. 1958. Dispersal, migration, longevity and death causes of *Strix aluco, Buteo buteo, Ardea cinerea* and *Larus argentatus*. Acta Vertebr. 1: 91–189.

Otterlind, G. 1948. Till gråtrutens (*Larus a. argentatus* Pont.) närings och spridningsekologi. Kungl. Fysiografiska Sällskapets I Lund förhandlinger 18: 36–56.

Paludan, K. 1951. Contributions to the breeding biology of *Larus argentatus* and *Larus fuscus*. Vidensk. Medd. Dansk naturh. Foren. 114: 1–128.

——— 1953. Nogle resultater af Københavns Zoologiske Museums Ringmaerkning af *Larus argentatus*. Vidensk. Medd. Dansk naturh. Foren. 115: 181–204.

Parslow, I. L. F. 1967. Changes in status among breeding birds in Britain and Ireland. Part 3. Br. Birds 60: 177–202.
Paynter, R. A. 1949. Clutch-size and the egg and chick mortality of Kent Island Herring Gulls. Ecology 30: 146–166.
Pearson, O. P. 1950. The metabolism of hummingbirds. Condor 52: 145–152.
Perrins, C. M. 1965. Population fluctuations and clutch-size in the Great Tit, *Parus major* L. J. Anim. Ecol. 34: 601–647.
Peters, H. M. & R. Müller. 1951. Die junge Silbermöwe (*Larus argentatus*) als "Platzhocker". Vogelwarte 16: 62–69.
Poulding, R. H. 1955. Some results of marking gulls on Steep Holm. Proc. Bristol Nat. Soc. 29: 49–56. (Reference not seen).
Rayfield, P. A. 1958. Rate of growth in Lapwing chicks. Bird Study 5: 34.
Rooth, J. 1956. Over het voedsel van de kiekendieven van de Boschplaat op Terschelling. Levende Nat. 59: 265–271.
——— 1957. Over het voedsel van de Zilvermeeuwen. Levende Nat. 60: 209–213.
——— 1966. Vogeltelling in het hele Nederlandse Waddengebied, augustus 1963. Limosa 39: 175–181.
Royama, T. 1966. Factors governing feeding rate, food requirement and brood size of nestling Great Tits *Parus major*. Ibis 108: 313–347.
Salomonsen, F. 1953. Fugletraekket og dets gåder. København, Munksgaard.
——— 1963. Oversigt over Danmarks fugle. København, Munksgaard.
Scheffé, H. 1959. The analysis of variance. New York, Wiley.
Schmidt, W. 1968. Vergleichend morphologische Studie über die Otolithen mariner Knochenfische. Arch. Fischereiwiss. 19, Beiheft 1.
Schönwetter, M. 1963. Handbuch der Oologie. Liefg. 7. Berlin, Akademie-Verlag.
Skoglund, W. C., K. C. Seegar & A. T. Ringrose. 1952. Growth of broiler chicks hatched from various sized eggs when reared in competition with each other. Poult. Sci. 31: 796–799.
Smith, N. G. 1966. Evolution of some arctic gulls (*Larus*): an experimental study of isolating mechanisms. Orn. Monogr. 4.
Smith, W. J. 1959. Movements of Michigan Herring Gulls. Bird-Banding 30: 69–104.
Spaans, A. L. 1959. Het Zilvermeeuwenprobleem op Vlieland. Levende Nat. 62: 25–29.
Spaans, A. L. & C. Swennen. 1968. De vogels van Vlieland. Wetensch. Meded. 75. Hoogwoud, Bureau K.N.N.V.
Spärck, R. 1951. The food of the North-European Gulls. Proc. Int. Orn. Cong. 10: 588–591.
Spitzenberger, F. 1961. Zur Ernährung einer istrischen Silbermöwen-Kolonie (*Larus argentatus michahellis*). Vogelwarte 21: 50–52.
Swennen, C. 1970. Vogelwaarnemingen op het IJsselmeer. Limosa 43: 1–10.
Swennen, C. & A. L. Spaans. 1960. Over de aantallen mossels op de strandhoofden van Vlieland. Zeepaard 20: 59–62.
Threlfall, W. 1968. The food of three species of gulls in Newfoundland. Can. Field-Nat. 82: 176–180.
Tinbergen, N. 1952. De "trek" van Zilvermeeuwen langs de Nederlandse kust. Ardea 40: 77–80.
——— 1953. The Herring Gull's world. London, Collins.
——— 1962. Foot-paddling in gulls. Br. Birds 55: 117–120.
Tucker, V. A. 1968. Respiratory exchange and evaporative water loss in the flying budgerigar. J. exp. Biol. 48: 67–87.
Vauk, G. & F. Gräfe. 1961. Fisch-Otolithen, ein wichtiges Hilfsmittel zur Nahrungsanalyse bei Lariden. Zool. Anz. 167: 391–394.
Vauk, G. & K. Löhmer. 1969. Ein weiterer Beitrag zur Ernährung der Silbermöwe (*Larus argentatus*) in der Deutschen Bucht. Veröff. Inst. Meeresforsch. Bremerh. 12: 157–160.
Vermeer, K. 1963. The breeding ecology of the Glaucous-winged Gull (*Larus glaucescens*) on Mandarte Island, B.C. Occ. Pap. Brit. Columbia Prov. Mus. 13.
——— 1970. Breeding biology of California and Ring-billed Gulls. Can. Wildl. Serv. Rep. Ser., Nr. 12.
Vonk, H. J., Grietje Brink & N. Postma. 1946. Digestion in the stomach of birds. I. The acidity in the stomach of young chickens. Proc. Kon. Ned. Akad. Wetensch. 49: 972–982.

Voous, K. H. 1960. Atlas van de Europese vogels. Amsterdam & Brussel, Elsevier.
Walters, J. 1961. Notes on the chicks of the Little Ringed Plover. Bird Study 8: 15–18.
Werner, C. F. 1963. Form und Grösse des Sacculus-Otolithen (Sagitta) der Gadidae. Zool. Anz. 170: 282–288.
White, H. C. 1957. Food and natural history of mergansers on salmon waters in the maritime provinces of Canada. Bull. Fish. Res. Bd. Canada 116: 1–63.
Wijngaarden, A. van. 1964. The terrestrial mammal-fauna of the Dutch Wadden-Islands. Z. f. Säugetierk. 29: 359–368.
——— 1967. Rapport over de verspreiding van de Noordse Woelmuis, *Microtus oeconomus arenicola* de Sélys Longchamps 1841, in Nederland. Zeist, RIVON.
Wilson, P. N. & D. F. Osbourn. 1960. Compensatory growth after undernutrition in mammals and birds. Biol. Rev. 35: 324–363.
Woodbury, A. M. & H. Knight. 1951. Results of the Pacific Gull color-banding project. Condor 53: 57–77.
Wynne-Edwards, V. C. 1962. Animal dispersion in relation to social behaviour. Edinburgh, Oliver & Boyd.

10. SAMENVATTING

In dit artikel worden de resultaten behandeld van een onderzoek naar de voedseloecologie van de Zilvermeeuw in Noord-Nederland (Fig. 1). Het doel van het onderzoek was kwantitatieve gegevens te krijgen over het aandeel dat het afval van de mens in het voedsel van deze vogels heeft en op deze wijze een bijdrage te leveren tot de discussie over de oorzaken van de populatiegroei van de soort in deze eeuw.

Een analyse van de terugmeldingen van Zilvermeeuwen die als kuiken op de Waddeneilanden zijn geringd laat zien dat de meeuwen uit dit gebied, evenals de meeste populaties in Noordwest-Europa, geen trekvogel zijn, maar na het broedseizoen in alle richtingen over een relatief klein gebied uitzwermen (Fig. 2–6, Tabel 1 en 2). De meeste meeuwen worden binnen 100 km van de ringplaats teruggemeld. Gedurende de vijftiger en zestiger jaren verplaatsten de meeuwen zich minder ver van de ringplaats dan in de eerste helft van deze eeuw, maar het verschil was alleen voor de eerstejaars vogels significant (Tabel 3). De verschillen worden toegeschreven aan de relatief gunstige voedselsituatie aan het begin van de dispersieperiode gedurende de laatste twee decennia als gevolg van de intensieve bestrijding van de soort in die periode. Deze had een extra sterfte van volwassen vogels in het broedseizoen en een geringe produktie aan jongen tot gevolg, waardoor de populatie aan het begin van de dispersieperiode steeds betrekkelijk klein was.

De meeste Zilvermeeuwen komen blijkens de ringgegevens niet vóór het einde van het vierde of vijfde levensjaar voor de eerste keer tot broeden.

Er is wel een tendens om in latere jaren als broedvogel terug te keren naar de geboortekolonie, maar deze is niet erg uitgesproken. Relatief veel meeuwen werden gedurende het broedseizoen op naburige eilanden teruggemeld (Tabel 4). Dit verspreidingspatroon werd toegeschreven aan de verstoring op de broedplaatsen door de intensieve bestrijding in de laatste twee decennia.

In het eerste levensjaar vindt de grootste sterfte plaats in september en oktober; dat is aan het einde van de dispersieperiode (Fig. 7). In het tweede en derde levensjaar is de sterfte min of meer gelijk over het jaar verdeeld. In latere jaren treedt de grootste sterfte gedurende het broedseizoen (mei–juli) op. Het sterftebeeld van de adulte vogels hangt waarschijnlijk niet samen met de intensieve bestrijding in de laatste decennia.

Omdat het grootste deel van de populatie gedurende het gehele jaar in een beperkt gebied verblijft, was het mogelijk de verspreiding buiten het broedseizoen door tellingen kwantitatief vast te leggen. Uit geregelde tellingen rond hoogwater op Terschelling en Vlieland is gebleken dat de aantallen op de Waddeneilanden na het broedseizoen snel afnemen (Fig. 8). Op Vlieland werd de afname gevolgd door een tijdelijke toename. De laagste aantallen werden op beide eilanden in de wintermaanden vastgesteld. In januari of februari was er echter al weer een duidelijke toename. Gedurende de wintermaanden fluctueerden de aantallen op beide eilanden onder invloed van de weersomstandigheden aanzienlijk.

Min of meer simultane tellingen in het gehele Waddengebied leverden totaal-aantallen van 33.000–39.000 Zilvermeeuwen op (Tabel 5). In de winter van 1966–1967 fluctueerde

het aantal volgens onze schattingen tussen 21.000 en 37.000 meeuwen, in de winter van 1967–1968 tussen 14.000 en minstens 28.000 vogels.

Gedurende 1967–1969 werden geregeld tellingen verricht op 13 vuilnisbelten op het vasteland van Friesland (Fig. 9 en 10, Tabel 6). Gedurende het broedseizoen waren de aantallen op de belten het laagst. Zij namen aan het einde van het broedseizoen toe en bereikten al in oktober het winterniveau. De aantallen bleven tot in april hoog. Gedurende de winterperiode waren de aantallen aan sterke schommelingen onderhevig. Deze fluctuaties bleken samen te hangen met de fourageermogelijkheden op het wad (Fig. 11 en Tabel 8).

In december 1967 werden in een betrekkelijk korte tijd vrijwel alle 104 vuilnisbelten op het vasteland van Friesland, Groningen en Drente geïnventariseerd (Fig. 12). De telling leverde een totaal van 26.097 Zilvermeeuwen op. Er werd berekend dat het aantal Zilvermeeuwen op deze belten gedurende de winter 1967–1968 moet hebben gefluctueerd tussen de 20.000 en minimaal 39.000 (Tabel 9).

De verdeling van de meeuwen over de vuilnisbelten was positief gecorreleerd met het aantal inwoners van de betrokken gemeenten (Fig. 13), hetgeen erop wijst dat de verspreiding van de meeuwen nauw samenhangt met de hoeveelheid voedsel die op de belten aanwezig is. Er werd verondersteld dat deze verdeling door intraspecifieke concurrentie tijdens de dispersieperiode tot stand komt.

Andere meeuwensoorten werden weinig op de belten aangetroffen. Dit hangt slechts gedeeltelijk samen met verschillen in de voedseloecologie van de diverse soorten. Elders in Nederland werden Kokmeeuwen namelijk wel talrijk op vuilnisbelten aangetroffen en blijkens inlichtingen van anderen is dat op sommige belten in het noorden van het land gedurende de zomermaanden eveneens het geval. Er werd verondersteld dat de Kokmeeuwen in het noorden van het land in de wintermaanden door de grotere Zilvermeeuwen door interspecifieke concurrentie worden verdrongen.

De totale Zilvermeeuwenpopulatie op het vasteland van Friesland, Groningen en Drente fluctueerde in de winter van 1967–1968 tussen 24.000 en minimaal 47.000 vogels (Tabel 11).

Het voedsel van volgroeide Zilvermeeuwen bestond voornamelijk uit mariene evertebraten uit de litorale en sublitorale zone (Tabel 12–14). In de loop van het onderzoek werden in de kolonies op Terschelling en Vlieland ruim 27.000 braakballen en faeces onderzocht. De samenstelling van de braakballen en faeces bleek in de loop van het seizoen sterk te veranderen (Fig. 14). Deze veranderingen werden toegeschreven aan verschillen in talrijkheid, bereikbaarheid en aantrekkelijkheid van de diverse prooisoorten.

Het voedsel van de jongen bestond voor het grootste deel uit vis (Tabel 16–22), voornamelijk Clupeidae, Gadidae en platvissen (Tabel 23 en 24). De Gadidae en platvissen waren geheel of grotendeels afkomstig van weggeworpen vangsten van de kustvisserij. Er werd berekend dat 1/5 tot 1/3 van het voedsel van de jongen vis betrof die via de visserij werd bemachtigd (Tabel 26). Etensafval werd in ongeveer 1/4 van de gevallen aangetroffen. Gemiddeld werd dus ongeveer 50% van het voedsel van de jongen door tussenkomst van de mens verkregen.

Er was een positieve correlatie tussen broedselgrootte en percentage meeuwen dat naast natuurlijk voedsel ook etensafval aan de jongen voerde (Fig. 16). Er werd verondersteld dat dit een reactie van de ouders was om aan de stijgende voedselbehoefte van de grotere broedsels te voldoen.

Jonge Zilvermeeuwen blijken in tegenstelling tot oudere meeuwen graten van vissen geheel te verteren.

Op grond van het verloop van de broedvogelstand van Eidereend, Bergeend en Kluut op Vlieland gedurende de laatste veertig jaar werd de conclusie getrokken dat de Zilvermeeuw op dit eiland niet als schadelijk kan worden beschouwd voor deze soorten, ofschoon de meeuwen ieder jaar een zware tol heffen van de eieren en jongen. Er werd verondersteld dat de gevolgen van de predatie door immigratie worden opgevangen.

Buiten het broedseizoen fourageert een groot deel van de populatie op vuilnisbelten en andere plaatsen met afval op het vasteland van Noord-Nederland. Op grond van diverse tellingen in het Waddengebied en op het vasteland werd berekend dat ten minste 32% van de totale winterpopulatie constant deze voedselbronnen benutte, terwijl het percentage bij ongunstige fourageermogelijkheden op de Waddenzee kon oplopen tot minstens 77%.

De voedselopname van Zilvermeeuwen die uitsluitend Kokkels aten bedroeg per laagwaterperiode gemiddeld 294 ruim één jaar oude Kokkels of 2.165 Kokkels van enkele maanden oud, of 167 ml kokkelvlees (Tabel 29).

Volgroeide meeuwen in gevangenschap gaven de volgende gemiddelde dagopnamen te zien: 363, 368 g Horsmakreel; 199, 229 g Sprot en jonge Haring; 48—101 g brood (Tabel 30, zie ook Fig. 17).

De totale voedselopname van twee groepen kuikens in gevangenschap bedroeg gedurende het kuikenstadium (6 weken) respektievelijk 9,2 kg versgewicht (2,5 kg drooggewicht) en 8,4 kg versgewicht (2,4 kg drooggewicht) vis per kuiken (Tabel 32, zie ook Fig. 19).

Volgroeide meeuwen bleken in gevangenschap in staat 8 dagen achtereen te vasten zonder merkbaar nadelige gevolgen. De meeuwen herstelden zich na een vastenperiode weer in korte tijd (Fig. 20), zodat werd verondersteld dat de soort aan een ongeregelde voedselvoorziening is aangepast.

In 1966 en 1967, maar niet in 1968, nam de groeisnelheid af van vroeg naar laat geboren kuikens (Fig. 23, Tabel 33). Dit werd zowel bij broedsels met 1 jong als bij broedsels met 3 jongen geconstateerd. Er werd verondersteld dat mogelijk de hoeveelheid water die de jongen in het droge duin door middel van dauw- en regendruppels tot zich kunnen nemen verantwoordelijk is voor de verandering in groeisnelheid in de loop van het seizoen. Bij het opkweken van kuikens in gevangenschap werd namelijk de indruk verkregen dat kuikens die niet in de gelegenheid waren te drinken minder eetlust vertoonden dan andere kuikens.

In diverse gevallen groeiden kuikens in broedsels met 1 jong harder dan in broedsels met 3 jongen (Fig. 23, Tabel 33).

De gewichtstoename van kuikens in supernormale broedsels was onregelmatig (Fig. 24). Diverse jongen groeiden bovendien zeer langzaam en bereikten in veel gevallen een veel lager maximum gewicht dan kuikens in normale broedsels. De jongen die onder een gewicht van 600 gram bleven werden alle tijdens het kuikenstadium of kort daarna doodgevonden. De diverse gegevens wijzen erop dat de soort in het Nederlandse Waddengebied vermoedelijk niet meer dan drie jongen kan groot brengen.

Jongen die naast natuurlijk voedsel etensafval kregen gevoerd bleken in diverse gevallen harder te groeien dan kuikens in overeenkomstige broedsels die alleen met natuurlijk voedsel werden gevoerd (Tabel 34).

Ondervoede kuikens bleken alleen een compenserende groei te vertonen als de voedselomstandigheden beter worden. Bij vogels in het wild zijn daarom de variaties in groeisnelheid vermoedelijk in de gewichten van de vliegvlugge jongen terug te vinden. De mogelijke invloed van dit gewicht op de overlevingskans werd besproken.

Er werd verondersteld dat de toename van de Zilvermeeuw in het Nederlandse Waddengebied in deze eeuw mogelijk is gemaakt door de beschermende maatregelen die in het begin van deze eeuw werden genomen, maar dat de beschikbare voedselhoeveelheid heeft bepaald tot welk niveau deze toename kon doorgaan.

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