J. Orn. 132, 1991: S. 427—437

Fledgling Production of Eiders *Somateria mollissima* in The Netherlands

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Introduction

The Eider-colonies in the Dutch Wadden Sea area represent the southernmost settlement in the breeding range of the species along the western coast of Europe (BAUER & GLUTZ VON BLOTZHEIM 1969, CRAMP & SIMMONS 1977). The population is growing and several new colonies became established since the first settlement was discovered in 1906 (reviewed in SWENNEN 1976). Ringing has shown that females breeding in these colonies remain completely philopatric and that young females, when breeding for the first time, are largely faithful to their natal colony (SWENNEN 1990). Therefore, the local production of fledglings, especially of female fledglings, will be an important factor determining later recruitment to the colonies.

The number of breeding pairs and the number of ducklings that hatch in the Dutch colonies do not show extreme fluctuations in successive years. However, the number of ducklings that fledge is highly variable, ranging between 0.00 and 1.99 fledglings per female in the five largest colonies (SWENNEN 1983). A high duckling mortality is a common phenomenon in Eiders (BAUER & GLUTZ VON BLOTZHEIM 1969). Duckling survival may be dependent on several factors. Two groups can be distinguished: the contribution of the female, mainly influenced by factors operating before hatching, and environmental factors operating directly upon the duckling after hatching. The present paper deals with the latter and presents data on the fledgling output of the colony on the Island of Vlieland over a period of 28 years. Comparable data on duckling survival were found only for the Ythan Estuary, Scotland (MENDENHALL & MILNE 1985). Their series comprises 13 years of which only 8 could be compared with weather data.

Methods

The size of the breeding colony

The number of breeding females is a measure of the size of an Eider-colony. Most estimates have been based on counts of Eiders along the shore in the first 10 days of May, when nearly all females breeding that year were on their nests. The surplus of adult males (counted males minus counted females) is considered to be equal to the number of breeding females (HOOGERHEIDE & HOOGERHEIDE 1958). A handicap of this method was the presence of huge numbers of non- breeders that had to be counted, often amounting to 4 to 5 times the number of local breeding pairs (SPAANS & SWENNEN 1968). The majority of the non-breeders are over-summering Eiders of the Baltic population (SWENNEN 1976, 1990).

It was assumed that the number of adult males and females was equal. A number of counts just prior to the breeding season proved this assumption to be correct. It was further assumed that also in the sub-adults the sex ratio was one. This could not be verified, as misidentifications of the sex of sub-adults was found to be unavoidable under field conditions (SWENNEN et al. 1989).

An additional method was to count nests in selected plots, usually concurrent with our ringing operations, or after most eggs were hatched. The percentual changes found between years were extrapolated over the whole colony. Data collected in 1979, when a complete count of nests was conducted, suggest that the counts of adults overestimate the actual number of nests. This means that especially since 1969 the size of the breeding colony may have been somewhat overestimated.

Fledgling output

Fledgling output was determined by counting the ducklings while the observers walked along the shore during high tide. The counts were conducted in the first week of July, when the ducklings were on average 5 to 7 weeks old (peak of hatching is approximately 23 May). In fact Eider ducklings fledge at an age of 8.5—10.7 weeks (BAUER & GLUTZ VON BLOTZHEIM 1969), but I found that when the ducklings become 8 weeks or older, they cannot always easily be distinguished from adults under the prevailing field conditions. The surveys were conducted over 27 years (1962—1988). A count of 1947 is added (HOOGERHEIDE 1950).

Sex ratio

Entire crèches of fledglings could be caught with a collapsible, portable funnel trap that was erected on sandy spots as soon as a crèche had been located. Thereafter the crèche was surrounded and driven to the trap by assistants walking or wading on the intertidal flats and with dinghies in the deeper water. Details of the trap are given elsewhere (SWENNEN 1988). Fledglings were ringed, sexed and set free again. The sex of the fledglings was determined on the basis of cloacal features (KORTRIGHT 1962, BAUER & GLUTZ VON BLOTZHEIM 1969). In later years, 601 (106 males and 495 females) of these fledglings were recaptured and then sexed on the basis of plumage characteristics (PALMER 1962, BAUER & GLUTZ VON BLOTZHEIM 1969). Differences were found in only 4 cases. In 1978, 278 fledglings drowned in a fishing net were also sexed. The dead ducklings were sexed by inspecting the secondary sexual characteristics of the syrinx (HUMPHREY 1958).

The sex ratio of fledglings in a crèche was never found to deviate significantly from the sex ratio in other crèches or of all fledglings caught in an area in a specific year. This indicates that, although exchange of ducklings between crèches could often be observed (SWENNEN 1989), separation based on sex did not occur in the ducklings. Therefore, a reliable sex ratio could be obtained without the necessity of catching all crèches.

Predators

The main predator of Eider ducklings in the Wadden Sea is the Herring Gull *Larus argentatus* (VAN DOBBEN 1934, SWENNEN 1983, 1989). The number of Herring Gulls during the duckling period is dependent on the size of their local breeding colony (SPAANS & SWENNEN 1968). Data on the number of breeding pairs are collected yearly by the Forestry Service and published in the Gull Reports of the Research Institute for Nature Management (RIN).

Weather

Mean air temperature and wind force over 10-day periods came from data of the meteorological observatory at Den Helder (about 35 km from Vlieland) published in the Monthly Weather Reports issued by the Royal Meteorological Institute (KNMI).

I should like to thank P. DUIVEN, J. ZUIDEWIND, the many students and volunteers who assisted in gathering the field data and the officers of the State Forestry Department on Vlieland, who always provided logistic support, J. HOOGERHEIDE, who introduced me in the problems of determining the size of the breeding population, Th. SMIT, Central Veterinary Institute, Lelystad, for identifying several pathogens and preparing the serum with antibodies of Goose Hepatitus virus for the field test, J. v. d. MEER and E. MEELIS for help with the statistics, and B. BAK, R. H. DRENT, J. G. VAN RHIJN and J. J. ZIJLSTRA for their suggestions for improving an earlier draft of the manuscript, and J. GUTT for preparing the German summary.

Results and Discussion

Fledgling production

The production of fledglings on Vlieland varied between 2 and 3200 per year over the 28 years for which data are available (Appendix). This corresponds with an average number of 0.342 fledglings per female per year, varying between 0.002 and 1.522. From the data on mean clutch size and mean hatching success (SWENNEN 1983) it can be computed that the average number of ducklings that hatched per female on Vlieland was about 4, varying between 3.1 and 4.6. Thus duckling mortality and not hatching failure was the main factor influencing reproduction success up to fledging.

The average sex ratio in 6,472 fledglings studied did not deviate significantly from unity (χ^2 = 0.08, d. f. = 1, n. s.). However, this does not hold for the individual years (Table). In 2 out of the 8 years the sex ratio differed significantly from one, with males

Sex ratio in Eider fledglings from different colonies in The Netherlands in different years. Probabilities given above dominant sex indicate deviations from an even sex ratio: χ^2-test, ** P <0.005, * P <0.05, no sign P >0.05 (n.s.).

Year	Vlieland		Terschelling		Ameland		Schier-monnikoog		Total		Females
	m	f	m	f	m	f	m	f	m	f	%
	**								**		
1978	636	538	—	—	—	—	—	—	636	538	45.8
1979	271	275	253	219	20	31	58	39	602	564	48.4
		*		*						**	
1980	55	80	104	140	—	—	69	77	228	297	56.6
1981	57	50	112	125	—	—	—	—	169	175	50.9
		*									
1982	231	292	289	262	55	66	—	—	575	620	51.9
1983	69	76	339	316	—	—	—	—	408	392	49.0
1984	80	79	222	227	—	—	—	—	302	306	50.3
1985	74	71	206	216	16	16	31	30	327	333	50.5
Total	1473	1461	1525	1505	91	113	158	146	3247	3225	49.8

dominating in one year, females in the other. As significant deviations in large series of tests can occur by chance, the sign test statistics on the values of the sex determinations of the different groups were combined. The sum of squares of the statistics follows a Chi-square distribution with 21 degrees of freedom, in our case giving χ^2 = 39.3, P <0.01. At hatching, the (secondary) sex ratio of Eiders on Vlieland does not deviate from unity, neither within a season (early, peak, late) nor between years (SWENNEN et al. 1979). An unbalanced sex ratio in fledglings must be caused by sex related mortality in the duckling stage.

Indications of such a selective mortality due to an infectious disease were found in one out of three years in large-scale rearing experiments (SWENNEN et al. 1979). As the mortality was female biased, it was thought that female ducklings were generally less resistant to diseases or had a lowered vitality. This opinion proved to be premature in view of new field data from which it appears that also male-biased mortality among ducklings may occur. The exact cause of sex-related mortality in ducklings is yet unknown and the scale and direction cannot be predicted. The question is relevant to the population dynamics of local populations, as female fledglings are predominantly recruited into their natal colony (SWENNEN 1990).

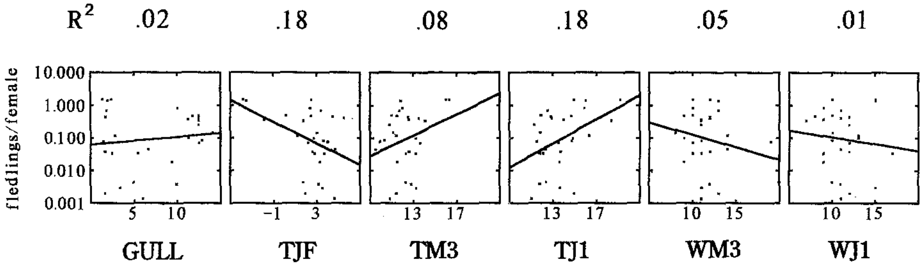
Number of predators and weather as possible determinants

Several factors may be involved in the extreme differences in fledging output: the number of ducklings hatched, the number of predators, the weather, the quality of the ducklings, the food supply, and diseases. Low temperatures and strong winds are usually considered detrimental to the survival of young birds. Therefore, mean air temperature and wind-force in the last 10 days of May (TM3; peak of hatching) and the first 10 days of June (TJ1; ducklings still small) might be critical. As winter temperatures influence quantity, quality and reproduction of benthic invertebrates (KRISTENSEN 1957, BEUKEMA & ESSINK 1986) that act as food for the Eiders in the Wadden Sea, also mean temperature of January and February (TJF; the coldest months) might indirectly influence duckling survival (data see Appendix).

To obtain an indication of the relative importance of the variables and the overall effect, the following model (in which t is the time from hatch to fledge, Y is the number of chicks, Y_0 is the number of chicks hatched, estimated by taking the number of females times the average number of hatchlings. Yt is the number of chicks grown into fledglings, FEM is the number of Eider females (nests), GULL is the number of gulls, which is assumed to be constant over the period from time = 0 to time = t, and c are constants). It has been assumed that the predation rate depends on the interaction between the number of prey and the number of predators:

$$dY/dt = c_0 \cdot Y \cdot \text{Gull, so } Y_t = Y_0 \cdot e^{c_0 \cdot \text{GULL} \cdot t}$$

So, assuming a multiplicative log-normally distributed error, the logarithm of the number of fledglings per female (Yt/FEM) is a linear function of GULL with normally distributed errors. Similarly, it has been assumed that this ratio is also a linear func-



Relations between number of fledglings per female and the size of the Herring Gull colony (GULL), temperature in January and February (TJF), temperature in the last 10 days of May (TM3), temperature in the first 10 days of June (TJ1), and the wind force (WM3, WJ1) in the same periods. Number of gulls x 1,000; temperatures in centigrades; wind force in 0.5 m/s. R^2 is the coefficient of determination. Only TJF and TJ1 are statistically significant ($P<0.05$).

tion of the weather factors TJF, TM3, TJ1, WM3, and WJ1. The number of fledglings per female appeared indeed to be positively related with TM3, TJ1, and GULL, and negatively related with TJF, WM3, and WJ1 (Diagrams and R^2 coefficients in Fig). This all suggests that low temperature in winter and high temperature at the end of May and the beginning of June, together with calm weather at the end of May and the beginning of June, and a large colony of Herring Gulls are profitable for fledging success. However, the scatter is large (Fig). A stepwise multiple regression analysis included only TJ1, which explained 18 percent of the total variance ($P = 0.024$). For each degree rise of mean June-temperature (TJ1) the number of fledglings per female was expected to increase by a factor of 1.5 (plus or minus the standard error 1.28—1.83). Note that the total range in the number of fledglings per female is equivalent to a factor of 400. Addition of any of the other variables did not lead to a significant increase of the explained variance ($P > 0.15$).

That the abundance of gulls does not negatively contribute to duckling survival may be surprising, as predation by Herring Gulls is undoubtedly the most obvious, immediate cause of death in Eider ducklings in The Netherlands (VAN DOBBEN 1934, SWENNEN 1989). However, gull predation is largely of a secondary nature, removing a doomed segment, i. e. weak and undernourished ducklings (SWENNEN 1989). Large gulls (*Larus argentatus*, *L. hyperboreus* and *L. marinus*) are important predators of ducklings everywhere in the breeding range of the Eider (e. g. GERASIMOVA & BARANOVA 1960, MUNRO & BÉDARD 1977). The reason why poisoning of breeding Herring gulls in their colonies was formerly carried out in The Netherlands was their predatory behaviour upon eggs and young of other birds, including the Eider (MÖRZER BRUIJNS 1956). After killing of about 110,000 adult gulls, the action was stopped (SWENNEN 1982) and the number of breeding pairs of both Herring Gulls and Eiders increased. Both species have probably benefitted by the greater peace on their common breeding grounds since then.

Also the factors temperature and wind contributed little to the explanation of the variation in the fledgling data. MENDENHALL & MILNE (1985) found, in stepwise multiple regression, a significantly negative effect of high winds, low temperatures and rainfall in a series of 8 years, but only when one year was omitted because of "its unusually high survival despite cold and windy weather". The conclusion may be that the observed fluctuations in weather of these first few weeks is not very critical to the survival of Eider ducklings. Possibly the other not quantifiable factors noted above are in fact crucial.

Food

In addition to fluctuations the data indicate a long-lasting period (1966—1977) during which massive fledging failure recurred periodically. Largely parallel to this fledgling failure in Eiders, some other long-term changes in productivity in the North Sea and adjacent waters have occurred. In the Dutch coastal waters blooms of the alga *Phaeocystis pouchetii* occurred regularly up to 1964, but they were less pronounced or even absent from 1969 onwards (Gieskes & Kraay 1977). This agrees fairly well with the decline of the production of Eider fledglings on Vlieland. Marked peaks of *Phaeocystis pouchetii* were found again from 1977 onwards in a study in the Marsdiep area from 1973 to 1985 (Cadée 1986). Another parallel phenomenon is that the stock of sprat *Sprattus sprattus* in the North Sea increased from about the early 1970s, and sharply decreased after 1978, while the larval production of the herring *Clupea harengus* was extremely low during the 1970s but increased sharply from 1977 onwards (Corten 1986). In about the same period, from the mid-1960s to the late 1970s, there was also a change in the plankton community in the western English Channel (Robinson & Hunt 1986). The relation with the long-term trends in marine production argues in favour of a link between the varying production in marine organisms and that of Eider fledglings.

The presence of benthic food items of a small size is indeed a prerequisite for fledgling success of Eiders (Swennen 1989). The abundance and species composition of small benthic invertebrates show large year-to-year fluctuations (Kühl 1972, Reise 1981). Franzmann (1989) suggested the importance of eutrophication for Eiders. It is beyond dispute that the nutrient concentrations in our coastal waters have increased during the last decades (Postma 1985). Also the concentration of micro-algae (Cadée 1986, Radach & Berg 1986), and the biomass of the macrozoobenthos has increased in the Dutch Wadden Sea since 1970 (Beukema & Cadée 1986). The same trend is visible in the fledgling production of the Eiders on Vlieland since 1970 (Appendix). It is tempting to relate these observations. However, the level of fledgling production was about the same in 1947, 1963—1966 and 1978—1987. Therefore a simple relation between fledgling production and increasing eutrophication seems highly unlikely.

Wide fluctuations in fledging success (0.01—1.3 fledglings per nesting female) have also been recorded from the Ythan estuary in Scotland (Mendenhall & Milne 1985). Their series (1962—1974) overlaps my data. In the overlap, there is no correlation between the two series in the total numbers of fledglings ($r = 0.31$, $P > 0.05$) or in the number of fledglings per female ($r = 0.32$, $P > 0.05$), although both areas had a peak in fledging success after the severe winter of 1963. Severe winters are usually followed by mass settlement of young benthic invertebrates in the intertidal zone (KRISTENSEN 1957), which means a good feeding opportunity for Eider ducklings.

Pesticides

Enhanced mortality of adult females occurred in the Vlieland colony at about the time the eggs hatched between 1963 and 1968, peaking in 1965 (SWENNEN 1972, 1982, 1983). This mortality was due to chlorinated hydrocarbons (mainly Telodrin and Dieldrin) in the Dutch coastal waters (KOEMAN 1971). Large numbers of breeding females were killed, which reduced total hatching. However, this pesticide-linked episode had no demonstrable effect on the survival of ducklings reaching the sea (Appendix). Pesticides were certainly not directly involved in the low fledgling success in the mid-seventies (SWENNEN 1989).

Diseases

In the course of the surveys some dead ducklings were found which had died of an illness. A few of these ducklings showed signs of Aspergillosis and some of Hepatitis with dark red bleedings of pinhead size or larger on the liver. The occurrence of such ducklings was rare, however, probably because the numerous gulls and crows removed dead and weak ducklings. Diseases as an important cause of death in ducklings older than one week became apparent during large-scale rearing experiments conducted in the period 1975—1977 (SWENNEN et al. 1979).

In 1977, the faeces and gullets of 34 large, captive ducklings were examined for several pathogens (*Aspergillus*, *Pasteurella*, *Salmonella*, *Trichomonas*) and various types of virus. All tests were negative. Via serum neutralization tests and agglutination tests blood samples were examined for various kinds of antibodies (Newcastle Disease virus, Celo virus, Inclusion Body Hepatitis virus, Reo virus, Gumboro virus, *Mycoplasma synovia*, *M. gallisepticum* and *Pasteurella multocida*). Most reactions gave negative or dubious results, but all samples reacted positively to Goose Virus Hepatitis (GVH).

In 1978, a test was conducted with newly hatched ducklings that were experimentally infected with either Goose Hepatitis Virus (MEEP 8) or with a variant strain (Le 34010, isolated from the liver of duck CDI 34010) and reared in captivity. Of the ducklings inoculated with MEEP 8, 65 % died (n = 20), of those inoculated with Le 34010, 20 % died (n = 20), and none of the controls died (n = 20). It was noted that the ducklings infected with MEEP 8 showed no escape reactions 7 days after inoculation. In the survivors, the disease caused severe retardation in growth and in some ducklings the growth of the bill was abnormal.

In spring 1979, 10 full-grown, wild Eiders were caught and tested for the presence of antibodies of GVH. Positive results were obtained from 2 males and 1 female, 1 male and 2 females were dubious and 3 males and 1 female were negative.

Also on Vlieland in 1979, a field test was conducted to study whether GVH has any effect on duckling survival in nature. Female Eiders with newly hatched young, heading for or about to reach the coast were intercepted and captured with the aid of a portable funnel trap. Half of the ducklings were given intra-muscular inoculations of 0.5 ml serum either in the breast or in the leg. The serum had been prepared by the Central Veterinary Institute from the surviving ducklings of the 1978 experiment. The methods used to produce the serum have been described by Yadin et al. (1977). Ducklings were marked in the right foot by punching a small hole in the inner web (controls), or in the outer web (serum treated). After a brood or a crèche had been caught, the adults were immediately examined or ringed and set free again. They usually waited in the near surroundings and came rapidly to their ducklings when they were collectively set free after treatment. In total, 2,931 ducklings (1,456 controls and 1,475 serum treated) were handled in the period 16 May to 4 June, but mainly between 21 and 28 May. The catching and handling of a crèche usually lasted only 15 to 20 minutes at most. After the main mortality was over in the second half of June ducklings were caught, ringed and examined on the nursery grounds. Of the 772 fledglings present, 743 could be caught, and 255 of these appeared to be marked. Of the marked birds 149 were serum treated and 106 were controls. The difference between treated and controls is statistically significant (G-test of independence G = 5.7, d. f. = 1, P <0.03), indicating a better survival in the inoculated birds.

Goose Virus Hepatitis (synonyms: Goose Influenza, Goose Pest) is mainly studied in domesticated waterfowl. Slow growth rate provides an early indication of the infection with the virus (Schettler 1971). Experimentally infected goslings died at an age of one to two weeks. In adult geese no signs of illness could be noted, but these adults produced antibodies that were passively transmitted to the eggs, making the goslings also immune during the first critical weeks of life (Hoekstra et al. 1973, Yadin et al. 1977). Therefore, it may be that a heavy infection in one year, killing most of the ducklings, will be beneficial to the offspring the next year, because of an immunization of the adults.

The occurrence of antibodies against GVH in wild adults and large ducklings, the fatal consequences of the illness in small captive ducklings, and the field evidence that injections with serum with Goose Hepatitis Virus antibodies has a positive effect on duckling survival indicate that GVH can be listed as one of the contributary causes of mortality among young Eider ducklings. Food scarcity is often the first primary cause of duckling mortality, operating mainly between 4—7 days after hatch (Swennen 1989). Under conditions of sufficient food, GVH may indeed prove to be the primary mortality factor, operating mainly in the age group of 2—3 week old ones. This interpretation of the impact of GHV in a wild population is of cource provisional as it is based on circumstantial evidence, but the hypothesis deserve to be followed up.

Both causes of death will generally go unnoted in the field because weak or slowly reacting ducklings are selectively taken by gulls (van Dobben 1934, Hoogerheide 1950, Belopolskii 1957, Tinbergen 1958, Swennen 1989). Observers will classify predation as the cause of death, which in fact is for the greater part removing ducklings doomed for other reasons. As GHV severely retards growth, the age of ducklings cannot precisly be estimated by size alone. Therefore, the primary cause of slow reaction in ducklings cannot be determined without time-consuming experiments as described earlier (SWENNEN 1989) or those described in this paper.

Summary

For 28 years, the survival up to fledging of Eider ducklings has been determined in the Dutch colony on Vlieland. On average 0.342 (0.001—1.528) ducklings per female fledged yearly. Within the ranges observed, the total number of ducklings that fledged seemed to be independent of the number of breeding females (range 800—2700) and the number of Herring Gulls in the study period. Indications were found of a sex-linked mortality occurring in some years. Correlations with a number of environmental factors suggested that low temperature in winter, high temperature at the end of May and the beginning of June, calm weather in May and June, and a high number of Herring Gulls were profitable for fledgling success. However, a stepwise multiple regression indicated only the temperature at the beginning of June as significant, explaining about 18 % of the total variance. The absence of a negative relation with breeding gull numbers confirms the interpretation of the role of the Herring Gull as a secondary mortality factor. Experiments showed that Goose Virus Hepatitis (syn. Goose Influenza or Goose Pest) was a primary cause of mortality among ducklings older than one week. The effect of diseases in the field was difficult to establish as diseased and weakened ducklings were usually eaten by gulls. A long-lasting fledgling failure was recorded from 1966 up to and including 1977. In the same period changes were noted in the biological systems in the North Sea.

Zusammenfassung

In einer Eiderenten-Kolonie auf der holländischen Insel Vlieland wurden die Überlebensraten der Küken 28 Jahre lang erfaßt. Im Mittel wurden jährlich 0.342 (0.001—1.528) Küken pro Weibchen flügge. Die Gesamtzahl der Küken war offensichtlich von der Anzahl brütender Weibchen (800—2700) sowie der Anzahl der Silbermöwen unabhängig. In einigen Jahren gab es Anzeichen für eine geschlechtsabhängige Sterblichkeit. Beziehungen zwischen der Rate flügger Jungvögel und einigen Umweltparametern, wie niedriger Temperatur im Winter, hoher Temperatur Ende Mai bis Anfang Juni, windarmes Wetter im Mai und Juni sowie der Präsenz vieler Silbermöwen ließen sich aufzeigen. Eine stufenweise multiple Regression zeigte jedoch, daß nur die Temperatur Anfang Juni einen signifikanten Einfluß hatte. Das Fehlen einer negativen Korrelation mit der Anzahl brütendee Möwen stützt die Annahme, daß die Rolle dere Silbermöwe als zweitrangig einzustufen ist. Versuche belegten, daß der Virus der Gänsehepatitis die Sterblichkeit von mindestens eine Woche alten Kücken unmittelbar bestimmte. Der Einfluß von Krankheiten konnte im Feld nur bedingt festgestellt werden, weil Möwen kranke und geschwächte Kücken üblicherweise fressen. Ein anhaltender Tiefstand des Aufzuchterfolges von 1966 bis 1977 fiel zeitlich mit allgemeinen Veränderungen der biologischen Verhältnisse der Nordsee zusammen.

Literature

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Appendix

Number of Eider fledglings (Fledgl), size of colonies of Eiders (Fem) and Herring Gulls (Gulls), mean temperature (°C) and mean wind force (0.5 m/s.) over the years of which data on fledglings were available. May3 means the last 10 days of May, and June1 means the first 10 days of June.

Year	Fledgl	Fem	Gulls	Temperature			Wind	
				Jan.+ Febr.	May3	June1	May3	June1
1947	1 370	900	1 400	—3.8	16.3	19.2	10	10
1962	200	2 600	1 500	4.0	9.9	11.5	19	13
1963	3 230	2 300	2 000	—3.5	11.8	16.0	13	15
1964	2 750	1 800	2 400	2.5	16.0	14.9	12	15
1965	1 050	1 500	1 900	3.4	11.7	12.5	13	11
1966	2	1 000	1 615	1.9	11.4	14.9	13	12
1967	380	850	1 751	4.5	12.5	12.8	12	12
1968	30	800	1 700	2.6	12.6	13.7	12	12
1969	40	1 200	2 505	2.8	12.3	12.1	11	17
1970	210	1 800	2 855	1.2	11.4	16.3	14	13
1971	5	1 700	3 365	3.5	13.2	13.6	11	15
1972	7	1 600	5 000	1.8	12.3	12.4	20	10
1973	50	1 500	5 500	3.7	13.2	11.8	10	9
1974	2	1 450	6 000	4.6	10.8	11.0	11	11
1975	72*	1 600	6 678	4.7	9.5	12.3	14	11
1976	33*	1 800	9 392	3.3	11.5	13.6	9	9
1977	7*	1 800	9 940	3.2	12.8	11.8	12	11
1978	1 611	1 900	10 050	2.4	12.0	15.9	10	9
1979	772	2 100	11 292	—1.8	12.6	14.0	11	9
1980	1 064	2 200	11 800	2.5	11.5	14.7	9	8
1981	202	2 050	11 270	2.7	13.2	14.8	9	13
1982	750	2 200	12 500	1.8	14.1	18.4	11	7
1983	205	2 500	12 820	3.6	10.3	14.7	11	10
1984	379	2 600	14 056	3.0	11.1	11.8	8	10
1985	168	2 400	12 500	2.2	13.6	13.5	10	12
1986	686	2 700	12 500	—0.5	10.8	11.3	11	12
1987	1 331	2 700	12 500	0.2	11.0	11.9	10	10
1988	1 113	2 700	12 500	5.5	13.5	12.9	12	11

*) The effective fledgling output was 93, 827 and 975 higher in 1975, 1976, and 1977, respectively, as a result of the release of ducklings that had participated in large-scale rearing experiments (SWENNEN et al. 1979, SWENNEN 1989).

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