DANISH REVIEW OF GAME BIOLOGY Vol. 14 No. 3

Distributions and movements of Eider *Somateria mollissima* populations wintering in Danish waters, analysed from ringing recoveries

by
HENNING NOER

Med et dansk resumé:
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Abstract

Noer, H., 1991: Distributions and movements of Eider *Somateria mollissima* populations wintering in Danish waters, analysed from ringing recoveries. - Dan. Rev. Game Biol. **14**(3).

Winter distributions of Eiders *Somateria mollissima* in Danish waters were analysed from recoveries of individuals ringed in Estonia, Finland, Sweden, Norway, Great Britain, and Holland. Emphasis of the analyses was placed on 1754 individuals recovered as shot. The majority of the recoveries (1,101) were ringed in Finland, most as nesting females. This material was analysed in detail. Recoveries reflect both autumn immigration to the Danish waters, winter distributions, and details of spring migration. Also, highly significant differences were found between years. The interpretation of the observed patterns is complicated by nearly continuous movements. Immigration of Baltic populations continues into December, while return movements from the Wadden Sea and/or the southern parts of the Baltic begin in late January. In addition to the latter movements, southward movements in the South Kattegat region and the inner Danish waters probably take place from late January as well. The net outcome is increasing concentrations of Eiders in the southern parts of the inner Danish waters throughout the winter. It is proposed 1) that the major part of the Eiders wintering in the northern Kattegat is the breeding populations of the Swedish West Coast and Norwegian Southeast Coast, and 2) that most of the Eiders wintering in South Kattegat, Storebælt and Lillebælt, and Sydfynske Øhav are from the Baltic populations.

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Preface

More than a million Eiders of Scandinavian origin pass Denmark each year. For the past 40 years Danish game biologists have therefore taken a natural interest in the species. In 1962 Knud Paludan analysed migration and winter distributions from some 200 ring recoveries, and wintering numbers and distributions were treated in 1974 by Anders Holm Joensen, who also treated other aspects affecting the ecology of the species in a number of publications between 1968 and 1976.

Besides the staging and wintering populations, there is a considerable breeding population of the species in Denmark, too. Intensive ringing schemes were initiated in the Stavns Fjord and Mandø colonies in 1970 by Anders Holm Joensen, and at Christiansø in 1972 by Niels Erik Franzmann. Continued until 1980, these investigations returned a material comprising 3,500 recoveries and 12,000 controls of ringed females. Analyses were under preparation by Niels Erik Franzmann, but due to his much too early death in 1987 the results were never published. Unfortunately, large parts of his work could not be reconstructed.

On the initiative of Helmuth Strandgaard, the former director of the research department the Nordic Council for Wildlife Research offered the financing of a two-year project of analysis and publishing of the most important parts of the material. The results of this project are the present paper and four following manuscripts, treating in detail aspects of migration, wintering, and population dynamics of the species. The contributions to the knowledge of the population biology of the Eider Duck resulting from these manuscripts have only been possible because of the timely support of Norway, Sweden, and Finland through the Council, which should be fully acknowledged here. More than 20 years ago, one of the reasons for the founding of the Council was the Danish bagging of Finnish and Swedish Eiders, emphasising the need for international cooperation when dealing with migratory species. By sponsoring the present project, the Nordic Council for Wildlife Research is thus fulfilling one of its original purposes in a convincing way.

Karsten Laursen
Director of Research Department, NERI

Contents

INTRODUCTION

The Danish waters are highly important as wintering quarters for waterfowl populations. More than 2 million ducks, swans, geese, and Coot *Fulica atra* winter in this area, and further numbers pass during spring and autumn (Joensen 1974a).

The most numerous species is the Common Eider *Somateria mollissima*. Aerial surveys conducted in the years 1968-73 revealed midwinter totals of 500,000-550,000 counted individuals (Joensen 1974a). Resumed from 1987, recent counts have reached totals of about 800,000 individuals (Laursen et al. in prep.). This increase possibly reflects the general growth of the North European Eider populations (Almkvist et al. 1974, Pehrsson 1978, Stjernberg 1982, Kullapere 1983, Hario and Selin 1988, Laursen 1989, Franzmann 1989). In addition to the midwinter counts, surveys in October-November and in March-April have been conducted since

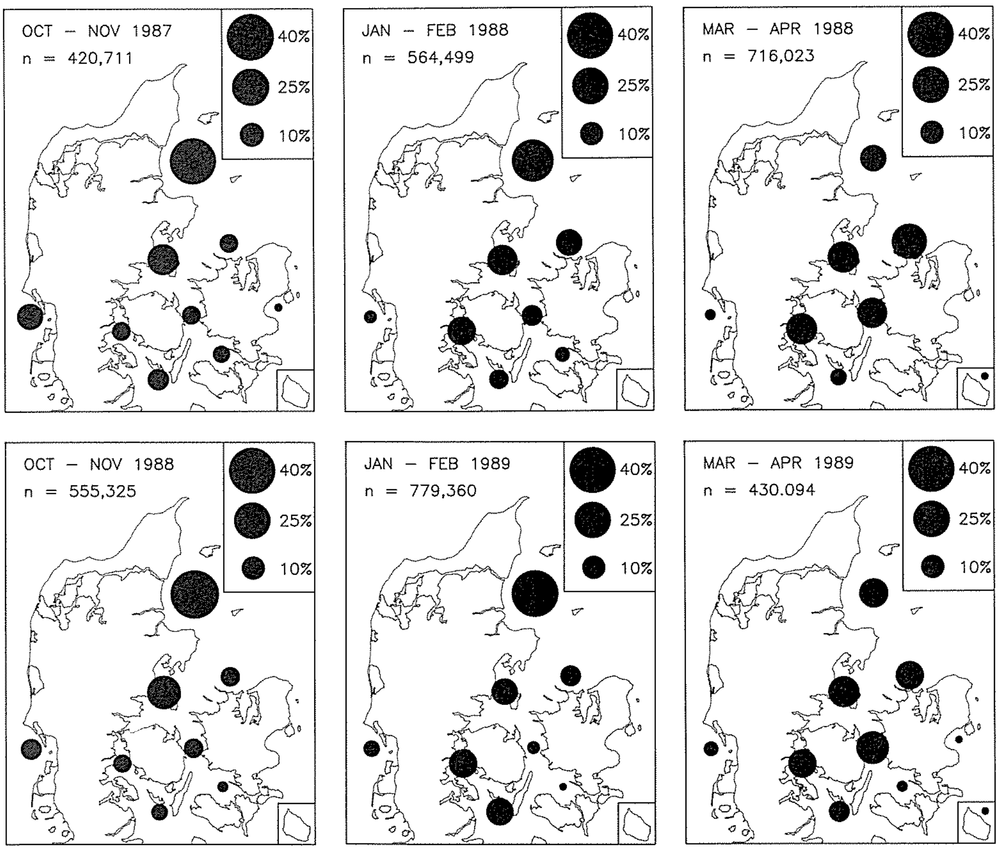

Fig. 1. Distributions and numbers of Eiders in Danish waters found in 6 aerial surveys 1987-89. In autumn surveys, the largest concentrations are observed in northern Kattegat, in midwinter surveys numbers have increased and Eiders are more evenly distributed, while in spring surveys concentrations are largest in the southernmost parts. Numbers counted in spring are high in early counts (March-April 1988) and lower in late counts (March-April 1989). Data from Laursen et al. (in prep.).

1987 (Laursen et al. in prep.). Numbers and distributions of Eiders in Danish waters throughout the winter period are thus fairly well known (Laursen et al. in prep.).

The detailed information obtained by the recent annual surveys has revealed that distributions and variatons in numbers of Eiders are very complex. Inspection of the surveys conducted since 1987 shows that characteristic changes take place throughout the winter period. Fewer individuals are counted in the autumn than in the midwinter surveys, and while in October the largest numbers occur in North Kattegat, the counts in February and March show that later in the winter the largest numbers occur in the southern parts of the inner Danish waters (Fig. 1). Corresponding numbers are given in Laursen et al. (in prep.).

These patterns in space and time mean either that different populations are involved, that continuous movements take place throughout the winter, or that these two factors act in combination. Analysis of ringing recoveries has shown that a large part of the Eiders wintering in Denmark belongs to the Baltic populations, though a few recoveries of Eiders ringed in South Norway and West Sweden indicated that the populations breeding there may winter in the Kattegat as well (Paludan 1962, Joensen 1974a). Recent analyses of recoveries of Eiders ringed in Great Britain and the Netherlands have shown that some Eiders of these populations are found in Danish waters, too (Swennen 1976, 1990, Baillie and Milne 1989). Thus, the composition of the wintering population of Eiders in Danish waters is complex, and at present it can only be investigated by further analyses of ringing recoveries.

Since 1970 the numbers of ringed Eiders recovered in Danish waters have increased considerably. While Paludan's (1962) analyses were based on about 100 recoveries of Eiders ringed in Sweden, the present number of recoveries of Eiders ringed outside Denmark exceeds 2,000. The purpose of this paper is to analyse recoveries from Danish wters of Eiders ringed elsewhere in Europe in order to improve the interpretation of the results obtained by aerial surveys. Emphasis is placed on seasonal changes in distributions of recoveries, but other aspects such as annual differences in patterns of recoveries that can be analysed from such a large material will be presented briefly. Recoveries of Eiders breeding in Denmark are presented elsewhere (Noer, in press).

ACKNOWLEDGEMENTS

The present study was sponsored financially by the Nordic Council for Wildlife Research. The staff at the Ringing Department of the Zoological Museum, Copenhagen, was very helpful and cooperative during the compilation of the material. Pertti Saurola and Jarmo Ruoho, the Ringing Department of the Zoological Museum of Helsinki, kindly provided updated text files on the recoveries of Finnish Eiders. Karsten Laursen critisized an earlier draft of the manuscript, and Georg Nehls and Stefan Bräger gave valuable suggestions on the movements between the Baltic and the Wadden Sea. Stefan Pihl and Flemming Pagh Jensen gave valuable information on increases of numbers in February. Without the support and cooperation of all of these persons and agencies the project would not have been realised.

MATERIAL AND METHODS

A total of 2,161 recoveries of Eiders ringed in Finland, Estonia, Sweden, Norway, Great Britain, and the Netherlands and recovered in Denmark have been available for analysis (Table 1). A few recoveries of individuals ringed in the German Wadden Sea and recovered in the Danish parts exist as well. All of these are local, and they have not been included.

The majority of the recoveries (81%) concerns individuals that have been shot. This is hardly surprising for a species that to a large extent winters offshore, but since shot individuals are far more likely to be recovered the presence of an open season in Finland, Sweden, and Denmark introduces a strong bias when numbers of recoveries from different countries are compared (Noer, in press). For the Eider, therefore, analyses of total (international) distributions should be based on the (much smaller) material of individuals recovered from 'other death causes', though this material may in itself be highly biased (Noer, in press). For a national analysis, however, the individuals recovered as shot are by far the largest and most homogeneous subset of the total material. Therefore, the analyses were based exclusively on bagged individuals. Data on other death causes have been included only for sparse data sets (excluded from statistical comparisons) and for comparison with distributions of shot individuals for the Finnish and Swedish data sets.

Due to the geography of the inner Danish waters, distributions of recoveries are skewed and in most cases bi- or multimodal. Accordingly, statistical analysis based on assumptions of normal distributions cannot be applied. Instead, an arbitrary division into subareas was used (Fig. 2). This division is based on the one used in the aerial counts (Joensen, 1974a), and most comparisons between distributions of recoveries have been done by means of χ^2-tests. These tests are undoubtedly less powerful than some recently published methods for comparisons between distributions of recoveries (e.g. Lokki and Saurola 1987),

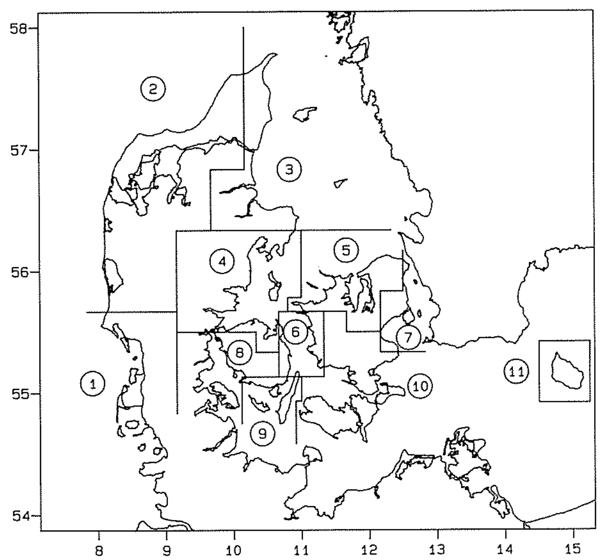

Fig. 2. Subdivision of Danish waters into count areas. Modified for computerisation from the one used in aerial surveys (Joensen 1974). Corresponding geographical names are: 1) Wadden Sea, 2) North Sea, 3) North Kattegat, 4) Southwest Kattegat, 5) Southeast Kattegat, 6) Storebælt, 7) Øresund, 8) Lillebælt, 9) Sydfynske Øhav, 10) Smålandshavet, and 11) Bornholm.

Table 1. Survey of recoveries of Eiders from Denmark. For each country of origin is given 1) the total number of recoveries, 2) the number of recoveries that has been ringed as pulli (numbers of recoveries of males and females given in parentheses), 3) the number of recoveries that has been ringed as adults (numbers of recoveries of males and females given in parentheses), and 4) the total number of individuals recovered as 'shot'.

	TOTAL	PULLI	ADULTS	SHOT
FINLAND	1355	180 (28,25)	1171 (3,1140)	1101
ESTONIA	67	19 (8,7)	42 (0,42)	49
SWEDEN				
Baltic	286	9 (1,1)	262 (3,248)	238
Kattegat	203	35 (5,7)	161 (2,155)	163
NORWAY	27	0	25 (0,25)	18
AT BRITAIN	14	6 (2,0)	6 (3,2)	9
HOLLAND	209	69 (60,1)	139 (100,38)	176
TOTAL	2161	318	1806	1754

but in most cases they suffice to demonstrate differences between sets of recoveries. Since the Eiders wintering in Denmark essentially are distributed along a N-S axis, another simple way of comparing patterns of distributions is to compare geographical latitudes of sets of recoveries by Median-tests (Siegel 1956). This has been used in some cases below, in the case of a two-sample comparison always with a Yates-correction (Siegel 1956).

RESULTS

Recoveries of Eiders ringed in Finland

Of the Finnish recoveries, 114 were ringed in the Åland Archipelago, while the rest were ringed in various colonies along the Gulf of Finland. No differences were found between patterns of recoveries from different areas, and only pooled results will be presented here.

Comparison of monthly distributions

Table 2. Results of χ^2-test comparing monthly distributions of recoveries of Eiders ringed in Finland (data in Appendix I). Each test compares distributions for a set of count areas over the five months of the open season (Fig. 2). The first step of the analysis tests whether the overall distribution in the Danish waters is constant throughout the 5 months, and a significant χ^2-statistic implies that the distribution changes. Since this is the case, various parts of the Danish waters are compared in the following steps in order to identify areas with similar temporal patterns of recoveries.

Count areas included	χ^2	df	P
1, 3, 4, 5, 6, 7, 8, 9, 10	108.86	32	<< 1%
1, 3, 4, 5, 6, 8, 9	60.11	20	<< 1%
3, 4, 5, 6, 8	35.86	16	0.3%
3, 4, 5	6.01	8	64.6%
6, 8, 9	18.23	8	2.0%
6, 8	3.00	4	55.8%
6, 9	12.91	4	1.2%
8, 9	12.34	4	1.5%

of recoveries (Figs 3-7, App. I) over count areas and months revealed highly significant differences (Table 2), implying that the distribution of recoveries within the Danish waters changes through the season. Exclusion of areas 1, 7, and 10 and, in the next step, 9, in both cases revealed significant differences between the count areas retained in the comparison (Table 2). Areas 3, 4, and 5 were not significantly different, while 6, 8, and 9 were. The difference was due to area 9, while areas 6 and 8 were similar (Table 2).

In general, therefore, the distribution of recoveries changes highly significantly through the winter period. Areas 7 and 10 have decreasing numbers of recoveries from October onwards, areas 3, 4, and 5

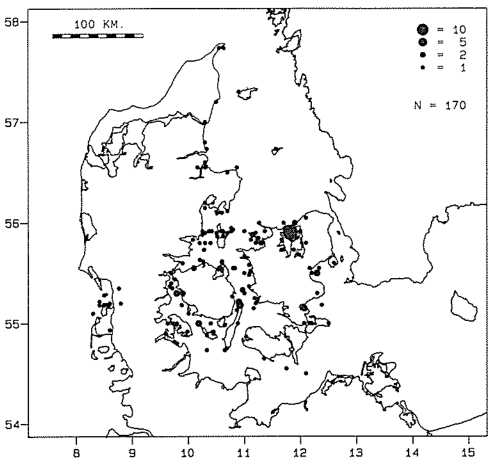

Fig. 3. Distribution of recoveries of Eiders ringed in Finland and recovered in Danish waters in October. Only individuals recovered as 'shot' are included.

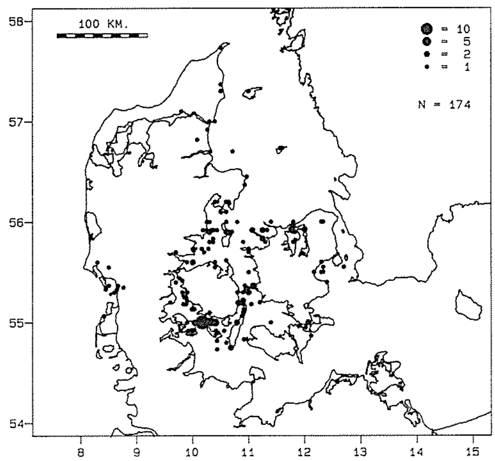

Fig. 5. Distribution of recoveries of Eiders ringed in Finland and recovered in Danish waters in December. Only individuals recovered as 'shot' are included.

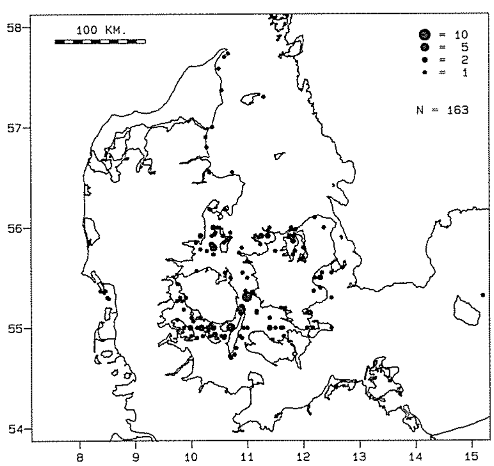

Fig. 4. Distribution of recoveries of Eiders ringed in Finland and recovered in Danish waters in November. Only individuals recovered as 'shot' are included.

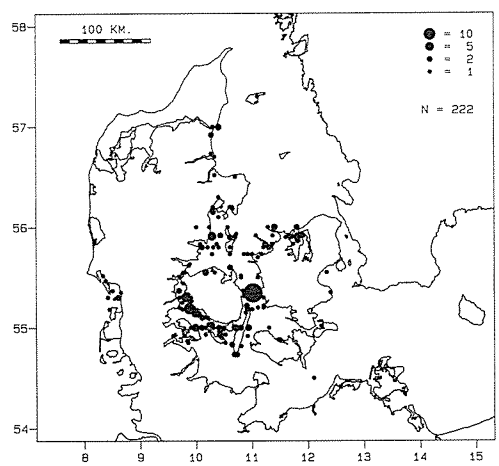

Fig. 6. Distribution of recoveries of Eiders ringed in Finland and recovered in Danish waters in January. Only individuals recovered as 'shot' are included.

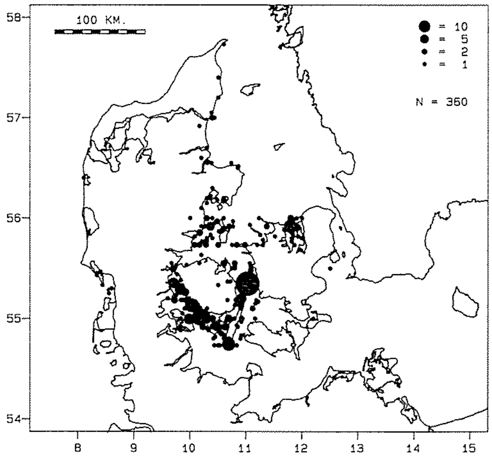

Fig. 7. Distribution of recoveries of Eiders ringed in Finland and recovered in Danish waters in February. Only individuals recovered as 'shot' are included.

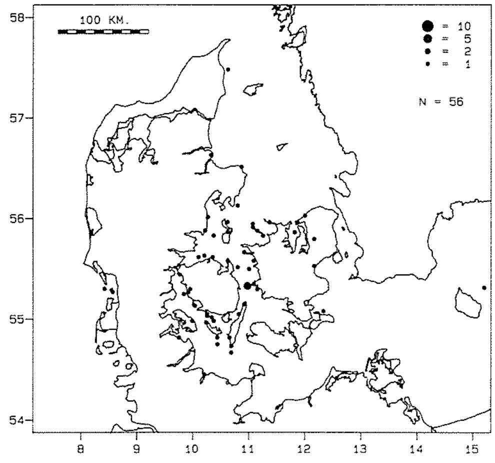

Fig. 8. Distribution of recoveries of Eiders ringed in Estonia and recovered in Danish waters in the period October-February. All death causes are included.

have almost equal monthly numbers of recoveries, while areas 6, 8, and 9 show strongly increasing numbers of recoveries in January and, particularly, February. This increase was most pronounced for area 9.

The number of recoveries is large enough to permit analysis of differences between years (App. II). Comparison between areas 4, 5, 6, 8, and 9 revealed highly significant differences ($\chi^2 = 77.75$, df = 52, P = 1.19%), and it is concluded that yearly differences between the distributions of recoveries exist at least for this data set.

Recoveries of Eiders ringed in Estonia

The recoveries stem from birds ringed on the Estonian West Coast, in particular at the islands Saarema (Ösel) and Hiiumaa (Dagö). Because of the sparse data, all recoveries from the period October to January (including 6 recoveries of individuals found dead) were pooled. The resulting distributions were similar to the distributions of Eiders ringed in Finland (Fig. 8, App. III). Recoveries from areas 1 and 3 indicate that part of the Estonian populations winters within these areas, though the bulk of the recoveries is from areas 4 and 5. Compared to the recoveries

*Table 3. Results of χ^2-comparisons of temporal distributions (monthly totals in Appendices I-VI) of recoveries from different populations. In all cases the tests have four degrees of freedom. Levels of significance are indicated as NS: not significant, * : 1% < P < 5%, ** : 0.1% < P < 1%, and *** : P < 0.1%.*

	ESTONIA	SWEDEN Baltic	SWEDEN Kattegat	NETHERLANDS
FINLAND	1.91 NS	11.01 *	4.69 NS	64.00 ***
ESTONIA		4.33 NS	2.67 NS	28.84 ***
SWEDEN Baltic			10.78 *	22.19 **
SWEDEN Kattegat				58.13 ***

Table 4. As Table 2. Comparisons of temporal distributions of recoveries of Eiders ringed at the Baltic coasts of Sweden (data in Appendix III).

Count areas included	χ^2	df	P
4, 5, 6, 8, 9, (7 + 10)	61.63	20	<< 1%
4, 5, 6, 8, 9	39.91	16	0.1%
4, 5	4.02	4	40.3%
6, 8, 9	9.49	8	30.3%

of Eiders ringed in Finland, the lack of concentrations of recoveries in areas 8 and 9 in February is obvious. Comparison between the temporal distributions of recoveries of Estonian and Finnish Eiders revealed no significant differences (Table 3).

Recoveries of Eiders ringed in Sweden

The Baltic populations

The majority of the recoveries (81%) were of birds ringed at Gotland. No differences were found between Eiders ringed on respectively Gotland and on the Swedish mainland. Though this lack of differences might be caused by small sample sizes, data were nevertheless pooled.

Comparisons between distributions of recoveries over areas and time (Figs 9-13, App. III) revealed highly significant differences (Table 4). In these comparisons, areas 7 and 10 were pooled because of small sample sizes. Exclusion of pooled areas 7+10 revealed significant differences between the remaining areas, while comparison between areas 4 and 5 respectively 6, 8, and 9 revealed no significance (Table 4). It is concluded that differences exist between on one hand areas 3, 4, and 5 and on the other areas 6, 8, and 9. Thus, overall patterns are much the same as for the Finnish Eiders, and it is concluded that there is a decreasing number of recoveries in areas 7 and 10 from October-November to January-February, while numbers in areas 8 and 9 increase and the monthly numbers of recoveries are relatively constant in areas 3, 4, and 5 (cp. App. III).

However, detailed comparisons with Eiders ringed in Finland suggest that although overall patterns are similar, slight differences exist. In general, recoveries of Eiders belonging to the Swedish populations tend to show more southerly distributions in the inner Danish waters (median-test on latitude of recovery (Siegel 1956)). Differences were significant for October (Median = 55°30'N, χ^2 = 8.93, df = 1, P << 0.01), insignificant for November and December pooled (Median = 55°22'N, χ^2 = 0.2428, df = 1, P = 62.22%), and significant for January and February pooled (Median = 55°19'N, χ^2 = 6.32, P = 1.19%). Moreover, the temporal distribu-

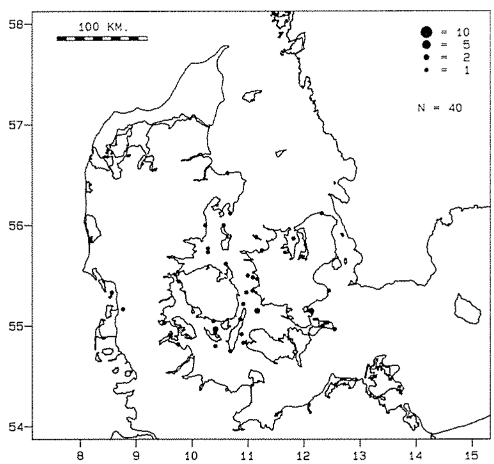

Fig. 9. Distribution of recoveries of Eiders ringed in Sweden (Baltic region) and recovered in Danish waters in October. Only individuals recovered as 'shot' are included.

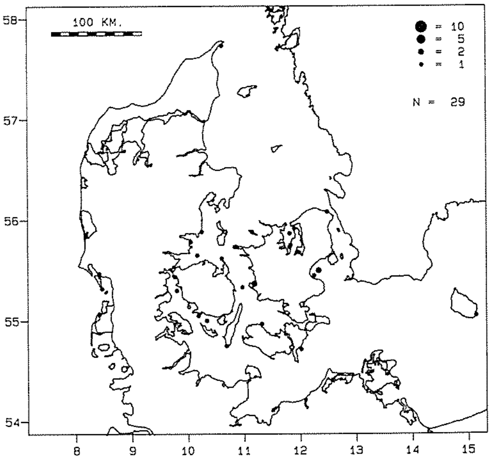

Fig. 10. Distribution of recoveries of Eiders ringed in Sweden (Baltic region) and recovered in Danish waters in November. Only individuals recovered as 'shot' are included.

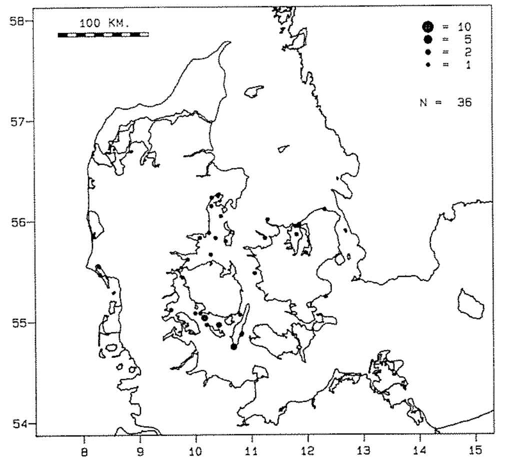

Fig. 12. Distribution of recoveries of Eiders ringed in Sweden (Baltic region) and recovered in Danish waters in January. Only individuals recovered as 'shot' are included.

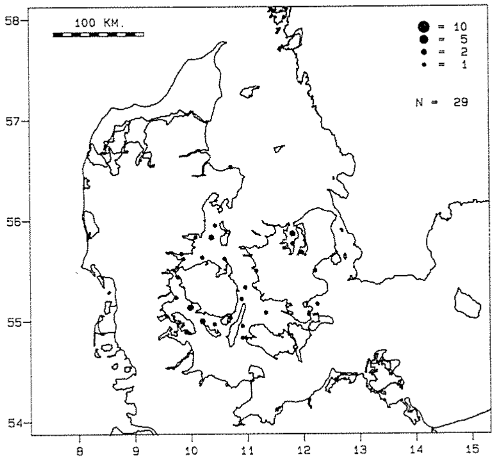

Fig. 11. Distribution of recoveries of Eiders ringed in Sweden (Baltic region) and recovered in Danish waters in December. Only individuals recovered as 'shot' are included.

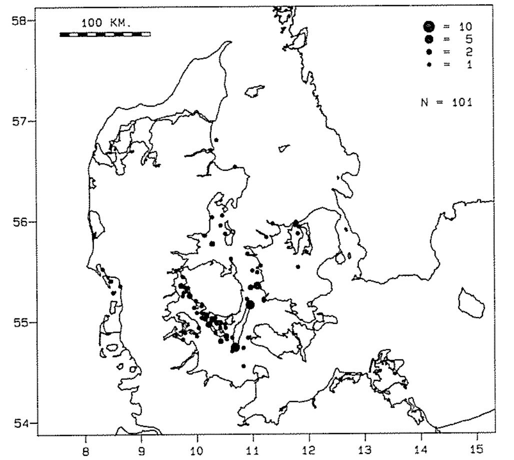

Fig. 13. Distribution of recoveries of Eiders ringed in Sweden (Baltic region) and recovered in Danish waters in February. Only individuals recovered as 'shot' are included.

tions of recoveries from these two areas differed significantly (Table 3). These differences mean that not only do recoveries of Eiders belonging to the Swedish Baltic populations have a more southerly distribution in October and in January-February, but relatively more recoveries are made in these months.

The Kattegat populations

Eiders ringed along the entire Swedish Kattegat coast were recovered in Denmark. Most recoveries, however, stem from the colonies at Hallands Väderö and Kungsbackafjorden (positions shown in Figs 14 and 15).

Recoveries of Eiders ringed South of 57° come from areas 3, 4, and 5 (Fig. 14, App. IV). In contrast, most of the recoveries of Eiders ringed on the Northern part of the Swedish West Coast are from area 3 (Fig. 15, App. V). The differences between the two data sets are highly significant (areas 3, 4, 5, and 6 pooled over time, χ^2 = 32.50, df = 3, P < < 0.01%).

The temporal distributions of the two sets of recoveries are similar (App. IV and V, χ^2 = 2.81, df = 4, P = 58.93%), and this is the reason why the two sets of recoveries from the Swedish Kattegat coasts were pooled in Table 3. After this pooling, the temporal distribution was not significantly different from that of the recoveries from Finland and Estonia, but significantly different from those of the Swedish East coast and Holland (Table 3).

Since geographical distributions of the recoveries of Eiders ringed on the Swedish Kattegat coasts do not change through the open season, comparison with the Baltic populations that reveal temporal variation is problematic. Therefore, such comparisons were not carried out. In the following it is assumed that these distributions are different.

Recoveries of Eiders ringed in Norway

A total of 33 recoveries of Eiders ringed in Norway were available. Sites of ringing were scattered along the entire Skagerrak coastline, and all birds were ringed as adult females (Table 1).

Recoveries of Norwegian Eiders were distributed almost exclusively in the northern part of area 3 (Fig. 16). Because of the small number of recoveries all death causes and months were pooled.

Comparison with the recoveries of Eiders ringed along the Swedish Skagerrak coast (North of 57°N, Fig. 15) revealed that the difference is significant (Median-test, Median = 56°43'N, χ^2 = 7.18, P = 0.74%).

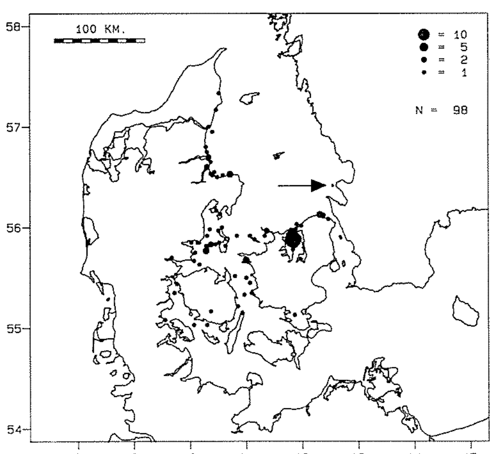

Fig. 14. Distribution of recoveries of shot Eiders ringed in Sweden (Kattegat coasts South of 57° N). Only individuals recovered as 'shot' October-February are included. The arrow indicates the position of Hallands Väderö, where most of the recovered individuals were ringed.

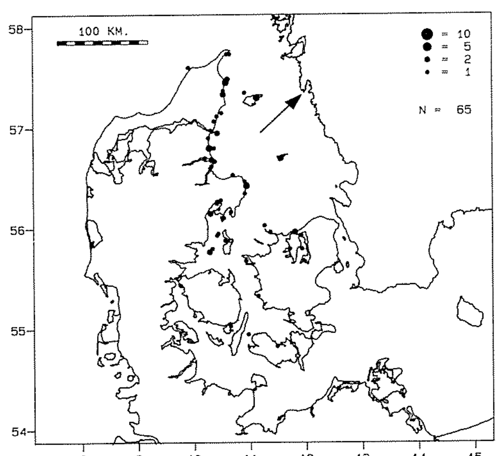

Fig. 15. Distribution of recoveries of Eiders ringed in Sweden (Kattegat coasts North of 57° N). Only individuals recovered as 'shot' October-February are included. The arrow indicates the position of Kungsbacka Fiord, where most of the recovered individuals were ringed.

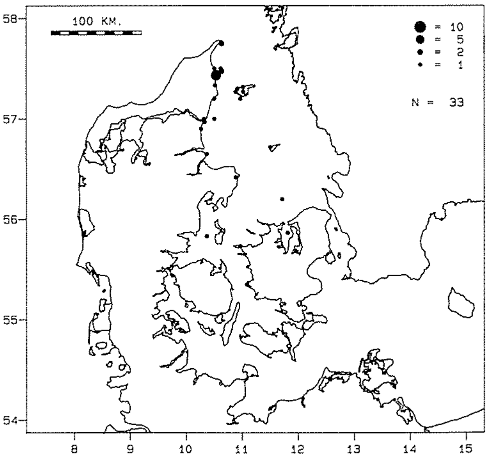

Fig. 16. Distribution of recoveries of Eiders ringed in Norway and recovered in Danish waters in October-February. All death causes are included.

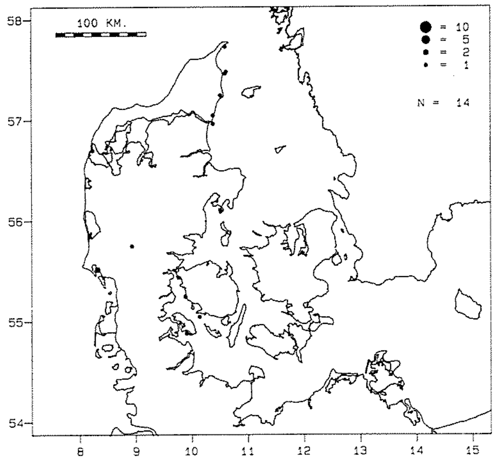

Fig. 17. Distribution of recoveries of Eiders ringed in Great Britain and recovered in Danish waters in October-February. All death causes are included.

Recoveries of Eiders ringed in Great Britain

A total of 14 recoveries exists of Eiders ringed in Great Britain. All have been ringed at Forvie, Scotland, either as ducklings or as winter visitors. Most were males (Table 1), probably on abmigration with Fennoscandian females (Baillie and Milne 1989).

The distribution of recoveries is shown in Fig. 17. Because of the sparse material, all death causes and periods were pooled, and no further analysis attempted.

Recoveries of Eiders ringed in the Netherlands

The recoveries included almost exclusively birds ringed at the islands Vlieland and Terschelling in the Dutch Wadden Sea. In the Netherlands, ringing of Eiders has included ringing of ducklings as well as of adults caught both at nest and by trapping. Trapping has been carried out both in the breeding and the moulting periods (Swennen 1976, 1990), and thus a relatively large number of males have been ringed. Though some females have been recovered in Denmark, the majority of the recoveries have been of males (Table 1). Because of the relatively small numbers of recoveries, sexes have been pooled.

For this part of the material, adults ringed in May probably represent breeding

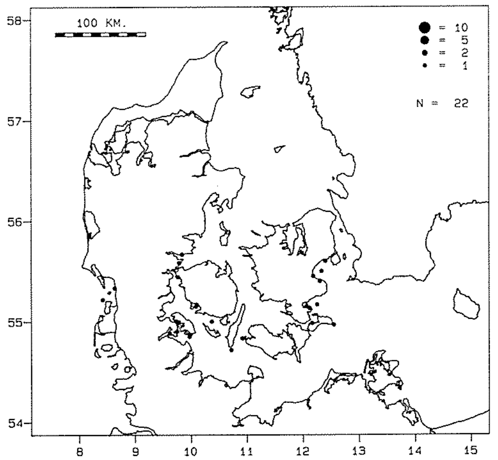

Fig. 18. Distribution of recoveries of Eiders ringed in the Netherlands April-June, i.e. as ducklings or adult males (pooled data from Appendices VI and VII) and recovered in the Danish waters in October. Only individuals recovered as 'shot' are included.

individuals, while adults ringed in July-August may be moulting individuals not belonging to the breeding population (e.g. Swennen et al. 1989). Accordingly, the recoveries were split (crudely) into three subsets, respectively individuals ringed as pulli, as adults before 1 July, and as adults after 1 July.

For birds ringed in April-June a number of October-recoveries from areas 7 and 10 have been made (Fig. 18, App. VII), while birds ringed after 1 July showed a

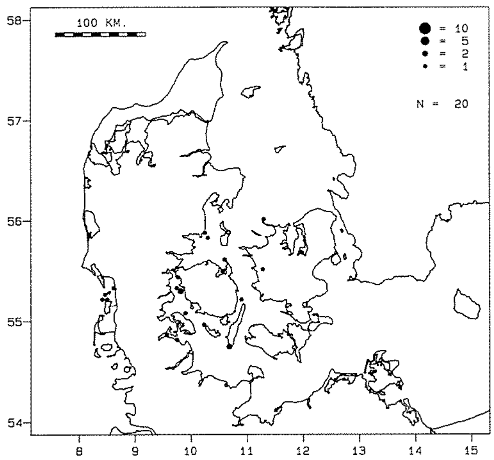

Fig. 19. Distribution of recoveries of Eiders ringed in the Netherlands July-September (data from Appendix VIII) and recovered in the Danish waters in October. Only individuals recovered as 'shot' are included.

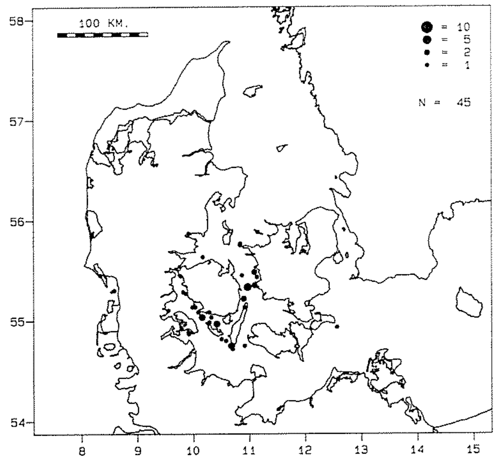

Fig. 21. Distribution of recoveries of Eiders ringed in the Netherlands April-June (pooled data from Appendices VI and VIII) and recovered in Danish waters in February. Only individuals recovered as 'shot' are included.

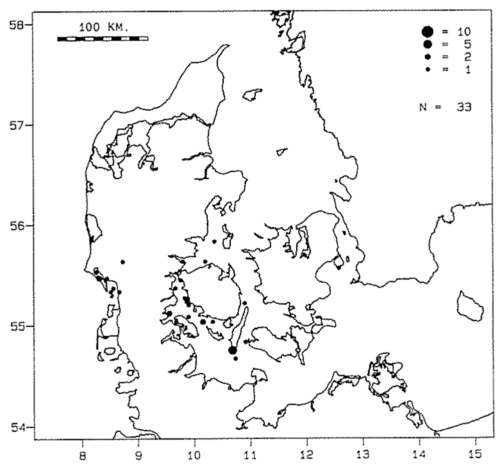

Fig. 20. Distribution of recoveries of Eiders ringed in the Netherlands and recovered in the Danish waters in the period November-January. Only individuals recovered as 'shot' are included.

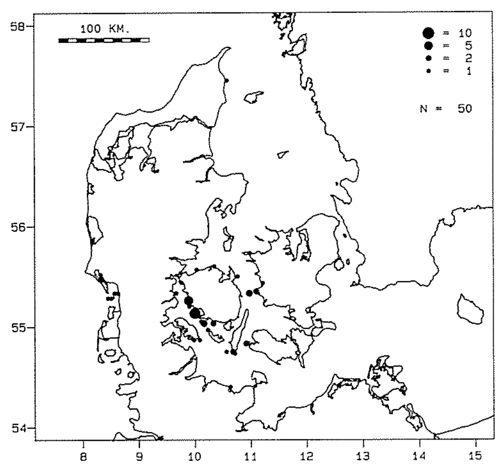

Fig. 22. Distribution of recoveries of Eiders ringed in the Netherlands July-September (data from Appendix VIII) and recovered in the Danish waters in February. Only individuals recovered as 'shot' are included.

more westerly distribution (Fig. 19, App. VIII). The data sets, however, are too small to permit meaningful testing. Due to sparse data, recoveries from November, December, and January were pooled (Fig. 20). In February, there are only minor differences between the distributions of birds ringed before and after 1 July (Figs 21 and 22). In general, all recoveries of birds ringed in the Netherlands showed distributions concentrated in the southernmost parts of the inner Danish waters.

The temporal distributions of the three sets of recoveries (App. VI-VIII, November-January pooled) showed no differences (χ^2 = 5.61, df = 4, P = 22.92%). Therefore, the three sets were pooled. χ^2-comparisons showed that the temporal distribution of these recoveries differed highly significantly from all other data sets (Table 3). In all cases, relatively fewer recoveries were made of Eiders ringed in the Netherlands in November, December, and January.

Since the temporal distribution of recoveries of Eiders ringed in the Netherlands differs from those of the other sets of recoveries, geographical comparisons have to be restricted in time. Comparisons of recoveries made in February revealed that the distributions of recoveries of Eiders ringed in the Netherlands are highly significantly different from those ringed in Finland (areas 4, 5, 6, 8, and 9 included in comparison, χ^2 = 52.84, df = 4, P << 0.01% (App. I and VI-VIII pooled)) and from those ringed on the Swedish East Coast (areas 4, 5, 6, 8, and 9 included in comparison, χ^2 = 25.08, df = 4, P << 0.01% (App. III and VI-VIII pooled)). In both cases, the distribution of the recoveries ringed in the Netherlands was more concentrated in the southern parts of the Danish waters.

DISCUSSION

Sources of bias

The patterns of recoveries presented above do not only reflect the distributions of the birds. They are also influenced by a number of sources of bias. The most important of these sources are 1) spatial and temporal variation in hunting effort, and 2) representativeness of ringed individuals.

Spatial and temporal variation in hunting effort

Spatial and temporal variation in hunting effort - defined as the number of active hours of hunting spent by hunters in the area - would obviously affect the patterns of recoveries, and these would no longer merely reflect the distribution of the population.

The Danish open season lasts from 1 October till 28 (29) February. Before 1970, most Eiders were bagged in October (Joensen 1974a, b, and 1978). This pattern, however, changed between 1970 and 1975 in some regions, detailed as areas 6, 8, and 9 in this paper (Noer et al. in prep.). In all other areas the temporal pattern of Eider hunting has remained largely unchanged. However, the proportion of the total Danish bag of Eiders shot in areas 6, 8, and 9 has been increasing during the same period, and today monthly numbers bagged - though still high in October - reach a minimum in November-December and then increase to a maximum in February (Noer et al. in prep.). More than 90% of the recoveries analysed in this paper have been made after 1970.

These changes in the geographical distribution of the Danish Eider bag could be due either to changes in the distributions of the birds, to changes in hunting effort, or to any combination of the two. Generally, however, numbers and hunting effort should tend to be positively intercorrelated, as hunters probably spend more time where the prospects of hunting success are good. Noer et al. (in prep.) argue that though the hunting effort undoubtedly has increased unproportionally in the three mentioned areas, changes in the distribution of Eiders probably underlie the changes in hunting effort. Granted this, it is assumed in the following that spatial and temporal variation in hunting effort tend to distort patterns of recoveries by exaggerating regional differences, rather than distorting the distributions completely.

Within any season, the hunting effort is influenced by weather, spells of strong winds often depressing numbers shot in any of the 5 months of an open season (Joensen 1974b), and ice conditions in some years leading to high numbers being bagged in January-February (Noer in prep.), and in others to an early closing of the season by Government Order (e.g. the 1978/79 season). This hardly affects the general comparison of different regions, but part of the differences between years found for the recoveries of Eiders ringed in Finland could be explained this way.

Representativeness of ringed individuals

Another aspect affecting the conclusions is the representativeness of the ringed individuals. In most cases ringing of Eiders has been done by catching on the nest, and therefore most recoveries are of adult females (Table 1). For the Eider, pair formation takes place in winter quarters (Spurr and Milne 1976), and males abmigrate to breed in the home colonies of their mates (Swennen 1976, 1990, Franzmann 1983, Baillie and Milne 1989, Noer in press). Patterns of movements may therefore differ for males and females. At least, this is the case for moult migration (Swennen et al. 1989). However, analyses of the recoveries from the two Danish colonies where males have been ringed suggest that even if moulting quarters and phenology of migration may vary between sexes, winter quarters do not differ (Noer in press). For those of the data sets presented in this paper where both males and females were represented, no differences in winter quarters were found either. Hence, pooling of sexes is considered justified for the present.

Moreover, in most countries ringing of Eiders has been done in a limited number of colonies. The discussion given below rests on the assumption that the investigated colonies are representative of the total Baltic and Kattegat/Skagerrak populations, but clearly further evidence is needed at this point too. Because of these limitations, the patterns of movements as outlined below should be viewed as hypotheses rather than definitive conclusions.

Movements

Eiders breeding at the Kattegat/Skagerrak coasts

The movements of the Swedish Kattegat and Norwegian Skagerrak populations are no reflected in the patterns of recoveries. This is presumably so because these movements cross open waters in Skagerrak and North Kattegat where no hunting takes place. As discussed below, Eiders from the Kattegat/Skagerrak populations probably arrive earlier at the wintering grounds in autumn and leave earlier in spring.

Eiders breeding in the Baltic

Movements in autumn and early winter
From visual and radar observations, the

autumn migration of the Baltic Eider populations is known to follow the East and South Coasts of Sweden (Carlsson 1962, Edelstam 1972, Alerstam et al. 1974). The main stream of migrants split up when entering the Danish waters. Part of the birds continue across South Jylland and enter the Wadden Sea (e.g. Swennen et al. 1989), while part of the migration continues to the Kattegat, some of it crossing Sjælland (e.g. Salomonsen 1972). The immigration into Danish waters is generally assumed to peak in early October (e.g. Paludan 1962). Numbers involved are discussed below.

In this paper, it has been found that for the Baltic populations numbers of recoveries in areas 7 and 10 are highest in October-November and then decrease (Tables 2 and 4, App. I and III). Since numbers of Eiders in these areas are very low also in midwinter surveys (Laursen et al. in prep., and Fig. 1) it is concluded that the recoveries from these areas reflect autumn immigration of the Baltic populations into the Danish waters.

The numbers of Finnish and Swedish recoveries in areas 7 and 10 are high also in November and December, indicating that immigration into the Danish waters continues until about medio December. This is also shown by the monthly numbers of recoveries (App. I and II): Though the shooting intensity in Denmark is much lower in November than in October (Paludan 1962, Joensen 1974a, b, and Noer et al. in prep.), the number of Eiders ringed in Finland and recovered in November equals the number recovered in October, implying a higher frequency of Finnish Eiders in November. Further evidence was obtained from the unpublished files of the late N.E.Franzmann, showing that Finnish Eiders are recovered both in Finland and along the Swedish East Coast (presumably on migration) until primo December. Accordingly, autumn immigration of Eiders into the Danish waters may be more prolonged than hitherto assumed.

Movements in spring and late winter

Spring emigration of Baltic Eiders from the Danish waters peaks from late March to early April, when visual and radar observations in Scania reach the highest densities (Alerstam et. al. 1974). This matches the breaking of the ice at the breeding grounds, which in the Gulf of Finland takes place in late April (Hario and Selin 1988). The majority of the migrants follows the South and East coasts of Sweden, but seemingly considerable numbers migrate directly from the Kattegat to the Baltic by crossing Scania (Alerstam et al. 1974). In Denmark, large flocks are regularly observed in late April crossing the island of Fyn and, when arriving at the coast of Storebælt, proceeding directly towards ENE (Rabøl and Noer 1970).

Prior to the spring migration proper, major movements take place within the Danish waters in late winter and early spring. For the Wadden Sea, an average number of 70,000 Eiders emigrate between medio February and medio March (Swennen et al. 1989), while for the inner Danish waters considerable changes in numbers and distributions between the midwinter and the spring surveys have been found (Fig. 1). For aerial surveys covering the German coasts of the western Baltic, large numbers have been reported to disappear between January and March (Kirchhoff et al. 1983, S. Bräger pers. comm.).

The aerial surveys made in Denmark indicate that numbers in the southernmost parts of the inner Danish waters increase throughout the winter (Fig. 1). For Storebælt, an increase of 80,000 individuals between January and March is observed (F.P.Jensen, pers. comm.), while for Lillebælt and Sydfynske Øhav, 160,000 individuals were counted on 13 January 1991 against 398,000 on 26 February 1991 (S. Pihl, pers. comm.).

The temporal changes in the distributions of recoveries presented in this paper fit these observations well. Due to the closing of the hunting season before the onset of departure for the breeding grounds in late March/early April this phase of movements is not well documented in the ringing recoveries, but for the late winter/early spring movements there much evidence exists.

For the Finnish and Swedish East Coast populations, highly significant increases in numbers of recoveries from areas 6, 8, and 9 were found in January and particularly February. Part of these increases is undoubtedly due to an increase in hunting effort (Noer et al. in prep.), but this part cannot be quantified at present. However, when numbers of recoveries from areas 6, 8, and 9 are pooled for 10-day periods through January and February and compared between populations, differences are highly significant (Table 5, $\chi^2 = 46.43$, df $= 20$, P $= 0.07\%$). Hence, composition of the concentrations in areas 6, 8, and 9 changes through this period, which cannot be due to increased hunting effort. As numbers counted in the region during these months increase, this change in composition of populations corresponds to immigration, judged from the data in Table 5 presumably from late January or early February onwards.

The late winter immigration into the Storebælt area is also reflected by visual observations. At Knudshoved, Eastern Funen (area 6), the proportion of males in migrating Eider flocks observed 1960-65 declined gradually from 80% in September to a minimum of 30% medio January, and after that increased until about 1 April (Rabøl and Noer 1970). This suggests autumn immigration of mainly females and young continuing until primo January, and a secondary immigration of flocks with a higher percentage of males from medio January onwards.

Potentially, recruitment areas for this immigration could be the Wadden Sea, where the percentage of adult males in winter is 50 or more (Swennen et al. 1989), the South coasts of the Western Baltic, or the Kattegat. Inspection of Tables 3 and 5 and App. I-VIII reveals that recoveries of Eiders ringed in the Netherlands increase unproportionally in February, and a similar increase was found in numbers of recoveries from the Danish Ertholmene population (Table 5). The Ertholmene population winters in the Wadden Sea (Noer in prep.). Hence, there is strong evidence suggesting that return movements from the Wadden Sea are involved. Since a further 50,000-70,000 Eiders disappear from the German coasts of the Baltic between January and March (Kirchhoff et al. 1983, and S. Bräger pers. comm.) it is also likely that immigration takes place from there.

Within the inner Danish waters, the relative numbers of recoveries from the

Table 5. Temporal distributions of recoveries from Store Bælt, Lille Bælt, and Sydfynske Øhav (areas 6, 8, and 9 in Fig. 2) in January and February. Recoveries included in the comparisons were ringed in A: Finland, B: Sweden (Baltic coasts), C: the Netherlands, D: Denmark (Ertholmene) and E: Denmark (Stauns Fjord and Saltholm pooled).

	A	B	C	D	E
1-10 January	31	6	4	8	8
11-20 -	48	2	5	12	13
21-31 -	41	8	7	16	11
1-10 February	50	22	15	19	14
11-20 -	76	24	28	31	42
21-29 -	99	29	54	55	36

Danish populations in Stavns Fjord and Saltholm in areas 5, 6, 8, and 9 increase in January-February (Noer, in press). Noer (in press) suggests that this pattern reflects southward movements of Eiders concentrating in these areas prior to spring migration, and that the Danish Eiders move to these areas as they follow flocks of Baltic Eiders with which they have mixed during autumn and winter. The patterns of particularly Finnish recoveries shown in this paper could fit this suggestion. Note that the temporal pattern in the increase in numbers of recoveries in areas 6, 8, and 9 is very similar for Finnish and for Danish Eiders (Table 5, χ^2 = 10.36, df = 11, P = 49.83%).

Besides the demonstration that the composition of the concentrations in areas 6, 8, and 9 changes through January and February (Table 5), the bias introduced by increased hunting effort in these areas could be evaluated by comparison with numbers of individuals recovered from death causes other than shooting. Inspection of the distributions of these recoveries (App. X-XII, recoveries from oil spills have been excluded), however, reveals only slight increases in numbers of recoveries from areas 6, 8, and 9 in late winter and early spring, and it is very clear that compared to the numbers of recoveries from the Kattegat region the relative numbers of recoveries from these waters are far smaller in this data set. This can be taken as an indication that the increase in numbers of recoveries from the southern parts of the inner Danish waters is mainly caused by an unproportional increase in hunting effort, but it could also mean that the recovery probability from death causes other than shooting is higher in the SW-Kattegat region. As large numbers of Eiders disappear from both the Wadden Sea and the South Coasts of the Western Baltic, and as aerial counts have demonstrated substantial increases in numbers of Eiders in areas 6, 8, and 9 during February, it is concluded the increases in numbers of recoveries reflect real changes in numbers of birds. Therefore, the recoveries from other death causes probably are the most biased part of the material.

Other movements

Evidence suggesting a return movement from the Wadden Sea to the southern parts of the Danish waters of a minimum of 50,000 Eider males after completion of moult in August-September was presented by Swennen et al. (1989). The possibility that these movements take place is, at least to some extent, supported by the recoveries of Eiders ringed in the Netherlands. For Eiders ringed April-June there are several recoveries in count areas 7 and 10 in October (Fig. 18). As for the Finnish and Swedish East coast recoveries, this probably represents autumn immigration from the Baltic into Danish waters. For Eiders ringed in July-September, no recoveries were made in count areas 7 and 10 in October (Fig. 19), and even if the two data sets are too small to permit reliable statistical testing this is taken to indicate that these recoveries have not entered the Danish waters from the Northeast. Rather, the distribution of these recoveries could be interpreted as reflecting immigration from SW (cp. the discussion of the late winter/early spring movements given above). Given that this is the case, the significantly lower numbers of recoveries of Eiders ringed in the Netherlands in November-January (Table 3) are notable, together with the concentration of the 33 recoveries from this period in the southernmost parts of the Danish waters (Fig. 20). This seems to indicate that to the extent Eiders return from the Wadden Sea in October to the Danish waters, they do not spread during winter, but remain in areas 6, 8, and 9. The low number of recoveries November-January would then be explained by the relatively low shooting pressure in these areas in autumn/early winter (Noer et al. in prep.).

The interpretation of the patterns of recoveries

As detailed above, the observed distributions of recoveries can be interpreted in more than one way. The following interpretation of the seasonal changes in numbers and distributions of Eiders in the Danish waters described above (Fig. 1) is proposed as being the most consistent with observations of migration and aerial surveys.

Most of the Kattegat/Skagerrak populations winter in the Danish parts of North Kattegat, as indicated by the low numbers counted along the Swedish West Coast and Norwegian South Coast in midwinter aerial surveys (Nilsson 1968, 1970, and 1973, and Nygård et al. 1988). Generally, these populations arrive earlier in autumn than the bulk of the Baltic populations. Immigration into Danish waters from the Baltic starts in late September/early October, but continues until primo or even medio December. The part of the Baltic populations that migrates to the Wadden Sea probably spends a minimum of time in the Danish waters, and the temporal differences (Table 3) suggest that these populations pass Denmark earlier in the autumn. According to this hypothesis, the northerly distribution of Eiders in the Danish waters in October/November surveys (Fig. 1) is due to uncompleted arrival of the Baltic populations. A summary of the autumn immigration according to this model is presented in Fig. 23.

At the time of the midwinter surveys, autumn immigration of the Baltic populations is completed, which accounts for the larger totals observed (Fig. 1). Immigration from the Baltic has mainly been to the southern parts of the inner Danish waters, which can explain the rather even distribution of the species over the Danish waters at this time of the year (Fig. 1). Return movements of Eiders from the Wadden Sea and immigration from the German parts of the Southwest Baltic are beginning to increase numbers of Eiders in areas 6, 8, and 9. A summary of the proposed midwinter distributions is given in Fig. 24.

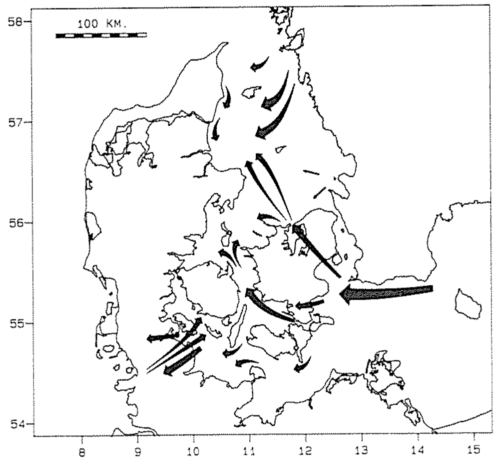

Fig. 23. Assumed patterns of autumn immigration of Eiders wintering in Danish waters. Immigration of the Kattegat/Skagerrak populations is assumed to take place earlier than immigration from the Baltic, the latter continuing into December. This model explains why the largest number of Eiders in Danish autumn aerial surveys are found in North Kattegat (Fig. 1). The presented differences in temporal distributions of recoveries from different populations is taken to suggest that the early immigration of Baltic Eiders to a large extent involves birds proceeding across the Danish waters to the Wadden Sea, while the southern parts of the inner Danish waters are 'filled' in late autumn.

At the time of the spring surveys, the bulk of the Kattegat/Skagerrak populations has left for the breeding grounds, which due to ice conditions will be accessible earlier in the spring than those of the Baltic populations. At the same time, large numbers of Eiders have moved from the Wadden Sea and the German parts of the Baltic to the southernmost parts of the inner Danish waters, where they concentrate prior to spring migration. Simultaneously, Baltic Eiders that have wintered in the Kattegat have moved to the South and concentrated along the North coast of Sjælland and in the Belts. Emigration from the Danish waters takes place in late March/early

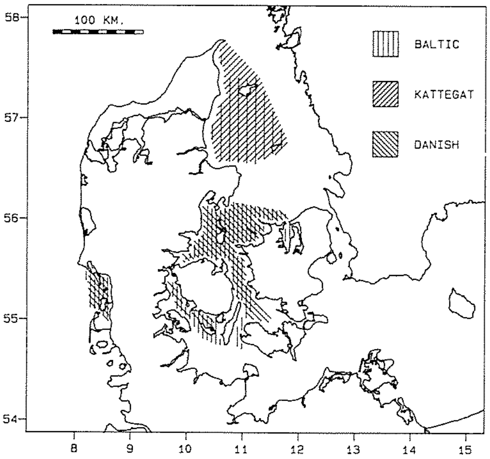

Fig. 24. Assumed midwinter distributions of different populations of Eiders in Danish waters. The map outlines the distributions in January-February, but it should be noted that almost continuous movements take place.

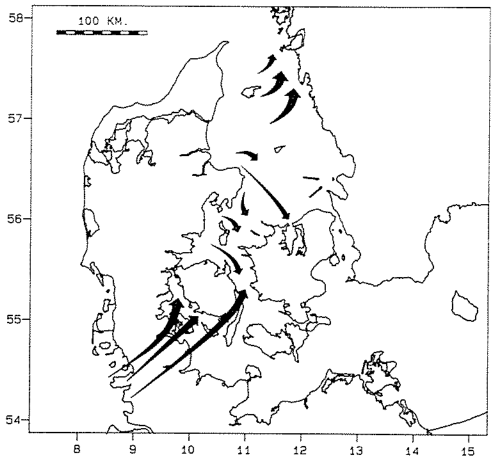

Fig. 25. Assumed patterns of movements in late winter/early spring of Eiders in Danish waters. These movements take place from late January (immigration from the Wadden Sea and the SW-Baltic) to March (emigration of the Kattegat/Skagerrak breeding populations from the Danish parts of North Kattegat), and would be reflected in aerial surveys as increasing concentrations in the southern parts of the inner Danish waters and decreasing numbers in North Kattegat. Hence, this model explains the observations presented in Fig. 1. The movements take place prior to the spring migration proper (late March/early April), where the Baltic populations emigrate from the Danish waters.

April, which means that numbers of Eiders may have dropped considerably in years where the aerial spring surveys are delayed (Fig. 1). A summary of the movements assumed to take place between January and March is given in Fig. 25.

Numbers involved

The size of the breeding populations on the Swedish West coast is assumed to be 70,000 pairs (Franzmann 1989), while 6,000 pairs were assumed to breed at the Norwegian Skagerrak coasts by 1980 (Røv et al. 1984). There are few recoveries of Eiders from these populations in the Wadden Sea (Anon. 1989), and as discussed above it is reasonable to assume that the major part of these populations winter in North Kattegat. As 75,000-80,000 breeding pairs probably correspond to a winter population of 250,000-300,000 individuals, the maximum numbers counted in area 3 during the Danish aerial surveys (abt. 320,000, Laursen et al. in prep.) indicate that the number of individuals from the Baltic populations wintering here is below 100,000 individuals. The Danish populations do only utilise these areas to a minimal extent in winter (Noer, in press).

The composition of concentrations in areas 4 and 5 (Fig. 2) is quite different. The majority of the Danish populations winter in this area (an estimated 50,000 individuals) and as revealed by the ringing recoveries the remainder of the Eiders wintering in this area can be assumed to be of Baltic origin. Danish aerial surveys reach midwinter totals of 150,000-250,000 individuals in these parts of the inner Danish waters, implying that 100,000-200,000 Baltic Eiders winter here. The concentrations in the southern Danish waters are probably completely dominated by the Baltic populations. These concentrations contribute a further 200,000 individuals.

Summing up these numbers, a maximum of 500,000 Baltic Eiders are assumed to be present in the Danish waters at the time of the midwinter counts (January). In combination with the 200,000-250,000 Baltic Eiders assumed to winter in the Wadden Sea (Swennen et al. 1989), these numbers correspond to roughly 250,000 breeding pairs in the Baltic. This figure contrasts sharply to the estimated numbers of breeding pairs (see also Laursen 1989), and in the comparisons between winter counts and breeding counts a deficit of about 1,000,000 individuals exists (Laursen 1989).

The numbers involved in the late winter/early spring movements cannot be estimated with certainty. An estimated 70,000 Eiders disappear from the Wadden Sea between 15 February and 15 March, a further 70,000 between 15 March and 15 April, and a further 50,000 between 15 April and 15 May (Swennen et al. 1989). In addition, 70,000 Eiders may immigrate from the SW-Baltic coasts in January-February. Based on these figures and on those obtained by aerial counts, the number of Eiders moving into the southernmost parts of the inner Danish waters in January-February may comprise between 250,000 and 400,000 individuals.

Differences between years and sets of recoveries

The observed differences between data sets indicate that variation in the general patterns exist. The differences between the Swedish (Baltic) and the Finnish sets of recoveries suggest that a larger fraction of the Swedish recoveries (which are mainly of birds ringed in Gotland) winter in the Wadden Sea and/or the Southwest Baltic. This is evidenced partly by the significantly more southerly distributions of recoveries from Denmark and partly by the differences between temporal distributions, relatively more recoveries of the Swedish population being made in October and February. Similarly, the relatively few recoveries of Estonian individuals in areas 6, 8, and 9 (Fig. 8) is taken to suggest that a smaller fraction of these winter in the Wadden Sea or the Southwest Baltic. At the same time, it is noteworthy that the temporal differences between sets of recoveries (Table 3 and App. I-VIII) show that the Eiders ringed in the Netherlands and in East Sweden – which presumably are Eiders wintering to a large extent South and Southwest of the Danish waters – are those with the relatively highest numbers of recoveries in October and February. This can be taken to indicate that the early autumn immigration in Denmark contains a high percentage of Eiders that fly on without wintering in Denmark. If this is true, the Eiders wintering in the Wadden Sea cannot be interpreted as 'overflow' resulting from a saturation of the inner Danish waters, but have to be viewed as a truly migratory part of the Baltic populations.

Moreover, differences between the Baltic colonies are small when compared to the differences between the Danish or Swedish Norwegian Kattegat/Skagerrak populations (Noer in press, and the present paper). Noer (in press) suggests that mixing of Eider flocks on autumn migration, in combination with a tendency for developing winter site fidelity, plays an important role in the determination of the observed patterns. Since the Baltic populations are concentrated along the East and South coasts of Sweden on migration – besides being numerically much larger – these populations can be assumed to mix during migration to a much larger extent than the Kattegat/Skagerrak populations, and the relatively smaller differences between colonies in the Baltic thus support this model. Quantification and comparison of the differences between colonies, compared to their relative isolation on migration, could undoubtedly contribute to the understanding of these problems. Such comparisons would be best undertaken if analyses of Eider recoveries were based on total sets of recoveries and not on the sets from any particular country – but this has been considered outside the scope of the present work.

Compared to the patterns revealed by recoveries of individuals ringed in the Netherlands and assumed to return to the Danish waters by crossing South Jylland, the pattern of recoveries of individuals ringed in Great Britain (Fig. 17) is peculiar. Judged from patterns revealed by recoveries from other populations with better known movements and from the fact that the probability of recovery is assumed to be smaller in the Northern parts of the Kattegat, the British Eiders recovered in area 3 probably enter the Danish waters through the Skagerrak, possibly in combination with Norwegian Eiders. One recovery of an Eider ringed in Great Britain and reported from Norway (Baillie and Milne 1989), seems to support this interpretation. The recoveries from areas 5 and 7 could be of individuals returning on autumn migration after breeding in the Baltic (Baillie and Milne 1989).

The differences between years found for the Finnish Eiders are presumably due partly to ice conditions ccounting for some years) and partly to slight variations in timing of the spring return movements from the Wadden Sea. In relation to the closing of the open season in Denmark on 28 (29) February, differences between years of less than 10 days in the time of the start of these movements would probably cause large fluctuations in numbers recovered. At least for some of these years, the detailed patterns of recoveries correspond to variation in the distributions of the birds as observed by the aerial counts (Noer unpubl.).

DANSK RESUMÉ

Fordelinger og trækbevægelser af overvintrende ederfugle *Somateria mollissima* bestande i de danske farvande, analyseret ud fra genmeldinger af ringmærkede fugle.

Store dele af de skandinaviske ederfuglebestande overvintrer i de danske farvande. Landsdækkende optællinger fra fly har flere gange resulteret i totaltal på 800.000 individer (Laursen et al. in prep.). Tællinger i oktober/november, januar/februar og marts/april har vist karakteristiske ændringer i antal og fordeling. I oktober og november findes de største antal i det nordlige Kattegat, i januar og februar er artens fordeling mere jævn, og det samlede antal er steget, og i marts og april findes de største koncentrationer i den sydlige del af de indre danske farvande (Fig. 1). På denne årstid kan det samlede antal være meget højt, hvis tællingen foretages inden starten af forårstrækket mod ynglepladserne (Fig. 1).

Baggrunden for disse karakteristiske fordelinger kan analyseres ud fra genmeldinger af ringmærkede ederfugle. Der foreligger ca. 2.100 genmeldinger fra en række nordeuropæiske lande (Tabel 1). Langt de fleste af de genmeldte fugle er ringmærket som kønsmodne hunner (ved fangst på reden), og over 80% er genmeldt som skudt. Hovedvægten i analyserne er derfor lagt på skudte fugle. Genmeldinger af danske ynglefugle behandles i en separat artikel (Noer in press).

På grund af en større ringmærkningsintensitet er størstedelen af materialet genmeldinger af finske (Fig. 3-7), svenske (Fig. 8-13) og hollandske (Fig. 18-22) mærkninger. Statistiske analyser af disse materialer viser klart, at fordelingerne ændrer sig gennem perioden oktober-februar, dvs. gennem jagttiden. Disse analyser er udført som simple χ^2-tests, der sammenligner de månedsvise antal af genmeldinger i forskellige delområder af de danske farvande (Fig. 2 og App. I-VIII). Både for de finske og for de svenske Østersø-bestandes vedkommende er billedet klart. Om efteråret er der et forholdsvist stort antal genmeldinger i Øresund og Smålandsfarvandet, mens fordelingen af genmeldinger i januar og februar viser en forøget koncentration i Storebælt, Lillebælt og Sydfynske Øhav. Det kan ligeledes vises, at der er mindre, - men statistisk signifikante - forskelle mellem de svenske og finske bestande. Genmeldinger fra den svenske vestkyst viser en mere nordlig fordeling i de danske farvande, især for fugle der yngler i det nordlige Kattegat (Fig. 14 og 15).Disse mønstre og forskelle mellem bestande kan ikke tillægges nogen definitiv fortolkning. Fordelinger af genmeldte fugle afhænger både af bestandenes fordelinger og af genmeldingssandsynligheden, f.eks. kan det forøgede antal af genmeldinger af baltiske ederfugle i de sydlige danske farvande tænkes forklaret både ved en øget koncentration af fugle og ved et øget jagttryk. Ud fra en række vurderinger af materialet kan der imidlertid opstilles en model for ederfuglebestandenes fordelinger i de danske farvande der er konsistent med observationerne. Denne model er skitseret i Fig. 23 (efterårstræk), 24 (midvinterfordelinger) og 25 (bevægelser i sen vinter/tidligt forår).

Det antages at næsten hele bestanden på den svenske vestkyst og norske sydkyst overvintrer i den danske del af det nordlige Kattegat (Fig. 24). Disse bestande udgør om vinteren 250.000-300.000 individer, og da antallet af ederfugle i det nordlige Kattegat om vinteren er 300.000-400.000 fugle indebærer antagelsen, at højst 100.000 baltiske ederfugle overvintrer i dette område. De overvintrende bestande i det sydlige Kattegat udgøres af de danske ynglebestande (ca. 50.000 individer) og 150.000-250.000 baltiske fugle. Bestandene i Storebælt, Lillebælt og Sydfynske Øhav er næsten udelukkende baltiske fugle, i alt cirka 200.000 individer.

Denne model kan forklare ændringerne i fordelinger gennem vintersæsonen (Fig. 1) ved at ynglebestandene i Nordkattegat og Skagerrak ankommer tidligere om efteråret og trækker tidligere til ynglekvartererne om foråret. Det må samtidig antages, at der i løbet af februar foregår et meget betydeligt tiltræk i Storebælt, Lillebælt og Sydfynske Øhav. Hovedparten af dette tiltræk formodes at komme fra Vadehavet, men sydgående bevægelser i de indre farvande på denne årstid spiller antagelig også en rolle. Denne øgede koncentration i den sydlige del af de indre farvande skønnes at omfatte 250.000-400.000 fugle, der årligt trækker til disse områder i løbet af februar, altså inden det egentlige forårstræk. Disse antal bekræftes af tællinger fra fly.

Резюме на русском языке:
Распределение и перелетные передвижения зимующих популяций обыкновенной гаги Somateria mollissima на датских водах. Анализированы на основании возвратов об окольцованных птицах.

Большая часть скандинавских популяций обыкновенной гаги зимует на датских водах. Охватывавшие всю страну подсчеты с самолетов несколько раз указали на общую численность в 800.000 особей (Лаурсен и др., подготовляется). Подсчеты в октябре/ноябре, январе/феврале и марте/апреле показали характерные изменения численности и распределения. В октябре и ноябре наибольшее количество наблюдается в северном Каттегате, в январе и феврале распределение этого вида более равномерно, и общая численность повышена, а в марте и апреле самые большие концентрации наблюдаются на южной части внутренних датских вод (Фиг. I). В это время года общая численность может быть очень велика, если подсчет произведен до начала весеннего перелета на места гнездования (Фиг. I).

Предпосылки этих характерных распределений можно анализировать на основании возвратов об окольцованных гагах. Имеется около 2.I00 возвратов из ряда стран Северной Европы (Табл. I). Преобладающее большинство птиц, о которых получены возвраты, окольцованы, будучи половозрелыми самками (пойманными на гнездах), и более 80% возвратов касаются застреленных птиц. При оценках наибольшее значение поэтому придано застреленным птицам. Возвраты о гнездующих в Дании птицах обсуждаются в отдельной статье (Ноэр, печатается).

Вследствии более значительной интенсивности кольцевания, наибольшую часть материала составляют возвраты о птицах, окольцованных в Финляндии (Фиг. 3 - 7), Швеции (Фиг. 8 - I3) и Голландии (Фиг. I8 - 22). Статистические анализы этих материалов ясно показывают, что распределения изменяются в течение периода с октября по февраль, т. е. сезона охоты. Эти анализы произведены путем простых испытаний способом x^2, причем сравнялись ежемесячные числа возвратов с разных отдельных частей датских вод (Фиг. 2 и Приложения I - VIII). Как о шведских, так и о финских популяциях получено ясное представление. Осенью сравнительно большое число возвратов получено с Эрезунда и Смоландских Вод, а распределение возвратов в январе и феврале свидетельствует о повышении концентрации в Большом и Малом Бельтах и архипелаге к югу от острова Фюн. Можно также показать, что состоят небольшие - но статистически значительные - разницы между шведскими и финскими популяциями. Возвраты с западного побережья Швеции указывают на распределение в датских водах дальше к северу, особенно птиц, гнездующих в Северном Каттегате (Фиг. I4 и I5).

Эти особенности и разницы между популяциями невозможно определенно объяснить. Распределения птиц, о которых получаются возвраты, зависят не только от распределения популяции, но и от вероятности возврата. Например, повышенное число возвратов о балтийских гагах с южных датских вод может объясняться как повышенной концентрацией птиц, так и повышенной интенсивностью охоты. Однако, исходя из ряда оценок материала можно составить модель распределений популяций гаг на датских водах, согласующуюся с наблюдениями. Эта модель схематически представлена в Фиг. 23 (осенний перелет), 24 (распределение в середине зимы) и 25 (перемещения поздней зимой / ранней весной).

Предполагается, что почти вся популяция с западного побережья Швеции и южного побережья Норвегии зимует на датской части Северного Каттегата (Фиг. 24). Эти популяции зимой составляют 250.000 - 300.000 особей, и так как число гаг на

Северном Каттегате зимой составляет 300.000 - 400.000 особей, это предположение приводит к выводу, что на этом водяном пространстве зимуют не более 100.000 балтийских гаг. Зимующие на Южном Каттегате популяции состоят из популяций, гнездующих в Дании (прибл. 50.000 особей) и 150.000 - 200.000 балтийских птиц. Популяции на Большом и Малом Бельтах и архипелаге к югу от острова Фюн являются почти исключительно балтийскими птицами, итого прибл. 200.000 особей.

Эта модель может объяснить изменения распределения в течение зимнего сезона (Фиг. I) тем, что гнездующие популяции на Северном Каттегате и Скагерраке осенью прибывают раньше, и весной раньше перелетают на места гнездования. В то же время нужно предположить, что в течение февраля происходит очень значительный прилёт на Большой и Малый Бельты и архипелаг к югу от острова Фюн. Предполагается, что главная часть этого прилёта происходит с морских отмелей на югозападе Ютландии, но некоторую роль также играют происходящие в это время перемещения к югу на внутренних водах. Эта повышенная концентрация на южной части внутренних вод включает 250.000 - 400.000 птиц, ежегодно перелетающих на эти водяные пространства в течение февраля, т. е. до настоящего весеннего перелета. Эти численности подтверждаются подсчетами с самолетов.

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APPENDIX

APPENDIX I. Spatial and temporal distribution of Eiders ringed in Finland and recovered as shot in Denmark.

Area	1	2	3	4	5	6	7	8	9	10	11	Tot.
October	10		13	34	40	25	6	18	11	13		170
November	3		10	30	27	23	8	12	30	19	1	163
December	9		15	36	24	20	6	20	36	8		174
January	8		11	42	31	43	2	41	36	8		222
February	6	1	15	60	44	71	1	66	88	8		360
Total	36	1	64	204	166	182	23	157	201	56	1	1089

APPENDIX II. Yearly distributions in Danish waters of Finnish Eiders recovered as shot in January and February.

	1971	1972	1973	1974	1975	1976	1977	1978	1980	1981	1982	1983	1984	1988
Area:														
1	1	1	2		4	1		1		1				
2		1												
3		2	2	1		2		3	1		1	3	1	2
4	7	3	5	8	4	3	4	4	5	4	7	13	3	12
5	5	6	5	3	4	3	4	1	5	2	5	5	6	3
6	4	3	3	3	8	7	5	11	8	9	9	11	5	8
7												1		
8	2	2	6	2	11	6	4	4	17	6	5	7	2	12
9	1	4	15	6	8	16	5	4	14	4	4	12	6	14
10		1			1	1		2		1		1		
11														

APPENDIX III. Spatial and temporal distribution of Eiders ringed in Estonia and recovered as shot in Denmark.

Area	1	2	3	4	5	6	7	8	9	10	11	Tot.
October	1			2		1			1		1	6
November				1	2	1		3				7
December			1	4	1	2			3			11
January	1			1	2	1			3			8
February			2	1	3	6		3	2			17
Total	2		3	9	8	11		6	9		1	49

APPENDIX IV. Spatial and temporal distribution of Eiders ringed in Sweden (Baltic) and recovered as shot in Denmark.

Area	1	2	3	4	5	6	7	8	9	10	11	Tot.
October	2		1	6	4	8	1	3	9	6		40
November	3		1	4	8	3	3	1	3	2	1	29
December			1	8	3	3	1	4	6	3		29
January	2			10	7	1		3	12	1		36
February	4		3	8	8	19		23	36			101
Total	11		6	36	30	34	5	34	66	12	1	235

APPENDIX V. Spatial and temporal distribution of Eiders ringed in Sweden (Kattegat coast < 57°N) and recovered as shot in Denmark.

Area	1	2	3	4	5	6	7	8	9	10	11	Tot.
October			5	6	9							20
November			2		7	1		1		1		12
December			5	4	7				1			16
January			4	9	9	1		1				24
February			4	4	9	6		2	1			26
Total			20	23	41	8		4	1	1		98

APPENDIX VI. Spatial and temporal distribution of Eiders ringed in Sweden (Kattegat coast > 57°N) and recovered as shot in Denmark.

Area	1	2	3	4	5	6	7	8	9	10	11	Tot.
October			8	1	2				1	1		13
November			3	3	1							7
December			12		2				1			15
January			7	1	1	1						10
February			10	8	2							20
Total			40	13	8	1			2	1		65

APPENDIX VII. Spatial and temporal distribution of Eiders ringed as pulli in the Netherlands and recovered as shot in Denmark.

Area	1	2	3	4	5	6	7	8	9	10	11	Tot.
October	4				1	1	1	2	2	1		12
November	1											1
December								1	2			3
January	1			1				3	2			7
February	3			1	1	9		14	8	1		37
Total	9			2	2	10	1	20	14	2		60

APPENDIX VIII. Spatial and temporal distribution of Eiders ringed as adults in April-June in the Netherlands and recovered as shot in Denmark.

Area	1	2	3	4	5	6	7	8	9	10	11	Tot.
October	1			2			3	5	2	4		17
November	1							2	1			4
December	1											1
January						1						1
February	1			2	2	6		3	12			26
Total	4			4	2	7	3	10	15	4		49

APPENDIX IX. Spatial and temporal distribution of Eiders ringed as adults in July-September in the Netherlands and recovered as shot in Denmark.

Area	1	2	3	4	5	6	7	8	9	10	11	Tot.
October	1			4		2		5	2			14
November				1			1	2	2			6
December	1								1			2
January	3			1				2	2			8
February	5		1	1	1	5		9	12			34
Total	10		1	7	1	7	1	18	19			64

APPENDIX X. Spatial and temporal distribution of Eiders ringed in Finland and recovered in Denmark (shot individuals excluded). A total of 58 recoveries resulting from oil spills have been excluded (45 from areas 3, 4, and 5 in 1971 and 1978).

Area	1	2	3	4	5	6	7	8	9	10	11	Tot.
June			1	1	1							3
July				5					2			7
August			1					2	1	2		6
September			1	2	2	2			1	1		9
October	1		2	6	2	1		3	1	3		19
November			1	1	4	4			3	5	1	19
December	2		3	4	4	3	1	1	4	1		19
January	1		1	6	5	7		4	4	2		30
February	1		2	3	4	6		4	4			24
March			2	5	6	4		2	5	1	1	26
April	3			6	5	1		1	3	4		23
May				2	1	1	1		2			7
Total	8		14	41	34	29	2	17	31	19	2	197

APPENDIX XI. Spatial and temporal distribution of Eiders ringed in Sweden (Baltic) and recovered in Denmark (shot individuals excluded).

Area	1	2	3	4	5	6	7	8	9	10	11	Tot.
June						1					1	2
July									1			1
August												0
September	1									1		2
October				3	1					1		5
November				1								1
December					1							1
January			1	4	2	2						9
February			1	4	2	3		2	2			14
March				1	1	1			2	1		6
April				1				1				2
May	1					1			1			3
Total	2		2	14	7	8		3	6	3	1	46

APPENDIX XII. Spatial and temporal distribution of Eiders ringed in Sweden (Kattegat) and recovered in Denmark (shot individuals excluded).

Area	1	2	3	4	5	6	7	8	9	10	11	Tot.
June				1								1
July									1			1
August	1		1		1			1				4
September							1					1
October			1		1							2
November			1	1	1					1		4
December			2	1	1							4
January			4	1								5
February			5	1								6
March			3	1	1							5
April			1		1	1						3
May			2		1							3
Total	1		20	6	7	1	1	1	1	1		39

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