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Population processes in the common eider *Somateria mollissima*

PROCEEDINGS FROM A WORKSHOP HELD AT KALØ
DURING 1 - 3 NOVEMBER 1991

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HENNING NOER & GEORG NEHLS

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Editorial

During 1-3 November 1991 more than 20 researchers from seven North European countries participated in an eider workshop entitled 'Population processes in the common eider *Somateria mollissima*', which was held at Kalø in eastern Jutland, Denmark.

At the end of the workshop it was decided that proceeding articles from the workshop should be published in a special issue of Danish Review of Game Biology, and Drs Henning Noer and Georg Nehls agreed to act as editors of the proceedings. At the end of the editing process in 1993, 6 articles were accepted for publication, but the publishing itself was delayed and has been postponed for several and various reasons.

Even though more than 10 years have gone since the workshop was held, I am happy - at long last - to be able to present this issue of Danish Review of Game Biology, which will be the last one as Danish Review of Game Biology back in 1994 merged with the Finnish Game Research and Swedish Wildlife Research to form the basis of the international journal WILDLIFE BIOLOGY. Thus the publication of this issue also marks the end of the era of the Nordic national journals.

November 2002

Technical Editor
Jan Bertelsen

CLUTCH SIZE IN SIX DANISH COMMON EIDER *SOMATERIA MOLLISSIMA* COLONIES: VARIATION IN EGG PRODUCTION

BREGNBALLE, T.

The aim of the present study was to quantify and discuss differences in common eider *Somateria mollissima* clutch sizes between the Stavns Fjord colony in the southwestern part of Kattegat and the Ertholmene colony in the southern Baltic. After having corrected for the effect of methods to estimate clutch size and for differences in the levels of egg predation, clutch sizes were 9.9% smaller in the stable Stavns Fjord colony than in the growing colony on Ertholmene. I suggest that the main reason for this difference in clutch size is that females at Ertholmene laid more eggs because of their easier access to high-quality food in winter and/or spring than females breeding in Stavns Fjord. The present paper also examines changes in clutch size during 1965-1992 in five colonies in the southwestern part of Kattegat. There were no clear negative effects of increased colony sizes on clutch sizes: Only in one colony and one period did clutch sizes decline as the size of the colony increased. After 1980, clutch sizes changed simultaneously in all five colonies indicating that egg production had changed due to common factors affecting food intake in late winter and early spring. The largest change in average clutch size after 1980 was a decline of 0.8-1.0 egg per clutch over a five-year period in four of the colonies, suggesting a macro-environmental change in the marine ecosystem of southwestern Kattegat.

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Compared to other sea duck species, the common eider *Somateria mollissima* lay large eggs but small clutches (Lack 1967, 1968). The laying of small clutches does not imply that clutch size is constant in space and time. Among colonies, average clutch size may differ with up to 3.5 eggs, i.e. from an average of 2.0 eggs per nest (Mehlum 1991) to an average of 5.5 eggs per nest (Gerasimova & Baranova 1960), and within the same colony the mean clutch size may vary over a series of years by up to 2.0 eggs (J.C. Coulson, unpubl. data). These variations in clutch size can greatly affect the population growth of an eider colony, although only so if a large proportion of the hatched ducklings survive to breed (Fig. 1).

The number of eiders breeding in two Danish colonies, Stavns Fjord and Ertholmene, developed differently during the 1970s (H. Noer, unpubl. data). The Stavns Fjord colony, located in southwestern Kattegat, increased in size during the 1960s but stabilised around 2,200 pairs in the 1970s, whereas the colony at Ertholmene continued to increase during the 1970s (for location and development of the two colonies see Lyngs 1992 and Bregnballe, Gregersen & Jepsen 2002). The first analyses of the possible reasons for the difference in population development revealed that clutches were smaller in Stavns Fjord than in the colony on Ertholmene. The fact that clutch size is smaller in some eider colonies than in others is usually ascribed to differ-

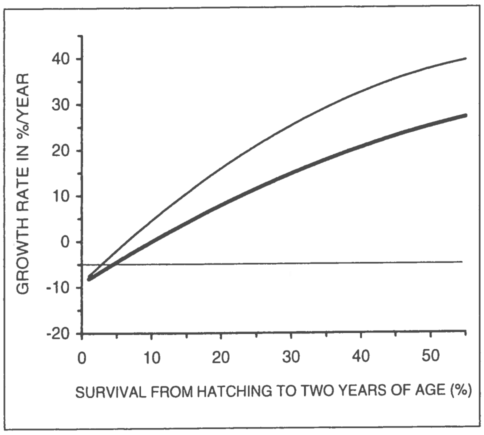

Figure 1. Theoretical simulation of the relationship between growth and survival from hatching until two years of age, using a clutch size of 3.5 (thick line) and 5.0 (thin line) as input values. The following standard input values were used in the Leslie matrix: an adult survival of 90% per year, a nesting success of 85%; 10% nested as 2-years old and the remaining as 3-years old.

ences in methods applied in estimating clutch size, and to differences in the amount of egg predation (Belopolskii 1957, Milne 1974, Ahlén & Andersson 1970, Swennen 1983, Mehlum 1991). However, differences in clutch size may also arise due to differences in the average number of eggs laid per female. The primary aim of the present paper is to identify and discuss the causes for the low clutch size in Stavns Fjord compared to that of Ertholmene.

Body condition reached prior to egg laying seems to affect the number of eggs laid in common eiders (Milne 1976, Erikstad, Bustnes & Moum 1993). Therefore, clutch size is likely to be sensitive to changes in the amount of food available in the wintering area, in the spring staging area and/or in the area near the colony. At some colonies, female eiders forage close to the breeding islets during the last days or weeks prior to the start of egg laying, and H. Noer (unpubl. data) suggested that the amount of food available close to the colony would decline in some colonies as the number of foraging eiders increased (with an increase in the colony size), and consequently food intake would deteriorate leading to smaller clutches. Studies in east England (J. C. Coulson, unpubl. data) and in the Gulf of Finland (Hario & Selin 1988, 2002) revealed significant changes in egg production, but food-related factors as a cause of the changes could not be identified. The secondary aim of this paper is to discuss the changes in clutch sizes in five Danish eider colonies in southwestern Kattegat based on the assumption that food stocks near the colony affect the egg production.

Study colonies, material and methods

On Ertholmene, eiders nest on two islets of 22 ha and 4 ha, respectively. Data included in the present paper refer only to the larger one of the two islets. In Stavns Fjord, eiders nest on 13 islets, varying between 1 and 51 ha in size. The location of the colonies is shown in Lyngs (1992) and Bregnballe et al. (2002).

The method applied in estimating clutch size on Ertholmene was different from the method applied in Stavns Fjord. On Ertholmene, clutch size was the maximum number of eggs recorded in each nest which was checked with an interval of five to seven days, whereas in Stavns Fjord, nests were checked only once, late in the incubation period. While checking the nests in Stavns Fjord, it was recorded whether females had been caught on the nest or not, and whether the nest cups contained no, small, medium or large amounts of down; this information was used to identify fully laid clutches.

To estimate the effect of partial egg predation on clutch size in Stavns Fjord, I divided the study area into 25 study units of 2.3 - 14.4 ha in size on five islets. The study units were defined according to vegetation structure and predator environment. This was done to identify areas in which only few or no eider clutches had been reduced in size due to egg predation.

The five colonies in southwestern Kattegat (Stavns Fjord, Hov Røn, Svanegrunden, Alrø Poller and Mågeøerne) included in the analyses of changes in clutch size all lie within 10-

50 km of each other (for location of the colonies see Fig. 1 in Bregnballe et al. 2002). Except for the Stavns Fjord colony, eiders bred on sandy islets up to 5.5 ha in size. Most clutches were laid in high grass and some in sea wrack. In Stavns Fjord eiders bred on elevated islets with many nests hidden in the scrub as well as on low islets with nests positioned in grass or sea wrack. Nests were checked once late in the incubation phase; the date of the nest check varied with up to 16 days among years and colonies. In this part of the present paper, average clutch size is defined as the average number of eggs present in all nests with eggs. The data available allow to test for the effect of colony size, number of breeding gulls and year class on the observed changes in clutch size.

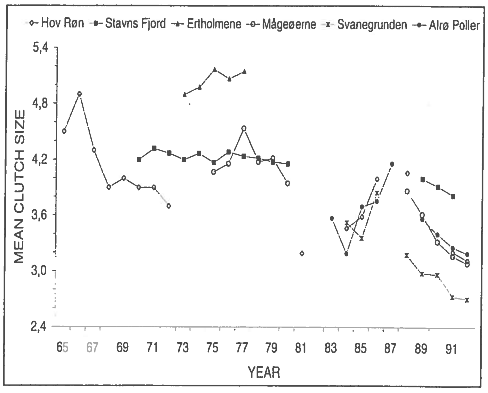

Figure 3. Mean clutch size of eiders on Ertholmene in the western Baltic Sea, and in five colonies in south-western Kattegat during 1965-1992. For number of nests included, see the text and Table 1. For all colonies except Ertholmene, the average clutch size includes incomplete clutches and clutches which lost one or more eggs to predators.

Results

Stavns Fjord versus Ertholmene

The proportion of nests with 1 - 4 eggs was higher in the Stavns Fjord colony (52.9%) than in the Ertholmene colony (28.6%; Fig. 2), and the average clutch size was lowest in Stavns Fjord in all years (Fig. 3). During the 1970s, the mean clutch size in Stavns Fjord (for 1971-1980; 1,129 < N < 1,763) was 4.25 ± 0.05 (SD) and on Ertholmene (for 1973-1977; 441 < N < 942) 5.03 ± 0.11 (SD), i.e. on average Stavns Fjord clutches contained 0.78 (15.5%) less eggs than clutches on Ertholmene. Part of this difference was due to the use of unequal methods in estimating clutch size, part of it was due to higher egg predation by gulls and crows in the Stavns Fjord colony than on Ertholmene. The clutch-size estimate from Stavns Fjord can be corrected for both of these effects by attempting to exclude incomplete clutches and clutches that may have lost eggs to predators.

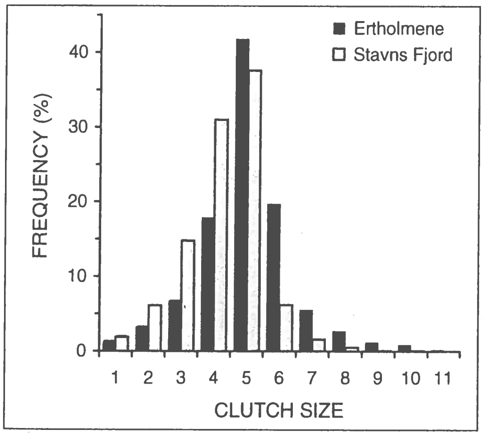

Figure 2. Mean frequencies (in %) of clutch sizes of eider nests in the Stavns Fjord colony during 1971-1980 (grey; 1,129 < N < 1,763) and in the Ertholmene colony in 1973 (black; N = 1,253).

Most of the incomplete clutches can be excluded from the clutch-size estimate by excluding both nests with small or medium amounts of down and nests from which females were absent or escaped before being caught (Fig. 4). In Stavns Fjord, the average clutch size was 4.42 ± 1.11 (SD) when estimated from fully laid clutches, i.e. nests where the female had been caught and the quantity of down had been high.

In Stavns Fjord, where some eggs were taken by gulls, crows and mammalian predators, clutch sizes were largest in nests positioned in the shrub on islands to which martens (*Martes* sp.) and red foxes (*Vulpes vul-*

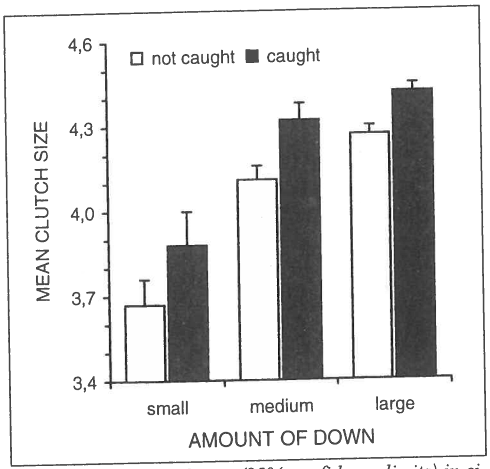

Figure 4. Mean clutch size (95% confidence limits) in eider nests given in relation to the amount of down in the nest cup and to whether the female was caught on the nests or not. Two-way ANOVA: for down, F = 135.9, df = 2, 15,457, P < 0.001; for caught/not caught, F = 76.5, df = 1, 15,457, P < 0.001; No interaction, F = 1.4, df = 2, 15,457, P = 0.25. For the down categories small, medium and large the sample sizes were; 792, 2,247, and 6,374 for 'not caught', and 373, 1,414, and 4,363 for 'caught', respectively.

pes) had no access. Assuming that none or only few of these clutches had been predated during egg laying or partially predated during incubation, the average clutch size was 4.53 for fully laid and unpredated clutches. On Ertholmene, almost all eider nests were sheltered against avian and mammalian egg predators, and only few clutches were reduced in size due to egg predation (Lyngs 1992).

After having corrected for the effect of the use of unequal methods and for the effect of egg predation, eider clutch size was on average 0.50 eggs (9.9%) smaller in Stavns Fjord than on Ertholmene.

Changes in clutch size in southwestern Kattegat

Clutch sizes declined at Hov Røn during 1966 - 1981 (see Fig. 3, Table 1). In the colonies Hov Røn, Svanegrunden and Alrø Poller, clutch size increased from 1984 (or 1985) to 1987 (or 1988). This increase was followed by a decline in the clutch size of 3.8 - 4.8% per year until 1992 (including the colony on Mågeøerne), and after five years the average clutch size had declined by 0.8 - 1.0 eggs

The early decline in clutch size on Hov Røn (during 1965 - 1972) occurred concurrently with an annual increase in colony size of 25% (correlation between clutch size and colony size: r = - 0.78, P = 0.038). The changes in clutch size in the other colonies and periods were not (negatively) correlated with changes in the number of breeding eiders (r > 0.09 for all).

Variation in the number of gulls did not seem to affect the changes in clutch size as the clutch size was neither correlated with the number of breeding gulls per eider nest nor with the total number of breeding gulls (colonies and periods tested both separately and together).

The individual clutch size also declined among older females in the period between the 1970s and 1989 - 1991 during which the mean clutch size declined in Stavns Fjord:

Table 1. Correlation coefficient of mean clutch size over year and the significance of change in clutch size in four eider colonies in southwestern Kattegat during 1965 - 1992.

Colony	Period	r	P	No. of years	Nests checked
Hov Røn	1965-1972	- 0.87	0.005	8	115-670
	1981-1986	+ 0.93	0.075	4	390-1000
	1988-1992	- 0.99	0.095	3	620-784
Svanegrunden	1986-1992	- 0.95	0.004	6	96-273
Alrø Polder	1983-1987	+ 0.79	0.113	5	108-248
	1987-1992	- 0.97	0.005	5	107-471
Mågeøerne	1988-1992	- 0.98	0.004	5	109-335

The average clutch size for 58 females 12-17-years old declined from 4.40 ± 1.1 (SD) in 1971-1980 to 4.02 ± 1.0 (SD) in 1989-1991 ($N = 118$ and $N = 65$; $t = 2.15$, $P < 0.05$). Therefore, recruitment of less productive year classes (Hario & Selin 1994) did not seem to have been causing the decline in clutch size in the Stavns Fjord colony.

Discussion

Differences in clutch size between the Stavns Fjord and Ertholmene colonies

Female eiders breeding in the Stavns Fjord colony live their whole life cycle in an environment completely different from that of females in the Ertholmene colony (Noer 1991), and the females may differ genetically and behaviourally. The difference in the colonies' average clutch size of 0.50 eggs may therefore have been caused by several factors.

Although egg dumping was observed on Ertholmene (Franzmann 1980), 10% of all egg-laying females should have laid all their eggs in nests of other females to account for the 0.50 egg difference in clutch size which is unlikely.

The difference in clutch size is more likely to be related to differences between the two colonies in the average number of eggs laid per female. Females breeding on Ertholmene may have laid more eggs because they nest near human settlements, because of larger body size or because they had access to more and better quality of food than females breeding in the Stavns Fjord colony. Female eiders on Ertholmene may have responded adaptively to a safe nesting environment, i.e. laid more eggs because they nested among houses on an inhabited island (*cf.* Hario & Selin 1987). However, the main reason for the differences in clutch size is more likely to be due to differences in fecundity rather than to differences in behaviour. High fecundity in eiders is often expressed in large clutches and large eggs (Hario & Selin 1987), and females on Ertholmene laid larger eggs than females in Stavns Fjord and other colonies (Table 2). Females on Ertholmene also weighed more than females in Stavns Fjord (H. Noer, unpubl. data) though it is unknown to what extent differences in clutch and egg size were due to differences in body size.

Females on Ertholmene may have reached higher pre-breeding weights and invested more resources in egg production (Erikstad et al. 1993) than females in Stavns Fjord because they had easier access to more high-quality food than females in Stavns Fjord. Milne (1976) found a significant correlation between mean weight of females in winter and mean clutch size in the following spring, and Erikstad et al. (1993) found that individual females varied their clutch size from one year to another dependent on their body weight at the onset of egg laying. Similar results have been found for other waterfowl species by e.g. Bengtson (1971), Ankney & MacInnes (1978) and Cooch, Lank, Rockwell & Cooke (1989).

The female eiders from the two Danish colonies are likely to have had access to dif-

Table 2. Mean egg length and width (in mm; $\bar{x}$) and ranges of egg dimensions for the two Danish colonies and one Finnish colony based on published data (N = number of eggs measured).

Trait		Stavns Fjord	Ertholmene[a]	Söderskär[b]
	N	425	408	403
Egg length, mm	$\bar{x}$	78.3	79.8	78.2[c]
	range:	71.5 - 88.4	69.2 - 88.5	
Egg width, mm	$\bar{x}$	51.3	52.2	51.5
	range:	47.1 - 55.0	48.8 - 55.3	

[a] Data from Franzmann 1980.

[b] Data from Laurila & Hario (1988) and Laurila (1988).

[c] Largest mean among the studies by Onno (1968), Haftorn (1971), Dementjev (1972) and Laurila (1988).

ferent amounts and qualities of food. As for female eiders breeding in the Baltics, most females from Ertholmene forage in the Wadden Sea area during winter, and south of the Danish island of Funen during early spring. Contrasting this, most of the eiders that breed in the Stavns Fjord forage in southwestern Kattegat throughout the whole year (Noer 1991). Eiders returning to Ertholmene have access to large stocks of blue mussels *Mytilus edulis* which have remained unexploited during winter, whereas females from the Stavns Fjord colony return to or stay close to the Fjord where the marine epifauna is exploited during most of the year.

The difference in clutch size between the two colonies may be part of a more general difference in egg production between populations from the Baltic Sea area and populations from the Kattegat area. The data available indicate that smaller clutches are laid in colonies along the Kattegat coasts than in colonies on the coasts of the Baltic Sea (Table 3, and for southwestern Kattegat colonies see Fig. 3). This may imply that the choice of wintering and spring staging areas affects the egg production, and/or when arriving to the breeding grounds, Baltic eiders profit from the access to food resources which have remained unexploited during winter.

Long-term changes in clutch size

In many areas common eiders stay close to their breeding colony during the last weeks or days before egg laying. However, it is not clear whether food intake at this time of the year affects the number of eggs laid by female eiders (Milne 1974, Swennen 1983, Hario & Selin 2002). The absence of detectable negative effects of colony size on clutch size in five of the six eider colonies in southwestern Kattegat may suggest that competition for food close to the colonies has been of little importance compared to other factors.

After 1980, the average clutch size changed simultaneously in all colonies (see Fig. 3). This suggests that egg production in the southwestern Kattegat colonies was affected by common factors. The female eiders are most likely to have been affected by regulatory factors in winter and early spring because

Table 3. Mean ($\bar{x}$) and range of clutch size in eiders in two colonies along the Kattegat coasts (Stavns Fjord and West Sweden) and three colonies along the Baltic Sea coasts (Ertholmene, South Sweden and Söderskär).

		Clutch size[a]		Effects of	
Region/Colony	Period	$\bar{x}$	Range	predation	Reference
Kattegat					
Stavns Fjord	1971-1980	4.53		no	this study
	1971-1980	4.43	(4.33 - 4.49)	+	
	1989-1991	4.23	(4.15 - 4.29)	+	
West Sweden	1982-1983	4.3	(4.3 - 4.4)	+	Götmark & Åhlund 1988[b]
Baltic					
Ertholmene	1973-1977	5.03	(4.88 - 5.15)	+	Franzmann 1980
	1992	4.93		+	Lyngs & Abrahamsen (1993)
South Sweden	1972-1974	4.73	(4.61 - 4.85)	+	Gerell 1985
Söderskär, Finland	1971-1985	4.93		no	Hario & Selin 1988
	1971-1985	4.74	(4.5 - 4.9)[c]	+	Hario & Selin 2000
	1986-1991	4.49	(4.3 - 4.7)[c]	+	Hario & Selin 2000

[a] Mean clutch size is the average of the yearly averages, except for Finland. To reduce the effect of differences in choice of method clutch sizes for Stavns Fjord were estimated from nests where the female had been caught and the quantity of down had been high.

[b] Estimated from data in Figure 2.

[c] From data in Figure 1.

at this time of the year, they forage in the same or almost the same areas in southwestern Kattegat. It is less likely, but not impossible that the amount and quality of food near all colonies changed simultaneously and to an extent that caused equal effects in all colonies.

Depletion of food stocks by wintering sea ducks may have affected food intake in winter and early spring (at nine aerial winter surveys in southwestern Kattegat 24,400-89,200 eiders were counted during 1987-1992; S. Pihl, pers. comm.). During 1985 - 1987 wintering sea ducks were excluded from foraging in large parts of southwestern Kattegat due to extensive ice cover, and it was during these years that the average clutch size increased (see Fig. 3). However, information on the impact on food stocks of eiders and the other sea duck species wintering in southwestern Kattegat is lacking. I conclude that the most recent decline in the eider clutch size (see Fig. 3) seems to be a result of macro-environmental changes in the marine ecosystem of southwestern Kattegat.

Acknowledgements - in preparing this paper, I have made use of data collected by many people employed at the Ministry of Environment and Energy. Without their fieldwork, I would not have had access to data on clutch sizes. Studies in Stavns Fjord were initiated by the late Dr. A.H. Joensen and E. Bøgebjerg in 1970 and continued by H. Noer and his co-workers in 1989. Other colonies in the southwestern Kattegat were counted mainly by M. Fog and J. Gregersen whom I would like to thank for kindly providing data. I thank H. Noer, J. Komdeur, S. Toft and two referees for useful help and suggestions on how to improve this manuscript.

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DEVELOPMENT OF COMMON EIDER *SOMATERIA MOLLISSIMA* COLONIES IN THE SOUTHWESTERN KATTEGAT, DENMARK: INFLUENCE OF PREDATORS AND IMMIGRATION

BREGNBALLE, T., GREGERSEN, J. & JEPSEN, P.U.

The development in the number of nesting common eiders *Somateria mollissima* at 13 sites in southwestern Kattegat, Denmark, was analysed using data from the 1950s to 1992. The total breeding population in the area reached 5,800 pairs in 1991-1992. At eight sites the numbers increased after colonisation, whereas at five of the 13 sites the numbers never exceeded 55 breeding females. A comparison of the distribution of successful colonies with the distribution of foxes and human activity suggests that the number of colonies in the southwestern Kattegat is limited by the distribution of 'peaceful' and safe nesting sites. Three of the colonies increased by 25-35% per year over 7-11 years. A simulation model was used to identify whether these high colony growth rates could be due to local reproduction alone, or whether immigration also contributed. The simulations indicated that immigration contributed to recruitment in the three colonies. The number of nests stabilised in five of the eight colonies, and the possible reasons for this stabilisation are discussed.

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The maximum size a regional breeding population of common eiders *Somateria mollissima* can attain will depend not only on the number of colonies that can be established, but also on the size that each colony will reach at saturation. The number of sites successfully colonised is high in some regions, e.g. the Söderskär archipelago in the Gulf of Finland (Hario & Selin 1988), but low in others, e.g. Kongsfjorden, West Spitsbergen (Mehlum 1991). Occurrence of mammalian predators and disturbance caused by human activities may force common eiders to move away from mainland areas and larger islands to isolated islets without mammalian predators and with little or no human disturbance (e.g. Laurila 1989, Swennen 1991). Mammalian predators and human activity may therefore affect the size of the breeding eider population by restricting both the distribution and the number of colonies. Thus, Mehlum (1991) suggests the common eider population in Kongsfjorden, West Spitsbergen, to have reached its maximum size, because all islets unreachable by the Arctic fox *Alopex lagopus* have become saturated with eiders. In our study, we compared data on the distribution of common eider colonies in the southwestern Kattegat, Denmark, with the distribution and occurrence of red fox *Vulpes vulpes* and human activities on islets and mainland coasts. We discuss whether human activities and presence of foxes are likely to have limited the number of colonies in the southwestern Kattegat.

Common eiders show a high degree of site fidelity to their natal colony, and they are especially faithful to the colony in which they breed the first year (Franzmann 1980, Swennen 1990, 1991). Hence, it has been assumed that dispersal of eiders from their natal or first selected breeding colony is unlikely to affect growth rates of other eider colonies (Swennen 1991). This assumption may not hold for the growth of newly established colonies, where even small scale immigration may affect the growth rate. One way to assess whether immigration adds to recruitment is to study the pattern and rate of colony growth. To determine whether observed growth rates are likely to be due, partly, to immigration, the first step is to estimate the highest growth rate attainable with local reproduction as the only source of colony growth. Maximum attainable growth rates can be estimated using deterministic population growth models (Larsson, Forslund, Gustafsson & Ebbinge 1988), so in this paper we compare model predictions with observed growth rates, and discuss the likelihood of immigration as an influencing factor in the development of eider colonies in the southwestern Kattegat. Our hypothesis was that growth rates higher than should be expected from the predictions based on local reproduction would indicate that immigration had actually contributed to the colony growth.

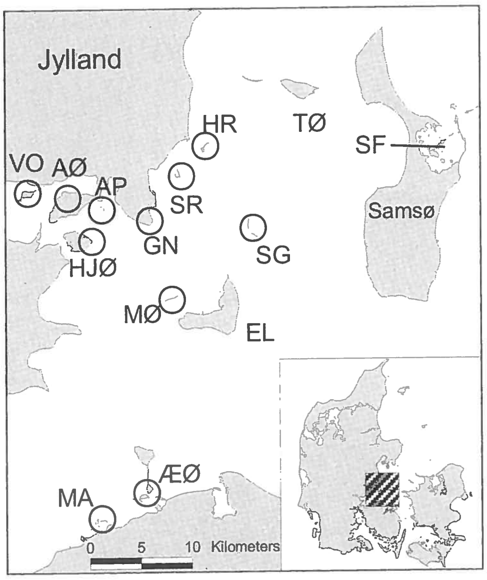

Figure 1. Study area in the southwestern Kattegat with location and names of islands, islets and peninsulas on which nesting eiders were recorded. VO = Vorsø, AØ = Alrø, AP = Alrø Poller, GN = Gylling Næs, SR = Søby Rev, HR = Hov Røn, TØ = Tunø, SF = Stavns Fjord, HJØ = Hjarnø, MØ = Møllegrunden, SG = Svanegrunden, EL = Endelave, MA = Mågeøerne, ÆØ = Æbelø. The sites ÆØ and VO include islets close to a main island.

Material and methods

Our southwestern Kattegat study area consisted of the mainland and island areas (Fig. 1), and the potential breeding sites included: 1) groups of tiny islets (sites SF, AP, MA; see Fig. 1 for abbreviations of site names) some of which were less than 0.02 ha, 2) single islets of 0.5- 57 ha (sites HR, SR, SG, VO, MØ, ÆØ; see Fig. 1) and 3) coast or coastal marsh on large islands and peninsulas on the mainland (sites TØ, AØ, GN, HJØ, EL; see Fig. 1). The geomorphology, flora and fauna on the islands HR, SR and MA are described in Fog (1973, 1982).

Nests of breeding common eiders were counted by a group of people who walked in a line across each islet; most of the people were from the Ministry of Environment and Ener-

Table 1. Input values used in the Leslie matrix to calculate clutch size, nesting success, proportions of females making their first breeding attempts and annual survival rates in eider populations in the southwestern Kattegat (see Fig. 3). Age at first breeding is given as the percentage breeding at each age class.

	Age groups	
Parameters	2 years	> 2 years
Clutch size (eggs/nest)	4.40	4.40
Nesting success	75%	75%
Proportion making first breeding attempts (%)	10%	90%
Annual survival rate	87%	87%

gy, but a few counts were carried out by voluntary ornithologists and hunters. In areas with few or dispersed nests (sites EL, GN and AØ) nest searching was not performed systematically in all years (see Fig. 3), but the coverage was extensive on all islets with increasing numbers of breeding common eiders. For the islet ÆØ, data were only available from 1960-1964, 1967-1969, 1980 and 1990. For the area SF, data for 1950-1965 were partly extrapolated, and nest censuses were carried out during 27 April - 4 May; in all other colonies nests were counted during 4 - 22 May. Due to both the year-to-year variation in dates of nest counting and initiation of egg-laying, a variable proportion of the nesting females may have been counted, and we are unsure whether this affected the estimated growth rates.

Information on red fox occurrence and human activity was extracted from published papers and notes made by observers, and letters and annual reports sent by local wardens to the Ministry of Environment and Energy.

We used a deterministic population model based on Leslie matrices to predict the maximum colony growth rate attained through local reproduction at various rates of duckling and subadult survival. Average input values selected for the deterministic population model are given in Table 1. The clutch-size value used (see Table 1) was chosen among the upper end of the observed values (see Table 3) because data were collected without discriminating between fully laid clutches and incomplete clutches (see Bregnballe 2002). The average nesting success was 63.0% in the HR colony (range: 48.4-76.0% for four years in which 125-416 nests were checked) and 75.3% in the SR colony (range: 63.4-94.9% for four years in which 58-291 nests were checked).

In Europe, up to 10% of common eider females may be breeding in their second year and the remaining 90% in their third year (Baillie & Milne 1983, Swennen 1991, H. Noer; unpubl. data), so we used these proportions in our model. As we had no estimates of female survival rates in the three rapidly growing colonies, we used unpublished data by H. Noer for females nesting in the SF colony.

Maximum survival during the period from hatching to the first year of breeding was set at 55% as this value is the highest recorded duckling survival in European studies (Hario & Selin 1989, 1991, Mendenhall & Milne 1985, Swennen 1991). Baillie & Milne (1983) reported a mean first year survival of 67% for a non-hunted population in Scotland, but supplied no maximum values. As the eiders in southwestern Kattegat are hunted, we expect the maximum first year and probably also the second year survival to have been lower than 75%. For the area SF, H. Noer (unpubl. data) found that 15% of the ducklings fledged during the 1970s were shot in their first year of life. Consequently, with the best possible conditions for ducklings and sub-

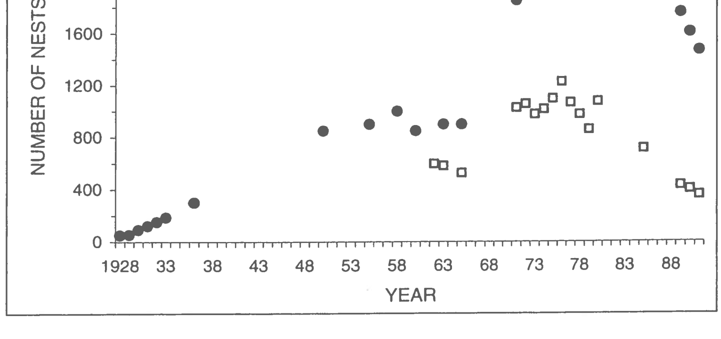

Figure 2. Total number of eider nests in Stavns Fjord (site SF; ●) and number of nests on four of the main breeding islets in Stavns Fjord (□) during 1928-1991. In 1907, 10 nests were found in Stavns Fjord.

adults about 50% might be expected to survive until fledging, and the annual survival for subadults would be 75% until the age of two years (i.e. until the start of breeding). This leads to a hypothetical total survival of 28% (0.50*0.75*0.75*100%) from hatching until the age of two years.

Results

Population development in the southwestern Kattegat

During the 19th century and the early 20th century the SF colony was the only common eider colony existing in the southwestern Kattegat (for references see Joensen 1973). In

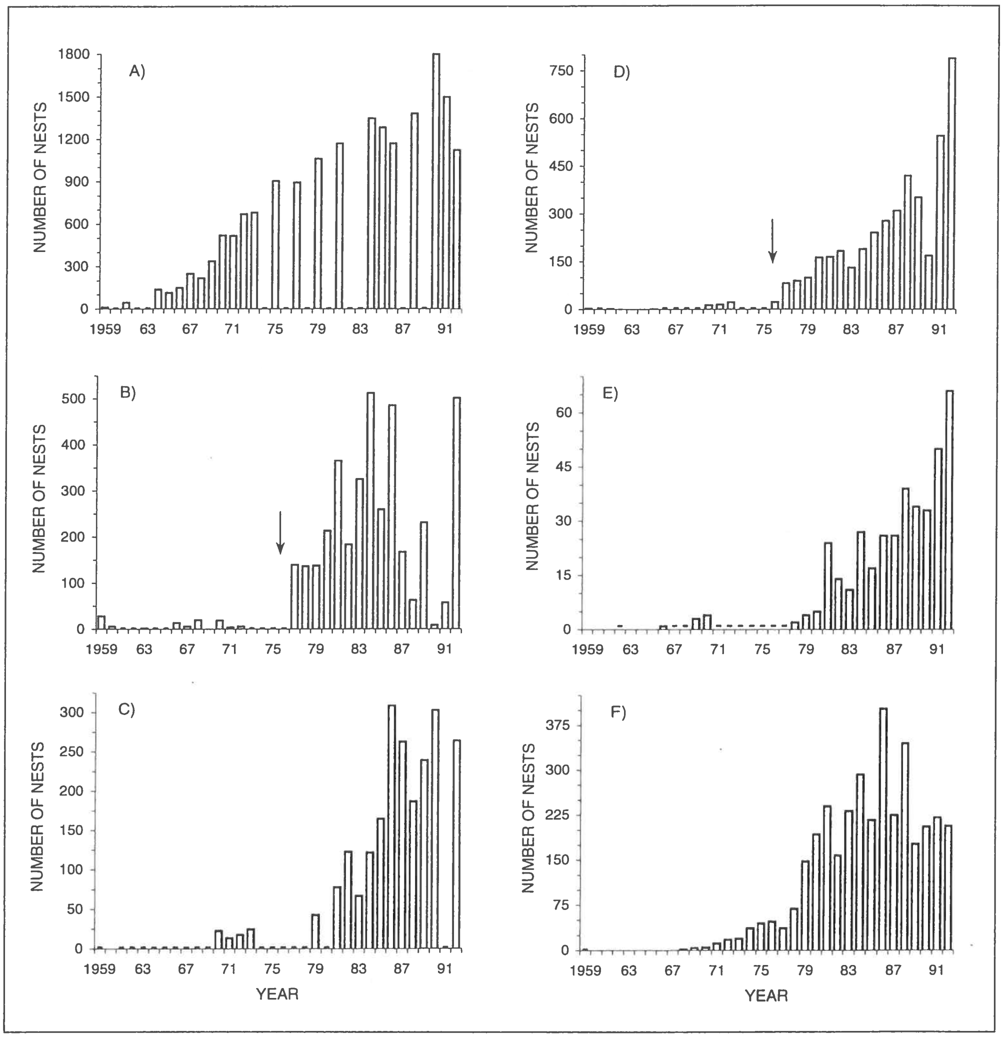

Figure 3. Number of eider nests at: A) Hov Røn (site HR), B) Søby Rev (site SR), C) Svanegrunden (site SG), D) Alrø Poller (site AP), E) Hjarnø (site HJØ), and F) Mågeøerne (site MA) during 1959-1992. Horizontal bars above the x-axis in specific years indicate absence of information on the numbers of nests in the respective years. The arrows in B) and D) indicate that admission to Søby Rev and Alrø Poller was prohibited from 1976 onwards.

Table 2. First years with recorded nesting eiders and more than 30 eider nests in the six successful colonies in southwestern Kattegat, and the number of years from first record of breeding to nesting of more than 30 females in relation to the occurrence of red foxes and the year in which protection against human disturbance was decided. Numbers in parentheses are the numbers of nests found in the first year of recorded nesting.

Colony/ Site	First year with recorded nesting of eiders	(N)	First year with > 30 nests	No. of years from first record to > 30 nests	Occurrence of red foxes	Protection against human disturbance
Hov Røn (HR)	1956[a]	(6)	1961	> 4	Never	1956
Søby Rev (SR)	1955[a]	(16)	1977	> 19	Regular	1976
Svanegrunden (SG)	1970[a]	(23)	1979	>9	Never	
Alrø Poller (AP)	1959	(2)	1977	18	Rare	1976
Hjarnø (HJØ)	1964	(2)	1988	24	Never	
Mågeøerne (MA)	1969	(2)	1974	5	Never	1968

[a] First year of recorded nesting eiders, but they probably started nesting in the site earlier than in the year given.

SF, the breeding number of eiders increased from 50 pairs in 1928 to 850 pairs in 1950 (Fig. 2). During the 1950s and 1960s, eiders settled in at least 13 new areas in southwestern Kattegat. On some of the colonised islands, breeding numbers developed rapidly between the second half of the 1960s and the mid 1980s (Fig. 3). The rate of population increase in southwestern Kattegat slowed down in the second half of the 1980s, but the breeding numbers continued to increase in the two colonies at AP and HJØ (see Fig. 3D, E). The total breeding population reached approximately 5,800 nesting females in 1991-1992.

Number and growth of colonies

On five islands or peninsulas (sites TØ, EL, GN, AØ, VO) on which red foxes or human activities occurred, breeding numbers never exceeded 55 nests, whereas on islands on which foxes occurred rarely (sites SR, AP) or never (sites HR, SG, HJØ, MA) the colonies continued to expand. In colonies where foxes occurred, or where incubating eiders were disturbed by human activity (sites SR, SG, AP, HJØ), many years elapsed between the first breeding record and the year when the breeding population exceeded 30 females (Table2). However, in sites HR and MA, where eiders were protected from human disturbance and foxes, the numbers of eiders increased soon after colonisation (see Table 2 and Table 3). In three colonies (sites SR, AP, SF), the breeding numbers increased dramatically only after the islets were protected from human disturbance (see Fig. 3 B, D for sites SR and AP). In site SF, where locals used to collect eggs (Paludan 1933), the number of eider nests increased rapidly after admittance to the main breeding islets was prohibited in 1928 (from 50 nests in 1928 to 300 nests in 1936).

Table 3. Period, number of years, growth rate (in % per year) and clutch size in five of the six eider colonies in southwestern Kattegat for the periods in which the numbers increased at a relatively constant rate.

		Number	Growth rate	Clutch size		
Colony/Site	Period	of years	% / year	x	N	Range
Hov Røn (HR)	1961-1972	11	27.8	4.1	8	3.7-4.9
	1972-1984	12	6.9	3.4	3	3.2-3.7
Svanegrunden (SG)	1979-1986	7	32.5	3.5	5	3.3-3.9
Alrø Poller (AP)	1977-1992	15	16.8	3.5	11	3.2-4.2
Hjarnø (HJØ)	1981-1992	11	6.6			
Mågeøerne (MA)	1971-1981	10	35.0	4.2	7	4.0-4.5

Table 4. Numeric increase in nest numbers and increase per year for periods in five of the six eider colonies in southwestern Kattegat during which abrupt increases in nest numbers happened.

Colony/ Site	Year/ period	No. of years	Numeric increase in nest numbers	Increase in % per year
Hov Røn (HR)	1959-1961	2	33	93.6
	1961-1964	3	93	45.3
	1966-1967	1	99	66.0
	1968-1969	1	108	46.8
	1969-1970	1	181	53.3
Søby Rev (SR	1972-1977	1	34	203.6
	1980-1981	1	76	71.0
Svanegrunden (SG)	1979-1982	3	80	42.0
	1981-1982	1	45	57.7
	1985-1986	1	144	87.3
Alrø Poller (AP)	1976-1977	1	59	256.5
	1979-1980	1	64	64.0
	1978-1981	3	74	51.5
Mågeøerne (MA)	1978-1979	1	79	114.5
	1978-1981	3	171	52.6

The colonies at HR, SG and MA were the fastest growing colonies in the southwestern Kattegat study area showing growth rates greater than 25% per year over a period of 11, 7 and 10 years, respectively (see Table 3). In these three and some of the other southwestern Kattegat colonies, nest numbers increased suddenly in some years (Table 4), especially before the numbers exceeded 300 pairs. The theoretical simulation of how population growth rates increase with increasing survival during the period from hatching to breeding shows (Fig. 4) that growth rates above 25% per year can be reached if more than 40% of the hatched ducklings survive until the age of two years.

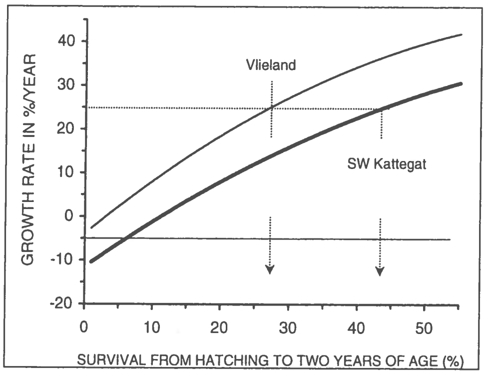

Figure 4. Theoretical simulation of the relationship between colony growth rate (in % / year) and survival (in %) from hatching to the age of two years (i.e. earliest start of breeding) in the southwestern Kattegat (thick line; based on data from Table 3) and in the colony on Vlieland in the Dutch part of the Wadden Sea (thin line). For the colony on Vlieland the following averages were used: 4.74 for clutch size, 80% for nesting success and 95.7% for annual adult survival (Swennen 1991).

Discussion

Number and growth of colonies

Our results suggest that the development of some colonies was affected by the occurrence of foxes and human activity. Disturbance caused by foxes and human activity may have exposed eider eggs to avian predators, and may thereby have affected the nesting success, and foxes may have predated eggs and females, and may thereby have affected both the nesting success and adult survival. It is also likely that females establishing new colonies avoided disturbed areas and preferentially settled where they had experienced no or low frequencies of disturbance and absence of mammalian predators whilst resting on land.

We believe that by the early 1990s, eiders had colonised most of the islands (within the region) on which they could nest with sufficiently high success to ensure a net recruitment. In the future, new colonies may, however, develop on the islets near site VO in the western part of the study area where two colonies (sites AP and HJØ) continue to increase (see Fig. 3D, E). We predict, however, that whether this will happen or not will depend on whether red foxes will occur or not.

In conclusion, it seems likely that the maximum size of the eider population in the southwestern Kattegat will be partly determined by the distribution and occurrence of foxes and human activities on islets and on the mainland coasts.

Did immigration add to recruitment?

The theoretical simulation of the relationship between the colony growth rate and the survival from hatching until two years of age (see Fig. 4) showed that growth rates above 25% per year may be reached if more than 40% of the hatched ducklings survived until the age of two years. A survival rate of 40% from hatching until the age of two years is high compared to the 28% we derived from the published maximum values for duckling survival and subadult survival (see Methods section). Thus, to obtain such a high survival rate ducklings and subadults must have experienced extremely good 'living conditions', and/or immigration may have taken place in the periods during which the colonies increased by more than 25% per year.

It is, however, also possible that adult survival has been underestimated, as our model value refers to a period of slow colony growth during which female survival may have been lower than during the early phases of the colony growth. Among other difficulties in our evaluation are that stochastic events may have stronger effects on small populations than on large populations, and we could not include this effect in our model because year-to-year variation in reproductive success, survival and non-breeding was unknown. Thus, although it seems unlikely, we cannot exclude the possibility that high growth rates were achieved purely by local reproduction.

The common eider colonies in the Dutch Wadden Sea (Swennen 1991) and the Black Sea (Ardamatskaya 1983) have also increased by higher rates than 25% per year over periods of more than five years. Because of high reproductive success and high survival in the Netherlands (Swennen 1991), local reproduction is more likely to have been a sufficient source for the observed 29.8% increase in the Dutch Vlieland colony than in the southern Kattegat colonies (see Fig. 4).

To reach the 29.8% yearly increase on Vlieland with a subadult survival of 75%, 35% of the ducklings must survive from hatching to the age of two years (see Fig. 4). Consequently, more ducklings should have survived from hatching to fledging than the maximum recorded during 27 years of studies on Vlieland (maximum was 36%; Swennen 1991). Therefore, duckling survival and subadult survival must have been extremely high in the period with high colony growth rates on the islands of Vlieland and Rottum. Alternatively immigration enhanced the population increase in the Dutch colonies in their first years of existence. Immigration may also have added to population growth in the common eider colony in the Black Sea, where the increase averaged 35% per year during the early years of expansion (Ardamatskaya 1983).

The sudden increase in some of the southwestern Kattegat colonies (see Table 4) supports our suggestion that immigration took place. However, year specific variation in the extent of non-breeding, in the timing of breeding and in duckling survival (e.g. Coulson 1984, Mendenhall & Milne 1985, Hario & Selin 1989, 1991, Swennen 1991) makes it difficult to use sudden increases in nest numbers as evidence for immigration. For example, large year-to-year variations in nest numbers occurring in some of the colonies after having exceeded 200 nests, indicate that a variable proportion of adults skipped breeding for one or more seasons. Counting errors arising either due to year-to-year variation in the timing of initiation of breeding or due to incomplete coverage may also have added to sudden increases in the nest numbers.

To conclude, we find it plausible that immigration added to the increase in nest numbers in some of the colonies in southwestern Kattegat.

Possible origin of new settlers and immigrants

New colonies may establish in areas in which eiders occur outside the breeding season and subadults spend their first years of life, e.g. the Wadden Sea (Joensen 1973, Swennen 1976, 1991) and the Black Sea (Ardamatskaya 1983). Female eiders from colonies in both eastern Kattegat and the Baltic Sea area occur in the southwestern Kattegat during winter (Noer 1991), where up to 95,000 eiders have been counted in winter (S. Pihl, pers. comm.) and many subadults remain during summer (P. Clausen, pers. comm.). Therefore, eiders that settled on the islands in the southwestern Kattegat during the 1950s and early 1960s may have originated both from neighbouring and more distant colonies.

Eiders hatched in 'saturated' colonies may have contributed to the growth in the neighbouring colonies. The high rates of increase in the colonies at SR, EL, AP and MA occurred when the numbers at SF and HR had levelled off (see Figs. 2 and 3); e.g., at SR the increase occurred when the increase at HR declined from 35.3% per year to 5.1% per year. That eiders from HR recruited or emigrated to SR, may suggest that the attractiveness of HR as a breeding place declined with increased colony size. Thus it is difficult to explain why some eiders settled at SR where foxes occurred in most years.

In the Dutch Wadden Sea fast growth of new colonies also coincided with declines in the growth rates of large neighbouring colonies (see Swennen 1991). The year-to-year changes in nest numbers on two neighbouring islands in the southwestern Kattegat (sites HR and SR) indicate that not all of the females remained site faithful to the colony in which they nested previously. Thus, in years when red foxes visited SR, nest numbers were low at SR but high in site HR, and vice versa in years when red foxes were not observed at SR (Table 5). In some years, sudden movements of female eiders to neighbouring colonies were also observed on the coast of Sjælland in the southeastern Denmark where nest numbers in a neighbouring colony (situated 4 km away) increased from 40 to 344 in one year (Sørensen & Woollhead 1982).

Colony size

Colony size may stabilise when resources like nest sites or food for females or ducklings become negatively affected by breeding numbers (H. Noer, unpubl. data), or when recruitment or survival declines for reasons unrelated to breeding numbers. Data by H. Noer (unpubl. data) on stabilsation of the SF colony in the 1970s suggest that the size of this co-

Table 5. Relationship between average numbers of female eiders nesting on Søby Rev and Hov Røn and whether red foxes were present on or absent from Søby Rev during 1984-1992, a period in which the total number of breeding eiders in the area was stable. Red foxes occurred on Søby Rev in 1987, 1988, 1990 and 1991.

	Average number of nests			
Island/ Site	With red fox on Søby Rev	Without red fox on Søby Rev	t	P
Søby Rev (SR)	75	399	375	< 0.01
Hov Røn (HR)	1560	1232	226	ns

lony is limited by factors associated with the breeding grounds themselves.

The stabilisation of the colonies at HR and SR seems to have occurred partly because more than 317 incubating females died in 1985. The declines in nest numbers at MA and SG are believed to have been partly caused by the disappearance of lyme grass *Elymus arenarius* and other vegetation which happened after cormorants *Phalacrocorax carbo sinensis* began nesting on the grounds of these islets. In site MA, the number of nesting cormorants increased from 120 to 1,982 pairs over a six-year period (1985-1991). In the same period the number of eider nests declined on islets with cormorants, but increased on a small and still vegetated islet. The year-to-year variation in nest numbers at MA indicates that some females either skipped breeding or moved to the nearby situated colony at ÆØ where numbers increased from 88 nests in 1980 to ca 850 nests in 1990.

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VARIATION IN GROWTH RATE AND BODY CONDITION OF COMMON EIDER *SOMATERIA MOLLISSIMA* DUCKLINGS WITHIN AND BETWEEN YEARS

CHRISTENSEN, T.K.

Growth rate and body condition of common eider ducklings were studied during 1990-1992 in the Stavns Fjord colony, Denmark. Correlation between body mass and tarsal length was used as a measure of body condition. There were no major differences in the rate of body mass increase or in mean body condition of ducklings from different rearing areas and between early and late hatched ducklings, but mean duckling condition showed highly significant differences between years. Correlation between estimates of growth rate and condition within and between years in relation to food abundance and availability was not found. There were no obvious relationships between body size and condition and environmental and population characteristics in separate years, which may ultimately determine foraging conditions, suggesting that growth and condition were not simply related to food abundance. Despite the variation in growth and condition between years, fledging success was not affected by mean cohort condition. Although the reasons for these patterns are poorly understood, the present results indicate that growth and condition characteristics of duckling cohorts may influence on future individual and cohort survival.

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Breeding females common eider *Somateria mollissima* are highly philopatric returning to breed in their natal colony throughout their reproductive life (Swennen 1990). As a consequence, the colony size is sensitive to variation in survival of duckling cohorts previously hatched from the colony.

Generally, eider ducklings experience very high mortality (Milne 1974, Swennen 1990), but mortality differs between years (Swennen 1989) with some cohorts surviving better than others. Similar cohort-variation has been found with respect to rate of recruitment (Milne 1974, Coulson 1984; H. Noer, unpubl. data) and body mass of breeding adult females (Hario & Selin 2002).

Variation in body mass of breeding females between specific cohorts (Hario & Selin 2002) suggests that cohorts recruiting to the breeding population may be of different value to the colony as body mass or condition of adult eiders is known to affect clutch size (Bustnes & Erikstad 1991, Hario & Selin 2002), post-breeding behaviour (Bustnes & Erikstad 1991) and possibly the frequency of non-breeding (see Coulson 1984).

During the brood rearing period, foraging conditions are the principal factors determining duckling growth and survival (Swennen 1989), but the correlation between juvenile foraging condition and final adult body size has not been studied in the eider. However, it has been found that differences in food quality during the period of juvenile growth explained about 10% of the observed variation in the size of adult barnacle goose *Branta leucopsis* (Larsson & Forslund 1991), implying that nutrient availability during juvenile growth affects the final adult body size (see James 1983, Boag 1987) which may in turn affect the fecundity and survival of adults. Thus, seasonal or annual environmental variation or differences in food abundance between different habitat types used as brood-rearing areas, may potentially influence on growth rate or body condition, and hence affect the development of the colonies.

In the present study I compared body condition of eider ducklings reared in two types of habitats to which broods show site fidelity, and compared the mean duckling condition in three successive breeding seasons. Comparison of the condition of early and late hatched ducklings was performed in one breeding season. Direct measures of food abundance was not possible due to inadequate sampling procedures.

Study area and material

My study was performed in the western part of Stavns Fjord, Samsø, Denmark (55°E54'N, 11°E39'E), where the breeding colony consisted of 1,400-1,600 pairs of common eider (Bregnballe 1993) which reared most of their ducklings within the Fjord area. Large shallow areas sheltered by many smaller islands and reefs provide good rearing and feeding sites. Algae are found in the deeper parts (1-2 m) of the Fjord (Fig. 1) with the highest densities in the northern archipelago, and consist primarily of the seaweeds *Fucus vesiculosus* and *F. serratus*. The intertidal flats have only a very sparse algal vegetation and consist of either sand/gravel or muddy sediments. As a consequence of the Fjord topography, ducklings tended to be reared in two types of habitats: a seaweed vegetated habitat and a sparsely vegetated intertidal habitat.

Observations were obtained from four more or less homogeneous areas containing the two major types of duckling rearing habitats (see Fig. 1). The areas 'North' and 'East' represented areas with extensive seaweed vegetation covering approximately 50% of total area (as estimated on the basis of transect counts). The areas 'West' and 'South' represented intertidal areas with an algae coverage of 10-20% in the deepest parts. In the areas North and East ducklings primarily foraged on the seaweed vegetation, whereas in the areas West and South foraging mainly occurred on the intertidal flats (Christensen 1992). Major changes in habitat structure did not occur in the four rearing areas during the years of study so changes in the foraging conditions between the study years could be outruled. Winters were very mild and storms or local ice formation only caused minor changes in algae coverage in the lower parts of the Fjord (pers. obs.). Data on spring temperatures (May-June; Table 1) were obtained from the nearest meterological station (Røs-

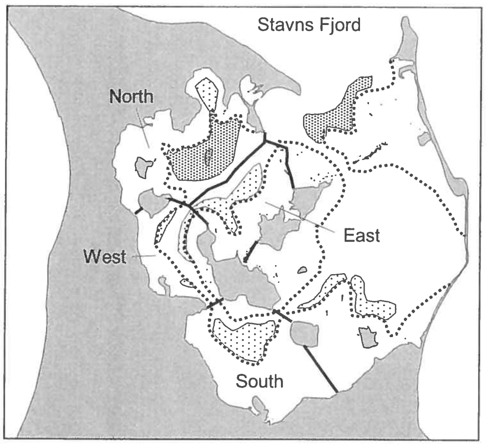

Figure 1. Location of the study area with the four brood-rearing areas North, West, East and South at Stavns Fjord, Denmark. Area East was used only in 1990 whereas the other areas were used during 1990-1992. Density of seaweed vegetation is given as > 0.2 plants/m² (densily hatched) and < 0.2 plants/m². Intertidal flats are located within the 1-metre depth cline (dotted line).

Table 1. Mean temperatures (°C) in May and June 1990-1992 based on data from Røsnæs lighthouse meteorological station.

	Normal	1990	1991	1992
May	10.8	13.0	9.5	12.4
June	14.8	15.3	12.3	17.6

næs lighthouse) located approximately 22 km southeast of the study area.

To allow for comparison of body condition of ducklings reared in the different areas, rearing site fidelity was examined in 1991. In each area ducklings were colour-marked with plastic tape glued to their down (with specific colours relating to rearing area) and ringed with a specially designed steel leg band. Colour marked ducklings were observed in declining numbers until day 15 after the marking, due to either loss of marks or death.

To obtain data on body condition, ducklings were caught in the areas North, West and East on 29-30 May 1990, whereas in the following year ducklings were captured in the areas North, West and South on 28-29 May and on 17-18 June 1991. In 1992 ducklings were captured on 9-12 June. A total of 140 ducklings were caught in 1990, and in 1991 and 1992 464 and 720 ducklings (including recaptures in 1991) were caught. For all ducklings, body mass was recorded to the nearest 5 g and tarsal length was measured to the nearest 1 mm.

I tested for differences in duckling condition for the different areas between May and June and between years using linear regression (Hald 1971) on plots of body mass and tarsal length in the third power and compared slopes and intercepts. The level of significance accepted was 5%, and statistical analyses only included ducklings with tarsal lengths of 38-55 mm. Although this was a conservative and subjective selection, these limits excluded both small ducklings which might still be digesting yolk, and older ducklings which might have ceased growing. In both cases, body mass of the ducklings may diverge from linear measurements. Omission of the largest ducklings from the samples also reduced the effect of increasing variance in the samples, making a better fit to the statistical assumption of equal variance. In analysing the differences between May and June 1991, ducklings captured in May and recaptured in June were omitted from the June sample.

Results

Rearing site fidelity

Brood tending eiders showed a high degree of site fidelity to their rearing areas. Of the 464 ducklings colour marked in 1991, 32 identifiable crêches were observed 77 times within 15 days after marking. Of these 32 crêches, only two were observed on six occasions foraging in an area which differed from the area in which they were marked. Similarly, only four (4.8%) out of 83 ducklings, ringed in May and recaptured in June, were caught in another area. Daily observations of identifiable broods from the areas West and South moving to and from a common night roost in area North, confirmed these results as these broods returned day after day to the same foraging sites in the areas West and South, although they should pass one or two neighbouring areas.

Condition

A comparison of duckling body condition within the months May 1990 and May and June 1991 was made from the regression statistics based on plots of body mass on tarsal length in the third power (Tables 2 and 3, Fig. 2). In 1990, ducklings from area East (with a seaweed coverage of about 50%) showed a higher rate of body mass increase than ducklings from area North, which, however, may have been caused by more large ducklings in this sample (see Fig. 2A). In May and June 1991, ducklings from area South (intertidal) had a consistently higher average body condition than ducklings from both area North (with a seaweed coverage of about 50%) and West (intertidal), although the difference in rate of body mass increase was only significant when compared to ducklings from area West in June (see Table 3, Fig. 2B, C). Thus, as no consistent trend was found data could not be used to elucidate whether ducklings reared in areas with a high degree of seaweed coverage (North and East) gained a better body condition than

Table 2. Sample sizes and regression equations of body mass and tarsus length cubed for ducklings captured in the Stavns Fjord study area during 1990-1992. Only ducklings with tarsal lengths of 38-55 mm are included.

			Equation		
	Area	N	Slope	Intercept	var (b)
1990	North	10	0.00240675	8.2342	0.000000173
	West	25	0.00292920	-16.9587	0.000000100
	East	34	0.00343662	-48.1902	0.000000041
1991 May	North	22	0.00411704	-59.1294	0.000000149
	West	49	0.00413366	-52.44	0.000000028
	South	47	0.00438103	-54.08	0.000000143
Total, May		118	0.00404288	-40.62	0.000000021
1991 June	North	43	0.00405814	-0.09	0.000000047
	West	26	0.00370790	30.90	0.000000086
	South	22	0.00461659	-52.11	0.000000072
Total, June		91	0.00416101	-10.26	0.000000022
Total 1990		69	0.00313447	-42.61	0.000000025
1991		209	0.00445739	-59.47	0.000000009
1992		565	0.00325574	20.80	0.000000003

Table 3. Comparison of linear regressions of duckling condition between the four rearing areas (North, West, South and East), for the different times of hatching and between different breeding seasons. Only ducklings with tarsal lengths of 38-55 mm are included.

		Regression statistics			
		Slopes		Levels	
		t	p	z	p
1990 (May)	N x W	0.99	ns	1.65	ns
	N x E	2.15	p<0.05	-	
	W x E	1.34	ns	1.56	ns
1991 May	N x W	0.04	ns	1.17	ns
	N x S	0.44	ns	3.06	p<0.01
	W x S	0.63	ns	2.53	p<0.05
1991 June	N x W	0.84	ns	0.46	ns
	N x S	1.52	ns	0.74	ns
	W x S	2.26	p<0.05	-	
1991 May x June	N x N	0.08	ns	4.19	p<0.001
	W x W	1.37	ns	5.27	p<0.001
	S x S	0.49	ns	1.68	ns
1991	May x June	0.86	ns	6.58	p<0.001
1990-91-92	1990 x 1991	6.18	p<0.001	-	
	1990 x 1992	0.64	ns	14.98	p<0.001
	1991 x 1992	1.46	p<0.001	-	

ducklings reared in intertidal habitats (West and South), or vice versa.

The comparison of body condition in early versus late hatched ducklings in the three areas in 1991 showed no differences in the rate of body mass increase (see Table 3). However, in the areas North and West the mean condition (slope levels) increased significantly in late hatched ducklings, but not in ducklings from area South (see Table 3, Fig. 2B, C), which indicated that the mean condition of late hatched ducklings in these two areas had increased to the level observed in ducklings in area South in both May and June. As a consequence, a significant increase in mean condition was found when pooled samples from May and June were compared (see Table 3). The fact that the seasonal increase occurred in both a seaweed covered habitat and an intertidal brood rearing habitat supports the suggestion of no specific habitat related relationship with duckling body condition.

Analyses of overall mean cohort condition revealed highly significant differences between years. The rate of body mass increase was significantly higher in 1991 than in 1990 and 1992 (Fig. 3, see Table 3). Consequently, ducklings from the 1991 cohort seemed to increase their body mass relatively faster than ducklings in the 1990 and 1992 cohorts and had a condition superior to ducklings from 1990 and 1992, even though the mean duckling body condition in 1992 was significantly higher than in 1990 (see Table 3).

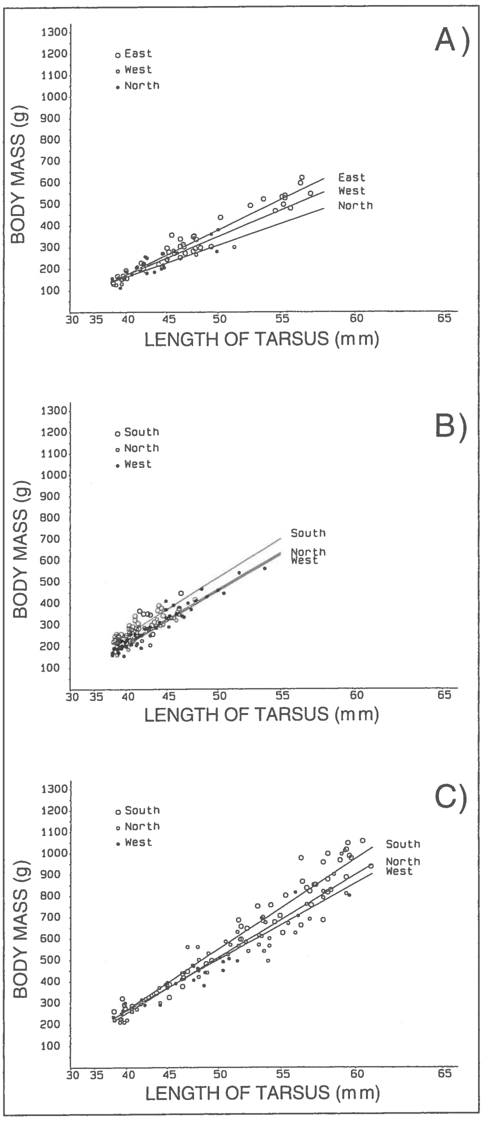

Figure 2. Duckling condition expressed as the relation between body weight (in g) and length of tarsus (in mm) for areas East, West and North in May 1990 (A) , for areas South, North and West in May 1991 (B) and for areas South, North and West in June 1991 (C).

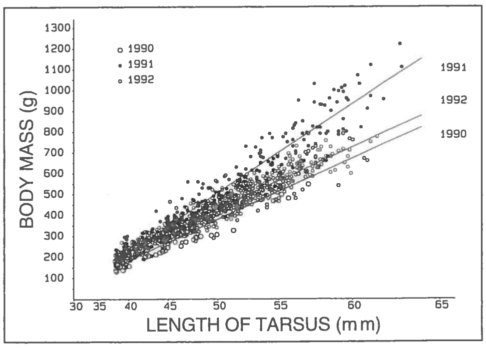

Figure 3. Duckling condition expressed as the relation between body weight (in g) and length of tarsus (in mm) of the total samples in Stavns Fjord for the years 1990-1992.

Discussion

The present study showed that common eiders were site faithful to specific areas within the colony nursery grounds during their brood rearing period. Due to topographical differences, ducklings were reared in two major types of habitats: one dominated by seaweed and one dominated by intertidal flats with very sparse algae vegetation. Despite the habitat difference and the associated potentially different foraging conditions, the observed variability in duckling body mass and condition between habitats and between early and late hatched ducklings were not found to be related to habitat differences. Within years, the variation in duckling condition was much smaller than between year cohorts, which suggests that environmental conditions between years were more important determinants of duckling growth than habitat or seasonal differences occurring within years.

Within-year variation in growth rate, body mass and condition of juvenile waterfowl have been related to spatial and temporal environmental variation (Larsson & Forslund 1991, Rhymer 1992). Even though growth rate is also related to maternal factors (Ricklefs & Peters 1981, Gustafsson 1986), differences in growth related to time of hatching, brood size or rearing area in geese, have not been affected by phenotypic components of female parents (Cooch, Lank, Rockwell & Cooke 1991a, Cooch, Jefferies, Rockwell & Cooke 1993). In the common eider, foraging condition has been found to be the principal factor determining duckling growth (Swennen 1989), and availability of food suitable to eider ducklings may vary with both season and habitat. Cantin, Bédard & Milne (1974) reported eider duckling food density to be highest in seaweed-dominated habitats. Although food densities were not examined in my study, duckling diet has been shown to differ between the two habitats, as it consists of mainly crustaceans and bivalves in the seaweed-dominated habitats and of polychaetes in intertidal habitats (Christensen 1992). Consequently, no indication was found that differences in prey had a significant effect on duckling growth and condition. It should, however, be noted that whereas foraging of eider ducklings in seaweed-dominated habitats was a solitary activity, ducklings in intertidal areas gathered around the brood-tending females who frequently trampled the substrate to free prey which might otherwise have remained unavailable to ducklings (Christensen 1992). This behaviour was observed much more frequently in the areas West and South than in areas East and North (Christensen 1992), and may have compensated for the low prey availability, i.e. the buried way of living of polychaetes.

Different cohorts

A positive correlation between temperatures in late May and early June and the fledging success of eiders has been shown by Swennen (1991a), and in the lesser snow goose *Anser c. caerulescens* reduced gosling growth occurred in years with cold, wet weather (Cooch, Lank, Rockwell & Cooke 1991b). In my study, the observed variation in condition between years was not positively correlated with spring temperatures, as the rates of body-mass increase was lower in the warm springs of 1990 and 1992 than in the cold spring of 1991. Although significant differences in mean duckling condition existed between 1990 and 1992, both of these cohorts must be classified as poor when compared to the condition of the 1991 cohort. Even with a positive correlation between ambient temperature and prey abundance, high temperatures might also have increased the risks of parasite infestation, which could have resulted in the slower duckling growth and poorer condition in 1990 and 1992 than in 1991. Simple calculations on data presented by Hario & Selin (1992) reveal that the level of parasite infection in ducklings varied between years in Finland, though a correlation with spring temperature did not exist. However, I did not investigate the parasite infection in ducklings in my study.

As my study did not focus on prey abundance, it is unknown whether differences in duckling growth and condition were related to changes in prey quantity or quality between years. A decline in food abundance leading to reduced growth in young waterfowl has been shown in years of high reproductive output and in periods of population increases (Pehrsson & Nyström 1988, Cooch et al. 1991b). In my study, exceptionally high reproductive outputs were recorded in 1992 (pers. obs.) which may have led to increased competition for resources that year, and may have resulted in a reduced growth rate and condition. However, as the number of ducklings recorded in 1990 was not high, increased competition due to a high reproductive output could not explain the poor growth rate and condition observed in the 1990 cohort. In contrast to the snow goose, for which a long-term decline in the body size of goslings possibly has occurred due to an over-exploitation of traditional feeding grounds during a period of population increase (Cooch et al. 1991b), cohort differences in growth rate and condition of eider ducklings is obviously not simply related to environmental conditions affecting the availability of food, or to short-term variation in population characteristics such as reproductive output and time of hatching. Whether this is a result of a more environmentally stable marine rearing habitat of eider ducklings providing plenty of food, compared to terrestrial foraging habitats of geese and freshwater ponds of dabbling ducks is, however, unknown.

The observed variation in mean cohort condition did not affect duckling survival to fledging. The prefledging mortality was estimated in 1990 and 1991, and was approximately 80% in both years (Bregnballe 1993). This implies: 1) that fledging success was not affected by duckling condition, and 2) that ducklings were able to survive in equal proportions despite differences in body condition. Compared to other studies, the duckling mortality was low in the Stavns Fjord colony (*cf.* 90-99%; Milne 1974, Mendenhall & Milne 1985, Swennen 1989), and may have been caused partly by insignificant gull predation in the study area throughout the prefledging period (Bregnballe 1993, pers. obs.), partly by the fact that any potential effect of parasites should be expected to be manifested in older ducklings (Mendenhall 1975) or in subadult birds (Swennen 1991b).

In conclusion it must be established that the observed variation in common eider duckling condition within and between years is environmentally induced. Genetic drift and natural selection cannot explain variation occurring in such a short time period. Although many aspects of causes to and effects of individual condition are poorly understood, e.g. condition of mother bird, egg size, duckling nutrient absorption, allometric growth and effects of parasites and sickness, the present cohort variation in growth rate and body condition suggests that the female part of common eider duckling cohorts may be of different value to their natal colony with respect to recruitment and lifetime breeding performance.

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COHORT-SPECIFIC DIFFERENCES IN REPRODUCTIVE OUTPUT IN A DECLINING COMMON EIDER *SOMATERIA MOLLISSIMA* POPULATION

HARIO, M. & SELIN, K.

After a steep increase lasting 15 years, the common eider *Somateria mollissima* population at the Söderskär bird sanctuary in the Gulf of Finland is currently declining at a rate of 6% per year. Concurrently with the decline, the annual mean clutch size has become smaller and more unstable over the years. This decline has been caused by less productive year classes entering the population; females recruited during the decline had significantly smaller clutches than females recruited during the population increase. They also weighed less at the start of the incubation period; yet, their egg size was similar to that of the older cohorts. These cohort-specific differences in clutch size and body weight applied only to birds laying in the peak laying period of the population (60% of the stock); the rest of the breeding stock had no influence on the variations in these parameters. Adult mortality has not changed over the two time periods (15% per year), whereas the recruitment rate is currently lower than in the period of increase, probably as a result of heavy duckling mortality. Intestine parasites do not seem to have caused the lowered fecundity; however, their role in duckling mortality remains a possibility.

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The underlying environmental factors influencing seabird population regulation are often hard to determine, and even when detected they have already been operating for many years. The common eider *Somateria mollissima* populations in the Baltic are known to have been increasing for decades; the only environmental factor known to be linked with this increase is eutrophication, leading to increased primary production in Baltic coastal waters and, in consequence, improved feeding conditions for the birds (Hario & Selin 1988).

At present, the common eider populations are declining in the central Gulf of Finland. The 40-year study at Söderskär reveals some marked changes in certain breeding parameters which call for other explanations in addition to changes in the feeding conditions.

Study area and material

The Söderskär bird sanctuary lies in the outer archipelago of the Gulf of Finland, about 25 km southeast of Helsinki. It consists of about 25 small islets and rocks. The total land area amounts to about 0.5 km^2 of which 'open skerries' (with patchy grassy vegetation but no uniform juniper *Juniperus communis* cover) account for 20 ha and 'wooded islets' (with large dense juniper cover and stands of aspen *Populus tremula* and Norway spruce *Picea abies*) for 30 ha. The area has been protected by law since 1930 and during the birds' breeding season it is only visited by researchers.

Each year all islets are searched thoroughly once or twice to locate all eider nests and to catch the females for ringing. Females have been captured in the study area every year since the 1950s. We have no possibilities of recognising the uncatchable portion of the population. For convenience, we consider it to be stable and score the 'new' unringed birds in our annual catch as 'first-breeders'. The clutch size and egg size of 'first-breeders' have proven to be smaller than those of the 'old' breeders (Hario & Selin 1987). Therefore, we have excluded this cohort (= previously unringed females) from the following analysis as its composition varies widely (from 10 to 34% of the breeding stock during 1971-1991) and introduces additional variance in the parameters we measured.

The analysis of clutch size, egg size and female weight is based on a subsample of 1,530 breedings of individually known 'experienced' females which had bred at least three times during the study period, i.e. during 1982-1991 (1982 was the first year when the timing of breeding was recorded for individually known females). This enables us to omit the 'maturation effect' found in young birds from the data (growing clutch size with growing number of breeding performances during the first 2-4 years, see Hario & Selin 1987).

The mean weight loss of females during incubation (g/day) was known from 175 breeding incidents. The duration of incubation was known from direct observation at 280 nests. For further information on field methods and delineation of study plots, see Hario & Selin (1988) and Laurila & Hario (1988).

Results

Population trends

The eider population of Söderskär increased ten-fold during 1949-1985 (Fig. 1). During 1949-1974 the population growth averaged 7% per annum and during 1975-1985 the population increased by 10% per annum. After 1985, the population has decreased by 34% over six years, i.e. nearly 6% per year. After a peak of 2,365 nests in 1985, we found only 1,555 nests in 1991.

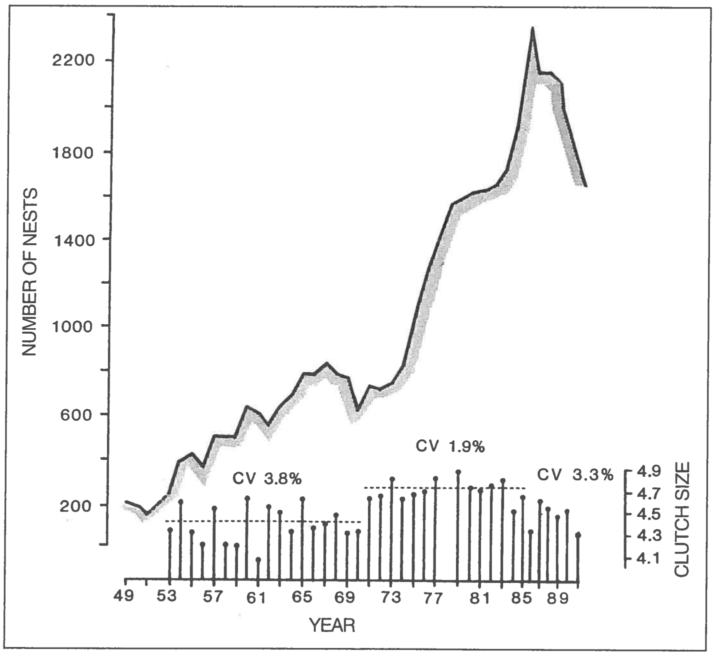

Figure 1. Population trend of eiders at Söderskär during 1949-1991 (continuous line) and yearly mean clutch size during 1953-1991 (bars) with average clutch size and coefficient of variation figures for different population trend phases (dashed horizontal lines).

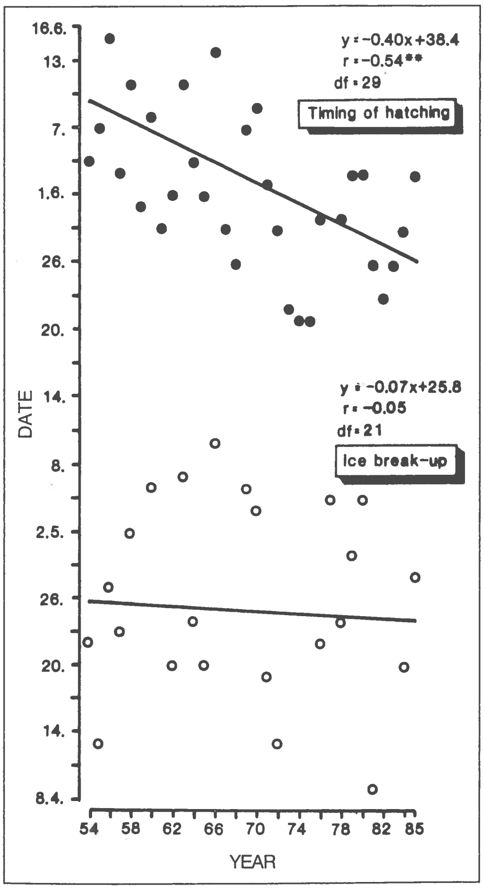

Figure 2. Regression lines of the yearly median hatching dates (●) and ice break-up dates (○) at Söderskär during 1954-1985 (data from Hario & Selin 1988).

Clutch size

Concurrently with the population growth, the clutch size increased markedly. During the steep increase in 1971-1985, the mean annual clutch size was 4.74 and before that, during 1953-1970, it was 4.44 (see Fig. 1). The mean clutch size also became more stable during 1971-1985, showing significantly less year-to-year variation than during 1953-1970 ($F = 4.01$, $df_1 = 17$, $df_2 = 14$, $P < 0.01$).

During the 1986-1991 population decline, the mean clutch size was 4.49 or 5%, i.e. 0.25 of an egg, below what it was during 1971-1985, and it became more unstable again, although due to the few years available (1986-1991) the variation did not differ significantly from that of the 1971-1985 period ($F = 3.025$, $df_1 = 5$, $df_2 = 14$; NS).

Timing of breeding and clutch size

During the long period of population growth in 1953-1985, the timing of breeding of the Söderskär eiders has changed progressively and significantly, and breeding now starts two weeks earlier than it did 30 years ago (Fig. 2). However, the timing of the break-up of the ice has not changed in the same period. Ice break-up is the most important abiotic factor affecting the laying date of eiders in the Gulf of Finland (Laurila & Hario 1988). Even though there is a strong correlation ($r = 0.77$, $df = 20$, $R = 59$) between the yearly median dates of hatching and the ice break-up, the long-term trends of these traits are not parallel.

Within-year, there is a marked seasonal decline in the clutch size of the Söderskär eiders which is attributable to the differences in relative timing of breeding between individual females. Early laying females lay larger clutches than late laying females (Fig. 3). The year effect on the timing of breeding has been smoothened by expressing the laying date as a deviation in days from the median date of laying (6 May) during 1982-1987.

The earlier the breeding occurs in relation to the population median the larger the clutch (see Fig. 3). The only exception is the extralimitally late females (laying 1-2 weeks later than the main breeding stock) which have larger clutch sizes than the other 'late' females. They seem to improve their production by taking longer to produce it. The 'late' females, arbitrarily the last third of the study cohort (Table 1), did not improve their egg production in contrast to the 'early' and 'median' females, which in their earliest breeding produced an average of 7 and 17% larger clutches than in their latest breeding (see Table 1). Hence, the clutch size variation of the population is modified by the 'early' and 'median' birds only, whereas the 'late' fe-

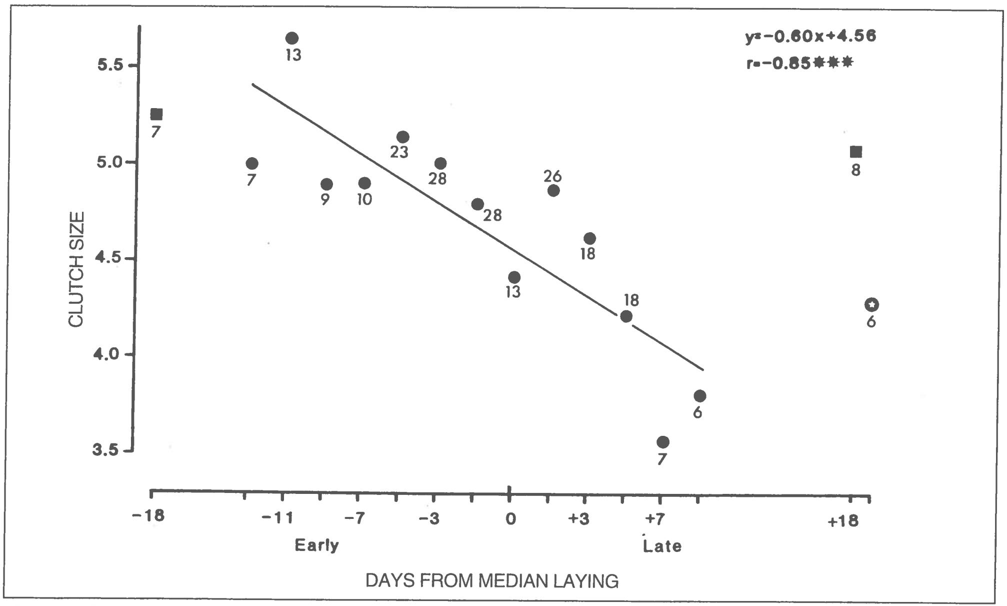

Figure 3. Relationship between clutch size of individual females and the timing of their laying according to the population median during 1982-1987 (6 May). In total, 220 breedings by 56 females, each breeding 3-6 times, were recorded. The figures denote sample sizes. Replacement clutches are marked with an asterisk in the symbol and extralimital clutches are marked with a square.

males seem to be insensitive to the timing of breeding.

We know from direct field observations that none of the extralimitally late breedings were replacements (see Fig. 3). There were six genuine replacement breedings in 1982-1983 (marked with an asterisk in Figure 3), all of which were the result of heavy disturbance (egg manipulation). The time interval between desertion of the initial clutch and laying of the replacement clutch ranged from 10 to 24 days (median 18 days). The timing according to the population median was about the same as in extralimitally late breedings

*Table 1. Comparison of clutch size, female weight and mean egg weight (mean ± SD) between the earliest and the latest breedings of individual eider females ranked according to relative timing, based on two-tailed t-test for matched pairs. The sample size of late laying females is smaller than those of early and median laying females. due to the low re-encountering rate in the field which may indicate non-breeding. *: P < 0.05 , **: P < 0.01 , ***: P< 0.001.*

		Calendar timing		
Relative timing of laying		Earliest	Latest	T-test
Early (N = 49)	Clutch size	5.1 ± 1.1	4.5 ± 0.9	t = 3.36**
	Female weight	2062 ± 129	2029 ± 157	t = 1.89 NS
	Mean egg weight	113.2 ± 5.9	112.0 ± 7.3	t = 1.28 NS
Median (N = 44)	Clutch size	5.0 ± 1.0	4.3 ± 1.0	t = 3.47***
	Female weight	1987 ± 123	1946 ± 167	t = 2.26*
	Mean egg weight	114.6 ± 5.8	112.3 ± 6.9	t = 2.50*
Late (N = 21)	Clutch size	4.6 ± 0.9	4.4 ± 1.0	t = 0.85 NS
	Female weight	1971 ± 166	1908 ± 174	t = 2.34*
	Mean egg weight	110.3 ± 4.5	108.4 ± 7.4	t = 1.26 NS

(median 19 days, range: 12-25 days), but the clutch size was suggestively smaller (4.3 ± 1.0 vs 5.0 ± 0.8, $t = 1.41$, $P < 0.1$) and the female weight was significantly lower (M. Hario & K. Selin, unpubl. data). This implies that replacement clutches are more labourious to produce, as the female has already lost some of her energy resources. Half the replacement clutches failed to hatch due to addled eggs and/or females giving up incubating. All the clutches in extralimitally late breedings hatched successfully.

Clutch size difference between population increase and decrease

Calendar timing has no effect on the mean clutch size of the whole population. The mean clutch size shows no apparent response to the annual median laying dates neither during the population increase in 1973-1985 ($r_s = 0.023$, $P = 0.924$) nor during the decrease in 1986-1991 ($r_s = 0.00$; Fig. 4). The long-term changes in clutch size occur parallel to the changes in population trends (see Fig. 1), and not to the trend in laying dates which progressively became earlier during the 30 years.

During the 1986-1991 population decline, about 60% of the clutches in our subsample were significantly smaller than the clutches laid during the period of population growth (Fig. 5). Their laying dates (21 April-5 May) make the peak laying period of this sample population (birds from the 'Project study area', Hario & Selin 1988). Of these 60%, about one fourth (150 clutches out of 700) was produced by the same females (N = 54) that were also active during the corresponding laying peak in 1982-1985. Their clutch size remained virtually constant (4.90 ± 1.13 (SD) vs 4.85 ± 0.91, Table 2). The average decrease in their clutch size, 0.05 of an egg or 1%, constitutes only 13% of the total decline in clutch size of this particular sample (0.364 of an egg). This reveals that the diminishing clutch size during the population decrease is caused mainly by less-productive year classes entering the population.

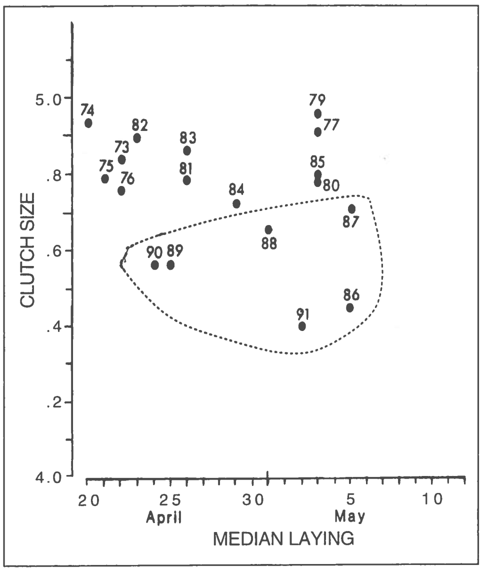

Figure 4. Mean clutch size of the Söderskär eider population in relation to the median laying date during the population increase in 1973-1985 (no data from 1978 were available) and during the population decrease in 1986-1991 (encircled).

Differences in female weight and egg size

A similar trend is found in female body weight at the start of the incubation period (see Fig. 5). During the population's laying peak, females weighed more in 1982-1985 than in 1986-1991. Again, the difference was a result of younger cohorts (recruited in the post-1985 era) having significantly lower body weight than the older cohorts, which, in turn, had kept their body weight constant (see Table 2). However, no similar cohort-specific difference existed in egg size (see Fig. 5).

The mean weight loss during incubation did not differ between the two population phases, albeit that only a minor part of the cohort could be measured in this respect (Fig. 6). Neither was there any difference in the duration of the incubation.

Why do early laying females with larger clutches and body weights lose more weight during incubation than late laying females (see Fig. 6)? This may simply stem from the

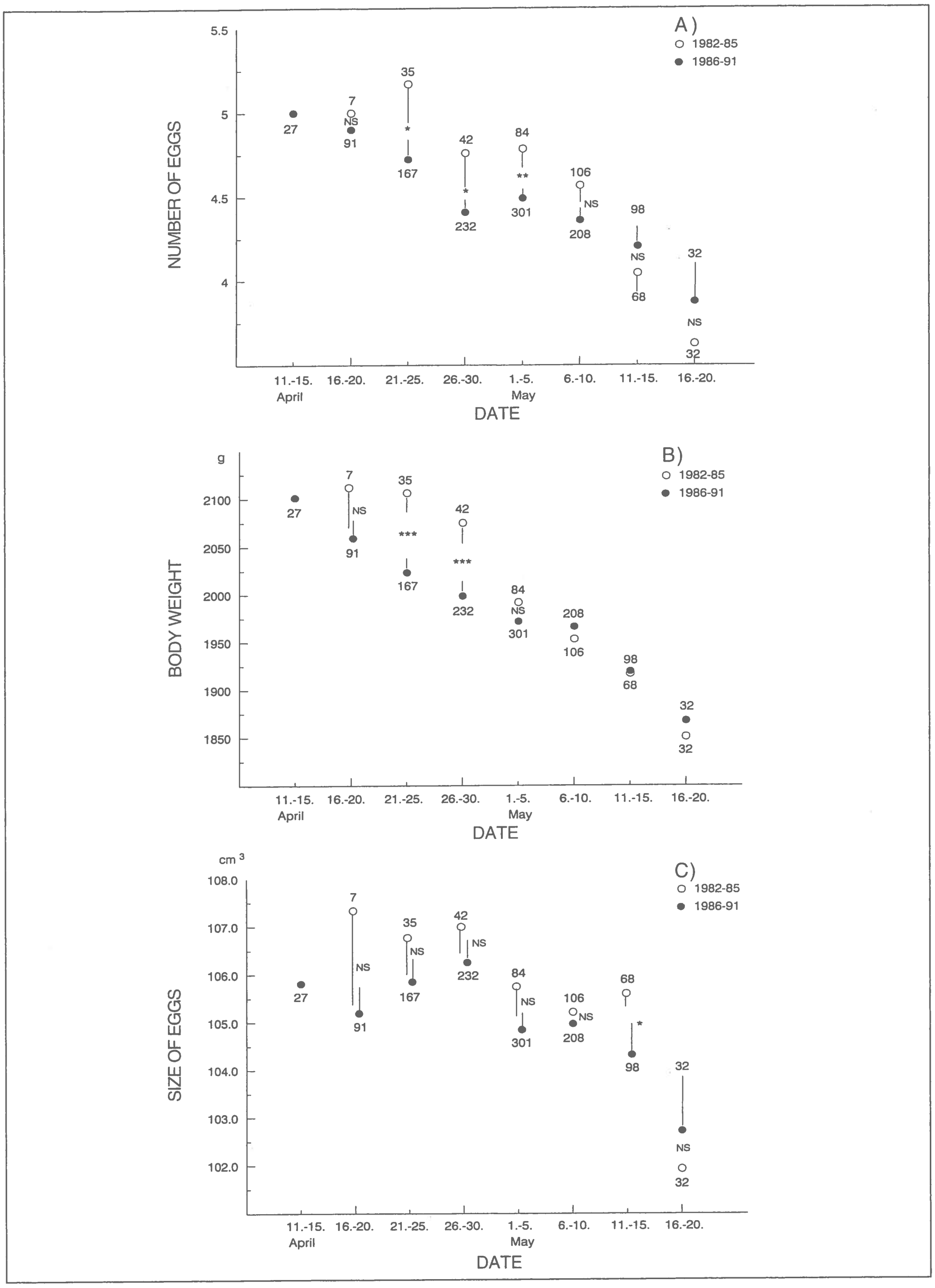

Figure 5. Differences in clutch size (A), in female body weight at the start of incubation (B), and in mean egg size/clutch (C) ($\bar{x}$ ± SE) between the population increase in 1982-1985 (○) and the population decrease in 1986-1991 (●). Figures denote the number of breedings which are ranked according to the timing of breeding. For further details, see text.

*Table 2. Differences (mean ± SD) in clutch size, female body weight (g) and mean egg size/clutch (cm^3) between females recruited during the population increase in 1982-1985 and females recruited during the population decrease in 1986-1991. First-time breeders have been excluded. Two-tailed t-test was used to give the difference. **: P < 0.01*

	Clutch size	Body weight	Egg size
Females recruited in 1982-1985 (N = 54)			
1982-1985	4.90 ± 1.13	2063 ± 130	105.7 ± 5.1
1986-1991	4.85 ± 0.91 NS	2050 ± 130 NS	104.6 ± 5.7 NS
Females recruited in 1986-1991 (N = 47)			
1986-1991	4.43 ± 1.09	1977 ± 127	105.8 ± 6.2 NS
Difference between cohorts	t = 2.779**	t = 2.588**	t = 1.275 NS

fact that they have larger bodies; thus, the heavy loss measured in crude weight makes an artefact.

Rate of recruitment

During 1986-1991, the rate of recruitment (% first-breeders of the breeding stock) fell below what is was when the population growth was steep (15% vs 23%; Mann-Whitney: U = -1.680, P = 0.093; Fig. 7). There is an apparent response by the population to the changes in recruitment. The five years of very high recruitment (30-34%, see Fig. 7) all occurred during the steep population increase (in the years 1976-1978, 1982 and 1985), whereas the lowest rates (11-18%) all were scored during the present decline (1987-1991). The annual survival of adult females has not changed over the two time periods; based on the capture-recaptures calculated using the programme RELEASE (Burnham, Anderson, White, Brownie & Pollock 1987)

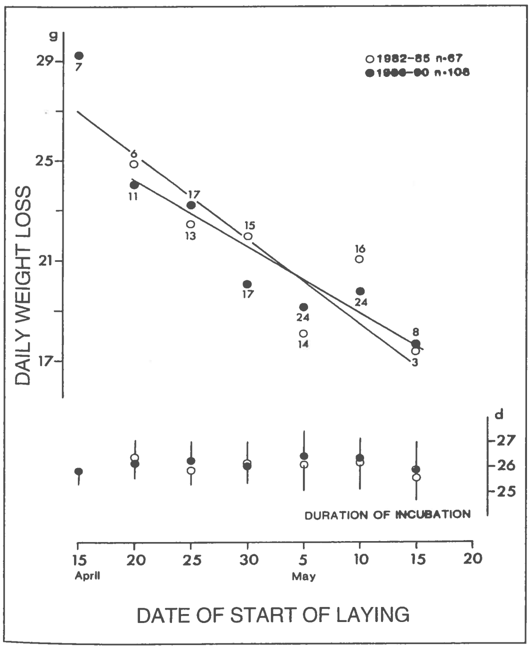

Figure 6. Mean daily weight loss of incubating eider females in the year of population increase (1982-1985; ○) and decrease (1986-1990; ●), and mean duration of incubation (days ± SD). Figures denote number of breedings which are ranked according to the timing of breeding.

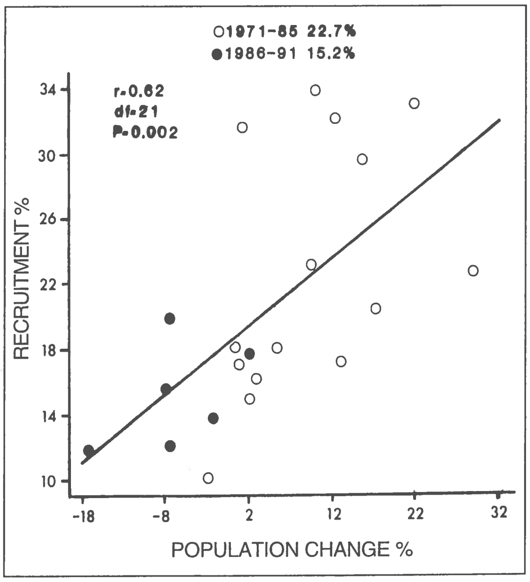

Figure 7. Mean annual rate of recruitment (% first-breeders) in relation to population change (% from the previous year) at Söderskär during the population increase (1971-1985) and decrease (1986-1991).

the mean annual survival was 0.8518 during 1982-1985 and 0.8762 during 1986-1990. There is no statistical difference between the years (Mann-Whitney: U = 5.00, P = 0.384). Hence, the mortality of ca 15% should be compensated for by a recruitment of similar size in a stable population. Because the present recruitment, indeed, equals the required 15% (see Fig. 7) and the population, nevertheless, declines, it seems possible that we overestimate the recruitment. This might be an outcome of the rather robust way of scoring the 'new' unringed birds as 'first-breeders' without being able to recognise the uncatchable portion of the population in any year. However, this error should remain about the same from year to year, not affecting the temporal changes in the recruitment rate or the survival rates in the model used (Cormarck-Jolly-Seber).

Duckling mortality

The low recruitment rate is partly an outcome of the very low fledging survival. During the 1986-1991 population decline, only 1-3% of hatchlings survived to fledging (Hario & Selin 1991). The mortality rate in the period of decrease was similar to that of the poor reproduction years in the late 1960s. In the 1970s, i.e. the period of population growth, the survival appeared far better, in some years reaching 25%. Typically, the survival rate is low in most of the years; there are only occasional peaks, but no such peak occurred during the 1986-1991 population decline (Hario & Selin 1991).

Discussion

The diminishing clutch size *per se* cannot explain the steep turn in our curve of colony size, since the Söderskär common eiders do not breed until they are 2-4 years old (Hario & Selin 1987), meaning that most of the decline would have been detectable only after 1988. Also, the timing of breeding was not involved in the clutch size variation, since calendar dates did not parallel with the mean clutch size (see Fig. 4), only the relative timing of 'early' and 'median' females (see Table 1). We can offer no explanation why the late laying females show no response to the timing of breeding nor to the population trends.

The eider population has decreased also in several other monitoring areas on the Finnish side of the Gulf of Finland; in some of these the decline is even more severe than that at Söderskär. The population trends bear close resemblance to that of the Kandalaksha reserve at the White Sea (e.g. Bianki & Koryakin 1990) (Fig. 8). In this area, the increase and subsequent decrease began about five years earlier than in the Gulf of Finland. According to Aleksej Koriakin (pers. comm. in 1991) the population is now fluctuating with no signs of a rapid increase.

We are not aware of the relevant population parameters of the Kandalaksha population except that the duckling mortality due to acanthocephalan parasites was exceedingly

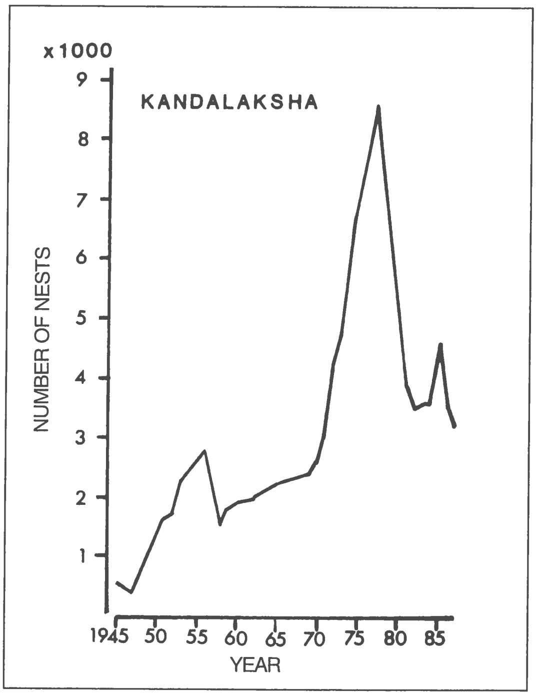

Figure 8. Population trends expressed as the number of eider nests at Kandalaksha at the White Sea during 1945-1985 (redrawn from Karpovic 1987).

high during the maximum growth of the population in 1976-1977: up to 83-87% of the small ducklings died then (Karpovic 1987). Of the several possible explanations for the fecundity decline at Söderskär we will shortly discuss the role of parasites.

Parasite burdens in dead eider females

During the 1987-1991 breeding seasons, all the eider females found dead in the Söderskär study area were collected, and those fit for examination were dissected and examined for intestine parasites.

All the females examined (46% of those found dead, N = 68) carried parasites (Table 3). A total of 75% scored the highest intensity rate of *Polymorphus minutus* (category 3 in Table 3, corresponding to over 100 worms per bird). About 16% scored category 2 (21-100 worms per bird), and 9% scored category 1 (1-20 worms). In addition, about 10% of the females also had large worm burdens of *Schistocephalus solidus* and/or *Lateriporus* sp. All the birds infected were severely emaciated and were apparently 'sick', but they still tried to feed in shallow waters by up-ending until the day they died.

Table 3. Number of adult female eiders and ducklings collected dead at Söderskär during 1987-1991, ranked in categories of infection (0-3) according to the abundance of acanthocephalan parasites found in intestines. For definition of the categories, see the text.

	Infection category				
Year	0	1	2	3	Total
Adults					
1987	0	0	0	0	0
1988	0	0	2	4	6
1989	0	2	0	4	6
1990	0	0	3	3	6
1991	0	1	0	13	14
Total	0	3	5	24	32
Ducklings					
1987	2	7	7	8	24
1988	0	1	2	11	14
1989	0	5	2	3	10
1990	0	1	1	4	6
1991	0	4	1	0	5
Total	2	18	13	26	59

Since parasite burdens cannot increase within the host, infection is possible only by ingestion of the infective larvae (cystacanth) with the food. The *Polymorphus minutus* cystacanth is transmitted to eiders by amphipods of the genus *Gammarus*, abundant crustaceans in the Baltic Sea (Segerstråle 1947, Kolding 1981, Kolding & Fenchel 1981). Natural worm loss from female eiders occurs during incubation (Thompson 1985a). Most of the dying females had heavy burdens of worms even though they had been in good condition only 5-10 days earlier at the completion of incubation. Their body weight at death was 20% lower than at the end of incubation (1,149 vs 1,441 g, N = 26), and their clutch size did not differ significantly from their individual clutch sizes in previous years (N = 82, z = 0.15, P = 0.88; z-test for matched pairs). The parasite infection of individual female eiders could not be predicted from reproduction parameters, and seemed to be accidental. Females do not normally jeopardise their breeding, and unfit females are more likely to skip breeding than to reduce clutch size or desert the clutch (see also Coulson 1984). The cohesive weight loss of incubating females during the two time periods and the similar duration of incubation in our material (see Fig. 6) indicate that female eiders can adjust the use of endogenous nutrient reserves to correspond to the clutch size without jeopardising the fate of the clutch e.g. through prolonged absence from the nest (no extra need for food intake). Their intensive incubation combined with heavy reliance on nutrient reserves seems to be a more optimal strategy than e.g. the ability to renest (Hario 1983). It is also noteworthy that the less-productive cohorts did not reduce the egg size during the present population decrease, but only the clutch size and body weight. Egg size can be considered a quality trait with a high proportion of genetic variation, and environmental factors have less influence on egg size than on clutch size (Laurila 1988).

To what extent parasites really were a cause of death is questionable. However, the low fecundity of the younger year classes compared with the older ones did not seem to be parasite-induced. Of the 37 known-aged eider females found dead and infected with acanthocephalan intestine parasites, 30 had entered the population during the population-growth period (before 1986) and seven had recruited during the population decline in 1986-1991. This corresponds to the present age distribution of the sample population in Figure 5 (G = 0.153; NS). Hence, transmission of the parasites was not biased towards the younger year classes. The average 'age' of the dead birds (= the number of years since they were first breeding) was 8.8 ± 4.1 years (range: 2-19 years, N = 37).

Moreover, as a further indication that the less-productive year classes were not more heavily committed by parasites than the productive ones, there was no significant difference between year classes in parasite load (number of worms/bird; ANOVA: F = 0.25, df = 1, 22, P = 0.63). Hence, parasite infection does not seem to be the cause of the overall reduction in fecundity rates in terms of smaller clutch size and lowered female body weight.

Parasite burden in ducklings

A large (N = 1,730) sample of gammarids was collected during 1989-1991 from two follow-up sites in the study area (Fig. 9). The gammarids were sorted by eye into groups of infected and uninfected individuals (for details, see Hario, Selin & Soveri 1992). The prevalence of the acanthocephalan larvae or cystacanth was highest at the beginning of the eider brood rearing period at both sites, but the abundance of the parasite was clearly higher in shallow sea-water ponds than in the littoral zone bladder-wrack vegetation (see Fig. 9). The former is the typical feeding habitat of young eider ducklings, and gammarids constitute a large proportion of the diet of both the ducklings and the escorting females. This also explains why sick females, being able to feed only in shallow waters, may accumulate great quantities of acantocephalans within a short time.

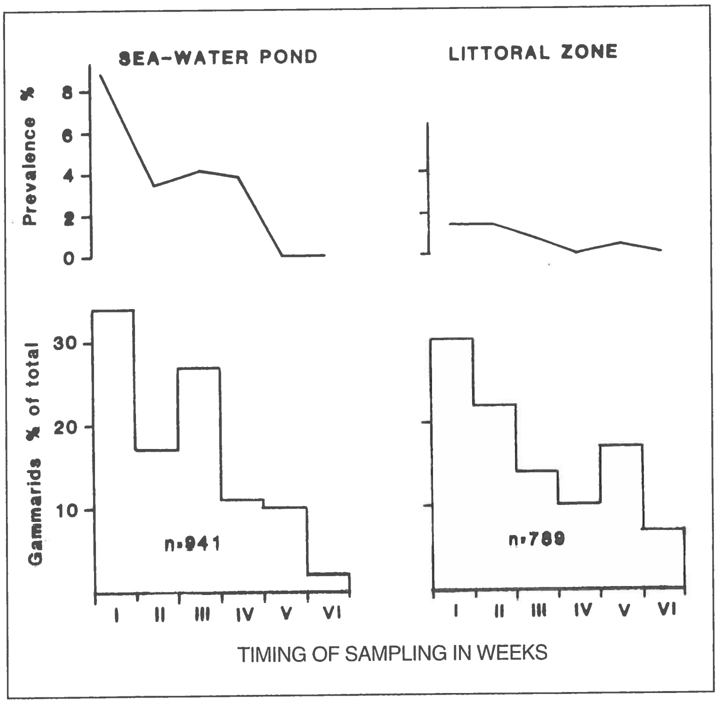

Figure 9. Prevalence of infection in gammarids in six different weeks (I-VI) of the eider brood rearing period at sea-water ponds and in the littoral zone, and occurrence of gammarids (% of the total number) in the respective weeks (from Hario et al. 1992).

The encountering rate of dead ducklings is probably lower than that of adult females. A total of 165 dead ducklings were found during 1987-1991; of these only 59 (36%) were suitable for examination. There was a greater variation in their parasite load than in that of adults (see Table 3). The years of heavy duckling mortality did not coincide with the years of heavy adult mortality.

The results do not allow a firm conclusion of the extent to which parasites affect duckling mortality. We suggest that the progressive decline in the abundance of gammarids at our two follow-up sites from 1989 to 1991 really reflects a reduction in the food stocks of eider ducklings (but see Salemaa 1987). This could be an outcome of the harmful effects of acanthocephalan worms on their intermediate host (lowering resistance and causing sterility in female gammarids; Crompton & Harrison 1965, Brown & Pascoe 1989). This assumption is currently being tested. If proved to be correct, then the parasite-induced regulation on duckling mortality acts via abundance of the intermediate host, gammarids, the preferred food item of eider ducklings.

Is food limiting?

For arctic nesting lesser snow goose *Chen caerulescens*, the reduced clutch size has been connected with probable food competition in an expanding population (Cooch, Lank, Rockwell & Cooke 1989). In the Baltic, the increase in the primary production of coastal waters has probably improved eider's feeding conditions. Unfortunately, no systematic monitoring of the abundance of the blue mussel *Mytilus edulis* has been conducted on the Finnish coast. Instead, marked fluctuations in biomass of certain soft-bottom bivalves have been noted, but these show local and temporal variations that neither seem to parallel the population trend of eiders nor the annual duckling survival (*cf.* the situation in the Netherlands, Swennen 1989).

Perhaps it is not necessary to presume that food itself is limiting, as only less than half of the present clutches at Söderskär are smaller and even these seem to confine to certain year classes. The same applies to female weight.

At present, there is little evidence to assess whether feeding at the breeding site contributes to clutch size. It may be for the maintenance mainly, restainining females from exerting their body reserves prior to egg laying. Dominance hierarchies could play a part in differences between individuals, so that older, more experienced females gain more food. However, the clutch size differences in this study do not stem from age-specific differences since all data confine to equally experienced females which have bred at least three times each. It is hard to believe that females would recognise year classes instead of age classes as they should when agonistic interactions modifying feeding rates would be the reason for the smaller clutch sizes of recent year classes.

Quantified food demands of adult eiders are high, especially when converted into numbers of mussels eaten per day (Swennen 1976, Thompson 1985b, Bustnes & Erikstad 1990). It is also clear that some females fail to gain a body condition sufficient to meet the physical demands of the long incubation (Korschgen 1977) and brood rearing (Bustnes & Erikstad 1991). Coulson (1984) found that eiders reduced the risk of death caused by breeding stress by avoiding breeding in certain years. The close relationship between the increased frequency of non-breeding and the decreased clutch size among females that chose to lay probably reflects the annual changes in the female 'condition' (Coulson 1984). In certain years females are less fit to breed, and the proportion of unfit females seems to increase when the population grows. In a sample of tagged birds, the incidence of non-breeding among late paired birds was as high as 77%, compared to 17% among early paired birds (Spurr & Milne 1976). Among the Söderskär eiders, the annual re-encountering rate of 'late' females is significantly lower than that of 'early' breeders (65% vs 73%, $\chi^2 = 3.84$, df = 1, $P < 0.05$, data from Table 1) indicating that the former are more liable to skip breeding. As was shown, the clutch size of 'late' females gives no response to the variation in timing; instead their strategy might be non-breeding in years of poor feeding conditions or high numbers of parasites.

However, non-breeding by itself does not explain the steady, continuous population decreases observed at Söderskär or at Kandalaksha.

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DO COMMON EIDERS *SOMATERIA MOLLISSIMA* EXHAUST THEIR FOOD RESOURCES? A STUDY ON NATURAL MUSSEL *MYTILUS EDULIS* BEDS IN THE WADDEN SEA

NEHLS, G. & KETZENBERG, C.

The feeding ecology of common eiders *Somateria mollissima* was studied on natural mussel *Mytilus edulis* beds in Königshafen on the island of Sylt, which forms a sheltered bay in the Wadden Sea of Schleswig-Holstein. The depletion of the mussel stocks was examined by comparing the size selection of eiders and the development of the structure of the mussel population. Eider numbers in Königshafen varied from 400 to 4,500 with the highest numbers recorded during autumn migration and winter. The eiders predominantly fed on mussels forming dense beds close to the low water line. In most months mussels formed the main part (>80%) of the eiders' diet. The importance of cockles *Cerastoderma edule* increased with increasing numbers of eiders in Königshafen. When eider numbers were at their maximum, up to 50% of the birds present were feeding aside the mussel beds. A significant negative correlation was found between the proportion of eiders feeding on the largest central mussel bed first occupied by eiders and the total numbers of eiders present in the area. This characterises this mussel bed as the preferred feeding ground and shows that a density regulation of eider numbers occurred. The size of the mussels selected by eiders showed a marked seasonal change with the largest mussels (median about 50 mm) being taken in midwinter and the smallest mussels (median about 35 mm) being taken after spawning in April. The biomass on the preferred mussel bed increased from 1,390 g AFDW (ash free dry weight) m^{-2} in June 1990 to 1,960 g AFDW m^{-2} in February 1991 and has remained at this level since then. In the meantime the density fell from 2,900 individuals m^{-2} to 1,700 individuals m^{-2}. The contrasting trends of density and biomass were explained by growth, as the median size of the mussels increased from 38 mm to 53 mm. Spatfall was estimated to contribute about 10% to mussel density annually and annual losses were calculated to amount to 20% of the mussels. A comparison of the changes in the structure of the mussel bed and the mussel sizes taken by eiders indicated that eider predation contributed significantly to mussel mortality. The constant biomass of the mussel bed, despite decreasing abundance, lead to the assumption that predation was compensated for by production. It is concluded that social interactions limit the density of feeding eiders below a level which would lead to prey exhaustion.

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A general consensus exists on the significance of limited food resources in determining the size of consumer populations. However, controversy exists on the problem of the frequency at which a given population will face situations of food shortage and at which level this mechanism acts (e.g. Newton 1980). Social interactions may determine which part of a population will have access to a given resource and which part will not. Resource depletion may thus be inhibited by behavioural mechanisms at a level below the actual capacity of a resource. This might be beneficial in the case of resources which are not renewed regularly and predictably, so that behavioural mechanisms allow utilisation for a longer period, though by a limited number of individuals only.

Extensive work on oystercatchers *Haematopus ostralegus* feeding in intertidal mussel beds, showed that interference limits the density of feeding birds, keeping the annual depletion even of the best feeding grounds and preferred size classes to 25-40% (e.g. Goss-Custard & Durell 1984, Zwarts & Drent 1981). Therefore, in the feeding territory of an oystercatcher, mussel abundance exceeds what the bird is able to consume during the time of its presence. It is thus generally accepted that territorial behaviour may limit population density independently of resource levels (Patterson 1980). Gregarious waterfowl, often feeding in large and dense flocks, represent another way of avian exploitation behaviour. There seems to be no upper limit for flock sizes, and feeding densities appear to be defined by the minimal individual distance between specimen. Depletion to an extent where a resource is no longer exploitable is a common feature and has been noted for herbivorous waterfowl (van Eerden 1984, Madsen 1988), diving ducks (Suter 1982) and eiders (Raffaelli, Falcy & Galbraith 1990), which may remove more than 80% of their food stocks in areas where densities are high. However, interference which results in a reduction in feeding rate as densities increase (Goss-Custard 1980) may cause a dispersal of birds and thus reduce local food depletion. The strength of interference depends on the aggression of the birds and their densities. The response to interference will depend on the available food resources. Considerable differences in dispersal and local predation pressure thus occur between species and between different areas, and prey depletion may be either positively or negatively density dependent (Bernstein, Krebs & Kacelnik 1991).

We investigated the predation of eiders on natural mussel beds in Königshafen in the northern part of the Wadden Sea. The common eider is one of the most numerous waterfowl species in the Wadden Sea and in terms of consumption the most important avian predator of the area (Smit & Wolff 1983). However, the consumption by eiders only reaches 12% of the average production of their prey species, i.e. mussels and cockles (Nehls 1991), and is considerably lower than reported from other areas. On the other hand, seasonal changes in the distribution of eiders within the Wadden Sea (Swennen, Nehls & Laursen 1989, Nehls 1989, 1991) may reflect local prey depletion.

In this paper we describe the seasonal pattern of the utilisation of mussel beds and compare the impact of eiders on different mussel beds. The aim of the study was to analyse the significance of eider predation on the density and structure of mussel beds and to assess whether behavioural responses to eider density or numerical responses to changing mussel populations affect predation pressure.

Study area and methods

Study area

Our investigations were carried out in Königshafen on the island of Sylt in the northern part of the Wadden Sea (Fig. 1). Königshafen is a shallow bay formed by a bending chain of dunes. The area encloses about 4.5 km^2 of tidal flats which are characterised by coarse sand. Tidal range averages 1.8 m and is smaller than in the more central parts of the Wadden Sea where tides may exceed 3 m. Since the 1930s mussel beds have increased

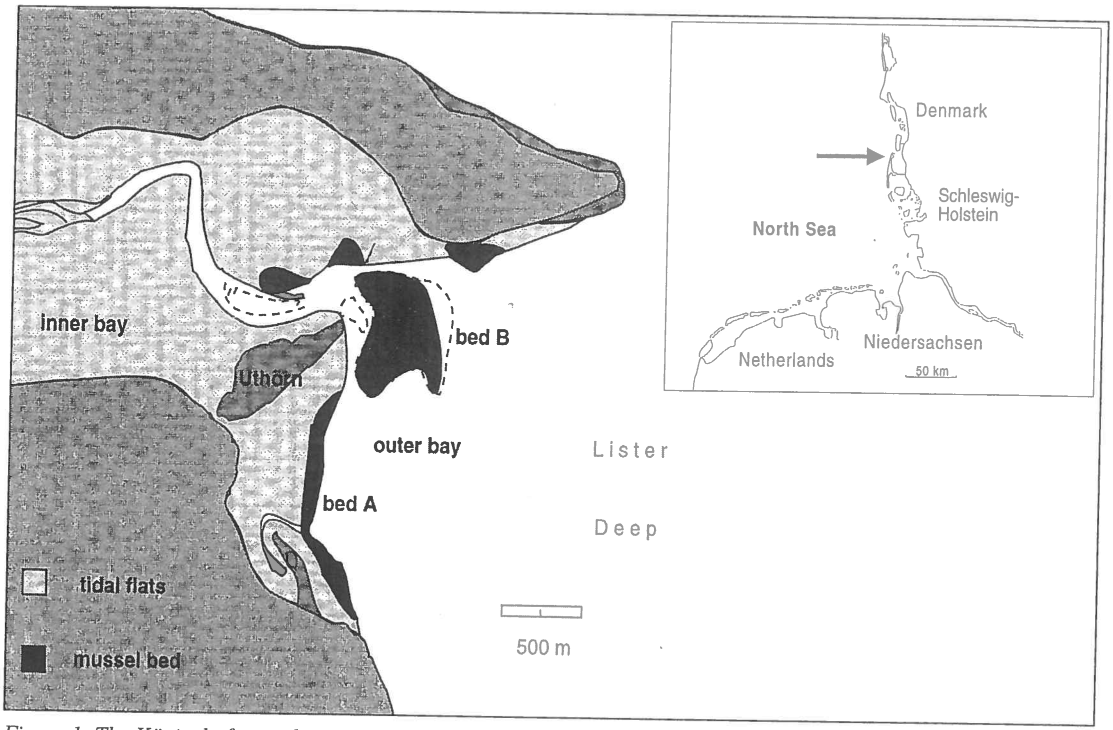

Figure 1. The Königshafen study area with distribution of mussel beds and tidal flats.

in the area and they cover about 5% of the mudflats during the time of the study. The productivity of the area is of the same magnitude as in other parts of the Wadden Sea (Asmus & Asmus 1990). Mussel beds form the most productive community and reach biomass values over 1.5 kg AFDW (ash free dry weight) m^{-2}, which exceeds the average biomass of the surrounding tidal flats (16-30 g AFDW m^{-2}) by far (Asmus 1987).

Eider numbers

From March 1990 to June 1992, eider numbers were surveyed every fortnight by ground based investigations. Their distribution on the feeding grounds was mapped every 15 or 30 minutes over whole tidal cycles for 49 days from an observation tower placed on the tip of the island of Uthörn (see Fig. 1). For this purpose the study area was subdivided into eight units where eider numbers and activity were monitored, thus allowing separate analysis of the different feeding grounds.

Eider food

Eider faeces were collected on a high tide roost on the island of Uthörn, adjacent to the mussel beds. Eider faeces contain a large proportion of indigestible fragments (e.g. mollusc shells and crab claws) which are easy to determine. As eiders tend to feed on one prey species at a time (Ketzenberg 1991, Nehls 1991), the majority of faeces contain fragments of only one prey species. To assess the proportion of the different species in the eiders' diet, we simply counted the number of faeces containing the different prey types on the roost. For detailed analysis a subsample of faeces was collected and washed through a sieve in the laboratory. The umbos of mussels were separated from the remains and were used to calculate the size of mussels taken by eiders. For calculation of mussel length (L) the following regression relating umbo width (U) and length of intact mussels was used:

$$L = 40.927 * U - 5.502 * U^2 - 9.638,$$
$$r^2 = 0.908, P = 0.0001, N = 101.$$

As the umbo*length relation may differ regionally, depending on age structure and growth condition of the mussels, this regression was based on biometric data of mussels from Königshafen. A non-linear regression in our study results from a high portion of older mussels because growth rate decreases with age whereas shell thickness continues to increase (e.g. Nehls 1991).

Mussel population

Most mussel beds of the Königshafen area are found close to the low water line where the bay opens to the deeper parts of the Wadden Sea. The intertidal mussel population of Königshafen concentrated in five beds of which two were regarded in this study, i.e. bed A, which stretches along the low-water line from Uthörn to the main island, and bed B, which is the largest mussel bed of the area, an island-like mussel bed between two gullies leading to the inner Königshafen (see Fig. 1).

Samples of mussels were taken using a 500 cm^2 corer. Numbers of samples per station varied from 4 to 6, depending on the purpose of sampling. In February 1991 only three samples per station were taken. Samples were sieved (mesh width 1.5 mm) and all mussels measured to the nearest millimetre. All samples were taken within patches of mussels. For establishment of length/frequency distributions, data from all stations were pooled. Biomass data were not measured directly but calculated using the following length/weight equation, which was derived from pooled data of all samples:

$$\ln \text{AFDW (g)} = \ln \text{lenght (mm)} * 2.962 - 11.643,$$
$$r^2 = 0.943, P = 0.0001, N = 282.$$

Due to the seasonal changes in the condition of the mussels the values presented here will differ somewhat from the real situation. However, for our purpose, which is to detect increases or decreases over a longer period, it seems justifiable to ignore the annual pattern of spawning and condition regaining.

Results

Eider numbers

Eiders visited Königshafen throughout the year with the lowest numbers below 500 nonbreeders during the breeding season (May-June) and the highest numbers with up to 4,500 during autumn migration (Fig. 2) Immigration of birds originating from Baltic breeding grounds started in June. During the moult-

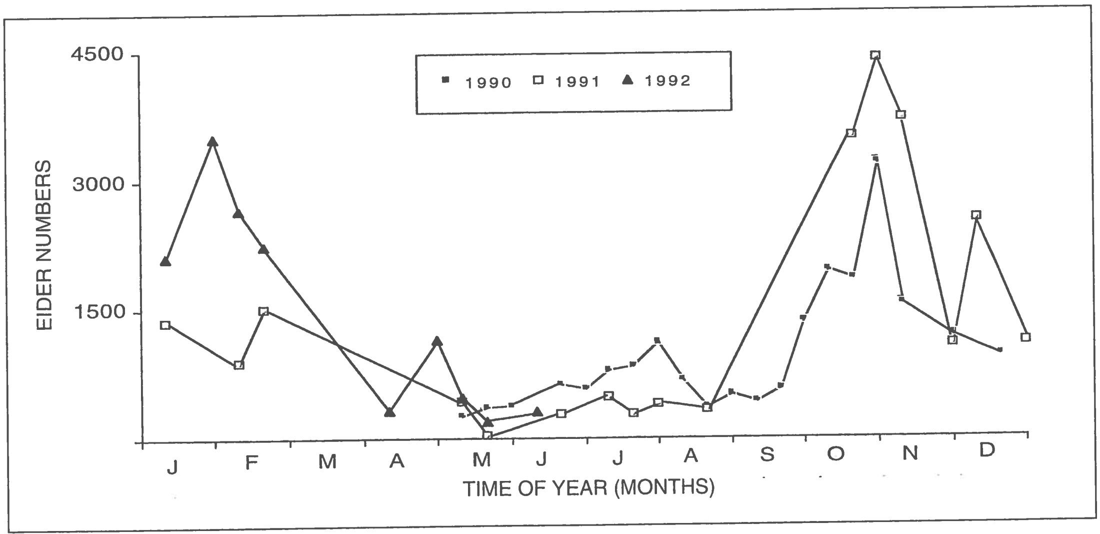

Figure 2. Phenology of eider numbers in Königshafen, based on fortnightly counts during 1990 - 1992

ing period (July-August) the eider population mainly consisted of immature birds (> 80%); this is in contrast to the large concentrations of moulting eiders in the Wadden Sea where > 80% of the population consists of adult males (Nehls 1991). Numbers of moulting eiders rarely exceeded 1,000 birds, because frequent disturbances caused by recreational activities drove the eiders away (Ketzenberg 1993). During autumn migration the composition of the eider population in Königshafen equalled that in the rest of the Wadden Sea, holding a slight majority of adult males. No obvious changes in numbers or phenology were detected during the study period.

Distribution on feeding grounds

Eiders foraged in mussel beds, gullies or tidal flats by diving or head-dipping. Trampling, which is mainly used to wash cockles out of the sediments, was rarely seen during the study period. The feeding activity was related to the tidal cycle with the activity being highest in periods of low water levels. On most mussel beds in Königshafen foraging activities and eider numbers were highest in the four hours of low tide level. However, the birds left the mussel beds when these became completely emersed. In the summer months, when eiders spent only little time feeding, the presence of the birds on the mussel beds was almost restricted to this period whereas in the winter months, when much more time was spent feeding, eiders were present on the mussel beds during the whole day except when the beds became dry. Many birds that foraged at mussel beds in the eastern part of Königshafen rested on the island of Uthörn during high tide and left by ebbing tide for the mussel bed and returned by rising tide to the roost, thus getting two times free transport to and from the roost.

Eiders predominantly used the mussel beds in the eastern part of Königshafen, where the bay opens to the Lister Deep. Daily variations in the spatial distribution within Königshafen were mainly attributed to human disturbances (see Ketzenberg 1993) or variations in the tidal amplitude. There was a significant negative correlation between eider numbers present in Königshafen and the proportion of eiders feeding at the mussel bed (Fig. 3). At times when eider numbers were low, the majority of birds were feeding at bed B, which thus could be characterised as the preferred, and first occupied, feeding ground

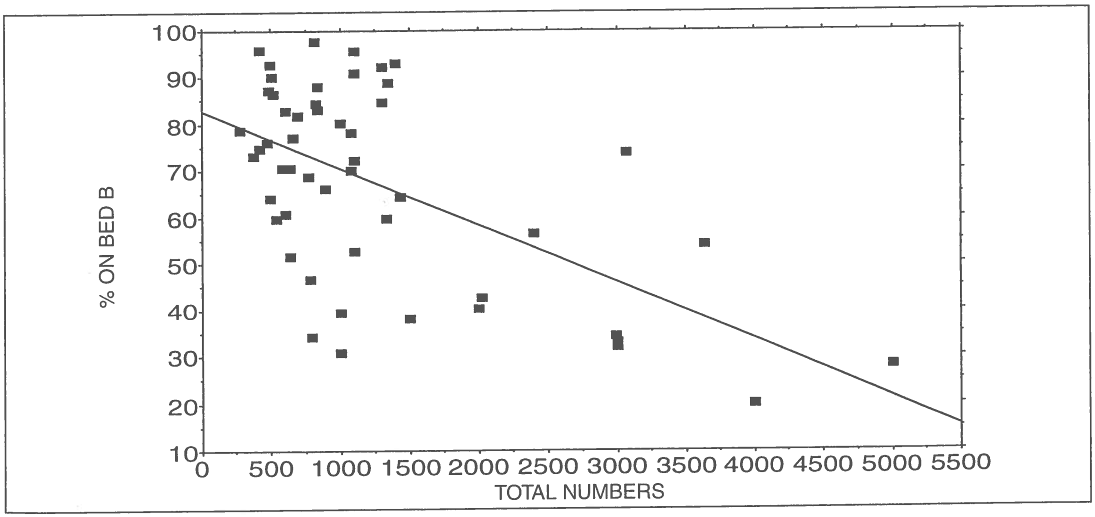

Figure 3. Correlation of eider numbers on mussel bed B and total numbers in Königshafen (r^2= 0.348, P = 0.0001). Data of counts from 1990 to 1992 are pooled. Numbers on bed B are maximum numbers during low water level, when feeding activities are highest, selected from continuous scan observations of the time from two hours before to two hours after low tide.

of Königshafen. In July, up to 90% of all eiders in Königshafen were feeding there. It further indicated that a density regulation occurs as eider numbers on bed B level off at about 1,000-1,500 individuals. When eider numbers increased during autumn migration, the birds dispersed over the total area of Königshafen and the proportion on bed B fell to 35%. During the time when maximum numbers were present (October-November) a large proportion fed aside the mussel beds at the tidal flats where mainly cockles were taken (compare Fig. 4), but as numbers went down in late winter, the birds once again concentrated on bed B, where up to 80% were found in spring. During the time of the study no marked annual differences in the spatial distribution and habitat utilisation of eiders in Königshafen were observed.

Eider food

The remains of 11 macrobenthic invertebrate species were identified in the faeces of eiders. Mussels, cockles and shorecrabs *Carcinus maenas* contributed significantly to the eiders' diet. Other species, including razor clams *Ensis directus*, hermit crabs *Eupagurus bernhardii*, seastars *Asterias rubens*, urchins *Echinoidea* sp. and snails *Littorna littorea* and *Crepidula fornicata* were taken regularly, but by very few birds only. Other species, such as ragworms *Nereis virens* were taken only occasionally. Mussels formed the main part of the eiders' diet in Königshafen for most of the year. In the period from May 1990 to February 1991, when faeces were investigated each fortnight, other species were only important as food items in May and October-November, and only in this period was the share of mussels in the eiders' diet below 80% (Fig. 4). Additional sampling in 1991 and 1992 revealed the same trend, with a relatively high portion of shorecrabs being taken in May and June and a share of about 50% of cockles in October and November.

Size selection

Eiders consumed almost all sizes of mussels available ranging from 5 to 63 mm, with median sizes varying within 32-52 mm. Despite the wide range of mussels that were consumed by eiders, strong selection of certain

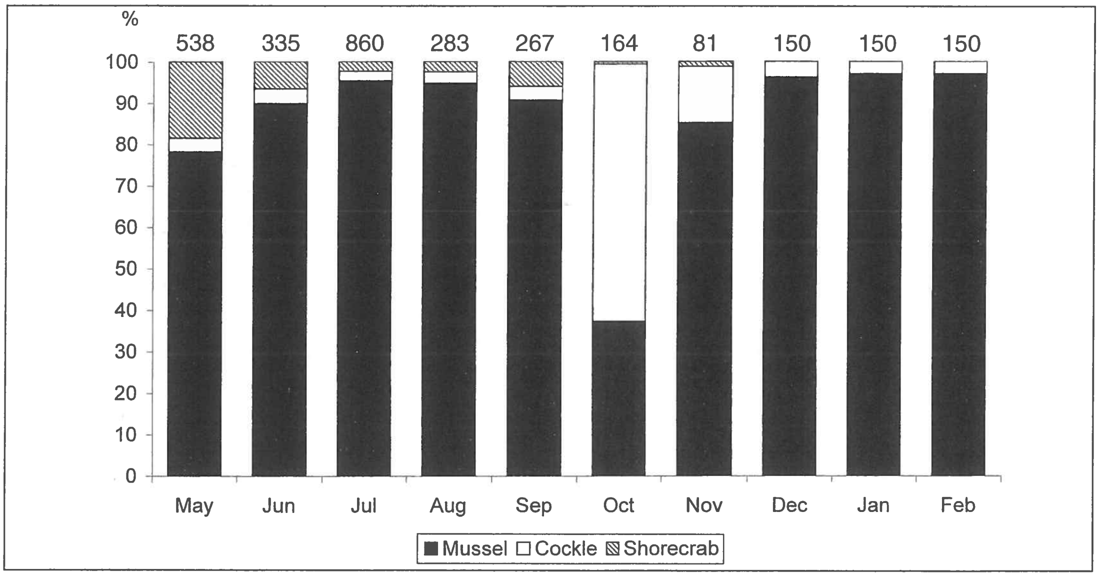

Figure 4. Seasonal changes in the composition of eider food in Königshafen as derived from indigestible fragments in faeces during 1990 - 1991. The bars give the percentages of faeces containing the most important food items. Numbers on top of the bars indicate sample sizes.

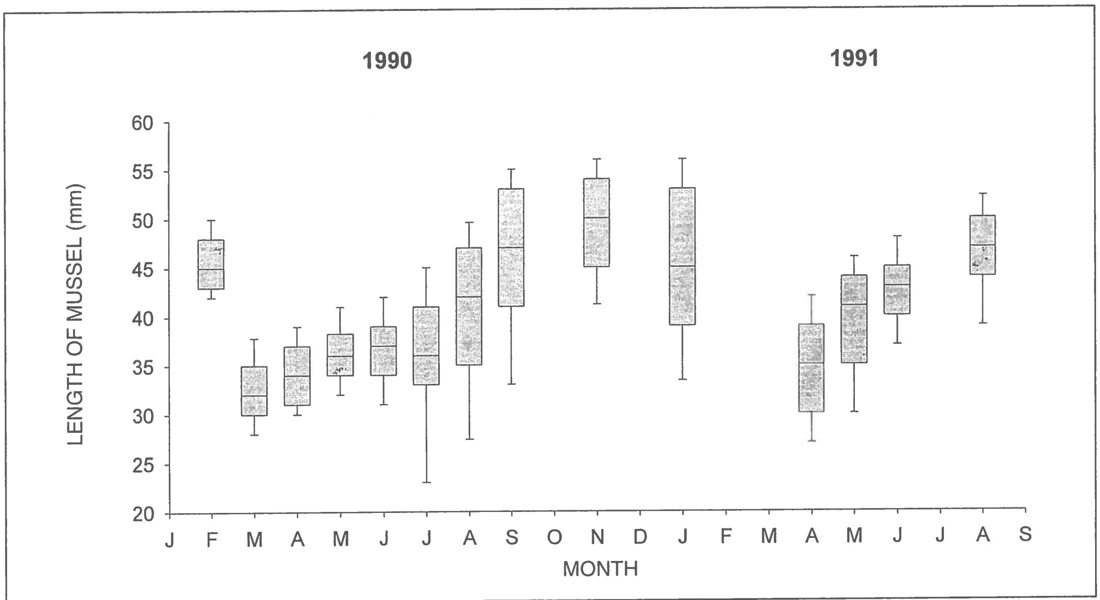

Figure 5. Seasonal changes in the sizes of mussels consumed by eiders during 1990 - 1992. Box plots indicate median, 50% (box) and 80% (bars) of the data.

sizes was found as shown by the seasonal variation of in the sizes of mussels taken by eiders based on data from 1990 to 1992 (Fig. 5). The sizes of mussels consumed showed a marked seasonal trend, with the largest mussels being taken during winter and the smallest being taken in late spring, which probably represents a response to changes in the condition of mussels due to spawning in spring (see Cayford & Goss-Custard 1990). Of all mussels consumed by eiders, 80% ranged in size within 30-55 mm. Eider predation thus concentrated on about one third of the sizes found in the mussel population on the beds studied (see below).

Mussel population and impact of eider predation

The mussel beds were not evenly covered with mussels. Mussel patches alternated with pools or bare sandflats. The coverage of bed B was estimated by aerial photographs taken in August 1992. The total area of mussel bed B was 0.14 km^2, of which 25-30% was covered with mussels. Bed A was estimated to contain a similar area covered with mussels, but as its borders were less clear and mussels were more spread out, it could not be accurately determined from the aerial photographs.

The structure of the mussel beds showed the characteristics of an older population formed by more than one year-class (Fig. 6). In June 1990 the length/frequency distribution of the mussels showed a maximum of around 40 mm. Mussels of this size probably represented the spatfall of 1987, which built up most of the mussel population in the Wadden Sea of Schleswig-Holstein at that time. Only very few mussels had reached their maximum length of about 70 mm, indicating that a high mortality of older mussels occurred in the time before the study, probably during the cold winters before 1987.

Changes in the structure of the mussel populations during the study period were caused by three different factors: 1) New spat recruited to the population, 2) growth of the mussels lead to an increase in average mussel size, and 3) predation, especially by eiders, caused size-specific mortality.

The changes in population structure from June 1990 to February 1991 differed between the two beds studied. Eider numbers on bed B were on average 2.5 times higher

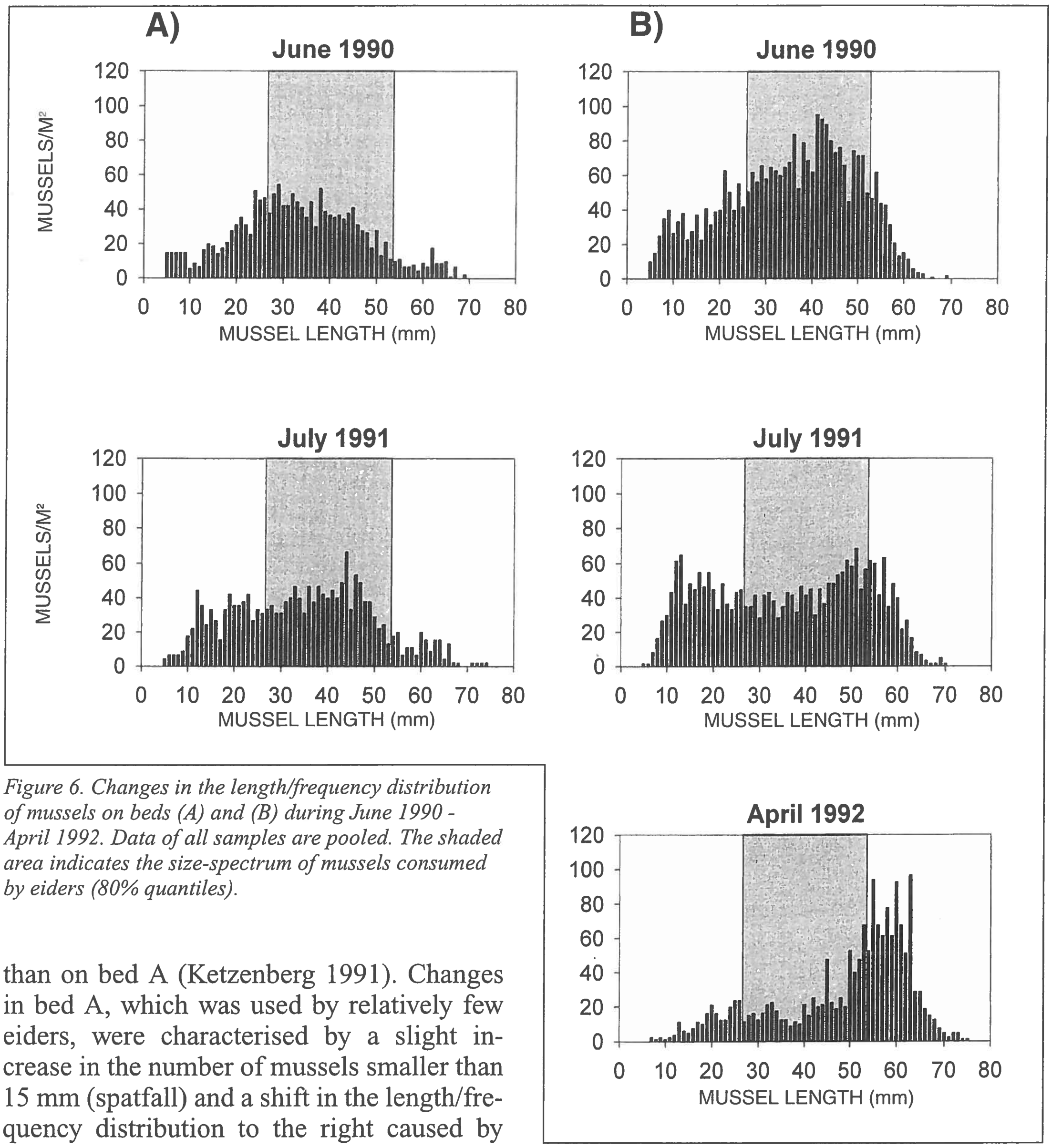

Figure 6. Changes in the length/frequency distribution of mussels on beds (A) and (B) during June 1990 - April 1992. Data of all samples are pooled. The shaded area indicates the size-spectrum of mussels consumed by eiders (80% quantiles).

than on bed A (Ketzenberg 1991). Changes in bed A, which was used by relatively few eiders, were characterised by a slight increase in the number of mussels smaller than 15 mm (spatfall) and a shift in the length/frequency distribution to the right caused by growth. However, the numbers of larger-sized mussels remained at a constant level (see Fig. 6). On bed B, which was intensively used by eiders, spatfall and growth was similar to those of bed A, but a decrease in the number of mussels ranging in size within 20-45 mm was observed. The abundance of mussels larger than 45 mm increased. However, the increase in the number of the larger mussels did not match the decrease in the number of smaller mussels and a reduction in the number of mussels larger than 20 mm was thus evident. Although some spatfall occurred after June 1990 the abundance of mussels decreased slightly (Table 1, Fig. 7). Losses of mussels occurred in the sizes which were taken by eiders most frequently (compare Fig. 6). On bed B, where the changes could be monitored over a longer period (bed A was damaged by ice in February 1991), mussel densities decreased until spring 1992 despite some additional spatfall during summer 1991 (see Figs. 6 and 7). Assuming a

Table 1. Mean density, median size and biomass of mussels on bed B (see Fig. 1) during June 1990 - April 1992. N gives the number of samples taken, density is expressed as individuals/m²and biomass as g AFDW/m².

Month	N	Mean density	Median size (mm)	Biomass/m²
June 1990	21	2899 ± 1306	38	1389
September 1990	24	2579 ± 1142	38	1400
February 1991	12	2465 ± 1029	37	1403
July 1991	16	2271 ± 691	37	1964
October 1991	16	1959 ± 693	47	1690
January 1992	16	2339 ± 1104	46	1805
April 1992	16	1695 ± 1887	53	1838

successful mussel recruitment of 250 mussels m^{-2} in both years, a decrease from 2,900 to 1,700 mussels m^{-2} represents some 50% mortality from June 1990 to April 1992. Losses occurred mainly in mussel sizes below 55 mm and in April 1992 the population was dominated by old, large-sized mussels (see Fig. 6 and Table 1). The biomass of the mussel bed followed a different trend and increased by 50% during the first year. Thereafter the biomass stayed more or less constant at about 1.8 kg AFDW m^{-2}. A substantial part of the mussel population escaped eider predation by growing to a size unsuitable for eiders. In April 1992 about half the mussels present on bed B had surpassed the size classes suitable for eiders (< 55 mm). In June 1990, 93% of the individuals and 79% of the biomass on bed B were suitable for consumption by eiders, but only 50% of the sizes and 27% of the biomass remained so in April 1992 (see Figs. 6 and 7). Considering the decrease in mussel abundance in bed B and the shift in the size frequency distribution towards larger sizes it appears that the density of mussels suitable for consumption by eiders decreased by two-thirds. An additional sampling in February 1993 showed this situation to be stable, with some recruitment keeping the density high and about two-thirds of the biomass consisting of mussels larger than 55 mm, thereby being out of reach for the eiders (see Fig. 7).

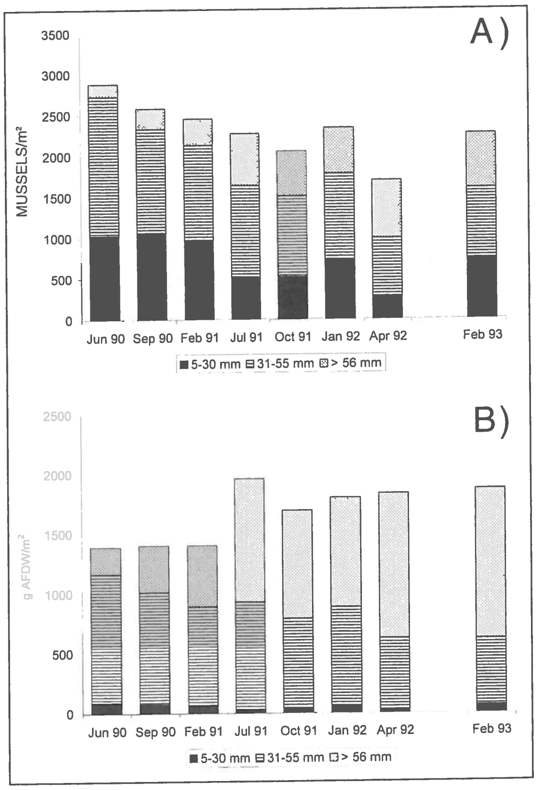

Figure 7. Density (A) and biomass (B) of mussel sizes on bed B during June 1990-April 1992. For comparison data for February 1993 are presented.

Discussion

Following an eider population increase (Laursen 1989), parts of the Wadden Sea have only recently become inhabited by eiders, and areas where eiders were scarce in the 1960s now hold several ten thousand eiders. However, in the northern and western parts of the

Wadden Sea where eiders were abundant before, numbers remained constant indicating that an upper limit of eider densities had been reached (Nehls, Bräger, Meißner & Thiel 1988, Swennen et al. 1989). Knowledge on the relation between eider predation and the dynamics of mussel beds in these areas may thus help us understand the underlying processes.

The population dynamics of mussels in the Wadden Sea are characterised by erratic spatfall and destructive events. Cold winters with extensive ice cover on the tidal flats and storms are the main factors influencing the abundance and distribution of mussel beds (Dankers, Koelemaij & Zegers 1989, Nehls & Thiel 1993). A common pattern is that a cold winter largely reduces the population and a strong spatfall restores it the next summer. However, in the time between two destructive events mussel beds are subject to predation by eiders and other predators, which have to adjust their behaviour and populations to highly variable food supplies.

Two contrasting developments occurred on the mussel beds in Königshafen during the study period. The abundance decreased but the biomass initially increased and then remained constant at a level of 1.8 kg AFDW m^{-2}. Size selection by eiders directed the predation pressure to a third of the mussel sizes and a reduction in the abundance of mussels in the sizes preferred by eiders was observed on bed B. However, annual losses even of the preferred mussels were relatively low. A proportion of mussels, which was high enough to ensure a constant biomass, escaped eider predation by growing larger than 55 mm. Predation by eiders was thus compensated for by production although little recruitment renewed the mussel population. At the end of the study period the majority of the mussels were no longer affected by predation by eiders. Similar findings were reported on eiders utilising mussel cultures in the Wadden Sea (Nehls & Ruth 1994). Because eiders do not affect the main part of adult mussels, which are the crucial part of the population for reproduction, it is concluded that eiders are not an important factor influencing the population dynamics of the mussels in Königshafen.

What are the reasons for the low predation pressure? The predation by eiders, like that of other waterfowl, may well lead to an exhaustion of their food resources. In the Ythan estuary in Scotland, eiders consume approximately 40% of the annual mussel production (Milne & Dunnet 1972) and may deplete preferred mussel beds by 80% over winter (Raffaelli et al. 1990). Predation rates by eiders on mussel beds of up to 55% have also been observed in Canadian waters (Guillemette, Himmelmann, Barette & Reed 1993). Eiders are numerous in the Lister Deep area which borders Königshafen and both moulting and wintering numbers often exceed 20,000 individuals (Nehls et al. 1988, Nehls 1991, G. Nehls, unpubl. data). The mussel beds in Königshafen formed an attractive food resource for eiders in the years of our study. Many mussel beds in the exposed parts of the Wadden Sea of Schleswig-Holstein were removed by severe storms in early spring 1990, but areas sheltered by islands, such as Königshafen, were not affected (Nehls & Thiel 1993). In the winters of 1990/91 and 1991/92 eiders concentrated in the areas east of the islands (G. Nehls, unpubl. data), so why did not more eiders occur in Königshafen? Foraging theory assumes that birds choose their feeding areas to maximise their intake, which is a function of patch quality, social interactions and individual performance (Kacelnik, Krebs & Bernstein 1992). Our data indicate that social interactions limit the number of eiders on the preferred feeding grounds in Königshafen. The development of eider numbers on bed B is characterised by the negative correlation of eider numbers present in Königshafen and the proportion feeding on this bed. This pattern has also been found in non-territorial waders (Goss-Custard 1980) and characterises such places as preferred feeding areas where densities are relatively high. The conclusion is based on the simple assumption that birds first occupy the best feeding areas and as densities increase, competition and thus interference increase and birds disperse and start to occupy suboptimal areas. A typical observation is that dominant birds occupy the best sites (e.g. Monaghan 1980, Ens & Goss-Custard 1984, Goss-Custard & Durell 1984). A negative effect of density on the food intake has indeed been found in Scottish eiders (Ashcroft 1976). The observation of eiders feeding aside the mussel beds on cockles during the time when numbers are highest indicates that part of the population has no access to the preferred feeding areas. The alternative hypothesis that eiders dispersed because the quality of the preferred area decreased, either through depletion by eiders or other factors, can be excluded as the number on bed B did not decrease. Furthermore, the effects of decreasing quality of feeding grounds would have lasted for the whole study period, as only little spatfall recruited to the mussel population. In both years cockles were only important for a short time in autumn. In late winter when eider numbers decreased, most birds were found once again on bed B. In April 1992, 80% of the 1,000 eiders remaining in Königshafen were found at bed B. As mussels may live in dense layers of more than 10 cm a large reduction of their abundance is possible before a response to the birds feeding efficiency occurs. The quality of a mussel bed is therefore not linearly related to mussel density but reaches a ceiling at a certain density. This might explain why a decrease in the densities of the preferred mussels did not affect its quality from the eiders' point of view.

The second factor mitigating any predation impact is the high biomass and production of the mussel beds in Königshafen. Biomass values of 1.8 kg AFDW m^{-2} represent the upper range of biomass values which intertidal or estuarine benthic communities can reach (see Asmus 1987) and are much higher than in other areas of the Wadden Sea of Schleswig-Holstein (M. Ruth, pers. comm.). Our finding, that the biomass did not increase beyond this level although annual mortality was low, indicates that individual growth of the mussels was density dependent. Food (e.g. planctonic algae) for a mussel bed is supplied by horizontal transport of the tidal currents, and mussels filter the overlying water column through their gills. At high densities mussel beds may substantially reduce their food resource (e.g. Asmus & Asmus 1991). Production can be regarded as limited by mussel density if the filtration capacity of the mussel bed is higher than the food supply from the water column. Under favourable conditions Wadden Sea mussels may reach a length of 50 mm within one or two years (Dankers et al. 1989), but in our study growth was much slower and by the end of the study few mussels had reached their maximal length of about 70 mm.

A combination of density regulation in eiders and a very high biomass of mussels thus leads to the conclusion that eider predation reduces mussel density, but production compensates for biomass losses. It is likely that eider numbers could be even higher without reducing mussel production, but it is unclear to what extent a reduction in mussel density would enhance growth of the remaining mussels. It will depend on the age structure of the mussel bed as production decreases with increasing size (Asmus 1987). Predation can be compensated for as long as the filtration capacity of the mussel bed is high enough to utilise their food resource completely and density dependent growth occurs. Apparently, this was the situation found in Königshafen.

Whether or not this situation is typical of the Wadden Sea depends on the structure of the mussel beds as well as on the mechanisms of density regulation in the eider. As the biomass of the mussel beds in Königshafen is at the highest possible level and the density of eiders has levelled off as a result of interference, predation does not depress the mussel population below its production capacity. This might be different in areas where mussels are spread out and the density of eiders, if related to the density of mussels, may reach a higher level. Although a clumping of resources should generally favour its depletion by predators, because intake rates will be less affected by decreasing prey abundance, a contrasting effect arises because the clumping of resources increases competition and thus interference (Milinski & Parker 1991). Consequently more birds may have access to a resource if it is spread out. This has been observed in oystercatchers feeding on mussel beds of the Wadden Sea, where the density of birds, as related to mussel bed surface, and hence predation impact was highest in areas with low mussel density (Zwarts & Drent 1981). This means, that the strongest predation pressure may not always occur in preferred areas. Mussel beds in other parts of the Wadden Sea generally show lower biomass values (500 g AFDW m^{-2}, M. Ruth, pers. comm.) than those found in Königshafen. Therefore the density of eiders in relation to mussel density may favour a stronger depletion of mussel beds in other areas. In the Ythan estuary, Scotland, where predation by eiders causes a substantial reduction in mussel stocks, dense mussel beds only reach one third of the biomass value found in Königs-hafen (Milne & Dunnet 1972).

It is thus important to know how eiders distribute over food resources of different quality. The distribution of birds over feeding grounds of different quality depends on the mean level of interference leading to aggregation in species with low interference and to dispersed foraging in species with high interference (Sutherland & Parker 1985). If no interference occurs, all members of a population are expected to concentrate in the best food patch and disperse after depletion equalises patch quality. At higher levels of interference, densities should follow a gradient of the quality of different feeding sites. However, aggregation may alter this pattern considerably. Birds may aggregate in flocks because they are attracted by their companions or simply because they have to share a rare resource (Pulliam & Caraco 1984). Although eiders may gather in large and dense flocks, interference within these groups apparently is higher than in other waterfowl, e.g. geese. In the Wadden Sea, aggressive interactions between feeding or resting eiders occur frequently (G. Nehls, pers. obs.). Flock formation in the Wadden Sea, where eiders rarely encounter predators, is at least partly, the result of clumped food resources: Observations of individually marked eiders only revealed a tide-induced synchronisation of the feeding behaviour of eiders and individual birds returning each tide to the same spots on the mussel beds (Ketzenberg 1991, Nehls 1995). When feeding on cockles, which are less aggregated than mussels, eider flocks disperse over large areas for foraging and may gather only on the roost (Nehls 1991). A dispersion of eiders in the Wadden Sea in relation to the quality of the feeding grounds is thus likely to occur. Feeding densities in other places will probably not be substantially higher than in Königshafen, though the feeding densities here may not represent the highest possible level.

This is in contrast to the findings of Guillemette et al. (1993) who observed high aggregation and synchronised foraging in the absence of aggressive interactions between eiders at mussel beds in Canadian reef habitats. Their results indicate aggregation as an important factor for habitat selection because of improved abilities to find suitable food patches: In large flocks the active part will always indicate the position of the food resource and serve as an orientation for birds resuming feeding after a rest. Although this behaviour has been observed in Königshafen (G. Nehls, unpubl. data) and in other tidal areas (Campbell 1978) during high tide, it is much less important in areas where most feeding activity occurs at low tide when mussels beds are exposed and visible. In contrast, tides restrict the availability of mussel beds to eiders and govern their activity pattern (Campbell 1978, Ketzenberg 1991, Nehls 1991, 1995), which can be regarded as a clumping of the resource in time and therefore should increase interference. As in our study, Campbell found that Scottish eiders used more feeding sites as numbers increased, but this was not the case in the Canadian study by Guillemette et al. (1993). Two different patterns of habitat exploitation in eiders can be distinguished: 1) Aggre-gation and synchronised foraging in areas where eiders predominantly feed by diving (Campbell 1978, Mudge & Allen 1980, Goudie & Ankney 1988, Ydenberg & Guillemette 1991, Guillemette et al. 1993), leading to a concentration of the predation rate in preferred areas which will facilitate an uneven distribution of predation pressure and favour local prey depletion, and 2) dispersed foraging in tidal areas (Campbell 1978, G. Nehls, pers. obs.) as a result of interference when aggregation is not beneficial, which should facilitate an even distribution of predation pressure.

Regarding the generally low predation in relation to the average total production of mussels in the Wadden Sea (12%, Nehls 1991), it can be concluded that prey exhaustion probably will not occur regularly, and seasonal changes in the distribution of eiders are only partly caused by depletion of the feeding grounds. Other factors may be more important, such as seasonal changes in food demand (Ketzenberg 1991, Nehls 1991) and size-selection (this paper) or increased sensitivity to disturbances during moult (Thiel, Nehls, Bräger & Meißner 1992, Ketzenberg 1993). However, our study was carried out at a time of relatively high mussel populations and the situation may change in times of small mussel populations. The fact that the number of eiders in Königshafen was not affected by a two-third decrease in their food source indicates that eiders may continue foraging until severe depletion of their food occurs. A much stronger depletion of the food sources than observed in our study is likely to occur at times of general food shortage, which may occur after cold winters (see Beukema 1979) or by overfishing of the mussel stocks (Laursen & Frikke 1987, Swennen 1991), when eiders concentrate on the remaining mussel beds.

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DEVELOPMENT AND POPULATION DYNAMICS OF COMMON EIDER *SOMATERIA MOLLISSIMA* COLONIES IN THE NETHERLANDS

SWENNEN, C.

This paper summarises the general development of common eider *Somateria mollissima* colonies in the Dutch Wadden Sea. All colonies settled between 1906 and 1947, starting with a few founder pairs. It took 5-20 years before the colonies exceeded 10 breeding pairs; this period was followed by a rapid exponential increase, gradually slowing with time. The oldest established colonies now show no further expansion, since limiting factors have come into operation. Clutch size did not change with increasing population, but fledgling output decreased significantly. Ringing shows that nearly all females recruit in their natal colony, whereas males show a high degree of natal and breeding dispersal. Because of the philopatry of the females, new breeding sites rarely become established. Natural mortality rates are low outside the breeding period. Predation of females and eggs represent the major limiting factors restricting eider colonies, since fledgling success determines overall growth rate in contrast to the findings of Coulson (1984).

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The European population of the common eider *Somateria mollissima* has shown dramatic changes in historical times. A southward expansion of breeding colonies started at the end of the 18th century when eiders first bred on the North Frisian Islands in the Wadden Sea area between 1785 and 1805 (Bauer & Glutz von Blotzheim 1969) and on the Scottish mainland in 1807 (Baillie & Milne 1989). Expansion and growth continued in the 20th century: eiders began to nest in The Netherlands on the West Frisian Islands in 1906 (van Heurn 1952), in Ireland in 1912 (Kennedy, Ruttledge & Scroope 1954) and in the Black Sea in 1975 (Ardamatskaya 1983). A fledgling was successfully reared in Lake Zürich in Switzerland (Anderegg 1989) and an unsuccessful clutch was found in Austria (Winding 1977).

Settlement typically followed a major distributional advance (300 km in the case of the Dutch colonies) followed by a phase of expansion in the vicinity of the new colony.

The discovery of nesting eiders in The Netherlands was a surprise. Unfamiliar eggs collected by islanders on the islands of Vlieland and Terschelling were shown to visiting ornithologists in 1906 and identified as eider eggs (van Heurn 1952). The settlement of such northern species contributed to the establishment of state nature reserves on the West Frisian Islands in 1925. The early settlement on Terschelling did not persist, but the one on Vlieland developed into a permanent colony. Besides the growth of the original breeding colony, the eider spread to become a common breeding bird in the Dutch Wadden area, nesting on all the islands and occasionally on the mainland coast (Swennen 1976). The Dutch colonies have shown rapid growth in the past, but the overall numbers have stabilised now, suggesting that limiting factors have come into operation as the population became larger. The present paper analyses the underlying population dynamics of the eider population in The Netherlands, in order to assess whether local production is sufficient to explain subsequent growth once a new colony has been founded.

Population units

The breeding populations of eiders on the West Frisian islands are well separated from neighbouring populations. Settlement on the adjacent East Frisian Islands (Germany) started much later (1934) and nesting was still irregular up into the 1980s (Bauer & Glutz von Blotzheim 1969, Swennen 1983a).

The overall Dutch eider population can be subdivided into discrete colonies on each of the larger islands (Fig. 1). Ringing has shown that this separation holds for the females only (Swennen 1990). A subdivision of a colony on an island is biologically less meaningful because nest-site fidelity is not complete (Swennen 1990) and female ducklings from one site may well recruit into another (C. Swennen, unpubl. data).

Development and sizes of the Dutch colonies

All Dutch colonies started with one or only a few nests. During the first 5-20 years, colony size remained below 10 nests, but this period was followed by a period of exponential increase at a rate of more than 20% per year (Table 1). The increase on Vlieland was interrupted by a short stationary phase (1937-1943) after which settlement on the other islands started. By 1960, colonies had become established on all six larger islands of the Dutch Wadden Sea.

Shortly after 1960, a sharp decline occurred, coinciding with high mortality among females during or just after incubation, but males and non-breeders were not affected (Swennen 1972). The mortality during 1962-

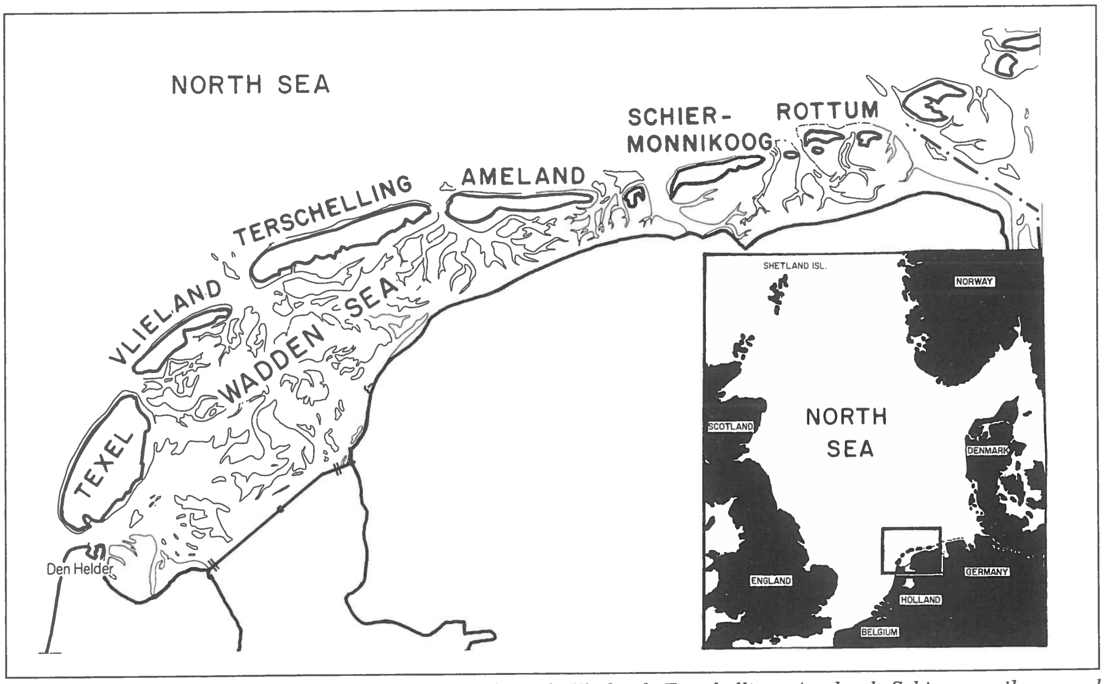

Figure 1. The study area, including the islands of Texel, Vlieland, Terschelling, Ameland, Schiermonnikoog and Rootum.

Table 1. Number of years between discovery of the first nest and the start of a clear increase in numbers (>10) (starting phase), the percentage of yearly increase in the exponential growth phase, and the total percentage of decrease caused by a pollution incident in the early 1960s

Colony	Duration of starting phase	Relative rate increase[1] from the end of the starting phase till 1960	% decrease in the number of nests during 1960-1968
Texel	1942 - 1947	28	95
Vlieland	1906 - 1925	17	75
Terschelling	1941[2] - 1946	27	55
Ameland	1945[3] - 1954	20	40
Sciermonnikoog	1941 - 1955	22	0?
Rottum[4]	1947 - 1968	22 (1968-86)	0

[1] According to the formula: $r = (\ln(N_t)-\ln(n_0))/t$ (Ricklefs 1973: 388)

[2] Earlier a few breeding attempts around 1906 (van Heurn 1952).

[3] Probaly also a few breeding attempts in the early 1930s (Valk 1976).

[4] The eiders breeding on the small island group conventionally summarised as Rottum can be considered to belong to one colony (Nolet 1988)

1968 (peaking in 1965) was caused by a pollution incident involving high concentrations of telodrin and dieldrin in marine invertebrates and fish in Dutch coastal waters (Koeman 1971). The impact of the pollution incident was largest on the westernmost colonies, situated closest to the mouth of the river Rhine, the source of contamination (Swennen 1972, 1976). After a 25% decrease in the total number of nests after 1960, the colonies recovered from 1,329 to 3,878 nests during 1968-1976, a mean rate of increase of 10.7% per year (see figures in Swennen 1976), compared to only 5% during 1976-1980 (see figures in Swennen 1983b). After 1980 data from some colonies are incomplete, but the numbers in all colonies appear to have stabilised in the 1980s, except in the relatively young colony on Rottum, where the number of nests is still increasing.

Vlieland is the oldest and remains the largest of the Dutch eider colonies. Its development has been studied regularly over the years. Its rate of increase slowed down gradually, from 29.8% per year during 1925-1936 to 13.5% per year during 1943-1959. Following a temporary reduction by 75% of the 1960 numbers in the pesticide period, the rate of increase (recovery) was only 4.7% per year during 1974-1988. The general form of the curve of the number of nests in the Vlieland colony is similar to that of Terschelling, which started later: a slow starting phase, an exponential growth phase, a decrease following the pollution incident in the early 1960s, with a subsequent recovery and slow expansion (Fig. 2). In the late 1980s, a small decrease was noted in the colonies on Vlieland and Terschelling.

The Rottum colony, on two of the easternmost and smallest of the West Frisian Islands, was still in its founding phase during the pollution incident. Its period of rapid growth coincided with the phase of slow growth or the stationary phase of the older colonies. Only in the late 1980s did the growth of the Rottum colony seem to level off (see Fig. 2).

Population parameters during the period of rapid increase

Little is known about the population parameters during the exponential growth phases of the Dutch colonies. Clutch sizes mentioned in the older reports are usually five, ranging within 3-6 eggs. This is about the same as the average of 4.74 found between 1964 and 1982 (Swennen 1983b). In the 1930s about 20% of the nests were destroyed by herring gulls *Larus argentatus*, crows *Corvus corone*

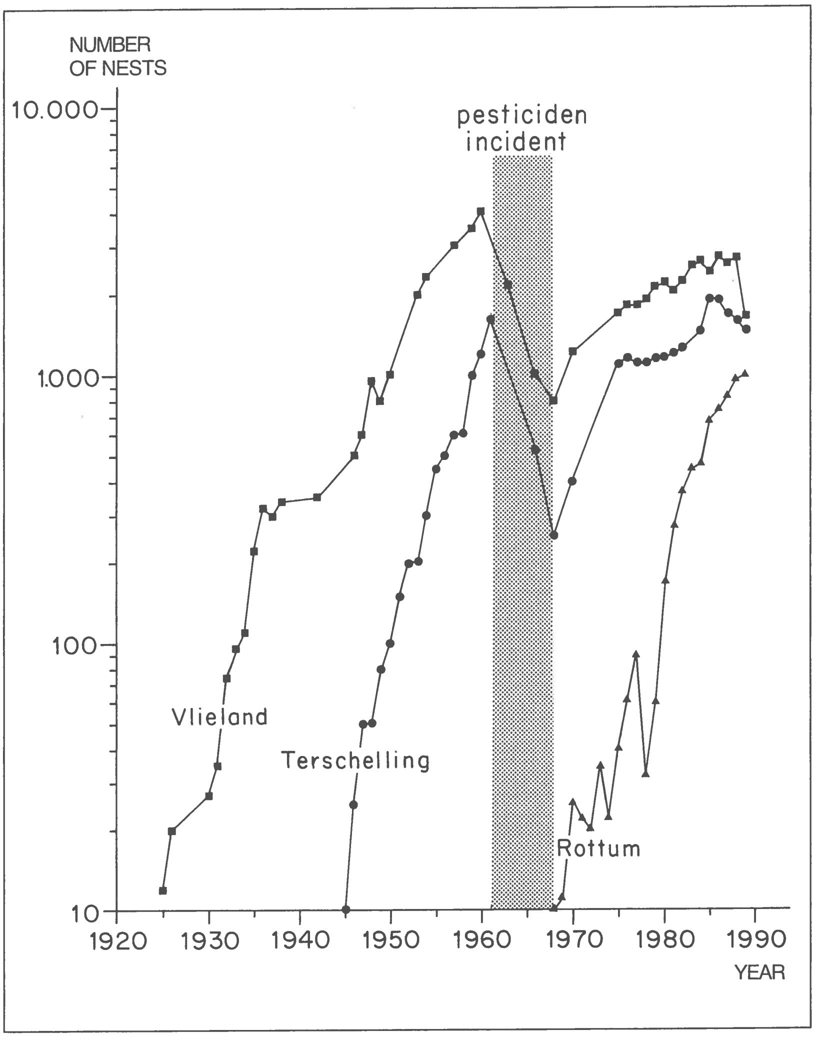

Figure 2. Number of eider nests on the islands of Vlieland, Terschelling, and Rottum during 1920-1988. (Vlieland and Terschelling after Swennen (1976), supplemented with later data; Rottum (= Rottumeroog and Rottumerplaat) after Nolet (1988) and van den Brink (1990)).

and man (van Dobben 1937). This percentage became lower after the culling of breeding herring gulls ended and the colony was less disturbed (Swennen 1983b).

Early recordings of fledging success do not exist. The Annual Reports of the State Forestry on Vlieland state the numbers of large ducklings for 1947 only. Hoogerheide & Hoogerheide (1958) give some numbers of one-year-old birds in spring as a measure of the fledging success in a previous year. We know now that this is not a reliable measure because subadults from the Baltic area also summer in the Wadden Sea (Swennen 1976, 1990). Only since 1963 have fledglings been counted systematically (Swennen 1983b, 1991).

Population growth can only occur when natality plus immigration exceed the sum of mortality and emigration. Mortality will probably have been low, as dead birds have not been reported during the breeding period (which is the peak mortality phase) and as hunting has been prohibited since the 1920s. The exponential increase suggests that growth mainly originates from local reproduction. Growth by a continued immigration would have given absolute increases with more or less constant additions without an initial stationary phase.

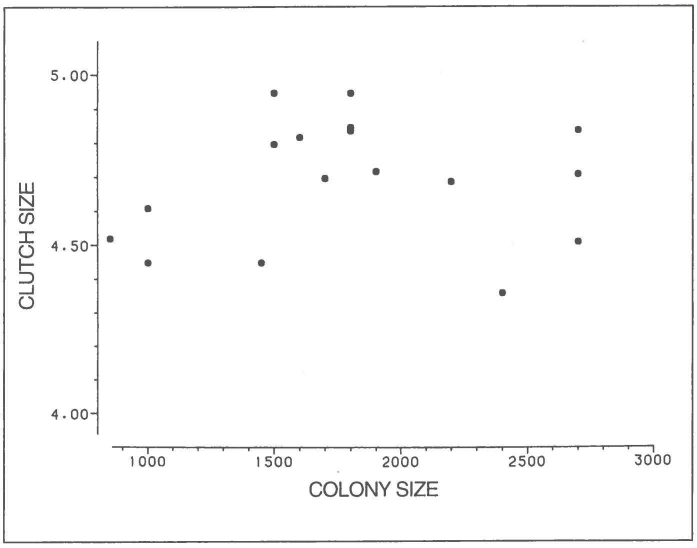

Figure 3. Relationship between the number of nests (colony size) and mean clutch size of the Vlieland eider colony (r= 0.11, N = 17, N.S.). (Data from Swennen, 1983b, and C. Swennen, unpubl. data).

Emigration and immigration

Recoveries of dead ringed birds and retraps or resightings of live birds indicated that nearly all juvenile females recruit into their natal colony when adult, and only a few (1.4%; N = 650) into the neighbouring colony (Swennen 1990). Recruitment from more distant colonies has not been established, but may have occurred on a negligible scale. None of the 7,422 breeding females handled had a foreign ring, while 1% of the females caught during the moulting period (N = 317) had been ringed abroad as fledglings (Swennen 1990). Once recruited, females do not change their breeding colony. Females are philopatric to their natal island and permanent residents, whereas males show a considerable amount of natal and breeding dispersal mainly moving into colonies in the Baltic Sea (Swennen 1990).

Natal and breeding philopatry is strongly developed in female eiders. The establishment of new colonies seldom occurs far from old breeding sites. Settlers must have lost their philopatry. Swennen (1990) suggests that this may happen when adult females are forced to oversummer outside their natal area, for example when they are physically unfit to go to their breeding site after moulting or wintering.

Estimation of the average recruitment rate

Eiders can raise only one brood per year. Mean clutch size per nesting female, i.e. the potential reproductive rate, does not seem to be influenced by population size (Fig. 3). Unhatched eggs and partial egg predation are rarely seen. Average clutch size measured was 4.74 ± 0.16 eggs (year-to-year variation: 4.45-4.95) in the Vlieland colony. Nest success varied. It went down to 66% during the pollution incident in the 1960s, but was 90-95.5% in 1959-1961 and 1970-1990 (Swennen 1983b). It may therefore be concluded that egg mortality is low in areas that are safe for the females.

Mean clutch size of Dutch eiders is on average slightly higher and the year-to-year variation is considerably lower than those of the eiders in the colony on the island of Coquet (England) studied by Coulson (1984): 4.47 ± 1.36 eggs (range: 3.78-5.40). Coulson's data suggest a decline in mean clutch size with increasing colony size.

The effective fecundity, defined as the mean number of young fledged per nesting female, i.e. when the young are two months of age, varies strongly in the Dutch colonies. The average number of fledglings per female seems to be negatively correlated with colo-

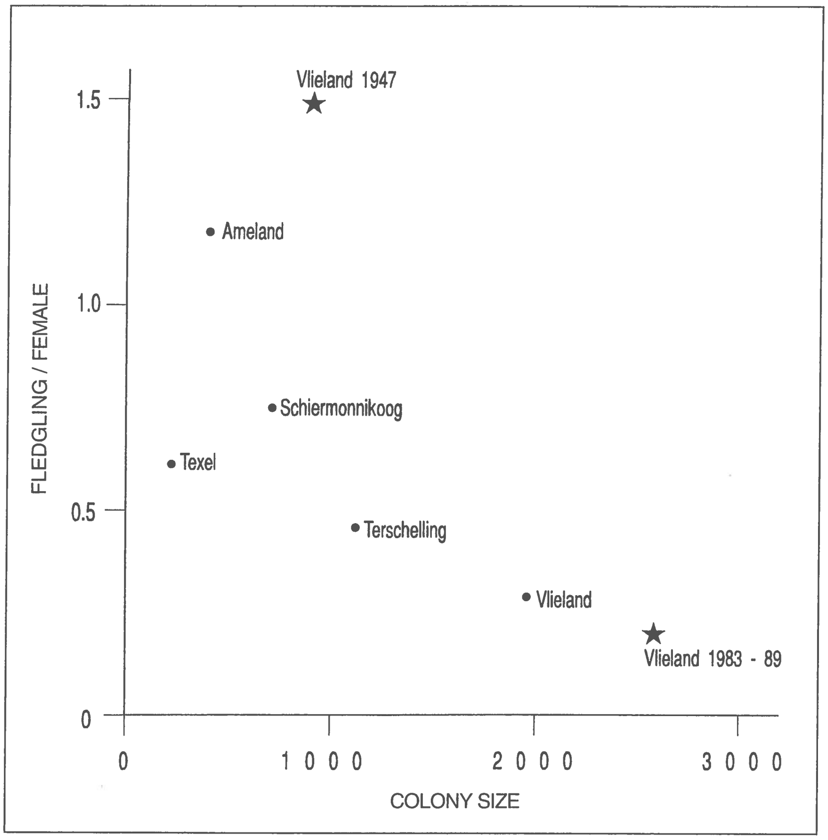

Figure 4. Relation between the mean number of nests (colony size) and the average number of eider fledglings produced per nesting female per year in the five main colonies during an 8-year period (1975-1983); data from Swennen (1983b). Two points (marked with asterisks) of the Vlieland colony have been added: 1947 when the colony was only 900 pairs and average held 2,600 pairs; data from Swennen (1991).

ny size (Fig. 4). Only the Texel colony does not fit well in the series, but see the paragraph on maximum colony size. Duckling mortality occurs during the two months between hatch and fledging. Mortality rates are highest within the first 10 days, peaking around day 5. Food density and feeding conditions are the critical factors. Young ducklings need a rich supply of small food items and enough time for feeding to survive (Swennen 1989b). Infectious diseases and parasites cause mortality among the older ducklings (Swennen 1991). In the Vlieland colony, survival up to the fledgling stage was studied for 27 years. Mainly due to variance in duckling mortality, a highly variable number (between 0.001 and 1.528; on average 0.366) of ducklings fledged per breeding female per year. On average half of the fledglings were females (Swennen 1991).

Subadult mortality occurs during the ca 21 months between fledging and first breeding. Subadult mortality in Dutch eiders often seems to be caused by hyper-infestations with *Polymorphus (Profilicollis) botulus*, an Acanthocephalid intestinal worm (Swennen & van den Broek 1960, and C. Swennen, unpubl. data). Subadult survival has not yet been determined; provisional figures range within 30-60%, depending on the range of years considered. In Scotland, subadult survival was estimated at 67% (Baillie & Milne 1982).

Age at first breeding

No ducks were found breeding in their second calendar year, but several in their third and later years. A provisional estimate indicates that about 37% start nesting in their third calendar year and the rest the following year (J. van der Meer & Swennen, unpubl. data). Baillie & Milne (1982) followed recruit-

Table 2. Monthly percentages of the annual numbers of ringed adult female eiders found dead in the Wadden Sea area during four periods and for the whole period of 1963-1988.

	Month												
Periode	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	N
1963/1968	1	0	1	1	41	46	9	0	1	0	0	0	373
1969/1975	2	3	3	6	19	39	13	3	4	2	2	4	100
1976/1981	3	7	3	11	26	21	9	7	3	6	1	3	122
1982/1988	7	6	7	4	16	20	8	8	8	8	3	5	297
1963/1988	3	4	3	6	26	32	10	4	4	4	1	3	892

ment of the 1976 cohort at Forvie (Scotland) and estimated that 26% of the two-year-old and 42% of the three-year old females bred, and that most females over three years of age attempted to breed.

Adult annual survival rates

Recoveries of ringed eiders give indications of mortality patterns over the year. Although the probability of finding and reporting ringed eiders may not be the same in all months, comparison between years and between males and females may give insight into the overall pattern.

In females, recoveries always peaked in May and June, the months of incubation and hatching. This was most extreme during the pollution incident in the early 1960s (Table 2). Deaths caused by pesticides have not been noted since 1968, although the breeding season remained the most risky period for adult females. Mortality outside the breeding period became gradually more important in the late 1980s and early 1990s. It is not yet clear what factor is responsible for the relative increase in recoveries outside the breeding season.

Contrary to the philopatric females, males gradually disperse (Swennen 1990). Hence recoveries of males can be split up into philopatric males found locally (no hunting) and dispersed males found abroad (Table 3). Philopatric males were most frequently reported from January to August. In most cases the real cause of death is not known. Oiling was the most frequently reported cause of death (19.2% of the recoveries of males in the Wadden Sea) and was highest in winter, with monthly averages of 33-48% from December to March inclusive. Oiled birds have been reported in all years, but 1969 and 1987 showed higher incidence when more than 70% of all recoveries reported oil as cause of death. Dispersed males were nearly all reported from the Baltic Sea and the Danish waters (Swennen 1990). Of these male eiders, 73.5% were reported to have been shot. Drowning in fishing nets was the second most reported cause of death (14.1%), followed by 'unknown' (8.3%). Only 1.7% was reported as being oiled. Hunting in Danish waters is largely responsible for the recoveries between October and February, and hunting in Finnish waters for the peak in April and May (see Table 3). Hunting completely obscures the natural death causes in recoveries from abroad.

Table 3. Monthly percentages of the annual number of ringed adult male eiders found dead in the Wadden Sea area (local) or abroad during 1965-1988.

	Month												
Area	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	N
Local	12	8	10	8	16	13	11	8	3	4	2	5	193
Abroad	4	17	3	14	39	3	1	1	4	9	3	2	420

A higher death rate in the first half of the year with a peak of deaths immediately after incubation, slightly later than on Vlieland, has also been found in England (Coulson 1984). Besides lower food density, the higher mortality in late winter and spring seems to be linked with reduced nutritional value per food item during the early part of the year (Beukema 1974). The movement towards land during the breeding season, with unfavourable conditions for feeding, increased agonistic behaviours, and a greater risk for contagious diseases may induce the peak in the mortality of both sexes during the reproduction period. The higher mortality amongst females during this period may result from the greater stress induced by the longer period on land, their complete fasting for about four weeks during incubation, followed by brood care for at least several days in poor feeding areas.

Provisional survival estimates based on ring recoveries of dead birds (Swennen 1972) indicated that annual survival fell to 0.49 during the peak of the pollution incident. However, from 1969 to the late 1980s the mean survival was 0.957, varying between 0.92 and 0.98. Reappraisal of adult survival from recapture of ringed females during the nesting period on Vlieland, spanning all 28 years of the study but excluding the pollution incident and the 1981 season when fieldwork started later than usual, provides an estimate of 0.95, which is in substantial agreement with the provisional value.

Coulson (1984) found survival rates of adult females varying between 0.756 and 1.000 (on average 0.895) in an English colony over a time span of 22 years. Baillie & Milne (1982) mention a mean annual survival of adult females of 0.96 in Scottish eiders.

Non-breeding

Each year a proportion of females do not breed, but the size of this proportion could not be determined. Usually, the estimates of the number of nesting birds did not fluctuate strongly. It is therefore concluded that the proportion of non-breeders did not fluctuate much either. However, unusually large numbers of females skipped nesting in 1968 and 1989. In 1989, the number of pairs along the coast was about the same as in the previous year at the beginning of the breeding season. However, in 1989 the number of nests was only about 65% of that in 1988. The number of non-breeding females remained high throughout the season. As in 1968, read rings on females resting ashore during high tide indicated that many of them had nested in previous years. Clutch-size and egg-volume were not significantly different between 1988 and 1989.

Weather may be an important factor; especially temperatures in March and early April. In 1968 and 1989, March was very mild with mean temperatures above the long-term average, while early April was cold with temperatures below the average and cooler than in March. Most eiders already came ashore in March where they stayed during April and the beginning of May, while food (cockles and mussels) densities were low in the coastal zone. The incidence of non-breeding females may reflect a food limitation around the larger colonies. Dutch eiders usually start egg-laying during April, immediately after arrival from offshore wintering grounds. Mean date of first eggs on Vlieland is 9 April ± 5.5 days (range: 1-23 April, N = 39 years). Most other females follow within one or two weeks. In the aberant years the birds started on 23 April. An early arrival followed by a delay in egg-laying caused by low temperatures might partly exhaust the reserves needed for laying and breeding. These reserves probably cannot be replenished near the breeding islands if food is locally scarce and bird density is high.

In England, Coulson (1984) observed an increased occurrence of non-breeding females as colony size increased. In two years of his 24-year study, more than 50% of the adult females did not breed. In years with extensive non-breeding, Coulson (1984) also found a significantly lower clutch size amounting to a 28% reduction.

Population balance

To test the premise that population increase in an individual colony is due to local reproduction measured rates of fledgling production can be compared with the number required to maintain population balance. Because of the strong male dispersal, analysis is restricted to females. The expected total lifetime production of daughters per female should exceed one. Hence

$$f\sum_{i=2}^{m} s_{(i)} b_{(i)} \geq 1$$

where f is annual fecundity, i.e. the expected number of daughters produced per breeding female per year, $s_{(i)}$ the survival probability up to age i, $b_{(i)}$ the proportion of breeders at age i and m the maximum age.

The proportion of breeders is assumed to be equal to 0% at age 1, 20% at age 2, 70% at age 3, and 100% at older age (J. van der Meer & Swennen, unpubl. data). Adult annual survival rate is assumed equal to 96%. Survival rate from age 2 to age 3 is set equal to 90%. Thus

$$s_2 f \geq \frac{1}{(0.2+0.9)\cdot(0.7+0.9)\sum_{i=4}^{m} 0.96^{I-3}}$$

When $m = 20$ then $s_2 f \geq 0.0859$, and when $m = 30$ then $s_2 f \geq 0.0655$. This means that on average a single daughter per female should reach the age of first breeding (age 2) once in every 12 year when $m = 20$, or once in every 15 year when $m = 30$. If one begins to count with the time of fledging, $s_{(2)}$ is approximately 50% (ranging from 35 to 65%). Hence f, the average number of female fledglings produced per breeding female per year, should be equal to 0.192 (when $m = 20$, or 0.131 (when $m = 30$), in order to assure that the population remains stable. It is assuring to note that this level of fledgling production has been achieved by the Vlieland colony in recent years (see the data points for 1975-1983 in Fig. 4) when the colony counts suggest a stable population (see Fig. 2). More importantly, the higher fledgling rates observed in the Vlieland colony during its active growth phase (1947) and for the other Dutch islands before the period of stability at the individual colony level (see Fig. 4) help to substantiate the claim that local production is sufficient to explain the observed population increase.

Theoretically, population growth rates could amount to about 50% per year with an average of 4.74 eggs (Swennen 1983b), a breeding success of 80% (van Dobben 1937), an even sex ratio at hatch (Swennen, Duiven & Reyrink 1979), first breeding in the third calendar year, hypothetical mortality rates of 35% up to first breeding, and 4% mortality per year in the adult females (see above). Such a theoretical rate of increase is sufficient to explain the observed lower rates of increase during periods of rapid exponential growth (see Table 1).

A control of the composition of the Vlieland colony

The importance of local production of female recruits for the maintenance of a colony is also shown amongst controls of ringed birds. Breeding females have been ringed on Vlieland nearly every year since 1963 (Swennen 1989a, 1990). Fledglings have been ringed since 1964 but only in some years. About 4,500 adult females and 10,500 fledglings have been ringed in the Dutch colonies. In the 1989 breeding season, controls amongst 109 ringed adult females showed that 55 were ringed as ducklings (50.5%). This percentage might have been higher because ring wear in the early part of the ringing study was such that the birds lost their rings after 6-20 years (Swennen 1968, C. Swennen, unpubl. data). Among ringed females retrapped in 1988 and 1989, 97 were ringed as ducklings during 1964-1974. None retained original rings, because all had been replaced during earlier controls (23 had had their ring replaced twice). Only a small percentage of the females could be reringed at a time. Therefore, many females without rings may have been retraps that had lost their original ring. Moreover, fledglings were ringed in only a few years and it was never possible to catch all fledglings. It would therefore appear from the ringing data that the greater part of the breeding female population was recruited from the local production of fledglings.

Maximum colony size

The Dutch part of the Wadden Sea is used by 100,000-200,000 eiders for wintering. Only about 10% of these birds belong to local breeding populations, the others originate from the Baltic Sea. While the total Baltic-Wadden-Sea population is still growing, the numbers of wintering birds in the Dutch Wadden Sea have not increased markedly since the 1970s. This suggests that the carrying capacity of this area for adult birds must now have reached its upper limits at an average of about 100 bird-days per ha per year (Swennen, Nehls & Laursen 1989). Local birds may have an advantage over foreigners, because the local colonies grew during this period. Up to the end of the 1980s, evidence for severe food limitation was not available for this part of the Wadden Sea.

The number of nests in several of the older Dutch colonies increased gradually slower and fluctuated or decreased in the late 1980s, while some young colonies were still growing. Population size appears to be approaching saturation level in these old colonies. Which density dependent processes limit these populations: adult survival, recruitment or both?

Coulson (1984) found a higher mortality in adult females and an increase in the proportion of non-breeders when his English colony became larger. The proportion of non-breeders could not be established in the Dutch colonies due to the large numbers of oversummering common eiders from the Baltic Sea, but a provisional analysis of the ringing data suggests that female mortality has increased in the 1980s. Several factors may be responsible. The expanding colony on Ameland entered an area with pools inhabited by high numbers of duck leeches, *Theromyzon tessulatum*, which caused heavy mortality among eiders exploring these pools as new nesting grounds in spring (C. Swennen, unpubl. data). Higher nest densities also have promoted outbreaks of contagious diseases on the breeding grounds when females are more susceptible because of the stress of the long fast. An epizootic of fowl cholera (pasteurellosis) killed nearly all nesting females in a section of the colony on Vlieland in 1984 (Swennen & Smit 1991), and similar cases have been found along the coast of Maine (Korschgen, Gibbs & Mendall 1978). Higher population densities also promote severe infestations with helminth parasites (Trematoda, Acanthocephala, Cestoda) causing weakening and even death in eiders (Swennen & van den Broek 1960, Thompson 1985). However, the somewhat higher mortality among adults seems to have only a minor effect on colony size.

Concerning recruitment, the data of Coulson (1984) suggest a decline in mean clutch size with colony size. No density effects on clutch size could be shown in the present study (see Fig. 3). There is, however, evidence for a density-dependent decline of the breeding output in the oldest colonies (see Fig. 4). This suggests that some form of competition or interference occurs during the brood-raising phase. Although no direct evidence for a possible mechanism can be advanced at this stage, it is illuminating to consider the total area of each island suitable for the young ducklings. The total nursery area of each island seems to correlate with the maximum colony size (Table 4). Data from the colonies of Ameland and Schiermonnikoog are incomplete but seem to fit

Table 4. Maximum number of nests in the stabilised eider colonies and the size of the area of nursery grounds.

Colony	Maximum size (nests)	Nursery area (km^2)
Texel	300	1.75
Terschelling	2000	8.25
Vlieland	3000	9.35

well in the series. The still growing Rottum colony (see Fig. 2) has a nursery area of 9.0 km^2. One must keep in mind that the nursery areas gradually differ in several quantitative aspects so that area alone is only a rough standard.

CONCLUSIONS

Data on colony growth, female philopatry, fledgling output and mortality, indicate that local reproduction is the main source of recruits into the Dutch eider colonies after the first settlement by one or a few pairs of immigrants. Continued immigration of birds from abroad could not be proved; if occurring, it plays a minor role.

Population size appears to be approaching the saturation level in several Dutch colonies. There is evidence for a density-dependent decline of the breeding output in the oldest colonies by some form of competition or interference during the brood-raising phase. Lower duckling survival appears to be the main cause of the decrease in growth of the older Dutch colonies.

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