Introduction
After a period of strong increase and establishment of new colonies in the Cormorant population of the IJsselmeer area, growth levelled off. This occurred after a lake-wide crash in breeding numbers in 1994, following a year with an extremely poor breeding success. In recent years, the Cormorants shift their breeding site more and more towards the central and northern parts of the nearby lake IJsselmeer. Here we analyse whether the redistribution of the birds in the different colonies resulted in stabilizing numbers and a maximised output of young per couple.

Key words: Cormorants, carrying capacity, population expansion, density dependence,

Methods and study area
Annually counts were made of breeding pairs in the IJsselmeer colonies, assessing breeding colonies’ output of fledglings later on (cf Van Eerden & Gregersen 1995 for methods). Distribution of adults over the feeding waters was based on monthly aerial counts, with additional information collected by observations from ships and from the shores.

Results
In the Netherlands Great Cormorants Phalacrocorax carbo sinensis breed in the IJsselmeer area in four colonies: Oostvaardersplassen, Lepelaarplassen, Naardermeer and Enkhuizen. All colonies are situated on the edge of the central lakes (183,000 ha of freshwater) in the eastern and southern part. The population development of the Dutch sinensis group has been extensively described by Van Eerden et al. (1991), Van Eerden & Gregersen (1995). The growth of the Dutch population has started from the old colony Naardermeer, in a well protected wetland at the southernmost part of the lake system. In 1970 about 2,000 pairs bred in Naardermeer, in 1985 this number had risen to 4,480 pairs. Part of the young produced in this colony did not settle in their ‘mother colony’ but was present as non-breeders in the IJsselmeer area during the 1970s. In 1978 the Oostvaardersplassen freshwater marsh was founded on new territory in the reclaimed Flevopolder, in 1985 Lepelaarplassen followed and very recently Enkhuizen-de Ven on the West shore in 1990. This growth ran parallel to expansion to other places in The Netherlands, Denmark and other localities in western Europe where sinensis breeds (Van Eerden & Gregersen 1995). The rapid increase in number of breeding pairs in new colonies could only be explained by the presence of a large non-breeding cohort. Later, also the returning young from the colony further speeded up numbers. Lepelaarplassen, which was founded between Naardermeer and Oostvaardersplassen, partly originated from Naardermeer birds, the shifting of colonies resulting in a better position for the individuals which had moved with respect to the distance to the fishing waters (Van Eerden & Gregersen 1995).
Suddenly, in 1994 the number of breeding pairs dropped dramatically (Fig. 1). Compared to the year before the maximum figures were Oostvaardersplassen 4,400 pairs (8,000, 55%), Lepelaarplassen 2,600 pairs (5,500, 47%) and Naardermeer 1,850 pairs (1,875, 99%). Thus, Naardermeer was amply affected. This sudden decline occurred in all colonies which rely for their food provisioning on lake IJsselmeer and Markermeer. Even the colony of Enkhuizen, only recently established, decreased from 509 pairs in 1993 to 296 in 1994. Naardermeer birds had started to exploit the lakes in the interior part of Noord-Holland and Utrecht as well as the border lakes between Flevoland and the mainland. This crash did not occur at other places in The Netherlands. There numbers stabilised or slightly declined (SOVON, A.J. van Dijk unpubl. data). Because of the importance of the IJsselmeer population for the country's total, the Dutch population experienced a decrease from 20,460 to just over 14,000 pairs. In later years the IJsselmeer population stabilized around 10,000 pairs (2000), whereas the Dutch population as a whole levelled off at some 20,000 breeding pairs. The Markermeer colony of Lepelaarplassen experienced another dramatic fall in numbers in 1999, the Oostvaardersplassen earlier also in 1987; these were, however, not recorded elsewhere in the region. The conclusion is that the IJsselmeer colonies, being the largest part of the breeding population in the Netherlands, crashed in number of breeding pairs because of one or several lake related factors.

![Figure 1. Number of breeding pairs in the IJsselmeer colonies (1970-2001)](image)

The colony of Enkhuizen has expanded recently and the mayor part of the nests were constructed on the ground in dry reed-land. The scarce presence of trees and bushes were occupied in an earlier stadium. The colony is still far from being limited by available nesting space. Predators like Fox (*Vulpes vulpes*), Polecat plus American Mink (*Mustela putorius* & *M. vison*) and possibly Pine Marten (*Martes martes*) may cause considerable mortality amongst young Cormorants and eggs. Ground-nesting is therefore nowadays very much restricted to the most remote parts in the old IJsselmeer colonies (islet situations). In the colony of Enkhuizen-de Ven still no foxes occur.
The recent occupation by Cormorants of the nesting site Enkhuizen is in line with predictions by the Hinterland hypothesis as formulated earlier (Van Eerden & Gregersen 1995). The new colony is situated closest to the central, least exploited part of the lake system.

**Fledging success and total reproductive output**

Besides the number of breeding pairs occurring in a colony, the breeding success in terms of number of fledged young per nest is a relevant measure of colony performance. The number of fledglings is a first indication of the expected development of the population on the longer term. The last couple of years this fluctuated between 0.25 and 1.0 fledged young per breeding pair for the old colonies (Naardermeer, Lepelaarplassen, Oostvaardersplassen). Earlier, during the 1980s, more young fledged, between 1.5 and 2.5 per nest on average (Van Eerden et al. 1991). The fluctuations often occur synchronously between the different IJsselmeer colonies. This is caused by a factor operating simultaneously on all IJsselmeer colonies: the wind-driven turbidity which affects detectability of fish (Van Eerden & Voslamber 1995). In terms of young production, 1993 was the worst year, since these data were gathered annually since 1981. This was the year preceding the crash in numbers. Already during and also after this event output of young was greater. Total number of young fledged fluctuated between 4,800 and 17,400 per annum. Again, the levelling off in reproductive rate is clearly visible suggesting a density dependent effect with total output stabilising around 10,000 young fledged. The colony of Lepelaarplassen, bordering the Lake Markermeer incurred another poor year in 1999 when both a sharp fall in numbers coincided with an extremely low breeding success. In fact this colony crashed for the second time in succession. The colony of Enkhuizen-de Ven is very productive still, even in the poor year 1999, consistent with the predictions of density dependence.

![Figure 2. Total output of young in the IJsselmeer colonies (1991-2001)](chart)
In conclusion we make two points here: first, breeding output is related to colony phase, expanding newly established colonies having a higher breeding success. Second, the colonies’ breeding output may increase after a so called crash event, a sudden decline in number caused by an external factor. Both effects point to density dependent production of young, i.e. a (food) limited capacity of the environment related to the number of birds that make use of it.

Discussion
In 2000 the colony near Enkhuizen started to expand (1355 nests) followed by an outburst resulting in 3,065 pairs in 2001. We suspect the growth in Enkhuizen therefore to originate from an exodus of Lepelaarplassen birds, the colony with the worst hinterland. The reduced number of fledged young per couple in the old colonies can be interpreted as a density dependent regulation. At the high density of breeding pairs, the food provisioning for the young would become more difficult which could lead to the production of fewer young. The question is why this crash was so severe and not just happened as a regular decline over more years? One of the proximate reasons might be the weather in 1994. In February a cold spell of two weeks occurred after a period of mild weather. Only by 24 February milder weather reached The Netherlands, but ice occurred at lake IJsselmeer well into the first week of March. It may well be that many birds which had come close to the colonies late February suffered from this cold spell and delayed breeding (or skipped breeding completely). Consequently, fewer eggs were laid (unpublished data K. Koffijberg), but fledging success was not extremely bad. The weather was probably important in delaying the onset of breeding but cannot explain the crash-like reduction in breeding numbers. The other colonies in The Netherlands experienced the same cold-start weather situation, but had no such drop in breeding numbers, so the prime factor must be linked to lake IJsselmeer.

Future developments
Breeding space has never been limiting colony size. All colonies are situated in rather young woods consisting of willow *Salix alba*, *S. viminalis*, *S. cinerea*, in Oostvaardersplassen and Lepelaarplassen and Black Alder *Alnus glutinosa* in Naardermeer. In all colonies, ground breeding also occurs, although this habit has decreased as a result of the presence of Red Foxes *Vulpes vulpes*. Also in future there will be enough space for breeding; the reforestation of the abandoned parts of the colonies takes time but may generate new possibilities within fifteen years from now. Foxes will undoubtedly reach Enkhuizen and may cause a further dispersal of this group. However, as pointed out by Van Rijn & Van Eerden (2002) some 75 sites in the area have potential as breeding place, so breeding space will not be limiting the colonies. After the crash observed in 1994 the population of the Great Cormorant has not recovered to the previously recorded number. Through density dependence a maximum number of breeding pairs is determined, most likely through competition between adults at the fishing waters. In the IJsselmeer situation the eutrophication process was responsible for the increase, enhanced by the over-fished situation leading to small sized fish. This pattern might be valid for the situation in many European freshwater and shallow coastal waters. If so, then the desired future with fewer nutrients and a sustainable fisheries aimed at higher stocks of predatory fish will definitely mean less space for Cormorants. Depending on the final lower levels of nutrient loads and on the resilience of the water systems (Scheffer 1993) the future state of many freshwater bodies supports fewer Cormorants. We therefore stress the importance of habitat and system management other than species management to reduce the conflicts with Cormorants. Only in this way the problems
encountered can be solved at a European scale, whereas other attempts will most likely fall into the category “mission impossible” (cf Van Eerden 2002).

References


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