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van Eerden, Mennobart R.; Voslamber, Berend

Published in:
Ardea

Publication date:
1995

MASS FISHING BY CORMORANTS *Phalacrocorax carbo sinensis* AT LAKE IJSSELMEER, THE NETHERLANDS: A RECENT AND SUCCESSFUL ADAPTATION TO A TURBID ENVIRONMENT

MENNOBART R. VAN EERDEN[1] & BEREND VOSLAMBER[1,2]

ABSTRACT The habit of mass fishing by Cormorants at lake IJsselmeer, The Netherlands, is a recent phenomenon. During the first half of the 1970s the birds changed behaviour probably as a result of the deteriorating under water visibility in the lake (3-4 m water depth). The behavioural switch coincided with years of high numbers of Smelt *Osmerus eperlanus* and Ruffe *Gymnocephalus cernuus* present in the southeastern part of lake Markermeer, the birds' main fishing area at that time. Social fishing by Cormorants is directed towards the catch of relatively small, pelagically dwelling fish. It is argued that for a large water system where social fishing is the rule, a minimum colony size of *c.* 1000 pairs is required. Typically each colony had one socially fishing group (4000-5000 birds) that slowly changed position through the course of the day. Depending on the direction of the wind the flock's position could greatly change between days. Hunting speed was measured and coincided with maximum swimming speed of medium sized fish prey (15-25 cm). Hunting speed increased during the season probably as a result of the greater swimming speeds of the fish at higher temperatures. Intake rate was closely linked to the birds' position within the flock indicating local depletion of the fished water layer. Mass fishing was especially rewarding at intermediate light intensities under water (50-80 cm Secchi depth, or 300-500 $\mu E.m^{-2}s^{-1}$ at 40 cm depth). The habit of pushing up the fish against the light back-ground of the clear top water layer was only possible when wind caused no greater turbidity than 40 cm Secchi depth (100 $\mu E.m^{-2}s^{-1}$) which is considered a breakpoint for this kind of behaviour. Adapting the habit of mass fishing effectively enabled the birds to exploit the turbid, rapidly changing environment which resulted in the extension of the foraging range thus maximising colony size relative to the resources available.

[1]Rijkswaterstaat Directorate Flevoland, P.O. Box 600, NL-8200 AP Lelystad, The Netherlands; [2]Zoological Laboratory, University of Groningen, P.O. Box 14, NL-9750 AA Haren, The Netherlands.

INTRODUCTION

Fish eating birds often hunt together to exploit a common prey. The birds form dense flocks, line- or V-formations to concentrate their prey. The behaviour has been recorded in various groups of species frequenting freshwater habitats as egrets, herons, spoonbills and waders (walking), pelicans (swimming), grebes, mergansers and cormorants (diving)(see Cramp & Simmons 1977, 1983). Also at sea, shearwaters, petrels, gannets, auks and penguins are commonly found in dense flocks when food is abundant (Nelson 1980). Bartholomew (1942) describes mass feeding in Double-crested Cormorants *Phalacrocorax auritus*.

The food habits of the Cormorants *P. carbo sinensis* of lake IJsselmeer in The Netherlands were studied intensively in 1938 (Van Dobben 1952) and 1971 (De Boer 1972). However, these authors never observed mass fishing to the extent as is recorded nowadays. During the 1970s an increasing number of Cormorants started breeding in The Netherlands, primarily as a result of expansion in the area of lake IJsselmeer (Zijlstra & Van Eerden

1991, Van Eerden & Gregersen 1995). First the numbers in the colony Naardermeer and later in Oostvaardersplassen and Lepelaarplassen increased considerably. Nowadays these colonies are among the biggest in Europe and mass fishing is the rule in the area of lake IJsselmeer. Already during the 1960s social fishing by the birds from Naardermeer was recorded incidentally in the border lakes between Flevoland and the mainland during late summer (Poorter 1967). In the course of 1970s the birds of Naardermeer changed their feeding behaviour from almost entirely solitary fishing (De Boer 1972) to fishing in large flocks. This was also the typical habit for Oostvaardersplassen birds in the 1980s. In the beginning the fishing flocks consisted of some hundreds of birds. Nowadays several thousands of birds (up to over 10 000) may be found in one flock.

The aim of this paper is to describe the apparent behavioural switch which occurred, to analyse the conditions under which mass fishing operates and to assess its possible benefits. The study was initiated during the summer of 1982 in the area of lake IJsselmeer and Markermeer (Voslamber 1988), and is extended here with recent data.

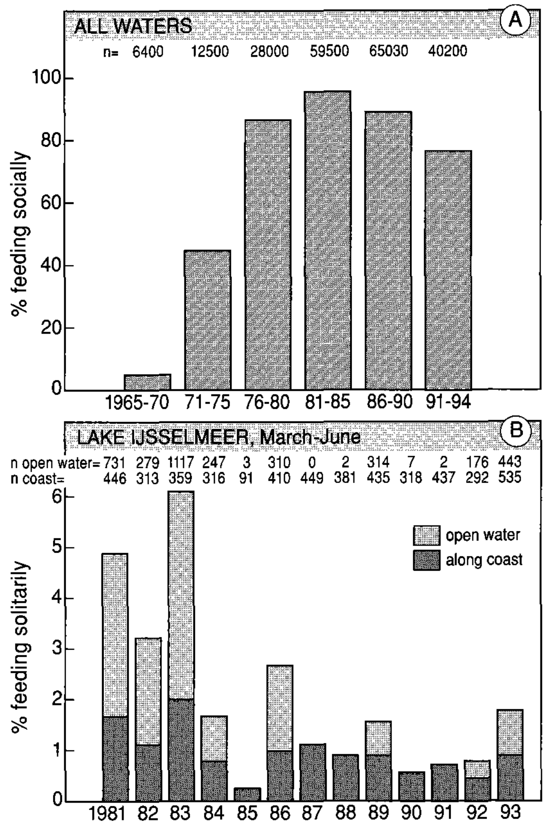

Fig. 1. Occurrence of mass fishing of Cormorants belonging to the IJsselmeer colonies Oostvaardersplassen, Lepelaarplassen and Naardermeer: (A) proportion of social fishing based on number of birds leaving the colony, March-June; (B) proportion of solitarily fishing birds based on monthly aerial counts of lake IJsselmeer and Markermeer (1981-1993). To avoid counts of nonbreeders the area comprised only the southern half of the lake where the colonies are situated.

METHODS

Occurrence of flocks

Observations from the edge of the colonies were used to assess the number of birds that attended either the socially fishing groups or went out to fish solitarily. Data before 1975 were drawn from De Boer (1972), partially reconstructed from student reports and through E.P.R. Poorter (pers. comm.). Monthly aerial counts of the entire lake were conducted since 1979. Directly within the area where birds from the nearby colonies habitually foraged (i.e. south of the line Medemblik - Rotterdamsche Hoek in the Noordoostpolder) the presence of singly foraging Cormorants was recorded during these counts to avoid the bias of counting or missing large flocks. We used the coastal zone (*c.* 2 km from the dike) which was counted integrally as well as 13 transects over open water to calculate the proportion of singly operating birds, relative to the number of birds in the colonies (breeding census).

During 1982 the positions of fishing flocks were determined on a daily basis throughout the breeding season. The flight traffic was used to determine the origin of the birds with respect to the colonies Naardermeer and Oostvaardersplassen. Flocks were registered from the shores of the lake using triangular positioning with the aid of distinct landmarks on the opposite shore. Also aerial and ship based observations were made, the latter using High Fix and, after 1986, Trident radio beacon navigation systems with an accuracy within *c.* 30 to 1 m respectively.

Fishing behaviour

To describe the movement patterns of the fishing flocks, their position was determined by means of a range-finder (Barr & Stroud, Glasgow, Rangefinder No. 12 MK VII, type FT37-No 817, 80 cm base). Flocks were spotted from a dike up to distances of 1.5 km. Changes in the position of the most dense, front part of the flock were used to calculate average swimming speed. Average density was estimated from mapping the contours of the flock and the total number of birds present, best counted at the time of break-up when birds flew away. Foraging success was determined by counting successful birds (with prey or swallowing), coming to the surface in runs of maximal 25 as watched through a telescope in fixed position. In this way any effects of within flock depletion could be assessed.

Flock fishing and light regime under water

Because turbidity was expected to play an important role in determining the birds' performance under water, observations on Cormorants were linked to an extensive programme of investigations about the water quality of lake Markermeer (Van Duin 1992). On a continuous basis environmental and under water light conditions at a depth of 0.4, 0.65 and 0.9 m. were registered from a pontoon, *c.* 3 km NE of Marken. Under water Quantum sensors LI-COR 192-SB were connected to a Campbell datalogger. Under water light was measured every minute and the average value per hour was stored in the database. Here we use the data from April-June 1988. Cormorants were recorded as present in the region when they were within a 5 km radius of the measuring unit, excluding the sheltered area of the Gouwzee which is known for its different light climate.

RESULTS

Occurrence of mass fishing

The development of mass fishing in the area of lake IJsselmeer happened quite recently, with a marked increase during the period 1970-1975 (Fig. 1A). In the past few years a tendency of increased solitary fishing becomes visible, which is caused by more birds feeding on the border lakes or inland on smaller sized waters. However, at lake IJsselmeer and Markermeer the aerial counts show that the proportion feeding solitarily continued to decrease during the 1980s, especially at the open water (Fig. 1B).

Figure 2 shows the daily pattern in number of birds attending the mass fishing aggregations. The massive early morning flight out of the colony to the common fishing site is followed several hours later by the first return flight causing a stabilisation of bird numbers on the water. During the 1980s birds from a colony usually stayed in one single fishing flock of 4-6000 Cormorants (maximum up to 10 000, including fledged young in July), with a continuous stream of birds flying back as a living chain, guiding the newcomers to the exact place.

Foraging patterns and intake rate

A flock consisted of a dense front (2-3 birds.m^{-2}, of which 1.5-2.5 birds.m^{-2} under water), mostly shaped as a half-moon. Behind the front a less dense (0.2-1.5 birds.m^{-2}) part follows, all birds swimming in the same direction, on the edges heading slightly outward. A large flock of 5000 Cormorants thus covers 0.5-0.8 ha while hunting in a cohesive flock, after lateral expansion of the front lines this may be even 2-3 ha, after which re-orientation follows. In the back lines birds are drying their wings and wait for a while before taking off to fly back to the colony. Others lagging behind fly to the front line to achieve a better position, often diving towards the approaching front. Typical flock configurations are depicted in figure 3, including the 'resting flock' consisting of birds waiting for further information of where to go. Such flocks occurred at times of

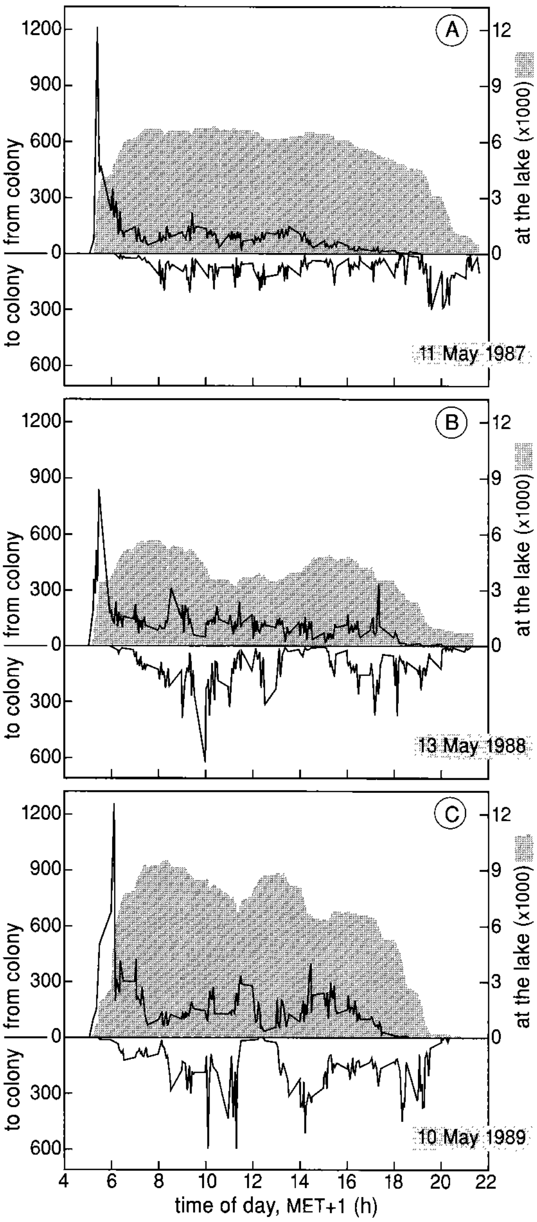

Fig. 2. Flight pattern to and from the colony Oostvaardersplassen throughout the day and the calculated number of birds fishing in a single social flock formation with: (A) uniform pattern; (B) two major flight peaks; (C) three peaks.

foggy weather or after the sudden break-up of the string of flocks of flying birds after a massive homeward flight. The newcomers then landed on the water somewhere on the track towards the fishing grounds without starting to fish.

While fishing, two distinct movement patterns could be recognised: (1) line-hunting and (2) zigzag-hunting. During line-hunting birds move through the water in a more or less straight line. From above, the flock is crescent shaped. A lot of birds fly from the rear to the front, which gives the observer the idea of a rolling flock. Seen from the side, zigzag-hunting gives the idea that the birds are diving in a disordered way. From above, however, we observed that the birds are searching a certain area while they are quickly changing direction (Fig. 3C). This is accompanied by a lot of splashing of water and many birds flying.

The two patterns of social hunting found were associated with the kind of prey the birds were after. Line-hunting was found especially when the birds were catching small fish like Smelt *Osmerus eperlanus* and Ruffe *Gymnocephalus cernuus*. Zigzag-hunting alternated always with line-hunting. It was recorded when the birds were catching larger fish (> 15 cm) like Roach *Rutilus rutilus* and Perch *Perca fluviatilis*. In this case foraging success during the preceding line-hunting phase was very low. We interpreted it as a way to concentrate and to exhaust fish in order to be able to catch them during the zigzag phase. Mean swimming speed during zigzag-hunting was higher than during line-hunting: 1.33 against 1.04 $m.s^{-1}$. In large lakes with a flat bottom like IJsselmeer this habit of social fishing is very successful, because fish cannot escape into crevices, neither under stones nor in the vegetation.

To understand these patterns functionally it is important to know the size of the fish that were actually caught. Sometimes it proved possible to estimate prey length in the field, but a better impression was got from otoliths found in pellets in the breeding colony the next day. The average length of fishes ingested as reconstructed from otoliths was between 5 and 25 cm (Fig. 4). The maximum swimming speed of a fish is roughly

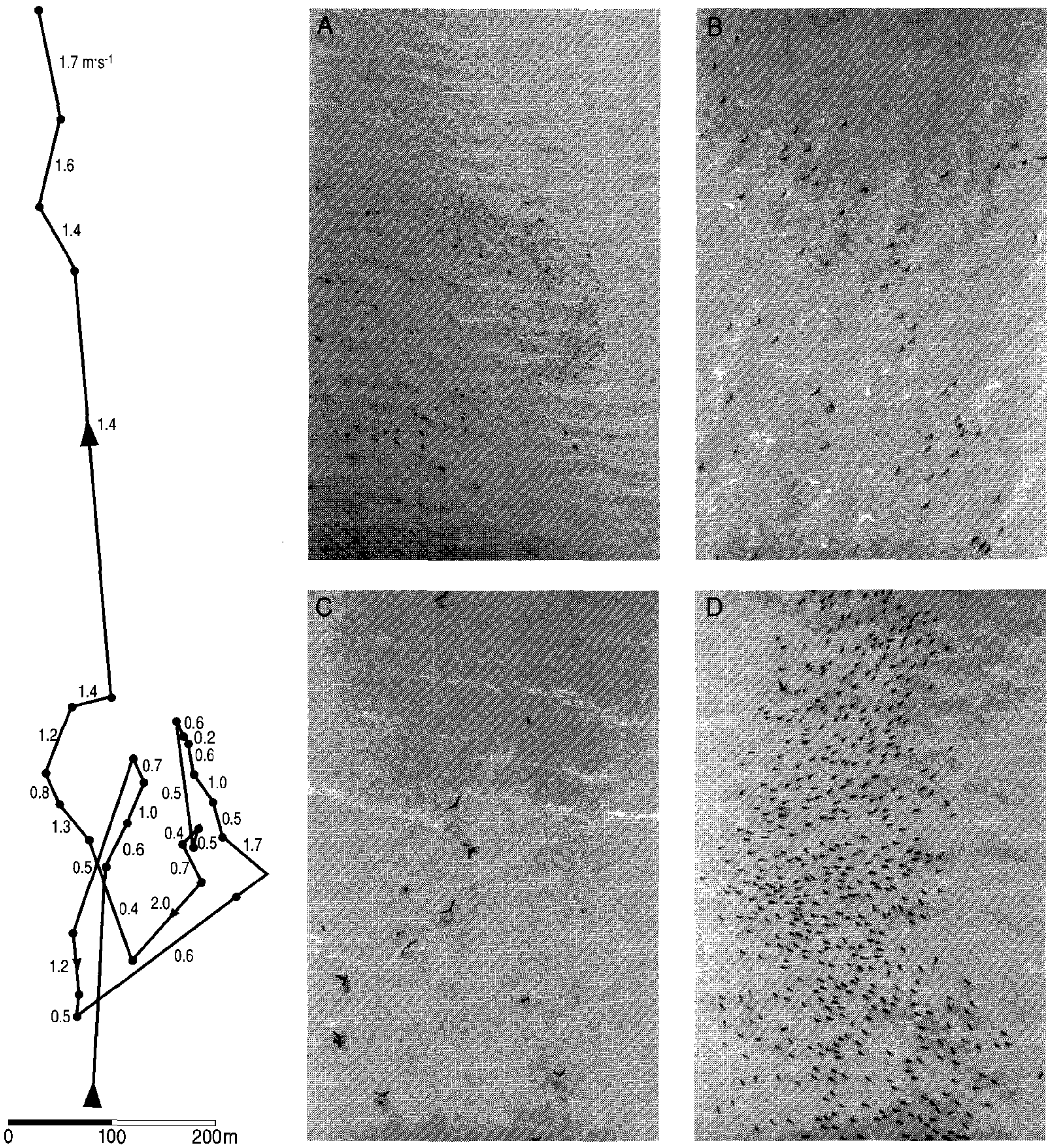

Fig. 3. Typical example of the movement pattern of a group of fishing Cormorants on 22 April 1982 as recorded by a rangefinder showing line-hunting and zigzag-hunting (left) and several overhead views of fishing flocks from aerial photographs (right): (A) typical half moon formation; (B) close-up of line hunting phase; (C) close-up of zigzag hunting with a lot of flying; (D) resting flock waiting for other birds indicating the exact location of the assembly of socially fishing birds.

estimated to be ten times its bodylength (see discussion in Voslamber 1988). So maximum swimming speed of the fish caught by Cormorants was about 0.5-2.5 $m.s^{-1}$. Fish can swim this maximal

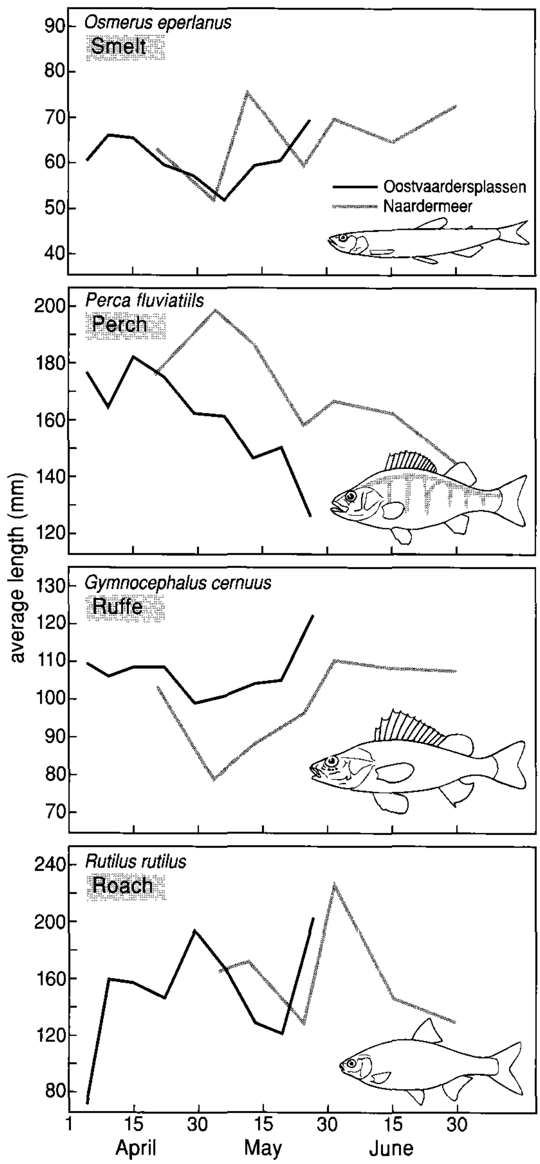

Fig. 4. Average fish length (mm) of the main species in the Cormorants' diet in the course of one breeding season, Oostvaardersplassen and Naardermeer, 1982. Notice the simultaneous pattern for both colonies and the overall decrease in average length of Perch taken.

speed only for a few minutes. After a period of burst speed a fish has to recover for a period of up to 24 hours (e.g. Wardle 1977). So if Cormorants are able to exhaust fish, they have a prey which is easy to catch. Average swimming speed of socially fishing Cormorants increased from 0.9 $m.s^{-1}$ in March till 1.4 $m.s^{-1}$ on average in May, steeply decreasing during the last days of May (Fig. 5A). In June average swimming speed again increased. These values are well above the estimated 0.6 $m.s^{-1}$ optimal swimming speed for a submerged diver like the Cormorant (Videler & Nolet 1990). The overall trend, pooling the data for 26 different days (1135 measured speeds) is statistically significant ($r_s = 0.37, p < 0.05$). Average hunting speed by Cormorants thus equals or exceeds maximum swimming speed of their main prey which means an effective exhaustion. The slight increase in swimming speed of the flocks might well be related to the higher swimming speed of fish due to the increased temperature in the course of the season. Also the decrease in average length of Perch which was noted, could be a result of the higher chance of escape of coarse fish at higher temperatures in the course of the spring. Figure 5B illustrates size and temperature dependent effects on swimming speed for 5, 10 and 20 cm Perch, after Wardle (1977, 1980).

During several occasions observations on intake rates over a longer period of time could be collected. Figure 6 shows one of such cases where Cormorants were fishing on Smelt. Foraging success was sharply linked to a bird's position within the flock, indicating a depletion of fish stocks within the waterlayers covered by the birds. This deduction from direct observation fits the generally recorded 'rolling' pattern of flocks, where birds from the back lines join or overfly the front to achieve a better position. Indirectly also the presence of scavengers as Black-headed Gulls *Larus ridibundus* indicated the presence of damaged fish which are being caught especially in the front lines of the fishing assembly.

The choice of the foraging location

The daily mapping of fishing flocks was used during the 1982 breeding season to find out whether there were regular patterns in the distribution over the lake. In fact no systematic pattern

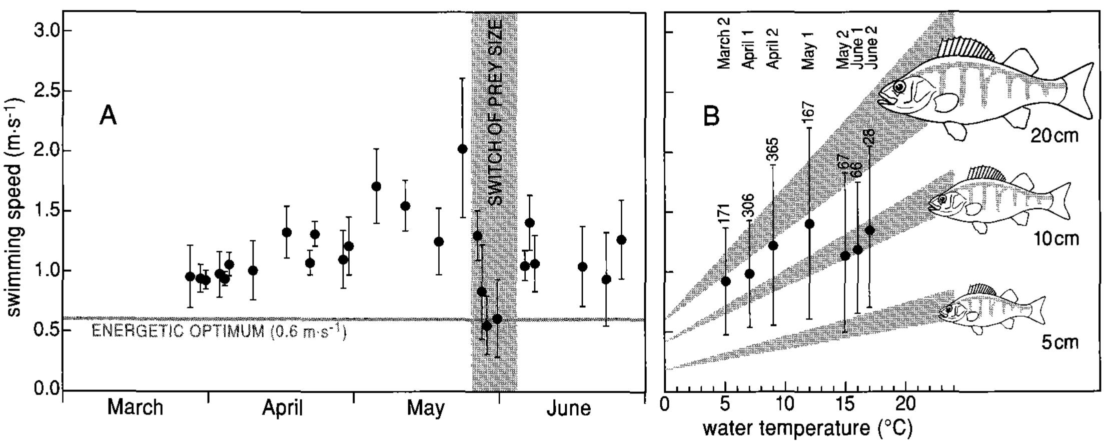

Fig. 5. (A) Swimming speed of mass fishing Cormorants (average per day ± 95% *C.L.* in the course of the season; (B) Maximum swimming speed of freshwater fish in relation to water temperature and fish size. Range per size class gives extremes in reported values according to Wardle (1977, 1980). Average swimming speed by Cormorants (± 95% *C.L.*) is also plotted against water temperature, taking all data from zigzag and line-hunting together. Notice the general increase in average swimming speed and the shift to a lower level late May, suggesting a switch to smaller prey which is in accordance with the data for Perch in Fig. 4.

was found, but instead there were great differences from day to day. It turned out that wind was an important factor determining the exact location of the mass foraging. How can wind influence the choice of the feeding place? Two factors appear to be important: (1) the cost of flying and (2) the availability / visibility of fish. Flight costs to and from a central place generally increase with wind force according to flight theory in the models of Pennycuick (1975, 1978). Wind direction and track direction are usually coupled, the birds were flying in most cases perpendicular to the wind direction at moderate wind speeds of 3-5 $m.s^{-1}$ (Van Eerden, unpubl.). So wind direction roughly sets the goal region, the birds determining the distance from the colony and thus the duration i.e. the energetic costs of the flight. At high wind speeds over 6 $m.s^{-1}$ the birds were wind-drifted, which caused compensatory flights.

Because Cormorants need to detect their prey visually, the clearness of the water seems very important in determining the final foraging spot. In a lake wind creates a water current and also waves may cause local 'upwelling' of bottom material (Van Duin 1992). In the shallow lake Markermeer (2-4 m water depth) this current of the water leads to suspension of the aqueous mudlayer present over large parts of the lake. This depresses penetration of light as wind speed increases (Fig. 7A). Different parts within the lake behave differently as a result of fetch length of the wind, the water depth and the type of bottom. However, at wind speeds over 8 $m.s^{-1}$ most parts become very turbid with Secchi depths under 40 cm all over the lake. The continuous registration of under water light attenuation near Marken, in lake Markermeer, showed that wind direction and wind force greatly influenced turbidity at intermediate levels of speed. As soon as the wind speed dropped, the water became more clear, an effect noticeable within 12 hours. Moreover the striking effect of sunshine was demonstrated, increasing under water light penetration up to a factor three (Fig. 7B-E). The Cormorants were recorded to fish within the region especially at days with intermediate under water visibility (Fig. 8). They were hardly present when underwater light levels dropped below 300 $\mu E.m^2.s^{-1}$ (measured at 40 cm water depth), although 70% of the season the light conditions were below this value. This value roughly compares to 50 cm Secchi depth. 40

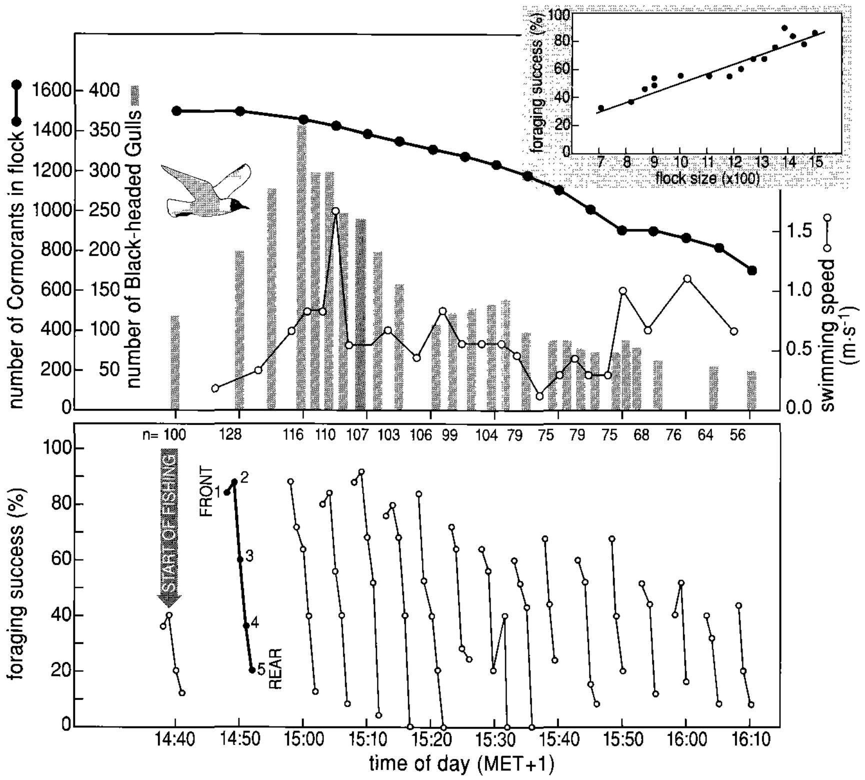

Fig. 6. Intake rate in relation to position within a flock of socially fishing Cormorants on Smelt, 31 May 1982. Notice the sharp decline in foraging success of birds not fishing at the front of the flock as well as the gradual decline of overall foraging success as time proceeds. Also indicated is the number of birds in the flock, calculated back from the flight traffic observed and the final count at the time of break-up. The number of scavenging Black-headed Gulls follows the general pattern of catching success in the Cormorants.

cm Secchi depth is considered an absolute lower limit for mass fishing.

DISCUSSION

Social fishing and colony size

The habit of social fishing is quite a recent phenomenon. Up to 1971 only irregular observations have been reported. Somewhere between 1972 and 1975 the population of Naardermeer switched to this technique almost completely. After 1975 most records confirm that social fishing was the rule at lake IJsselmeer. What was the reason for that marked switch?

A certain minimum number of birds needs to be present in the colony in order to keep the flock in action, as well as the flight traffic going throughout the day. Birds flying out follow incoming birds upstream as well as birds flying ahead. This *va et vient* principle guides the newcomers to the exact place that lays well out of sight of the colony. Because the position of the fishing flock may change over the day a continuous updating of information is necessary. Could colony size be too low to allow for social fishing? The recently established colonies Oostvaardersplassen (1978) and Lepelaarplassen (1985, Zijlstra & Van Eerden 1991) consisted in their first years only of birds fishing solitarily. For Oostvaarders-

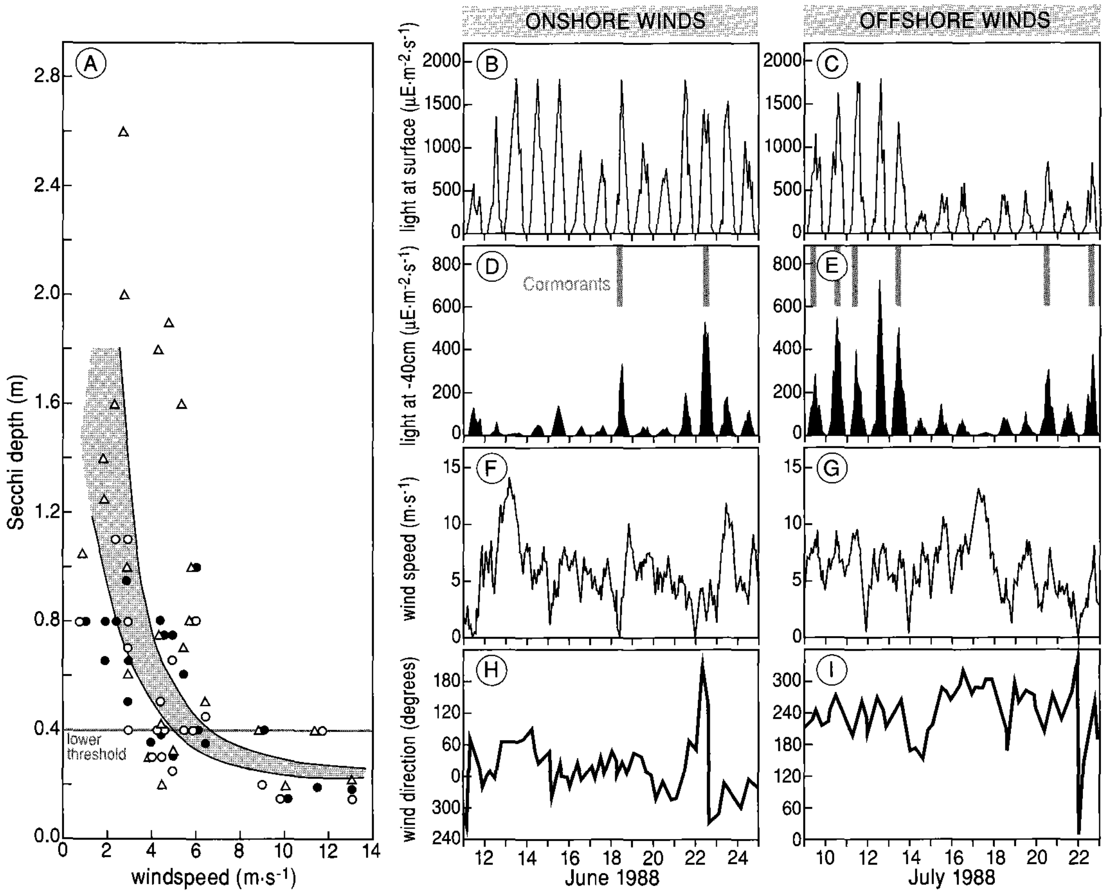

Fig. 7. Light climate under water at lake Markermeer: (A) Under water penetration of light (Secchi depth) in relation to wind speed at three different locations. For Cormorants a lower critical level of 40 cm Secchi depth was found below which no foraging birds were observed as long as better visual conditions were available. Notice the general deterioration of light conditions as wind speed exceeds 8 $m.s^{-1}$; (B) - (E), simultanuous registration of light at surface, at 40 cm water depth, wind speed and wind direction, as measured from a pontoon showing poor under water light conditions during times of northerly winds (fetch length > 10 km); (F) - (I) idem with better light conditions during SW winds (fetch length < 3 km) and marked effect of sunshine in the period 9-13 July 1988. Presence of Cormorants indicated for different days. Data about light regime (B-I) from E.H.S. Van Duin.

plassen social fishing was first observed regularly in the third year: 1980 with 1100 breeding pairs present. For Lepelaarplassen this was also in the third year after the settlement, i.e. 1987, with 1050 breeding pairs. These data support the view of the existence of a lower limit of colony size in relation to social fishing in a large lake.

Number, however, is not the self-evident factor for this behaviour. The size of the colony at Naardermeer in the early seventies was well above 1000 breeding pairs while still solitary fishing predominated. Also at the time that the colony Wanneperveen was well over 2000 breeding pairs social fishing was never observed (Van Dobben 1952, 1995). Moreover, many Danish colonies are well above 1000 pairs without any social fishing being apparent as occurs at lake IJsselmeer. The obvious difference is that the under water light re-

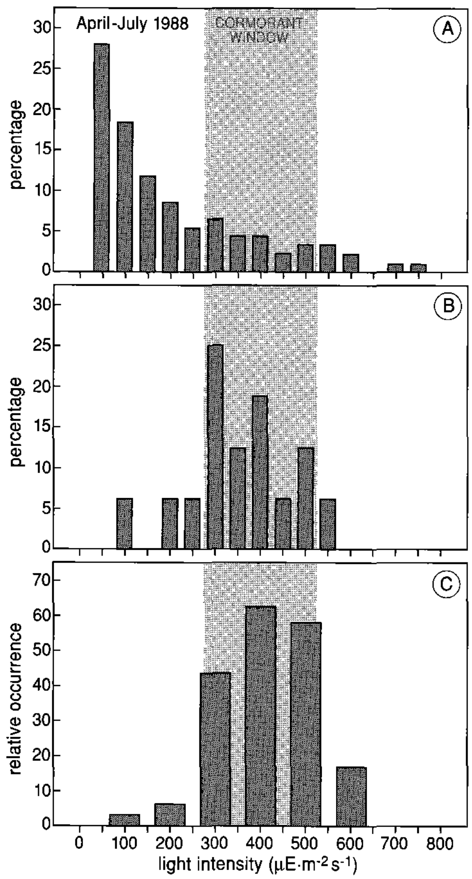

Fig. 8. Continious registration of under water light conditions (maximum per day at 40 cm water depth) near Marken and the presence of fishing Cormorants in the region (radius of 5 km): (A) Frequency distribution of daily light levels in the period April-July 1988; (B) idem at times when Cormorants were present in the region; (C) proportion of days with fishing Cormorants according to a certain light level.

gime is substantially more turbid at places where mass feeding predominates. In the Danish inshore areas of the Baltic, summer values of Secchi depth of 2-5 m are common (own obs.).

As a consequence of the habit of social fishing the birds can now exploit a much larger region than before. Based on the fact that birds follow each other to the common fishing place, figure 9 illustrates the presumed relationship between colony size and range use. Unless other factors become limiting, the number of breeding birds is of direct influence on the possible length of the 'commuting chain' between colony and foraging site. That birds indeed use the location of other groups to guide them was observed several times during foggy weather. Cormorants flying out sometimes get no further information about where to go and settle on the water waiting for other birds. The same also occurs under good visibility conditions after a sudden break-up of the flock with massive return flights to the colony being followed by a quiet period with hardly any

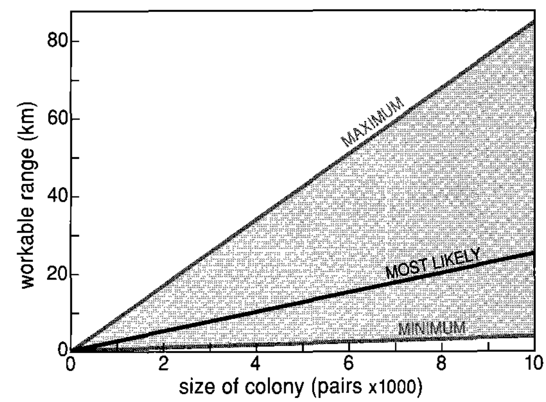

Fig. 9. Hypothetical relationship between colony size and foraging range to be covered by birds flying along a line, following out- and in-flying colony members. The range to be covered is set by the maximum number of commuting flocks within sight of each other, both to and from the spot of social fishing. A day of 14 hours was assumed with each pair going out twice, uniformly distributed over the day. Birds are assumed to return in a uniform way from the fishing place. The maximum range estimate assumes that all birds would fly solitarily with a detection distance for other birds of 900 m. The minimum range assumes birds flying in flocks of 20 and a 900 m (bad weather) detection distance. The central line ('best guess') is based on the assumption of flocks of 20 birds and a detection rate of 5400 m, the maximum distance for which birds were observed to react upon each other in the field under fair weather conditions. The maximum size for a colony of *sinensis* in western Europe as recorded in recent times has been indicated.

traffic. However, under normal conditions birds leaving the colony only have to follow the ongoing traffic to find the rendezvous. When at a certain site foraging is no longer profitable, the birds switch feeding site which is quickly transmitted to the newcomers by the returning birds.

Social fishing and fish stocks

Although the number of breeding pairs seems important, the proximate factor determining the behavioural switch must have been something else. Mass fishing is only rewarding at high prey densities. The species composition in lake IJsselmeer consists of several species which occur in high numbers, e.g. Ruffe, Smelt and the yearlings of Perch, Pikeperch *Stizostedion lucioperca* and Roach. The fish are regularly distributed over large areas according to sonar recordings (Van Eerden, unpubl.). Until 1970 fishing with trawls was common practice. Because of the by-catch of large quantities of small Perch, Pikeperch and Eel *Anguilla anguilla* this fishery was stopped. Although still under discussion, this change is likely to have had a positive effect on the density of young fish but also on the smaller species like Smelt and Ruffe. As shown by fish stock surveys in the southern part of lake Markermeer during 1973 and 1974, twice the density of Smelt and Ruffe was present compared to the average for the period 1966-1991 (Lanters 1992). At the same time, by increasing the fishing effort on large predatory fish by extensive gill-net fishery during the winter half year, the stocks of Perch and Pikeperch are kept well below their biological capacity (Van Densen *et al.* 1990, Buijse 1992), resulting in a lowered predation pressure and thus possibly higher stock of small fish. Both effects loaded the Cormorants' dice and both have contributed to the behavioural switch of the Cormorants in the early 1970s.

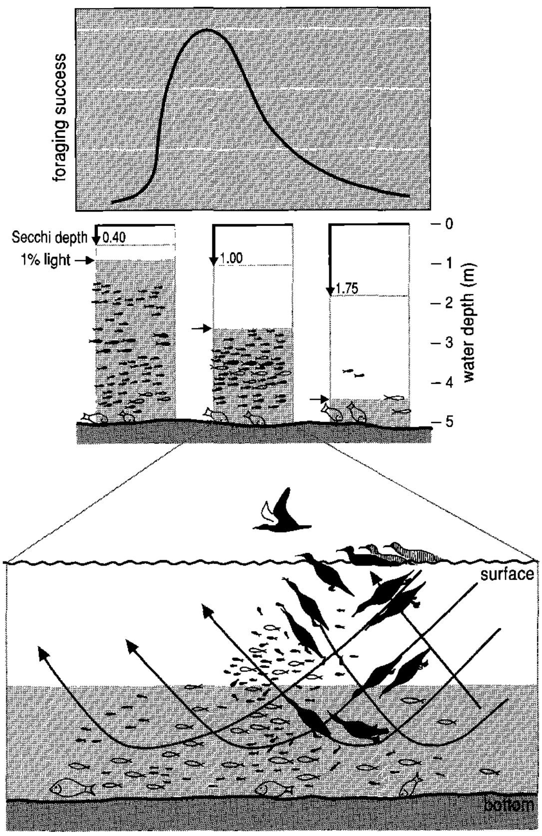

Fig. 10. Scheme illustrating the supposed optimal level of under water light conditions for socially fishing Cormorants. The effect of different levels of light under water is related to the vertical distribution of fish. Based on echo soundings most fish tend to stay during daytime at depths below 1% light, relative to the surface. At intermediate light levels the Cormorants can effectively push up the fish from the dark zone into the clear top layer where they are being caught. Arrows indicate diving paths in the front section, birds from behind diving underneath the the upward swimming Cormorants.

Optimal turbidity?

We know that the under water visibility worsened during the past twenty years (Rijkswaterstaat yearbooks). In general terms eutrophication has caused a continuous increase of algeal densities up to a factor ten compared to the situation in the 1930s (Wibaut-Isebree Moens 1954, Postma 1966, De Wit 1980, Berger 1987). Moreover the construction of large waterworks (embankment of Southern Flevoland in 1968, closing of the dike Enkhuizen - Lelystad in 1975) in the same period has altered the conditions of the currents, causing an increased turbidity in the southern part of lake IJsselmeer (the area now known as lake Markermeer). We suppose that mass feeding was the result of the deteriorating conditions for solitary foraging. Since social fishing can be practised efficiently in turbid waters only, the behavioural switch occurred. Two factors are important with respect to improved catchability of the prey. The birds may herd the fish (line hunting) and thus concentrate the density of their prey, adjusting their swimming speed to the maximum burst speed of the prey causing exhaustion. Secondly, the front of diving birds under water is thought to push up the fish hiding in the darker part of the water column up into the clear surface layers where they can be detected and subsequently taken. Figure 10 shows this hunting system in a schematic way.

Ideally the concentration effect works best at intermediate light levels. Fish is then still abundant and regularly distributed in the darker part of the watercolumn. The lighter part is not too deep which both saves diving costs and lessens the chances of escape for fish that are pushed up. Evidence for the existence of an upper limit of under water visibility which makes mass fishing no longer profitable is twofold. First, the clear water in the westernmost Baltic (Secchi depths 2 - 6 m) has not led to any mass fishing comparable to the IJsselmeer situation in colonies of equally large size. However, Danish ringed birds when present late summer at lake IJsselmeer are known to perform this behaviour all the time, which shows the environment and not the birds to be different. Second, during an extreme period of clear water in spring 1993 (Secchi depth well over 1.50 m), caused by the absence of the planktivorous Smelt, the social fishing completely stopped and birds moved away towards the turbid canals inland as well as to the turbid region of the mouth of the river IJssel (Ketelmeer) and the border lakes. Therefore we argue that at a water depth of 4-5 m an optimal light intensity under water could well exist, from our data provisionally estimated between 50 and 80 cm Secchi depth, or 300-500 $\mu E.m^{-2}s^{-1}$ measured at 40 cm below the surface.

CONCLUSIONS

In conclusion we state that the deteriorating visibility conditions, the supposed change in the composition of the fish community towards more and smaller prey after the stop of trawling in 1970 enforced by increasing numbers since the protective measures after 1965 were all factors that have contributed to the behavioural switch towards mass feeding. Combination of the advantages of the change of habit has turned an ecologically negative development into a more beneficial situation than it was at the time of the solitary fishing. This change of behaviour, which may have resulted in an increased carrying capacity of the lake through range extension and a possibly higher yield per ha, may well have contributed to the extensive growth of the population of Cormorants, at least in The Netherlands.

ACKNOWLEDGEMENTS

We appreciate the cooperation with Maarten Platteeuw, Menno Zijlstra, Jan Muller and several others who assisted in collecting the data. Thanks to Rijkswaterstaat skippers Bertus Bakkes (ms Flevomeer), Leo de Ronde (ms Markermeer), Arie Burggraaf (ms Elise) and Bram van der Meer (ms Noord Holland) who provided additional data on flock positions. Bram bij de Vaate and Menno Zijlstra participated in the aerial counts. Rudolf Drent foresaw already in 1976 the usefulness of a rangefinder in the study of flock movement in birds. He kindly put the equipment to our disposal. Wouter Dubbeldam and Kees Koffijberg were of help in computerising the data. Rudolf Drent, Menno Zijlstra and Leo Zwarts gave useful comments on various drafts of this paper. Willem Dekker of RIVO (Netherlands Institute for Fishery Investigations) kindly allowed us to cite their fishery data.

REFERENCES

Bartholomew, G.A. 1942. The fishing activities of Double-crested Cormorants on San Fransico Bay. Condor 44:13-21.

Berger, C. 1987. Habitat en ecologie van *Oscillatoria*

agardhii Gom. Thesis University of Groningen, 233 pp.
Buijse, A.D. 1992. Dynamics and exploitation of unstable percid populations. Thesis Agricultural University Wageningen, 167 pp.
Cramp, S. & K.E.L. Simmons (eds) 1977. The birds of the western Palearctic, Vol. 1. Oxford University Press, Oxford.
Cramp, S. & K.E.L. Simmons (eds) 1983. The birds of the western Palearctic, Vol. 3. Oxford University Press, Oxford.
De Boer, H. 1972. De voedselbiologie van de Aalscholver. Report. Rijksinstituut voor Natuurbeheer, Leersum.
De Wit, J.A.W. 1980. Aspecten van de waterkwalteit in het IJsselmeergebied. H_2O 13:251-256.
Lanters, R.L.P. 1992. The spatial ditribution of six major fish species in lake IJsselmeer, The Netherlands, in relation with environmental conditions. Report Binvis 92-06, Rijksinstituut voor Visserijonderzoek, IJmuiden
Nelson, J.B. 1980. Seabirds, their biology and ecology. Hamlyn, New York
Pennycuick, C.J. 1975. Mechanics of flight. In: D.S. Farner & J.R. King (eds) Avian Biology Volume 5:1-75. Academic Press, New York.
Pennycuick, C.J. 1978. Fifteen testable predictions about bird flight. Oikos 30:165-176.
Poorter, E.P.R. 1967. Aalscholverconcentraties in het Eemmeer. Limosa 40:255.
Postma, H. 1966. Observations on the hydrochemistry of inland waters in The Netherlands. Proc. I.B.P. Symposium 1966, Amsterdam and Nieuwersluis.
Van Densen, W.L.T., W.G. Cazemier, W. Dekker & H.G.J. Oudelaar 1990. Management of the fish stocks in lake IJssel, the Netherlands. In: W.L.T. Van Densen, B. Steimetz & R.H. Hughes (eds) Management of freshwater fisheries. Proc. Symp. EIFAC, Göteborg:313-327. Pudoc, Wageningen.
Van Dobben, W.H. 1952. The food of the Cormorant in The Netherlands. Ardea 40:1-63.
Van Dobben, W.H. 1995. The food of the Cormorant *Phalacrocorax carbo sinensis*: old and new research compared. Ardea 83:139-142.
Van Duin, E.H.S. 1992. Sediment transport, light and algal growth in the Markermeer. Thesis Agricultural University Wageningen, 274 pp..
Van Eerden, M.R. & J. Gregersen 1995. Long-term changes in the northwest European population of Cormorants *Phalacrocorax carbo sinensis*. Ardea 83:61-79.
Videler, J.J. & B.A. Nolet 1990. Costs of swimming measured at optimum speed: scale effects, differences between swimming styles, taxonomic groups and submerged and surface swimming. Comp. Biochem. Physiol. 97:91-99.
Voslamber, B. 1988. Visplaatskeuze, foerageerwijze en voedselkeuze van Aalscholvers *Phalacrocorax carbo* in het IJsselmeergebied in 1982. Flevobericht 286. Rijksdienst voor de IJsselmeerpolders, Lelystad.
Wardle, C.S. 1977. Effects of size on the swimming speeds of fish. In: T.J. Pedly (ed.) Scale effects in animal locomotion. Academic Press, London.
Wardle, C.S. 1980. Effects of temperature on the maximum swimming speed of fishes. In: M.A. Ali (ed.) Environmental Physiology of Fishes: 519-531. Plenum Press, New York.
Wibaut-Isebree Moens, N.L., 1954. Plankton. In: L.F. De Beaufort (ed.) Veranderingen in de Flora en Fauna van de Zuiderzee: 90-155. Zuiderzeecommissie Nederlandse Dierkundige Vereniging.
Zijlstra, M. & M.R. Van Eerden 1991. Development of the breeding population of Cormorants *Phalacrocorax carbo* in The Netherlands till 1989. In: M.R. Van Eerden & M. Zijlstra (eds) Proceedings workshop 1989 on Cormorants *Phalacrocorax carbo*: 53-60. Rijkswaterstaat directorate Flevoland, Lelystad.

SAMENVATTING

Sociaal vissen bij Aalscholvers in Nederland is een betrekkelijk nieuwe ontwikkeling. De vogels hebben hun gedrag ingrijpend veranderd tussen 1972 en 1974 (Fig. 1). Tegenwoordig vissen de meeste vogels in reusachtig grote groepen (4000-6000 exemplaren), waarbij iedere kolonie één visplaats heeft waarmee de vogels een pendeldienst onderhouden (Fig. 2).

Met behulp van een afstandsmeter werd de verplaatsing van vissende groepen vastgelegd en hieruit kon de snelheid worden berekend. Het bleek dat twee fasen kunnen worden onderscheiden: het lijnjagen waarbij vis wordt opgedreven ($1.04\ m.s^{-1}$) en het zigzagjagen waarbij de vis wordt gevangen ($1.33\ m.s^{-1}$, Fig. 3). De snelheid waarmee de Aalscholvers door het water gaan is zo groot dat de bejaagde vis uitgeput raakt.

Afhankelijk van temperatuur en lichaamslengte ligt de maximum zwemsnelheid van een 5-25 cm lange vis tussen de $0.5\text{-}2.5\ m.s^{-1}$. In de loop van het seizoen gaan Aalscholvers sneller zwemmen, vermoedelijk als gevolg van het temperatuureffect op de vis. Eind mei kwam hieraan een eind doordat de vogels overschakelden op kleinere vis (Fig. 4 en 5).

Het foerageersucces van jagende Aalscholvers was

afhankelijk van de positie in de groep wat wijst op een efficiënt afvissen van de beviste waterlaag (Fig. 6). Sociaal vissen trad in het bijzonder op bij een bepaald lichtklimaat onder water, niet te helder maar zeker niet te troebel (50-80 cm Secchi diepte of 300-500 $\mu E.m^{-2}s^{-1}$ gemeten op 40 cm diepte, Fig. 7-9). Het gedrag waarbij vissen vanuit de donkere waterlagen door de massaal oprukkende vogels tegen de lichte toplaag worden gedrukt en vervolgens gevangen (Fig. 10) is alleen mogelijk wanneer de Secchi waarde niet lager is dan 40 cm.

Voor de plotselinge gedragsverandering is een aantal faktoren verantwoordelijk. Door de aanleg van de Houtribdijk (1965-1975) tussen Enkhuizen en Lelystad veranderde het stromingspatroon in het zuidelijk deel waardoor de troebeling toenam. Voor solitair vissende Aalscholvers werd de situatie dus ongunstiger, voor sociaal vissen juist gunstiger. Voor 1970 maakte de beroepsvisserij op het IJsselmeer intensief gebruik van sleepnetten (kuil- of trawlsysteem). Na 1970 schakelde zij over op de fuikenvisserij 's zomers en een intensief gebruik van staande netten ("staand want") 's winters. Deze vangtuigen werken veel selectiever op grote vis. Hierdoor kon aanvankelijk de stand aan kleine vis sterk toenemen. Samen met de - door beschermende maatregelen - toegenomen populatie Aalscholvers heeft dit geleid tot de plotselinge gedragsverandering.

De conclusie is dat door sociaal te gaan foerageren de vogels beter gebruik hebben kunnen maken van de aanwezige vis in het meer. De bevlogen afstanden zijn groter (tot 70 km) en vermoedelijk is ook de oogst per oppervlakte-eenheid groter dan wanneer alle Aalscholvers solitair zouden jagen.