The Food of the Cormorant in the Netherlands

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The food of the Cormorant in the Netherlands

by

W. H. VAN DOBBEN

Contents.

1. Introduction.

As far back as the memory of men reaches there have always been large rookeries of Cormorants in the Netherlands. The nests are situated exclusively in trees. The birds belong to the subspecies *Phalacrocorax carbo sinensis* (SHAW and NODDER).

The fishermen have always considered the Cormorant to be a dangerous rival and consequently it was persecuted. Only its great vitality and faculty of adaptation have saved the bird from extermination in this densely populated country.

In the years between 1920 and 1930, however, the total number of breeding pairs had decreased to 1200 (BROUWER 1926, 1927). The fear that this typical and decorative bird would disappear from the landscape of our large rivers and seashores has led to a certain protection and since then the number has increased. It appeared that it was sufficient to leave a rookery undisturbed to obtain a quick recovery. The rookery at Wanneperveen increased from 500 nests in 1932 to 2000 nests in 1939; the rookery at Lekkerkerk during the same period from 500 to 1200 nests. So the problem arose again and the interests of the fishery had to be taken into account.

One of the main reasons for the persecution of the Cormorant is the devastation caused in the nesting trees. Almost every tree inhabited by Cormorants dies within 5 years. As long as it stands upright and affords sufficient nesting sites it remains in use, but before long the birds are obliged to occupy a neighbouring part of the wood, causing serious damage in a short time. The chief reason why the trees die so soon may be the Cormorant's habit of using living twigs as well as dead ones for the building of its nest. The trees are completely plundered. Its remarkable physical strength enables the bird to do so. Herons and Rooks take only dead twigs and do not kill their nesting trees.

The excrements of the Cormorant too are very damaging to green leaves. Not many plants succeed in surviving under the nesting trees. Nettles are relatively insensible. Among trees the elder is rather resistant.

The owner of the largest rookery, the „Vereeniging tot Behoud van Natuurmonumenten" (Society for the Preservation of Nature Monuments in the Netherlands) would not take action against the birds before an inquiry had been made into the influence of the Cormorant on the fish population.

The "Nederlandsche Vereeniging tot Bescherming van Vogels" (Society for the Protection of Birds in the Netherlands) took the initiative for such an investigation. The results are formulated in the following pages. The data underlying this inquiry were collected mainly in the large rookery near the village Wanneperveen (fig. 1). It is situated in the wood of a large decoy, consisting mainly of alder and birch.

In the second rookery, about 15 kilometers East of Rotterdam (fig. 2)

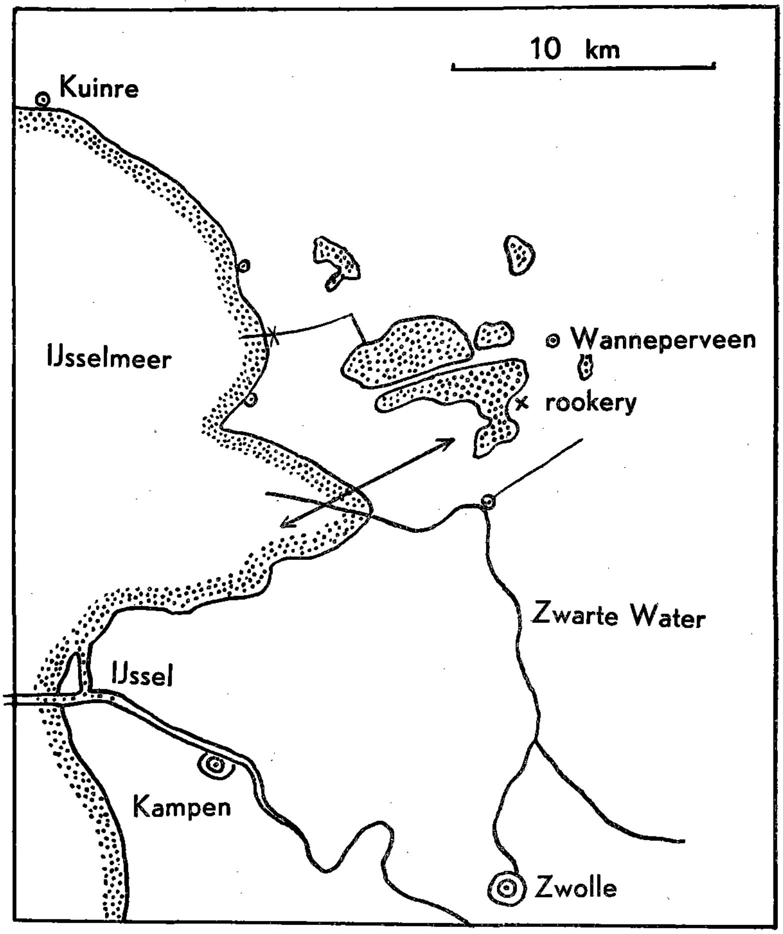

Fig. 1. The environment of the rookery near Wanneperveen; IJsselmeer (= IJssel-lake), the former Zuiderzee. The main route of the birds is indicated by an arrow.

near the river Lek, a number of fishes was collected by Mr. A. Kortlandt. This breeding place is also situated in the wood of a decoy ("Lekzicht"). It was here that Kortlandt made his extensive studies on the behaviour of the Cormorant (Kortlandt 1938, 1940).

From a third large settlement, situated at the time in the "Biesbosch"

(25 km SE of Rotterdam) 65 fishes were obtained by mediation of Mr. VAN TIENHOVEN.

In a little rookery near the Hook of Holland ("Staelduinen") some

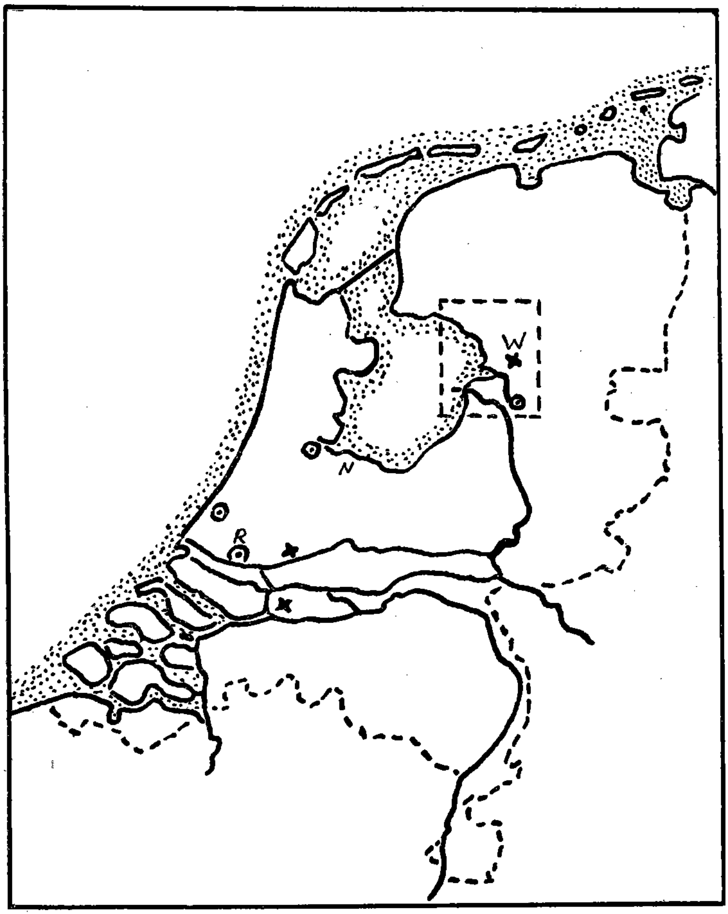

Fig. 2. (x) The situation of the 3 largest Cormorant rookeries in the Netherlands (1938-1939). R: Rotterdam; N: Naardermeer; W: Wanneperveen.

fishes were collected by Mr. LAARMAN. I am greatly indebted to these gentlemen for their kind assistance.

That Cormorants eat fish is generally known. On the food of the Southern Cormorant, however, little has been published if it is taken into account how easy ejected fishes can be collected in a disturbed rookery.

"The Handbook of British Birds" (WITHERBY 1947) reports: "almost entirely fish, both fresh- and salt-water species ... nearly all kinds not too large ..., but eels are favourite prey".

The "Handbuch der Deutschen Vogelkunde" (NIETHAMMER 1938) mentions "Fische, besonders Aale, im Meere Plattfische".

Sofar I know the most detailed report on the subject is published by MADSEN and SPÄRCK (1950). These authors examined the stomachs of 365 Southern Cormorants shot in Danish rookeries situated near island coasts at the approaches to the Baltic; the birds were sent by the hunters to the Institute of Game Biology. (In my opinion this method has a serious drawback, for a shot Cormorant ejects from the stomach as much fish as possible before it dies.) 258 birds contained recognizable food remains originating from 687 fishes, from which 2% true fresh-water species, 18.5% Eel (mostly taken from salt water) and the rest marine species, especially Herring (36.8% !).

2. Objects and methods.

The object of the investigation was to make an inquiry into the following questions:

The composition of the food, the share of several fish species.

The origin of the food.

The daily rations of old birds and young ones.

The relations between the fish population on the hunting grounds and the composition of the Cormorants food.

The influence of the Cormorant on the persecuted species of fish.

The methods used were mainly the following:

Examination of ejected meals and pellets.

Observations of the movements of the birds.

Feeding experiments with young Cormorants.

Observations at the nests.

Examination of samples taken from the fishing grounds of the birds by human fishery.

3. General remarks on the food and the hunting grounds.

Cormorants feed on fish almost exclusively. The vomits sometimes contain remains of other animals, e.g. Mollusca or Polychaeta, from which may be assumed, however, that they originate from the stomachs of captured fishes.

There is some evidence that, rarely, other animals are taken. Mr. J. HOOGERHEIDE saw a Cormorant taking nestlings of a Sheldduck near Huizen on the former Zuiderzee. Balkan Cormorants seem to take swallows, which fly low over the water (BERNATZIK 1929). A few large shrimps and two crabs are recorded from the rookery near the Hook of Holland and from Lekkerkerk. KORTLANDT (1940) mentions a water-rat. In the rookery at Wanneperveen, however, thousands of vomits examined contained only fish. The hunting method of the bird—diving in open water—and its preference for large prey may be accepted as an adaptation to the capture of fish.

From my observations no clear proof could be obtained that a certain species of fish is preferred. I often noticed the same species of fish several times under the same nest, but this may be explained by a preference for a hunting ground with limited choice. At Wanneperveen some birds regularly produce "dark" fishes from peaty waters.

The preference for certain hunting grounds is very clear. The Wanneperveen rookery is situated on the shore of a lake but practically no Cormorant ever fishes there, although it is not neglected by human fishery.

94.5% of the birds make the 7 kilometer trip to the IJsselmeer (fig. 1), the rest goes in other directions. The reason is obvious: the lake ("Belterwiede") is poorly populated compared with the IJsselmeer. There is an indirect method to verify the origin of the food. The inhabitants of the IJsselmeer are remarkably light coloured. The Eels are light brown, the dark streaks of the Perches look very faint. Fishes from "inland" waters are much darker, more clearly marked. In the ejected meals of the Wanneperveen Cormorants the typically light coloured fishes form an overwhelming majority.

The abundance of *Acerina* in these vomits points to the same direction —this fish is numerous in the IJsselmeer, not in inland waters.

These facts agree with the movements of the birds leaving and approaching the rookery—except in the early spring, when the stream of Cormorants leaving for the fishing grounds does not go to the IJsselmeer but to the lower course of the rivers IJssel and Zwarte (= black) Water. The reason is not quite clear.

The Ruffe, Roach and Perch they bring back from these expeditions are typical inhabitants of the IJsselmeer. Moreover it is a wellknown fact that fishes show a tendency to swim upstream in the spring. The rich population of the IJsselmeer may eventually crowd the only two rivers available and Cormorants are quick to exploit such a situation. During April the stream of fishing Cormorants is switched gradually from the rivers to the IJsselmeer.

The following experience illustrates the preference of the Cormorant for a densely populated water.

On a tour along the Zwarte Water on April 7, 1939 I saw several Cormorants fishing singly in the river. As usual they showed a tendency to avoid each other. In several pools inside the river dike (scars from old breaches in the dike called "wiel" in Dutch) no birds were fishing. Only one pool had 5 visitors. Exactly this one carried a notice: "fishing prohibited" and the name of an angling club. I was informed that fish was set here regularly. The Cormorant generally accepts no lead when fishing. I presume that these 5 birds had detected the spot independently and by chance, remembering it and returning regularly. In this way the whole rookery will at last give priority to the richest hunting ground available.

The acreage of the area visited by Cormorants fishing on the lake is not easy to determine. Southwards they go not much farther than the mouth of the IJssel (fig. 1) northwards they can be seen as far as Kuinre. How far they go westward on the lake I cannot state but it is sure that the fishing is not confined to the coastal zone. There is no reason to suppose that the birds go farther westward than southward, so the fishing area of the Wanneperveen rookery will be limited to the NE part of the lake, comprising about 400-500 sq. kilometers [1]).

The Cormorants fishing near Amsterdam, for instance, do not breed in the Wanneperveen rookery, they are non-breeding birds sleeping in the famous Naardermeer (see fig. 2 ; in later years a rookery was formed here). The birds fishing near the dike separating the IJsselmeer from the sea sleep on the sand flats of the Frisian Islands. In the Wanneperveen rookery not one sea fish has ever been observed.

4. The journey to the lake.

In the early morning twilight the rookery awakes and a mass start begins (fig. 3). The exodus soon decreases in strength but continues hour after hour. It is clear that most birds do not start as soon as possible. Indeed many birds can be seen sleeping on a branch near the brooding partner long after sunrise.

One hour after the mass start the return begins. Towards noon the returning birds outnumber the departing ones. At about 4 p.m. a mass return takes place. Departing birds gradually become less frequent although they are seen almost till sunset. The returning stream decreases gradually, dying down after sunset, an odd bird only returning in the first darkness.

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1) This part was drained in 1941 and later on reclaimed.

Cormorants never fish in the dark hours as herons do. As a rule a bird departs on its own initiative, but on the way a tendency to join other birds leads to the forming of flying groups, including as a rule not many more than 10 birds. It happens, however, especially in the early morning, that a large group starts simultaneously. One bird influences the other, the impulse waves through the rookery. The birds whirl through the air, many falling back into the trees; some 100 meters from the rookery the rest gathers and gets into formation, forming a straight line or a V, like geese do. Such a group can often be seen decreasing speed and almost hovering for a short time. This strange behaviour may be repeated several times. I had to witness this many times before I understood the reason. The leading bird takes the initiative and it is clear that by stopping in the air it tries to leave the leading place to the following bird. This one defends its position by stopping too and so on. The situation closely resembles the tactics of bicycle racing. The conclusion may be drawn that the birds are fully conscious of the fact that the leader has the most strenuous role. After some hovering one Cormorant, perhaps a hungry one, takes the first place "for Heaven's sake" and the troop goes off again.

Another form of wavering is performed when a troop turns round, often under the influence of homing birds. This may indicate a hesitation between two favoured places, the nest and the fishing grounds. When the weather is fine the troops leaving the rookery rise gradually. When they cross the dike of the IJsselmeer they have reached an altitude of more than 100 meters. Then they stop wingbeating and glide down in the original direction till they almost reach the surface of the water about 1 kilometer from the coast. Here the wing-beating is resumed. The troop begins to dissolve, the birds dispersing and seeking their own way. Descending upon the water is not often observed. At the point were the majority of the Cormorants reaches the lake, fishing near the coast is rarely seen.

The behaviour of the homing birds is quite different. There are meeting places where the birds gather after fishing. One meeting place was situated on the little pier of the water-mill south of Blokzijl (fig. 1) another, much larger one, on the water south of the pier of the Zwarte Water. I suppose that this meeting place originally was on the pier, but that the birds were disturbed by the activity of the "Zuiderzeewerken" (draining-works).

Little troops come from the lake and descend as a whole or partly on the meeting place. At intervals a large group tears itself away and makes for home. At first it flies at a moderate altitude but after reaching the coast it begins to turn round, describing huge loops in the air and rising gradually. Wing-beating alternates with gliding.

Generally the movement points slanting upward into the direction of the rookery. With the weather fine and clear some troops maintain this queer behaviour till half way home or even farther, reaching a height of about 1 km. Then the troop flies a short time straight in the direction of the rookery. Long before reaching the point just above home the descent begins. The troop dissolves itself and each bird glides down along a spiral line at a break-neck speed.

Standing on the dike I could follow such a circling group with the glass (8 ×) till it descended into the rookery. The distance is 7 km, the time was 10 minutes. A direct course would have taken about 6 minutes. The reason for this remarkable behaviour is not clear. The fact that the circling starts when a troop reaches the coast made me suppose that upward airstreams play a role. The circling of homing birds has, however, often been observed under circumstances ruling out this explanation. It seems more likely that an aversion of the Cormorant to flying over land, especially to flying low over land is responsible for the phenomenon.

Only when the visibility is very poor no circling takes place, the birds then flying rather low and direct to the rookery.

5. The fishing.

When a Cormorant decides to fish, it descends upon the water. After a short time it begins to dive. It stays under water for a quarter or half a minute and waits about 12 seconds between each dive. Normally only a few of the dives meet with succes. This is easy to establish, for the swallowing of the prey takes place above water. After "nibbling" and turning the prey it is swallowed head first. The fishing continues and is not finished before a good haul is made.

What is happening under water is not so easy to ascertain. The only thing I personally did see was that a Cormorant swims under water using its legs simultaneously; the bird "leaps" forward and does not use its wings.

According to Portielje (1927) the bird fishes in a zigzag line near the bottom; according to Kortlandt it catches the prey with a sudden leap, stretching the neck.

Kortlandt (1940) assumes also that generally the fishing takes place near the bottom. English authors (Steven 1933, Lack 1945) express the same opinion about *Ph. c. carbo.* MADSEN and SPÄRCK (1950) state that "the fishes eaten by the Cormorant (in Denmark) are mostly bottom forms", but simultaneously record the (pelagic) Herring as the most numerous prey. I could find no clear proof for a preference for bottom forms compared with pelagic fishes. It must be added of course that in the shallow Dutch inland waters the pelagic fishes live also very near to the bottom.

The fish usually bears traces from the hooked upper mandible of the bird. The only wound to be found upon most vomited fishes is clearly caused by this formidable weapon. In a large number of fishes I noted the place where the wound was found. It appears that most of the fishes are caught just behind the gills. The wound is situated at the side of the fish, generally near the back, an indication that it is caught from above. The catch just behind the head secures the best hold on a sprawling fish.

The Eel forms an exception to the rule. Some individuals bear the trace of the Cormorants bill behind the head but the majority appears to be taken at the snout. An explanation of this fact is given in chapter 18.

Social fishing has often been mentioned in literature. I only saw it once.

On the 14th of June 1938 I observed a troop of several hundreds fishing north of the mouth of the Zwarte Water in the IJsselmeer in shallow, overgrown water, where fishing by single birds was generally not observed.

The distance was large and the activity decreased quickly. Under heavy splashing the troop moved first in one, then in another direction. It formed no long front line, rather a compact patch of birds. The stragglers often rose from the water and descended in front of the foremost birds. The diving did not resemble the normal behaviour, the birds rather making short sorties under water.

Swallowing of food was in fact observed. The whole action appeared adapted to drive fishes from their hiding places between the water plants.

6. The frequency of the fishing expeditions.

When the total number of birds leaving daily for the fishing grounds is divided by the number of birds living in the rookery, the average number of fishing expeditions for one bird must be obtained. This seems to be a simple calculation but it is not so easy to collect the right figures to make it. We can count the nests in use and so find the number of breeding birds. In 1939 this was a little more than 4000.

There are, however, non-breeding birds sleeping regularly in the rookery and they are not so easy to account for. These birds sit at night between the nesting birds as well as apart in groups of trees next to the rookery. There are at least hundreds of them, perhaps thousands.

A count to establish the number of birds leaving and entering the rookery was made on May 24 and 25, 1939. No fledged young were present at the time to confound the result. As an observation point I choose a small high bridge 1 km to the west of the rookery.

The first day a count was made from 3 p.m. till darkness and the second day from darkness till 3 p.m. The daily movements are very regular and the two days were of the same type of weather (sunny with eastern wind) so it seems permissable to add the results (fig. 3). In total 7704 Cormorants left the rookery and 8632 returned. The latter figure must be accepted as the right estimate for the number of fishing expeditions. The homing birds are much easier to count because they approach the rookery from a great altitude. The leaving birds fly low and more dispersed. The main reason for the discrepancy, however, forms the mass departure in the early twilight when many birds are overlooked.

We come to the conclusion that about 8600 fishing expeditions are made by 4000 breeding birds and an unknown number of non-breeding birds. The latter as a rule go in the morning and return in the afternoon, each individual appearing once in the calculation. The breeding birds, having young at the time, are expected to go to the fishing grounds several times. It is clear, however, that their average number of expeditions does not exceed two.

When each breeding bird goes twice, this accounts for 8000 returns, the rest (600) coming to the account of the non-breeders. When the latter, however, are more numerous, the only possible conclusion can be that a part of the breeding birds goes only once a day to the fishing grounds.

Observations at the nests, as will be shown in chapter 12, lead to the conclusion that regarding parents with half-grown young, as a rule one goes fishing once, the other twice a day. So the 4000 breeding birds account at the end of May for 6000 journeys, non-breeders being responsible for the remaining 2600.

The latter figure is higher than expected, it seems improbable that the numbers of non-breeding birds lie above 2000. Moreover we have to take into account that our starting point (8600) has been deduced from parts of two days, which may permit a variance of several hundreds.

It is sure, however, that all evidence available leads to the conclusion that the numbers of daily trips are very low.

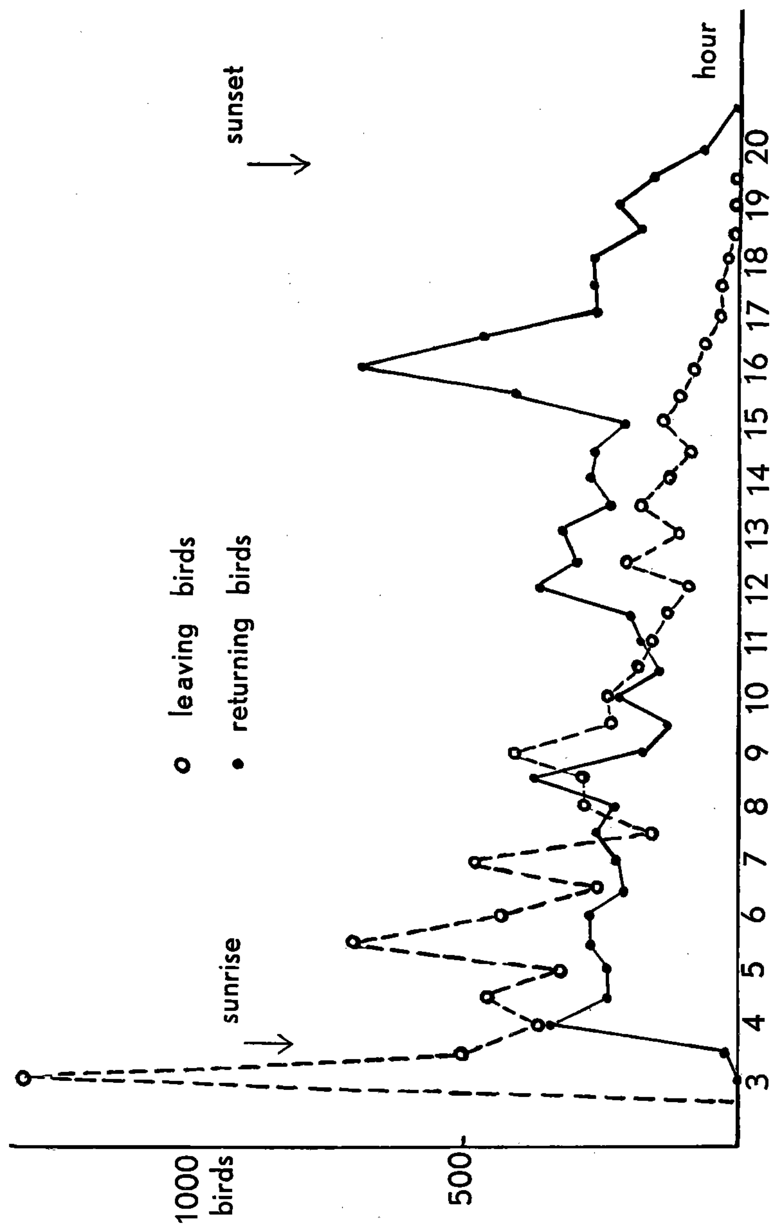

Fig. 3. The number of birds leaving and approaching the rookery every half hour during one day (May 24 and 25, 1939).

This is very remarkable, for a Cormorant might easily go several times a day to the IJsselmeer. Two facts, however, must be recognised. In the first place the Cormorant seems to dislike this journey (circling, hesitating). In the second place the large stomach enables the bird to carry a day's meal at a time. The digestion is so slow that it makes little difference whether the fishing is divided over the whole day or done in the early morning.

It is clear, however, that parents fishing not only for their own needs but also for 3 large young, must carry a daily ration for $2\frac{1}{2}$ cormorant each, weighing about 1000 grammes (see chapter 10 and 13).

Even for a large Cormorant this is not possible, 750 grammes being the maximum load. There is, however, a chance of avoiding this difficulty. When a Cormorant, immediately after its arrival at the fishing grounds, begins to fish and then sits down some hours to digest enough food for its own needs, it will make room for a second catch, this time to feed the young. In such a case it will be sufficient to carry 600 grammes (for $1\frac{1}{2}$ young) to the rookery. It is clear that in such a way even a Cormorant with large young ones may be able to limit its daily fishing trips to one.

In chapter 12 where the observations at the nests are recorded it will be shown that the feeding of the young indeed begins rather late in the morning.

It is a fact that a Cormorant spends only a little part of the day in fishing. Few other species are so often seen sitting quietly for a long time at the same spot. It must be remarked that it is impossible for this bird to fish for any long time, because the feathers do not protect it sufficiently against the water. HEINROTH (1927) explains this by the fact that the large wings cannot be hidden in the body feathers so completely as is done by ducks. KORTLANDT (1940) assumes that the structure of the feathers is responsible. It also seems that the skin of the Cormorant is highly pneumatic, probably a protection against the frequent cooling by cold water (GROEBBELS 1932).

Several authors stress the point that the Cormorant goes to the water only for fishing. KORTLANDT even remarks that, properly speaking, this bird is a hydrophobic ! This may be somewhat exaggerated. On several occasions I saw Cormorants resting on the water, e.g. when the rookery was disturbed early in the season. Then a troop of several hundreds floated on the water of the Belterwiede till all was quiet. It struck me, however, that in such a situation they float much higher on the water than when fishing, thus probably succeeding in keeping dry.

Little birds, e.g. passerines, spend the larger part of the day in search of food; when they have young, even the whole day. Large birds require relatively less food, so that the Cormorant can better be compared with a bird of the same size.

The heron, for instance, spends undoubtedly far more time in fishing than the Cormorant. Moreover its average prey is much smaller. For a Cormorant it is a common event to catch a prey satisfying its whole daily need. It seems to me that the Cormorant, in comparison with other animals feeding on large prey, has an easy life. Its prey is numerous and its fishing technique apparently superior. In this respect it is perhaps comparable with the Peregrine Falcon, also a successful hunter spending most of its time in idleness.

The rapid increase of these species when undisturbed by man possibly bears some relation to this fact.

7. The vomiting.

The data on the food of the Cormorant recorded in this paper originate almost exclusively from ejected meals collected in the rookeries. The vomiting is mainly a reaction to disturbance. When the rookery is disturbed the birds on the nests stretch their necks. When the danger disappears, the tension is broken by shuffling of feathers or by producing droppings. When, however, it approaches, the birds react by vomiting or flight, or both.

While vomiting the bird moves its head slowly to and fro; the corresponding sounds resemble those made by humans under similar conditions. This behaviour may be a nervous symptom without any biological significance. It is, however, not impossible that an enemy trying to climb the nest tree is scared by the vomiting or his attention diverted by the fishes falling down as a kind of ransom.

The supposition is allowed, too, that a flying Cormorant frees itself from ballast by vomiting. It is a fact that brooding birds often fly with difficulty; it is not uncommon to see such a bird falling from the nest, being apparently too stiff to get on the wings. Such a bird will vomit vehemently. Non-brooding birds also vomit when the colony is disturbed.

Large young birds, even those which cannot yet fly, show the same reaction.

When a rookery is visited daily to collect ejected meals, the birds grow more or less accustomed and react less intensely. After some days' interval the accumulation was always greater. Persons new to the birds induced increased vomiting. Policemen in uniform appeared to stimulate the vomiting considerably. Each ejected meal was noted separately. The fishes were identified and measured; for partly digested ones the length was estimated. On a following visit all old remains had disappeared. The ducks, rats, crows and herons living in the rookery were responsible.

The Blue Herons especially followed my steps at a safe distance and disputed with each other over the half digested fishes. Rats and ducks cleared the rest in darkness. The Carrion-Crows exploit each disturbance in the rookery by stealing eggs and fishes.

I never saw an adult Cormorant take a vomited fish from the earth; a fledged young did it once.

8. The digestion.

Ejected meals from Cormorants may contain totally undigested fishes as well as partly digested ones. Figure 4 can illustrate how this is possible.

The stomach of the Cormorant is a club-shaped, thin-walled and very extensible organ. It enables the bird to swallow a fish as long as its own body. When a Pike measuring 40 centimetres in length is carried, the tail can be seen in the half-open bill of the bird, waiting for the digestion of the head. When such a fish is vomited, its body is luke-warm, but the tail very cold.

The intestine is about half a centimeter wide and measures 2-3 meters in length. It is situated behind the stomach, ascending to make several spiral windings before descending to the cloaca. The digestion is restricted to the lowest part of the stomach. Normally the fishes are placed with the head down. Gliding gradually into the digestion zone the head is attacked first, with a rather sharp contrast between the digested and undigested part. So it is possible that fishes are produced with undamaged body but without head.

When a little fish lies crosswise in the lower part of the stomach it is digested over its full length simultaneously. Eels form a clew in the stomach; it often happens that parts of the middle are digested whilst head and tail are undamaged. The habitus of a vomited fish enables us to reconstruct more or less the position it held in the stomach.

By section on young Cormorants in captivity it was learned that a column of fishes as shown in figure 4 glides into the digestion zone at a speed of about 1.5 centimeters in one hour. The complete digestion of one large fish (Pike-Perch) measuring 30 cm in length lasts about 15 hours; the hind part disappears rapidly after gliding down crosswise in the digestion zone. It appears that the rumours about the fantastic speed with which the Cormorant digests its food, are not true. This explains how it is possible that a bird after brooding for hours may produce an entirely undamaged fish.

The capacity of the stomach is not easy to determine. A grown-up young Cormorant in captivity, a very large and healthy specimen, refused food after receiving 500 grammes. Only 4 hours later it accepted another 200 grammes. The largest meals I ever obtained from adult birds weighed about 750 grammes. This may be a limit; it is exactly the same weight as reported by MADSEN and SPÄRCK (1950) as a maximum.

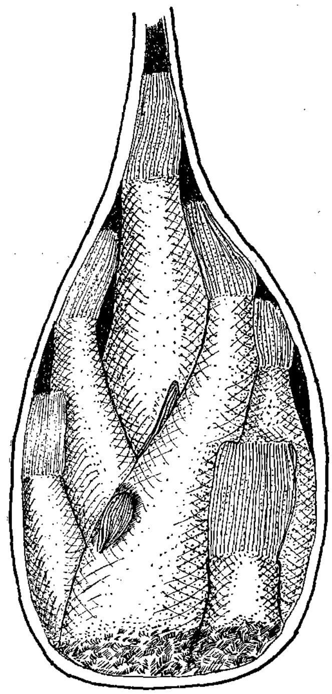

Fig. 4. Stomach of a Cormorant filled with Roach. Estimated length of the fish 12, 14, 15, 15, 18 and 19 cm, total fresh weight about 275 gr.
Brooding bird May 4, 1940.

During the digestion process the flesh is liquified and disappears into the intestine. What happens exactly with the bones and scales of the prey is not quite clear. STRESEMANN (1927) points out that all bones are dissolved in the stomach of the Cormorant, but this is certainly not always the case. I have fed young Cormorants for weeks without observing ejected bones, so that it must be assumed that the fishbones were digested. There is no doubt, however, that adults in freedom eject most of the bones and scales, for a large part in the form of pellets and without many signs of damage. This made me initially assume that the gastric juice is non-acid, but this proved to be untrue.

The gastric juice of a large young Cormorant, half an hour after feeding with a little piece of fish, appeared to contain 136 mgrs/equivalent HCl/L, the pH being 0.9 ! This was a practically pure secretion of the stomach. Other samples, somewhat mixed with digested fish, gave the following pH-values: 1.3; 1.9; 2.9 [1]). It would be surprising if fishbones escaped digestion in such an acid milieu. Other observations indicate, however, that in practice the gastric juice is largely neutralised. Three hours after feeding a complete meal, a mixture of liquified fish taken from the stomach gave a pH-value 4.6. This may explain the fact that even towards the end of the process, when only bones and scales remain, these are not digested.

Miss MENNEGA (1938) has drawn attention to the fact that during

1) The material was sucked from the stomach with a small rubber tube swallowed by the bird. This proved to be a very simple and effective technique.

digestion of large quantities, pH-values in the stomach of some birds are surprisingly high (for a heron > 3.5) while the pepsine-optimum lies at 2.4. This discrepancy is as yet unexplained.

In the (few) stomachs examined I found only remains of fresh meals, which gave the impression that all bones are removed daily in some way [1]).

A part may be digested, even in old birds. A large part is simply vomited. Finally large quantities of pellets are found under the nests.

These pellets are oblong, varying in length from 4 to 7 cm. Each pellet is surrounded by a mucous membrane. During a section of a large young Cormorant I had the opportunity to observe the origin of such a pellet. It appeared that the pituitary lining of the gizzard was pushed off and enveloped the undigested remains of the food. This process is perhaps the normal ending of each meal for an adult Cormorant.

After the removal of the pellet a new lining may be formed to receive a new meal and to be pushed off in its turn.

MADSEN and SPÄRCK (1950) observed in 7 (out of 365) Cormorant stomachs a "more or less advanced shedding of the cuticle". These stomachs were entirely or almost empty.

The pushing off and vomiting of the lining of the stomach in birds is mentioned by GROEBBELS (1932), but few details are given.

BARTLETT (1869) gives the following communication: A hornbill in captivity regularly threw up the entire epithelial lining of the gizzard, containing undigested food. It was clear that a quick regeneration took place (confirmed by W. H. FLOWER 1869). BARTLETT (1881) later on made a similar observation with an *Ahinga* and writes: "I feel particularly anxious to call the attention of persons keeping cormorants to this habit, as it is highly probable that this bird does the same thing".

BARTLETT gives no indication that this may be a mean to remove undigestable rests of food. FORBES (1881) has examined and described one of the objects thrown up by *Ahinga*. It was identical with the epithelial lining of the stomach.

As confirmed by the microscope, the mucous membrane of the pellet of the Cormorant, however, has no cellular structure.

So far as I know, the pellets of other birds have no mucous cover. The pellet of an owl, for instance, must be formed in quite a different

1) LUMSDEN and HADDOW (1946) often observed in the stomach of the Shag *(Phalacrocorax aristotelis)* large numbers of worn otolithes and do not mention pellets at all. There seems to be a large difference between the two related species in this respect. LUMSDEN and HADDOW also report otolithes in the faeces. I never observed solids in the droppings of *Ph. carbo*. MADSEN and SPÄRCK (1950) never found accumulated otolithes in the stomachs of the Southern Cormorant.

way compared with the Cormorant. STRESEMANN (1927) records that owls may produce more than one pellet after one meal, whilst the Cormorant can form one pellet only after each meal.

9. The pellets as a means to establish the daily ration.

It is clear that the contents of pellets can show us the composition of the food equally well as the vomited fishes do. The bones, scales and otolithes make it easy to determine the prey. Moreover, the pellet may inform us about the size of the preceding meal. For brooding birds this meal will generally form a daily ration (see p. 26).

These considerations justify a careful analysis of pellets, especially of those from brooding birds. Therefore a number of pellets was collected under nests with eggs on May 5, 1940. It proved possible to determine every single fish involved and to estimate its length and weigth. Table I gives some results. It is clear that the portions forming one pellet agree fairly well with the estimate of the daily meal, which will be given in the following chapter.

It appears further that no complete skeletons are found in the pellets; generally at least half of the bones are missing. The way in which the pellets are formed excludes the possibility that a part of the bones remains behind, so that the missing part must be either digested or vomited before the forming of the pellet. One may ask whether it is possible under these circumstances that the remnants of a whole fish disappear. This seems unlikely, the remnants of all fishes involved being mixed together. When finally a pellet is formed each fish will be represented at least by some bones.

10. The "complete ejected meal" as a means to establish the daily ration.

It is not easy to determine the daily food ration of an animal in wild state. It is impossible to follow all doings and dealings of a bird in freedom.

There are circumstances, however, enabling us to form an opinion on the requirements of the Cormorant. In the former chapter the pellets were mentioned.

Furthermore a part of the ejected meals represent complete stomach contents, being the result of one visit to the fishing grounds. As Wanneperveen birds brooding eggs, generally make only one fishing tour a day, the capture from this tour can be accepted as a daily ration.

When a Cormorant vomits it is questionable, of course, whether the

TABLE I

Estimated length and weight of fish, whose remains were found in 19 Cormorant pellets, collected under nests with eggs; May 5, 1940.

Each fish is represented by a figure.

Length of each separate fish (in cm)	Total fresh weight in grammes
Roach 10, 2 × 14, 2 × 15, 2 × 18	290
Roach 13, 14, 15, 17, 18	260
Roach 2 × 15, 2 × 18	220
Roach 3 × 14, 18; Ruffe 30 × 7½	380
Roach 19; Perch 20; (one fish hook and 3 pieces of bark)	200
Ruffe ± 40 little specimens, estimated	300
Ruffe 15 × 6½	90
Perch 24; Ruffe 3 rather large specimens	300
Roach 12, 13, 18, 19; Ruffe 8 rather large and many small ones	400
Roach 10, 14, 15, 16; Perch 15; Ruffe 10, 12, 2 × 14	290
Roach 13; Perch 12, 13; Ruffe 3 × 14, 3 × 12	250
Roach 13, 18; Ruffe 28 × 10; (one water snail)	380
Roach 18; Perch 2 × 16; Ruffe 14	210
Ruffe 18 × 10; 17 × 6½	380
Roach 13, 2 × 16, 18; Ruffe 12, 13, 14	290
Roach 16, 17; Perch 15; Ruffe 10 × 5, 8 × 10, 3 × 14	390
Roach 15, 18; Perch 15; Ruffe 10 × 10	250
Roach 22; Perch 17, 20; Ruffe 10, 12	330
Roach 15; Perch 12; Ruffe 20 × 7½, 4 × 14	330
Average about	300

complete contents of the stomach are thrown out or only a part. In some cases this question can be solved with ease. It sometimes happens that the whole column of fishes leaving the stomach remains intact, the shape of the stomach being clearly represented. The digestion zone (fig. 4) can be distinguished and in such a case there is no doubt as to whether the vomit is complete.

Usually, however, the meals do not remain intact, the Cormorant shaking its head to and fro, the fishes flying right and left. Notwithstanding that, it is also possible in these cases to judge the completeness of the ejected meal. When half digested fishes are present we may suppose that all undamaged fishes, lying of course in the upper part of the stomach, are thrown out. When we fit the half digested fishes together we can reconstruct more or less the original column with its digestion zone and judge whether fishes are missing.

Now it is possible that some fishes are already completely disgested and that their bones are not thrown out. In such a case we could not accept the ejected meal as a complete one. When the vomits are collected early in the morning there is little chance, however, that a fish has already disappeared.

As the judgment of an ejected meal in its completeness requires much routine I waited until 1940 (May 3 and 4) to collect data on this matter. The situation was favourable at the time. The rookery had not yet been disturbed that year so the vomiting was intense. Most of the birds had eggs or newly hatched young, so that they were still fishing for their own requirements only. As a result I considered 29 out of 123 meals as complete. They are recorded in table II. The original weight of the half digested fishes is estimated according to their size.

We come to the result that these "complete meals", representing in most cases a daily ration, include generally between 200 and 500 grammes of fish.

On May 4 the average was 335 grs., on May 5 285 grs., the first day with mixed food being more representive.

It is remarkable that large portions always contain big fishes. Portions consisting of little fishes generally do not reach a weight of 300 grammes. This gives a valuable indication of the point at which a fishing Cormorant is satisfied. When only little fishes are taken the final stomach contents will approach the limit at which a feeling of satisfaction is reached. When, however, a big fish is captured towards the end of the hunting, this limit will be passed. So the complete vomits consisting of little fishes indicate the need of the Cormorant more exactly than those containing big fishes.

Judging from these data we may conclude that a portion of 250 to 300 grammes of fish a day can satisfy a brooding Cormorant. It is clear, however, that the average consumption is higher.

The hunger of a Cormorant taking less than 300 grammes may soon be satiated thanks to a big capture the day before.

We must also allow for the possibility that the daily need of a Cormorant with young ones is larger, much more energy being required. Moreover, table III shows that in 1939 many vomits from brooding birds equalled or exceeded the largest rations of May 1940. In 1939 the food situation seemed excellent, as will be explained later on. Taking all these facts into account it seems to me that the average need of a

TABLE II

Complete ejected meals, May 1940.
Each fish is represented by a figure.

Length of each separate fish (in cm)	Total fresh weight (estimated) in grammes
May 4	
Ruffe 10, 13; Smelt 9; Eel 4 × 14, 12 × 21, 4 × 26....	320
Tench 27..........	330
Roach 17, 20, 3 × 15	260
Roach 19, 3 × 15, 17	250
Tench 30	425
Eel 4 × 22, 25, 26; Ruffe 2 × 8; Roach 15, Bream 15..	190
Bream 23; Roach 20, 15	260
Pike-Perch 17, 28; Roach 19; Ruffe 4 × 6, 9, 11; Perch 8, 9; Eel 20, 21, 21, 25	390
Perch 3 × 19, 20; Ruffe 6, 8	370
Roach 15, 18; Perch 13, 15, 21	300
Roach 30	380
Pike-Perch 38	500
Pike-Perch 38	500
Roach 13, 14, 15; Ruffe 8, 10; Perch 10, 19, 20	330
Roach 13; Bream 19; Ruffe 3 × 10, 4 × 11, 6, 8; Perch 20	310
Roach 4 × 17	230
Roach 13, 2 × 15, 3 × 16, 20	340
Average	340
May 5	
Roach 12, 14, 15, 2 × 17, 19	280
Roach 14, 18, 19, 2 × 20	370
Roach 10, 12, 13, 18, 19, 20	300
Roach 2 × 15, 19, 20, 21	360
Roach 12, 14, 2 × 15, 18, 19	275
Roach 3 × 14, 3 × 15, 17	260
Roach 12, 2 × 15, 2 × 18, 19	310
Roach 12, 15, 16, 17, 19, 23	400
Roach 11, 3 × 15, 16, 18	245
Roach 2 × 14, 24	320
Roach 2 × 16, 19, 20	290
Average	285

TABLE III

Large ejected meals from March-April 1939.
Each fish is represented by a figure.

Length of each separate fish (in cm)	Total fresh weight (estimated) in grammes
March 13	
Pike 35	240
Roach 5½, 3 × 6½, 8, 9½, 10, 12, 12, 14, 14, 21; Ruffe 6½ 7 × 9, 10, 11	360
Roach 19, 35	600
Roach 9, 13; Pike-Perch 30	230
Bream 17, Pike-Perch 33	350
Bream 18, 22, 23	300
Pike 39	380
April 6	
Tench 27	330
Roach 32	460
Roach 13, 16, 17, 18; Tench 25	470
Pike 40	420
Pike 40	420
Rudd 20; Pike-Perch 34	440
Tench 34, Eel 40	660
Pike 40	420
Pike 40	420
Roach 12, 13, 15, 28; Perch 8	420
Roach 17, 22; Bream 16, 20; Pike-Perch 30	500
Pike-Perch 32, 33	560
Pike-Perch 34	340
April 7	
Roach 8, 10; Ruffe 5, 8; Bream 10, 18, 19; Perch 9, 10, 18	250
Pike-Perch 34	340
Pike-Perch 2 × 30	400
Roach 20, Bream 25	225
Pike-Perch 2 × 30	400
Perch 18, Bream 30	400
Pike-Perch 2 × 30	400
Bream 10, 25, 30	500
Bream 33	400
Perch 2 × 7, 27	350
Roach 16, 2 × 17, 21 (dark colour !)	275
Roach 32	460
Roach 2 × 15; Bream 15; Pike 14, 28	250
Roach 14, Ruffe 9, 10, Pike-Perch 34	370
Perch 13, Tench 2 × 24	500
Bream 32	300
Pike 39	380
Pike-Perch 33, 34	640

Wanneperveen Cormorant does not exceed 400 grammes a day. This estimate agrees with the daily requirement of a large young at full growth (chapter 13) and it is unlikely that this ration lies below that of an adult bird.

It is of interest to compare my estimate with the food requirement recorded for other birds.

Daily requirement of	% of body weight	Author
Little birds (summer)	50	RÖRIG (1903)
Starling (summer)	50	RÖRIG (1903)
Kestrel	33	RÖRIG (1903)
Kestrel	20-25	UTTENDÖRFER (1939)
Peregrine Falcon	20	HEINROTH (1927)
Heron	16,5	HEINROTH (1927)
Pelican	30	GROEBBELS (1932)
Cormorant (*Ph. ater*)	55 (!)	MATTINGLEY (1927)
Cormorant (*Ph. auritus*)	27	WETMORE (1927)
Cormorant (*Ph. c. sinensis*) ...	37.5	HEINROTH (1927)
Cormorant (*Ph. c. sinensis*) ...	20	MADSEN and SPÄRCK (1950)
Cormorant (*Ph. c. sinensis*) ...	20	my estimate

Nearly all these figures originate from birds in captivity; my estimate seems to be comparatively low. The question arises whether the Wanneperveen Cormorants eat as much as they can. The question is discussed in chapter 13.

11. The feeding of the young.

Young Cormorants are fed on the stomach contents of their parents. Newly hatched young ones are constantly and carefully covered, the parents relieving each other in the same way as while brooding the eggs. Now and then the old bird moves somewhat aside till a chicken can free its head and reach the bill of the parent. Then it wags its head and a feeble twittering is heard. The old bird vomits up a piece of fish and enables the young one to take it bit by bit from the side of the bill.

Such a piece of fish clearly comes from the digestion zone of the stomach (figure 4). It cannot be called half digested; it is a part loosened from a fish by the digestive process. An examination of some 8 newly hatched Cormorants fallen from the nests showed that their stomachs contained no or very few fishbones. It was clear that these very young birds had only received parts easy to swallow, often from large fishes.

The Cormorant does not change its prey at the moment of the hatching, for instance taking especially small fishes for the young birds [1]).

The feeding of newly hatched chickens often takes place hours after the arrival of the covering parent. It is possible that the required material cannot be obtained from a full stomach, where it must pass a column of undigested food (see fig. 4).

When the young ones are about one week old, the feeding gradually begins to take place in quite a different way. When an old bird appears on the nest, it is stormed by the young. Uttering a cry resembling the screeching of a wheel-barrow (tshe-wee-de) they wag their heads and touch the gular sack of the old bird. When the flight feathers are developped the begging young wave their wings. The parent stays motionless with raised bill and stretched neck. Sometimes it shows a tendency to move its head out of reach, the young making frantic efforts to restore the situation. When everything takes a normal course the old bird will make some swallowing movements and slightly open the bill. Suddenly the head of a young one plunges from the side into the beak of the old bird and disappears deep into the oesophagus. It can be seen as a moving knob in the parents neck. In this way the food in the stomach is reached by the young bird and usually already swallowed before the head is withdrawn. The first young often gets whole fishes, the following come to partly digested prey. I often saw large young Cormorants vomit fishes with digested head and tail, while the middle was intact. In such a case the head was digested by the old bird which always swallows a fish head first. While the young are fed, the fishes are not turned, so in the young bird the tail of the fish goes down first. In the case of a large Pike-Perch one may ask how this is possible without wounding by the sharp stickles of the fins. When a young Cormorant withdraws its head before swallowing, the fish is always turned; so this instinct is already early developed.

When the young Cormorants are fledged and begin to make trips in the neighbourhood, the feeding as a rule still takes place on the nesting site. The nest often disappears rapidly by negligence and robbing. When a parent is willing to feed, it takes a place on the nesting site and awaits the things to come. It will never be asked for food by strange

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1) On June 2nd 1939 I shot a ♀ on her return to the nest with just hatched young at 2.10 p.m. Its weight was 2.1 kg (empty). The stomach contained one large Roach (24 cm) and one Eel (47 cm), fresh weight together about 450 grammes. The fishes had been captured about 6 hours before (estimate).

young birds (as for instance young Sandwich Terns would do) the attitude towards strange old birds being very hostile.

When one of the own young becomes hungry, it flies to the nesting site and finds its parent. Immediately a feeding follows. Sometimes the old bird seems frightened by the onslaught of its child and flees. Then a wild pursuit follows and a feeding is forced elsewhere, looking almost like an act of violence.

Sometimes old birds can be observed pouring showers of water over the nestlings, from the stomach. The thirsty young ones try to catch the water, but their behaviour is not very adequate as KORTLANDT (1940) has described in detail.

12. The number of feedings.

In the Wanneperveen rookery birds brooding eggs as a rule change place twice a day: for instance a bird brooding during the night may be relieved at 11 a.m. and may return at 4 p.m.

When the young ones hatch this rule is continued provisionally, the old birds do not undertake special hunts to get food for their young. The chickens are fed "from stock", often hours after the relieving.

When the feeding method has changed as described in the former chapter the young are fed as a rule immediately after the arrival of a parent. Such a feeding is also divided into several efforts, some of which may lead to nothing. This can last for half an hour, pauses included. When one young is satisfied, another follows. A young bird receiving nothing will beg the more frantically at the arrival of the other parent. A series of feedings performed by one parent without leaving the rookery will be called one feeding in the following considerations.

During observations of several nests with young birds aged from 3 to 4 weeks, it soon appeared that the daily number of feedings is very low, beginning rather late in the day. Within 5 hours after sunrise only very few feedings are observed. Six hours after sunrise feedings get more frequent. It is, however, no exception to observe a nest with large young birds from sunrise till 2 o'clock p.m. without noticing a feeding.

My observations of 1938 and 1939 gave the impression that the young birds are fed as a rule only twice a day, once by each parent, the old birds maintaining the routine of one hunting trip each. The only indication of more daily feedings by one parent came from fledged young. To check this point, the 30th May 1943 8 nests were kept under observation from sunrise till sunset (5.20-21.50 double summer time), which I omitted to do in 1938-39.

In the following summary of these observations the periods are given during which each parent was absent, its return always being followed by relieving the partner and feeding the young birds.

1. 3 young birds about 2 weeks old.
   parent A absent: 9.30—15.20
   parent B absent: ? —7.20; 15.30—17.37
2. 3 young birds about 10 days old.
   parent A absent: 13.30—16.25
   parent B absent: 8.15—12.30; 16.30—20.50.
3. The same situation.
   parent A absent: 18.24—21.37
   parent B absent: ? —8.53; 12.10—15.30.
4. 2 young birds 3 weeks old.
   parent A absent: 8.00—14.03
   parent B absent: 14.09—18.02
5. Eggs.
   parent A absent: 11.00—15.45
   parent B absent: 16.20—19.20
6. 3 young birds about 3 weeks old.
   parent A absent: 10.05—12.40; 18.30— ?
   parent B absent: 13.30—18.30
7. 2 young birds about 4 weeks old.
   parent A absent: ? —10.40; 17.35— ?
   parent B absent: 11.40—17.35
8. 3 young birds about 4 weeks old.
   In the morning A is present but does not feed although the young ones beg vehemently. About noon this parent disappears.
   At 15.45 B arrives and feeds (it is almost murdered by the young !)
   17.18 A comes and feeds.
   B departs and is not yet returned at the end of the observation.

The following conclusions can be drawn from these observations. It appears to be almost a rule for birds with half-grown young that the parent fishing early in the day goes again after the partner has had its turn. So one parent fishes once, the other twice. This conclusion agrees with the result of the counting recorded in chapter 6.

Birds brooding eggs make one tour each. Although in this case only one nest with eggs was observed, previous observations have convinced me that this is the rule.

The conclusion already drawn in 1938 and 1939 that the first daily feedings take place rather late in the morning is confirmed by these observations. The feeding of the nestlings in nest 1 at 7.20 is abnormally early. The others were fed for the first time at: 12.20, 8.53 a.m., 14.03, 12.40 and 10.40 a.m.

In the following table the duration of the absence is recorded for both parents:

Nest no.	Parent fishing once	Parent fishing twice
1	5 h. 50 min.	> 2 h. and 2 h. 7 min.
2	2 h. 55 min.	4 h. 15 min. and 4 h. 20 min.
3	3 h. 13 min.	> 3 h. 33 min. and 3 h. 20 min.
4	6 h. 3 min.	
	3 h. 54 min.	
5 (eggs)	4 h. 45 min.	
	3 h. 0 min.	
6	5 h. 0 min.	2 h. 35 min. and > 3 h. 20 min.
7	5 h. 55 min.	> 5 h. 20 min. and > 4 h. 15 min.
8	5 h. 18 min.	> 10 h. 25 min. and > 4 h. 32 min.

The old birds stay away from home for a rather long time and we can be sure that the larger part of this time is spent in idleness. Then the bird has the opportunity to digest food for its own need which enables it to give to the young eventually all fishes carried home. The best use of the situation can be made when the old bird loads to capacity immediately before the return. I have the impression that especially birds with large nestlings do so regularly.

It is necessary to emphasize that the relations described in this chapter form no rule for all Cormorant rookeries. At Lekkerkerk where the rookery is situated neat the river Lek, the birds go fishing several times a day, as KORTLANDT told me.

13. The daily ration of the nestlings.

Observations at the nests are unable to give us an exact idea of the quantity of fish fed by the parents to young Cormorants. Large fish can often be swallowed only after the withdrawal of the nestling's head from the throat of the old bird. Such observations cannot be generalized, however.

When a young bird vomits it is impossible to judge whether the stomach is emptied completely, for it contains partly digested and undigested fishes mixed together. Large vomits of young birds lay between 200 and 300 grammes (fresh weight of fishes, table IV) but it is not certain whether a part of a fish has been digested by a parent.

Many meals consist of one large fish or the remains of it. Because a young may be fed several times a day we are never certain whether an ejected meal represents a daily ration.

TABLE IV

Large ejected meals of nestlings in 1938.
Each fish is represented by a figure.

Lentgh of each separate fish (in cm)	Total fresh weight (estimated) in grammes
June 14	
Roach 9, 2 × 11, 2 × 12, 13; Ruffe 3 × 7, 8	130
Pike-Perch 17, Perch 17, Roach 17, Ruffe 7, Smelt 15 × 8	220
Eel 18, 20, 23, 2 × 25, 26	110
Roach 8, 12, 2 × 13, 15, 19; Perch 16; Ruffe 7, 8	250
Roach 14, 17, 18	160
Roach 14, Eel 2 × 22, 13; some little Smelt	120
Eel 2 × 24, 34	120
Roach 10, 13, Smelt 30 × 8	150
Burbot 30	500 (?)
Eel 2 × 23, 24, 3 × 25, 26	150
Roach 12, 17; Perch 15; Ruffe 2 × 7, 8, 9, 10	160
June 15	
Eel 18, 20, 21, 22, 23, 24; Ruffe 6	110
Roach 2 × 12, 14; Bream 14; Ruffe 8	100
Eel 24, 25, 35	130
Eel 18, 22, 2 × 23, 24, 2 × 25	130
Roach 13, 2 × 15; Ruffe 8	110
Roach 16, 18	120
20 large Sticklebacks	100
Tench 27	330
June 17	
Eel 20, 24, 2 × 25, 26, 28; Roach 12	160
Roach 11, Smelt 30 × 8	140
Bream 2 × 16, 2 × 18	230
Roach 20	100
Roach 11, 20	110
Roach 22	130

The result of some sections was the following: A large nestling vomited Eel: 20, 20, and 22 cm; Roach 12 cm. After it had been caught it produced Eel: 25, 25 and 26 cm. Killing the bird I found yet another Eel: 25 cm in the stomach. Together 8 fishes with a fresh weight of about 150 grammes. This may be the result of one feeding (the young was alone).

Three nestlings of about 3 weeks old, weighing about 1.7 kilogrammes each had the following stomach contents:

Eel	21, 22, 26 cm	(fresh weight 53 grammes)
Eel	26 cm	(fresh weight 25 grammes)
Eel	25 cm	(fresh weight 23 grammes)

These Eels originated from one feeding in the morning. The stomachs contained no bones, they had received no more food earlier in the day.

At 14 p.m. the mother arrived, a little bird weighing 1.9 kg (empty). It was shot.

The stomach contained:

1	Roach	18 cm, fresh weight	70 grammes,	totally digested
1	Roach	14 cm, fresh weight	30 grammes,	half digested
1	Pike-Perch	30 cm, fresh weight	220 grammes,	head digested
12	Ruffes	8-9 cm, fresh weight	180 grammes,	6 half digested
Total capture		....	500 grammes	of which about 150 grammes digested

For the young 350 grammes of fish were available and it is questionable whether the mother would have given all the food she carried. If she did so and divided the food equally between the young, each one would receive 117 grammes (a honest division is impossible in this case because of the large Pike-Perch).

Then the young would receive 170, 142 and 140 grammes, after two fishing tours of the parents. The father would certainly have departed at 14 p.m. for a second tour if I had not intervened. It would have been impossible for him, however, to bring the ration of this day per young above, let us say, 400 grammes.

Because the shooting in the rookery was undesirable, I have abstained from further sectioning and tried to approach the problem in another way.

Some young birds were held in captivity and fed on a daily ration. It was tempting to use for this purpose young birds fallen from the nests and I did start with them, but they seemed never to be quite normal so that later on I took young birds from the nests.

The following experiment dates from 1938:

From a nest with 3 nestlings being about 3 weeks old and very different in size, the middle one was taken after weighing of all three.

It received 300 grammes of fish daily. After 18 days all three were weighed again with empty stomachs. The result was:

	Nestling with ration of 300 grms.	Large brother	Small brother
June 27, begin of the experiment	1875 gr.	2125 gr.	875 gr.
July 5	2000 gr.		
July 11	2125 gr.		
July 16	2125 gr.	2125 gr.	1875 gr.

It appears that in this case the daily ration of 300 grammes was sufficient to give the young Cormorant in captivity the same weight as his large brother fed by the parents. It is very surprising that the latter apparently had reached its top weight so early. The little one, which initially looked quite abnormal seemed to have taken advantage from the removal of one of the rivals. It had recovered a great deal at the end of the experiment.

In 1939 experiments were carried out with 5 nestlings. As a control 3 young birds from one nest were weighed.

The result was this:

In captivity	No. 1 3 weeks old daily ration 200 grms.	No. 2 3 weeks old daily ration 300 grms.	No. 3 4 weeks old daily ration 200 grms.	No. 4 4 weeks old daily ration 280 grms.	No. 5 4 weeks old daily ration 320 grms.
May 19 (beginning)	1230 gr.	1400 gr.	1900 gr.	1750 gr.	2150 gr.
June 5	1450 gr.	1800 gr.	1700 gr.	1700 gr.	2250 gr.

Controls (4 weeks old)

	No. 6	No. 7	No. 8
May 19	1600 gr.	1400 gr.	1400 gr.
June 5	2500 gr.	2200 gr.	2100 gr.

At the end of the experiments the birds were weighed with empty stomachs, they had received no food that morning.

It must be remembered that adult Cormorants vary in weight between 1700 and 2600 grammes, so that a young bird weighing 1700 grammes may have reached its maximum.

It seems clear, however, that a daily ration of 200 grammes of fish is insufficient to warrant a normal increase in weight. The young ones receiving this ration were very meagre, though not backward in development. The birds receiving 300 grammes were rather normal, but it is obvious that the controls have received more from their parents.

It seemed to me that the state of nourishment of the young Cormorants at Wanneperveen was better in 1939 than in 1938. This may be caused by the rich capture of Pike-Perch in May 1939. The young Cormorant seems to possess a large amount of adaptivity. When it is somewhat undernourished it gets meagre but develops normally. When the undernourishment makes even this impossible, the bird is able to recover when the food situation improves (the "small brother" of 1938).

With passerines this is impossible. When the development is hampered here, a young bird cannot recover. Of course there is a large difference between the development of a young Cormorant staying 7-8 weeks in the nest and that of a young songbird completing its nestling period in a quarter of that time. It is evident that such an intensive process cannot bear any deflection. Accordingly young songbirds require relatively far more food than their parents; this does not hold for the Cormorant.

When we estimate the daily ration of a well-fed young Cormorant weighing 2000 grammes at 400 grammes this means 20% of the body weight and about the same as my estimate for adult birds.

Heinroth (1927) records 500 grammes for 4 weeks old nestlings and 750 grammes for adults. I have offered 750 grammes daily during a short period to a very large young Cormorant and learned that it is possible indeed to force it upon the bird. Once it took 1000 grammes within 16 hours. It is very doubtful, however, whether ever one nestling receives so much from its parents. The often moderate state of nourishment of the young, especially in 1938, indicates that at the time the average daily ration did not reach 400 grammes. Besides I accept this as one of the signs that the life conditions of the Cormorants in Wanneperveen are not quite optimal, notwithstanding the richness of their hunting grounds. Another sign is the small size of the clutches, mainly 3-4 eggs, giving generally 2-3 young birds (I only saw once a nest with 4 young ones). Moreover second broods are rare.

I assume that there is a relation between these facts and the low number of daily visits to the feeding grounds. All this may be the result of the aversion to the flight over the land route separating rookery and IJsselmeer, described in chapter 4. It sounds unlikely that such a strong flyer should be handicapped by a ten minutes flight; the handicap, however, may be purely psychological.

A comparison with the colony of Lekkerkerk, where the birds nest right next to their main fishing grounds, visit the river frequently, have larger clutches (mainly 4-5 eggs) and often brood twice, may give a justification of my assumption.

14. The total requirement of the colony at Wanneperveen.

My estimate of the total consumption of the Wanneperveen rookery is based on the following population figures:

Adult birds 4000; non-breeding birds 2600; nestlings 5000.

Further it is assumed that the adults arrive from March 1 and that their numbers are completed in April. The non-breeding birds arrive mainly in April. The young birds take their part from May 15 and are accepted as full consumers from July 1.

On the basis of a daily requirement of 400 grammes the total consumption of such a population amounts to 740.000 kg till October 1 [1]). This food originates, as stated before, for about 94.5% from the IJsselmeer. The landings by human fishery from this lake totalled in 1939: 2.100.000 kg Eel, 2.600.000 kg Pike-Perch, about 5.000.000 kg Ruffe and 1.000.000 kg Smelt. So it appears that the capture of the Cormorants (about 700.000 kg) cannot be treated as negligable.

Much depends on the share of valuable fishes in this capture. In the chapters discussing Eel and Pike-Perch this question will be approached in detail.

The figure 700.000 should be accepted as a maximum, perhaps reached in the "rich" year 1939. I am convinced that the consumption in 1938 was (perhaps 20%) lower.

15. The fish population of the IJsselmeer.

An exact knowledge of the fish population available is of great importance to judge the feeding habits of the Cormorant. In cases as Lekkerkerk, where the birds fish in large rivers as well as in several polder waters with quite different inhabitants it is much more difficult to get information than in Wanneperveen, where the IJsselmeer with its wellknown population is the main hunting ground.

The following facts are derived from publications of HAVINGA (1938, 1939).

After the disappearance of the salt in the IJsselmeer following the

1) Towards the end of September the rookery is gradually deserted. It is not certain whether the departing birds leave the IJsselmeer immediately. Ringed young birds from Lekkerkerk are found in France and Italy from September, and in North Africa from October onwards. Besides, it is certain that other young birds are still in the Netherlands at the same time.

close of the dike in 1932, a few species of fresh water fishes living at the time in the fresh parts of the Zuiderzee near the IJssel mouth have spread rapidly.

From these the Perch, Roach, Bream, and in a lesser degree White Bream have formed a close population in the shallow coastal waters. In the south and east parts of the lake this zone is several miles wide.

Locally *Potamogeton* fields are developed.

More locally or rarely other species as Pike, Carp and Gudgeon occur and in my opinion it is certain that the Tench must be common locally, although this view could not be accepted by Mr. HAVINGA. Two fresh water species, Ruffe and Pike-Perch have spread over the whole lake. In a far less degree this is also the case with the Bleak. From the old inhabitants of the Zuiderzee the Smelt and the Eel have maintained themselves in the IJsselmeer, the Eel increasing in numbers.

The typical salt water fishes disappeared except for some Flounder.

The following figures from test fishings in the coastal zone of the NE part of the IJsselmeer (the fishing ground of the Wanneperveen rookery) were placed at my disposal by Mr. HAVINGA (13 fishings, from June 1938 till April 1939).

Ruffe	135000 specimens	Bream	950 specimens
Smelt	25000 specimens	White Bream .	50 specimens
Eel	1380 specimens	Bleak	1 specimen
Pike-Perch	435 specimens	Carp	15 specimens
Perch	121 specimens	Flounder	1 specimen
Roach	1736 specimens	Stickleback ...	many specimens

These figures undoubtedly give only a part of the true proportions. The figure for Eel is low because the samples were taken during daytime. Fishing at night would provide about 4 times more. The Tench is not represented, whereas the Cormorants land many Tench together with typical IJsselmeer fishes.

In the *Potamogeton* fields near the coast the proportions may differ from those shown on this list.

Notwithstanding this the results of the fishing tests are of great value in forming an opinion of the population of the lake.

16. The composition of the food.

The data underlying my conclusions originate mainly from the rookery at Wanneperveen. In the years 1938, 1939 and 1940, respectively 8443, 4306 and 526 fishes were collected here from Cormorant vomits. In the two first years this was done regularly, often twice a day. Figures 5 and 6 give a survey of the share of several species of fish in the course of the breeding season. Figure 16 gives a similar survey for the rookery at Lekkerkerk, concerning 540 fishes only.

In my opinion it may be permitted to accept the vomited fishes as a reliable sample of Cormorant food. It is imaginable that big fishes overcharging the birds more or less are thrown out more easily than small prey. The observations in the rookery do not give the impression, however, that a close relation consists between the stomach contents and the

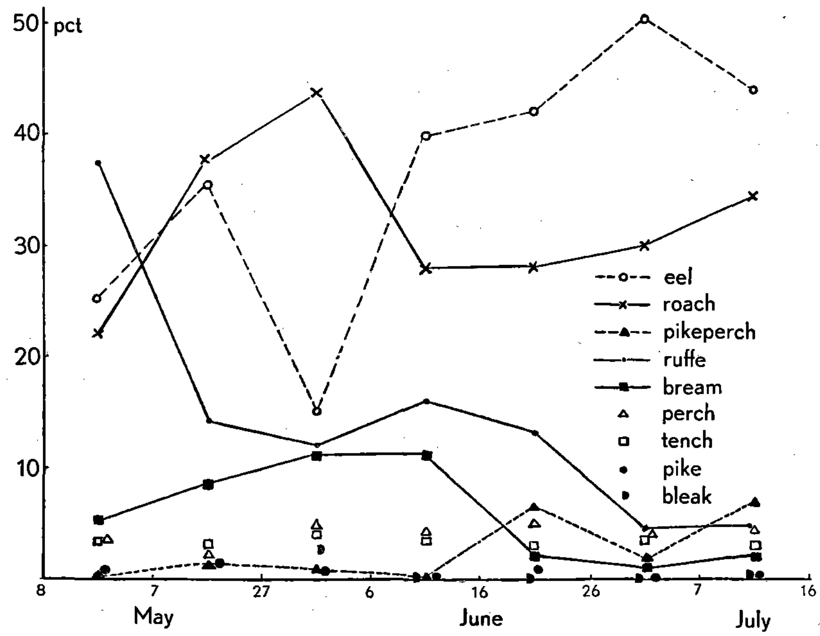

Fig. 5. Percentages of several fish species landed by the Wanneperveen Cormorants during May, June and July 1938. Smelt and Stickleback excluded.

tendency to vomiting. Disturbed Cormorants vomit even when their stomach is practically empty.

It is very interesting to compare the composition of the food in a certain rookery with the fish population of the hunting grounds.

The capture of the Cormorants is of course a reflection of this fish-population, although not a true reflection.

The differences between the fish available and the fish captured originate mainly from:

a. the preference towards large fishes;

b. the ease with which a species can be captured, its accessibility.

The average size of the Cormorant prey is larger than that of the total fish population. Fishfry to a length of 6 cm is rarely taken. MADSEN and SPÄRCK (1950) state that Danish Cormorants usually do not take fish below 15 cm.

Sticklebacks and little Smelts are infrequently taken in spite of their large numbers. From little species the elder generations are preferred.

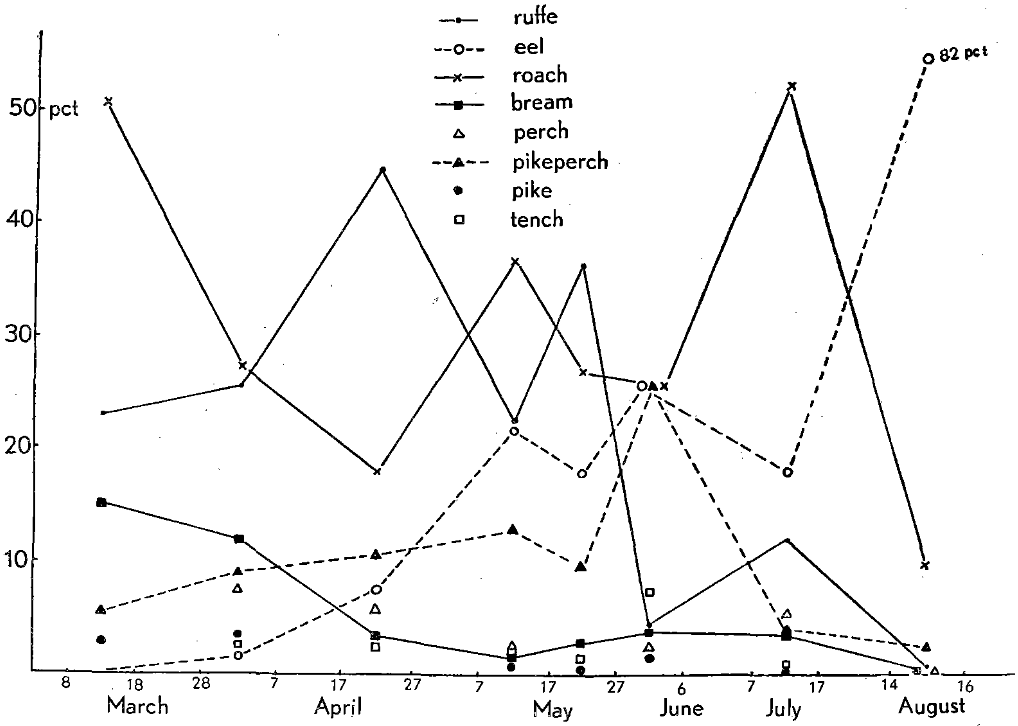

Fig. 6. As fig. 5 for several periods in the spring and summer of 1939.

This will be illustrated in the following chapters. From very large species of fish such as Pike and Pike-Perch the elder generations cannot be mastered by the Cormorant, the birds restricting themselves to the half-grown individuals.

The accessibility of a species depends on its habits, there are indications that slow swimmers are preferred to fast swimmers of the same size and that fishes swimming freely are taken more easily than those living hidden between waterweeds. Instances of this will also be given in the following chapters.

17. The fluctuations in the composition.

A glance at the figs. 5, 6, 7 and 8 immediately shows that the composition of the food is far from constant. There are annual, seasonal and even diurnal fluctuations.

Differences between two years can be explained without difficulty by alterations in the fish population. Seasonal changes are due to alterations

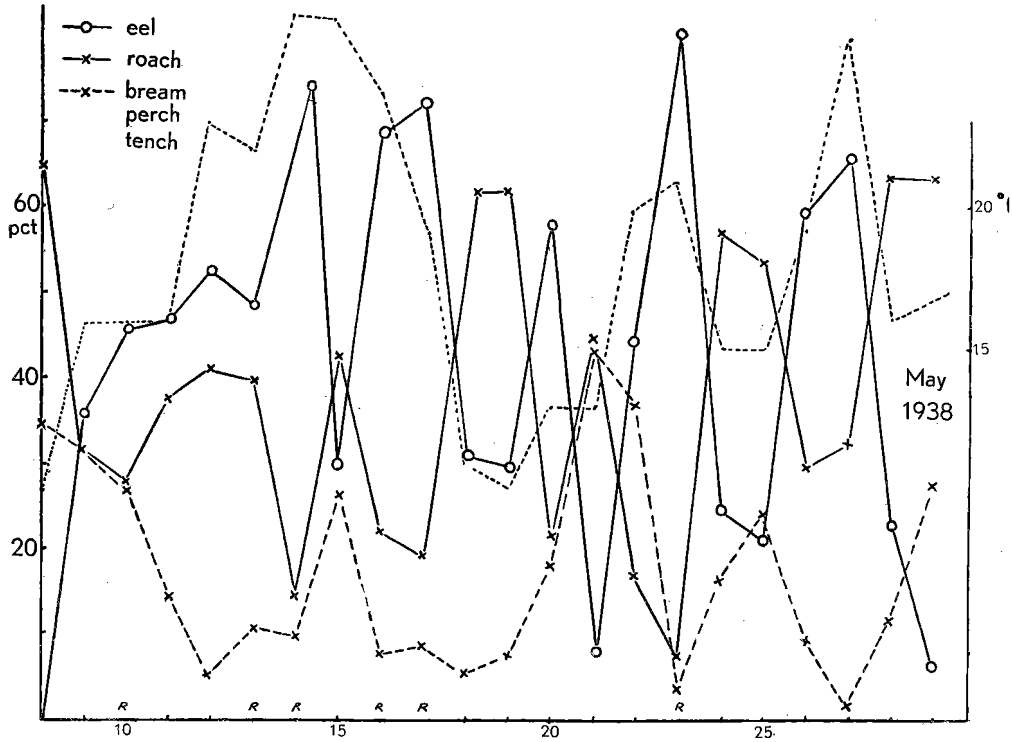

Fig. 7. Percentages of several fish species (without Smelt, Stickleback and Ruffe) landed by the Wanneperveen Cormorants during successive days in May 1938. ------- : optimal daily temperature in degree Celsius. R: Ruffe abundant.

in behaviour or size of the fishes in the course of a season as will be shown in the following chapters.

Moreover figs. 7 and 8 show that the numerical relations between the species can change enormously on successive days. These changes are mainly connected with the weather. In the first week of May for instance. Eels are only landed in sunny weather. Roach, Bream and Ruffe prevail when it is cold.

When only a part of the day is sunny, the composition of the food changes accordingly. As will be shown in chapter 18, these relations are ruled by the accessibility of the Eel.

Some daily fluctuations may be explained by a changing preference of the birds for parts of the fish-water with different population. On fine sunny days from the second half of May onward it is a rule that from the morning till afternoon the landings of Roach decrease whereas

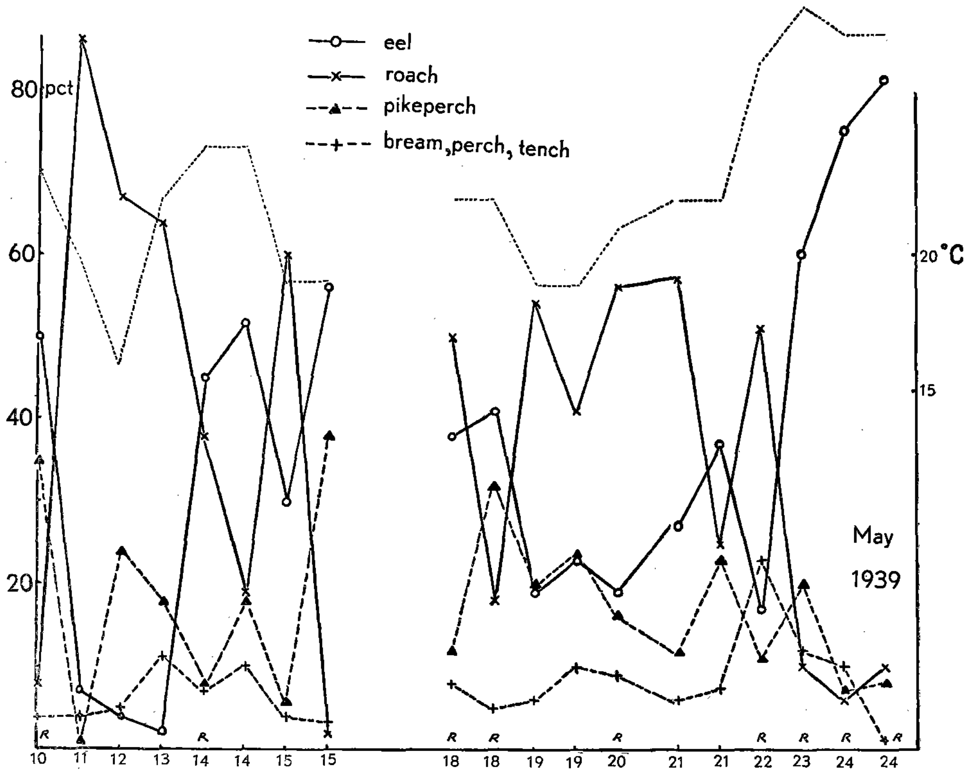

Fig. 8. As fig. 7, for May 1939. In cases where one date appears twice, the first figure refers to the morning, the second the afternoon.

the Eel and the Pike-Perch increase (fig. 8). This is explicable when we remember that the Roach is numerous only in the coastal zone of the IJsselmeer, whereas Eel and Pike-Perch are not restricted to any part of the lake. When a majority of the Cormorants fishes in the coastal zone at dawn and in the centre of the lake in the afternoon, the relation in the capture will be as mentioned above.

Although I am not in the position to prove this by direct observation, some indirect support can be given.

In chapter 12 we saw that a fishing tour of a Cormorant as a rule lasts for 3-5 hours. From the observations recorded in fig. 3 it appears, however, that in the early morning many birds return after a one hour's absence. It is unlikely that those birds go far from home, they probably fish in the coastal zone. Moreover, I suppose that these are mainly birds brooding eggs (compare chapter 12). The absence of birds making their tour later in the day as a rule lasts longer. This fits very well with the supposition that they go farther from home and may visit the centre of the lake.

Our knowledge about the behaviour of both birds and fishes is very incomplete and in some cases it is quite impossible to explain very striking fluctuations in the capture.

It is difficult to understand for instance why on some days (27 May 1939 !) masses of one year old Roaches were landed, dirted with green algae. Apparently one or another uncommon situation in the lake had enabled the Cormorants to catch them easily, perhaps in social fishing.

Hardly a single observation was made in the Wanneperveen rookery to indicate a relation between the spawning season of any fish species and an increased capture by the Cormorants.

Madsen and Spärck (1950) also report seasonal changes, partly connected with the spawning season. This applies to the Herring, which is taken when it comes near the coast in autumn and spring. Mackerels are only taken in summer, when they come into Danish waters. The Flounder is reported absent in one cold season, when it stays in deep water. The Eel is called a "constant element in the food" by these authors. Their observations begin in April and are, in my opinion, insufficient to justify this statement.

18. The Eel, *Anguilla anguilla* (L.).

In the Netherlands the Eel is considered to be the principal food of the Cormorant; the Dutch name of this bird "Aalscholver" means: Eel-Cormorant. It is true indeed that the Eel is an important prey but it is not easy to determine whether there is a real preference for it. It is remarkable that the number of Eel collected in the rookery varies strongly with the season and the weather. It seems that at one time the Eel can be captured easily, while at other times it is difficult to obtain.

Looking at fig. 6 we see that before May import of Eel is rather insignificant. With the approach of the summer the import increases till on warm days in July the Eel undeniably becomes the principal food.

At first sight the reason of this change seems clear: the human fishery of Eel also begins towards the summer. It is well known that in the winter this fish disappears into the mud and that it begins to "walk" (as the Dutch fishermen say) when the temperature of the water increases. This holds, however, for night-time only, the human fishery accordingly being executed at night. The Cormorant on the contrary fishes only at daytime when the Eel as a rule hides in the mud. HEINROTH (1927) asks how it is possible that a daytime bird can capture such a nocturnal animal in large quantities! There are some indirect indications enabling us to answer this question. In the first place almost all Eels produced by the vomiting Cormorants have a typical injury at the rostrum, their noses are squeezed and reddish. It appears further that on warm and sunny days Eels' heads often protrude more or less from the mud.

Mr. I. KRISTENSEN described the behaviour of Eels in captivity to me as follows: with every rise of temperature—in the afternoon in the sun or in the winter in a heated room—the Eels lift their heads out of the sand, making a swinging movement and respiring vigorously.

It can easily be imagined how an Eel, surprised by a Cormorant in such an attitude will try to withdraw its head, the nose being the last part of the body to disappear. It is likely that this behaviour makes the Eel an easy prey during suitable weather and explains the mass supply on warm summer days.

We cannot, however, exclude the possibility of a real preference and an adaptation to a special hunting method.

In the first weeks of my presence in the rookery when I knew nothing of these facts it struck me at once that a deterioration of the weather was followed by a decrease of the import of Eel. For instance May 20, 1938 the following fishes were found:

	Morning, weather fine and sunny	Afternoon dark and rainy
Eel	54	3
Roach	3	18
Perch	1	5
Tench	3	4
Bream	0	5
Ruffe	15	1

A comparison of bright and dark days in May shows this difference clearly. Figs. 7 and 8 show that every rise in temperature accords with an increase in the landing of Eel.

Later in the summer, however, it is a common event to observe a large import of Eel on dark days. This supports the assumption that it is the reaction of Eels to temperature that limits their accessibility and not for instance the transparancy of the water, which is of course better during bright, calm weather.

Apart from the weather, the time of day also influences the import of Eel. On fine sunny days the Cormorants take more Eel in the afternoon than in the morning (so in contrast with days as May 20, 1938). Fig. 8 gives several instances. An explanation is given in chapter 17.

Fig. 9 shows that the bulk of the landed Eel has a length of 18 to 26

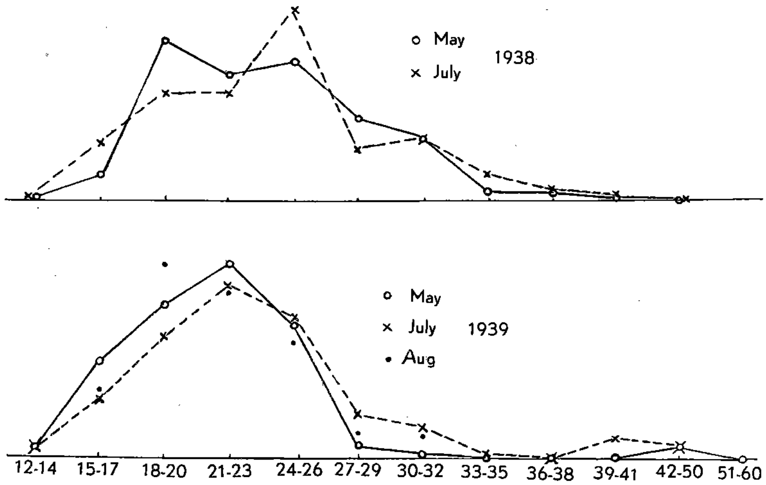

Fig. 9. Length frequency distribution of the Eel landed by the Wanneperveen Cormorants during some months in 1938 and 1939. Length in cm.

cm. Eels over 35 cm are infrequently observed. The reason is simply that large Eel is scarce in the IJsselmeer. The Cormorant is able to capture Eels measuring for instance 60 cm. When such large specimens are found in Wanneperveen they are usually of a dark colour, showing their origin from peaty inland waters.

Little Eels measuring 10-18 cm in length are rarely taken, although they are of course more numerous than the larger specimens.

One of the principal objects of my investigation was to determine the influence of the Cormorant on the Eel population. For this purpose it is necessary to estimate the amount of Eels taken during the whole season. For the sake of simplicity we may suppose that before May no Eel is taken, that in May 20% of the total weight of food consists of Eel and in June-September 35%. So we come to almost 200.000 kg in total, about 2.5 millioen specimens over 26 cm (average weight 40 grammes) and 5 million specimens under this length (average weight 20 grammes). This would mean that every year 7.5 million Eels are taken from hunting grounds measuring 400-500 sq. km, so one Eel from every 50-60 sq. m. One may ask whether this results in a difference between the NE corner of the lake and the rest of the IJsselmeer. Mr. HAVINGA informs me that indeed a slight difference exists. It is possible, however, that this difference would be larger if there was no communication between the two parts, so that the hunting grounds of the Cormorant would receive no large scale completion.

The question as to how far the heavy toll taken by the Cormorants influences the density of the Eel population can be judged only by a comparison with the human fishery and its consequences. Against the 7.5 million Eels captured by the Cormorants, about 55 million are taken from the IJsselmeer yearly by fishermen. This is calculated from the total weight landed in 1939.

According to HAVINGA (1939) it is obvious that this intense fishery has an enormous influence on the population of the lake. The scarcity of big Eels is a clear indication. In a conversation Mr. HAVINGA told me that at least 75% of the Eels settling in the lake are taken by fishery after reaching the legally established length (28 centimeters). If the Cormorants had left their 7.5 million Eels alone, approximately 75% of this number would have been captured by the fishermen too. The chance that the Eels might die by other causes in the mean time is not taken into account, man and Cormorant presumably being the main enemies. The result of these considerations is that 5.625.000 Eels were withheld from the human fishery by the Cormorants, being about 10% of the 55 million landed in 1939.

It must be emphasised that this conclusion is an estimate of the maximum damage and should not be generalised.

19. The Pike-Perch, *Stizostedium lucioperca* (L.).

The Pike-Perch is sharply persecuted by the Cormorant as might be expected for a fish of this size. As the history of the numerous 1937 born generation shows, this applies only to a limited age. Till May 1938 when this generation was about one year old, its representatives measuring 18 cm in length, only few specimens were observed in the Wanneperveen rookery. Towards July, when by rapid growth a length of 20 cm was reached, the import increased to 7% of all captured fishes. From elder generations only 16 specimens (length 30-36 cm) were observed during 1938.

In March 1939 the 1937 generation was almost 2 years old and measured about 33 cm in length. Till May the landings increased from 5 to 13% of all captured fishes (see fig. 6). This rise continued until the first half of June, when the huge proportion of 25% was reached. This means that more than half the total weight of the Cormorant food consisted of Pike-Perch. From this moment a rapid decrease began. In July only 4% of the captured individuals consisted of Pike-Perch, in August 2%.

This remarkable fact can be explained by the rapid growth of the fish. In July already 10% of the 1937 generation had surpassed the length of 40 cm. The curve of the average growth, derived from observations by HAVINGA (1939) is reproduced in fig. 10. The average length of the Pike-Perch captured by the Cormorants, however, did not increase after May 1939. This is without doubt due to the fact that Pike-Perch over 34 cm can be captured only with difficulty and specimens over 36 cm not at all. Since the 1937 generation surpassed this length the Cormorant must restrict itself to the backward individuals. As specimens under 36 cm became more and more rare, the capture decreased accordingly. The increase of the import from March till June may be explained by the gradual appearance of the Pike-Perch in the coastal zone, the species hibernating in deep waters.

In 1938 we should expect the 1937 born generation to be more numerous than in 1939, it was, however, captured less, as already mentioned. This may be explained as follows: in 1938 the one year old Pike-Perch did not exceed many other, still more numerous fishes (Roach e.g.) in size and desirability.

Moreover the Pike-Perch is a fast swimmer and probably less easy to capture. There was no special reason for the Cormorant to prefer it as there would be the following year. The growing desirability also may be partly responsible for the increasing import from March till June 1938, apart from the migration of the species towards coastal waters.

In 1938 the size of the captured Pike-Perch increased with the growth of the 1937 generation (fig. 10) this in contrast with 1939. As the Cormorant prefers large specimens we would expect that in 1938 the average length of the captured fishes would be greater than the average length in freedom.

According to fig. 10 this is not the case. It must be remarked, however, that the length of the long and almost always partly digested Pike-Perch is not easy to estimate. I think it possible that in 1938, the first year of the observations, the length of the Pike-Perch was systematically underestimated.

The fry of this species measures in June 4.5 cm in length, in August already 15 cm! In 1939 such specimens were not observed, although they were rather numerous in the IJsselmeer (HAVINGA 1939). So this stage is practically safe for the Cormorant. From the 1938 born generation only 4 specimens were observed in 1939. This is due to the competition

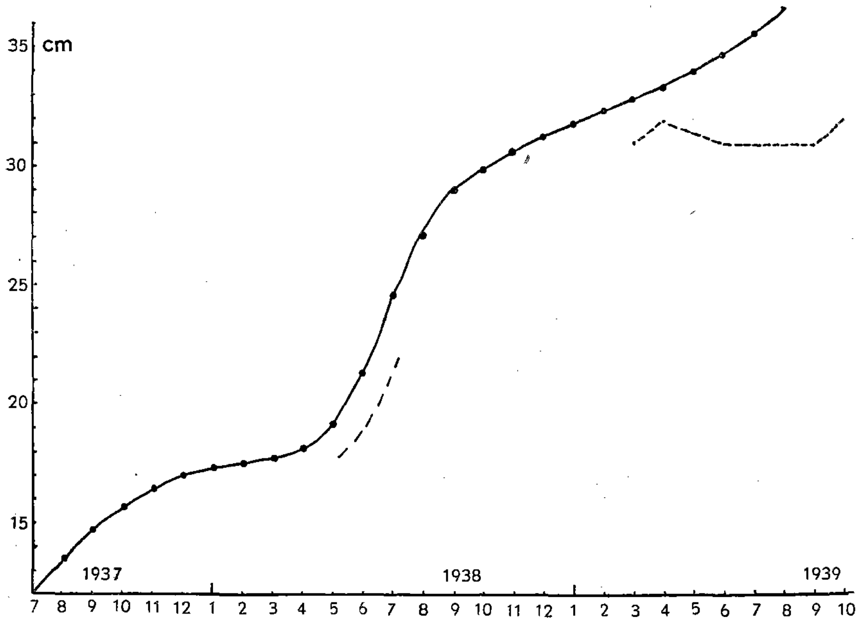

Fig. 10. Growth of the 1937 born generation of Pike-Perch in the IJsselmeer (after figures from HAVINGA 1939). Dotted lines: Average length of Pike-Perch landed by the Cormorants.

by the elder generation and to the failure of the propagation in the cold spring of 1938. We draw the Conclusion that Pike-Perch in the first year of its lifetime is safe from the Cormorant. In the second year it is taken in small numbers from June probably until the end of the breeding season. In the third year it is captured in increasing numbers from March till the summer, when the danger suddenly ends. The influence of this short but intense persecution is not easy to determine. In March 1939 35% of the total weight of the food consisted of Pike-Perch, in the beginning of June even 60%. On the base of these figures I estimate the total weight of the captured Pike-Perch in 1939 at 155.000 kg, comprising 620.000 specimens.

In a conversation with me Mr. HAVINGA estimated that 80% of the Pike-

Perch in the IJsselmeer is captured by human fishery after reaching the legal length of 40 cm.

Then they have an average weight of 750 grammes. When we neglect other causes of death, man and Cormorant being the only enemies of large specimens, we come to the conclusion that 496.000 Pike-Perch from the generation born in 1937 were withheld from the human fishery by the Cormorant. This means a loss of at least 375.000 kg. In the last months of 1939 the fishermen had already landed more than 2 million kg Pike-Perch measuring 40-45 cm (HAVINGA 1939) and in total between 3 and 4 million kg have been marketed from this generation.

The loss caused by the Cormorant population can therefore be roughly estimated at 10%, which agrees remarkably well with the corresponding figure for the Eel.

An indirect influence of the Cormorant on this valuable fish is improbable. The food of the Pike-Perch consists mainly of Smelt (HAVINGA 1939) and this little fish is taken only in small numbers by the Cormorant.

20. The Ruffe, *Acerina cernua* (L.).

All Ruffe imported into the Wanneperveen rookery by the Cormorants show the light tint of the IJsselmeer population. According to HAVINGA (1938) the Ruffe is the most numerous fish in this water, in the coastal parts as well as in the centre of the lake, its numbers being enormous. It is captured by the Cormorants in fair numbers but it is by no means the principal food.

Only from early spring until the second half of May the Ruffe may during some days happen to be the most numerous prey, sometimes reaching 50% of the imported individuals. Later on, during full summer the import decreases and eventually becomes insignificant. The reason for this relative lack of interest of the Cormorant must be found in the smallness of this fish. Excepting the fry, the size of the bulk of this species varies from 6 to 10 cm in length, its weight averaging from 5 to 15 grammes. The largest Ruffe I ever saw measured 16 cm in length and weighed 15 grammes. Such specimens, however, are rare in the IJsselmeer.

When hunting Ruffe the Cormorant clearly prefers the large specimens. In the spring of 1938 one year old Ruffe and elder generations were found in proportions of 5 : 1 in the IJsselmeer. This fact was established by measuring a sample collection of 134 specimens, which were obtained by human fishery. Simultaneously, with those imported by Cormorants, proportions of 1.7 : 1 were found. This proves once more that the Cormorant selects its prey. It is clear that the length frequency distribution of the Ruffes captured by Cormorants (fig. 11) does not give a true picture of the population in the lake.

In spite of the selection towards the larger specimens, the majority of the imported Ruffe was one year old in 1938. In 1939, however, almost no one year old specimens were observed; an overwhelming majority being two years old. Moreover the total consumption was

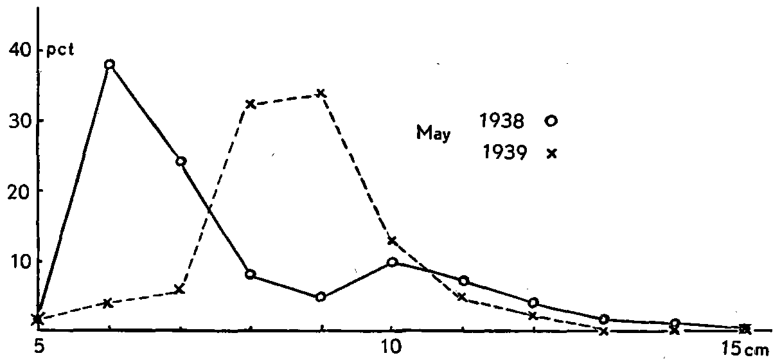

Fig. 11. Length frequency distribution of the Ruffe landed by the Wanneperveen Cormorants in May 1938 and 1939.

higher. The reason was this: in 1937 the fishfry survived very well, better by far than in the cold spring of 1938. The generation born in 1937 was in 1938 one year old and appeared in the food of the Cormorant on a large scale only owing to its great numbers.

In 1939 the same generation was two years old and had grown even more desirable because of the increased size of its members, thus expelling the younger generation from the interest of the Cormorants. In this season the 1938 born generation was probably even outnumbered absolutely by its predecessor.

The decrease in the import of Ruffe towards the summer is closely connected with the increase in the availability of the Eel. Besides, it is remarkable that these two species often appear in the same meals.

These may all originate from the centre of the lake. It is probable that the Ruffe is never taken in large numbers in the coastal zone, where it always has the competition of larger fishes such as Roach, Bream and Perch. In the centre of the lake the Eel is the favorite prey, but only in the summer. In the early spring Cormorants fishing in the centre and not being so lucky as to capture a Pike-Perch, are obliged to take Ruffe or Smelt, the first being preferred. As towards the summer the Eel grows more available, the interest of the Cormorant is deflected from the Ruffe, and this species is gradually replaced by Eel. When these considerations are justified, large imports of Ruffe should coincide with low numbers of coastal fishes and eventually with high numbers of Eel and Pike-Perch.

Figs. 7 and 8 show that this relation prevailed fairly well in 1938, but was doubtful in 1939, when the Ruffe was far more desirable by its size and could compete with larger species. It is doubtful whether the Cormorant has any influence on the enormous Ruffe population of the IJsselmeer. In the early spring of 1939 the import sometimes reached a level of 5-600 kg daily, whilst the total stock in the IJsselmeer was estimated at some tens of millions kg by HAVINGA (1938).

21. The Roach, *Leuciscus rutilus* (L.).

This fish can be called the typical prey of the Cormorant in the Netherlands. During the whole breeding season it forms an important part of the food, surpassed only temporarily by other species. In the rookeries near the large rivers this is yet more clear than at Wanneperveen (fig. 16).

This proves no special preference, however; the Roach is a common and rather large fish, its shoals swim in open water easily attracting attention.

The import of Roach in the Cormorant rookeries is rather regular, no clear seasonal differences are observed. Even on warm summer days when the import of Eel reaches its maximum, the Roach maintains its place better than any other fish.

The largest Roach found in a rookery measured 30 cm in length and weighed about 500 grammes, the smallest 5 cm and 5 grammes. The majority measured from 10 to 20 cm and weighed 10-100 grammes. Of course the length frequency distribution recorded in fig. 12 gives no true reflection of the Roach population; in the lake the youngest generations form a far larger majority. Here again we trace the preference of the Cormorant towards large fishes. Besides, the relation between the generations is not constant.

In May 1938 the majority of the captured Roaches was one year old (length 5-12 cm). In July most members of this generation were 13-15 cm long. Now they expelled the elder generations still more from the interest of the Cormorant by their growth. In May 1939 we find the same generation two years old, measuring 16 to 18 cm length. Again it forms the majority and surpasses the following, one year old generation (compare May 1938)!

The fact that in May 1938 the one year old generation dominates and in May 1939 the two years old generation, may again be explained by the better surviving of the fishfry in the warm spring of 1937 in comparison with the cold spring of 1938. The two year old fishes are more desirable and will be captured more except when their absolute numbers lay too far behind those of the following generation.

In July 1939 the one year old generation dominates again; I presume

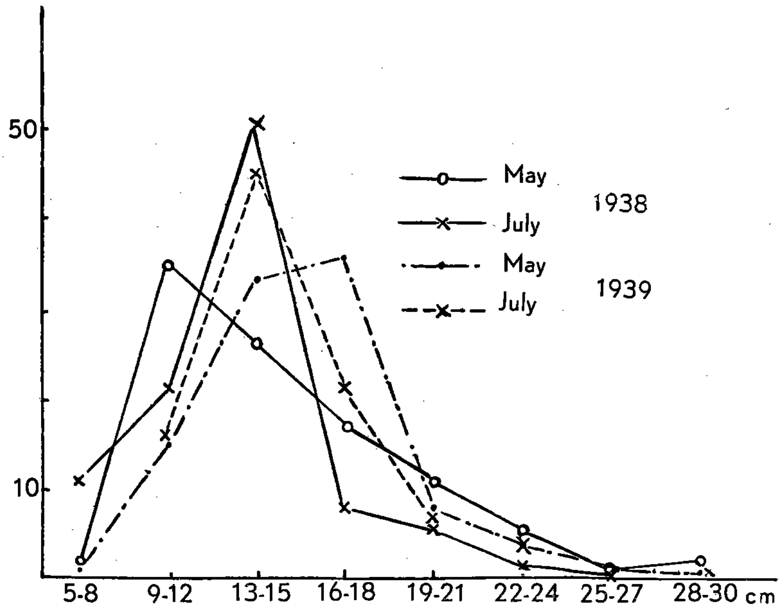

Fig. 12. Length frequency distribution of the Roach landed by the Wanneperveen Cormorants during some periods in 1938 and 1939.

that at this moment it had become more attractive by its rapid growth.

It is clear, however, that it cannot exceed the elder generations in the same way as its predecessor did in 1938.

In Wanneperveen we may estimate the share of the Roach at 1/3 of the imported weight. This means 233.000 kg, half of which may concern fishes over 20 cm, perhaps 600.000 specimens with an average weight of 200 grammes. The other half may concern 3.200.000 Roaches with an average weight of 35 grammes. This heavy toll has not prevented the species forming a dense population in the coastal zone of the IJsselmeer.

The further increase of the species seems to be hampered by the lack of suitable spawning grounds in the IJsselmeer. Under these circumstances it is unlikely that the Cormorant has much influence on the spreading of the Roach in the lake.

An overwhelming majority of the landed Roach has the light tint of IJsselmeer fishes. However, dark specimens from inland waters are regularly observed, often together with *Scardinius erythrophthalmus* (L.), the Rudd, which does not seem to live in the IJsselmeer.

22. The Bream, *Abramis brama* (L.) and the White Bream, *Blicca björkna* (L.).

Abramis and *Blicca* are not easy to distinguish, especially when only half digested parts of fishes are available. Thus the two species are

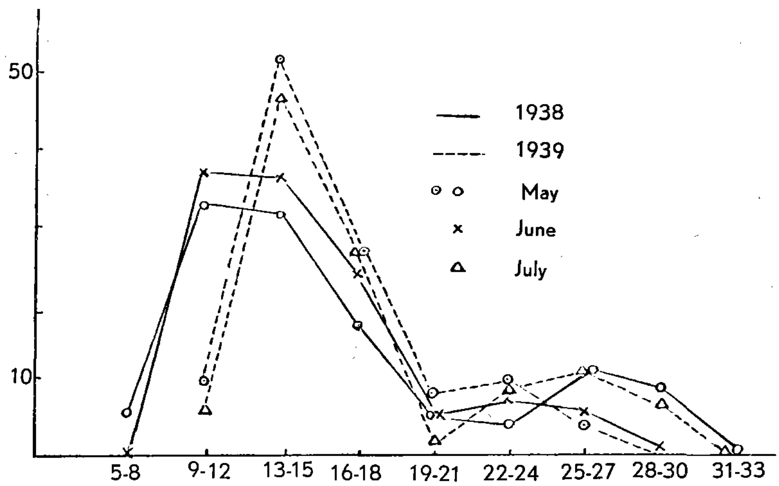

Fig. 13. Length frequency distribution of the Bream. As fig. 12.

combined, *Abramis* forming without doubt a large majority. Figures from fishing tests show that in the IJsselmeer the relation is 85 : 15.

In Lekkerkerk 10-20% of the captured fishes belonged to these species. In Wanneperveen the share was not so large and less constant. In the early spring it could reach a level of 15%, later on decreasing rapidly. The Roach is captured far more, absolutely and relatively. From the figures recorded in chapter 15 it appears that in the coastal zone of the IJsselmeer the Roach is twice as numerous as the Bream. The Cormorants, however, capture 4-10 times more Roaches. The reason may be found in the behaviour; the Bream is more or less nocturnal, living more hidden.

Fig. 13 shows the composition of the Bream capture, giving a double-topped curve. Two groups can be distinguished, the first measuring

10-18 cm in length (presumably one and two years old) the second 22-33 cm (4 years and older). This is not accidental, the figures from Lekkerkerk show the same tendency (fig. 17). The fact that two species are taken together cannot be made responsible. There is no relation with the spawning season. The solution of the problem may be found in particularities in the life history of the Bream.

Mr. I. KRISTENSEN told me that Bream reaching a certain age, change their habits. The young generations live more or less pelagic as Roach do, but large specimens generally feed grubbing in the bottom, taking mainly little Mollusca as *Sphaerium* and *Pisidium*. From figures given by HAVINGA (1941) can also be inferred that IJsselmeer Bream over a length of 19 cm take more bottom fauna, in casu: the larvae of *Tendipes plumosus* and Oligochaeta (*Tubifex*, *Limnodrilus*).

This change in diet is confirmed by HARTLEY (1947) mentioning 18 cm as the critical size. I suppose that there is a relation between this change in behaviour and the experience that Bream reaching this size becomes more accessible for the Cormorant. It seems that large bottom fishes such as mature Bream and Tench are easy to catch.

23. The Perch, *Perca fluviatilis* (L.).

In the Wanneperveen rookery 3 to 5% of the imported fishes belonged to this species, without clear seasonal changes. In Lekkerkerk the share of the Perch was larger, it increased towards July to 25%. This may be accidental, however, the total numbers of available fishes being low.

In the IJsselmeer the Perch occupies the same region as the Roach i.e. the coastal zone. After a remarkable spreading following the disappearance of the salt from the lake, no further increase took place so that the density of the population lies far behind that of the Roach. In mixed meals we find the Perch mostly together with this species. An overwhelming majority shows the remarkable lack of colour which characterizes all inhabitants of the IJsselmeer. The dark streaks are very faint, the red fins less bright than normal. In contrast sometimes very dark specimens were seen, originating from peaty inland waters.

Fig. 14 shows the length frequency distribution of the collected Perch. Here the same relation can be observed as with the Roach. In May 1938 the one year old generation dominates owing to the success of the 1937 propagation. In July 1938 a large part of this generation measures 10 cm in length. In May 1939 the average length is 13-15 cm, this now two years old group dominates strongly, one year old specimens are rarely taken. In July 1939 the two year old Perch reach a length of 16-18 cm.

It is clear that the bulk of the capture is one or two years old, elder fishes being of course far less numerous. Only 4 individuals over 25 cm were observed (one measured 30 cm). Perch of this length may be generally too big for the Cormorant to be swallowed, thanks to their

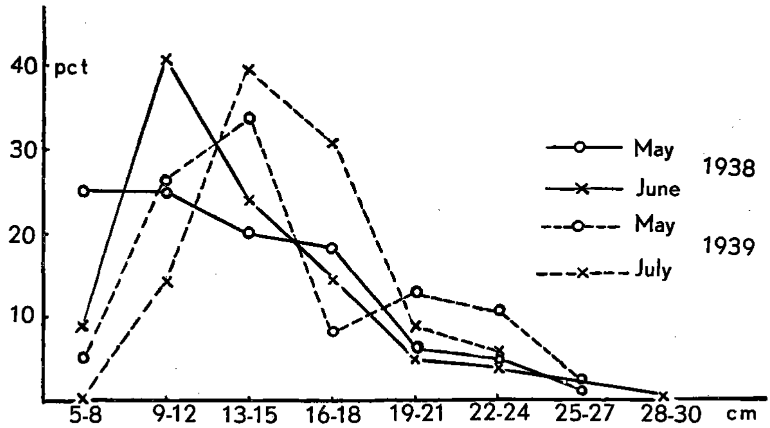

Fig. 14. Length frequency distribution of the Perch landed by the Wanneperveen Cormorants during some periods in 1938 and 1939. Length in cm.

plump posture. The total quantity of Perch taken by the Wanneperveen Cormorants in one breeding season can be estimated at 4% of the total weight consumed, that is to say at 28.000 kg.

24. The Tench, *Tinca tinca* (L.).

As figs. 5, 6 and 16 show, the Tench is regularly imported in the Cormorant rookeries. The total numbers captured are not so large in comparison to other species, but the fact that especially very big Tench is taken, makes its share in the total weight of food rather high. It is remarkable that many more specimens measuring over 20 cm in length are found than smaller ones (fig. 15).

This seems to be a rule in all Dutch Cormorant rookeries (fig. 17). We can be certain that in freedom the younger generations are much more numerous than the 3-5 years old Tench which are so frequently imported by the birds. It seems, however, that elder individuals are easier to capture.

After reading my manuscript, I. Kristensen assured me that observations on Tench in captivity had convinced him that young Tench live much more hidden in the water vegetation than large specimens. Here of course lies the possibility of an explanation.

The origin of the Tench imported in Wanneperveen is not quite clear. Remarkably light coloured specimens occur next to dark ones, but the difference is not so clear as it is for many other species. Owing to their size the Tench are often the only prey produced by a vomiting Cormorant. When there are companions these often originate from inland waters, but mostly from the IJsselmeer.

Mr. HAVINGA informed me that the Tench is unknown as an inhabitant of the IJsselmeer. It is not impossible, however, that the vast rush fields (*Scirpus lacustris* L.) near the IJssel delta lodge Tench.

In Wanneperveen the share of the Tench in the total weight of food

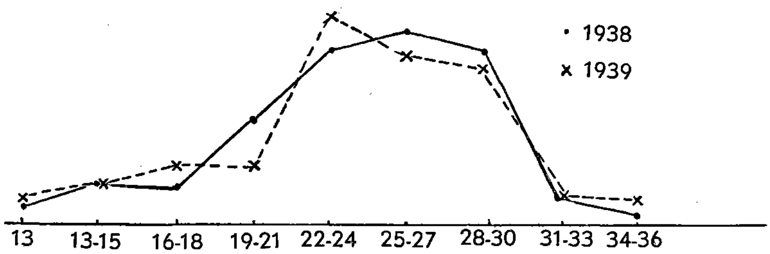

Fig. 15. As fig. 14. Length frequency distribution of the Tench.

was in 1938 about 17%. This means 125.800 kg; in the full season about 700 kg is landed daily, comprising 2300 specimens with an average weight of 300 grammes.

It is remarkable that the origin of these large quantities is so difficult to trace.

25. The Pike, *Esox lucius* (L.).

The share of the Pike in the food of the Dutch Cormorant is not large; as a rule it is less than 1%. Only in the early spring can it be somewhat higher.

The majority of the captured Pike is rather large. For instance during March, April and May 1939 6 Pike measuring 13-21 cm in length (presumably one year old) were found in the Wanneperveen rookery against 19 specimens between 28 and 42 cm (probably 2, partly 3 years old).

In July 1939 only two Pike were found, both belonging to the large group. We expect the one year old Pike to be more numerous than the two year old generation and their size is surely sufficient to attract the Cormorants' attention.

Nevertheless they are neglected. We may explain this in the same way as for Pike-Perches. The Pike is a fast swimmer, when surprised starting with enormous speed. It will not make an easy prey, only large and very desirable specimens will induce a Cormorant to pursuit.

In the early spring the Pike easily attracts attention by its activities during the spawning period. This may be the reason for the larger import during this season.

In the IJsselmeer the Pike is by no means numerous and is restricted to the overgrown parts of the coastal zone. Whether the Pike imported in Wanneperveen originate from here or from inland waters I failed to notice.

26. The Smelt, *Osmerus eperlanus* (L.).

This species was landed regularly but never in very large numbers although it is very common in the IJsselmeer. It is not represented in the text figures. In May 1938 it was frequently found in fair numbers; complete balls of one year old specimens were observed daily. On 14 June, 7 meals were found containing together 128 specimens. These specimens measured only 7-8 centimetres in length. In general only few Smelt over 10 cm are observed in the vomits. Samples from the landings of fishermen confirmed to me that large Smelt is rare in proportion to small ones. It may be assumed that this is the reason for the little interest shown by the Cormorant. In 1939 the species was observed only sporadically.

27. The Three-spined Stickleback, *Gasterosteus aculeatus* (L.).

Large specimens measuring 7 cm in length and weighing 3-4 grammes were found regularly in the rookery. The species is not represented in the text-figures. Especially in May 1938 they were found daily, in July, however, the species was observed no more.

In May 1939 they were less common, all little species being scarce at the time owing to the interest of the Cormorant in Pike-Perch!

In the meals the Stickleback is often present between other species but sometimes complete balls were found, containing more than 100 specimens apparently collected with great patience. In the IJsselmeer the Stickleback is extremely numerous, especially near the coast.

28. The Bleak, *Alburnus alburnus* (L.).

This little fish is landed regularly in small numbers. It was represented in a sample of fish caught in the centre of the lake and consisting mainly of Smelt and Ruffe. The Bleak is probably the only cyprinoid inhabiting the open water of the IJsselmeer.

29. The Gudgeon, *Gobio gobio* (L.).

A small number of Gudgeons measuring 12-14 cm in length were found both in Wanneperveen and in Lekkerkerk.

30. Rare findings from Wanneperveen.

The following species were observed sporadically:

Burbot, *Lota lota* (L.).

Wanneperveen 5 specimens (Lekkerkerk 1 sp.). All measuring about 30 cm.

Crucian carp, *Carassius carassius* (L.).

Wanneperveen 9 ex., measuring 10-15 cm.

Barbel, *Barbus barbus* (L.).

Wanneperveen 2 specimens.

31. A comparison between Wanneperveen and the rookeries of the large rivers, the occurrence of salt water species [1]).

In 1938 I received 450 fishes from the large rookery near Lekkerkerk, thanks to the care of KORTLANDT. Fig. 16 gives the percentage of the more common fishes during the season. In fig. 17 the length frequency distribution is given for several species. As in Wanneperveen, the Eel appears to be an important food, increasing towards the summer. The average size is larger, presumably because the waters near Lekkerkerk are less overfished than the IJsselmeer.

The percentage of the Roach and its size seems comparable in the two rookeries. In Lekkerkerk the Rudd is also represented regularly in small numbers. The Bream is relatively taken more at Lekkerkerk; it is remarkable that here too we notice the fact that the frequency distribution shows a second top for large specimens. The position of the Tench is again comparable to Wanneperveen, the large size of the average individual included.

Little Perches, presumably one year old, were taken more and more towards the summer. Pike and Bleak were represented in small numbers. The Smelt was not observed in 1938, Ruffe recorded once. Two Gudgeons and 1 Burbot were found.

From the Awaite Shad (*Alosa fallax* (Lac.) or *Clupea alosa-finta* Hoek) mature specimens of 28-40 cm are sometimes observed in Lekkerkerk (May 1 sp., June 7 sp., July 1 sp.). This migrating fish belongs obviously to the largest prey a Cormorant can take. In 1941 *Osmerus* was added

1) The data given in this chapter are not quite complete, because some notes were lost during the critical winter 1944-45.

to the list. May 10 and 18 KORTLANDT found two vomits with large Lamperns (*Lampetra fluviatilis* (L.), having a length of 30 cm) both under the same nest.

Apart from the freshwater fishes, forming a large majority at Lekkerkerk, some salt water species are landed, as the following instances show:

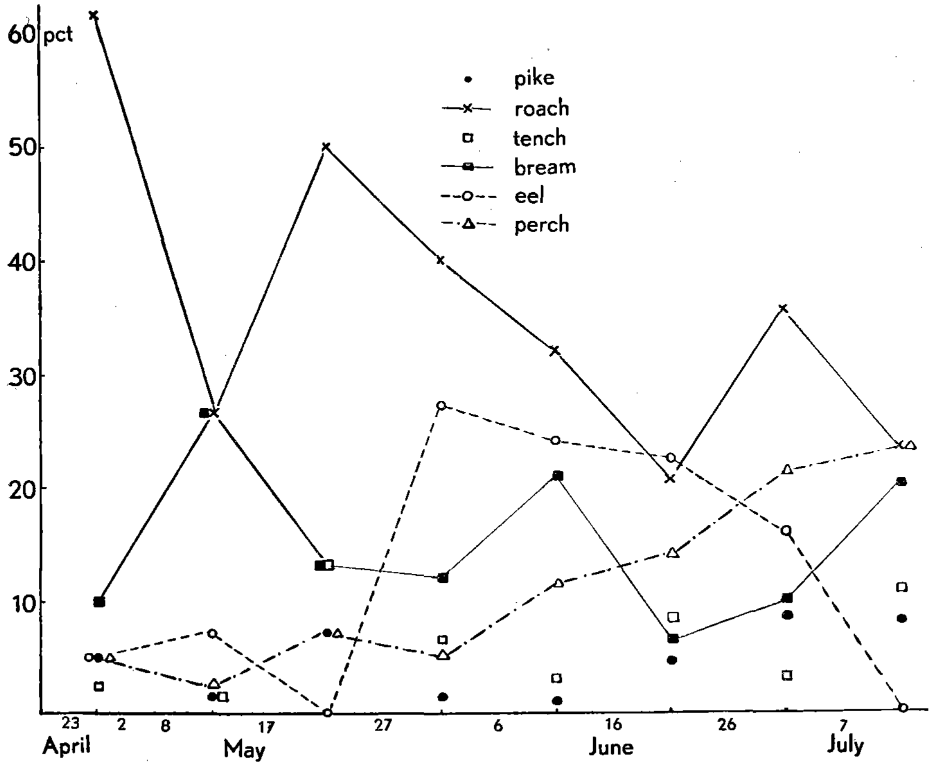

Fig. 16. Percentages of several fish species landed by the Lekkerkerk Cormorants in 1938.

Flounder (*Pleuronectes flesus* L.) June and July 1938: 6 sp.; summer 1947: 7 sp., all 7-9 cm in length (one 17 cm).

Viviparous Blenny (*Zoarces viviparus* L.) about July 1, 1938: 1 sp. June 1941 this species was again recorded, together with *Centronotus gunnellus* (L.) and *Cottus scorpius* (L.) !

The list can be closed with some little *Solea vulgaris* L. from June 1941, a crab (species?) and some large Shrimps (*Crangon crangon* (L.)). After examination of the Crustacea I came to the conclusion that they did not originate from a fish stomach. Now we come to the question as to where these salt water organisms are taken. The Flounder prefers brackish water, at least in the warm season and goes rather far upstream in the estuaries. A vomit with *Zoarces*, *Centronotus* and *Cottus*, however, must originate from salt waters.

Lekkerkerk is situated 40 km from the North Sea and I doubt whether

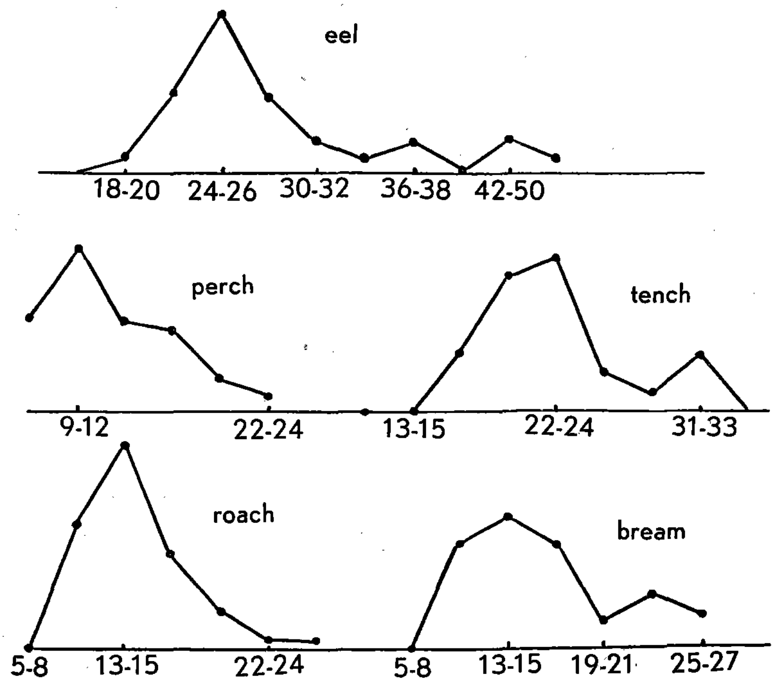

Fig. 17. Length frequency distribution of some species landed in Lekkerkerk in 1938. Length in cm.

this distance is acceptable for a nesting Cormorant. When the birds fly 26 km southwards they reach the estuary of the Merwede (called: Hollands Diep). The fact that from the rookery "Keizersdijk" only fresh water fishes are recorded does not make it probable that much sea fish is available in this neighbourhood.

So the origin of the sea organisms in Lekkerkerk is not quite clear. It must be taken into account that large quantities of sea water enter the Nieuwe Waterweg near Hook of Holland with the tide and flow in the direction of Rotterdam. It is possible that far inland in deep gullies the salinity of the water is sufficient to support marine species.

From the rookery at the "Keizersdijk" in the "Biesbosch" (delta-region of the Merwede, fig. 2) 68 fishes were examined in 1939:

April-May: Roach 17 sp., Rudd 1 sp., Bream 3 sp., Perch 3 sp., Gudgeon 2 sp., Smelt 1 sp.

June-July: Awaite-Shad 15 mature sp., Eel 19 sp., Roach 4 sp., Tench 2 sp., Bream 1 sp.

This sample shows that these birds fish at least mainly in fresh waters and generally do not reach the salt streams round the Zealand Isles.

Finally some vomits from Staelduinen near the Hook of Holland were placed at my disposal by Mr. LAARMAN.

Birds from this rookery were seen fishing in the North Sea, often near the beach in the surf. They also visit inland waters. Their behaviour proves that the Southern Cormorant does not avoid the sea as a hunting ground in the breeding season. The following fishes were found:

Perch 2 sp., Roach 3 sp., Gudgeon 2 sp., Awaite-Shad 1 large sp. (40 cm !), *Pleuronectes* 6 sp., 13-17 cm (4 *P. limanda*, 2 *P. flesus*), *Solea* 1 sp. (17 cm).

Already in 1938 *Crangon* was reported here. In 1941 a pellet was found, consisting only of this species. I accept this as a further proof that the Cormorant takes large Shrimp directly. A medium sized *Carcinides moenas* (L.) may also be taken directly. *Crangon* is recorded by STEVEN (1933) for the Common Cormorant.

SERVENTY (1938) found a "crab" and a "shrimp" in the stomach of the Australian *P. carbo*.

After MADSEN and SPÄRCK (1950) Danish Southern Cormorants mainly fish in the sea (see p. 5 of this paper). These authors do not believe that Crustaceans are taken regularly.

32. Parasites.

All Cormorants in the Wanneperveen rookery are infected by a little yellow coloured nematod, belonging to the genus *Contracaecum*. All specimens collected were females, so it was not possible for Mr. J. MONTAGNE (Utrecht) to whom I am much indebted for his kind assistance, to determine whether the species was *C. microcephalum* or *C. spiculigerum*. NIETHAMMER (1938) records *C. spiculigerum* for the Cormorant. MADSEN and SPÄRCK (1950) record an almost 100% infestation with parasites (presumably *Contracaecum spiculigerum*) for Danish birds.

This parasite lives freely in the stomach of the Cormorant. At the moment in which a fish is damaged by digestion, the worms intrude into its body. Thus practically each vomit contains *Contracaecum*, which may be easily mistaken for a fish parasite. The nematod seems to do little harm to its host, taking only a small part of the digesting food.

They are never very numerous; large numbers would be removed easily by vomiting.

The manner of feeding from the stomach contents of the parents may lead to an early infection of each young Cormorant. According to NIETHAMMER (1938) the normal infection takes place by fishes. According to SERVENTY (1938), however, *Contracaecum* has one host only.

Another parasite I found in the Cormorant vomits is *Ligula intestinalis* L. This cestod has a complicated life history. The adult animal lives in the intestine of fish-eating birds, especially ducks. The eggs leave the body and hatch in the water. The larvae infect Copepoda (*Cyclops strenuus* L. is mentioned in literature) and develop here to the precercoid stage. When the first host is eaten by a Cyprinoid, the parasite pierces the intestine and develops in the abdominal cavity to a plerocercoid, becoming a true tape worm measuring 20 cm in length and being about 1 cm broad.

When the host is a little fish or when more than one *Ligula* is present the full size is not reached. The parasite fills the abdominal cavity to a damaging extent, the gonads of the host do not develop when a full grown *Ligula* is present. The wall of the belly gets thin and looses the scales. When the fish dies the tapeworm manages to get out and has a chance to be eaten by a bird. The infection can, however, also take place by the eating of a whole infected fish. The parasite settles in the intestine of the bird and reaches maturity in 4 days, its size remaining the same. With this the cyclus is closed.

I could not succeed in explaining the part the Cormorant is playing towards *Ligula*. It is a fact, however, that numerous infected Roaches are landed from the IJsselmeer by the birds. All totally undamaged Roaches available were tested in the period May 25-July 16, 1938:

From 170 Roaches measuring 10-14 cm 26 (15.3%) were infected.

From 136 Roaches measuring 15-27 cm 40 (30%) were infected.

It is of interest to compare these figures with data collected from Roaches landed by the fishermen from the same grounds:

June 16, 1938. From 171 Roaches (19-24 cm) 11 (6.4%) were infected.

June 24, 1938. From 321 Roaches (19-24 cm) 20 (6.6%) were infected.

When we accept this relation (6.5% infected) as representative for the part of the lake visited by the Cormorants (as I think it is permitted) the conclusion is this:

The Cormorant captures relatively more infected fishes than sound ones. The significance of this fact is discussed in the following chapter.

Moreover it is clear that one year old Roach are less frequently occupied by *Ligula* than elder generations. Of course they have had less time to get infected.

Generally the plerocercoid is fullgrown, younger stages were rarely observed. It seems that it reaches the full size quickly and then manages to stay for a long time at this stage. Taking into account the high proportion of infected Roaches landed by the Cormorants and the enormous numbers consumed, we must suppose that every Cormorant is regularly infected. A calculation shows that as an average every three days a Wanneperveen Cormorant eats an infected Roach. Should the Cormorant be a suitable host for the parasite, we might expect each bird to be heavily infested, old ones as well as young.

This is not the case. Several large young Cormorants appeared to be free from *Ligula*. From 3 adult birds, only one carried a *Ligula* in the intestine.

Some experiments were undertaken to determine whether *Ligula* develops to maturity in a Cormorant. Efforts to infect 3 fledged young Cormorants in captivity by feeding them with infected Roaches failed, however. After 4 days nothing was found in the intestine.

According to some authors, for instance NIETHAMMER (1938), the Cormorant is a suitable host for *Ligula*, but as a rule fish-eating ducks (*Mergus* for instance) are recorded.

My experience indicates that a *Ligula* eaten by a Cormorant has little chance for further development; a large majority at least seems to perish. It is possible, however, that very large losses are normal and that the few succeeding specimens are sufficient to let the species survive.

The pond of the decoy situated in the centre of the Wanneperveen rookery is linked with open water by a ditch. At the mouth of this ditch I captured a dozen one year old Roaches; 50% was infected by *Ligula*. This high proportion is no rule in the neighbouring waters; I take this as an indication that the pond in the rookery is heavily infected.

This does not prove, however, the participation of the Cormorants; for the half-tame ducks (*Anas platyrrhynchos* L.) of the decoy, which eat so many remains of the vomits, may be the mediators.

33. The possibility of a favourable influence exerted by the Cormorant on the fish population.

In the preceding chapter it was shown that the Cormorants take 30% Roaches infected by *Ligula* from a population where the proportion is only 6.5%. This relative preference for infected fishes can be explained by the supposition that these animals are handicapped when a shoal is persued by a Cormorant and thus more easily taken.

This is a matter of general importance. It is often supposed that an animal of prey exerts a favourable influence by taking mainly ill or abnormal specimens. Facts supporting this hypothesis are rare, however.

In our case it is possible that the Cormorant itself spreads the disease which it seems to suppress, but this does not affect the principle.

When the Cormorant is really a suitable host for *Ligula*, we have the interesting situation that a parasite enlarges its chances, because infected fishes are more easily taken. It is not improbable that the Cormorant may suppress the development of a contagious disease among fishes in this way, but no further indications in this direction were observed.

34. Summary.

The food of the Cormorant, *Phalacrocorax carbo sinensis* (Shaw and Nodder) in the Netherlands.

The investigation was carried out in a large rookery (about 2000 nests, situated on trees), near the former Zuiderzee (fig. 1). The birds take their food for 94% from the north-eastern part of the IJsselmeer, generally within a distance of 25 km from home. The fishing is restricted to the daytime. The movements to and from the rookery (fig. 3) are discussed in chapters 4 and 6.

Social fishing was observed only once.

There are many indications that the birds dislike the (7 km) journeys over land to the lake and try to limit them to a minimum. Brooding birds go as a rule once a day, birds with nestlings once or twice. The number of feedings is accordingly low (chapter 12). This is made possible by the large capacity of the stomach (fig. 4) which may contain a maximum of 750 grammes of fish. In a rookery situated near the hunting grounds the birds seem to fish more frequently.

When a rookery is disturbed, many fishes are ejected, which makes it easy to obtain samples of the food. In the years 1938, 1939 and 1940, 13000 fishes were examined. Hours after taking its meal a Cormorant can vomit undamaged parts of fishes and even whole fishes, while the digestion is rather slow and limited to the deeper part of the stomach (fig. 4).

From some of the vomits it could be established that they were complete. When such vomits are collected early in the morning from brooding birds they generally represent a daily ration. Two series of complete vomits averaged resp. 340 and 285 gr. (tables II, III).

Another means to form an opinion on the food and the daily ration was found in the analysis of pellets (table I). Although the gastric

juice of a Cormorant proved to be very acid (pH 0.9) the fishbones are generally removed undigested by vomiting, often in the form of pellets. In the latter case the pituitary lining of the gizzard is pushed off and envelops the bones and scales remaining from a meal. It could not be established whether pellets are formed after each meal, but it is probable that a pellet includes the remains of one fishing tour.

It was established experimentally that a large young Cormorant develops normally on a daily ration of 300 gr, but remains meagre. 100 gr. more give it an excellent appearance.

The calculations about the total requirement of the rookery are based on an average daily ration of 400 gr (about 20% of the body weight) for adults and large young. The total requirement of a rookery with 4000 adults, 2600 non-breeding birds and 5000 young during one season is estimated at 740.000 kg.

The fish population of the IJsselmeer is characterised by the fact that only few species are numerous (chapter 15). Eel, Pike-Perch, Smelt and Ruffe occur in the whole lake; Roach, Bream and Perch are mainly restricted to the coastal zone. These species are captured by the Cormorants in large quantities, except the Smelt (figs. 5, 6). In addition many Tench are taken, often together with fish showing the typical light colour of all inhabitants of the IJsselmeer. Their origin, however, is not quite clear.

The share of several species in the food of the Cormorant is presumably determined by the preference towards large fishes and their accessibility. The latter quality depends on living habits and swimming speed.

Specimens under a weight of 6 gr are rarely taken. The largest fishes recorded are: Pike, Awaite-Shad (both measuring 40 cm), Pike-Perch (38 cm), Roach, Perch, Tench (all about 30 cm) and Eel (65 cm). Apart from the Eel, such specimens represent a weight of about 500 gr.

The composition of the food shows many fluctuations (fig. 5-8). Differences between two successive years indicate changes in the fish population.

Seasonal changes are due to alterations in size or behaviour of the fishes. Daily fluctuations are mainly connected with the weather and ruled by the accessibility of the Eel.

In chapter 18-24 the most important fish species are discussed separately.

The Eel. In the early spring no Eels are landed. The capture begins with sunny days in May and shows a clear connection with rises in temperature (figs. 7, 8).

The majority of the Eel shows an injury at the nose. It is supposed that they are surprised by the Cormorant when they, in warm weather, lift the head out of the mud. The length frequency distribution of the captured Eel is recorded in fig. 9.

It is calculated that the rookery took 7.5 million Eel from the IJsselmeer, while fishermen landed 55 million specimens. The actual damage is estimated at 10%.

The Pike-Perch. In 1938 and 1939 a large majority of the Pike-Perches in the IJsselmeer belonged to the 1937 born generation. Their growth is recorded in fig. 10. In 1938 few specimens were captured from this generation, although they were numerous and sufficiently large. Other numerous fish from the same size may have been easier to capture. In 1939, when the generation from 1937 excelled by its size, increasing quantities were taken from March till June (fig. 6), when the larger part measured more than 36 cm and could no more be managed by the birds. In total 620.000 specimens were taken in 1939. While a large majority of the whole stock is taken by human fishery after reaching the legally established measurement (40 cm) it is certain that some damage is caused by the Cormorants. This damage is estimated at 10% of the total yields of the Pike-Perch fishery.

Length frequency distributions of the Ruffe, the Roach, the Bream, the Perch and the Tench, landed by the Cormorants are recorded in figs. 11-15. The relative high proportion of elder generations reflects the preference toward large fishes. The changing share of age groups can be explained by numerical differences between successive generations.

A large majority of the victims is 1 or 2 years old. An exception is formed by the Tench, which is taken mainly at an age of 3 years and more. This may be explained by the fact that young specimens live hidden between the waterweeds, while mature Tenches feed at the bottom in open places.

The length frequency distribution of the Bream indicates that this fish becomes less accessible towards a length of 17-18 cm but is taken at an increasing scale at a larger size. This coincides with a change in behaviour and diet, after which the Bream more or less accepts the habits of a large Tench.

The Pike is taken in small numbers mainly at a length of 30-40 cm in the spring. There may be a connection with the spawning season.

Smelt and Stickleback are taken occasionally only, obviously because of their small size.

Chapter 31 gives some data from Cormorant rookeries near the large rivers.

In Lekkerkerk (fig. 2) a small number of real saltwater fishes is recorded. During June large mature Awaite-Shads are landed occasionally. Birds from a rookery near Hook of Holland fish in the North Sea as well as in inland waters. Large Shrimps were recorded as a prey.

In chapter 32 the parasites are discussed. Almost every Cormorant stomach is infested with the little nematod *Contracaecum*, which seems to do no harm. It could be established that from the large Roaches taken by the birds from the IJsselmeer, 30% was infested with the large cestod *Ligula intestinalis* L., while in the fishwater the rate was only 6.5%. It can be assumed that the parasite increases the accessibility of the fish by hindering its movements. It could not be proved that the Cormorant is a suitable final host for the tapeworm, so it remains uncertain whether the bird plays a role in the spreading of the disease it seems, at first sight, to suppress.

Literature cited.

Bartlett, A. D., 1869: Remarks upon the habits of the hornbill (*Buceros*). Proc. Zool. Soc. London.

——, 1881: Remarks upon the habits of the Darter. Proc. Zool. Soc. London.

Bernatzik, H. A., 1929: Ein Vogelparadies an der Donau. Berlin, Wien, Zürich.

Brouwer, G. A., 1926 and 1927: De bedreigde broedplaatsen van de Aalscholver in Nederland. Ardea 15 and 16.

Forbes, A. W., 1881: Note on Mr. Bartletts communication on the habits of the Darter. Proc. Zool. Soc. London.

Groebbels, Fr., 1932: Der Vogel. Berlin.

Hartley, P. H. T., 1947: The natural history of some British fresh water fishes. Proc. Zool. Soc. London 117 (1).

Havinga, B., 1938, 1939, 1940: De ontwikkeling van de vischstand in het IJsselmeer. Maandoverzicht omtrent de uitkomsten der visscherij en Meded. van de Rijksinstituten voor visscherij-onderzoek. Dep. van Economische Zaken, 's-Gravenhage.

——, 1941: De veranderingen in de hydrografische toestand en in de macrofauna van het IJsselmeer gedurende de jaren 1936-1940. De biologie van de Zuiderzee tijdens haar drooglegging. Meded. van de Zuiderzeecommissie, afl. 5.

Kortlandt, A., 1938: De uitdrukkingsbewegingen en -geluiden van *Phalacrocorax carbo sinensis* (Shaw and Nodder). Ardea 27 (1-2).

——, 1940: Eine Übersicht der angeborenen Verhaltungsweisen des Mittel-Europ. Kormorans. Archives Néerlandaises der Zoologie 4 (4).

Lack, D., 1945: The ecology of closely related species with special reference to Cormorant and Shag. The Journal of Animal Ecology 14.

Lumsden, W. H. R. and A. J. Haddow, 1946: The food of the Shag in the Clyde Sea area. The Journal of Animal Ecology 15 (1).
Madsen, F. J. and R. Spärck, 1950: On the feeding habits of the Southern Cormorant (*Phalacrocorax carbo sinensis* Shaw) in Denmark. Danish Review of Game Biology I, 3.
Mattingley, A. H. E., 1927: Cormorants in relation to fisheries. The Condor 29.
Mennega, A. W. M., 1938: Waterstofionenconcentratie en vertering in de maag van enige vertrebraten. Dissertatie Utrecht.
Niethammer, G., 1938: Handbuch der Deutschen Vogelkunde II. Leipzig.
Portielje, A. F. J., 1927: Zur ethologie bzw. psychologie von *Phalacrocorax carbo subcormoranus* (Brehm). Ardea 16.
Rörig, G., 1903: Studien über die wirtschaftliche Bedeutung der insectenfressenden Vögel. Untersuchungen über der Nahrung unserer heimischen Vögel, mit besonderer Berücksichtigung der Tag- und Nachtraubvogel. Arbeiten aus der Biologischen Abteilung für Land und Forstwirtschaft. Berlin.
Serventy, D. L., 1938: The feeding habits of Cormorants in S.W. Australia. Emu 38.
Steven, G. A., 1933: The food consumed by Shags and Cormorants around the shores of Cornwall (England). Journal Mar. Biol. Ass. Plymouth 19.
Uttendörfer, O., 1939: Die Ernährung der Deutschen Raubvögel und Eulen und ihre Bedeutung in der heimischen Natur. Neudamm.
Wetmore, A., 1927: The amount of food consumed by Cormorants. The Condor 29.
Witherby, H. F. c.s., 1947: The Handbook of British Birds IV. London.

Some historical data on the relation between wind direction and migration of Chaffinches (*Fringilla coelebs* L.)

by

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25th Publication of the foundation „Vogeltrekstation Texel"

In a paper on the autumn-migration of Scandinavian Chaffinches (Deelder 1949) I concluded a correlation between the direction of prevailing winds in autumn and the number of birds passing in concentrated migration over the duneland district in Holland. Migration is strong in years which are characterized by an excess of winds from the SW. quarter and weak when winds from the NE. quarter are abundant.

This conclusion was based on observation records for a limited