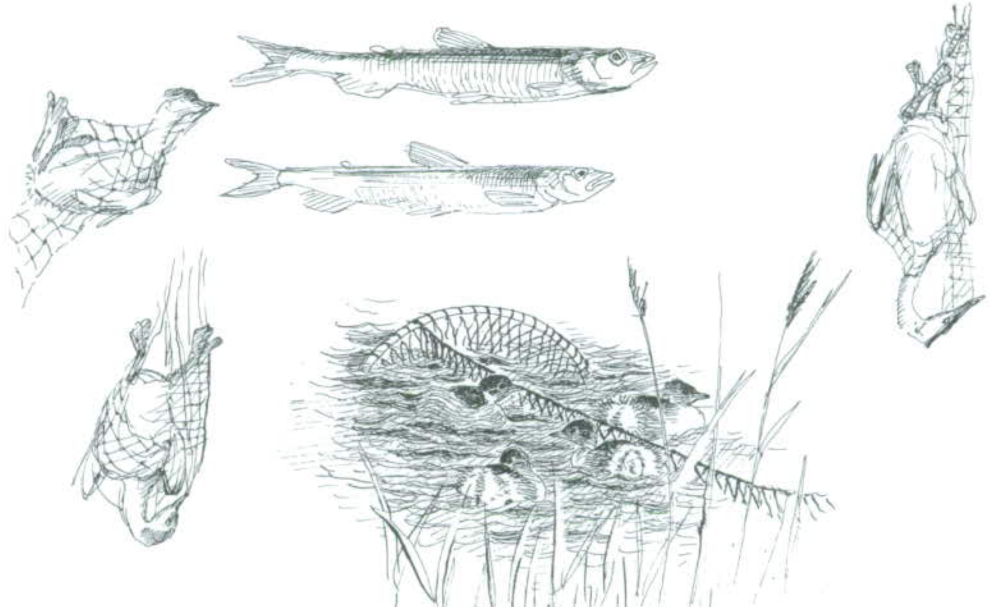

Seasonal changes in the diet of Great Crested Grebes *Podiceps cristatus* indicate the constraints on prey choice by solitarily pursuit-diving fish-eaters

This study examines how prey size and diet composition of Great Crested Grebes *Podiceps cristatus* change in the course of the non-breeding season (August-March). The analysis is based on an examination of the contents of oesophagi and stomachs of more than 1300 grebes which drowned accidentally in gill-nets while foraging at lake IJsselmeer, a large inland lake in the Netherlands, in 1978-1985.

Almost all recorded prey were fish, with Smelt *Osmerus eperlanus* contributing 85% to the total of 26 754 identified fish-prey. Prey abundance in the lake consisted of an overall 70% Smelt on the basis of numbers (beam-trawl surveys).

Seasonal changes in diet were correlated with an increase in diving depth, as inferred from drowning depth, no differences between males and females being apparent. For all months, grebes that drowned deeper contained less Smelt but more large prey.

Body size correlated with ingested fish size, but the correlation was only occasionally significant within the sexes, females being on average 10% smaller than males. Females took on average smaller prey and more Smelt than males (overall 74% and 56% respectively of total mass).

In the course of the autumn and winter season, the size of the ingested prey increased, an effect which could be accounted for by concurrent changes in prey availability through temperature dependent swimming speed.

A conceptual model was developed to predict patterns in diet, in terms of constraints imposed on the predator by the opportunities provided by the abiotic and biotic environments. Evaluating the predictions of the prey choice hypothesis, we conclude that swimming speed of both fish and grebes is the most important variable influencing the prey choice of Great Crested Grebes. A decrease in water temperature leads to a decrease in the maximal swimming speed of fish, and thus to an increase in the maximal length of fish that can be captured. Greater water transparencies in autumn and winter allow grebes to detect prey visually in deeper water, where larger fish are found. Because the prey concurrently withdraw into even deeper regions, deeper diving grebes are not able to compensate for their higher travel costs by ingesting more fish.

Introduction

In many marine and freshwater ecosystems, fish-eating birds are major consumers of the secondary production (White 1957, Evans 1973, Nilsson & Nilsson 1976, Furness 1978, Furness & Cooper 1982, Bourne 1983, Croxall *et al.* 1985). Possible conflicts with human fishery interests have led to a number of studies modelling the interactions between fish stocks and numbers of fish-eating birds (*e.g.* Furness 1982, Nettleship *et al.* 1984, Wood 1985, Linn & Campbell 1992). The predictive power of such studies is hampered by a lack of basic ecological knowledge, such as the distribution and size of fish stocks and the underwater feeding behaviour of the birds. Little information exists on the biological reasons behind prey choice and the question what limits local bird densities (Duffy *et al.* 1987b, *cf.* Piersma 1987). The scarcity of information must partly be due to the fact that the feeding habits are not very open to direct observations, which is particularly so for pursuit-diving water birds (but see Wilson & Wilson 1988, Wiersma *et al.* 1995). This is not only because most of the action takes place under water, but also because of the scale of their daily foraging movements (Wilson 1985, Van Eerden *et al.* 1993, Van Eerden & Voslamber 1995) and the general inhospitality of their environment to man. To overcome the difficulties of behavioural foraging studies in the field, a few studies have examined underwater feeding in captive pursuit-diving water birds (Duffy *et al.* 1987a, Sjöberg 1988).

Great Crested Grebes *Podiceps cristatus*, which are solitarily and visually hunting, foot-propelled, pursuit-diving and fish-eating birds, have the additional problem of feeding often in turbid waters in which underwater observations are simply impossible. Simmons (1977), O'Donnell (1982), Mayr (1986) and Ulenaers *et al.* (1992) have attempted to study the food of Great Crested Grebes by recording the type and size of prey brought to the surface. In the latter study it was concluded that the grebes took smaller fish than available in the shallow (1 m deep) fish pond. Although such data may give a biased picture, as small items may already have been swallowed under water, they indicate the limited capability to catch all fish within the size range that can be swallowed. Madsen (1957), Geiger (1957), Smogorchevski (1959), Doornbos (1984) and Büttiker (1985) studied food choice by analysing the oesophageal and stomach contents of purposefully collected grebes. However, these studies may be biased because of selection on the birds shot, and/or result in birds without any prey in the gullet because they were inactive.

This paper presents oesophageal and stomach contents of 1319 Great Crested Grebes which accidentally drowned in fishing nets in lake IJsselmeer, the Netherlands, during the non-breeding season. We try to infer the most important environmental correlates of the seasonal changes in diet. In order to do so, the description of the diet of grebes will be framed by a conceptual model which describes the factors influencing the prey choice of a pursuit-diving predator.

A conceptual model

In order to understand the mechanisms behind the diet choice of the grebes in turbid water, a conceptual model was made *a priori*. To describe the foraging process it is divided in three steps: prey detection, capture and handling plus ingestion.

Detection - At lake IJsselmeer we never observed Great Crested Grebes searching the underwater world from the surface. We therefore infer that at our sites the grebes dive and only then detect their prey, as they are approaching from below (*cf.* Fig. 1). The factors which influence the detection and capture of fish-prey, presented in Figure 1, are possibly correlated with attributes of the predator, the prey and the environment.

The depths which grebes are "profitably able to reach" (*i.e.* their diving performance) may depend on age dependent skill and body size (Piatt & Nettleship 1985, Duffy *et al.* 1987a). The depth to which a grebe has to dive to encounter a fish depends on the species (Smelt *Osmerus eperlanus* is mainly pelagic; Roach *Rutilus rutilus*, Perch *Perca fluviatilis* and Pikeperch *Stizostedion lucioperca* live deeper in the water column; Ruffe *Gymnacephalus cernuus* is epibenthic), and on the size and age of the fish (*e.g.* Karst 1968). The time of the day (*e.g.* Narver 1970, Northcote & Rundberg 1970, Piersma *et al.* 1988) and the time of the year (*e.g.* Bohl 1980) also affect the depth of living, which may be due partly to the direct influence of light. With increasing light intensities, which cause surface living fish to move to deeper water, birds may also take more bottom-dwelling prey.

studied on a large scale, allowing for a comparison of recovery between the different types of reed. The previously heavily grazed sites already recovered in the first season without grazing. Average height of shoots was between 184 and 207 cm (tussocks and inter-space combined). Average stem diameter varied between 5.11 and 5.95 mm for four out of the five types. Only type 3 lagged behind (Table 4). Shoot density was still highest in the previously most heavily grazed types, but was already more than 75% lower than at the time of exploitation by the geese. The previously grazed reeds were extremely powerful in the production of seeds. The number of panicles per m^2 was highest in type 2, 1 and 3 respectively, being six to nine times higher than in the ungrazed type 5. Also panicle size increased, which meant in all a ten to fifteen fold larger seed output as compared to the ungrazed stands.

Table 4. *In situ* recovery of different types of *Phragmites* within one year without grazing. Data reflect the performance of reed as recorded in September 1987 along the same trajectories as presented in Table 2 for the grazed situation. Panicles expressed as number per 100 shoots, *Archanara* stem borer infection given as percentage of shoots.

	Shoot length			Stem diameter			Shoot density			Panicle density	Litter layer	*Archanara* infection	
	cm	SD	N	mm	SD	N	N m^{-2}	SD	N	N 100^{-1}	cm	%	N
Zone													
1	185	37	114	5.37	1.32	60	521	90	21	41	0	0	62
2	207	40	92	5.66	1.30	58	373	88	15	44	4	0	59
3	184	31	259	5.04	1.36	145	263	160	24	31	10	34	148
4	203	35	264	5.95	1.39	96	180	8	12	26	10	52	101
5	195	17	149	5.11	1.04	74	231	70	6	5	35	16	74

Archanara infestation was found only in type 3, 4 and 5 and not in the previously most heavily grazed stands 1 and 2. Type 4 suffered most, which coincided with the largest average stem diameter. The lowering of the water level allowed a measurement of the amount of accumulated litter present at the bottom. A gradually increasing amount was found from hardly any in type 1 to 30 - 40 cm in type 5.

The process of recovery over five consecutive years was recorded by an enclosure experiment set up in 1985, when grazing was excluded in an area previously exploited by geese. The area (100 m^2) included tussocks of reed with unvegetated bare mud and water in between (type 3). After the grazing ban, new growth already resulted in the first year in many runners and a quick invasion of the space in between the tussocks, which themselves became less important and eventually died off (Table 5). Shoot density in the tussocks dropped significantly over these five years (Spearman $r_s = -0.9$, $P = 0.01$). In the first two years, shoot density was higher inside than outside the tussocks (t-test, $P < 0.0005$), thereafter lower ($P < 0.001$). Stem diameter in the newly colonised area was larger than inside the tussocks in all years (t-tests, $P < 0.0005$), although the difference became less in later years (Spearman $r_s = -1.0$, $P = 0.01$). Again *Archanara* stemborers rapidly took over the role of most important herbivore under the new condition of absent goose grazing. The newly colonised areas were already infested in the second year, the tussocks to a lower extent and not before the fourth year after grazing had ceased. We conclude that growth inside tussocks is a direct result of the grazing pressure by geese.

Table 5. Changes in various parameters of *Phragmites* before and after the start of the exclosure experiment in the moulting area in 1985. Measurements refer to shoots (type 3) growing in tussocks (caused by goose grazing) as well as the space in between. *P* indicates level of significance according to *t*-tests comparing tussocks and interspace within one year. See text for trends over the years.

	Shoot density (N m^{-2})					Stem diameter (mm)				
	1984	1985	1986	1987	1988	1984	1985	1986	1986	1987
Tussocks	1320	848	789	139	32	3.1	3.7	4.2	5.1	4.3
Interspace	0	4	144	219	114	8.5	8.4	7.6	7.9	6.2
P	0.0005	0.0005	0.0005	0.0001	0.0001	0.0005	0.0005	0.0005	0.0005	0.0005

	Average shoot height (m)					*Archanara* infection (N per 100 shoots)				
	1984	1985	1986	1987	1988	1984	1985	1986	1987	1988
Tussocks	1.2	1.8	2.6	2.3	1.6	0	0	0	0	14.3
Interspace	0	1.4	2.1	2.6	2.5	0	0	12.6	21.4	57.5

Discussion

Effects of grazing

Goose grazing had no apparent effect on the overall distribution of *Phragmites* in the marsh. The yearly event of mass defoliation of the reeds has led to the formation of several types, which are clearly distinguishable in the field. The most heavily grazed stands resulted in a low coverage (8 - 15%), but in terms of production per unit of vegetated area gave a higher yield than the undamaged stands (Table 2). Seed production was highest in the slightly grazed areas. It decreased sharply with increasing grazing pressure.

Both the enclosure and the drawdown experiments showed the great power of recovery of the previously heavily grazed types. Already after one growing season without goose grazing, the average stem diameter no longer differed among the types *i.e.* in relation to the preceding grazing pressure. This was caused by the many thick shoots developing in the space between the tussocks. The small scale enclosure experiment showed that the tussocks themselves gradually disappeared after the continuous grazing pressure had ceased (Table 5), whilst serving only as temporary but effective mounds during periods of grazing. The tussocky growth pattern prevents the geese from destroying the plant completely. The remaining leaves are in the centre and are hardly accessible to them. During winter, the uprooting of stolons by geese and swans is very much hampered due to the protective dense cover of dead shoots, which strongly conflicts with the habit of trampling holes.

Experiments by Van der Toorn and Mook (1982) studying different forms of stress on stands of *Phragmites* showed a consistent inverse relationship between density and diameter of shoots. They assume a surplus of buds of different size to be responsible for this. Larger buds develop first, possibly as a result of competition for nutrients and water. Only when the first developed meristems die will the smaller ones develop into shoots. The experiment results indicate a stress induced, increased density of smaller stems (up to a factor 4 increase). Our results fit in with this framework. However, the stress that was caused by geese in our study area managed to induce stem densities 2.4-3.9 times higher than the maximum values recorded by Van der Toorn and Mook (1982) in the same polder.

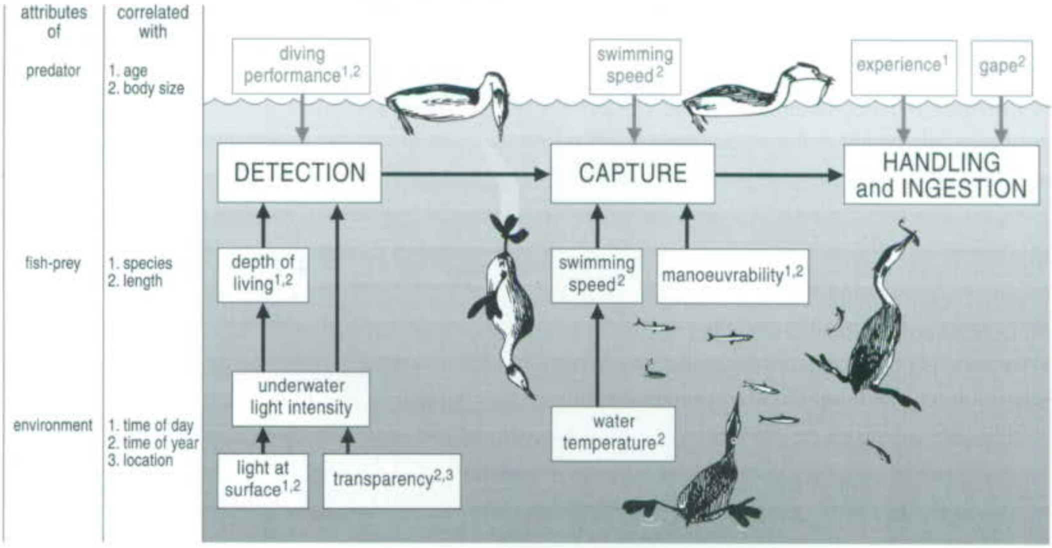

Figure 1. Conceptual hypotheses of the factors influencing the detection, capture and ingestion of fish-prey by Great Crested Grebes. From top to bottom, the thin-lined boxes list the factors ("attributes"), related to predator, prey and environment respectively, that influence eventual prey ingestion. In addition, the column on the left lists the measured variables that may correlate with the different factors, since the factors themselves have not directly been measured by us. Factors like visual acuity, mode of foraging (solitary *versus* social) and manoeuvrability of the predator were assumed to be constant in this within-species comparison. The directions of arrows point out the causal relations (in the case of factors influencing actions) or the order of the actions. Grebe drawings by Jon Fjeldså.

Ambient illumination directly influences the distances at which prey can be detected (Vinyard & O'Brien 1976). Underwater light intensity depends on the amount of light on the water surface (a function of time of the day, the weather and time of the year) and the transparency (or turbidity) of the water. Detection distance is also a function of prey size (Ware 1973, Confer & Blades 1975) and contrast. Grebes are assumed to overcome the problem of a very small contrast by approaching from below. In the same way Cormorants *Phalacrocorax carbo* (Van Eerden & Voslamber 1995) and Smew *Mergus albellus* (Chapter 18) hunt their prey from below, the flock-hunting habit of these species was, however, never observed in grebes at lake IJsselmeer.

Since the reactive distance of teleost fishes has been shown to be asymptotic with body length (Ware 1973), and since the coloration (and hence inherent contrast) of the fish species taken by grebes on lake IJsselmeer is much the same, both variables are assumed here to be constant.

Capture - Due to the notable sexual differences in body size and therefore in drag and relative muscle mass, differences in diving performance can be expected. The larger male Great Crested Grebes can perhaps achieve a higher swimming speed than the females due to their larger muscle volume.

Webb (1978) was unable to find differences in fast-start performance in teleost fishes of different body shape. However, large differences exist in maximum burst speeds related to fish length (Wardle 1977, Videler 1993) and to water temperature (Wardle 1980, Videler 1993). These relationships are quantitatively depicted in Figure 2. Maximum underwater swimming speed was recorded between 1.1 and 1.3 m s^{-1} (3.8-4.8 km hr^{-1}: Fig. 2B). Since the water temperature in lake IJsselmeer shows a seasonal variation of no less than 16 °C (Fig. 2C), which must greatly influence the size of fish which are

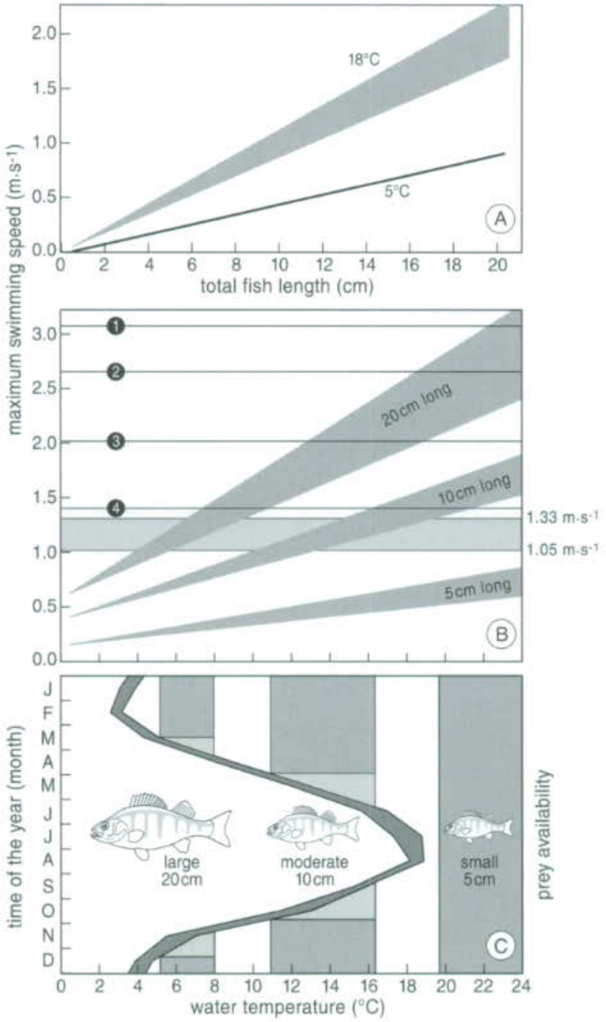

Figure 2. Maximum swimming speeds of poikilothermic teleost fishes are approximately linearly correlated with total length (A) and water temperature (B). (A) and (B) are constructed from data for a range of teleost fishes presented by Wardle (1977 and 1980), assuming that fish move forward with about 0.7 times their (total) length at each tailbeat (= stride; Wardle & Videler 1980, Wardle 1980). The shaded areas indicate the total range in reported values. The horizontal lines and area indicate the swimming speeds of various pursuit-diving bird species. 1: maximum speed over 10 m of juvenile Jackass Penguins *Spheniscus demersus* (Wilson 1985), freshly moulted adults attain even higher speeds; 2: highest estimated bottom speed of Cape Cormorants *Phalacrocorax capensis* (Wilson & Wilson 1988: Fig. 7). This species is approximately the same size as Great Crested Grebes; 3: upper limit of swimming speeds of Black Guillemots *Cepphus grylle* recorded by Uspenski 1956; 4: highest measured underwater swimming speeds of two flightless South American grebe species *Podiceps taczanowskii* and *Rollandia microptera*, calculated under the assumption that they travelled along the bottom (derived from data in Figs. 21 and 22 in Fjeldså 1981); Shaded bar indicates range observed for Great Crested Grebes diving in 0.30 m deep water (pers. obs.). Panel (C) shows the seasonal variation in water temperatures in lake IJsselmeer over the study period August 1978-December 1985 (database WAKWAL; area indicates 95% confidence interval around mean per month). According to panel (B) the seasonal prey availability for Great Crested Grebes has been indicated for three size categories by the dark-shaded areas. The light-shaded areas indicate fish not accessible to the grebes. In addition, the width of the columns gives an indication of the numerical presence of the three categories of fish.

able to outswim the grebes (Fig. 2B), we predict considerable changes in prey choice over the seasons as the water temperature changes. Small fish of 5 cm would be attainable all year long, 10 cm long fish from November until May and 20 cm long fish only in the coldest months: December until February (Fig. 2C). Fish types which have a greater manoeuvrability may have a better chance of escaping predation after being detected. We doubt, however, whether there are significant species and size specific differences in manoeuvrability over the range of fish sizes taken (*cf.* Fuiman & Webb 1988).

Handling and ingestion - If the diameter of a fish-prey is an important variable in deciding whether it can be ingested or not (Fjeldså 1981, Piersma 1988b), the relative thickness or "roundedness" of a prey species should correlate negatively with its ingested size. Such size limits were found by Büttiker (1985: Figs. 4 and 5) for Great Crested Grebes feeding on Roach and Perch in a Swiss lake. At lake IJsselmeer young Bream *Abramis brama* may be expected to impose ingestion problems because of its high-backed shape. A factor that additionally acts in this respect is experience of the predator. We may expect age-related differences to exist as well. We expect that adult birds are able to consume larger prey than first-winter grebes.

Methods

Study area

The largest lake in the Netherlands, lake IJsselmeer, was created in 1932 by closing off the Zuiderzee from the Wadden Sea by a dike. In 1975 lake IJsselmeer was divided into two parts, lake IJsselmeer (1225 km^2) and lake Markermeer (700 km^2). Along the north-eastern shores, lake IJsselmeer has extensive sandy shallows less than 3 m deep. The rest of the lake is 3-5 m deep with a rather flat sandy bottom, with only soft clay in some 5-7 m deep trenches in the centre. Lake Markermeer is 2.5-4.5 m deep, with a uniform flat bottom of mostly soft silt and clay. Sandpits occur scattered in the lake, down to *c.* 25 m deep (Voslamber *et al.* 1995). Lake IJsselmeer is fed by the polluted river Rhine. It is eutrophic with large fish stocks (300-500 kg ha^{-1}: Willemsen 1983). Due to algal bloom and sediment loads, the transparency of the water is usually less than 1 m (Secchi-depth value).

Diving depths, morphometrics and diet analysis of grebes

Grebes were obtained from fishermen around the lake during August-March in 1978-1985. The birds had drowned in gill-nets, standing 1.2 m high on the bottom of the lake. From August to October the majority of birds came from lake Markermeer. From November until March the birds came both from the northern and southern parts. The position of the drowned grebes was recorded by using nautical charts. Water depth was either directly recorded by fishermen or looked up on the chart. We assume that drowning and diving depth of the grebes are closely correlated. By keeping records of the fishing locations of the fishermen contributing to the study with caught birds, a correction could be made of the location of catch of the foraging grebes and fishing intensity. All birds were stored at -20 °C within 36 hrs after drowning. The grebes were thawed, weighed, described, aged as juvenile (first-winter) or adult (≥ second-winter) birds (see Piersma 1988a for methods), and sexed.

Food items found in the oesophagus were never digested, so the total length of the fish could be measured directly. Stomach contents, comprising balls of feathers with fish debris (Piersma & Van Eerden 1989), were either immediately refrozen, or stored in 96% ethanol for up to 6 months. The fish fragments consisted of vertebrae, scales, otoliths, parts of jaws and pharyngeal bones. The lengths of the otoliths of the right side of the head (which equal those on the left side: Doornbos 1980) of Smelt and the Percid species, were measured to the nearest 0.1 mm. Their otoliths being so brittle, lengths of the right pharyngeal bones of Roach and Bream were measured instead.

Sampling of the fish population

The fish population in lake IJsselmeer was sampled in August-October 1985 and 1986, with a 15 m long beam-trawl. The trawl had a mesh which decreased from 45 mm stretched width at the opening of the net to 15 mm at its end. A bag of 10 mm mesh width was attached over the end of the trawl to account for the smaller sized fish. The opening was 7 m wide and 1.2 m high. With iron chain-weights of 60 kg added to the front of the trawl, the net was towed along the bottom. Towing speed was held constant at 5 km hr^{-1}. Fishing took place between 9 and 15 h. The fish were sorted to species and size classes (5 g intervals) and the numbers of individual fishes in each class counted.

Samples of fish from catches made in lake IJsselmeer in late autumn and winter were used to determine the relationships between otolith, pharyngeal bone and fish dimensions and fresh and dry mass (see Chapter 16, Van Eerden *et al.* 1993). For Smelt, the mass of fishes whose remains were found in the stomach had to be calculated in two steps: first total length and then mass was estimated. This was necessary due to slight wear of their fragile otoliths. For the other species direct regression equations were used. For all species the relationships between otolith, pharyngeal bone and total fish length on the one hand and total fish length, fresh and dry mass on the other are presented in Table 1.

Results

Morphometrics of grebes

For all linear body dimensions, males are larger than females (Table 2; Piersma 1988a). The sexual size dimorphism is most pronounced in bill length, with males having on average a 12% longer bill than

Table 1. Equations to estimate total fish length (FL, in cm) and fresh mass (FM, in g) from otolith length (OL, in mm), pharyngeal bone length (PL, in mm) or total fish length, for the main prey species of Great Crested Grebes at lake IJsselmeer. Samples of fish collected between October and February were used to determine the equations. We tried to select fish from the approximate range of sizes eaten by grebes (*i.e.* between 3 and 20 cm). The length estimate of Smelt incorporates a correction for wear in the stomach.

Species	Equations	R^2	N
Smelt *Osmerus eperlanus*	$FL = 2.8 \times OL + 1.9$	-	-
	$FM = 0.0028 \times FL^{3.231}$	0.99	17
Roach *Rutilus rutilus*	$FL = 1.494 \times PL + 1.472$	0.99	27
	$FM = 0.0630 \times OL^{2.919}$	0.99	27
	$FM = 0.0030 \times FL^{3.498}$	0.99	40
Ruffe *Gymnocephalus cernuus*	$FL = 1.999 \times OL + 0.097$	0.83	44
	$FM = 0.0595 \times OL^{3.380}$	0.98	18
	$FM = 0.0081 \times FL^{3.170}$	0.99	33
Perch *Perca fluviatilis*	$FL = 2.810 \times OL - 0.340$	0.67	13
	$FM = 0.0992 \times OL^{3.674}$	0.98	20
	$FM = 0.0051 \times FL^{3.347}$	1.00	20
Pikeperch *Stizostedion lucioperca*	$FL = 4.236 \times OL - 3.366$	0.94	18
	$FM = 0.0420 \times OL^{4.407}$	0.95	18
	$FM = 0.0034 \times FL^{3.305}$	0.99	18

Table 2. Morphometrics of, and the extent of sexual size dimorphism in, the studied population of Great Crested Grebes, the two age classes taken together. Coefficients of variation (CV) are calculated as (SD/average) × 100%. Sexual size dimorphism is expressed as the ratio between male and female dimensions (M/F ratio; *cf.* Jehl & Murray 1986). Data recalculated from Table 1 in Piersma (1988a), except for structural size (defined as body × wing × keel × 0.0001: Piersma 1984), which was calculated again from the same database. Sample sizes are about 700, both for males and females (but for tarsus length about 375). Body length in cm, other linear dimensions in mm, and structural size in 100 cm^3 (not cm^3, as in Piersma 1984: Table 7).

Dimension	Males			Females			Sexual size dimorphism
	Average	CV(%)	(Range)	Average	CV(%)	(Range)	
Body length	54.64	3.3	(45-61)	50.87	3.2	(46-59)	1.07
Wing length	198.64	2.6	(174-215)	188.74	2.5	(171-205)	1.05
Bill length	51.43	6.2	(39-59)	46.09	5.2	(35-52)	1.12
Tarsus length	65.64	3.9	(57-74)	61.77	4.0	(50-69)	1.06
Keel length	80.74	4.7	(67-92)	75.48	4.8	(61-89)	1.07
Structural size	87.72	8.2	(52-111)	72.71	8.2	(55-94)	1.21

females. Note, however, that between the sexes all body dimensions show overlap in size. In addition to being most sexually dimorphic, bill length also shows most intra-sexual variation.

As a compound measure of the body size of Great Crested Grebes we have taken here "structural size", which can be defined as the reserve-independent (skeletal or emaciated) mass of a bird (Wishart 1979). Piersma (1984) found that in Great Crested Grebes structural size (a three-dimensional measure) is best approximated by the multiplication of body, wing and keel length. For each sex, structural size appears to be even more variable than bill length (Table 2). It is also the most sexually dimorphic amongst the body size variables.

The average fresh body mass of Great Crested Grebes changes considerably over the non-breeding season (Piersma 1988a). Birds are lightest in August-September (females = 1000 g, males = 1150 g). They subsequently increase in mass, due to the deposition of fat, to essentially a stable mass level from November until March (females = 1130 g, males = 1270 g).

The fish community

As is shown by this (Table 3) and earlier studies (Willemsen 1983, Cazemier 1986), the fish community of lake IJsselmeer consists of six common species (Smelt, Roach, Bream, Ruffe, Perch and Pikeperch) and three less common species (Eel *Anguilla anguilla*, Three-spined Stickleback *Gasterosteus aculeatus* and Flounder *Platichthys flesus*). Smelt contributes over half the total numbers of fish, while Roach and Bream contribute over half the total biomass (Table 3; *cf.* Willemsen 1983 for IJsselmeer).

There are some differences between the fish populations in the two compartments of lake IJsselmeer (Table 3). Although Willemsen (1983) asserts that lake IJsselmeer contains less Ruffe than lake Markermeer and more Smelt, Roach and Bream, we can only support this with the data from 1986 for the cases of Ruffe (a difference which is not significant) and Roach. In August 1986, 1$^+$ (second-summer < 18 cm) Perch and 1$^+$ Pikeperch (< 25 cm) were most abundant in lake IJsselmeer. Based on analyses for the period 1966-1993, when 23 fixed sites were subject to systematic monitoring, Knijn and Dekker (1993) show higher 0$^+$ stocks for lake IJsselmeer compared to lake Markermeer for Pikeperch, Perch, Smelt, Roach and Bream. Only for Ruffe is lake Markermeer consistently more important.

Throughout the summer and the early autumn (May-October) fish in lake IJsselmeer grows in

Table 3. Differences between the fish stocks in lake IJsselmeer and lake Markermeer: masses (kg) and numbers of different species caught with a beam-trawl in the period 18-21 August 1986. The sampling locations ($N = 13$ in the northern, and $N = 6$ in the southern part) were evenly spread over the entire area. At each location the net was towed along the bottom, over a transect of one km. Differences between the averages were tested with two-sided Student's t-tests. The very small catches of Eel *Anguilla anguilla*, Three-spined Stickleback *Gasterosteus aculeatus* and Flounder *Platichthys flesus* are not included.

Species	Category	IJsselmeer		Markermeer		two-sided Student's t-test	P-value
		Average	SD	Average	SD		
Smelt	Mass	5.0	5.7	6.8	4.5	0.74	NS
Roach		14.9	20.9	0.7	1.1	2.45	0.05
Bream		12.6	14.6	13.8	26.2	0.10	NS
Ruffe		0.9	1.3	7.5	7.7	2.25	NS
Perch (< 18 cm)		5.1	3.5	1.5	1.3	2.94	< 0.05
Perch (≥ 18 cm)		3.1	3.8	3.9	2.2	0.42	NS
Pikeperch (< 25 cm)		1.1	1.2	0.2	0.2	2.63	< 0.05
Total		44.3	33.5	34.9	34.5	0.56	NS
Smelt	Number	1630	1554	3311	2908	1.33	NS
Roach		100	142	1187	1207	2.20	NS
Bream		232	406	8	12	1.99	NS
Ruffe		12	14	11	20	0.14	NS
Perch (< 18 cm)		362	224	81	60	4.21	< 0.005
Perch (≥ 18 cm)		16	18	27	18	1.24	NS
Pikeperch (< 25 cm)		91	86	17	18	2.97	< 0.05
Total		2443	1423	4642	3242	1.59	NS

length. Figure 3 summarises the changes in average length of Smelt, Ruffe and Perch as recorded by our regular sampling in 1985 and 1986. The growth of Smelt and Perch stops in September, but the growth of (especially the 1^+, second-summer) Ruffe continues into October (Fig. 3). Absolute growth rates of the two cohorts of the three species did not differ much during the examined period of the year. Between species and year classes, second-year Perch show most variation according to place and year in the timing of growth termination and in the length attained before winter. Willemsen (1983) was unable to detect any systematic differences in the growth rates of fish in lake IJsselmeer compared to lake Markermeer, nor could we.

Prey choice and diet composition

Fish made up virtually all of the recorded prey items. Smelt formed the majority (26 754 or 85%) of the identified prey (Fig. 4). Ruffe (9.3%) and Perch (4.5%) constituted the rest. In August and September, the time of the year that the grebes assemble in large flocks in a few areas of lake IJsselmeer to moult their wings (Piersma 1987), remains of insects and plants were commonly recorded, sometimes containing tens of individual insect items. Since it is unlikely that the occasionally recorded crustacean, polychaete, insect and plant remains contribute significantly to the daily food intake of Great Crested Grebes, we shall not discuss them further.

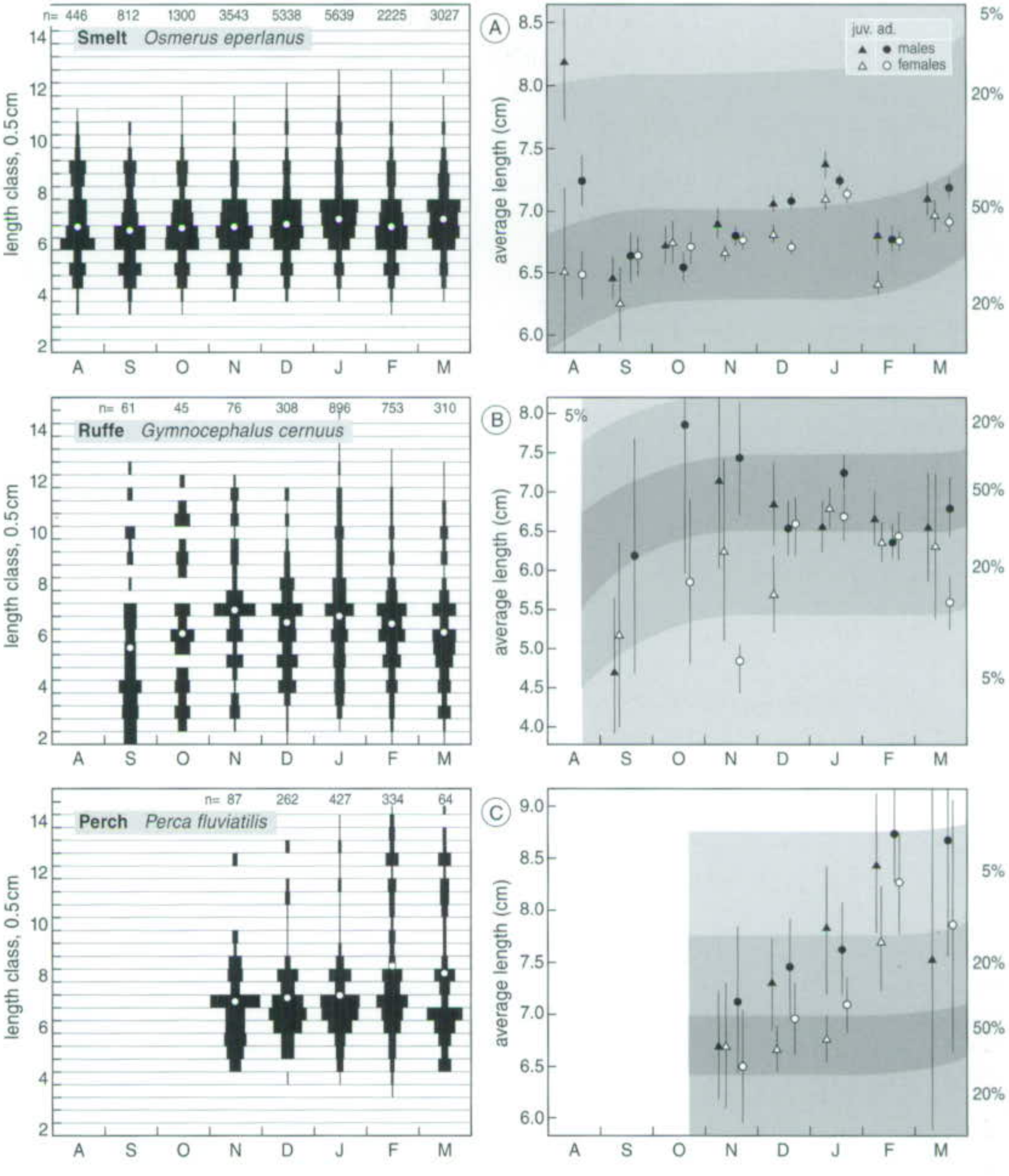

Figure 3. Seasonal changes in the length-frequency distributions of Smelt, Ruffe and Perch ingested by Great Crested Grebes at lake IJsselmeer (left) and in the average lengths of Smelt, Ruffe and Perch ingested by the four age and sex classes (dots in right panels). Open circles in the left panels indicate overall monthly average fish lengths. The vertical bars around the averages in the right panels indicate 95%-confidence intervals. *Shading in right panel*: Seasonal changes in the average lengths of the 0⁺ (first-year) cohort of Smelt, Ruffe and Perch in lake IJsselmeer. The graphs are compiled from data for autumn 1985 in Piersma and Muller (1987), and from data for autumn 1986 in Lindeboom (1988). The heavily-shaded area encloses 50% of lengths present, the medium-shaded area encloses 40% and the lightly-shaded area 10% of the lengths present in the different periods.

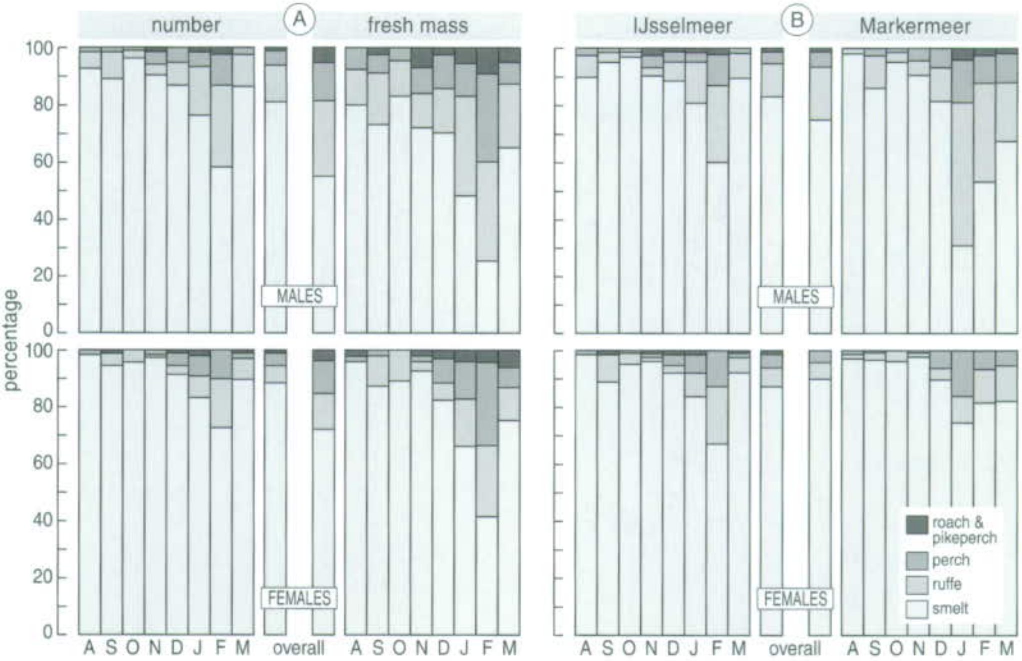

Figure 4. (A) Seasonal changes in the diet composition by number (left) and by fresh mass (right) of male and female Great Crested Grebes at lake IJsselmeer. (B) Seasonal changes in the diet composition (in fish numbers) of male and female Great Crested Grebes in the two compartments of lake IJsselmeer: IJsselmeer and lake Markermeer. For the yearly averages (middle columns) all contrasts are statistically significant from zero (χ^2-test, df = 3, $P < 0.001$). For males, IJsselmeer *vs.* Markermeer, $\chi^2 = 107.5$; for females, IJsselmeer *vs.* Markermeer, $\chi^2 = 37.0$, for IJsselmeer, males *vs.* females, $\chi^2 = 302.5$; for Markermeer, males *vs.* females, $\chi^2 = 301.5$). For the overall averages (middle columns), the differences between the diet (in numbers) of males and females are statistically significant ($\chi^2 = 178.4$, df = 3, $P < 0.001$).

The relative dimension of the prey is an important factor which determines prey choice. This explains the virtual absence of young Bream, a "high-backed" species, from the diet of Great Crested Grebes at lake IJsselmeer. The negative correlation among prey species between diameter relative to length (thickness) and ingested size suggests that gape may limit the ingestion of large individuals of the "thickest" species.

Figure 5 shows that this is not the only factor when all fish-prey species are examined together. However, the availability of different length classes complicates this overall picture: Smelt and Ruffe longer than 10 cm were rare in lake IJsselmeer. If we only compare Smelt with Ruffe, it is clear that grebes took smaller individuals of the thicker-bodied Ruffe. For the remaining three species, for which there are no such clear availability problems over the given range in size, the prediction does also hold. Larger individuals of the most elongated species (Pikeperch) were eaten compared to Roach and Perch. Roach and Perch longer than 15 cm were not eaten, despite their abundance in lake IJsselmeer (Piersma & Muller 1987, R. Lindeboom unpubl. data).

Since no systematic and significant differences were found between the diets of juvenile and adult Great Crested Grebes (χ^2-tests, $P > 0.05$), the data for the two age groups are pooled. Although the diet composition differed between males and females (Fig. 4A), and between birds captured in the northern

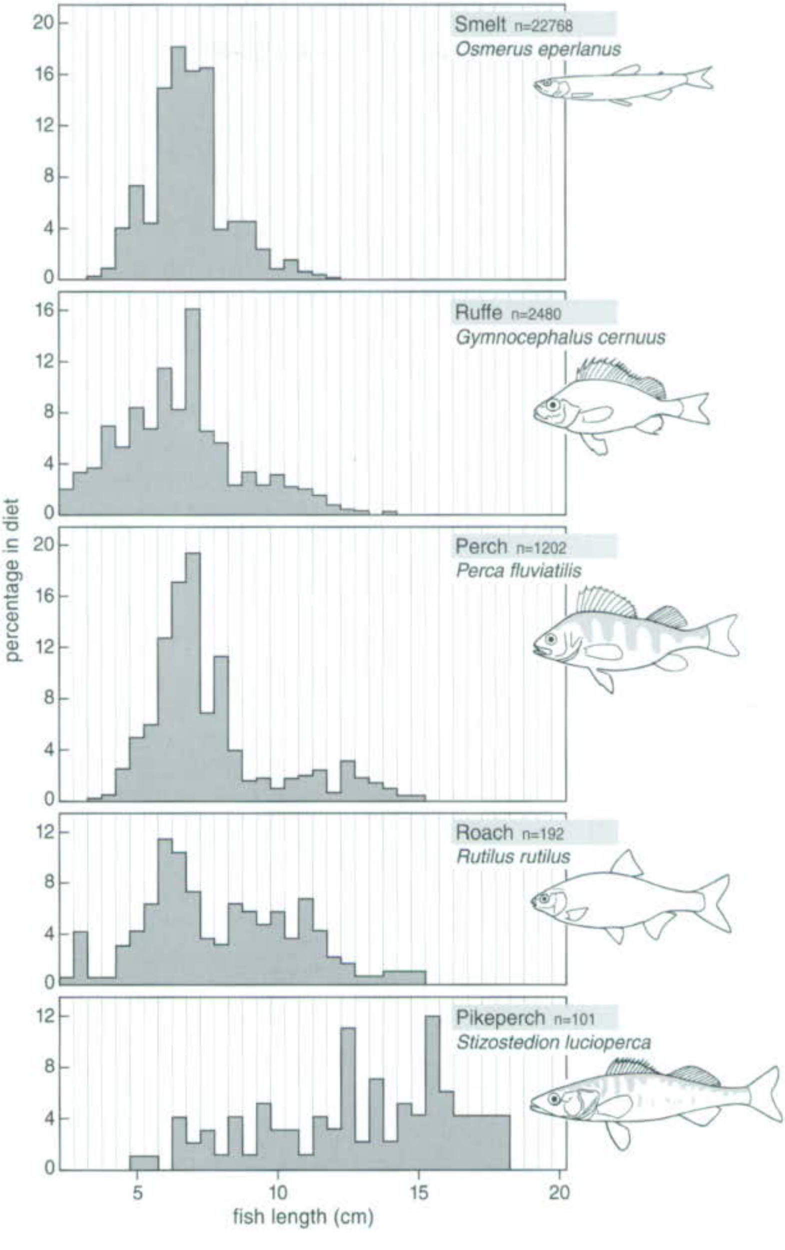

Figure 5. Frequency distributions of the lengths of the five most important fish species ingested by Great Crested Grebes in lake IJsselmeer. The fish species are arranged (from top to bottom) in order of increasing fish length consumed. The maximum height/maximum length ratios are approximately 0.15 for Smelt, 0.21 for Pikeperch, 0.25 for Ruffe, 0.29 for Roach and 0.33 for Perch.

and southern part of lake IJsselmeer (Fig. 4B), the seasonal patterns for the various categories were highly comparable. For all sex and area categories, the numerical contribution of Smelt to the diet remained high (> 90%) throughout the period August-November, and then decreased. In lake IJsselmeer the relative contribution of Smelt was lowest in February, in lake Markermeer in January. The decrease in the contribution of Smelt in winter was compensated for by an increase in the contribution of Ruffe (especially in males) and Perch, and to a lesser extent Pikeperch and Roach.

Because of their relatively small size and mass, Smelt formed a smaller part of the daily intake than expected from their numerical abundance (Fig. 4A). Over the entire season on the basis of weight, Smelt formed 56% of the fish mass ingested by males and 74% of the intake of females. Ruffe and Perch contributed most to the remaining intake.

A shift in prey size

For both sexes, the average prey mass was largest in February when the heaviest prey species (Pikeperch, Perch and Roach) predominated in the diet. Individual fish masses also peaked in this month (Fig. 6). For each prey species, females ingested prey with a smaller mass than males. Overall, average individual prey mass differed with 0.6/2.5 × 100 = 24% in favour of the males.

Season and sex/age related variations in the size of ingested prey of the main prey species (Smelt) are investigated in Figure 6, presented against the background of the overall growth patterns. The majority of Smelt eaten by Great Crested Grebes belonged to the 0^+ yearclass (Fig. 6). Relatively large Smelt were ingested in August, when the grebes still ate a lot of the 1^+ yearclass. This is probably a result of the as yet limited availability of proper sized (35 cm long) 0^+ Smelt (Fig. 3, Van Eerden *et al.* 1993). From September to January the size of ingested Smelt increased, an effect which cannot be accounted for by a simultaneous growth of the two yearclasses of Smelt (Fig. 3). In February the average size of ingested Smelt dropped to the September-October level to increase again in March. The lat-

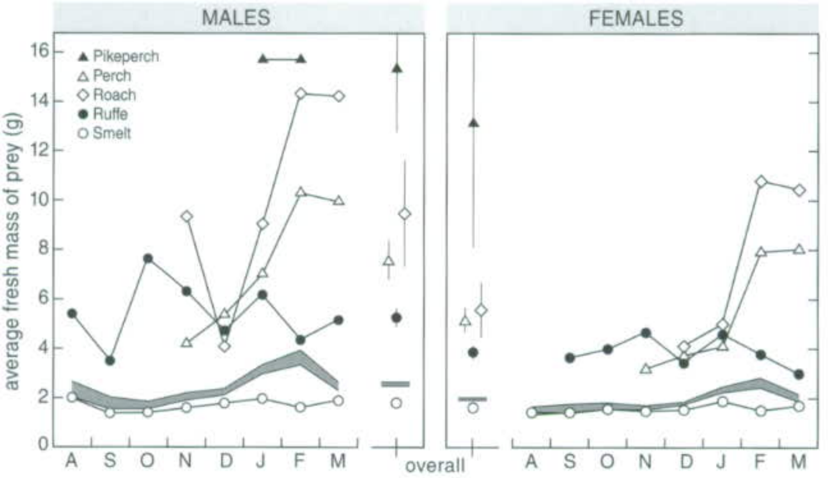

Figure 6. Seasonal changes in the average mass of fish ingested by male and female Great Crested Grebes at lake IJsselmeer. Different prey species are indicated with different symbols (monthly averages; the bars around the overall averages show the 95%-confidence intervals). The average mass of ingested prey is indicated by the shaded area, which encloses the 95%-confidence intervals of the monthly averages.

Table 4. Analysis of variance of the effects of month, sex and age on the lengths of different fish species ingested by Great Crested Grebes at lake IJsselmeer. For Smelt and Ruffe females ate smaller fish than males. In the case of Perch, females ate smaller fish than males, and juveniles smaller fish than adults.

Effect	Smelt ($N = 22\,769$)		Ruffe ($N = 2481$)		Perch ($N = 1202$)		Roach ($N = 192$)		Pikeperch ($N = 79$)	
	R^2 (%)	P-value	R^2 (%)	P-value	R^2 (%)	P-value	R^2 (%)	P-value	R^2 (%)	P-value
Month	2.18	< 0.001	2.23	< 0.001	6.54	< 0.001	9.45	0.003	21.33	0.001
Sex	0.51	< 0.001	0.61	< 0.001	2.03	< 0.001	1.76	0.039	-	0.259
Age	-	0.777	-	0.127	0.38	0.026	2.27	0.019	-	0.326
Month × Sex	0.28	< 0.001	0.75	0.008	-	0.660	-	0.338	-	0.999
Month × Age	0.12	< 0.001	-	0.045	-	0.472	-	0.989	11.54	0.011
Sex × Age	0.02	0.023	-	0.448	-	0.338	-	0.293	4.03	0.044
Month × Sex × Age	0.10	< 0.001	0.84	0.001	-	0.809	3.64	0.001	-	0.073

ter changes cannot be explained by changes in the lengths of present Smelt either. Female Great Crested Grebes tended to eat smaller Smelt than males. There were no systematic differences between the sizes of Smelt eaten by juvenile and adult birds.

Most Ruffe eaten by Great Crested Grebes belonged to the 0^+ yearclass (Fig. 5). The average size of ingested Ruffe increased from September until November (Fig. 6). This effect can partly be explained by the concurrent growth of Ruffe in the months of September and October (Fig. 3). Ruffe eaten by females tended to be smaller than Ruffe eaten by males. No differences in the size of Ruffe eaten by juveniles and adults are apparent.

The average size of ingested Perch increased from November until February and levelled off in March (Fig. 6). This increase was due to both an increase in the size of ingested Perch of the two yearclasses and to an increasing proportion of Perch belonging to the 1^+ yearclass (Fig. 3). The seasonal increase in average size cannot be explained by a simultaneous increase in the size distribution of Perch in lake IJsselmeer. Male Great Crested Grebes tended to eat larger Perch than females, the differences between juvenile and adult birds again not being apparent.

A three-way analysis of variance to investigate simultaneously the effects of time of the year, sex and age on the length of the ingested prey of all species (Table 4) confirmed that the time of the year explained 2-20% of the variation in prey size. Sex (and henceforth size) of Great Crested Grebes also explained part of the variation in prey size, but the age of the predator was generally unimportant. Interactions between the three effects only explained an appreciable part of the variation in the case of Pikeperch.

In the foregoing analysis, the body size of the predator as it is related to size of the ingested prey was implicated in the effect of sex: male Great Crested Grebes are bigger than females (Table 2). To examine the effects of body size more directly, we have correlated size of ingested prey to various components of body size of grebes that captured it (Table 5). Over all birds (pooling the two sexes) the various components of body size are indeed positively correlated with prey size (apart from Pikeperch). For the elongated Smelt and Pikeperch, the size of the larger sex (males) is negatively correlated with prey size. In the case of Roach, the size of the smaller sex (females) is positively correlated with prey size. There are no obvious differences in the way in which different body size variables correlate with prey size. For example, bill length does not generally correlate better than structural size.

Diving depth and prey choice

Having described seasonal changes in prey size, prey mass and diet composition, we now examine

Table 5. Pearson correlation coefficients between lengths of ingested fish of five different species and the various body dimensions of the Great Crested Grebes that ate them. Negative correlations are in italics. NS indicate correlation coefficients which are not statistically significant at the 5%-level. When no values are presented, $N < 10$. Body, wing, keel, tarsus and bill are length measurements, structural size is a volume measure (see Table 2).

Fish species	Predator category	Sample size (range in *N*)	Body dimensions					
			Body	Wing	Keel	Struc. size	Tarsus	Bill
Smelt	Both sexes	10 360-22 690	+0.079	+0.041	+0.032	+0.056	+0.019	+0.064
	Males	4264-9960	NS	*-0.042*	*-0.042*	*-0.036*	*-0.048*	NS
	Females	6091-12 641	+0.069	NS	NS	NS	NS	+0.029
Ruffe	Both sexes	697-2481	+0.085	+0.079	+0.039	+0.075	+0.162	+0.078
	Males	497-1545	NS	NS	NS	NS	+0.131	NS
	Females	200-907	+0.133	NS	*-0.080*	NS	NS	+0.147
Perch	Both sexes	429-1202	+0.134	+0.055	+0.110	+0.112	NS	+0.102
	Males	180-555	NS	*-0.082*	NS	NS	*-0.128*	NS
	Females	249-647	NS	*-0.072*	+0.095	NS	NS	NS
Roach	Both sexes	93-192	+0.309	+0.272	+0.272	+0.312	+0.337	+0.187
	Males	32-78	NS	NS	NS	NS	NS	NS
	Females	61-114	+0.287	+0.245	+0.312	*-0.366*	*+0.403*	NS
Pikeperch	Both sexes	77-79	NS	NS	NS	NS	-	NS
	Males	56	NS	*-0.363*	*-0.399*	*-0.423*	-	NS
	Females	21	NS	+0.347	NS	NS	-	NS

whether part of the variation in prey choice can be explained by the details of the catching location. A variable that changed dramatically in the course of the season is the depth at which the grebes drowned (Fig. 7). In autumn, Great Crested Grebes only were collected in water less than 6 m deep. From November onwards grebes also foraged in deeper water, down to a depth of 22 m in February. Although males tended to dive deeper than females, the sexual differences were not statistically significant (Mann-Whitney *U* tests for monthly and overall averages, $P > 0.05$).

As the grebes drowned in deeper waters, the numerical contribution of Smelt to the diet decreased and was replaced by Ruffe, Perch, Pikeperch and Roach (Fig. 8). This was true for all birds combined, for males and females, for different times of the year and for different areas (IJsselmeer *vs*. Markermeer). The average lengths of ingested fishes also changed in relation to drowning depth (Fig. 9). Grebes which drowned in water 12-23 m deep contained smaller Smelt than grebes caught in shallow waters (< 6 m), but Pikeperch (caught by females) was on the contrary larger in deeper water (ANOVA's, $P < 0.05$). For Smelt, Roach, Perch (males) and Ruffe (males) fish length was larger between shallow and middle deep waters (6-11 m; ANOVA's, $P < 0.05$).

Those Great Crested Grebes that drowned in deeper water caught larger prey species and larger individuals of the large prey species than the birds that drowned in shallower water, so the average ingested prey mass increased with depth with 1.5 to 2 g for males and females, respectively (ANOVA's, $P < 0.0001$: Fig. 10A). In spite of this, the ratio between prey mass and water depth at the drowning location decreased with increasing drowning depths (Fig. 10B). If drowning depth would linearly relate

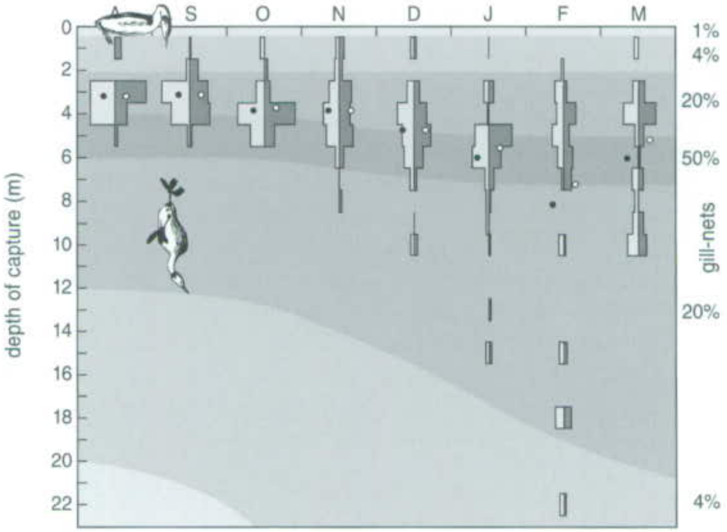

Figure 7. Seasonal changes in the depths at which male and female Great Crested Grebes drowned in gill-nets in lake IJsselmeer. The figure presents frequency distributions of the bottom depths on which the 1.2 m high gill-nets were standing in which the grebes drowned. Closed and open circles indicate the monthly averages for respectively males and females. The average depths at which the whole population gill-nets are found in different months have been indicated.

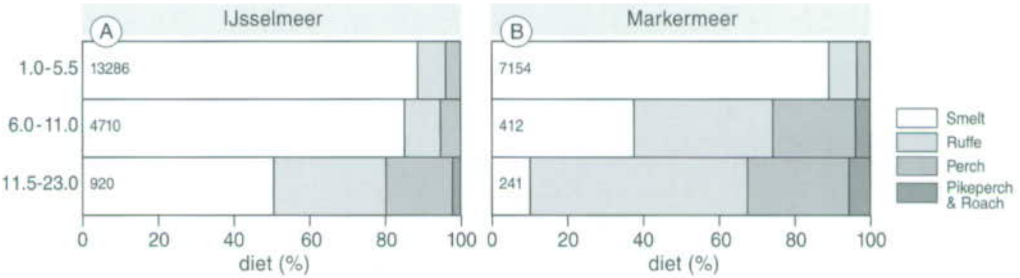

Figure 8. The depth-related numerical diet compositions of Great Crested Grebes in lake IJsselmeer (A) and lake Markermeer (B).

to time spent under water and energy expenditure, for deep dives to be more profitable than shallow dives a grebe should thus capture more prey per deep than per shallow dive.

In an attempt to disentangle the effects on average prey mass identified in Figure 10, a four-way analysis of variance was carried out (Table 6). The effects of depth, sex, area (IJsselmeer or Markermeer) and period (time of the year) contributed significantly to the explanation of the variation in prey mass. However, since "period" added significantly to the explanation of variance in prey mass, independently of the other factors, the analysis suggests that the change in diet composition over the winter cannot exclusively be explained by changes in drowning (diving) depth. There must thus be one or more additional environmental factors that change in the course of the winter (*e.g.* water temperature), making large fish-prey easier to catch.

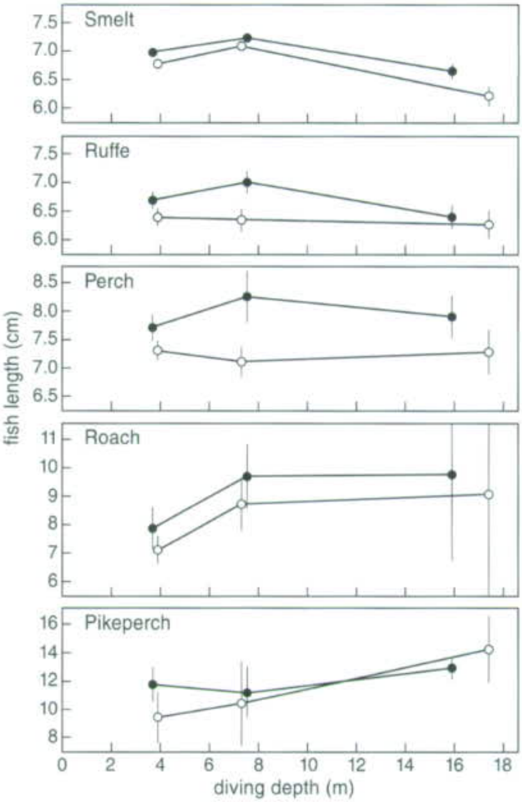

Figure 9. Prey-fish lengths in relation to the depths at which the Great Crested Grebes that ate them were caught in lake IJsselmeer. Overall averages with 95%-confidence intervals are presented for the three depth classes defined in Figure 8 for males (closed circles) and females (open circles).

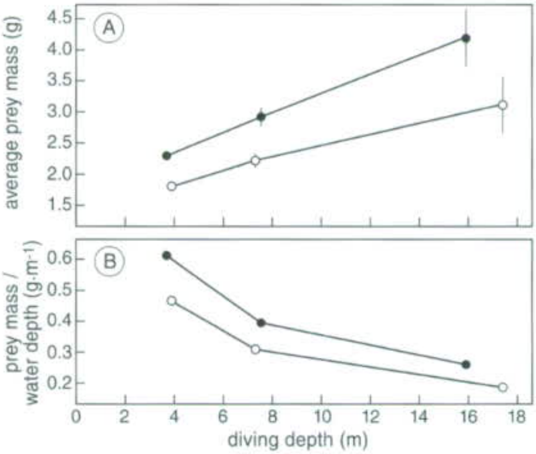

Figure 10. Prey-fish mass in relation to the depths at which the Great Crested Grebes that ate them were caught in gill-nets in lake IJsselmeer (A) and an index of yield (prey mass/vertical diving distance, one-way) in relation to depth (B). In (A) overall averages with 95%-confidence intervals for males (closed circles) and females (open circles) are presented.

Table 6. Analysis of variance of the effects of drowning depth (three depth classes, Fig. 8), sex of the predator, foraging area (IJsselmeer and Markermeer) and period of the year, on the fresh mass of ingested fish by Great Crested Grebes at lake IJsselmeer. Based on average water temperature the periods are: August-October (= 1), November, December and March (= 2) and January and February (= 3). 26 723 cases were processed. The significant effect for area means that birds from lake IJsselmeer ingest on average lighter fish than birds from lake Markermeer. The significant effect of period means that birds ingested increasingly heavy prey in the course of the winter season, a trend which is reversed in March, independently of the effects of other variables.

Effect	R^2 (%)	*P*-value
Depth	0.93	< 0.0001
Sex	0.89	< 0.0001
Area	0.13	< 0.0001
Period	1.43	< 0.0001
Depth × Sex	0.04	0.004
Depth × Area	0.97	<0.001
Depth × Period	-	0.051
Sex × Area	0.02	0.020
Sex × Period	0.08	0.001
Area × Period	-	0.123
Depth × Sex × Area	0.03	0.012
Depth × Sex × Period	-	0.907
Depth × Area × Period	0.06	0.001
Sex × Area × Period	-	0.835
Depth × Sex × Area × Period	-	0.194

Discussion

Prey and predator based constraints on prey choice

Prey size limits the range of ingestible prey in a medium sized predator like Great Crested Grebes. Only 0^+ and in some fish species also 1^+ cohorts are present in the diet. These form biologically the majority of prey items within each species, except for those which show irregular reproduction. In lake IJsselmeer and Markermeer, Roach (peaks in: 1979, 1983, 1989), Bream (1983, 1989), Perch (1980, 1982, 1985, 1986, 1989) and Pikeperch (1983) show such pattern of erratic reproductive success (Buijse 1992, Knijn & Dekker 1993), and we may argue to what extent variation in abundance of the first-winter cohort might have affected prey selection. During the period of this study, 1979-1990, all potential prey species have had bumper years without any noticeable effect on the diet of the grebes. The almost absence of 0+ Bream, a high-backed species, in the diet of Great Crested Grebes (9 fishes captured over 26 762 identified prey), can therefore be explained by problems of ingestion rather than low abundance.

From our data we may conclude that within the group of slender-built prey species like Smelt and Pikeperch, it must be performance of the predator rather than gape size that limits prey size, an argument which was also invoked to explain why small-sized Slavonian Grebes *Podiceps auritus* captured larger Smelt than the larger-sized Red-necked Grebe *P. grisegena* (Piersma 1988b). Extending the discussion to Great Crested Grebes, we find that the latter (and largest) grebe species captured only marginally larger Smelt than Slavonian Grebes. This indicates that, in respect to the size of Smelt taken, differences in the swimming performances of the two species are not discernible, and that bill size is of no importance at all in determining Smelt size captured. Also lengths of Ruffe and Perch taken by Slavonian Grebes spanned the same range as was found for Great Crested Grebes in this study. Only when the incidence of larger prey species in the diet is concerned, a tendency is observed that the larger predators took more large fish species.

Within the large sample of Great Crested Grebes, differences between prey dimensions of males and females suggest a sexual difference in performance. We found that the smaller females fed on smaller sized prey, irrespective of prey species (Table 4). Also, a larger part of the diet of females is taken up by the smallest species (Smelt) than in males (Fig. 4). The finding that males take more of the epibenthic living Ruffe than females (Table 5), suggests that males may have a greater diving performance than the smaller females, although female Great Crested Grebes dive as deep as males (Fig. 7, but see Hofer 1969). It is perhaps most likely that the sexual differences in ingested size within each prey type are explained by a sexual difference in swimming performance. We hypothesise that females have lower maximum swimming speeds than males, possibly because they are smaller.

Environmental constraints on prey choice

The most significant seasonal changes in the diets of Great Crested Grebes at lake IJsselmeer are the increasing size of ingested individuals of all fish species in the course of autumn and late winter (a trend which is reversed in early spring), and the replacement in midwinter of Smelt by the larger fish species Ruffe, Perch, Roach and Pikeperch (Figs. 4 and 6). According to the conceptual model (Fig. 1) two basic environmental factors could in theory explain the larger sizes of ingested fishes, as well as the decreased percentages of Smelt in mid-winter: (1) increasing transparencies permit grebes to detect prey at larger depths, and since the large prey species live deeper, to detect larger prey; (2) decreasing water temperature reduces the maximum swimming speeds of fish (Fig. 2), which enables the grebes to capture bigger prey after detection.

The seasonal variations in water temperature (Fig. 2C) could partly explain why the size of the three main prey species increased (Smelt, Ruffe and Perch, Fig. 6) during the period when the fish populations showed no growth (Fig. 3). Decreasing water temperatures could also explain why larger and presumably more profitable prey species than Smelt were taken in mid-winter (the monthly average mass-percentages of Smelt in the diet of grebes are positively correlated with monthly average water temperatures, both for males ($r = 0.70$, $N = 8$, $P < 0.05$) and for females ($r = 0.70$, $N = 8$, $P < 0.05$). During all months, grebes which drowned deeper contained less Smelt and contained larger Pikeperch and Roach, a negative correlation exists between the percentages of Smelt and the monthly average drowning depths (males: $r = -0.91$, $N = 8$, $P < 0.01$ and females: $r = -0.94$, $N = 8$, $P < 0.01$).

Grebes which drowned at increasing depths did so with increasing ambient transparencies (Fig. 11): grebes are apparently able to detect large and deep (epibenthic) living prey in clear water only. Since transparencies of more than 60 cm also occur at times of the year other than January and February, when water temperatures are higher, we additionally conclude that only when water temperatures are low, do large prey swim slow enough for grebes to take the trouble to dive deep and capture them.

The small size of Smelt eaten in February remains to be explained. Since the size of Smelt decreases with drowning depth (Fig. 9), an *ad hoc* explanation might go as follows: in February the birds concentrate on the large and deep living prey and only supplement their diet with the most easily captured (smallest) Smelt, which they encounter en route (like in benthos-feeding Eiders, R.C. Ydenberg pers. comm.).

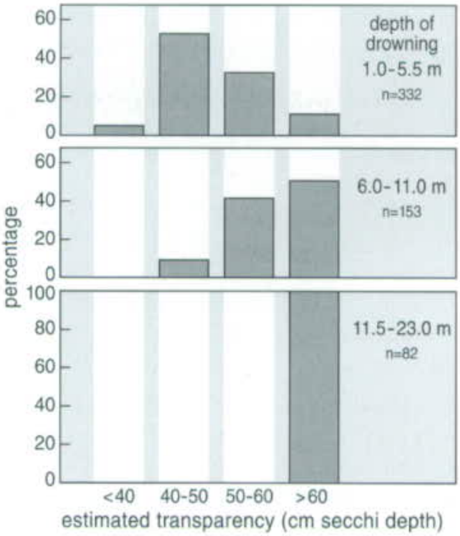

Figure 11. The depths at which Great Crested Grebes drowned in lake IJsselmeer in January and February correlates positively with the estimated transparency at the capture-sites. Secchi-disc transparencies at capture sites were estimated from average values for wind speed and direction, measured on the capture date in the area (Houtrib; from daily weather reports issued by KNMI in De Bilt), and data from database WAKWAL of RIZA, Lelystad. The three depth distributions are statistically different ($\chi^2 = 304.7$, df = 6, $P < 0.001$).

Conclusions

An evaluation of the *a priori* prey capture model results in the support of 8 out of 14 predictions (Table 7). Not upheld were predictions about age related foraging skill and age and morphometric dependent capability of deep dives. Our distinction of age classes on the basis of plumage and gonads, which only resulted in two categories, was possibly too crude to allow a proper distinction. The other possibility, that foraging skill would be completely indifferent among birds from the first autumn onwards, seems unlikely. Apparently deep dives can be made with the same effort by small and large grebes. Predictions about prey capture which are linked to the ability to manoeuvre were supported in favour of the larger sized grebes. At first sight the slight differences in prey choice which are the result of differences in structural size may seem ecologically insignificant. All grebes seem to eat *grosso modo* the same array of prey sizes and species. The fact *that* we demonstrated these differences, however, is of great importance when one is to judge the balance between prey abundance and predator density. Apparently larger grebes can also take larger and faster fish, as they will meet under water the same prey composition as the smaller conspecifics. Size range extension probably enlarges prey biomass within reach and the pattern observed is not the result of active selection. The larger and/or more mobile prey in the diet of the larger grebes thus implicitly reflects the scarcity of winter prey. If the more abundant smaller sized fish were within easy range, we would expect that the entire diet would be composed of this group. This is apparently not the case, and the size range extension can thus be interpreted as a sign that all fish which is encountered upon during a dive is pursued.

The most striking outcome of this study was the seasonal variation in environmental conditions that led to considerable changes in the type and size of fish-prey that are eaten by Great Crested Grebes.

Table 7. A list of possible correlations and qualitative predictions related to the choice between a variety of fish prey species by Great Crested Grebes at lake IJsselmeer, based on the conceptual prey choice model presented in Figure 1, compared with the results of this study.

Category	Attribute	Proven or possible correlations	Predictions about prey choice	Model
PREDATOR	Diving performance	Increases with age	Older birds dive deeper, and feed on deeper living prey	Rejected
		Increases with body size	Males dive deeper than females Larger birds of either sex dive deeper than smaller birds	Rejected Probably Rejected
	Swimming speed	Increases with body size	Larger birds take the faster fish types	Supported
	Experience in handling	Increases with age (handling time decreases)	Older birds take fish that are more difficult to handle	No evaluation
	Gape width allowing ingestion	Increases with body size	Larger birds take fish with a larger cross-section	Supported
PREY	Depth of living	Depends on the species	Smaller birds take more pelagic prey Younger birds take more pelagic prey	Supported Rejected
		Increases with size	Smaller birds take smaller fish Younger birds take smaller fish	Supported Rejected
		Increases with increasing underwater light intensities	When light circumstances are better, only larger birds can take larger prey	Supported
	Swimming speed	Depends on the species Increases with size (Fig. 2)	Larger birds take faster species Larger birds take fish with greater lengths	Supported Supported
		Increases with temperature (Fig. 2)	Birds take larger and faster fish when the water temperature is lower	Supported

The temperature of the water appeared to influence greatly which fish sizes are attainable as prey: as water temperature decreases, burst swimming speeds of fish decrease as well. This means that the larger and faster fish are no longer able to escape from the pursuing predators. Since larger fish live more near the bottom, they can only be detected when the transparency of the water is high. Temperature and underwater light climate are thus important determinants of the bird's prey choice. The same factors were affecting prey availability in Cormorants *Phalacrocorax carbo*, at the same lake in summer (Van Eerden & Voslamber 1995).

By the same token, this study showed that the predation risk for different fish species, or even size cohorts within one species, is not constant over winter, but varies according to an environmental and predator based attainability. During late winter, more large prey become available as prey for this predator, which is important in models which aim at estimating the effect of predators on cohort or size group survival.

Bottom haul during fish survey, Vrouwenzand lake IJsselmeer, October 1985.

Great Crested Grebes which, in order to compensate for extra costs for thermoregulation in winter, must eat about twice as much as in late summer (Chapter 5, Wiersma *et al.* 1995), may be slightly facilitated to do so because of this enlargement of the prey size range available to them. On the other hand, the larger grebes seem better off during the coldest period. Our sample indeed shows this shift: from September until December we collected 171 adult males against 188 adult females. In January-February this was 177 adult males against 144 adult females, which is statistically different ($\chi^2 = 3.82$, $P = 0.05$). In first-winter grebes no such shift was apparent.

The environmental correlates of prey choice being approximately identified, it would now be of great interest to take Great Crested Grebes into the laboratory. Experiments under controlled conditions along the lines of pioneering studies by Swennen and Duiven (1977) and Sjöberg (1988), could not only provide crucial tests of the correlative evidence presented here, but could also lead to the formulation of quantitatively predictive prey choice and predation models. Such studies and the resulting models could do much to help us to come to terms with this ecologically important but intractable group of pursuit-diving birds.

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Chapter 18

Social fishing in wintering Smew *Mergus albellus* enhances prey attainability in turbid waters

Maarten Platteeuw, Mennobart R. van Eerden & Jan H. Beekman

Social fishing in wintering Smew *Mergus albellus* enhances prey attainability in turbid waters

In winter, Smew may gather by thousands in the area of lake IJsselmeer, the Netherlands. In the 1980s this was the only haunt where major concentrations of the species were known to occur on their entire flyway in western Europe (5000-12 000 birds regularly). As the reasons for this concentration were poorly understood, this formed the start of a study on the feeding ecology of this fish-eating bird.

Smew ate almost exclusively small fish, 95% ($N = 19\,528$) of all prey identified consisting of fish between 4-9 cm. Gullet analyses of 236 Smew, freshly obtained after having drowned in fishing gear while foraging, showed the importance of a single prey species, Smelt *Osmerus eperlanus* (92% based on numbers, 80% on mass). Beside, Smew showed a positive selection for (also pelagic) Perch and Pikeperch and avoided the bottom-dwelling Ruffe and the spiny Three- and Ten-spined Stickleback. Roach was neither preferred nor avoided. Smew took more small individuals than could be expected from the abundance of the different cohorts (Smelt, Perch, Ruffe and Roach).

By a description of the foraging track of the birds and records of fish density over the water column it could be shown that Smew abundance was related to a certain combination of water transparency and fish density, the ducks avoiding both the lowest and the highest light intensities (Fig. 8) as well as the lowest fish densities.

Smew always fished in flocks. Only if total numbers present were below 250 birds no social fishing was observed. Birds in larger flocks were more successful in prey capture, as indicated by content of gullet of birds caught in fish nets during foraging.

It is concluded that by attending a communal roost and by foraging in dense flocks, Smew are able to exploit fish densities that would be out of reach for solitary operating predators. Yet, the entire harvest the birds made out of the total stock available to them was less than 0.25% of the Smelt that were within reach in that part of the water column under exploitation by the flock. This stresses the marginal gain rate of the birds in this turbid environment, which is not likely to have an impact on the fish stock at all. The other way around, however, the fact that Smew are susceptible to changes in a food supply which may seem superfluous at first sight, corroborates the special status of the species in Europe, which only harbours a few suitable wintering places.

Introduction

The aggregation of birds in groups, in roosts, breeding colonies or while actually foraging, is a widely occurring phenomenon. Several factors have been suggested for the explanation of this phenomenon, such as: (1) clumped food resources attracting birds from over a wide area, (2) safety against predators, (3) pooling of relevant information on spatial variations in food availability, (4) co-operative feeding on a mobile prey, enhancing food availability for each individual flock member (*e.g.* Ward & Zahavi 1973, Krebs 1974, Pöysä 1987, Kersten *et al.* 1991). These explanations are not mutually exclusive and thus flocking behaviour may have evolved as a consequence of any combination of the factors mentioned. Though aware of the possibility that flock formation may only be the consequence of the clumping of food resources or a means to reduce individual predation risk, in this paper we are looking for field evidence for the possible contributions of the two food-related factors to flock formation in wintering fish-eating Smew *Mergus albellus*.

In temperate climatic zones gregarious behaviour is particularly common outside the breeding season. Many birds then abandon their breeding territories, which are no longer able to sustain their food needs, and have to look for alternative areas to spend the winter. Since these areas are often less well-known to the birds and, in general, food resources become scarcer during the winter season, the predictability of daily feeding success for any individual bird lessens considerably at this time of year. It is therefore that the theory of bird aggregations serving as an up-to-date information pool on the best feeding sites (Ward & Zahavi 1973) is such an appealing one. The need for well updated information on spatial variations in food distribution would seem to be particularly great in birds depending on food resources that are highly unpredictable with respect to abundance, distribution and attainability.

Piscivorous bird species foraging on large stretches of open water are among the most obvious examples of birds that consistently face uncertainties as to where to find their prey, how much of it will be available and which percentage of the available stock will actually be detectable and, subsequently, catchable. Fish are highly mobile prey items, that occur in temporally and spatially varying distributions over all three dimensions as a function of *e.g.* season, time of day, water temperature, light conditions and characteristics of aquatic sediments (*cf.* Chapters 15-17, Wiersma *et al.* in prep., Piersma *et al.* 1988, Van Eerden *et al.* 1993). Each (combination) of these factors may in its turn influence both the fish's own prey distribution and their ability to avoid predation. Particularly some small-sized pelagic fish species most vulnerable to (avian) predation feed on zooplankton, which is detected by eye (*e.g.* Blaxter 1966). Therefore, these fish can only forage when underwater light conditions exceed a certain minimum level (*e.g.* Blaxter 1966, Bohl 1980), but in the meantime they also have to avoid the clearest waters where they are easily detected by their predators (both birds and predatory fish; *e.g.* Piersma *et al.* 1988). This rather structural unpredictability of fish attainability may in fact be one of the most prominent reasons for many fish eating bird species to breed in colonies, and associate in flocks, where relevant information can be obtained from other flock members on at least a daily basis (Ward & Zahavi 1973, Krebs 1974). By living in colonies or joining in night roosts at least once a day, each individual flock member may take advantage of the pooled information on food availability over a much larger surface area than by operating strictly on its own. An example of this mechanism was shown by Van Eerden & Voslamber (1995) for flock feeding Cormorants *Phalacrocorax carbo* in the breeding season. The foraging range these birds may cover, while commuting between the colony and the (single) feeding site, was supposed to be strongly dependent upon colony size: the larger the colony, the longer the chain of commuting flocks within sight distance of each other. This directly implies that larger assemblies of birds can explore more terrain, even on occasions when the entire flock forages at the same site.

Apart from roosting or breeding together in flocks, many piscivorous birds even forage in flocks. This has been described for wading birds (herons and spoonbills; Krebs 1974, Hafner *et al.* 1982, Cezilly *et al.* 1990, Kersten *et al.* 1991), for plunge-diving seabirds (gannets, boobies, gulls, terns, etc.; Leopold & Platteeuw 1987) and for swimming and/or surface-diving birds (*e.g.* penguins, cormorants, pelicans and mergansers; Bartholomew 1942, White 1957, Huntingdon & Roberts 1959, Des Lauriers & Brattstrom 1965, Källander *et al.* 1970, Whitfield & Blaber 1978, Beintema 1980, Wilson 1985, Van Eerden & Voslamber 1995). In many occasions this so-called "social fishing" may merely be caused by a casual coincidence of circumstances causing fish to concentrate in harvestable densities in a relatively small and accessible patch within the range of a colony or roost. In a number of well-studied cases, individual intake rates of flock members in these circumstances were shown to be higher than among birds fishing individually (*e.g.* Krebs 1974, Hafner *et al.* 1982). This sort of events has been described including estimates of prey densities for flocks of feeding seabirds, fishing on small pelagic fish driven to the surface by large predatory fish or by cetaceans (Au & Pitman 1986, 1988) and for Little Egrets *Egretta garzetta* feeding in flocks on near-surface concentrations of small fish in open patches of water during periods of low oxygen contents (Kersten *et al.* 1991). Concentrations of fishing Goosanders *Mergus merganser* have been shown to attract conspecifics looking for a site to feed. This attraction grew stronger as the fishing flocks became larger (Wood 1985a, b, Wood & Hand 1985), which suggests a flock size dependent harvesting rate. Nonetheless, individual food intake could not be shown to increase with the flock size in these instances, possibly because of unnaturally high densities of recently stocked salmonids.

In some instances, authors have suggested that the technique of social fishing in itself may be one of the factors inducing fish to concentrate in easily harvestable densities. Circumstantial evidence for this positive effect on intake rates of individual flock members by co-operative social fishing has been accumulated for White Pelicans *Pelecanus onocrotalus* (Whitfield & Blaber 1978) as well as for Cormorants (Van Eerden & Voslamber 1995). Generally, however, neither estimates nor indications of individual intake rate are available.

It may be clear that tests as to whether (either or both) the pooled information on food availability in flocks and a general increase of individual food intake due to co-operative feeding techniques can actually contribute to flock formation in the field are difficult to undertake and therefore scarce. In most winters the southern fringe of the Dutch freshwater lake IJsselmeer is visited by up to a few thousand Smew, which generally make use of one single night roost (Fig. 1) and are often seen foraging in flocks of varying sizes in the adjacent open water areas (Källander *et al.* 1970, Beintema 1980). Aerial surveys over the entire lake system show that, under ice-free conditions, virtually all Smew concentrate close to the coast and well within the reach of the night roost. Together with the fact that most birds exclusively live on one single prey species (0+ Smelt *Osmerus eperlanus*), this situation provided excellent conditions for simultaneously taking record of bird behaviour in relation to fish abundance.

This paper provides evidence for the hypotheses that: (1) the regular aggregation of all wintering Smew of the area in a central roost enabled them to explore the entire area within their flying range and find the most profitable feeding site and (2) the habit of fishing in flocks may under certain circumstances facilitate individual intake rates.

Methods

Study area

The Dutch lake IJsselmeer area (Fig. 1) is a former estuary closed off from the sea in 1932, and currently consists of two large freshwater components: lake IJsselmeer in the north (*c.* 125 000 ha) and lake Markermeer in the south (*c.* 70 000 ha). The water system is fed by the river IJssel, a branch of the river Rhine, and thus both lakes are eutrophic and relatively turbid. Average water depths are about 5 m in the north and some 3-4 m in the south. In the north most of the soil consists of sand, while in the southern part mostly clayish sediments have been deposited. Clay soils in the north are restricted to the bottoms of some former tidal gullies and of former sandpits, because of their greater depths.

Long-term censuses and detailed observations

From 1980 onwards, monthly aerial surveys of water birds have been carried out in both lakes, using a

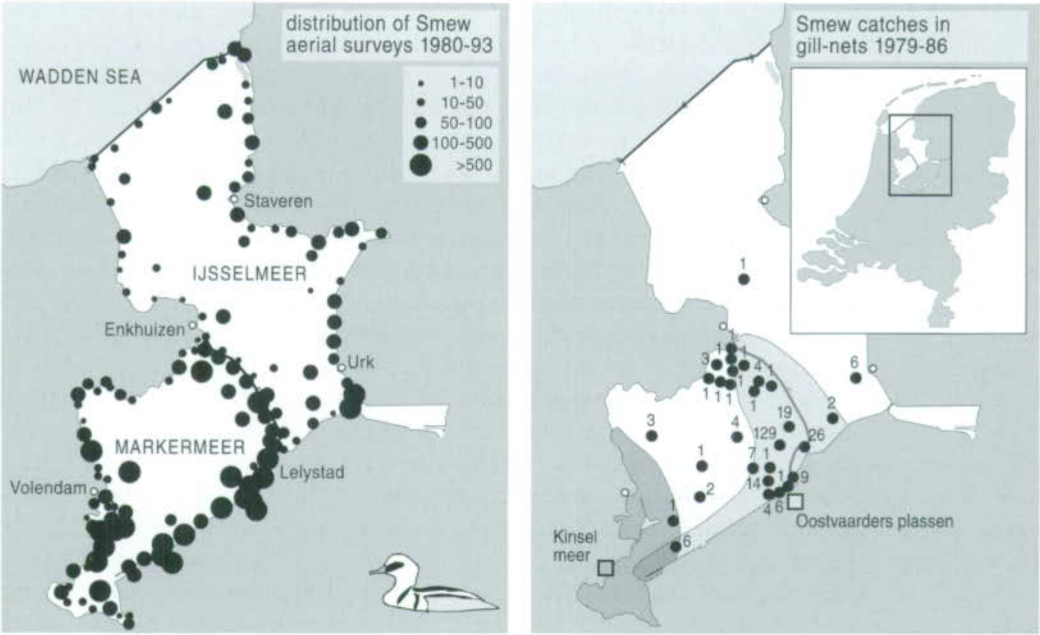

Figure 1. Location of study area in lake IJsselmeer area within the Netherlands; distribution of Smew based on maximum numbers during aerial counts and gill-net catches. Main roosts and foraging areas covered from each roost have also been indicated. The more widespread distribution as derived from aerial counts results from periods of frost, when ice-holes determine the foraging possibilies.

high-winged Cessna 172 aeroplane. During each count, which lasted 5-6 h, the entire shoreline (including adjacent inland waters) was covered while the open water was sampled by flying regularly spaced-out loops at a fixed height (150 m) and a constant speed (145 km h^{-1}). Along the shorelines all water birds were identified and counted by one observer, while during the loops only the birds within a fixed angle were noted. For this paper the results for Smew have been used for the period 1980-1993, merely to establish their preferred sites within the entire lake IJsselmeer region.

Throughout the years several roost sites of Smew have been localised along the southern fringe of the lake IJsselmeer area (Fig. 1). Only two of them can be considered to be main roosts which habitually hold up to a few thousand individuals (often comprising the entire wintering population of the moment): Oostvaardersplassen and Kinselmeer. Birds roosting at Oostvaardersplassen cover foraging areas in the southern and eastern parts of lake Markermeer (and sometimes in southern lake IJsselmeer), while birds roosting at Kinselmeer forage in the south-western and western parts of lake Markermeer (Fig. 1). In 1987/88 (a mild winter), seven systematic surveys of roosting Smew were carried out at these two sites as well as on two of the secondary roosts (Gouwzee and Lelystad-Haven). During these surveys five observers were posted at different sites from about 1.5 hours before sunset until a quarter of an hour after. All Smew entering the roost sites were counted and, if possible, the entire roosting flock was also checked regularly.

During one winter (1987/88) frequent surveys for foraging Smew were carried out along the southern fringe of the lake IJsselmeer area, where the birds usually concentrate in the period that the lake remains ice-free (Fig. 1). As a rule these surveys were carried out once a week, but in the proximity of the fish sampling dates this frequency was stepped up to twice a week. The water surface was scanned with the naked eye, while slowly driving by car along the dikes. Every 2 km a stop was made, during which an additional binocular scan took place. When visibility was lower than 2 km, more stops were made to ensure that no birds were being missed. During these censuses each flock was registered separately in order to analyse gregariousness of the Smew present. Birds were counted while at surface; when very actively hunting, counting was postponed until the ducks were in a more quiet phase. Very often the most accurate counts of large flocks were attained when the birds went aloft flying.

Finally, daily activity patterns of flocks of Smew were registered throughout the period of daylight by keeping a constant watch during four days in January and February 1988. During these observations more detailed information on feeding habits was collected as well, such as swimming speed, diving frequency and searching path. Flock position (location and area covered) was recorded using a military range-finder (Barr & Stroud 12 MK VII, type FT37). This also enabled us to draw conclusions about bird density while foraging up to a distance of 1.5 km from the shore.

Fish availability, prey choice and food selection

During the period of the detailed surveys, monthly fish samplings were executed over the same area. Concurrently, data were collected on water transparency, as this was judged to be a potential key factor in the detectability of the fish. Fish densities were estimated along 22 fixed transects in the same area each month from November until March. Most of these transects were sampled by means of echo sound recordings (Lowrance type fish-finder), enabling us to estimate vertical as well as horizontal distribution patterns (see also Chapter 15, Piersma *et al.* 1988). In order to estimate real fish densities from echo sound recordings, some of the transects were trawled simultaneously with a 7 m beam trawl, with which surface as well as bottom hauls were carried out over the same distance as the echo sound recordings. This way it proved to be possible to estimate both species composition and fish density in terms of individuals per volume unit. The number of fish per m^3 (FD) could be calculated from the number of echoes per m^3 (E) according to the equation:

$$\mathrm{FD} = 2.714\mathrm{E}^{0.712} \; (R^2 = 0.74, N = 16, P < 0.05).$$

Species were sorted out and weighed, either as a whole or as subsamples. Length frequency distributions of all fish species caught were also determined in order to estimate biomass by means of specific exponential regression equations of fish mass on fish length (Doornbos 1980, Platteeuw 1985).

Availability of fish was approximated by determining the available biomass for different zones of underwater light climate. Based on the measurements of transparency in cm Secchi, the depths at which light intensity reaches 1% and 0.1% are calculated by the formula $l = l_0 \times e^{-rd}$, in which l is light intensity at depth d, l_0 is light intensity at the surface (set at 100%) and r is the coefficient of extinction (Bohl 1980). For the calculation of r it was assumed that at a depth of 2.5 times the measured value of transparency in cm Secchi, light intensity was 1% of the surface light (Van Eerden & Voslamber 1995). Thus, three water layers were distinguished, *e.g.* the "clear" layer (1-100% of surface light), the "crepuscular" layer (0.1-1% of surface light) and the "dark" layer (< 0.1% of surface light).

Gullet analysis of Smew that had accidentally drowned in gill-nets provided information on prey choice and size of prey consumed. Birds were collected daily from fishermen all around lake IJsselmeer (Fig. 1) and were stored in freezers (-20 °C) before dissection. For diet analysis we used both direct measurements of fresh fish from the oesophagus and indirect measurements of otoliths from stomach contents. In order to overcome problems with wear of otoliths, we had to correct reconstructed fish length from otoliths by comparing species specific length frequencies from gullet and stomach contents (Feltham 1990, Zijlstra & Van Eerden 1995). Oesophagus filling was determined

Table 1. Percentage of Smew numbers counted at the two main roosts of Oostvaardersplassen and Kinselmeer or at secondary roosts during seven complete roost surveys in the winter of 1987/88.

	Oostvaardersplassen	Kinselmeer	other	*N*
8 December	92.3	0	7.7	3431
23 December	64.4	33.7	1.9	3960
6 January	4.8	0	95.2	21
21 January	67.6	30.9	1.5	1545
3 February	92.7	0	7.3	1486
15 February	43.6	29.7	26.7	1925
1 March	89.3	0	10.7	56
total	72.7	19.2	8.1	12424

by identifying and measuring all fish items in the oesophagi and subsequent back calculation of their summed fresh mass and energy content (regression equations by Doornbos 1979, 1980, Platteeuw 1985). Cumulative fish mass in the oesophagus was used as a measure of foraging success, as birds which are caught while foraging are to be expected being halfway their foraging bout. All birds obtained at the same date, at the same site and by the same fisherman were assumed to belong to the same flock.

Results

Choice of fishing site

The distribution of Smew within lake IJsselmeer, based on monthly aerial surveys from 1980 through 1993 as well as on localities where individual birds got entangled in gill-nets in 1979-1986 (Fig. 1), clearly shows that the birds concentrate in the southern and south-western parts of the area (*e.g.* lake Markermeer). This coincides with the proximity of rather protected and quiet stretches of water inshore, such as Oostvaardersplassen nature reserve and the small lake Kinselmeer, possibly the most appropriate sites for night roosts (*e.g.* Beintema 1979, 1980). The average feeding zone that is covered from each roost shows little overlap. Also in the winter of 1987/88 the main roost was most of the time in Oostvaardersplassen, where generally well over 60% of all Smew censused were found (Table 1). The second most important roost at Kinselmeer was in use in four out of seven cases, then holding about 30% of the wintering population at that particular moment. Other secondary roosts generally harboured less than 30% of the Smew present, except in early January when heavy south-westerly winds had reduced the total number of birds down to a mere 21 individuals (Table 1). Except for early January, therefore, the vast majority of wintering Smew in 1987/88 foraged in the same area as was found during the long-term census (Fig. 1). Birds can occur outside the main area at times of frost, when ice holes dictate the feeding possibilities; this explains the difference in distribution as shown by aerial counts over many years and the pattern derived from catches by fishermen and counts during relatively mild weather.

Even within the Smew survey area, which was chosen to cover the entire range of the lake IJsselmeer area within reach of the main roost at Oostvaardersplassen, the birds did not spread out evenly while foraging during the day. In fact, four distinct areas could be distinguished throughout the season: the eastern and the southern part of lake Markermeer, the rather protected harbour of Lelystad-

Large aggregation of Smew *Mergus albellus*, Lake Markermeer, January 1982. Birds from the scattered groups move to join the flock in front of the picture. Note still water conditions that often occur prior to freezing.

Haven and the south-eastern part of lake IJsselmeer (Fig. 1). These foraging sites were normally within 5-10 km, and never further than 15 km from the roost.

Immediately after arrival in early December, most birds were found in the eastern and southern parts of lake Markermeer (Fig. 2). From 20 December onwards, however, numbers decreased and eastern lake Markermeer was completely abandoned. This coincided with an abrupt change in weather: a north-easterly anticyclone in the first half of December with cold weather was followed by a period of severe south-westerly gales. This caused large scale re-suspension of silt in the eastern parts of lake Markermeer and a corresponding lowering of the underwater visibility there. Up until the end of January, the main concentrations within the survey area occurred in southern lake Markermeer and at Lelystad-Haven. The roost counts indicated that in early January the alternative feeding sites in the western and south-western parts of lake Markermeer have been in use for at least a short while. This part of the lake is less affected by diminishing visibility during south-westerly and westerly winds than the preferred sites in eastern lake Markermeer (see Van Eerden & Voslamber 1995). While numbers in the survey area gradually increased again by the end of January and in February, virtually all birds were seen at Lelystad-Haven during the entire latter month and in early March (Fig. 2). The south-eastern part of lake IJsselmeer was never visited by significant numbers of Smew, nor was the rest of the area.

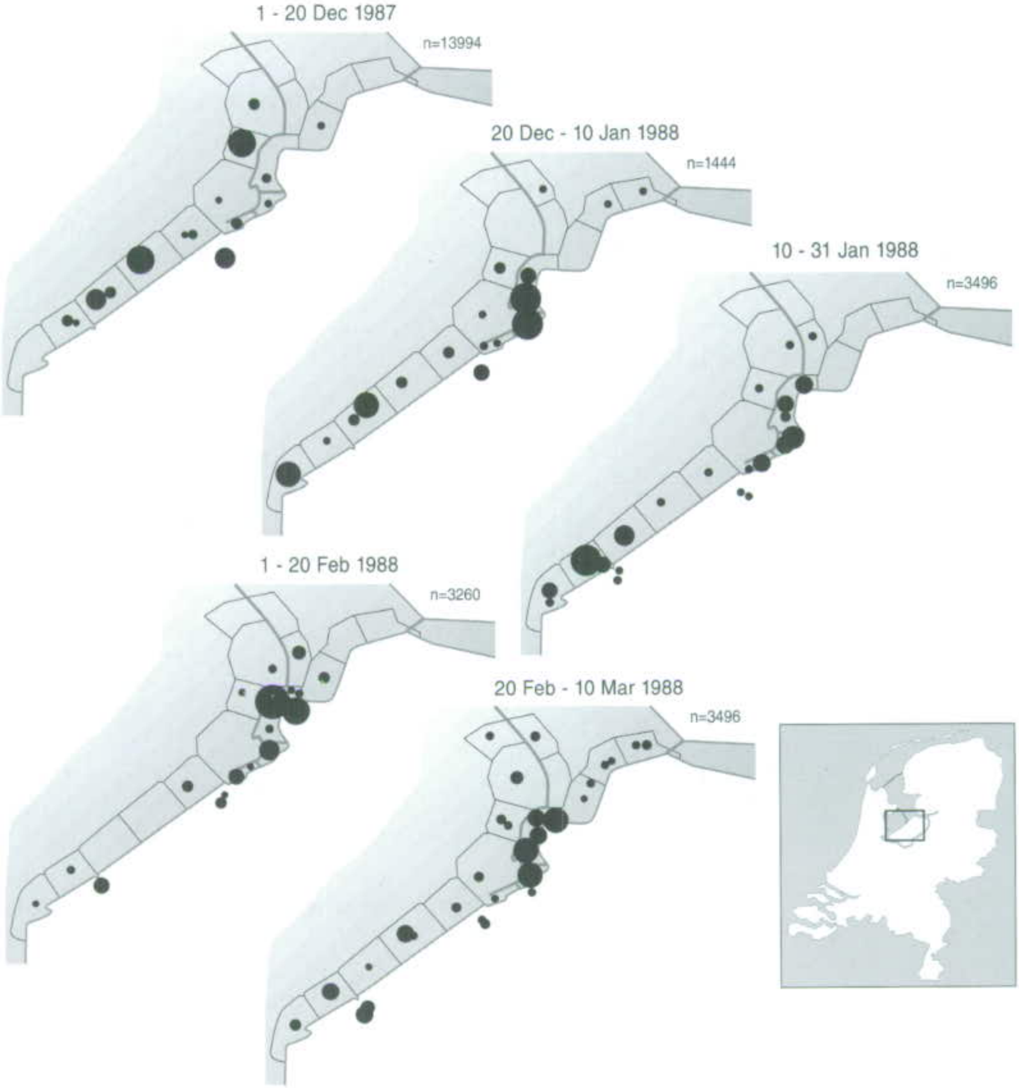

Figure 2. Distribution of Smew within the study area throughout 1987/88; size of dots provides an indication to the proportion of the cumulative number of birds counted at the different sites. Flocks plotted inland occurred on marskes and canals.

Flocking behaviour

Smew were, as a rule, very gregarious in the study area. Whenever more than 250 birds were present during a survey, the vast majority of them was found in flocks of over 200 individuals (Fig. 3). Greater numbers of birds present resulted in even larger flock sizes (of up to over a 1000 birds), but there was no tendency to expand flock size in proportion to the increase in numbers present. When the numbers present were smaller than 250 birds, flock sizes were, of course, lower and the tendency for individual birds to join in proportionately large flocks was distinctly less marked (Fig. 3). When less than 50 birds were present, even none of them were found in flocks of more than 10 birds. From this pattern of flock-

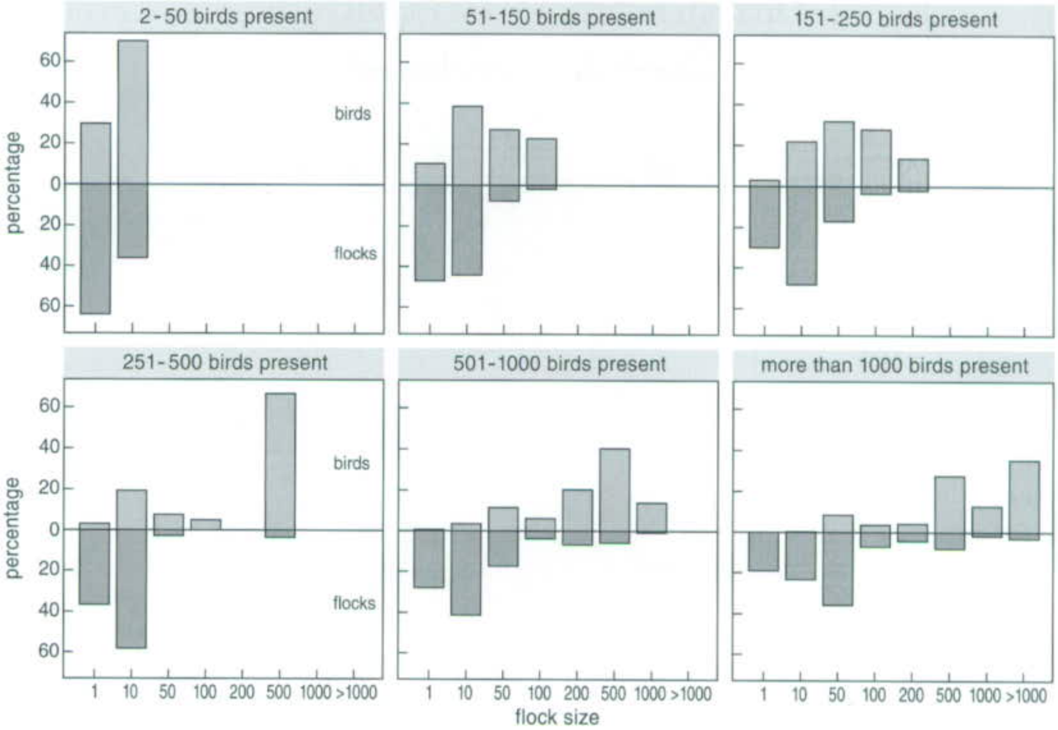

Figure 3. Frequency distribution of numbers of birds in flocks and flock sizes for different numbers of Smew present, along the same survey transect in the eastern part of lake Markermeer.

ing, it may be deduced that Smew are especially inclined to form relatively large flocks when the numbers present permit them to join together in groups of at least 200 individuals. Flocks of 500-1000 or even more than 1000 birds were, however, generally avoided. In other years, when total numbers were between 6000-12000 Smew, foraging did take place in flocks of 1500-1800 birds.

Foraging behaviour

The roost at Oostvaardersplassen was generally left between sunrise and an hour afterwards. Continuous observations throughout the day on 12 January 1988 showed that Smew spent about seven hours at the foraging sites on the lake before returning to the roost. Most of this time was actually spent foraging (75.1%, 5.3 h). Foraging activity did not show distinct peaks at any particular time of the day, periods of active fishing being regularly interspersed with periods of resting (23.4% of the time). The remaining 1.5% of the time spent at the lake was dedicated to flying movements from patch to patch or induced by disturbances by ships. An actively foraging flock of Smew was found to spend 67.7% of its time actually diving, while just a mere 32.3% was spent at the water surface. Smew thus devoted 3.6 h of their active day to diving. Although we did not succeed in following the flocks continuously on other days, we conclude from partial observations that foraging Smew spend on average between 3.5 and 4 hours per day diving.

From a total of 16 measured searching paths of fishing flocks, with 179 "checkpoints", on four days in January and February 1988, a mean overall rate of transport was calculated of 0.65 m s^{-1}

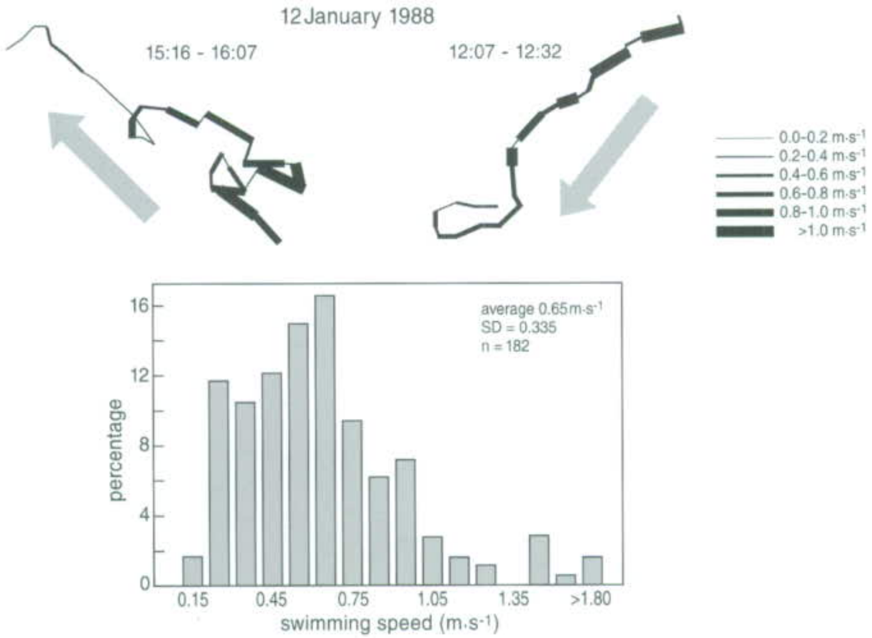

Figure 4. Two examples of Smew searching paths and frequency distribution of surface swimming speeds in foraging flocks, based on 179 'checkpoints' from 16 searching paths in January and February 1988.

($SD = 0.335$, $N = 179$). This speed for the entire flock ranged from 0.12 to 2.38 m s^{-1} and fluctuated widely over consecutive stretches (Fig. 4). The general pattern was that periods of high swimming speeds preceded rapid changes of direction and "loops" (Fig. 4). This suggests that during periods of maximum swimming speed the fish are driven together by the flock, while subsequent harvesting of the exhausted fish takes place while swimming more quietly and erratically.

Flock size (X) was related to the width of the stretch covered, approximated as

$$Y_{\mathrm{stretch}} = 0.2 + 0.1\ X_{\mathrm{flocksize}}$$

with stretch width in m. Assumptions for this approximation were that the average width of a fishing flock, expressed in bird widths, was about twice the size of the flock, that an individual bird width amounted to 20 cm and that each bird could look (and search) under water over a distance of about 10 cm in both directions. The length of the active day at the feeding grounds lasted 5.25 h on average which, in combination with the average speed of the flock of 0.65 m s^{-1}, equals about 19 km of foraging track covered in one dimension. The surface area of water searched daily (A_{searched}) by a flock of X Smew can thus be estimated as 19 000 x ($0.2 + 0.1\ X_{\mathrm{flocksize}}$) m^2.

Underwater swimming speed could not be measured directly. Nonetheless, since an average dive of a flock fishing Smew lasted for about 10 s and the maximum swimming speed of a flock along the surface could easily reach 1.75 m s^{-1}, some estimates of maximum underwater swimming speed could be made under various assumptions on diving depth. Throughout the entire winter the "clear" water layer ranged on average until a depth of 1 m, the "crepuscular" layer from 1 to 1.5 m and the "dark" layer from 1.5 m to the bottom at about 4 m. Assuming a more or less "triangular" trace of a Smew dive, three possibilities are considered (Fig. 5). A bird may dive towards the bottom and back, it may dive to

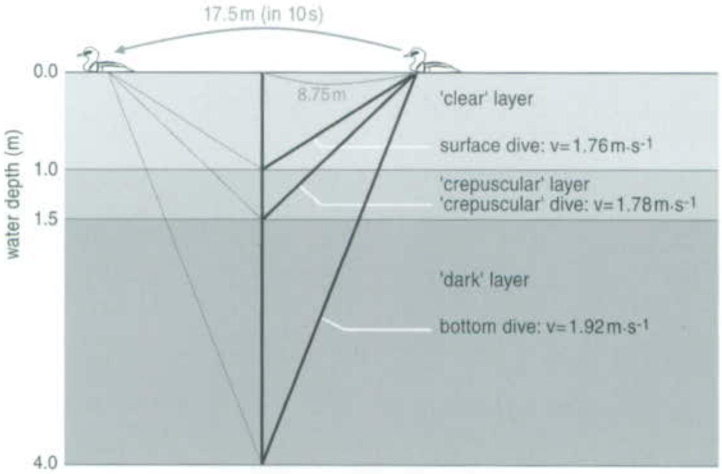

Figure 5. Schematic derivation of average underwater swimming speed of a flock foraging Smew at a measured surface swimming speed of 1.75 m s^{-1} under three assumptions of diving depth.

Table 2. Total numbers and estimated biomass of fish species caught during five sampling dates along the southern fringe of the lake IJsselmeer area, the Netherlands, in 1987/88. For the most common species, fish length has been indicated separately for surface and bottom trawls.

Species	Fish stock				Fish length (mm ± SE_x)		
	number	%	biomass (g)	%	surface	bottom	*P*
Smelt *Osmerus eperlanus*	73 099	85.7	123 604	27	67.9 (0.15)	69.6 (0.20)	NS
Ruffe *Gymnocephalus cernuus*	9 380	11.0	55 038	12.0	77.0 (1.66)	75.3 (0.26)	NS
Three-spined Stickleback *Gasterosteus aculeatus*	1 052	1.2	1 250	0.3	55.2 (0.36)	52.4 (4.6)	NS
Perch *Perca fluviatilis*	955	1.1	41 165	9.0	134.2 (0.70)	134.4 (1.64)	NS
Roach *Rutilus rutilus*	472	0.6	19 710	4.3	62.6 (5.72)	106.8 (3.24)	<0.001
Bream *Abramis brama*	196	0.2	206 210	45.0			
Pikeperch *Stizostedion lucioperca*	87	0.1	10 040	2.2			
Eel *Anguilla anguilla*	9	0.0	820	0.2			
Ide *Leuciscus idus*	6	0.0	35	0.01			
Ten-spined Stickleback *Pungitius pungitius*	6	0.0	-	-			

the limit of the "crepuscular" layer and back and it may limit its diving effort to the "clear" layer. A flock moving at 1.75 m s^{-1} along the water surface will cover 17.5 m during the 10 s of an average dive, so a bottom diver will move below the surface at an average speed of 1.92 m s^{-1}, a "crepuscular" diver will do so at 1.78 m s^{-1} and a surface diver at 1.76 m s^{-1}.

Fish community

In winter, Smelt was by far the most numerous fish species throughout the study area, ranging from 70-75% by number in southern lake Markermeer and IJsselmeer to well over 90% in eastern lake Markermeer and Lelystad-Haven, the overall proportion being *c.* 85% (Table 2). On the basis of biomass, Smelt only came second (27%) after Bream *Abramis brama* (45%), in which individual fish are much larger and heavier (Table 2).

Within the group of potential prey for Smew (< 12 cm), no difference existed in fish lengths between bottom and surface trawls for Smelt, Ruffe *Gymnocephalus cernuus*, Perch *Perca fluviatilis* and Three-spined Stickleback *Gasterosteus aculeatus* (Table 2).

Fish densities (predominantly Smelt) also showed some marked seasonal fluctuations over the different areas (Fig. 6). In the southern part of lake Markermeer the highest densities (up to 2.5 fish individuals per m^3) were found at the end of November, just before the arrival of the Smew, and in March, when the birds started to leave again for their breeding areas. From December through February average fish density here ranged between 0.4 and 1.5 individuals per m^3. In eastern lake Markermeer mean fish densities were similar to the densities in the south throughout the winter, but lacked the marked peaks. At Lelystad-Haven a marked increase in fish density took place during the winter: first in the south-west and later in the north-east, suggesting a migration of fish (mainly Smelt) from lake Markermeer to lake IJsselmeer (sluices partially open in winter). This impression is corroborated by a noticeable increase in fish density at lake IJsselmeer, north of the sluices by late February and March. However, densities in the latter area remained as a rule below the level of 1.0 fish per m^3. Based on the proportion of Smelt, length frequency distribution and the relationship between length and fresh mass, Smelt densities were estimated in kg ha^{-1} for all sampling sites for every month between November 1987 and March 1988.

Diet, prey size selection and flock effect

Six fish species were taken by Smew of which Smelt constituted 92.4% (numbers) and 80.4% (mass).

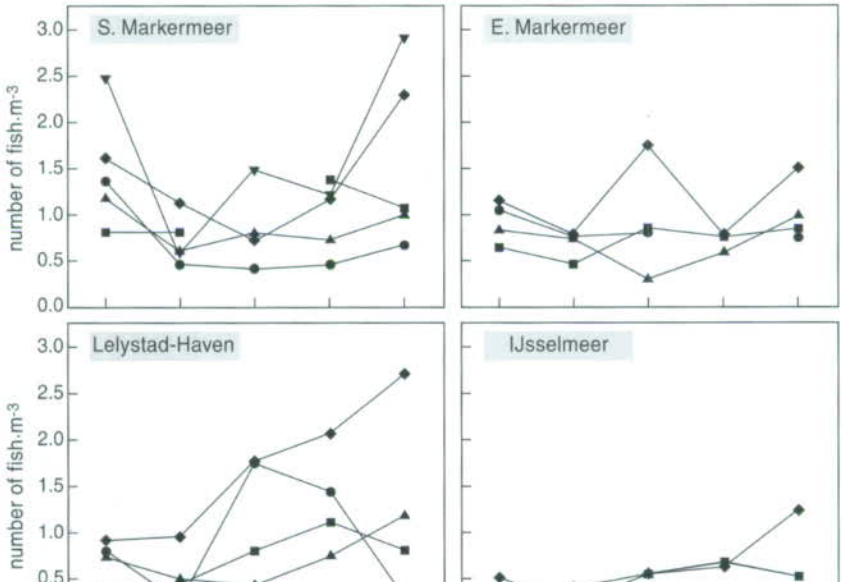

Figure 6. Fluctuations in fish density (70-90% Smelt *Osmerus eperlanus*) in four parts of the study area. Fish density was assessed in fixed transects by sonar recording.

Table 3. Diet of Smew based on the analysis of 236 gullet and stomach contents. Total number of identified fishes was 2 014 (oesophagus) and 17 513 (stomach). Fish size reconstructed from otoliths from stomach contents was corrected for wear (see Methods). Ivlev's E (range -1 +1) was calculated to assess selectivity of prey choice.

Fish species	numbers			mass		
	% on offer	% taken	Ivlev E	% on offer	% taken	Ivlev E
Osmerus eperlanus	86.8	92.4	0.30	68.1	80.4	0.32
Gymnocephalus cernuus	10.9	4.4	-0.45	27.3	10.2	-0.54
Gasterosteus aculeatus	1.2	0.1	-0.85	0.7	0	-1.00
Perca fluviatilis	0.5	2.3	0.65	3	8.1	0.48
Rutilus rutilus	0.4	0.8	0.34	0.7	0.8	0.07
Stizostedion lucioperca	0.07	0.2	0.48	0.1	0.5	0.67
Leuciscus idus	0.007	0	-1.00	0.02	0	-1.00
Pungitius pungitius	0.007	0	1.00	0.0006	0	-1.00

Next in importance were Ruffe (4.4% and 10.2%), Perch (2.3% and 8.1%). Roach *Rutilus rutilus* and Pikeperch *Stizostedion lucioperca* accounted for less than 1% of the Smew's diet, while only two Three-spined Sticklebacks were found out of 19 527 identified prey items. Related to fish abundance, taking all fish from the trawl surveys of 12 cm and less as potential prey, Ivlev's selection index E was calculated according to formula $E = (r - p) / (r + p) - 2rp$, with r and p the fractions in diet and fish on offer respectively (Jacobs 1974). Smew showed a preference for the pelagic species Pikeperch, Perch and Smelt. The demersal Ruffe was negatively selected just as the spiny sticklebacks.

Except for Roach (peak in January), Ruffe, Perch and Pikeperch were taken more frequently in March, at the end of the winter season ($\chi^2 = 1497.7$, 43.7 and 840.0 respectively, df = 2, $P < 0.005$), while Ruffe was caught relatively more frequently in lake IJsselmeer (11% of prey items *vs.* 3.6 % in lake Markermeer, $N = 17\ 133$). Compared to females, males ate more prey other than Smelt (9.5%, $N = 10\ 362$ in males *vs.* 5.7%, $N = 6894$ in females), while no difference existed between the first-winter and older birds (8.3%, $N = 4970$ in first-winter and 7.8%, $N = 12\ 286$ in older birds).

About 95% of the prey caught by Smew ranged between 4 and 9 cm. In relation to the frequency of sizes on offer, Smew caught on average smaller fish than available (Fig. 7). It is interesting to note that this also holds for comparisons within the same year class.

The question of how individual Smew could take advantage of foraging in dense flocks could not be answered by direct observation. Instead we used the filling of the gullet (fresh mass of fish only) in relation to the number of birds caught simultaneously in one net. After $\log(N + 1)$ transformation of the strongly negatively skewed data a multiple regression analysis was performed. In this analysis other variables were also included which could affect prey uptake. When selecting only birds with fish in their oesophagus, *i.e.* the successful birds at the time of catch, four variables: SEX (standardised Beta -0.19), YEAR (-0.14), DEPTH (-0.095) and FLOCK (+0.109) explained most of the variance (adjusted $R^2 = 0.049$, $F_{4,166} = 3.175$, $P = 0.015$). However, only one variable, SEX, was statistically significant ($t = -2.477$, $P = 0.014$) on its own and corrected for all other effects accounted for most of the effect (adj. $R^2 = 0.029$). If the zero birds are included, a better fit of the model is obtained (adjusted $R^2 = 0.095$, $F_{4,213} = 6.716$, $P < 0.001$). FLOCK (+3.49), SEX (-0.116), TOTLENG (-0.107) and YEAR (-0.103) formed the best combination. Interestingly, however, only FLOCK proved to be statistically significant in its own, accounting for most of the explained variance ($R^2 = 0.084$, $F_{1,216} = 20.827$, $P < 0.001$). Birds joining larger flocks thus had accumulated more prey than those from smaller flocks,

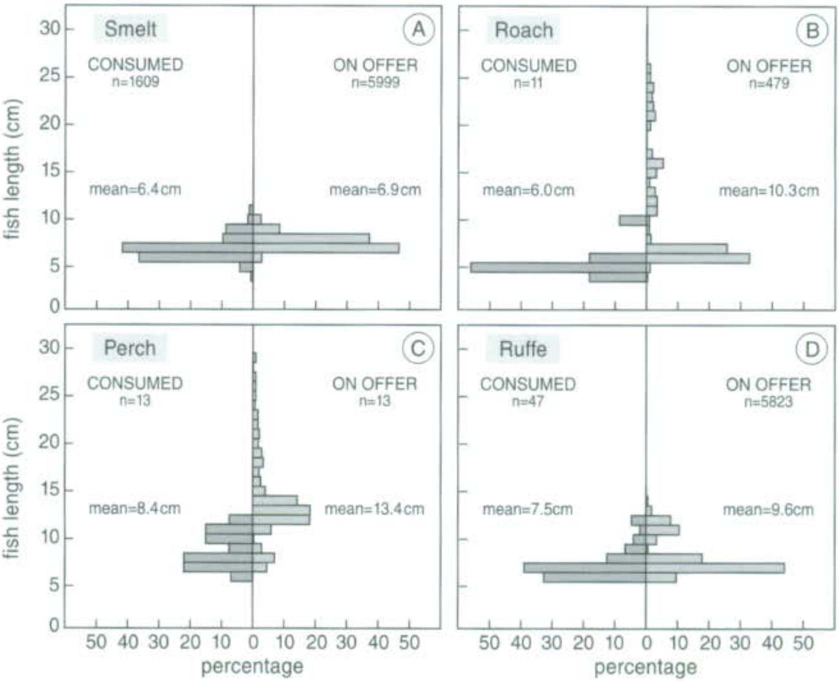

Figure 7. Size selection among Smew: comparison of fish length distributions among fresh fish from oesophagi of drowned Smew and fresh fish caught in winter 1987/88 for Smelt *Osmerus eperlanus*, Roach *Rutilus rutilus*, Perch *Perca fluviatilis* and Ruffe *Gymnocephalus cernuus*.

whereas males tended to be more successful than females. Bird age, structural size and fat load had no effect on the oesophagus filling.

Fish attainability and distribution of Smew

During the winter a distinct positive relationship was found between the estimated Smelt density (in kg ha^{-1}) at any particular sampling site and the mean number of Smew days spent in its immediate vicinity in the period following the sampling (Fig. 8). Although this tendency to visit the areas with the highest Smelt densities was observed throughout the winter, the correlation generally accounted for 18-37% of the explained variance and was virtually absent between December and January (R^2 = 0.025) when bird numbers reached a minimum.

Although important, overall Smelt density is not the only factor which determines foraging site selection in Smew. Beside sheer abundance of a prey, its actual availability to a predator is also influenced by its detectability. Smew, being visual hunters, are supposed to be hampered by the rapid changes in water transparency that may occur in lake Markermeer as a result of silt re-suspension from the bottom by wind-induced wave activity (Van Duin 1992). This may quickly change the foraging conditions at different localities within the study area, and the birds are likely to shift foraging sites accordingly. Moreover, the vertical distribution of the planktivorous Smelt is also likely to be influenced by water transparency, with the fish tending to avoid the higher water layers when transparency is high (*cf.* Bohl 1980).

For the most important three months of Smew presence (December 1987-February 1988) the vari-

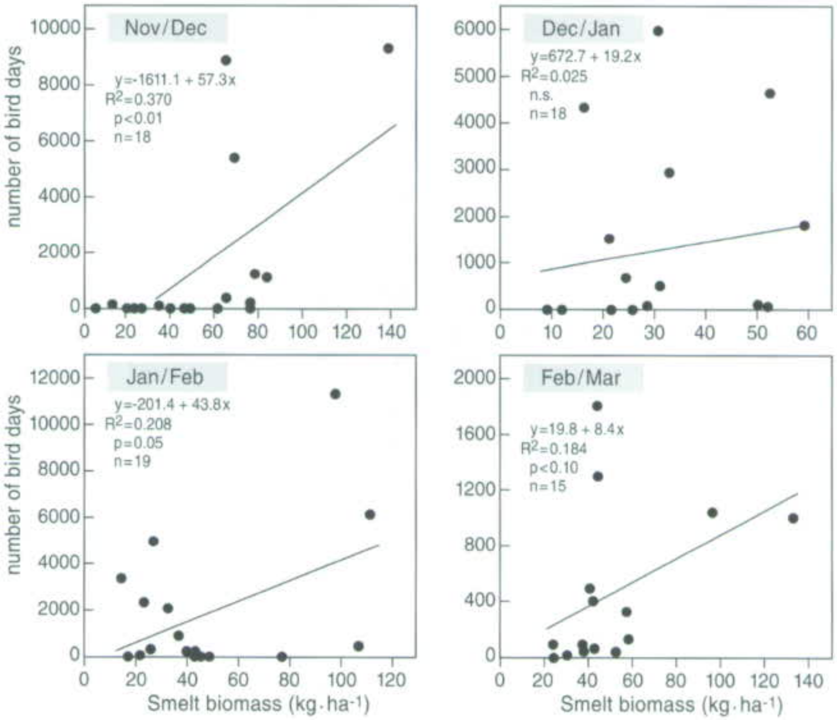

Figure 8. Relationships between Smelt density (kg ha^{-1}) estimated during fish sampling and Smew days following each fish sampling.

ations within the study area of vertical distribution of echoes indicating fish presence are shown in connection to these three water layers in Figure 9. In the same figure the number of Smew days spent at the same patches and in the same periods is also depicted. In southern as well as in eastern lake Markermeer and at Lelystad-Haven, marked decreases in Smew exploitation of patches coincided with decreasing light intensities, while fish densities near the surface remained more or less constant. However, a period of relatively clear water, but low fish density near the surface in southern lake Markermeer in February, did not attract any Smew and neither did the invariably clear waters of lake IJsselmeer, even when fish densities near the surface were comparatively high (*e.g.* in January and March). Note the spatial differences but also the erratic pattern of prey abundance with respect to underwater light climate.

We used multiple regression to determine the set of variables which contributed most significantly to Smew numbers. Using the method of backward deletion of terms, we entered site, date and fish density. The latter was computed as the total fish density and the fish density within different levels of underwater light intensity (total, 1% and 0.1% light levels). The model that best explained Smew abundance, included fish density within the light and crepuscular zone (1% light of surface), (*Attfish*, N m^{-3}). Including area and date did not contribute significantly, and Smew density (Y) could be expressed as $Y = 0.00133 \times Attfish$. This model, including underwater light intensity in relation to Smelt density, showed a better fit than was achieved when the overall Smelt density was used (adjusted $R^2 = 0.74$, $F_{1,58} = 168.9$, $P < 0.001$).

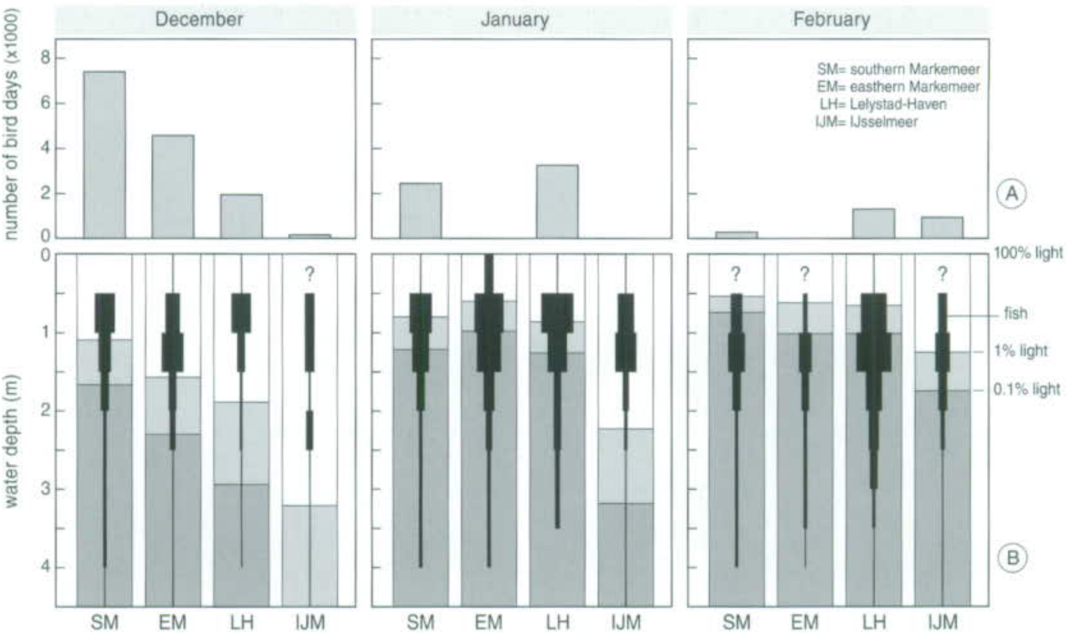

Figure 9. Variations in the vertical distribution of fish and number of Smew days in relation to water transparency, separately for three months during the winter 1987/88. Note the deterioration of underwater visibility from December to February and the response in bird numbers, as well as the site selection in relation to the availability of Smelt.

Thus, Smew abundance was related to a certain combination of water transparency and fish density: the ducks avoided the lowest and the highest light intensities (Fig. 9) as well as the lowest fish densities (*cf.* Fig. 8).

Discussion

Flock foraging and food finding

Throughout the years, most Smew wintering in the Dutch lake IJsselmeer area are consistently found along the southern fringe of the area, generally preferring the eastern and southern parts of the southernmost of the two lakes (lake Markermeer). Within this reduced range two different foraging areas corresponding to two main roost sites can be distinguished. By far the most important one of these roosts, which generally holds 60-90% of all Smew present, is situated at Oostvaardersplassen, the other one at the small lake Kinselmeer farther to the south-west (Fig. 1). Both roosts consist of shallow water surrounded by Reed beds *Phragmites australis*. When ice conditions delimit use of these areas, Smew roost in ice-holes and along dikes close ashore. When not completely frozen, Smew keep to the eastern part of lake Markermeer. We therefore do not consider the presence of a suitable roost the ultimate factor to determine Smew distribution on the scale of the lake.

From the roost at Oostvaardersplassen, feeding areas (mostly within a range of 10 km) in the eastern and southern parts of lake Markermeer are covered as are the harbours of Lelystad-Haven (Fig. 1), while from Kinselmeer the western and south-western fringes of lake Markermeer are visited. The foraging areas in the eastern range seem to be the first choice areas, the areas in the west only being used when conditions in the east deteriorate because of onshore winds. On the scale of lake IJsselmeer as a whole, Smew concentrated in the area of the highest turbidity. The sandy bottoms of lake IJsselmeer are less susceptible to re-suspension because of the waves, hence the underwater visibility is higher (Van Duin 1992) at a higher average density of Smelt (Dekker 1997). Strong onshore winds indeed made the birds move away, probably because the underwater visibility became too low (Secchi depths < 20 cm).

Within the range covered from the main night roost, Smew proved to be very gregarious. Moreover, it has been shown that within reach of the roost, foraging sites are chosen on the basis of a combination of Smelt density and water transparency. Sites with very low fish densities were avoided and so were the lowest as well as the highest water transparencies. Lowest water transparencies during this present study occurred by the end of December 1987 and the first half of January 1988, when persisting south-westerly gales caused a strongly reduced underwater visibility in eastern lake Markermeer. As a response, Smew gradually moved westwards where more sheltered waters occurred, and up to 30% of all birds present temporarily shifted their night roost. However, it was observed that when total numbers present fell below 250 individuals, both attendance of the main roosts and the habit to forage in flocks decreased significantly. A logical explanation could be that whenever feeding conditions are favourable for at least a few hundred Smew, these birds tend to make use of either of the two well-known main roosts, and utilise flock formation during the day as a means to track the most favourable patches within their particular roost's range. The birds are thus able to take quick advantage of each other's assessments of foraging conditions (water transparency and Smelt density), in the same way as suggested for breeding Cormorants in the same area by Van Eerden and Voslamber (1995).

The avoidance of the clearest waters is at first glance rather surprising for a visual hunter such as Smew. However, pelagic fish such as Smelt tend to avoid the clearest waters (at least during daytime), therefore occurring closer to the bottom or sooner being inclined to seek protection in large shoals (*e.g.* Bohl 1980). It seems reasonable to assume that fish will be more easily detected when approached from below by a predator than when approached from above (*e.g.* Wilson 1985, Piersma *et al.* 1988, Van Eerden *et al.* 1988, Van Eerden & Voslamber 1995). Moreover, an approach from below carried out in a simultaneous way by a group of birds is bound to result in a concentration of fish in the more transparent upper water layer, and in reducing the possibilities of escape towards darker and safer depths (Van Eerden & Voslamber 1995). This consideration may be the crux to understand why the clearest waters are avoided by socially fishing Smew. At daytime their favourite prey will not be available in the higher water layers, where they would be too easily detectable by both avian predators and predatory fish such as large Perch or Pikeperch. Chasing the fish towards the water surface by approaching it from below becomes therefore impossible when water transparencies are high. This is supposed to be the reason for the almost complete avoidance of the western and central part of lake IJsselmeer, an area well-known for its Smelt density. In this area Goosander *Mergus merganser* is hunting in large flocks in a similar way as Smew in lake Markermeer (MRE unpublished data). Being much larger (two and a half times the size of Smew), this species can probably dive with greater ease to greater depths, which it needs to if, analogous to the Markermeer situation, Smelt is to be hunted under similar light conditions.

Flock foraging, individual yield and impact on fish population

The observations as to the choice of the fishing patch and the actual foraging habits strongly suggest that flocking behaviour, while actually foraging, is generally of advantage to the individual bird. By driving the fish together and exhausting it, each participant of a flock may get the chance to increase its foraging intake. Comparison of oesophagus filling, both in terms of fresh fish mass and energy content, among birds caught in gill-nets in varying numbers per day and site indeed suggests that the attainable fish load is higher among birds foraging in larger flocks. Nonetheless, the variation in mean oesophagus filling, though still positively related to minimum flock size of the birds drowned, was only explained for 17-18% by variations in minimum flock size. Thus, an individual bird may have better chances for filling its oesophagus in larger flocks, but the possibilities to increase the intake rate for every participant of the flock may decrease when flock sizes become larger. For Cormorants hunting in flocks for Smelt such a "within-flock" depletion was demonstrated (Van Eerden & Voslamber 1995). This phenomenon is likely to explain the apparent reluctance to join together in flocks of more than 500 birds, even when the numbers of Smew present would easily permit the formation of such flocks.

Smew were generally absent in areas with a density of Smelt less than 0.3 m^{-3}. The largest flocks were observed between densities of 0.3-0.6 fish m^{-3} with a smaller average flock size at higher densities (1-2.5 m^{-3}). Average swimming speed of Smew under water, approximated at 1.75 m s^{-1}, is enough to exhaust fish at lengths of 15 cm (Wardle 1975, 1977). Fish taken by Smew was on average 4-9 cm, so most of 0+ cohorts of the species present in the area are completely within reach of this predator. Only Pikeperch, of which the 0+ winter group exists of fish between 15-20 cm is in the upper region of reach. Smew took extremely small individuals of this species (8.5-11 cm), which is consistent with this swimming speed hypothesis. Yet it is remarkable that Smew took smaller than average sized fish of four of the commonly occurring species of the 0+ cohort (Fig. 7). As the observed difference is greater than the (marginal) difference in average fish size over the water column (Table 2), restricted feeding to the upper water layers cannot explain this phenomenon. Instead, lower swimming speed of the smaller fish may be directly responsible for this. During the winter, the average length of Smelt, Ruffe, Perch and Pikeperch caught increased somewhat, which, because of the absence of growth of the fish, is in line with the aforementioned. Fish-eating Great Crested Grebes *Podiceps cristatus* in the same area also took larger prey as winter proceeded (see Chapter 17). This was explained by lower water temperatures, which caused larger individual fish to get within reach of this predator.

Of the amount of 320 tonnes of fresh mass of Smelt estimated to be present at the onset of the winter of 1987/88, the visiting Smew, with an average individual body mass of 730 g, consumed between 70 and 95 tonnes. For this calculation it is assumed that DEE (Daily Energy Expenditure) equals 3-4 times BMR (Basal Metabolic Rate; *cf.* Platteeuw *et al.* 1992, De Leeuw 1997), BMR is 307.6 $M^{0.734}$ in which M is body mass in kg (Aschoff & Pohl 1970), assimilation efficiency is 0.80 for fish-eating birds (Castro *et al.* 1988) and caloric value of Smelt amounts to 5 kJ g^{-1} fresh mass (Platteeuw 1985). Individual daily food needs are then 182-242 g of fresh mass. Thus, during the winter concerned here Smew only consumed between 2.2 and 2.9% of the available fresh mass of their preferred prey species, a proportion so low that the effect of this predation on the fish population is likely to have been negligible.

We have also tried to assess possible effects of foraging flocks of Smew on local food availability. It has been shown that Smew seem able to actively fish the upper 1.5 m of the water layer, *i.e.* the light layer and the crepuscular layer. In a single day a flock of X birds is thus able to cover a volume of $A_{searched} \times 1.5 = [19\,000 \times (0.20 + 0.1\ X)] \times 1.5\ m^3$ of water. Within this searching space the same flock of X birds will need to catch on average a daily Smelt biomass of 182 to 242 times X grams of fresh fish in order to provide for the daily food needs of each flock member. The Smelt densities measured in the field at different sites and times were combined with the number of Smew present at the same site and time. The total amount of fish theoretically detectable was estimated as the product of Smelt density at a certain site and a certain time with the amount of fish they could have found within the search area covered that day. Thus, it was found that in most of the cases only between 0.10 and 0.50% of the Smelt present inside the search area was needed to cover all the birds' daily needs. This seems to imply that (1) at any time the available local food stocks do not suffer from depletion by Smew predation and (2) all sites hold more than sufficient food supply at any time to support the number of birds present. The first implication is likely to be true, but the second one is not, since it has been shown that the sites with the lowest fish densities are actively abandoned by the birds, indicating low profitability. This apparent discrepancy may be understood by realising that most of the fish present within the Smew's search area may either not be detectable (*e.g.* because they escape towards the dark water layer when the birds start diving) or not be harvestable (*e.g.* because they succeed in escaping the actual chase).

At this stage we cannot determine the actual lower threshold below which fishing is impossible. However, this study has clearly shown that large numbers of Smew are associated with particular fish densities in relation to underwater light climate. At first sight these densities seem extraordinarily high in comparison with the yield of the birds. In relation to the predictability of the winter haunt for several months these densities have to be reconsidered; a 0.005 fraction of captured Smelt over a winter season of 100 days means a capture rate of every second Smelt in the area of surveillance. The fact that the limited area in use by the Smew is part of a much wider system means a further spread of risk of depletion to occur. The turbid Markermeer system thus provides an attractive food source for this highly versatile group of birds. Further knowledge about the fish densities at the few other sites where large numbers turn up in Europe is urgently needed to tackle the question of how these birds divide themselves over the wintering areas. In IJsselmeer/Markermeer we observed a poor relationship with Smelt densities but this may also be judged in relation of the European alternatives which are in the Baltic (Švazas *et al.* 1994) and German Bight.

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Smelt *Osmerus eperlanus*, when abundant in large numbers consistute the most important prey item for fish-eating water birds at lake IJsselmeer and lake Markermeer.