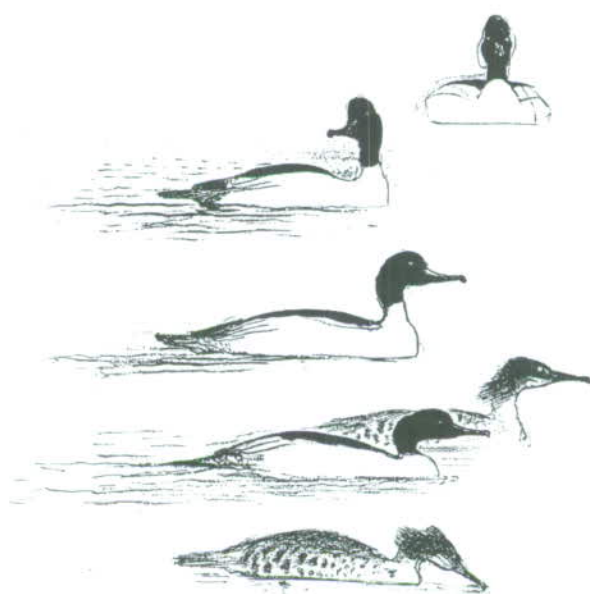


Chapter 19

Sex-dependent differences in exploitation of fish stocks in Red-breasted Mergansers *Mergus serrator* utilising a two-prey system in winter

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Sex-dependent differences in exploitation of fish stocks in Red-breasted Mergansers *Mergus serrator* utilising a two-prey system in winter

This study focuses upon habitat use and prey exploitation by a fish-eating predator, the Red-breasted Merganser *Mergus serrator*, while wintering at lake IJsselmeer, the Netherlands. The bird's diet, based on identification of fresh fish by gullet and stomach analysis of 1609 birds collected, was dominated mainly by two species, Smelt *Osmerus eperlanus* and Eel *Anguilla anguilla*, constituting 95% of all prey identified ($N = 10\ 296$). The consumption of Eels hidden in the mud occurred very locally, as wintering Eels are present at relatively great depths (5-7 m) in soft substrates. Smelt was caught more pelagically and over a wider range (depth and locality) in the lake. A strong sexual dimorphism in body dimensions was apparent, associated with a different prey choice. The larger male mergansers hunted both Smelt and Eel, the females, however, mainly caught Smelt. A clear prey switch towards Eel occurred during stormy weather, which induced low visibility under water hampering in its turn hunting for Smelt. Females were less successful in catching Eel which required more and deeper dives. The prey switch had different consequences for the estimated daily energy expenditure. In males the increase in DEE was estimated conservatively from being c. $3.1\text{--}3.4 \times$ Basal Metabolic Rate (BMR) during Smelt hunting to $5.2\text{--}6.4 \times$ BMR during Eel hunting. It was concluded that the larger males (both adult and first-winter birds) possess a greater propulsion power than females, enabling them to perform deeper dives at a relatively lower cost. The (rare) Eel hunting by females (both adult and juveniles) was calculated to raise the daily energy expenditure to $6.1\text{--}7.9 \times$ BMR in this group, which is higher than can be sustained on a daily level. Associated with these high levels of energy expenditure, adult females lost body mass at the time of the prey switch. On the other hand, in adult males especially the structurally larger birds and birds with a better condition were involved in the diet switch towards Eel.

Habitat segregation within this species of fish-eating birds thus leads to a reduced intraspecific competition and, as a result, to a strongly skewed sex ratio if conditions only permit hunting for Eel (harsh weather, possibly also low Smelt stocks).

Introduction

Wintering Eels *Anguilla anguilla* are, at least in temperate climates, known to be largely inactive (Larsen 1972, Neveu 1981, Bernat *et al.* 1988) and spend most of the cold season hidden inside the sediments of their freshwater habitats (Van Dobben 1952, Lecomte-Finiger & Prodon 1979). Exploitation of Eel by piscivorous birds is generally hampered by this combination of caching and lack of activity, as has been demonstrated in the case of the Cormorant *Phalacrocorax carbo*, a notoriously visual hunter, in the Netherlands (Van Dobben 1952). His study showed Eel to be particularly vulnerable to Cormorant predation on warm and/or sunny days in late spring and summer, when individual fishes stick their heads out of the mud in which they are hidden. Since the vast majority of piscivorous birds

are generally assumed to locate their prey by sight (Eriksson 1985), the secretive habits of Eel, especially in winter when low water temperatures set limits to muscular activity, would seem to be a rather effective way of avoiding avian predation.

Detailed research on foraging habits of both Goosander *Mergus merganser* and Red-breasted Merganser *M. serrator* in Sweden, however, has indicated that these two piscivorous duck species may employ two rather different foraging tactics (Sjöberg 1985, 1988). First, the detection of prey from the surface followed by subsequent pursuit diving (e.g. Salyer & Lagler 1940, White 1957, Mills 1962) and, second, the locating of prey while actually under water by probing more or less at random inside cavities or other possible hiding places for fish. The first tactic is employed when good underwater light conditions prevail, and the detection of fish by sight is relatively straightforward. Red-breasted Mergansers have been reported repeatedly as predators of salmonid fish in a clear water, riverine habitat (White 1939, Sjöberg 1985, Feltham 1990). In worse light conditions (i.e. in more turbid waters or while foraging at night) the second tactic would be more rewarding (Sjöberg 1985). Thus, both species of merganser may actually adopt active tactile searching for prey species hidden along the bottom, when ambient conditions favour such a hunting strategy. Given this adaptation of mergansers, which seems to be particularly well-developed among Red-breasted Mergansers (Sjöberg 1988), even wintering Eel, being almost completely buried in the soil, would become vulnerable to bird predation. Indeed, Madsen (1957) found an important proportion of Eel in the stomachs of Goosanders, caught between October and February in Danish waters, hereby demonstrating that the supposed winter inactivity does not completely preclude predation during this season. Feltham (1990) showed that Red-breasted Mergansers took Eel as the most important alternative prey after salmonids (6% based on mass during spring).

In the relatively turbid water of lake IJsselmeer, the Netherlands, both species of merganser are known to winter in important numbers (e.g. Van Eerden & Bij de Vaate 1984). While Goosanders seem to concentrate their fishing efforts primarily on the pelagically living Smelt *Osmerus eperlanus*, comparable to the situation in their main alternative wintering area in the SE Baltic (Švažas *et al.* 1994), Red-breasted Mergansers in lake IJsselmeer exploit Eel as an important alternative prey beside Smelt (Van Eerden & Bij de Vaate 1984, Buijse *et al.* 1993).

As a sedentary and hidden prey, Eels in winter constitute specific challenges to the predator compared to the free swimming fish which are in a three dimensional space. This paper describes the extent and importance of Eel predation vs. other prey in winter at lake IJsselmeer. We focus on the diet of the Red-breasted Merganser, with special emphasis on the occurrence of prey-switching and sexual segregation.

Methods

From a series of seven consecutive winters (1979/80 through 1985/86), a total of 1684 Red-breasted Mergansers were collected which had accidentally drowned in gill-nets while foraging. Gill-nets are used in winter for the commercial catch of Perch *Perca fluviatilis* and Pikeperch *Stizostedion lucioperca*. For the purpose of this study a network of fishermen from various localities all around lake IJsselmeer was set up, which required daily visits to the harbours to collect the birds caught (Fig. 1). All birds were identified as to age (first-winter or adult, by inspection of plumage and gonads) and sex. Birds were labelled and stored in freezers (-20 °C) before dissection in order to examine the contents of oesophagus and proventriculus. Furthermore, many of the birds were examined in more detail describing biometrics, moult and also, for a representative sample, body reserves. The combined mass of the right breast muscles (*pectoralis* and *supracoracoideus*) was considered to be a measure of pro-

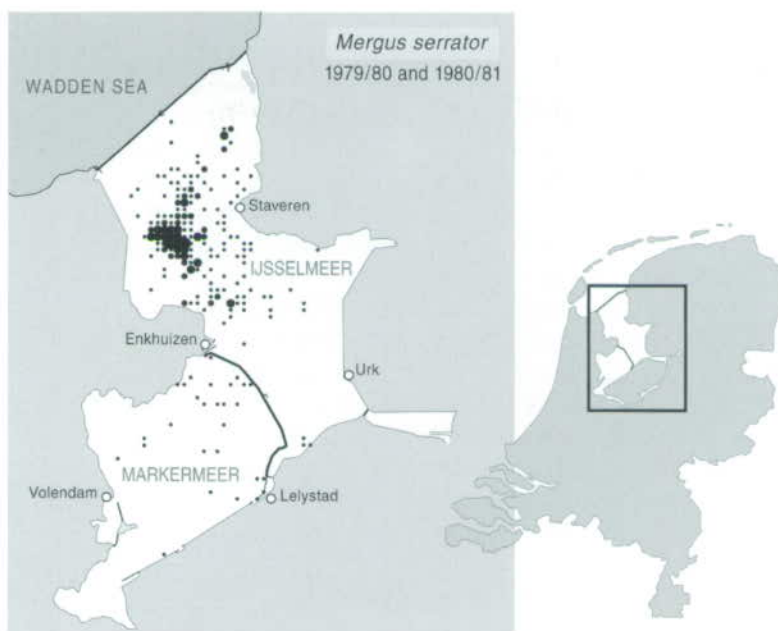


Figure 1. Location of lake IJsselmeer area within the Netherlands and distribution of Red-breasted Mergansers caught within this area. The distribution of the birds has a strong concentration in the deepest parts of the lake, where former tidal gullies occur.

tein reserves, while the amount of abdominal fat was determined (to the nearest 0.1 g) as a measure of lipid reserves. Abdominal fat mass (AF) had a linearly positive correlation to total lipid mass (TF), as determined by Soxhlet extraction with petroleum-ether according to the formula:

$$TF = 63.9 + 19.0 \times AF \quad (r = 0.821, P < 0.001).$$

Information on the exact location (nearest km) and diving depth (0.1 m) at the time of drowning was derived from the data provided by the fishermen upon request.

Food remains collected from oesophagus and proventriculus generally consisted of complete and still undigested fish. All these fishes were identified to species level and their length was measured to the nearest mm. Fresh mass was estimated by species specific regression equations obtained from samples of the same material. Smaller samples were analysed for water, protein and lipid content, as well as for caloric value. Water content was determined by comparing fresh mass to dry mass (2 days in a ventilated stove, 70 °C). Protein content was calculated as $6.25 \times \text{Kjeldahl N}$ and lipid content was determined by Soxhlet extraction with petroleum-ether. Caloric values were obtained by summation of caloric values of lipid and lipid-free dry mass, both measured by an adiabatic bomb calorimeter.

Results

Site and water depth in relation to diet

The vast majority of Red-breasted Mergansers of which the exact location of drowning was known,

were caught in the northernmost sector of lake IJsselmeer (91%, $N = 478$), north-west of the line Enkhuizen - Staveren (Fig. 1). Even within this reduced part of the study area, a concentration of birds occurred at the most central part, right inside the area of the former tidal gullies, where water depths reach 6-7 m and the bottom consists of clay. Outside these deepest parts, the water depth varies from 3 to 5 m and the bottom is mainly sandy. Except for dredging-pits, elsewhere in lake IJsselmeer water depth hardly ever surpasses 5 m and, correspondingly, sandy bottoms prevail as well. Here c. 9% of the birds were found and less than 1% were caught at lake Markermeer, to the south-west of the dike between Enkhuizen and Lelystad (Fig. 1), where water depth ranges from 3 to 4 m and a very mobile layer of silt covers the larger part of the bottom.

Diving into the clayey gullies was associated with the composition of the bird's diet, in which Eel constituted an important part (41%, $N = 10\,296$ of all individual prey items identified from 1426 birds). The highest densities of Eel hidden in the bottom are to be expected in the finest, clayey sediments (Lecomte-Finiger & Prodon 1979). Indeed, at depths of 4.5-7 m the number of Eel found per bird was much higher than in less deep water, while Smelt as most important alternative prey (53% of the prey items) was found in highest densities in birds caught at depths of 2.5-4 m (Fig. 2). Additionally Ruffe *Gymnocephalus cernuus* (2.8%), Roach *Rutilus rutilus* (1.3%) and Perch *Perca fluviatilis* (1.2%) were also identified; however, they played a role of minor importance.

Prey composition over the season and through the years

The seasonal distribution of the foraging locations and abundance of Red-breasted Mergansers showed a remarkable difference between winters, the vast majority of birds being recovered in only one season, i.e. 1980/81 (81% of all birds, $N = 1609$). Even more surprising was the striking difference in prey choice between the seasons with the largest sample sizes 1979/80 and 1980/81. Among mergansers which contained prey in the oesophagus, Eel made up 4% of the prey in 1979/80 ($N = 1770$), while in 1980/81 51% of the bird's diet ($N = 8277$) consisted of this species in all months (cf. Fig. 3). Moreover, individual success of Eel fishing was also higher in the second winter, expressed as the average number of Eel per bird with a filled oesophagus (0.66, SD 2.28 in 1979/80 vs. 3.86, SD 4.03 in 1980/81; cf. Fig. 3).

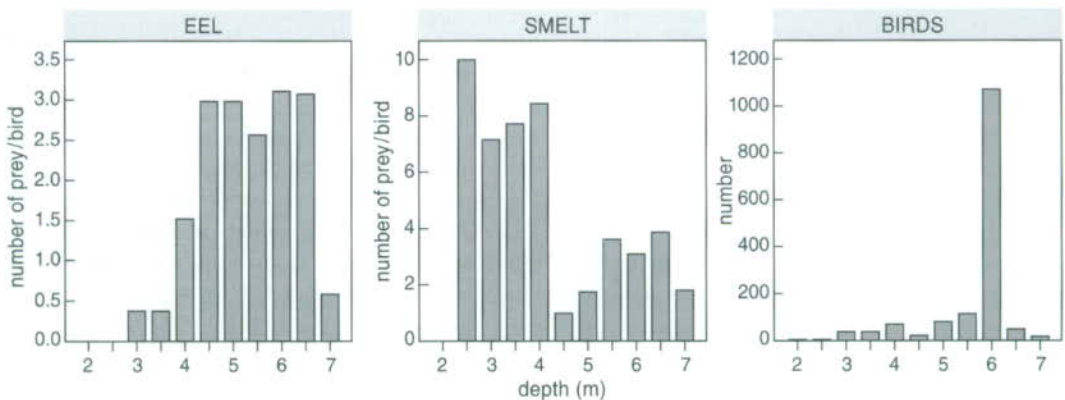


Figure 2. Average number of Eel and Smelt recorded per bird drowned at various water depths. Only gullet content has been analysed, being directly related to the place and depth at which each bird was caught. "Empty" birds are included in the calculation, using sex and depth as estimators for prey choice category. For comparison the distribution over water depths of the birds that were obtained has been given as well, showing the extreme concentration of the birds in the gullies (10-25% of catching effort by fishermen).

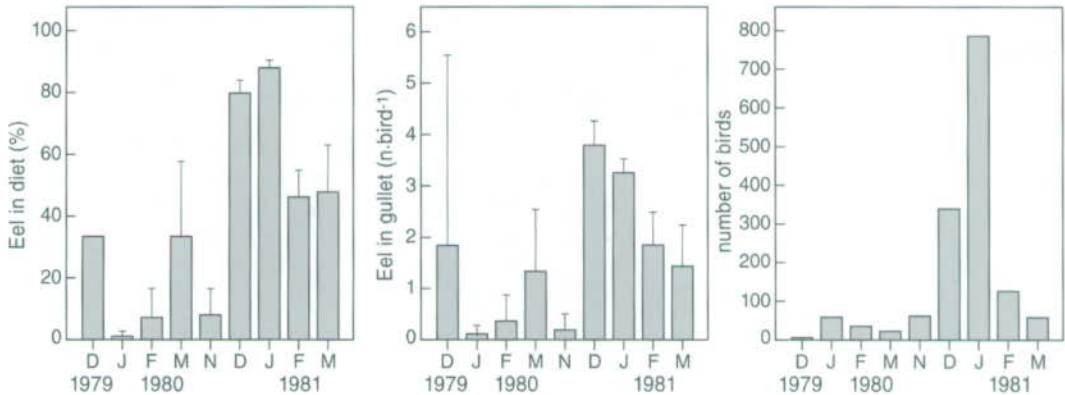


Figure 3. Seasonal occurrence of Eel (percentage and number in diet) in comparison to the number of Red-breasted Mergansers obtained. Upper 95% confidence limits have been indicated.

Most Eels were taken during mid-winter in December and January, while Smelt showed the opposite pattern with a relatively higher percentage occurrence in autumn and spring. Both time of year and sex significantly determined the bird's diet (MANOVA, $F = 9.53$, $P < 0.001$). A significant interaction between sex and month occurred ($F = 5.07$, $P = 0.025$), because females switched later and to a lesser extent to an Eel diet. The overall model gave no significant effects on Eel consumption for total body mass, mass of breast muscles, structural size and age. That Eel hunting was not only confined to one season became clear when analysing birds from other winters as well. Comparing all seasons with more than 20 birds caught, 1981/82, 1983/84 and 1986/87 showed also the importance of Eels in the diet of males (40-70% on the basis of mass), while 1985/86 was statistically significant a peak year with over 90% Eels in the diet of adult male Red-breasted Mergansers (Fisher LSD test, Wiersma 1996). Also in females the pattern is quite consistent, the percentage Smelt being rather constant over the years (50-60% based on mass). 1980/81 had relatively many Eels in the diet (45% based on mass), the other seasons showed fewer Eels (10-25%). Although significantly different among years, the diet consisted always of one of the two main prey species, Smelt or Eel.

Within the period of December 1980 to February 1981, when 1206 mergansers were collected (84% of the combined total of the first two seasons; $N = 1434$), wind direction, wind force and air temperature all significantly influenced the day-to-day occurrence of Eel among all prey items (ANOVA's, F -values 19.4, 24.2 and 7.7 respectively, $P < 0.0001$). On a daily basis, the highest incidence of Eels was found during strong winds from northerly, westerly or south-easterly direction coinciding with relatively high air temperatures. In absence of any wind no Eel was caught at all. Weather conditions thus contributed greatly to the composition of the birds' diet.

Body dimensions of predators

Differences between male and female Red-breasted Mergansers are not only expressed by plumage characteristics, but also by clear differences in structural size. These differences apply to adult as well as to first-year birds (Table 1). All sex related differences in structural size were statistically significant (t -tests, $P < 0.0001$). Moreover, first-year males were consistently smaller than adults of the same sex with respect to all measurements taken. These differences were particularly significant for total length (TL), wing length (WL) and sternum length (SL; t -test, $P < 0.0001$), but markedly less pronounced for

Table 1. Averages of structural size measurements in Red-breasted Merganser; total length (TL), wing length (WL), culmen length (CL) and sternum length (SL) of sex and age classes.

	TL (cm)		WL (mm)		CL (mm)		SL (mm)	
	male	female	male	female	male	female	male	female
adult								
mean	60.6	54.9	257.0	235.0	58.8	52.9	125.5	113.0
SD	1.3	1.4	5.3	5.5	2.3	2.0	4.0	4.3
N	874	147	878	147	854	143	237	57
first-year								
mean	59.2	53.6	244.8	226.7	58.4	52.9	123.9	111.4
SD	1.4	1.6	4.9	5.3	2.2	2.0	4.0	3.6
N	295	187	296	187	290	181	95	87

culmen length (CL; $t = -2.43$, $P < 0.015$). Within the group of females, culmen length even turned out to be not statistically different between first-year birds and adults ($t = 0.11$, $P = 0.915$), while the other measurements were (t -test, $P < 0.017$). This means that, although first-year birds are not yet fully grown, they possess a relatively long bill. In the case of females, there is even no distinction in bill size between adults and first-year birds.

As a consequence of larger body dimensions in males than in females and in adults than in first-year birds, much the same sex and age related differences are found in condition measurements, such as body mass, dry mass, abdominal fat mass and mass of the breast muscles (Table 2). All these measurements positively correlate with structural size, expressed as either $0.0001 \times TL \times WL \times SL$ in case of the first three or as $0.0001 \times SL^3$ in case of the latter (Fig. 4).

Sexual dimorphism and prey composition

The fact that gullets almost invariably contained either Eel or Smelt and seldom a mixture of both, suggests the existence of a dichotomy in prey capture techniques associated with the two habitats. Of 616 birds containing five or more prey items, 85% had either exclusively consumed Eel or had eaten no Eel at all (Fig. 5). Among the birds collected, Eel was overall the most important prey, 63% based

Table 2. Average body condition measurements of sex and age classes of Red-breasted Mergansers wintering at lake IJsselmeer: fresh body mass (FM), dry body mass (DM), abdominal fat mass (AF) and fresh mass of breast muscles (BM).

	FM (g)		DM (g)		AF (g)		BM (g)	
	male	female	male	female	male	female	male	female
adult								
mean	1485	1122	548.7	420.0	8.35	5.99	96.02	74.46
SD	116	108	77.7	87.5	4.30	3.54	7.70	6.62
N	877	146	228	50	235	55	236	56
first-year								
mean	1392	1072	499.3	398.3	8.31	7.64	90.95	71.29
SD	103	91	66.7	63.2	4.38	4.72	7.53	5.63
N	295	187	93	77	95	83	96	83

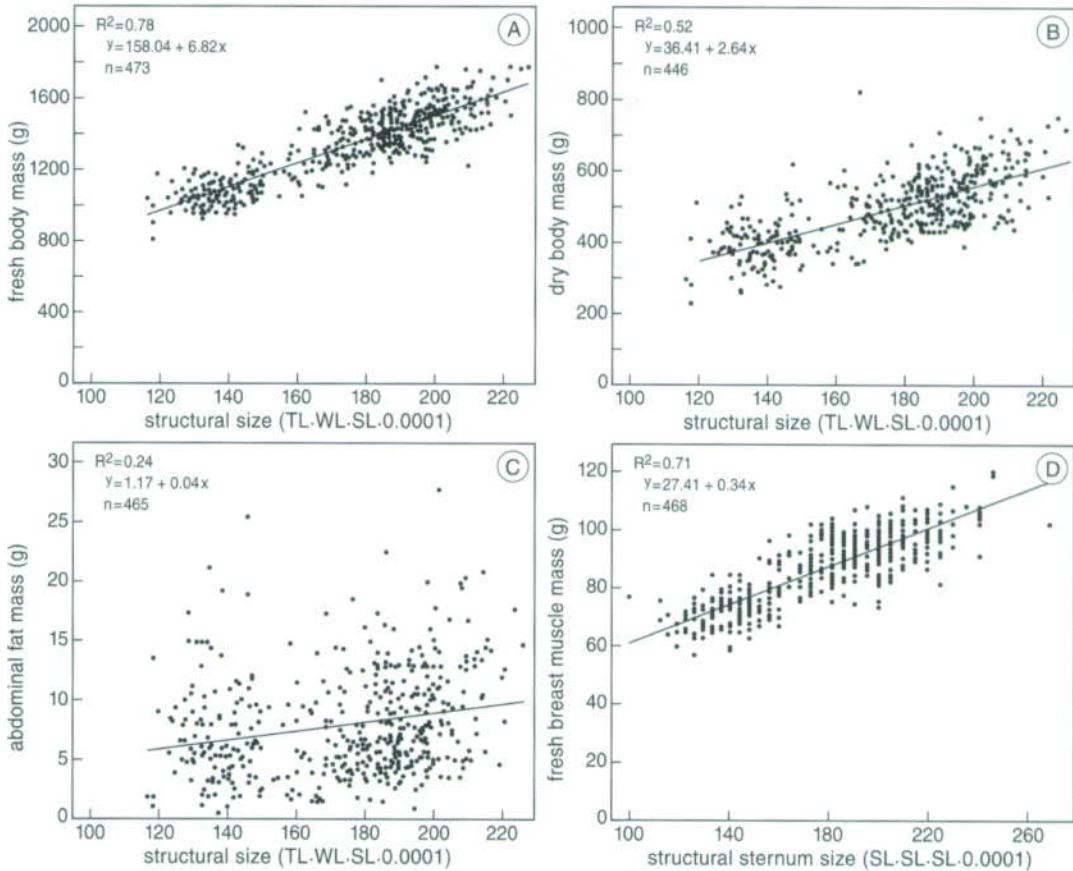


Figure 4. Linear relationships between structural size and fresh body mass, dry body mass, abdominal fat mass and fresh breast muscle mass. Structural size was expressed using combinations as total body length (TL), wing length (WL) and sternum length (SL).

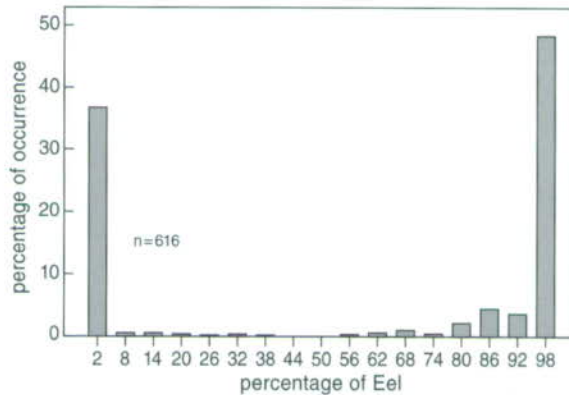


Figure 5. Frequency of the percentage of Eel among prey items in individual Red-breasted Mergansers containing five or more prey in their gullet. A clear dichotomy of either few (diet consists of Smelt) or many Eel is apparent.

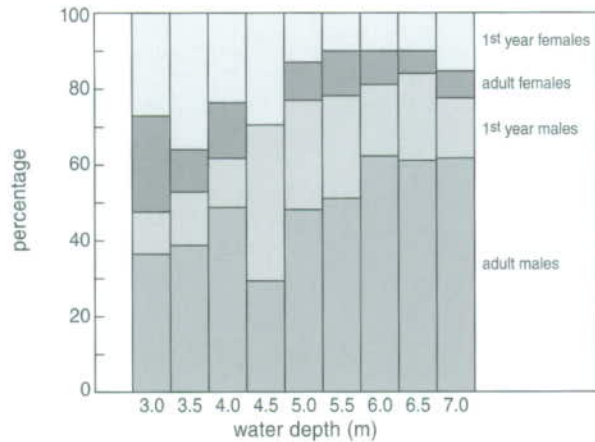


Figure 6. Sex and age composition of Red-breasted Mergansers in relation to the depth of drowning.

on mass. Second to Eel came Smelt, which constituted 31% of all prey consumed based on mass.

These findings indicate that the exploitation of hidden Eel involves a completely different fishing strategy than the pursuit of the pelagically living Smelt. Individual mergansers going for Eel have to dive to the deepest parts of the lake and search along the bottom to locate their prey by probing in the bottom, while birds hunting for Smelt visually detect and catch their prey during more superficial dives. Considering the rather different diving behaviour likely to be involved in either of these two hunting methods, we conclude that birds use different strategies of food exploitation, which seem mutually exclusive.

The fact that males are larger than females and adult birds larger than first-year individuals, may have consequences in relation to the ability to perform deeper dives. A greater proportion of males (adults as well as to a lesser extent first-year birds) was found among the birds drowned at depths of over 5 m than among the casualties from lower depths (Fig. 6). Also, if distinguished by main prey consumed, among "Eel consumers" (50% or more of the prey items belonging to this species) a higher proportion of adult males and a lower proportion of first-year females were found than among "Smelt consumers" (with less than 50% Eel; Fig. 7). The distribution of the sex and age classes over both consumer categories differed significantly from the expected distribution ($\chi^2 = 138.3$, $df = 3$, $P < 0.0001$). The sex and age composition found among birds without fresh fish in their oesophagus ("empty" birds; Fig. 7) is intermediate. Extrapolation of the prey preferences in the sex and age classes to the same classes among "empty" birds suggests that about 70% of them would have tried to catch Eel and about 30% Smelt. Among the "empty" males even up to 75-80% are likely to have been hunting for Eel, while among the "empty" females the proportion of Eel hunters would have been about 50%.

These marked differences in prey choice between the four sex and age classes suggest a relation between size and physical ability to dive towards the greatest depths for Eel. Differences in fresh body mass or measures of structural size ($0.0001 \times TL \times WL \times SL$ or $0.0001 \times SL^3$) between "Eel consumers" and "Smelt consumers" can be analysed within each of the sex and age classes as well. Among adult males, structural sternum size was significantly larger in "Eel consumers" (two-tailed $t = -3.02$, $df = 180$, $P < 0.003$) which fits the pattern, while among first-year females body mass was higher in "Smelt consumers" (two-tailed $t = 2.37$, $df = 67$, $P = 0.013$). In both of the first two winters, body mass peaked in December-January in males. In females this was only the case in 1979/1980. In 1980/1981 a

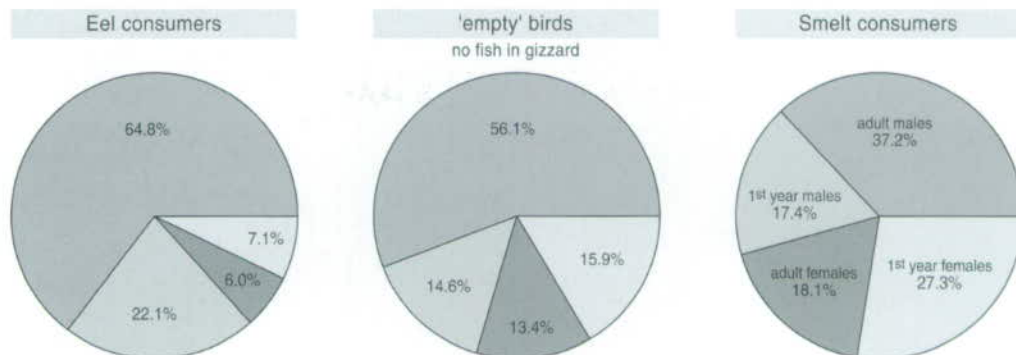


Figure 7. Sex and age composition of "Eel consumers" (50% or more Eel) and "Smelt consumers" (less than 50% Eel) as well as "empty birds" (unsuccessful at time of catch).

marked 8% drop in body mass was apparent for adult females from December (1260 g, SE 28) to January (1161 g, SE 14), coinciding with the prey switch towards Eel. Between the other categories no significant differences in body mass existed.

In order to analyse the relationship between the different variables determining structural size, body condition, diving depth and diet in more detail, a partial correlation analysis was carried out between body mass, mass of pectoral muscles, bill length and (log transformed) percentage Eel in the diet (only prey containing mergansers). For four sex and age classes separately, Pearson's r was corrected for month, water depth and structural size, all being significant terms in a multiple regression analysis with body mass as dependent variable. Concerning diet related factors, the proportion of Eel in the gullet was positively correlated with body mass in adult males ($r = 0.17$, $P = 0.024$). In adult females the relationship was not significant ($r = 0.28$, $P = 0.098$) and no relationship was apparent in juveniles. In adult males also breast muscle mass was correlated with the fraction Eel in the gullet ($r = 0.17$, $P = 0.021$). These results indicate that, at least in adult males, body condition was better in birds that performed deep dives in search for Eel.

Longer-billed birds had, corrected for structural size, a lower body mass in adult males ($r = -0.23$, $P = 0.002$ and adult females ($r = -0.39$, $P = 0.018$). This negative relationship existed also with pectoral muscle mass in juvenile males ($r = -0.31$, $P = 0.007$), adult males ($r = -0.34$, $P < 0.001$) and adult females ($r = -0.56$, $P < 0.001$). As bill length has no relationship with observed diet composition, the interpretation of these findings remains unclear.

Beside the observed tendencies for males to dive deeper and include a higher proportion of Eel in their diet, males had also caught somewhat larger individuals (Fig. 8). Both in adult and first-year birds, the average length of Eels was significantly greater in males than in females (t -test on log-transformed values, $P = 0.004$). No significant differences existed in average prey length between different age classes of the same sex.

Foraging success

Content of the gullets of both Smelt and Eel hunters was negatively skewed when considering load size per bird (Fig. 9). However, Smelt fishing mergansers contained on average four to five times as many individual fishes in the oesophagus as birds that had hunted for Eel (Table 3). This difference was highly significant in all sex and age classes (Mann-Whitney U -test, $P < 0.0001$). In spite of the higher individual prey mass and the higher energy content of Eel, the average amount of energy ingested by

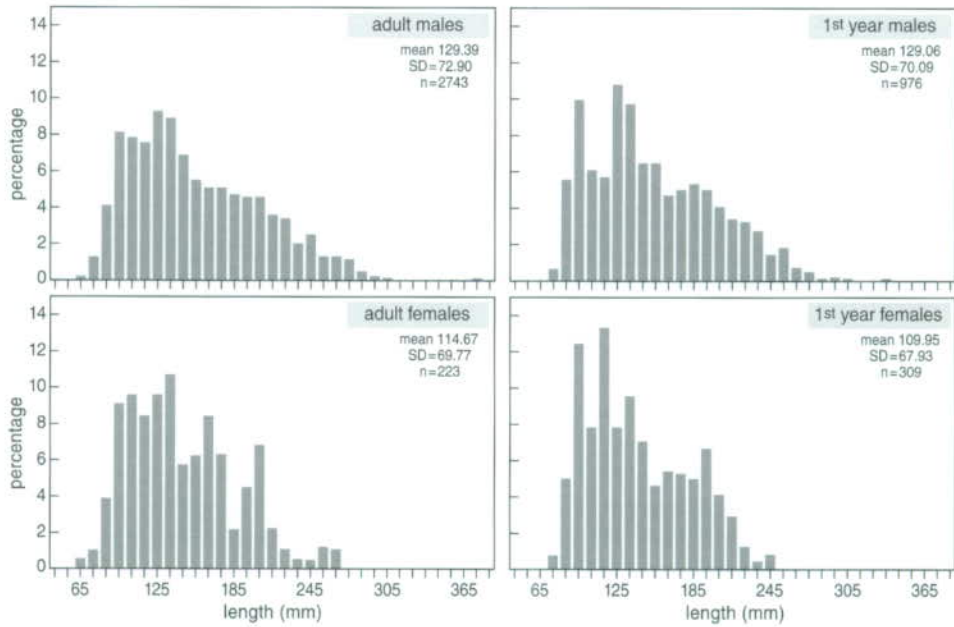


Figure 8. Length frequencies of Eel caught by different sex and age categories of Red-breasted Mergansers. Peak values in prey size taken occur for elvers which are present in the lake during their first winter.

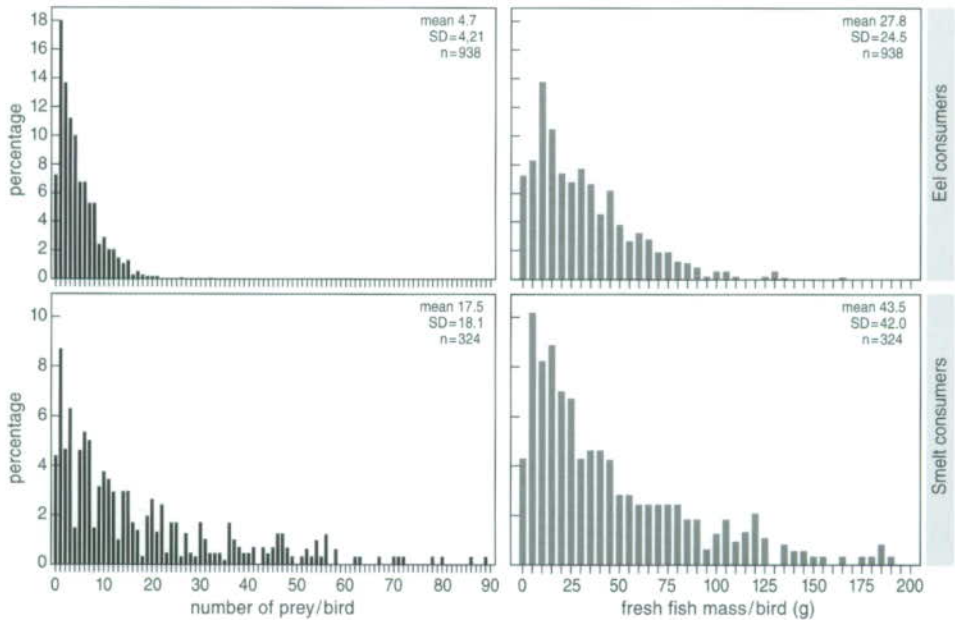


Figure 9. Negatively skewed frequency distributions of gullet content in terms of prey number and total fresh mass, apart for Eel hunting and Smelt hunting Red-breasted Mergansers.

Table 3. Fishing yields per bird of both successful and unsuccessful Red-breasted Mergansers at the time of drowning, expressed in number of prey, total prey mass (g), energy content (kJ) and energy content in multiples of corresponding Basal Metabolic Rate (BMR), calculated on the basis of individual fresh body mass according to Aschoff and Pohl (1970). The proportions of Eel and Smelt hunters among unsuccessful birds are estimated, assuming the same sex and age composition in these two categories as in successful birds.

		prey number		prey mass (g)		energy content (kJ)		multiples of BMR		N
		mean	SD	mean	SD	mean	SD	mean	SD	
adult male	'Eel'	4.7	4.1	29.1	24.6	195.3	175.4	0.47	0.42	602
	'Smelt'	17.9	18.4	45.9	41.8	234.3	213.0	0.56	0.50	125
Mann-Whitney	U		19449.5		30143.5		34482.5		34468.0	
	P		0.0000		0.0005		0.1413		0.1395	
first-y male	'Eel'	5.0	4.4	29.3	25.7	193.7	181.7	0.49	0.45	258
	'Smelt'	19.9	19.9	50.5	47.7	257.0	244.7	0.64	0.59	56
Mann-Whitney	U		2640.5		4461.0		5046.0		5004.0	
	P		0.0000		0.0156		0.2170		0.1870	
adult female	'Eel'	3.7	4.4	19.0	20.0	117.1	123.3	0.35	0.37	61
	'Smelt'	16.3	16.8	38.6	39.7	194.6	202.9	0.55	0.56	57
Mann-Whitney	U		697.0		1169.0		1307.0		1330.0	
	P		0.0000		0.0022		0.0201		0.0289	
first-y female	'Eel'	4.4	4.4	20.4	21.1	120.5	128.4	0.38	0.40	73
	'Smelt'	16.0	17.2	38.7	39.5	194.9	201.8	0.58	0.59	86
Mann-Whitney	U		1585.5		2251.5		2439.0		2489.5	
	P		0.0000		0.0022		0.0155		0.0247	
all birds	'Eel'	4.7	4.2	27.8	24.5	184.1	172.5	0.46	0.42	938
	'Smelt'	17.5	18.1	43.5	42.0	220.8	214.6	0.58	0.55	324
Mann-Whitney	U		77104.0		124710.5		141099.0		136891.5	
	P		0.0000		0.0000		0.0549		0.0077	

Eel consumers tends to be less than in Smelt consumers. The differences were, however, not significant in adult and first-year males (Mann-Whitney *U*-tests, $P = 0.14$ and $P = 0.22$ respectively), but were so in adult and first-year females (Mann-Whitney *U*-test, $P < 0.02$; Table 3). Not only does an individual Eel on average constitute a higher biomass intake than a Smelt, the nutritional value in terms of energy content is also higher in Eel (21.1 kJ g^{-1} dry mass vs. 20.3 kJ g^{-1}). This difference is particularly marked in Eels of more than 20 cm length. The protein content, however, is more or less similar for the two prey species (about 68-74% of dry mass), except for the largest Eels of over 20 cm, which contained only 46% of protein on dry mass basis. Thus, for all mergansers a switch in prey choice from Smelt to Eel will generally result in a decline of food intake in terms of number, biomass and energy content. If gullet content is expressed as fraction of (size related) BMR, Table 3 shows that when hunting for Smelt, all sex and age categories do equally well ($0.50\text{-}0.64 \times \text{BMR}$), whereas for Eel, females have lower

ratio's (0.37-0.40) than males (0.42-0.45). We used these fractions as the best estimates with respect to energy intake in relation to requirements. We will return to this point as these differences in apparent foraging success have wide implications for the energy budget of the mergansers. Surprisingly, both for Smelt as Eel, the juveniles did slightly better than the adults of the same sex (Table 3).

Discussion

Methodological rationale and sampling errors

The question could be raised how the way in which the sampled birds were collected from fishermen, might affect the conclusions. We will discuss this matter for three levels *i.e.* distribution, prey choice and foraging success.

Distribution

During the years of sampling, a lake-wide scheme was set up to collect drowned birds. Fishermen were requested to bring in all birds caught, not discriminating among species. Since many other diving birds, such as *Aythya* ducks or Smew *Mergus albellus*, which were collected simultaneously, were primarily recovered from the shallower sandy parts of lake IJsselmeer or from lake Markermeer (see Chapter 14 and 18), the apparent preference of foraging Red-breasted Mergansers for the deepest parts (Fig. 1 and 2) is not the result of biased fishery activities. This is corroborated by the finding that virtually all live Red-breasted Mergansers counted during the monthly aerial surveys (1980-1997) were seen here (MRE, unpubl. data).

Prey choice

Red-breasted Mergansers wintering in lake IJsselmeer were found to feed primarily on Smelt and Eel. Smelt is a pelagically living species, that even in winter generally inhabits the higher water layers (Beekman & Platteeuw 1994), while Eel spends the cold season buried in the bottom sediment (Van Dobben 1952, Lecomte-Finiger & Prodon 1979). Thus, the fact that individual mergansers had almost invariably eaten either Smelt or Eel was considered to indicate the existence of two completely different foraging tactics, *e.g.* relatively superficial diving and active pursuit of prey located by eye or bottom-directed diving and grabbing stationary prey located by probing in the mud. However, the gill-nets are placed stationary at the lake bottom, which may cause a selection towards deep diving birds. Mergansers that would remain in the uppermost water layers, are not sampled at all, especially not in areas of deep water. The difference in water depth at which Smelt divers and Eel divers were found (Fig. 2), is caused merely by different catching locations (gullies and lake floor). As Smelt density is also high in the upper and middle water layers of the gullies (Dekker 1997), the fact that Eel-divers rarely contained Smelt indicates the existence of a pronounced prey preference. While diving for the bottom, they have passed twice the zone in which Smelt is present, which rules out the possibility that the conclusion is caused by sampling bias.

Foraging success

We used the number of fresh fish in the oesophagus as a measure of foraging success. This is reasonable when both the probability of drowning and the number of prey taken per minute of foraging time do not systematically vary throughout a fishing bout. The amount of fish in the oesophagus at the moment of drowning is expected to show a normal distribution within Eel as well as within Smelt consumers. However, oesophagus content, both expressed in number of prey and in total prey mass, was strongly skewed negatively in both groups (Fig. 9). This suggests that either the probability of being



Male Red-breasted Merganser *Mergus serrator*, victim of gill-net fishery.

trapped in a gill-net decreases towards the end of a fishing bout and/or the intake rate of individual prey items does. If searching for prey would mean a more horizontal movement under water, then the chance of getting trapped in a fishing net depends on the phase within a fishing bout. A decrease in intake rate with foraging time could also be the combined effect of depletion of the foraging patch and satiation of the foraging bird. In spite of these effects on the frequency distribution of the oesophagus contents, it still seems appropriate to consider average oesophagus content as a relative measurement of foraging success.

Weather dependent prey detectability

The most suitable sediments for Eel to hide in are found in the former tidal gullies in the northern part of lake IJsselmeer, where water depths reach 5-7 m and the bottom is covered by clay (Lecomte-Finiger & Prodon 1979). Within lake IJsselmeer, Smelt too is more numerous in the northern part, but it is markedly less confined to the deepest gullies than Eel. The locations of recovery of most mergansers indicate a strong preference of the species for the same part of the area as fishing grounds. The choice for Smelt or Eel is likely to depend on the relative profitability of each of the alternative prey species at the moment of fishing. The profitability is a function of abundance, detectability and nutritional value of both fish species, as well as of the energetic costs of the predator involved with either of the two foraging techniques.

Smelt abundance may vary considerably over seasons, but was remarkably similar in 1979 and 1980 (Buijse 1992, Buijse & Dekker 1996). Perhaps even more important than actual abundance, the detectability of Smelt may vary greatly, even on a daily basis, according to the amount of up-welling of silt through wave activity. High winds, especially from northerly, north-westerly and south-easterly directions (cf. Fig. 1), are causing high waves over large stretches of water. The force of these waves induces the finest sediment particles to re-suspend into the water column, thereby hampering light penetration and correspondingly causing a deterioration of underwater visibility. In view of the minor differences in the census of elvers entering the IJsselmeer system in the two winters considered, the abundance of small Eel is unlikely to have differed a great deal in the first two winters considered,

while the relative abundance of the most frequent length classes (9–14 cm) was in 1979/80 even higher than in 1980/81 (Dekker 1987a, b). Therefore, the massive switch in prey choice towards Eel in the latter season from December 1980 onwards, is probably attributable to the high incidence of strong winds in both December 1980 and January 1981 and not to a greater prey abundance. The reduced immigration of elvers into lake IJsselmeer which occurred from 1982 on (Dekker 1987a, 1997) has, so far, not prevented mergansers to switch again to Eel during at least three seasons after the decline occurred (Wiersma 1996). To answer the question of existence of a possible lower threshold in elver density we should have detailed information about the actual density in the hibernating area in the deep gullies. Future work is necessary to unravel this point in more detail.

Another point that deserves attention with respect to the interpretation of the diet data is the number of mergansers that is actually present. As pointed out earlier, Red-breasted Mergansers were especially numerous in the catches during periods of windy weather. However, the number of birds that were landed by fishermen by far exceeded the estimates by the aerial counts or counts from ships (Beintema *et al.* 1980). Only a wind dependent influx of birds from the Wadden Sea to lake IJsselmeer could explain this discrepancy. Red-breasted Mergansers are common in winter on salt water habitats like the Wadden Sea (Smit & Wolff 1981). If this hypothesis is right, than Eel feeding can be regarded as the best alternative the birds have to respond to deteriorating foraging conditions of their main prey. Our study clearly shows that superficial interpretation of the data could easily lead to false conclusions, despite the large sample sizes and the consistency of the patterns. We conclude that Red-breasted Mergansers, if present at lake IJsselmeer, are essentially inclined to feed on the salmonid Smelt, if conditions of underwater visibility permit them to locate this prey. When, however, underwater visibility diminishes because of high wind-induced turbulence, only part of the birds are able to change their foraging strategy towards Eel hunting at greater depths. Probably many more birds from elsewhere join the birds already present.

Eels hidden inside the sediment are presumably located upon touch. Detectability of this prey is unlikely to be hampered by low underwater visibility and may even be enhanced somewhat by the higher water temperatures that usually coincide with mild, stormy winters. In summer, Eels were shown to be more active when strong wind or other factors increase the hydro-dynamics of their environment (Corsi & Ardizzone 1985), while winter activity seems also to be stimulated by higher air (and water) temperatures (*cf.* Bernat *et al.* 1988). Thus, the same circumstances that hamper detection and catchability of Smelt do not apply, or may be even slightly favourable, to Eel. Foraging costs remain to be explained to make a full comparison possible.

Foraging energetics and prey choice

Smelt is considered the first choice prey in the system, because foraging success was markedly lower among Eel fishing birds than among Smelt hunters. Among the mergansers with a filled oesophagus, birds without any Eels contained on average 45.29 g (SD 38.04) fresh fish mass, birds with up to 50% Eel 42.75 g (SD 33.08), birds with 50–99% Eel 40.72 g (SD 26.78) and finally birds with only Eel just a mere 28.38 g (SD 23.30). Moreover, Smelt-fishing mergansers contained on average four to five times as many individual fishes in the oesophagus than birds that had hunted for Eel (Table 3). Although mean fresh mass of an individual Eel caught was 6.0 g against a mere 2.3 g for an individual Smelt, this did not compensate for the lower energy content of the gullet of Eel eaters (Table 3). Especially females incurred a lower yield, even if corrected for body mass.

Within adult males, the largest category if body mass is concerned, feeding on Eel was associated with a higher body mass than within those hunting for Smelt. On the contrary, Eel hunting was negatively correlated with body mass in juvenile females, being the smallest size category. These observations suggest that Eel hunters, diving to depths of 5 m and more, are the heavier birds in the population.

With their lower foraging success, the females (and especially the juvenile females) are supposed to face unfavourable conditions when applying this foraging tactic.

In order to compare the profitability of both tactics, an approximation of foraging effort in relation to prey uptake is needed. In order to do so, we had to assume several parameters and to construct an energy budget based on activity-specific costs. For this, we will derive several parameters from trials with Tufted Duck *Aythya ferina* and Scaup *A. marila* in a semi-natural diving device which were conducted in order to measure the energy expenditure in these diving species during winter (De Leeuw 1996, 1997).

- *Basal Metabolic Rate* (BMR) was estimated from the allometric relationship using fresh mass of mergansers caught during the study, according to Aschoff and Pohl (1970). We used 480 kJ day^{-1} (adult male), 458 kJ day^{-1} (juvenile male), 392 kJ day^{-1} (adult female), 379 kJ day^{-1} (juvenile female).
- *Resting Metabolic Rate* (RMR) for birds resting on the water's surface was estimated using the allometric relationship derived by De Leeuw (1996). We used 11.23 J s^{-1} (adult male), 10.61 J s^{-1} (juvenile male), 8.79 J s^{-1} (adult female) and 8.44 J s^{-1} (juvenile female).
- *Foraging depth* was assumed to be constant in the two strategies, for Smelt hunters at 2 m, Eel hunters at 6 m.
- *Diving costs* were split into costs during the actual dive (descent, foraging bout and ascent) and recovery costs after the birds have surfaced. Diving costs were determined allometrically by the relationship derived by De Leeuw (1997) for birds on cold water. We used 25.3 J s^{-1} (adult male), 24.2 J s^{-1} (juvenile male), 20.7 J s^{-1} (adult female) and 20.0 J s^{-1} (juvenile female). Costs for recovery were estimated to be equal to actual diving costs during dives to 2 m and a factor 1.5 higher for dives down to 6 m water depth (De Leeuw 1997).
- *Diving time*: Based on the experiments with Tufted Ducks as mentioned before, the duration of a dive to 6 m was assumed to last twice the time needed for a dive to 2 m. No compensatory behaviour, such as the reduction of the number of dives as depth increased, as was the case in Tufted Ducks during periods of cold water (De Leeuw 1997), was assumed to occur in Red-breasted Mergansers. Extra costs for warming-up the ingested food were not taken into account either. In benthos-feeders, which may need 2000 g of fresh mussels (including shells) for a 1000 g duck (Chapter 14, De Leeuw 1997), this led to extra costs for thermoregulation and caused the behavioural adaptation of shortening the time spent diving (De Leeuw 1997).
- *Flight costs* were estimated from allometric formulae in Norberg (1990). We used 79.0 J s^{-1} (adult male), 75.0 J s^{-1} (juvenile male), 62.9 J s^{-1} (adult female) and 60.6 J s^{-1} (juvenile female).
- *Time budget* was not studied by direct observation in this species; the distance from the shore and the probable occurrence of night feeding (Eels) prevented this. Instead, we used a conservative estimate of 3-4 h of diving in Smelt hunting mergansers, which equals the 3-4 hours of diving found in Smelt hunting Smew at lake IJsselmeer (Chapter 18, Platteeuw *et al.* in prep.). Applying both ends of this range, this gave a range in estimated DEE, rather than one value. Flight was conservatively estimated at 20 minutes per day for all categories, being the same for both prey types. Red-breasted Mergansers showed no distinct roosting behaviour with associated commuting flights.
- *Foraging success* was estimated from gullet content of the drowned birds. Corrected for body mass of the predator, the ratio of Eel to Smelt was calculated for each sex and age class from data in Table 3. By this factor an estimate was obtained for the prolonged diving time necessary during Eel hunt relative to Smelt. The values used are 1.362 (adult male), 1.306 (juvenile male), 1.829 (adult female) and 1.684 (juvenile female).

Since Eel hunting invariably takes place at greater depths, it seems logic to assume that the larger body

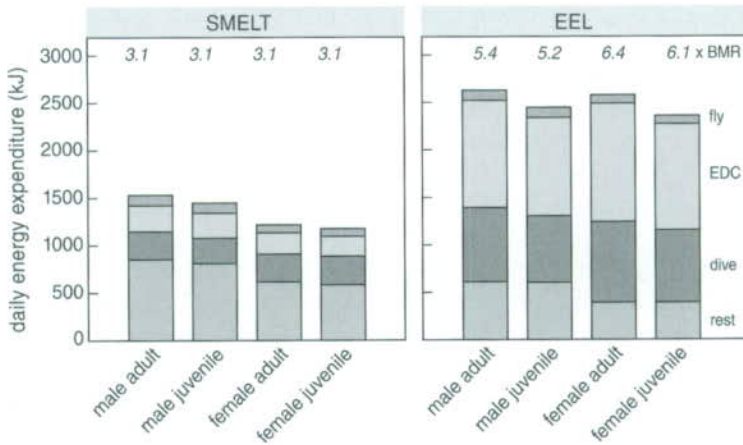


Figure 10. Reconstruction of daily energy expenditure of different sex and age classes of Red-breasted Mergansers exploiting either Smelt or Eel. DEE has been estimated conservatively using data from the literature in estimating energy costs per activity. A three hours diving period was assumed in the case of Smelt hunting, from which the values for Eel hunting were derived using data about foraging success per category. In female mergansers Eel hunting is surpassing the upper metabolic ceiling of $DEE_{max} = 6 \times BMR$ (Weiner 1992, Hammond & Diamond 1997), caused by an increase of costs for diving and dive-recovery costs (EDC) in combination with lower foraging success. See text for upper estimates of DEE.

size of males enables them to feed more efficiently on Eel than females, catching both more and larger fish. Indeed, our calculations suggest that the larger body size of males, associated with a higher level of Basal Metabolic Rate (BMR, Aschoff & Pohl 1970) and, correspondingly, a higher absolute level of working capacity (Drent & Daan 1980, Kirkwood 1983, Weiner 1992), grants them a larger amplitude of possible extra energy expenditure. This means that, although the larger and heavier males have to spend more energy to descend than the smaller females (in absolute terms), their maximum working level is so much higher, that they can more easily cope with these costs than females. Moreover, females are additionally penalised by their lower foraging success.

The constructed energy budgets for the four sex and age categories have been depicted in Figure 10. When involved in Smelt hunting we estimated a DEE for all categories between $3.1\text{--}3.4 \times BMR$. For Eel hunters the estimates are much higher, $5.2\text{--}6.4 \times BMR$ in males and $6.1\text{--}7.9 \times BMR$ in females. If compared to the maximum sustainable level of energy metabolism as put forward by Kirkwood (1983) and Weiner (1992), Eel hunting is for males already close to the edge, but for females completely out of reach. In their review of this physiologically determined "upper benchmark" (Drent & Daan 1980) of what is achievable by any living vertebrate organism, Hammond and Diamond (1997) state that reported ceiling values of sustained peak daily energy expenditure (DEE_{max}) range between 4.3 and 6.7 times resting metabolic rate (RMR). Out of 69 reported studies, only 12 were above 5.5 times RMR, which stresses the extreme conditions under which the Red-breasted Mergansers operate in winter at lake IJsselmeer. We consider our approximation of the daily energy budget as rather conservative, taking only a low (and fixed) value of 20 minutes per day for flight and not applying any extra costs for warming-up the ingested food. Concerning Eel hunting, we did not take into account extra costs for thermoregulation caused by wind chill and extra cost for transport because of drift in stormy weather. The estimates are therefore supposed to represent minimum levels for energy expenditure and corroborate the conclusions drawn before.

In conclusion we state that the rather simple, two-prey-system of lake IJsselmeer in winter is open only to one sex in particular, the males. Even for this group, foraging on Eels in winter is probably close to their metabolic ceiling. The fact that also the juvenile males behave similarly with respect to prey choice and foraging success is interesting, because it suggests that not experience (foraging skill or socially related behaviour) allows the prey switch, but body size alone, which is physically related to diving performance. The fact that we failed to find correlations between diet composition and structural or condition parameters within all age and sex categories does not necessarily mean that these factors play no role. Except for a technical reason because of smaller sample sizes, one biological explanation may be that we analysed only birds which could perform the switch as they were able to balance the budget, without marked consequences for body condition. That the switch can only be made by an a-select fraction of the birds is also shown by the biased sex and age ratios over the diet-groups. Besides the low number of females compared to males in the overall catches: 277 females (21%) against 1041 males (79%), also the division of the age categories over the food types is remarkable. In adult males 83% was recorded as Eel hunter, in first-winter males this was 82% while in adult females 52% and in juvenile females just 46% was recorded as such (Table 3).

The smaller habitat range of females compared to males makes the former more vulnerable to bad weather conditions. It may be one of the reasons for the well-known segregation of the sexes over the winter range, with female and juvenile birds spending the winter in more temperate regions (Bauer & Glutz von Blotzheim 1969).

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References

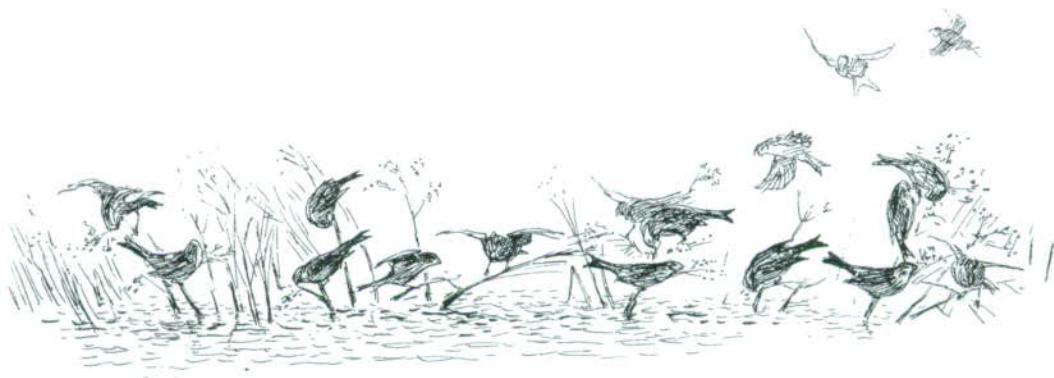
- Aschoff, J. & H. Pohl 1970. Der Ruheumsatz von Vögeln als Funktion der Tageszeit und der Körpergrösse. *J. Orn.* 111: 28-47.
- Bauer, K.M. & U.N. Glutz von Blotzheim 1969. *Handbuch der Vögel Mitteleuropas*. Akademische Verlagsgesellschaft, Frankfurt am Main.
- Beekman, J.H. & M. Platteeuw 1994. Het Nonnetje *Mergus albellus* in het IJsselmeergebied. Internal report 37 LIO, Rijkswaterstaat, Directorate Flevoland, Lelystad.
- Beintema, A.J., L.M.J. Van Den Bergh, G.J. Müskens & T.A. Renssen 1980. Atlas van de vogels op het IJsselmeer. Rijksinstituut voor Natuurbeheer report 80/2, Leersum, the Netherlands.
- Bernat, Y., J. Lobón-Cerviá & P.A. Rincón 1988. Números y densidades de anguilas (*Anguilla anguilla* L.) en un río cantábrico. *Rev. Biol. Univ. Oviedo* 6: 95-108.
- Buijse, A.D. 1992. Dynamics and exploitation of unstable percid populations. PhD thesis, Wageningen Agricultural University, Wageningen, the Netherlands.

- Buijse, A.D., M.R. Van Eerden, W. Dekker & W.L.T. Van Densen 1993. A trophic model for IJsselmeer (The Netherlands), a shallow eutrophic lake. In: V. Christensen & D. Pauly (eds.) Trophic models of aquatic ecosystems. ICLARM Conference Proceedings 26: 90-94.
- Buijse, A.D. & W. Dekker 1996. Uncertainty in fish stock assessment based on bottom trawl surveys in Lake IJsselmeer. In: I.G. Cowx (ed.) Stock assessment in inland fisheries. Fishing News Books, Oxford: 260-279.
- Corsi, F. & G.D. Ardizzone 1985. Some environmental conditions affecting Yellow Eel catchability. *Oebalia* XI-2, N.S.: 561-571.
- De Leeuw, J. 1996. Diving costs as a component of daily energy budgets in aquatic birds and mammals: generalizing the inclusion of dive-recovery costs demonstrated in Tufted Ducks. *Can. J. Zool.* 74: 2131-2142.
- De Leeuw, J. 1997. Demanding divers. Ecological energetics of food exploitation by diving ducks. *Van Zee tot Land* 61, Rijks-waterstaat Directorate IJsselmeergebied, Lelystad; PhD thesis University of Groningen, the Netherlands.
- Dekker, W. 1987a. De rode-aal-stand van het IJsselmeer. *Visserij* 40: 97-102.
- Dekker, W. 1987b. Analysis of length frequency data by an ANOVA type model. European Inland Fishery Advisory Commission (FAO), Eel Working Group, Bristol.
- Dekker, W. 1997. Visstand en visserij op het IJsselmeer en het Markermeer: de toestand in 1996. Rijksinstituut voor Visserijonderzoek, Rapport C002/97, IJmuiden, the Netherlands.
- Drent, R.H. & S. Daan 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* 68: 225-252.
- Eriksson, M.O.G. 1985. Prey detectability for fish-eating birds in relation to fish density and water transparency. *Orn. Scand.* 16: 1-7.
- Feltham, M.J. 1990. The diet of Red-breasted Mergansers (*Mergus serrator*) during the smolt run in N.E. Scotland: the importance of Salmon (*Salmo salar*) smolts and parr. *J. Zool. Lond.* 222: 285-292.
- Hammond, K.A. & J. Diamond 1997. Maximal sustained energy budgets in humans and animals. *Nature* 386: 457-462.
- Kirkwood, J.K. 1983. A limit to metabolisable energy intake in mammals and birds. *Comp. Biochem. Physiol.* 74: 1-3.
- Larsen, K. 1972. Studies on the biology of danish stream fishes. III. On seasonal fluctuations in the stock density of Yellow Eel in shallow stream biotope and their causes. *Medd. sra. Dan. Fisker. Havunders.* 7: 23-46.
- Lecomte-Finiger, R. & R. Prodon 1979. Etude expérimentale du comportement fouisseur de la Civelles (*Anguilla anguilla* L.): le choix d'un substrat. *C.R. Acad. Sc. Paris* 289: 741-743.
- Madsen, F.J. 1957. On the food habits of some fish-eating birds in Denmark. *Dan. Rev. Game Biol.* 3: 21-83.
- Mills, D. 1962. The Goosander and Red-breasted Merganser in Scotland. *Wildfowl Trust Rep.* 13: 79-92.
- Neveu, A. 1981. Variations saisonnières et journalières de l'alimentation de l'Anguille (*Anguilla anguilla* L.) dans des conditions naturelles. *Acta Oecologica/Oecologia Applicata* 2: 99-116.
- Norberg, U.M. 1990. Vertebrate Flight. Springer Verlag, Berlin.
- Salter, J.C. & K.F. Lagler 1940. The food and habits of the American Merganser during winter in Michigan, considered in relation to fish management. *J. Wildl. Manage.* 4: 186-219.
- Sjöberg, K. 1985. Foraging activity patterns in the Goosander (*Mergus merganser*) and the Red-breasted Merganser (*M. serrator*) in relation to patterns of activity in their major prey species. *Oecologia (Berlin)* 67: 35-39.
- Sjöberg, K. 1988. Food selection, food-seeking patterns and hunting success of captive Goosanders *Mergus merganser* and Red-breasted Merganser *M. serrator* in relation to the behaviour of their prey. *Ibis* 130: 79-93.
- Švačas, S., W. Meissner & H.W. Nehls 1994. Wintering populations of Goosander (*Mergus merganser*) and Smew (*Mergus albellus*) at the south eastern Baltic coast. *Acta Ornithologica Lituanica* 9-10: 56-69.
- Van Dobben, W.H. 1952. The food of the Cormorant in The Netherlands. *Ardea* 40: 1-63.
- Van Eerden, M.R. & A. Bij de Vaate 1984. Natuurwaarden van het IJsselmeergebied. Flevovericht 242, Rijksdienst voor de IJsselmeerpolders, Lelystad.
- Weiner, J. 1992. Physiological limits to sustainable energy budgets in birds and mammals: ecological implications. *Trends Ecol. Evol.* 7: 384-388.
- White, H.C. 1939. The food of *Mergus serrator* on the Margaree River N.S. *J. Fish. Res. Bd. Canada* 4: 309-311.
- White, H.C. 1957. Food and natural history of mergansers on salmon waters in the maritime provinces of Canada. *Bull. Fish. Res. Bd. Can.* 116.
- Wiersma, P. 1996. Dieet en conditie van overwinterende Middelste en Grote Zaagbekken in het IJsselmeergebied, 1979-1987. Rijkswaterstaat, RIZA werkdocument 96.086X, Lelystad.

Chapter 20

Evaluation and synthesis: the carrying capacity of Dutch freshwater wetlands for water birds outside the breeding season

Mennobart R. van Eerden



Evaluation and synthesis: the carrying capacity of Dutch freshwater wetlands for water birds outside the breeding season

Food production and food availability are of paramount importance in explaining distribution and abundance of water birds in Dutch freshwater wetlands outside the breeding season. More specifically, this treatise showed the tight relationships between the attainable fraction of total food on offer and bird numbers. In contrast to the agricultural food stocks, use of natural resources is seen to be close to the maximum.

At present, wetlands form but a tiny fraction of their extent in ancient times; still their international importance as staging and wintering habitat for millions of water birds warrants continuous concern in relation to nature management, conflicts with agricultural interests and land-use planning. Underlying knowledge about the reasons *why* and *how* the different habitats are used is scanty and the wish to extend this knowledge formed the basis for the present study about carrying capacity related issues in Dutch freshwater wetlands.

Evidence is presented how birds exploit patches of food, ranging in scale from 0.01m² - 2000 km². Food exploitation is subject to strict foraging rules which lead in many cases to depletion of food stocks. As a consequence, the birds have to shift food type locally or have to move away. Social factors such as dominance relations between flock members but also family structure in monogamous species may govern the lowest level down to which a food patch can be harvested. Also the geographical position along the flyway is important in this respect; minimising time of migration may lead to underuse of food stocks *en route*.

If the exploitation levels of food stocks are compared over an array of species, representing the major trophic guilds, we showed that the exploitation level of food supplies increased in the order fish-eaters, benthos-eaters and plant-eaters. Reasoning from a parallel decline in costs of foraging, this leads to the conclusion that herbivores are time-limited whereas piscivores are energy-limited. In the benthivores both time and energy expenditure set limits to the exploitation of resources. The fact that these prey are sessile, makes them more readily exploitable than fish, which show active escape behaviour in a three dimensional space.

Management directives from this study comprise several focal points. In general, Dutch freshwater wetlands are too static and cut off from natural large scale events. This loss of habitat dynamics resetting succession leads to a deterioration of natural values, even in the case of the larger wetlands. It is suggested either to bring back natural dynamics by connecting smaller systems to larger units or, even more important, to restore the natural forces which may ensure the re-setting of succession. By restoring the free-play of currents, ice, tidal movement and possibly fire, the typical pioneer situations can be maintained. These pioneer stages are of prime importance for plant and animal life characteristic for riverine or lake-bound environments. In case that active management by natural forces is excluded because of other reasons than nature management, more costly tools such as grazing, cutting and water level management can be applied. In any case, these measures are to be preferred above a management of "doing nothing".

This study has put forward arguments that further knowledge should be obtained in the sequence fish-eaters, benthos-eaters and plant-eaters. Not only is habitat of herbivores easier to restore and main-

tain than areas which function for benthos and fish-eaters, also knowledge about habitat exploitation in these purely aquatic groups is currently far less complete than is the case for plant-eaters. Extrapolating from the current trend in water quality (Hosper 1997, Noordhuis *et al.* 1997), these aquatic groups deserve further attention and measures to safeguard their territories. Concerning the herbivorous water birds, emphasis should be laid on creating or restoring natural feeding conditions where it is possible.

Nature development which is currently being carried out in aquatic environment in the Netherlands (IJsselmeer, large rivers, delta area), focuses too much on physical measures and landscape-based habitat modification. Not just the appearance, but the internal, food producing capacity of a wetland should play a leading role in future projects.

Carrying capacity revisited

Long-term changes

Wetlands in the Netherlands have greatly changed in appearance and total surface area has declined enormously, at least over the last 7000 years. Agricultural areas have expanded and presently play a prominent role as catchment area for herbivorous water birds. Transitional zones in both terrestrial and aquatic habitats are especially scarce, due to large scale waterworks and sector management. As a consequence the water bird composition has shifted strongly to a Man-dependent community. Narrow margins cause a limited buffer capacity when food is scarce or weather conditions grow worse. Conflicts with agriculture and fisheries may arise frequently and are likely to increase in future, unless alternative feeding sites can be offered.

A reconstruction was made of the composition and abundance of water birds, using palaeo-geographic maps of the Netherlands in relation to habitat-specific bird density. Of the wetland types, raised bogs, fen-peat and freshwater marshlands greatly declined. Fish-eaters, benthos-eaters and herbivores depending upon natural feeds declined, while those herbivores which switched to agricultural food increased. The brackish water areas almost completely disappeared, whereas tidal mudflats did not change that much in total surface area since the Early-Subatlantic, 2100 years ago.

The period after 1350 AD was conclusive with respect to the onset of irreversible changes (Chapter 2). We consider the situation around 1350 AD as a reference for the prospects of today's nature without the overriding impact of Man. The prominent role of agriculture has nowadays led to the attraction of large numbers of herbivorous ducks, geese and swans. Many of these species have responded to the highly fertilised swards with increasing numbers. As especially the larger species are nowadays fully dependent upon agricultural foods, a vulnerable situation has developed with respect to changes in agricultural practice. In future, an increasing conflict with agriculture is foreseen because of the fact that lower levels of N-fertilisation will be applied to grasslands. As a consequence the birds will redistribute themselves over the existing alternatives; seedlings of agricultural crops are a likely alternative for grass, if biomass is not limiting. This food which is qualitatively comparable to the best pastures is, however, more vulnerable to the effects of grazing (Chapter 3, Van Eerden *et al.* 1996).

Fish-eaters are also increasingly the subject of complaints by fisheries authorities (see EIFAC 1988 for position statement in Europe). In small scale freshwater areas such as ponds and stocked impounded river stretches just a few birds can cause a serious loss of fish as has been recorded in Cormorants *Phalacrocorax carbo* (Moerbeek *et al.* 1987, Seiche & Wünsche 1996, review in Veldkamp 1996). The simultaneous use of large scale water bodies for different purposes such as nature conservation, recreation and fisheries also entails potential conflicts, although economical proof for damage

to the fisheries in these large scale systems is often lacking or disputable (Suter 1991, 1997 but see Staub *et al.* 1992).

Constraints on waterfowl in winter

Water birds in winter are constrained by either low water temperatures, a digestive bottle-neck, food density, or a combination of these constraints. This limits habitat choice and influences individual foraging behaviour by setting an upper limit to the extractable energy; the food situation may dictate the migratory behaviour, which is costly in terms of energy expenditure. Migratory patterns may be either characterised as versatile with flexible time schedules of when to arrive and how long to stay, or traditional with pre-determined goals with little annual variation. In extreme cases a mass die-off in waterfowl may occur if food conditions become marginal.

Water birds in winter use much of their energy for thermoregulation. Experiments with intact, plumage dry carcasses of water birds showed the strong effect of degree of water contact to heat loss. If completely submerged (diving position) birds lost 4.8 times more heat per unit of time than while on land and birds in swimming position lost 2.2 times more heat than on land. Body mass was the most important determinant of heat transfer. In a semi-natural diving device, De Leeuw (1997) could verify increased energy expenditure during cold weather with live diving ducks, using the doubly labelled water technique. Body mass, in relation with the degree of water contact, can be used as gross predictor for the costs of thermoregulation, being largest for smaller birds during diving or swimming. Generally, higher conductance will lead to a tendency toward a further southward wintering of the smaller species, although especially small birds (1 kg and less) may use the tactic of leaving the water if possible. Given this constraint by cold water, provision of wetlands with resting areas where birds can spend part of the day out of the water could be an important measure to increase the carrying capacity of wetlands by reducing the costs of living of the water birds (Chapter 4). Natural, gently sloping shores with unvegetated soils as well as islets or inundated meadows could serve this function. On the other hand, some bird species, such as mergansers and grebes, preferably do not rest on land. For these birds during severe cold ice edges can function as resting place, while they feed in the ice holes nearby. That winter conditions with cold water impose extra costs for water birds, was confirmed by a study on the prey choice and prey mass ingested by Great Crested Grebes *Podiceps cristatus*. Low water temperatures caused almost a doubling of prey intake compared to the late summer situation just after wing moult (Chapter 5). This knowledge is important if one is to model energy flow through the food-web (for lake IJsselmeer see Buijse *et al.* 1993).

Food quality differs greatly and this affects the energy budget of birds. Plant food, though often abundant, is usually of poor quality from a nutritional point of view. Also benthic organisms with an external skeleton or clams bear a large tare fraction which has to be processed by the digestive tract. Bulk feeders among the water birds, such as the herbivorous swans, geese and ducks as well as the benthos-eating diving ducks incur a constraint set by a limited digestive capacity. Not the rate of food uptake, but the digestion of food may impose limits to the amount of energy that can be assimilated. In a comparative study, the smallest herbivore, Teal *Anas crecca* was shown not to forage on green leaves because of a metabolisable energy uptake which would be below its threshold level. Larger species in the guild of avian herbivores digested food better, caused by longer retention times of food in the gut (Chapter 6). These findings are relevant for the evaluation of the species-specific use that water birds can make of an area. In relation to the question of possible damage to agricultural crops, this knowledge can be used to either lure birds away from the vulnerable crops or to increase carrying capacity of natural areas by providing conditions where the preferred vegetation can develop. As a consequence of

the existence of digestive bottle-necks, the water birds are obliged to show a strong selection of the highest quality resources. In the herbivores which were studied under field conditions, this was obvious by a continual selection for high nitrogen/low crude fibre content of their food (Chapters 9, 10, 11, 12).

Benthivorous diving ducks showed a strong preference for the highly rewarding small mussels, but this selection was absent when birds had to dive and were consequently time-constrained (Chapter 13 and De Leeuw & Van Eerden 1992). Habitat selection in order to reduce diving costs by choosing the shallowest foraging grounds paralleled an increase of the energy content of the mussels in shallow compared to deeper waters (Chapter 13, 14). This could not preclude that due to the limited availability of shallow areas in lake IJsselmeer at present, the birds faced a rapidly deteriorating food supply as winter proceeded (Chapter 14 and De Leeuw 1997).

The consequences of food shortage are often not obvious. Migratory behaviour enables birds to move to alternative sites. The costs and consequences of such behaviour are difficult to assess, especially as the breeding areas of the migratory birds are often far away from the wintering areas. In Brent Geese *Branta bernicla* it could be demonstrated that spring food conditions were of influence on fattening rate and subsequent breeding performance (Prop & Deerenberg 1991, Ebbinge & Spaans 1995). It is not unlikely, therefore, that autumnal feeding conditions also affect survival, but data to demonstrate this are not available. Owen *et al.* (1992) showed that Barnacle Geese were in positive energy balance in October and November, whereas they demonstrated an energy deficit by food uptake only in December and January. Stored body fat was used to balance the budget. On the other hand, the effect of short-stopping *i.e.* shortening the migratory pathway has a positive effect on survival as shown by data on Greylag Geese *Anser anser* wintering in the Netherlands as compared to conspecifics wintering in southern Spain (Persson 1992, L. Nilsson pers. comm.)

Chapter 7 deals with the ultimate effect of food shortage. We described a mass die off in diving ducks which were deprived of food for several weeks in late winter. Instead of wandering away, the birds awaited better weather, which, however, did not appear in time. We concluded that the mal-reaction by the ducks, which was observed simultaneously in Switzerland, was the result of the moment in time, when the bad weather occurred, in relation with an already depleted food supply; if the cold spell had come (as usual) earlier in the winter season, the birds would have reacted properly by moving away. The findings stress the extreme dependence upon food stocks as well as the narrow gateways which the birds pass through. Most likely, the tradition of using these resources year after year, in connection with the extreme scarcity of top-food localities in Europe in late winter, has given rise to this wait-and-see strategy, with occasionally fatal results.

Foraging rules determine patch use

Food exploitation in water birds is subject to foraging rules which are used in order to yield the highest energy return per unit of time. Food depletion by waterfowl in nature is often occurring, the birds having to shift to another food type because of scarcity of the preferred source. Food attainability explains differences in observed patch harvest levels and is based on net food intake rate in relation to the amount of daily metabolisable energy that is required. Food density may affect fattening rate and in some cases evidence was found for a density dependent energy uptake for individuals. In most cases the available fraction of the preferred food source limits the use that birds can make of it. Social factors may also affect patch harvest levels and in many cases threshold levels are discernible, which are the lowest levels of food density that can be harvested under the prevailing conditions.

Foraging strategies to exploit patches comprise at least three different tactics. In all cases under study, birds showed a positive resource dependent harvest *i.e.* when more food is available, also more is extracted from the patch. Food density is important in directing patch harvest and the final food density left behind corresponds to the lower limit of intake rate which is energetically acceptable to the consumer. Giving up density of a patch (GUD) is adjusted in relation to the environmental (average) patch density as was found in experiments with Teal *Anas crecca* (Chapter 9). These experiments also showed that, depending upon the conditions, different foraging tactics may be optimal. The techniques applied to obtain seeds from water or mud are different and this led to differences in the optimal size of seeds selected by the birds. In uncertain, highly variable environments Teal were found to allocate their time more or less equally to the patches, thus applying a *Fixed Time Strategy*. However, later on, when the food situation was less uncertain, they changed to a *Bayesian Foraging Strategy* (Chapter 9). When this strategy is applied, the birds use prior information, based on previous patch information; as a consequence of imperfect knowledge of patch density, richer patches become underused, poorer patches by contrast overused. It is suggested that the habit of foraging in flocks may contribute to this exploitation pattern. When flock attendance is more important for an individual than actual GUD of the patches under exploitation, enforced overuse of the poorer patches and underuse of richer patches can easily be understood.

Bayesian foraging was also found in Greylag Geese exploiting seeds of *Agrostis stolonifera* and *Suaeda maritima* (Chapter 10) and in Wigeon *Anas penelope* feeding on seeds of *Salicornia brachystachya* (Chapter 8, and unpublished data). Confirming the experimental results in Teal, wild Bewick's Swans *Cygnus columbianus bewickii* also changed strategy in relation to the level of food abundance. For most of the time the swans were Bayesian foragers, while applying a *Rate Assessor Strategy* when food density was low (Chapter 10). So, the water birds were shown to behave along predictable lines and to respond to the constantly changing food supply by appropriate adjustment of the numerical response and time in patch. Threshold levels of food density which allowed no further exploitation were commonly found in herbivores and benthivores and in some cases also in piscivores (Chapter 16), for which group threshold levels are very difficult to study.

Social dominance also influenced patch use patterns as was shown in experiments with Teal and in wild Bewick's Swans. As Bewick's Swans forage in family units, it could be demonstrated that larger families, though dominant, leave at a higher GUD than small families, families without young and single birds. Patch exploitation is thus dependent on several factors which are not only governed by the food supply itself. Clearly, feeding strategies in waterfowl are not to be considered as fixed, species specific properties but depend instead on several factors of which the effect changes over time. Of course, food density in relation to the available fraction, remains the most important predictor for the use that water birds can make of a patch. In all cases described in this work a positive resource dependent harvest of food items was recorded; this fact, in relation to the depletion effects which were causing the birds to move away or to shift to less profitable feeds, shows that for many situations food was limiting the use that wild birds could make of a patch. Only in the case of fish-eaters this information is less clear; however, evidence was given that also here attainability of the food (influenced by underwater light in Great Crested Grebes and Smew *Mergus albellus*, Chapter 15, 17 and 18, or sex-related structural size in Red-breasted Mergansers *Mergus serrator* affecting diving performance, Chapter 19) determines prey intake.

That availability of natural food in wetlands in the temperate region is scarce is demonstrated by this study. Competition for common supplies between or within species is no exception but more likely a rule. As demonstrated in Chapter 8, Barnacle Geese could achieve a better position with respect to their harvest of *Salicornia* in competition with the earlier arriving Wigeon, by speeding up their migration in autumn. Another example has been worked out in Chapter 12, where moulting Greylag Geese, as a

result of different levels of crowding by conspecifics in the reed marsh, were presumed to utilise a different fraction of their fat reserves, in order to overcome the scarcity of the natural food stock. These links between food density, bird densities and individual body condition, are the first steps to quantifying the mechanism behind density dependent regulation of populations.

Stopover ecology: scaling up the patch

It is possible to scale up local patch use patterns to higher levels (area, zone or entire stopover site along the flyway). This allows predictions about the carrying capacity *i.e.* the number of birds that can be sustained by the area and the occurrence of dietary switches. For herbivorous water birds convincing results were obtained, being somewhat less clear in benthivorous diving ducks and least prominent in the piscivorous mergansers and grebes. These differences are probably not attributable to a biologically different concept, but are due to the increasing complexity of defining the attainable fraction of the birds' food supply.

What evidence do we have that patch use patterns on a small scale can be extrapolated to larger areas, up to an entire stopover site? At the scale of lake Lauwersmeer (*c.* 90 km²) we showed that food stocks could be quantified to predict bird numbers in larger areas. In particular, this is true for the herbivorous water birds up to the scale of vegetation units in a given year. In Bewick's Swans feeding on *Potamogeton* (Chapter 10) and Greylag Goose foraging on seeds of *Agrostis stolonifera* (Chapter 11), it was shown that birds responded closely to the density of the preferred food on offer in different patches. However, food density accounted only for a numerical response when a threshold density was surpassed.

If the food supply is easy to reach and is above threshold densities, the numerical response by birds is straightforward. The best example we know so far comes from our study of Teal which fed on seeds of (mainly) *Ranunculus sceleratus* in Oostvaardersplassen (M.R. Van Eerden & M. Zijlstra, unpubl. data). As shown by Figure 1A these large scale assessments of the food supply are closely followed by the maximum number of Teal that frequented the area from year to year. As the relationship in this case is linear we must assume that the area is inspected each year by enormous numbers of birds. However, only in case of a rewarding food supply do they prolong their stay and subsequently build up in numbers. For Bewick's Swans, again a relationship existed between annual food abundance and bird numbers. Figure 1B depicts the relationship for the Borderlakes whereas also for Lauwersmeer scaling up was possible (J.H. Beekman and M.R. Van Eerden, unpublished).

In benthos-eating diving ducks feeding on *Dreissena* mussels we had too few data to construct a relationship between lake-wide sampling of benthos and duck numbers over the years. This might be possible in future if *Dreissena* continues to decrease in stock at lake IJsselmeer/Markermeer as is expected (see Chapter 14 and discussion in De Leeuw 1997). The sampling of large (25 - 50 km²) sub areas did show a relationship between mussel biomass, water depth and duck numbers already, which makes clear that also in this group scaling up of small patches to larger areas is valid.

In fish-eating water birds the situation is even more obscured by the fact that the available fraction of the food supply is so difficult to measure. A preliminary investigation of the long-term changes in Smelt *Osmerus eperlanus* biomass and bird numbers shows, except for the trough-years, a weak relationship (unpubl. data). This will be partly caused by the overriding effect of underwater visibility as was shown for Great Crested Grebes in Chapter 15 and 16 and for Smew in Chapter 18, but also because of the role of alternatives on a much larger scale. In species, where prey attainability is so important and at the same time so unpredictable, both between and within years, we would expect the birds to sample their possibilities at a very large scale. However, that in fish-eaters also a direct

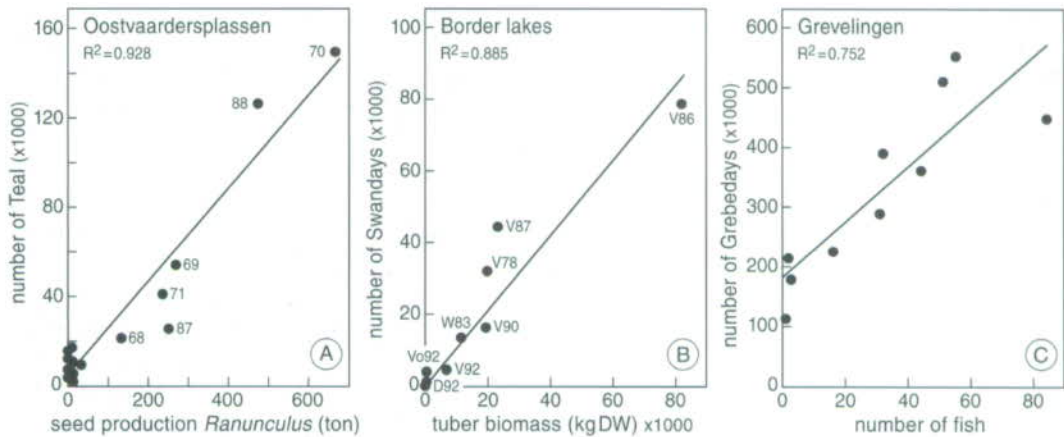


Figure 1. Scaling-up patch use data to the level of an entire stopover site. (A) Herbivorous Teal *Anas crecca* in Oostvaardersplassen feeding on seeds of the annual pioneer vegetation consisting of *Ranunculus sceleratus*. (B) Bewick's Swans *Cygnus columbianus bewickii* in the Borderlakes of Flevoland exploiting the tuberbanks of the macrophyte *Potamogeton pectinatus*. (C) Piscivorous Great Crested Grebes *Podiceps cristatus* in lake Grevelingen in relation to the stock of *Gobiidae* (after Doornbos 1984). Data points refer to years.

response to their food stocks can occur, was shown by data in Doornbos (1984) in the saline lake Grevelingen. In this study on grebes, a neat relationship was demonstrated between density of gobies *Gobiidae* and grebe numbers in different years (see Fig. 1C). Crucial in this respect is the observation that the water in the Grevelingen at that time was crystal clear by Dutch standards (Secchi depths 2 - 6 m). For the IJsselmeer system, which because of its turbidity is more typical for an estuarine environment, we demonstrated the crucial role of underwater light conditions on prey attainability (Chapter 17 and 18).

Stopover ecology: food-based migratory traditions

Migration habits affect exploitation of food supplies. Tradition-based species are associated with long range migration and predictable food sources. Opportunistic species tend to have a shorter migration distance and react promptly to changing food supplies.

Some species of waterfowl traditionally return to the same stopover sites each year, while other species do not. One of the factors determining the degree of tradition to return to a site may be related to the predictability of the food supply. In herbivores, perennial plant species are more predictable than annual species. Birds feeding on animal prey face on average less predictable situations than plant-eaters. There are, however, many exceptions to these generalisations. Yet there are some interesting points to make within one guild: among herbivores, birds which dig up rhizomes (roots, stolons, tubers) of perennial species would be more tradition-based, an obligate seed-eater as Teal exploiting pioneer plants on the contrary would react opportunistic to new food supplies. Similarly it can be hypothesised that among diving birds, fish-eaters exploiting unpredictable prey would be more versatile than benthos-eaters feeding on sessile prey.

In the case of Wigeon and Barnacle Goose the latter responded with a speeding up of their migration in reaction to the new and expanding *Salicornia* food stocks. However, it took several years before

this new migration pattern was realised (Chapter 8). The apparent time lag in response was unlikely to be due to limited bird numbers. Another example is shown by the colonisation by Stoneworts *Characeae* in the Borderlakes of Flevoland and its use by Bewick's Swans. Although *Characeae* replaced Sago Pondweed *Potamogeton* rapidly in the period 1987-1990, the migratory swans did not forage on this food until 1994 (pers. obs.), i.e. four years after it had become the dominant underwater vegetation (monitoring by Rijkswaterstaat, F. Zant). The swans continued to feed on the remaining Pondweed patches, while sedentary Mute Swans *Cygnus olor* already exploited the new food source. After the food switch numbers have increased rapidly, culminating until now with 11 500 Bewick's Swans (46% of flyway population, Scott & Rose 1996) feeding on *Chara aspera* and *Nitellopsis obtusa* (see Noordhuis 1997) according to an aerial count 31 October 1997 (M.R. Van Eerden, M. Zijlstra, J.H. Beekman). These examples show that building up a new tradition takes time. Why does it take so long to store knowledge into the memory of the birds and to apply this knowledge by altering the migration schedule on the level of a significant part of the population as was the case in Barnacle Geese and Bewick Swan? In view of the discussion in Chapter 6, it may well be that mass food switches only occur if the food stock involved is stable and can reward the consumer for several consecutive weeks in a row. This may allow the digestive machinery to become adapted to specific requirements necessary to digest the new food type. This could either be a change in length of the total tract or a modification of the microflora (McWilliams *et al.* 1997). This likely cost factor, associated with a dietary switch may be one of the reasons for the postponed reaction to the new food supply. Moreover it is probably no coincidence that both species are long-lived, long-range migrants, flying over large distances between stopover sites. It is imaginable that it does not pay to rely immediately on a suddenly occurring new food supply; a dependable food source can, however, eventually enter the migratory programme. Research into this direction is needed in order to predict dietary switches on the medium term for different species other than just from the calorific return to the consumer, as is usually done in classical foraging theory.

Migratory time-table and patch use

The migratory time-table, in relation to the annual rhythm of the consumer and the food situation of other staging sites on the flyway, additionally determine local patch harvest levels. This means that not only local food supplies dictate the level of harvest, but that also food density at a much wider scale influences local processes.

Patch harvest levels, food choice and hence carrying capacity may differ according to the position of the foraging area on the flyway level. Depletion at a final station might occur down to a lower level than during a halt at a stopover site.

In Lauwersmeer, Greylag Geese *Anser anser*, underway from Norway to southern Spain, showed a preference for the highest quality of plant food available. Experiments with captive geese showed that they were capable of using other plant parts and species in the vegetation, however at the expense of a longer foraging period. It was concluded that the geese, being time constrained on their autumn migration, tend to select the best feeds in order to gain fat at a maximum rate, thus minimising migration time (Chapter 11). This resulted in a Giving Up Density of twice the level in captive birds, showing an apparent underuse of the stock of *Agrostis* seeds and several plant species of the vegetation available to them.

On the contrary, many Bewick's Swans *Cygnus c. bewickii* (exploiting the tubers of Sago Pondweed *Potamogeton pectinatus* soon after arrival, later on switching to arable crops or grass (cf. Beekman *et al.* 1991) in the Netherlands are at the end of the migratory flyway to the winter quarters (neck-collar

study J.H. Beekman). Repeated measurements of Giving Up Densities over the years showed that the swans in recent years exerted less effort to exploit Sago resulting in higher GUD's than those that were found before 1989. We suggested that the food situation *en route*, i.e. in the Baltic, had become better, thus allowing the swans to put less effort in tuber digging in the Dutch sites in order to attain the required autumnal fat load. The swans were supposed to judge the food supply in relation to their body condition, the time of year and the site along the flyway (Chapter 10). These results are relevant when one is to judge food supplies in relation to the carrying capacity for individual species of birds. Especially surprising was the finding that the relative and not only the absolute level of food availability on the flyway needs to be taken into account. Stopover sites in general have to offer better food conditions than wintering sites, as the food demands of the birds are higher during this phase.

Based on the data collected in this study and using unpublished data from other areas further upstream, Figure 2 depicts the idealised use that water birds could make of different stopover sites along the flyway. It has been assumed that in the northern arctic and boreal breeding and staging areas no satiation of habitat exists at present. In some species, namely the herbivorous Barnacle Geese and possibly the Bewick's Swan, this may not be true. These species are highly subsidised in winter due to high quality grasslands (Chapter 3), whereas in summer they utilise rather specific parts of coastal, respectively estuarine areas, which nowadays may be of limiting capacity. But for most species further downstream the flyway, satiation of the preferred habitats occurs and an increasing number of birds tend, according to the model, to be forced aside to lower ranking sites. In the wintering sites in western Europe, suitable habitats are even more limited. The consequence of such a pattern of a downstream decrease of capacity of wetland areas is that a premium is set on fast migration to the southern sites.

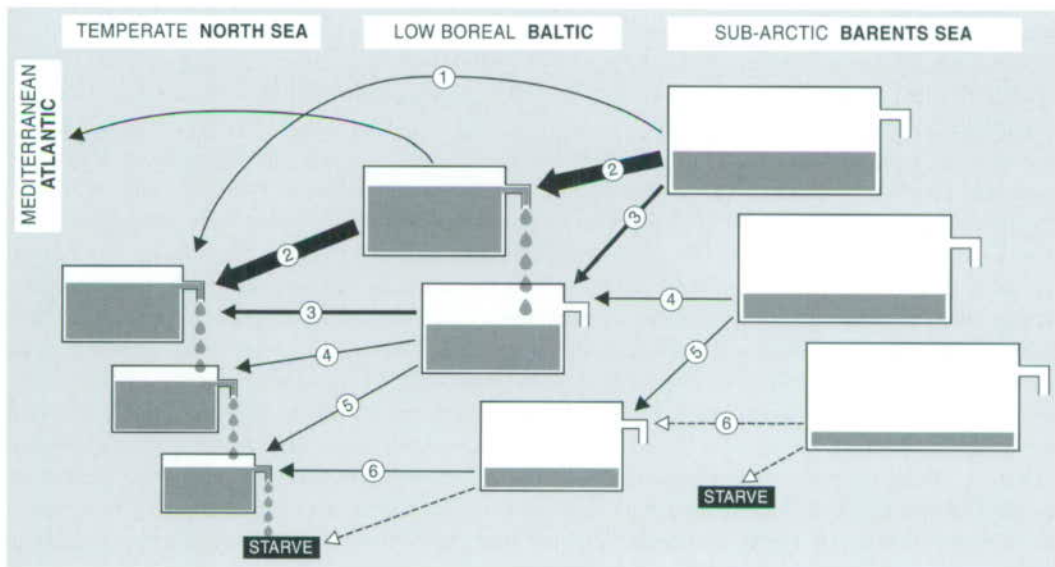


Figure 2. Qualitative model showing schematic use of stopover sites by water birds during autumn migration. For three regions habitats have been plotted in descending quality and the use by birds has been indicated by the filling of the tubs. Note the limited capacity of stopover sites further south along the flyway. Numbers refer to migration routes, 1 = long-range migrants using few stopover sites, 2 = migrants using most rewarding stopover sites, 3-6 cascade of use of sub-optimal stopover sites along the flyway. Note the viewpoint that in the temperate region of the North Sea, most wetlands are used at maximum capacity.

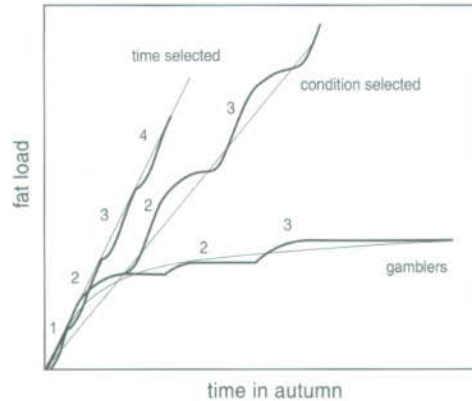


Figure 3. Model of fattening rate of birds using stopover sites of different quality or lagging behind in exploratory sequence. For reasons of simplicity, loss of condition due to migration has not been depicted but is supposed not to vary as a function of fattening rate and being equal for all birds which cover the entire route. Note the sigmoid curve of fattening rate as function of time at each stopover site (1-4). Three different cases of migration in relation to timing of exploitation at a given stopover site have been depicted.

Given lower fattening rates at second choice sites, a bird incurs an increasing cost by not belonging to the early arriving group. Timely fattening up in relation to the possibility to choose an energy saving tail-wind (see Piersma 1994 (pp. 131 - 134) in waders, Ebbinge 1989, Piersma & Van de Sant 1992 in geese) might even allow the birds to over-fly stopover sites.

In a schematic way, Figure 3 shows three possible situations with respect to habitat exploitation and migration speed. Birds are considered to arrive among the first, in the middle group, or in the tail end to exploit the available food stock in a given wetland along the flyway. Because flight costs are assumed to be equal for reasons of simplicity, the graphs quickly show the difference in migration speed and concurrent (cumulative) fattening rate as a function of the timing of exploitation. Dependent on the relative size of the food supply at each stopover site and the need to reach the farthest site in time, birds can use different strategies as to exploit a certain food stock. The Greylag Geese *Anser anser* which migrated from Norway to Spain and passed through the Netherlands used an "early and fast" strategy with an underuse of the food stock of *Agrostis stolonifera* seeds (Chapter 11). Barnacle Geese *Branta leucopsis* were shown to be able to hasten their migration speed in autumn as a result of an increased food stock, which, however, they had to share with Wigeon *Anas penelope* (Chapter 8). Undoubtedly these geese have overflowed staging areas further to the north on their way to the Lauwersmeer, a pattern which was reversed when the food supply diminished again. Bewick's Swans *Cygnus c. bewickii* tended to use Sago *Potamogeton pectinatus* tubers in relation to body condition, which we associated also with the change of food supplies, but then at stopover sites further north along the flyway (Chapter 10). Further research into this topic of differences in habitat use, consequences for body condition and fitness would seem extremely rewarding, keeping in mind that different populations as well as individuals within one population adopt a different migration, and hence foraging strategy.

Foraging costs and patch exploitation: trophic considerations

Foraging costs of the consumer and energetic return of food also determine patch harvest levels and thus carrying capacity of a stopover site. Species with high levels of daily energy expenditure (DEE) due to high foraging costs use only a tiny fraction of natural food stocks compared to species with lower levels of energy expenditure. The low-cost, low-income herbivores exert generally the highest exploitation rates which occur in natural situations. High-cost, high-income piscivores have low levels of energy extraction which run parallel to extensive use of space and *vice versa*. The benthivores, combining relatively high costs for foraging with intermediate food quality, take an intermediate position as does their average harvest level.

In an inter-species comparison we expect foraging costs to increase from herbivore < benthivore < piscivore and may question whether patch harvest differs between groups. A literature study on harvest levels by water birds from different foraging guilds, representing consumers of the major trophic levels, shows large differences between species. From Table 1 it appears that average level of harvest is highest among herbivores, lower but variable in benthivores and lowest in piscivores. If we consider the actual amount of energy extracted the pattern is as follows. On an annual basis ($\text{kJ m}^{-2} \text{y}^{-1}$) over an on average 2-5 months staging period, fish-eaters account for 5-20 kJ m^{-2} , benthos-eaters 50-250 kJ m^{-2} . For plant-eaters the pattern is more diverse, ranging from 150-500 kJ m^{-2} in foliage eaters in spring and winter to 350-900 kJ m^{-2} in seed-eaters in autumn. The highest values were found for the moulting Greylag Geese being 1000-5500 kJ m^{-2} when defoliating reeds. These results show the same trend as was found in the cropping level, but the range in energy extraction is much larger. Grossly speaking, a factor ten exists between primary, secondary and tertiary consumers. This is in the same order as the difference between the level of annual production for the major trophic levels (Odum 1959), and underlines the differences in spacing behaviour between fish-eaters (low density), benthos-eaters (intermediate density) and plant-eaters (high density).

If we consider the various cost factors for different groups of water birds adapted to a different foraging mode, the following conclusion suggests itself. Low-cost, low-income herbivores have the possibility to extend their foraging time within the limits set by the digestive capacity of the gut (Karasaov 1990). They occur in the highest densities as do their food resources. On the other hand, high-cost, high-income piscivores are not time but energy constrained. Maximum level of costs spent foraging are considered roughly the same for all groups (Table 2). Because of their behaviour spending much time on and under water, the benthos- and fish-eaters spend more energy to compensate for heat loss than herbivores do (see Lovvorn & Gillingham 1996, de Leeuw 1997). Figure 4 depicts the idealised transect across a typical wetland, showing the main avian consumers in it together with levels of harvest (% cropped) and in terms of gross energy extracted ($\text{kJ m}^{-2} \text{y}^{-1}$). As outlined before, the guilds with a high level of daily energy expenditure take the lowest toll and *vice versa*.

Implications for wetland development, conservation and research

Restoring dynamic systems

For the down-stream end of the fly-way of water birds, where Man has the greatest impact on nature, the recommendations from this study are as follows: In the Netherlands it is necessary to develop, restore and preserve wetlands large enough to have a fair level of internal dynamics, *i.e.* eroding forces such as wind, wave, ice and other natural forces. These can set-back succession and ensure the contin-

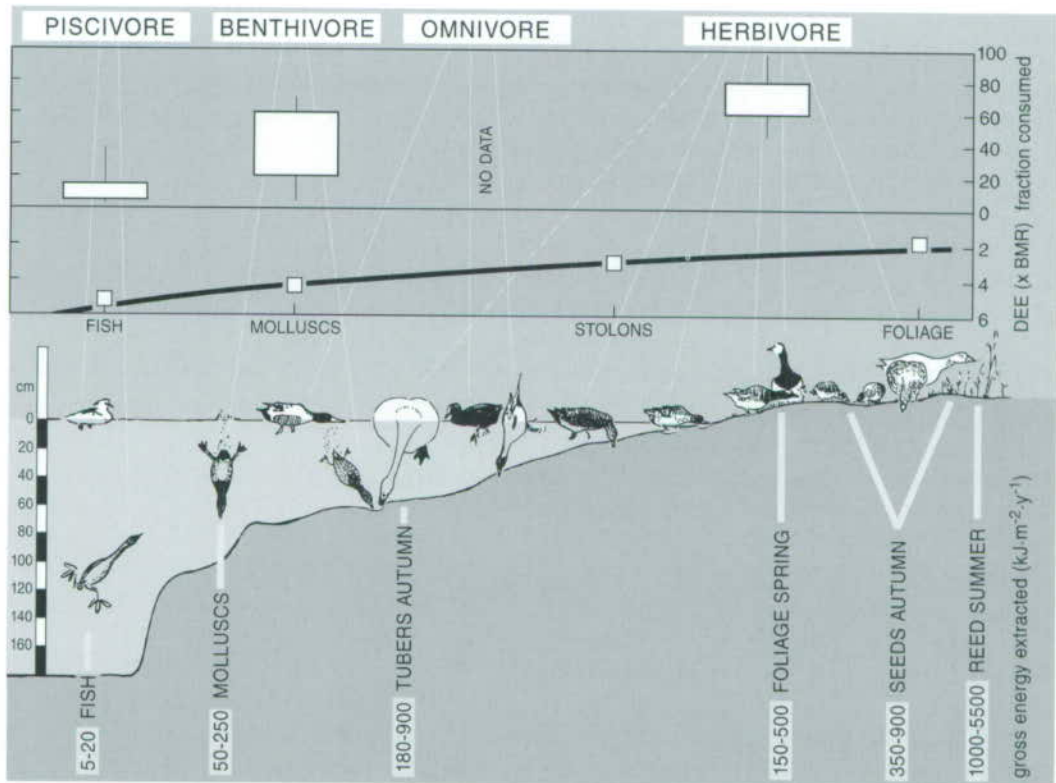
Table 1. Exploitation level by water birds of resources belonging to different trophic levels. Indicated has been maximum harvest levels of food stocks at a community level.

Guild ¹	Consumer	Food species	Food type ²	% ⁴ eaten	Remarks	Place	Reference
P	<i>Phalacrocorax carbo</i>	Cyprinidae, Percidae	fish	5-15	summer	L. IJsselmeer NL	Van Dam <i>et al.</i> 1995 M.R. Van Eerden unpublished
P	<i>Phalacrocorax carbo</i>	Cyprinidae, Percidae	fish	11	winter	L. Ketelmeer NL	Platteeuw <i>et al.</i> 1992
P	<i>Phalacrocorax carbo</i>	<i>Rutilus</i>	fish	17-20	winter	Gravel pits Maas NL	Noordhuis <i>et al.</i> 1997
P	<i>Phalacrocorax carbo</i>	Percidae	fish	5-10	winter	L. Markermeer NL	Beekman & Platteeuw 1994
P	<i>Phalacrocorax carbo</i>	various species	fish	3	year round	L. Chiemsee D	Keller 1995
P	<i>Phalacrocorax carbo</i>	<i>Salmo salar</i>	fish	6-13	summer	County Mayo IRL	MacDonald 1988
P	<i>Phalacrocorax carbo</i>	Cyprinidae, Percidae	fish	11	winter	L. Wolderwijd NL	Dirksen <i>et al.</i> 1995, Noordhuis <i>et al.</i> 1997
P	<i>Podiceps cristatus</i>	Gobiidae	fish	36	winter	Grevelingen NL	Doombos 1984
P	<i>Mergus serrator</i>	Clupea	fish	28	winter	Grevelingen NL	Doombos 1984
P	<i>Mergus serrator</i>	<i>Gasterosteus</i>	fish	11	winter	Grevelingen NL	Doombos 1984
P	<i>Mergus merganser</i>	Salmonidae	fish	< 10	spring	Br. Columbia CAN	Wood 1987a
P	<i>Mergus merganser</i>	trout	fish	8-21	winter	Teeside UK	Carter & Evans 1988
P	<i>Mergus merganser</i>	<i>Oncorhynchus</i>	fish	10-22	spring	Br. Columbia CAN	Wood 1987b
P	<i>Mergus merganser</i>	<i>Oncorhynchus</i>	fish	19-39	spring	Br. Columbia CAN	Mace 1983 in Ruggerone 1986
P	<i>Mergus merganser</i>	Salmonidae	fish	1-2	spring	R. Halselva N	Kålås <i>et al.</i> 1993
P	<i>Mergus albellus</i>	<i>Osmerus</i>	fish	< 3	winter	L. Markermeer NL	Doombos 1979
B	Seaducks	<i>Mytilus</i>	mollusc	5-35	winter	Baltic S	Nilsson 1970, 1980
B	<i>Somateria mollissima</i>	<i>Mytilus</i> , <i>Cardium</i>	mollusc	13	winter	Wadden Sea D	Nehls 1989, 1995
B	<i>Somateria mollissima</i>	<i>Mytilus</i>	mollusc	48-69	winter	Gulf of St. Lawrence CAN	Guillemette <i>et al.</i> 1996
B	<i>Somateria mollissima</i>	<i>Mytilus</i>	mollusc	18-24	winter	Kielerbucht D	Kirchhof 1979
B	<i>Somateria mollissima</i>	<i>Cardium</i>	mollusc	19-55	winter	Kielerbucht D	Kirchhof 1979
B	<i>Aythya fuligula</i>	<i>Dreissena</i>	mollusc	23	winter	L. Ermatingerbecken	Zuur 1983
B	<i>Aythya fuligula</i>	<i>Dreissena</i>	mollusc	43	winter	L. Untersee CH	Suter 1982a,b
B	<i>Aythya fuligula</i>	<i>Dreissena</i>	mollusc	8-11	winter	L. Neuchâtel CH	Pedroli 1981
B	<i>Aythya fuligula</i>	<i>Dreissena</i>	mollusc	15-50	winter	L. IJsselmeer NL	Chapter 14, Van Eerden <i>et al.</i> in prep.
B	<i>A. fuligula</i> , <i>A. marila</i>	<i>Dreissena</i>	mollusc	57	winter	L. Erie USA	Hamilton <i>et al.</i> 1994
B	<i>A. fuligula</i> , <i>A. ferina</i>	Chironomidae	insect larvae	92	winter	L. Klingnau CH	Willi 1970
H	<i>Anas platyrhynchos</i>	Barley	seeds	85-93	summer	Flevoland NL	M.R. Van Eerden unpublished
H	<i>Anas acuta</i>	Wheat	seeds	80-97	summer	Flevoland NL	M.R. Van Eerden unpublished
H	<i>Anas penelope</i>	<i>Agrostis</i>	leaves	69-88	spring	Lauwersmeer NL	Platteeuw & Spaans 1983
H	<i>A. penelope</i> , <i>B. leucopsis</i>	<i>Salicornia</i>	seedheads	70-85	autumn	Lauwersmeer NL	Ch. 8, Van Eerden 1984
H	<i>Branta leucopsis</i>	<i>Cerastium</i>	seedheads	60-90	summer	Spitsbergen N	M.R. Van Eerden unpublished
H	<i>Branta leucopsis</i>	<i>Salix</i>	leaf-buds	70-80	summer	Spitsbergen N	Prop <i>et al.</i> 1984
H	<i>Branta leucopsis</i>	<i>Saxifraga</i>	flowers	10-45	summer	Spitsbergen N	M.R. Van Eerden unpublished
H	<i>Branta leucopsis</i>	<i>Cochlearia</i>	leaves	40-90	summer	Spitsbergen N	M.R. Van Eerden unpublished
H	<i>Branta leucopsis</i>	<i>Equisetum</i>	plants	60-80	summer	Spitsbergen N	M.R. Van Eerden unpublished
H	<i>Branta leucopsis</i>	<i>Lolium</i>	leaves	75	winter	Caerlaverock GB	Owen <i>et al.</i> 1992
H	<i>Branta bernicla</i>	<i>Plantago</i>	leaves	80	spring	Schiernmonnikoog NL	M.R. Van Eerden in Prins <i>et al.</i> 1980
H	<i>Anser anser</i>	<i>Phragmites</i>	leaves	70	summer	Oostvaardersplassen NL	Ch. 12, Van Eerden <i>et al.</i> in prep.
H	<i>Anser anser</i>	<i>Agrostis</i>	seeds	75	autumn	Lauwersmeer NL	Ch. 11, Van Eerden <i>et al.</i> in prep.
H	<i>Anser anser</i>	<i>Phleum</i>	seedheads	47-77	summer	Oostvaardersplassen NL	A. Muis & J. Diender unpublished
H	<i>Anser anser</i>	Oilseed rape	leaves	45-75	autumn	Flevoland NL	M.R. Van Eerden unpublished
H	<i>Anser fabalis</i>	Sugar beet	rootcrops	65-88	autumn	Flevoland NL	M.R. Van Eerden unpublished
H	<i>Cygnus c. bewickii</i>	<i>Potamogeton</i>	tubers	60-90	autumn	Lauwersmeer, Borderlakes NL	Ch. 10, Van Eerden <i>et al.</i> in prep.
H	<i>Cygnus cygnus</i>	Oilseed rape	leaves	50-78	winter	Flevoland NL	M.R. Van Eerden unpublished

¹ P = Piscivore, B = Benthivore, H = Herbivore² based on food stock;³ proportion harvested of original food stock

Table 2. Approximated foraging costs, time spent foraging and daily energy expenditure for foraging guilds.

Foraging guild	Food	Foraging costs (x BMR)	Time spent foraging (h) ¹	Field metabolic rate (x BMR) ²	Time spent not foraging (h)	Total DEE (x BMR) ³
Piscivore	fish	10	3 - 4	4.5	20 - 21	5.2 - 5.4
Benthivore	mussels	6	5 - 7	4.0	17 - 19	4.4 - 4.6
Herbivore	stolons	3.5	8 - 12	2.5	12 - 16	2.8 - 3.0
Herbivore	foliage	2.0	10 - 18	1.5	6 - 14	1.7 - 1.9

¹ Maximum range² Not foraging, water temperature < 5 °C³ According to time energy budget over 24 h⁴ Assuming BMR not to vary between groups (see Daan *et al.* 1990).**Figure 4.** Schematic cross-section through a freshwater wetland with typical avian consumers in it. The approximated costs for foraging, expressed as multiples of Basal Metabolic Rate (BMR) and the (gross) energetic return of the food taken ($\text{kJ m}^{-2} \text{y}^{-1}$) have been indicated together with harvest levels experienced in nature. The low-cost herbivores take the greatest toll from their food plants, whereas in fish-eaters, having a high-cost feeding mode, the lowest levels of exploitation are found (see text for further explanation).

uation of the important primary phase which is, a.o. most important for water birds. If the natural forces are unable to guarantee these cyclic events in primary wetlands, an active management should be carried out trying to replace these natural processes. Applying this kind of measures to existing Dutch wetlands is necessary to increase the food availability and therefore the current carrying capacity for water birds. Water management by applying fluctuating water levels is to be preferred over stagnant levels. Letting nature run its own course in wetland areas which are of limited size (<1000 ha) but are supposed to keep their pioneer character and henceforth carrying capacity for water birds, without an active management to replace these natural forces is a *contradictio in terminis*. We have seen that in the enclosed wetlands of recent origin high natural values may occur. However, without active management these values are under constant pressure and tend to turn down, although often only after a considerable time (15 - 25 years in freshwater marshes, >50 years in large lakes). These rather long periods complicate the discussion and decision making about the direction of nature management. If natural forces are absent or not effective enough in this respect, it is a matter of choice as either to bring back the natural dynamic or substitute it by management measures such as grazing and cutting (Bakker 1989, 1997, Bakker *et al.* 1997), bio-manipulation of water bodies (Hosper 1997) or water level manipulations (Van Eerden 1995, Vulink & Van Eerden 1998). An example of such substitution management is shown by Figure 5. Teal responded with enormous numbers to the water level induced vegetation changes. Of course above all, an attempt should be made to bring back the natural dynamics, because this will guarantee best that the processes which are aimed at, will indeed occur. An additional argument is the cost-effectiveness of such measures, which are undoubtedly lowest for the natural or near-natural situations on the long-term. There is an urgent need for studies to show the effect of re-opening of barrier dams on chances for a return of dynamic situations in relation to a sustainable, long-term carrying capacity of the system.

A focus on specific groups

On a European scale the vulnerability of the fish-eaters is apparent. Shallow open freshwaters constitute an endangered habitat. At present three major wetlands hold most of the fish-eating water birds in the Netherlands in winter: IJsselmeer, Markermeer, Grevelingen and Krammer Volkerak. The latter two are recently closed off parts of former estuaries with fish stocks not yet in equilibrium. Lake IJs-

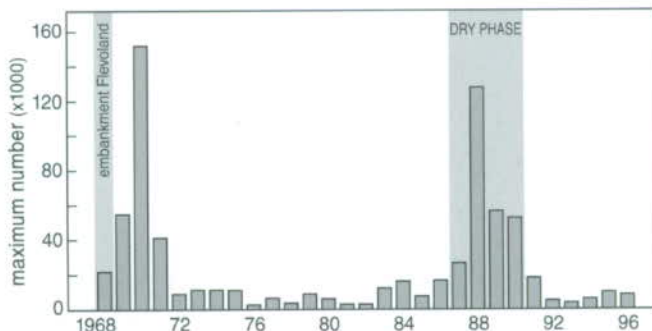


Figure 5. Example how active management in a freshwater wetland can affect carrying capacity for water birds. Due to periods of low water tables in the Oostvaardersplassen marsh, pioneer vegetation could develop to an explosive extent, which was followed immediately by a numerical response of Teal *Anas crecca*. The first peak in bird abundance was natural, because of embankment of the polder in 1968, the second peak was induced by active management of the water table (draw-down period 1987-1990), inducing a second outburst of the pioneer vegetation.

selmeer and Markermeer are important because of their size and the abundance of a land-locked population of the small salmonid Smelt. Also because of the differences in levels of habitat exploitation between the major ecological groups of water birds, conservation priorities should focus in hierarchical order from fish-eaters, benthos-eaters to plant-eaters. Further research concerning the quantification of food-consumer relationships should also follow this sequence. Especially conditions as to maintain fish populations that are present in densities high enough to serve as food for fish-eating birds should be striven for, in a system that is large enough to avoid the risk of overuse. As especially small fish serve as bird food, the productivity of the system is important as well as the presence of small-sized species such as Smelt in the IJsselmeer (1932) at present. Also in smaller sized former estuaries as Haringvliet (1971), Krammer Volkerak (1987), Lauwersmeer (1969) and Grevelingen (1971), priority should be given to measures which could lead to a sustainable use of fish, benthos and aquatic and littoral vegetation by water birds (and Man where appropriate). Considering the herbivores, the development of systems where large scale aquatic macrophytes such as Sago Pondweed *Potamogeton* spp. and Stoneworts *Characeae* occur, seems promising (cf. Noordhuis 1997). The re-establishment of brackish waters could bring back tuber producing *Scirpus maritimus*, and natural marshlands where bulbs of *Triglochin palustris* form an attractive part. These management practices are important in order to reinforce the natural carrying capacity of Dutch wetlands; the measures should aim, by focusing on wetland birds, at bringing back also the other plant and animal species which are as much, or more vulnerable than the birds are.

Investing in research along the flyway

On a higher level, that of the flyway of the water birds, research priorities should aim at quantifying existing food supplies, identifying digestive or other ecological bottle-necks and predicting future developments with respect to the sustainability of the ecosystems involved. Research abroad is an essential step forward if we are to safeguard the flyway systems in future times. Not only increased efforts by specific research and inventories, but also investment of (western) money is necessary to book progress. This requires a close co-operation between different research institutes in the Netherlands and abroad.

This approach is likely to give the best results if research effort is divided over the different foraging guilds. Especially the benthos- and fish-eating water birds will need much attention before this goal can be achieved. In the herbivores, the approach with the aid of satellite images seems promising (cf. Beekman *et al.* 1996).

Evaluating wetland values

The significance of wetlands in an international context is often evaluated by listing of areas which meet the so-called 1% criterion (Atkinson-Willes 1976). This standard is applied world-wide and serves as an independent estimator which accounts for differences in population size. Given the results of this study, again a division into different ecological groups would seem to provide a more sensitive measure. Instead of taking the total flyway population of each species, a weighting factor should be applied, being in the order 1 for herbivores, 3-5 for benthivores (and tentatively planktivores) and 10-15 for piscivores. The factors are relative to the consumption levels experienced among the different groups (see Fig. 4) and take into account the ecological role the species play in the food-web of the system. Especially when one is to compare the quality of different wetlands in a (inter)national context such a correction would seem useful. In this respect a further refinement can also be made by a thorough distributional analysis. Some species are concentrated in just a few hot-spots and in particular the very few alternative sites of sufficient capacity to compare with the IJsselmeer emphasise how important this habitat really is. Especially the species with patchy distribution patterns deserve an accounting

system more sensitive than 1% of flyway population accounted for. Relative scarcity of the key habitats requires detailed work along the entire flyway.

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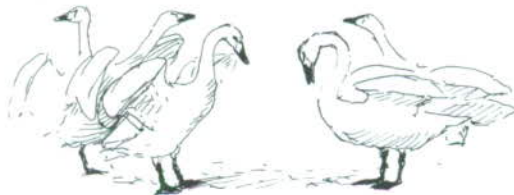
References

- Atkinson-Willes, G.L. 1976. The numerical distribution of ducks, swans and coots as a guide in assessing the importance of wetlands in midwinter. Proc. Int. Conf. on Conservation of Wetlands and Waterfowl, Heiligenhafen 1974: 199-271.
- Bakker, J.P. 1989. Nature management by grazing and cutting. Kluwer, Dordrecht.
- Bakker, J.P. 1997. Natuurbeheer in kustsystemen. Openbare les Rijksuniversiteit Groningen, 28 oktober 1997.
- Bakker, J.P., P. Esselink, R. Van der Wal & K.S. Dijkema 1997. Options for the restoration and management of coastal salt marshes in Europe. In: K.M. Urbanska, N.R. Webb & P.J. Edwards, Restoration ecology and sustainable development, Cambridge University Press, Cambridge: 212-248.
- Beekman, J.H., M.R. Van Eerden, Y.N. Mineyev, L. Luiguijoe & H. Den Hollander 1996. Landsat satellite images for detection of submerged macrophytes: in search of potential stop-over feeding sites for Bewick's Swans *Cygnus columbianus bewickii* along their migration route. In: M. Birkan et al. (eds.) Proceedings of the Anatidae 2000 Conference, Strasbourg 1994. Gibier Faune Sauvage 13: 421-450.
- Buijse, A.D., M.R. Van Eerden, W. Dekker & W.L.T. Van Densen 1993. Elements for a trophic model for IJsselmeer (the Netherlands), a shallow eutrophic lake. In: V. Christensen & D. Pauly (eds.) Trophic models of aquatic ecosystems. ICLARM Conf. Proc. 26: 90-94.
- Carter, S. & P. Evans 1988. The Goosander in relation to Salmon fisheries. Ibis 130: 589.
- Daan, S., D. Masman & A. Groenewold 1990. Avian basal metabolic rates: their association with body composition and energy expenditure in nature. Am. J. Physiol. 259: R333-R340.
- De Leeuw, J.J. 1997. Demanding Divers. Ecological energetics of food exploitation by diving ducks. Van Zee tot Land 61, Rijkswaterstaat Directorate IJsselmeergebied, Lelystad; PhD thesis University of Groningen, the Netherlands.
- Dirksen, S., T.J. Boudewijn, R. Noordhuis & E.C.L. Martejn 1995. Cormorants *Phalacrocorax carbo sinensis* in shallow eutrophic freshwater lakes: prey choice and fish consumption in the non-breeding period and effects on large-scale fish removal. Ardea 83: 167-184.
- Doorbos, G. 1979. Winter food habits of Snew (*Mergus albellus* L.) on lake IJssel, the Netherlands: Species and size selection in relation to fish stocks. Ardea 67: 42-48.
- Doorbos, G. 1984. Piscivorous birds on the saline lake Grevelingen, the Netherlands: abundance, prey selection and annual food consumption. Neth. J. Sea Res. 18: 457-497.
- Ebbinge, B.S. 1989. A multi-factorial explanation for variation in breeding performance of Brent Geese *Branta bernicla*. Ibis 131: 196-204.
- Ebbinge, B.S. & B. Spaans 1995. The importance of body reserves accumulated in spring staging areas in the temperate zone for breeding in Dark-bellied Brent Geese *Branta b. bernicla* in the high Arctic. J. Avian Biol. 26: 105-113.
- EIFAC (European Inland Fisheries Advisory Commission) 1988. Report of the EIFAC working party on prevention and control of bird predation in aquaculture and fisheries operations. EIFAC Technical Paper 51.
- Guillemette, M., A. Reed & J.H. Himmelman 1996. Availability and consumption of food by Common Eiders wintering in the Gulf of St. Lawrence: evidence of prey depletion. Can. J. Zool. 74: 32-38.
- Hamilton, D.J., C.D. Ankney & R.C. Bailey 1994. Predation of Zebra Mussels by diving ducks; an enclosure study. Ecology 75: 521-531.
- Hosper, H. 1997. An ecosystem approach to the restoration and management of shallow lakes in the Netherlands. PhD thesis, University of Wageningen, Wageningen, the Netherlands.

- Karasaov, W.H. 1990. Digestion in birds: chemical and physiological determinants and ecological implications. *Studies in Avian Biology* 13: 391-415.
- Kålås, J.A., T.G. Heggberget, P.A. Bjørn & O. Reitan 1993. Feeding behaviour and diet of Goosanders (*Mergus merganser*) in relation to salmonid seaward migration. *Aquat. Living Resour.* 6: 31-38.
- Kirchhof, K. 1979. Nahrungsökologische Untersuchungen an benthosfressenden Enten in der Hohwachter Bucht. Diplomarbeit, University of Kiel.
- Lovvorn, J.R. & M.P. Gillingham 1996. Food dispersion and foraging energetics: a mechanistic synthesis for field studies of avian benthivores. *Ecology* 77: 435-452.
- MacDonald, R.A. 1988. The Cormorant (*Phalacrocorax carbo*) in relation to Salmon fisheries. *Ibis* 130: 590.
- McWilliams, S.R., D. Afik & S. Secor 1997. Patterns and processes in the vertebrate digestive system. *Trends Ecol. Evol.* 12: 420-422.
- Meininger, P.L. & F.A. Arts 1997. De Strandplevier *Charadrius alexandrinus* als broedvogel in Nederland in de 20e eeuw. *Limosa* 70: 41-60.
- Moerbeek, D., W.H. Van Dobben, E.R. Osieck, G.C. Boere & C.M. Bungenberg De Jong 1987. Cormorant damage prevention at a fishfarm in the Netherlands. *Biol. Cons.* 39: 23-38.
- Nehls, G. 1989. Occurrence and food consumption of the Common Eider (*Somateria mollissima*) in the Wadden Sea of Schleswig Holstein. *Helgol. Meeresunters.* 43: 385-393.
- Nehls, G. 1995. Strategien der Ernährung und ihre Bedeutung für Energiehaushalt und Ökologie der Eiderente (*Somateria mollissima*) (L., 1758). PhD thesis, University of Kiel.
- Nilsson, L. 1970. Food-seeking activity of south Swedish diving ducks in the non-breeding season. *Oikos* 21: 145-154.
- Nilsson, L. 1980. Wintering diving duck populations and available food resources in the Baltic. *Wildfowl* 31: 131-143.
- Noordhuis 1997. Watersysteemrapportage Randmeren. RIZA rapport 95.003, Rijkswaterstaat RIZA, Lelystad.
- Noordhuis, R. 1997. Biologische monitoring zoete rijkswateren: watersysteemrapportage Randmeren. RIZA rapport 95.003.
- Noordhuis, R., E.C.L. Marteijn, R. Noordhuis, S. Dirksen & T. Boudewijn 1997. The trophic role of Cormorants *Phalacrocorax carbo* in freshwater ecosystems in the Netherlands during the non-breeding period. In: M. Gromadzki & J. Gromadzka (eds.) Proceedings third international conference on Cormorants in Europe, Polish Academy of Sciences, Institute of Ecology, Gdansk. *Ekologia Polska* XLV. No 1/1997: 249-262.
- Odum, E.P. 1959. *Fundamentals of Ecology*. Saunders, Philadelphia.
- Owen, M., R. L. Wells & J. M. Black 1992. Energy budgets of wintering Barnacle Geese: the effects of declining food resources. *Ornis Scand.* 23: 451-458.
- Pedroli, J.C. 1981. Les relations entre la Moule Zébrée *Dreissena polymorpha* (Pallas) et les oiseaux aquatiques. PhD thesis, University of Neuchâtel, Neuchâtel.
- Persson, H. 1992. De invloed van de jacht op de omvang van de broedpopulaties van de Grauwe Gans *Anser anser*. *Limosa* 65: 41-47.
- Piersma, T. 1994. Close to the edge: energetic bottlenecks and the evolution of migratory pathways in Knots. PhD thesis University of Groningen, Het Open Boek, Den Burg, Texel, the Netherlands.
- Piersma, T. & S. Van de Sant 1992. Pattern and predictability of potential wind-assistance for waders and geese migrating from West Africa and the Wadden Sea to Siberia. *Ornis. Svecica* 2: 55-66.
- Platteeuw, M., J.H. Beekman, T.J. Boudewijn & E.C.L. Marteijn 1992. Aalscholvers *Phalacrocorax carbo* in het Ketelmeer buiten de broedtijd: aantallen, prooikeuze en voedselaanbod. *Limosa* 65: 93-102.
- Platteeuw, M. & B. Spaans 1983. Beweiding: een zinvol beheer ten behoeve van waterwild? Student report, University of Groningen.
- Prop, J., M.R. Van Eerden & R.H. Drent 1984. Reproductive success of the Barnacle Goose *Branta leucopsis* in relation to food exploitation on the breeding grounds, western Spitsbergen. *Norsk Polarinst. Skr.* 181: 87-117.
- Prins, H.H., R.C. Ydenberg & R.H. Drent 1980. The interaction of Brent Geese (*Branta bernicla*) and Sea Plantain (*Plantago maritima*) during spring staging: field observations and experiments. *Acta Bot. Neerl.* 29: 585-596.
- Prop, J. & C. Deerenberg 1995. Spring staging in Brent Geese *Branta bernicla*: feeding constraints and the impact of diet on the accumulation of body reserves. *Oecologia* 87: 19-28.
- Ruggerone, G.T. 1986. Consumption of migrating juvenile salmonids by gulls foraging below a Columbia River dam. *Trans. Am. Fish Soc.* 115: 736-742.
- Scott, D.A. & P.M. Rose 1996. Atlas of *anatidae* populations in Africa and western Eurasia. Wetlands International Publication

41. Wetlands International, Wageningen.

- Staub, E., A. Krämer, R. Müller, Ch. Ruhle & J. Walter 1992. Einfluß des Kormorans (*Phalacrocorax carbo*) auf Fischbestände und Fangerträge in der Schweiz. Schriftenreihe Fischerei 50, Bundesamt für Umwelt, Wald und Landschaft, Bern.
- Suter, W. 1982a. Der Einfluß von Wasservögel auf Populationen der Wandermuschel *Dreissena polymorpha* (Pall.) am Untersee/Hochrhein (Bodensee). Schweiz. Z. Hydrol. 44: 149-161.
- Suter, W. 1982b. Vergleichende Nahrungsökologie von überwinternden Tauchenten (*Bucephala*, *Aythya*) und Bläßhuhn (*Fulica atra*) am Untersee-Ende/Hochrhein (Bodensee). Orn. Beob. 70: 225-254.
- Suter, W. 1991. Der Einfluß fischfressender Vögelarten auf Süßwasserfisch-Bestände: eine Übersicht. J. Orn. 132: 29-45.
- Suter, W. 1995. The effect of predation by wintering Cormorants *Phalacrocorax carbo* on Grayling *Thymallus thymallus* and Trout (*salmonidae*) populations: two case studies from Switzerland. J. Appl. Ecol. 32: 29-46.
- Ulenaers, P., J. Van Vesslem & A.A. Dhondt 1992. Foraging of the Great Crested Grebe in relation to food supply. J. Anim. Ecol. 61: 659-667.
- Van Dam, C., A.D. Buijse, M.R. Van Eerden, J.G.P. Klein Breteler & R. Veldkamp 1995. Aalscholvers en beroepsvisserij in het IJsselmeer, het Markermeer en noordwest-Overijssel. Report Reference Centre for Nature Management IKC, Wageningen, the Netherlands.
- Van Eerden, M.R. 1984. Waterfowl movements in relation to food stocks. In: P.R. Evans, J.D. Goss-Custard & W.G. Hale (eds.) Coastal waders and wildfowl in winter. Cambridge University Press, Cambridge: 84-100.
- Van Eerden, M.R., J.T. Vulink, G.K.R. Polman, H.J. Drost & W. Oosterberg 1995. Oostvaardersplassen, 25 jaar pionieren op een weke bodem. Landschap 12: 23-39.
- Van Nes, E.H. & E.C.L. Marteijn 1991. Watervogels in het Volkerak-Zoommeer; ontwikkelingen in de eerste twee jaar na afsluiting (1987-1989). Limosa 64: 155-164.
- Veldkamp, R. 1996. Cormorants *Phalacrocorax carbo* in Europe. A first step towards a European management plan. National Forest and Nature Agency, Copenhagen, Denmark and National Reference Centre for Nature Management, Wageningen the Netherlands.
- Vulink, J.T. & M.R. Van Eerden 1998. Herbivory and waterlevel regime as key operators for ecosystem development in Dutch man-made wetlands. In: M.F. Wallis de Vries, J.P. Bakker & S.E. Van Wieren (eds.) Grazing and ecosystem management. Chapman & Hall, London, in press.
- Wood, C. C. 1987a. Predation of juvenile Pacific Salmon by the Common Merganser (*Mergus merganser*) on eastern Vancouver Island. I: Predation during seaward migration. Can. J. Fish. Aquat. Sci. 44: 941-949.
- Wood, C. C. 1987b: Predation of juvenile Pacific Salmon by the Common Merganser (*Mergus merganser*) on eastern Vancouver Island. I: Predation of stream-resident juvenile salmon by merganser broods. Can. J. Fish. Aquat. Sci. 44: 950-959.
- Zuur, B., W. Suter, A. Kramer 1983. Zur Nahrungsökologie auf dem Erntinger Becken (Bodensee) überwinternder Wasservögel. Orn. Beob. 80: 247-262.



Samenvatting

*Wo grade, wenn man nichts versteht
der Schnabel um so leichter geht*

Wilhelm Busch

Dit werk is de neerslag van een onderzoek naar de draagkracht van Nederlandse zoetwatergebieden (*wetlands*) voor water- en moerasvogels. In een heel scala van verschillende biotopen, ondiep en diep open water, ondergedoken waterplanten, zoetwatermoerassen en brakke graslanden zijn studies verricht naar de relaties tussen de aanwezige voedselvoorraad en de benutting ervan door watervogels.

Daarnaast is de huidige situatie voor wat betreft het voorkomen van *wetlands* in Nederland vergeleken met de toestand voordat de mens zijn overheersende rol in het landschap ging spelen. Het bleek dat viseters en bodemfauna-eters in aantal zijn afgenomen door inpoldering en drainage van natte gebieden. Ook de rol van de landbouw als voedselleverancier voor de planteneterende watervogels is belicht. Deze heeft voor de planteneterende watervogels een enorme verhoging van de draagkracht betekend; met name de grote soorten zijn een groot deel van het jaar afhankelijk van wat de landbouwgebieden te bieden hebben.

In de winter krijgen watervogels te maken met vier belangrijke beperkingen, die bepalend zijn voor het inschatten van de draagkracht van de *wetlands*. Naast bereikbaar voedsel zijn drie ervan terug te voeren op de fysiologie van de vogels zelf. De afkoeling door het water schroeft het metabolisme op, waardoor de voedselconsumptie van de in het water levende soorten in de winter tenminste een factor twee hoger is dan in de nazomer. De planteneters en mosseleters hebben daarnaast een probleem bij het verwerken van hun voedsel, dat van relatief lage kwaliteit is. De planteneters hebben daardoor een tijdsprobleem terwijl de benthoseters een gecombineerd tijds- en energieprobleem hebben door de hoge energetische kosten van het duiken. De viseters hebben een relatief hoog kostenniveau voor levensonderhoud en worden daarnaast geconfronteerd met zeer onvoorspelbare prooien, die bovendien moeilijk waarneembaar zijn en veel energie vragen om te vangen. Als de lasten voor de watervogels hoger zijn dan de baten kan er aanzienlijke sterfte optreden, zoals is aangetoond bij mosseletende duikeenden.

Voedselbeschikbaarheid speelt een cruciale rol bij de draagkracht van de Nederlandse *wetlands*. Uit het onderzoek zijn regels afgeleid hoe voedselbronnen worden benut en tot welke ondergrens het voedsel beschikbaar is. Watervogels putten de natuurlijke hulpbronnen uit tot een niveau dat energetisch rendabel is. Daarna stappen ze over op voedsel van minder hoge kwaliteit (energie-inhoud, bereikbaarheid), of ze vertrekken naar elders. De productie en beschikbaarheid van voedsel neemt af in de reeks bovengrondse plantaardige biomassa (zaden, bladeren), ondergrondse biomassa (wortels, knollen en bulbillen), bodemfauna, vis. De kosten van voedsel zoeken en levensonderhoud door de watervogels die erop gespecialiseerd zijn nemen in dezelfde volgorde toe. De viseters komen daarmee in de laagste dichtheden voor (hebben het grootste ruimtebeslag) gevolgd door benthoseters en planteneters.

Aan deze vaststelling kunnen gevolgen worden verbonden voor het beleid ten aanzien van ontwikkeling, beheer en onderzoek van *wetlands*. De Nederlandse *wetlands* zijn van grote (internationale) betekenis als pleisterplaats en overwinteringsgebied voor watervogels. Voor de herbivoren onder de watervogels zijn de *wetlands* vooral een plek waar wordt gerust. Voedsel wordt verkregen op het boerenland waar soms sprake is van schade. Deze soorten zijn sterk afhankelijk van het landbouwbeleid, aangezien de kwaliteit van het voedsel door de rassenkeuze en de bemestingsgraad wordt bepaald. Een teruglopende kwaliteit van de landbouwgewassen ten gevolge van een verminderde stikstofgift zal mogelijk leiden tot een herverdeling van de vogels, die vooralsnog geen alternatieven hebben door het wegvallen van de natuurlijke voedselbronnen.

Bij een ongewijzigd beleid bestaat een niet gering risico dat ook de natuurwaarden van de belangrijkste water- en moerasgebieden binnen afzienbare termijn sterk zullen afnemen. Veel van de belangrijkste *wetlands* zijn recent ontstaan door de aanleg van polders (Zuiderzeeproject) en de afsluiting van zeegaten (Deltaproject, Lauwersmeer, IJsselmeer). In deze gebieden, die ecologisch gezien erg jong zijn, komen watervogels in de eerste 25-50 jaar na aanleg van nature in hoge dichtheden voor. Echter, de voortgaande successie zal ertoe leiden dat, zonder aanvullende maatregelen, deze waarden gestaag in betekenis zullen afnemen. Terugbrengen van de bij deze systemen behorende natuurlijke dynamiek is een mogelijkheid om dit proces tot staan te brengen. Dat is temeer belangrijk daar elders belangrijke *wetlands* zijn verdwenen en de druk op de overgebleven gebieden verder zal toenemen.

Bij natuurontwikkeling in *wetlands* zou daarom het voedselweb in het systeem als basis moeten dienen voor de te nemen maatregelen en niet alleen de landschappelijke waarde die vooral een esthetisch oogmerk dient.

Uitgangspunten en vraagstelling

Water vormt de kern van het leven. Natte natuurgebieden zijn van onschatbare waarde voor bijzondere leefgemeenschappen. Zoetwatergebieden zijn schaars op mondiaal niveau; de ondiepe, 's winters niet bevrozende delen vormen een belangrijk toevluchtsoord voor watervogels. In Nederland gaat het daarbij voor wat betreft de eenden, ganzen en zwanen om c. 3,5 miljoen vogels (Koffijberg *et al.* 1997, Rose 1995, Rose & Scott 1994).

Veel van de oorspronkelijk natte gebieden zijn gedraineerd, ontgonnen en van bestemming veranderd. Het is daarom van groot belang de bestaande gebieden te beschermen door regelgeving en een adequaat beheer. Daarnaast is het van belang nieuwe gebieden te creëren die als *wetland* kunnen functioneren. Om deze te kunnen inrichten en te beheren is kennis nodig van het ecosysteem. De samenstelling van de componenten (inventarisatie), de veranderingen erin (*monitoring*) en de relaties tussen de componenten in het systeem (procesonderzoek) vormen de pijlers van het ecosysteem onderzoek. Het onderzoek dat hier wordt beschreven heeft tot doel voor een aantal karakteristieke Nederlandse *wetlands* een analyse te maken van de relaties die er bestaan tussen watervogels en hun voedsel. In dit onderzoek staat het begrip *Carrying Capacity*, het dragend vermogen van *wetlands* voor de verschillende groepen, centraal.

Opzet van het onderzoek en methoden

Als leidraad bij het onderzoek kan de schematische doorsnede door een *wetland* dienen (Hoofdstuk 1, Figuur 2). De verschillende onderzoekssituaties zijn hierin via de nummers van de betreffende hoofdstukken terug te vinden. Deze figuur komt terug in de synthese in Hoofdstuk 20 (Figuur 4), wanneer

generaliserende conclusies worden getrokken na koppeling van de resultaten uit de verschillende deelstudies.

Het onderzoek belicht vooral de rol van voedsel als factor die het voorkomen van watervogels in de winter bepaalt. Bij de beschrijving van de voedselkeus is steeds geprobeerd eventuele selectie aan te tonen voor voedselsoorten of lengteklassen binnen een soort.

Herbivore watervogels produceren met grote regelmaat keutels; hierin is het aanwezige celwandmateriaal van de gegeten planten nog goed herkenbaar en op soort te brengen en zodoende kan een goed beeld van het dieet worden verkregen. De keuteltellingen zijn in het veld een maat voor de begrazingsdruk als het interval tussen twee opeenvolgende keutels bekend is. De vegetatie werd bemonsterd op samenstelling en kwaliteit. Soms werd daarbij gebruik gemaakt van luchtfoto's om de grootschalige patronen in beeld te brengen.

Benthivore duikeenden werden op hun voedselvuchten gevolgd met behulp van radar. Vogeltellingen op het IJsselmeer werden uitgevoerd vanuit de lucht. De bodemfauna werd integraal gekarteerd in het IJsselmeer en Markermeer in 1981/1982 en opnieuw in 1994/1995. Dode eenden die 's nachts op de voedselgronden gevangen waren in staand water werden van vissers betrokken. Analyse in het laboratorium gaf informatie over prooikeus, biometrie en conditie.

Bij de viseters werd de voedselsituatie vooral met proefbevissingen vastgesteld, aangevuld met sonarmetingen in transecten. Ook hier werden dode vogels verzameld voor dieet studies. In totaal werden c. 10 000 vogels verzameld, waarvan 4500 duikeenden, 2000 futen, 2500 zaagbekken en 1000 overige soorten.

De gebieden waar is gewerkt ten behoeve van deze studie zijn weergegeven in Hoofdstuk 1, Figuur 1. Vaak betrof het recent ingepolderde terreinen. Door de snelheid van successie werden deze gebieden beschouwd als voorbeeld van natuurlijke experimenten, waarbij de grote aantallen aanwezige watervogels de mogelijkheid boden meetbare gegevens te verkrijgen.

De opbouw van de studie is als volgt. In Hoofdstuk 1 wordt een inleiding gegeven in de relaties tussen vogels en voedsel. Dieren gedragen zich niet willekeurig, maar nemen iedere dag beslissingen waarheen te gaan, hoe lang te blijven en wat te eten. De *Optimal Foraging Theory* beschrijft de voedselkeuze van het dier in een optimale situatie, waarbij het volledige kennis heeft van terrein en voorkomen van voedsel. De zogenaamde *patch-use models* geven een beeld van het gedrag van een consument bij het aanboren van een *patch*, een discrete eenheid te exploiteren voedsel. Bij de rangschikking van de overige 19 hoofdstukken zijn vier delen te onderscheiden: deel I Achtergrond (hoofdstukken 2 en 3); deel II Ecologische beperkingen (hoofdstukken 4-7); deel III Watervogels en voedselbenutting (hoofdstukken 8 - 19); deel IV Synthese (hoofdstuk 20).

Deel I: Achtergrond; veranderende wetlands in Nederland

In Hoofdstuk 2 is een palaeo-geografische reconstructie gemaakt van de avifauna in verschillende perioden, tot c. 7000 jaar geleden. Als basis diende een landschapsbeschrijving uit iedere periode, die werd gekoppeld aan schattingen van de vogeldichtheid op grond van de huidige vogelaantallen in vergelijkbare habitats. Het blijkt dat de omvang van de *wetlands* enorm is geslonken en dat met name brakwatergebieden nagenoeg zijn verdwenen. Als gevolg daarvan is de opvangcapaciteit voor vis-etende en bodemfauna-etende watervogels sterk afgenomen.

In Hoofdstuk 3 wordt de rol van de intensivering van de landbouw onder de loep genomen. Geconcludeerd wordt dat tenminste 11 soorten planteneters sterk in aantal zijn toegenomen als gevolg van het gunstige voedselaanbod voor deze groep. Alle grotere soorten ganzen en zwanen zijn voor 4-7 maanden per jaar afhankelijk van landbouwgewassen. Dit geeft aan hoe kunstmatig de situatie voor deze

groep inmiddels is geworden, maar ook hoe kwetsbaar de soorten zijn voor veranderingen in het gevoerde landbouwbeleid. Vragen omtrent schade voor de landbouw en de betekenis van natuurgebieden voor de herbivoren worden besproken.

Deel II: Ecologische beperkingen

In het winterhalfjaar komen de watervogels in aanraking met een aantal beperkende factoren. Deze factoren zijn mede bepalend voor de draagkracht van een gebied en zijn om deze reden nader bestudeerd.

In Hoofdstuk 4 wordt de thermoregulatie bij watervogels besproken. Door registratie van het temperatuurverloop in gave lichamen van dode watervogels kon worden vastgesteld dat lichaamsgewicht een belangrijke factor is die de warmteoverdracht bepaalt. Vet had geen invloed, maar de mate waarin de vogels in contact komen met water bleek zeer belangrijk. Ten opzichte van een dier op het droge, werd voor zwemmen en duiken een verhoging van de warmteoverdracht gevonden van respectievelijk een factor 2,2 en 4,8. De aanwezigheid van ondiepe oevers waar de vogels de rustperiode kunnen doorbrengen zonder in contact met het water te zijn, is van grote betekenis als kostenbesparende, en daarmee draagkracht verhogende factor. In de midwinter kunnen ijsranden in grote watersystemen dezelfde functie hebben voor visetende zaagbekken.

In Hoofdstuk 5 wordt aangetoond dat bij in het wild levende vogels ook inderdaad sprake is van een verhoging van de energie-behoefte in de winter om de kosten van afkoeling te compenseren. Futen op het IJsselmeer blijken in de winter in koud water twee keer zoveel te eten als in de nazomer.

In Hoofdstuk 6 wordt het probleem van de verteerbaarheid bij de herbivoren besproken. Bij deze groep heeft een oppervlakkige vertering van het opgenomen plantenmateriaal tot gevolg dat de vogels veel tijd aan eten moeten besteden, soms wel 15 uur per dag. De grotere soorten verteren het voedsel beter dan de kleinere soorten dankzij een langere verblijftijd in het maag-darm kanaal. Bij dezelfde doorloopsnelheid van 0.2 mm s^{-1} is het voedsel langer onderweg in de langere tractus van de grote ganzen en zwanen ten opzichte van die van de kleine ganzen en eenden. Kleine vogelherbivoren zijn daardoor gevoeliger voor veranderingen in de kwaliteit van het voedsel dan grotere soorten. Ze zijn gedwongen selectiever te foerageren: de kleinste onderzochte soort, de Wintertaling, is niet in staat op een dieet van grasbladeren te leven, zoals de iets grotere Smient wel kan. Plantenzaden zijn, samen met ondergrondse plantendelen zoals tubers, stolonen en bulbillen, voedsel van superieure kwaliteit en van groot belang om vetreserves aan te leggen in het najaar.

In Hoofdstuk 7 wordt een massale sterfte besproken onder duikeenden. Deze vond plaats onder invloed van koud weer, bij voedselschaarste en laat in de tijd (februari-maart 1986). Het onvermogen van de eenden om nog weg te trekken wordt verklaard door een combinatie van factoren, waarbij de tijd in het jaar de eenden waarschijnlijk op het verkeerde been heeft gezet; in normale winters is de kans op een zo laat intredende langdurige vorstperiode minimaal en voldoet afwachten van de koude-inval in de meeste gevallen.

Deel III: Watervogels en voedselbenutting

Foerageerstrategieën

Watervogels zoeken hun voedsel niet *at random*, maar volgen een bepaalde foerageerstrategie. Bij de herbivoren kon de zogenaamde *Fixed Time Strategy* worden vastgesteld (bij Wintertalingen in een hoogst onvoorspelbare omgeving (Hoofdstuk 9) en ook de *Rate Assessor Strategy* (bij Kleine Zwanen in een omgeving met een lage dichtheid aan Fonteinkruidknollen (Hoofdstuk 10). Bij een aantal

soorten was in het veld sprake van de zogenaamde *Bayesian Foraging Strategy*. Daarbij bezit het dier een zekere voorkennis bij de beoordeling van de voedselvoorraad. De vogels zijn niet in staat de kwaliteit van de *patches* exact in te schatten; ze benaderen deze zo goed mogelijk op grond van reeds opgedane kennis. *Bayesian Foragers* zullen, op grond van de verwachting van de kwaliteit van de gemiddelde patch, een rijke plek onderbenut laten en een arme overbenutten. De gewoonte van veel watervogels om in groepen te fourageren draagt ook bij tot onderbenutting van rijke, en overbenutting van arme plekken. Omwille van het verblijf in de groep zullen vogels die geconfronteerd worden met slechte plekken, toch doorgaan met voedsel zoeken; rijke plekken zullen worden opgegeven als de groep vertrekt op grond van de gemiddelde benutting van de gehele voedselvoorraad.

Er zijn drempelwaarden in de voedseldichtheid waar beneden het niet lonend is voor vogels om de bron verder te exploiteren. Fraaie voorbeelden van dergelijke voedseldrempels werden vastgesteld bij Kleine Zwanen die de knolletjes van Schedefonteinkruid uit de waterbodem opgraven (Hoofdstuk 10). Ook bij Grauwe Ganzen die de zaden van Fioringras afritsen werd zo'n drempel gevonden (Hoofdstuk 11). Experimenteel kon worden vastgesteld dat wilde ganzen een hogere drempel ($c. 12 \text{ g m}^{-2}$) hanteerden dan in experimenten met tamme ganzen op dezelfde vegetatie werd gevonden (5.8 g m^{-2}). De hogere drempel bij de wilde ganzen werd in verband gebracht met de tijdsdruk waaronder deze vogels opereren. Op doorreis naar Spanje verblijven ze slechts enkele weken in het gebied en benutten de voedselvoorraad zodoende niet uitputtend.

Bij de op Driehoeksmosselen fouragerende duikeenden werd een aanwijzing verkregen dat ook hier sprake is van een ondergrens ($c. 50 \text{ gFW m}^{-2}$); deze grens verschoof naar hogere waarden bij toenemende diepte (Hoofdstuk 14), zoals werd verwacht op grond van de toenemende duikkosten van de eenden. Ook kon in een experimentele situatie in het veld worden vastgesteld dat de exploitatie van de mosseldichtheid in een *patch* afhankelijk is van de omgevingsdichtheid. In een rijke omgeving wordt dezelfde dichtheid minder ver teruggebracht dan in een arme omgeving. Ook hier kan het fourageren in groepen weer de reden zijn voor de gevonden patronen.

Bij de visetende soorten bepaalt de lichthoeveelheid onder water de bereikbaarheid van de prooi. Voor Futen in de rui was het mogelijk om kritische dichtheden voor de belangrijkste prooi-soort, Spiering, aan te tonen (Hoofdstuk 16). Bij Nonnetjes die in de winter in groepen de dan aanwezige Spiering bejagen kon de keuze van de vogels worden verklaard vanuit de visdichtheid in combinatie met het onderwater lichtklimaat. Het in groepen vissen stelt de vogels in staat de Spiering te concentreren in de bovenste waterlaag, maar dit gaat het best bij intermediaire lichtomstandigheden (Hoofdstuk 18).

Uitputting van de voedselvoorraad

Voedsel is niet ongelimiteerd voorhanden, en daarnaast is niet al het aanwezige voedsel toegankelijk of energetisch rendabel te exploiteren. Door traditievorming kunnen tijdens de voor- en najaarstrek betrouwbare voedselbronnen jaarlijks worden geëxploiteerd. Bij de herbivore ganzen werd aangetoond dat deze traditievorming door de aanwezige voedselvoorraad kan worden beïnvloed. In de loop van acht jaar kwamen Brandganzen zo'n drie weken eerder naar de Lauwersmeerpolder om er te kunnen profiteren van de rijke voorraad Zeekraalzaad die ze met de eerder in de tijd arriverende Smienten moesten delen. Toen de versnelling in het trekschema niet langer beloond werd doordat de voedselvoorraad terugliep vanwege natuurlijke successie, kwamen de ganzen weer later naar het gebied toe. Dat betekent dat voedselvoorraden op een hoog schaalniveau worden gewogen (Hoofdstuk 8). Ook de rui-traditie bij de Grauwe Gans in de rietmoerassen in Flevoland (Hoofdstuk 12) is een voorbeeld van zo'n langjarige reactie op een nieuwe voedselbron. Ondanks het feit dat Riet al vanaf 1972, vier jaar na de inpoldering van Zuid Flevoland, dominant aanwezig was in de polder, duurde het toch tot het eind van de jaren 80 voor de hoogste aantallen ruiers werden geteld. De toename in de Oostvaardersplassen

liep echter parallel met de aantalstoename in west Europa zodat er geen sprake was van een vertraagde reactie omdat de fractie ruiers ten opzichte van het totaal ongeveer gelijk bleef. Het nieuw ontstane gebied kon uitgroeien tot de belangrijkste ruiplaats voor de soort in Europa.

Bij de graszaad-etende Grauwe Ganzen in de Lauwersmeer zijn aanwijzingen dat de benutting van de vegetatie ondergeschikt was aan het primaire belang zo snel mogelijk in Spanje te zijn. Niet de gehele zaadvoorraad van Fioringras werd benut, en andere soorten planten werden nauwelijks in het dieet gekozen, terwijl de experimenten met ganzen in een ren op de vegetatie aantoonde dat dit wel degelijk lonend was. Optimalisering van de timing van de trek was hier belangrijker dan het continueren van de opgebouwde conditie op andere soorten (bij een overigens langere werkdag, Hoofdstuk 11).

Kleine Zwanen, afkomstig uit de Russische broedgebieden pleisteren op de herfsttrek in het Baltische gebied, vergelijkbaar met de Grauwe Ganzen die in Nederland op weg naar Spanje een tussenstation aandoen. Op de herfsttrek eten de zwanen bij voorkeur waterplanten. Het onderzoek in het Lauwersmeer heeft aangetoond dat de Kleine Zwanen de knollen van Fonteinkruid in de periode na 1989 minder sterk begrazen dan ervoor (Hoofdstuk 10). Deze verandering werd in verband gebracht met een mogelijke verandering in het voedsel in het Baltische gebied; de zwanen zouden in afhankelijkheid van de opgebouwde conditie, in Nederland meer of minder moeite doen voor een uitputtende exploitatie van het voedsel. Zo worden voedselvoorraden niet alleen beoordeeld op grond van hun lokale beschikbaarheid, maar ook op grond van de voedselrijkdom op andere pleisterplaatsen van de *flyway*.

Bij benthoseters en viseters beschikken we niet over dergelijk gedetailleerde informatie. De onder water levende prooien zijn daarvoor te moeilijk te karteren. Vast staat dat de oogstbare fractie veel lager is dan bij de herbivoren (zie onder). Kuifeenden hadden problemen met de exploitatie van in kluiten aangehechte Driehoeksmosselen, die vooral op de gemakkelijk bereikbare ondieptes voorkomen (Hoofdstuk 13). De zwemsnelheid van vissen is, naast de diepte en het lichtklimaat, de belangrijkste factor die de bereikbaarheid voor viseters verklaart. In Hoofdstuk 17 wordt aangetoond dat de watertemperatuur via het effect op de zwemsnelheid van de koudbloedige vis de vangkans beïnvloedt. In de loop van de winter gingen Futen steeds grotere prooien vangen, ondanks het feit dat er geen groei optrad. Ook op grotere diepte werden grotere prooien gevangen, echter alleen bij rustig weer en relatief heldere omstandigheden. Nog ingewikkelder was de situatie bij Middelste Zaagbekken. In Hoofdstuk 19 wordt beschreven hoe alleen de structureel grotere mannetjes in staat zijn Aal te vangen uit de geulen van het noordelijk deel van het IJsselmeer. Bij winderig weer (slecht doorzicht) werden palingen gevangen, terwijl bij rustig weer Spiering werd gevangen door alle geslacht- en leeftijdsgroepen. Het energetisch dure aalvangen was alleen mogelijk voor mannetjes, die daarvoor wel op een niveau van energieuitgave van c. 5,5 x BMR balanceerden.

Sociale status en verschillen in benutting

De sociale status van vogels is van invloed op het niveau van benutting. Bij Wintertalingen werd in een experimentele situatie vastgesteld dat de sociaal ondergeschikte vogels *patches* van lagere kwaliteit benutten (Hoofdstuk 9). Bij in het wild levende Kleine Zwanen werd vastgesteld dat grote families, die sociaal dominant zijn over eenlingen en paren, op de rijkste plekken voedsel zochten; omdat grote families echter een aaneengesloten areaal *patches* voor alle familieleden nodig hebben, is hun "opgeefmoment" eerder en de hoeveelheid voedsel die in de *patch* achterblijft dus hoger dan bij kleine families en zwanen zonder jongen (Hoofdstuk 10).

Trofisch niveau en verschillen in benutting

De voedselbereikbaarheid verschilt tussen herbivore, benthivore, en piscivore watervogels. In Hoofd-

stuk 20 is een samenvatting gegeven van de gevonden exploitatie niveaus in deze en andere studies. Het blijkt dat de hoogste benuttingsgraad van natuurlijke voedselbronnen wordt gevonden bij de herbivoren, gemiddeld 60-80%. Bij de bodemfauna-eters is dit 20-60%, terwijl de viseters de laagste fracties te zien geven: gemiddeld 5-15%. Deze verschillen zijn ook aanwezig in absolute niveaus van energie-onttrekking ($50-5500 \text{ kJ m}^{-2} \text{ y}^{-1}$). De waarneming dat in dezelfde volgorde de kosten van voedsel zoeken toenemen, evenals de dagelijkse energie-uitgave, is frappant. Hiermee geassocieerd is het ruimtebeslag van viseters het grootst, dat van mosseleeters intermediair en dat van planteneters het kleinst.

Deel IV: Synthese; implicaties voor onderzoek, ontwikkeling en beheer van wetlands

Over de rol van viseters in watersystemen is onvoldoende bekend. Dringende vragen voor de nabije toekomst zijn hoe de viseters 's winters duurzaam aan vis kunnen komen en hoe het dilemma van de afgesloten watersystemen opgelost kan worden. Lauwerszee, Grevelingen en IJsselmeer zijn alle drie belangrijke leefgebieden voor viseters, maar vooral de kleinere systemen (Lauwerszee, Grevelingen) worden gekenmerkt door een afname van de aantallen. Te vrezen valt dat dit op termijn ook voor het IJsselmeer verwacht kan worden (vgl. Hoofdstuk 14 voor duikeenden, De Leeuw 1997). De toegenomen waterkwaliteit zorgt voor grotere helderheid, waardoor het vissen moeilijker wordt. Herstel van de natuurlijke dynamiek kan leiden tot een structurele toename van trekvis en benthos, hetgeen voor watervogels ook op de lange termijn een gunstige voedselsituatie garandeert. Daarvoor is het noodzakelijk dat experimenten worden opgezet, analoog aan en zo mogelijk op grotere schaal dan die in het Haringvliet.

Anderszijds heeft de toegenomen helderheid een positief effect op de terugkeer van waterplantenvegetaties ten behoeve van herbivore watervogels. Het spectaculaire herstel van kranswieren in de Randmeren van Flevoland en elders heeft enorme gevolgen voor de draagkracht van deze gebieden voor herbivore en benthivore watervogels (Noordhuis 1997).

Wat betreft implicaties voor natuurontwikkeling kan gesteld worden dat deze studie heeft aangetoond dat een aantal gerichte maatregelen genomen kan worden om de draagkracht te vergroten. Eén ervan is het voorzien van watergebieden (waar nodig) van eilanden en ondieptes waar watervogels in de winter het contact met het water (en dus sterke afkoeling) kunnen verminderen tijdens het rusten. Een andere betreft het herstellen van de van nature voorkomende gradiënt-situaties, als voedselweb gegevens aangeven dat componenten uit het systeem ontbreken. Het huidige beleid, waarbij *ad hoc* acties nog vaak domineren, is te marginaal georiënteerd (oeverbeheer) en teveel gericht op landschappelijk aanzien alleen. In plaats daarvan zou het interne draagvlak meer moeten worden vergroot door het creëren van duurzaam te benutten voedselvoorraden.

Literatuur

- De Leeuw, J.J. 1997. Demanding Divers. Ecological energetics of food exploitation by diving ducks. PhD thesis, University of Groningen; Van Zee tot Land 61, Rijkswaterstaat, Directorate IJsselmeergebied, Lelystad, the Netherlands.
- Koffijberg, K., B. Voslamber & E. Van Winden 1997. Ganzen en zwanen in Nederland. Overzicht van pleisterplaatsen in de periode 1985-94. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.
- Noordhuis, R. (ed.) 1997. Biologische monitoring zoete rijkswateren: watersysteemrapportage Randmeren. RIZA rapport 95.003.
- Rose, P.M. 1995. Western Palearctic and south-west Asia waterfowl Census 1994. IWRB Publication 35, IWRB, Slimbridge.
- Rose, P.M. & D.A. Scott 1994. Waterfowl population estimates. IWRB Publication 29, IWRB, Slimbridge.

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