

Results

Feeding performance in relation to diving depth

The daily mussel consumption and diving behaviour of Scaup in the outdoor diving cages are summarized in Table 1. Mussel consumption was on average 2240 gFW.d⁻¹, which is equivalent to a metabolizable energy intake of 1120 kJ.d⁻¹. At a diving depth of 1 m, food consumption was significantly higher than at a depth of 3 m, but body mass was probably not maintained in the deep diving conditions, suggesting that the ducks were not in energy balance during these trials. The considerable effects of a single defecation (approximately 30 gFW) and meal size on body mass measurements, however, did not allow a more rigorous analysis. Dive duration increased with depth, while the number of dives per day tended to decrease with diving depth. Apparent intake rates also tended to decrease with depth (ANOVA: $F_{2,36} = 6.9$, $P < 0.05$), although differences between depths were not significant. Similar trends with diving depth were found in Tufted Duck at water temperatures below 10 °C (De Leeuw *et al.* *subm.*). The average daily food intake of 1607 gFW.d⁻¹ (964 kJ.d⁻¹), and apparent intake rates of the smaller sized Tufted Duck (body mass *ca.* 600 g) reported in De Leeuw *et al.* (*subm.*) were approximately 15% and 25% lower than in Scaup (800 g).

Intake rate of mussel clumps

Apparent intake rate (AIR) at a water depth of 3 m varied with the degree of byssal attachment of mussels ('tight clumps', 'moderate clumps' (see previous section), and 'loose mussels'; ANOVA: $F_{2,55} = 12.2$, $P < 0.001$), while AIR was higher in Scaup than in Tufted Duck ($F_{1,55} = 6.2$, $P = 0.02$), in particular when feeding on 'moderate clumps' (Student's *t*-test: $t = 2.7$, $P = 0.01$; see Fig. 3). AIR was significantly lower when feeding on 'tight clumps' than when feeding on 'moderate clumps' in both species (Tufted Duck: $t = 3.22$, $P = 0.004$; Scaup: $t = 3.03$, $P = 0.008$). In Scaup, there was no difference in AIR between 'moderate clumps' and 'loose mussels', but Tufted Duck were able to profit more from unattached mussels than from moderately attached mussels ($t = 2.2$, $P < 0.05$).

The byssal attachment of individual mussels in the population of 'moderate clumps' varied considerably between loose mussels (10-20% of biomass) and more

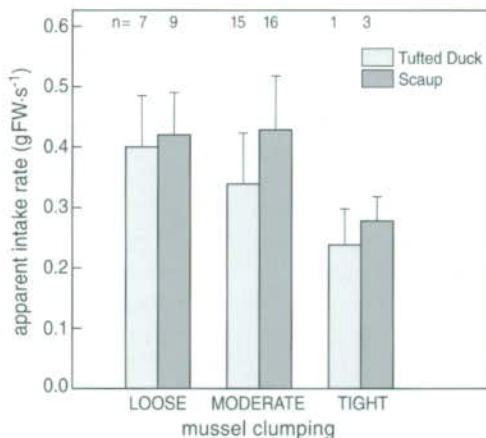


Fig. 3. Average ($\pm$ SD) apparent intake rates of mussels differing in their byssal attachment ('loose mussels', 'moderate clumps', and 'tight clumps') of Tufted Duck and Scaup feeding at a diving depth of 3 m (n is the number of experimental days).

or less tightly clumped mussels, and it seems reasonable to assume that AIR could vary accordingly with the proportion of clumps in the population. As consumption of a particular batch of mussels proceeds, the proportion of clumps might change due to depletion, thus affecting AIR. This hypothesis was tested by performing an analysis of covariance (ANCOVA) on AIR with the percentage of mussels consumed in a trial as a covariate. Because AIR varies with water temperature and diving depth (De Leeuw *et al.* *subm.*), these parameters were also introduced in the model as covariates, and individual duck as a factor. The percentage of mussels consumed ranged from 20-80% in both species, but did not affect AIR in Tufted Duck (Water temperature: $F_{1,56} = 52.5$, $P < 0.001$; Depth: $F_{1,56} = 7.2$, $P = 0.01$; Duck: $F_{2,56} = 12.8$, $P < 0.001$; after backward deletion of interactions ($P > 0.05$) and Percentage of mussels consumed $F_{1,55} = 0.02$, $P = 0.65$) and Scaup (Water temperature: $F_{1,74} = 9.5$, $P = 0.003$; Depth: $F_{1,74} = 8.8$, $P = 0.004$; after backward deletion of interactions, Duck ($P > 0.05$), and Percentage of mussels consumed $F_{1,73} = 0.1$, $P = 0.80$). This suggests that the ducks did not strongly select for either unattached mussels or tight clumps, or, if so, this did not affect the intake rates.

Size selection

Both Tufted Duck and Scaup showed a slight preference for mussel sizes in the range of 7 to 16 mm (Fig. 4), although mussel sizes in the entire size range up to 30 mm were taken. Tufted Ducks feeding on unattached mussels under equivalent diving conditions (De Leeuw & Van Eerden 1992) were more selective than the ducks feeding on mussel clumps in this study. Analysis of covariance was used to test for effects of depletion (percentage of biomass consumed per trial, 30–65% in both species), water temperature, and diving depth (covariates), and species (factor) on the selectivity for the most preferred size classes (7–16 mm). There was no difference in selectivity for these small sizes among diving depths and species (ANCOVA, $P > 0.05$), although Scaup tended to be less selective than Tufted Duck (Fig. 4). Selectivity decreased with the percentage of biomass consumed ($F_{1,50} = 9.2$, $P = 0.004$) and increased with water temperature ($F_{1,50} = 10.4$, $P = 0.002$).

Depletion did not affect the apparent intake rate (AIR, see previous section), but its effect on selectivity may indirectly influence feeding effort *via* the energy value of mussels, because the condition of mussels decreases slightly with mussel size. In order to facilitate comparison between trials and species, the relationship between mussel size and condition of mussels (in

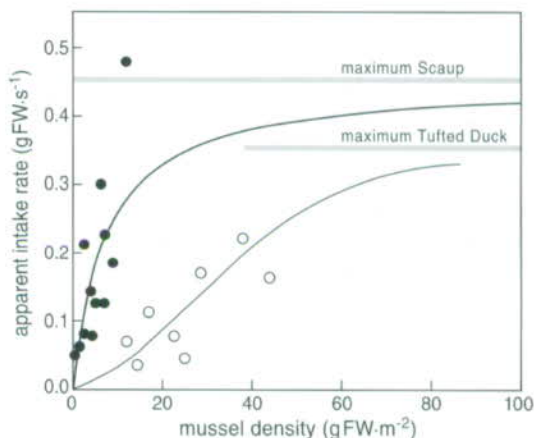


Fig. 5. Functional response of Scaup and Tufted Duck feeding on mussel clumps in a 45 m² basin. The maximum intake rates were derived from ducks feeding in diving cages at mussel densities of more than 2000 gFW.m⁻². A 'type 2' functional response curve (Holling 1959) was fitted for the Scaup ($y = (0.45x) / (7.4 + x)$), and a 'type 3' curve for Tufted Duck due to refusals to feed at densities below 10 gFW.m⁻² (sigmoidal curve fitted by eye).

kJ.gFW⁻¹) was standardized to the energy values of mussels calculated for the Scaup experiments while fresh weights were approximated from dry shell weights (see Methods). The standardized mussel conditions decreased by less than 2% in Tufted Duck and less than 1% in Scaup when the percentage of biomass consumed increased to 60% (multiple regression: Species: $t = 6.2$, $P < 0.001$, Biomass: $t = 6.5$, $P < 0.001$). Size selection of mussels in clumps thus seems a negligible factor in the feeding performance of Scaup and Tufted Duck.

Intake rate and mussel density: the functional response

The apparent intake rates (AIR) were strongly related to densities below 50 gFW.m⁻² when the mussel clumps were randomly distributed (Fig. 5). AIR is determined by the handling time of mussels swallowed underwater and the searching time for encountering mussel clumps. For practical reasons, the 'type 2' functional response (Holling 1959) can be described as: $AIR = ax / (b + x)$, where x is density, a is the asymptotic handling time coefficient, and b is the searching

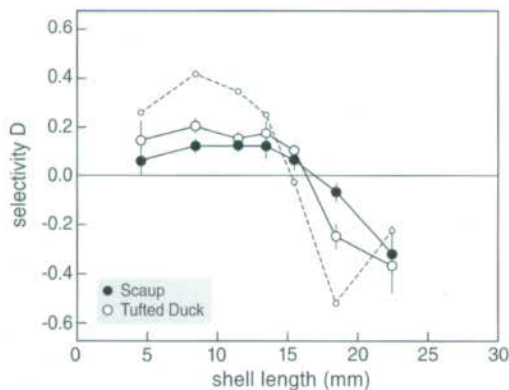


Fig. 4. Average ($\pm$ SE) selectivity in relation to mussel shell length for Tufted Duck and Scaup feeding on mussel clumps (solid lines). The broken line indicates the selectivity of Tufted Duck feeding on unattached mussels at a diving depth of 3 m (De Leeuw & Van Eerden 1992).

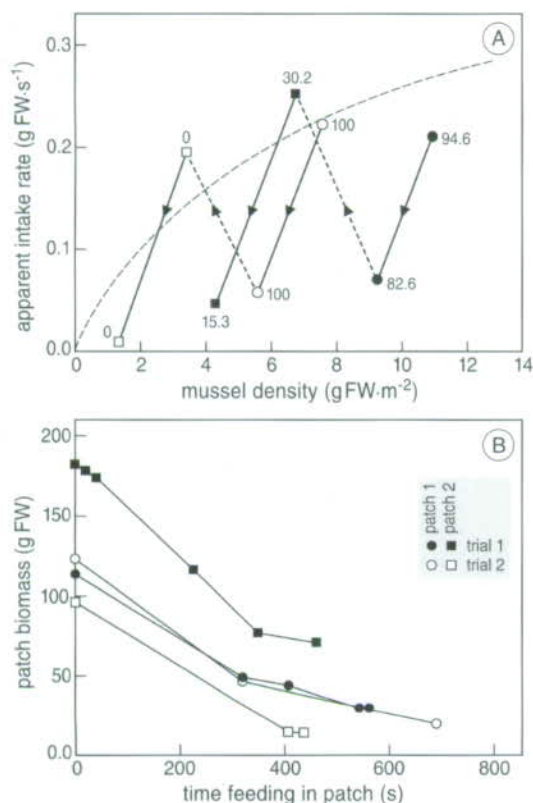


Fig. 6. A. Intake rate of Scaup in relation to the density of mussels when clustered in 2 patches. The average mussel density in the basin decreases from right to left in both trials, due to depletion by the ducks. Broken lines indicate the switch from feeding at the patch which was encountered first (circles) to feeding at the second patch (squares). Labels at the data points indicate the percentage of dives in the first patch encountered. The dashed line indicates the functional response curve of Scaup from Fig. 5. **B.** Decrease in biomass of a patch in relation to feeding time spent in each patch.

time coefficient (Lovvorn & Gillingham 1996). The handling time coefficient a (i.e. the maximum intake rate) was determined from intake rates observed in Scaup and Tufted Duck feeding in the diving cages at mussels densities of more than 2000 gFW.m⁻², and linearly interpolated to a diving depth of 1.5 m. The searching time coefficient b was subsequently fitted to the Scaup data using the least squares criterion ($a = 0.45$, $b = 7.4$). Thus, intake rate was 50% of the maximum value at a density of 7 gFW.m⁻² in Scaup,

but searching for mussels seems not of great influence to intake rates at mussel densities above 30 gFW.m⁻², where intake rates are mainly determined by handling of mussels. Intake rates of Tufted Duck were considerably lower than in Scaup at these low mussel densities. Moreover, Tufted Duck refused to feed at densities below 10 gFW.m⁻², although they were occasionally observed diving, probably in search for a more rewarding food source. For this reason, a sigmoidal 'type 3' functional response is more appropriate (Royama 1971).

When mussels were offered in 2 patches, intake rates of Scaup did not decrease monotonously with decreasing total mussel density in the basin, as observed in the randomly distributed mussels, but, in contrast, varied strongly with depletion ('saw-tooth' curves, Fig. 6A). The ducks continued to feed at the first patch that was encountered until intake rates dropped by more than 70% due to depletion of that patch and loss of feeding time during search for the next patch. Upon finding the second patch, intake rates were high again until the second patch was also depleted. Within patches, the rate of decrease of mussel biomass was similar in all trials (Fig. 6B). The results of this experiment suggest that the ducks did not perceive a sort of average density in the feeding area (basin), but instead treated patches individually and depleted them sequentially rather than searching for areas with the highest food densities. Intake rates when feeding on mussels clustered in patches were lower on average than when feeding on randomly distributed clumps.

Food processing rate

The apparent intake rate (the food intake per dive) provides insight in the efficiency at which food can be obtained by diving. However, the time to recover between dives is ignored if we use the apparent intake rate as the currency. Also, the rate of food gain may not be restricted by the rate of diving (including recovery periods) but rather by the rate at which food is processed. The rate of food processing was approximated from diving activity recordings, which yield the longer term rate of cumulative food gain, assuming a constant food gain per dive over the experimental period. The cumulative intake of three Scaup diving to 5 m over a time span of 42 h is graphically illustrated in Fig. 7. Periods of constant food intake last for several hours and alter-

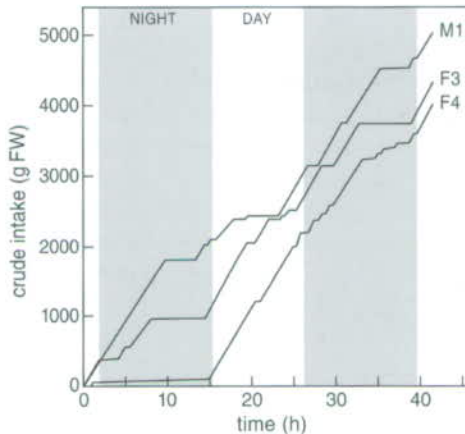


Fig. 7. Crude intake of mussels during 42 h in three Scaup diving for mussels at a depth of 5 m. The cumulative food gain was determined from diving activity, assuming a constant yield per dive over the entire feeding period.

nate with long resting periods. The timing of resting periods is quite different between the three individuals in this example and seems not related to day or night. Also, the ducks apparently did not always aim at achieving energy balance within a period of 24 hours. For example, duck F4 commenced with feeding only 15 h after the start of the experiment, but from then on continued to feed for 20 h at a constant rate. Despite the variation in timing of long resting periods, the maximum crude intake rate (slope of the curves) was very similar over periods of several h in all birds. These periods of high food intake consisted of a regular pattern of feeding bouts (a number of dives in quick succession and longer resting periods), as illustrated by a sequence of pause durations between dives of duck M1 (Fig. 8). Feeding bouts of 4 to 5 dives alternated with resting periods of 6 to 8 min. Per feeding bout 35 gFW of mussels were ingested (8 g per dive). This is close to the maximum amount of *ca.* 40 gFW of mussels found in the esophagi of 2322 dissected wild Scaup which had drowned as bycatches in fishing nets in Lake IJsselmeer (De Leeuw & Van Eerden 1995). It appears that the esophagus is filled during a feeding bout and mussels are crushed in the gizzard afterwards. Because the storage capacity of the esophagus is limited (less than 2% of the daily needs), food must be processed

rapidly. The maximum difference in body mass between the end of the resting phase of 8 h (empty gastrointestinal (GI) tract) and the end of the feeding phase (full GI tract) in the feeding time restriction experiments was *ca.* 90 g, suggesting that the amount of mussels in the gizzard and intestines (thus excluding 35 g of mussels in the esophagus) probably does not exceed 55 g. At a maximum crude intake rate of $220 \text{ gFW} \cdot \text{h}^{-1}$ in the example of M1 (Fig. 7 and 8) and a maximum storage capacity of 90 g, the throughput time of mussels would be 25 min. In agreement with this estimate, is the observation in Scaup diving for mussels in the basin in Haren, that the first defecation appeared 23 min (SD 6 min, $N = 14$) after the start of feeding. During this short period of time, the shells are crushed in the gizzard and the mussel flesh is digested.

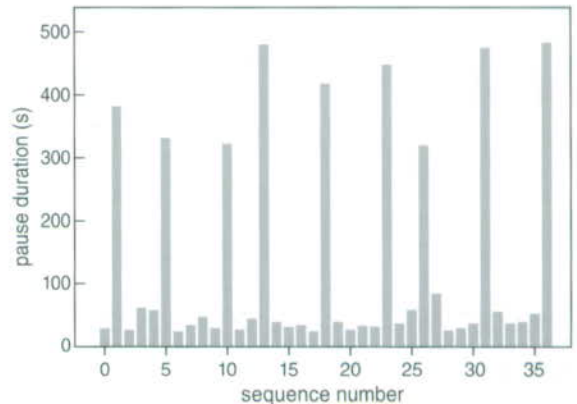


Fig. 8. Sequence of pause durations between dives of Scaup M1 diving to 5 m during 1.3 h of feeding (see Fig. 7).

The short-term resting periods between dive bouts may reflect both recovery from diving and (or) time needed for food processing (crushing mussel shells in the gizzard and digestion of flesh in the intestines). The question as to whether the observed rate of food gain reflects the maximum food processing rate or the maximum diving rate was further explored by restricting the daily feeding time to 16 h and comparing the cumulative food gain (crude intake) and the cumulative dive duration for Scaup diving to 1 m and 5 m, respectively, to create the maximum difference in diving costs

(Fig. 9). The examples shown demonstrate that the rate of food gain was similar between diving depths, but that the rate of diving was higher in deeper diving ducks. Since both diving costs and recovery duration are proportional to dive duration (De Leeuw 1996), the rate of food processing is apparently the limiting factor and recovery time from diving adjusted accordingly.

Because the rate of food processing seems mainly determined by the rate of food assimilation, it is more appropriate to express these rates per unit of digestible matter or in their metabolizable energy equivalent ($\text{kJ}\cdot\text{h}^{-1}$ crude feeding time). Concurrent estimates of daily metabolic rates from doubly labelled water, time-energy budgets, and food consumption data suggest that an assimilation efficiency as high as 85% is a proper estimate for mussel feeding birds, even though 95% of the ingested matter is indigestible (De Leeuw

et al. *subm.*). Thus, energy assimilation rates (EAR) are apparently independent of the energy content of mussels relative to the amount of indigestible matter.

In order to compare rates of food processing under different conditions and to assess the maximum energy assimilation rate (EAR_{max}), the average rates over 3-h periods (i.e. 6–8 times the estimated throughput time of mussels and thus reflecting the absorption rate) were calculated (Fig. 10). The frequency distributions of EAR in 3-h periods of Tufted Duck diving to 5 m under three different conditions: (1) feeding at high water temperatures (21°C) on clumps (mussels of high energy value, $0.6 \text{ kJ}\cdot\text{gFW}^{-1}$) and (2) loose mussels (low energy value, $0.45 \text{ kJ}\cdot\text{gFW}^{-1}$), respectively, and (3) ducks feeding on clumps at low water temperatures ($3\text{--}7^\circ\text{C}$) have been collected in Fig. 10A. EAR was not significantly different between mussels of different en-

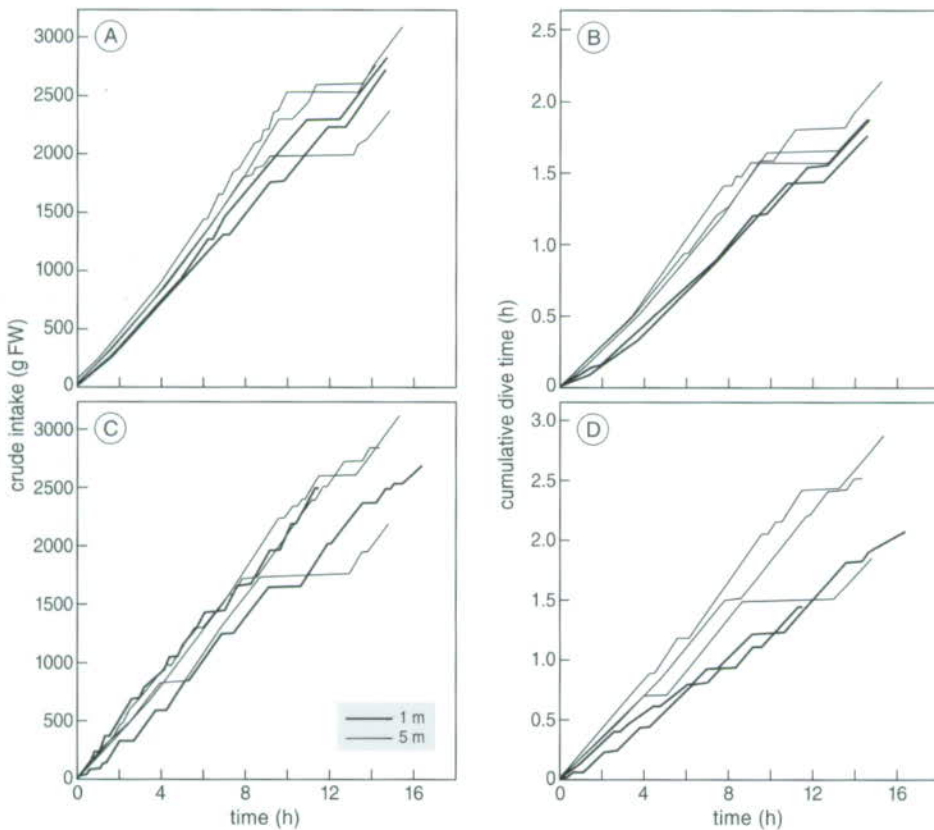


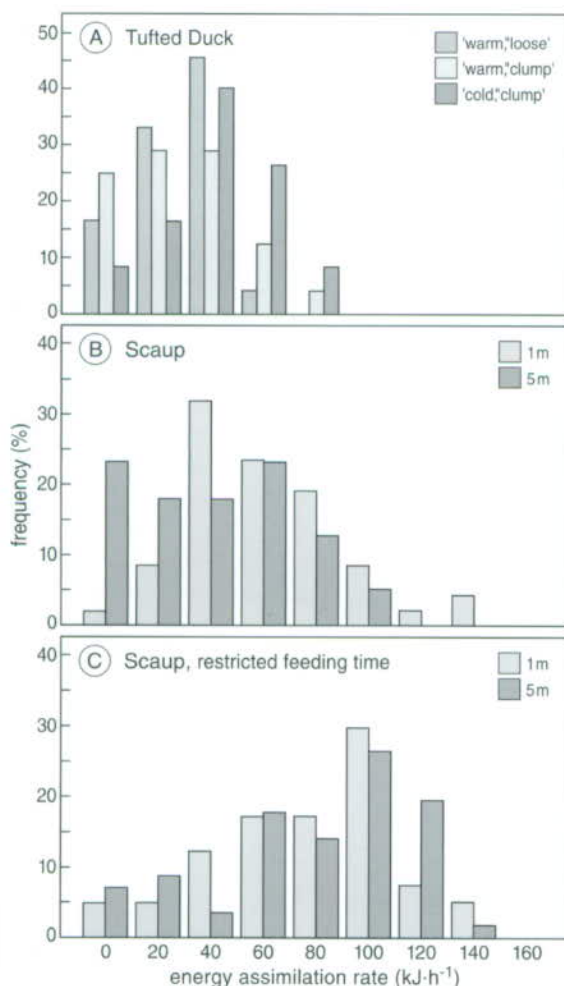
Fig. 9. Crude food intake and cumulative dive duration of Scaup M1 (A and B) and F4 (C and D), respectively, at diving depths of 1 m and 5 m during 16-h feeding periods.

Table 2. Energy expenditure of Scaup during the resting phase (7.6 h, no food offered) and during the feeding phase (10.9 h, mussels offered at a depth of 3m) determined from doubly labelled water measurements. Water temperature was 3.5 °C. The net excess diving cost (EDC) was approximated by subtracting the cost of heating up the ingested food mass from the difference in energy expenditure between the feeding phase and the resting phase.

Duck	Body mass (g)	Metabolic rate (W)		Dive duration (s)	Consumption (g)	EDC ($J \cdot s^{-1}$)
		Rest	Feeding			
M1	755	6.9	14.8	3501	1230	53
M2	770	6.1	13.1	2832	1265	55
F3 ¹⁾	700	6.2				
F4	715	8.8 ²⁾	14.4	2646	1605	59 ²⁾

¹⁾ Duck F3 did not eat during the entire measurement period

²⁾ Duck F4 was actively diving during the resting phase. For calculating the excess diving cost, the average of the resting values of the other three ducks (6.4 W) was used.



ergy value (Kolmogorov-Smirnov test, $Z = 1.15$, $P = 0.14$) with a maximum rate at about 80 $kJ \cdot h^{-1}$. EAR tended to be higher under cold conditions (K-S $Z = 1.68$, $P = 0.007$), reflecting the higher daily food consumption and thus higher average food processing rates in winter. In Scaup, the frequency distributions of EAR in the experiments with restricted feeding time were skewed to the right (Fig. 10C) as compared to the two-day unrestricted feeding times (Fig. 10B; K-S test, $Z = 2.84$, $P < 0.001$), but the maximum assimilation rate (EAR_{max}) of ca. 120 $kJ \cdot h^{-1}$ (ca. 240 $gFW \cdot h^{-1}$) was similar and did not vary with diving depth (K-S $Z = 0.52$, $P = 0.95$).

Feeding costs

Doubly labelled water measurements of Scaup in the diving cages were obtained during both resting periods and periods of feeding activity while diving to 5 m. The average metabolic rate was 6.4 W during the resting period of 7.6 h (excluding duck F4 which was actively diving) and 14.1 W during the feeding phase of 10.9 h (Table 2). Because the average food consumption dur-

Fig. 10. Frequency distributions of average assimilation rates during 3-h periods. **A.** Tufted Duck feeding on 'clumps' (0.6 $kJ \cdot gFW^{-1}$) at 21 °C ('warm', $N = 24$ 3-h periods) and 'loose' mussels (0.45 $kJ \cdot gFW^{-1}$; $N = 24$), and feeding on 'clumps' at 3.5 °C ('cold', $N = 72$). **B.** Scaup diving to 1 m ($N = 39$) and 5 m ($N = 52$) during 48-h unrestricted feeding trials, and **C.** during trials with feeding periods restricted to 16 h (1 m: $N = 45$; 5 m: $N = 52$).

ing the feeding phase was only 60% of normal values, this feeding metabolic rate should be maintained for 1.7 times longer than the 10.9 h in this experiment (i.e. 18.5 h) to meet the daily energy demand. The daily energy expenditure (DEE) can thus be approximated from the daily fraction of time feeding (at 14.1 W) and resting (at 6.4 W) yielding a DEE of $(18.5/24) \times 14.1 + ((24-18.5)/24) \times 6.4 = 12.3$ W or 1063 kJ.d^{-1} . This value is within 5% of the average of 1120 kJ.d^{-1} (or 2240 gFW.d^{-1}) estimated from daily food consumption data of Scaup (Table 1).

The energetic costs of food processing can be estimated from the energy necessary to warm up the ingested food mass from the ambient water temperature of 3°C to a core body temperature of 41°C (heat capacitance of mussels $2.8 \text{ J.g}^{-1}.\text{C}^{-1}$), assuming full substitution of heat generated by crushing shells and digestion for thermoregulation (De Leeuw *et al.* in prep.). This fraction was subtracted from the energy expenditure in excess over the resting phase, to estimate the net excess diving cost (EDC, De Leeuw 1996), which thus amounts to 56 J.s^{-1} spent underwater. This value is 12% higher than EDC measured in Tufted Duck at equivalent water temperatures (50 J.s^{-1} spent underwater, De Leeuw 1996).

The metabolic rate of resting and diving Scaup can also be estimated from body mass corrected values of oxygen consumption measurements obtained in the smaller sized Tufted Duck (body mass 600 g, Scaup 750 g), assuming that these costs scale to body mass by an exponent of 0.8 and 0.72, respectively, in diving birds (De Leeuw 1996). This would yield to 6.8 W for resting and 59 W for excess diving costs, respectively, which are only 6 and 5 % higher, respectively, than the values derived from the above mentioned doubly labelled water measurements in Scaup.

Discussion

Adjustment of diving activity to food processing rate

The maximum energy assimilation rates (EAR_{max}) were closely similar under different conditions of diving depth, time available for foraging (Scaup), and mussels of different energy value (Tufted Duck). At an EAR_{max} of *ca.* 80 kJ.h^{-1} in Tufted Duck and

110 kJ.h^{-1} in Scaup, the retention time was *ca.* 25 min. This seems a short period of time for efficient digestion, given the large amounts of indigestible matter (water and shell fragments) in the intestines (Dade *et al.* 1990). For example, Kersten & Visser (1996) measured a retention time of 28 min in Oystercatchers *Haematopus ostralegus* (body mass 500 g). These birds ingest the flesh of mussels *Mytilus edulis* without shells, but yet their intake is limited by digestion during low tide feeding periods. Thus, it seems reasonable to assume that the observed maximum food processing rates in this study cannot be exceeded without major adjustments of the gastro-intestinal tract (though Karasov (1996) indicated that many birds may be flexible in this respect). It is questionable whether these maximum rates can be sustained for much longer than several hours, because other metabolic processes than absorption in the intestines might become limiting. The maximum rate of metabolizable energy intake estimated from the allometric equation of Kirkwood (1983) is 40 kJ.h^{-1} in Tufted Duck and 50 kJ.h^{-1} in Scaup, respectively, which correspond well with the observed daily average assimilation rates in both species (Fig. 10). A notable example was Scaup F4 (the continuous diver in Fig. 7) which succeeded to feed for 24 h at a rate of energy gain of 75 kJ.h^{-1} . This would imply that longer resting periods between feeding periods are vital and that a considerable amount of energy must be stored in body tissues when feeding at EAR_{max} .

Even if foraging could be maintained at EAR_{max} until the daily energy requirements are met, the limited capacity of food storage both in the esophagus and in the intestines (imposed by the extraordinarily large mass of water and shells of mussels), would still imply a large time penalty for mussel-feeding diving ducks, as more than 95% of their daily food requirements must be digested at the feeding sites. For example, Scaup in this study would need more than 11 h to meet their daily needs, while Tufted Duck would need at least 13 h.

The timing of diving activity is apparently structured by the rate of food processing. The number of mussels gained in a dive bout indicated that the esophagus was filled with mussels, followed by a resting period of 5-10 min to crush the shells and start to digest the flesh. During a dive bout, Tufted Duck suffer from

a notable drop in body temperature, which is proportional to dive duration and the amount of cold food ingested, and the ducks need to cease diving regularly to recover from heat loss (De Leeuw *et al.* in prep.). The rate of recovery depends on the metabolic rate and perhaps long recovery durations (more than 20 min) reduce the total energetic investment in heating up the body. As demonstrated in Scaup, however, recovery periods between dive bouts are usually less than 10 min and seem to be adjusted to the rate of food processing rather than vice versa. An obvious advantage of short recovery durations is a reduction in the total duration of rest at the water surface on the foraging grounds and the accordingly longer duration of rest at sheltered day-time roosts. In the wild, diving ducks usually feed at night and rest during the day, probably because thermostatic or locomotory costs are higher at the wind-exposed foraging grounds than at the roosting sites.

Although the food intake rate itself is usually not limiting the energy procurement, the efficiency of food gathering may indirectly influence the amount of food to be processed, and thus the time needed for food processing, owing to the high feeding costs in these birds. Diving costs contribute *ca.* 25% to the daily energy expenditure of Scaup and Tufted Duck in winter, while the energy costs of food processing account for a similar amount in the daily energy expenses (Table 1 and 2; De Leeuw *et al.* *subm.*). A decrease in intake rate results in higher diving costs to obtain a given quantity of food. This extra cost must be compensated by a higher daily food intake, which also increases the food processing costs and, in turn, further increases diving costs to obtain this extra food. Thus, diving ducks face the problem that any adverse effect on feeding performance will disproportionately increase the total feeding effort on a daily basis and consequently the daily energy expenses and foraging times.

Size or site selection?

When feeding on clumps, Tufted Duck and Scaup showed a slight preference for the smaller sizes, Tufted Duck being more selective than Scaup. It must be noted that the observed selectivity for small sized mussels may partly reflect passive selection, as young (small) mussels tend to settle on older mussels at the peripheral positions of a clump and are thus more ac-

cessible to the ducks. Selectivity may be limited by the short time available for selection while diving at high energetic costs. Tufted Duck actively selected small mussels when these were not attached to any substrate and could be efficiently strained by a waterflow ('suction-feeding'), but even under these relatively favourable feeding conditions, selectivity was relaxed in diving compared with non-diving birds (De Leeuw & Van Eerden 1992).

The difference in selectivity between the species can be explained by a difference in handling ability which is related to bill morphology (cf. Goudie & Ankney 1986). Scaup accidentally caught in fishing nets in the Lake IJsselmeer area had larger bills (mean length 43 (females) - 44 (males) mm, height 17.4 - 17.9 mm; $N = 612$) than Tufted Duck (mean bill length 39 (females) - 40 (males) mm, height 14.7 - 15.2 mm; $N = 672$; De Leeuw & Van Eerden 1995), which would facilitate the ingestion of large mussels in Scaup. Also, Scaup are able to ingest bunches of mussels that are torn off from mussel clumps and swallowed as if they were single items, thereby increasing intake rate. Such bunches of (small) mussels have been frequently found in the esophagi of dissected wild Scaup, but rarely in Tufted Duck (M.R. van Eerden, unpublished data). Indeed, intake rates differed strongly between the two species when feeding on mussel clumps in contrast to feeding on unattached mussels, although tight clumps at the other extreme were difficult to handle in both species, probably because the broad bill is not suitable for grasping closely attached mussels. Thus, Tufted Duck seemed to prefer smaller sizes and seemed to be hindered more by the byssal attachment of mussels than Scaup. Tufted Duck also feed more often on other small prey items than Scaup (De Leeuw & Van Eerden 1995).

The mussel sizes found in the esophagi of wild ducks caught in fishing nets in Lake IJsselmeer and Lake Markermeer varied widely (Fig. 11, redrawn from De Leeuw & Van Eerden 1995). Mussel sizes up to 30 mm were recorded, which are the largest sizes in the population. Mussel sizes in Scaup were slightly larger than those in Tufted Duck. Both species consumed large amounts of mussels which were larger than the preferred size classes in the experiments. More small mussel sizes were taken in Lake Markermeer than in Lake IJsselmeer in both species (although

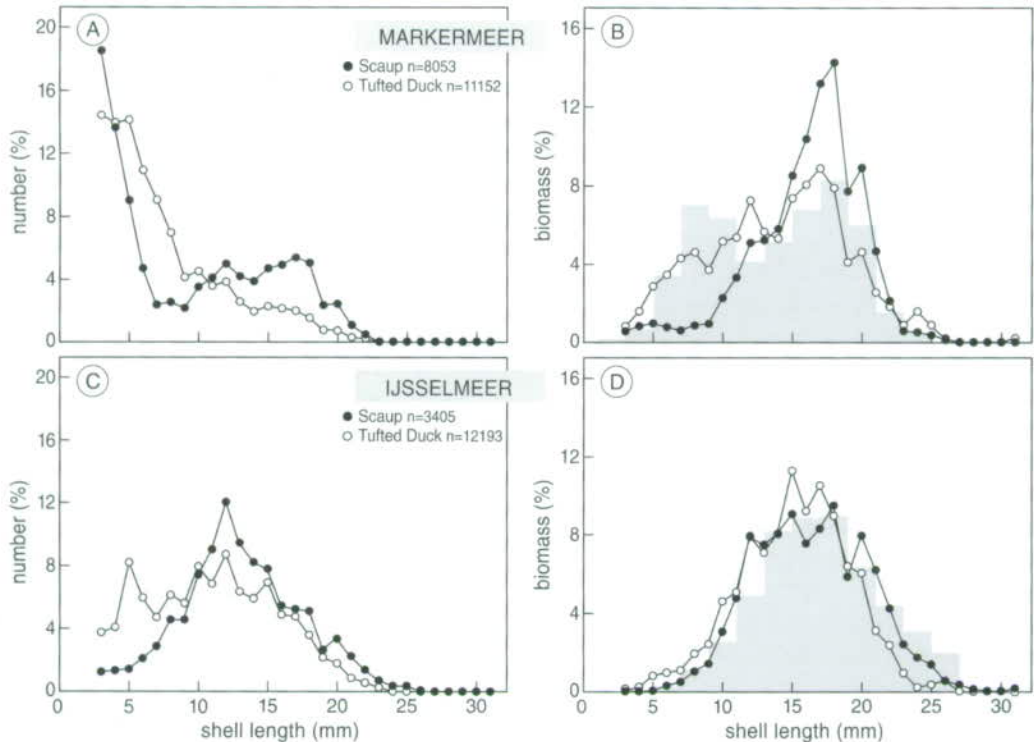


Fig. 11 Mussel sizes found in the esophagi of 445 Tufted Duck and 461 Scaup caught in fishing nets in Lake Markermeer and of 216 Tufted Duck and 960 Scaup caught in Lake IJsselmeer, respectively. *N* refers to the number of mussels measured. Percentages of numbers of mussels (left-hand panels) and fresh biomass (right-hand panels) are given. All size distributions were significantly different from each other (Kolmogorov-Smirnov 2-sample tests, $P > 0.05$). Data from De Leeuw & Van Eerden (1995). The shaded boundaries indicate size distributions of mussels in early winter as obtained from bottom samples in Lake Markermeer ($N = 1038$) and Lake IJsselmeer ($N = 1246$; Bij de Vaate, unpublished data).

this difference is small with respect to biomass), which probably reflects the distribution of sizes available in both lakes rather than active selection.

Mussel size seemed to have a smaller effect on intake rate than the byssal attachment of mussels. However, byssal attachment of mussels increases with shell length (Fig. 12A), thus favouring smaller sizes. The byssal attachment of mussels decreased with water depth and tended to be lower in Lake Markermeer than in Lake IJsselmeer (Fig. 12B; Van Eerden & De Leeuw, unpublished data). The difference in average byssal attachment is even larger between both lakes because of the prevailing smaller mussel sizes in Lake Markermeer. Because Tufted Duck seemed relatively more efficient in handling small, unattached prey that

can be easily swallowed underwater, in contrast to ingesting large prey items or several mussels attached by byssal threads, Lake Markermeer seems to offer a more profitable habitat with respect to (gross) intake rate for Tufted Duck than Lake IJsselmeer.

Giving up density of mussels

Depletion of the food source by up to 80% did not affect intake rate, owing to the wide range of sizes accepted when feeding on clumps, and therefore only slight shifts in the size distribution of the mussel population on offer. Also, as the proportion of large mussels increased only slightly during depletion, the gradual decrease in energetic return of a given feeding effort seemed negligible (less than 2 % after depletion of

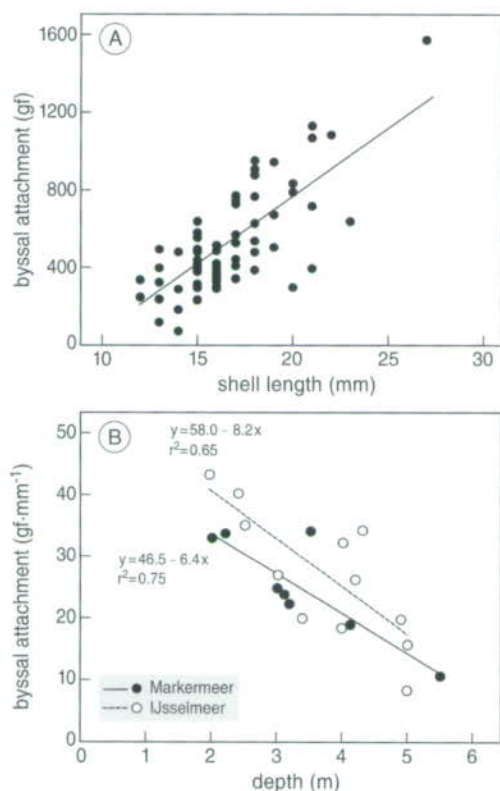


Fig. 12. A. Example of byssal attachment of mussels from Lake IJsselmeer at a water depth of 3 m in relation to mussel size. Byssal attachment was measured by tearing off a mussel from a clump through gently pulling a *Pesola* unster clasp around the shell. B. Byssal attachment (attachment force per mm size class) in relation to water depth in Lake Markermeer and Lake IJsselmeer (difference between lakes was not significant; ANCOVA, $P > 0.05$). Data from Van Eerden & De Leeuw (unpublished).

65% of the available mussels). Apparently, mussel size selection has no effect on the feeding effort of diving ducks when feeding on mussel clumps.

Depletion reduces, however, the density of the food source and thus will increase the searching effort. From the functional response curves, it appeared that Scaup were feeding very efficiently at low mussel densities. This suggests that searching for food is only limiting at extremely low densities, while handling prey (swallowing mussels underwater or the amount of mussels that can be transported to the surface) is usu-

ally limiting. The result of the patch experiment (Fig. 6) suggests that Scaup prefer to deplete patches sequentially rather than searching for sites with high food densities. This is in accordance with the expectation that handling time mainly determines intake rate and only at very low densities will searching for food affect the intake rates. However, there seemed to be a considerable time penalty to switch between patches. Feeding in large flocks, as often observed in the IJsselmeer area, probably reduces search time for recovering patchily distributed prey (Ranta *et al.* 1993).

Intake rates of Tufted Duck were considerably lower at low mussel densities than intake rates of Scaup. It seems unlikely that searching efficiency (swimming speed and the active area of encountering prey, Tome 1989) was that much lower in Tufted Duck, because body size, and therefore hydrodynamic propulsion efficiency (Lovvorn & Jones 1991), is not greatly different between the two species (*ca.* 25% difference in body mass). A more likely explanation is that the Tufted Ducks aimed to search for a more rewarding feeding site, instead of 'making the best of a bad job'. This was also reflected by the refusal of these ducks to feed at densities below 10 gFW.m⁻².

As a consequence of increasing searching effort with depletion, diving may become too costly for further exploitation of the food source and ducks have to give up foraging in that patch. Because diving costs are high (*ca.* 25% of the daily energy expenditure at non-limiting mussel densities in this study) and the daily budget may approach an energetic 'ceiling' under field conditions (De Leeuw *et al.* *subm.*), intake rate of diving ducks should be high to maintain energy balance. Intake rate of Scaup was still 90% of the maximum values at a density of 60 gFW.m⁻² and 80% at 30 gFW.m⁻², according to the functional response curve. A crude approximation of the minimal intake rate required under winter conditions can be made by calculating the lowest intake rate at which the daily energy expenditure approaches the maximum metabolizable intake rate according to Kirkwood (1983). For Scaup with a body mass of 750 g this amounts to 1435 kJ.d⁻¹ or a daily food consumption of 2870 gFW.d⁻¹. From the energy budget data, we obtain maintenance costs of 553 kJ.d⁻¹ (resting birds), while the energy required for heating up the cold ingested food mass amounts to 305 kJ.d⁻¹. Thus, a maximum of 1435-553-

305 = 577 kJ can be devoted to diving, or 10300 s to obtain 2870 gFW of mussels, which is equivalent to an intake rate of 0.28 gFW.s⁻¹ (62% of the maximum intake rate). This would be feasible at mussel densities of at least 12 gFW.m⁻². This is an absolute lower threshold density, because other additional cost factors like flight, increased thermoregulatory costs at wind-exposed feeding sites or the extra diving costs for searching suitable feeding sites are not included. If these additional costs were only 10% of the daily expenses, minimal intake rates should be more than 80% of the maximum values observed in this study. Giving-up densities can thus be conservatively estimated to be higher than 30 gFW.m⁻². This level may slightly increase with diving depth because intake rates are lower at greater depth (Table 1). Mussel densities observed in the field after periods of intense predation by diving ducks confirm that this is a realistic estimate indeed (Table 3). The giving-up densities of Scaup and Tufted Duck are in the same range and increase slightly with diving depth.

A corollary of the necessarily high intake rate is that feeding success, i.e. the probability of finding mussels in a heterogeneous feeding area, should be consistently high. To assess the relative importance of searching efficiency for feeding success of Tufted Duck and Scaup in the wild, I revert again to dissected birds caught in fishing nets in the Lake IJsselmeer area (De Leeuw & Van Eerden 1995). The relative feeding success rate was approximated from the fraction of ducks caught with food in the esophagus, as these birds were presumably exploiting a food patch successfully. The absolute percentage may be higher, because the probab-

ility of being entrapped in a fishing net at the bottom is lower in ducks diving mainly vertically while exploiting a food patch (filling the gullet) than in ducks searching for food (empty esophagus) which move more horizontally over the bottom, thus suffering a high probability of encountering a fishing net. The fraction of birds caught with mussels in the gullet can thus only be used as an index for feeding success. This index was 0.57 ($N = 327$) for Tufted Ducks diving between 2 and 4 m in Lake Markermeer and 0.52 ($N = 217$) for ducks diving in Lake IJsselmeer. In Scaup, the success rate index was 0.71 ($N = 431$) for Lake Markermeer and 0.63 ($N = 709$) for Lake IJsselmeer, respectively (De Leeuw & Van Eerden 1995). This suggests that (1) Scaup feed more efficiently than Tufted Duck (according with the experiments presented in this study), and (2) that feeding success was higher in Lake Markermeer than in Lake IJsselmeer. Lake-wide surveys by means of bottom sampling suggest indeed a more homogeneous distribution of mussels and a higher probability of encountering mussels in Lake Markermeer (Van Eerden *et al.* in prep.).

Habitat use determined by differential foraging skills?

Tufted Duck and Scaup showed great similarities in their foraging behaviour when feeding on *Dreissena*, both in the field and in experiments. The smaller sized Tufted Duck, however, has a stronger preference for small mussels that can be easily ingested and seems to be hindered more by byssal attachment of mussels in clumps than Scaup. Also, searching effort may disproportionately reduce intake rate in the Tufted Duck.

Table 3. Lowest densities of *Dreissena polymorpha* after periods of intense predation by diving ducks. Only single prey situations in which more than 70% of biomass disappeared during the predation period are included.

Predator species	Habitat	Water depth (m)	Density (gFW.m ⁻²)	Reference
<i>Aythya fuligula</i>	River (Upper Rhine, Switzerland)	1.0	30	Suter 1982b
		1.3	32	
		3.5	50	
<i>Aythya fuligula</i>	Pond Leblanc (Belgium)	3.3	50-100	Draulans 1982
<i>Aythya fuligula</i>	Lake Markermeer (The Netherlands)	2.5	65	Van Eerden <i>et al.</i> (in prep.)
		3.5	60	
<i>Aythya marila</i>	Lake IJsselmeer (The Netherlands)	2	47	Van Eerden <i>et al.</i> (in prep.)
		3	60	

Table 4. Parameters for estimating the net energy intake rate of Tufted Duck and Scaup feeding on Zebra Mussels at a water depth of 3 m in Lake IJsselmeer (IJ) and Lake Markermeer (M).

	Lake	Tufted Duck	Scaup	Reference ¹
Apparent intake rate (gFW.s ⁻¹)	M	0.40	0.42	1
	IJ	0.34	0.42	1
Metabolizable energy content (kJ.gFW ⁻¹)	M	0.40	0.40	2
	IJ	0.48	0.48	2
Diving cost (W)		50	56	1,3
Food heating cost (kJ.g ⁻¹ .°C ⁻¹)		2.8	2.8	4

¹) References: (1) This study, (2) De Leeuw (unpublished), (3) De Leeuw (1996), (4) De Leeuw *et al.* (subm.)

These differences in foraging skills correspond qualitatively with the observed segregation of the two species in the IJsselmeer area when local differences in prey properties are taken into account. In Lake Markermeer, mussels are smaller (Bij de Vaate 1991), their substrate attachment by byssal threads is less developed (Fig. 12), and the probability of encountering mussels (reducing searching efficiency) is higher (Van Eerden *et al.* in prep.) than in Lake IJsselmeer. However, growth conditions of mussels are more favourable in Lake IJsselmeer (Bij de Vaate 1991), hence improving the nutritional value of mussels in this part of the lake system: the energy content of mussels collected at a water depth of 3 m in Lake IJsselmeer (metabolizable energy content (MEC) 0.48 kJ.gFW⁻¹) proved to be considerably higher than that of mussels collected in Lake Markermeer (MEC 0.40 kJ.gFW⁻¹; unpublished data). Since both energetic costs and benefits are higher in Lake IJsselmeer than in Lake Markermeer, the net energy intake rate can be used as a currency to evaluate the profitability of both parts of the lake for diving ducks. Food intake rates were approximated on the basis of apparent intake rates (AIR) observed in ducks feeding on 'moderate clumps' as obtained in this natural fashion from a water depth of 3 m in Lake IJsselmeer (see Table 4). For the smaller mussels with low byssal attachment in Lake Markermeer, I assumed that AIR equals that of feeding on unattached mussels. By subtracting the energetic costs for diving (DC) and heating up the ingested food (assuming a heat capacitance of 2.8 kJ.g⁻¹.°C⁻¹ and a difference in body and ambient water temperature of 38 °C, FC = 2.8 x 38 x AIR) the net energy intake rate can be calculated as AIR x MEC-DC-FC kJ.s⁻¹ spent underwater (Fig. 13).

From the net intake rates, it appears that Scaup greatly benefit from the high energy returns of mussels in Lake IJsselmeer because intake rates are not affected by the larger size or strong byssal attachment of mussels. For Tufted Duck, this benefit is far less since the byssal attachment of mussels in Lake IJsselmeer reduces intake rate.

The implications for habitat selection also depend on the minimal intake rates that the ducks must achieve to balance their energy budget. This can be approxi-

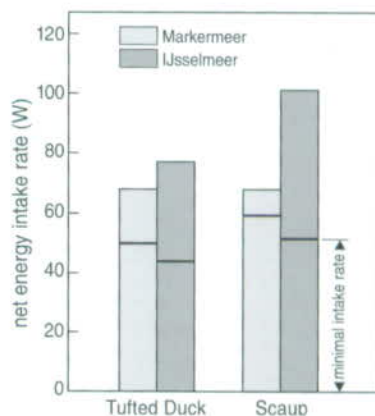


Fig. 13. Net energy intake rates estimated for Tufted Duck and Scaup feeding in Lake IJsselmeer and Lake Markermeer at a water depth of 3 m. Intake rates are based on the maximum values observed in ducks feeding on mussels clumps with moderate byssal attachment in case of Lake IJsselmeer and on unattached mussels in Lake Markermeer. The higher net intake rates in Lake IJsselmeer are due to the high energy content of mussels in this part of the lake system. Minimal intake rates required for energy balance are indicated by crossbars.

mated by calculating the minimal intake rates required to keep the energy expenses below the 'metabolic ceiling' suggested by Kirkwood (1983), analogous to the calculation made in the previous section. Assuming that Tufted Duck can maximally expend 1185 kJ.d⁻¹ and Scaup 1435 kJ.d⁻¹ according to Kirkwood, it becomes apparent that Scaup require considerably higher intake rates to support their larger body mass than Tufted Duck, and that Scaup have to perform almost maximally to balance their budgets in Lake Markermeer (Fig. 13). This can explain the strong preference of Scaup to winter in Lake IJsselmeer. This preference can be relaxed by the smaller Tufted Duck which needs less energy on a daily basis, even though feeding in Lake IJsselmeer might be more profitable.

Competition with the larger (probably dominant) Scaup, might drive Tufted Duck to Lake Markermeer, while the high energetic demands of Scaup are a driving force to monopolize the most profitable areas in Lake IJsselmeer. Other factors than competition (e.g., the distance between feeding sites and suitable roosting areas, the susceptibility to wind-exposed feeding sites, the likelihood of discovering suitable feeding areas) doubtless play a role in habitat selection too. Considering foraging skills in isolation is thus insufficient to determine the profitability of feeding habitats. More detailed analyses on prey distribution combined with energetic models, that can approximate the complex interplay between foraging costs and variable energetic returns from mussels under different field conditions, might give answers to questions as to what extent habitat use can be attributed to differences in optimal feeding conditions and competition, and to what extent mussel populations can be exploited by diving ducks.

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Chapter 9

Synthesis: An energetic approach to habitat use and food exploitation limits of diving ducks in the IJsselmeer area

Joep J. de Leeuw



Synthesis:

An energetic approach to habitat use and food exploitation limits of diving ducks in the IJsselmeer area

Introduction

Patterns of food exploitation by wintering diving ducks feeding on Zebra Mussels *Dreissena polymorpha* in the Lake IJsselmeer area have been described in Chapter 2. The large numbers of diving ducks consumed a small fraction (< 20%) of the total food stock in normal winters. The number of birds and their habitat use proved to correspond with local and annual variations in food supply. The segregation in spatial distribution of Tufted Duck *Aythya fuligula* and Scaup *A. marila*, the observed shifts to deeper water in the course of the winter, and local depletion of mussel populations suggested that variations in food stock may be important criteria for habitat suitability or may even limit the number of birds wintering in the area. Also, properties of the prey such as size, attachment to the substrate, and density of mussels affected food exploitation, suggesting that foraging skills and energy costs of feeding may give cues to understand the observed patterns. In subsequent chapters (3-8), the foraging behaviour and energetics of the main species, Tufted Duck and Scaup, were examined in experiments with captive birds feeding on mussels under conditions that approached the natural situation.

The aim of this chapter is to investigate the exploitation mechanisms of diving ducks and to identify maximum sustainable levels of predation on Zebra Mussels in the IJsselmeer area. As outlined in Chapter 1, an energetic model approach will be used to integrate the foraging energetics of Tufted Duck and Scaup with habitat use and feeding conditions observed in the field. The model quantifies the energetic implications of foraging decisions relevant to wintering diving ducks. These decisions have reference to (1) properties of the prey (energy content of mussels, byssal attachment, density of mussels), (2) diving depth, (3) probability of finding food patches, and (4) flight distance

between roost and foraging site. In addition, switching to alternative feeding areas and the role of competition in habitat use will be discussed (Fig. 1).

The following steps will be undertaken to tackle the questions concerning habitat suitability and limitations to food exploitation:

1. The foraging energetics model is presented to explore the feeding options that diving ducks face in the wintering area. The model constructs field energy budgets in relation to different environmental parameters.
2. Predictions concerning the profitability of foraging sites are derived from the energy model.
3. Model predictions are tested against the observed habitat use and numerical responses to changing food conditions in the course of the winter and in relation to the two sampling periods 1981 and 1992.
4. Limitations to predation and their implications for carrying capacity are discussed.

The foraging energetics model

To analyse the food and habitat choices of diving ducks in the IJsselmeer area, I will use estimates of daily energy expenditure (DEE) as a criterion for habitat selection and exploitation capabilities, presuming that the energy expenses are related to survival probabilities. It is generally believed that waterfowl populations are regulated by winter mortality (e.g., Von Haartman 1971, Nilsson 1984, Owen & Black 1990) and there is increasing evidence that sustained high levels of energy expenditure have implications for survival. For example, high daily energy expenses may suppress the functioning of the immune system, thereby increasing the susceptibility to disease (Apanius 1993, Deerenberg 1996). A correlation between life span and

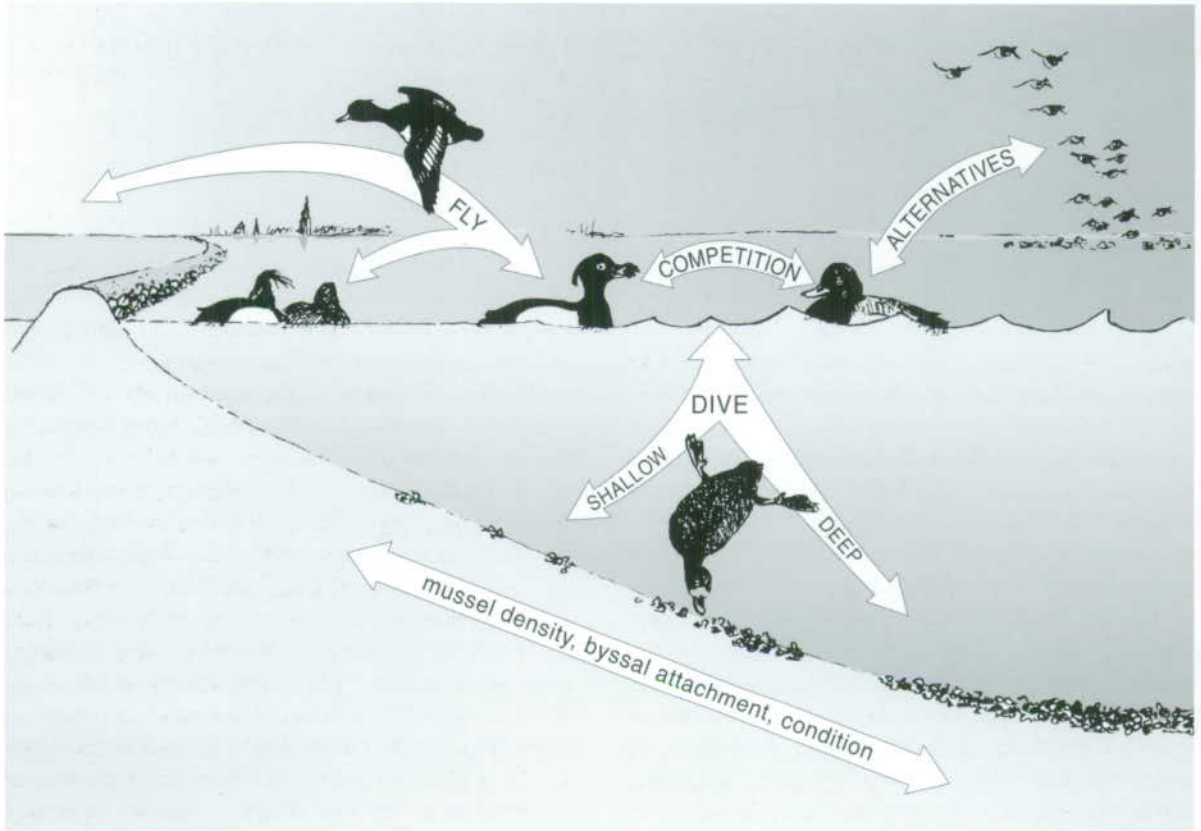


Fig. 1. Behavioural decisions for food and habitat selection of Tufted Duck and Scaup feeding on Zebra Mussels in the IJsselmeer area.

metabolic rate as formulated in the 'rate of living' theory (Pearl 1928) has been demonstrated in experiments in which metabolic rate was manipulated through ambient temperature (e.g. Miquel *et al.* 1976) or food restriction (Pieri *et al.* 1992), as well as by comparative studies (Pearl 1928, Sacher 1978). The repercussions of high energy costs may not become directly apparent, but high levels of energy turnover may entail a higher risk of mortality for long periods afterwards. For example, Kestrels *Falco tinnunculus*, that were forced to work at high energy levels in order to raise their experimentally enlarged broods, suffered a significantly increased risk to die during the following months in winter (Daan *et al.* 1996). Likewise, high costs in winter might reduce the probability of successful breeding attempts of diving ducks in the following breeding sea-

son. We may thus assume that foraging decisions are governed by their effects on the energy balance of diving ducks (see also Fig. 2 in Chapter 1) and that food exploitation is delimited by energetic considerations via their fitness consequences.

The costs of a cold dive

Food exploitation by diving is a time and energy consuming activity, even for species of diving duck which fully rely on this mode of foraging and are well adapted to diving. The basic problem of feeding by diving is the limited oxygen supply available during breathhold. Therefore, foraging times at the bottom are short, while much time and energy must be devoted to travel between the food source and the surface to breathe. This is particularly costly during dives in wa-

ter deeper than 4 m when diving ducks may partly rely on anaerobic metabolism, as suggested by the foraging behaviour of Tufted Duck and Pochard (Chapter 4). Respirometry experiments with diving Tufted Duck revealed that foraging costs are extremely high in cold water, due to the poor insulation of the compressed air layer in the feathers while diving (Chapter 5). In addition to the hydrodynamic costs to overcome buoyancy, the increased heat loss during diving incurs an incremental thermoregulatory cost which amounts to approximately half the total diving costs. Body temperature of Tufted Duck drops when diving in cold water and a considerable amount of energy is invested for recovery after diving, as could be shown by the use of implanted heart rate and body temperature transmitters (Chapter 6). Accounting for these costs of delayed recovery (relevant for constructing energy budgets) yields higher values of diving costs than suggested in earlier studies which were mainly focused on the actual diving phase (e.g., Woakes & Butler 1983, Lovvorn & Jones 1991, Bevan & Butler 1992, Stephenson 1994). Moreover, our experiments demonstrated that the ingestion of large amounts of cold food contributes to a drop in body temperature, while recovery from heat loss proved to be time-consuming. Under semi-natural conditions with Tufted Duck and Scaup diving for Zebra Mussels, the energy needed for thermoregulation was the main cost factor explaining the high daily expenses, as revealed from food consumption and doubly-labelled water measurements (Chapters 7 and 8). An interesting feature was to find that the obligatory energy cost for warming up ingested food in winter seemed to be larger than the heat generated by crushing shells and digestion of flesh. As a corollary, the expected energy cost to compensate heat loss from food ingestion can be used to estimate the food processing costs under cold conditions. The daily energy expenses (DEE) proved to be close to supposed maximum sustainable levels (e.g. Kirkwood 1983, Hinds *et al.* 1993). Consequently, foraging costs of diving ducks must be neatly fitted within narrow margins of their energy budgets. We may thus expect that foraging decisions are focused on an efficient use of energy and time with regard to diving and the amount of food to be ingested to balance their budget. Both net rate of energy intake and foraging efficiency (the most common currencies in foraging theory) are reflected in the DEE of

wintering diving ducks, because foraging costs mainly determine energy expenditure. Therefore, DEE is very useful to evaluate both foraging decisions and possible energy constraints.

From captive to field energy budgets of Tufted Duck and Scaup

Energetic costs and feeding performance of captive Tufted Duck and Scaup were measured in outdoor semi-natural environments (Chapter 7 and 8). Although these conditions approached the thermal environment in the field, at least two differences can be noted. First, in contrast to the captive birds, free-living diving ducks deposit considerable fat stores to survive cold spells when food may be difficult to find (ice cover or high feeding costs). Along with the increase in fat load, some organs increase in size as well. For example, flight muscles of fat birds are larger than those of lean ducks (De Leeuw & Van Eerden 1995). Average body mass of wild Tufted Duck and Scaup is 1000 g and 1300 g, respectively (based on ducks caught in fishing nets between November and March; De Leeuw & Van Eerden 1995), i.e. approximately 1.65 times the body masses of the captive birds. Secondly, free-living diving ducks fly between their day-time roosts and feeding grounds at night (Chapter 2). The larger body size and foraging flights will incur extra energy costs above the energy budgets of Tufted Duck and Scaup as measured under the semi-natural diving conditions. These extra costs have to be estimated to translate the energy budgets of captive birds into field energy budgets.

The diving duck energy budget is composed of the following components (see Table 1):

Maintenance costs. The minimal resting costs are basal energy costs (the minimal requirements to sustain the metabolic machinery) and the costs to maintain a constant body temperature at rest. Because fat is metabolically inactive tissue (Blaxter 1989), basal metabolic rate (BMR) correlates best with lean body mass (Piersma *et al.* 1996). Lean body mass was estimated from fat-free dry masses of carcasses of 733 Tufted Duck and 1549 Scaup caught in winter in fishing nets in the IJsselmeer area, assuming a water content of 67% of dry fat-free tissue. Lean body masses were on

Table 1. Parameters used in field energy model of wintering Tufted Duck and Scaup at a water temperature of 3 °C. Diving costs are expressed as excess over resting costs (EDC).

Component	Tufted Duck	Scaup
Body mass (g)	1000	1300
Lean body mass (g)	720	995
Maintenance ¹ (W)	7.0	8.9
Food heating (J.g ⁻¹ .°C ⁻¹)	2.8	2.8
Diving ¹ (EDC, W)	52	58
Flight (W)	68	84
Maximum energy assimilation rate (EAR _{max} , W)	30	40
Maximum MEI ² (kJ.d ⁻¹)	1713	2070

¹) Maintenance and diving costs were assumed to decrease linearly with increasing water temperature with an intercept at a body temperature of 41 °C.

²) Maximum metabolizable energy intake, according to Kirkwood (1983), calculated on the basis of total body mass ($1713 \times \text{BM}^{0.72} \text{ kJ.d}^{-1}$)

average 720 g (Tufted Duck) and 995 g (Scaup), averages that did not vary between November and March (De Leeuw & Van Eerden 1995). These values are 25 to 30 % higher than in captive Tufted Duck and Scaup (assuming a minimal fat percentage of 5% in lean birds, T. Piersma, pers.comm.). To my knowledge, no studies have addressed the relationship between body mass and thermal conductance within individuals. Several factors may influence this relationship. The surface area to volume ratio is lower, suggesting a relatively lower heat loss, in bigger birds. Although fat seems to have no effect on thermal conductance (De Vries & Van Eerden 1995), the temperature of the metabolically inactive fat tissue could be maintained at a lower level to reduce thermoregulatory costs. Furthermore, it is questionable whether the plumage will have the same insulating properties in fat and in lean individuals. The perfusion of fat tissue seems to vary considerably in dissected animals, possibly in response to the deposition or utilization of fat stores (M.R. van Eerden, pers. comm.). Here, I will assume that maintenance costs (basal metabolic rate plus thermoregulatory costs in resting birds) scale proportionally to lean body mass. Variation in maintenance costs with water temperature (below the thermoneutral zone at ca. 15–20 °C, De Leeuw 1996) were calculated assuming a linear relationship with water temperature between 3° and 10 °C, the cost line cutting the temperature axis at 41 °C (body temperature, see Chapter 6). This would

yield maintenance costs of 7.0 W in Tufted Ducks and 8.9 W in Scaup resting on water at an average winter temperature of 3 °C.

Swimming. Swimming costs below a speed of 0.5–0.6 m.s⁻¹ are very low in Tufted Duck (at 0.4 m.s⁻¹ 10% higher than resting values; Woakes & Butler 1983) and are not considered incremental in the model.

Diving. Hydrodynamic costs of diving Lesser Scaup *Aythya affinis* (body mass ca. 600 g) increased only by 2% with fat mass increasing from 35 to 190 g (Lovvorn & Jones 1991). Average maximum fat mass was 220 and 250 g in wild Tufted Duck and Scaup, respectively (De Leeuw & Van Eerden 1995). Therefore, hydrodynamic diving costs were estimated to be 3% higher in winter-fattened ducks as compared to near-lean ducks diving in captivity with estimated fat contents of less than 40 g. Fat does not affect thermal conductance of submerged ducks (De Vries & Van Eerden 1995), and I assume here that thermoregulatory costs of diving were similar in captive and wild ducks. Diving costs in excess over maintenance costs are thus estimated at 52 J.s⁻¹ (Tufted Duck) and 58 J.s⁻¹ (Scaup) at a water temperature of 3 °C (Chapters 5 and 8). As in maintenance costs, variation in diving costs with water temperature were approximated by assuming a linear slope with temperature between 3° and 10 °C with the intercept at 41 °C (body temperature).

Food processing. Feeding costs are estimated from the calculated cost to heat up the cold food mass to body temperature, assuming a specific heat of $2.8 \text{ kJ.g}^{-1}.\text{°C}^{-1}$ for Zebra Mussels. All the heat generated by digestion of food and shell crushing in the gizzard is assumed to compensate the high (obligatory) thermoregulation costs in winter, as demonstrated in Chapter 6 and 8.

Flight. Flight costs were estimated from Masman & Klaassen (1987), provisionally accepting an aspect ratio of 0.06 and 0.08 of Tufted Duck and Scaup, respectively (M. Klaassen, pers. comm.). Flight metabolic rates were estimated at 68 W in Tufted Duck (average winter body mass 1000 g) and 84 W in Scaup (1300 g).

Fat stores. Diving ducks deposit fat stores in autumn (mainly in November at water temperatures of 3–10 °C). The energetic costs of fat deposition were approximated from the energy density of fat (39.3 kJ.g^{-1} ; efficiency of transforming metabolized energy into fat is 0.88; Kersten & Piersma 1987) and the average increase in fat mass of the wintering population estimated from carcass analyses, with a maximum of 3 g.d^{-1} in Tufted Duck ($N = 327$) and 4 g.d^{-1} in Scaup ($N = 333$; De Leeuw & Van Eerden 1995).

Maximum metabolism. Empirical evidence suggests that the daily rate of energy use is limited to values of approximately 4 to 5 times the basal metabolic rate (e.g., Drent & Daan 1980, Kirkwood 1983, Hinds *et al.* 1993, Karasov 1996, Ricklefs *et al.* 1996). Although it is questionable whether these levels are really energetic constraints rather than average maxima (Peterson *et al.* 1990, Weiner 1992), even higher sustained levels of energy expenditure might have repercussions for survival as discussed earlier. In the following analyses, I will often refer to the widely accepted maximum level of energy turnover suggested by Kirkwood (1983) to scale the metabolic performances needed for food exploitation. Although I do not assume an explicit energy constraint, DEEs exceeding the Kirkwood level will be considered critical.

For a proper implementation of costs in the energy budgets, the following components of feeding performance in free-living ducks had to be estimated:

Feeding time. Crude feeding time (i.e. minimum time required at the feeding sites) is assumed to be proportional to DEE when feeding at the maximum rate of energy assimilation (EAR_{max} , see Chapter 8). Extrapolations based upon lean body masses give values of EAR_{max} amounting to 30 and 40 W for free-living Tufted Duck and Scaup, respectively.

Intake rate. Food intake rate in relation to water depth, mussel density, and byssal attachment were measured in captive Tufted Duck and Scaup (Chapter 7 and 8). I assume similar intake rates for wild birds, because there were no differences in structural size of the foraging apparatus (bill length and height) between captive and wild ducks. Intake rates were linearly interpolated between depths (Chapter 8). Note that the effect of diving depth on daily energy costs are mediated only by differences in apparent intake rates (energy gain per second diving) in relation to diving depth (assuming water temperature remains constant), as diving costs per second underwater do not vary with depth (Chapter 5). In Lake Markermeer, mussels are smaller on average than in Lake IJsselmeer and the degree of byssal attachment of mussels to a substrate of dead marine shells is low. These small clumps of loosely attached mussels are probably easily 'strained' by Tufted Duck and here I will provisionally accept similarly high intake rates as measured in ducks feeding on unattached mussels. In Scaup, intake rates were not dependent on byssal attachment except for extremely 'tight' mussel clumps from the shallowest areas in Lake IJsselmeer (see Chapter 8).

Energy content of mussels. The condition of mussels varied considerably between different sampling locations (unpublished data). The metabolizable energy content of mussels (kJ.gFW^{-1}) was lower in Lake Markermeer than in Lake IJsselmeer, owing to less favourable growing conditions in the former (Bij de Vaate 1991). In Lake IJsselmeer, the energy content decreased with water depth (Fig. 2). From the limited data currently available, it appears that mussels in the northern part of Lake IJsselmeer (NY) are in better condition than in the southern part (SY; ANCOVA with depth; $F_{1,9} = 5.2$, $P < 0.05$; no annual differences could be noted). Factors like growing conditions for mussels (concentration of chlorophyll; Bijkerk 1995) or wind-

induced mixing of the water column in the more exposed northern part of the lake could explain this difference. In Lake Markermeer, energy content of mussels was in the lower range of IJsselmeer mussels

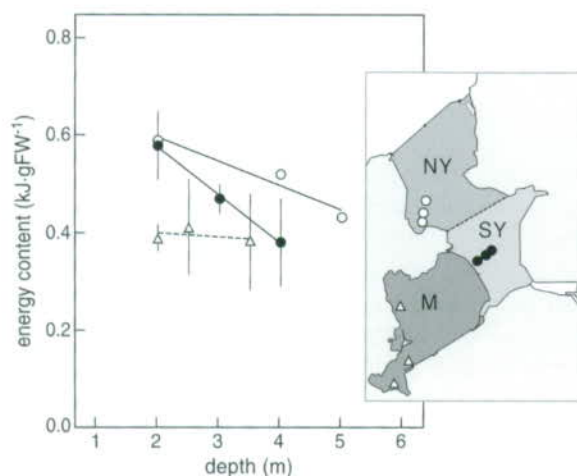


Fig. 2. Condition of mussels in early winter. The average ($\pm$ SD) conditions over three depth gradients are given. Energy content of mussels is significantly lower in the southern part of Lake IJsselmeer (SY; three sampling years) than in the northern part (NY; one sampling year). In Lake Markermeer, mussel condition is low and does not vary with water depth; De Leeuw, unpublished data.

(mean 0.40 kJ.gFW^{-1} , SD 0.08 , $N = 11$), but did not vary with depth between 1.9 and 3.5 m (linear regression, $r^2 = 0.04$, $P = 0.76$).

DEE as a criterion for habitat suitability

As argued above, minimizing DEE at energy balance is here used as a currency for habitat selection decisions. DEE is calculated in two steps. First, the daily costs for maintenance and flight are assessed for a certain feeding site and roost (fixed costs) and subsequently the additive feeding costs are calculated in order to achieve energy balance. For every unit of foraging effort (a dive), energy is gained by food intake (depending on intake rate and energy content of mussels), while the energy costs of diving and food processing increase, as graphically illustrated in Fig. 3. The energy expenditure at the point where the expenses meet the gains equals DEE at energy balance.

Predicting the profitability of foraging sites

In the subsequent analyses, the energetic implications of foraging decisions concerning habitat and prey parameters (see Fig. 1) will be investigated. The qualitative predictions from the model generally hold for both

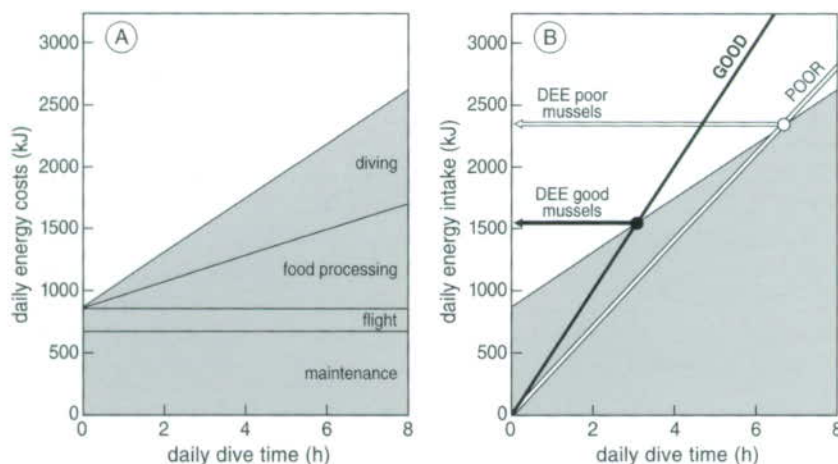


Fig. 3. Graphical representation of the energy model for estimating the DEE at energy balance. The example shows simulated data for Scaup feeding on mussels of poor condition (water depth 4 m) and good condition (2 m). **A.** Total energy expenditure increases for every unit of feeding effort (here expressed as the total daily duration of diving), due to high costs of diving and food processing. **B.** The rate of energy gain from digestion of mussels depends on mussel condition. DEE at energy balance is found where the energy gain meets the total energy expenses.

Tufted Duck and Scaup, although different aspects of habitat choice are only given for the species for which field data are available to test the predictions quantitatively. Where possible, predictions are made for both species. As a first approximation, DEEs are estimated for average winter conditions at a water temperature of 3 °C, a diving depth of 3 m (Lake Markermeer) or 3.5 m (Lake IJsselmeer) and a daily flight duration of 12 min, which corresponds to a commuting distance between roost and foraging site of 5–6 km (Chapter 2). In most cases, the relationship between DEE and feeding parameters are presented graphically in order to visualize the sensitivity of deviations in parameter values for estimates of DEE.

The doom of depth

Feeding conditions are unfavourable at greater water depths, because (1) diving effort increases with depth (decrease in apparent intake rates (AIR, Chapter 8), and (2) the energy content of mussels decreases with depth (Fig. 2). The combined effect implies a steep increase in DEE with greater foraging depths, as illustrated for Scaup feeding in Lake IJsselmeer (Fig. 4). Foraging costs (all costs above maintenance and flight costs) increase from 35 to 60% of DEE with depth increasing from 2 to 5 m. DEE exceeds the energetic maximum according to Kirkwood (1983) by 20% when feeding on mussels in poor condition at a depth of 4 m (location SY) and in Lake Markermeer. At the better conditions in the northern part of Lake IJsselmeer, the increase in DEE is less dramatic. The increased diving effort with greater water depth has only a moderate effect on DEE (5% increase from 2 to 3.5 m) when mussel condition is constant as appears from the Markermeer situation. From the sharp increase in DEE with depth and local differences in mussel condition, we may expect:

- (1) a strong preference for feeding in shallow water in Lake IJsselmeer, i.e. mussels at water depths below 4–5 m are virtually unharvestable,
- (2) acceptance of greater feeding depths in the northern part of the lake (NY), and
- (3) virtually no utilization of Lake Markermeer by Scaup.

Depletion of the profitable shallow areas will reduce

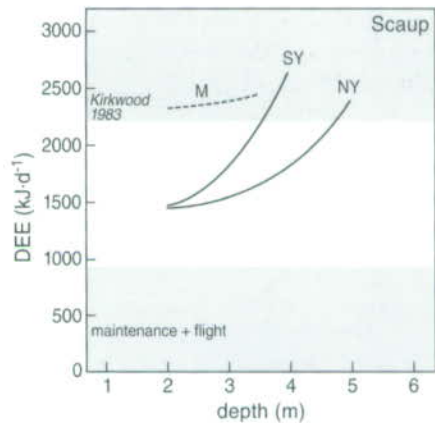


Fig. 4. Predicted daily energy expenditure at balance (DEE) in relation to water depth, according to the energy model. Maintenance and flight costs are fixed values in this example. The effect of differences in mussel condition between SY and NY (Fig. 2) is illustrated by solid lines. DEE exceeds Kirkwood's supposed maximum at depths of 4–5 m. DEE also exceeds the metabolic ceiling for the poor mussel conditions in Lake Markermeer ($0.48 \text{ kJ} \cdot \text{gFW}^{-1}$, independent of depth).

intake rate when mussel densities become low, thereby increasing the foraging costs to maintain energy balance. Eventually, it would pay the ducks to shift to deeper water. The relationship between intake rate and DEE at 2, 3, and 4 m (with average mussel conditions per depth class) is depicted in Fig. 5. Maximum intake rates decrease slightly with depth (Chapter 8), but DEE strongly increases because of the poor condition of mussels at depth. Intake rates at 2 m might be lower, because of the relatively strong byssal attachment of most of the mussel population at this depth (see Chapter 2). However, even if the entire population would consist of the most tightly attached mussels, and intake rate would be as low as $0.28 \text{ gFW} \cdot \text{s}^{-1}$ (Chapter 8), DEE at a depth of 2 m would not exceed the DEE at 3 m. The following predictions can now be added:

- (4) Scaup should feed at a depth of 2 m until intake rate drops below $0.28 \text{ gFW} \cdot \text{s}^{-1}$ before utilizing foraging sites at 3 m.
- (5) Thereafter, mussels at 2 and 3 m should be exploited simultaneously until DEE has increased to the 4 m level.

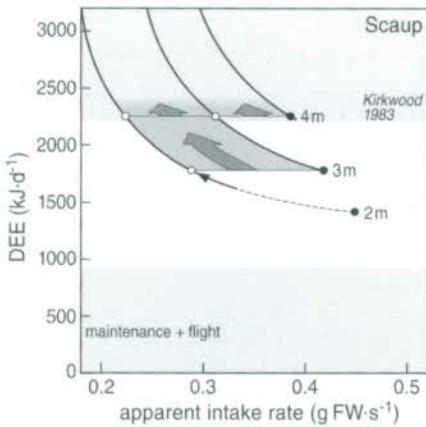


Fig. 5. Predicted DEE at energy balance in relation to apparent intake rate for different water depths. Average mussel conditions in Lake IJsselmeer were used (0.59, 0.48, and 0.41 kJ.gFW⁻¹ at depths of 2, 3, and 4 m, respectively). If intake rate at 2 m would drop to 0.28 gFW.s⁻¹ when food becomes scarce due to depletion, it would be equally efficient to feed at 3 m (shaded area). Arrows indicate trends in DEE with consecutive depletion of foraging sites at 2 and 3 m water depth (see text).

- (6) Mussels at 4 m should only be exploited at high densities in predictable areas, because a drop in average intake rate (as a result of reduced feeding success) would increase the daily energy costs to levels higher than Kirkwood's supposed maximum. As noted earlier, the critical depth also depends on local variation in mussel condition.
- (7) In line with prediction 5 and 6, it also follows that Scaup should give up feeding at 2 and 3 m, when mussel densities would become too low to maintain intake rates above 0.22 and 0.32 gFW.s⁻¹ (ca. 80% of the maximum intake rates), respectively, because DEE would exceed the Kirkwood level at lower mussel densities. According to the functional response curve presented in Chapter 8, this threshold density would be approximately 30 gFW.m⁻². Depending on the heterogeneity in mussel distribution, this value may in fact be higher (see below).

Shore-bound versus wind-exposed feeding

Diving ducks often spend the day at sheltered inshore roosts, where they can rest at low energy cost, because

swimming costs are low and thermal conductance is minimal while the bill and one leg are tucked in the feathers (see Chapter 6). However, suitable roosting sites may be at considerable distance from feeding sites imposing high energy costs of daily foraging flights. From an energetic point of view, diving ducks should only commute between day-time roosts and foraging sites, if resting costs at the roost are sufficiently lower than at the foraging site to compensate the flight costs. Although there are no data available to simulate these extra resting costs imposed by wind (convective heat loss) and waves (swimming, vigilance, instead of resting with head and leg in the feathers), we can compare the effect on DEE of a certain increase in resting costs and the estimated flight costs. In the model of Fig. 6, I assume that maintenance costs are minimal (i.e., comparable to the captive conditions) at the day-time roosts, but higher at foraging sites. Assuming that maintenance costs were only 10% higher at the foraging site than at the roost, the simulation shows that the distance to the roost should be less than 2.5 km for Tufted Duck wintering in Lake Markermeer (Fig. 6A). If maintenance costs were 20% higher, roosts should be less than 4.7 km from foraging sites, and less than 6 km at 30% higher maintenance costs. Maximum commuting distance should decrease again at further increases in maintenance costs at the foraging site (Fig. 6B). The reason is that total feeding time at the foraging site would increase so far (more than 18 hours a day) that the time that could be spent at the roost would become too short to benefit from low resting costs. Before discussing the implications of these results, a brief investigation of the sensitivity of the model to parameter values of flight and maintenance costs seems appropriate. The estimate of flight costs according to Masman & Klaassen (1987) used in this study yielded an estimate of flight costs equivalent to only 50% of the widely accepted aerodynamic model values of Pennycuik (1989), and thus seems a conservative estimate. Nevertheless, flight costs are notoriously difficult to measure and many empirical attempts overestimate flight costs (M. Klaassen & Å. Lindström, pers. comm.). Even if the actual flight costs would be as much as 30% lower than the value accepted here (i.e. 35% of the Pennycuik prediction), the maximum predicted distance between roost and foraging site should still be less than 8 km (instead of

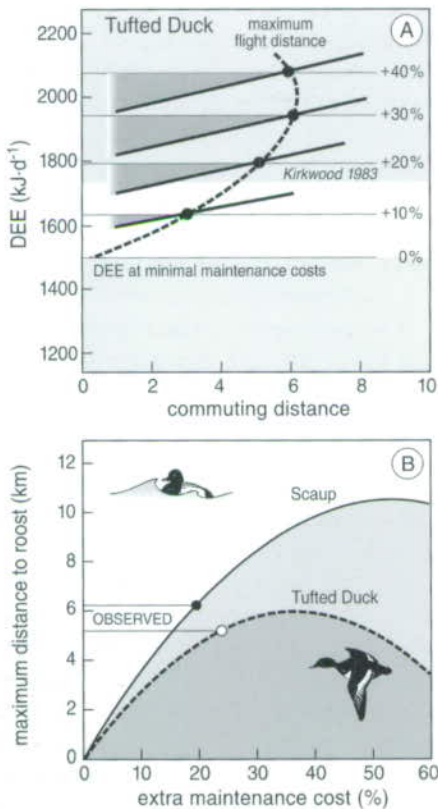


Fig. 6. A. Predicted DEE at energy balance of Tufted Duck in relation to commuting distance between foraging sites and day-time roosts (solid lines) for different estimates of the extra maintenance costs at the foraging site relative to the roost (thin lines). The shaded areas where flight costs are lower than the costs of remaining at the foraging sites indicate the estimated range of flight distances, while the estimated maximum commuting distance is shown by the curve. B. Predicted maximum commuting distance as a function of the extra maintenance costs at the foraging site relative to the costs at the roost, for which minimal maintenance costs were assumed. The symbols plotted on the curves are the average foraging flight distances of Scaup and Tufted Duck observed by radar in late winter (February-March).

6) according to the model. If, on the other hand, minimal maintenance costs would be 20% lower than the current estimates, the maximum flight distance would be less than 7.5 km (instead of 6 km). It can thus be concluded that the model is rather robust to perturbations of its parameters.

For comparison, the same analysis was conducted for Scaup (see Fig. 6B), revealing that the maximum commuting distances for this species are longer. The following predictions can now be made:

- (8) Commuting distance between foraging sites and roosts should be short, favouring coastal feeding areas.
- (9) Foraging flight range of Scaup should be greater than that of Tufted Duck.
- (10) Scaup and Tufted Duck should remain at the foraging sites, if the nearest roost is further away than the boundaries depicted in Fig. 6.

In general, this analysis advocates the crucial importance of roosting areas where diving ducks can rest undisturbed, as flight costs have a considerable impact on DEE.

Probability of finding suitable feeding sites

The high energy costs of feeding and energy budgets that are close to metabolic ceilings, in particular in wintering Tufted Duck, imply that feeding success must be high to maintain energy balance. For example, a reduction in foraging success of 20% from maximum values will incur an increment in DEE of 25% in Tufted Duck (Fig. 7), thereby exceeding the energetic ceiling supposed by Kirkwood (1983). Though less dramatically than in Tufted Duck, DEE of Scaup also increases exponentially at lower intake rates (Fig. 5). Because of these extremely narrow margins, we may expect that diving ducks favour areas with high densities of mussels and a high probability of encountering mussels. In the IJsselmeer area, the spatial distribution of mussels seems to vary considerably in different parts of the lake system and between years (Fig. 1 in Chapter 2). The fine grain, or first-order patchiness, as perceived by the ducks could not be exactly assessed because bottom samples with a Van Veen grab (0.04 m², Chapter 2) cover a much smaller unit of area than a diving duck can scan in a single dive (at least 1 m² when feeding on mussels). Therefore, diving ducks may perceive a more homogeneous distribution of mussels than expected from the variation in bottom samples. Hence, considering larger scale variation at the level of patches is more appropriate for diving ducks. In order to locate these patches, however,

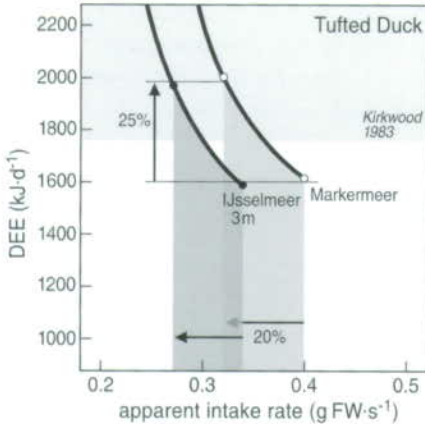


Fig. 7. Predicted DEE at energy balance in relation to apparent intake rate of Tufted Duck in Lake Markermeer and Lake IJsselmeer when feeding at a water depth of 3 m. The energy content of mussels was 0.48 (IJsselmeer) and 0.40 kJ.gFW⁻¹ (Markermeer), respectively. A drop in intake rate of 20% would incur a 25% increment in DEE, exceeding Kirkwood's maximum level.

ducks must sample the environment by diving, thus at high energy cost. Diving ducks usually feed in large flocks of hundreds or thousands of birds, probably because flocking behaviour may enhance individual feeding success. Coarse-level information about feeding patches may be obtained from the feeding success of neighbouring conspecifics (Pöysä 1992). In general, flock size is larger when food is less predictable (e.g. Pöysä 1992, Ranta *et al.* 1993). We may thus assume that large units of area could be sampled by feeding flocks, but, at the same time, only large, more or less homogeneous areas are profitable for large flocks (i.e. allow a high individual food intake rate). As argued in Chapter 2, the giving-up density of a feeding flock may depend on the heterogeneity of the mussel distribution. In the more heterogeneous areas, a considerable fraction of individuals in a feeding flock will face the threshold density (30 gFW.m⁻²) in patches with low mussel densities, while others are still feeding in higher density patches, which are only partially exploited. Although the individuals within a flock may concentrate around high density patches, some patches will become more isolated relative to their depleted surroundings. Consequently, these patches are more and more difficult to locate each night and the area will

be abandoned leaving the higher density patches not fully exploited, as was demonstrated in Chapter 2. Thus, the average giving-up density in a heterogeneous area will be higher than the threshold density of a fully exploited patch. Here, I will provisionally accept a general giving-up density of 50 gFW.m⁻², based upon field measurements of mussel densities observed after intense predation by diving ducks (Table 3 in Chapter 8). It must be stressed that this giving-up density does not reflect a mechanistically defined threshold, but rather a conservative approximation within a range of densities at which diving ducks should stop foraging. As shown in Chapter 2 (Fig. 10), the local giving-up density is often considerably higher.

To approximate the effect of coarse-level patchiness on habitat suitability, the probability of encountering mussels was estimated from the lake-wide surveys of mussels in 1981 and 1992 (Chapter 2). Grid cells of 2x2 km with average densities of more than 50 gFW.m⁻² (conservative giving-up density) were accepted as a functional feeding unit, which can sustain a flock of diving ducks for several days. For example, one grid cell with an average density of 200 gFW.m⁻² converts to an available biomass of 4 000 000[m²]*(200-50)/1000[kg] = 600 000 kg, or ca. 150 000 bird days, which is equivalent to, for instance, 1 week for a flock of 20 000 birds. The 50 gFW.m⁻² giving-up density excludes 9% of the total biomass in the area. This value differs only slightly from the 30 gFW.m⁻² threshold density earlier derived from the experiments in captivity (see Chapter 8) which would exclude ca. 4% of the mussel biomass. As a relative estimate for the probability of encountering mussels in a grid cell, I will use the percentage of bottom samples in which mussels were found. The profitability of feeding sites is further delimited by water depth due to poor conditions of mussels and long flight distances from shore-bound roosts. From the earlier model predictions, we may assume that feeding at depths below 3.6 m in the southern part of Lake IJsselmeer and 4.4 m in the northern part is no longer profitable. To predict the attendance of birds to potential feeding areas, all grid cells in deeper water and with average mussel densities below the giving-up density (50 gFW.m⁻²) are excluded (Fig. 8). Selecting only the areas within the predicted maximum flight ranges of Scaup (8 km) and Tufted Duck (6 km) from commonly used, large day-time roosts (based on

monthly counts in the three years centered around the lake-wide mussel surveys, see Chapter 2), only a limited number of grid cells reflect profitable feeding sites in the IJsselmeer area. Both the number of profitable grid cells and the probability of encountering mussels increased in Lake IJsselmeer, but decreased in Lake Markermeer between the 1981 and 1992 survey. The following predictions concerning patchiness in the mussel distribution will be tested:

- (11) The number of bird days within each potential foraging area (circles in Fig. 8) should be related to the biomass, the probability of encountering mussels, and the number of cells meeting the profitability criteria (as a crude approximation of the isolation of potential feeding sites) in that area,
- (12) In general, the numbers of Scaup in Lake IJsselmeer should have increased between 1981 and 1992, while the numbers of Tufted Duck should have decreased in Lake Markermeer.

Prediction of seasonal shifts in profitability

The necessity to shift to deeper water in the course of the winter and the energetic implications resulting from this are demonstrated for Scaup wintering in Lake IJsselmeer, using estimates of available biomass of mussels, the number of Scaup in the area, and their estimated energy budgets. I used a discrete 'switch-of-depths-model' for simplicity (depth classes of 1 m with mean mussel conditions observed per depth zone), while all parameters of the model are calculated for 10^{-d} periods. The available mussel biomass is calculated from the lake-wide survey in 1992 (assuming a giving-up density of 50 gFW.m⁻²). The number of Scaup in each 10-d period is approximated from interpolated values of the averages of monthly aerial surveys between 1990 and 1995 (mild winters without significant ice cover). Balancing their budget, Scaup also rely on fat stores as energy supplies. The average rate of deposition and utilization of fat is approximated from carcass analyses of drowned ducks caught in the IJsselmeer area (De Leeuw & Van Eerden 1995). The

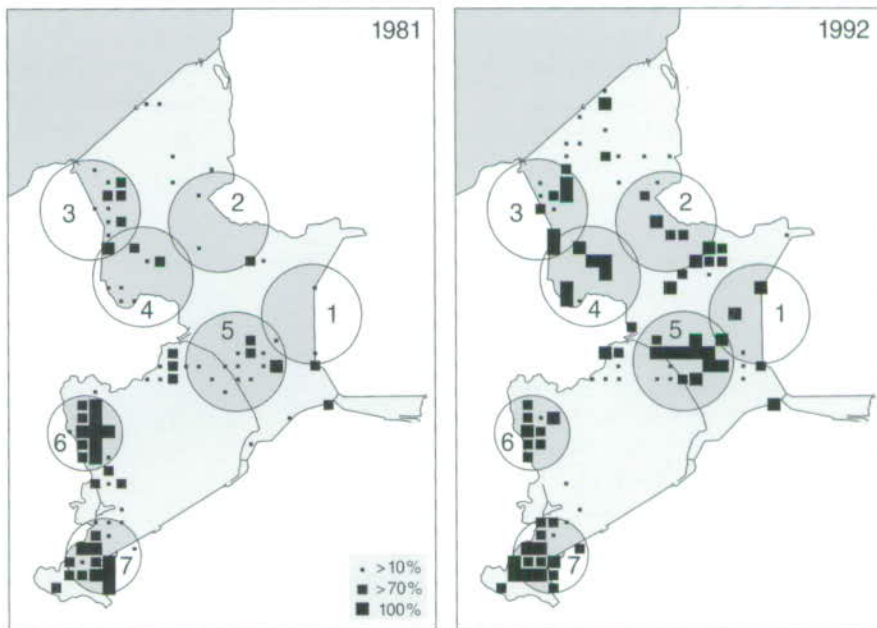


Fig. 8. Profitable foraging sites (based on 2x2 km grid) at depths less than 3.6 m (SY) or 4.4 m (NY) in the IJsselmeer area in 1981 (A) and 1992 (B). Average mussel density per grid cell is at least 50 gFW.m⁻² (giving-up density). Probability of feeding success per cell was estimated from the percentage of bottom samples (0.04 m²) with mussels (see text).

number of Scaup, their fat stores, and the available biomass per depth class allow the following predictions (see Fig. 9):

- (13) Scaup arriving in October-November should start to exploit shallow foraging sites, when favourable conditions of relatively high water temperature and high energy value of mussels allow deposition of fat stores.
- (14) The ducks should switch to foraging sites at 3 m when the shallowest areas are depleted by early December and the large numbers of Scaup in midwinter should switch to 4 m in late January.
- (15) Upon the switch to water depths at 4 m, where energy balance could not be maintained below Kirkwood's maximum, fat stores should decline.
- (16) As a consequence of the long feeding times in late winter needed to process the large amounts of food of low nutritional value, the expectation is that Scaup can no longer afford to feed only at night, and thus they should partially forage during the day.

Depending on local conditions of biomass available at different depths and the condition of mussels, the time of switching to deeper water and the associated predictions may vary.

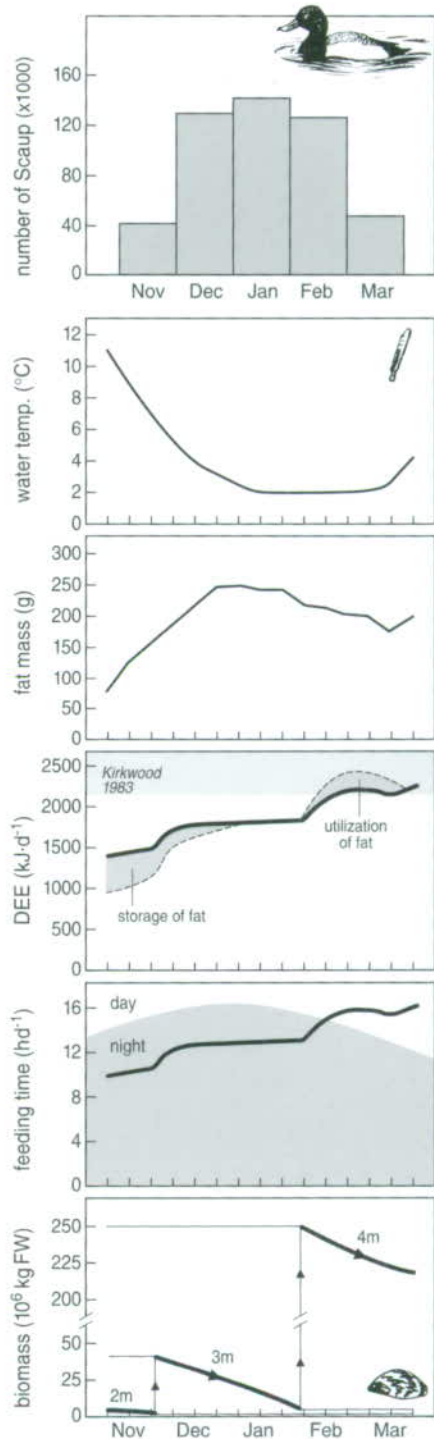


Fig. 9. Seasonal shifts in exploitation of *Dreissena* in Lake IJsselmeer by Scaup during winter. According to the depletion model, Scaup should start at the shallowest depth and shift to deeper water in the course of the winter (lower panel). **A.** Average number of Scaup in Lake IJsselmeer from monthly aerial surveys between 1990 and 1995. **B.** Water temperature decreases in November and early December to the February average of 2 °C. **C.** Fat mass of 1407 Scaup caught in fishing nets in Lake IJsselmeer (De Leeuw & Van Eerden 1995). **D.** DEE at energy balance (dashed line) and DEE corrected for storage and utilization of fat stores (solid line), approaching Kirkwood's maximum in late winter. **E.** Total feeding time exceeds the night-time hours (shaded area) in late winter. **F.** Decline in mussel biomass at different depth zones (initial biomass estimated from 1992 survey).

Do the predictions match field observations?

Shallow foraging areas are the most profitable ones.

A major prediction from the energy models presented in the previous sections is that diving ducks should show a strong preference for shallow foraging sites, because of the high energy content of mussels, low diving effort, and the short distance between shore-bound roosts and feeding sites. Only if shallow areas are depleted should the ducks shift to deeper waters. Radar observations of foraging flights of Tufted Duck and Scaup (see Chapter 2 for details) neatly match these predictions. Both species exploited the shallow, coastal zones early in winter and were feeding in deeper water, further off-shore, in late winter. Concurrently with the exploitation of shallow areas in the southern part of Lake IJsselmeer in early winter, Scaup were feeding at greater depth in the northern part of the lake (Fig. 10), which accords with the observed higher mussel condition in the north. Also, Scaup moved further north in the course of the winter (see monthly distribution maps of Scaup in Chapter 2). Contrary to prediction, Scaup were also frequently feeding at depths of *ca.* 5 m in late winter, but it is questionable whether Scaup could maintain energy balance at these depths (Fig. 9, see next section).

Utilization of fat stores.

Diving ducks often rely on their fat stores in late winter as an extra energy supply (cf. Ryan 1972, Hohman *et al.* 1993, Lovvorn 1994a). The model predicted that Scaup were not able to maintain energy balance below the Kirkwood level upon the shift to deep, unprofitable feeding areas forced upon them by depletion of shallow waters. The shift coincided with a decline in fat mass as measured from carcass analyses of drowned ducks (De Leeuw & Van Eerden 1995), suggesting that fat was used as an energy subsidy. The rate of decline in fat mass in carcasses was *ca.* 50% higher in Tufted Duck than in Scaup, indicating a stronger reliance on bodily energy stores in the smaller Tufted Duck, which is more sensitive to heat loss. In severe winters, ice cover may prohibit feeding at favourable feeding sites. Scaup with a midwinter fat mass of 300 g can survive a fortnight without additional feeding (maintenance costs 800 kJ.d⁻¹ and an energy density of 39 kJ.g⁻¹ fat) or a couple of days longer when also utilizing bodily

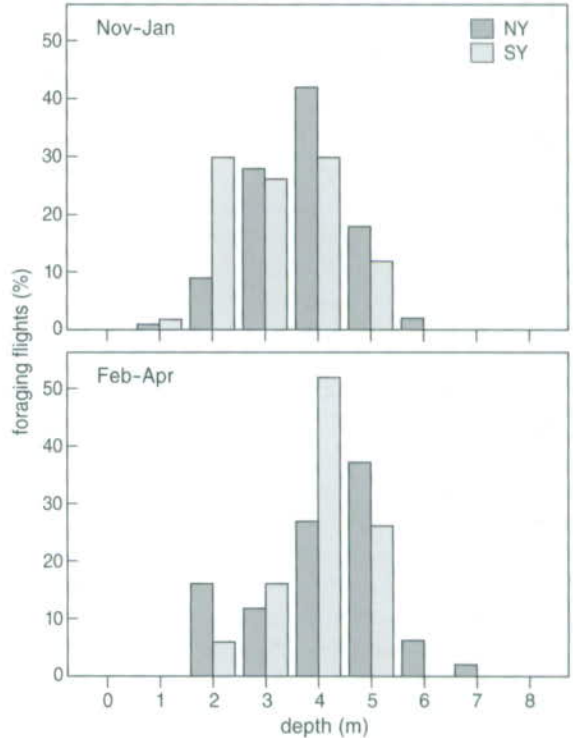


Fig. 10. Frequency distribution of foraging depths of Scaup based on radar observations of feeding flights (Chapter 2 for details) in northern (NY) and southern IJsselmeer (SY) in early and late winter showing shift to deeper water in late winter.

protein reserves. Tufted Duck (fat mass 200 g) can survive a similar period. In the last 20 years, there were 5 winters in which the IJsselmeer area was covered with ice for longer than a month. In those winters, Tufted Duck and Scaup could only have survived in alternative, ice-free habitats. Tufted Duck usually move to rivers, while Scaup are frequently found in the Wadden Sea or North Sea down south to France during such ice episodes. Food availability in these alternative areas and the survival chances of these severe winter movements are largely unknown. A notable exception was the dramatic starvation of tens of thousands of Tufted Duck and Scaup in Switzerland and the Dutch Wadden Sea, respectively, in late February and March 1986 (Suter & Van Eerden 1992). This example demonstrates that alternatives may not always be within reach of the ducks and that the combined effect

of low food availability and long cold spells can take a heavy toll.

Short flight distances.

Flight distances observed by radar were usually well below 10 km, with late winter averages of 5.3 km for Tufted Duck, and 6.3 km for Scaup and in early winter even less (Chapter 2). This confirms that roosts are indeed often close to the foraging sites and that Scaup fly further than Tufted Duck, as predicted from Fig. 6. Nilsson (1970, 1972) mentioned that commuting distances of Tufted Duck and Scaup in the southern Baltic Sea (Sweden) were on average 2-5 km. Foraging flights were sometimes considerably longer than 10 km, not matching the predictions. However, diving ducks may shift roost sites and foraging sites according to the prevailing winds and upon depletion. Moreover, the model implicitly assumed that diving ducks maintained energy balance within a day. This is not necessarily the case. For example, in severe weather with strong winds, it might pay the ducks to remain longer at sheltered roosts and compensate the increased reliance on bodily energy stores later, under more favourable conditions. Lovvorn (1994a) observed that Canvasbacks *Aythya valisneria*, Redheads *Aythya americana*, and Lesser Scaup *Aythya affinis* reduced or stopped feeding during very cold weather, while Kestenholz (1994) demonstrated from recaptures of individual Tufted Duck wintering at Lake Sempach, Switzerland, that these birds were able to adjust their body mass throughout the winter, suggesting considerable flexibility in this respect.

The fact that diving ducks do fly between roosts and foraging sites, might suggest that resting costs are often considerably higher (at least 20-25%, see Fig. 6) at exposed foraging sites than at sheltered ponds or coastal zones. In addition, the location of roost sites depends on wind direction and feeding areas may be chosen accordingly. However, when the near-shore zones are depleted in late winter, Scaup often remain at the foraging sites (Chapter 2), probably accepting high maintenance costs. Also, the usual huge flocks observed in winter (sometimes more than 30 000 individuals) tend to break up by the end of the winter and both species show day-active feeding, as predicted from Fig. 9. A shift from night-feeding to actively foraging during the day later in the winter season was

also recorded in Tufted Duck feeding on Zebra Mussels in the Upper Rhine (Suter 1982), and Scaup and Tufted Duck feeding on *Mytilus* and other bivalves in the Baltic Sea in southern Sweden (Nilsson 1970, 1972).

Threshold densities.

As mentioned earlier, the predicted giving-up densities match well with the lowest densities measured by the end of the winter after intensive predation, although locally patches at shallow depths remained unexploited (Fig. 11). An associated question is to what extent local populations can recover from such intense predation, for example within a growing season or over several years. This is particularly relevant to the annual predictability of finding suitable feeding sites by diving ducks. It is possible that diving ducks take advantage of food sources at foraging areas which can be exploited year after year to enhance their survival chances.

Reproduction and growth are well-studied in *Dreissena*. Fecundity is extremely high, amounting to 1 million eggs per spawning event (Sprung 1990), while mussels grow within one season (April-August) to

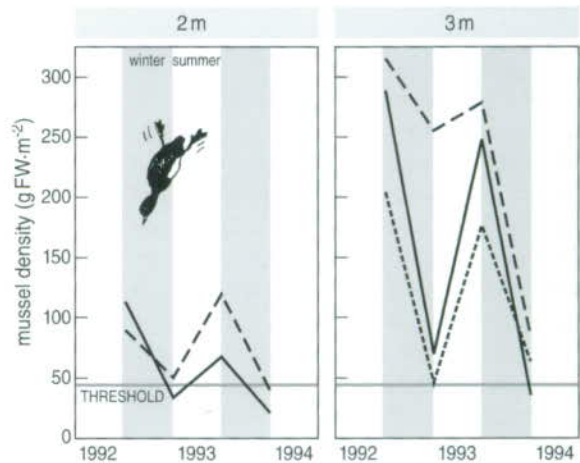


Fig. 11. Variation in mussel densities due to predation by Scaup in winter (shaded boundaries) at sampling stations at Enkhuizerzand, Lake IJsselmeer, and growth and settlement in summer. Predicted threshold densities, where Scaup should give up foraging at 2 and 3 m ($30\text{--}50\text{ gFW.m}^{-2}$) are indicated. Notice that one sampling station at 3 m was not exploited in 1992/93, but depleted to a similar extent as the other stations in the next winter.

shell lengths of 10–15 mm (Bij de Vaate 1991). In addition, veligers (the larval stage) may be transported from the rivers Rhine and IJssel and settle in the IJsselmeer (Bij de Vaate 1991). Colonization of the IJsselmeer area by Zebra Mussels occurred within 2 years, starting 4 years after closing the dyke when the area had transformed from a marine-brackish estuary to a freshwater lake. Favourable feeding sites of Scaup in Lake IJsselmeer sampled in autumn and spring showed that the density of mussels is reduced to threshold levels by predation during winter, but had recovered by the next growing season, upon which mussels were exploited again up to threshold levels in the following winter (Fig. 11). Note that one sampling plot at 3 m was not exploited in the first year, but utilized in a similar fashion as the other sites in the second winter. These examples demonstrate the enormous growth potential for recovery after intense predation within one season, allowing sustained annual exploitation by diving ducks.

Predictable feeding areas.

The energetic costs of searching for food patches, in particular in a heterogeneous area, appears the most likely explanation for the apparent underexploitation of rich patches. Flocking behaviour and the concentration of diving ducks around large, predictable feeding areas, as shown in Fig. 8, seem vital to achieve a sufficiently high intake rate to maintain energy balance. To approximate the effect of patchiness on bird attendance, the predictability of finding mussels was calculated as the probability of encountering mussels by bottom sampling (10 samples per grid cell were taken). Linear regression analyses were carried out with the number of bird days of Scaup in each of the encircled areas and the biomass above a certain threshold of predictability (10–100%). In Lake IJsselmeer, the number of Scaup correlated best with biomass in grid cells with a probability of encountering mussels of at least 70% ($r^2 = 0.69$, $P = 0.003$, see Fig. 12). If cells with lower probabilities are included, the relationship becomes weaker ($r^2 = 0.55$, $P = 0.011$, when all cells are included). Similarly, the number of Scaup correlated well with the number of grid cells meeting the profitability criteria of sufficiently high biomass (i.e. above threshold density) and shallow depths in the area ($r^2 = 0.81$, $P < 0.001$). Also, the total number of Scaup

days spent in the selected areas increased between 1981 and 1992 from 6.1 to 9.2 million bird days, which nicely corresponds with an increase in 'predictable biomass' (above the 70% encounter rate criterion) from 66.8 to 90 million kgFW. In contrast, the total biomass in the selected areas (thus including unprofitable grid cells) slightly decreased from 113 (1981) to 96 million kgFW (1992). This again gives support to the importance of shallow, homogeneous mussel areas for the number of birds that can spend the winter there. The decrease in numbers of Tufted Duck also corresponds to the decline in harvestable biomass, in particular in the most southern part of Lake Markermeer (area 7 in Fig. 8 and 12). The harvestable biomass in Lake Markermeer in 1981 seemed to be underexploited, however. A possible reason is that 1981 was a year with high spat fall in Lake Markermeer (Bij de Vaate 1991). As this would mean a sudden increase in available biomass, the wintering population of Tufted Duck might not have been able to respond within the season. Like the Scaup data, the numbers were very close to the maximum number of bird days that could survive on the harvestable biomass. This maximum was calculated on the basis of the minimal food requirements per bird (approximated at 4 kg per day).

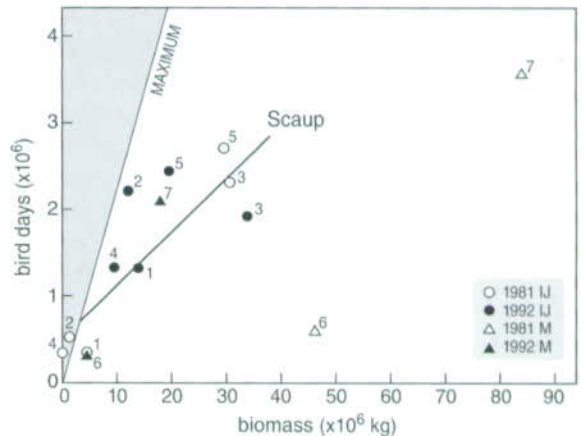


Fig. 12. The number of bird days in relation to mussel biomass in profitable areas. Profitable areas were selected by excluding deep water, low mussel densities, and low encounter rates of mussels (see text for details). Notice differences between years and Scaup (IJsselmeer, IJ) and Tufted Duck (Markermeer, M). Numbers indicate areas depicted in Fig. 8.

A more rigorous analysis of the influence of the probability of finding food on profitability hinges on a proper sampling regime of patchiness on a scale relevant to feeding ducks. This, in practice, may be a difficult task to realize as also pointed out by Lovvorn (1994b) and Lovvorn & Gillingham (1996). In their study of exploitation patterns of Canvasbacks in the field, using a comparable foraging energetics model, these authors attributed deviations from model predictions mainly to shortcomings in an adequate assessment of patchiness of the food supply.

Why do Tufted Duck and Scaup segregate?

Although both Tufted Duck and Scaup can be found at all feeding sites known in the IJsselmeer area, the vast majority of both species was clearly segregated: Scaup were mainly found in Lake IJsselmeer and Tufted Duck in Lake Markermeer and the southern boundary of Lake IJsselmeer (Chapter 2). The preference of the Scaup for Lake IJsselmeer is best explained by the high energy value of mussels, in particular at shallow depths, as compared to the relatively poor condition of mussels in Lake Markermeer (Fig. 4). Tufted Duck, on the other hand, might benefit from higher intake rates when feeding on small mussels with a low byssal attachment as found in Lake Markermeer, whereas Scaup seemed indifferent in this respect (see Chapter 8). However, the Tufted Duck's benefit from a moderate byssal attachment does not off-set the relatively poor condition of mussels in Lake Markermeer: as in Scaup, Tufted Duck can balance their budget at a lower DEE in the shallower parts of Lake IJsselmeer (2 m and 3 m) than in Lake Markermeer (at 3 m) as depicted in Fig. 13 (even if it is assumed that the ducks are feeding exclusively on 'tight clumps'). An energetic perspective therefore only predicts underuse of the 4 m zone in Lake IJsselmeer, but not the massive shift to Lake Markermeer as actually observed. We may thus pose the question why Tufted Duck were not observed in larger numbers in Lake IJsselmeer. Three possible explanations will be discussed: (1) the importance of sheltered foraging sites and roosts along the coast and at inland ponds around Lake Markermeer, (2) the probability of encountering mussels, and (3) competition with the larger-sized Scaup.

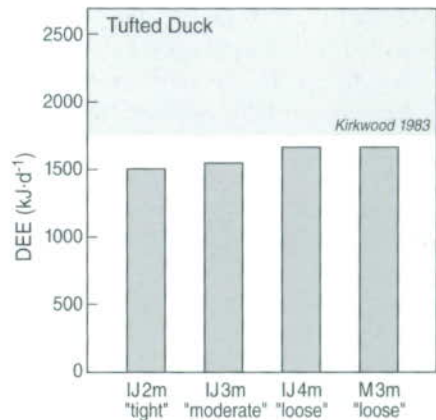


Fig. 13. Daily energy expenditure (DEE) estimated for Tufted Duck feeding on tightly, moderately, and loosely attached mussels at 2, 3, and 4 m in Lake IJsselmeer (IJ), respectively, and loosely attached mussels in Lake Markermeer (M).

Sheltered roosts and feeding grounds.

Diving ducks can enjoy savings on resting costs not only at sheltered roosts but also at foraging sites, because a major proportion of the total feeding time is spent resting at the surface in order to process the food (shell crushing and digestion). As can be seen in Fig. 6A, DEE of Tufted Duck was generally extremely high, approaching Kirkwood's suggested maximum at commuting distances of 5 km and extra maintenance costs at the foraging sites *ca.* 20% higher than minimal values. Owing to its smaller size, Tufted Duck is more susceptible to heat loss than Scaup. Therefore, the availability of nearby sheltered resting sites appears to be an important criterion for the profitability of foraging sites. The prevailing wind direction in the IJsselmeer area is south-west, while the east wind is the coldest. Lake Markermeer not only offers more sheltered feeding grounds along its west coast than Lake IJsselmeer, but there are also many sheltered roosting areas available behind dykes and dams, in particular in the most southern part (e.g., Lepelaarsplassen, Pam-pushaven, IJhavens of Amsterdam, Kinselmeer, Gouwzee; see Fig. 4 in Chapter 1 for topography). Scaup enjoy broader margins in DEE, allowing longer flights and higher maintenance costs. Observations confirm that Scaup switch frequently between roosting sites at either the west coast or east coast of Lake IJ-

selmeer, depending on wind direction. On the other hand, Scaup often stay at more off-shore foraging sites in late winter, facing the more wind-exposed conditions in Lake IJsselmeer (as depicted in the maps of Figure 4 in Chapter 2).

Tufted Duck also seemed to be more sensitive to variation in mussel density than Scaup, probably because searching efficiency is lower and a reduction in intake rate more strongly affected DEE. The analyses of gullet contents of drowned ducks from which the relative feeding success was derived (see Chapters 2 and 8) confirmed this difference in probability of encountering mussels between the species and between the lake compartments, favouring Lake Markermeer where the probability of encountering an exploitable mussel patch is higher.

In conclusion, Tufted Duck's preference to feed in Lake Markermeer cannot be adequately explained by higher net intake rates than in Lake IJsselmeer, but extra savings on resting costs and a higher probability of finding food could explain this choice. These aspects of habitat suitability, however, are extremely difficult to quantify in terms of contributions to a diving duck's energy budget, as they require exact figures of searching efficiency at different locations through the winter and estimates of wave-exposed resting costs.

Competition.

Even more difficult to quantify is the possible role of competition in the segregation of the two species. Tufted Duck and Scaup sometimes utilize the same feeding grounds and have widely overlapping diets. Tufted Duck arrive earlier (October) in favourable feeding areas, but leave these areas when large numbers of Scaup invade (Chapter 2). This seems a clear example of exploitation competition: the mussels eaten by Tufted Duck could otherwise have been eaten by Scaup and *vice versa*. But more direct competition may also play a role: although interspecific aggressive behaviour is rarely observed in free-living diving ducks (but see Siegfried 1976), the segregation of the species might well be a result of interference competition, the larger sized Scaup dominating Tufted Duck. For example, Scaup might monopolize the highly favoured feeding site at Enkhuizerzand (Lake IJsselmeer), a large scale shallow area (2-3 m) with evenly distributed, relatively high densities of mussels in good condition

(area 5 in Fig. 8 and 12). Scaup can be found here in large flocks of 10 000 to 30 000 birds throughout winter. Also, in the northwestern part of Lake Markermeer Scaup have appeared since 1990, while Tufted Duck seem to abandon the area (Chapter 2). Fretwell & Lucas (1970) developed the concept of the ideal-free distribution (IFD), which predicts that individuals spread themselves evenly over the available resources as far as they can gain profit. However, when individuals differ in their foraging and competitive ability, as was shown to be the case among Tufted Duck and Scaup, habitat segregation will occur, the more so in habitats where food availability is difficult to predict (Rosenzweig 1991). This phenomenon can also explain the tendency for segregation between males, females and juveniles within the species (see Chapter 2, Choudhury & Black 1990, De Leeuw & Van Eerden 1995).

Implications for carrying capacity

Carrying capacity is reached when incoming birds are unable to make use of the harvestable food sources. The predictions of the energy model regarding the question when diving ducks reach their limits to food exploitation were strongly supported by field data (Table 2). Most importantly, it could be shown that the number of birds in particular areas correlated closely with the biomass that could be harvested at maximum sustainable levels. In order to predict the carrying capacity of the entire lake system of the IJsselmeer area, the total biomass that can be harvested has to be estimated. Assuming that diving ducks ideally deplete shallow areas before exploiting deeper mussel populations, the question translates to the available biomass for a certain number of bird days that can be spent at a given depth range (see Fig. 14). As an average figure based on the energy model, it can be assumed that daily food consumption of an average diving duck increased linearly with water depth from 3 to 5.5 kg mussels over a depth range of 2 to 6 m, due to increasing diving costs, flight distance, and lower quality mussels at the greater depths. As in earlier examples, I assumed a giving-up density of 50 gFW.m⁻² (excluding *ca.* 9% of the total biomass), and a minimal probability of encountering mussels of 70% (excluding another 20% of the total biomass). Mussels in the depth range from 2 to 4 m

Table 2. Overview of predictions from the energetic model and supporting evidence from field observations on Tufted Duck and Scaup.

	Prediction	Confirmed by observations?	
		Tufted Duck	Scaup
Preference for shallow water and shifts to deeper water due to depletion	1, 4, 5, 6, 13, 14	yes	yes
Northern IJsselmeer more profitable than southern part and Markermeer	2, 3	no	yes
Giving-up density at least 30 (-50) gFW.m ⁻²	7	yes	yes
Short flight distances	8	yes	yes
Scaup fly further than Tufted Duck	9	yes	yes
Duck numbers correspond with changes in profitable mussel biomass	11, 12	yes	yes
Utilization of fat stores in late winter	15	yes	yes
Daytime feeding in late winter	10, 16	yes	yes

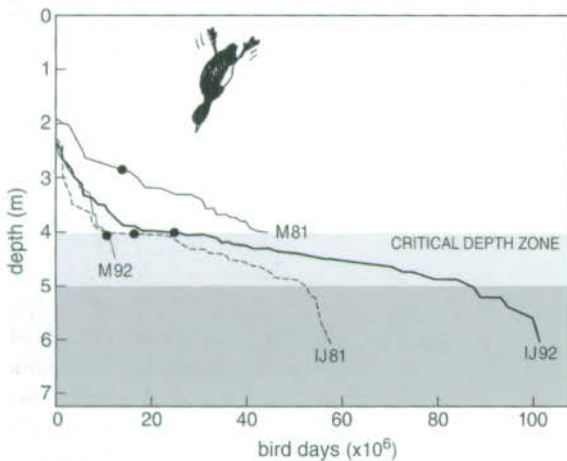


Fig. 14. Number of bird days in relation to water depth. The cumulative bird days are based upon depth-dependent estimates of harvestable biomass in Lake Markermeer (M) and Lake IJsselmeer (IJ) in 1981 and 1992, respectively. Harvestable biomass was calculated from 2x2 km grid cells with threshold densities of 50 gFW.m⁻² and a probability of encountering mussels per bottom sample (0.04 m²) higher than 70%. Daily mussel consumption was assumed to increase with depth (2-6 m) from 3 to 5.5 kgFW.bird⁻¹.d⁻¹. The number of bird days in mild winters (no ice cover) in the periods 1980-84 and 1990-95, respectively, are indicated on the curves. Bird days of Tufted Duck, Scaup, Pochard, and Goldeneye are combined. The critical depth zone of 4-5 m can only be exploited at high cost, depending on local variations in mussel condition and patchiness in mussel distribution.

are readily harvestable according to the energy models presented. In the range of 4 to 5 m, mussels are superabundant, but most mussel beds are more than 8 km

off-shore and mussels are in poor condition, although there may be considerable local variation in this respect. In general, this depth range can probably only be exploited at very high energy costs (DEE above the suggested maximum sustainable levels), and it is questionable whether diving ducks can maintain energy balance while feeding for long at these depths. The carrying capacity can thus be estimated as the number of bird days that can be spent up to depths of 4 m.

The average number of bird days of all mussel-consuming diving ducks (Tufted Duck, Scaup, Pochard, and Goldeneye) observed in mild winters without ice cover in the periods 1980-84 and 1990-95, respectively, are plotted in Fig. 14. Three out of four estimates demonstrate that carrying capacity must have been reached as the number of bird days intersect the critical depth zone at 4 m. Only Lake Markermeer was apparently underexploited in 1981. The high numbers of Scaup observed since 1990 correspond with the increase in available biomass in Lake IJsselmeer, while the recent decrease in numbers of Tufted Duck matches the strong decline in mussel biomass in Lake Markermeer.

Future perspectives

This study gives evidence that diving ducks can harvest only a fraction (20% on average) of the total mussel biomass in the IJsselmeer area. The condition of mussels proved to be an important criterion for the profitability of foraging sites. Investigations on depth-dependent and local variations in mussel condition could

further improve our insight to what extent exploitation by diving ducks is limited. Also, the probability of finding food, both at the level of patches (for the individual) and of larger units of profitable area for feeding flocks, seems an important criterion for habitat selection. Sampling programs of patchiness at levels relevant to diving ducks linked to field measurements of the foraging effort and habitat use of individual birds (for instance by radio telemetry) could further enhance our understanding of where and how diving ducks can forage profitably. The implications for carrying capacity could be refined when these conditions can be quantified.

The ecological energetic approach proved to be successful to elucidate the patterns in distribution of ducks and patch exploitation. The measurements on foraging energetics and insights into habitat use presented in this study can be applied more generally to study food exploitation in aquatic ecosystems. For example, the possible impact of diving ducks could be investigated in other *Dreissena* dominated water bodies, such as the Great Lakes of America where Zebra Mussels might conquer the indigenous benthic fauna. It would be a challenge to extend the approach to other trophic systems, for example where the benthic community is dominated by Chironomidae, or to other diving duck species, such as Eider *Somateria mollissima* and Black Scoter *Melanitta nigra* feeding on bivalves in the marine environment. An extension to fish-eating divers such as the Cormorant *Phalacrocorax carbo* which can be studied in the same lake-system provides an especially promising perspective.

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Samenvatting

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Duikende en Driehoeksmosselen

Elke winter komen grote aantallen duikende vanuit hun noordelijker gelegen broedgebieden naar het IJsselmeer. De talrijkste soorten zijn de Kuifeend (maximaal 150 000 per winter) en de Toppereend (maximaal 200 000), die hier een cruciaal overwinteringsgebied vinden waar soms bijna de helft van de Europese populatie verblijft. Deze vogels leven van allerlei bodemdieren die ze opduiken, maar opmerkelijk is de zeer sterke voorkeur voor Driehoeksmosselen, een talrijk schelpdier in zoetwatergebieden. Wanneer deze soort zich in een gebied vestigt nemen de aantallen overwinterende duikende vaak navenant toe, zoals bijvoorbeeld in Zwitserse meren rond 1970 en recent in de Great Lakes in Amerika werd vastgesteld. In het IJsselmeergebied is de Driehoeksmossel algemeen sinds de verzoeting na de afsluiting in 1932. De sterke link tussen de talrijke duikende en mosselen vormt een belangrijke schakel in het ecosysteem van het IJsselmeer. Als filteraars van algen, bijvoorbeeld, wordt Driehoeksmosselen een belangrijke functie toegedicht met betrekking tot de waterkwaliteit. In dit onderzoek is gekeken in welke mate duikende deze voedselbron exploiteren. Ook wordt een antwoord gezocht op de vraag of de aantallen duikende die in het gebied overwinteren afhangt van de hoeveelheid Driehoeksmosselen.

Draagkracht: wanneer is het voedsel op?

Hoe goed duikende ook zijn aangepast aan het voedselzoeken onderwater, een deel van het voedsel blijft onbereikbaar voor ze. Hoeveel dat is wordt bepaald door het vermogen van de eenden om voldoende voedsel per dag te vinden. De fractie van de voedselvoorraad die een voldoende hoge voedselopname garan-

deert bepaalt het aantal vogels dat kan overwinteren, ofwel de draagkracht van het IJsselmeergebied. De voedselopname die duikende kunnen halen wordt bepaald door eigenschappen van de mosselen (prooien) en van de omgeving (habitat). Duikende hebben steeds maar kort de tijd om onderwater voedsel te zoeken, omdat ze voortdurend naar het wateroppervlak moeten om adem te halen. Daarom is het bijvoorbeeld van belang hoe diep ze voor de mosselen moeten duiken, hoe lang ze er naar moeten zoeken en hoe snel de mosselen kunnen worden doorgeslikt. Wanneer voedselzoeken niet meer rendabel is, is de draagkracht bereikt en moeten vogels het gebied verlaten of gaan ze dood. Hoe meten we echter wat rendabel is? Alles wat een levend wezen doet heeft te maken met energie-omzettingen. Als we het gedrag van duikende kunnen uitdrukken in energie-uitgaven en de opname van voedsel als energie-opname, zijn we in staat om te bepalen onder welke omstandigheden de energiekosten niet meer opwegen tegen de baten van voedselzoeken. Anders gezegd, we kunnen met deze kosten-baten analyses 'beslissingen', die duikende nemen bij het kiezen van hun voedsel en hun voedselgebieden, meetbaar maken en de meest rendabele opties aangeven. We kunnen dan dus ook in zekere zin voorspellen hoe duikende gebruik maken van het IJsselmeergebied en wanneer de voedselvoorraad niet meer toereikend is.

Naast metingen aan de voedselvoorraad en het aantal duikende in het IJsselmeer was het dus nodig om nauwkeurige metingen te doen aan de manier van voedselzoeken en de energie-huishouding van duikende. Omdat duikende vaak 's nachts actief zijn en onderwater voedselzoeken was het onmogelijk om dit in het veld te doen met vrijlevende vogels. Vandaar dat veel van deze metingen gedaan zijn in experimenten met duikende onder gecontroleerde omstandigheden, waarbij zoveel mogelijk de natuurlijke wintersituatie in het IJsselmeer werd nagebootst.

Voedselopname

Duikendeen slikken prooien in hun geheel door. De schelpen van Driehoeksmosselen worden gekraakt in de gespieerde maag. Vervolgens gaat de schelpmassa de darmen in en wordt het vlees verteerd.

De grootte van de schelp bepaalt hoe snel deze kan worden ingeslikt. Kleine mosselen (tot ca. 1.5 cm) worden met een soort filtertechniek uit een waterstroom gezeefd die wordt opgewekt in de snavel tijdens het voedselzoeken onderwater. Grotere mosselen (tot 3 cm) daarentegen worden een voor een naar binnen gewerkt; dat kost meer tijd. Omdat per duik maar weinig tijd op de bodem besteed wordt (10-12 seconden), nemen duikendeen grotere mosselen ook vaak mee naar het wateroppervlak om ze daar door te slikken. Hoewel er in de grotere mosselen meer vlees en dus energie zit, leveren kleine mosselen meer energie op per tijdseenheid. De voedselopname werd gemeten in experimenten met Kuifeenden en Toppereenden die doken naar Driehoeksmosselen op diepten tot 5 m in zogenaamde duikkooien in een zuigerplas bij Lelystad. Met behulp van een computergestuurd detectiesysteem met infra-rood licht werd de duikactiviteit van de eenden (4 per soort) dag en nacht geregistreerd gedurende enkele maanden. Uit deze experimenten bleek dat Kuifeenden en (in mindere mate) Toppereenden inderdaad een voorkeur hebben voor de kleinere mosselen. Door de hoge tijdsdruk tijdens het voedselzoeken onderwater zijn ze echter niet heel selectief en accepteren ze ook veel mosselen van groter formaat.

Driehoeksmosselen produceren vaak byssusdraden

waarmee ze zich vasthechten aan een harde ondergrond (andere mosselen of dode schelpen). De zeeftechniek werkt dan niet en de mosselen moeten worden losgetrokken van het substraat voordat ze kunnen worden ingeslikt. Bij de Kuifeend is daardoor de voedselopnamesnelheid lager bij het eten van zogenaamde mosselkluiten dan wanneer ze losliggende mosselen kunnen verzamelen met de filtertechniek. Toppereenden zijn wat groter en kunnen ook meerdere kleine mosselen die aan elkaar zitten doorslikken, waardoor de opnamesnelheid veel minder wordt beïnvloed door de byssusdraden. Alleen in uitzonderlijke gevallen zitten mosselen zo stevig vast dat ook bij Toppereenden de opnamesnelheid omlaag gaat.

De duikactiviteit bleek te bestaan uit een zeer regelmatig patroon van een reeks duiken kort achter elkaar (kleine maaltijden) afgewisseld met langere pauzes van ongeveer 10 minuten. Tijdens het duiken wordt de slokdarm gevuld met ca. 35 g mosselen die worden gekraakt in de daaropvolgende pauze en vervolgens worden verteerd. Dit gaat in hoog tempo: een mossel zit gemiddeld slechts 25 minuten in het eendelichaam. Een mossel bestaat grotendeels uit schelp en water, slechts ongeveer 5% is vlees. Omdat de vleesinhoud van mosselen zo klein is hebben duikendeen dagelijks grote hoeveelheden nodig om hun energiebehoefte te dekken. In de winter kan dat oplopen tot enkele kilo's per dag (3 maal hun lichaamsgewicht). Omdat slechts een geringe hoeveelheid mosselen tegelijkertijd verwerkt kan worden in het lichaam (en weinig voedsel kan worden opgeslagen) moet bijna al dat voedsel ter plekke worden verteerd. De vertering is, ook bij andere vogels, vaak de beperkende factor in de energieopname



en duikeenden moeten daarom het grootste gedeelte van een etmaal op de fourageergronden doorbrengen, waarbij het voedselzoeken voortdurend wordt onderbroken door verteringspauzes.

Mosselen vormen niet altijd een rijkgedekte tafel. Op veel plaatsen zijn mosselen schaars of komen ze in sterk wisselende hoeveelheden voor. Duikeenden zoeken voedsel op de tast en de voedselopname hangt dan ook af van de kans om mosselen op de bodem tegen te komen. De invloed van de ruimtelijke verspreiding van mosselen op de voedselopname werd onderzocht bij Kuifeenden en Toppereenden die doken in een groot basin (bodempoppervlak van 50 m²). Duikeenden bleken efficiënt te kunnen zoeken: alleen bij zeer lage mosseldichtheden (minder dan 50 g.m⁻²) werd de snelheid van energieopname beduidend minder. Bij grotere dichtheden is vooral het inslikken van de prooi beperkend. Wanneer mosselen homogeen verspreid waren was de gemiddelde opnamesnelheid hoger dan wanneer dezelfde hoeveelheid mosselen sterk geclusterd was. Blijkbaar kostte het in het laatste geval veel tijd om de rijke mosselplekken te vinden.

Energetische kosten van duiken en voedsel verwerken

Duiken is uit energetisch oogpunt een kostbare manier van voedselzoeken. De beperkte hoeveelheid zuurstof die in het lichaam kan worden opgeslagen maakt het noodzakelijk om voortdurend op en neer te pendelen tussen het wateroppervlak en de bodem. Bij diepere duiken (5 m) wordt bijna de helft van de duiktijd besteed aan het reizen. Om toch voldoende tijd over te houden om voedsel te zoeken op de bodem neemt de totale duiktijd toe met de diepte. Er zijn aanwijzingen dat duikeenden al bij diepten vanaf 4 m gedeeltelijk gebruik moeten maken van anaerobe stofwisseling (een kostbare manier om zuurstof uit te sparen).

Een oorzaak van het hoge zuurstofverbruik tijdens het duiken is de grote inspanning die is vereist om onderwater te blijven. Voor een goede isolatie tegen het koude water hebben duikeenden een waterdicht verenpak waarin lucht wordt vastgehouden. Onderwater zorgt dit voor een sterke opwaartse kracht die overwonnen moet worden met krachtige zwembewegingen van de poten. Op grotere diepte wordt de lucht

samengedrukt en neemt die oprijfkracht af, maar ook de isolerende werking van de lucht in het verenkleed. Vooral bij duiken in koud water verliezen duikeenden daardoor veel warmte, zoals in een experiment kon worden afgeleid uit een sterk verhoogde zuurstofopname van Kuifeenden naarmate de watertemperatuur lager was. De zuurstofopname werd gemeten door Kuifeenden te laten duiken in een 6 m diep aquarium vanuit een perspex box aan het wateroppervlak, waarin nauwkeurig de zuurstofconcentratie kon worden bepaald. De mate van afkoeling in het lichaam tijdens het duiken en de daarmee gepaard gaande energie-uitgaven werden gemeten bij Kuifeenden die werden voorzien van een hartslag- en temperatuurzendertje in de buikholte. Uit deze experimenten bleek dat de afkoeling door het duiken aanzienlijke energetische kosten met zich meebrengt.

Ook bleek daaruit dat het inslikken van de enorme hoeveelheden koude Driehoeksmosselen een grote kostenpost vormt op de dagelijkse energie-uitgaven, omdat veel energie geïnvesteerd moet worden in het op peil houden van de lichaamstemperatuur. De warmte die vrijkomt bij het verteren van het voedsel en door de spieractiviteit van de maag bij het kraken van de mosselen kon overigens worden gebruikt om dit warmteverlies gedeeltelijk te compenseren. Het duiken en voedselverwerken vormen bijna de helft van het totale winter-energiebudget van duikeenden. Maar zelfs het rusten op water onttrekt al veel warmte aan de vogels bij lage temperaturen. Duikeenden rusten vaak op luwe plaatsen, met één poot en de snavel in de veren om het warmteverlies zoveel mogelijk te beperken. Al met al bereikt het energiebudget in de winter waarden rond het maximum dat vogels kunnen handhaven. Doordat de energiekosten zo hoog zijn, stellen duikeenden hoge eisen aan hun omgeving om een rendabele voedselexploitatie mogelijk te maken.

Welke voedselgebieden zijn aantrekkelijk?

In 1981 en 1992 is het voorkomen van Driehoeksmosselen in het hele IJsselmeergebied (1925 km²) onderzocht door bodemmonsters te nemen in een regelmatig grid van 2x2 km-hokken. Daaruit bleek een grote variatie in de verspreiding van de mosselen die onder meer verband houdt met de bodemgesteldheid

en de waterdiepte. De dichtheid mosselen (biomassa per m²) neemt over het algemeen toe met de diepte tot ongeveer 5 m en neemt dan af. De ruimtelijke verspreiding van de aantallen duikeenden, die maandelijks werden geteld vanuit een vliegtuig gedurende een periode van 20 jaar, kwam in grote lijnen overeen met de verspreiding van Driehoeksmosselen, al bleken vooral ondiepe plekken een onevenredig groot aantal vogels aan te trekken. Dit werd bevestigd door de verspreiding van duikeenden die waren verdrongen in visnetten tijdens het voedselzoeken 's nachts en door radarwaarnemingen van nachtelijke voedselvuchten vanaf de dagrustplaatsen langs de kust. Opmerkelijk was dat de twee talrijkste soorten duikeenden grotendeels gescheiden voorkomen in het gebied, Toppereenden vooral in het IJsselmeer en Kuifeenden in het Markermeer.

Gedetailleerde bemonsteringsprogramma's op locaties waar veel duikeenden werden waargenomen toonden aan dat duikeenden soms een aanzienlijk deel van de biomassa wegnamen, maar ook dat sommige mosselgebieden slechts gedeeltelijk of in het geheel niet werden benut. Daarnaast kwam vast te staan dat eigenschappen van de populatie Driehoeksmosselen lokaal sterk konden verschillen. De hoeveelheid vlees in een mosselschelp van zekere lengte (mosselconditie) varieerde bijvoorbeeld sterk en dit leek samen te hangen met de groeicondities van mosselen. In het IJsselmeer zijn Driehoeksmosselen gemiddeld in betere conditie dan in het Markermeer, maar de conditie neemt sterk af in dieper water. In het noordelijke deel van het IJsselmeer werden ook betere mosselen aangetroffen dan in het zuidelijke deel. Hetzelfde geldt voor de mate waarin mosselen zich vasthechten met byssusdraden: de aanhechting is gemiddeld wat sterker in het IJsselmeer dan in het Markermeer en neemt af met de waterdiepte.

De invloed van deze variatie in omgevingsfactoren op het energiebudget van duikeenden (en daarmee de aantrekkelijkheid van gebieden) werd onderzocht met behulp van een energiemodel. Daarmee werden de dagelijkse energie-uitgaven berekend op basis van de metingen aan voedselopnamesnelheid en de energetische kosten onder verschillende voedselomstandigheden. Ook kon daarmee worden aangegeven wanneer gebieden vermoedelijk niet langer rendabel geëxploiteerd konden worden.

Alleen ondiepe gebieden zijn rendabel

De modelberekeningen lieten zien dat de energetische kosten sterk oplopen met de waterdiepte. Dit was niet zozeer het gevolg van het feit dat duikeenden niet zo diep zouden kunnen duiken, alswel vanwege de sterk verminderde conditie van de mosselen in diep water. Daardoor moeten veel grotere hoeveelheden mosselen worden opgedoken en verwerkt dan nodig is in ondiep water. Het model voorspelt dat in het IJsselmeergebied duikeenden niet veel dieper dan 3.5 tot 4.5 m zouden moeten duiken om hun energiebalans te kunnen handhaven. Deze ondergrens hangt af van de lokale mosselcondities. Bovendien liggen de diepere delen verder uit de kust. Met een schatting van de vliegkosten op basis van literatuurgegevens kon worden berekend dat voedselgebieden niet veel verder dan enkele kilometers van de dagrustplaatsen verwijderd zouden moeten liggen omdat anders vliegkosten te zwaar op het budget zouden drukken. Bij Toppereenden zou de maximale afstand gemiddeld niet meer dan 8 km moeten zijn en bij Kuifeenden slechts 6 km. Deze schattingen komen goed overeen met waarnemingen in het veld: de gemiddelde vliegafstanden die werden waargenomen met radar liggen inderdaad binnen de voorspelde maxima en duikeenden toonden een sterke voorkeur voor ondiepe, kustgebonden plekken. In het noordelijk deel van het IJsselmeer doken Toppereenden overigens dieper dan in het zuidelijk deel zoals werd verwacht op basis van de gemeten verschillen in mosselconditie. Bovendien waren Toppereenden bereid gemiddeld iets verder te vliegen dan Kuifeenden. Op grond van schattingen van de biomassa op verschillende diepten en de voedselbehoefte van duikeenden kon worden berekend dat in de loop van de winter de voedselvoorraden uitgeput raken in de ondiepe delen. Dit werd wederom bevestigd door de waarnemingen in het IJsselmeergebied die een verschuiving naar voedselgebieden op grotere diepte lieten zien later in de winter. De berekeningen suggereerden ook dat duikeenden later in de winter, wanneer de rendabele gebieden zijn uitgeput, problemen krijgen om de energiebehoefte te blijven dekken. Uit analyses van verdrongen eenden blijkt inderdaad dat ze de vetvoorraden aanspreken die ze in de vroege winter, onder gunstige voedselcondities, konden aanleggen.

Hoe worden rendabele gebieden gevonden? Door de variatie in verspreiding van de Driehoeksmosselen



Belangrijke voedsel- en rustgebieden van overwinterende duikeenden in het IJsselmeergebied (K = Kuifeend, T = Toppereend; secundaire gebieden licht getint). De grote pijlen geven indicaties voor noord-zuid gradiënten met betrekking tot de benutting van Driehoeksmosselen door duikeenden. In het noordelijk deel is de conditie van mosselen beter, maar is het habitat en de groeivorm van mosselen minder aantrekkelijk voor duikeenden. De kleine pijlen geven verplaatsingen aan in de loop van de winter. In het oostelijk deel van het Markermeer ruïen in de nazomer ongeveer 30 000 Kuifeenden en Tafelreenden.

zijn de beste voedselgebieden niet precies te voorspellen. Het zoeken naar de rijke voedselplekken is energetisch gezien kostbaar omdat de vogels steeds moeten duiken. Gebieden met een grote kans om mosselen aan te treffen (homogene verspreiding) zijn daarom het meest in trek. Om die plekken te kunnen vinden zoeken duikeenden in grote groepen van duizenden vogels hun voedsel, waarbij elke vogel ook informatie over het succes van andere zoekende individuen kan gebruiken. Dit stelt echter ook eisen aan de grootte van de voedselgebieden. Analyses van de aantallen duikeenden die werden geteld in mosselrijke sectoren in het IJsselmeer en de op grond van modelberekeningen rendabel geachte plekken binnen die sectoren toonden een duidelijk verband met de beschikbare mosselbiomassa. Bovendien kwamen ver-

anderingen in de benutbare hoeveelheid mosselen in die sectoren (op grond van metingen in 1981 en 1992) sterk overeen met de waargenomen veranderingen in aantallen duikeenden: een toename van het aantal Toppereenden in het IJsselmeer en een afname van het aantal Kuifeenden in het Markermeer.

Is de draagkracht van het IJsselmeergebied bereikt?

Modelberekeningen lieten zien dat rendabele gebieden grotendeels worden geëxploiteerd. Als er meer duikeenden zouden zijn of wanneer ze langer in het gebied zouden blijven, zouden Toppereenden naar onrendabel geachte voedselgebieden moeten uitwijken.

De waargenomen toename van het aantal overwinterende Toppereenden tussen 1981 en 1992 kwam bovendien overeen met de toename van de mosselen in geschikte voedselgebieden in het IJsselmeer. Hieruit mogen we concluderen dat de draagkracht voor Toppereenden wordt bereikt, ook al wordt slechts 20% van de aanwezige biomassa benut. Het Markermeer is nauwelijks een alternatief voor Toppereenden omdat de conditie van de mosselen waarschijnlijk te gering is om de hoge energiebehoefte te dekken.

Voor de kleinere Kuifeenden kon worden berekend dat het Markermeer wel kon worden benut, zij het op de grens van haalbaarheid. Daarbij is het van belang dat ze op luwe plekken voedsel kunnen zoeken en kunnen rusten; dit is met name mogelijk in het meest zuidelijke deel van het Markermeer en het IJmeer. Toch zouden Kuifeenden, net als de Toppereenden, uit het oogpunt van energie-opname, ondiepe gebieden in het IJsselmeer moeten prefereren boven het Markermeer. Vermoedelijk speelt concurrentie met de grotere Toppereenden een belangrijke rol. Deze lijken een monopoliepositie te handhaven in de favoriete gebieden in het IJsselmeer en er zijn aanwijzingen dat Kuifeenden vroeg in de winter goede gebieden verlaten zodra de Toppereenden daar arriveren. Evenals bij Toppereenden suggereren de parallelle afname in mosselbiomassa tussen 1981 en 1992 in het Markermeer en het teruglopende aantal Kuifeenden dat ook voor hen de grens wordt bereikt.

De benadering vanuit de energetica van het gedrag van individuele vogels in combinatie met uitvoerige monitoring van de aantallen duikeenden en Driehoeksmosselen is een vruchtbare gebleken om de beperkingen aan de voedselexploitatie op te helderen. Dat de ogenschijnlijk oneindige ruimte van het open water van IJsselmeer en Markermeer slechts in beperkte mate kan worden benut, heeft consequenties als het gaat om veranderingen in het ruimtegebruik of het ecosysteem zelf. De ondiepe gebieden als Enkhuizerzand, Kreupel, Vrouwenzand en IJmeer zijn daarbij van buitenproportionele betekenis voor de opvangcapaciteit van het totale IJsselmeergebied voor duikeenden.

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