Food intake rates and habitat segregation of tufted duck Aythya fuligula and scaup Aythya marila exploiting zebra mussels Dreissena polymorpha

de Leeuw, J.J.

Published in:
Ardea

FOOD INTAKE RATES AND HABITAT SEGREGATION OF TUFTED DUCK *AYTHYA FULIGULA* AND SCAUP *AYTHYA MARILA* EXPLOITING ZEBRA MUSSELS *DREISSENA POLYMORPHA*

JOEP J. DE LEEUW[1,2]

De Leeuw J.J. 1999. Food intake rates and habitat segregation of Tufted Duck *Aythya fuligula* and Scaup *Aythya marila* exploiting Zebra Mussels *Dreissena polymorpha*. Ardea 87: 15-31.

The foraging skills of Tufted Duck *Aythya fuligula* and Scaup *Aythya marila* feeding on Zebra Mussels *Dreissena polymorpha* were studied in experiments under semi-natural diving conditions with relevance to the IJsselmeer/Markermeer area (large lakes in the centre of The Netherlands, former Zuiderzee area), the major freshwater wintering site of both species in Europe. Daily consumption of mussels (based on fresh mass) was about two to three times the body mass of the birds because of the large water and shell content and consequently low nutritional value of mussels. Feeding costs (diving and processing food) were about 50% of daily energy expenses in winter, as revealed from doubly labelled water measurements. Food intake rates decreased with the degree of byssal thread attachment of mussels in Tufted Duck, while intake rates of Scaup were only affected when mussels grew in tightly attached clumps. Food intake rates were usually 15-25% lower in Tufted Duck than in the 25% heavier Scaup. Both species were able to swallow all mussels available in the population, though smaller mussels were slightly favoured. Scaup had higher food intake rates at low mussel densities than Tufted Duck, but intake rates seemed unaffected at densities higher than ca. 100 gFM m^{-2}, which is similar to giving-up densities observed in the field. Feeding activity consisted of short feeding bouts of a number of dives in quick succession to fill the esophagus with mussels, followed by longer resting pauses of 5-10 minutes to crush mussel shells in the gizzard and digest the flesh. The limited capacity to store food in the gut (less than 5% of the daily requirement) and long digestive pauses imply that diving ducks must spend a large fraction of the day on the feeding grounds. The differences in feeding skills between the two species correspond qualitatively with their spatial segregation in the IJsselmeer area when local differences in prey properties are taken into account.

Keywords: *Aythya fuligula* - *Aythya marila* - *Dreissena polymorpha* - food intake - habitat segregation - diving - digestion - IJsselmeer - foraging behaviour

[1]Zoological Laboratory, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands and Rijkswaterstaat, Directorate IJsselmeergebied, P.O. Box 600, 8200 AP Lelystad, The Netherlands; [2]Present address: Netherlands Institute for Fisheries Research, P.O. Box 68, 1970 AB IJmuiden, The Netherlands, E-mail: joep@rivo.dlo.nl

INTRODUCTION

The adjoining freshwater lakes IJsselmeer and Markermeer (total surface area 1925 km^2) in the Netherlands, are a major wintering area in Europe for Tufted Duck *Aythya fuligula* (average winter maximum *ca.* 90 000 birds) and Scaup *A. marila* (average maximum ca. 140 000; see Fig. 1). Tufted Duck are found predominantly in the southern Lake Markermeer while Scaup reside mainly in the northern IJsselmeer. Both species feed almost exclusively on Zebra Mussels *Dreissena polymorpha* (Bij de Vaate 1991). Lake-wide surveys of the distribution of Zebra Mussels and

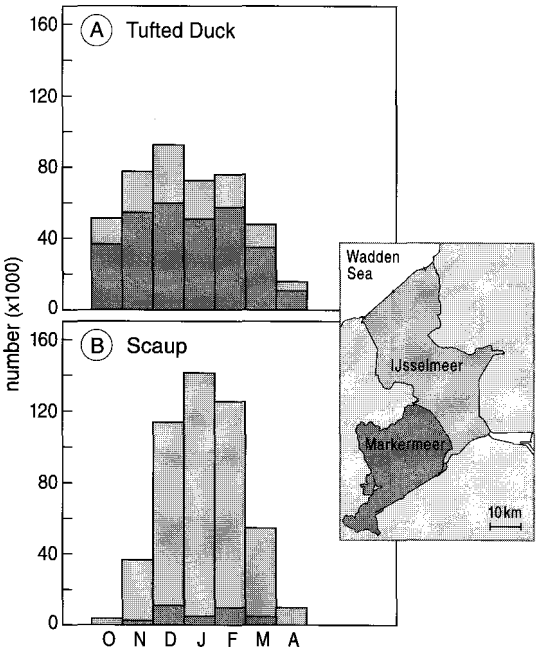

Fig. 1. Average number of wintering Tufted Duck (**A**) and Scaup (**B**) in the IJsselmeer and the Markermeer between 1980 and 1995. Four severe winters in which the lakes were ice-covered for more than 2 weeks (low numbers of diving ducks) are excluded.

the spatial and temporal distribution of diving ducks in the area revealed that these ducks prefer to feed on mussels in the shallowest parts of the lakes (De Leeuw 1997; Van Eerden 1997). Only 10-20% of the total food stock is annually harvested by diving ducks, but locally patches can be exploited by more than 90%.

Many studies suggest that maximization of energy intake rate is a major criterion for food and habitat selection (see Stephens & Krebs 1986 for a review). Intake rates depend on the feeding skills of individuals, food availability, and interference between competing individuals (e.g. Siegfried 1976; Rosenzweig 1991; Ranta *et al.* 1993; Sutherland 1996), and a variety of models have been developed to relate variations in feeding rate with habitat use (Rosenzweig 1991; Sutherland 1996).

In this paper, I address the feeding performance of Tufted Duck and Scaup in relation to their habitat use in the IJsselmeer/Markermeer area, with particular reference to local differences in prey properties. Zebra Mussels range in shell length from several mm to a maximum of *ca.* 30 mm. They often produce byssal threads for attachment to a substrate of shells, forming loose or tight clusters ('mussel clumps'). However, mussels are also found unattached, particularly at water depths over 4 m. Due to differences in growth conditions for mussels, the average shell length of mussels is about 25% lower in the Markermeer than in the IJsselmeer (Bij de Vaate 1991). Both species of diving duck regularly dive up to 5 m deep and ingest mussels whole. The calcareous shells are crushed in the muscular gizzard. Energy costs of feeding are high in these birds, owing to high thermoregulatory costs when diving in cold water, and to considerable costs to heat up the large amounts of cold ingested food (up to three times their body mass daily; De Leeuw 1996; 1997). Food intake rates (gross intake over dive time) thus have direct implications for energy and time budgets of diving ducks in addition to habitat parameters (see Fig. 2). Properties of the prey are presumed to be the primary determinants of food intake rates in this study. For example, handling time of mussels may depend on prey size and byssal attachment of mussels, while searching for mussels depends on the distribution of the prey (density and patchiness). These prey properties in turn depend on properties of the habitat, especially water depth.

Feeding behaviour of diving ducks is often difficult to study in the field, because the birds mainly feed at night and ingest mussels underwater. Information on mussel size selection and foraging success in both lake compartments was obtained from bycatches (over 3000 ducks) from the gill net fishery in the area. More detailed observations on intake rates were obtained in experiments with captive Tufted Duck and Scaup feeding on Zebra Mussels under semi-natural conditions. Variations in intake rate with diving depth, byssal attachment of mussels, and mussel length were studied in diving cages 5 m deep. In addition, daily food consumption and energy expenditure

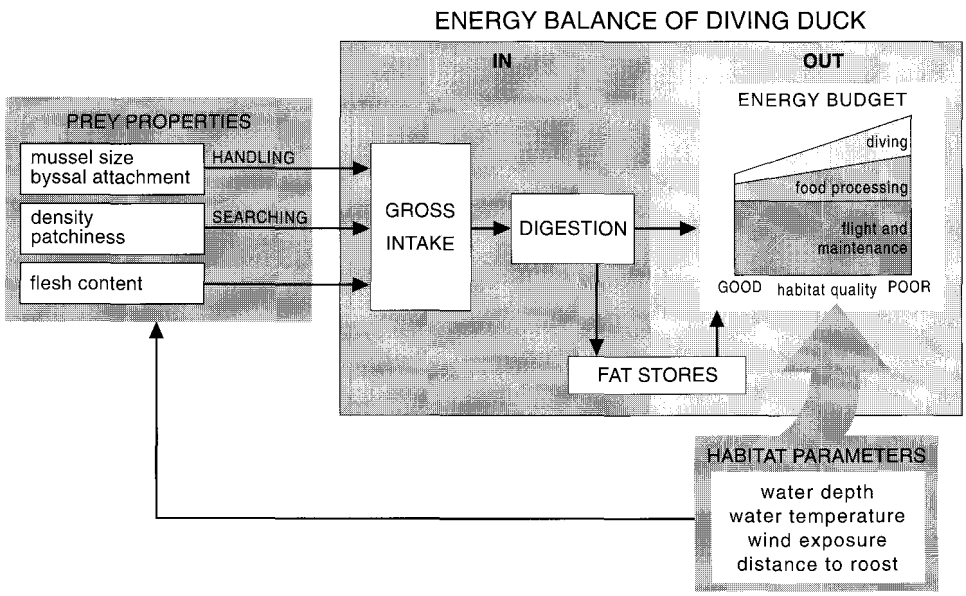

Fig. 2. The relationship between habitat properties and the energy balance of diving ducks in their wintering habitat. Prey properties of Zebra Mussels primarily determine food intake rate. Both habitat parameters and food intake influence the energy expenses, as visualised by the relative foraging costs in poor and good quality habitats.

(using the doubly-labelled water technique) were measured in resting and feeding Scaup to determine foraging costs and net energy intake rates (energy intake minus energy costs of foraging) and compared to earlier published results for Tufted Duck (De Leeuw *et al.* 1999). The effect of mussel density on intake rate (the 'functional response') was studied in separate experiments with ducks diving in a large artificial pond (45 m^2, 1.5 m deep). The differences in feeding performance between the two species of diving duck are discussed in relation to observed feeding conditions in the IJsselmeer and the Markermeer.

METHODS

Field data on feeding conditions

Diving ducks drowned in gill nets used in the commercial fishery were collected from local fishermen (De Leeuw & Van Eerden 1995; Van Eerden 1997). In total, 45 vessels provided 1136 Tufted Duck and 2182 Scaup during winter months (November-March) between 1979 and 1990. Depth at which the birds were caught was either provided by the fishermen or derived from a nautical chart. Food items in the esophagus were counted and mussel shell lengths were measured individually to the nearest mm. The proportion of ducks with mussels in the esophagus was used as an index of foraging success of both species in either lake (De Leeuw & Van Eerden 1995; Van Eerden 1997). Mussels were dredged at different depths in both lake compartments (12 stations across the IJsselmeer and 8 stations across the Markermeer) as part of a long-term study on the population structure of Zebra Mussels (further details in Bij de Vaate 1991; Van Eerden 1997). From samples of 100-250 mussels, the attachment strength of byssal threads of individual mussels was measured by tearing off a mussel from a clump through gently pulling a Pesola scale clasped around the shell. The length of each shell was then measured to the nearest mm.

Diving cages

An outdoor diving device was constructed to simulate winter feeding conditions. Four 1x1 m and 5 m deep cages of wire-netting were fixed to a floating pontoon in an 8 m deep sand pit. Diving depth in each cage was manipulated by moving a feeding tray (1x1 m) with the aid of 4 ropes. Diving behaviour was continuously recorded by a computer-controlled infrared light detection system scanning the water surface areas of each cage (details in De Leeuw *et al.* 1999). During two winters, three Tufted Ducks (2 males, 1 female; mean body mass *ca.* 600 g) and four Scaup (2 males, 2 females; mean body mass *ca.* 800 g), which were obtained from a commercial waterfowl breeder, were trained for 7 weeks to dive for Zebra Mussels. During the training period before the experiments, the ducks acclimated to the experimental protocol and could adjust their physiology to diving conditions (Butler & Turner 1988) and to processing mussel shells in the digestive tract (Piersma *et al.* 1993). The birds were kept singly in the diving cages and were fed fresh Zebra Mussels offered on the feeding trays at depths of 1, 3, or 5 m. In the first 3 weeks, depth was increased gradually, thereafter depth was manipulated randomly. To minimise disturbance, the pontoon was visited only once every one or two days for about one hour in the afternoon. First, the ducks were caught, weighed and kept in dark boxes. The food trays were lifted to the surface and the remaining mussels were weighed. Visual inspections of the bottom of the cages by SCUBA-divers indicated that less than 1% of the mussels dropped by the ducks missed the food trays. A batch of fresh mussels was weighed, offered on the trays, and the trays were lowered down. Afterwards, the ducks were weighed again and released into their cages. Daily mussel consumption was calculated from the mass difference of mussels between subsequent visits. Average food intake rates were determined by dividing food consumption by total time spent underwater per experimental trial. These intake rates include both mussels swallowed underwater and mussels that were brought up to the surface and swallowed after surfacing. The time required for the latter could not be measured in this set-up. In this paper, I will refer to apparent intake rate (AIR) to compare the food consumed relative to the time spent diving under different feeding conditions of diving depth and byssal attachment of mussels.

Mussels and feeding conditions

Zebra Mussels were dredged weekly in the IJsselmeer from a favoured feeding site of wild ducks at a water depth of 3-3.5 m. The majority of these mussels (80-90%) lived as mussel clumps and were offered in this natural fashion to the ducks in most experiments. To test the effect of mussel clumping on apparent intake rate, mussels were detached from their substrate ('unattached mussels') in 7 trials with Tufted Duck and 9 trials with Scaup. Also, intake rates of ducks feeding on 'tight clumps' (strong byssal attachment) were measured in 11 trials with Tufted Duck and 3 trials with Scaup.

Selection for mussel shell length while feeding on mussel clumps was determined from the difference in size distributions in samples of 200-400 g fresh mass (gFM, equivalent to 200-600 mussels) measured before and after 24-h feeding trials. In Tufted Duck, 12 trials at water temperatures between 3°C and 22°C and diving depths of 3 and 5 m were analysed and in Scaup 11 trials of diving to 1, 3, or 5 m at water temperatures between 3 and 7°C. The selection for length classes was determined from the selectivity index $D = (r - p) / (r + p - 2rp)$, where r and p are the fraction of a length class in the diet and on offer, respectively (Jacobs 1974). Positive values of D (0-1) indicate selection for that length class. Length classes were 3-7 mm, 8-11 mm, 12-13, 14-15 mm, 16-17 mm, 18-21 mm, 22-26 mm (cf. De Leeuw & Van Eerden 1992).

Factors for converting mussel intake (fresh mass, FM) to energy intake were derived from the length distributions of mussels selected by Scaup and Tufted Duck, the fresh mass (including shells) and flesh content (dry mass, DM) of mussels of different lengths, and the energy density of flesh (22.5 kJ gDM^{-1}; Bij de Vaate & De Leeuw,

unpublished data). Assuming an energy assimilation efficiency of 85% for the dry mass of flesh (De Leeuw *et al.* 1999), the conversion factors were 0.5 kJ gFM^{-1} for whole mussels for Scaup, and 0.6 kJ gFM^{-1} for Tufted Duck. DM of flesh were determined in 7 length classes of mussels between 8 and 22 mm (10 individuals per even mm length class) for each of the size selection samples. DM did not vary with date of collection or experimental conditions (Analysis of Covariance of $\log_{10}$-$\log_{10}$ transformed data of DM and shell length (L, covariate), n.s.), so data were pooled: $DM(mg) = 0.0069L^{2.721}$ (n = 880 mussels) for Scaup, and $DM(mg) = 0.0074L^{2.752}$ (n = 400) for Tufted Duck. DM of empty mussel shells were also determined for the Scaup experiments; $DM(mg) = 0.069L^{2.82}$ (n = 880). Dry mass of shells consisted on average of 35% of the total fresh mass. The difference in energy conversion factors for mussel clumps used in the two species is caused by local and (or) annual differences in body condition of the mussels used.

Food processing rate

The rate of food processing was estimated from diving activity recordings including resting periods, which yield the longer-term rates of cumulative food gain (crude intake rate), assuming a constant food gain per dive equal to the daily mussel consumption divided by the total number of dives. To estimate the maximum rate of food processing, feeding time was restricted in experiments with Scaup by removing all food during the day (7 to 8 h), and offering mussels only at night (15 to 16 h). Thus, we stimulated nocturnal feeding as commonly observed in diving ducks in the wild (Van Eerden 1997). During the day, the food tray was maintained at a depth of 1 m, so that the ducks could check with minimal diving effort that no food was available.

Energy expenditure of foraging

Energy expenditure was measured with doubly labelled water in four Scaup during a resting period of 8 h and a subsequent feeding period of 11 h with mussels offered at a depth of 3 m. This experiment followed the feeding time restriction experiments (see preceding section) at a water temperature of 3.5 °C. The experimental procedure and calculations were equivalent to those described for Tufted Duck in these diving cages (De Leeuw *et al.* 1999). In short, 1 ml of an isotope mixture of D_2O and $H_2{}^{18}O$ (30 atom percent ^2H and 60 atom percent ^{18}O) was injected into the abdominal cavity. The turnover of hydrogen and oxygen isotopes was determined from blood samples (15 µL) drawn from a wing vein, after equilibration (1.5 h after injection of isotope mixture) and at the end of an experimental period. CO_2 production was calculated according to Heyman & Roberts (1990), including fractionation factors for evaporative water loss (1 g h^{-1} in Tufted Duck (De Leeuw *et al.* 1999) and assuming 1.2 g h^{-1} in the larger Scaup). An energetic equivalent of 26 $kJ.L^{-1}$ CO_2 (based on the composition of flesh of Zebra Mussels: 76.1% protein, 8.4% fat, 15.5% carbohydrates) was used to calculate energy expenditure.

Mussel density

The effect of mussel density on food intake rate was studied in experiments with Tufted Duck and Scaup trained to dive in a large artificial pond (9x5 m and 1.5 m deep) at the Zoological Laboratory, Haren, The Netherlands. The visibility (Secchi-disc) was about 0.5 m (max. 0.7 m) during the experiments. Four Scaup (2 males, 2 females) and 6 Tufted Duck (4 males, 2 females) were used. Diving behaviour was observed from a hide next to the pond. Mussel densities were in the range of the lowest densities found after extensive predation in late winter in the IJsselmeer area. Mussel clumps were individually marked with paint on the substrate shell, weighed on a balance (accurate to 0.1 g), and haphazardly distributed on a net spread out over the bottom of the pond (net area *ca.* 30 m^2). After 30-60 dives had been observed, the clumps were recovered, weighed, and offered again. This was repeated once or twice. Afterwards, the mass of the dead shells was measured and subtracted from total clump mass to calculate the initial biomass of live mussels. Twelve trials

with Scaup (2 ducks per trial) and 8 trials with Tufted Duck (3 ducks per trial) were conducted with mussel densities varying between 5 and 50 gFM m^{-2}. The intake rates are compared with the intake rates observed in the diving cage experiments with ducks feeding at high mussel densities of > 2000 gFM m^{-2} by linearly interpolating the 1 and 3 m values of AIR to the 1.5 m in the density experiments.

RESULTS

Field feeding conditions

The mussel lengths found in the esophagi of wild Scaup and Tufted Duck had a wide range (Fig. 3). Mussel lengths up to 30 mm, the largest sizes in the population, were recorded. Both species took more small mussel sizes in the Markermeer than in the IJsselmeer in both species. Selectivity, however, could not be tested by comparing length distributions in the field and in the diets of the ducks because of strong local and annual differences in length structure of the mussel populations (Bij de Vaate 1991). Tufted Duck ate

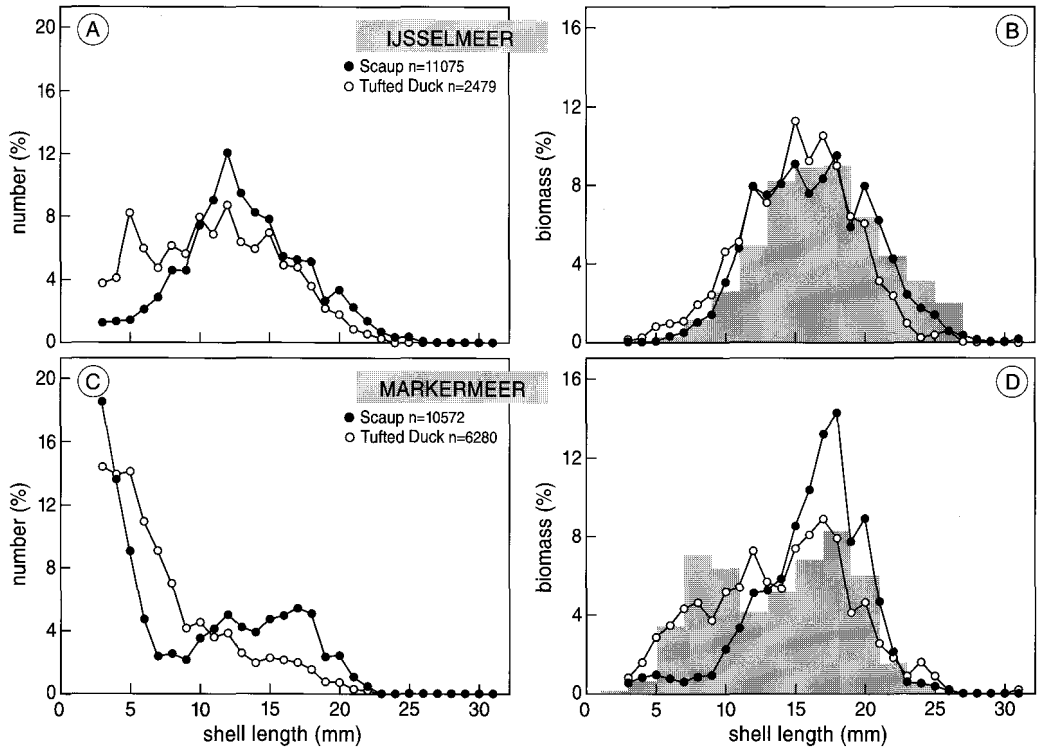

Fig. 3. Mussel sizes found in the esophagi of 216 Tufted Duck and 960 Scaup bycaught in fishing nets in the IJsselmeer (A, B) and of 445 Tufted Duck and 461 Scaup caught in the Markermeer (C, D), respectively. *n* refers to the number of mussels measured. Percentages of numbers of mussels (A, C) and fresh biomass (B, D) are given. Each pair of size distributions differs significantly (Kolmogorov-Smirnov 2-sample tests, $P < 0.05$). The shaded boundaries indicate size distributions of mussels in early winter as obtained from bottom samples in the IJsselmeer ($n = 1246$) and the Markermeer ($n = 1038$; Bij de Vaate, unpublished data). Differences in size distributions of diets and bottom samples are partly due to local and annual variation.

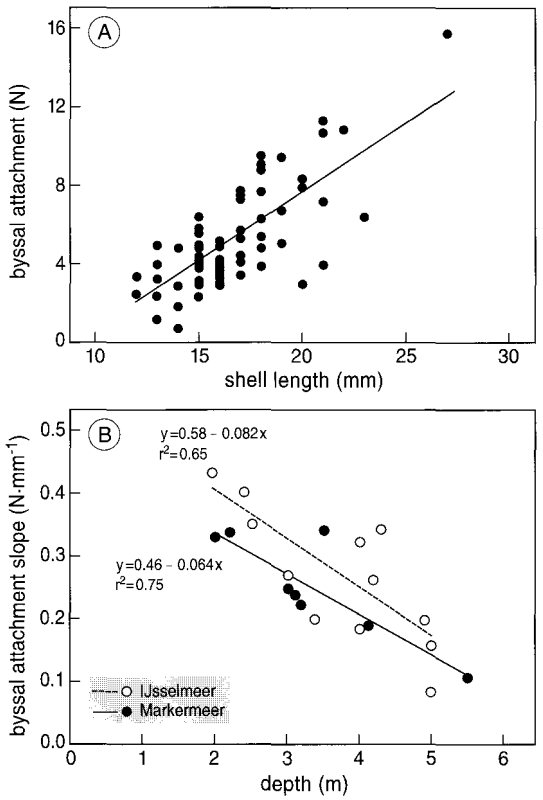

Fig. 4. (A) Example of byssal attachment strength of mussels from the IJsselmeer at a water depth of 3 m in relation to mussel size. Byssal attachment was measured by tearing off a mussel from a clump through gently pulling a Pesola balance clasped around the shell. (B) Length-independent byssal attachment (slopes of regressions of the type depicted in A) in relation to water depth in the IJsselmeer and the Markermeer. Data from Van Eerden (1997).

smaller sizes, especially first-year mussels, in the Markermeer than Scaup (Kolmogorov-Smirnov 2-sample tests, $P < 0.05$ for both lakes).

Byssal attachment of mussels increased linearly with shell length (Fig. 4A). The length-independent byssal attachment (the slope of the linear relationship between shell length and byssal attachment) decreased with water depth and was lower in the Markermeer than in the IJsselmeer (ANCOVA, $F_{1,18} = 5.3$, $P < 0.05$) (Fig. 4B). The difference in average byssal attachment is larger between both lakes because smaller mussel sizes (weakly attached) prevail in the Markermeer.

The fraction of birds caught with mussels in the esophagus can be used as an index for feeding success (Van Eerden 1997). This index was 0.57 ($n = 327$) for Tufted Ducks diving between 2 and 4 m in the Markermeer and 0.52 ($n = 217$) for ducks diving in the IJsselmeer. In Scaup, success rate index was 0.71 ($n = 431$) for the Markermeer and 0.63 ($n = 709$) for the IJsselmeer, respectively (differences between species ($G = 98.6$, $df = 3$) and lakes ($G = 83.0$, $df = 3$) and the interaction term ($G = 79.5$, $df = 2$) were significant (all $P < 0.005$), following calculation procedures in Sokal & Rohlf (1981), pp 750-763). This suggests that feeding success was higher in Scaup than in Tufted Duck, and was higher in the Markermeer than in the IJsselmeer.

Feeding performance in relation to diving depth

Daily mussel consumption and diving behaviour of Scaup and Tufted Duck in the outdoor diving cages are summarised in Table 1. Mussel consumption of Scaup was on average 2240 gFM d^{-1}, which is equivalent to a metabolizabale energy intake of 1120 kJ d^{-1}. Dive duration increased with depth, while 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 adjacent depth classes were not significant (Tukey tests, n.s.). Similar trends with diving depth were found in Tufted Duck at water temperatures below 10°C (Table 1; De Leeuw *et al.* 1999). For the smaller Tufted Duck (body mass *ca.* 600 g), mean daily food intake and apparent intake rates were about 15% and 25% lower than in Scaup (*ca.* 800 g).

Intake rate of mussel clumps

Apparent intake rate (AIR) at a water depth of 3 m did not differ between Scaup and Tufted Duck at 'unattached' and 'tight' degrees of byssal attachment (Student's *t*-tests, n.s.), but AIR was greater for Scaup at 'moderate' degrees of byssal

Table 1. Average (SD) daily food intake and related parameters of four Scaup and three Tufted Duck feeding on mussel clumps at different diving depths in winter at water temperatures between 3 and 7 °C. Apparent intake rate is the food intake rate per second underwater. Significant differences between depths are indicated (ANOVA with Tukey-test, $P < 0.05$ denoted by different letters (a,b,c)).

	Scaup			Tufted Duck		
	Depth (m)			Depth (m)		
	1	3	5	1	3	5
Number of experimental days	10	20	15	11	21	8
Food intake (gFM d^{-1})	2521 (615)	2039 (546)	2299 (477)	1661 (242)	1572 (296)	1623 (193)
Metabolizable energy intake (kJ d^{-1})	1260 (308)	1020 (273)	1150 (239)	967 (145)	943 (178)	974 (116)
Dive duration (s)	11.1 (1.1)^a	17.7 (1.1)^b	23.5 (1.9)^c	9.8 (1.9)^a	15.8 (1.6)^b	20.9 (1.9)^c
Number of dives per day	496 (132)^a	278 (77)^b	273 (75)^b	497 (37)^a	315 (47)^b	290 (40)^b
Apparent intake rate (gFM s^{-1})	0.46 (0.10)^a	0.42 (0.09)^{a,b}	0.36 (0.07)^b	0.35 (0.08)^a	0.32 (0.11)^{a,b}	0.27 (0.05)^b
Body mass (g)	806 (41)	806 (38)	820 (35)	601 (29)	586 (38)	580 (54)

attachment ($t_{15,17} = 2.7$, $P < 0.01$; Fig. 5). AIR was significantly lower when birds were feeding on 'tight clumps' than when feeding on 'moderate clumps' in both species (Tufted Duck: $t_{11,15} = 3.2$, $P < 0.005$; Scaup: $t_{3,16} = 3.0$, $P < 0.01$). In Scaup, there was no difference in AIR between 'moderate clumps' and 'unattached mussels', but Tufted Duck were able to profit more from unattached mussels than from moderately attached mussels ($t_{7,15} = 2.1$, $P < 0.05$).

Size selection

At diving depths of 1, 3, and 5 m combined, both Tufted Duck and Scaup selected mussel lengths in the range of 7 to 16 mm (Fig. 6), although mussels in the entire range up to 30 mm

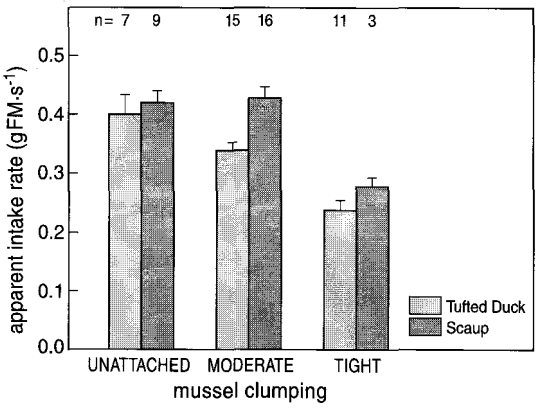

Fig. 5. Average (± SE) apparent intake rates of mussels differing in their byssal attachment ('loose mussels', 'moderate clumps', and 'tight clumps') of Tufted Duck and Scaup feeding at a diving depth of 3 m. *n* gives the number of experimental days.

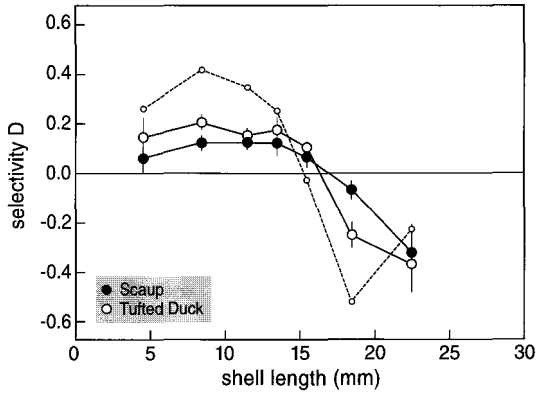

Fig. 6. Average (± SE) selectivity in relation to mussel shell length for Tufted Duck and Scaup feeding on mussel clumps (solid lines; diving depths of 1, 3, and 5 m combined). The broken line indicates the selectivity of Tufted Duck feeding on unattached mussels at a diving depth of 3 m (De Leeuw & Van Eerden 1992).

were taken. Tufted Ducks feeding on unattached mussels at 3 m depth (De Leeuw & Van Eerden 1992) were more selective than ducks feeding on mussel clumps in this study (standard errors of data for clumped mussels pooled for all depths are low enough to allow comparison with data for unattached mussels at 3 m only). There was no significant difference in selectivity for selected length classes (7-16 mm) among diving depths and species (Analysis of covariance, n.s.).

Intake rate and mussel density: the functional response

The relationship between intake rate and food density, the 'functional response curve', generally shows a phase of rapid increase in intake rate with density followed by a plateau at higher densities where encounter rates no longer depend on food density and intake rates are determined by handling time (Holling 1959). Apparent intake rate (AIR) of Scaup and Tufted Duck was strongly related to mussel densities below 50 gFM m^{-2} when clumps were distributed over a 45 m^2 pond (Fig. 7). Functional response curves could not be estimated because there are no data of intake rates at intermediate mussel densities. However, plateau intake rates can be estimated from average intake rates observed at the extremely high mussels densities of > 2000 gFM m^{-2} used in the experiments with Scaup and Tufted Duck feeding in the diving cages (data presented in Table 1). The rapid phases of increase, at 50% of these plateau intake rates, were found at mussel densities of 10 gFM m^{-2} in Scaup and 35 gFM m^{-2} in Tufted Duck. This suggests that Scaup maintained higher encounter rates at low mussel densities than did Tufted Duck.

Food processing rate

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. 8. Periods of constant food intake lasted for several hours and alternated with long resting bouts, both at day and night. Despite the variation in timing of long resting periods, maximum crude intake rate (slope of

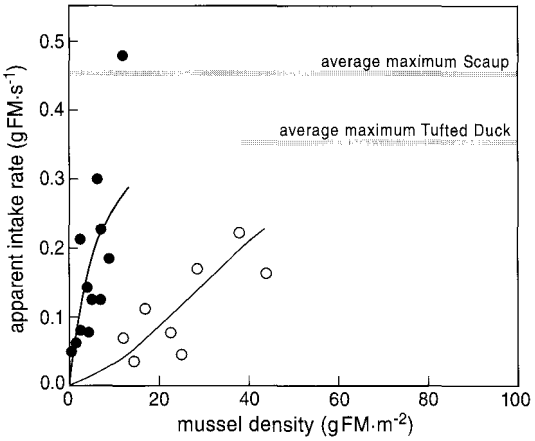

Fig. 7. Apparent intake rate of four Scaup and six Tufted Ducks in relation to density of mussel clumps in a 45 m^2 pond 1.5 m deep. The average maximum intake rates were derived from ducks feeding in diving cages at mussel densities of more than 2000 gFM m^{-2}.

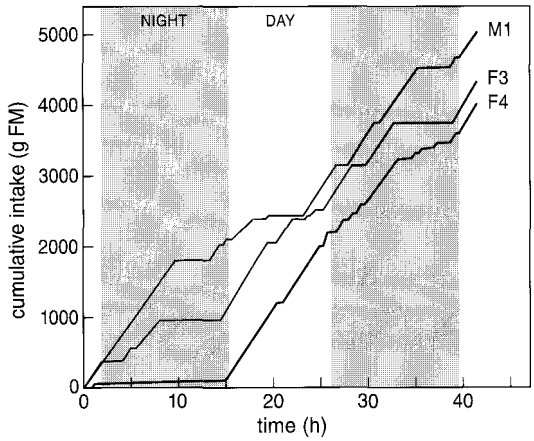

Fig. 8. Cumulative intake of mussels during 42 h in three Scaup diving for mussels at a depth of 5 m. Cumulative food gain was determined from diving activity, assuming a constant intake per dive over the entire feeding period.

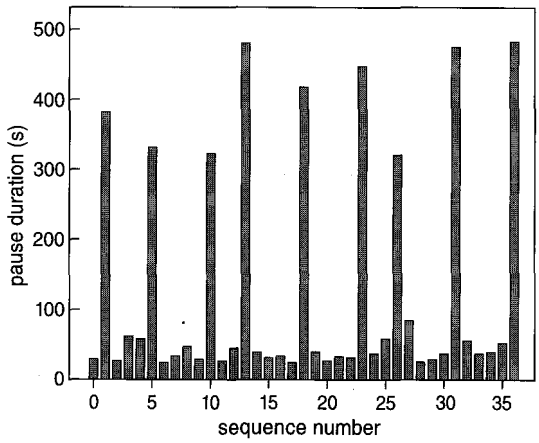

Fig. 9. Sequence of pause durations between dives of Scaup M1 diving to 5 m during 1.3 h of feeding.

the curves) was very similar over periods of several hours 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. 9). Feeding bouts of 4 to 5 dives alternated with resting periods of 6 to 8 min. On average, 30 gFM of mussels were ingested per feeding bout (SD = 16, n = 1102 feeding bouts). The maximum amount of mussels found in esophagi of 2322 dissected wild Scaup which had drowned as bycatches in fishing nets in the IJsselmeer was *ca.* 40 gFM (De Leeuw & Van Eerden 1995). It appears that the esophagus is filled during a feeding bout and mussels are crushed in the gizzard afterwards. The storage capacity of mussels in a duck's body was estimated from the maximum difference in body mass between the end of the resting phase of 8 h (empty gastro-intestinal (GI) tract) and the end of the feeding phase (full GI tract) in the feeding time restriction experiments. The 3 highest values of 44 body mass difference measurements were 80 g, suggesting that the amount of mussels in the gizzard and intestines (thus excluding 30 g of mussels in the esophagus) probably does not exceed 50 g. At an average crude intake rate of 214 gFM h^{-1} in the feeding time restriction experiments (see below) and a maximum storage capacity of 80 g, throughput time of mussels would be 22 min. In agreement with this estimate is the observation in Scaup diving for mussels in the pond in Haren, that the first defecation appeared 23 ± 1.7 min (mean ± SE, 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.

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 of whether the observed rate of food gain reflects maximum food processing rate or maximum diving rate was further explored by restricting daily feeding time to 16 h and comparing cumulative food gain (crude intake) and cumulative dive duration for four Scaup diving to 1 m and 5 m, respectively, to create the maximum difference in diving costs (illustrated for 2 birds in Fig. 10). Sometimes longer resting periods were made (up to several hours), but these were excluded from the analyses. A bout criterion interval of 14 minutes (method described in Martin & Bateson 1988) was used, which resulted in the removal of 2% of the resting periods. Dive rate was lower at 1 m (7.8 min submerged h^{-1}) than at 5 m (9.7 min h^{-1}; $t_{61,91} = 7.3$, $P < 0.001$), but the rate of food gain was similar at both depths (210 and 216 gFM h^{-1}, respectively; $t_{61,91} = 1.1$, n.s., Fig. 11C). This suggests that the rate of diving was adjusted to the rate of food processing.

Crude intake rates were lower in Tufted Duck (mean ± SE) 90.5 ± 2.0 gFM h^{-1}, n = 97 feeding bouts) than in Scaup (168.0 ± 4.8 gFM h^{-1}, n = 72 bouts; t = 14.4, $P < 0.001$) when ducks were diving for mussel clumps at 5 m depth (Fig. 11). Intake rates of Scaup were higher when feeding time was restricted to 16 h per day (213.6 ± 3.2 gFM h^{-1}, n = 152) compared to unrestricted feeding times (t = 8.24, $P < 0.001$). The latter results suggest that intake rates are not strictly limited by processing time under normal conditions and that the ducks can increase processing rates if neces-

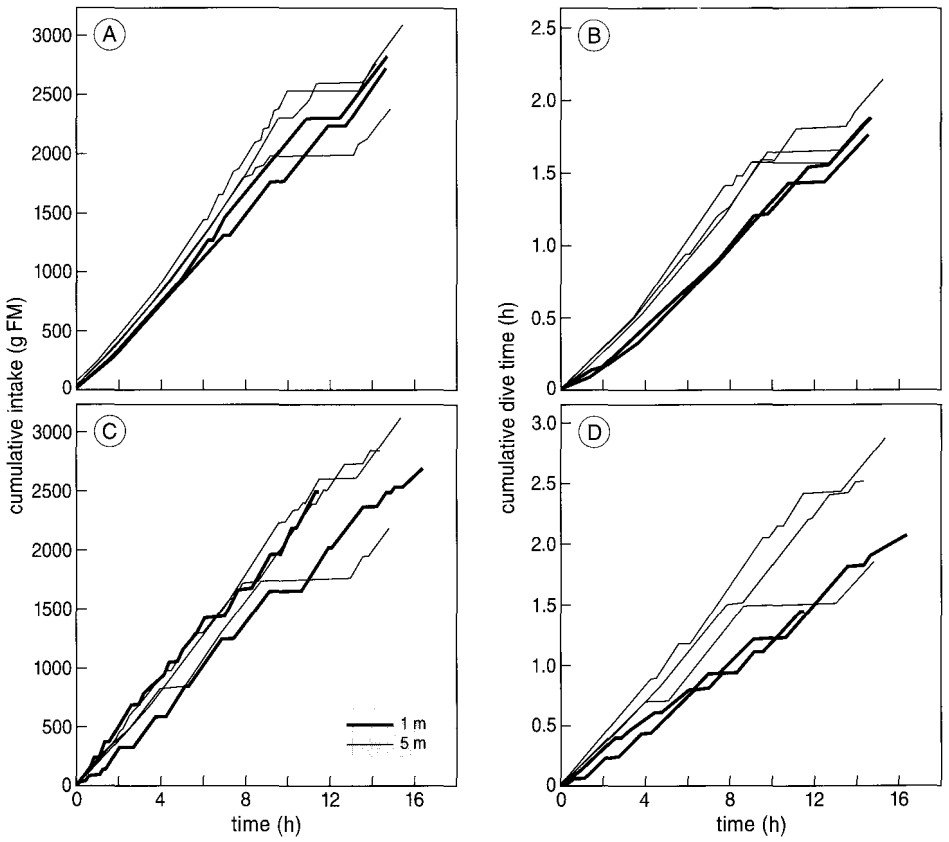

Fig. 10. Cumulative food intake (A, C) and cumulative dive duration (B, D) of Scaup M1 (A, B) and F4 (C, D), respectively, at diving depths of 1 m and 5 m during 16-h feeding periods.

sary. However, they appear to prefer processing food at a rather constant, but submaximal rate (Fig. 10), which seems to govern alternate periods of diving and resting (Fig. 9).

Feeding costs

Average metabolic rate of Scaup 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 average food consumption during the feeding phase was only 60% of normal values (Table 1), this feeding metabolic rate should be maintained for 1.7 times longer than the 10.9 h in this experiment 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) x 14.1 + ((24 - 18.5) / 24) x 6.4 = 12.3 W (1063 kJ d^{-1}). This value is within 5% of the average of 1120 kJ d^{-1} (or 2240 gFM d^{-1}) estimated from daily food consumption data of Scaup (Table 1).

The higher costs during the feeding period can be attributed to energy costs for diving and food processing. Energy costs of food processing include crushing mussel shells in the gizzard, digestion of flesh, and warming up the ingested cold food mass. All heat produced from shell crushing and digestion can probably be used to warm the ingested food, because no energy costs for feeding in excess of the obligatory need for thermo-

Table 2. Energy expenditure of Scaup during resting (7.6 h, no food offered) and feeding (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 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	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.

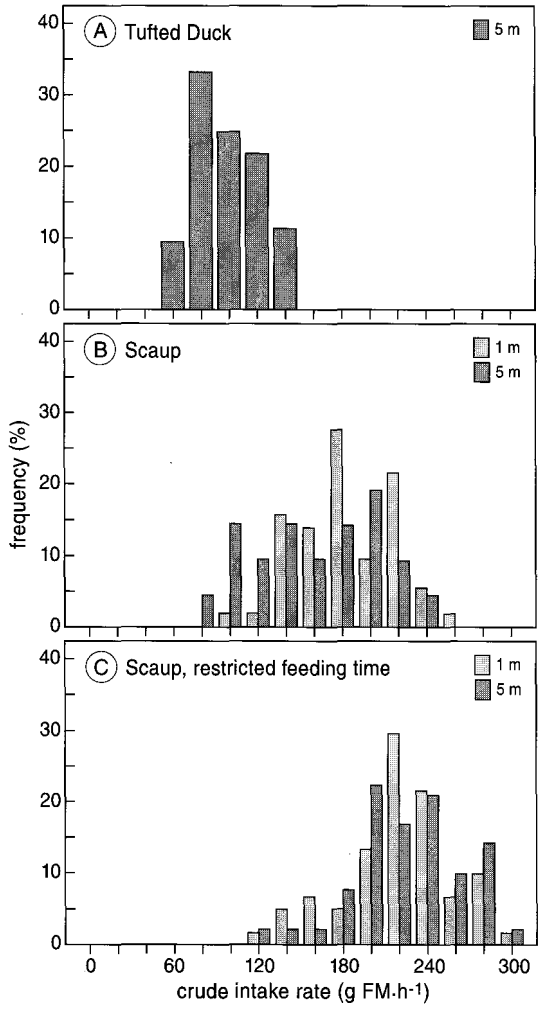

Fig. 11. Frequency distributions of average crude intake rates including resting periods. (A) Three Tufted Duck feeding on mussel clumps at 5 m (n = 97 episodes with resting durations < 14 min). (B) Four Scaup diving to 1 m (n = 51) and 5 m (n = 21) during 48-h unrestricted feeding trials. (C) Four Scaup diving during trials with feeding periods restricted to 16 h (1 m, n = 61; 5 m, n = 91).

regulation after food ingestion could be demonstrated in mussel-feeding Tufted Ducks, as discussed in De Leeuw *et al.* (1998). Therefore, feeding costs can be simply estimated from the energy necessary to warm up the ingested food mass from ambient water temperature of 3°C to a core body temperature of 41°C (heat capacitance of mussels 2.8 J g^{-1} $°C^{-1}$). By subtracting these feeding costs and resting costs from total energy expenditure in the feeding period, energy costs for diving (in excess over resting costs) can be estimated. This excess diving cost (EDC; De Leeuw 1996) amounts to 56 J s^{-1} spent underwater (averaged for three birds; Table 2). This value is 12% higher than EDC measured in Tufted Duck at equivalent water temperatures (50 J s^{-1} spent underwater, De Leeuw 1996).

Metabolic rate of resting and diving Scaup can also be estimated from body-mass corrected values of oxygen consumption obtained in the smaller-sized Tufted Duck (body mass 600 g, Scaup 750 g), assuming that resting and diving costs scale to body mass by an exponent of 0.80 and

0.72, respectively, in diving birds (De Leeuw 1996). Thus, we find 6.8 W for resting and 59 W for excess diving costs, which are only 6 and 5% higher, respectively, than the values derived from the doubly labelled water measurements in Scaup.

DISCUSSION

Adjustment of diving activity to food processing rate

At a crude intake rate of *ca.* 210 g h^{-1}, the retention time of Scaup was *ca.* 23 min. Grandy (1972) found a retention time of 30 min in Black Ducks *Anas rubripes* feeding on *Mytilus* shells. 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; Karasov 1996). Kersten & Visser (1996) measured a retention time of 28 min in Oystercatchers *Haematopus ostralegus* (body mass 500 g), which ingest only the flesh of mussels *Mytilus edulis*.

The timing of diving activity is apparently determined 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 empty the esophagus. During these resting episodes, ducks also recover from body heat loss imposed by diving (De Leeuw *et al.* 1998). The limited capacity of food storage both in the esophagus and in the intestines (less than 5% of the daily needs), implies 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 13 h, while Tufted Duck would need almost 15 h to process their daily food ration. The maximum time that can be spent at sheltered day-time roosts would therefore be less than 11 h (Scaup) and 9 h (Tufted Duck), respectively. Since foraging costs are high in diving ducks, any adverse effect on feeding performance will increase the daily energy expenses (and food requirements) and thus the daily foraging times. This may explain why in late winter, when feeding conditions deteriorate, diving ducks tend to remain on the feeding grounds instead of fly to their sheltered daytime roosts (Van Eerden 1997).

Size or site selection?

When feeding on clumps, Tufted Duck and Scaup showed a slight selection for smaller mussel lengths (Fig. 6). The observed selectivity for small mussels may partly reflect availability, as young (small) mussels tend to settle on older mussels at peripheral positions of a clump and are thus more accessible to ducks. Selectivity may be limited by the short time available for selection while diving at high energy 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 selection experiments with moderately attached clumps showed no difference between the two species (Fig. 6), but Tufted Duck appeared to eat smaller mussels than did Scaup in the Markermeer (Fig. 3). This may suggest that Tufted Duck more strongly prefers patches with small mussels than do Scaup, rather than that they select smaller sizes.

Giving up density of mussels

Depletion reduces the density of the food source and thus it increases searching effort. From Fig. 7, it appeared that Scaup could maintain high intake rates at mussel densities as low as 30-60 gFM m^{-2}. 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 usually limiting intake rates.

Mussel densities observed in the field after periods of intense predation by diving ducks confirm that diving ducks are able to deplete mussel

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.

Species	Water system	Water depth (m)	Density (gFM m^{-2})	Reference[1]
Tufted Duck	River Rhine (Switzerland)	1.0	30	1
		1.3	32	
		3.5	50	
	Pond Leblanc (Belgium)	3.3	50-100	2
	Markermeer	2.5	65	3
		3.5	60	
Scaup	IJsselmeer	2	47	3
		3	60	

[1]) References: (1) Suter 1982, (2) Draulans 1982, (3) Van Eerden 1997

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 the IJsselmeer (IJ) and the Markermeer (M), and in experimental cages (Exp).

	Lake	Tufted Duck	Scaup	Reference[1]
Apparent intake rate (gFM s^{-1})	M	0.40	0.42	1
	IJ	0.34	0.42	1
Metabolizable energy content (kJ gFM^{-1})	M	0.40	0.40	2
	IJ	0.48	0.48	2
Diving cost (W)	Exp	50	56	1,3
Food heating cost (kJ g^{-1} $°C^{-1}$)	Exp	2.8	2.8	4

[1]) References: (1) This study, (2) De Leeuw (1997), (3) De Leeuw (1996), (4) De Leeuw *et al.* (1998, 1999)

beds to densities of 30-60 gFM m^{-2} (Table 3), corresponding to the range at which the functional response curves appear to reach the asymptote (Fig. 7). The giving-up densities of Scaup and Tufted Duck are in the same range and increase slightly with diving depth. Since foraging costs are high, however, feeding success, i.e. the probability of finding mussels in a heterogeneous feeding area, should be consistently high. Lake-wide surveys by means of bottom sampling suggest indeed a more homogeneous distribution of mussels and a higher probability of encountering mussels in the Markermeer (Bij de Vaate 1991). Also, feeding success of diving ducks estimated from esophagus contents indicated that mussel encounter rates were higher in the Markermeer than in the IJsselmeer.

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, seems to prefer small mussels (Fig. 3) and may be hindered more by the byssal attachment of mussels in moderate clumps (Fig. 5) than Scaup. 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 the Markermeer, mussels are smaller (Bij de Vaate 1991), their substrate attachment by byssal threads is less developed (Fig. 4), and the probability of encountering mussels (reducing searching effort) is higher (Van Eerden 1997) than in the

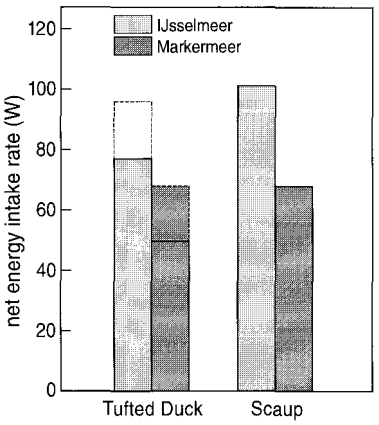

Fig. 12. Net energy intake rates estimated for Tufted Duck and Scaup feeding in the IJsselmeer and the Markermeer at a water depth of 3 m. Intake rates are based on the values observed in ducks feeding on musselclumps with moderate byssal attachment in The IJsselmeer and on unattached mussels in the Markermeer. In Tufted Duck the potential difference between unattached (higher intake rates) and moderately attached mussels is indicated by dashed lines; there was no difference in Scaup (Fig. 5). The higher net intake rates in the IJsselmeer are due to the higher energy content of mussels in this part of the lake system.

IJsselmeer. However, the energy content of mussels in the IJsselmeer (metabolisable energy content (MEC) 0.48 kJ gFM^{-1} at a depth of 3m, De Leeuw 1997) proved to be higher than that of mussels in the Markermeer (MEC 0.40 kJ gFM^{-1}). Thus, both energy costs and benefits are higher in the IJsselmeer than in the 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. By subtracting the energy 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 between 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. 12). In the Markermeer most mussels (> 60%, Van Eerden 1997) live unattached, but in the IJsselmeer less than 30% occur unattached (mainly in deep water) while the majority are found in 'moderate clumps' (tight clumps are rare in both lakes and are not considered here). Because intake rates of Scaup are not affected by the byssal attachment of mussels (Fig. 5), Scaup greatly benefit from high energy returns of mussels in the IJsselmeer, explaining its preference for this part of the lake. In contrast, for Tufted Duck net intake rates in both lakes are much closer, since the generally stronger byssal attachment of mussels in the IJsselmeer reduces intake rate.

Other factors than foraging skills (e.g., distance between feeding sites and roosting areas, susceptibility to wind-exposed feeding sites, likelihood of discovering feeding areas, and competitive ability of Scaup *vs.* Tufted Duck) doubtless play an important 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 about the extent to which habitat use can be attributed to differences in optimal feeding conditions and to what extent mussel populations can be exploited by diving ducks.

ACKNOWLEDGEMENTS

I am most grateful to Jeroen van der Brugge, Hans Gerritsen, Martine Greve, Jan van der Kamp, Ingrid Nijholt, Stef van Rhijn, and Fulco Zegwaard for assistance during the long lasting experiments. Vincent Wigbels and Hans Roosenberg are thanked for allowing me to work at the 'Natuurpark Lelystad'. Leo de Ronde, Gerrit Kooij, and Kees Berkeveld are greatly acknowledged for collecting the innumerable fresh mussels. Tosca Boeré, Sjoerd Veenstra, and Roelie Wiegman helped care for (and catch!) the ducks in Haren. Mennobart van Eerden was very helpful and stimulating at all stages of the project. The manuscript improved from comments of Rudi Drent, Marcel Kersten, Mardik Leopold, Theunis Piersma, and two anonymous referees.

REFERENCES

Bij de Vaate A. 1991. Distribution and aspects of population dynamics of the Zebra Mussel *Dreissena polymorpha* in the Lake IJsselmeer area, The Netherlands. Oecologia 86: 40-50.

Butler P.J. & D.L. Turner 1988. Effect of training on maximal oxygen uptake and aerobic capacity of locomotory muscles in Tufted Ducks *Aythya fuligula*. J. Physiol. 401: 347-359.

Dade W.B., P.A. Jumars & D.L. Penry 1990. Supply-side optimization: maximizing absorptive rates. In: Hughes R.N. (ed.) Behavioural Mechanisms of Food Selection (NATO ASI Series G20): 531-556. Springer-Verlag, Berlin.

De Leeuw J.J. 1996. Diving costs as a component of daily energy budgets of aquatic birds and mammals: generalizing the inclusion of dive-recovery costs demonstrated in Tufted Ducks. Can. J. Zool. 74: 2131-2142.

De Leeuw J.J. 1997. Demanding divers. Ecological energetics of food exploitation by diving ducks. Ph.D. thesis, University of Groningen, Groningen. Van Zee tot Land 61, Rijkswaterstaat, Directorate IJsselmeergebied, Lelystad, The Netherlands.

De Leeuw J.J. P.J. Butler, A.J. Woakes & F. Zegwaard 1998. Body cooling and its energetic implications for feeding and diving of Tufted Ducks. Physiol. Zool. 71: 720-730.

De Leeuw J.J. & M.R. van Eerden 1992. Size selection in diving Tufted Ducks *Aythya fuligula* explained by differential handling of small and large mussels *Dreissena polymorpha*. Ardea 80: 353-362.

De Leeuw J.J. & M.R. van Eerden 1995. Diving ducks in the Lake IJsselmeer area, the Netherlands: population structure, biometry, moult, condition, and food choice. Flevobericht 273, Rijkswaterstaat Directorate IJsselmeergebied, Lelystad.

De Leeuw J.J., M.R. van Eerden & G.H. Visser 1999. Wintering Tufted Ducks *Aythya fuligula* diving for Zebra Mussels *Dreissena polymorpha* balance feeding costs within narrow margins of their daily energy budget. J. Avian Biol. 30 182-192.

Draulans D. 1982. Foraging and size selection of mussels by the Tufted Duck *Aythya fuligula*. J. Anim. Ecol. 51: 943-956.

Goudie R.I. & C.D. Ankney 1986. Body size, activity budgets, and diets of sea ducks wintering in Newfoundland. Ecology 67: 1475-1482.

Grandy J. IV 1972. Digestion and passage of Blue Mussels eaten by Black Ducks. Auk 89: 189-190.

Heyman M.B. & S.B. Roberts 1990. Determination of total energy expenditure in infants using doubly labelled water. In: Chapman T.E., R. Berger, D.J. Reijngoud & A. Okken (eds) Stable isotopes in paediatric nutritional and metabolic research: 51-66. Intercept Ltd, Hampshire.

Holling C.S. 1959. Some characteristics of simple types of predation and parasitism. Can. Entomol. 91: 293-320.

Jacobs J. 1974. Quantitative measurements of food selection. A modification of the Forage Ratio and Ivlev's Electivity index. Oecologia 14: 413-417.

Karasov W.H. 1996. Digestive plasticity in avian energetics and feeding ecology. In: Carey C. (ed.) Avian Energetics and Nutritional Ecology: 61-84. Chapman & Hall, New York.

Kersten M. & W. Visser 1996. The rate of food processing in the Oystercatcher: food intake and energy expenditure constrained by a digestive bottleneck. Funct. Ecol. 10: 440-448.

Kirkwood J.K. 1983. A limit to metabolisable energy intake in mammals and birds. Comp. Biochem. Physiol. 1A: 1-3.

Martin P. & P.P.G. Bateson 1988. Measuring Behaviour. An Introductory Guide, 2nd edition. Cambridge University Press, Cambridge.

Piersma T., A. Koolhaas & A. Dekinga 1993. Interactions between stomach structure and diet choice in shorebirds. Auk 110: 552-564.

Ranta E., H. Rita & N. Peuhkuri 1993. Patch exploitation, group foraging, and unequal competitors. Behav. Ecol. 6: 1-5.

Rosenzweig M.L. 1991. Habitat selection and population interactions: the search for mechanism. Am. Nat. 137: 5-28.

Ricklefs R.E. 1996. Avian energetics, ecology, and evolution. In: Carey C. (ed.) Avian Energetics and Nutritional Ecology: 1-30. Chapman & Hall, New York.

Siegfried W.R. 1976. Segregation in feeding behaviour of four diving ducks in southern Manitoba. Can. J. Zool. 54: 730-736.

Sokal R.R. & F.J. Rohlf 1981. Biometry, 2nd edition. Freeman, New York.

Stephens D.W. & J.R. Krebs 1986. Foraging Theory. Princeton University Press, Princeton.

Suter W. 1982. Der Einfluss van Wasservögeln auf Populationen der Wandermuschel *Dreissena polymorpha* am Untersee/Hochrhein (Bodensee). Schweiz. Z. Hydrol. 44: 149-161.

Sutherland W.J. 1996. From individual behaviour to population ecology. University Press, Oxford.

Van Eerden M.R. 1997. Patchwork. Patch use, habitat exploitation and carrying capacity for water birds in Dutch freshwater wetlands. Ph.D. thesis, University of Groningen, Groningen. Van Zee tot Land 65, Rijkswaterstaat, Directorate IJsselmeergebied, Lelystad, The Netherlands.

SAMENVATTING

Kuifeenden *Aythya fuligula* en Toppereenden *Aythya marila* overwinteren massaal in het IJsselmeergebied, waar ze voornamelijk Driehoeksmosselen *Dreissena polymorpha* eten. Beide soorten duikeenden leven grotendeels gescheiden in het gebied: Toppereenden vooral in het IJsselmeer, Kuifeenden vooral in het Markermeer. Onderzocht werd in hoeverre deze verdeling kan worden verklaard uit verschillen in haalbare voedselopnamesnelheden. Deze snelheden hangen af van eigenschappen van de mosselen, zoals schelpgrootte, de aanhechting met byssusdraden aan andere schelpen en de ruimtelijke verspreiding. Opnamesnelheden werden gemeten in een reeks experimenten met vogels die in gevangenschap naar mosselen doken onder omstandigheden die zo veel mogelijk de natuurlijke winterconditie benaderden. In het Markermeer zijn de Driehoeksmosselen gemiddeld wat kleiner dan in het IJsselmeer, de aanhechtingssterkte van de mosselen is er minder en er treedt minder kluitvorming op. Uit de experimenten blijkt, dat Kuifeenden in het Markermeer een aanzienlijk hogere opnamesnelheid kunnen halen (bijna 20% meer) dan in het IJsselmeer. Bovendien zijn de mosselen in het Markermeer homogener verspreid, waardoor het foerageersucces ook hoger zou kunnen zijn. Bij de grotere Toppereenden speelt de aanhechtingssterkte van de mosselen nauwelijks een rol en neemt de opnamesnelheid pas bij zeer lage mosseldichtheden af. Doordat de energie-inhoud van mosselen in het IJsselmeer hoger is dan in het Markermeer, is de netto-opname voor Toppereenden er ook aanzienlijk hoger, hetgeen hun sterke voorkeur voor dit deel van het gebied kon verklaren. Bij Kuifeenden is het verschil in netto-opname tussen beide gebieden echter gering, omdat de effecten van de sterkere byssusaanhechting en de grotere energie-inhoud van de mosselen elkaar bijna opheffen. Naast voedselopnamesnelheid kunnen ook andere factoren, zoals concurrentie tussen beide soorten duikeenden en de aanwezigheid van luwe plekken voor dagrustplaatsen, ertoe bijdragen dat de kleinere Kuifeenden, die uit energetisch oogpunt gevoeliger zijn voor wind, het Markermeer verkiezen.

Received: 19 February 1997, accepted 20 March 1999
Corresponding editor: Mardik F. Leopold