How *Dreissena* sets the winter scene for water birds: dynamic interactions between diving ducks and zebra mussels

The Zebra Mussel in Europe

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Abstract

Diving ducks are in winter tightly linked to areas with mass occurrence of *Dreissena*. In Europe and North America the large lakes form main wintering areas for these *Aythya* species. The predator-food relationship is necessary to be understood before one is to set management goals for the water bird species. We describe this both from the predator's viewpoint (food availability, foraging energetics) as well as from the prey's position (impact on stocks, trends in population, predation and reproductive ability). For Lake IJsselmeer the data on birds and zoobenthos span a range of over twenty years, which allows conclusions at the system level, supplemented by studies from elsewhere.

Introduction

The zebra mussel is an invasive species in Western Europe with a potential to become very abundant upon settlement, often dominating the benthic community. The establishment and expansion of *Dreissena polymorpha* in Western Europe in the 20th century has been well documented (see Schloesser et al., 1994 for review). Diving ducks depending on benthic fauna have shown to respond quickly to newly established zebra mussel populations, both through complete diet switches and through changes in their wintering distributions (Géroudet, 1966, 1978; Leuzinger and Schuster, 1970; Pedroli, 1977, 1981; Suter and Schifferli, 1988). At many freshwater lakes and shallow river sections, diving ducks of the genus *Aythya* now rely on the zebra mussel as a major food source in winter, indicating that zebra mussels are perceived as a real feeding bonanza. Indeed, the current winter distributions of species like tufted duck (*A. fuligula*) and scaup (*A. marila*) correspond well with large lakes with high densities of zebra mussels (Fig. 1). In particular those larger lakes are favoured which are located close to the 0°C January isotherm (in Europe especially Lake IJsselmeer, The Netherlands, and alpine lakes, Switzerland). These lakes are most of the winters ice-free and not too far from the breeding grounds in northern and eastern Europe. Likewise, the more recent invasion of zebra mussels in the Great Lakes has been followed by a strong response in diet and numbers of North American wintering diving duck species (see Mitchell and Carlson, 1993 for *Aythya affinis*, Schloesser et al., 1994 for documentation of zebra mussel invasion).

Where abundant populations of zebra mussels have a strong impact on the number of diving ducks, these birds can concurrently have a strong impact on mussel populations as well. Some studies report that diving ducks can exploit mussel stocks for more than 90% over winter (e.g. Suter, 1982c; Werner et al., 2005), but lower rates of exploitation seem to be more common. In fact, the exploitation of mussels by diving ducks highly depends on local conditions (e.g. De Leeuw, 1997; Van Eerden, 1997). Water depth, mussel size, condition and growth forms determine the dynamic interplay between the occurrence of mussels and their value as food source for diving ducks (De Leeuw, 1999). The interactions between zebra mussel populations and wintering diving ducks in Lake IJsselmeer, The Netherlands, has been studied for more than 20 years through many surveys, field studies and laboratory experiments, most of these reported in Van Eerden (1997), De Leeuw (1997) and Noordhuis et al. (2010).

At Lake IJsselmeer zebra mussels occur at depths of 1-6 m, all within potential reach of the avian predators (recorded winter maxima over 300,000 birds). Mussel densities in the lake are far beyond those in the nearby rivers and inland lakes. The IJsselmeer case therefore is considered a
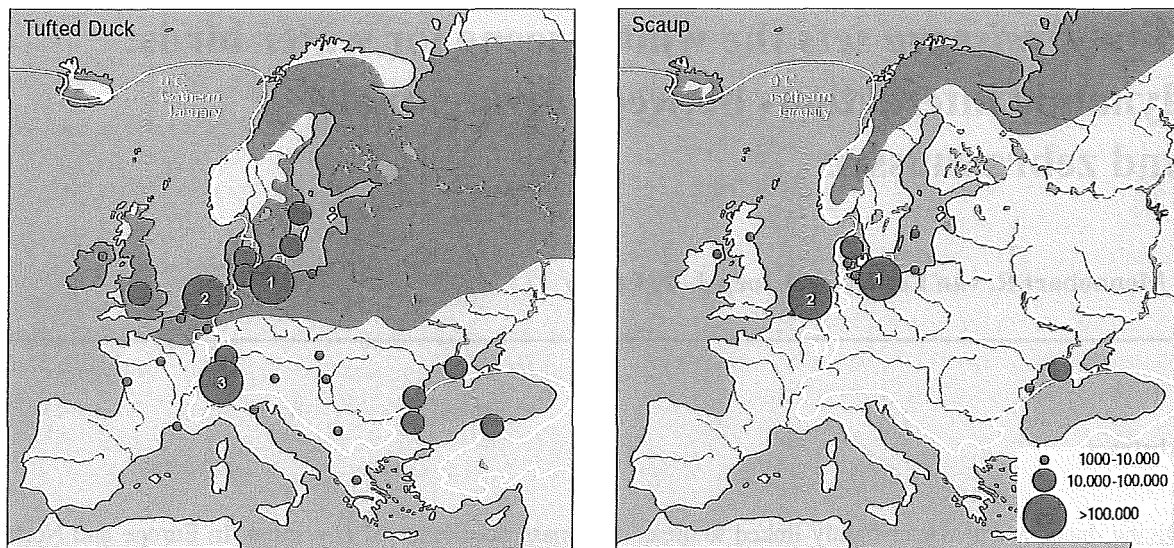
Figure 1. Breeding distribution (shaded) and major wintering areas (dots) of tufted duck and scaup. Tufted ducks breed in north and eastern Europe and move west and south to wintering habitats close to the 0°C January isotherm in the southern Baltic Sea (1) and large freshwater areas, such as the Lake IJsselmeer area in The Netherlands (2) and subalpine lakes of Switzerland (3), or river sections and ponds. B. Scaup breed further north than tufted duck and winter in marine coastal areas of the southern Baltic Sea, the freshwater Lake IJsselmeer, and the Black Sea (Data from: Cramp and Simmons, 1977; Ridgill and Fox, 1990; Rose and Taylor, 1993; Durinck et al., 1994).

major, but discrete foraging site on the flyway level. Nearest stations for diving ducks are all at a considerable distance: the Baltic and north German waters at 300-800 km and the south German and Swiss lakes at 800-1,200 km. Therefore, knowledge on both the distribution of this benthic food source and its use by diving ducks is considered of major importance to assess the carrying capacity of the system. Many of the sites where *Dreissena* forms the staple food are placed under the EC Bird and Habitat Directive, meant to safeguard the internationally commuting populations of wild birds by adequate managing the water systems.

In this chapter we explore the dynamic interactions between zebra mussels and diving ducks to demonstrate how spatial distribution and growth patterns of zebra mussels are shaped by predation on the longer term and how in turn an energetic ceiling sets limits to exploitation by diving ducks.

Optimal foraging rules and the carrying capacity theorem

Foraging animals are considered to follow economic rules in order to survive in a constantly changing world. Energy expenditure and prey profitability are important currencies, which determine local conditions for exploitation of prey. This so called optimal foraging behaviour (e.g. Charnov, 1976) predicts exploitation of natural resources by wild animals to be governed by strict rules, which have in common that the animals can only harvest the energetically profitable fraction of the total prey amount on offer. Following this individual-based harvesting of natural resources, the overall effect of an entire wintering population of predators

or even different populations of related species, which may compete for the same food items, is thus limited by the harvestable amount of food. The carrying capacity concept, i.e. the food-based natural upper level of use by wild animals in a certain habitat, is widely accepted as theory, but field measurements, especially at the level of stop-over or wintering sites, are scarce due to the difficulties of assessing food availability and bird use at measurable scale.

The migratory behaviour of the birds even implies a European scope on feeding, resting and breeding opportunities. This most likely involves decision making at different levels of scale, both in terms of habitat choice as in time. Table 1 lists these decision variables. In this chapter we will concentrate at the feeding level and down to individual prey items. The *Dreissena*-diving duck interplay in large lakes allows comparisons to be made at the level of the lake community. We will shortly discuss the implications at wintering habitat and flyway level.

Material and methods
Study area

Lake IJsselmeer is a large, shallow freshwater lake since 1932 when this former estuary was closed off from the Wadden Sea by the barrier dam Afsluitdijk. Water tables are at a fixed level through regulation by discharge sluices. Embankments have reduced the area to its current size of almost 2,000 km². Since 1975 a dike separates the larger northern compartment (IJsselmeer, 1,225 km², average depth 4.5 m) from the southern compartment (Markermeer, 700 km², average depth 3.6 m). Depth profiles vary with former sand

Table 1. Decision parameters for free-flying diving ducks with respect to spatio-temporal differences of habitat scope.

Decision level	Decision variables	Examples of options
Flyway	Phenology of life cycle events (breeding, moult, migration, wintering)	Aquatic ecosystems in boreal and temperate zone with seasonally predictable patterns of food availability; water temperature and ice conditions
Wintering habitat	Freshwater, brackish or marine foraging, level of disturbance	Estuaries, lakes, rivers and ponds, level of predators
	Food group and climatic conditions	Baltic Sea, Wadden Sea, (*Mytilus edulis*) IJsselmeer, Swiss lakes, (*Dreissena polymorpha*) Water temperature, ice conditions
	Scale of roosting and foraging habitat	Mass flock foraging (sharing of information, safety against predators), or single birds
Feeding area	Water depth	Shallow or deep water
	Flight distance	Close or distant feeding areas
	Prey predictability	Large homogeneous areas, smaller patches
	Prey density	Mussel banks, scattered mussels
Prey	Size	Small or large mussels
	Attainability	Unattached mussels or strong byssal attachment, occurrence as singles or clumps, occurrence under stones
	Quality	Mussel condition (high or low energy content), shell structure (thin or thick)

banks and tidal gullies, as well as artificially deepened areas (ships traffic, sand extraction). The estuarine past continues to show, however, because of very flat bottoms in most of the lake area. The River IJssel (northern branch of the River Rhine) discharges directly into IJsselmeer. Residence time of water is 4-6 months in IJsselmeer and 12-24 months in Markermeer. Water quality has changed markedly with initially a period of eutrophication, reaching a peak in the late 1970s, followed by ongoing nutrient reductions since the 1980s. Nutrient levels were on average higher in IJsselmeer than in Markermeer (for further details see Noordhuis et al., 2010). Ice cover, which lasted longer than 20 days occurred only in less than 30% of the winters since 1975, whereas during most winters the lake never completely freezes over. This makes the site an attractive and predictable winter haunt for migratory waterbirds (Van Eerden, 1997).

Surveys of zebra mussels

Lake-wide surveys of zebra mussels were carried out in 1981, 1992/1993 and 1999/2000. Mussels were collected using a Van Veen grab (400 cm²) on ca 450 stations (10 sub samples each) in a regular 2x2 km grid (Bij de Vaate, 1991). Live mussels were sorted out on board after a sieving procedure to eliminate soil (1 mm mesh). Mussel densities were expressed in bio-volume (ml m⁻²), a reliable estimate for total fresh mass ($Y=0.074X + 43.74$; $R^2=0.965$, $p<0.001$).

Detailed field mapping was carried out at the shallows of Enkhuizerzand, where mussel stocks were followed prior to and after the wintering season. Long-term changes of mussel stocks were recorded at two sites, taking 10 samples (0.04 m² each) per month (1981-1984). We choose two sites adjacent to large daytime roosts of either tufted duck or scaup to detect any similarities in patterns of food abundance, predator density and predation levels. Experimentally enriched trays with mussels allowed assessment of patch use at the greatest detail (Van Eerden, 1997).

Surveys of diving ducks

The number and distribution of diving ducks was assessed from monthly aerial surveys of water birds at their daytime roosts that were carried out since 1980, using a high-winged Cessna 172 flying at an altitude of 150 m and a speed of 130-150 km h⁻¹. We used data of five winter seasons (total number of bird days spending the winter at IJsselmeer and Markermeer) corresponding with large-scale zebra mussel surveys. All ducks using the IJsselmeer system as feeding area were included in the counts, so including the inland roosts in marshes and ponds.

The use of nighttime foraging areas was studied using radar (AEI 651, 1 cm beam; 9.445 GHz, parabolic antenna in a mobile caravan connected to a 220 V diesel generator). Flight direction and the lengths of foraging flights from day-

time roosts were assessed during the early evening hours at total darkness. The radar was positioned at the coast, usually on top of a dike at close range to a main diving duck roost. This allowed tracking flocks of birds (mainly tufted duck *A. fuligula* and scaup *A. marila*) up to 10 km distance, sometimes 15 km when ducks flew high. Tracks were usually much shorter, ending at the foraging location. Movements were either photographed from the screen (time exposure) or directly plotted on a map. Additional information was collected from returning flights of ducks in the morning by direct observation from vessels and the coast. Track direction from vessels was recorded with the aid of the ship's radar, which was, compared to the shore-based equipment, less sensitive to the small bird echoes. On the other hand, ship-based observations allowed longer distances to be recorded because of the ship's position between the foraging area and roost. Tracks were entered in a GIS, which allowed calculation of distance flown, and water depth at the foraging location.

Diet and food consumption

Diving ducks, which had been drowned in gill nets used in the commercial fishery, were collected from local fishermen around the IJsselmeer area. In total, 45 vessels provided 6,954 ducks over the period 1979-90. Dissection of drowned birds took place in the laboratory after thawing of the frozen bodies (-20°C). Content of the gullet of 6,052 ducks was sorted out and food items were counted. In case of small prey, sub-samples were counted and extrapolated volumetrically. *Dreissena* shells were always measured individually to the nearest mm.

Food intake of *Dreissena* by diving ducks was estimated using data collected on captive tufted duck and scaup in a semi-natural diving device where food consumption and energy expenditure were recorded (De Leeuw, 1999; De Leeuw et al., 1999). Food consumption was corrected for body size of wild ducks as obtained from drowned individuals. Here we use daily rations in the field of 3,200 gFW for tufted duck, 3,600 g for scaup, 3,300 g for pochard (*Aythya ferina*) and 2,900 g for goldeneye (*Bucephala clangula*). Coot (*Fulica atra*), being partly herbivore, is provisionally set at 2,000 gFW.

Foraging behaviour and energetics of diving ducks

Diving behaviour, daily rations of zebra mussel consumption, and energetics of tufted duck and scaup were studied under semi-natural outdoor conditions (pontoon with diving cages) and in indoor 6 m deep aquaria (De Leeuw, 1996, 1999; De Leeuw and Van Eerden, 1992; De Leeuw et al., 1998, 1999). These studies allowed to construct daily energy budgets depending on local foraging conditions (diving depth, water temperature, growth form of zebra mussels

(single or in clumps), mussel condition (flesh content)), and were combined with the data of distance between daytime roosts and nighttime foraging areas (De Leeuw, 1997). The energy balance model is used to compare foraging decisions and predict the distribution of diving ducks over the lake and the carrying capacity of IJsselmeer and Markermeer for wintering diving ducks (De Leeuw, 1997, 1999).

Results
Changes in distribution of zebra mussel populations

Zebra mussels colonized the entire area soon after 1932, but densities were found to vary strongly with local conditions, of which depth and the occurrence of substratum for settlement (dead marine shells or unionid bivalves) were structuring most.

Distribution maps of *Dreissena* over the entire lake in 1981, 1992/93 and 1999/2000 show large spatial variation in mussel biomass (Noordhuis et al., 2010). High mussel densities occurred in the southeastern part of Lake IJsselmeer, at the outflow of the river IJssel as well as in the southwestern part of Lake Markermeer. High densities also occurred on the steep ridges adjacent to the former tidal gullies, particularly in northern IJsselmeer. Mussels were scarce or absent in the eastern part of Lake Markermeer and the central parts and the northwestern coastal regions of Lake IJsselmeer. Part of the areas without mussels coincided with deeper water and a bottom covered by soft and recently deposited silt (Bij de Vaate, 1991; Noordhuis et al., 2010).

Comparing the three lake-wide investigations (Fig. 2), spanning an eighteen years interval, this general distribution pattern held for all years, but densities varied considerably (Noordhuis et al., 2010). In Lake IJsselmeer, *Dreissena* abundance increased between 1981 and 1992 from 397 x 10⁶ to 672 x 10⁶ kg FW. In 1999, the population had decreased to 533 x 10⁶ kg FW. In Lake Markermeer, however, *Dreissena* abundance decreased between 1981 and 1992 from 218 x 10⁶ kg FW to 86 x 10⁶ kg FW, while the distribution patterns remained similar. In 1999-2000 the Markermeer population had further dropped to 40 x 10⁶ kg FW. The large differences between the years resulted from marked changes in mussel densities especially those occurring at deeper water (> 4.5 m in IJsselmeer, > 3.5 m in Markermeer, Fig. 2). In Markermeer a large shift in depth distribution is apparent after 1981, caused by the continuous deposition of silt in this newly created lake (1975, see Noordhuis et al., 2010).

Mussel density increased from 1 to 5 m water depth, steeply falling thereafter (Fig. 3A). More than 60% of total biomass is situated at depths greater than 4 m. On average, mussels were larger at greater depths and associated with higher densities. Condition of mussels, however, decreased with increasing water depth (Fig. 3B). At greater
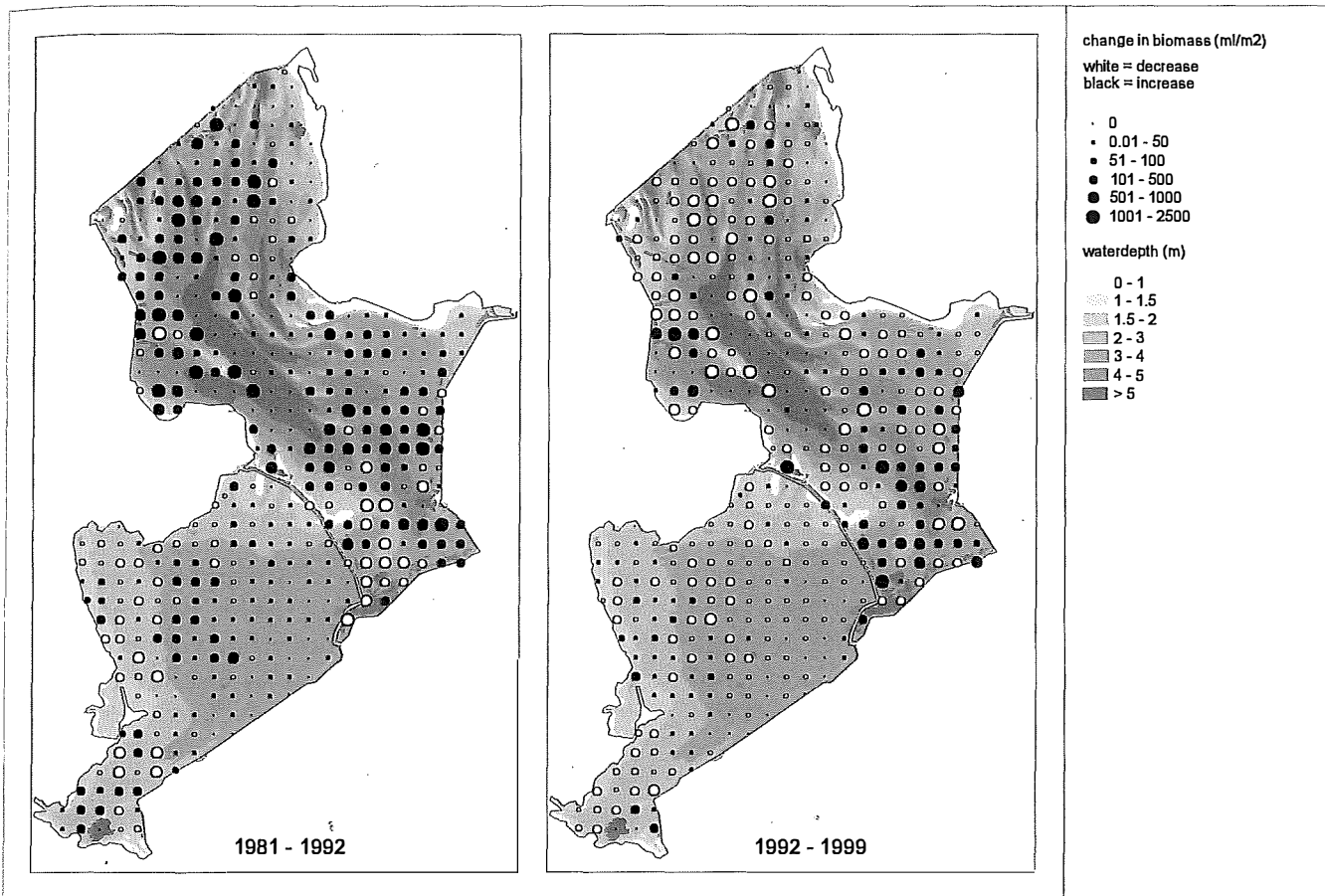
Figure 2. Change in biomass distribution of zebra mussels in IJsselmeer and Markermeer between surveys in 1981-1992 and 1992-1999. Depth contours indicated. Notice the increase in the northern and central parts of Lake IJsselmeer in the first interval and a decrease there as well as in the greater part of Lake Markermeer over the second interval.

depths the population consisted for about 60% of unattached mussels, laying on the bottom or densely packed in beds, whereas in shallow water this was only 20%, the rest growing in clumps, often tightly attached to old marine shells (Van Eerden, 1997).

Numbers, diet and habitat selection by diving ducks

Among the avian benthos feeders, tufted duck and scaup were the most abundant winter visitors. Tufted ducks were present from July until April, with peak numbers feeding on *Dreissena* between November and February (60-85,000, maximum 150,000). Scaup were numerous between October and April, with peak numbers somewhat later, from December until February (100-125,000, maximum 220,000) (Van Eerden, 1997). Tufted duck frequented the southern part of the lake system, whereas scaup were more common in the northern part. Each species has its own roosting centres where large flocks return year after year, although part of the population is regularly distributed along the shores of the lakes during daytime.

The stomach analyses of diving ducks accidentally drowned in fishing gear demonstrated that *Dreissena* was indeed the most important prey item during winter months (November-March). Pochard (chironomid larvae) and coot (vegetative matter) were less specialized *Dreissena* feeders (Table 2).

Radar observations: seasonal patterns and differences between species

Foraging tracks, as observed by radar and extended by visual observation, showed that most ducks flew at least several kms from the coast before landing to feed (Fig. 4). The roosts were situated in the same region as the foraging areas. The roosting concentrations dissolved between 1-1.5 h after sun-set, invisible to the human eye. Most birds returned to the roosts already 1 h before sunrise, although in the course of the morning ducks were seen arriving from their foraging grounds, especially under calm wind conditions. No midnight movements to and from roosts were ever observed. Tufted duck generally flew less far (4.0 km) than scaup (5.0 km, $F_{1,1026}=37.5$, P< 0.001). During the second
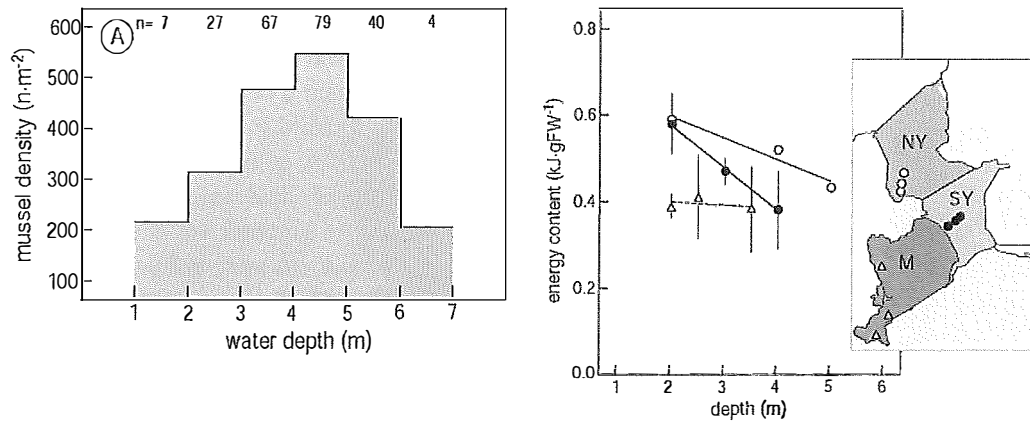
Figure 3. Characteristics of *Dreissena polymorpha* at Lake IJsselmeer and Markermeer: **A**. Density of *Dreissena* in relation to water depth (data lake-wide survey 1981). **B**. Condition (energy content) of *Dreissena* in relation to water depth (De Leeuw, 1997). The average (± SD) conditions over two 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).

part of the winter longer distances were travelled by both species (3.1 km and 5.3 km, $F_{1,661}=109.1$, P<0.001 in tufted duck, 4.3 km and 6.3 km $F_{1,364}=47.4$, P<0.001 in scaup). Diving depth, as derived from radar observations of foraging locations, varied between the species in the course of the season and for different parts of the lake system. Combining all data into a multiple regression model, significant effects existed for species (tufted duck diving less deep than scaup, Student's t=4.24, P=0.0001), site (Markermeer more shallow dives than northern part of IJsselmeer, deepest in northern part t=10.87, P<0.00005) and period (early winter less deep than late winter t=5.50, P<0.00005). The overall difference between the two species was partly due to the fact that the majority of tufted ducks were based at the shallower Lake Markermeer. However, also for southern IJsselmeer, where both species occurred in large numbers, a difference existed, but surprisingly, tufted duck were recorded here at somewhat greater depths than scaup in early winter (3.7 and 3.2 m, respectively, ANOVA $F_{1,185}=9.76$, P=0.0022). In late winter no difference in average feeding depth was found here (tufted duck 4.0 m, scaup 4.0 m, $F_{1,102}=0.0$, P=0.917).

Zebra mussels as prey for diving ducks

Diving ducks are skilful predators on zebra mussels. The broad bill is well equipped for collecting many small prey items during a single dive. Especially small, unattached mussels (spat and young mussels less than 15 mm) can be collected by a water suction-flow generated by small bill movements (De Leeuw and Van Eerden, 1992). Small mussels are, therefore, highly preferred over larger mussels. Mussels are swallowed whole, whereupon the mussel shells are crushed in the muscular gizzard. Large mussels are more difficult to swallow and, because of thicker shells, harder to crush. Moreover, most zebra mussels produce byssal threads with which they attach themselves to hard substrate, often other zebra mussels, thereby forming clumps. Tight clumps are even more difficult to handle. In experiments with captive ducks trained to dive in outdoor cages (see methods, De Leeuw, 1999; De Leeuw et al., 1999), tufted duck showed 20% lower intake rates while feeding on mussel clumps as compared to unattached mussels with similar size composition. The somewhat larger scaup, however, was more efficient in handling mussel clumps and did not show significantly lower intake rates as compared to feeding on unattached mussels.

The extent to which zebra mussel populations are exploited by diving ducks depends thus largely on the profitability of the potential feeding spot with respect to the availability of mussels. As pointed out in Van Eerden (1997) it is not unlikely that the mussels in tightly attached clumps

Table 2. Importance of *Dreissena* as staple food for individual water bird species wintering at lake IJsselmeer and Markermeer based on gizzard and stomach content analyses (see Van Eerden 1997 for further details).

Species	Dreissena % of diet (mass)	Number of stomachs analysed
Scaup, *Aythya marila*	99.9	1,394
Goldeneye, *Bucephala clangula*	95.7	311
Tufted duck, *Aythya fuligula*	95.0	632
Pochard, *Aythya ferina*	89.3	90
Coot, *Fulica atra*	65.5	128

result from the "shaping" of the population by the continuous heavy predation by diving ducks on the shallowest areas.

Diving ducks as predators on *Dreissena*

Are there measurable long-term effects of predation on the benthos community? By simultaneous monitoring of *Dreissena* and diving ducks in Lake Markermeer (Pampushaven) and IJsselmeer (Trintelhaven) we found contrasting differences in predation and subsequent changes in mussel population (Fig. 5). Within one winter season tufted duck always preceded scaup, although total numbers of both species differed enormously between the two regions under study. If we consider the mussel plots that were sampled on a monthly basis, it became evident that, over a five years period, adult mussels increased at the site used by scaup and decreased at the site used by tufted duck. We showed that the decrease was accompanied by an irregular spat production and concurrently high numbers of tufted duck. Especially the high peak of first year mussels in summer 1982 was followed by large numbers of ducks, which caused an almost complete disappearance of the peak in mussel spat. Together
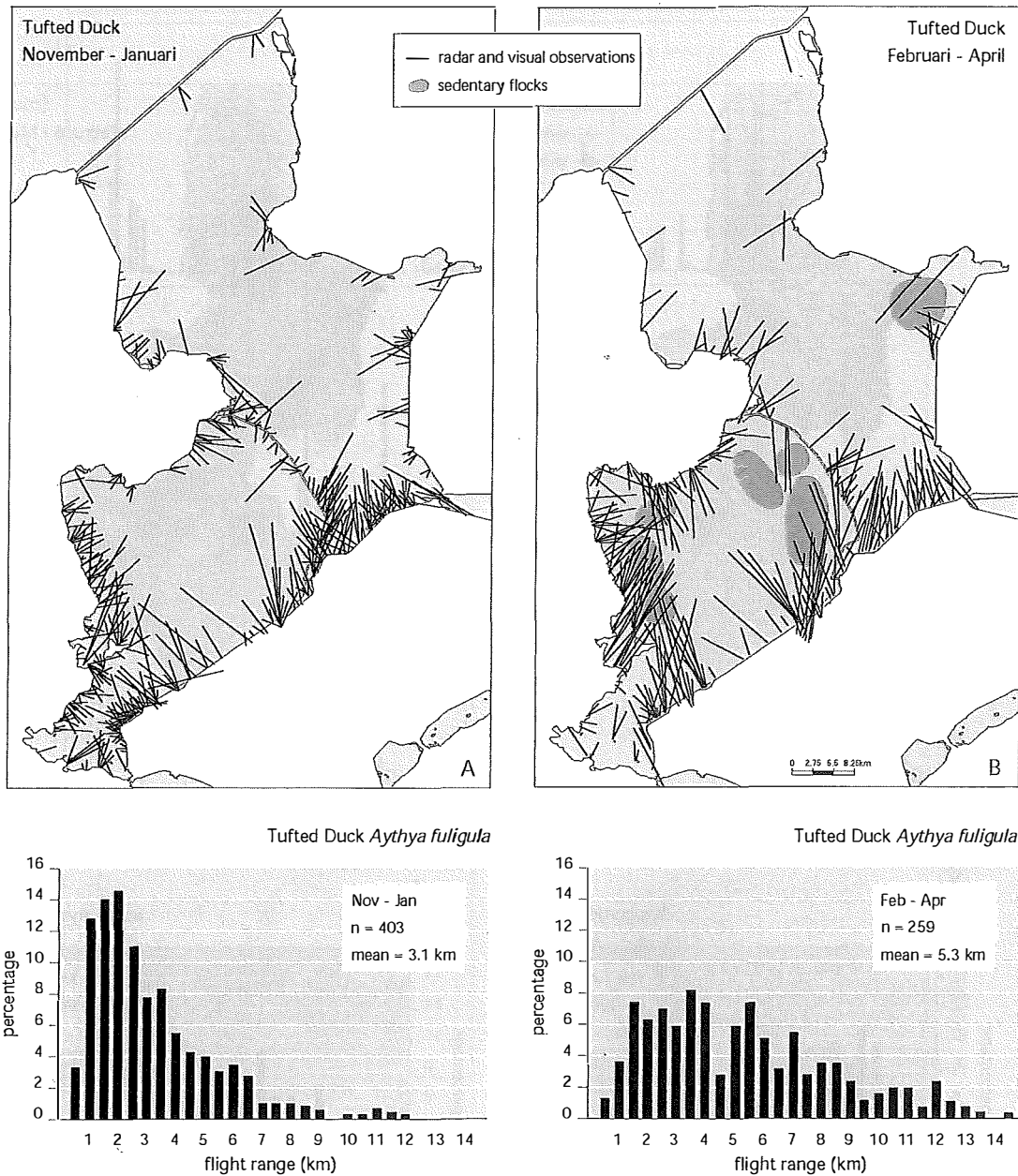
Figure 4. Foraging flights of tufted duck as recorded by radar and visual observations in (**A**) early and (**B**) late winter. (**C**) and (**D**) idem for scaup. Notice spatial segregation of the two *Aythya* species and the general link between positions of roosts and the use of foraging areas. Late winter positions of sedentary, non-commuting duck flocks are indicated. Frequency distributions of the length of foraging flights for the same data are depicted in the lower panels.

with the drop in numbers of adult mussels the winter before, this caused the dramatic collapse of the (local) population (Van Eerden, 1997). Radar observations the next winter (1983/1984) showed that ducks were no longer foraging at the site; but in 1984/1985 this proved to be again the case, after a slight recovery of the mussel bank. Also at Lake IJsselmeer tufted duck preceded scaup within one season. However, the regular production of spat here enabled the population to grow, despite regular setbacks due to avian predation. As tufted duck are known to be able to prey efficiently on spat by suction feeding (De Leeuw and Van Eerden, 1992), this species might be responsible for the main reduction in first year mussels (3-7 mm), whereas both species prey on older mussels (8-18 mm). From the viewpoint of the dynamics of the mussel population depredation by ducks has an annual effect (local patch depletion and shaping because of size and structure selectivity) as well as a long-term effect (biomass development and size distribution).

Energy budget sets the upper limits of exploitation

The decisions by diving ducks at the level of feeding area and prey characteristics (Table 1) can be further explored using an on-the-site-energy-balance model (Fig. 6), which estimates the energetic gains from intake of mussels against the energetic costs to exploit a potential feeding spot. The
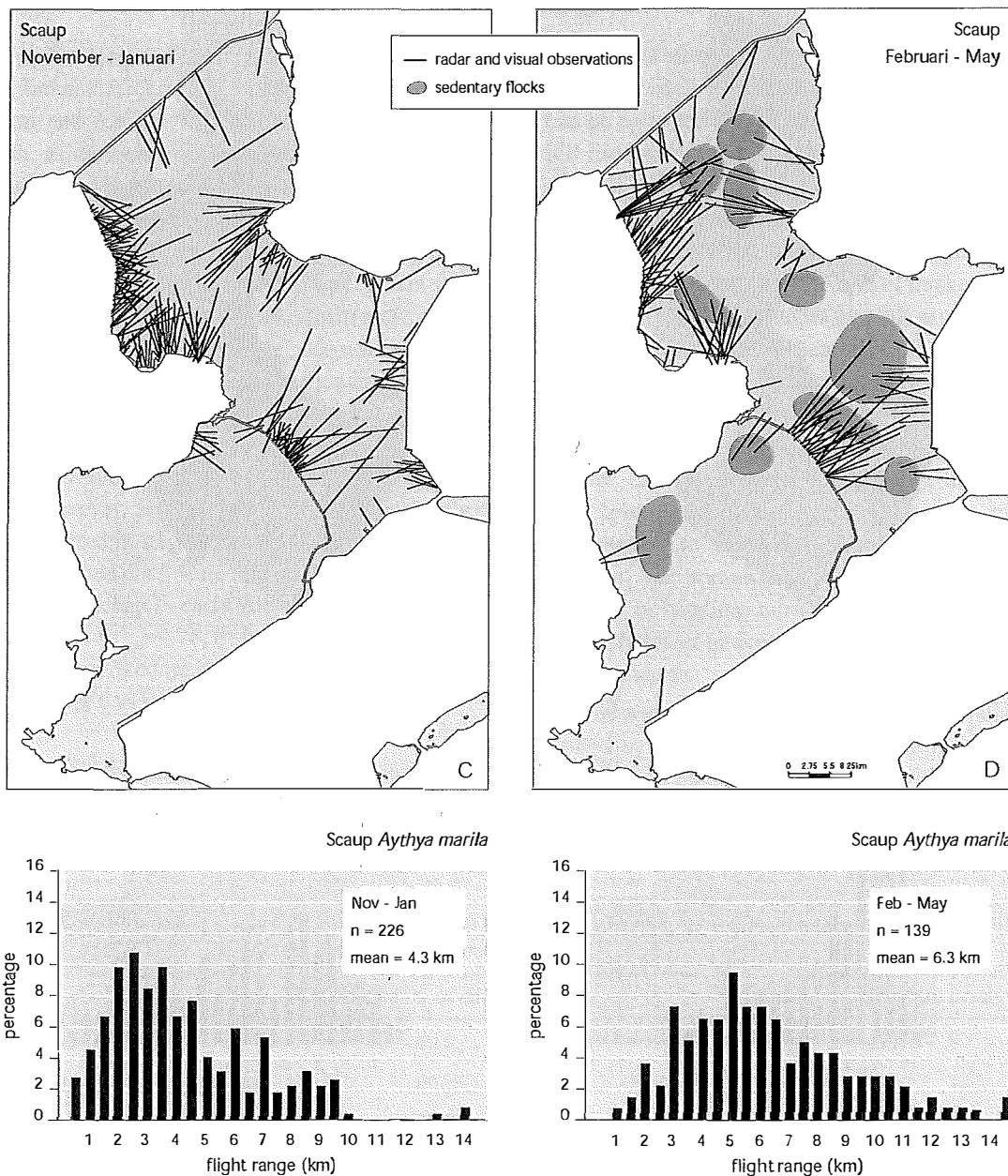

Figure 4. (continued).

energetic costs that diving ducks incur are composed of the following components:

Maintenance costs: the energy costs to maintain basal metabolic functions in the body and to maintain the body temperature above 40°C in a strongly cooling environment with winter water temperatures close to zero (De Leeuw et al., 1998).

Diving costs: costs to dive for food. Diving costs increase with water depth because diving ducks have to dive for longer times paddling against the upthrust and because

of stronger heat loss at greater depth where increased pressure reduces the insulative properties of the air trapped in the feathers (De Leeuw, 1996; De Leeuw et al., 1998).

Food-processing costs: the costs to crush the mussel shells and heat up the large amounts of fresh mussels ingested (see below) from just above zero (winter water temperature) to above 40°C (body)(De Leeuw et al., 1998). Because mussels are swallowed whole, the ingested mass consists for about 95% of indigestible shells and water. Crushed shells and most of the water leave the bird as faeces.
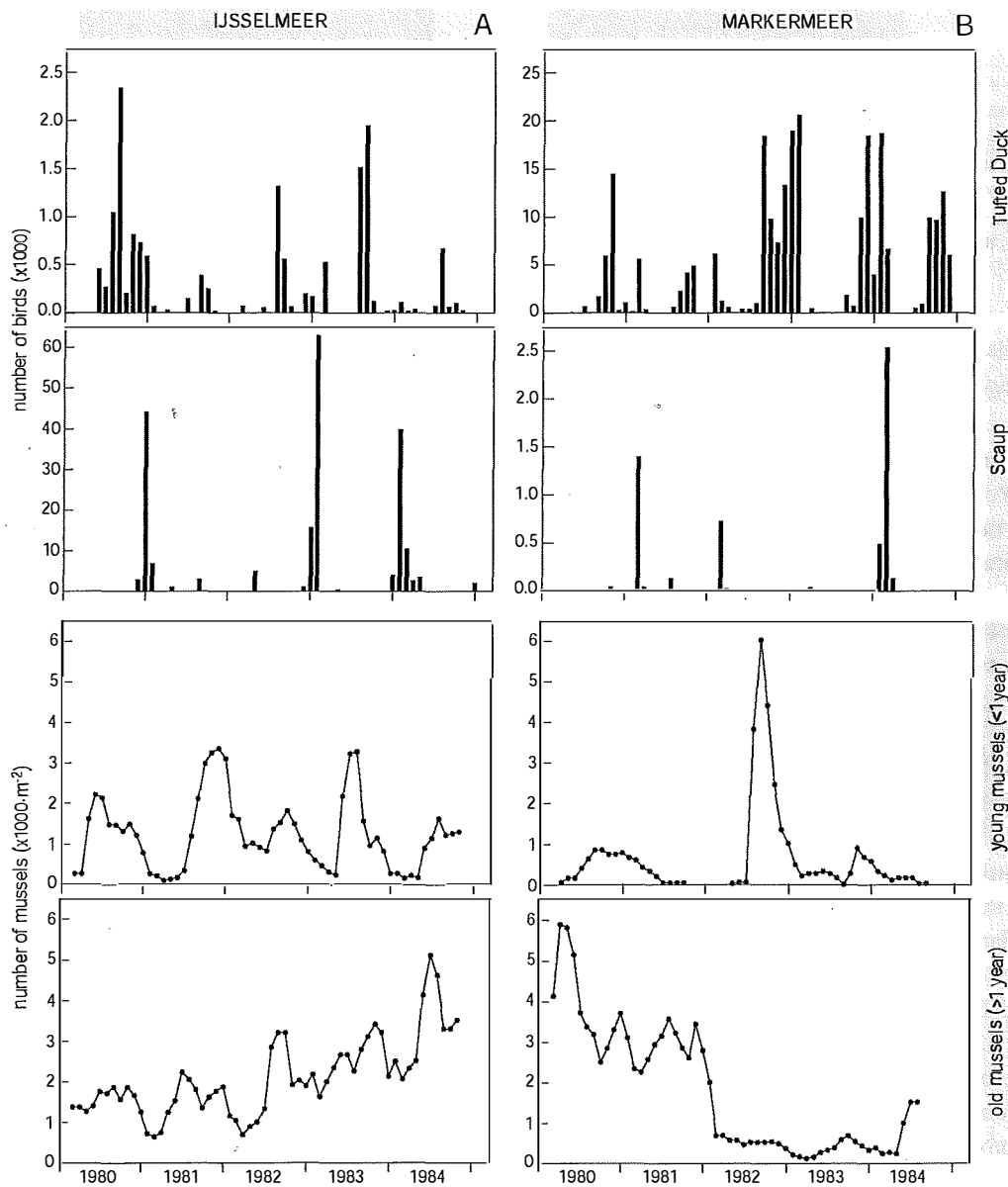

Figure 5. Monitoring of *Dreissena* and ducks at two sites over a period of five years, based on monthly sampling of benthos and counts of ducks at the main nearby roosts. Benthos data expressed as three-point running means after data in Bij de Vaate (1991). At site **A** (Enkhuizerzand, IJsselmeer) regular production of spat fall led to a slowly increasing mussel population, despite annual predation by diving ducks (mainly scaup). At site **B** (Pampus, Markermeer) irregular spat fall and extremely heavy predation during the winter 1981/82, when the site was one of the few open places in Lake Markermeer, led to the disappearance of *Dreissena*, without recolonisation on the longer term. Notice the seasonal sequence in presence of tufted duck before scaup and the general concordance between the number of tufted duck and the occurrence and depletion of one year old mussels.
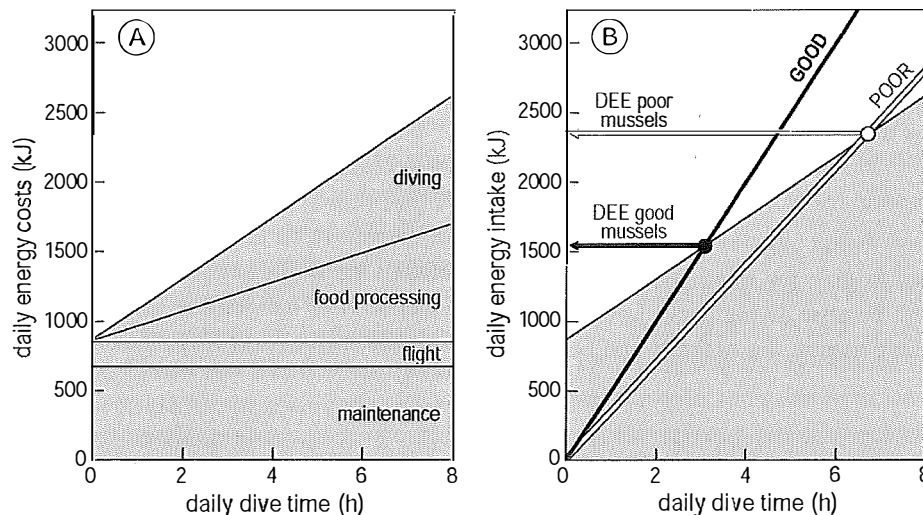
Figure 6. Energy balance model for estimating the daily energy expenditure (DEE) of diving ducks at energy balance (De Leeuw, 1997). The example shows simulated data for scaup feeding on mussels of poor'condition (water depth 4 m) and good condition (2 m). **A.** Total energy expenditure increases for 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.

Flight costs: costs to commute between daytime roosts (usually the sheltered zones along the shore) and nighttime foraging areas in the open areas of the lake (De Leeuw, 1997).

The components of the energy-balance model were estimated for tufted duck and scaup in a set of metabolic studies carried out with captive birds diving and foraging on mussels under semi-natural conditions (De Leeuw, 1996, 1997, 1999; De Leeuw et al., 1998, 1999). In these studies energy costs were measured for different foraging options with regard to diving depth, water temperature, mussel size and growth form, covering the natural ranges as found in IJsselmeer and Markermeer. The results are summarized in Table 3. The variation in flesh content (Fig. 3B) turned out to be of major importance for the energy budget (Fig. 6). When the flesh content of *Dreissena* is low, diving ducks would need to eat more in order to meet their daily energy demands, but to achieve this they should dive more frequently and have to handle also larger amounts of cold indigestible material (shells and water). In IJsselmeer the flesh content of mussels is strongly related to water depth: at a depth of ca. 5 m the flesh content is 30% lower than at 2 m. As a result, deeper areas can only be exploited at extremely high-energy costs (Fig. 7). Deeper areas therefore offer only marginal feeding opportunities; probably they can only be exploited on negative energy budgets when diving ducks must rely on body fat reserves stored during more profitable conditions in early winter (De Leeuw, 1997). The mussels in the Markermeer area had already in the 1980s lower flesh contents than in the IJsselmeer (Van Eerden, 1997). This situation even worsened parallel to the numerical crash in Markermeer after 1992 (Noordhuis et al., 2010).

Long-term dynamics in distribution of benthos and birds

In Fig. 8 lake wide mussel survey dynamics are compared to changes in numbers of diving ducks separately for the two lakes and thereby for the two main consumers, tufted duck and scaup. If we correlate total biovolume with bird presence a positive correlation exists (R^2=0.53, P<0.01, N=6). Using available biovolume instead (IJsselmeer 30 ml m^{-2}; ≤ 3.75 m and Markermeer 40 ml m^{-2}; ≤3.50 m, for scaup and tufted duck, respectively) the correlation remains about the same (R^2=0.54). If we leave 1999 IJsselmeer out (see below) the correlation increases to R^2=0.87, P<0.01, N=5. Notice the fact that quite a lot of the datapoints lay very close to the required minimum available mussel stock as indicated in Fig. 8. This means that the food requirements of the diving ducks are very close to the carrying capacity of the lake system.

Discussion
Zebra mussels as staple food of the benthic community of large lakes

Diving ducks are not the only consumers of *Dreissena*. Consumption of small *Dreissena* by fish such as roach (*Rutilus rutilus*) occurs mainly in summertime (Prejs et al., 1990) and thus can be ruled out as factor causing over-winter loss of mussels. However, predation by roach on benthic food in summer may cause a change in the benthic community and, therefore, it might affect the carrying capacity for wintering diving ducks (Winfield et al., 1992).

The role of *Dreissena*, being a keystone species in the trophic foodweb of many freshwater lakes nowadays, is comparable to that of the blue mussel (*Mytilus edulis*) in

Table 3. Exploitation limits of *Dreissena* by diving ducks, set by water depth, flight distance and prey characteristics.

Foraging characteristic	Relevant range	Effect	Energetic impact on daily energy budget	Reference
Water depth	Shallow (2m) - deep (5 m)	Energy loss (dive duration and cooling)	+10%	De Leeuw, 1996, 1997; De Leeuw et al.,1998
Flight distance between daytime roost and nighttime foraging area	Small (0 km) - large (30 km)	Energy loss	Ca 5-10% (depending on options for finding shelter at daytime roosts)	De Leeuw, 1997
Prey density	Mussel banks - lower threshold	Intake rate	Ca. 20% (lower threshold depends on foraging abilities!)	De Leeuw, 1997, 1999
Size	Small - large mussels	Intake rate	Ca. 10-20%	De Leeuw and Van Eerden, 1992
Attainability (attachment with byssus threads)	Unattached mussels - clumps	Intake rate	Tufted duck: +20% Scaup: <5%	De Leeuw, 1999
Quality (flesh content)	High (0.6 kJ/gFW) - low (0.4 kJ/gFW)	Energy gain/ energy loss (diving/cooling)	+60%	De Leeuw, 1997, Fig. 7

marine habitats. This species is preferred food for scaup in early autumn and winter. A crash of *Mytilus* in the Dutch Wadden Sea in 1989, caused by intensive fishing on young and older mussels (Dankers et al., 1999), was followed by a strong increase in scaup numbers in the nearby Lake IJsselmeer during a period of seven seasons (1988/89-1994/95). The influx was paralleled by a synchronous influx of tufted duck, coot and pochard during the first part of this period, probably attracted because of the higher stock of *Dreissena* in IJsselmeer during the early 1990s. Interestingly, these obligate freshwater species showed a less prolonged period of elevated numbers than did scaup (coot and tufted duck four seasons (1989/90-1992/93), pochard and goldeneye three seasons (1988/89-1990/91)).

Rather than coot, tufted duck and pochard, scaup may more easily switch between marine and freshwater systems and in relation to this may use other shellfish than the freshwater molluscs to which the other species are confined. The almost doubled numbers of scaup in this period thus lasted four years longer than in the other species. First in 1995/96, (one season after the first big spat fall of *Mytilus* after the harsh winter of 1994/95), the number of scaup in IJsselmeer declined and numbers in the western Wadden Sea increased. The poor feeding conditions in the Wadden Sea thus forced the IJsselmeer system to take up temporarily some 36 million extra scaup days, corresponding to an extra consumption of ca 130 million kg of *Dreissena*. Could this extra influx have affected the mussel stocks in Lake IJsselmeer? The distribution maps of *Dreissena* (Fig. 2), point to the greatest losses in the deeper areas in the northern part of IJsselmeer, merely

overlapping with the nighttime distribution of scaup (radar studies and drowned birds, see also Van Eerden, 1997). As a similar decline did not occur at the deeper areas in the southeastern part of the lake, we conclude that the cumulative harvest over seven winter seasons by scaup, rather than a common abiotic factor, was responsible for this. Another effect of cascading response of declining food conditions in one lake to another was observed in tufted duck. Higher
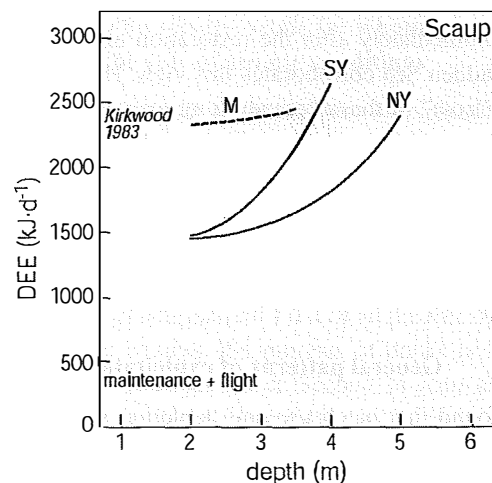

Figure 7. Predicted daily energy expenditure at balance (DEE) in relation to water depth, according to the energy balance model for three different locations with contrasting mussel conditions (Fig. 3B). NY=northern IJsselmeer, SY=southern IJsselmeer, M=Markermeer. The shaded area indicates the supposed maximum daily energy expenditure according to Kirkwood (1983), indicating that exploitation of Markermeer and the deeper areas of IJsselmeer occurs at the energetic limits of diving ducks.
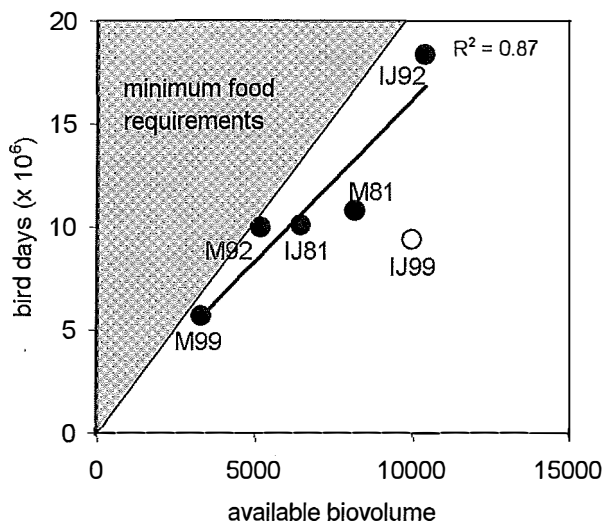
Figure 8. Relationship between mussel availability and diving duck numbers. Bird days per winter season (Sept-March) of tufted duck and scaup (total in five years around sampling of mussel stock) and lakewide survey of available mussels for Markermeer and IJsselmeer. Available biovolume of zebra mussels in ml m^{-2}.

numbers in Lake IJsselmeer paralleled the declining food stocks in Lake Markermeer (see Noordhuis et al., 2010) and corresponding lower numbers of ducks. Since 1990/91 more tufted ducks are present in IJsselmeer compared to the years before, although the influx in IJsselmeer was less than the decline in Markermeer. This is in line with the conclusion of the carrying capacity being reached. Deteriorating food supplies cause lower numbers and redistribution over other, less profitable areas. For tufted duck the shift to the deeper IJsselmeer incurs higher diving costs (see radar observations and table 3). The declining number of scaup from the IJsselmeer immediately after the restoration of *Mytilus* stocks in the Wadden Sea corroborates this view. However, the associated "cost" of these cascading movements can not simply be observed from shifts in bird numbers alone; instead, more information would be required on the alternatives of the birds that left the preferred area and, perhaps more important, what their associated costs were in terms of declining body condition or lowered chances on future survival.

General patterns of exploitation

We found that patch use and depletion levels of *Dreissena* varied greatly from one site to another (depth, density, growth pattern and distance from roost) and from year to year (Van Eerden, 1997). Predation at one spot may result in heavily depleted patches whereas other parts remain untouched. Exploitation of zebra mussels by diving ducks in a large lake operates at different levels of decision. First, the exploitation of different patch levels at different sites within a region (first order patch level). Choosing a forag-

ing and roosting site, diving ducks tend to minimize costs for transport (short flight tracks) and to minimize costs for extra locomotion at the roost (shelter against waves, avoidance of disturbance). First order patch exploitation tends to maximize energy intake by selection of small prey, where possible. Second, the macro choice of where to forage (second order patch level) and associated with this the choice of a suitable roost site.

Size selection effects could be demonstrated as the ducks selected smaller, fast growing zebra mussels in a better than average condition (Van Eerden, 1997). Shallow areas were found to be the most profitable, despite the low mussel densities, lower total abundance, and stronger byssal attachment of mussels compared to average (clumps rather than single mussels). The energetic constraints of the diving ducks are thus very much focused on the factor of mussel quality. For a large lake system this means that large parts of the population are out of reach for the predators.

Social foraging, detectability of hot spots in a dynamic environment

Generally speaking, the feeding on *Dreissena* by diving ducks resulted in a relatively underexploitation of rather isolated, rich patches, of mussel banks at greater depths and of mussels occurring in large clumps. The richest mussel beds at depths of 4 m and more, were only partially exploited and this only during the latter part of the winter season. This is probably due to imperfect knowledge of the environment (night-time foraging under water, the scale of the habitat) and further limitations imposed by the flock-feeding habit (Van Eerden, 1997).

The choice of a certain foraging area by a flock of several thousands of birds is likely to be influenced by the average quality of the site rather than by peak values. This average is supposed to affect bird density and to determine the number of nights the site is in use. In other words, general giving-up density (GUD) is likely to be determined by the average for the site (several km^2) and is affected by local mussel quality (flesh content, attainability). In such an exploitation system the relatively scarce rich patches will be underused and poorer than average patches will be overused with respect to their GUD.

Patch experiments showed no physical limits to ingestion, such as mussel size and occurrence of mussels in clumps (Van Eerden 1997). However, trials with captive birds did show a reduction in net intake rate for larger mussels and mussels in clumps (De Leeuw and Van Eerden, 1992; De Leeuw, 1999). Patch quality therefore is important to the individual, but patch exploitation by individual birds is apparently subservient to the flock's attendance to the site. First order patch exploitation by individual ducks may thus obey

the higher order of common decision making by the members of the group, over a much larger area than individual flock members can experience themselves. The mechanism behind this may simply be available time for exploitation in combination with a constant harvest rate, adjusted to the average yield of the site. However, we showed that diving ducks do possess the ability to allocate more time and/or to concentrate in larger numbers at the best patches.

By their highly social, flock-feeding behaviour, spending their inactive phase at huge communal roosts, individual ducks may profit from the knowledge available in the group, e.g. to which feeding sites they should fly, to achieve the most profitable prey uptake. Radar observations on the foraging tracks demonstrated the short periods of movement to and from the feeding areas (75% of all movements within 20 minutes) and the concentrated direction of the flight paths which support the idea of a strong social cohesion amongst the flock members of a roost. As we have seen above, this communal harvest does not lead to an overall depredation of all mussels within potential reach of the ducks.

Carrying capacity in large freshwater lakes: the upper limits to predation

Exploitation rates can thus be predicted from local conditions and because of enormous differences in growing conditions the carrying capacity parameters differ for the individual cases. Is this consistent with other studies, which have recorded predation levels in relation to biomass on offer? In large scale water bodies at the Swedish coast Nilsson (1970, 1980) estimated a 6% (5-35%) loss by wintering sea ducks exploiting the common mussel *Mytilus edulis*. Consumption by eiders *Somateria mollissima* was calculated to amount a 13% loss for mussels and cockles *Cerastoderma edule* in the German part of the Wadden Sea (Nehls, 1989, 1995). Guillemette et al. (1996) report for individual reefs in a tidal environment in the Gulf of St Lawrence, Canada, 48-69% depletion of *Mytilus* due to eider predation. For *Dreissena*, Pedroli (1981) reported 22% loss in lake Neuchâtel, Switzerland with depths up to 9 m. Hamilton et al. (1994) found a 57% decline in a recently colonized *Dreissena* population at a stretch of lake Erie due to predation by diving ducks (depth 5-7 m). Suter (1982c) estimated with >95% the highest recorded impact of diving ducks on bivalves (*Dreissena*) in a smaller scaled, riverine area of Untersee/Hochrhein, Switzerland (depth 1 m). Likewise Werner et al. (2005) demonstrated a large impact on *Dreissena* by tufted ducks in Lake Bodensee, Germany (>90%). Although not always stated explicitly, we conclude from these studies that the highest measured impacts coincide with: 1) smaller water bodies, 2) shallower situations or 3) better mussel condition due to limnological circumstances (trophic level, influence of river).

In conclusion, predictability and size of the food stock in relation to foraging costs (scale of the total habitat in relation to water depth) appear to be important factors, which determine the harvestability of the benthic community, in particular *Dreissena*. The large lakes form predictable feeding conditions for large numbers of ducks. Not only the total amount of benthos is important, also the within lake buffering of local differences in food supply. By their social foraging habit, the ducks are probably able to share the under water information about the best available options. Crashes of the food stock in one lake may result in a temporally higher impact of the birds on the mussels in nearby lakes.

Effect of predation on high quality mussels for reproduction

Local setbacks in mussel stocks may be caused by avian predation. In most cases, the frequent spawning by *Dreissena* results in a rapid recolonization of the population after one growing season. In the case of extremely heavy predation described by Suter (1982c) and Cleven and Frenzel (1992) mass immigration of 1^+ mussels took place, facilitated by the water current. A factor, which is still open for discussion, is the effect of predation by diving ducks on fleshy mussels at shallow depths in relation to the reproductive capacity of the lake. It is unknown whether veliger larvae are being produced by all parts of the population at the same rate. If the reproducing part of the *Dreissena* population is confined to that of the highest condition, than the selective predation pressure by the diving ducks on these mussels may have a greater effect than judged by numerical examination of the percentage loss.

Who sets the scene for whom: the role of abiotic conditions

So far we have tackled the problem of exploitation from the point of view of the predator; we showed the gross effects of predation on structuring and shaping the population. However, our main conclusion was that *Dreissena* determines the possibilities the birds have to settle themselves during winter. What other factors might be responsible for the observed changes in mussel abundance? First of all the role of ice winters. During ice winters, the number of ducks is lower, so overall predation rates are lower. Second, in years after complete ice cover, *Dreissena* spat fall is often more abundant than during years following mild, ice-free winters (A. bij de Vaate, pers. comm). Both effects would result in potential expansion of the population. On the other hand the formation of ice in shallow lakes causes damage to mussel populations because of the effects of ground ice, which may move mussels up to the surface where they freeze over (Van Eerden, unpubl. data). Could the latter effect be the main reason for the large-scale developments, which occurred in IJsselmeer?

All three lake wide investigations were preceded by two or three harsh winters in years prior to the sampling; so mussel spat will not have been the limiting factor for differences in overall mussel stock. The investigation in 1982/83 had a total of 266 icedays in the five years preceding the inventory. The second investigation in 1992/93 was characterised by much milder weather: 121 icedays in the total of five preceding winters. Finally, the 1999/2000 investigation had a total number of icedays of 201 in the five preceding winters, so again colder. Despite predation by birds the series of mild winters may well have contributed to the observed increase in mussel stocks in IJsselmeer in this period.

Another important abiotic factor is anoxia in summer due to high water temperatures and little wind. Even in shallow lakes as IJsselmeer this may occur (Berger, 1987) and may cause mortality of mussels. Among the highest average temperatures per month (> 20°C) since 1901 rank July 1994 (21.4°C), July 1995 (20.1°C) and August 1997 (20.5°C), all in the second interval when a large decline was observed. In the first interval, only July 1983 (20.1°C) was extremely warm. Therefore, besides a strong predation also the negative effect of high summer temperatures may have contributed to the decrease in the period 1992-1999. Can we separate both effects? In Fig. 2 we depicted the spatial distribution of change in mussel population and noticed a general decrease NW of the line Lemmer-Trintelhaven, whereas SE of that line large areas occurred with increased stands. If high temperatures would have caused mass mortality, this would have occurred lake-wide, thus also in the SE part of lake IJsselmeer, which was not the case. In conclusion we therefore state that predation caused by scaup was very likely the main reason behind the dramatic fall in mussel stocks in the northern part of Lake IJsselmeer. However, the high summer temperatures may well have caused a lowered body condition of the mussels, which would explain the lower than expected number of bird days in that period compared to the available zebra mussel biovolume in 1999.

Elsewhere we described the combined effect of sedimentation of silt and predation on the mussel stocks in lake Markermeer (Noordhuis et al., 2010).

Although not quantifiable at the level of the lake as yet, it is very likely that effects of low and high temperature as well as silt contribute negatively to the *Dreissena* stocks. Especially in combination with intensified predation (which occurs because of cascading effects outside the water system), large decreases may occur. However, because of the enormous regenerative ability of the species, it is able to withstand large losses.