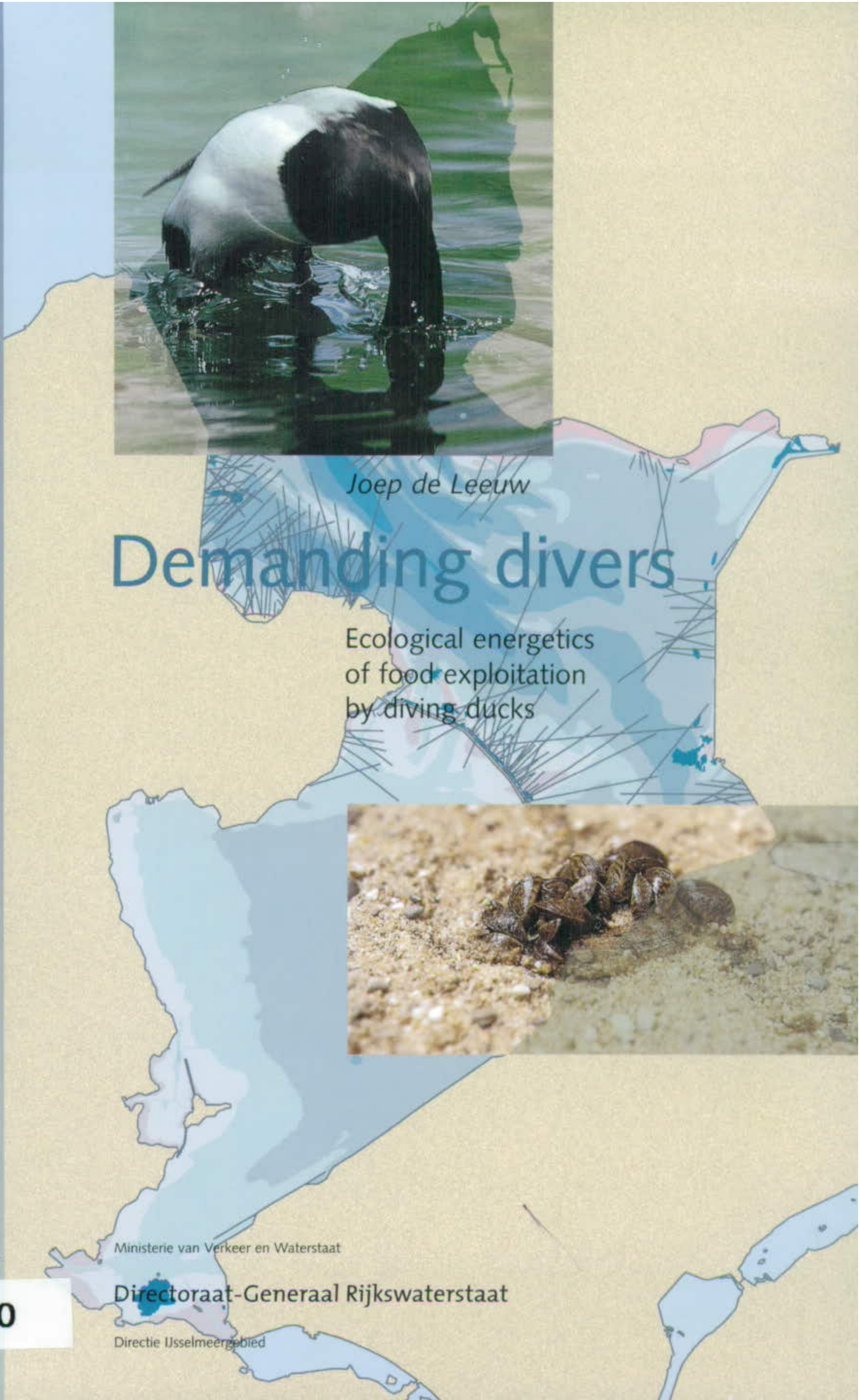
van zee tot land

DEMANDING DIVERS Joep de Leeuw



Joep de Leeuw

Demanding divers

Ecological energetics of food exploitation by diving ducks

Ministerie van Verkeer en Waterstaat

Directoraat-Generaal Rijkswaterstaat

Directie IJsselmeergebied

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Dit rapport vormde tevens het proefschrift waarop de auteur op 2 mei 1997 promoveerde aan de Rijksuniversiteit te Groningen.
Als promotor trad op Prof. Dr. R.H. Drent.

Demanding divers
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UITNODIGING

voor het bijwonen van de verdediging van het proefschrift
en de daarbij behorende stellingen op
vrijdag 2 mei 1997 om 16.15 uur precies
in de aula van het Academie-gebouw, Broerstraat 5 te Groningen.

Na afloop is er een receptie in het Academie-gebouw.

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Stellingen

behorende bij het proefschrift
Demanding divers.
Ecological energetics of food exploitation by diving ducks
van Joep J. de Leeuw

1. Hoewel onderzoek naar het gedrag van individuele dieren aanzienlijke terreinwinst heeft geboekt, staat de vertaling ervan naar de draagkracht van gebieden nog in de kinderschoenen.

   Sutherland 1996. From Individual Behaviour to Population Ecology.

2. Biomechanische modellen voor het schatten van duikkosten, waarbij de *aerobic efficiency* geijkt wordt met respirometrische metingen gedurende de actieve duikperiode*, onderschatten de thermoregulatorische component van het duiken vooral bij extrapolatie naar grotere duikdiepten.

   *) Lovvorn & Jones 1991. Can. J. Zool. 69: 2879.

   Dit proefschrift.

3. Het Stavoren's gezegde "Sneeuw op de luiken doet de duikers duiken" is energetisch verklaarbaar.

4. De verbluffende fenotypische flexibiliteit die dieren vertonen om zich aan te passen aan veranderingen in hun milieu* vereist dat experimenteel onderzoek wordt uitgevoerd over een breed traject van fysiologisch en ecologisch relevante condities. Het vergt grote creativiteit van onderzoekers om op basis van noodgedwongen kleine steekproeven wetenschappelijk gefundeerde uitspraken te doen.

   *) Piersma & Lindström 1997. TREE 12: 134.

5. Wanneer men de verwachte fitness consequenties van gedrag afhankelijk veronderstelt van het totale energiebudget, dient men bij analyses van fourageerbeslissingen ook de kosten in de periode dat niet wordt gefourageerd te betrekken.

   Vrij naar: Houston 1995. Behav. Ecol. 6: 393.

   Hoofdstuk 9.

6. De aanleg van de Houtribdijk heeft er mede toe geleid dat de aantallen Driehoeksmosselen zijn afgenomen in het Markermeer en toegenomen in het IJsselmeer.

7. Ruimtelijke patronen in aquatische ecosystemen worden vaak beschreven aan de hand van aantrekkelijk gekleurde kaartbeelden. Aangezien de onderliggende biologische processen doorgaans samenhangen met de waterdiepte is dit een te oppervlakkige benadering.

8. In de huidige explosie van natuurontwikkelingsplannen schuilt het gevaar van onderschatting van reeds aanwezige natuurwaarden.

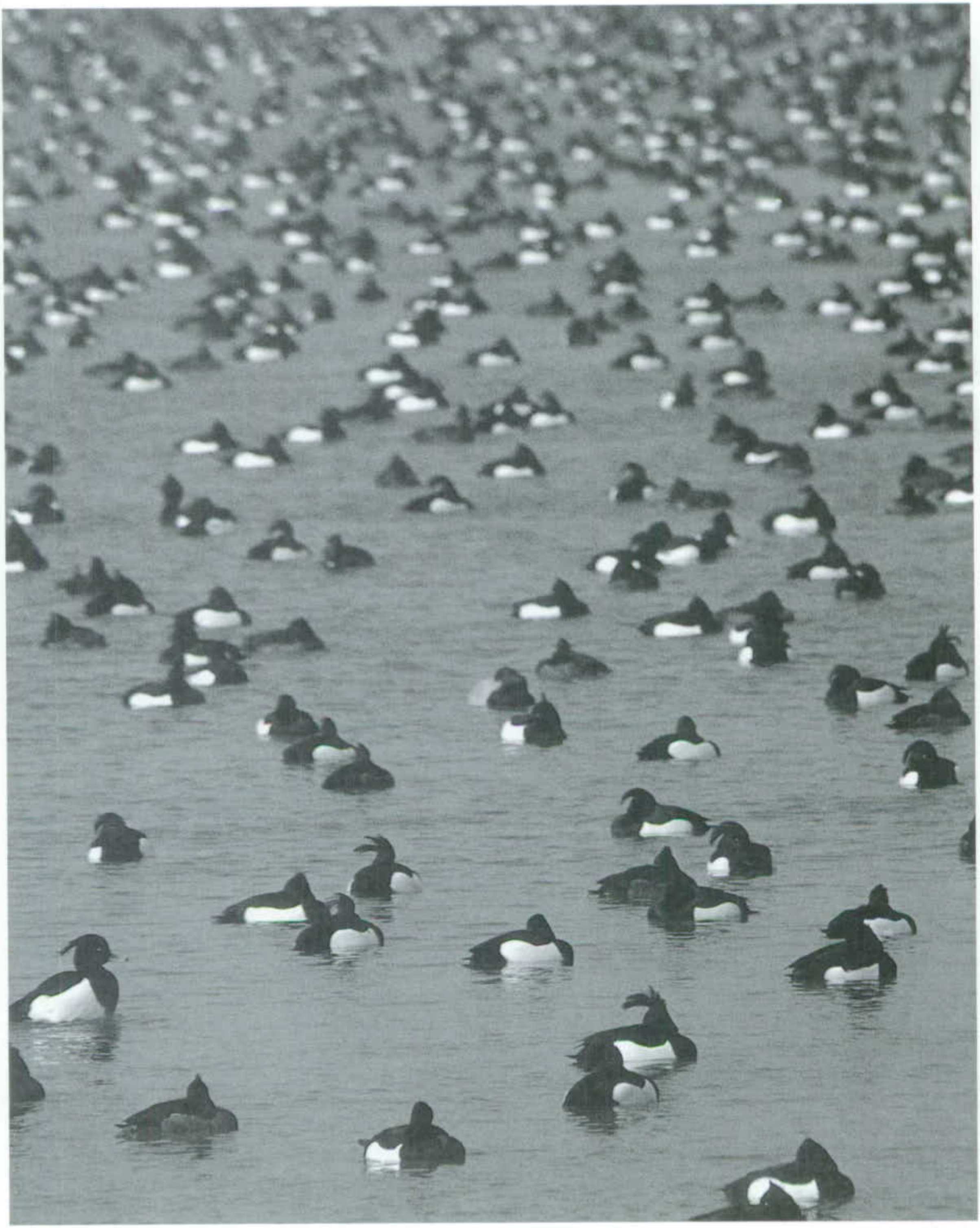
9. Het nut van een maatschappelijke discussie over een tweede grote luchthaven is discutabel zolang in Nederland het massaal sparen van airmiles wordt gestimuleerd.

10. Het imago van de tabaksplant vanuit het gezichtspunt van de volksgezondheid zal aanmerkelijk verbeteren wanneer deze door genetische manipulatie in staat is menselijk haemoglobine te produceren.

    Dieryck *et al.* 1997. Nature 386: 29.

11. Het succes van de als *mountain-bike* uitgeruste *city-bike* is niet begrijpelijk vanuit het oogpunt van energetische efficiëntie. Mogelijk is het "handicap-principe"* meer van toepassing.

    *) Zahavi 1975. J. Theor. Biol. 53: 205.



figuren: Dick Visser en Fiel v.d. Veen (pag. 28, 32, 33, 35)
omslag: Fiel v.d. Veen
foto's: Joep de Leeuw, Mennobart van Eerden (pag. 10, 22)
DTP en drukwerk: Evers Litho & Druk
coördinatie productie: Henk Bos

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Chapter 1

Introduction


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Introduction

Diving ducks and their benthic food resources

Diving ducks of the genus *Aythya* are specialized consumers of benthic food resources in freshwater and marine ecosystems. They are accomplished divers, morphologically and physiologically suited for an aquatic life style. The caudally positioned legs and webs between the toes facilitate propulsion underwater (e.g. Lovvorn & Jones 1991), the sensible receptors in the tip of the bill effectively recognize food items while feeding at the bottom (Kooloos *et al.* 1989), and the structure of feathers assures a waterproof plumage (Rijke 1969), factors enabling these birds to exploit aquatic food sources. Nevertheless, diving is a strenuous activity for these birds. Among North-American species of diving duck, for example, the size of the heart relative to body size was found to increase with water depth, reflecting the heavy oxygen demand of diving (Bethke & Thomas 1988).

Diving ducks are opportunistic feeders capitalizing on a variety of underwater organisms, including plants, molluscs, insects, worms, crustaceans, and fish eggs (e.g. Madsen 1954, Olney 1963, Nilsson 1972, Pedroli 1981, Suter 1982). The Zebra Mussel *Dreissena polymorpha* is the most abundant bivalve in eutrophic stagnant and flowing waters in Europe and comprises the major food source of many diving ducks wintering in these freshwater ecosystems, such as Tufted Duck *Aythya fuligula*, Pochard *A. ferina*, and Scaup *A. marila*, and to a lesser extent Goldeneye *Bucephala clangula* and Coot *Fulica atra*. The establishment and expansion of Zebra Mussels in western Europe this century is well documented (see Schloesser *et al.* 1994 for recent bibliography). Migration routes and wintering distribution of Tufted Duck and Pochard altered markedly in response to the invasion of *Dreissena* in the great lakes of Switzerland and Germany (Géroudet 1966, Leuzinger & Schuster 1970, Jacoby & Leuzinger 1972, Pedroli 1981). Increasing numbers of diving ducks were also recorded in the Great Lakes of North-America after the recent introduction of Zebra Mussels here (e.g. Wormington & Leach 1992, Mitchell & Carlson 1993).

The Lake IJsselmeer area in The Netherlands is nowadays the main freshwater wintering site in western Europe of Tufted Duck and Scaup (Fig. 1), where they feed almost exclusively on Zebra Mussels for six months a year. Maximum numbers in winter amount to 150 000 Tufted Duck (20% of NW-European population) and 200 000 Scaup (50% of NW-European population; M.R. van Eerden, pers. comm.). Zebra Mussels rapidly expanded in the area four years after closing off the lake in 1932 when it was transformed from a marine-brackish estuary of a branch of the River Rhine into a shallow freshwater lake of originally 3650 km^2, and presently 1925 km^2 (Bij de Vaate 1991, Smit *et al.* 1993). Most mussels occur at depths between 2 and 6 m (Bij de Vaate 1991), well within reach of the avian predators. The impact of mussels as filterers of the water column has been stressed by Reeders *et al.* (1989) and Reeders & Bij de Vaate (1990), stating that the entire water body of the lake is filtered once or twice each month and that mussels might be able to affect algal biomass. Extensive predation of mussels by great numbers of diving ducks in winter might, therefore, indirectly influence water quality.

The international importance of the IJsselmeer area as the main wintering site of diving ducks on their West-European flyway on the one hand and the possible impact of predation on the population of Zebra Mussels on the other hand formed the main incentive to study the food exploitation mechanisms of diving ducks and to address the question as to what extent the predation is a sustainable resource use. This knowledge finds a practical application in habitat management considerations.

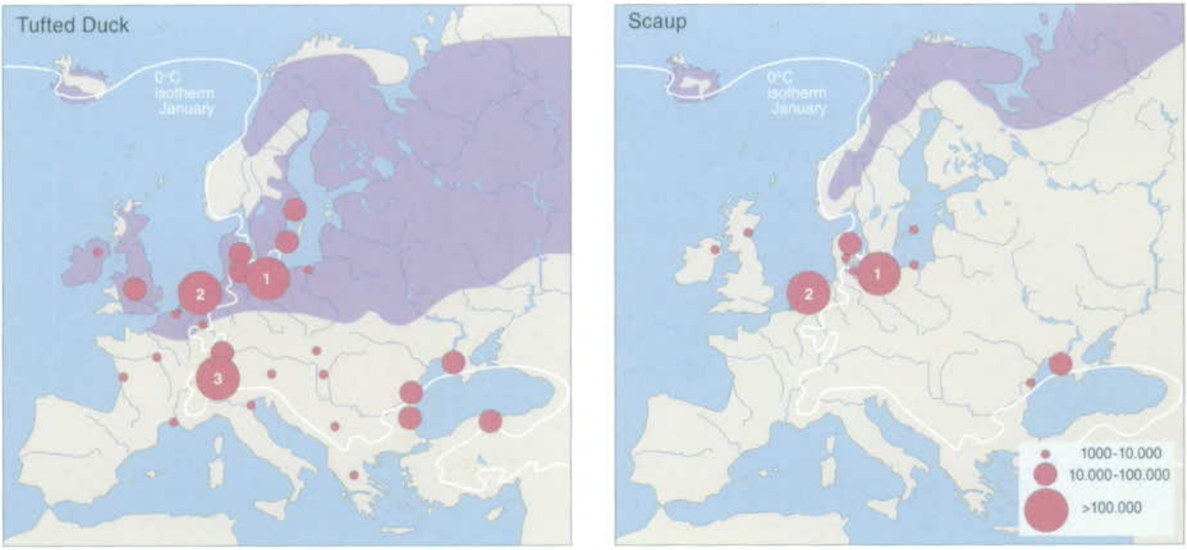


Fig. 1. Important wintering sites and breeding areas of diving ducks in Europe. **A.** Tufted Duck breed in north and eastern Europe and move west and south to wintering habitats in the southern Baltic Sea (1) and large freshwater areas, such as the Lake IJsselmeer area in The Netherlands (2) and subalpine 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 & Simmons 1977; Ridgill & Fox 1990, Rose & Taylor 1993, Durinck *et al.* 1994).

Carrying capacity and foraging energetics

The increasing interest in the effects of habitat loss and habitat changes on population sizes has recently inspired a number of investigations concerning habitat use and the concept of carrying capacity. This concept is based on the commonsense notion that there must be a limit to the number of animals that can be supported by resources in an area. Goss-Custard (1985) defined carrying capacity to be reached when no more birds can establish themselves in the area and the immigration of any further individual will result in the death or emigration of another. Studies on Grey Plovers *Pluvialis squatarola* (Moser 1988) and Brent Geese *Branta bernicla* (Ebbinge 1992), for example, have shown that birds emigrate to other areas when preferred sites became 'saturated' as the population increased. However, such a saturation process does not necessarily imply that an absolute maximum is reached, but could also indicate that utilization of secondary sites had become more profitable than a further increase in the density of birds in the favoured areas. Also, saturation of an area is often difficult to identify from bird numbers, even if the area would be at carrying capacity. In fact, we depend on some sort of 'natural experiment' that could demonstrate an overflow to other areas in response to changes in population size and (or) food supply (Fig. 2). Demographic analyses of the numbers of birds using a certain area are, therefore, often insufficient to test for carrying capacity, as argued by Ens *et al.* (1994) and Goss-Custard *et al.* (1996).

Another, more deterministic approach to evaluate the concept is to examine the underlying biological mechanisms that may delimit utilization of food resources. This in general requires thorough studies on the behavioural ecology of individuals which can be integrated in population models (see Rosenzweig (1991) and Sutherland (1996) for compilations of models aiming to do so). Also, knowledge on the food supply is essential to assess the harvestable fraction which is limited by constraints on food and energy intake of the birds (see below). Empirical studies on sustainable resource use, such as the long-term studies of Zwarts (1996) on waders and the population dynamics of their prey in the Wadden Sea, revealed that the survival of birds like Oystercatchers *Haematopus ostralegus* was related to the food intake rate that individuals could achieve in winter. This field approach on the basis of feeding behaviour of individual birds has also proven to be very fruitful for understanding large-scale food exploitation patterns, e.g. those of herbivorous waterfowl in the Lauwerszee area, The Netherlands (Van Eerden 1984).

A general framework to understand the behaviour of animals is individual-based optimization theory (e.g., Stephens & Krebs 1986, Krebs & Kacelnik 1991). Where animals feed, which prey they take, how long they stay at a particular foraging site, etc., can be seen as 'behavioural decisions' without implying conscious choice of the animal (Krebs & Kacelnik 1991; see Table 1 for examples of decision variables and options of diving ducks analysed in this study). Foraging decisions can be studied from an optimality perspective assuming that an animal chooses the option which will eventually maximize its fitness. The currency that animals should maximize or minimize is for practical reasons usually an indirect, fitness-related measure. The net rate of energy gain (energy intake minus foraging costs) is a currency that animals could maximize if there is a draw-back on foraging time, and this currency has great appeal in the literature of Foraging Theory (see Stephens & Krebs 1986 for review). Other currencies like energy efficiency maximization (the

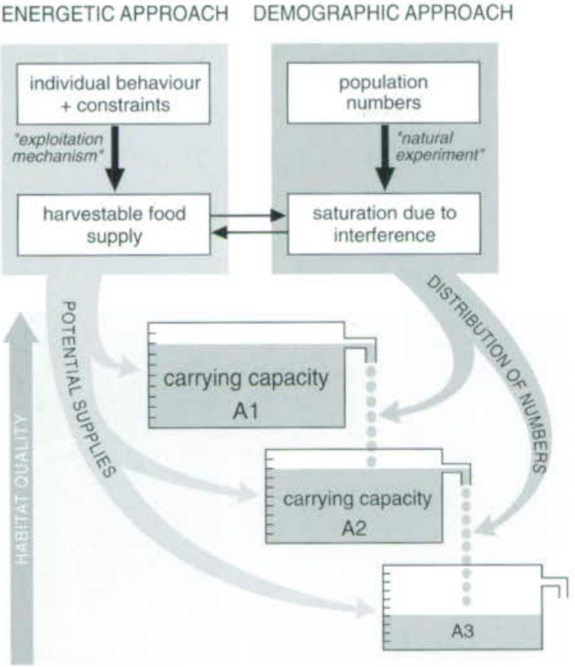


Fig. 2. Two lines of approach to the carrying capacity concept. The demographic approach is based on changes in population numbers and their distribution to identify saturation of areas. The energetic approach aims to estimate the harvestable food supply in an area from energetic limitations to food exploitation by individuals. The combination of both lines of approach is used to estimate the sustainable number of birds in specific areas (A1, A2, A3) and thus their carrying capacities.

Table 1. Overview of behavioural decisions of diving ducks concerning their foraging on Zebra Mussels in the IJsselmeer area during winter. Decisions at the level of wintering habitat down to prey properties are investigated in this study.

Decision level	Decision variables	Examples of options
Flyway	Breeding, moult, migration, wintering	Aquatic ecosystems in subantarctic and temperate zone with seasonally predictable patterns of food availability
Wintering habitat	Open water, roosting and foraging sites, food availability	Baltic Sea, IJsselmeer, Swiss Lakes, rivers and ponds
Feeding area	Water depth	Shallow or deep water
	Prey predictability	Large homogeneous areas, patches
	Prey density	Mussel banks, depletion
Prey	Size	Small or large mussels
	Attainability	Strong byssal attachment (clumps) or unattached mussels
	Quality	Mussel condition (low or high energy content)

rate of energy gain divided by the rate of energy expenditure) may be more appropriate under circumstances of constraints to the daily energy expenses (e.g. Ydenberg *et al.* 1994, Houston 1995). The logic of energy-related currencies is that every biological activity requires transformation of energy. Energetic studies assessing the costs and benefits of behavioural options are nowadays a universal tool for a quantitative understanding in animal ecology (see Ricklefs (1996) for review).

Towards an energetic model of predation by diving ducks

Diving ducks often gather in large concentrations in open habitats so that wintering population numbers can be surveyed with relative ease. A variety of field studies have been carried out to assess the impact of food exploitation on benthic food resources, for example by estimating the expected food consumption of birds counted in a specific area (e.g. Nilsson 1972, Stanczykowska *et al.* 1990, Nehls 1995), and (or) estimating the removal of prey biomass during periods of predation (e.g. Nilsson 1969, 1980, Willi 1970, Pedroli 1981, Suter 1982), sometimes refined by the use of exclosures to discriminate between natural mortality and predation (Smith *et al.* 1986, Hamilton *et al.* 1994, Mitchell *et al.* 1994). These studies are very useful to approximate the extent of predation, but they are usually not very specific with respect to food and habitat characteristics, nor to limitations set by the foraging abilities of the predators. Conclusions concerning carrying capacity and the possible impact of predation on benthic food populations are, therefore, difficult to draw from these studies and even more difficult to predict. To achieve this, we need also to study the foraging behaviour of diving ducks in relation to habitat characteristics (Fig. 2). There is, however, very little information on detailed foraging activities of diving ducks, because they are often nocturnal, difficult to approach, and feeding underwater. Hence, detailed studies on foraging behaviour must include experiments with captive birds.

Aspects of energy gain, such as food and prey size selection, have been studied in relation to prey profitability, which accounts for time and energy costs of searching and handling prey, for example in Canvasbacks *Aythya valisineria* (Ball 1994), Tufted Duck and Pochard (Draulans 1982, 1987), and Eider *Somateria mollissima* (Beauchamp *et al.* 1992, Nehls 1995), while Tome (1988) studied food patch depletion in captive Ruddy Duck *Oxyura jamaicensis*. The results of these studies broadly matched optimal foraging predictions which assumed that these ducks maximize the net rate of energy gain. The next step is the much more complicated translation of foraging behaviour to habitat use. Lovvorn & Gillingham (1996) took a pioneering step with an energetic model to link the foraging energetics of Canvasbacks to the spatial distribution of their prey. Their model, based upon biomechanical estimates of diving costs and measurements of food intake rate, demonstrated the importance of feeding costs and prey profitability for explaining the behaviour of the birds, although quantitative predictions of patch use were only partially supported by field measurements. In this study, I examine food exploitation by diving ducks along the same lines of reasoning, but on the basis of direct measurements of foraging energetics and feeding performance (both under controlled conditions) and at the large scale of a key wintering site.

Outline of the thesis

The main goal of this study is to analyse which factors determine the carrying capacity of a large lake ecosystem and to predict effects of possible habitat changes on diving duck numbers and the sustainability of resource use. Lake IJsselmeer is a relevant study area for both conservational and scientific reasons, as a large proportion of the European wintering population of diving ducks is exploiting a relatively simple single-prey system (Van Eerden & Bij de Vaate 1984). This allows us to quantify the impact and distribution patterns of diving ducks in relation to prey availability on a large scale in a discrete wintering area (see Fig. 1 and Chapter 2).

A behavioural energetic approach will be taken to analyse the mechanisms of food and habitat selection by diving ducks as the foraging decisions are assumed to be motivated by energetic considerations. The energy balance (gains and costs) of diving ducks is related to properties of the prey and the environment

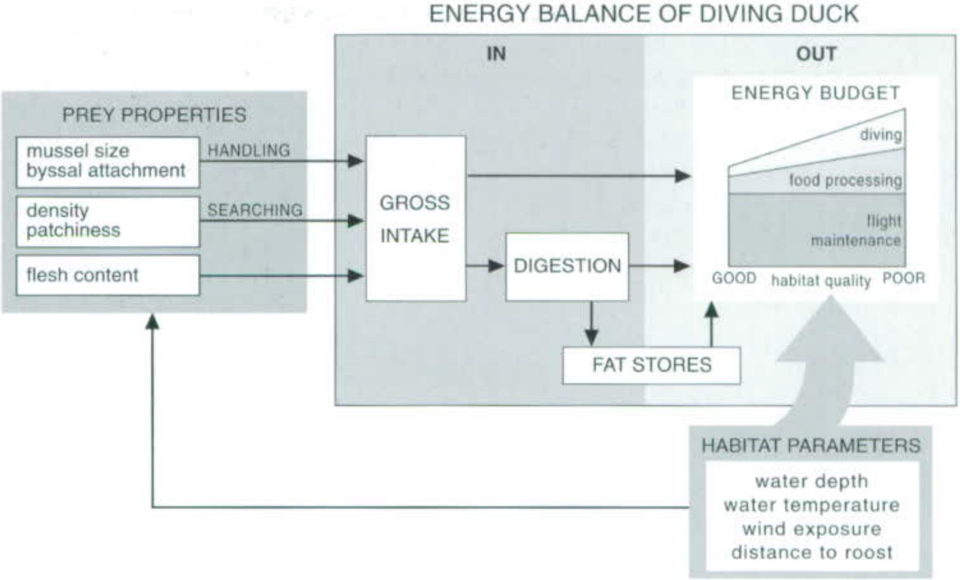


Fig. 3. Energy balance of diving ducks in relation to properties of the wintering habitat. Prey properties of Zebra Mussels primarily determine energy gain. The physical environment and food intake influence the energy expenses, as visualized by the relative foraging costs in poor and good quality habitats. In balancing the budget, diving ducks can temporarily store or utilize fat as an energy source.

(Fig. 3). For example, prey size and its attachment to the substrate, the nutritional value of prey, and prey distribution may determine food and energy gain, while physical properties of the environment, such as water depth, temperature, and wind exposure, may affect the energy expenses. Costs and benefits can be strongly interrelated: food intake, for example, also determines energy expenditure, when costs of obtaining food by diving and processing food in the body are taken into account. The components of the energy budget examined in this study are (1) maintenance costs (basal costs and energy costs to maintain a high body temperature in a cold environment), (2) activity costs (diving for food, flight), and (3) food processing costs, including warming up cold ingested food to body temperature, crushing mussel shells in the muscular gizzard, and digestion of food. The majority of these components have not been quantified earlier or were studied without reference to the field situation faced by wintering diving ducks. In this study, the mechanisms of habitat use will be investigated by closely integrating laboratory experiments and field measurements and observations in the IJsselmeer study area (Fig. 4).

As most of the work is carried out with close reference to the IJsselmeer situation, Chapter 2 starts with a detailed description of the diving ducks and food exploitation patterns observed in the area. With this in mind, I will focus on the necessary details of foraging behaviour and energetics in the following chapters (3-8) to arrive in the final chapter (9) at the IJsselmeer area again with an energetic model of the exploitation of Zebra Mussels by diving ducks.

The question as to whether the IJsselmeer area reaches carrying capacity is firstly approached on the basis of field measurements of the spatial and temporal distribution of diving ducks and Zebra Mussels in the area (Chapter 2). Seasonal and annual shifts in habitat use are derived from monthly aerial surveys of daytime roosts of diving ducks over a twenty-year period, while foraging areas at night are detected from radar observations and from bycatches of ducks in fishing nets. Habitat use will be related to lake-wide surveys of the distribution of Zebra Mussels. Local exploitation patterns in relation to prey properties and physical characteristics of the environment are analysed to refine questions and hypotheses concerning the mechanisms underlying habitat selection and the carrying capacity concept.

The foraging skills and different components of the energy budget of diving ducks were, for practical reasons, studied using captive Tufted Duck and Scaup, the two most important predators of Zebra Mussels in the area. A variety of experiments were conducted under conditions which approached the natural situation as closely as possible in order to facilitate the incorporation of the results into field models.

A first exploration of how diving ducks select and handle prey underwater is presented in Chapter 3, which reports feeding experiments on the profitability of differently sized prey. Handling techniques of Tufted Duck are analysed in relation to the size of mussel shells to explain size selection patterns when these birds have to dive for their food.

In Chapter 4, dive time budgets of Tufted Duck and Pochard are analysed with respect to the basic problem of feeding by diving, namely the limited oxygen supply during breathhold. Hence, little time is available for foraging at the bottom, while much time and energy

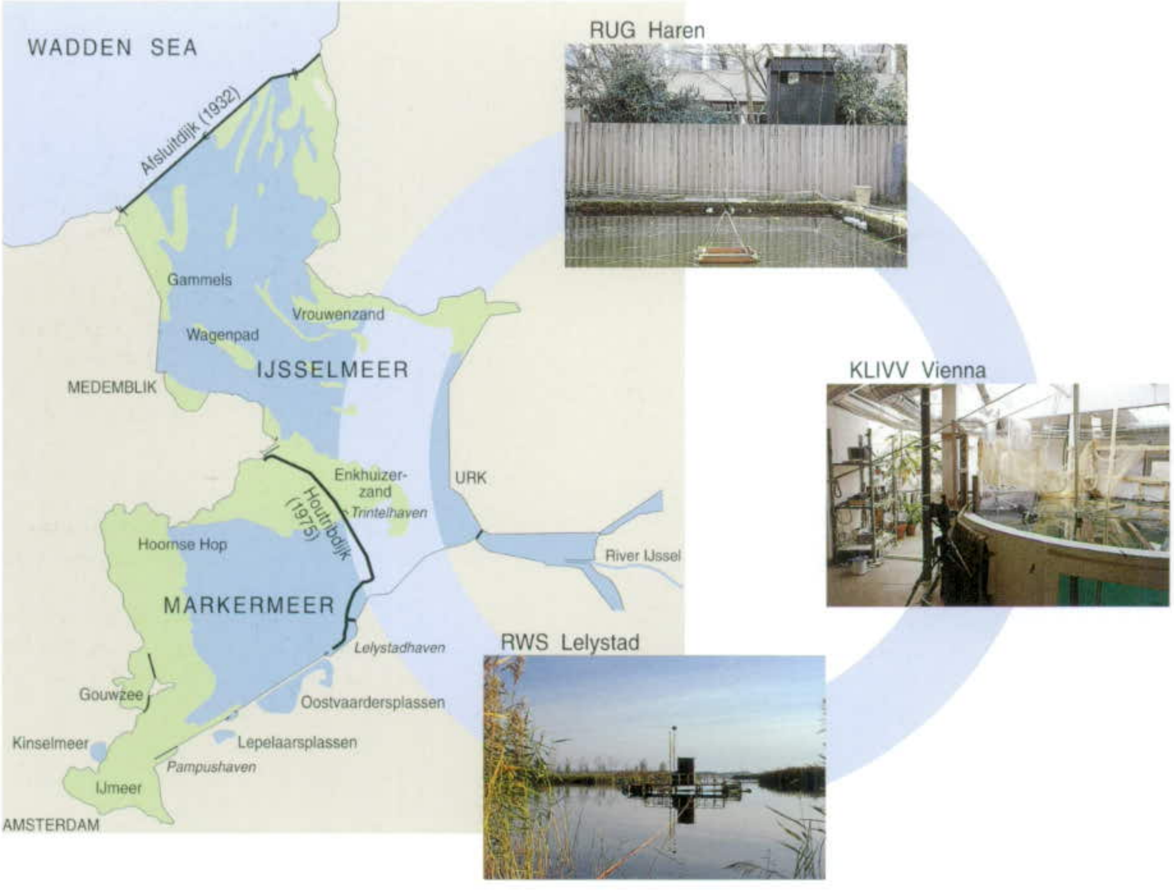


Fig. 4. The IJsselmeer study area and the additional experimental study sites: outdoor diving cages in 'Natuurpark Lelystad' (Rijkswaterstaat Lelystad; Chapters 3, 7, 8), outdoor basins at the Zoological Laboratory (RUG Haren; Chapters 6, 8), and an indoor diving tank at the Konrad Lorenz Institut für Vergleichende Verhaltensforschung (Vienna, Austria; Chapter 4, 5, 6). The IJsselmeer area (1925 km^2) is a shallow, freshwater lake since the closing off by the Afsluitdijk in 1932. The Houtribdijk (1975) subdivides the lake system into the northern Lake IJsselmeer and southern Lake Markermeer.

must be devoted to travel between the food source and the surface to breathe, in particular in deep water. The hypothesis is tested that ducks use both aerobic and anaerobic pathways during diving as suggested from theoretical models predicting particular depth-dependent time budgets.

The energy costs of being fully submerged when diving are addressed in Chapter 5. In Tufted Ducks diving from a respirometry box, energy costs were assessed with particular emphasis on the inclusion of dive-recovery costs which have not been specifically accounted for in previous studies. This is, however, of ecological relevance if we are to construct energy budgets and to evaluate foraging decisions. Variations in diving costs with underwater activity and water temperature are further analysed using existing literature, from which also allometric relationships are derived for diving costs in birds and mammals.

In addition to diving costs, it was necessary to quantify food processing costs to complete energy budgets (Chapter 6). In particular, the ingestion of large amounts of cold Zebra Mussels (upon diving in cold water) is supposed to affect body cooling and recovery times. Heart rate and body temperature transmitters are used to quantify the energy costs associated with cooling in unrestrained feeding Tufted Duck.

The energetic implications of living in cold water are investigated in Chapter 7. Daily energy and time budgets of Tufted Duck feeding on Zebra Mussels in outdoor, semi-natural diving cages are examined in concurrent measurements of mussel consumption, doubly labeled water estimates of energy expenditure, and reconstructed time-energy budgets. The latter are based on energetic measurements derived in the foregoing chapters and automatic recordings of diving activity of the birds.

In Chapter 8, the differential habitat use by Tufted Duck and Scaup in the IJsselmeer area, as described in Chapter 2, is further explored on the basis of variations in food intake rates of both species in relation to prey and habitat properties, such as mussel size, mussel density, and water depth. The foraging skills of Tufted Duck and Scaup are determined in a variety of experiments with ducks diving under semi-natural conditions.

Finally, I integrate the foraging energetics of diving ducks and habitat properties of the IJsselmeer area in an energetic model to predict exploitation patterns and habitat use of Tufted Duck and Scaup in relation to the carrying capacity concept (Chapter 9).

References

Ball, J.P. 1990. Active diet selection or passive reflection of changing food availability: the underwater foraging behaviour of Canvasback Ducks. In: R.N. Hughes (Ed) Behavioural Mechanisms of Food Selection (NATO ASI Series G20): 95-107. Springer, Berlin Heidelberg New York.

Beauchamp, G., Guillemette, M. & Ydenberg, R. 1992. Prey selection while diving by Common Eiders *Somateria mollissima*. Anim. Behav. 44: 417-426.

Bethke, R.W. & Thomas, V.G. 1988. Differences in flight and heart muscle mass among geese, dabbling ducks and diving ducks relative to habitat use. Can. J. Zool. 66: 2024-2028.

Bij de Vaate, A. 1991. Distribution and aspects of population dynamics of the Zebra Mussel *Dreissena polymorpha* (Pallas 1771) in the lake IJsselmeer area (The Netherlands). Oecologia 86: 40-50.

Cramp, S.E. & Simmons, K.E.L. 1977. Handbook of the Birds of Europe, the Middle East and North Africa, The Birds of the Western Palearctic. Oxford University Press, Oxford.

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

Draulans, D. 1987. Do Tufted Duck and Pochard select between differently sized mussels in a similar way? Wildfowl 38: 49-54.

Durinck, J., Skov, H., Jensen, F.P., Pihl, S. 1994. Important marine areas for wintering birds in the Baltic Sea. Ornis Consult Report 1994: 1-110, Copenhagen.

Ebbinge, B.S. 1992. Regulation of numbers of Dark-bellied Brent Geese *Branta benicla bernicla* on spring staging sites. Ardea 80: 203-228.

Ens, B.J., Piersma, T. & Drent, R.H. 1994. The dependence of waders and waterfowl migrating along the East Atlantic Flyway on their coastal food supplies: what is the most profitable research programme? Ophelia Suppl. 6: 127-151.

Géroudet, P. 1966. Premières conséquences ornithologiques de l'introduction de la Moule Zébrée *Dreissena polymorpha* dans le lac Léman. Nos Oiseaux 28: 301-307.

Goss-Custard, J.D. 1985. Foraging behaviour of wading birds and the carrying capacity of estuaries. In: R.M. Sibly & R.H. Smith (Eds) Behavioural Ecology: Ecological Consequences of Adaptive Behaviour, pp. 169-188. Blackwell Scientific Publications, Oxford.

Goss-Custard, J.D., West, A.D., Clarke, R.T., Caldow, R.W.G. & Durell, S.E.A. le V. dit. 1996. The carrying capacity of coastal habitats for Oystercatchers. In: J.D. Goss-Custard

(Ed) The Oystercatcher. From Individuals to Populations, pp. 327-351. Oxford University Press, Oxford.

Hamilton, D.J., Ankney, C.D. & Bailey, R.C. 1994. Predation of Zebra Mussels by diving ducks: an exclosure study. Ecology 75: 521-531.

Houston, A.I. 1995. Energetic constraints and foraging efficiency. Behav. Ecol. 6: 393-396.

Jacoby, H. & Leuzinger, H. 1972. Die Wandermuschel *Dreissena polymorpha* als Nahrung der Wasservögel am Bodensee. Anz. Ornothol. Gesellschaft Bayern 11: 26-35.

Kooloos, J.G.M., A.R. Kraaijeveld, G.E.J. Langenbach & G.A. Zweers 1989. Comparative mechanics of filter feeding in *Anas platyrhynchos, Anas clypeata* and *Aythya fuligula* (*Aves: Anseriformes*). Zoomorphology 108: 269-290.

Krebs, J.R. & Kacelnik, A. 1991. Decision making. In: J.R. Krebs & N.B. Davies (Eds) Behavioural Ecology, an Evolutionary Approach. Blackwell Scientific Publications, London.

Lambeck, R.H.D., Goss-Custard, J.D. & Triplet, P. 1996. Oystercatchers and man in the coastal zone. In J.D. Goss-Custard (Ed) The Oystercatcher. From Individuals to Populations, pp. 289-326. Oxford University Press, Oxford.

Leuzinger, H. & Schuster, S. 1970. Auswirkungen der Massenvermehrung der Wandermuschel *Dreissena polymorpha* auf die Wasservögel des Bodensees. Orn. Beob. 67: 269-274.

Lovvorn, J.R. & Gillingham, M.P. 1996. Food dispersion and foraging energetics: a mechanistic synthesis for field studies of avian benthivores. Ecology 72: 435-451.

Lovvorn, J.R. & Jones, D.R. 1991. Body mass, volume, and buoyancy of some aquatic birds, and their relation to locomotor strategies. Can. J. Zool. 69: 2888-2892.

Madsen, F.J. 1954. On the food habits of diving ducks in Danmark. Dan. Rev. Game Biol. 2: 157-266.

Mitchell, C.A. & Carlson, J. 1993. Lesser Scaup forage on Zebra Mussels at Cook nuclear plant, Michigan. J. Field Ornithol. 64: 219-222.

Mitchell, C.A., Custer, T.W. & Zwank, P., J. 1994. Herbivory on shoalgrass by wintering Redheads in Texas. J. Wildl. Manage. 58: 131-141.

Moser, M.E. 1988. Limits to the number of Grey Plovers *Pluvialis squatarola* wintering on British estuaries: an analysis of long term population trends. J. Applied Ecol. 25: 473-485.

Nehls, G. 1995. Strategien der Ernährung und ihre Bedeutung für Energiehaushalt und Ökologie der Eiderente *Somateria mollissima*. PhD Thesis. Christian-Albrechts Universität, Kiel.

Nilsson, L. 1969. Food consumption of diving ducks wintering at the coast of South Sweden in relation to food resources. Oikos 20: 128-135.

Nilsson, L. 1972. Habitat selection, food choice, and feeding habits of diving ducks in coastal waters of South Sweden during the non-breeding season. Ornis Scand. 3: 55-78.

Nilsson, L. 1980. Wintering diving duck populations and available food resources in the Baltic. Wildfowl 31: 131-143.

Olney, P.J.S. 1963. The food and feeding habits of Tufted Duck *Aythya fuligula*. Ibis 105: 55-62.

Pedroli, J.C. 1981. Les relations entre la Moule Zébrée *Dreissena polymorpha* et les oiseaux aquatiques. PhD Thesis. University of Neuchâtel, Neuchâtel.

Reeders, H.H., Bij de Vaate, A. & Slim, F.J. 1989. The filtration rate of *Dreissena polymorpha* in three Dutch lakes with reference to biological water quality management. Freshwater Biol. 22: 133-141.

Reeders, H.H. & Bij de Vaate, A. 1990. Zebra Mussels *Dreissena polymorpha*: a perspective for water quality management. Hydrobiologia 200: 437-450.

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

Ridgill, S.C. & Fox, A.D. 1990. Cold weather movements of waterfowl in western Europe. IWRB Special Publication No. 13, IWRB, Slimbridge.

Rijke, A.M. 1969. Wettability and phylogenetic development of feather structure in water birds. J. Exp. Biol. 52: 469-479.

Rose, P.M. & Taylor, V. 1993. Western Palearctic and Southwest Asia waterfowl census 1993. IWRB, Slimbridge.

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

Schloesser, D.W., Bij de Vaate, A. & Zimmerman, A. 1994. A bibliography of *Dreissena polymorpha* in European and Russian waters: 1964-1993. J. Shellfish Res. 13: 243-267.

Smit, H., Bij de Vaate, A., Reeders, H.H., Van Nes, E.H. & Noordhuis, R. 1993. Colonization, ecology, and positive aspects of Zebra Mussels *Dreissena polymorpha* in the Netherlands. In: T.F. Nalepa & D.W. Schloesser (Eds) Zebra Mussels. Biology, impact, and control, pp 55-77. Lewis, Boca Raton.

Smith, L.M., Vangilder, L.D., Hoppe, R.T., Morreale, S.J. & Brisbin, I.L. 1986. Effect of diving ducks on benthic food resources during winter in South Carolina, U.S.A. Wildfowl 37: 136-141.

Stanczykowska, A., Zyska, P., Dombrowski, A., Kot, H. & Zyska, E. 1990. The distribution of waterfowl in relation to mollusc populations in the man-made lake Zegrzynskie. Hydrobiol. 191: 233-240.

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

Suter, W. 1982. Vergleichende Nahrungsökologie von überwinternden Tauchenten *Bucephala, Aythya* und Blässhuhn *Fulica atra* am Untersee-Ende/ Hochrhein (Bodensee). Orn. Beob. 79: 225-254.

Sutherland, W.J. 1996. From Indvidual Behaviour to Population Ecology. Oxford University Press, Oxford.

Tome, M.W. 1988. Optimal foraging: food patch depletion by Ruddy Ducks. Oecologia 76: 27-36.

Van Eerden, M.R. 1984. Waterfowl movements in relation to food stocks. In: P.R. Evans *et al.* (Eds) Coastal waders and wildfowl in winter. Cambridge University Press, Cambridge.

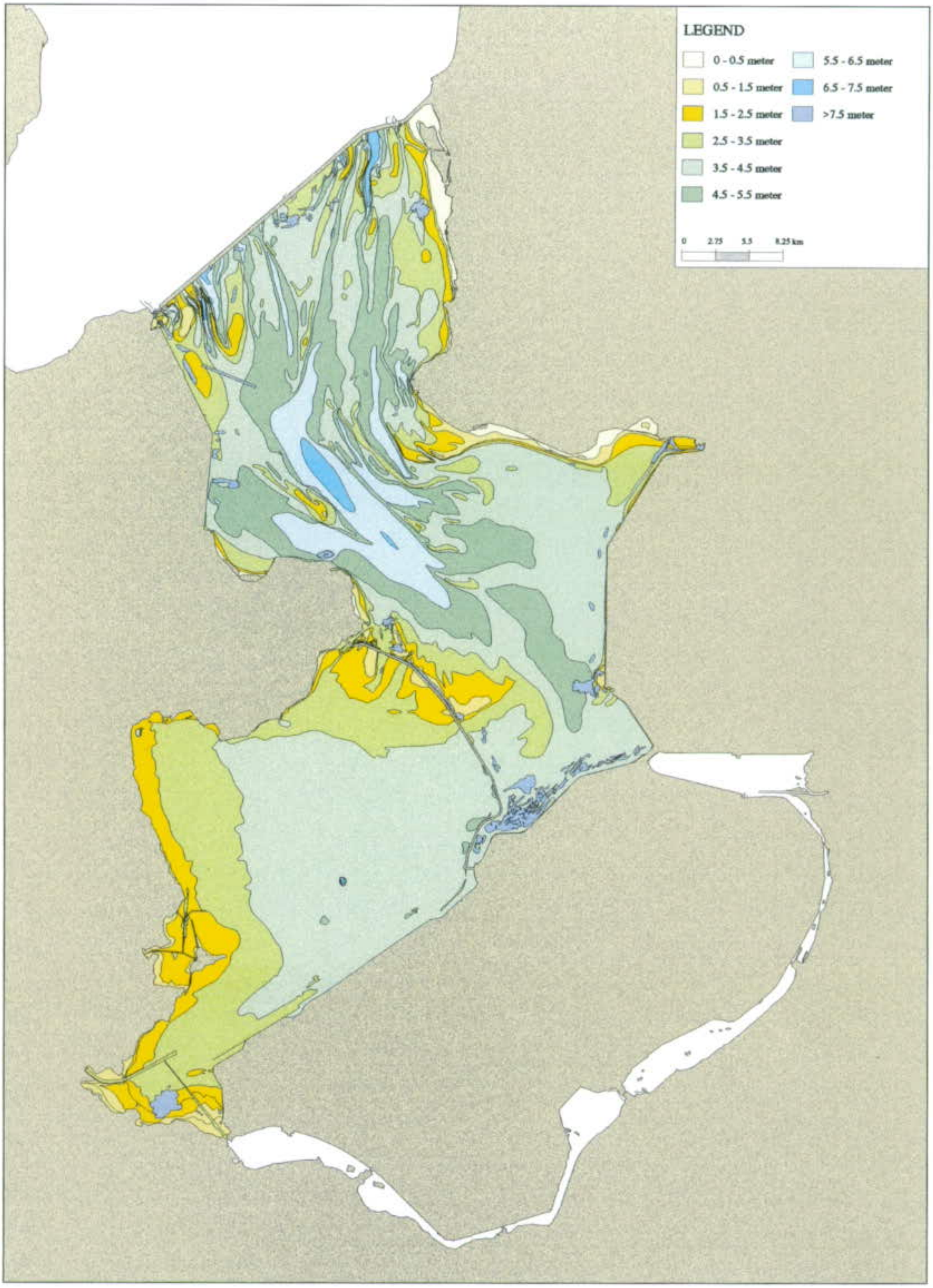
Van Eerden, M.R. & Bij de Vaate, A. 1984. Natuurwaarden van het IJsselmeergebied. Flevobericht 242, Rijksdienst voor de IJsselmeerpolders, Lelystad.

Willi, P. 1970. Zugverhalten, Aktivität, Nahrungserwerb auf dem Klingnauer Stausee häufig auftretender Anatiden, insbesondere von Krickente, Tafelente und Reiherente. Orn. Beob. 67: 183-217.

Wormington, A. & Leach, J.H. 1992. Concentrations of migrant diving ducks at Point Pelee National Park, Ontario, in response to invasion of Zebra Mussels *Dreissena polymorpha*. Can. Field-Naturalist 106: 376-380.

Ydenberg, R.C., Welham, C.V.J., Schmid-Hempel, R., Schmid-Hempel, P. & Beauchamp, G. 1994. Time and energy constraints and the relationships between currencies in foraging theory. Behav. Ecol. 5: 28-34.

Zwarts, L. 1996. Waders and their estuarine food supplies. Van Zee tot Land 60, Rijkswaterstaat Directie IJsselmeergebied, Lelystad.



Water depth zones in the IJsselmeer area.

Chapter 2

A field test of the carrying capacity concept in wintering diving ducks: do high foraging costs delimit exploitation of Zebra Mussels?

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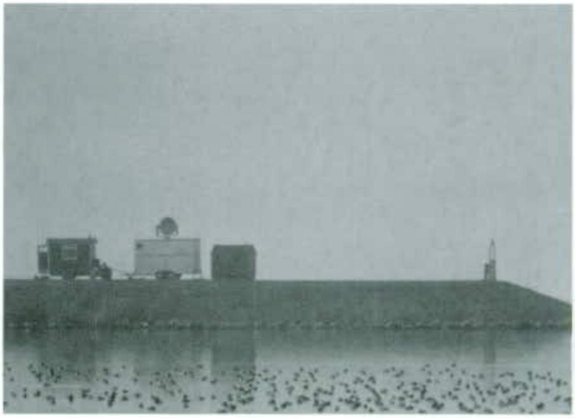


A field test of the carrying capacity concept in wintering diving ducks: do high foraging costs delimit exploitation of Zebra Mussels?

Food exploitation patterns of diving ducks were studied in the field in order to investigate whether a major wintering area, the IJsselmeer (1925 km^2), the Netherlands, is now filled to capacity. During the period 1975-1995, we monitored the habitat use of four species of benthivorous diving duck, the Tufted Duck *Aythya fuligula*, Pochard *A. ferina*, Scaup *A. marila*, and Goldeneye *Bucephala clangula*, and the Coot *Fulica atra* (total winter maxima of more than 300 000 birds). The almost complete dependence on Zebra Mussels *Dreissena polymorpha* was demonstrated by analyses of gullet contents of birds drowned in gill nets when foraging at night. Distribution of day-time roosts and foraging areas at night corresponded in general with the spatial distribution of mussels as revealed from two lake-wide surveys. A strong spatial segregation was found, however, among the main predators, Scaup residing in the northern part (IJsselmeer) and Tufted Duck in the southern part (Markermeer). Mussel biomass was estimated at 615 million kg (fresh mass) in 1981 and 758 million kg in 1992. The total annual predation by ducks amounted to 40-70 million kg in average to poor winter seasons (low number of ducks due to ice cover) and 90-135 million kg in peak years. This corresponds to an overall biomass reduction owing to diving duck predation of 5-22%.

Patch use patterns on a smaller scale were strongly affected by mussel biomass and water depth. Ducks did not equalize differences in patch density over large areas probably due to the flock-feeding habit and imperfect knowledge of patchiness. Giving-up mussel densities at the end of the predation period were inversely related to supposed costs for exploitation (water depth). Nevertheless, field experiments with introduced patches suggested that the birds could assess local patch quality (at the level of 1 m^2) in terms of density and condition of the mussels in relation to the local environment. Locally, diving ducks were able to remove more than 90% of the mussel stock.

Food consumption in the field seemed to follow optimality rules such as to (1) minimize duration of foraging flights, (2) concentrate at the most profitable areas with respect to food intake (depending on food density and prey properties) and (3) to minimize diving costs (water depth). During daytime the birds roosted in wind-protected areas which contributed to save maintenance costs. The diving ducks' habitat use and patch exploitation strategies imply that only a fraction of total food supplies can be harvested each year; high costs for exploitation of the prey may limit further use. The observation that the strong increase since 1988 in numbers of Scaup, the dominant species in the guild, was followed by a shift in distribution of Tufted Duck and later on by a decline in their numbers, gives support to the hypothesis that the diving ducks compete for the same, limiting food source.

Introduction

Carrying capacity and food exploitation theory

A great deal of work has been carried out to describe how birds forage, which decisions they take in order to choose their foraging habitat and how food patches are exploited. In contrast to an overwhelming set of hypotheses and theories describing these individual choices from a theoretical (optimality) point of view (Stephens & Krebs 1986, Rosenzweig 1991), relatively few studies have provided experimental evidence for these theories from either laboratory or the field. In a recent review, Maurer (1996) found no more than 14 out of 63 studies (22%) which gave quantitative support to one of the set of optimal foraging models tested, while 30% falsified the predictions. The concepts of foraging theory thus seem far from explaining patterns of how birds distribute themselves over resources available to them and, more specifically, how food exploitation occurs. Nevertheless, models that link the foraging behaviour of birds to the spatial distribution of their prey might be a promising tool to unravel foraging mechanisms, for example to identify the possible constraints on patch use imposed by foraging energetics (Lovvorn & Gillingham 1996).

Despite the uncertainty about the mechanisms underlying food exploitation patterns, the concept of carrying capacity has found much appeal amongst workers concerned with implications of habitat loss for various populations of animals. As defined by Goss Custard & Durell (1990), capacity has been reached when birds emigrate or starve as food density declines to such a level that minimum intake rates are no longer met. One of the premises for studies that aim to test this concept is that food density must be measurable on a scale large enough to identify effects on a significant part of a population of consumers.

We studied food exploitation by migratory diving ducks over an entire winter period and attacked the carrying capacity problem in species characterized by high costs of foraging. Our study site was chosen as to have a scale large enough (1) to attract a considerable number of birds, (2) to analyse within-habitat differences of distribution of both prey and predator, and (3) to assess measurable effects by avian predators which virtually feed on a single prey species. In many situations, diving ducks may choose from several prey species differing in profitability, which may strongly affect the behaviour of the predator (Pehrsson 1984, Guillemette *et al.* 1992).

We tested the following predictions according to foraging theory and in relation to an *a priori* model of carrying capacity:

(A) Diving ducks remove a significant portion of total food stocks available to them, and hence numbers and distribution are related to food abundance.

(B) Food consumption and distribution of predators in the field are governed by optimality rules which predict that behavioural costs and benefits play a decisive role. Costs considered in this study are (1) flight costs between foraging areas and roosting sites, (2) diving costs in relation to water depth, (3) extra maintenance costs at roost sites (thermoregulation and wave-dependent locomotion). Maximizing the foraging benefits predicts concentration of the diving ducks at the most profitable areas with respect to food intake rates (determined by properties of the prey and prey density) and energy costs (dive depth, shelter at roost site).

The study was carried out over the period 1975-1995 in order to analyse the possible development of predatory impact and carrying capacity on the longer term. We used both natural fluctuations in food supply as well as experimentally created patches to determine food exploitation patterns and numerical responses of diving ducks to food availability. Our aim on the longer term is to integrate field data collected on food consumption and harvest rates with specifically designed experiments on foraging behaviour and energetics of diving ducks in a multi-factorial model of distributional ecology.

Foraging costs of aquatic predators

Waterbirds spend most of the winter in water at low temperatures and hence incur high energetic costs for thermoregulation (De Vries & Van Eerden 1995, De Leeuw 1996). Being continuously on the water and also completely submerged when feeding, diving ducks are considered expensive foragers as suggested in many studies. For example, De Leeuw *et al.* (subm.) found by measurements of daily energy expenditure (DEE) and food consumption under semi-natural conditions, that Tufted Ducks *Aythya fuligula* increased DEE by 70% from summer (2.5 times the basal metabolic rate, BMR) to winter (4.2 BMR). This level of energy expenditure is close to the upper ceiling of metabolizable energy which can be achieved according to Kirkwood (1983). In Eider ducks *Somateria mollissima*, Nehls (1995) calculated an increase in DEE from 3 to 4.3 BMR from summer to winter. Wiersma *et al.* (1995) concluded from an extensive study on stomach analyses a similar increase from ca. 3 to 5 BMR from late summer to winter in Great Crested Grebes *Podiceps cristatus*.

The *Aythya-Dreissena* "trait d'union"

At many freshwater lakes and shallow river sections, diving ducks of the genus *Aythya* rely on the Zebra Mussel *Dreissena polymorpha* as their main food source in winter. The establishment and expansion of *Dreissena* in western Europe during this century has been well documented (see Schloesser *et al.* 1994 for recent bibliography). The increase in Europe has had a marked effect on the number of wintering diving ducks (Géroudet 1966, 1978, Leuzinger & Schuster 1970, Pedroli 1977, 1981, Suter & Schifferli 1988). Recently, *Dreissena* has invaded North America and has evoked a quick response to diving ducks in the area of the Great Lakes (see Mitchell & Carlson 1993 for *Aythya affinis*, Nalepa & Schloesser 1993 for documentation of invasion). The recent invasion by the species of North America has caused great concern because of the tremendous success of the colonisation and the unforeseeable impact this will have on the ecology of the waterbodies in question.

Although not the only avian consumers of this prey in Europe, the diving ducks Tufted Duck *Aythya fuligula*, Scaup *A. marila*, and Pochard *A. ferina* form the majority of the predators in most situations, sometimes accompanied by Goldeneye *Bucephala clangula* and Coot *Fulica atra* (Suter 1982b). Consumption 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 the 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).

Several studies have described the impact of wintering diving ducks on their food supply. Predation can be substantial (see discussion) with the highest values of more than 95% of the mussel population consumed in the river Rhine area in Switzerland (Suter 1982a), but winter losses are often considerably lower.

In the IJsselmeer area (192 500 ha), a shallow eutrophic lake system in the Netherlands, Zebra Mussels occur at depths of 1-6 m, all within potential reach of the avian predators (winter maxima over 300 000 birds). Mussel densities in the lake are far beyond those in the nearby rivers and inland lakes. The IJsselmeer area is therefore considered a 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 800-1200 km. Therefore, knowledge on both the distribution of benthic food and its use by diving ducks is considered of major importance, not only to assess carrying capacity of the system, but also as a field test of hypotheses arising from foraging theory and distributional ecology.

Methods

Study area

The study was conducted at the IJsselmeer area, the largest system of freshwater lakes in NW Europe west of the 0 °C isotherm of January. Situated at the lower end of a branch of the river Rhine, the water is eutrophic and watertables are maintained at fixed levels with the aid of sluices in the barrier dam which separates the lakes from the Wadden sea. The lake system is divided since 1975 into two parts: Lake IJsselmeer in the north (1225 km^2) into which flows the river IJssel and Lake Markermeer in the south (700 km^2), which is now isolated from the river. Average depth is 4.5 m for the northern part and 3.2 m for the southern part. Therefore, almost the entire lake bottom is considered of potential importance as foraging ground for benthos-feeding ducks. Ice cover which lasted longer than 20 days occurred only in 30% of the winters (1975-1995), whereas during most winters the lake never completely froze over. This makes the site an attractive and predictable winter haunt for migratory waterbirds (Van Eerden & Bij de Vaate 1984, Van Eerden & Zijlstra 1986).

Distribution of Zebra Mussels

Lake-wide mapping of *Dreissena* was carried out in 1981 and 1992. Mussels were collected from vessels using a van Veen grab (400 cm^2, Bij de Vaate 1991). Sampling stations were chosen in a regular grid over the entire lake in order to assess the large scale heterogeneity in mussel distribution as an estimate of second-order patchiness (see Kotliar & Wiens 1990). For practical reasons a grid of 2 x 2 km was chosen, yielding over 400 sampling stations. At each station 10 samples were taken, describing a circle with a diameter of ca. 100 m. Water depth and bottom characteristics were recorded at each sampling station (see Bij de Vaate 1991 for details). Mussel density was expressed on the basis of fresh weights ($gFW.m^{-2}$), which was in some cases converted to ashfree dry weight (AFDW) using the relationship that on average 1 gFW is equivalent to 0.025 g AFDW. Four levels of habitat scale were distinguished: (1) lake (several hundreds of km2), (2) region (5-25 km^2), (3) site (5-25 ha), and (4) patch (5-25 m^2).

The ship's position could be determined within an accuracy of 5 m using the Trident radio beacon system. This enabled the revisiting of exactly the same areas at the level of patches before and after winter. Structural parameters of the *Dreissena* community recorded were biomass (gFW), growth form (percentage occurrence as clumps, unattached mussels, or mussel bank), and population structure (frequency of mussel sizes, accurate to the nearest mm).

Number and distribution of diving ducks

Waterfowl were counted once per month (1980-1995) from the air using a high-winged Cessna 172 aeroplane flying at 150 m altitude and at a speed of 130-150 $km.h^{-1}$. As the aerial flights revealed that all diving ducks on the lake were present at daytime roosts close to the shore, we also used earlier shore-based counts from the period 1975-1979. Bird numbers were expressed as bird days per winter (October-April). Distribution was recorded using *ca.* 150 distinct count sectors such as stretches of shoreline, harbours and small inland waterbodies. Most diving ducks, except Goldeneye and Coot, were inactive during daytime. Only during periods of ice cover and in late winter or early spring, Tufted Duck and Scaup were observed foraging during daytime, which was recorded separately.

In order to relate the distribution of diving ducks to mussel density, a mussel index figure was calculated for each transect of lake shore. This was based on the weighted average of all stations sampled in the lake, divided by their distance to the transect of shoreline. Monthly bird counts per transect were pooled into two periods each winter (October-December and January-March). We used two ten-year periods of counts, grouped around the two years of integral mapping of *Dreissena*, 1975-1985 (map 1981) and 1986-1995 (map 1992). To account for exposure to wind and waves, each transect was categorised at a 5 point scale from fully exposed to sheltered relative to the prevailing SW wind.

We used radar (AEI 651, 1 cm beam; 9.445 GHz, parabolic antenna in a mobile caravan connected to a 220 V diesel generator) to study the direction and, if possible, the lengths of foraging flights 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 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 echos. Ship-based observations, however, allowed longer flight 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 6954 ducks over the period 1979-90. Information was collected about the place of recovery ($N = 5820$), usually accurate to 1 km. Depth at which the birds were caught was either provided by the fishermen or abstracted from a nautical chart. Fishing intensity was provisionally estimated in a 2 x 2 km grid on a scale from 1 to 5, using information by the fishermen and the number of nets that were put overboard, also taking account of fishing effort without a bycatch of ducks. The information collected during the most intensive years (1979-1981) was extrapolated to the other years when a limited number of fishermen were asked to deliver the collected ducks. This information was used to map the foraging locations of the ducks, corrected for fishing effort (duck numbers divided by fishing intensity).

Dissection of drowned birds took place in the laboratory after thawing of the frozen bodies (-20 °C). Content of the gullet of 6052 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.

Because diving ducks were caught while foraging, we used the proportion of ducks with mussels in the esophagus as a crude index of foraging success.

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, subm.). Food consumption was corrected for body size of wild ducks as obtained from drowned individuals. Here we use daily rations in the field of 3200 gFW for Tufted Duck, 3600 g for Scaup, 3300 g for Pochard and 2900 g for Goldeneye. Coot, being partly herbivore, is provisionally set at 2000 gFW. For this species, counts in October in areas rich in aquatic vegetation (*Potamogeton, Characeae*) were excluded from the analyses, as Coots are entirely dependent upon plant food in this period (M.R. Van Eerden, unpublished).

Predatory impact

Sites were selected for estimating exploitation rates at typical diving duck localities, spaced across the lake system (1984-86 and 1992-95). Each site was 100x250 m and 50 samples (0.04 m^2 each) were taken before and after the main predation period by diving ducks (*i.e.* September-October and March-May). Samples were taken regularly spaced across the station and with exact location recorded by Trident. Samples were sorted for living mussels, which were counted and the combined weight was taken per sampling station (expressed as $gFW.m^{-2}$). Where relevant, the observed predation was analysed with respect to small scale heterogeneity of mussel distribution or first-order patchiness (Kotliar & Wiens 1990), using the exact locations of the grab samples before and after winter. In all cases the average for each site was calculated and compared before and after winter.

Experimentally created patches of 1 m^2 were set out filled with mussels, using steel trays bordered by a 10 cm high edge. Mussels were collected from a shallow area (< 3 m), to ascertain that mussels were in good condition (high flesh content, see below). Mussels were either offered in clumps or as unattached mussels (after manually detaching the mussels from their substrate), depending on the experiment. During descent the trays were covered by a lid which was removed by a scuba diver after the tray was positioned on the lake bottom. These experimental patches were situated within areas naturally occupied by *Dreissena*. Each group of 8-10 patches was accompanied by two exclosures, using the same 1 m^2 tray, but covered with a lid with 1 cm steel mesh wire, to account for natural mortality. Two experiments were carried out. First, patches were set out at depths of 1.5, 2.5. 3.7 and 4.5 m, (8 trays per depth class) and filled with differently sized clumps, (5-10 kg FW). In the second experiment, two times 10 patches were positioned at the same depth (3.4 m) and in the same region (1.5 km apart), but in two contrasting natural mussel densities, in order to study giving-up densities in relation to patch density and environmental quality. The trays were left in the field during the entire winter season (Dec.- Apr.).

Size selection was studied comparing frequency distributions of mussels before and after winter using Jacobs' selectivity index D (see Jacobs 1974):

$D = (r-p)/(r+p-2rp)$, with p the fraction of each length class before winter and r the fraction lost during winter, respectively.

Long-term changes in *Dreissena* were recorded at two sites, taking 10 samples (0.04 m^2 each) per month (1981-1984). We chose two sites adjacent to large day-time roosts of either Tufted Duck or Scaup to detect any similarities in patterns of food abundance and predator density.

Data analyses

Mussels were measured to the nearest mm, but mussels less than 3 mm were discarded from analyses. Biomass was expressed as $gFW.m^{-2}$ unless stated otherwise.

All statistical analyses were made using SPSS (Norusis 1988). Multiple regression and MANOVA models were used to analyse effects of the different parameters measured. To facilitate interpretation, no more than two-way interactions of terms were taken into account and non-significant interactions were deleted by backward exclusion. Where necessary, data were log-transformed to achieve normality. An acceptance level of $P < 0.10$ was used to determine whether mussel biomass had declined over winter or not. In all other cases the level of acceptance was set at 0.05. In order to find the best estimator of mussel biomass per m^2 in mussel areas (see lake-wide surveys), original data were log(n+1) transformed before taking the arithmetic mean. This was necessary because of the strong skewness of the data. Total mussel biomass for the entire lake was calculated on the basis of the arithmetic mean of all (regularly dispersed) samples.

Radar observations on track length and direction of foraging flights, as well as the position of drowned birds were entered in a GIS, using ARCINFO as database. This allowed determination of water depths at the foraging locations observed.

Results

Distribution and patchiness of food

Distribution maps of *Dreissena* over the entire lake in 1981 and 1992 show high spatial variation in mussel biomass (Fig. 1). High mussel densities occurred in the southeastern part of Lake IJsselmeer, at the outflow of the river IJssel (a branch of the river Rhine) 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

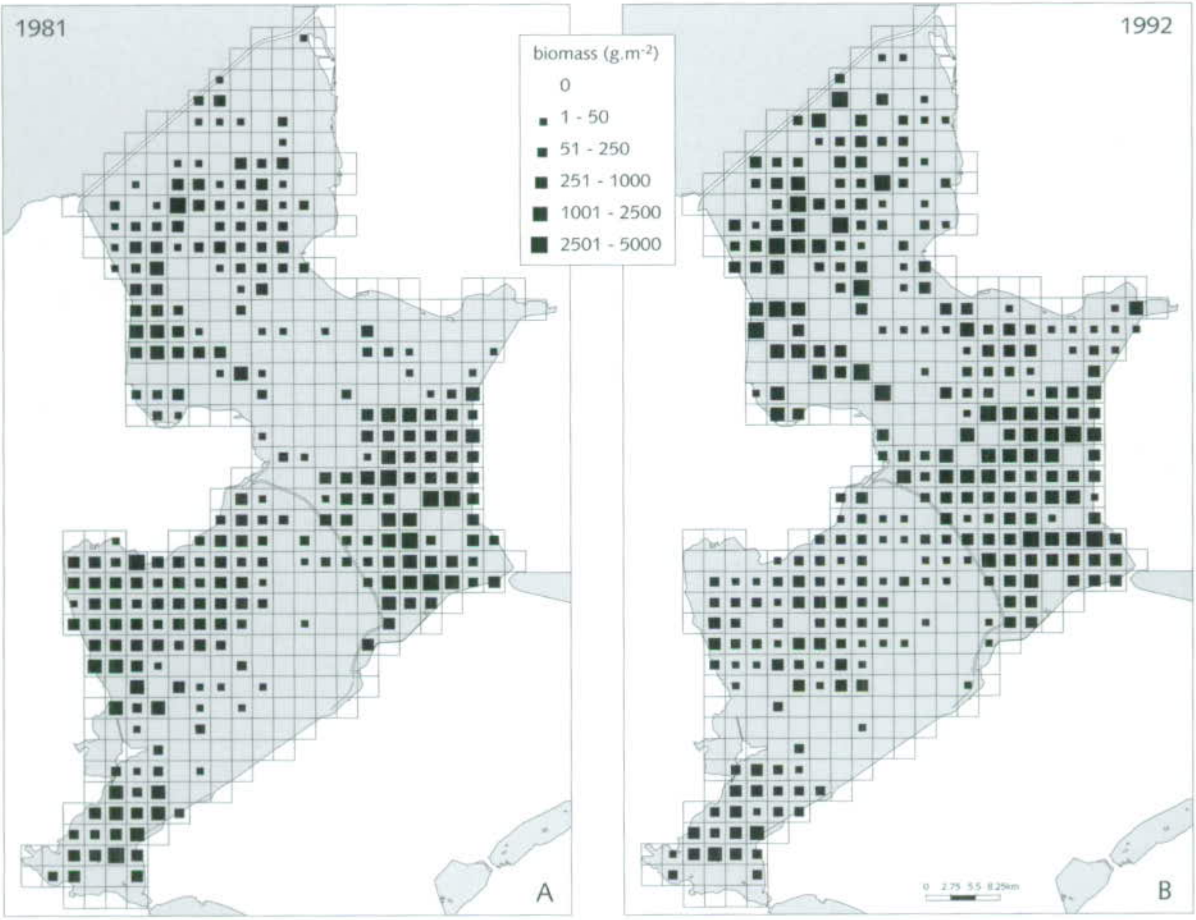


Fig. 1. Distribution of Zebra Mussels *Dreissena polymorpha* in the IJsselmeer area in 1981 and 1992. Biomass is expressed as average gFW.m^{-2} per grid cell (2 x 2 km). Notice the overlap in general pattern of abundance, corresponding with water depth and soil characteristics. In 1992 mussels were more widely distributed but mean densities were lower than in 1981.

Table 1. Distribution and density of mussels in Lake IJsselmeer (IJ) and Lake Markermeer (M), according to lake wide surveys in 1981 and 1992. Mussel density is expressed as percentages of biomass (gFW) per sample (400 cm^2) and as the average density per m^2 where mussels occur (average of log-normal transformed data). Biomass (in 10^6 kgFW) for the entire lake is calculated on the basis of arithmetic means of all samples (*N*).

Year	Lake	*N*	Percentage of biomass ($g.sample^{-1}$)					Mean density	Total biomass
			0	1-20	21-65	66-135	136-350	$g.m^{-2}$	$kg.10^6$
1981	M	1659	63.3	18.4	14.9	2.5	0.9	563.1	218
	IJ	2802	72.1	12.3	11.0	2.6	1.9	678.8	397
1992	M	1480	48.9	43.3	6.9	0.7	0.1	104.6	86
	IJ	2647	49.8	26.9	14.2	5.0	4.2	401.7	672

northwestern coastal regions of Lake IJsselmeer. Part of the areas without mussels coincided with deeper water and a bottom covered with soft, recently deposited silt (Bij de Vaate 1991).

Comparing both lake-wide investigations, spanning an eleven year interval, the general pattern held for both years. However, mussels were more evenly distributed in 1992 in both IJsselmeer and Markermeer, according to the larger fraction of samples with mussels (Table 1). Despite a similar incidence pattern in Lake Markermeer in both years, a much lower density was found in 1992 (86.10^6 kgFW compared to 218.10^6 kgFW), whereas in Lake IJsselmeer total mussel biomass had increased from 397.10^6 to 672.10^6 kgFW (Table 1). Combination of data from the two lakes yielded a total of 615.10^6 versus 758.10^6 kgFW in 1981 and 1992, respectively.

Mussel density increased from 1 to 5 m water depth, falling steeply thereafter (Fig. 2A). More than 60% of total biomass is situated at depths greater than

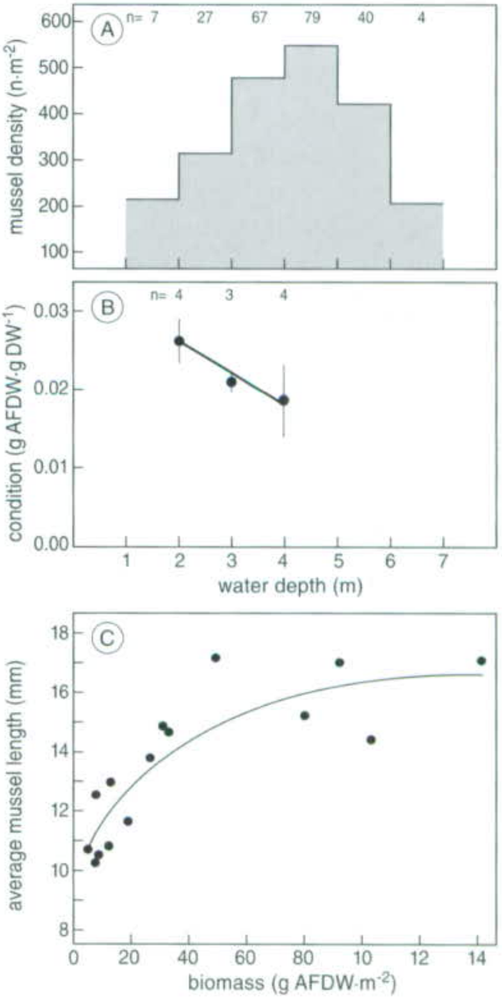


Fig. 2. Characteristics of *Dreissena polymorpha* at Lake IJsselmeer and Markermeer: **A.** Effect of water depth on density of Zebra Mussels (based upon the 1981 survey). **B.** Relationship between condition of mussels (dry flesh mass relative to total mass) and water depth in Lake IJsselmeer (De Leeuw, unpublished). **C.** Average mussel size of sub-populations in Lake IJsselmeer in relation to mussel density. Each data point is based on 50 bottom samples (0.04 m^2 each).

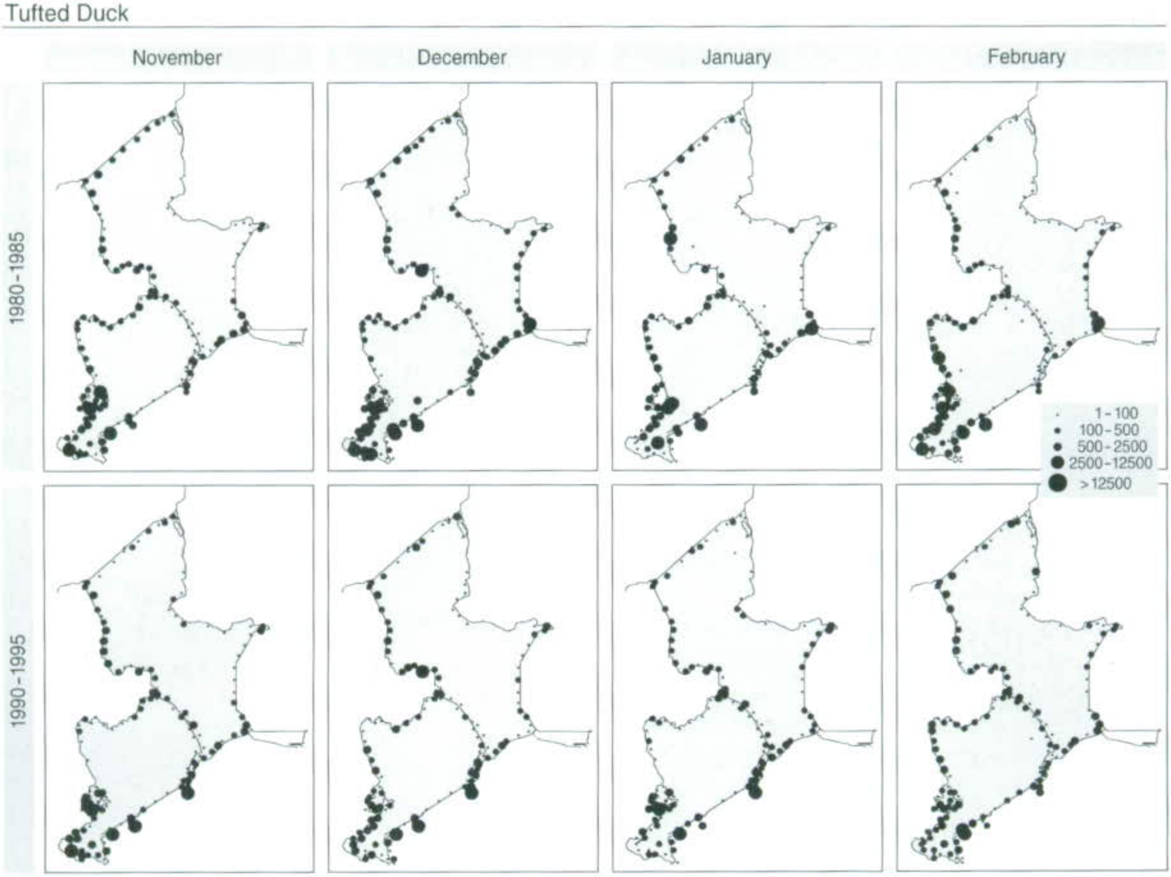
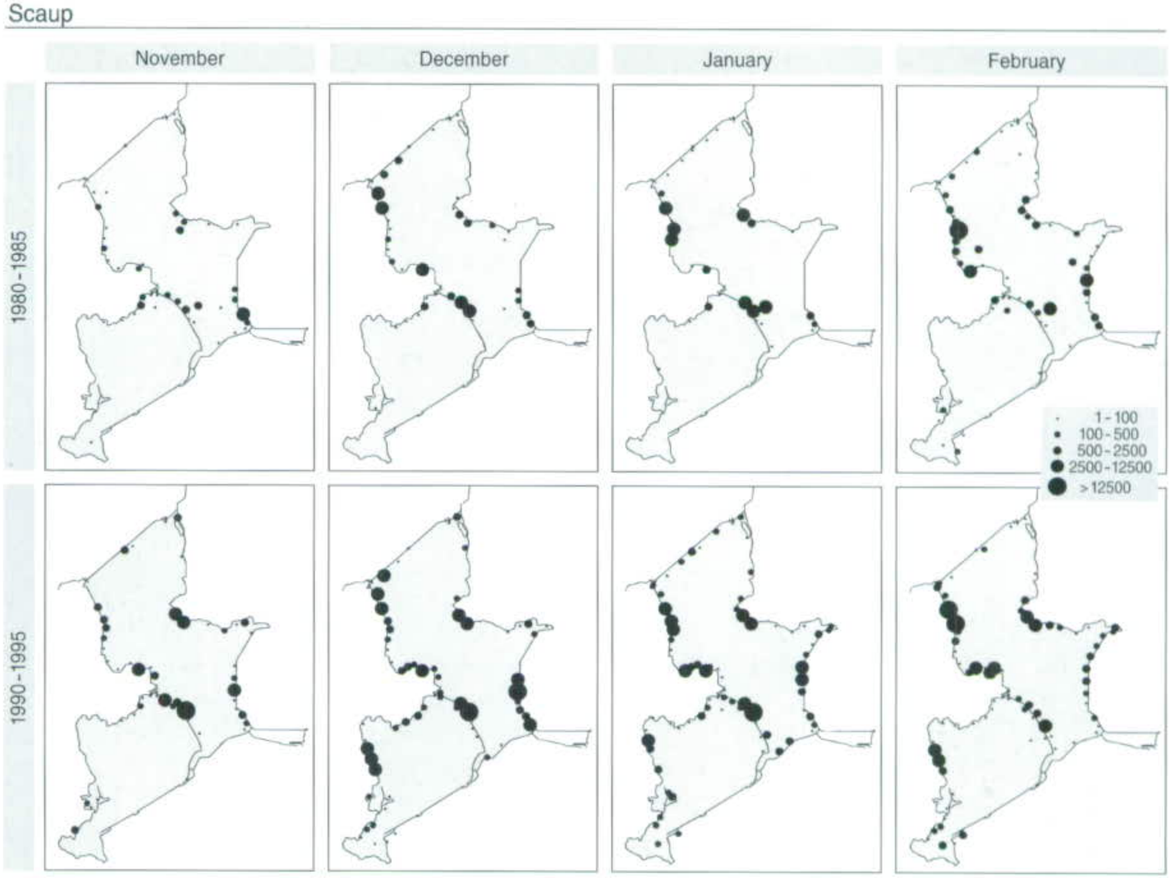


Fig. 3. Spatial distribution and number of Tufted Duck and Scaup at day-time roosts at Lake IJsselmeer and Lake Markermeer, according to monthly aerial counts in winter in two periods. Each trajectory depicts the five-year mean of bird numbers. Notice the range extension of Scaup in the second period as well as the spatial segregation of the two species.

4 m. Condition of mussels, however, decreased with increasing water depth in Lake IJsselmeer (Fig. 2B). On average, mussels were larger at greater depths in particular in areas with high mussel densities (Fig. 2C). At greater depths, 60% of the population consisted of unattached mussels spread over the bottom or densely packed in beds. In shallow water this fraction was only 20%, the rest growing in clumps, often tightly attached to dead marine shells (mainly *Mya arenaria*). As shown by visual observation of the lake bottom, densities may vary considerably over short distances whereas in other cases large homogeneous patterns exist (see below).

Number and distribution of predators

Among the avian benthos feeders, Tufted Duck and Scaup were the most abundant winter visitors. Tufted Duck were present from July until April, with peak numbers 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). Tufted Duck frequented the southern part of the lake system, Scaup were more common in the northern part (Fig. 3). Each species had separate roosting centres where large flocks returned year after year, although a smaller part of the population was reg-



ularly distributed along the shores of the lakes during daytime.

Foraging tracks, as observed by radar and extended by visual observation, showed that most ducks flew at least several km 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 sunset, 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 (mean of entire winter 4.0 km) than Scaup (5.0 km, $F_{1,1026} = 37.5$, $P < 0.001$). During the second part of the winter longer distances were travelled for both species (3.1 km in November-January and 5.3 km in February-April, $F_{1,661} = 109.1$, $P < 0.001$ in Tufted Duck, 4.3 km and 6.3 km, $F_{1,364} = 47.4$, $P < 0.001$, in Scaup).

The offshore situation of foraging grounds of diving ducks was corroborated by the distribution of drowned birds, caught while foraging at night. As during daytime, and parallel to the radar observations but based on many more days, most drowned Scaup originated from Lake IJsselmeer and most Tufted Duck

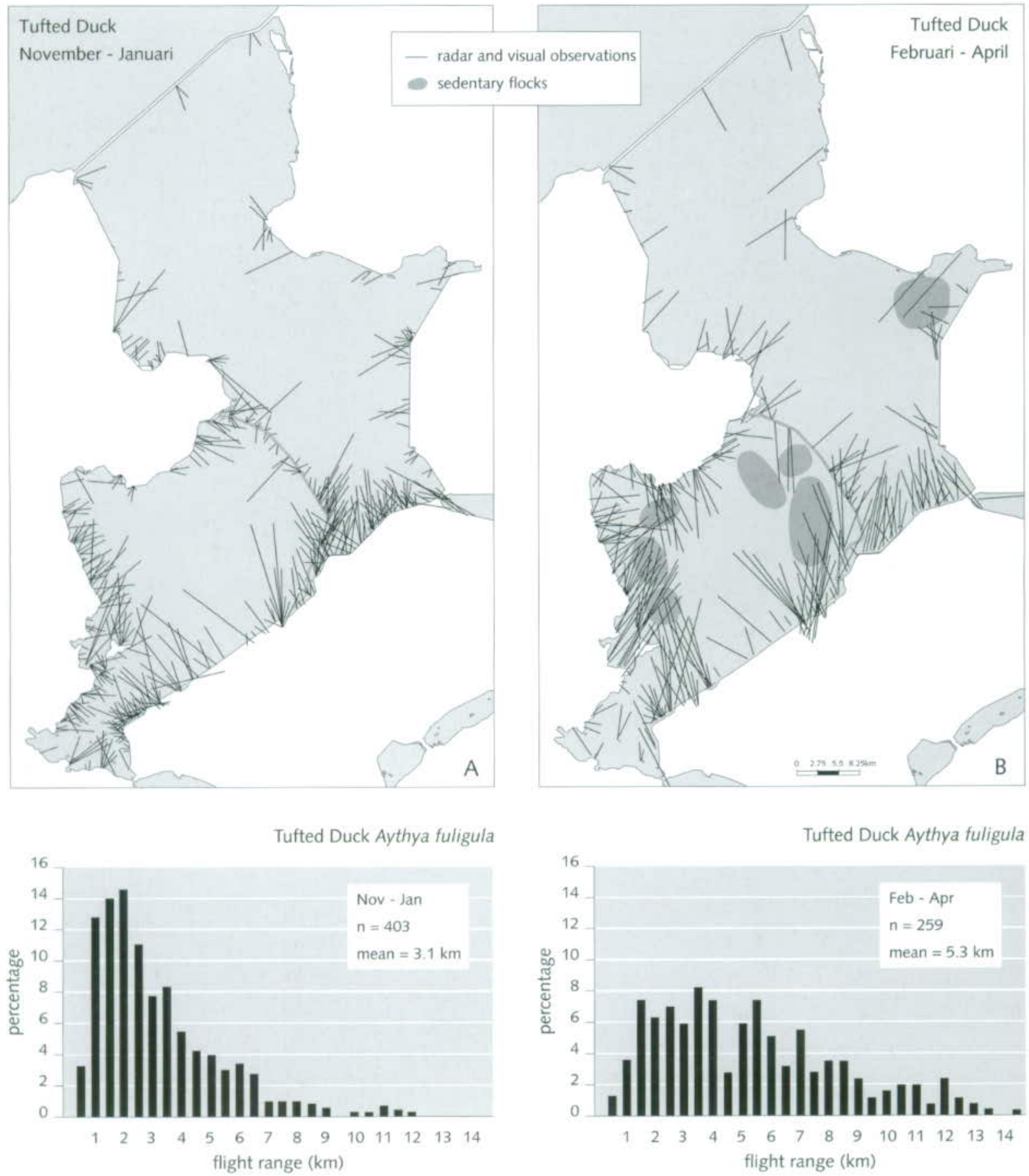
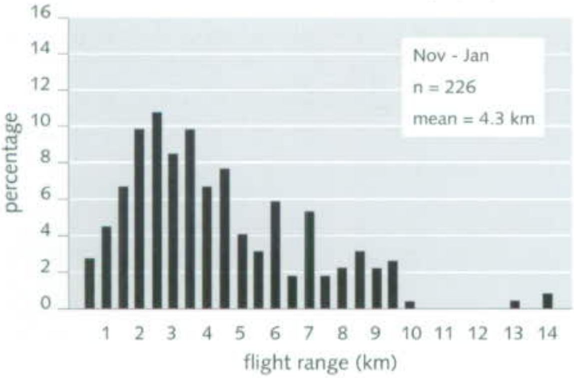


Fig. 4. Foraging flights of Tufted Duck as recorded by radar and visual observations in (**A.**) early and (**B.**) late winter. **C. D.** idem for Scaup. Notice spatial segregation of the two *Aythya* species and the general link between positions of roosts and the use of foraging areas. Late winter 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.

Scaup *Aythya marila*



Scaup *Aythya marila*

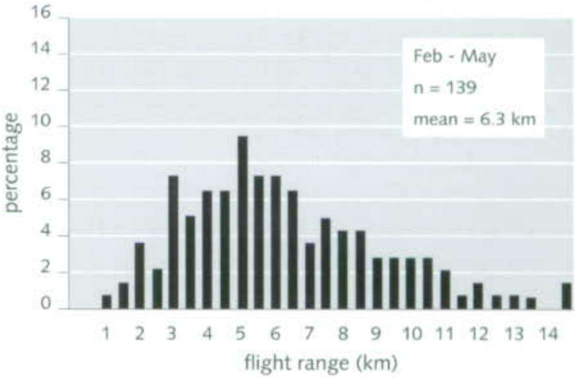


Table 2. MANOVA analysis of variance for number of diving ducks at day-time roosts in relation to the factors 'exposition' (5 classes against the prevailing SW wind), 'time of year' (months between November and February), 'period' (1975-1985 and 1986-1995), and 'lake compartment' (IJsselmeer, Markermeer). A full model including all two-way interactions was run whereafter non-significant interactions were deleted backwards. As covariate musselindex was calculated from the weighted mean of presence of mussels over a maximum of 400 stations (2x2 km grid cells) divided by the distance to each of the 160 potential roosts. Analyses were performed for three species and 4 depth ranges (m) for which the mussel index was calculated.

	Tufted Duck *A. fuligula*				Scaup *A. marila*				Pochard *A. ferina*			
	0-2.5	0-3.5	0-4.5	0-5.5	0-2.5	0-3.5	0-4.5	0-5.5	0-2.5	0-3.5	0-4.5	0-5.5
Factors												
Exposition	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.020	0.003	0.004
Month	0.013	0.013	0.013	0.013	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lake	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.000	0.000
Period	0.247	0.810	0.529	0.196	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.001
Expo*lake	0.000	0.000	0.000	0.000	0.003	N.S.	N.S.	N.S	.N.S	.N.S.	N.S.	N.S.
Expo*period	0.000	0.001	0.007	0.028	0.023	0.025	0.022	0.021	N.S.	N.S.	N.S.	N.S.
Month*lake	N.S.	N.S.	N.S.	N.S.	0.001	0.001	0.001	0.001	N.S.	N.S.	N.S.	N.S.
Lake*period	N.S.	N.S.	N.S.	N.S.	0.000	0.0000	.000	0.000	N.S.	N.S.	N.S.	N.S.
Covariate												
Musselindex	0.000	0.001	0.725	0.090	0.000	0.000	0.000	0.000	0.000	0.000	0.007	0.000
Adjusted R^2	0.34	0.32	0.31	0.32	0.35	0.36	0.33	0.33	0.13	0.13	0.12	0.13

from Lake Markermeer (Fig. 5). Adjusted for fishing intensity, concentrations of ducks occurred at the shallower places (2-3 m depth), which are found in Lake IJsselmeer at Enkhuizerzand, Vrouwenzand and the gradient-rich slopes along the former tidal gullies in the northern part of the lake. In Lake Markermeer the western half attracted more ducks than the eastern, deeper part. There were no ducks reported from the extreme south, because fishing activity is almost absent in this region (but see radar observations). In addition to the direct observations by radar, the cumulative distribution shows the vast area of underwater habitat in use by the different species.

The distribution of the ducks over their daytime roosts in midwinter (peak numbers in November-February) was correlated with the distance and density of *Dreissena* in the lake system, as shown by multivariate analysis (MANOVA, Table 2). Also wind exposure and lake compartment had a significant effect, both by their interaction with mussel stock. When analysed for different depth zones, these relationships persisted up to 3.5 m in Tufted Duck, but could be extended to 4.5 m in Scaup and Pochard (Table 2). The full model accounted for 12-35% (adjusted R^2) of the total variation in actual bird numbers at the roost.

In mild winters, the predation pressure as expressed in bird days of the two species combined, varied between 12-29 x 10^6 bird days in the period 1975-84 and 19-31 x 10^6 for the period 1985-94 (Fig. 6). A marked increase in the number of Scaup appeared in 1988, whereafter numbers stabilized at a level 70% higher than that of the 1970s. Tufted Duck numbers remained remarkably stable for a long period, but during the last years of the period of study numbers tend to decline. Comparing the two lakes, Tufted Duck, Pochard, Goldeneye, and Coot showed an overall decline in Lake IJsselmeer, whereas Scaup increased sharply over the same period. For most species this decline set

Fig. 5. Distribution of locations where diving ducks were caught in gill nets while foraging at night (October-March 1979-1990). The number of duck catches were corrected for fishing intensity (see text). Notice the spatial segregation between the species similar to that recorded by radar (Fig. 4), but also the wide range of use of the lake area, due to the cumulative data collection over many days and several years.

➔


Tufted Duck
October - March
number of birds
corrected for
fishing intensity
. 1
. 2 - 5
▪ 6 - 10
■ > 10
Scaup
October - March
A
B
Pochard
October - March
Goldeneye
October - March
0 2.75 5.5 8.25km
C
D

in between 1975 and 1985. The decline in numbers in Lake IJsselmeer was parallelled by a temporary increase in the same period in Lake Markermeer, followed by a decrease in number during the second half of the 1980s, except for Coot which shows strong fluctuations.

Ice cover led to a significant reduction of bird abundance (Linear regression of number of days with ice cover and total number of bird days (x 10^6) for Tufted Duck: $R^2 = 0.42$, slope -0.078, $P < 0.001$; Scaup: $R^2 = 0.24$, slope -0.097, $P = 0.024$).

Diet, food intake and foraging effort in winter

Based on gullet analyses of drowned ducks, winter diet consisted for more than 90% of *Dreissena* (Table 3). All species, except Scaup, took other benthic prey as well (> 5% based on number of prey items). The other prey consisted of freshwater species of molluscs (Gas-

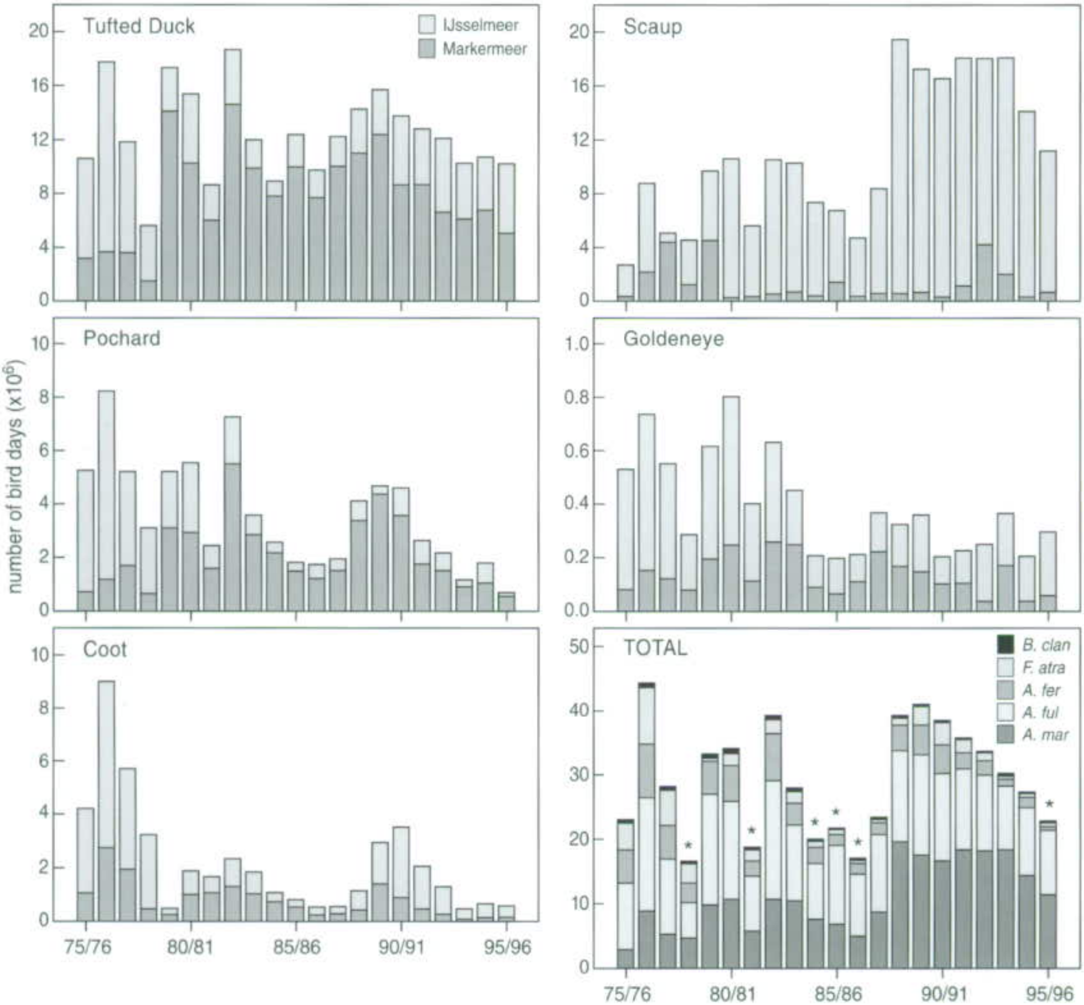


Fig. 6. Number of bird days per year (October-March), for the five species which consume *Dreissena*, separately for Lake IJsselmeer and Lake Markermeer. Except for Scaup, a general decline is apparent for four species at Lake IJsselmeer (1975-1995), which was, except for Coot, parallelled by a temporary increase at Lake Markermeer. Notice the effect of severe winters indicated by asterisks.

Table 3. Diet of diving ducks in the IJsselmeer area during winter (November-March) separated for different sex and age classes (juv = first winter birds). Listed is percentage occurrence of food items by number, for *Dreissena* also by fresh mass.

	Pochard		Tufted Duck				Scaup				Goldeneye			
	A. ferina		*A. fuligula*				*A. marila*				*B. clangula*			
	M	F	M	M	F	F	M	M	F	F	M	M	F	F
	ad	ad	ad	juv	ad	juv	ad	juv	ad	juv	ad	juv	ad	juv
N	67	23	340	69	147	76	684	88	517	105	112	28	123	48
Percentage by mass														
Dreissena	87.5	94.5	93.7	98.2	95.0	97.8	99.9	99.9	99.9	99.7	99.9	99.9	97.0	80.2
Percentage by number														
Dreissena	19.9	65.7	31.9	67.7	40.7	62.8	98.5	99.5	97.4	94.6	97.3	98.0	76.4	89.4
Potamopyrgus	1.8	0.2	19.4	16.0	16.0	13.8	0.4		0.2	1.6		1.4	2.25	0.7
Valvata	0.0	0.6	0.6	0.3	0.2	0.5	0.0	0.2					2.7	
Pisidium	39.3	2.1	38.6	13.5	28.2	22.8	1.0	0.3	2.4	3.5	1.5	0.7	18.4	
Ostracoda	27.5	7.5	9.3	2.5	14.5						1.2			0.2
Chironomidae	11.6	23.9	0.1		0.2									0.8
Tubificidae														0.8
Gammarus			0.0		0.2	0.1			0.0	0.3			0.2	8.2

Table 4. Apparent foraging success of diving ducks, as determined from the proportion of esophagi containing Zebra Mussels. Diving ducks drowned in gill nets, and were caught at night at different depths while foraging. Sample sizes are given in brackets.

	Pochard *A. ferina*	Tufted Duck *A. fuligula*	Scaup *A. marila*	Goldeneye *B. clangula*
Markermeer	50.0 (26)	52.3 (568)	71.0 (639)	45.5 (209)
2-3 m	54.5 (11)	61.4 (83)	64.8 (54)	47.3 (146)
3-4 m	50.0 (6)	54.9 (244)	72.4 (377)	50.0 (42)
4-5 m	50.0 (8)	46.7 (240)	70.9 (206)	25.0 (20)
IJsselmeer	38.2 (131)	50.0 (390)	63.2 (1487)	38.7 (532)
2-3 m	27.3 (44)	49.1 (55)	53.1 (113)	34.2 (149)
3-4 m	40.0 (55)	53.7 (162)	64.4 (596)	45.0 (220)
4-5 m	64.7 (17)	52.7 (131)	64.8 (526)	36.7 (128)
5-6 m	20.0 (5)	25.0 (12)	64.9 (208)	25.0 (8)
>6 m	44.4 (9)	36.4 (22)	30.8 (13)	33.3 (21)

tropoda, Bivalvia), worms (Tubificidae), insects (Chironomidae) and crustaceans (Gammaridae). Occasionally, seeds of macrophytes such as *Scirpus maritimus* were found. Exceptional was the finding of one Goldeneye which had eaten ten small fish (0+ Smelt *Osmerus eperlanus*, 4.7-5.2 cm).

Apparent foraging success (AFS), as defined by the proportion of birds with an esophagus containing one or more mussels, increased from Pochard (40.1%, *N* = 157) and Goldeneye (40.6%, *N* = 741), *via* Tufted Duck (51.4%, *N* = 958) to Scaup (65.6%, *N* = 2126). For all species, AFS was higher in Lake Markermeer than in Lake IJsselmeer. AFS increased with water depth up to *ca.* 4 m in Lake IJsselmeer, whereafter it declined again (Table 4). This pattern reflects the increasing mussel density, and thus the probability of encountering mussels, with depth (Fig. 2A). If AFS is compared for the different months of the winter season, Tufted Duck showed a gradual decline as winter proceeds, whereas the opposite is true for Scaup (Table 5). Despite the lower number of birds that were caught, the data for Goldeneye also suggest higher success rates as winter proceeds.

Diving depth, as determined from radar observations of foraging locations, varied between the species in the course of the season and for different parts of the lake system (Table 6). Combining all data into a multiple regression model, significant effects existed for species (Tufted Duck diving less deep than Scaup, Student's $t = 4.24$, $P = 0.0001$), lake compartment (in Lake Markermeer more shallow dives than in Lake IJsselmeer, deepest dives in the northern part (NY), $t = 10.87$, $P < 0.00005$) 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 *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 (Tufted Duck 4.0 m, Scaup 4.0 m, $F_{1,102} = 0.0$, $P = 0.917$).

Size dependent mortality

All four species ate mussels covering the entire size

Table 5. Apparent foraging success of diving ducks in relation to period of year and dive depth between 3 and 6 m (see Table 4). Data refer to Lake IJsselmeer.

Month	Pochard *A. ferina*	Tufted Duck *A. fuligula*	Scaup *A. marila*	Goldeneye *B. clangula*
November	39.4 (33)	56.8 (74)	48.3 (89)	25.0 (32)
December	54.2 (24)	51.5 (99)	56.3 (135)	37.7 (130)
January	46.2 (26)	53.5 (129)	68.2 (550)	43.5 (168)
February	4.0 (25)	47.6 (21)	61.3 (217)	43.7 (135)
March	75.0 (8)	44.0 (25)	64.8 (244)	25.0 (32)

Table 6. Night-time foraging depths of Tufted Duck and Scaup in three lake compartments in early and late winter (M = Markermeer, SY = Southern IJsselmeer, NY = Northern IJsselmeer). Depths were determined from radar tracks of foraging flights with the aid of GIS.

Depth (m)	Scaup *A. marila*					Tufted Duck *A. fuligula*			
	Nov-Jan			Feb-Apr		Nov-Jan		Feb-Apr	
	M	SY	NY	SY	NY	M	SY	M	SY
1	1	1	1	3	5				
2	2	13	10	2	8	63	8	17	4
3	1	11	33	5	6	105	28	82	15
4		13	49	16	14	52	91	40	40
5		5	21	8	19	1	11	1	9
6			2		3				4
7					1				1
Mean	2.0	3.2	3.7	4.0	4.1	2.9	3.7	3.2	4.0

ANOVA on differences between periods: Tufted Duck, Markermeer $F_{1,362} = 8.52$, $P = 0.0039$, IJsselmeer South $F_{1,214} = 5.45$, $P = 0.0195$; Scaup IJsselmeer South $F_{1,73} = 11.8$, $P = 0.0011$, IJsselmeer North $F_{1,165} = 4.81$, $P = 0.0281$

range (3-27 mm) and, as discussed elsewhere, local differences in mussel population are reflected in the birds' diet (De Leeuw & Van Eerden 1995). Based on 32 samples of length frequency distributions before and after the winter period, Fig. 7A-D shows relative losses for each length class, combined for depth categories. Expressed as the dimensionless Jacobs' D (Jacobs 1974), a strong loss of juveniles under 5 mm was apparent at all sites but the deepest. Except for the shallowest sites, mortality increased with mussel size over the range 5-25 mm, with marked losses at sizes larger than 20 mm. This increase tends to be stronger at greater water depths. However, at the most shallow sites (depth 1.6-2.5 m), a reversed trend is visible with most mortality occurring in mussels with shell lengths

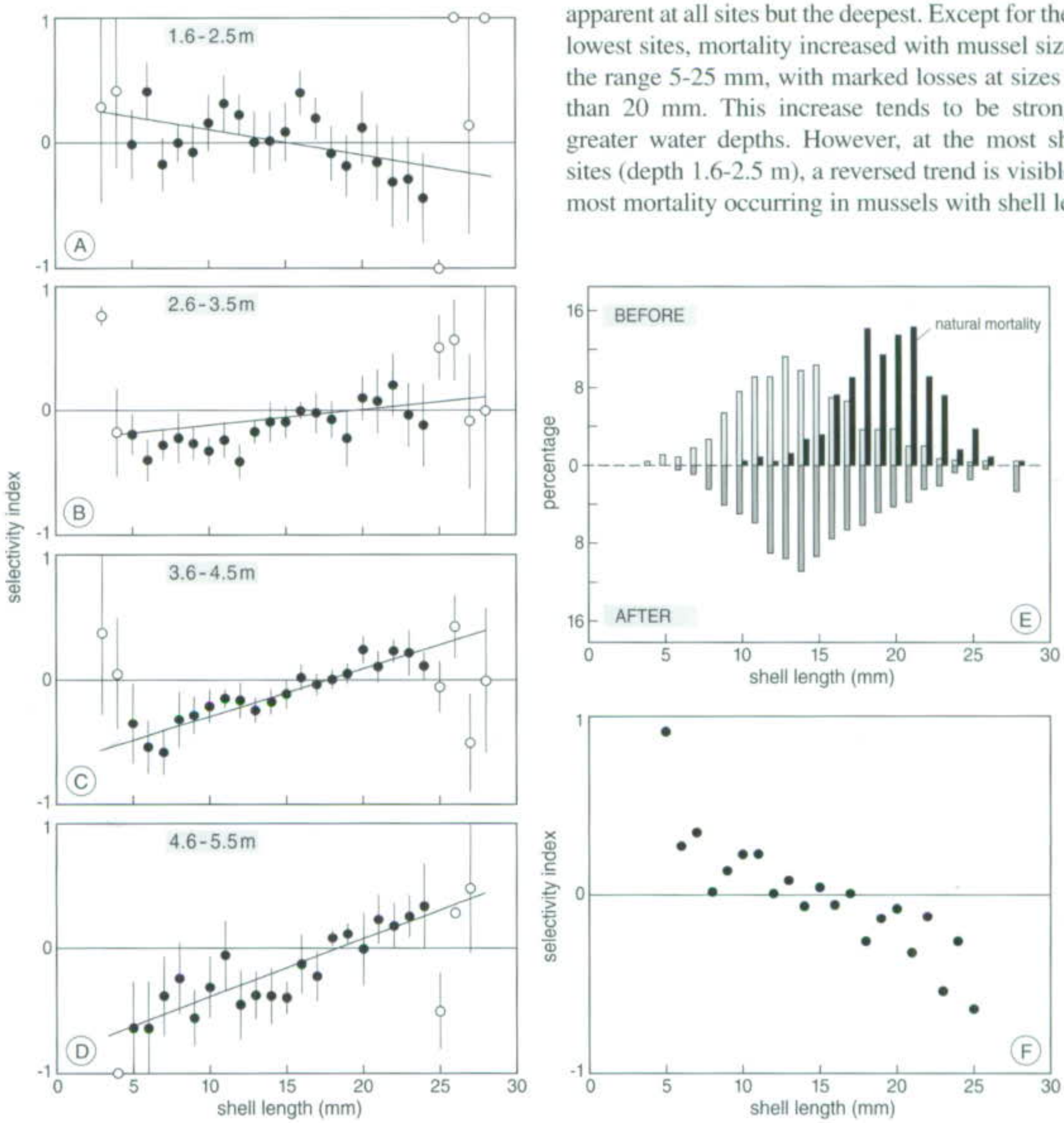


Fig. 7. A.-D. Relative disappearance of mussel sizes over winter, as measured in the field at 32 sites during the winters 1984/85, 1985/86 and 1992/93. The frequency distributions are based on mass per length class and a selectivity index (Jacobs 1974) was calculated (bars give standard errors). The data have been arranged according to water depth. Except for the shallowest areas, all populations incur the greatest losses in mussels larger than 20 mm. **E.** Frequency distribution of mussel size before and after winter from predation trays offered at a depth of 3.4 m, and natural mortality by length class as recorded in two exclosures. **F.** Selectivity by diving ducks feeding on mussels at 3.4 m water depth, after correction for natural losses.

Table 7. Distribution of total biomass (% gFW) over unattached mussels (Sol.) and clumps of different size categories (gFW) before and after predation by diving ducks in winter 1984/85. Chi^2 tests used for comparison of distributions within each site (** = $P < 0.005$, *** = $P < 0.0005$).

Site	Depth (m)	Before				After				
		Sol.	< 2 g	2-5 g	> 5 g	Sol.	< 2 g	2-5 g	> 5 g	P
Markermeer										
B	3.1	71.4	2.4	13.4	12.9	37.6	1.9	11.0	49.5	***
C	3.7	52.8	3.6	18.6	25.0	45.1	1.5	16.7	36.7	***
IJsselmeer										
E	2.0	19.5	0.6	11.7	68.2	13.4	0.2	1.5	85.0	***
F	3.5	45.7	10.5	17.7	26.2	9.5	2.2	16.0	72.3	***
G	4.2	68.8	9.5	16.0	5.6	43.6	7.6	19.9	28.9	***
D	4.9	39.1	0.8	14.2	45.8	35.3	2.4	16.0	46.3	**

less than 20 mm. A multiple regression of Jacobs' D for the range 5-25 mm showed significant effects for both shell length ($P < 0.001$) and water depth ($P = 0.019$), the latter effect being due to the contrasting data of depth class < 2.5 m. Excluding these data, no effect for depth could be demonstrated in the other three classes.

To account for mortality other than predation by diving ducks, data from exclosures were used, in combination with records of mussel predation from experimental trays positioned on the lake bottom (depth 3.4 m). In this experiment an age dependent mortality was found, with higher losses in the older age classes. In terms of fresh biomass, this mortality amounted to 16% on the basis of fresh mass (Fig. 7E). After correction of the frequency distribution for this death cause, the effect of duck predation alone could be estimated. Fig. 7F shows that diving ducks took mussels less than 15 mm relatively more often than could be expected on the basis of their presence.

In conclusion, diving ducks tend to take the smaller mussels from the population on offer, especially at depths down to 2.5 m. Moreover, age dependent mortality occurs, which is mostly confined to the larger size classes of *Dreissena*.

Clumps and unattached mussels

In the winters 1984/85 and 1985/86, clumped and unattached mussels were sampled and weighed separately before and after the predation period. Unattached mussels accounted for 40-70% of total biomass in most sites. In general, unattached mussels declined over winter, whereas the proportion of clumps greater than 5 g increased (Table 7). In sites where a significant reduction in overall biomass was found, this was due to the loss of the fraction unattached mussels ($F_{1,188} = 7.4$, $P = 0.007$) while for the total mass present in clumps no reduction could be demonstrated ($F_{1,188} = 1.1$, $P = 0.289$). Mussels in clumps thus showed a higher survival over winter than did unattached mussels. However, a closer examination of clump biomass (in a separate experiment) revealed also some predation on clumps. In this experiment, a total of 2829 clumps were weighed individually (accurate to 0.1 gFW). In sites with a significant reduction in total biomass, average biomass per clump decreased over winter from 3.12 to 2.45 gFW ($F_{1,2086} = 32.0$, $P < 0.001$). In sites with no overall reduction in mussel biomass, average clump mass was not significantly different before (2.65 g) and after (2.51 g) winter ($F_{1,711} = 0.4$ $P > 0.50$).

When 16 experimentally composed patches (4.5-12.5 kgFW.m^{-2} in trays exposed to predation) were filled with clumps of different weight classes (mean 6.5, 9.2, 13.8, 20.7 gFW), no differences were found with respect to loss rates in relation to either clump size, water depth (1.5-4.5 m) or biomass on offer (multiple regression, adjusted $R^2 = 0.01$, $F = 1.06$, $P = 0.42$). Biomass of *Dreissena* was reduced from several kgs to an average of 1200 gFW.m^{-2}, which

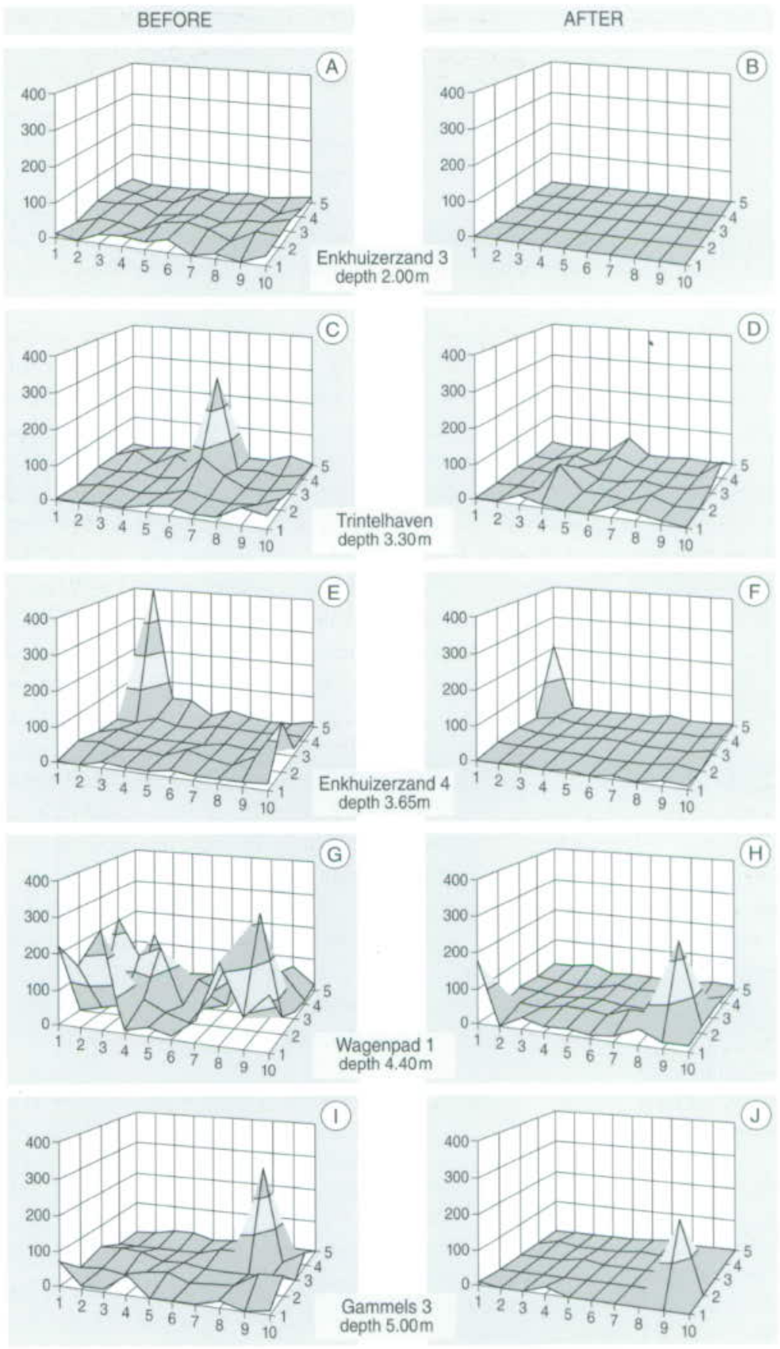


Fig. 8. Patch use by diving ducks, showing first-order exploitation as measured by detailed sampling of a rectangular plot (100x250 m) before and after visitation by diving ducks. Mussels are more abundant at greater depth, but predatory effects predominate at the lower densities in shallow water. Predation did not equalize initial differences in patch density leaving high density patches only partially exploited.

shows that ducks were able to exploit patches containing only mussels in clumps.

From these data we conclude that, in the field, diving ducks rely particularly on unattached mussels but do take mussels from clumps in addition.

Patch use

Fig. 8 illustrates patch use by diving ducks in relation to water depth (increasing biomass) and heterogeneity at the level of several tens of m^2 (first-order patchiness). Diving ducks did not even out first-order patchiness within one season by a complete reduction of peak densities at the different stations. Instead, in most cases where a significant reduction in biomass occurred, originally rich patches remained discernable after predation had taken place. Remarkably, the rather low biomass at the shallowest sites was evenly exploited. Overall, rich patches lost more mussels compared to poorer patches within the same site.

Experimentally created patches (250-4000 g mussels per tray on offer) were set out in either a rich or a poor environment with respect to mussel density. The trays were filled with high quality mussels from the shallow 2.5 m zone (see Fig. 2B), which were manually detached from their substrate and presented in a single layer of mussels. The two sites were in the same region, at the same depth (3.4 m), but about 1.5 km apart. As in the naturally occurring patches, rich patches lost more mussels than poor patches. The giving-up densities were weakly related to initial mussel biomass in the trays, but strongly related to average biomass available in the environment (plateau values in Fig. 9). In the rich environment, significantly more mussels were left over than in the poor environment (1920 vs 291 gFW.m^{-2}). This happened also in the experimental patches (933 vs 422 gFW.m^{-2}, Student's $t = 6.23$, $P < 0.0001$). If we compare the level of depletion of the environment of the introduced patches, the rich site lost on average 1300 gFW.m^{-2} and ended down at a level of 1920 gFW.m^{-2} ($P = 0.007$), whereas at the poor site, except for the predation trays, no significant reduction in biomass occurred (287 vs 291 gFW.m^{-2}, $P = 0.97$). The experimental patches with high quality mussels, however, were depleted further than their environment at the rich site. At the poor site, the introduced patches were depleted down to a level 2.2 times lower than at the rich site, although the final densities in these patches were still 1.5 times higher than in the environment.

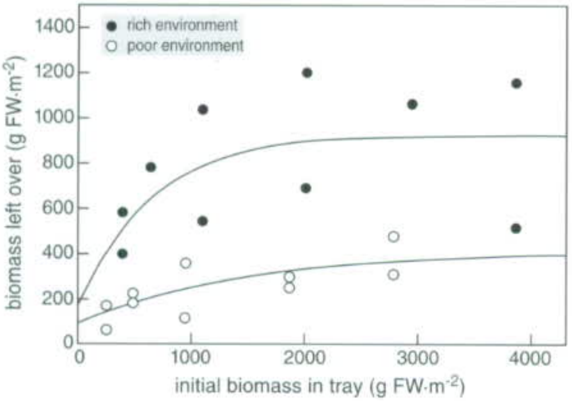


Fig. 9. Exploitation of experimentally created patches of 1 m^2, filled with high quality mussels (250-4000 gFW). Two sets of 10 patches were situated in either a rich or a poor environment. Water depth was 3.4 m at both sites. Ducks exploited denser food patches more intensively than less dense patches and giving-up density was lower at the site with the lower environmental density. Compared to the environment, at the rich site ducks surpassed the threshold for the site in general, which is explained by the higher quality of mussels in the experimental patches. At the poor site this was not the case, possibly due to low numbers of ducks at the site (see text for further explanation).

This experiment shows that diving ducks apparently adjusted their foraging effort at the level of patches with respect to the relative benefit of the patch (density and quality of mussels) in relation to that of the patch environment.

Impact of predation on mussel stocks

Reduction in biomass over winter was studied in the period 1983-1995. Significant loss occurred in 20 out of 50 cases in the period 1984-1987 (40%) and 29 out of 49 cases in the period 1992-1995 (59%). Many sites thus remained unpredated over winter.

When considering three categories of water depth (< 2.5, 2.6-3.5 and 3.6-4.5 m), in each of them a significant positive relationship existed between initial mussel biomass and the amount left over. Sites with initially more mussels lost, however, on average more biomass than poor sites. Average biomass consumed per station was also strongly affected by water depth

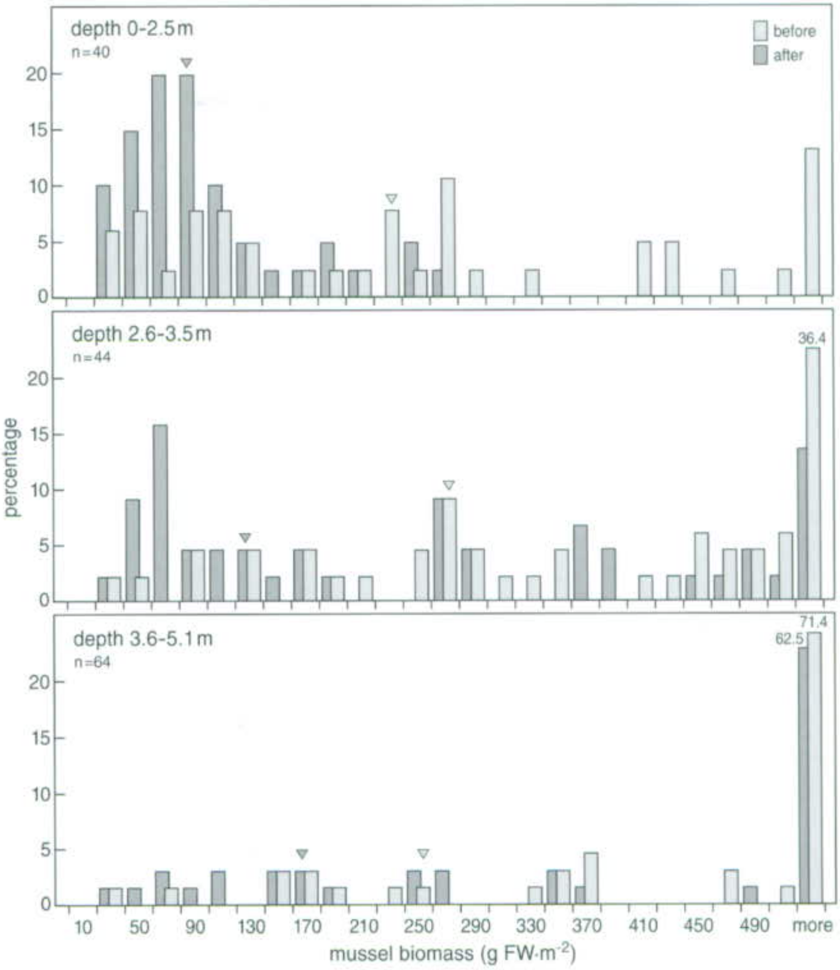


Fig. 10. Mussel densities recorded before and after winter in 148 natural plots in the period 1983-1994 in relation to water depth. Arrows indicate the median for densities less than 500 $gFW.m^{-2}$, showing an increase with depth. The fraction of higher densities also increased with depth, but was apparently not utilized by diving ducks.

(Fig. 10). At sites deeper than 4 m, significantly less predation occurred than at shallower sites and the level down to which the birds had depleted their food stocks, increased with increasing depth.

Combining data of mussel biomass for the entire lake system and consumption rates by the different diving duck species allows estimation of the relative share in predation of each species. For the periods around the two years of lake-wide sampling of the IJsselmeer area, the greater part of mussel consumption by consumers of *Dreissena* could be attributed to Tufted Duck (1975-1985: 45%, 1986-1995: 37%) and Scaup (1975-1985: 30%, 1986-1995: 51%). In total, predation by ducks amounted to $40\text{-}70.10^6$ kgFW in average and poor seasons and $90\text{-}135.10^6$ kgFW in peak years when high numbers are present. This corresponds to a biomass reduction due to predation of 5-22%. In Lake IJsselmeer predation accounted for a 10-13% loss in biomass at maximum. In Lake Markermeer, maximum predation was estimated at 18% of biomass in the ear-

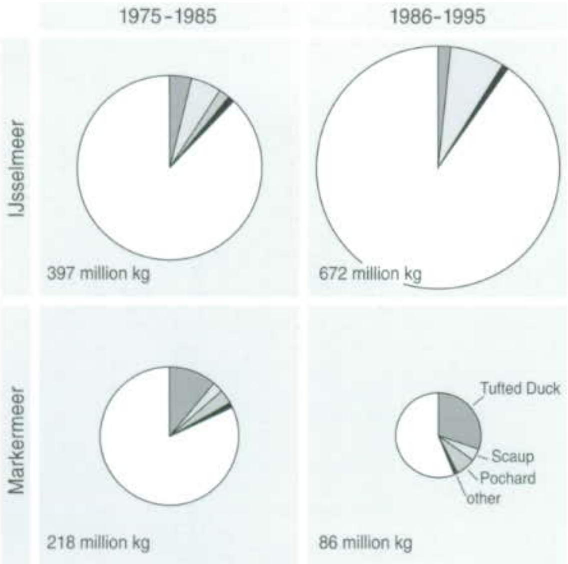


Fig. 11. Pie diagrams showing mussel predation by different diving duck species. Total amount of mussels available at Lake IJsselmeer and Lake Markermeer was calculated from the lake wide surveys in 1981 and 1992. The consumption by diving ducks (mean of winters of 1975-1985 and 1986-1995, respectively) was calculated on the basis of monthly aerial counts and species-specific consumption rates.

lier period, but 44% in the period 1986-1995 (Fig. 11).

We might explore impact also by long-term effects of predation on the benthos community. By simultaneous monitoring of *Dreissena* and diving ducks in Lake Markermeer (Pampushaven) and Lake IJsselmeer (Trintelhaven) we found contrasting predation patterns and subsequent changes in mussel population (Fig. 12). Within a 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 is evident that, over a five year period, adult mussels increased at the site in Lake IJsselmeer and decreased at the site in Lake Markermeer. The decrease in Lake Markermeer was accompanied by an irregular spat fall of mussels and 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 with the drop in numbers of adult mussels the winter before, this caused the dramatic collapse of the local mussel population. Radar observations the next winter (1983/1984) showed that ducks were no longer foraging at the site, but in 1984/1985, after a slight recovery of the musselbank, this was again the case. Also at the IJsselmeer site, Tufted Duck preceded Scaup, though in lower numbers. The regular production of spat here enabled the population to grow, however, despite regular set-backs due to avian predation. As Tufted Duck are known to prey efficiently on spat by a suction-feeding technique (De Leeuw & Van Eerden 1992), this species might be responsible for the main reduction in first year mussels, whereas both species prey on adult mussels.

Discussion

Exploitation patterns in the *Aythya-Dreissena* "trait d'union"

With respect to patch density after exploitation, we showed "underuse" of some rich patches. This is probably due to imperfect knowledge of the environment (night-time foraging underwater) and further limitations imposed by the flock-feeding habit. The choice of a certain foraging area by a flock of several thousands of birds is probably influenced by the average quality of the site (as experienced by most flock members) rather than by peak densities, which only a limited number of birds will come across. In other words, the average quality is supposed to affect bird density and the number of nights the site is in use. Consequently, the giving-up density (GUD) is likely to be determined by the average food density of the site (several km^2) and local food quality (flesh content and byssal attachment of mussels). In such an exploitation system, the relatively scarce rich patches will be underexploited compared to the average GUD.

Patch experiments suggested no physical limits to ingestion, such as mussel size and occurrence of mussels in clumps. However, trials with captive birds showed a reduction in intake rate for larger mussels and mussels in clumps (De Leeuw & Van Eerden 1992, De Leeuw, subm.). Patch quality is, therefore, important to the individual, but, as we see it, patch exploitation by individual birds is subservient to the flock's at-

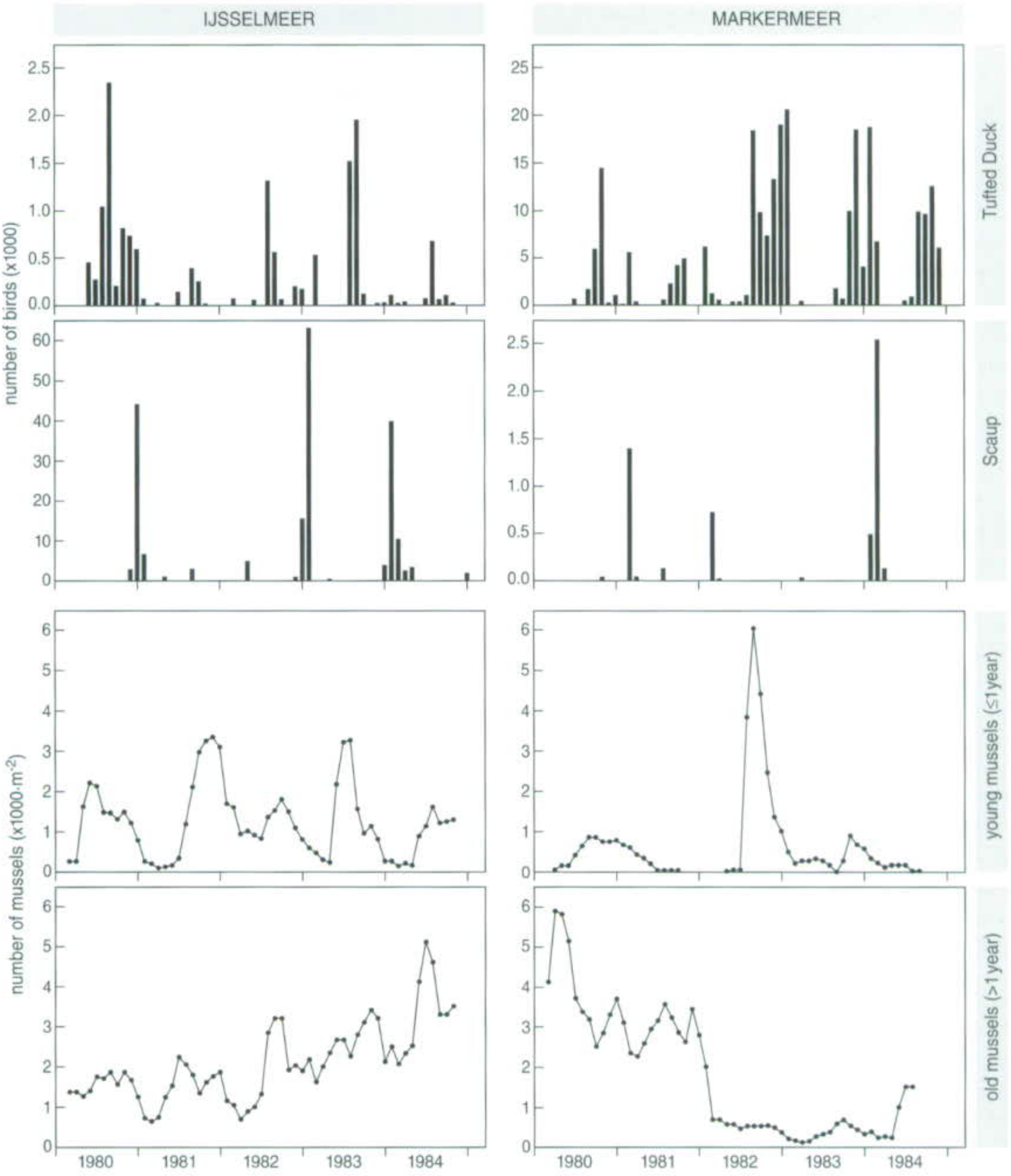


Fig. 12. Monitoring of *Dreissena* and ducks at two sites over a period of five years, based on monthly sampling of benthos and counts of ducks at the main nearby roosts. Benthos data expressed as three point running means after data in Bij de Vaate (1991). At site A (IJsselmeer) regular production of spat fall led to a slowly increasing mussel population, despite annual predation by diving ducks (mainly Scaup). At site B (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 re-colonisation 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.

tendance to the site. The advantage of flock feeding is that individuals can gain much more information on local food densities from flock members than they are able to gather by sampling the lake bottom on their own (Pöysä 1992, Ranta *et al.* 1993) by diving at high energy cost. 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 experience themselves. Nevertheless, we showed that diving ducks are able to allocate more time and/or to concentrate in larger numbers at the better patches. For example in Fig. 8, isolated rich patches lost far more mussels than the average of the environment (Enkhuizerzand and Trintelhaven), although their final density remained higher than the average. In areas with a high frequency of rich patches, as was the case at greater depth, some patches remained entirely unexploited whilst others became fully grazed down (see Fig. 8, Wagenpad 4.4 m depth).

The experiments with food trays showed that rich patches might be exploited to a density even lower than that of the environment, but in this case superior quality mussels were offered in environments of contrasting density (Fig. 9). The high quality mussels in the rich site were exploited down to a lower level than the environment. This was not true for the poor environment, which was, except for the trays, hardly exploited at all. The fact that the final densities in the two experiments differed, suggests that ducks foraged in denser flocks or spent more time in the rich patches at the poor site. The results indicate that the ducks are not only able to recognize and to respond to differences in mussel density but also to a different quality over short distances.

The tendency of a higher GUD at greater depths is in qualitative agreement with the marginal value theorem (Charnov 1976), predicting a higher GUD in less rewarding sites. In our case, deeper sites mean a longer travel distance (both for flight from coastal roosting sites and diving to depth) and a lower flesh content of the mussels. More data are needed about flight costs, diving costs, and profitability of the prey encountered, before a more quantitative test can be achieved.

The selection for relatively small mussels, especially at the shallower sites, may be caused by the higher flesh to shell ratio in small mussels (Draulans 1982, 1984, De Leeuw & Van Eerden 1992). The near absence of size selection in sites deeper than 2.5 m (Fig. 6), however, suggests a general time constraint on the foraging ducks caused by water depth. Depth related exploitation patterns were also found in other studies (Pedroli 1977, Draulans 1982, Nehls 1995, Lovvorn & Gillingham 1996).

To conclude, exploitation of Zebra Mussels by diving ducks may operate at different levels of decision. First, the choice of feeding flocks where to forage (second-order patch level) and associated with this the choice of a roost site. Diving ducks seemed to choose their foraging and roosting sites from the perspective of minimization of energy costs for transport (short flight tracks) and costs for extra locomotion at the roost (shelter against waves, avoidance of disturbance). Secondly, individual decisions are made with respect to the exploitation at the level of patches and sites within a region (first-order patch level). These decisions are apparently taken from the perspective of maximization of energy intake by selection of small, unattached prey where possible. This selective behaviour for small prey was also exhibited in the diet choice of the smallest species of diving duck and, in the larger species, by the dominant sex (males) and age classes (adults).

The overall pattern of exploitation of Zebra Mussels showed a positive density dependent harvest and was typified by the underuse of the richest patches which we think is the result of imperfect knowledge of the patch structure underwater. In terms of foraging strategy, diving ducks exploiting Zebra Mussels in winter can thus be categorised as Bayesian foragers (Green 1980, 1984, Valone & Brown 1989), adjusting their feeding effort to what they expect from average patch quality in a site without knowledge of the actual first-order patchiness.

Similar patterns of patch use have been described in laboratory experiments with Ruddy Duck *Oxyura jamaicensis*, which proved to obey predictions of giving-up times according to the marginal value theorem, although they sometimes foraged longer in high density patches than predicted for an omniscient bird (Tome 1988). A parallel to our work is also found in the field study of Lovvorn (1994) and Lovvorn & Gillingham (1996) who developed a foraging model for Canvasbacks *Aythya valisineria* to relate the behaviour of the ducks to the spatial distribution of their vegetative food (winter buds of *Vallisneria*). Field sampling before and after the period of exploitation revealed that 50% of the food stock was consumed in profitable areas, while the average decline in all sampling stations was only 20%. Patch quality in terms of biomass per bud (rather than the number of buds per unit of area) mainly determined the behaviour of the ducks. Water depth proved also important according to biomechanic estimates, although the ducks performed only shallow dives (depth < 1 m) in this study. The giving-up densities in the field were generally lower than predicted by a simulation on the basis of estimated foraging energetics, suggesting that the decision of Canvasbacks to leave the lake mainly depended on depletion of areas with densities that allow profitable foraging.

Sustainable use and foraging energetics

We showed that patch use and depletion levels varied greatly from one site to another (depth, density, growth pattern and distance from roost) and from year to year. Generally speaking, the feeding on *Dreissena* by diving ducks resulted in an apparent under-exploitation of rich patches, of patches at greater depths, and of mussels occurring in clumps. The richest mussel beds at depths of 4 m and more, were only partially exploited and only during the latter part of the winter season. The conclusion from these findings is that predation levels by diving ducks might be limited by high costs outweighing the net foraging benefits for the avian predators. The limited use the birds exhibit on the total food stocks becomes evident when total biomass and total food consumption by diving ducks is calculated (Fig. 11). The predation levels of 10-18% (occasionally 44%) of the food stock are consistent with other studies in large scale water bodies. Nilsson (1970, 1980) estimated predation losses of 5-35% by wintering diving ducks exploiting the Common Mussel *Mytilus edulis* and other molluscs in the Baltic Sea. Consumption by Eiders *Somateria mollissima* was calculated to amount to a 13% loss for mussels and cockles *Cerastoderma edule* in the German part of the Wadden Sea (Nehls 1989, 1995). Guillemette *et al.* (1996) reported 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 a 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 owing to predation by diving ducks (depth 5-7 m). Suter (1982a) estimated the highest recorded impact of diving ducks on bivalves (*Dreissena*) in a smaller scaled, riverine area of Untersee/Hochrhein, Switzerland (depth 1-3 m) where 95% of the mussel stock was consumed. Predictability and size of the food stock in relation to foraging costs (water depth) appeared to be important factors which determined the harvestability of the benthic community in these studies.

By their highly social, flock-feeding behaviour, spending their inactive phase at huge communal roosts, individual ducks may benefit from the knowledge available in the group, as to which feeding sites they should fly to in order 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, however, this communal harvest does not lead to an overall depletion of mussels within potential reach of the ducks. Instead, the exploitation seems to be limited by factors constraining the harvest of the larger part of mussel biomass, in particular at greater depth. The consequence of such a limit is the survival of large cohorts of Zebra Mussels. From our long-term study we conclude that local set-backs in mussel stocks may well be caused by avian predation. In most cases, the frequent spawning by *Dreissena* results in a rapid re-colonization of the population after one growing season (but see Fig. 12 for the combined effect of poor recruitment and heavy predation). Subsequent to the extremely heavy predation described by Suter (1982a) in the upper Rhine, mass immigration of 1+ mussels took place, facilitated by the water current, which could sustain the mussel population.

Towards a multi-species model of carrying capacity

How are bird numbers determined and how can patterns of distribution be explained? The ideal free concept of Fretwell & Lucas (1970) supposed in its most simple form that interference between individuals is the factor that determines distribution and limits the degree of concentration of predators at food areas. Also depletion of food stocks may sometimes play an important role with respect to distribution of predators (Tome 1988, Mitchell 1990). Patch use models of prey exploitation taking into account one of these factors have refined our thinking about habitat use (see, for example, Rosenzweig 1991). However, field studies at a larger scale, linking field evidence of distributional ecology to theory, are scarce. A recent example is a study on Cranes *Grus grus*, avian herbivores with the possibility of visual food density assessment (Alonso *et al.* 1995, Bautista *et al.* 1995). From this study both arguments for the existence of interference and for patch depletion affecting individual intake rates were found. Sutherland and Allport (1994) found field evidence for their non-interference model with depletion as the most important factor determining competition among individuals in a study of two species foraging in the same area, Bean Geese *Anser fabalis* and Wigeon *Anas penelope*.

In the *Aythya-Dreissena* system at Lake IJsselmeer five species of avian predators act together when consuming a common invertebrate prey. Along four lines of evidence we will explore the question raised in the beginning of this paper as to whether ducks achieve the highest sustainable energy intake possible and what evidence we have to decide whether or not the carrying capacity of the system has been reached.

1. Maximization of energy intake

While exploiting *Dreissena*, diving ducks seemed to obey foraging rules qualitatively. Areas with highly profitable mussels received more attention, which could be ascertained at various levels of scale: lake, region, site, and patch. The fact that size selection was apparently operating only at depths less than 2.5 m, points to a time constraint on the foraging ducks, set by water depth. Apparent foraging success differed among the species, being highest in Scaup and lowest in Pochard. At greater depth, foraging success was higher in all species corresponding with the density of *Dreissena*. In Tufted Duck apparent foraging success declined as winter proceeded, but in Scaup and Goldeneye it increased, probably owing to shifts to deeper water in late winter.

We conclude from these observations that the diving ducks experienced a deteriorating food supply in the course of winter, but that not all species are equally affected. In line with this, accumulated mass of winter body fat peaked in December and declined rapidly thereafter in the Pochard, but fat mass was continually high until January in the Tufted Duck or even February in the Scaup (De Leeuw & Van Eerden 1995).

2. Minimization of energy expenditure

The relationship between the night-time use of mussels and the daytime distribution of diving ducks over different roosts suggests a trade-off between the costs of commuting flights and the profitability of a certain foraging site. The degree of exposition to wind and waves was a major factor explaining the distribution of the diving ducks, suggesting that during daytime that ducks aim to minimize extra energy costs for maintenance (compensatory paddling to overcome wind drift, extra costs for thermoregulation). Later on during the winter season commuting flights were longer in both Tufted Duck and Scaup, while shifting to deeper water. This also points towards the general tendency for minimizing energy costs favouring shallow, near-shore foraging sites. The fact that Scaup and Pochard but not Tufted Duck showed a relationship with abundance of mussels at 4.5 m water depth and more, underlines the different ability between the species to exploit Zebra Mussels. Apparently, Scaup and Pochard are able to exploit a greater range in water depth than the smaller sized Tufted Duck.

3. Competition and habitat segregation

Are there reasons to support the idea that the large scale food exploitation by different species of diving ducks is modulated by competition? The five species have widely overlapping diets and are, therefore, competitors for the same prey. Tufted Duck and Scaup, the main players in the game of utilizing the available fraction of the *Dreissena* food source, do not mix freely over the daytime roosts. Also, the extended distribution of Scaup over more roosts, as numbers went up during the 20 years of this study, has been parallelled by a retreat of Tufted Duck and Pochard in Lake Markermeer (Fig. 3 and 12), again pointing towards competition.

The increase in mussel biomass in Lake IJsselmeer, which seems to have occurred in the second half of the 1980s, was paralleled by a strong increase in the number of Scaup, while Tufted Duck, by contrast, under-went no marked change in total numbers at the same time (Fig. 6). The latter species partly shifted to Lake Markermeer where since 1991/1992 a decline has become apparent. This coincides with the decline of the mussel stock in Lake Markermeer which was further corroborated by a strong tendency of decline in Coot, Goldeneye, and Pochard in this lake compartment. Because of the fluctuations in numbers, long-term trends will become more clear in future years. Recall that the calculated fraction of mussels consumed by diving ducks remained roughly the same, except for the second period in Lake Markermeer (Fig. 11), which might be interpreted as a kind of over-exploitation followed by a numerical response.

4. Competition and diet selection

The subtle differences in prey choice between different species that was demonstrated by the diet analyses (Table 3) may be considered in relation to the accessible fraction of the total food stock. The age and sex related tendencies to take also other prey than Zebra Mussels as observed in Tufted Duck, Pochard, and Goldeneye, may either point to slight differences in habitat choice and/or feeding techniques. The very small gastropods, chironomids, ostracods and microbivalves found in the diet can only be taken up by the suction-feeding method which is also used for straining small mussels underwater (De Leeuw & Van Eerden 1992). The incidence of other prey in the diet might thus be regarded as a reflection of the birds being selective with respect to energy intake. The fact that even within Pochard and Tufted Duck, females and juveniles tend to feed more on a pure *Dreissena* diet than males and adults do (Table 2 and Van Eerden, unpubl. data), suggests a difference in foraging skill. The position of Scaup and Goldeneye is somewhat different. Because of its size, the Scaup diet only comprises *Dreissena*, irrespective of sex and age classes. It is possible, therefore, that Scaup is unable to achieve a net intake rate high enough to sustain its energy demands from prey smaller than mussels under winter conditions. Goldeneye, the species with the strongest sexual dimorphism in structural size, underlines this viewpoint. The large males (both adult and juvenile) of this species were pure *Dreissena* eaters, like Scaup, whereas the females took many more small prey, like Tufted Duck and Pochard (Table 3). Food and habitat segregation within species are mechanisms to avoid direct competition (Rosenzweig 1991).

At Lough Neagh, an ecosystem where *Dreissena* is lacking, Winfield & Winfield (1994) found Scaup and Pochard to be almost entirely confined to chironomid larvae, unlike Tufted Duck and Goldeneye, which also exploited small molluscan and crustacean prey. Our data may also be compared with that of the guild of seaducks studied by Goudie and Ankney (1986). They found the larger species, Common Eider and Black Scoter *Melanitta nigra* to be mussel and echinoderm feeders, whereas the small Long-tailed Duck *Clangula hyemalis* and Harlequin Duck *Histrionicus histrionicus* consumed also large amounts of crustaceans in addition to small mollusc prey. Moreover, the smaller species took more energy rich food as compared to the larger species.

To sum up, if food stocks were really as superabundant as they seemed, we would neither expect these species, sex, and age related differences to occur, nor the observed increase in foraging effort (flight distance and diving depth) in the course of the winter. Also the numerical response to changes in mussel stock or availability of mussels in relation to the abundance of other species of diving duck is noteworthy in this respect. Our tentative conclusion is that capacity for avian consumers of *Dreissena* is reached in most years. We do stress the importance of a multi-species approach to further quantify the carrying capacity problem. To achieve this goal, further monitoring of changes in the duck and benthos populations will be necessary, together with experiments with captive ducks which are underway to provide the indispensable data on intake rates and foraging energetics in relation to habitat and prey properties.

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References

Alonso, J.C., J.A. Alonso & L.M. Bautista, 1994. Carrying capacity of staging areas and facultative migration extension in Common Cranes. J. Appl. Ecol. 31: 212-222.

Bautista, L.M., J.C. Alonso & J.A. Alonso, 1995. A field test of ideal free distribution in flock-feeding Common Cranes. J. Anim. Ecol. 64: 747-757.

Bij de Vaate, A., 1991. Distribution and aspects of population dynamics of the Zebra Mussel, *Dreissena polymorpha* (Pallas, 1771), in the Lake IJsselmeer area (The Netherlands). Oecologia 86: 40-50.

Charnov, E.L., 1976. Optimal foraging: the marginal value theorem. Theor. Popul. Biol. 9: 129-136.

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

De Leeuw, J.J. (subm.) Food intake rates and habitat segregation of Tufted Duck and Scaup exploiting Zebra Mussels in the IJsselmeer area. Ardea.

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. Duikeenden in het IJsselmeergebied. Flevobericht 373, Rijkswaterstaat Directorate IJsselmeergebied, Lelystad 106 pp. (ISBN 90-1137-0).

De Vries, J. & M.R. Van Eerden, 1995. Thermal conductance in aquatic birds in relation to the degree of water contact, body mass and body fat: energetic implications of living in a strong cooling environment. Physiol. Zool. 68: 1143-1163.

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

Draulans, D., 1984. Sub-optimal mussel selection by Tufted Ducks *Aythya fuligula*: test of a hypothesis. Anim. Behav. 32: 1192-1196.

Fretwell, J.D. & H.L. Lucas Jr., 1970. On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheoretica 19: 16-36.

Géroudet, P., 1966. Premières conséquences ornithologiques de l'introduction de la "moule zébrée" *Dreissena polymorpha* dans le Lac Léman. Nos Oiseaux 28: 301-307.

Géroudet, P., 1978. L'évolution du peuplement hivernal des oiseaux d'eau dans le canton de Genève (Léman et Rhône) de 1951 à 1977. Nos Oiseaux 34: 207-220.

Goss-Custard, J.D. & S.E.A. Le V. dit Durell, 1990. Bird behaviour and environmental planning: approaches in the study of wader populations. Ibis 132:272-289.

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

Green, R.F., 1980. Bayesian birds: a simple example of Oaten's stochastic model of optimal foraging. Theor. Pop. Biol.18: 244-256.

Green, R.F., 1984. Stopping rules for optimal foragers. Am. Nat. 123: 30-40.

Guillemette, M., R.C. Ydenberg & J.H. Himmelman, 1992. The role of energy intake rate in prey and habitat selection of Common Eiders *Somateria mollissima* in winter: a risk-sensitive interpretation. J. Anim. Ecol.61: 599-610.

Guillemette, M., A. Reed & J.H. Himmelman, 1996. Availability and consumption of food by Common Eiders wintering in the Gulf of St. Lawrence: evidence of prey depletion. Can. J. Zool. 74: 32-38.

Jacobs, J., 1974. Quantitative measures of food selection. A modification of the Forage ratio and Ivlev's Electivity Index. Oecologia 14: 413-417.

Hamilton, D.J., C.D. Ankney. & R.C. Bailey, 1994. Predation of Zebra Mussels by diving ducks: an exclosure study. Ecology 75: 521-531.

Kirkwood, J.K., 1983. A limit to metabolisable energy intake in mammals and birds. Comp. Biochem. Physiol. 74: 1-3.

Kotliar, N.B. & J.A. Wiens, 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos 59: 253-260.

Leuzinger, H. & S. Schuster, 1970. Auswirkungen der Massenvermehrung der Wandermuschel *Dreissena polymorpha* auf die.

Wasservögel des Bodensees. Orn. Beob. 67: 269-274.

Lovvorn, J.R., 1994. Biomechanics and foraging profitability: an approach to assessing trophic needs and impacts of diving ducks. Hydrobiologia 278: 223-233.

Lovvorn, J.R. & M.P. Gillingham, 1996. Food dispersion and foraging energetics: a mechanistic synthesis for field studies of avian benthivores. Ecology 77: 435-452.

Maurer, B.A., 1996. Energetics of avian foraging. In: C. Carey (ed.) Avian Energetics and Nutritional Ecology pp 250-279, Chapman & Hall, New York.

Mitchell, C.A. & J. Carlson, 1993. Lesser Scaup forage on Zebra Mussels at Cook nuclear plant, Michigan. J.Field Ornithol. 64: 219-222.

Mitchell, W.A., 1990. An optimal control theory of diet selection: the effects of resource depletion and exploitative competition. Oikos 58: 16-24.

Nalepa, T.F. & D.W. Schloesser, 1993. Zebra Mussels: biology, impact, and control. Lewis Publ. Boca Raton.

Nehls, G., 1989. Occurrence and food consumption of the Common Eider *Somateria mollissima* in the Wadden Sea of Schleswig Holstein. Helgol. Meeresunters. 43: 385-393.

Nehls, G., 1995. Strategien der Ernährung und ihre Bedeutung für Energiehaushalt und Ökologie der Eiderente *Somateria mollissima* (L.,1758). Ph.D. Thesis, University of Kiel, Kiel.

Nilsson, L., 1970. Food-seeking activity of south Swedish diving ducks in the non-breeding season. Oikos 21: 145-154.

Nilsson, L., 1980. Wintering diving duck populations and available food resources in the Baltic. Wildfowl 31: 131-143.

Norusis, M.J., 1988. SPSSPC+ Statistical Package. Chicago.

Pöysä, H., 1992. Group foraging in patchy environments: the importance of coarse-level local enhancement. Ornis Scand. 23: 159-166.

Pedroli, J.C., 1977. Relation entre les oiseaux aquatiques et *Dreissena polymorpha* Pallas dans le Lac de Neuchâtel. Orn. Beob. 74: 86-87.

Pedroli, J.C., 1981. Les relations entre la Moule Zébrée *Dreissena polymorpha* (Pallas) et les oiseaux aquatiques. Dissertation, University of Neuchâtel, Neuchâtel.

Pehrsson, O., 1984. Diving duck populations in relation their food suplies. In: P.R. Evans, J.D. Goss-Custard & W.G. Hale (eds.) Coastal waders and wildfowl in winter pp. 101-116. Cambridge University Press, Cambridge.

Prejs, A., K. Lewandowski & A. Stanczykowska-Piotrowska, 1990. Size selective predation by Roach *Rutilus rutilus* on Zebra Mussel *Dreissena polymorpha*: field studies. Oecologia 83: 378-384.

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.

Schloesser, D.W., A. Bij de Vaate & A. Zimmerman, 1994. A bibliography of *Dreissena polymorpha* in European and Russian waters: 1964-1993. J. Shellfish Res. 13: 243-267.

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

Suter, W., 1982a. Der Einfluß von Wasservögel auf Populationen der Wandermuschel *Dreissena polymorpha* (Pall.) am Untersee/Hochrhein (Bodensee). Schweiz. Z. Hydrol. 44: 149-161.

Suter, W., 1982b. Vergleichende Nahrungsökologie von überwinternden Tauchenten (*Bucephala*, *Aythya*) und Bläßhuhn (*Fulica atra*) am Untersee-Ende/Hochrhein (Bodensee). Orn. Beob. 70: 225-254.

Suter, W. & L. Schifferli, 1988. Überwinternde Wasservögel in der Schweiz und ihren Grenzgebieten: Bestandsentwicklungen 1967-1987 im internationalen Vergleich. Orn. Beob. 85: 261-298.

Sutherland, W.J. & G.A. Allport, 1994. A spatial depletion model of the interaction between bean geese and wigeon with the consequences for habitat management. J. Anim. Ecol. 63: 51-59.

Tome, M.W., 1988. Optimal foraging: food patch depletion by Ruddy Ducks. Oecologia 76: 27-36.

Valone, T.J. & J.S. Brown, 1989. Measuring patch assessment abilities of desert granivores. Ecology 70: 1800-1810.

Van Eerden, M.R. & A. Bij de Vaate, 1984. Natuurwaarden van het IJsselmeergebied. Flevobericht 242. Rijksdienst voor de IJsselmeerpolders, Lelystad.

Van Eerden, M.R. & M. Zijlstra, 1986. Natuurwaarden van het IJsselmeergebied: prognose van enige natuurwaarden in het IJsselmeergebied bij aanleg van de Markerwaard. Flevobericht 273. Rijksdienst voor de IJsselmeerpolders, Lelystad.

Wiersma, P., T. Piersma & M.R. Van Eerden, 1995. Food intake of Great Crested Grebes *Podiceps cristatus* wintering on cold water as a function of various cost factors. Ardea 83: 339-350.

Winfield, I.J & D.K. Winfield, 1994. Feeding ecology of the diving ducks Pochard *A. ferina*, Tufted Duck *Aythya fuligula*, Scaup *A. marila* and Goldeneye *Bucephala clangula* overwintering on Lough Neagh, Northern Ireland. Freshwater Biol. 32: 467-477.

Winfield, I.J, D.K. Winfield & C.M. Tobin, 1992. Interactions between the Roach *Rutilus rutilus*, and waterfowl populations of Lough Neagh, Northern Ireland. Environmental Biology of Fishes 33: 207-214.

Chapter 3

Size selection in diving Tufted Ducks *Aythya fuligula* explained by differential handling of small and large mussels *Dreissena polymorpha*

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Size selection in diving Tufted Ducks *Aythya fuligula* explained by differential handling of small and large mussels *Dreissena polymorpha*

We studied prey size selection of Tufted Ducks feeding on fresh water mussels under semi-natural conditions. In experiments with non-diving birds, we found that Tufted Ducks use two techniques to handle mussels. Mussels less than 16 mm in length are strained from a waterflow generated in the bill ('suction-feeding'), while larger mussels are picked up and handled singly. Suction-feeding on small mussels proved to be more profitable. In the non-diving situation, the ducks preferentially took the smallest mussels on offer. It is suggested that smaller mussels incur lower costs of crushing mussel shells in the gizzard. Ducks diving for mussels preferred suction-feeding on all mussels up to about 16 mm in order to minimize the costs of diving. The selectivity for small mussels increased with diving depth (1-5 m), probably because ducks diving deeper spend more time at the bottom collecting small mussels, before a larger mussel is taken to the surface and ingested afterwards. We conclude that the two handling techniques we described for Tufted Duck open up an extensive feeding niche for benthic feeding diving ducks.

Introduction

Birds feeding by diving must regularly interrupt feeding to return to the water surface to breathe. In most birds, dive times are short (i.e. less than one minute; Dewar 1924, Kooyman 1989) and consequently the decision of which prey to take will be focussed on collecting prey in very short feeding bouts. Recently, it has been shown that prey choice may be influenced by the period of time over which foraging decisions take place (see Lucas 1990, for review).

In this study we examine prey choices in a diving bird, the Tufted Duck. In the wintering areas in western Europe, Tufted Ducks mainly feed on Zebra Mussels *Dreissena polymorpha* (e.g. Bij de Vaate 1991). All mussels are swallowed whole and crushed in the muscular gizzard. Shell fragments and flesh pass together through the gastro-intestinal tract. Both in field studies (Pedroli 1981, Draulans 1982) and in captivity (Draulans 1982, 1984, 1987), it has been shown that Tufted Ducks select particular mussel sizes. Draulans studied size selection in relation to the profitability of the prey and found that Tufted Ducks selected smaller mussels than would be expected. His explanation was that the birds avoided the risk of taking mussels that were too large to be swallowed and hence unprofitable (Draulans 1984). In his experiments, however, the ducks did not have to dive for the mussels.

Tufted Ducks in the wild feed predominantly by diving at depths up to 5 m (Willi 1970, Nilsson 1972, Draulans & De Bont 1980). The aim of this paper is to study the impact of diving on prey size selection. Experiments were carried out with captive Tufted Ducks diving under semi-natural conditions. In experiments with non-diving birds, we were able to determine the profitability of differently sized mussels.

Material & Methods

Mussels

Zebra Mussels were collected weekly in lake IJsselmeer, The Netherlands, in November and December 1987. Mussels attached in clumps were detached from their substrate and separated by cutting the byssus. Dry weights (24 hours, 70 °C) and ash weights (90 minutes, 450 °C) were measured for 10 mussels per size class with shell lenghts of 3, 5, 7, 9, 11, 13, 15, 17, 19, 21, and 23 mm. Shell lengths were measured to the nearest mm. The relationship between ash-free dry weight of mussels including the shell (*AFDW*, g) and mussel shell length (*L*, mm) is described by the power function: log AFDW = 2.727 x log L-5.007 ($r^2 = 0.992$).

Experiments without diving

Two hand-reared Tufted Ducks (a male and a female, body mass 450-500 g) were used in the experiments. The ducks were kept separately in cylindrical wire-netting cages. Room temperature was about 15 °C. Food consisted of mixed grains and water *ad lib*. In addition, Zebra Mussels were offered regularly to avoid possible alteration of the gastro-intestinal tract (Kehoe *et al.* 1988). The experiments were carried out when the ducks were fully grown, at an age of 6 to 8 months.

Handling times were measured by offering a known number of mussels of one mm length class at a time in a dish with about 3 cm water. The birds were watched from behind a blind. Handling time, defined as the time between picking up and complete swallowing a mussel, was measured using a stopwatch with an accuracy of 0.1 s. Because sometimes mussels were taken rapidly in the flow of water sucked into the bill and thus processed simultaneously, handling time was also calculated as the duration of a bout of continuous handling divided by the number of mussels taken. The number of mussels offered was varied in successive trials, thus ensuring a spread in the number of mussels taken in one bout. The experiments were carried out at different times of the day and never lasted longer than two hours. Mussels of different size classes were offered in a random order to exclude effects of satiation. The profitability of each size class was calculated as the gross intake of organic material (AFDW) per mussel of that size class per second handling time.

Selection of mussel sizes from a field population was determined by taking a random sample of 200 gram wet weight (400 to 500 mussels of known size). The mussels were offered in an oval dish (about 30 x 18 x 5 cm) containing water (3 cm). Foraging time was measured using a stopwatch with an accuracy of 0.1 s. The dish was removed regularly to measure the shell length (to the nearest mm) of all remaining mussels. Afterwards, the remaining mussels were offered again and foraging was continued. This procedure was repeated, until the ducks refused to consume more mussels.

Experiments under semi-natural diving conditions

Three Tufted Ducks (1 adult male, 1 adult female, and 1 subadult male, body masses varying between 500 and 680 g) were succesfully trained to dive for mussels. They were kept singly in cages fixed to a pontoon in an 8 m deep water-filled sandpit. Each cage was constructed of an iron frame with wire netting and consisted of a deep shaft (1 x 1m, 5m deep). At the water surface the cages were enlarged by 0.5 m (0.5 m deep), to give a total swimming area of 1 x 1.5 m. A board (20 x 20 cm) was placed in the shallow part of the cage a few centimeters above the water for the birds to rest. Food was offered on a tray (1x1 m with upright edges of 15 cm) in the dive shaft. Diving depth was manipulated by changing the level of the tray. Three months before the experiments started the birds were placed in their cages and fed on mixed grains. Diving depth was increased steadily up to 5 m. Thereafter, the diet was gradually altered to mussels over 4 weeks. Each day around noon, the birds were weighed, the remaining mussels were collected and total wet weight was measured, a sample was drawn from which mussel sizes were later determined, and an entirely new batch of mussels of known wet weight was offered. The experiments were conducted in November and December under normal local winter conditions, with water temperatures slightly above freezing (2-5 °C).

Size selection was measured by taking samples of 150-250 gram wet weight (about 300 to 800 mussels) drawn before and after one day of consumption. Mussel sizes were measured to the nearest millimetre. The consumption per size class was calculated from the total weight loss of mussels in the tray after 24 hours and the changes in frequency distributions of size classes (2 mm each). The birds proved to consume up to 2 kg wet weight of mussels per day. The level of depletion was manipulated by varying the amount of mussels on offer (offering a smaller amount resulted in a greater level of depletion). An amount of 10, 8, 6, 5, and 4 kg wet weight was offered at a depth of 1.25 m. Ten, 8, and 6 kg was offered at a depth of 2.5 and 3.75 m, and 10 and 8 kg at 5.0 m, sufficient for the ducks to maintain their body weights. Tests without ducks proved that no mussels were lost from the tray as a consequence of experimental handling or water movement, and that the inaccuracy of wet weight measurements influenced the estimated consumed fractions by less than 5%.

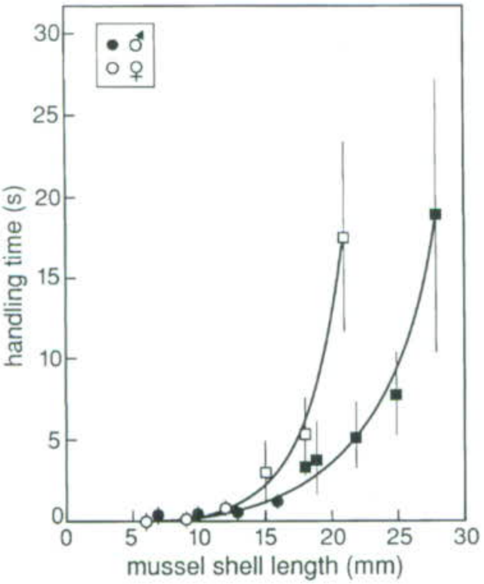

Fig. 1. Handling time per mussel (mean ± SD) in relation to mussel shell length (*open symbols* female, *closed symbols* male; *circles* suction-feeding, *squares* picking).

We used the selectivity index D as proposed by Jacobs (1974) for comparison of size selection under different conditions. D is a derivative of Ivlev's electivity index E and has the advantage of being insensitive for changes in relative frequencies of the resource population as a consequence of consumption. If r is the relative frequency of a certain size class in the diet and p the relative frequency of that size class in the resource population, then: $D = (r - p) / (r + p - 2rp)$. Values of D are between -1 and 1. If $D > 0$ that size class is preferred, if $D < 0$ that size class is selectively neglected. Because mussels were unequally distributed over size classes (see Fig. 3), calculations of the selectivity parameter D would be inaccurate in the lower and higher end of the size class range. To minimize this problem, size classes were pooled as follows: 1-6 mm, 7-10 mm, 11-12 mm, 13-14 mm, 14-16 mm, 17-20 mm, and 21-26 mm. Values of D were not significantly different between the three ducks for all size classes (ANCOVA, $F_2 = 1.33$, $P = 0.27$). Therefore, the data were lumped for further analyses.

Results

Profitability in relation to mussel size and handling technique

Handling time increased with mussel shell length (Fig. 1). Mussels larger than 15 mm in the case of the female and 17 mm in the male were picked up individually. Much time was spent orienting the large mussels in the bill to achieve a suitable position for swallowing. Mussels larger than 18 mm in the female and larger than 25 mm in the male caused increasing difficulties and about one third of these larger mussels were rejected after being handled for 10-20 s. The largest mussels eaten were 25 mm for the female and 30 mm for the male. Mussels up to about 16 mm were taken up in bouts, i.e. a number of mussels was collected in the bill, before they were swallowed. These smaller mussels were collected in a water-suction-flow generated by rapidly repeated tongue movements. Tufted Ducks sieving mussels in this way resemble dabbling ducks filtering seeds from water (Kooloos *et al.* 1989). The time spent handling mussels in a bout was linearly related to the number of mussels in that bout. The slope of each line represents the mean handling time per mussel, as shown in Fig. 1.

The two size-related handling techniques greatly affect the profitability of the mussels (Fig. 2). The

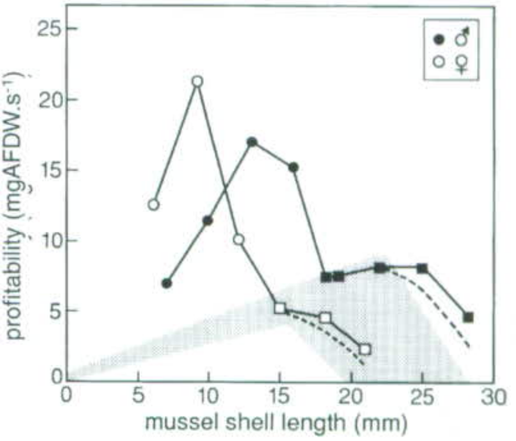

Fig. 2. Profitability curves of male and female duck (symbols as in Fig. 1). For comparison the range of profitability curves from Draulans (1984, 1987) is given (shaded area). Broken lines indicate profitability including rejected items.

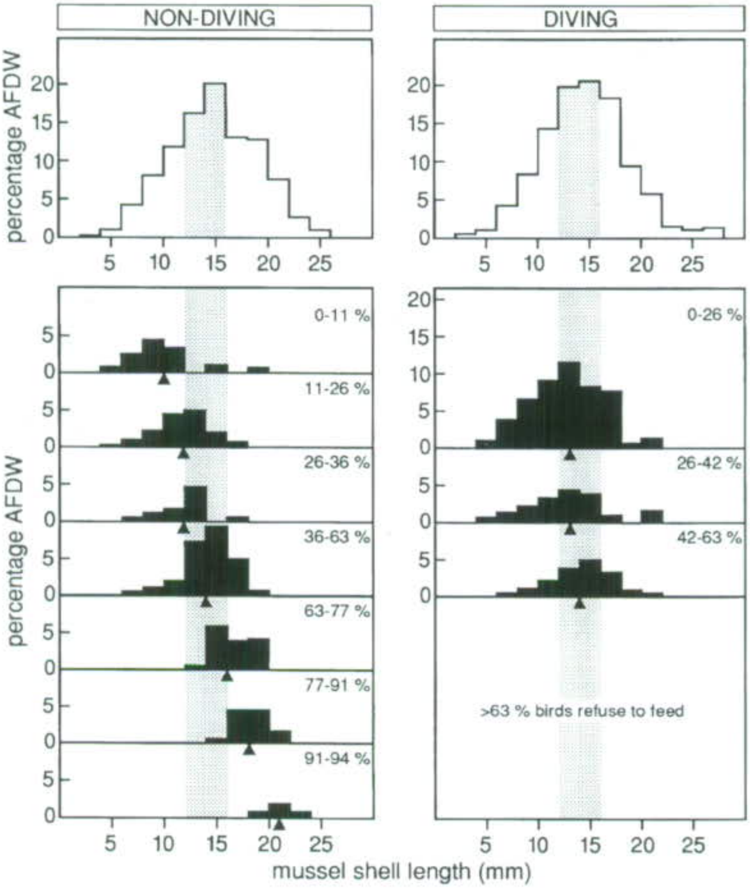

Fig. 3. Size selection from a field population of *Dreissena polymorpha* in a male duck in a non-diving situation (left) and a male duck diving to 1.25 m. The upper diagrams show the distribution of AFDW over size classes in the initial population (white). In the lower diagrams the fractions of AFDW taken from the initial population are shown in successive intervals of consumption (black) indicated by percentages. Triangles (▲) indicate the median mussel size per interval. Shaded areas show the most profitable size range (see Fig. 2)

peaks of the curves reflect the high intake rate of small mussels in a suction-flow. In the male bird, a second peak seems to appear, representing the individually handled larger mussels. The average profitability of the largest mussels was in fact lower than indicated, because they were sometimes rejected. Draulans (1984, 1987) found the highest profitability for the largest mussels. The high peak for small mussels in our curves did not show up in the experiments undertaken by Draulans, who offered mussels without water. His birds did not have the opportunity to generate a water-flow and, consequently, the profitability of small mussels was much lower. For larger mussels the curves in the two studies are in good agreement. In conclusion, in the presence of water, feeding on small mussels sieved from a suction-flow is more profitable than picking up individual, larger mussels.

Preference for mussel size under non-diving and diving conditions

Size selection of mussels from field populations is illustrated for a male duck eating from a dish (non-diving) and one diving to 1.25 m (Fig. 3). In the non-diving situation, the duck apparently chose the smallest

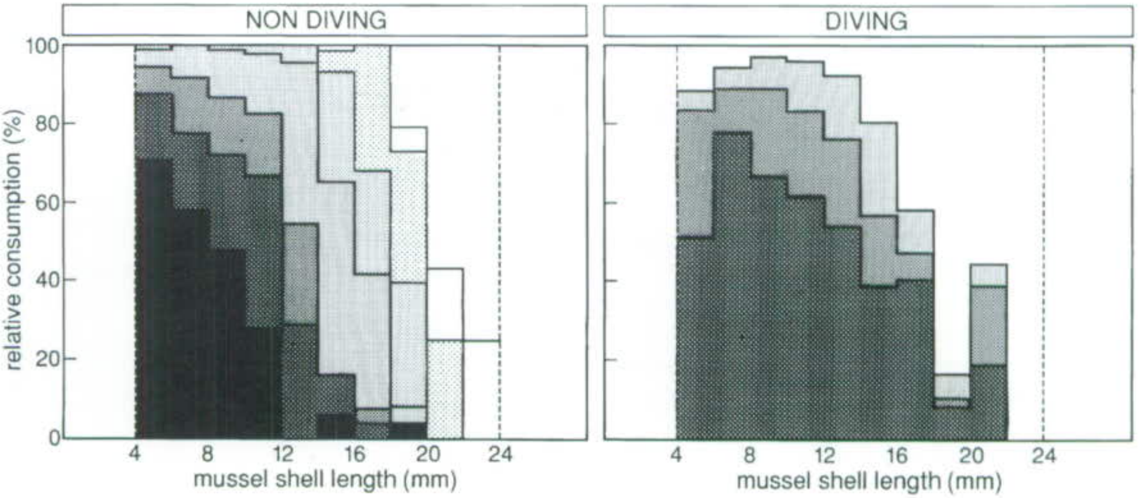

Fig. 4. Relative consumption of mussel sizes (cumulative percentages per size class) for a male duck in the non-diving situation (left) and a male duck diving to 1.25 m (right). Subsequent intervals of consumption (see Fig. 3) are ordered from dark to light.

mussels on offer and gradually took larger mussels, when the smaller ones became scarce. In the diving situation, a wider range of mussel sizes was taken and a shift towards larger mussels was not found. The relative consumption of size classes allows comparison of the two selection patterns (Fig. 4). The cumulative size distributions of the depletion intervals (computed on a AFDW basis) of 0-26% and 0-36% (0-42% in case of the diving situation), respectively, are significantly different between the non-diving and diving situation (Kolmogorov-Smirnov two sample test, $P < 0.001$ and $P < 0.05$, respectively), whereas the size distributions up to 63% (i.e. all small mussels are taken by suction-feeding in both situations) are not significantly different. Thus, in contrast to the clear shift from smaller to larger mussels in the non-diving situation, the diving bird continued to feed on all mussel sizes up to 16 mm. This pattern prevailed until almost all small mussels were taken. At that stage, the diving subjects refused to eat more mussels. The same patterns were found in the other birds of the two groups (non-diving and diving, respectively), indicating that differences in selection are due to diving, indeed, rather than to individual differences.

In the non-diving situation, the intake rate of mussels changed along with the shift in mussel sizes taken (Fig. 5). Intake rates increased, when on average larger mussels were taken, up to sizes of about 16 mm, whereupon intake rates dropped to a much lower level. The sharp decline in intake rates coincides with a change in handling technique: when mussels that can be strained from a suction-flow become scarce, the in-

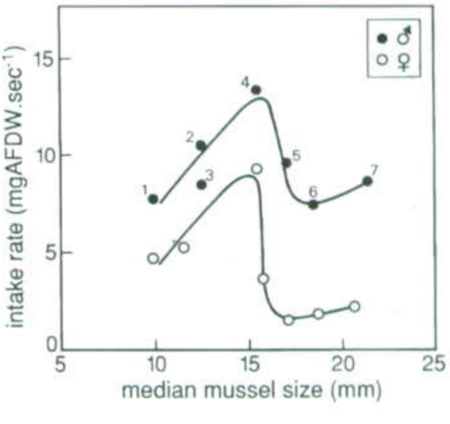

Fig. 5. Intake rates of mussels from a field population as a function of the median mussel size taken in successive intervals of consumption in the non-diving situation (● male, ○ female). Numbers correspond with successive intervals in Fig. 3 (left panel). Curves are fitted by eye.

take of small mussels becomes less efficient, presumably because of the interference of the progressively more abundant, larger mussels that must be picked up individually.

Selectivity under different diving conditions

Size selection under different conditions was compared by means of the selectivity parameter D (see Material and Methods). Linear regression analysis was used to determine whether resource depletion and diving depth influenced the selectivity for certain size classes. Resource depletion had no significant effect on the selectivity parameter D in all size classes ($P > 0.05$). Thus, the strategy of selection was independent of the abundance of the size classes, although the diving birds refused to eat when small mussels were no longer available (see Fig. 3). Selectivity was closely related to diving depth. A positive correlation was found for selectivity for the second, third, and fourth size class (7-10 mm, 11-12 mm, 13-14 mm, resp.; $P < 0.001$). Selectivity for the fifth size class (14-16 mm) was not related to diving depth ($P > 0.05$) and a negative correlation was found for the sixth size class (17-20 mm; $P < 0.05$). These relationships are illustrated in Figure 6. There were no significant correlations with diving depth for the first (1-6 mm) and seventh size class (21-26 mm), probably because of the low numbers of mussels on offer.

Figure 6 also shows a marked switchpoint in selectivity for mussel sizes of 15-16 mm, which, again, coincides with the switchpoint in handling techniques (see Fig. 2 and Fig. 5). In conclusion, the ducks became more selective towards the smaller mussels that could be handled in bouts when diving to greater

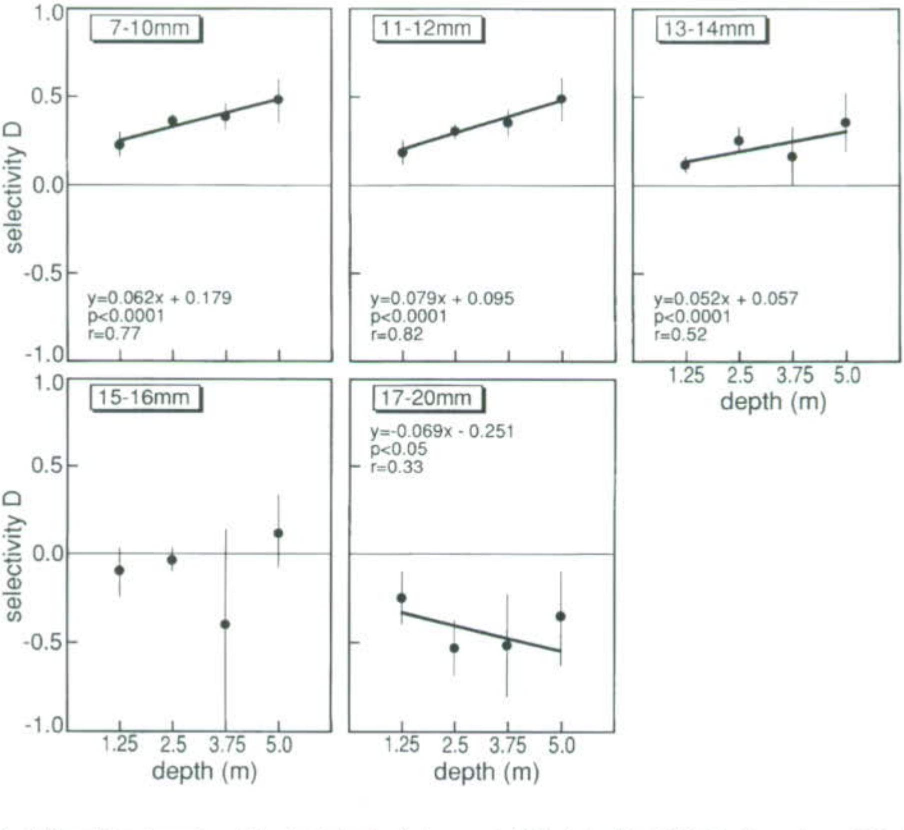

Fig. 6. Selectivity for different size classes in relation to diving depth (mean selectivity index D ± 1 SD). Positive values of D indicate preferred sizes. Significant changes in selectivity are indicated.

depths. This suggests a shift in the proportion of feeding on small mussels, using the 'suction-flow' technique, relative to the 'pick-up' technique for larger mussels.

Discussion

Profitability of suction-feeding

Small mussels proved to be most profitable in our study, due to the high intake rate of mussels by 'suction-feeding'. The implications of this technique on foraging behaviour can be considerable, although several criteria have to be met to allow suction-feeding. Prey items must be small and occur in high densities and, of course, they must be obtained from water. Draulans (1982) found that Tufted Ducks preferred smaller prey sizes (10-15 mm) when he offered mussels in a ditch with turbid water, than when mussels were offered on the border of the ditch without water (15-20 mm most preferred). Draulans believed that excluding visual cues in the former made the ducks choose conservatively smaller mussels in order to avoid the risk of taking mussels being too large to handle efficiently. Our data, however, show that the preference for smaller mussels can also be explained entirely by the higher profitability of small mussels, when obtained by suction-feeding in water.

Conditions of high densities of small, single food items are often met by diving ducks, for example in high densities of spat of *Dreissena polymorpha*, but also other food types, e.g. fry-eating Surf Scoters *Melanitta perspicillata* (Vermeer 1981) or Goldeneyes *Bucephala* spp. (Vermeer 1982). Pochard *Aythya ferina*, Scaup *Aythya marila*, Goldeneye, and Tufted Duck often feed on micro bivalves, *Pisidium* spp., small gastropods, *Hydrobia* spp., *Potamopyrgus* spp., benthic ostracods, or plant seeds (Madsen 1954, Olney 1963, Olney 1968, Nilsson 1972, own obs.). Thus, suction-feeding on small prey (< 5 mm) could be widespread. We believe that suction-feeding, as an alternative for consuming larger bivalve prey, opens up an extensive feeding niche for benthic feeding diving ducks.

Size selection and the costs of foraging

The selection patterns shown in Fig. 3 and 4 may indicate that Tufted Ducks select mussel sizes by indifferently accepting all mussels smaller than a certain threshold size. The opening at the bill tip determines which prey sizes can enter the bill (Kooloos *et al.* 1989) and thus sets the upper threshold of acceptance. In the non-diving situation, the ducks only accepted the smallest mussels available and the level of acceptance was raised in response to depletion of the smaller sizes. In the diving birds, the level of acceptance was fixed at a mussel size of about 16 mm, thus accepting all mussels that could be strained by suction-feeding. This foraging technique implies that small, less profitable mussels will also be sucked into the bill. Although small food items (diameter 2 mm) already grasped in the bill can be rejected concurrently with retaining larger items (Kooloos *et al.* 1989, Ball 1990), it might be time consuming or impossible to reject mussels of about 7-10 mm while retaining the most profitable sizes of 10-15 mm. Therefore, rejection of the smallest size classes may be unprofitable when suction-feeding.

In the non-diving situation, the ducks initially took smaller mussels than the most profitable sizes (Fig. 2 and 3). In the diving birds, however, the most profitable and most abundant sizes were also included in the diet. On average, the diving birds accepted larger prey than the non-diving birds. We found no individual differences within the two groups, suggesting that the differences in size selection were due to diving, indeed. Similarly, Ydenberg (1988) found that White-winged Scoters *Melanitta fusca* feeding at the water surface chose smaller Blue Mussels *Mytilus edulis* than when diving. Could this be a general difference between diving and non-diving animals? And if so, what can account for this discrepancy? In many studies, where non-diving birds preyed on relatively large bivalve prey, smaller items than the most profitable sizes were favoured, for example in all experiments carried out by Draulans (1982, 1984, 1987) on Tufted Duck and Pochard. Profitability is measured as the gross energy intake per unit handling time. The proper rationale, however, would be the net energetic gain per unit handling time, thus subtracting the costs of foraging from the energy gain (Stephens & Krebs 1986). The preference for the smaller prey sizes is probably a consequence of the habit of crushing the mussels in the gizzard. The energetic cost for crushing is related to shell thickness, thus favouring smaller mussels. On the other hand, the gullet might operate most efficiently, when it is filled with a mixture of prey sizes, as Ydenberg (1988) proposed. This 'mixed bag' hypothesis could explain the consumption of a few larger mussels in addition to the favoured, smaller ones. This is best shown in the diving situation (Fig. 3 and 4). However, an alternative hypothesis is available for taking additional large mussels by diving birds (see next section). It is interesting to note that size selection of Zebra Mussels by the ciprinid fish *Rutilus rutilus* (which is not time constrained by breathing trips to the water surface) could be explained by the ratio of crushing resistance of mussel shells and the energy content of mussels of different size (Prejs *et al.* 1990). Bustnes & Erikstad (1990) found that the flesh content relative to shell weight of Blue Mussels decreased with mussel size and suggested that Common Eiders *Somateria mollissima* selected small sizes to minimize the daily intake of shell material. Thus, mussels smaller than the size category assuring highest intake rates may in fact be more profitable in terms of net energy gain for the ducks in the non-diving situation.

Diving ducks have also to pay the costs of collecting food under water (the metabolic rate during submersion is about 3.5 the resting rate in the Tufted Duck, Woakes & Butler 1983), due to transit between surface and bottom and work to overcome buoyancy. An associated cost is the subsequent recovery period at the surface (again at 3.5 resting metabolic rate). The diving birds chose a diet in which all mussels up to 16 mm were included, thus increasing their intake rate. In doing so, the costs of collecting prey under water were minimized, but the birds accepted consequently higher costs of food processing (crushing shells and digestion) afterwards. The ducks in the non-diving situation interrupted foraging for about 10 minutes to unload the gullet by crushing the mussel shells, when approximately 15-20 g wet weight of mussels was taken. Based on this observation, diving ducks consuming about 1500 g wet weight each day may need up to 15 hours to process their food. Wild birds do not exceed 3 hours of diving time per 24 hours (Suter 1982). We believe that in general diving ducks minimize the time spent diving, thereby maximizing gross energy intake rate. Any extra time spent under water would increase the costs of foraging. The expected lower efficiency of crushing and digestion (e.g. Speakman 1987, Dade *et al.* 1990) might be compensated by longer intervals between foraging bouts to process food, thus extending the period of foraging.

Foraging strategy in response to short dive times

Selectivity for the smaller size classes increased with diving depth and no effect of mussel density was found. These findings seem to contradict results of field experiments of Draulans (1982), who found less selective prey choice with increasing diving depth and lower densities of mussels. In the field experiments carried out by Draulans (1982), however, mussels were attached in clumps. Mussel sizes are unequally distributed in clumps (smaller ones closer to the edge) and clumps as a whole can be taken to the surface (own observations), limiting the choice of prey sizes. Thus, selectivity may depend on the number of mussels taken per clump, which in turn may depend on diving depth. Therefore, feeding on clumps is complicated and should be further studied.

Considering the way different sized mussels are handled according to our observations (small mussels up to 16 mm in a suction-flow versus picking up larger mussels), we may expect that these handling techniques are mutually exclusive (see Fig. 5). Handling large mussels may occur while surfacing, as is the case for example in mussel-feeding White-winged Scoter (Ydenberg 1988), Scaup (own observations) and Common Eider (Swennen 1976). Large mussels can be picked up at the bottom (one at a time) and handled at the surface without extra costs for diving. Draulans (1982), however, has already suggested that Tufted Ducks may prefer smaller sizes, when time at the bottom is limited, because several small items would yield more energy per dive than a single large food item. For species like Tufted Duck, adapted to take small prey, a functional strategy would be taking up small mussels in a run first and at the end, when bottom time is nearly over, pick up a larger one. The timing of taking a particular prey size can be explained in terms of lost opportunity (Stephens & Krebs 1986). Taking a large item at the beginning of a dive would prohibit taking any more mussels in a dive and is thus not the optimal strategy. Not taking a large item at the end of a dive is unprofitable, because no further diving costs are required to get the extra food item. Observations by means of a video-camera mounted just above the tray with mussels showed that Tufted Duck do indeed feed in runs and that larger items are taken to the surface (unpublished data). It was also found that the time spent foraging at the bottom increased with diving depth. Wilson & Wilson (1988) regard diving birds as central-place-foragers (Orians & Pearson 1979) and predicted that diving birds should increase their foraging time under water at greater depths in order to use their dive time most efficiently. We suggest, therefore, that selectivity for small size classes increased with diving depth, because in deeper dives more time was spent to take small mussels in a run, before a large mussel was picked up.

Analyses of gullet contents of a variety of diving ducks, such as Goldeneye, species of the genus *Aythya*, Common Scooter *Melanitta nigra*, and Eider, show that food items smaller than 10 mm are most frequently ingested (on weight basis), while most individuals consume few items larger than 15 mm (e.g. Madsen 1954, Olney 1963, Olney 1968, Nilsson 1972). This implies that observations on (large) prey handled at the surface are likely to underestimate both diet diversity and food intake rates.

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References

Ball, J.P. 1990. Active diet selection or passive reflection of changing food availability: the underwater foraging behaviour of Canvasback Ducks. In: R.N. Hughes (Ed) Behavioural Mechanisms of Food Selection (NATO ASI Series G20): 95-107. Springer, Berlin Heidelberg New York.

Bij de Vaate, A. 1991. Distribution and aspects of population dynamics of the Zebra Mussel *Dreissena polymorpha* (Pallas 1771) in the lake IJsselmeer area (The Netherlands). Oecologia 86: 40-50.

Bustnes, J.O. & K.E. Erikstad 1990. Size selection of Common Mussels *Mytilus edulis* by Common Eiders *Somateria mollissima*: energy maximization or shell weight minimization? Can. J. Zool. 68: 2280-2283.

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

Dewar, J.M. 1924. The bird as a diver. Witherby, London.

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

Draulans, D. 1984. Suboptimal mussel selection by Tufted Ducks *Aythya fuligula*: test of a hypothesis. Anim. Behav. 32: 1192-1196.

Draulans, D. 1987. Do Tufted Duck and Pochard select between differently sized mussels in a similar way? Wildfowl 38: 49-54.

Draulans, D. & A.F. De Bont 1980. Een analyse van het duiken naar voedsel van de Kuifeend *Aythya fuligula* buiten het broedseizoen. Gerfaut 70: 251-260.

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

Kehoe, F.P., C.D. Ankney & R.T. Alikauskas 1988. Effect of dietary fiber and diet diversity on digestive organs of captive Mallards *Anas platyrhynchos*. Can. J. Zool. 66: 1597-1602.

Kooloos, J.G.M., A.R. Kraaijeveld, G.E.J. Langenbach & G.A. Zweers 1989. Comparative mechanics of filter feeding in *Anas platyrhynchos*, *Anas clypeata* and *Aythya fuligula* (*Aves: Anseriformes*). Zoomorphology 108: 269-290.

Kooyman, G.L. 1989. Diverse Divers, Physiology and Behavior. Springer, Berlin Heidelberg New York.

Lucas, J.R. 1990. Time scale and diet choice decisions. In: R.N. Hughes (Ed) Behavioural Mechanisms of Food Selection (NATO ASI Series G20): 165-185. Springer, Berlin Heidelberg New York.

Madsen, F.J. 1954. On the food habits of diving ducks in Danmark. Dan. Rev. Game Biol. 2: 157-266.

Nilsson, L. 1972. Habitat selection, food choice, and feeding habits of diving ducks in coastal waters of South Sweden during the non-breeding season. Ornis Scand. 3: 55-78.

Orians, G.H. & N.E. Pearson 1979. On the theory of central place foraging. In: D.J. Horn, R.D. Mitchell & G.R. Stairs (Eds) Analysis of Ecological Systems: 154-177. Ohio State University Press, Columbus.

Olney, P.J.S. 1963. The food and feeding habits of Tufted Duck *Aythya fuligula*. Ibis 105: 55-62.

Olney, P.J.S. 1968. The food and feeding habits of Pochard *Aythya ferina*. Biol. Cons 1: 71-76.

Pedroli, J.C. 1981. Les relations entre la Moule Zebree *Dreissena polymorpha* et les oiseaux aquatiques. PhD thesis, University of Neuchâtel.

Prejs, A., K. Lewandowski & A. Stanczykowska-Piotrowska 1990. Size-selective predation by Roach *Rutilus rutilus* on Zebra Mussel *Dreissena polymorpha*: field studies. Oecologia 83: 378-384.

Speakman, J.R. 1987. Apparent absorption efficiencies for Redshank *Tringa totanus* and Oystercatcher *Haematopus ostralegus*: implications for the predictions of optimal foraging models. Am. Nat. 130: 677-691.

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

Suter, W. 1982. Vergleichende Nahrungsökologie von überwinternden Tauchenten *Bucephala*, *Aythya* und Blässhuhn *Fulica atra* am Untersee-Ende/ Hochrhein (Bodensee). Orn. Beob. 79: 225-254.

Swennen, C. 1976. Populatie-structuur en voedsel van de eidereend *Somateria m. mollissima* in de Nederlandse Waddenzee. Ardea 64: 311-371.

Vermeer, K. 1981. Food and populations of Surf Scoters in British Columbia. Wildfowl 32: 107-116.

Vermeer, K. 1982. Food and distribution of three *Bucephala* species in British Columbia waters. Wildfowl 33: 22-30.

Willi, P. 1970. Zugverhalten, Aktivität, Nahrungserwerb auf dem Klingnauer Stausee häufig auftretender Anatiden, insbesondere von Krickente, Tafelente und Reiherente. Orn. Beob. 67: 183-217.

Wilson, R.P. & M.P.T. Wilson 1988. Foraging behaviour in four sympatric cormorants. J. Anim. Ecol. 57: 943-955.

Woakes, A.J. & P.J. Butler 1983. Swimming and diving in Tufted Ducks *Aythya fuligula* with particular reference to heart rate and gas exchange. J. Exp. Biol. 107: 311-329.

Ydenberg, R.C. 1988. Foraging by diving birds. In: H. Ouellet (Ed) Acta XIX Congressus Internationalis Ornithologici (Vol. II): 1832-1842. University of Ottawa Press, Ottawa.

Chapter 4

Adjustments in the diving time budgets of Tufted Duck and Pochard: is there evidence for a mix of metabolic pathways

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Adjustments in the diving time budgets of Tufted Duck and Pochard: is there evidence for a mix of metabolic pathways

Predictions of models for the optimal allocation of time over the dive cycle for divers using aerobic and anaerobic respiration, were tested using experimental data on the Tufted Duck *Aythya fuligula* and Pochard *A. ferina*. Patterns in the dive cycle were highly correlated with water depth. In both species, foraging time increased with water depth up to 3 m. In the Pochard, foraging time subsequently declined before increasing again at around 4 m. Qualitatively similar patterns in foraging time are predicted by the model based on the use of aerobic and anaerobic respiration, the 'mixed metabolism' model. As predicted by this model and previous 'aerobic' models, foraging time decreased in response to increasing substrate depth (used to increase foraging costs), while surface time was not affected. Paddle rates, used as an indicator of foraging costs, however, did not increase. In response to lower water temperature (used to increase the energetic costs of both the travel and foraging phases of the dive), surface times increased as predicted, except at the shallowest depth class. The predicted relationship between foraging time and diving costs is complex, being dependent on water depth and a number of other parameters; the observed trends were non-significant. Ascent duration was found to decrease with decreasing water temperature, but no significant changes occurred in descent duration. Estimates of paddle rates and travel speeds suggest that foraging is on average more costly than travelling (ascent and descent combined), diving costs decrease with depth and travel speeds change subtly with depth.

Introduction

While divers are believed to rely predominantly on aerobic respiration, there is considerable evidence that they may combine aerobic and anaerobic respiration during extended dives (Jones *et al.* 1988, Ydenberg & Forbes 1988, Kooyman 1989, Ydenberg & Clark 1989, Croll *et al.* 1992, Stephenson *et al.* 1992, Chappell *et al.* 1993, Stephenson 1994).

We previously presented models (Houston & Carbone 1992) predicting the manner in which aerobic divers allocate time over the dive cycle (see also Carbone & Houston 1994). In Carbone & Houston (1996), we extended this work to include the use of two metabolic pathways. The 'mixed metabolism' model assumes a simultaneous use of the two pathways. This model provides predictions for deep water dives of long duration. In this paper, we test a number of qualitative predictions from both the previous 'aerobic' and 'mixed metabolism' models using the results from diving experiments on two species of diving duck, the Tufted Duck *Aythya fuligula* and Pochard *A. ferina*. The experiments were conducted at depths up to 5.5 m under conditions that allowed for detailed observation of underwater behaviour.

During a foraging bout, divers make repeated trips between the underwater foraging site and the water surface. We subdivide this into three periods of the dive cycle: foraging time (at the underwater feeding site), surface time (recovery) and return travel time (from the surface to the feeding site and back). We assume that divers aim to maximize the proportion of time of the dive cycle devoted to foraging. Both types of dive models are based on balancing either oxygen load or anaerobic metabolite load over the dive cycle. These models also assume a decrease in rates of uptake of oxygen (or rates of anaerobic metabolite assimilation) with the amount of oxygen or metabolite acquired (see also

Kramer 1988). Thus, higher rates are achieved when the diver maintains smaller loads of oxygen or metabolite in the body. The predicted time budgets are strongly influenced by travel time (related to water depth) and rates of energy use underwater, but are not particularly sensitive to food intake (Houston & Carbone 1992, Carbone & Houston 1994).

The qualitative predictions of the 'mixed metabolism' model vary substantially depending on the parameter values (Carbone & Houston 1996). Given moderate differences in the efficiency of aerobic and anaerobic respiration, the patterns against travel time are qualitatively similar to the previous 'aerobic' models. When large differences in efficiency are assumed, however, there is a 'doubling' of the general patterns observed in the previous models. Thus, in the 'mixed metabolism' model, patterns in foraging time with travel time range from having a single peak (as in the previous models) to having a second peak before the final decline. The corresponding pattern in surface time changes from having one region where surface time increases abruptly (near the combined aerobic-anaerobic dive limit) to having two such regions, one at the depth where the second peak in foraging time begins, and a second around the diver's combined aerobic-anaerobic limit (Figure 3a,c in Carbone & Houston 1996).

The 'aerobic' models predict that increasing the costs of foraging reduces foraging time for all depths, without influencing surface time, while increasing foraging and travel costs results in both a decrease in foraging and an increase in surface time (Houston & Carbone 1992). These same predictions hold for the 'mixed metabolism' model except where the pattern in foraging time has two peaks. In this instance, the predicted patterns are difficult to test qualitatively because an increase in foraging and travel costs may either decrease or increase foraging time depending on the water depth (Figure 8a-c in Carbone & Houston 1996).

The diving experiments were designed to provide qualitative tests of a number of these predictions. We examined the effect of water depth, water temperature and substrate depth. Water depth was varied to test the effect of increasing travel time. Water depth experiments were also conducted under a range of water temperatures to test the effects of different rates of underwater energetic expenditure through the loss of body heat ('water temperature experiments'; e.g. Kooyman *et al.* 1976, Wilson *et al.* 1992). Substrate depth was used to vary energetic expenditure while foraging (repeated from Carbone & Houston 1994). Additionally, paddle rates and travel speeds were used to provide crude estimates of levels of buoyancy and energetic expenditure while foraging.

Methods

We conducted the experiments between 17 April 1993 and 25 March 1994, in an indoor aquarium at the Konrad Lorenz Institute, Vienna, Austria. The ducks were obtained from wildfowl breeders, and were allowed at least 8 weeks to acclimatize to the experimental conditions during which time they lived in the experimental tank. The aquarium building was maintained at approximately room temperature. Experimental trials in the evening were conducted under artificial light, otherwise the birds were kept under a natural light regime. Twelve Tufted Duck (six males, six females) and seven Pochard (three males and four females) were trained, although not all of these participated in all of the experiments. The experiments were conducted in the main section of the tank which was circular (diameter of 3.9 m) and 5.7 m deep. An additional section of the aquarium (2.6 m long, by 2.5 wide, by 1.0 m in depth) was partitioned from the experimental chamber and was used to hold non-experimental birds during the experiments.

The Tufted Duck were provided with a background diet of wheat, duck pellets and grit. During the experiments the birds were fed mealworms, which they appeared to prefer to their background diet. For the Tufted Duck, the background food was withheld until the experiments were completed (for a minimum of 2 h). The Pochard received several trials in a day (up to six), and so were only given experimental food during this period.

A tray 1.1 m^2 in area by 16 cm deep was suspended in the centre of the experimental section of the tank (Fig 1). This could be adjusted to different water depths from two sets of ropes and pulleys. The mealworms were divided into roughly equal amounts and placed in four 0.25 m^2 sub-trays, which were placed within the main tray. The sub-trays were lined at the bottom with a fine metal mesh which allowed water to

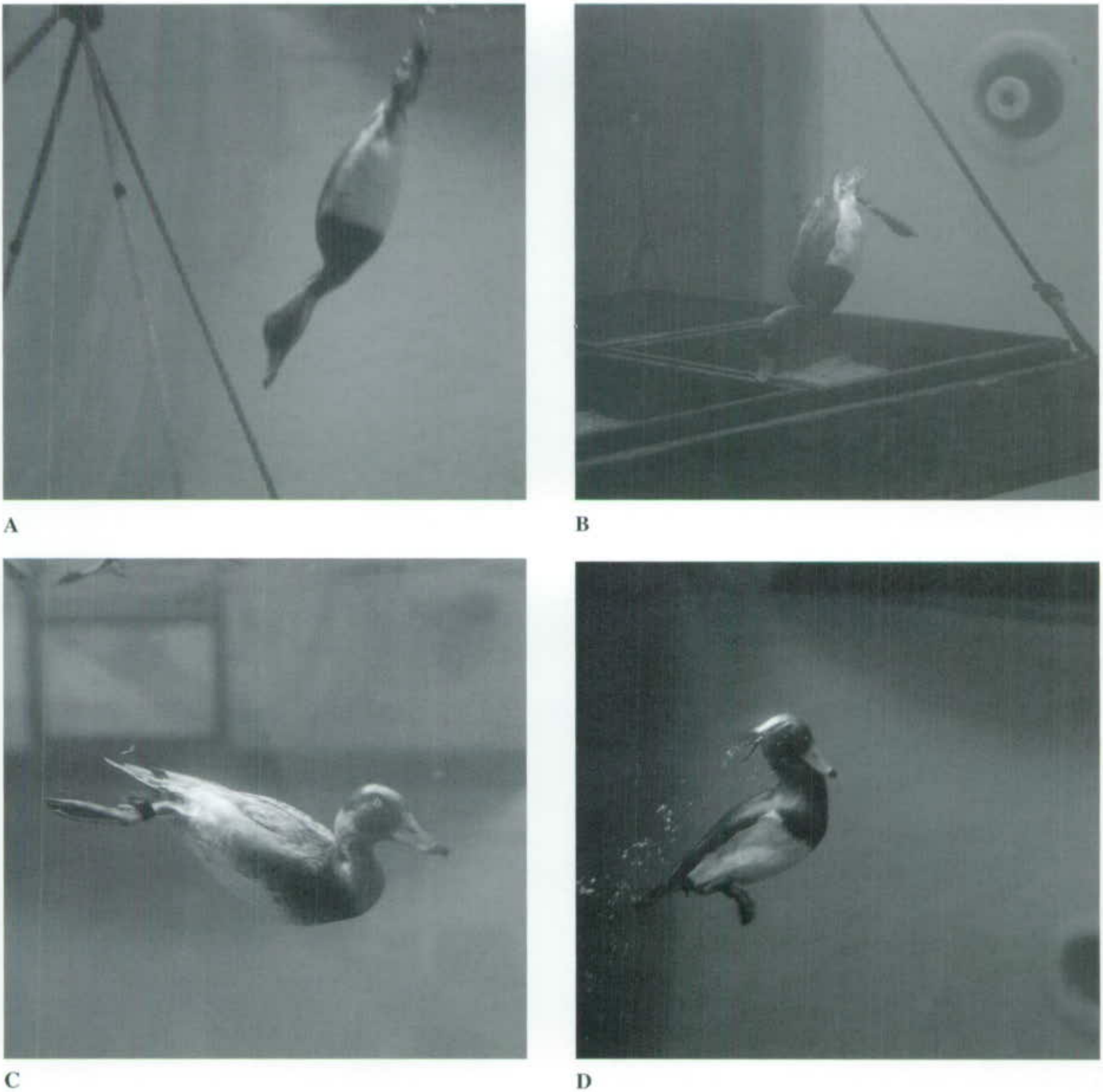

Fig. 1. Tufted Duck feeding underwater in the experimental diving tank. **A.** Descending to the feeding tray. **B.** Feeding on mealworms at the tray. **C.** Turning its body position from head-down during feeding to head-up during ascent. **D.** Ascending passively to the surface through buoyancy. The air bubbles around the head are respiratory gas expired prior to surfacing.

pass through, making them lighter to handle. During the water depth and sand depth trials, mealworms were spread evenly across the bottom of the sub-trays and then covered with sand. During the water temperature and paddle rate experiments, the food was left uncovered on top of the sand.

Trials were performed individually for the Tufted Duck and in groups for the Pochard (see below). The assignment of the trials was according to a stratified-random schedule. In the water depth trials for the Tufted Duck, all trials on a given day were conducted at the same depth. We monitored the birds using two video cameras, one placed at the surface and another placed in front of a window near the food tray. The images from the cameras along with sound recorded with an underwater microphone and a time code (0.1 s accuracy) were mixed down onto a single video recorder via a Panasonic digital AV video mixer, which was in a room adjacent to the experimental area. The descent, foraging, ascent and surface periods could be clearly heard through the monitor (see also Carbone & Houston 1994). Although visibility conditions were generally excellent, we occasionally required the audio recordings when birds were momentarily out of the field of view of the cameras. We monitored duration of each stage of the dive cycle either directly during the experiments using the monitor (sand depth experiments only), or by use of a video player with a toggle control and the time code accurate to 0.1 s. These records were then logged onto a personal computer. To determine an appropriate maximum duration for surface time, we conducted a bout criterion interval analysis (Martin & Bateson 1988) on two separate databases, both of which suggested that 35 s was an appropriate (conservative) value (this differs from the 20 s maximum used in Carbone & Houston 1994). In the Tufted Duck depth trials this resulted in the removal of only 30 (2.0%) of a total 1460 recorded surface times. All trials conducted on individual birds were stopped when the bird became distracted from feeding after completing a bout of dives. As in Carbone & Houston (1994), we did not observe any consistent changes in diving time budgets during the trial period due to possible changes in motivation (e.g. satiation).

During the sand depth trials, the mealworms remaining at the end of the trial were sifted from the sand and counted. By calculating the total foraging time and the number consumed during a trial, we could determine the average rate of food intake while at the food tray.

Water depth experiment

This experiment was designed to determine the effects of water depth on the duration of stages of the dive cycle. The trials were conducted at 0.5 m (Pochard) or 1.0 m (Tufted Duck) depth intervals ranging from a depth of 0.5 m to 5.5 m (Pochard) and 4.5 m (Tufted Duck). By the end of the experiment, each bird (with a few exceptions) had been tested at all depths. Water temperatures ranged from 8.0 to 12.0 °C.

The Tufted Duck performed the trials individually, usually one trial for each bird per day (12 birds). The duration of these trials varied depending on the behaviour of the bird. In these experiments, the tray con-

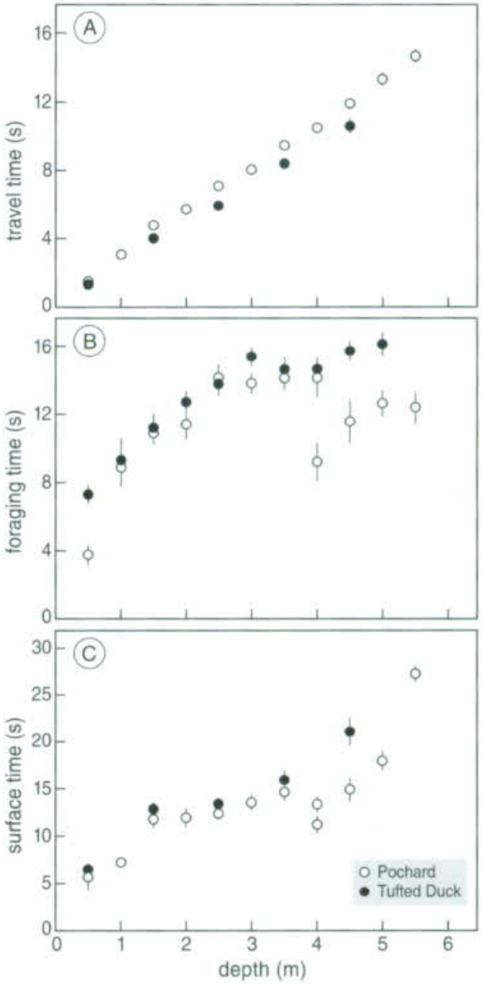

Fig. 2. Average time budgets (± SE) against water depth for the Pochard and Tufted Duck. **A.** Return travel time. **B.** Foraging time. **C.** Surface time. Each point is the average of 12 Tufted Duck (except preliminary data on foraging time) or 7 Pochard for a particular depth.

tained 26.0 g live weight of mealworms (approximately 300) which were covered with 2.0 cm of sand and renewed after each trial. Additional water depth data on Tufted Duck foraging times from preliminary trials were included for comparison (Fig. 2b). We could not, however, compare surface times from the preliminary trials, as these were not obtained.

The Pochard were more nervous in these experiments and so were not tested individually, but instead performed the trials as a group. Seven birds (three males and four females) completed these experiments. The birds were given 100 g live weight of mealworms (approximately 1150) which was renewed after each trial. The time budgets of each bird (identified from coloured leg rings and sex) were determined after the trials from the video recordings. These trials were allowed to continue for between 2 and 3 h, during which time the food would have been almost completely consumed. Feeding activity occurred in bouts, with intermittent periods of rest. All surface times of greater than 35 s were excluded (see above). We repeated the trials at 4.0 m because of a temporary difficulty with visibility through the glass. The data from the original trial were readable from the video recording. As the mean for the repeat trial (under conditions of better visibility) was significantly lower than the original, both sets of data are presented in the analysis (see below).

Sand depth experiment

Sand depth was used to manipulate rates of energy expenditure while foraging, but it also influences the rates of food intake (Carbone & Houston 1994). We monitored foraging paddle rates to provide an approximate estimate of energy expenditure. We used two depths of sand: 2.0 and 4.0 cm. The food tray contained 26.0 g live weight of mealworms and was lowered to a depth of 3.5 m. Ten Tufted Duck (five males, five females) completed this experiment. Water temperatures ranged from 12.0 to 13.0 °C.

Water temperature experiment

The lowest water temperatures after refilling the tank were around 6.0 °C, but over approximately 2-3 weeks this increased to approximately 21.0 °C, providing a range of temperatures for the experiments. We pooled the data for temperatures of 7-11 °C ('low') and 20-23 °C ('high'), and conducted the experiment at three depths; 1.0 m, 3.0 m and 5.0 m. Five Tufted Duck (two males, three females) completed this experiment.

Paddle rate and travel speed experiment

Another set of water depth experiments were conducted at depths of 3.3 m and 5.5 m. In these experiments we estimate descent and ascent speeds and paddle rates (during descent and foraging), by using a third camera placed in a horizontal position in front of a viewing panel at the 2.5 m mark. We measured the number of paddles and durations of descent from the surface to the first 2.5 m and then from 2.5 m to the final depth (either 3.3 m or 5.5 m). Corresponding data on ascent durations were also obtained. We calculated descent and ascent speeds and paddle rates from these data. Five Tufted Duck (two males, three females) completed this experiment.

Statistical analysis

We used repeated measures ANOVA to test variation in time budgets with water depth and water temperature. In the Pochard data, one female (with the least data) and the first trial at 4.0 m were removed for the ANOVA in order to balance the design (this female was included for other analyses). Subjects were nested in sex and cross factored against depth or temperature (sex was not treated as a factor in the water temperature analysis). Linear and polynomial regression and paired t-tests (two-tailed) were also used in the analysis

Results

Effect of depth

For both the Pochard and Tufted Duck, all diving time budgets were correlated with depth (Fig. 2a-c). Changes in return travel time with depth were strongly linear (Fig. 2a), suggesting that rates of travel were approximately constant (repeated measures ANOVA: Tufted Duck: Depth, $F_{4,58} = 471.4$, $P < 0.0001$; Sex, $F_{1,10} = 0.53$, NS; Sex x Depth, $F_{4,58} = 0.49$, NS; Pochard: Depth, $F_{10,64} = 449.3$, $P < 0.0001$; Sex, $F_{1,4} = 0.74$, NS; Sex x Depth, $F_{10,64} = 0.49$, NS).

Mean foraging duration was also highly correlated with depth in both species (Fig. 2b; repeated measures ANOVA: Tufted Duck: Depth, $F_{4,58} = 61.9$,

$P < 0.0001$; Sex, $F_{1,10} = 1.74$, NS; Sex x Depth, $F_{4,58} = 0.61$, NS: Pochard: Depth, $F_{10,64} = 26.1$, $P < 0.0001$; Sex, $F_{1,4} = 6.3$, $P < 0.1$; Sex x Depth, $F_{10,64} = 1.47$, NS). The patterns in foraging time in the Pochard and Tufted Duck were both significantly non-linear. In the Pochard database, there were significant differences in the two sets of trials conducted at 4.0 m (paired *t*-test: mean difference = -5.04, $t = -4.47$, $df = 6$, $P = 0.004$). We decided, therefore, to conduct two separate analyses for each of these trials (Fig. 3 a, b). In both sets of analysis, significantly more variation was explained by a third order polynomial than a second order polynomial (with original 4.0 m trial: $Y = -1.45 + 12.26x - 3.11x^2 + 0.24x^3$; x, $P = 0.0001$; x^2, $P = 0.0002$; x^3, $P = 0.0061$, Fig. 3a; with repeat 4.0 m trial: $Y = -2.96 + 15.40x - 4.63x^2 + 0.43x^3$; x, $P = 0.0001$; x^2, $P = 0.0001$; $x^{3\cdot}$ $P = 0.0001$; Fig 3b). A similar pattern was found in the mean foraging times of the Tufted Duck, although the third order polynomial was non-significant (preliminary data included; $Y = 3.75 + 7.39x - 1.71x^2 + 0.14x^3$, x, $P = 0.0002$; x^2, $P = 0.037$; x^3, $P = 0.14$, second order polynomial: $Y = 2.56 + 5.34x - 0.55x^2$; x, $P = 0.0001$; x^2, $P = 0.002$; see Fig. 2b).

Surface durations in both species were highly correlated with water depth and significantly non-linear (Fig. 2c). In the Pochard the interaction between sex and depth was significant (repeated measures ANOVA: Tufted Duck: Depth, $F_{4,58} = 55.3$, $P < 0.0001$; Sex,

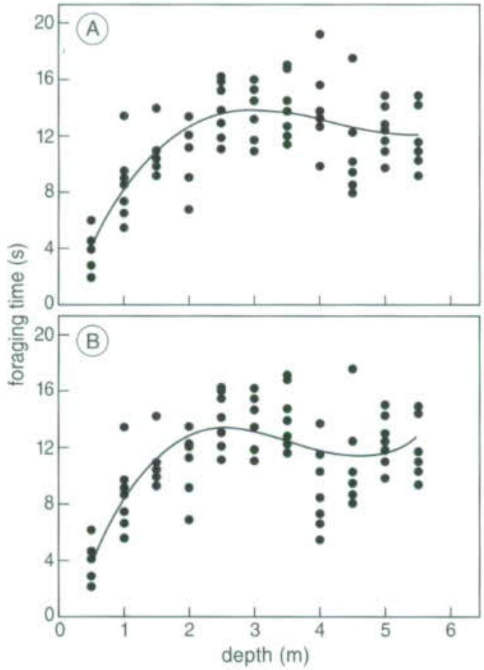

Fig. 3. Polynomial regression analysis of Pochard foraging time against water depth (trial means), **A.** including original 4.0 m trials and **B.** including repeat 4.0 m trials. See text for details.

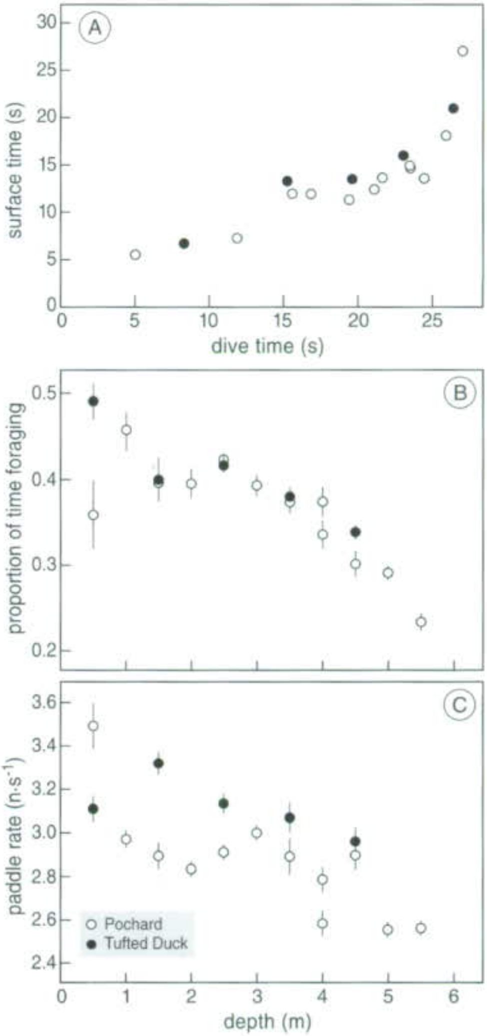

Fig. 4. Average (± SE) surface time against dive time (**A.**) and proportion of time foraging (**B.**) and paddle rate (**C.**) against water depth. Each point is the average of 12 Tufted Duck, or seven Pochard for a particular depth.

$F_{1,10}$ = 0.45, NS; Sex x Depth, $F_{4,58}$ = 1.25, NS; Pochard: Depth, $F_{10,64}$ = 52.8, $P < 0.0001$; Sex, $F_{1,4}$ = 0.57, NS; Sex x Depth, $F_{10,64}$ = 2.95, P = 0.007). In both species, a third order polynomial explained significantly more of the variation than a second order polynomial (Tufted Duck: $Y = 0.72+14.06x-5.21x^2 + 0.69x^3$, x, P = 0.0004; x^2, P = 0.004; x^3, P = 0.004, Pochard: $Y = -2.91 + 17.32x-6.36x^2 + 0.76x^3$, x, P = 0.0001; x^2, P = 0.0001; x^3, P = 0.0001).

There was a significant decline in the proportion of time spent foraging with water depth in both species (repeated measures ANOVA: Tufted Duck: Depth, $F_{4,58}$ = 17.6, $P < 0.0001$; Sex, $F_{1,10}$ = 1.26, NS; Sex x Depth, $F_{4,58}$ = 1.49, NS; Pochard: Depth, $F_{10,64}$ = 14.2, $P < 0.0001$; Sex, $F_{1,4}$ = 5.69, $P < 0.01$; Sex x Depth, $F_{10,64}$ = 0.43, NS; Fig. 4a).

Figure 4b shows surface time against the dive duration for the purpose of comparison with other diving studies, and because it is commonly used as an indicator of a shift to anaerobic respiration (see below).

The paddle rates while foraging declined with water depth in both species (Fig. 4c). In the Pochard, males had significantly higher paddle rates (repeated measures ANOVA: Tufted Duck: Depth, $F_{4,58}$ = 12.0, $P < 0.0001$; Sex, $F_{1,10}$ = 1.57, NS; Sex x Depth, $F_{4,58}$ = 1.36, NS; Pochard: Depth, $F_{10,64}$ = 26.5, $P < 0.0001$; Sex, $F_{1,4}$ = 8.73, $P < 0.05$; Sex x Depth, $F_{10,64}$ = 0.44, NS).

Effect of sand depth

The Tufted Duck significantly reduced the time spent foraging in response to increasing sand depth, but surface time was not affected (Table 1). Paddle rates (used as an approximate measure of energy expenditure), however, did not increase significantly in response to an increase in sand depth. Consumption rates declined significantly as sand depth increased.

Table 1. Average (±SE) duration (s) and paddle and consumption rates (n.s^{-1}) of Tufted Duck feeding at sand depths of 2.0 cm and 4.0 cm.

	Sand depth			
	2.0 cm	4.0 cm	*t*	*P*
Foraging time	16.1 (0.6)	13.5 (0.7)	4.13	0.003
Surface time	18.2 (1.6)	17.4 (1.9)	0.60	NS
Paddle rate	3.06 (0.07)	3.03 (0.06)	0.34	NS
Consumption rate	0.46 (0.03)	0.14 (0.03)	4.95	0.0008

Water depth of 3.5 m, *t*- and *P*-values refer to paired *t*-tests, two-tailed. *N* = 10 (Tufted Duck).

Table 2. Average (±SE) duration (s) of different phases of the dive cycle of Tufted Duck diving at low and high water temperatures.

Depth (m)		Water temperature			
		7.0-11.0 ºC	20.0-22.0 ºC	*t*	*P*
Descent	1	1.57 (0.11)	1.68 (0.09)	1.44	NS
	3	4.48 (0.34)	4.73 (0.38)	1.00	NS
	5	7.58 (0.64)	7.39 (0.51)	0.75	NS
Foraging	1	7.47 (0.68)	8.32 (0.71)	0.95	NS
	3	12.45 (1.24)	11.72 (1.07)	1.15	NS
	5	12.47 (1.17)	12.91 (1.74)	1.60	NS
Ascent	1	1.71 (1.11)	1.81 (0.12)	1.79	NS
	3	3.56 (0.20)	4.44 (0.24)	7.18	0.002
	5	5.26 (0.50)	6.35 (0.62)	5.26	0.005
Surface	1	10.03 (0.27)	12.00 (0.91)	2.26	NS
	3	17.13 (1.14)	15.18 (1.07)	4.65	0.018
	5	21.41 (2.36)	17.40 (2.01	4.58	0.01

t- and *P*-values refer to paired *t*-tests, two-tailed. *N* = 5 (Tufted Duck).

Effect of water temperature

Water temperature did not have a significant effect on descent duration (Table 2). Ascent duration, however, was significantly less at low temperatures, except at 1.0 m. No significant trends in foraging time were observed, but surface time increased significantly in response to decreasing temperature except at 1.0 m.

Paddle rates and travel speeds

An analysis of the paddle rates and travel speeds suggests that energy expenditure and travel speed change with water depth (Table 3). Paddle rates during the descent were significantly lower after 2.5 m than from the surface to 2.5 m. Descent speeds were consistently higher during the first stage of the descent, but these differences were not significant. Ascent speeds were significantly higher in the second phase of the ascent in both the 3.3 and 5.5 m trials, suggesting greater buoyancy at shallow depths.

Table 3. Average (±SE) paddle rate ($n.s^{-1}$), descent and ascent speeds ($m.s^{-1}$) for the paddle rate and descent speed experiments. Travel period is divided into 'upper range' (0-2.5 m) and the 'lower range': remaining distance to the food tray (either 3.3 m or 5.5 m).

Depth (m) of food tray		Depth range Upper	Lower	*t*	*P*
Paddle rate					
Descent	3.3	4.53 (0.097)	4.01 (0.093)	3.65	0.022
	5.5	4.57 (0.079)	3.88 (0.096)	9.24	0.0008
Speed					
Descent	3.3	0.748 (0.061)	0.690 (0.039)	1.50	NS
	5.5	0.782 (0.064)	0.694 (0.054)	2.19	0.094
Ascent	3.3	1.67 (0.088)	0.822 (0.067)	13.59	0.0002
	5.5	1.16 (0.087)	0.940 (0.067)	5.68	0.0047

t- and *P*-values refer to paired *t*-tests, two-tailed. $N = 5$ (Tufted Duck).

Descent speeds during the first phase of descent were faster in the trials at 5.5 than at 3.3 m (paired *t*-test: mean difference = -0.034; $t = 3.30$, $df = 4$, $P = 0.03$; Table 3). While there were no differences in descent paddle rates (paired *t*-test: mean difference = -0.044; $t = 1.44$, $df = 4$, NS), paddle rates during foraging were significantly lower at 5.5 m than at 3.3 m (paired *t*-test: mean difference = 0.30; $t = 6.81$, $df = 4$, $P < 0.003$). Ascent speed during the second half of the ascent (0-2.5 m) was significantly higher in the 3.3 m trials (paired *t*-test: mean difference = 0.51; $t = 10.75$, $df = 4$, $P = 0.0004$).

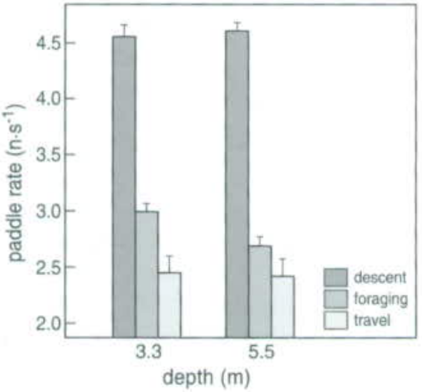

Fig. 5. Average (± SE) paddle rate during descent, foraging and travelling (descent plus ascent) for depths of 3.3 m and 5.5 m. $N = 5$ (Tufted Duck).

We also compared paddle rates during foraging and average paddle rates during the travelling period (including the ascent, where the birds float to the surface; Fig. 5) in order to estimate the relative energy expenditure of foraging and travel phases of the dive (referred to in Houston & Carbone 1992 and Carbone 1992). Although paddle rates during descent were higher than during foraging (shown in Fig. 5 for comparison), the average paddle rates during travel (with ascent duration included) were lower. This difference was significant at the 3.3 m trial but not at 5.5 m (3.3 m: paired *t*-tests: mean difference = 0.57; $t = 3.99$, $df = 4$, $P < 0.02$; 5.5 m: mean difference = 0.26; $t = 2.38$, $df = 4$, $P < 0.08$).

Discussion

A number of qualitative predictions of the models presented in Houston & Carbone (1992) and Carbone & Houston (1996) were supported by our results.

Water depth

The durations of all stages of the dive cycle were significantly correlated with water depth. The return travel time was proportional to depth, suggesting that travel speed is approximately constant (see also below).

Patterns in foraging time with depth for both species were significantly non-linear. A third order polynomial provided a significantly better fit in Pochard, but the same analysis was not significant in the Tufted Duck. This analysis suggests that at least in the Pochard the pattern in foraging time might have two turning points, which is qualitatively similar to the predictions of the mixed metabolism models given large differences in the metabolic efficiencies of aerobic and anaerobic respiration (Carbone & Houston 1996). The patterns in foraging time were similar in both species, but more pronounced in the Pochard. Given that Pochard are thought to be poorer divers (Willi 1970, Nilsson 1972), they may be less effective than the Tufted Duck at anaerobic respiration.

Two sets of depth trials were conducted on the Pochard at 4.0 m: the mean foraging time of the repeated trial was significantly lower than that of the original. This result is surprising given that foraging time increased consistently up to 3.5 m and again after 4.5 m. Very similar foraging times were also found in the Tufted Duck for the 0.5-3.5 m range. The predicted foraging times for the 'mixed metabolism' model are highly variable in the region between the two peaks (Carbone & Houston 1996). Foraging times in this region appear to be particularly sensative to a number of parameters (see e.g. the effects of K_2, α_2, m_w in Figures 4a, 5a, 3a and 8 in Carbone & Houston 1996). It is possible, therefore, that diving time budgets are less consistent in this region. These results suggest a need for further tests in this depth range.

Surface time increased non-linearly with water depth in both species. These results are qualitatively similar to changes in the predicted patterns in both sets of models (Houston & Carbone 1992, Carbone & Houston 1996). While there was an upturn in surface times in both species around the 3.5 m depth, there was no indication of the second upturn predicted by the mixed metabolism model given large differences in the efficiencies of the two metabolic pathways. We would not expect to see this, however, unless the bird dived in water deep enough for it to approach its combined aerobic-anaerobic dive limit. The longest dives observed in this study were well below estimated aerobic dive limits (see below).

The proportion of time spent foraging declined with depth in both the Pochard and Tufted Duck. This is a general prediction of models in which the proportion is maximized (e.g. Carbone 1992, Carbone & Houston 1996).

Paddle rate declined with increasing water depth by 27.2% in the Pochard (from 3.53 strokes.s^{-1} to 2.57 strokes.s^{-1}) and by 10.8% in the Tufted Duck (from 3.32, at 1.5m, to 2.96 strokes.s^{-1}), suggesting that the reduction in buoyancy may have a substantial impact on the energetic costs during deep dives (see e.g. Lovvorn *et al.* 1991, Stephenson 1994). A similar trend was observed in the foraging paddle rates obtained from the paddle rate experiment (see below).

The effects of buoyancy were not included in the diving models and this may influence the predicted patterns. Changes in buoyancy with depth, however, should be gradual and are not a likely explanation for the abrupt changes in foraging time observed in this study.

The relationship between surface time and dive duration (Fig. 4) is presented for the purposes of comparison with other diving studies (Dewar 1924, Stonehouse 1967, Nilsson 1972). Surface time increases roughly in proportion with depth up to 3.5 m and thereafter increases more rapidly. Such trends have been used to indicate a decline in aerobic efficiency and a reliance on anaerobic respiration (Nilsson 1972, Kooyman *et al.* 1980, Kramer 1988, Hörning 1992, Kooyman & Kooyman 1995). We predict (Carbone & Houston 1996) that upturns in this relationship can occur either in the region where the diver begins to rely on anaerobic respiration, or near the combined aerobic-anaerobic limit.

Sand depth

In the Tufted Duck, increasing the depth of sand covering the food significantly reduced foraging time but did not influence surface time. Similar results were observed in the Pochard (Carbone & Houston 1994). If increasing sand depth increases the energetic costs of foraging, the reduction in foraging time is consistent with the predictions of Kramer (1988), Houston & Carbone (1992) and Carbone & Houston (1996).

The paddle rates, which were used to estimate energy expenditure, did not differ significantly between the two sand depths. This result does not support our assumption that sand depth influences the energetic costs of foraging. Other aspects of diving behaviour, such as body angle, stroke amplitude, or head probing rate (described in Tome 1990), may have provided a better indicator of energy expenditure while foraging. If diving birds adjust energy expenditure through a combination of different types of underwater behaviour, this may explain the large variation in paddle rates found in this study. These results suggest a need for monitoring the energy expenditure of diving birds directly (see e.g. Woakes & Butler 1986, Butler 1988, Bevan & Butler 1992) while they feed in different substrate conditions.

It is also possible that the reduction in foraging time was due to other factors. For example, sand depth also had a strong effect on rates of mealworm consumption (see also Carbone & Houston 1994), and this could have influenced the motivation of the birds. Rates of consumption, however, did not affect foraging times in the Pochard (Carbone & Houston 1994), nor did intake rates have a strong effect on the predicted foraging times (Houston & Carbone 1992) and so we assume it is not a major factor here.

Water temperature

Water temperature did not influence descent durations, but ascent duration significantly decreased with decreasing temperature in all but the shallowest depth class (1.0 m). The buoyancy of the birds might be higher at lower temperatures as a result of having a greater air load either in the respiratory system (as a means of increasing oxygen storage, see Keijer & Butler 1982), owing to higher energetic costs, or in the feathers in order to enhance insulation. This would be consistent with the finding that ascent speed increased in response to lower water temperature. Although one might expect the corresponding descent rates to be lower, it is possible that other factors such as an increase in swimming effort in response to increasing energetic costs might have masked this effect. Similar arguments have been made about flight speed optimization (Pennycuick 1989, see also Thompson *et al*. 1993).

Alternatively, the birds may reduce ascent speed in order to scan the surface prior to surfacing in order to avoid other birds or predators (Beauchamp 1992). The birds appeared able to adjust ascent speed by changing their body angle. An increase in energy costs may have forced them to increase ascent speed at the cost of reducing the time available for scanning.

The models predict that surface time should increase with increasing underwater costs for all depths (Houston & Carbone 1992, Carbone & Houston 1996). In the Tufted Duck, surface times were greater at low water temperatures in all but the shallowest depth class.

Under conditions where the mixed metabolism model produces two peaks in foraging time, predicted changes in foraging time with temperature and depth are complex and therefore difficult to test. The observed trends in foraging time were non-significant and variable.

The objective of the water temperature experiment was to vary the energetic costs of diving (both during the travel and foraging phases of the dive). The impact of water temperature on the energetic expenditure of divers has been examined by Wilson *et al*. (1992), who suggested that this effect may increase with depth because water pressure reduces the thickness of the insulation layer from the feathers.

Bevan & Butler (1992) found that average energetic expenditure by Tufted Ducks while underwater was not influenced by water temperature. These experiments, however, were conducted only at a depth of 0.6 m and temperature effects may be minimal at such depths. Our behavioural results are consistent with the results of Bevan & Butler (1992) in that we found no significant effects at the shallowest depth class. Bevan & Butler (1992) found, however, that body temperature, at low water temperatures, declined significantly over the entire diving bout. This suggests that divers may delay the full cost of recovery until after the diving bout. Such effects are not included in our models (see Discussion in Carbone & Houston 1996).

Adjustments in travel speed and paddle rates

Ascent speeds changed with depth, being faster at 0-2.5 m. No significant variation in descent speeds was observed. Increases in buoyancy at shallower depths may have increased ascent speed. Descent speeds were also higher in this region in the 5.5 m trials. Diving ducks may jump higher out of the water at the start of deep dives (observed in Tufted Duck and Pochard, Willi 1970) and this may increase the initial speed of descent. Ascent speeds were higher in the 0-2.5 m region in the 3.3 m trials than in the 5.5 m trials. This result is difficult to explain in terms of differences in buoyancy or air loads.

Paddle rates during the descent were higher than during foraging. Average rates across the travel period (including both descent and ascent) were 19.3% lower at 3.3 m (travel $2.42.s^{-1}$ versus foraging $3.00.s^{-1}$) and 9.6% lower at 5.5 m (travel $2.44.s^{-1}$ versus foraging $2.70.s^{-1}$) than the average during foraging. This suggests that average energetic costs during the foraging phase of the dive are higher than during the travel phase in shallow water, but that this difference declines with increasing depth.

In our companion paper (Carbone & Houston 1996), we suggest that the variation in foraging time with depth might provide the most reliable indicator of a shift to anaerobic respiration. Pochard had foraging times with two turning points with the second turning at around 3.5 m; a similar, but non-significant pattern was observed in the Tufted Duck. The relationship between surface time and dive time also increased abruptly at about 3.5 m for both species.These results are qualitatively similar to the predictions of the mixed metabolism model and suggest a degree of reliance on anaerobic respiration at depths of 3.5 m.

The estimated aerobic dive limit for the Tufted Duck is 44 s (see Butler 1988). The maximum mean dive duration in this study was under 30 s or 68% of this estimate. Based on the aerobic capacity alone, we would not expect these birds to rely on anaerobic metabolism. Woakes & Butler (1986) found, however, that in Tufted Duck, when energy expenditure during surface swimming was similar to that estimated for diving (Woakes & Butler 1983), lactic acid levels in the blood increased dramatically. Jones *et al.* (1988) used these results to argue that diving duck may rely on anaerobic respiration during normal diving activity.

A number of authors argue that divers use a combination of aerobic and anaerobic respiration while diving (Kooyman 1989, Croll *et al.* 1992, Chappell *et al.* 1993, Stephenson 1994). In most studies, however, it is still not known to what extent and when they rely on anaerobic respiration. Research using a combination of behavioural and physiological measures would be needed to test further the mixed metabolism model to see whether patterns in diving time budgets can reliably indicate the use of anaerobic respiration.

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References

Beauchamp, G. 1992. Diving behavior in Surf Scoters and Barrow's Goldeneyes. Auk 109: 819-827.

Bevan, R.M. & Butler P.J. 1992. The effects of temperature on the oxygen consumption, heart rate and deep body temperature during diving in the Tufted Duck *Aythya fuligula*. J. Exp. Biol. 168: 199-217.

Butler, P.J. 1988. The exercise response and 'classical' diving response during natural submersion in birds and mammals. Can. J. Zool. 66: 29-40.

Carbone, C. 1992. Behavioural and Ecological aspects of diving in Pochard *Aythya ferina*. D.Phil. Thesis. Oxford University.

Carbone, C. & Houston, A.I. 1994. Patterns in the diving behaviour of the Pochard *Aythya ferina*: a test of an optimality model. Anim. Behav. 48: 457-465.

Carbone, C. & Houston, A.I. (1996). The allocation of time over the dive cycle: an approach based on aerobic and anaerobic respiration. Anim. Behav. 51: 1247-1255.

Chappell, M.A., Shoemaker, V.H., Janes, D.N., Bucher, T.L., Maloney, S.K., 1993. Diving behavior during foraging in breeding Adelie Penguins. Ecology 74: 1204-1215.

Croll, D.A., Gaston, A.J., Burger, A.E. & Konnoff, D. 1992. Foraging behavior and physiological adaptations for diving in Thick-billed Murres. Ecology 73: 344-356.

Dewar, J.M. 1924. The Bird as a Diver. London: H. F. and G. Witherby.

Hörning, M. 1992. Die Ontogenese des Tauchverhaltens beim Galapagos Seebären *Arctocephalus galapagoensis* (Heller 1904). Ph.D. Thesis, University of Bielefeld.

Houston, A.I. & Carbone, C. (1992). The optimal allocation of time during the dive cycle. Behav. Ecol. 3: 233-262.

Jones, D.R., Furrilla, R.A., Heis, M.R.A, Gabbott, G.R.J. & Smith, F.M. 1988. Forced and voluntary diving in ducks, cardiovascular adjustments and their control. Can. J. Zool. 66: 75-83.

Keijer, E. & Butler, P.J. 1982. Volumes of the respiratory and circulatory systems in Tufted and Mallard Ducks. J. Exp. Biol. 101: 213-220.

Kooyman, G.L. 1989. Diverse Divers, Physiology and Behaviour. London: Springer-Verlag.

Kooyman, G.L., Gentry, R.L., Bergman, W.P. & Hammel, H.T. 1976. Heat loss in penguins during immersion and compression. Comp. Biochem. Physiol. A. 54: 75-80.

Kooyman, G.L. & Kooyman, TG. 1995. Diving behavior of Emperor Penguins nurturing chicks at Coulman Island, Antarctica. Condor 97: 536-549.

Kooyman, G.L., Wahrenbrock, E.A., Castellini, M.A., Davis, R.A. & Sinnett, E.E. 1980. Aerobic and anaerobic metabolism during voluntary diving in Weddell Seals, evidence of preferred pathways from blood chemistry and behaviour. J. Comp. Physiol. 138: 335-346.

Kramer, D.L. 1988. Behavioural ecology of air breathing by aquatic animals. Can. J. Zool. 66: 89-94.

Lovvorn, J.R., Jones, D.R., and Blake, R.W. 1991. Mechanics of underwater locomotion in diving ducks, drag, buoyancy and acceleration in a size gradient of species. J. Exp. Biol. 159: 89-108.

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

Nilsson, L. 1972. Habitat selection, food choice and feeding habitat of diving ducks in coastal waters of southern Sweden during the non-breeding season. Ornis. Scan. 3: 55-78.

Pennycuick, C.J., 1989. Bird Flight Performance. Oxford University Press, Oxford).

Stephenson, R. 1994. Diving energetics in Lesser Scaup *Aythya affinis* (Eyton). J. Exp. Biol. 190: 155-178.

Stephenson, R., Hedrick, M.S. & Jones, D.R. 1992. Cardiovascular responses to diving and involuntary submergence in the Rhinoceros Auklet *Cerorhinca monocerata* (Pallas). Can. J. Zool. 70: 2303-2310.

Stonehouse, B. 1967. Feeding behaviour and diving rhythms of some New Zealand shags *Phalocrocoracidae*. Ibis 109: 600-605.

Thompson, D., Hiby, A.R. & Fedak, M.A. 1993. How fast should I swim? Behavioural implications of diving physiology. Symp.Zool.Soc.Lond. 66: 349-368.

Tome, M.W. 1990. Underwater foraging behavior of Canvasbacks, Lesser Scaups and Ruddy Ducks. Condor 90: 168-172.

Willi, P. 1970. Zugverhalten, Activität, Nahrungserwerb auf dem Klingauer Stausee häufig auftretender Anatiden, insbesondere von Krickente, Tafelente und Reiherente. Orn. Beob. 67: 183-217.

Wilson, R.P, Hustler, K., Ryan, P.G., Burger, A.E., & Nöldeke, C.E. 1992. Diving birds in cold water, do Archimedes and Boyle determine energetic costs? Am. Nat. 140: 179-200.

Woakes, A.J. & Butler, P.J. 1983. Swimming and diving in Tufted Ducks *Aythya fuligula*. J. Exp. Biol. 120: 215-231.

Woakes, A.J. & Butler, P.J. 1986. Respiratory, circulatory and metabolic adjustments during swimming in the Tufted Duck *Aythya fuligula*, with particular reference to heart rate and gas exchange. J. Exp. Biol. 107: 311-329.

Ydenberg, R.C. & Clark, C. 1989. Aerobiosis and anaerobiosis during diving by Western Grebes, an optimal foraging approach. J. Theor. Biol. 139: 437-449.

Ydenberg, R.C. & Forbes, L.S. 1988. Diving and foraging in the Western Grebe. Ornis. Scan. 19: 129-133.

Chapter 5

Diving costs as a component of daily energy budgets in aquatic birds and mammals: generalizing the inclusion of dive-recovery costs demonstrated in Tufted Ducks

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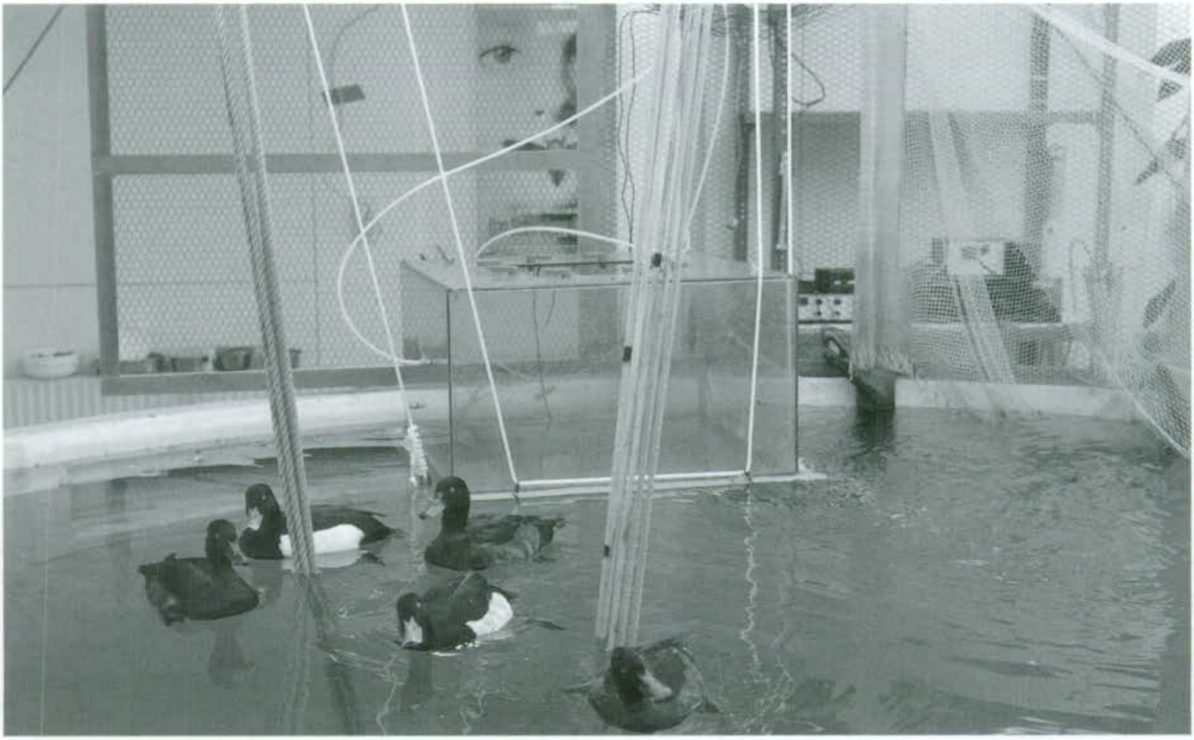

Diving costs as a component of daily energy budgets in aquatic birds and mammals: generalizing the inclusion of dive-recovery costs demonstrated in Tufted Ducks

Metabolic studies on freely diving birds and mammals are reviewed and allometric relations of diving costs are presented. A distinction can be made between three different types of diving costs: (1) metabolic rate during submergence, relevant in estimating aerobic dive limits, (2) average metabolic rate during diving and breathing intervals (MR_d), and (3) diving costs as the excess over resting costs (EDC). EDC is the most comprehensive measure, integrating energy costs over entire dive series with subsequent longer term recovery from heat loss or anaerobic metabolism. Respirometry experiments with Tufted Duck *Aythya fuligula* diving in a 5.7 m deep indoor tank, demonstrated that in this species diving costs, expressed as EDC, increased at lower water temperatures. MR_d was not significantly related to temperature, and probably reflects only the hydrodynamic and not the thermoregulatory component of diving costs. In general, the usual practice of measuring metabolic costs only during diving activity seems insufficient to estimate the total costs of diving. Studies that include longer term recovery (e.g., doubly labelled water measurements over entire foraging trips) yield more complete estimates of diving costs. To take diving costs into account in an animal's energy budget, estimates of EDC are more appropriate than MR_d.

Introduction

To date, one of the major problems in studies on the metabolic costs of diving has been that oxygen consumption during submergence cannot be measured using conventional respirometry techniques (e.g., Castellini *et al.* 1985, Culik *et al.* 1996, MacArthur & Krause 1989). Regression analyses of postdive oxygen consumption measurements on dive and surface durations have been used to estimate the diving metabolic rate for the purpose of calculating aerobic diving capacity (e.g., Castellini *et al.* 1992, Culik *et al.* 1996, Fedak *et al.* 1988, Ponganis *et al.* 1993, Woakes & Butler 1983). These measurements do not account for the metabolic demands of surface activity or thermoregulation. Moreover, foraging models focusing on diving animals have demonstrated that the dive cycle (dive and subsequent recovery at the surface) is a more appropriate metabolic and temporal unit for developing an understanding of the behaviour of divers (e.g., Carbone *et al.* 1996). But even the average metabolism over a series of dives, including recovery metabolism during breathing intervals, may not account for all metabolic costs of diving. It has been demonstrated in Tufted Ducks *Aythya fuligula* (Bevan & Butler 1992), Muskrats *Ondatra zibethicus* (MacArthur 1984), and Weddell Seals *Leptonychotes weddelli* (Kooyman *et al.* 1980), for example, that body temperature declined after a dive series and that metabolic rate may be elevated for more than 1 h as animals subsequently recover from heat loss or anaerobic respiration. In most papers on the energetics of diving, no explicit distinction is made between the underwater phase, the dive cycle (including breathing intervals), and longer term recovery.

A meaningful distinction between three types of diving costs can be made with reference to the time frame of measurements: (1) the metabolic rate during submergence to calculate the aerobic dive limit or hydrodynamic propulsion efficiency of divers (e.g., Woakes & Butler 1983, Castellini *et al.* 1992, Ponganis *et al.* 1993), (2) the average metabolic rate over the dive cycle as an estimate of the rate of oxygen use dur-

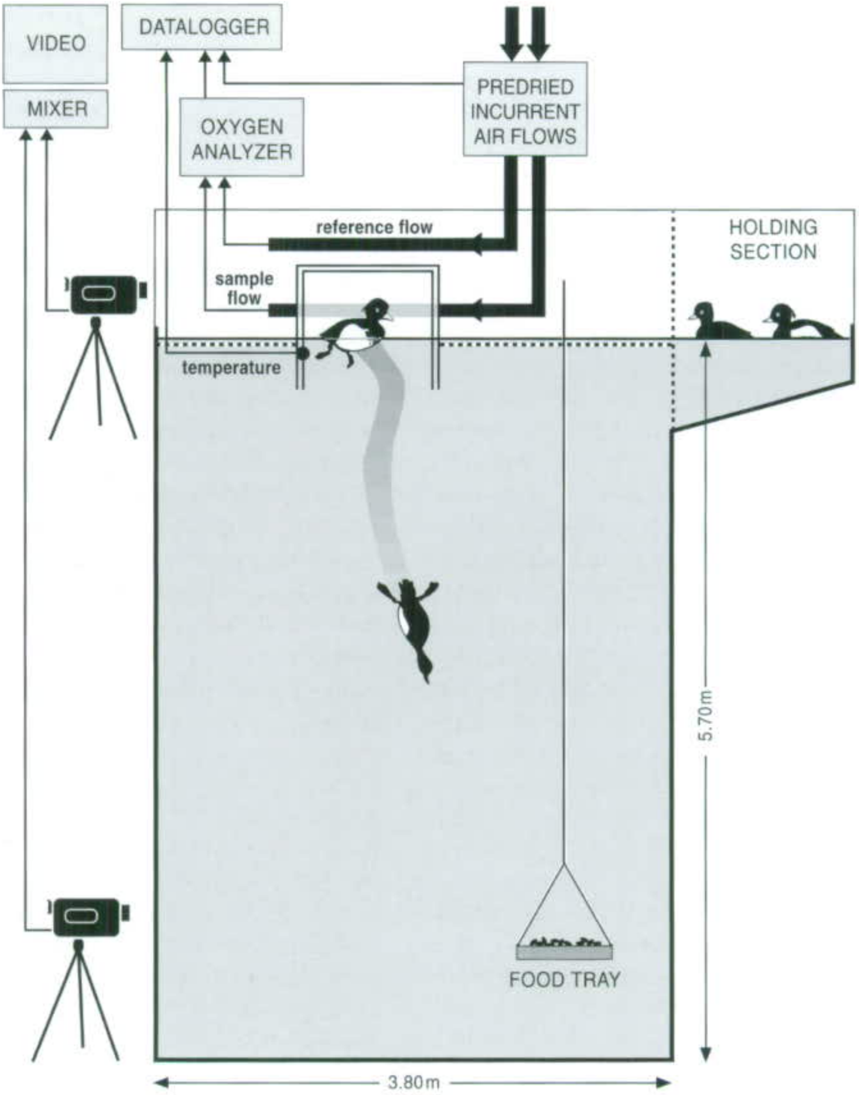

Fig. 1. Diving tank and respirometry setup. The water depth to the food tray was either 2.2 or 5.5 m. Birds were kept in the visually separated holding section of the tank, when they were not being used in the experiments.

ing diving activity (e.g. Culik *et al.* 1996), in this paper referred to as the diving metabolic rate (MR_d), and (3) the costs of diving as the excess over resting costs, including both recovery from heat loss or anaerobic metabolism after a series of dives and all surface activity associated with diving, such as grooming and preening (e.g,. MacArthur 1984, MacArthur & Krause 1989). The latter will be defined in this paper as the excess diving cost (EDC). In contrast to 1 and 2 which are calculated from the oxygen consumption during short breathing intervals between dives (see Culik *et al.* 1996), EDC includes the whole period of elevated metabolism due to diving activity (see MacArthur 1984). Therefore, EDC can only be applied to entire dive bouts rather than single dives in a bout. Regression of diving activity data on average foraging trip metabolism can also provide information on diving costs in terms of EDC (Costa 1988, Nagy *et al.* 1984), although care should be taken with the interpretation of estimates of activity-specific metabolism (Wilson & Culik 1993). From an ecological perspective, EDC is the most informative measure of diving costs, as it translates directly as the contribution of diving to an animal's daily energy budget.

To explore the consequences of applying different time frames of measurement, this paper concentrates on the distinction between the two major types of diving costs, the metabolic rate during diving activity (MR_d) and the longer term excess diving cost (EDC). Woakes & Butler (1983) and Bevan & Butler (1992) reported that the metabolic rate of Tufted Ducks during diving appeared to be independent of water temperature, but body temperature was significantly lower after diving in cold water. This suggests that the ecologically relevant thermoregulatory component of diving costs is not quantified when diving costs are expressed as MR_d rather than as EDC (cf. MacArthur 1984). This hypothesis is tested by applying both MR_d and EDC calculations to novel respirometry data on Tufted Ducks diving to 2.2 and 5.5 m (within the normal depth range for wild birds) at different water temperatures. The problem of the time frame for diving cost measurements is further analysed using existing literature, from which allometric relationships were derived for diving costs in birds and mammals. Variation in diving costs is explained in terms of differences in underwater activity and water temperature, and the different types of diving costs are discussed.

Material & Methods

Eight Tufted Ducks (5 males, 3 females) were trained to dive in a 5.7 m deep indoor tank at the Konrad Lorenz Institut für Vergleichende Verhaltensforschung, Vienna, Austria (Fig. 1). During the 4-week training period, the surface area (10 m^2) of the tank was covered with wire netting in a stepwise fashion, while a respiration box (60x60 cm, 35 cm high) allowed the birds to perform their normal behaviour at the water surface (resting, wing flapping and preening). After the ducks had adjusted to the experimental conditions, they made voluntary feeding dives from the respiration box to a food tray (1 m^2) containing mealworms at depths between 2 and 5.5 m. Between dives they usually rested or preened in the box. Some birds, however, spent most of their diving time engaged in subsurface swimming rather than diving vertically. Only 3 ducks (2 males, 1 female, with mean body masses of 615 (duck M1), 672 (M2), and 592 g (F1)) managed to dive directly between the respiration box and the feeding tray and these ducks were used in the subsequent experiments. Oxygen consumption was measured during each 4-h trial (one trial per bird each day) using an Applied Electrochemistry S-3A oxygen analyser. Oxygen concentration in the box varied between 20.3 and 20.9%. Oxygen concentration in the sample system and in the reference system (Fig. 1) was measured continuously, and averages over 10-s intervals were stored on a Squirrel 1200 datalogger. The airflow to the box and reference flow were maintained at 400 L/h (STPD) using Brooks 5850E mass flow meters. Incurrent airflows and the sample flow to the oxygen analyser were dried over predried molecular sieves (3 Å). Water temperature was recorded continuously using a digital thermometer (accurate to within 0.1 °C) 10 cm below the water's surface in the respiration box.

Owing to the relatively large size of the respiration box and therefore the large wash-out effects on changes in gas concentration, the instantaneous oxygen consumption was calculated from the difference in oxygen concentration between successive 10-s intervals, using the exponential model described by Bartholomew *et al.* (1981). Small measurement errors are exponentially enlarged by this model. To reduce this noise in the data, 6-point running geometric means (i.e., average per minute) were calculated. This could not fully control for minor fluctuations due to the oxygen analysing system (see the deviations around zero metabolism in Fig. 2). Oxygen consumption data were converted to their energetic equivalent of 20 kJ/L O_2 (Bevan & Butler 1992) assuming a respiratory exchange ratio of 0.8 (Bevan *et al.* 1995).

Resting metabolic rates (RMR) in water were determined from the lowest 10-min averages recorded in resting periods of at least 30 min duration. RMR refers to the metabolic rate of absorptive, thermoregulating ducks (at water temperatures probably below the thermoneutral zone, see Bevan & Butler 1992).

MR_d over entire dive bouts was calculated for dive

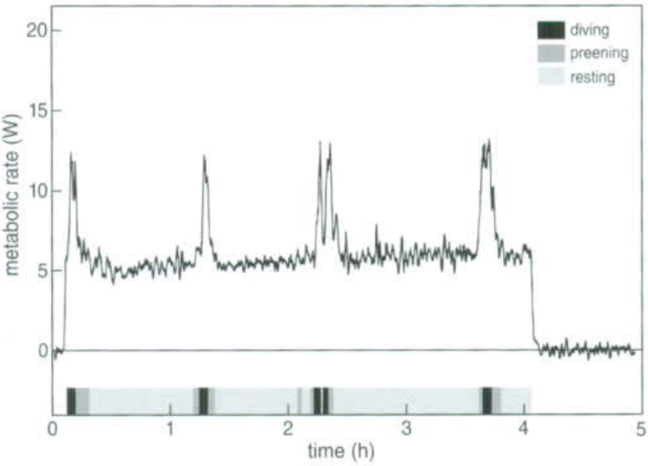

Fig. 2. Changes in instantaneous metabolic rate and activity pattern during one trial of duck F1. Diving depth was 5.5 m and water temperature 12 °C. Resting metabolic rate increased slightly in the course of the trial, probably because of the heat increment of feeding while digesting mealworms. Fluctuations around zero metabolism before and after the trial show the effect of measurement errors after correction for wash-out effects (Bartholomew *et al.* 1981).

bouts longer than 2 min:

$$MR_d = VO_{2\ \mathrm{total\ dive\ bout}} / (\Sigma t_{\mathrm{dive}} + \Sigma t_{\mathrm{surface}}),$$

where Σt_{dive} and $\Sigma t_{\mathrm{surface}}$ are the total dive and surface durations in a dive bout. Dive bouts were usually clearly separated in time (Fig. 2). The energy investment in diving (EDC), the excess oxygen consumption over the resting rate, was calculated over the period from the first dive in a bout until the metabolic rate returned to the resting level:

$$EDC = (VO_{2\ \mathrm{total}} - \dot{V}O_{2\ \mathrm{rest}} \cdot t_{\mathrm{total}}) / \Sigma t_{\mathrm{dive}}.$$

The recovery period after diving was defined as the time between the end of the last dive in a bout and the time when the metabolic rate returned to the resting level. In each trial, two to eight dive bouts could usually be quantified. Short subsurface exploratory dives sometimes interfered with feeding dives in a dive bout. These underwater episodes were included in calculations of the total dive time in a bout, but dive bouts with more than 25% exploratory dives were excluded from the analyses.

The experiments were carried out at water temperatures of approximately 7 °C (after the tank was refilled with cold water) to 23 °C (*ca.* 2 weeks after the tank was refilled) to manipulate the thermoregulatory response. Dives were either shallow (2.2 m) or deep (5.5 m). Two video cameras were used to observe the behaviour of the birds in the respiration box and at the food tray, respectively (Fig. 1). The video images were recorded simultaneously with a timer (accurate to the nearest 0.1 s) via a Panasonic AV video mixer and were later analysed. Diving activity was subdivided into different phases of the dive cycle: descent, foraging at the food tray, ascent, and surface time (Table 1). Surface times longer than 50 s were considered resting periods, using a conservative bout criterion interval calculated from the data set (cf. Carbone *et al.* 1996). The durations of diving, resting, and preening per dive bout were related to the excess oxygen consumption during that dive bout.

Results

Diving behaviour and energy expenditure in Tufted Ducks

The durations of different phases of the dive cycle of dives to the food tray at 2.2 and 5.5 m are summerized in Table 1. The average numbers of dives per bout var-

Table 1. Average (SD) durations (s) of different phases of the dive cycle and numbers of dives per bout for three Tufted Ducks diving at feeding depths of 2.2 and 5.5 m.

Duck	Depth	n	Descent	Foraging	Ascent	Dive	Surface	Number of dives per bout
M1	2.2	53	3.0 (0.4)	12.2 (3.1)	5.6 (1.7)	20.9 (3.5)	21.6 (9.3)	2.9 (1.2)
	5.5	67	7.7 (0.9)	12.4 (3.4)	7.9 (1.2)	28.1 (3.4)	27.2 (10.7)	1.8 (0.9)
M2	2.2	85	5.1 (3.5)	11.8 (4.5)	6.9 (1.6)	24.7 (3.4)	19.2 (4.4)	10.6 (4.6)
	5.5	74	9.8 (1.5)	12.3 (2.9)	7.9 (1.2)	30.0 (3.0)	28.6 (7.0)	7.5 (4.5)
F1	2.2	51	7.4 (2.8)	9.0 (2.1)	4.2 (0.6)	22.0 (4.1)	18.2 (10.6)	3.4 (1.6)
	5.5	112	8.9 (1.8)	8.1 (2.6)	7.2 (0.5)	24.2 (2.6)	29.3 (10.5)	3.9 (1.6)

ied between 2 and 10 with depth (ANOVA, $F_{1,117} = 4.5$, $P = 0.04$) and individual ($F_{1,117} = 63.2$, $P < 0.001$). The durations of descent, foraging, ascent, and recovery did not vary with water temperature (ANCOVA with duck and depth as factors and water temperature as covariate, $P >> 0.05$ for all variables). Only duration of descent for dives to 5.5 m increased by 0.1 $s.°C^{-1}$ ($P = 0.002$). ANOVA was used to test for differences between depths (2.2 and 5.5 m) while differences between individuals were significant ($P < 0.05$). Dive durations were longer at greater depth ($F_{1,128} = 110.2$, $P < 0.001$), owing to longer durations of descent ($F_{1,131} = 211.1$, $P < 0.001$) and ascent ($F_{1,131} = 40.8$, $P < 0.001$). Foraging times at the food tray did not differ between the depths ($F_{1,134} = 0.4$, $P = 0.52$) or individuals ($F_{1,134} = 0.2$, $P = 0.67$). Average surface durations increased with depth ($F_{1,94} = 13.5$, $P < 0.001$), but did not vary among individuals ($F_{1,94} = 0.0$, $P = 0.97$). Descent and ascent were 1-2 s longer than those reported earlier for Tufted Ducks in the same tank (Carbone *et al.* 1996), probably as a consequence of the time penalty incurred by diving to and from the small surface area of the respiration box relative to the total surface area of the tank.

The average EDC per trial and RMR decreased significantly with rising water temperature (Fig. 3, least-squares linear regression weighted by the number of dive bouts: $EDC = 54.6\text{-}1.43xT$, $r^2 = 0.40$; $P < 0.0001$; $RMR = 5.88\text{-}0.11xT$, $r^2 = 0.62$, $P < 0.0001$) and there was a nonsignificant trend in MR_d with temperature ($MR_d = 16.5\text{-}0.23xT$, $r^2 = 0.02$, $P = 0.26$). Diving depth did not significantly affect EDC (ANCOVA, $F_{1,128} = 0.32$, $P = 0.63$), or MR_d ($F_{1,128} = 3.0$, $P = 0.06$). Preening time increased significantly with EDC ($F_{1,128} = 123.1$, $P < 0.001$), bout dive duration ($F_{1,128} = 51.3$, $P < 0.001$), and water temperature ($F_{1,128} = 9.3$, $P = 0.003$), while individual differences were significant ($F_{2,128} = 6.5$, $P = 0.002$). Preening was considered part of diving activity, since all preening behaviour observed was associated with diving behaviour (either between dives in a bout or immediately after a dive bout, see Fig. 2). The duration of recovery after a dive bout strongly increased with EDC ($F_{1,130} = 30.0$, $P < 0.001$), while individual differences were not significant $F_{1,130} = 3.0$, $P = 0.06$). After diving and preening, the metabolic rate was still elevated for at least 10 min before it became indistinguishable from resting values.

Discussion

Water temperature and diving costs in Tufted Ducks

MR_d estimates obtained in this study are comparable to values reported earlier for shallow (0.6-1.7 m) diving *Aythya* species (Woakes & Butler 1983, Bevan & Butler 1992, Stephenson 1994; see Table 2). It has been suggested that deeper diving ducks have higher air loads in the air sacs for oxygen storage (Keijer & Butler 1982) and in the plumage to provide increased insulation against water pressure at depth (Wilson *et al.* 1992). This might increase the hydromechanical costs of overcoming buoyancy (Lovvorn & Jones 1991). However, in the present study no difference was found in diving costs between 2.2 and 5.5 m (water pressure 1.22 and 1.55 atmospheres, respectively), so the extent to which diving depth might affect the energy costs of diving remains unclear. Owing to compression of the

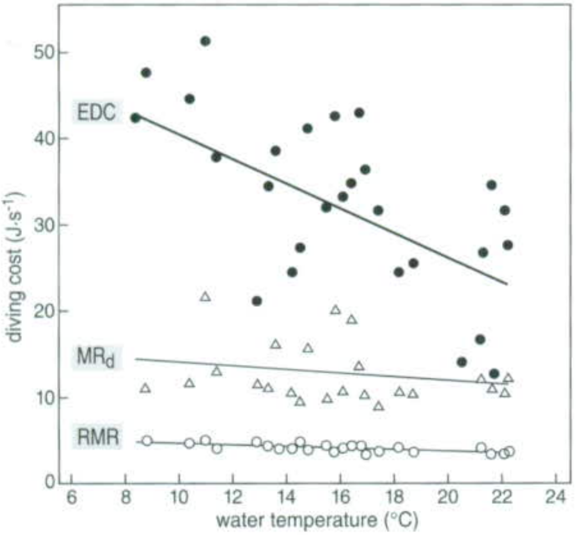

Fig. 3. Excess diving cost (EDC) and metabolic rates during diving activity (MR_d) and resting on the water surface (RMR) in relation to water temperature for three Tufted Ducks. Data points are per-trial averages. Regression equations are weighted by the number of dive bouts per trial: EDC = 54.6-1.43x, $P < 0.0001$, $MR_d = 16.5\text{-}0.23x$, $P = 0.26$, RMR = 5.88-0.11x, $P < 0.0001$.

volume of air in the feathers and respiratory system at depth, the hydrodynamic costs of overcoming buoyancy are lower at greater depths, as is shown by the decrease in paddling rates while foraging at the food tray (Carbone *et al.* 1996). On the other hand, heat loss increases with compression of the air layer in the feathers (Kooyman *et al.* 1976). Thus, changes in depth affect the hydrodynamic and thermoregulatory costs in opposite directions and might have obscured any depth effect on diving costs in this study. Although diving costs per second spent underwater did not differ between the two depths, dive durations and surface durations were longer at 5.5 m, and the proportion of time spent foraging in a dive cycle was, on average, 33% lower at 5.5 m than at 2.2 m (ANOVA, $F_{1,123} = 41.1$, $P < 0.001$). Deeper diving is therefore less efficient, and thus it is more costly to obtain a specific amount of food.

There was no significant relationship between MR_d and water temperature, which is similar to the finding of Bevan & Butler (1992), but in contrast, EDC was strongly related to temperature (Fig. 3). This suggests that during diving energy is mainly used to overcome hydrodynamic forces, but the extra thermoregulatory costs of being underwater are largely paid *after* a series of dives. The increased heat loss at lower temperatures will thus result in a drop in body temperature during the underwater phase of the dive. Indeed, Bevan & Butler (1992) showed that body temperature was significantly lower after diving in cold water (7.4 °C) than after diving in water at 23 °C. In his study on Muskrats, MacArthur (1984) demonstrated that there is a close correlation between the decline in body temperature after diving and the postdive excess oxygen consumption. This indicates that ducks and Muskrats are not actively maintaining body temperature during diving, to avoid competition for oxygen between thermogenic tissues (e.g., shivering muscles) and the hypoxia-sensitive core tissues. Saving oxygen for hydromechanical purposes enables diving animals to maximize the proportion of time spent foraging over the dive cycle (see Carbone *et al.* 1996). The delay in recovery from cooling until after the dive bout might coincide with the longer pauses in diving activity for digestion of food.

The analysis showed a strong correlation between preening time and both excess metabolic costs and water temperature, suggesting that preening is a response to body cooling during diving. Grooming and preening behaviour associated with diving has also been found in Common and Thick-billed Murre (Croll & McLaren 1993), Muskrat (e.g., MacArthur 1984), Mink (Stephenson *et al.* 1988), and Sea Otter (Costa & Kooyman 1984). MacArthur (1984) argued that not only may grooming and preening serve to maintain a waterproof pelage or plumage, but heat generated by this activity could supplement nonshivering thermogenesis. In his study, metabolic recovery from diving was prolonged in Muskrats prevented from grooming.

Diving costs in birds and mammals

To generalize the problem of including postponed dive-recovery costs from body cooling and anaerobiosis, metabolic studies from the literature of diving birds and mammals were analysed. In the compilation of diving costs (Table 2), only data from animals engaged in voluntary dives were used, as the metabolic rates of restrained animals or animals forced to dive are significantly lower than those of voluntarily diving animals