Diet and habitat use of scoters *Melanitta* in the Western Palearctic - a brief overview

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If patterns of scoter distribution and abundance are to be understood, there is a need to know upon which prey items these birds feed, how they obtain these prey items and the habitats from which these food items are most easily harvested. Dietary studies and descriptions of habitats exploited by Common and Velvet Scoter in the non-breeding season are reviewed. The existing literature strongly suggests that, outside of the breeding season, these species forage mainly upon marine bivalve molluscs (especially those less than 4cm long) that live on the surface or within the upper 3cm of clean, coarse, sandy substrates in waters less than 20m deep. Although there is a large energetic cost to diving, handling and crushing such prey prior to digestion, such sedentary prey items often occur in very high densities, offering a locally abundant and predictable feeding resource. Since single species often dominate the diet, but dominant food items differ between feeding areas, it seems likely that scoters simply take whatever prey is locally available in sufficient abundance to fulfil nutritional needs. Large differences in documented prey size frequency distributions suggest that scoters may not select for specific prey size classes below an upper digestive limit. However, in the absence of any precise understanding of how scoters obtain their prey, nor any simultaneous studies of available benthic food abundance and size class distributions in scoter diets, it is not possible to confirm if differences simply reflect differences in profitability between different prey at different sites at different times of the year. There remains a considerable need to study the basic feeding ecology and the behaviour of scoters and their prey if their patterns of distribution and abundance are to be better understood.

Key Words: feeding ecology, Common Scoter, Velvet Scoter, bivalve molluscs, diving ducks

Of all the factors determining the distribution of organisms, the extent and availability of food is assumed to be of central importance. For Common *Melanitta nigra* and Velvet Scoters *M. fusca*, which spend the majority of their time in shallow marine waters, food supply is likely to play a major role in determining how birds are distributed in time and space. Although little is known about the potential predators of these birds, it seems likely that the response to risk of natural predation plays at best a secondary role in determining how scoters distribute themselves at sea. Certainly, the role of quasi-predator stimuli (such as human disturbance) apparently can play a major modifying role in the distribution of scoters locally. In order to understand why scoters occur where they do, when they do, it is important to understand what features of the food supply characterise those areas where scoters are especially abundant or remain for prolonged periods of time. So what precisely are the major features that characterise moulting and wintering habitats used by scoters in the Western Palearctic?

This question needs to be addressed in a number of ways. Firstly, there is a need to be able to determine the diet and link the abundance of dietary prey species to the habitats that support the greatest densities of those prey items. Secondly, there is a need to understand the way in which the birds exploit their prey, since conditions may restrict the availability of prey of suffi-

cient profitability to the predators. In this case, 'sufficient profitability' is defined as prey that yields sufficient energy/nutrient gain per unit handing time to ensure profitable foraging (*sensu* Zwarts *et al.* 1992). This is especially important amongst organisms that crush the tough outer shells of ingested molluscs in a muscular gizzard to obtain nutrients and energy. In the Common Eider *Somateria mollissima*, Nehls (1995) showed that 50-60% of the ingested energy was expended in capturing, handling, processing and digesting prey. In birds that dive to feed on benthic organisms in the open sea, physiological limits on the depths to which predators can dive may further affect the availability and profitability of prey in deeper water. Energetic models and empirical observations suggest that diving ducks show strong preferences for foraging in the shallowest waters, but that prey depletion may force birds to shift to deeper waters as a season progresses (Lovvorn & Jones 1991; van Eerden *et al.* 1997; de Leeuw 1997, 1999; de Leeuw *et al.* 1999). Hence, selection of rich prey resources may change in time and space because of changes in water depth and depletion of the food base. Furthermore, prey items may be too cryptic, lie too deep in the sediment or dig themselves too deep to be easily accessible or available to the predators (Piersma 1994; Kube 1996). Hence, an apparently suitable rich benthos exhibiting high biomass may effectively lie beyond the reach of the feeding apparatus of foraging scot-

ers. Even when abundant and available to predators, the size of prey (eg too small to be profitable or too large to be physically ingested) may affect the profitability of predation. Prey biomass alone may thus not reflect the suitability of a given area to a given predator. Indeed, in one of the larger investigations of benthos communities and scoter distributions, Degraer et al. (1999) found no good correlation between bivalve and scoter densities, perhaps because water depth played such a significant role in determining the distribution of the predators. For this reason, this synthesis draws on unpublished grey and published literature to briefly consider not merely the favoured prey species of scoters, based on existing information, but also their abundance and habitat use, and those factors likely to affect the suitability of the available prey.

Diet

Studies show that both Common and Velvet Scoter consume many bivalve molluscs (Madsen 1954; Cramp & Simmons 1977; Stempniewicz 1986; Bräger & Nehls 1987; Meissner & Bräger 1990; Durinck et al. 1993; Schricke 1993; Bräger et al. 1995; Leopold et al. 1995; Leopold & van der Land 1996; Hughes et al. 1997; Degraer et al. 1999; Zydelis 2002). The most frequently reported species are those listed in **Tables 1 and 2**. In addition to bivalve molluscs, gastropods (such as whelks Nassarius and periwinkles Littorina) are also taken to a lesser

degree (Schricke 1993; Aulert & Sylvand 1997). Crustaceans (isopods, amphipods and small crabs), annelids, echinoderms and fish may also figure in the oesophagus contents (Cramp & Simmons 1977; Stempniewicz 1986; Schricke 1993; Byrkjedal et al. 1997; Frengen & Thingstad 2002; Zydelis 2002). Several observers report a more varied diet amongst Velvet Scoter and consider that this is because they tend to forage closer to the coastline than Common Scoter, resulting in a more diverse diet and more prey items typical of rocky or stony shores (eg Madsen 1954; Cramp & Simmons 1977). Nevertheless, in both scoter species, molluscs comprised more than 95% of the diet by frequency and 80% by volume, so it is clear that these represent the dominant prey items.

The composition of prey items varies considerably between studies - for instance in Lithuania, Common Scoter was found to have consumed most frequently Macoma balthica, with relatively high proportions of polychaetes and isopods, whereas Velvet Scoter took mainly Mya arenaria (Zydelis 2002). In contrast, in the Gulf of Gdansk, Poland, Stempniewicz (1986) found that Mya arenaria, Macoma baltica and Cardium lamarcki were the most important items for both scoters. This contrasts with the dominance of Spisula in North Sea coasts of Denmark and the Netherlands (Offringa 1991; Durinck et al. 1993; Leopold et al. 1995; Leopold 1996). Analyses of the oesophageal content of shot scoters

Table 1. Commonly reported mollusc species present in the diet of Common Scoter, giving typical sediment type used by each organism (based on McMillan 1973 and other sources), the origin of the study and the source reference.

Species	Substrate	Region
Macoma balthica	Mud/sand	Belgium[1], Britain[7], Danish Baltic[4], Sweden[5], Lithuania[6], German Baltic[12], Danish Baltic[13]
Cardium edule	Sand	Danish Wadden Sea[3], Britain[7], Poland[1], German Baltic[12], Danish Baltic[13]
Mytilus edulis	Various	Danish Baltic[4], Britain[7], White Sea[10], German Baltic[12]
Mya arenaria	Sand	Lithuania[6], Poland[11], German Baltic[12], Danish Baltic[13]
Spisula subtruncata	Sand	Belgium[1], Netherlands[2,8], Danish Wadden Sea[3]
Cyprina islandica	Sand	Geman Baltic[12], Danish Baltic[13], Danish Wadden Sea[13]
Donax vittatus	Sand	Belgium[1], Britain[7]
Tellina tenuis	Sand	Belgium[1], Britain[7],
Littorina spp.	Various	Danish Baltic[4], Britain[7]
Venus gallina	Sand	Danish Baltic[4], Britain[7]
Mactra corallina	Sand	Netherlands[9], Britain[7]
Pharus legumen	Sand	Britain[7]
Spisula elliptica	Sand	Britain[7]
Lutraria lutraria	Mud/sand	Britain[7]
Scrobicularia plana	Estuarine mud	Britain[7]
Gibbula cineraria	Various	Britain[7]
Cardium echinatum	Sand	Britain[7]
Abra alba	Mud/sand	Belgium[1]
Tellina fibula	Sand	Belgium[1]
Barnea candida	Wood/peat/clay	Belgium[1]
Nassarius reticulatus	Various	Danish Baltic[4]
Cardium scarbrum	Sand	Danish Baltic[4]
Nucella sp.	Various	Danish Baltic[4]
Neretina fluviatilis	Brackish	Danish Baltic[4]
Musculus nigra	Sand	Danish Baltic[4]
Mya truncata	Sand	German Baltic[12]
Cardium lamarcki	Sand	Poland[11]
Ensis sp.	Sand	Danish Wadden Sea[13]

Taxonomy follows McMillan (1973).
Source references: [1]Degraer *et al.* (1999), [2]Leopold *et al.* (1995), [3]Durinck *et al.* (1993) [4]Madsen (1954), [5]Nilsson (1972), [6]Zydelis (2002), [7]Hughes *et al.* (1997), [8]Offinga (1991), [9]Bottelier (1938), [10]Bianki (1992), [11]Stemniewicz (1986), [12]Meissner & Bräger (1990), [13]see text.

Table 2. Commonly reported mollusc species present in the diet of Velvet Scoter, giving typical sediment type used by each organism (based on McMillan 1973 and other sources), the origin of the study and the source reference.

Species	Substrate	Region
Spisula subtruncata	Sand	Danish Wadden Sea[3], Danish Baltic[4]
Cardium edule	Sand	Danish Wadden Sea[3], Danish Baltic[4]
Macoma balthica	Mud/sand	Danish Baltic[4]
Mytilus edulis	Various	Danish Baltic[4]
Nassarius reticulatus	Various	Danish Baltic[4]
Littorina littorea	Various	Danish Baltic[4]
Venus gallina	Sand	Danish Baltic[4]
Bittium reticulatum	Various	Danish Baltic[4]
Gibbula cineraria	Various	Danish Baltic[4]
Buccinum undulatum	Various	Danish Baltic[4]
Nucula nitida	Sand	Danish Baltic[4]
Macoma calcarea	Sand	Danish Baltic[4]
Mya truncata	Mud/sand	Danish Baltic[4]
Bela turricula		Danish Baltic[4]
Massarius pygmaea		Danish Baltic[4]
Mucula nitida	Various	Danish Baltic[4]
Cyprina islandica	Sand	Danish Baltic[4]
Aporrhais pes-pelicani		Danish Baltic[4]

Taxonomy follows McMillan (1973).
Source references: [3]Durinck *et al.* (1993), [4]Madsen (1954).

from Ebeltoft Vig in Eastern Jutland (Denmark) were dominated by *Musculus nigra* and *Mya arenaria* in samples from the winters of 1986/1987 and 1987/1988, but *Cardium edule*, *Macoma balthica* and *Cyprina islandica* in 1989/1990 (K. Asferg, in litt.). *Cardium edule* and *Cyprina/Ensis* spp. respectively (K. Asferg, in litt.) dominated samples taken from Common Scoter shot off Læsø (Danish Kattegat)

and in the Juvre Dyb (Danish Wadden Sea). Finally, indirect evidence for Common Scoters relying on bivalve species such as *Abra alba*, *Tellina* spp. or *Cardium edule* comes from observations of large flocks situated over areas with very high densities of these potential prey species in Dutch waters (van Steen 1978; Leopold *et al.* 1995).

The results from all these studies share the common dominance of one

or another bivalve in the diet of Common Scoter examined, although the specific prey species may vary between areas. This local predominance that is characteristic of most studies suggests that Common Scoter take those mollusc species that are most abundant, albeit that they utilise different species at different locations depending on the composition of the marine benthic community. Locally, this may therefore even result in some prey items being taken preferentially. For example, Common Scoter in the Gulf of Gdansk fed selectively on *Mya arenaria* and *Cardium edule*, and avoided *Mytilus edilus*, which occurs in the diet elsewhere (Stempniewicz 1986). However, as data on diet and benthos availability were not studied simultaneously, prey selection in Common Scoter has still to be demonstrated. One extreme case of dietary selectivity can be found in Bauer & Glutz von Blotzheim (1969), who reported the stranding of a ship laden with beans on Heligoland in the German Bight in the 1800s, which attracted 1,000 Common Scoters to forage on spilled beans for up to one month!

It is misleading to leave the impression that Common Scoter eat only bivalve molluscs. A number of accounts report gastropod molluscs, and there are consistent reports of birds taking significant proportions of polychaetes, echinoderms and small crustaceans, such as isopods (eg Madsen 1954; Byrkjedal *et al.* 1997; Žydelis 2002). It seems highly likely that these are often taken when encountered on sandy-bottomed habitats with sufficient frequency in sufficient abundance to figure in the diet. Likewise, Velvet Scoter exhibit a more varied range of dietary items than Common Scoter. Nevertheless, in terms of frequency and biomass, it is fair to conclude that the majority of the diet in the animals studied has comprised bivalves, and therefore the local distribution and abundance of scoters is likely to be strongly influenced by the local abundance and availability of these benthic organisms.

Substrate type

All the accounts listed above suggest that Common Scoter favour feeding on areas of sandy bottom (see also the habitats normally occupied by prey species in **Tables 1 and 2**). Here, they most commonly take immobile prey, which can be detected and consumed, on the bottom or in the most superficial layer. Almost all of the important prey items are typical of sand substrates, although *Mytilus edulis* is one apparent exception. Intriguingly, the Common Scoter does appear to consume large amounts of *Mytilis edulis* at some locations studied (eg Schricke 1993; Hughes *et al.* 1997), but Madsen (1954) suggested that they did not take them from hard, submerged rock reefs, as do Common Eiders. Blue mussels will attach themselves to any hard surface with their byssus threads (including to shells of conspecifics) and are hence reported from areas of pure sand, mud and scattered boulders (Franz & Harris

1988; Newell 1989). Seaducks feeding on blue mussels must mainly tear the mussels apart from each other, so the sediment type has little effect on the birds' ability to forage on this food source. It may therefore be that even this species is derived from sandy substrates where it occurs and is encountered by scoters.

On this basis, it appears therefore that scoters are to a high degree selecting for shallow in- or epi-faunal species which live in coarser substrates, especially sands, such as the bivalve molluscs, dog whelk gastropods, isopods and annelid (especially Pectinarian) worms. Quite how the prey are obtained remains unknown. However, it can be assumed that the upper 4.5cm horizons (ie the extent to which a scoter bill can penetrate the sediment based on measurement of bill length, shown in Figure 4.10 on page 54 of Kube 1996) are sifted or siphoned in some way to abstract individual prey. Certainly, such sediments are easier to sift through for relatively large bivalves than, for example, finer clays, muds and silts and substrates of high organic content.

Both scoter species are known to feed on *Spisula subtruncata*, which is widely distributed in Danish waters less than 20m deep, forming part of the 'Venus community' that characterises sandy substrates as defined by Thorson (1979). This type characterises the typical benthic community in many of the internationally important areas used by scoters in moult and winter periods around the Danish coasts. This sandy sediment benthic community is also common and widespread throughout eastern North Sea coasts, and extends to the west coast of Britain, including the North Wales coast and Liverpool Bay (Mackie 1990) and Carmarthen Bay (Lownds 1982; Hughes *et al.* 1997) where Common Scoter are also abundant.

Madsen (1954) was convinced that Velvet Scoter foraged closer to the coast than Common Scoter, with the result that they took more rocky shore species, such as periwinkles and crabs. Nevertheless, he concluded that the Velvet Scoter was also a sandy substrate specialist, predominantly taking a very similar array of sand-dwelling bivalve species to those taken by Common Scoter (**Table 2**).

Availability - distribution in substrate

Although *Cardium* spp., *Spisula* spp. and *Donax* spp. always lie in the top 2cm of the substrate, other bivalves bury themselves deeper in the substrate, where they are unavailable to feeding scoters. Assuming that Common Scoter are only able to extract prey items 4.5cm down into the sediment, deeper burying, older and larger specimens of *Mya arenaria* (Kube 1996), *Echinocardium* (Byrkejdal *et al.* 1997) or *Ensis* spp. may be beyond reach, particularly of young, inexperienced birds (Aulert & Sylvand 1997).

It is therefore important in any consideration relating to how to characterise the attractiveness of the benthic

fauna that the accessibility of the prey within the substrate is adequately known. This requires a sampling procedure that can identify the depth within the substrate at which prey organisms normally lie, since this can affect both accessibility and prey size distributions (see Kube 1996). Furthermore, prey can show a range of escape responses that could render them inaccessible to potential predators. *Spisula elliptica* uses its muscular foot to 'leap' 6-8cm from potential predators (Thorson 1979) while *Pharus legumen* and *Ensis directus* can rapidly bury themselves 15-20cm down in the substrate, making it hard even for humans to capture them (Swennen *et al.* 1985; Fish & Fish 1989; Hughes *et al.* 1997). This also presents some challenges for designing adequate protocols to sample the normal undisturbed distribution of the in-fauna within the sediment column. Hence, the presence of such members of a species- or biomass-rich bivalve in-fauna may not equate to ideal foraging conditions for scoter, and any benthic surveys anticipated to attempt to correlate bird abundance with benthic communities need to take these factors into consideration.

Availability - size class distribution

Prey can only be considered 'available' if it is ingestible (ie it can be swallowed and digested). Some prey species are too small to be worth ingesting, others too large to be physically swallowed (Draulans 1984), whilst the shells of others may be too well armoured to be profitably cracked open in the gizzard. Many diving ducks are known to take large single items to the surface before swallowing them (Ball 1990; de Leeuw & van Eerden 1992; Nehls 1995; Byrkjedal *et al.* 1997). Therefore, below the absolute upper threshold of prey size imposed by ability to swallow, the handling time involved in processing large prey items can reduce intake rates or profitability (Draulans 1982). The energetic costs of crushing shells also increases with increasing shell length (Piersma *et al.* 1993a; Nehls 1995), which may impose another energetic constraint upon the taking of large bivalves. Attempting to eat very large prey may also prove hazardous: large razor clams (*Ensis* spp.) as well as very large mussels or mussels with abundant attached barnacles may even kill birds if they damage the oesophagus or get stuck in the throat (Swennen 1976; Jukema 1979; Swennen & Duiven 1989).

Madsen (1954) stated that the preferred size of the hard-shelled mollusc food items ingested by Common Scoter ranged from 5-10mm up to 20mm, with *Mytilus* consumed up to 30mm long and *Mya* spp. up to 40mm long, but gave no details of frequencies. He also concluded that Velvet Scoter, being slightly larger than Common Scoter, took slightly larger prey, potentially swallowing *Buccinium undulatum* individuals up to 60mm long. He reported this species taking soft prey (such as fish and worms) of longer length, but conceded the normal upper limit for hard-

shelled prey would probably be c.50mm. Kube (1996) recorded Common Scoter feeding on *Mya arenaria* specimens of between 5mm and 30mm length. Stewart (cited in Hughes *et al.* 1997) found that the average size of *Donax vittatus* taken by Common Scoter in Carmarthen Bay, South Wales, was 28mm. Meissner & Bräger (1990) found a mean shell size of 15.3mm amongst ingested *Cyprina islandica* from a sample of Common Scoter from the German Baltic, with very few specimens larger than 30mm. In what can be considered a sympatric study of bivalve size selection, Durinck *et al.* (1993) found no differences in size class distributions between the two scoter species off the west coast of Denmark amongst either *Cardium edule* or *Spisula subtruncata* (see **Figure 1**). There were significant differences between the size class distributions of the two bivalve species, suggesting that neither predator selected for a specific size class but rather took a 'representative' subset of what was available to it.

Overall, in the literature there is considerable variation in the size class distributions of bivalve prey taken by Common Scoter (**Figure 2**). The presence of large numbers of very small prey items in the sample from Helgenæs, east Jutland (Danish Baltic, November 2001), suggests that there is not an obvious 'lower' critical threshold that limits prey size within the range measured here, since none of the abundant prey was found to exceed

10mm in size. In this situation, it may well have been the ease of extraction of large numbers of very small prey that made such foraging profitable under these circumstances. Under other circumstances, whilst it may be more effective to consume larger bivalves, it would also make no sense to reject smaller specimens once harvested. The interesting feature is the normal distributions shown by these frequency distributions that differ markedly in their means. These data are extremely hard to interpret, since they draw from non-random samples of birds taken from different areas in Danish waters at different times of year. The differences could therefore reflect differences in selection of size classes by the birds (because of different nutritional requirements at different times of year or the difference in profitability of different sizes of prey items, for example). On the other hand, these differences could merely reflect the random selection of birds taking whatever is the most profitable prey in proportion to their availability locally. It is impossible to distinguish between these two possible interpretations with our available knowledge, but, based on the available information, it seems likely that there is an upper limit on the size of hard prey taken, which seems to be around 30-40mm. It also seems likely to be the case that the wide range of prey sizes within the range taken reflects the local conditions in some way. However, considerably more research needs to be undertaken before one can be certain
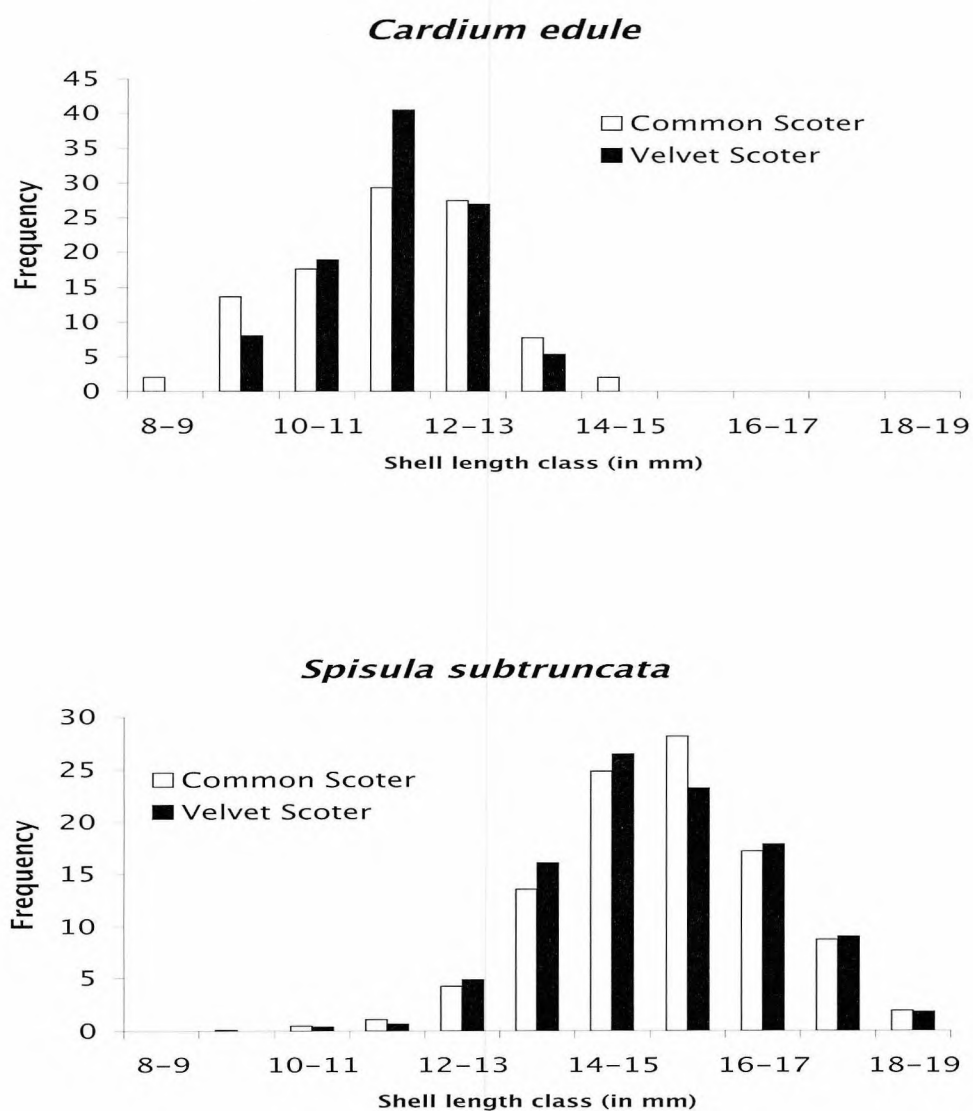
Cardium edule

Spisula subtruncata

Figure 1. Frequency distribution of shell lengths of *Cardium edule* (upper) and *Spisula subtruncata* (lower) taken by Common and Velvet Scoter (data from Durinck *et al.* 1993).
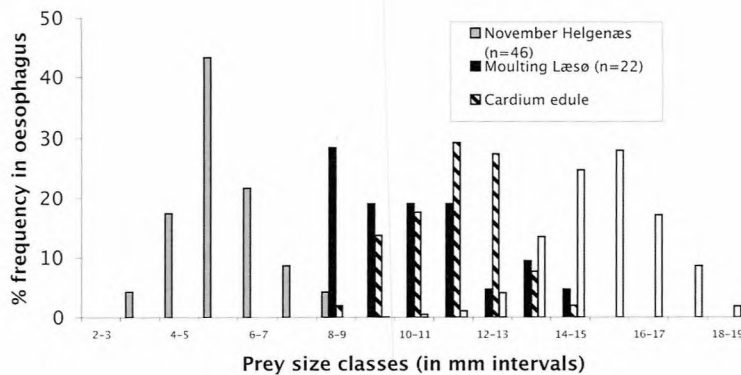
Figure 2. Frequency distributions of bivalve shell lengths of prey items taken from the oesophagus of Common Scoters killed in Denmark. These are: (i) Helgenæs, east Jutland, Danish Baltic, November 2001 (n=46, unpublished data), (ii) south of Læsø, Danish Baltic, August 2001 (n=22, unpublished data), (iii) *Cardium edule* and (iv) *Spisula subtruncata* taken in the Danish North Sea (latter two datasets from Durinck *et al.* 1993).

that scoters exploit available profitable bivalve populations rather than show a high level of selection for specific sizes classes.

Water depth

All other things being equal, scoters would be expected to dive in the shallowest water necessary to obtain their food. Locomotory costs of diving are second only to flight in terms of energy expenditure (c.3.5 times basal metabolic rate, Woakes & Butler 1983, 1986), so foraging represents a trade-off between the food gain obtained from a dive to the bottom versus the costs of travel and handling. It would therefore be expected that scoters select for the shallowest foraging areas possible, consistent with the highest available suitable prey biomass. Assessments of the depths exploited by scoters vary considerably between authors and presumably reflect local water column depth and benthic community types. For the Common Scoter, Dewar (1924) recorded 81% of dives between 2.2 and 3.7m depth (maximum 6.7m), yet Madsen (1954) claimed that 10-20m was the 'normal' diving depth for Common Scoter and 14-30m for Velvet Scoter. On the breeding areas, the normal diving depths for Common Scoter are 1-3m (Dementiev & Gladkov 1952; Cramp & Simmons 1977) and 2-5m for Velvet Scoter (Cramp & Simmons 1977). Recent aerial surveys of moulting and wintering Common and Velvet Scoter in Ålborg Bugt, eastern

Denmark (see Petersen *et al.* 2003) show that birds were localised over a mean water depth of 5.93m (+0.015 S.E., n=16,605 bird observations) in July. However, as the winter progressed, the mean water depth associated with localisations fell in a predictable fashion through each of the winter months to reach to 9.40m (+0.019 S.E., n=30,805) in April, and this pattern was consistent between three different years. The results of these aerial surveys showed that a mere 0.015% of 568,543 non-flying Common Scoter were observed at positions with water depths of >20m (Petersen *et al.* 2003).

In summary, scoter are not randomly distributed at sea: they select for specific benthic communities and the energetic constraints on diving versus derived energy and nutrient gain constrains them to select shallow water, which appears to be less than 20m in most of the western Palearctic. More data are required on the interplay between prey biomass, prey availability, prey quality and water depths to understand foraging dynamics in tidal waters and in response to food depletion.

Discussion

The widespread distribution and abundance of diving ducks suggest that they are unlikely to be restricted to any particular type of food but readily take whatever prey is available in sufficient quantity. Certainly, local dominance of species in the diet does vary with local prey abundance (eg Nilsson 1972; Durinck *et al.* 1993). Nevertheless, it is extremely difficult from the available literature to determine prey selectivity of scoters. Very few of the studies sampled the benthic communities and the diet of scoters at the same point in time and space. In general terms, it would certainly appear that scoters take whatever bivalve mollusc species is most abundant where they feed, and it is apparent that the prey species vary throughout the non-breeding range of these ducks. Hence in Lithuanian, Polish and German Baltic coasts, Common Scoter consumed the locally abundant *Mya arenaria*, in Danish Baltic waters *Cardium edule* was predominantly taken where this species is abundant, in Danish and Dutch Wadden Sea waters *Spisula subtruncata* was taken, whilst in NW France mainly *Donax vittatus* was taken. In this sense, the diet appears to simply reflect local abundance, the major constituents of the benthic communities dominating the diet in most studied situations. There is a need to undertake specific synchronous studies of benthic communities and diet of scoters in a number of different situations throughout their non-breeding range to establish feeding selectivity in terms of species and size class distributions.

Extremely little is known about factors affecting site selection, given that ducks show little evidence of strong species or size selection. This is especially interesting, since scoter are conspicuously mobile, with small flocks

flying daily between favoured feeding areas, apparently monitoring the quality of their feeding environment. Common Scoter wintering off The Netherlands' coast will sometime switch en masse to alternative sites tens of kilometres distant (eg after severe disturbance from shell fisheries or mass mortality of *Spisula*, M.F. Leopold, pers. comm.), suggesting prior knowledge of these alternative feeding grounds. Nevertheless, the basis for site selection remains obscure. In The Netherlands, for example, scoters have been described spending a whole winter on a *Spisula* bank where prey averaged 10mm shell length, returning the following year when the *Spisula* had grown to c.20 mm, and again the following year when they had reached 25-30mm (Offringa 1991; Leopold 1996). Here, prey size and prey density changed between three consecutive years (although the water depth clearly did not) because the *Spisula* was not replenished by good spat fall, yet this single age class in one area apparently supported 100,000 Common Scoter for three consecutive winters. Studies failed to demonstrate the specific impacts of birds on the *Spisula* stocks of such a bank because other agents (such as fisheries, winter mortality and storm damage) had a far greater impact on their distribution and abundance (Leopold *et al.* 1998). In this context, there appears little evidence for either prey depletion or size class frequency selection playing a role in feeding site selection for this large

aggregation of Common Scoter.

Scoters do seem to prefer to feed in sandy substrates during moult and winter. Not only do most of the most frequently consumed prey items occur in such substrates, but also the sites of many of the most important concentrations are characterised by sandy sediment types. These include the Danish Ålborg Bugt area south of Læsø (probably the most important moulting and wintering site for the species in the world) and the eastern North Sea coastline. However, the presence of this community type does not guarantee the presence of scoters, so clearly there is more to habitat selection than just benthic community and sediment type. The information presented here comes mainly from the Baltic and North Sea areas, which represent the core of the non-breeding range of the scoter species in the Western Palearctic. Although the wintering sites of coastal Portugal, Spain and North Africa are more peripheral to the range, it is interesting to speculate about the potential differences in feeding profitability of the exploited habitats in this region, not least to understand the potential benefits that justify the extra energy expenditure needed to fly there from the main centres of the wintering range.

This review has also highlighted the lack of knowledge relating to seasons other than autumn and winter. Most of the studies presented here have not considered potential changes in prey composition in late winter and spring

prior to migration to breeding areas. Several diving duck species include fish roe in their diet during pre-breeding staging (and at other times of the annual cycle as well), and this may explain anomalous shifts in scoter distributions in spring to normally unoccupied areas in inshore Danish waters. Since these periods in the life cycle may be critical for accumulation of pre-migration and pre-breeding nutrient and energy stores, and hence affect breeding success, this lack of knowledge identifies a priority area for future investigations. Furthermore, it would be extremely profitable if it were possible to incorporate information on diet with the characterisation of seasonal use, sediment types and general benthic community types in any compilation of a site inventory for non-breeding scoters in the Western Palearctic.

Researchers still have no idea about how scoter locate, capture and handle their prey, but it seems likely that the combination of high prey encounter rate and the ease of probing and siphoning in sand combine to make foraging in these substrates highly profitable. Some diving ducks are known to probe and dig in soft substrates for single food items (eg Suter 1982; Ball 1990) and it seems likely that scoters may use this feeding technique, especially for prey items towards the upper end of the size spectrum selected. Long-tailed Duck *Clangula hyemalis* and Tufted Duck *Aythya fuligula* are thought to strain small (<16mm) prey items from sediments by creating a strong water flow generated in the bill. This is thought to be a common filtering technique used by many benthic feeding diving ducks, perhaps including scoter, to sift small prey items (Madsen 1954; Böhme 1992; de Leeuw & van Eerden 1992; Kube 1996). If this is the case, the relatively 'clean' sandy substrates, with little organic or fine mud fractions, would enable simple differentiation of prey items using this type of feeding technique and may contribute to the explanation of why this substrate type is selected. This could also explain how other food items, such as annelids, crustaceans (especially isopods and amphipods, which inhabit the upper sand horizons) and even small fish figure in the diet of some individuals. Direct observational studies of feeding techniques in captivity would be useful. However, observations of their natural feeding techniques (perhaps in the wild using remote underwater video methods) would be highly desirable to understand the basic feeding ecology of these species, establish prey capture techniques and perhaps gain insights into fine-grained habitat selection. Knowledge of how prey items are extracted from the substrate would also assist in understanding what proportion of the potential benthos biomass is actually available to diving scoters. Earlier, it was speculated that prey more than 4.5cm below the surface was totally unavailable to foraging scoters, but bivalves may show diurnal patterns in their vertical distribution and this again deserves further

investigation. Is bivalve biomass so great in the upper 2cm of rich sandy substrates that scoters have no need to probe deeper? Even the most rudimentary understanding of how these birds feed is lacking.

The differences in mean prey size from different sites at different times based on different prey make it difficult to distinguish between the hypotheses that scoter select for specific prey size or that they simply take prey in proportion to their availability. The remarkable similarity between the size class frequencies of the *Cardium* and *Spisula* taken by Common and Velvet Scoter in the Danish North Sea suggests that the birds are taking prey in proportion to their availability. Differences in bill and gape size and morphology between these two predator species might be expected to create differences only in maximal prey size between the two scoter species. Prey selection within a selected site can only be established by the simultaneous study of the available benthos and scoter prey. This remains a priority area of research for the future.

In summary, scoters seem to prefer foraging in clean, sandy substrates that support benthic communities rich in bivalve biomass. Within such sites, prey species are probably taken in proportion to their abundance. This would make the identification of suitable habitat signatures relatively simple throughout the Western Palearctic and enable a crude extrapolation of the potential food resource available to the populations of the two species. Unfortunately, although such a calculation could be interesting, understanding of the feeding ecology of the Common and Velvet Scoter remains poor. There exists an abundant literature on the seasonal and annual variations in the benthic fauna of intertidal sediments as these relate to consumers (wading birds, Wanink & Zwarts 1993; Zwarts & Wanink 1993). These have enabled the interpretation of the distribution and abundance of the predator (in this case the waders) in terms of the abundance, availability and distribution of their prey. This has been achieved both by measuring feeding intake rates (eg Goss-Custard *et al.* 1982; Zwarts *et al.* 1992) and by comparing available prey distribution with wader densities (eg Zwarts *et al.* 1990; Piersma *et al.* 1993b). In these studies, it has been shown that shorebirds can remove substantial proportions of the macrozoobenthos biomass (10-20%), a depletion rate which affects foraging profitability and hence the distribution of predators (Zwarts & Drent 1981; Meire 1993). The offshore submarine theatre for foraging scoters restricts our ability to undertake such studies for seaducks, which are difficult even to count and map accurately, let alone to observe in preferred feeding habitats. Food choice has only been estimated from stomach content analysis (see references above) or inferred from the benthos present at preferred sites, and diet selection and prey handling studies of diving ducks have

remained in the domain of laboratory experiments (eg Draulans 1982; de Leeuw & van Eerden 1992).

The challenge is clear: if researchers are to be able to make the simplest of predictions of where, when and in what numbers moulting, wintering and pre-breeding scoters occur in relation to their food supply, they need to understand more about their basic foraging ecology and behaviour and their prey. It is evident that, just as in intertidal systems, the fraction of bivalve prey harvestable by scoters will depend upon energy density, body weight, biomass, burying depth and behaviour of the prey as well the nature of the sediment, the depth of the water column that sits above it and the level of disturbance to the site. As in the case of waders harvesting the intertidal benthos, the consumption rates of the predator scoters will deplete prey in a manner that will also affect local profitability of the food supply and levels of interference between foraging individuals and modify predator densities. The challenge is to be able to understand the basics of these systems in a hostile and difficult environment in which to carry out research. Nevertheless, to be better able to relate the distribution of non-breeding scoter to their food supply and begin to make some predictions about the effects of changes in habitat or habitat loss on scoter populations, investment must be made in such research in the future.

Acknowledgements

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