Diet (preferences) of Common Eiders *Somateria mollissima*

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Introduction

Eiders are large sea ducks, which feed on a large variety of prey species. They usually specialize on one or more prey species in any one situation and the list of known prey species is long. The prey may be attached to a hard substratum or buried in the sand; it may occur singly or clumped; it may be small (i.e. smaller than 1 cm) or large (> 7 cm); it may be soft or hard-shelled or spiny; it may be taken while the bird is walking on dry land or it may be taken while submerged at tens of meters. This would suggest that eiders can live and survive under many different circumstances and indeed they do. They may live, for instance, on a mixed diet of sea-urchins and very small (< 1 cm) mussels in kelp-dominated areas (St Lawrence Bay, Canada; Guillemette et al., 1993) or on medium-sized mussels (10-40 mm) in northern Norway and the Baltic and Wadden Seas (Madsen, 1954; Bustnes & Erikstad, 1990; Kallenborn et al., 1994). The ducks, particularly those in the Wadden Sea, may also prey on much larger mussels of up to 7 cm (Nehls, 1991; 1995). In Norway, eiders have shown great versatility, living either on large clams of up to 5.4 cm or on tiny fish-eggs, both at water depths of 25-50 m (Brun, 1971; Gjøsæter & Sætre, 1974). Notwithstanding this suite of possibilities globally, eiders usually focus on bivalve molluscs and on blue mussels in particular. In most situations, at least one other prey species is also important. In the Wadden Sea, cockles fulfill this role (reviews in Camphuysen, 1996; Leopold et al., 2000), but it is largely unknown whether mussels and cockles are interchangeable for individual ducks and to what extent other prey species might supplement the diet when both primary species are scarce. The question remains as to which parts of mussel and cockle stocks can be utilised by the eiders. This is important information for the management of the Wadden Sea, for instance, for decisions regarding the amounts of mussels and cockles needed to be set aside for the ducks as both are fished on a large, industrial scale in the Wadden Sea (Ens, 2000). This contribution aims at describing the known diet and dietary preferences of eiders.

Because eiders have such a wide variety of possible staple diets, one might wonder if they are capable of utilizing any food source. In any case, food should be available within the right but wide size and correct depth ranges, be sufficiently abundant, and have a positive energy return meaning that hunting, catching and processing costs combined must be outweighed by the calorific contents and subsequent energy gains. Still, even if eiders could survive on very different foods under a given set of conditions, the energy expended during feeding might still make one type of food more favorable than another. Also, some energy-rich foods may create problems. Crabs carry a potentially lethal parasite load, while the long and sharp razor clams, as well as very large mussels or mussels covered with barnacles may cause more direct physical damage or even kill the bird (Swennen, 1976; Jukema, 1979; Swennen & Duiven, 1989). For these reasons, Swennen (1976) considered that eiders prefer relatively small and smooth, and hence safe prey. Nehls (1995) has added to this picture the notion that selection of certain size classes is also influenced by handling costs and energetic returns (flesh contents). Larsen & Guillemette (2000) and Leopold et al. (2000) found evidence that depth at which prey occurs, may also be limiting, and that depth interplays with prey size.

Actual Diet and Prey Preferences in the Wadden Sea: What Can and Cannot be Eaten?

The Wadden Sea is highly productive, but only a few species are particularly abundant. Most of the very abundant worm-species are of very little importance to eiders. Other abundant foods like the clams, *Mya arenaria* and *Ensis directus*, generally live too deeply buried or grow fast to sizes too large for the ducks to swallow, to be of much use to them. Some animals that live within reach and are super-abundant in places, are apparently too small to be profitable. These species include the mud snail *Hydrobia ulvae*, for example, while fish eggs are never available in large quantities. This leaves the eiders in the Wadden Sea with a limited number of prey species. Of these, mussels and cockles form the sta-

ple diet in most available studies, but these are supplemented by the Tellinid *Macoma balthica*, the starfish *Asterias rubens*, the crab *Carcinus maenas* and the periwinkle *Littorina littorea*. Recently, i.e. since about 1990, eiders have also moved to the North Sea coastal zone, to feed on the clam *Spisula subtruncata*.

Mussels and cockles. Mussels and cockles have been found to be the staple diets in all major diet studies within the Wadden Sea proper. Eiders, as seen from aerial and ship-based surveys throughout the international Wadden Sea, mainly reside over mussel culture plots, natural mussel beds and sand flats with high densities of cockles (Nehls, 1989; 1995; Swennen, 1991; Baptist et al., 1997; Berrevoets et al., 2000; Laursen et al., ms; pers. obs.). However, mussel culture plots become of little importance to eiders in the breeding and moulting season in summer (Swennen et al., 1989) when the birds avoid areas that are often disturbed by working mussel fishermen. Many large-scale studies have shown that these two bivalves form the bulk of the diet throughout the entire Wadden Sea, but also that much variation exists between places, seasons and years (Pethon, 1967; Swennen, 1976; Oranjewoud, 1983; Nehls, 1989; Asferg, 1990; Kallenborn et al., 1994; Hilgerloh, 1999; 2000; Laursen et al., ms). One of the two prey species alone may form over 90% of the diet at certain locations. For eiders feeding on cockles, this is hardly surprising, as they feed essentially in a one-prey species situation. Some small *Mya* or large *Macoma* that are encountered in the process of digging up cockles, are obviously not rejected as food and form most of the remainder of the diet in such situations. Likewise, mussels form the bulk of the biomass on natural mussel beds and on culture plots, but associated crabs, starfish or periwinkles may also be eaten. From these results, it is not immediately clear that the ducks actually do prefer mussels and cockles. They obviously prefer locations with a high biomass of suitable prey, and in the Wadden Sea, this happens to be mussel and cockle beds. In other areas of the world, mussels and cockles are substituted by other species, if these are more readily available.

Macoma. The brightly colored Baltic Tellins are very obvious in faeces and are noted in many studies but Macoma was only once (Laursen et al., MS) found as an important source of food. Many *Macoma* will be too small to be profitable and most of the larger animals live relatively deep in the sediment, especially in winter (Zwarts & Wanink, 1993). Parasite-infected *Macoma* crawl towards and over the surface, but eiders, like Oystercatchers *Haematopus ostralegus*, may dislike such individuals (Hulscher, 1982). On top of this, large *Macoma* are very hard-shelled and thus take a relatively high amount of energy to be broken down in the birds' stomachs (Camphuysen et al., submitted).

Mya. Sand Gapers quickly become an unsuitable prey for eiders in that they become too deeply buried for the birds to dig them up and too large to swallow. In general, only young animals are suitable prey. We know very few studies where feeding on *Mya* was observed on more than a very limited scale. Nyström et al. (1991) found that (juvenile) eiders ate young *Mya* (< 2 cm shell length), in the Baltic. Kallenborn et al. (2000) also found *Mya* in drowned eiders in the Baltic. Very little is known of *Mya* as eider food in the Wadden Sea. Swennen (1976) did not find this species in 4441 faeces samples.

Ensis. Razor Clams seem an unsuitable food at first because of their shape and burying capacity (Swennen et al., 1985), but they are apparently eaten in certain situations. In autumn 2000, a flock of several hundred eiders was seen, apparently feeding, on a site off Vlieland in the North Sea coastal zone, where *Ensis directus* was commercially fished and presumable the only abundant biomass (J. van Dijk, pers. comm.). Laursen et al. (MS) actually found *Ensis* in stomachs of shot birds. From 1986-88, it constituted over 50% of all prey items in one of their study areas.

Littorina. Periwinkles have often been found in faeces and stomachs of eiders in the Wadden Sea, but are rarely considered as an important food source. In one study in Canada, periwinkles were found to be important prey to juvenile eiders (Cantin et al., 1974). For the Wadden Sea there is also evidence that at least some individuals may focus on this prey, possibly after they have become severely infested with the parasite *Proficollis botulus* (Swennen, 1976). There is some anecdotal evidence that in times of food shortage, more eiders may switch to eating periwinkles (Swennen in Abrahamse & Revier, 1991; Cadée, 1991). *Littorina* is probably predominantly eaten in the high intertidal zone and on rocky shores, i.e. on dikes at the fringes of the Wadden Sea, where juvenile and sick, adult eiders are the most abundant (Swennen, 1976). Eiders may not be able to break down the opercula of *Littorina* in their stomachs and more than likely must regurgitate these remnants, possibly making *Littorina* a less preferred prey of healthy eiders (Swennen, 1976; but see Laursen et al., MS: *Littorina* also found in healthy adults). The problems of removing these parts may

also explain why *Littorina* is often recorded as prey in stomachs of starved eiders.

Asterias rubens. Starfish are eaten regularly, particularly on sublittoral mussel beds and mussel culture plots. It is unclear whether starfish are merely 'bycatch' to mussel-feeding eiders, or if some birds actually focus on this prey. One study (Oranjewoud, 1983) found starfish and crabs (the two species are placed together in this study) to be the dominant prey in winter, indicating that such prey gain importance when mussels reach a low flesh content at that particular time of year.

Carcinus maenas. Crabs are regularly taken by most eiders in the Wadden Sea, as most eiders carry at least some of the parasites that have these crabs as their first intermediate host (Swennen & Van den Broek, 1960; Camphuysen et al., submitted). Crabs are dangerous prey, both during handling (pincers!) and after digestion, as many carry parasites, which are potentially lethal to the ducks. Eating crabs is thus often seen as a sign of poor feeding capability, and mostly observed in juvenile, inexperienced or otherwise impaired birds that feed in shallow, near shore waters, or as a sign of a lack of more suitable food (Camphuysen et al., submitted). In this respect, it is interesting to note that at least one other bird has, like eiders, shown mass die-offs in connection with a presumed switch from preferred prey (fish) to crabs. Great Northern Divers (or Common Loons) *Gavia immer* have shown several such mass die-offs around Florida, USA, and their stomachs and guts were found to contain unusual quantities of crab-associated parasites (McIntyre, 1988; Forrester et al., 1997). In contrast to the notion that crabs are prey to be avoided, Swennen (1976) considered that eiders actually like eating crabs. Laursen et al. (MS), however found crabs in the stomachs of juvenile eiders in particular, suggesting that adult birds prefer to, or are better able to, feed on other prey, i.e. mussels and cockles.

Fish eggs. Different species of soft-bodied prey have been noted as food sources for eiders in the Wadden Sea, but never in great quantities. Fish eggs are rarely available in large amounts in the Wadden Sea. Swennen (1976) only mentions that eiders (rarely) took eggs of Bull-rout *Myoxocephalus scorpius*, a bottom dwelling fish that spawns among rocks and other hard substrates, e.g. mussel beds.

Spisula subtruncata. Through Shells are a new and important prey species for eiders in the Netherlands. In 1989/90, large numbers first took to the Dutch North Sea coastal waters, which was apparently in response to a structural food shortage of mussels and cockles in the Wadden Sea (Leopold et al., 1995; 2001) and a simultaneous increase of *Spisula* in the North Sea. *Spisula* became the staple diet of eiders in the (Dutch) North Sea (Den Hollander, 1993; Leopold, 1996). All things considered, *Spisula* would have good returns compared to the other important burying bivalve, the cockles. In a comparison of shell mass, shell strength and flesh contents, Camphuysen et al. (submitted) demonstrated *Spisula* to be a profitable prey species, provided that large specimens can be eaten. In fact, eiders were demonstrated to be able to live only on large (> 1.5 cm, preferably even > 2.5 cm) specimens (Leopold et al., 1998; 2000). However, all things are not equal, in that cockles can be found in very shallow waters, while *Spisula* occur at water depths of 5-15 meters and considerable effort must go into diving, which is needed to find and catch these bivalves. Without energetical measurements of eiders feeding on different prey at different water depths, the question whether *Spisula* could be a preferred prey or just a secondary prey in times of shortage of mussels and cockles, remains unresolved. There is some evidence both ways. Non-oil related eider mortality was highest in 1990/91 and 1999/2000, when prey in the Wadden Sea was apparently in short supply (Camphuysen et al., submitted). However, mortality was normal in 1992/93, when the highest numbers of eiders frequenting the North Sea *Spisula* banks was recorded.

Size or Quality Selection in Different Prey Species

Given that mussels and cockles, and possibly *Spisula* are the most important prey, the next question is whether eiders prefer a certain size or quality. The birds may do so in a two-step process: first, by selecting a feeding site where prey size or quality are generally profitable and second, by selecting the most profitable prey from within that site. In the Wadden Sea, subtidal, cultured mussels are the most profitable (Camphuysen et al., submitted) and therefore, the vast majority of eiders in the Dutch Wadden Sea (where most culture plots are located) reside over these mussels, if they are made available (no ice, no disturbance by fishermen; Berrevoets et al., 2000; Leopold et al., 2000). Depth, however, may be a limiting factor for feeding on mussels. Larsen & Guillemette (2000) found that eiders very much prefer natural beds at water depths shallower than 6 m, than beds at 6-12 m. Mussels on the culture

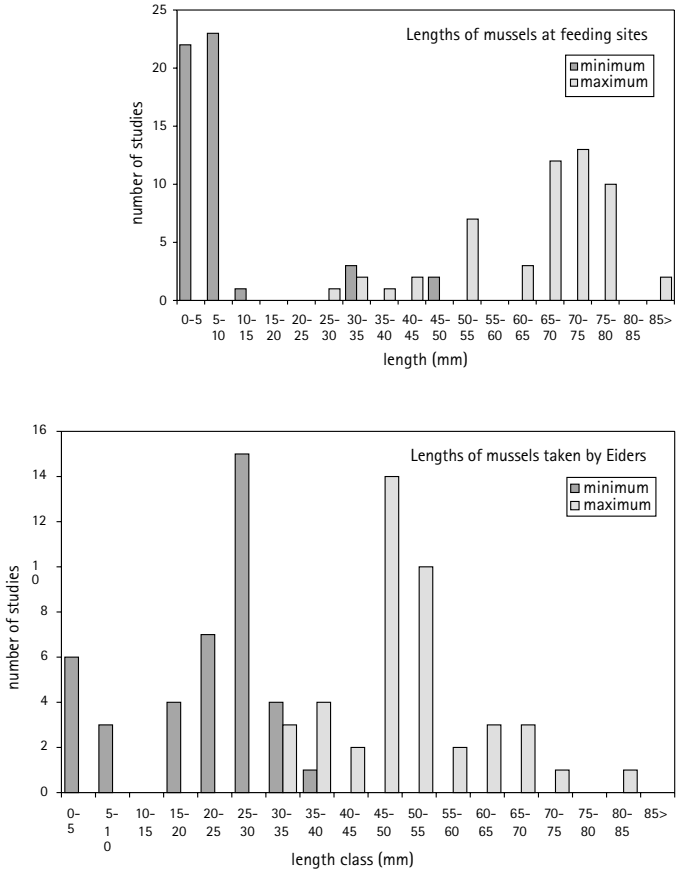
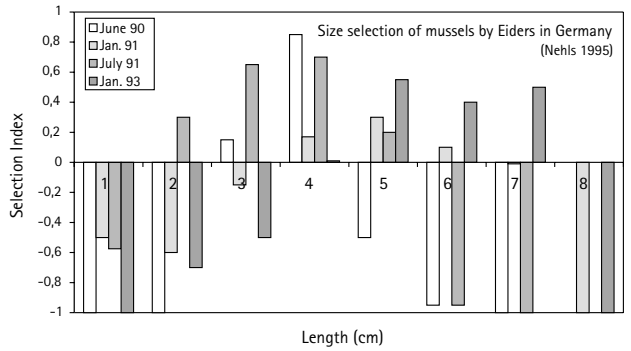


Figure 1: (top) Minimum and maximum lengths of Blue Mussels at eider feeding sites. (bottom) Minimum and maximum lengths of Blue Mussels taken by eiders. Along the Y-axis, the number of studies or sub-studies is given in which a particular minimum or maximum is given.

plots have thinner shells and are less well attached to each other than intertidal ones, and for this reason only, should be the preferred food of eiders (Bustnes, 1988; Bustnes & Erikstad, 1990; Nehls, 1995).

Size Selection in Mussels

Mussels from natural intertidal beds and subtidal culture plots differ greatly in their profitability, and studies of prey selection on natural mussel beds cannot simply be extrapolated to culture mussels. Unfortunately, most studies on size selection have been carried out on natural mussel beds. A further problem when trying to understand the process of size selection from data in these studies is that most studies only provide the range (smallest and largest) taken and do not compare the fraction taken from the prey on offer. An overview of size ranges of mussels taken worldwide is given in Fig. 1. For the Wadden Sea, only a few studies are available. Swennen (1976) concluded, from a wealth of field work conducted in the 1960's and 70's, that: eiders 'clearly took much smaller molluscs than were available on the flats', but gives no quantitative data on prey availability. He also suggests (in Swennen et al., 1989) that molluscs of 1-2 cm would be the preferred prey and speculates that the birds might deplete the stocks of small sized molluscs over winter, thus forcing the birds to gradually take larger and larger mussels until they must take mussels that are considered to be of 'commercial size' in late winter. Nehls (1995) agrees with the suggestion that size of ingested mussels increase during the winter, but he, and also Bustnes (1988) and Bustnes & Erikstad (1990), offers an explanation for this based on feeding energetic. Eiders maximize energetic returns, therefore subtle differences in flesh contents and shell masses between different size classes govern the birds' feeding decisions over winter. Nehls (1995) found, that on intertidal mussel beds in the German Wadden Sea, eiders selected a size range of 2-5 cm in summer and of 4-7 cm in winter (Fig. 2a). A similar pattern of size selection was found in Canada (Hamilton et al., 1999), but within a size spectrum of much smaller mussels (Fig. 2b). Laursen et al. (MS) found, that in shot birds in Denmark, mussels taken (range 3-5 cm) differed from those actually on offer (0.5-7 cm), indicating that the eiders did not select either the largest or the smallest mussels available. However, if the mussels on offer were on average small (mainly smaller than 3 cm) the eiders selected the largest mussels (3-5



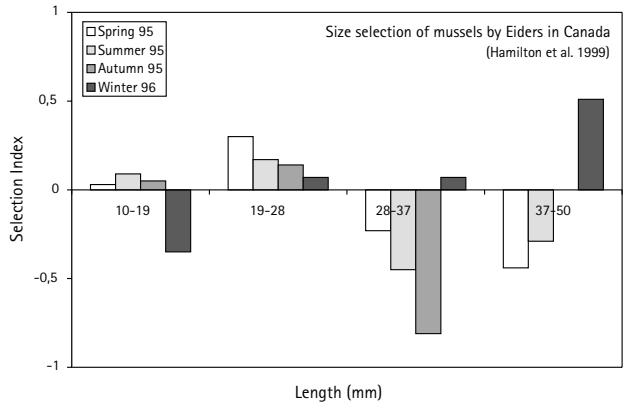


Figure 2: (a) Size selection of Blue Mussels by eiders feeding on natural intertidal mussel beds in the German Wadden Sea (after Nehls, 1995). (b) Size selection of Blue Mussels by eiders feeding at Canadian rocky shores (Hamilton et al., 1999).

cm) present. There are no data on size selection by eiders on the Dutch culture plots, which are the most important feeding sites of the Wadden Sea. Larsen & Guillemette (2000) found, that on subtidal natural mussel beds in Denmark, the eiders mainly fed at depths of less than 6 m. Most culture plots fall within this range. They also argue that flesh to shell mass ratios are highly unfavorable in larger mussel sizes and observed that at depths greater than 6 m, the mussels could reach sizes that were too large to be profitable for the eiders, thus indicating a high predation pressure. Mussels in beds in deeper waters were thus unprofitable for two reasons: they occurred too deep and were too large.

Size Selection in Cockles

Surprisingly, even less is known about size selection in cockles, although selection in this rather uniform, intertidal prey would be much easier to study than in mussels. Both studies on distribution of eiders over the Wadden Sea and diet studies show cockles to be important prey, but just how they compare to mussels and which cockles are the most suitable prey remains unknown. An overview of ranges of size taken by eiders is given in Fig. 3. Swennen (1976) has provided eiders with cockles on unburied feeding trays and under these highly artificial circumstances, the eiders always took the smallest cockles from those on offer. This was especially true if large cockles were offered. There are no field studies that compare cockles taken with those locally present. There are only some general suggestions that cockles would be less profitable than mussels if flesh to shell masses were compared (Camphuysen et al., submitted). Also, feeding on cockles seems to be restricted by the tidal cycle in that this prey is mainly taken when a little water is present on the feeding site. Cockles living in very muddy sediments are avoided (Nehls, 1991; 1995).

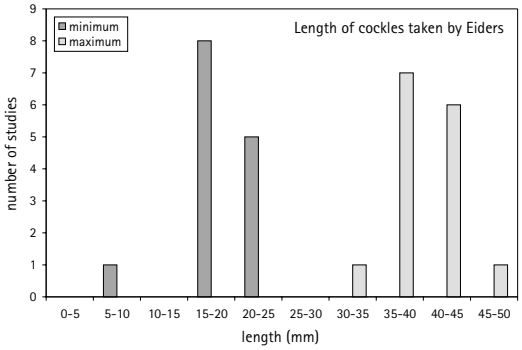


Figure 3: Minimum and maximum lengths of cockles eaten by eiders in different studies.

Size Selection in Spisula

Size selection in *Spisula* has not been directly studied, through the comparison of sizes taken to sizes on offer. However, Leopold et al. (2000) compared eider distribution and size distribution of *Spisula* in the Dutch North Sea and found that eiders always selected sites with the largest *Spisula*. *Spisula* smaller than 1 or 1.5 cm seem to be too small. Eiders were also found to prefer *Spisula* banks at relatively shallow depths (< 10 m).

Discussion

Eiders can take many different prey items, but in the Wadden Sea, the mussel is probably the most important prey. Mussels are reliable prey as they are always present, unless the beds are grossly over fished, as happened in 1990 (Beukema, 1993; Camphuysen et al., submitted). Cockles are the next most important prey and are also energetically profitable, but cannot be taken throughout the entire tidal cycle. These occur in very low densities after mass die-offs in severe winters and have thicker shells than (cultured) mussels. *Spisula subtruncata* is now the third most important prey, but has two main disadvantages: it occurs in relatively deep waters and the prey stock may be unreliable as evidence shows that mass die-offs have occurred in severe winters.

Most prey sizes can be taken by eiders, but they seem to prefer medium sized prey. The most important piece of knowledge that we still lack in this respect is the feeding decisions eiders make, both on mussel seed and on culture plots, and on cockle beds. As we do not know what is present on the different culture plots (Smaal et al., 2000), distribution of the birds over the range of plots available cannot be understood. Taking this one step further, we do not know what, if anything, the eiders select from within these plots. Neither size selection of mussels or the selection of mussels versus other prey present, such as starfish and crabs, within plots has been studied here. It is in this area that additional studies are most urgently needed to understand what exactly eiders do in the Wadden Sea. Opportunities are there, if fishermen and scientists can work together, as the constant stocking, restocking/relocating, growth and final removal of mussels from the plots form an immense feeding 'trial' for eiders. Tapping into this large-scale 'experiment' will be the challenge for the immediate future. Work on site and size selection in cockles is an easier task to address, as it can be done on foot and without information, which is currently only available to fishermen.

References

Abrahamse, J. & H. Revier, 1991. Kees Swennen over Eidereenden en schelpdiervisserij. Waddenbulletin 26, pp 123-125.

Asferg, K.,1990. Diet of Eiders in the Danish waters, with notes on other seaduck species. Summ. lect. Joint Meeting IWRB's West. Pal. Seaduck Database. IWRB Newsletter December 1990, p 31.

Baptist, H.J.M., R.H. Witte., P. Duiven & P.A. Wolf, 1997. Aantallen Eidereenden *Somateria mollissima* in de Nederlandse kustwateren en de Waddenzee in de winters 1993-97. Limosa 70, pp 113-118.

Berrevoets, C.M., H.J. Baptist & R. Witte, 2000. Analyse Eidereenden Waddenzee/Waddenkust/Hollandse Kust. Werkdocument RIKZ/IT/2000.841. Rijksinstituut voor Kust en Zee, Middelburg. 25 pp.

Beukema, J.J.,1993. Increased mortality in alternative bivalve prey during a period when the tidal flats of the Dutch Wadden Sea were devoid of mussels. Netherlands Journal for Sea Research 31, pp 395-406.

Brun, E., 1971. Predation of *Chlamys islandica* by *Somateria* spp.. Astarte 4, pp 23-29.

Bustnes, J.O., 1988. Selection of Blue Mussels, *Mytilus edulis*, by Common Eiders, *Somateria mollissima*, by size in relation to shell content. Canadian Journal of Zoology 76, pp 1787-1790.

Bustnes, J.O. & K.E. Erikstad, 1990. Size selection of Common Mussel *Mytilus edulis* by Common Eiders, *Somateria mollissima*: energy maximization or shell weight minimization. Canadian Journal of Zoology 68, pp 2280-2283.

Cadée, G.C., 1991. De Alikruik (*Littorina littorea*) als Eidereend voedsel. CB Ned. Malac. Ver. 262, pp 876-880.

Camphuysen, C.J., 1997. Ecologisch profiel van de Eidereend *Somateria mollissima*. RIKZ-werkdocument 96.146x, Nederlands Instituut voor Onderzoek der Zee, Texel. 125 pp.

Camphuysen, C.J., C.M.Berrevoets, H.J.W.M. Cremers, A. Dekinga , R. Dekker, B.J. Ens., T.M. van der Have, R.K.H. Kats, T. Kuiken, M.F. Leopold , J. van der Meer & T. Piersma, MS. Mass mortality of Common Eiders *Somateria mollissima* in relation to commercial fisheries and fisheries management in the Dutch Wadden Sea, submitted to Journal of Applied Ecology.

Cantin, M., J. Bédard & H. Milne, 1974. The food and feeding of Common Eiders in the St. Lawrence estuary in summer. Canadian Journal of Zoology 52, pp 319-334.

Ens, B.J., 2000. Berekeningsmethodiek voedselreservering Waddenzee. Alterra rapport 136, Wageningen.

Forrester, D.J., W.R. Davidson, R.E. Lange, R.K. Stroud, L.L. Alexander, J.C. Franson , S.D. Haseltine, R.C. Littell & S.A. Nesbitt, 1997. Winter mortality of Common Loons in Florida coastal waters. Journal of Wildlife Diseases 33, pp 833-847.

Gjøsæter, J. & R. Sætre, 1974. Predation of eggs of Capelin (*Mallotus villosus*) by diving ducks. Astarte 7, pp 83-89.

Guillemette, M., J.H. Himmelman & C. Barette, 1993. Habitat selection by Common Eiders in winter and its interaction with flock size. Canadian Journal of Zoology 71, pp 1259-1266.

Hamilton, D.J., T.D. Nudds & J. Neate, 1999. Size-selective predation of Blue Mussels (*Mytilus edulis*) by Common Eiders (*Somateria mollissima*) under controlled field conditions. Auk 116, pp 403-416.

Hilgerloh, G., 1999. Year to year changes in the share of Cockles (*Cerastoderma edule*) and Blue Mussel (*Mytilus edulis*) in the food of Eiders on six Frisian islands. Senckenbergiana maritima 29, pp 71-73.

Hilgerloh, G., 2000. Interregional similarities in the food composition of Common Eiders (*Somateria mollissima*). Seevögel 21, pp 108-111.

Hollander, N. den, 1993. Zwarte Zeeëenden (*Melanitta nigra*) en schelpdiervisserij. Student report, Nederlands Instituut voor Onderzoek der Zee en DLO-Instituut voor Bos- en Natuuronderzoek, Texel.

Hulscher, J.B., 1982. The Oystercatcher *Haematopus ostralegus* as a predator of the bivalve *Macoma balthica* in the Dutch Wadden Sea. Ardea 70, pp 89-152.

Jukema, J., 1979. Eidereend *Somateria mollissima* als slachtoffer van mossel *Mytilus edulis*. Limosa 52, pp 73-74.

Kallenborn, R., E.Hartwig &tH.Hühnerfuss, 1994. Vergleich der Nahrung von Eiderenten (*Somateria mollissima (L*).) aus Oehe-Schleimünde mit Ergebnissen aus unterschiedlichen Nord-und Ostseegebieten.). Seevögel 15, pp 31-37.

Larsen, J.K. & M. Guillemette, 2000. Influence of annual variation in food supply on abundance of wintering Common Eiders *Somateria mollissima*. Marine Ecology Progress Series 201, pp 301-309.

Laursen, K., K.S. Asferg & J. Frikke, MS. Impact of mussel fishery on Eider Duck *Somateria mollissima* in the Danish Wadden Sea.

Leopold, M.F., 1996. *Spisula subtruncata* als voedselbron voor zee-eenden in Nederland. BEON Report 96-2, Programmabureau BEON, Rijksinstituut voor Kust en Zee, Den Haag. 58 pp.

Leopold, M.F., H.J.M. Baptist, P.A. Wolf & H. Offringa, 1995. De Zwarte Zeeëend *Melanitta nigra* in Nederland. Limosa 68, pp 49-64.

Leopold, M.F., M.A. van der Land & H.C. Welleman, 1998. *Spisula* en zee-eenden in de strenge winter van 1995/96 in Nederland. Beon-rapport 98-6. Rijksinstituut voor Kust en Zee, Den Haag. 51 pp.

Leopold, M.F., R.K.H. Kats & B.J. Ens, 2000. Aanvullend onderzoek voedselbeschikbaarheid Eidereend *Somateria mollissima*: literatuuroverzicht voedselecologie. Unpublished working report, Alterra, Texel.

Leopold, M., C. Berrevoets & M. van Roomen, 2001 (in press). Scoters in the Netherlands (1860 - 2000). Proc. Wetlands International Seaduck Specialist Group Meeting, Kalø, Denmark, 2000. NERI Techn. Rept.

Madsen, F.J., 1954. On the food habits of the diving ducks in Denmark. Danish Review for Game Biology 2, pp 157-266.

McIntyre, J.W., 1988. The Common Loon: Spirit of Northern Lakes. University of Minnesota Press, Minneapolis. 228 pp.

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

Nehls, G., 1991. Eiderenten im schleswig-holsteinischen Wattenmeer. Corax 14(3), pp 1-66.

Nehls, G., 1995. Strategien der Ernährung und ihre Bedeutung für Energiehaushalt und Ökologie der Eiderente (*Somataria mollissima* (L., 1758)). PhD thesis, Christian-Albrechts Universität, Kiel. 173 pp.

Nyström, K.G.K., O. Pehrsson & D.Broman, 1991. Food of juvenile Common Eiders (*Somateria mollissima*) in areas of high and low salinity. Auk 108, pp 250-256.

Oranjewoud Ingenieursbureau, 1983. Onderzoek naar overwinterende Eidereenden in de westelijke Waddenzee. Petroland BV, Den Haag. 36 pp.

Pethon, P., 1967. Food and feeding habits of the Common Eider *Somateria mollissima*. Mytt Magison for Zoologi 15, pp 97-111.

Swennen, C., 1976. Populatiestructuur en voedsel van de Eidereend *Somateria mollissima* in de Nederlandse Waddenzee. Ardea 64, pp 311-371.

Swennen, C., 1991. Ecology and population dynamics of the Common Eider in the Dutch Wadden Sea. PhD-thesis, University of Groningen. 144 pp.

Swennen, C. & E. van den Broek, 1960. *Polymorphus botulus* als parasiet bij de Eidereenden in de Waddenzee. Ardea 48, pp 90-97.

Swennen, C. & P. Duiven, 1989. Eidereend *Somateria mollissima* gestikt in Amerikaanse zwaardscheden. Limosa 62, pp 153-154.

Swennen, C., M.F. Leopold & M. Stock, 1985. Notes on growth and behaviour of the American razor clam *Ensis directus* in the Wadden Sea and the predation on it by birds. Helgoländer Meeresuntersuchungen 39, pp 255-261.

Swennen, C., G. Nehls & K. Laursen, 1989. Numbers and distribution of Eiders *Somateria mollissima* in the Wadden Sea. Netherlands Journal for Sea Research 24, pp 83-92.

Zwarts, L. & J.H. Wanink, 1993. How the food supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body weight, burying depth and behaviour of tidal-flat invertebrates. Netherlands Journal for Sea Research 31, pp 441-476.

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