Hunting from motorboats displaces Wadden Sea eiders Somateria mollissima from their favoured feeding distribution

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Hunting of eiders *Somateria mollissima* from motorboats is common in Danish marine waters, and to reduce hunting pressure on eiders and other diving duck species in Denmark, motorboat hunting was banned within 42 marine sites covering an area of 2,934 km^2, although the effects of this regulation have to date not been examined. Our case study analyses the effects of excluding motorboat hunting from an area of 682 km^2 of the Danish Wadden Sea (hereafter the 'Study Area') which also supported a large area of blue mussel beds, the preferred food for eiders. Our study covered the entire Danish Wadden Sea (total area 1,225 km^2) during the hunting seasons (October-February) of 1980-2003 using 85 aerial surveys of eiders and motorboats used by hunters. Eider numbers increased by 56% in the Study Area following the ban on motorboat hunting despite a 50% reduction in the eider flyway population over the same period. There was a significant negative relationship between the density of hunter motorboats and that of eiders on a small geographical scale (1.8-2.5 km). Motorboat hunting in the Study Area also affected eider distribution at larger geographical scales (4-12 km), displacing eiders from the Study Area offshore from the Wadden Sea into the North Sea. Following the ban on motorboat hunting, most eiders occurred in the Study Area. Winter (21 December-31 January) body condition of eiders was greater in the Study Area than the body condition of eiders in the Offshore Area during autumn (20 October-20 December). Eider abundance relative to blue mussel biomass significantly increased after motorboat hunting was banned in the Study Area, but there was no such change during winter after the hunting ban. Since the ban on motorboat hunting in the Study Area, eider numbers throughout the entire Danish Wadden Sea seem to be regulated by total blue mussel biomass.

Key words: blue mussel, body condition, displacement, eider, hunting free marine areas, Somateria mollissima, trade off, Wadden Sea

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Waterfowl shooting is widespread in many European countries, especially in inland freshwater areas in coastal marshlands. Inland studies show that hunting activity disturbs dabbling ducks and geese affecting numbers and local distribution (Bell & Owen 1990, Madsen 1994, Madsen & Fox 1995, Fox & Madsen 1997, Evans & Day 2001, Vaananen 2001, Tamisier et al. 2003). Coastal studies are fewer, but these also demonstrate effects of shooting on distribution and feeding activity of dabbling ducks, swans and coots (Madsen 1998, Darren & Day 2002, Bregnballe et al. 2003). Levels of disturbance caused by hunting depend on the type of hunting activity, e.g. mobile shooting punts cause greater disturbance to dabbling ducks, swans and coots than stationary shooting punts (Madsen 1998). Compared to mobile punts rowed by oars, motorboats are highly mobile and are therefore expected to present stronger disruptive stimuli to birds. Nevertheless, only one study has demonstrated local displacement of motorboat hunting (Salvig et al. 1994).

Denmark's shallow marine waters support up to 1.5 million diving ducks during the non-breeding season (Laursen et al. 1997a, Pihl et al. 2001). Many of these occur several kilometres offshore, which has established a tradition in Denmark to hunt diving ducks from motorboats, which is not practiced in other countries. The annual Danish eider *Somateria mollissima* bag is currently ca. 76,000 individuals (Asferg 2004), of these, 71% of the bagged eider ducks were shot by hunters using motorboats (Clausager 2004).

The Danish Game and Wildlife Management Act limits the speed of motorboats used for hunting to a maximum speed of 9.7 knots, although during hunting this is restricted to 2.7 knots. Eiders can be hunted during the daytime from 1 October until the end of February, although within SPA-areas (Special Protection Areas covered by the EU-Bird Directive, which include the Danish Wadden Sea) the open season ends on 31 January. From 1979 and 1987, hunting from motorboats was forbidden in 42 marine areas in Denmark covering 2,934 km^2, with the aim of reducing hunting pressure on eiders and other diving duck species. In the Wadden Sea, these areas were extended in 1992 (see later). Despite protection from motorboat hunting inside these areas for two decades, the effects on diving ducks of establishing hunting free marine zones have yet to be examined. Our study focused on eider numbers and their displacement due to hunting from motorboats, and took advantage of the banning of hunting from motorboats inside the Danish Wadden Sea (between the mainland and the islands to the west) in spring 1992 (Fig. 1).

According to predation risk theory, habitat choice is the outcome of decisions that balance the trade-off between predation risk and resource richness (Frid & Dill 2002). As a result, it is predicted that sustained, intense disturbance stimuli may cause habitat shifts at the cost of reduced access to resources, but that animals will reaccess resources in habitats previously affected by disturbance stimuli once these stimuli are removed (Frid & Dill 2002). Applying these formulations to our study, we predicted that motorboat hunting a) would reduce the number of eiders in the Study Area, b) would be inversely related to eider densities, and c) would prevent eiders from distributing themselves in accordance with the biomass density of their preferred food resource blue mussels. We tested a) and b) by comparing eider numbers and distribution before and after motorboat hunting was stopped in 1992 in the Study Area. To examine c), we used the approach of Guillemette & Himmelman (1996), testing the prediction that eider numbers during the non-breeding season are correlated with food availability, following a simple ideal free distribution (Fretwell & Lucas 1990). In our study, we analysed the relationships between blue mussel biomass and eider abundance before and after motorboat hunting was banned, and tested whether there was a correlation between the two parameters which would suggest that hunting from motorboats had not influenced the eiders in their exploitation of the blue mussel stock. A lack of such a correlation, however, would not automatically suggest that hunting from motorboats had a negative effect on the eiders' exploitation of blue

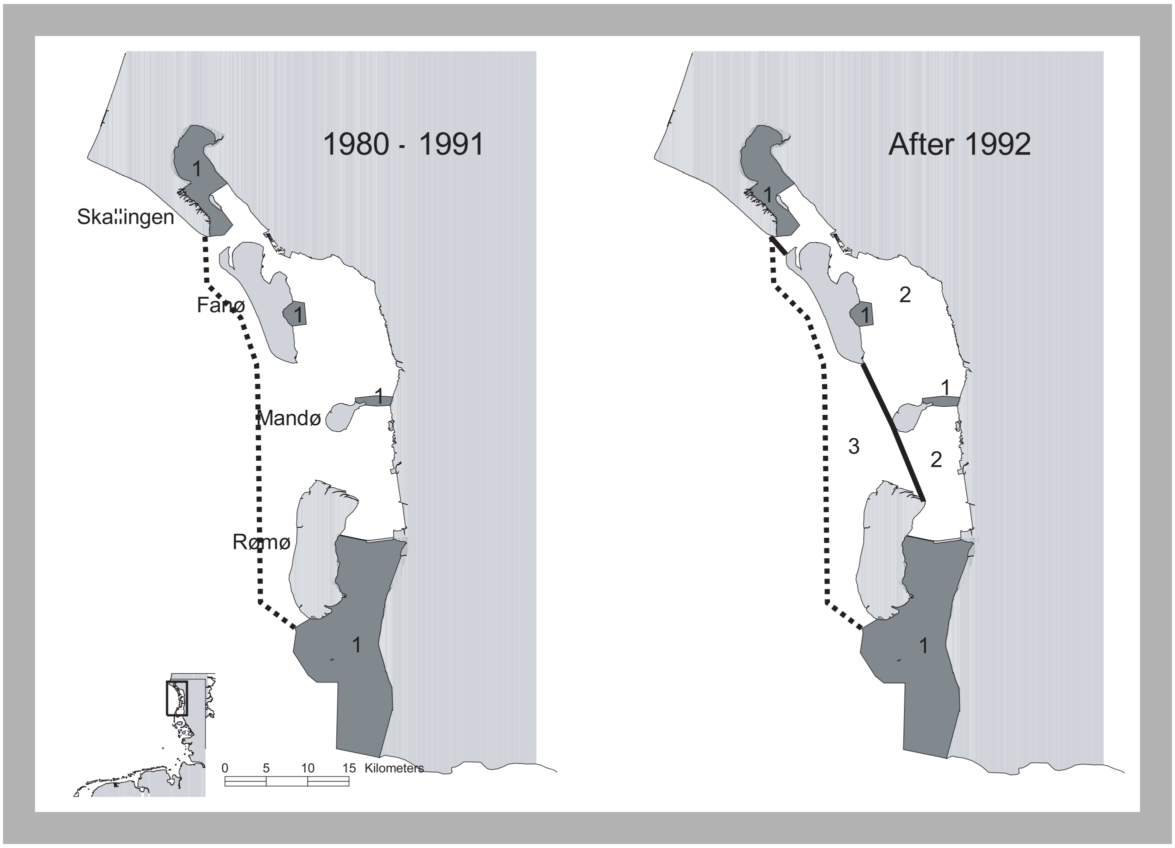

Figure 1. The Danish Wadden Sea showing the survey area from the mainland coast to the dotted line west of the islands (Fanø, Mandø, Rømø). During 1980-1991, motorboat hunting was banned in four areas (1) called Refuge Areas. After 1992, motorboat hunting was also banned in the Study Area (2), but allowed in the Offshore Area (3) when the motorboats were anchored. Inserted is a map of the entire Wadden Sea with the Danish part indicated.

mussel, because the quality and accessibility of blue mussel, and the availability of alternative food items could also influence the results (Nehls et al. 1997).

Study site

The Danish Wadden Sea constitutes the northern part of the Wadden Sea, comprising up to about 10% of the total area (see Fig. 1). The Danish Wadden Sea covers 1,225 km^2, of which 60% is intertidal with an amplitude of 1.8 m. A peninsula (Skallingen) to the north and three major islands (Fanø, Mandø and Rømø) to the west border the area, separating it from the North Sea. To manage hunting and public access, the Danish Wadden Sea became a wildlife reserve in 1979, and hunting from motorboats was not allowed in four sites (two larger and two smaller sites, hereafter called the Refuge Areas) extending to 321 km^2 (see Fig. 1). In spring 1992, the regulation of hunting and public access in the wildlife reserve was revised and hunting from motorboats was banned between the mainland coast and westwards to a line connecting the islands and the peninsula. This area of 635 km^2 is hereafter called the Study Area (see Fig. 1). The area west of the line connecting the peninsula and the islands is referred to as the Offshore Area (269 km^2), and hunting from active sailing motorboats was also forbidden there, although it was still allowed to hunt eiders from motorboats at anchor. From 1992, the open season for eider ducks was also confined to 1 October-31 January in the Danish Wadden Sea. The Refuge Area, the Study Area and the Offshore Area are in this paper collectively referred to as the Danish Wadden Sea.

Methods

A total of 85 aerial surveys were performed from October to the end of February during 1980-2003 covering the Danish Wadden Sea. From 1980-1991 we made almost one survey per month (56 surveys), while during 1992-2003 less surveys were made (29 surveys, Fig. 3).

Two observers in the aircraft identified and estimated the numbers of eiders and motorboats with hunters. All observations were assigned to one of 59 subareas, of which 24 were situated in the Study Area (see maps in Laursen et al. 2008). The aircraft flew at a speed of ca. 130 km/hour at ca. 60 m, but only on days with suitable weather conditions, i.e. visibility of > 5 km, wind speed of < 25 km/hour and no rain. Surveys were carried out at high tide, starting 2.5 hours before maximum water level and lasted 3-4.5 hours. The same route was followed during each survey, and the same, trained observers (eight different individuals of which one of the two participated in all surveys) were used during the entire study. The count procedure estimated 'total count' of waterbirds from aircraft following Pihl & Frikke (1992). Counts of eiders surveyed from aircraft were very highly correlated with simultaneous ground counts in the same sites on the same days (relative difference between ground and aerial counts: 1.1% ± 19.0 (mean ± SE); Laursen et al. 2008). This is helped by the fact that eiders do not flush from the water surface at the approach of an aircraft, and the light coloured males are conspicuous and draw attention to the location of flocks.

The inverse correlation between hunting motorboats and the number of eider ducks was analysed on both small and large geographical scales. Small-scale effects were tested for using observations from all 24 subareas within the Study Area, and all information was included from eiders in subareas where motorboats were also recorded. The size of the 24 subareas varied between 3 and 35 km^2 (average 13.5 km^2). The subareas can be considered as roughly having a squared form, hence, if eider ducks moved out of a subarea, they flew 1.8-2.5 km (minimum and maximum distance) if they were situated in the centre of a subarea. Large-scale displacement was examined by comparing the main distribution of eiders in the Study Area and in the Offshore Area. The distances measured between the areas frequently used by eiders in the two areas varied by 4-12 km, as minimum and maximum distances (Laursen et al. 1997b).

Blue mussels *Mytilus edulis* are together with cockles *Cerastoderme edule* the preferred food items for eiders (Swennen 1976, Kats 2007). The biomass of blue mussels was estimated annually in the Danish Wadden Sea during 1986-2003 using a combination of ground sampling and aerial photographs (Kristensen & Borgstrøm 2005). In 1984 and 1985, information was only available from the amount of landed mussels, and for these two years, the biomass of blue mussel was estimated as two times the landed amount (a conservative estimate compared to the relationship established in the two following years (Kristensen & Hoffmann 2000, P.S. Kristensen pers comm.)). The vast majority (> 98%) of blue mussels were located in the Study Area and the Refuge Area, and no culture mussel beds occur in the Danish Wadden Sea.

Body conditions of 36 male and 24 female eiders collected in the Offshore Area (autumn 1986) and the Study Area (winter 1987) were calculated as body mass divided by wing length (Christensen 2001).

The open season for eider ducks extends from the beginning of October to the end of January/February the following year. To simplify the notation of the hunting seasons in this paper, only the first year is mentioned, e.g. the open season 1980/81 is referred to as 1980. Also, we refer to motorboats used for hunting as simply 'motorboats'.

The change in eider duck abundance in the Study Area during the period following the ban on hunting from motorboats was so pronounced (see below) that for some of the following analyses, the period from October-January was divided into two seasons: 20 October-20 December (autumn) and 21 December-31 January (winter) in an attempt to identify reasons for the change in numbers. The first part of October and the whole month of February were excluded due to immigration and emigration of eiders ducks in the Wadden Sea (Noer 1991). The dates of 20 and 21 December were chosen to define the two seasons and to ensure almost the same number of observations in each season.

Results

Motorboat numbers and activity

During 1980-1991, when hunting was allowed in the Study Area, an average of 6-10 motorboats were recorded per survey in October-February, with no differences between months (ANOVA, data log + 1 transformed: $F = 0.51$, $df = 4$, $P = 0.73$, N: see Fig. 3). From 1980-1991 to 1992-2003, when hunting in the Study Area was banned, the average motorboat number per survey decreased significantly from 6.6

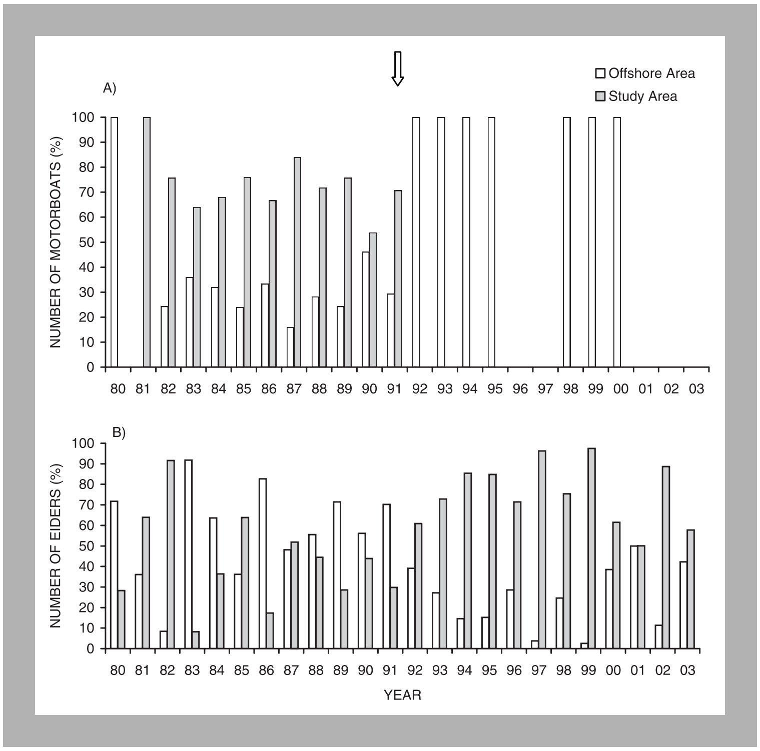

Figure 2. The relative distribution (%) of A) motorboats and B) eiders between the Offshore Area and the Study Area during 1980-2003. The arrow indicates spring 1992, when motorboat hunting was banned in the Study Area.

motorboats before the ban to 1.1 motorboats after the ban (t-test with unequal variances, data log+1 transformed: $t = 5.88$, $df = 80$, $P < 0.001$).

During 1980-1991, the average relative distribution of motorboats between the Offshore Area and the Study Area was 32.8% and 67.8%, respectively (Fig. 2A). After 1991, motorboats were only recorded in the Offshore Area, except for two motorboats observed on transit through the Study Sea (not shown in Fig. 2A). Marked differences in hunting practice were observed between the Offshore Area and the Study Area probably due to differences in the roughness of sea conditions. In the Offshore Area, a large proportion of the motorboats were observed west of the deep water channel between Skallingen and Fanø and west of that between Fanø and Mandø (see Fig. 1). In addition, many of the motorboats were seen at anchor near sand banks and deeps, obviously waiting for the eider ducks to pass when moving in response to the tidal current. In contrast to this, motorboats in the Study Area were widely spread, actively seeking out flocks of eider ducks to hunt.

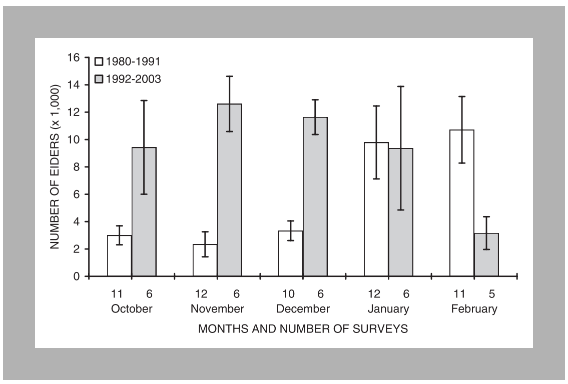

Figure 3. Eider numbers (mean±SE) during October-February in the Study Area for the periods 1980-1991 (motorboat hunting was allowed) and 1992-2003 (motorboat hunting was banned). There were statistical differences between the monthly eider numbers during 1980-1991 compared to 1992-2003 except for January ($P < 0.05$, Wilcoxon Two-Sample Test). Number of surveys for the two periods is indicated below the x-axis.

Eider numbers

An average of ca. 7,800 eiders per survey was recorded in the Refuge Area, and this number was stable during 1980-1991 (average 7,000 individuals) and 1992-2003 (average 8,700 individuals). In the Study Area, average eider numbers increased (by 58.6%) from 5,800 individuals in 1980-1991 to 9,200 individuals in 1992-2003 (t-test, data log+1 transformed: $t = -2.24$, $df = 83$, $P = 0.03$). Changes in numbers counted in the Study Area from 1980-1991 to 1992-2003 (when motorboat hunting was banned) were not evenly distributed between all months. Eider duck numbers increased in October, November and December in the study area after the ban of motorboat hunting (see Fig. 3). However, the numbers were stable in January and decreased in February. In the Offshore Area, the average number of eider ducks decreased from 9,400 individuals during 1980-1991 to 2,700 individuals during 1992-2003 (t-test, data log+1 transformed: $t = 3.34$, $df = 22$, $P = 0.003$).

The average total eider numbers per survey in the Danish Wadden Sea showed no changes from 1980-1991 (average 22,500 individuals) to 1992-2003

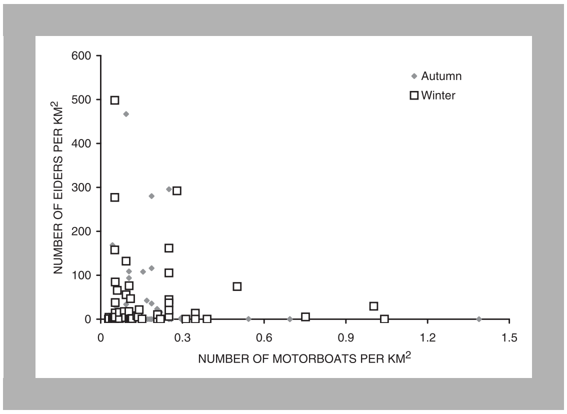

Figure 4. Relationship between number of eiders per km^2 and number of hunting motorboats in the Study Area during October-January 1980-2003. Observations are shown for autumn (20 October-20 December) and winter (21 December-31 January) seperately.

(21,500 individuals) (t-test, data log + 1 transformed: t = -0.39, df = 83, P = 0.60).

Displacement of eiders

During 1980-1991, a small scale displacement of eiders in the Study Area was detected in relation to density of motorboats (Fig. 4), with a threshold in eider duck density at about 0.3 motorboats per km^2. The average eider density was significantly higher below this threshold (29.7 individuals per km^2, N = 141) than above it (5.6 individuals per km^2, N = 21) showing a negative effect on eider duck density in subareas with high densities of motorboats (t-test, data log + 1 transformed: t = 2.21, df = 161, P = 0.03).

Eider densities during both autumn and winter showed a threshold density shift at about 0.3 motorboats per km^2 (see Fig. 4). However, eider density was significantly lower (χ^2 = 4.8, P < 0.05, df = 1) in autumn (average number below/above 0.3 motorboats per km^2: 21.2/0.1 eiders) compared to winter (average number below/above 0.3 motorboats per km^2: 45.5/15.3 eiders). This result shows that eider densities increased from autumn to winter in the Study Area. However, because a threshold was evident in both seasons, eiders reacted to hunting from motorboats in a similar fashion in both of the two seasons.

Large scale displacement was evident from the Offshore Area to the Study Area (see Fig. 2B). During 1980-1991, when motorboat hunting occurred in the Study Area, a relative larger proportion of the eiders occurred in the Offshore Area (average = 40.2%, range 4-77%) compared to the Study Area. During 1992-2003, when motorboat hunting was banned in the Study Area, the distribution was reversed, and a smaller proportion of eiders occurred in the Offshore Area (average = 14.1%, range 1-44%), and the relative number increased in the Study Area (Wilcoxon two-sample test: Z = -3.03, P = 0.02).

During autumn 1980-1991, 75.6% of the eiders occurred in the Offshore Area compared to 48.5% during winter, and in the Study Area, 24.4% occurred in autumn and 51.5% during winter. The differences in distribution between autumn and winter was statistically significant (χ^2 = 15.5, P < 0.001, df = 1).

Biomass of blue mussels

Annual average blue mussel biomass increased from 33,400 tons during 1984-1991 to 52,800 tons during 1992-2003, although, one year was responsible for most of the increase (1994 with 117,000 tons). The majority of the blue mussel biomass was located in the Study Area both before (73%) and after 1992 (71%), and most of the remaining blue mussel stock was situated in the Refuge Areas. For both autumn and winter, the relationship between mussel

Table 1. Linear regression model to predict eider numbers (x 1,000) based on blue mussel biomass (x 1,000 tons) during autumn and winter 1984-1991 (years with motorboat hunting in the Study Area) and 1992-2003 (years without motorboat hunting in the Study Area). NS: not statistically significant.

Area	Period	Parameter estimate	Partial R^2	F	P	N
Study Area						
Autumn	1984-1991	0.039	0.141	0.98	NS	8
Autumn	1992-2003	0.134	0.237	1.87	NS	8
Winter	1984-1991	0.516	0.433	6.1	<0.05	8
Winter	1992-2003	0.248	0.631	10.26	<0.05	10
Wadden Sea						
Autumn	1984-1991	-0.002	0.000	0.00	NS	8
Autumn	1992-2003	0.060	0.042	0.26	NS	8
Winter	1984-1991	0.196	0.072	0.46	NS	8
Winter	1992-2003	0.347	0.561	10.21	<0.05	10

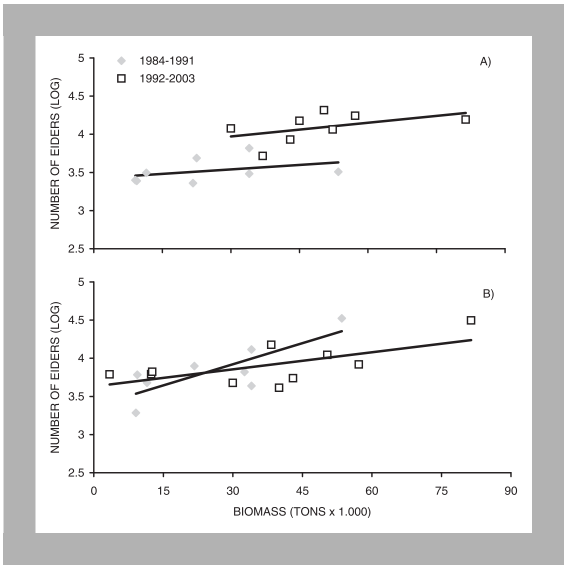

Figure 5. Relationship between blue mussel biomass and eiders numbers (log) in the Study Area during 1984-1991 (motorboat hunting allowed in the Study Area) and 1992-2003 (motorboat hunting banned in the Study Area) for A) autumn (20 October-20 December) and B) winter (20 December-31 January). For significance and number of observations, see Table 1.

biomass and eider numbers in the Study Area was analysed for the periods with (1984-1991) and without (1992-2003) motorboat hunting. During autumn 1984-1991 and 1992-2003 there were weak relationships between biomass and eider numbers (Table 1, Fig. 5A). However, the relationship between biomass and the eider numbers in the Study Area was stronger during the years without hunting from motorboats (1992-2003) than during the years with motorboat hunting (see Fig. 5A; ANCOVA: $F = 14.78$, $P < 0.002$, $df = 1$).

There were significant, positive relationships between blue mussel biomass and eider numbers both in the period with (1984-1991) and without (1992-2003) motorboat hunting in the Study Area during winter (see Table 1, see Fig. 5B).

Considering the overall relationships between blue mussel biomass and the eider numbers in the Danish Wadden Sea during autumn/winter, pre- and post-1992, the only significant relationship was found in winter during the years after motorboat hunting was banned in the Study Area (see Table 1).

Body condition index

Body condition indices of both adult male and female eider ducks were higher in the Study Area during winter compared to autumn in the Offshore Area (Table 2). Body mass increased for males by 0.146 kg (6.2%) and for females by 0.297 kg (14.2%).

Discussion

The number of hunting motorboats was higher in the Study Area than in the Offshore Area, which supports Laursen's (1985) estimation that about 3,000 eiders were shot annually in the Study Area compared to 700 eiders in the Offshore Area.

Blue mussel biomass

Eiders prefer to feed on blue mussels, and there was a significant correlation in winter between the blue mussel biomass and the eider density both with and without motorboat hunting in the Study Area. The correlation between mussels and eiders was also improved during autumn when the hunting ceased and the eider numbers increased. The result shows that hunting displaced the eiders during autumn in the Study Area to the Offshore Area, and then post-hunting, the bird numbers increase in the Study Area, indicating that they prefer to stay there. During winter there was no change in numbers in the Study Area pre- and post-hunting, which shows that the eiders used this area despite a high hunting pressure. The body condition showed that eiders staying in the Study Area had higher body mass during winter than eider in the Offshore Area during autumn. These results indicate that the eiders during autumn just stay in the Offshore Area, but later they have to accumulate body mass for spring migration and

Table 2. Body condition index (body mass, kg/wing length, mm) and body mass (kg) of adult eider females and males collected in the Offshore Area and in the Study Area during autumn 1986 (1 October-20 December) and winter 1986-1987 (21 December-28 February). Body condition index and body mass were tested by use of a t-test.

	Autumn, Offshore		Winter, Study Area		Body condition		Body mass		
Sex	Body condition	Body mass	Body condition	Body mass	t	P	t	P	N
Female	6.91	2.090	7.70	2.387	2.44	<0.05	2.99	<0.02	10, 14
Male	7.42	2.348	7.95	2.494	2.11	<0.05	2.47	<0.01	14, 22

breeding and thus move to the Study Area to feed on blue mussels. That means that the balance of the trade off between food availability and predation risk is shifted as the winter progresses, i.e. more birds move into a more risky but high-quality habitat like the Study Area as winter progresses.

Gill et al. (2001) argue that the decision of whether to stay in an area despite human disturbance or to leave it depends on the availability of alternative suitable habitats nearby. Swennen et al. (1989) concluded that the eider number during winter in the Wadden Sea is food dependent. All together, this indicates that the eiders in our study have no alternative than moving into the Study Area to feed on blue mussels and increase their body condition in spite of a high hunting activity in the area.

These results support the predation risk theory (Frid & Dill 2002) which states that habitat choice of animals is the outcome of decisions that balance the trade-off between predation risk and resource richness, and they also confirm Clark's (1994) results that animals may run a risk to increase their reproductive fitness.

The surveys from aircraft were carried out on days with good weather, which were also the type of days when hunters in motorboats were most active, perhaps overestimating the relative density of motorboats. Eiders may therefore experience many undisturbed days and relatively few days with disturbance. This may explain why eiders took the apparent risk of staying in the Study Area, and that their reaction was so pronounced when the motorboat hunting took place. Lima & Bednekoff (1999) showed that behavioural reaction of a prey species depends on the lengths of exposure to predation risk and that the reactions are expected to be strongest in brief or rare periods of high predation risk. Luttberg et al. (2003) argue that if interference competition is high, in some cases, the prey are able to benefit from increasing their foraging effort when predation risk is high and the interference competition therefore low. This could be the case for eiders feeding in large numbers on the same mussel banks of restricted size. In a study on human disturbance, Mallord et al. (2007) conclude that food limitation was the driving force behind the density-dependent relationships found in their study. These factors contribute to explain why the eiders took the higher risk in the Study Area during winter.

Considering the Danish Wadden Sea as a whole, we found no correlation between eider numbers and blue mussel biomass during autumn (1984-1991 and 1991-2003) or during winter 1984-1991. However, a significant correlation was found during winter after 1992 when motorboat hunting was banned in the Study Area. These results indicate that hunting from motorboats had an effect on the eiders' exploitation of blue mussels before 1992. After 1992, the number of eiders in the Wadden Sea seems to be regulated by the blue mussel biomass.

Displacements

Eiders were displaced by motorboats both locally and also to the Offshore Area since there was no refuge place in the Study Area where they could escape disturbance effects as described by Frid (2003). Several studies have shown that shooting activity forces wildfowl to depart discrete areas and seek out less disturbed places, including areas or habitats not commonly used by the species (Bell & Owen 1990, Madsen & Fox 1995). Madsen (1988) demonstrated that shooting activity prevented brent geese *Branta bernicla* and wigeons *Anas penelope* from utilising areas with a high biomass of eelgrass. However, at night, when shooting was not allowed, both species moved into these sites to feed. A large experimental study in Danish marine waters showed that shooting activity prevented herbivorous waterfowl from exploiting eelgrass (Madsen 1998). In Northern Ireland, Evans & Day (2001) found that shooting prevented large proportions of four diving duck species from feeding during daytime near to the shore, but they came ashore at night to feed in the absence of shooting. In our study, density of eiders was inversely related to density of motorboats on both small (1.8-2.5 km) and larger geographical scales (4-12 km) and the effect was so pronounced that a large proportion of eider ducks obviously preferred to move to and remain in the Offshore Area. The surveys were performed during daytime, and we have no information on the distribution of eiders at night, when it is possible that the eiders returned to the Study Area to feed after disturbance ceased.

In addition to hunters, natural predators may also influence birds' choice of feeding place and utilisation of the landscape (Ydenberg et al. 2007). The displacement patterns found in this study could be caused by raptors, e.g. peregrine *Falco peregrinus* and white-tailed eagle *Haliaeetis albicilla*, which occur in the Danish Wadden Sea and exploit the rich waterbird numbers during the non-breeding season. But it does not explain the negative relationship between motorboats and the density of eiders, together with the simultaneous change in the eiders distribution the year after hunting was stopped in the Study Area, since the predator species are constant in their seasonal, temporal and spatial occurrence.

Eider numbers

Several studies show that waterfowl numbers are locally reduced by hunting activities (see reviews by Bell & Owen 1990, Madsen & Fox 1995 and Tamisier et al. 2003). Experimental studies in coastal waters in Denmark demonstrated that dabbling duck numbers increased fourfold or more in areas closed to hunting activity (Madsen 1998, Bregnballe et al. 2003). Studies in Britain also showed clear increases in dabbling duck numbers after hunting was banned in coastal areas (Darren & Day 2002). Establishment of 53 shooting free reserves in Denmark during 1993-2002 covering about 1,100 km^2 of coastal waters and marsh land areas increased the dabbling duck numbers by up to ca. 70% compared to the number present before hunting activity was stopped. However, in these areas the diving ducks species (pochard *Aythya ferina*, tufted duck *A. fuligula* and goldeneye *Bucephala clangula*) did not show any changes in numbers before and after the hunting was banned probably due to very little hunting activity on the open water bodies after these species in particular (Clausen et al. 2004). Studies in Canada of mixed species flocks of diving ducks (*Aythya* spp.) also showed little response to hunting due to low shooting activity (Knapton et al. 2000). In the Danish Wadden Sea we found an average density of 0.008 motorboats km^{-2} overall, although densities were greatest in the Study Area where they had an effect on eiders at densities above 0.3 motorboats km^{-2} (see Fig. 3). The effect was also confirmed by the increase of 58.6% in eider numbers after 1992 when motorboat hunting was banned in the Study Area. However, based on total eider numbers in the Danish Wadden Sea, there was no significant change before and after 1992 when the Study Area was closed for motorboat hunting, showing that the eiders had locally redistributed themselves after the hunting ban in 1992.

A prerequisite for obtaining the result as predicted, that hunting reduce the number of eiders, is that other factors, such as the size of the flyway population of eiders, were constant during the study period. In fact, the Wadden Sea-Baltic population of eiders was nearly halved during the study period. Unfortunately, this population which breeds mainly around the Baltic coasts and about 60% of which winters in Danish waters (Laursen 1989, Durink et al. 1994) is not monitored annually. However, countrywide aerial surveys showed that the Danish eider numbers nearly halved from the late 1980s to the late 1990s (Laursen et al. 1997a, Pihl et al. 2001, Petersen et al. 2006), with similar reductions in numbers from other parts of the non-breeding area (Desholm et al. 2003). During the same period, eider numbers in the Danish Wadden Sea were more or less stable, which indicate that the relative importance of the Danish Wadden Sea as a wintering area for eiders has increased during this period.

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References

Asferg, T. 2004: The Danish game bag during the hunting season 2002/2003. - Technical report from NERI, no. 491, 24 pp. (In Danish).

Bell, D.V. & Owen, M. 1990: Shooting disturbance, a review. - IWRB Special Publication no. 12: 159-171.

Bregnballe, T., Madsen, J. & Rasmussen, P.A.F. 2003: Effects of temporal and spatial hunting control in waterbirds reserves. - Biological Conservation 119: 93-10.

Christensen, T.K. 2001: Effects of duckling body condition on hunting vulnerability in juvenile and immature common eiders Somateria mollissima. - Wildlife Biology 7: 97-104.

Clark, C.W. 1994: Antipredator behavior and the asset-protection principle. - Behavioral Ecology 5: 159-170.

Clausager, I. 2004: Wing collection in Denmark from the hunting season 2003/04. - NERI Technical Report No. 504, 70 pp. (In Danish with an English summary).

Clausen, P., Bøgebjerg, E., Hounisen, J.P., Jørgensen, H.E. & Petersen, I.K. 2004: Reserve network for migratory birds. - NERI Technical Report No. 490, 141 pp. (In Danish).

Darren, M.E. & Day, K.R. 2002: Hunting disturbance on a large shallow lake: the effectiveness of waterfowl refuges. - Ibis 144: 2-8.

Desholm, M., Christensen, T.K., Scheiffarth, G., Hario, M., Anderson, Å., Ens, B., Camphuysen, C.J., Nilsson, L., Waltho, C.M., Lorentsen, S-H., Kuresoo, A., Kats, R.H.H. & Fox, A.D. 2003: Status of the Baltic/Wadden Sea population of the Common Eider Somateria m. mollissima. - Wildfowl 53: 167-203.

Durinck, J., Skov, H., Jensen, F.P. & Pihl, S. 1994: Important Marine Areas for Wintering Birds in the Baltic. - Ornis Consult report, Copenhagen, 109 pp.

Evans, D.M. & Day, K.R. 2001: Does shooting disturbance affect diving ducks wintering on large shallow lakes? A case story on Lough Neagh, Northern Ireland. - Biological Conservation 98: 315-323.

Fox, A.D. & Madsen, J. 1997: Behavioural and distributional effects of hunting disturbance on waterbirds in Europe: implications for refuge design. - Journal of Applied Ecology 34: 1-13.

Fretwell, S.D. & Lucas, H.L. 1990: On territorial behaviour and other factors influencing habitat distribution in birds. - Acta Biotheoretica 19: 16-36.

Frid, A. 2003: Dall's sheep responses to overflights by helicopter and fixed-wing aircraft. - Biological Conservation 110: 387-399.

Frid, A. & Dill, L. 2002: Human-caused disturbance stimuli as a form of predation risk. - Conservation Ecology 6: 11. Available at: http://www.consecol.org/vol6/iss1/art11

Gill, J.A., Norris, K. & Sutherland, W.J. 2001: Why behavioural responses may not reflect the population consequences of human disturbance. - Biological Conservation 97: 265-268.

Guillemette, M. & Himmelman, J.H. 1996: Distribution of wintering common eider over mussel beds: does the ideal free distribution apply? - Oikos 76: 435-442.

Kats, R.K.H. 2007: Common eiders Somateria mollissima in the Netherlands. - Alterra Scientific Contributions No. 19. Atterra and the University of Groningen, 334 pp.

Knapton, R.W., Petrie, S.A. & Herring, G. 2000: Human disturbance of diving ducks on Long Point Bay, Lake Erie. - Wildlife Society Bulletin 28: 923-930.

Kristensen, P.S. & Hoffmann, E. 2000: Fishery for blue mussels in Danish waters 1989-1999. - DFU report no. 72-00, 38 pp. Danish Fishery Research Institute, Charlottenlund. (In Danish with an English summary).

Kristensen, P.S. & Borgstrøm, R. 2005: Danish Wadden Sea; fishery of mussels (Mytilus edulis L.) in a Wildlife Reserve? - In: Laursen, K. (Ed.); Monitoring and Assessment in the Wadden Sea. Proceedings from the 11. Scientific Wadden Sea Symposium, Esbjerg, Denmark, 4-8 April, 2005. NERI Technical Report No. 573, pp. 113-122.

Laursen, K. 1985: Waterfowl and wader shooting in the Danish Wadden Sea and South Jutland. - Danske Vildtundersøgelser 39: 1-60. Vildtbiologisk Station, Kalø, Denmark. (In Danish with an English summary).

Laursen, K. 1989: Estimates of Sea Ducks Winter Populations of the Western Palaearctic. - Danish Review of Game Biology 132, No. 6, 22 pp.

Laursen, K., Frikke, J. & Kahlert, J. 2008: Accuracy of total counts of waterbirds from aircraft in coastal waters. - Wildlife Biology 14: 165-175.

Laursen, K., Pihl, S., Durink, J., Hansen, M., Skov, H., Frikke, J. & Danielsen, F. 1997a: Numbers and Distribution of Waterbirds in Denmark 1987-1989. - Danish Review of Game Biology 15, no.1: 1-181.

Laursen, K., Salvig, J. & Frikke, J. 1997b: Waterbirds in relation to human activity in the Wadden Sea 1980-1995. - NERI Technical Report No. 187, 73 pp. (In Danish with an English summary).

Lima, S.L. & Bednekoff, P.A. 1999: Temporal variation in danger drives antipredation behaviour: the predation risk allocation hypothesis. - American Naturalist 153: 649-659.

Luttberg, B., Rowe, L. & Mangel, M. 2003: Prey state experimental design affect relative size of trait- and density-mediated indirect effects. - Ecology 84: 1140-1150.

Madsen, J. 1988: Autumn feeding ecology of herbivorous wildfowl in the Danish Wadden Sea, and impact of food supplies and shooting on movements. - Danish Review of Game biology 13, no. 4: 1-32.

Madsen, J. 1994: Impacts of disturbance on migratory waterfowl. - Ibis 137: 567-574.

Madsen, J. 1998: Experimental refuges for migratory waterfowl in Danish wetlands. II. Tests of hunting disturbance effects. - Journal of Applied Ecology 35: 398-417.

Madsen, J. & Fox, A.D. 1995: Impacts of hunting disturbance on waterbirds - a review. - Wildlife Biology 1: 193-207.

Mallord, J.W., Dolman, P.M., Brown, A. & Sutherland, W.J. 2007: Qualifying density dependence in a bird population using human disturbance. - Oecologica 153: 49-56.

Nehls, G. 1989: Occurrence and food consumption of the Common eider, Somateria mollissima, in the Wadden Sea of Schleswig Holstein. - Helgoland Marine Research 43: 385-393.

Nehls, G., Hertzler, I. & Scheiffarth, G. 1997: Stable mussel Mytilus edulis beds in the Wadden Sea - They're just for the birds. - Helgoland Marine Research 51: 361-372.

Noer, H. 1991: Distribution and movements of eider Somateria mollissima populations wintering in Danish waters, analysed from ringing recoveries. - Danish Review of Game Biology 14, no. 3: 1-32.

Pihl, S. & Frikke, J. 1992: Counting birds from aeroplane. - In: Komdeur, J., Bertelsen, J. & Cracknell, G. (Eds.); Manual for Aeroplane and Ship surveys of Waterfowl and Seabirds. - IWRB Special Publication 19: 8-23.

Pihl, S., Petersen, I.K., Hounissen, J.P. & Laubek, B. 2001: Country wide aerial survey of waterbirds, winter 1999/2000. - NERI Technical Report No. 356, 46 pp. (In Danish with an English summary).

Petersen, I.K., Pihl, S., Hounisen, J.P., Holm, T.E., Clausen, P., Therkildsen, O. & Christensen, T.K. 2006: Landsdækkende optælling af vandfugle januar-februar 2004. - NERI Technical Report No. 606, 76 pp. (In Danish).

Salvig, C.J., Laursen, K. & Frikke, J. 1994: Surveys of Human Activities and their Effects on Numbers and Distributions of Waterfowl in the Danish Wadden Sea. - Ophelia Suppl. 6: 333-337.

Swennen, C. 1976: Populatie-structure en voedsel van de Eidereend Somateria m. mollissima in de Nederlandse Waddenzee. - Ardea 64: 311-371. (In Dutch).

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

Tamisier, A., Bechet, A., Jarry, G., Lefeuvre, J.C. & Le Maho, Y. 2003: Effects of hunting disturbance on waterbirds. A review of literature. - Revue d'Ecologie - La Terre et la Vie 58: 435-449. (In French with an English summary).

Vaananen, V.M. 2001: Hunting disturbance and the timing of autumn migration in Anas species. - Wildlife Biology 7: 3-9.

Ydenberg, R.C., Butler, R.W. & Lank, D.B. 2007: Effects of predator landscapes on the evolutionary ecology of routing, timing and moult by long-distance migrants. - Journal of Avian Biology 38: 523-529.