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ORIGINAL PAPER

Managing hunted populations through sex-specific season lengths: a case of the Common Eider in the Baltic-Wadden Sea flyway population

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Abstract Management of harvested wildlife populations aims to protect species from overexploitation and ultimately extinction, by regulating exploitation towards achievable sustainable levels. However, assessments of impact and sustainability of implemented management actions on a population level are scarce. This study assesses effects of changes in hunting season length imposed on the Baltic-Wadden Sea Common Eider *Somateria mollissima* population, including differential restriction on hunting of the sexes. The potential impact of these changes on the population was assessed by simple demographic matrix projections. Since the early 1990s, this population has declined at ca. 6.3 % per annum, and the male/female ratio among shot birds has fallen from 3:2 to about 3:1. Concerns in Denmark regarding the conservation status and sustainability of contemporary levels of exploitation resulted in shortening the open season by 44 and 46 days for females and 13 and 15 days for males from the hunting seasons 2004/2005 and 2011/2012 onwards, respectively. These reduced the kill of adult females by 82 %, adult males by 31 %, juvenile females by 58 % and juvenile males by 55 %. The observed reduction in the kill of adult females following both changes in 2004/2005 and 2011/2012 matched the expected changes based on the seasonal distribution of sexes in the bag prior to the change. Post 2004/2005 hunters killed more adult males, but shot markedly fewer juvenile birds than expected. Demographic modelling of the female population showed that the effects of the reduced hunting would correspond to an increase in the annual population growth rate from the previous −6.3 to −3.6 % (post 2004) and −1.6 % (post 2011). The model also predicted that a full ban on hunting female eiders (adults and juveniles) would lead to a positive population growth rate of 0.7 %. Taking into account the conservative model estimates and natural variations in annual breeding success, the implemented changes in sex-specific regulation of hunting may potentially be an effective management tool to halt the decline of the Baltic-Wadden Sea eider population, potentially rendering such levels of hunting sustainable under prevailing conditions.

Keywords Hunting · Sex differentiation · Bag size · Common Eider · *Somateria mollissima* · Wildlife management · Population development

Introduction

Long-term, sustainable human exploitation, especially through recreational hunting, is a common feature of many vertebrate populations (cf. Errington 1956). However, there are many examples of populations that have declined or even gone extinct due to exploitation, and overexploitation is still recognised as a contributing factor to population declines in a substantial number of threatened species worldwide (e.g. Ludwig et al. 1993; Casey and Myers 1998). With rising environmental pressures, management interventions play an increasing role in safeguarding global biodiversity and in maintaining viable populations (Pimm et al. 1995; Johannes 1998). Management has been successful in enhancing population size in a large number of exploited species, e.g. American moose *Alces alces* (Timmermann 2003), South African fur seal *Arctocephalus pusillus* (David and van Sittert 2008), pink-footed geese *Anser brachyrhyncus* in NW Europe (Madsen et al. 1998) and several goose populations in North America (cf. Alisauskas et al. 2011). However, in many common and traditionally hunted species, there is an increasing need for more adaptive management, where the effects of

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specific regulations can be tested against competing model predictions to assess the relation between hunting regulation and conservation status (Williams and Johnson 1995).

Following the principles of sustainable exploitation (Hilborn et al. 1995; Sutherland 2001), management of hunted populations has often involved implementation of restrictive actions (e.g. changing season length, setting daily quotas, imposing bag limits on specific sex and age groups, or geographical restrictions), to adjust the level of harvest/exploitation to declines in abundance (Heusmann and McDonald 2002; Menu et al. 2002; Gauthier and Lebreton 2004; Norman et al. 2004). In general, it is assumed that restricting hunting/exploitation will reduce the hunting bag and increase population size (Dooley et al. 2010; but see Poysa et al. 2013). However, population responses may depend on density dependence and hunters' responses to changes in hunting opportunities and are unlikely to be simple (cf. Kokko 2001; Pellikka et al. 2005). Indeed, reduced levels of hunting may not always reduce bag sizes, as hunters may adjust to or overcompensate their kill as a result of changes in hunting opportunities (Johnson et al. 1986). Hunter responses to management may depend on hunting type or traditions (e.g. subsistence hunting, supplementary household hunting or recreational sport-hunting) and may vary with game species and even with the motivation behind the implemented changes (Sunde and Asferg 2014). Applying restrictions to hunting should therefore be carefully assessed to determine both the immediate effect on bag size and the resulting impact on changes in population size (Elmberg et al. 2006). Such an evaluation is a prerequisite to secure sustainable levels of exploitation that also attain long-term management goals, such as maintaining population size and range.

The Baltic/Wadden Sea flyway population of the Common Eider *Somateria mollissima* is traditionally hunted in Finland, Sweden and Denmark, with recent annual bag sizes of approximately 4,000–6,000 (2010), 5,000 (2008) and 40,000–60,000 (2011) birds, respectively. Since the 1990s, the size of this population has almost halved (Desholm et al. 2002; Ekroos et al. 2012a) and the sex ratio changed from 3:2 adult male/adult female ratio to the present ca. 3:1 (Ekroos et al. 2012a; Lehikoinen et al. 2008), implying that the reproductively active female segment of the population has declined more dramatically than that of males.

Since the vast majority of the total annual bag taken on the wintering areas takes place in Danish waters (Noer 1991; Christensen 2005), Denmark has a special responsibility to ensure that hunting of eiders is performed in a sustainable way (as required under the EU Bird Directive, Habitat Directive and Ramsar, Bern and Bonn conventions). Concerned by falling population levels, reproductive success and relative numbers of fecund females, Denmark changed the regulations relating to hunting of eiders in the winter season of 2004/2005 and again in 2011/2012, as part of a continuing programme overseen by the Danish Wildlife Committee which assesses the national levels of hunting exploitation and the population status of all game species. These regulatory changes were aimed at safeguarding the reproductively more 'valuable' females by introducing alterations to the sex bias in the hunting bag, by shortening the open season on females more than for males (Anonymous 2004; Anonymous 2010). In this study, the numerical responses in the hunting bag of the Common Eider in Denmark are evaluated for their effectiveness, following implementation of these changes. To explore the potential effects of these changes in management practice on population development, and hence to provide an assessment of sustainability, population growth rate estimates were obtained through demographic modelling, taking into account the changes in survival associated with reduced hunting kill.

Materials and methods

Hunting data

Data on the total annual bag of eiders in Danish waters were obtained from the Danish Hunting Bag Record (Strandgaard and Asferg 1980) which has gathered species-specific bag data on a county basis since 1948 based on mandatory annual reports from all persons holding a hunting license. Historical changes to the reporting system, potentially leading to variable reporting frequencies in different time periods, have been corrected for, based on questionnaires directed at license holders that have not submitted reports (Asferg 1996; Asferg and Lindhard 2003).

Data on the age and sex composition of the eider bag were obtained from the Danish Wing Survey (see Clausager 2004 and references therein, www.bios.au.dk/vinger). The Danish Wing Survey relies on voluntary contributions of wings of shot game bird species and has been running since 1982 to supplement the Hunting Bag Record data on game birds. Based on plumage characteristics, all wings are determined to sex and age (Boyd et al. 1975). Since 1982, an average of 1,886 (range 906–4,150) eider wings has been examined, annually representing 1.3–4.0 % of the total eider bag (1996-2012).

Confidence in the accuracy of ageing and sexing eiders from the plumage characteristics of single wings is considered to be high. Since the start of the wing survey in 1982, only four different people have been making these determinations and all have been trainees for extended periods before working solo, and besides, eiders are easy to determine to sex and age (cf. Boyd et al. 1975). Adult males can be divided into first, second, third, fourth and fifth year or older of age, while females can only be divided into first year and older birds. Determining the sex from the wings of first-year birds was based on wing shape (longer tertial feathers in males than in females) and colour of the small underwing rim of feathers in the alula area, which are more conspicuously patchy/flecked in females. In addition, later in the hunting season, many first-year birds could be sexed from the appearance of a few adult feathers in the proximal wing area.

The representativeness of the temporal and geographical distribution of the hunter-collected eider wings submitted to the Danish Wing Survey has previously been evaluated with respect to the overall distribution. The monthly distribution of wing survey data was significantly correlated to the seasonal distribution of ring recoveries, as was the county distribution with the geographical distribution of the county wise bag sizes (Noer et al. 1995; Christensen 2005). Hence, the wing data was considered to be reasonably unbiased.

Changes in hunting regulation

During 1996/1997 to 2003/2004, the open season on eiders in Denmark was 1 October to 28(29) February. From the 2004/2005 season until 2010/2011, the open season on eider females was shortened by 1.5 months (44 days), to the period from 1 October to 15 January, whereas the open season on males was reduced by 13 days, ending on 15 February. The most recent change, implemented from the 2011/2012 season, reduced the open season on females by an additional 45 days to 1 October to 31 November and the open season on males by an additional 15 days to 1 October to 31 January.

Data analyses

In analysing changes in the hunting bag related to the management changes implemented from the hunting season 2004/2005, the period 1996/1997–2003/2004 was compared to the post-change period 2004/2005–2010/2011 and to the data from the seasons 2011/2012–2012/2013. In all winters since 1996, winter conditions have been generally comparable, with the latest severe ice winter occurring in the 1995/1996 winter, although some severe cold spells occurred in the winters of 2009/2010 and 2010/2011. However, none of these later years resulted in special protection due to meteorological conditions, even though the occurrence of sea ice may have prevented hunting in local areas during parts of January and February.

Special protection of females and juvenile eiders in Danish waters was implemented in local areas affected by outbreaks of avian cholera epizootics in 1996, 2001 and 2003 (Christensen et al. 1997; Pedersen et al. 2003). Designed to protect local birds that were present close to the affected breeding colonies during the very early hunting season (no hunting from 1 October to 15 November), these purely local measures are not considered to have any significant effect on the overall national bag size, as the majority of the bag is taken in the latter half of the season.

To estimate the overall sex and age classes in the annual kill of eiders, the annual total bag obtained from the Danish Bag Statistic was multiplied by the annual proportions of sex and age classes obtained from the Danish Wing Survey. The average bag size and 95 % confidence limits were then calculated separately for the periods before and after the two management changes to test for significant change. One-tailed statistical analyses were made using ANOVA and differences were accepted at alpha <0.10, as the expected results of the hunting restrictions were reductions. As it has previously been shown that the annual bag of eiders among individual eider hunters was stable despite the population decline (Christensen 2005), the overall population reduction was not considered as an alternative explanation to declining annual bag sizes.

The exact dates associated with the wing survey data allowed calculations of the expected bag size of all four age and sex groups following the implemented changes in hunting season length in both 2004/2005 and 2011/2012. Bag size following a change in season length was calculated as 'bag size $(t+1)$=bag size $(t)\times$average proportion shot $(1-y)(t)$', where t denotes the time periods 1996/1997–2003/2004, 2004/2005–2010/2011 and 2011/2012–2012/2013 and y is the proportion of birds shot in the part of the season going to be closed in $t+1$. Confidence limits on expected bag size were calculated from the annual proportions in each time period.

Population modelling

To assess the relative effect of the changes in hunting regulations on growth of the reproductive female population, a simple demographic population model was constructed, based on the principles of Leslie matrices (Caswell 2001; Duriez et al. 2005; Gilliland et al. 2009). The model was designed as an age-structured projection matrix including six age classes (ducklings, first-, second-, third- , fourth- and fifth-year birds) considering only the female segment of the population. Model parameters (clutch size=4.3 eggs per nest and hatching success=95.5 %) were obtained from a previous 8-year survey of a Danish breeding population (Christensen and Noer 2001), whereas age-dependent breeding propensity (0 % as 1 year old, 14 % breeding as 2 years old, 45 % as 3 years old, 77 % as 4 years old and 100 % at age 5 years and older), annual adult (0.848) and duckling survival to 1 year of age (0.117) were based on an unpublished ring recovery study at a Danish colony (H. Noer and E.B. Hansen, unpublished). The sex ratio of hatchlings was set at 50 % (Swennen 1991).

To simulate the actual population development and size, the basic demographic model was constructed with an initial stable population of 520,000 breeding females (the average of 560,000 and 480,000 breeding eiders recorded in 1991 and 2000 with an assumed stable number of breeding birds (Desholm et al. 2002; Ekroos et al. 2012a)), characterised by adult survival (S_{stable}) and growth rate=0 %. This stable period was followed by a period of a 6.3 % annual decline (corresponding to a 48 % decline during 9 years reported by Ekroos et al. (2012a)). The population decline was obtained by adjustment to adult survival only (with a survival rate: $S_{decline}$). To assess the effects of the changes in hunting on female eiders, the change in the actual number of females bagged of both adult and juveniles was built into the model by a corresponding change in survival rates. The rate of change in survival rates was calculated relative to the basic model that describes a stable population ($\Delta S_{2004} = S_{2004} - S_{stable}$ and $\Delta S_{2011} = S_{2011} - S_{stable}$, for both adults and juvenile females) and the difference in survival added to the survival values calculated for the previous period (survival from 2004 = $S_{decline} + \Delta S_{2004}$ for both adults and juveniles; survival from 2011 = $S_{2004} + \Delta S_{2011}$ for both adults and juveniles). Growth rate estimates were calculated from changes in breeding numbers during a 10-year period, encompassing the years 9 to 19 in the model array.

Uncertainties associated with population modelling potentially include process uncertainty related to variation in demographic parameters in time, observational uncertainty in all included population-specific parameters and model uncertainty. In a long-lived species as the eider, breeding parameters and survival are generally stable parameters, with survival being the principal determinant of population growth. Hence, the parameters included in the present model are considered reasonably unbiased and are comparable to values obtained in other studies (cf. Gilliland et al. 2009 and references therein, see discussion). Concerning potential demographic changes, i.e. earlier first-time breeding in a declining population, it is unknown to what extent such adaptations has taken place in the Baltic eider population in recent years. However, with the eider being characterised by low annual reproductive outputs, even small changes in adult survival in the eider populations are assumed to minimise potential effects from demographic changes considerably. Adjusting survival in the present modelling approach is considered as the most reliable way to evaluate effects of the changed hunting practice (cf. Gilliland et al. 2009), although model predictions should be interpreted carefully. Given scarce data on most model parameters, no attempt was made on estimating variation on model outputs. Likewise, bootstrapping confidence intervals from model growth rate estimates did only show extremely small deviations from mean estimates (not shown), providing no meaningful information of natural variation.

Results

Numbers shot

The total estimated numbers of adult and juvenile eiders shot in Danish waters before and after the change in hunting regulation in 2004/2005 and 2011/2012 are shown in Fig. 1. The reduction by 44 days in the hunting of female eiders in 2004/2005 coincided with a significant 60 % reduction in the annual bag of adult females from a previous average of 17,300 to an average of 6,900 (ANOVA: $F_{1,13}$=55.16; P<0.001), a mean annual 'saving' of ca. 10,400 adult females. The reduction by 13 days in the hunting season of males in 2004 had no significant effect on the numbers of adult males shot (ANOVA: $F_{1,13}$=0.247; P=0.628). The bag of males thus showed an unchanged level of around 39,000 individuals bagged annually during the period 1996 to 2010. The reduction in season length by a further 46 days in the hunting of females and 15 days in the hunting of males which took effect from the hunting season of 2011/2012 showed marked reductions in the annual hunting bag of approximately 3,800 adult females and 10,700 males (Fig. 1). With non-overlapping confidence limits, these reductions were considered significant.

Although the new legislation explicitly regulates the hunting of females, there were also changes in the bag of both sexes of juvenile eiders from 2004 to 2005 and potentially from 2011 to 2012. In 2004, annual average reductions were approximately 3,600 juvenile females (37 %) and 7,800 juvenile males (49 %). The difference was significant for males (ANOVA: $F_{1,13}$=6.31; P= 0.026) but just failed to achieve statistical significance for females (ANOVA: $F_{1,13}$=3.01; P=0.106). After 2010/2011, the data suggest a further reduction in the bag of around 2,100 juvenile females and 900 juvenile males, although the changes were not considered significant, as the confidence limits were overlapping. In total, the annual average bag size of eiders in Denmark during the period 1996/1997–2003/2004 to 2004/2005–2010/2011 thus declined from 82,500 to 59,100, and even further since 2011/2012 to 41,600 birds annually, encompassing total reductions in the bag of adult females of 82 %, adult males of 31 % and 58 and 55 % reductions in the bag of juvenile females and males, respectively.

Compared to the period 1996–2003, the reductions in bag sizes following the reductions in the lengths of the hunting seasons in 2004/2005 and in 2011/2012 showed that the female bag size almost fitted with the predicted reductions (Fig. 2, upper). The bag reduction in adult males taken after 2004/2005 was less than expected, suggesting that hunters almost fully compensated for the new restrictions by shooting similar numbers of males during a shortened season. The change in the bag of males after

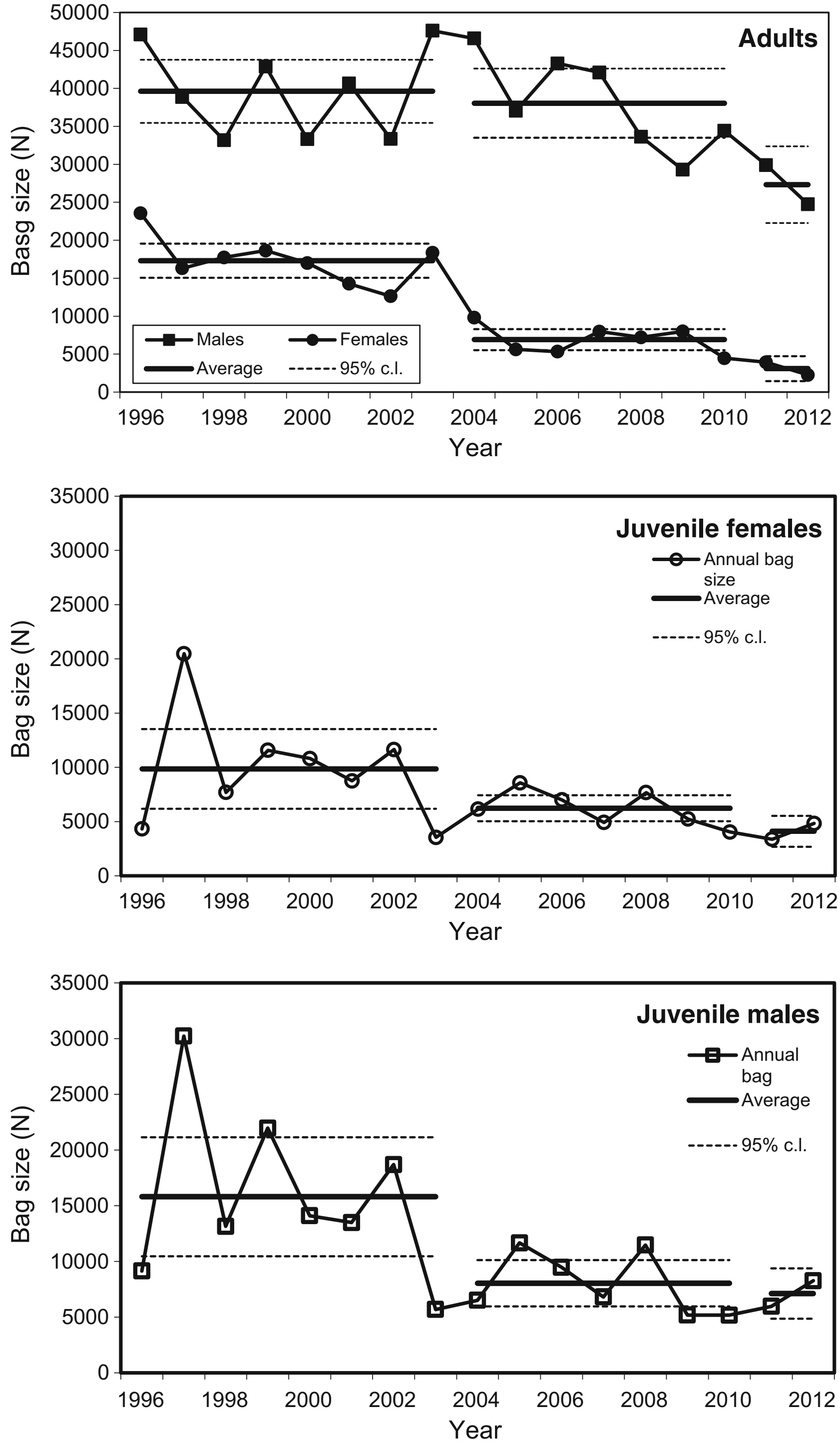

Fig. 1 The Danish bag size of adult and juvenile eiders during the seasons 1996/1997–2012/2013. The average (*bold lines*) and 95 % confidence intervals (*dotted lines*) are shown for the periods 1996/1997–2003/2004, 2004/2005–2010/2011 and 2011/2012–2012/2013

2011 was almost in full correspondence with the change expected of the further shortening of the season (Fig. 2, lower). For both juvenile males and females, the reductions in hunting season in 2004/2005 showed much larger reductions than expected, indicating that hunters actively avoided shooting juvenile birds. As for adults, the bag size of juveniles changed as expected following the change in 2011/2012 (Fig. 2).

Population impact

Modelled population prediction of changes in the numbers of breeding female eiders in the Baltic-Wadden Sea flyway as a result of the changed hunting practice in 2004/2005 and 2011/2012 is shown in Fig. 3. The changes were implemented during a period when the population already showed an annual decline of 6.3 %. By incorporating the reduced hunting

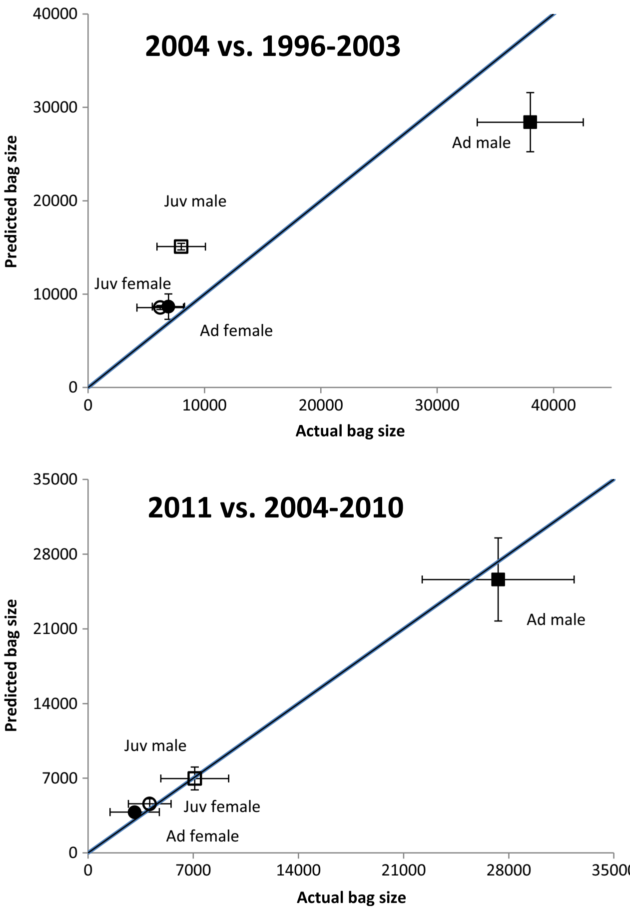

Fig. 2 Actual versus predicted bag size reductions following shortening of the hunting seasons in 2004/2005 and 2011/2012, estimated from the temporal distribution of the bag of either sex and age class during the preceding period

kill of both adult and juvenile female eiders as increased survival rates (see Table 1), the model predicts that the population annual growth rate changed from −6.3 to −3.6 % as a result of the shortening of seasons in 2004/2005. The additional restrictions on hunting implemented in 2011/2012 potentially result in a further change in annual growth rate to a present level of −1.6 % (Table 1).

To obtain a stable population level at the present level of ca. 290,000 breeding eiders under prevailing demographic conditions, the model predicted that the hunting kill of adult female eiders should be reduced by a further ca. 3,900 individuals annually or that of juvenile females should be reduced by ca. 4,500. With an average annual bag size of 3,100 adult females, a complete hunting ban on adult females would not restore the population trend to a stable level, but results in a population annual growth rate of −0.9 %. However, as a complete ban of hunting females also will affect the kill of juvenile females, the full effect of closing hunting on both adult and juvenile females would, according to the present model, result in a positive annual population growth rate of 0.7 % (Table 1).

Discussion

Changes in bag size

The changes in hunting regulations sought to protect females more than males (by reducing the length of the seasons more for females than for males) in a declining eider population. To the extent that we can measure, the reduction in season length was effective in attaining the management goal, by reducing the bag of adult females by up to 82 % and of adult males by up to 31 %. It also had the effect of reducing the juvenile female and male bags by up to ca. 58 and 55 %, respectively. The bag size of adult females generally followed the bag size

Fig. 3 Modelled development of the female eider population showing the estimated effects on population development of reduced hunting in 2004/2005 and 2011/2012 and if hunting on both adult and juvenile females was completely closed. The legend shows the population annual growth rate for the initial declining population (−6.3 %) and the resulting change following reduced hunting (cf. 'Materials and methods')

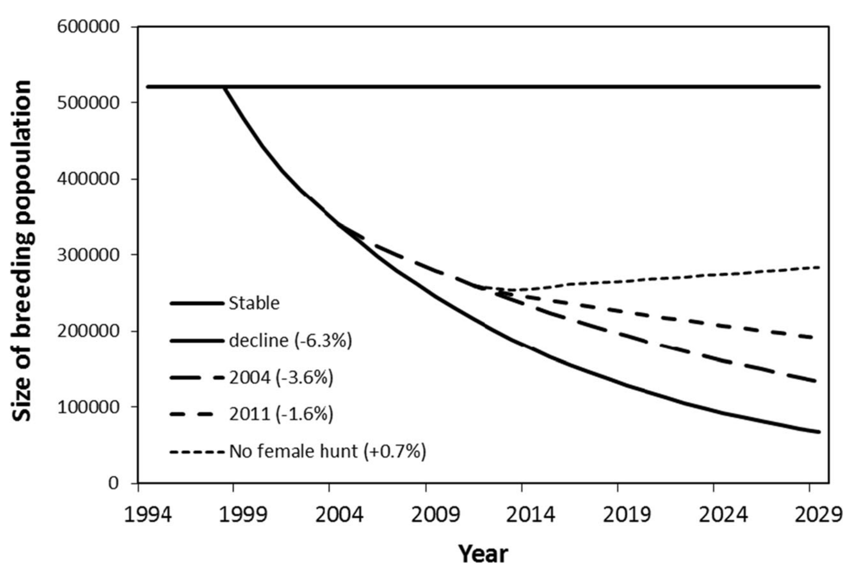

Table 1 Modelled survival rates of female eiders relating to stable and declining breeding populations, and the estimated survival rates resulting from the reduced female hunting kill from 2004/2005 and 2011/2012, given that all other factors are unchanged

	Survival rates		Bag size reduction (*N*)		Population growth rate (%)
	Adult	First year	Adult	First year	
Stable population, 1990–2000 level	0.848	0.117			0.0
6.3 % annual decline	0.781	0.117			−6.3
Reduced female hunting, 2004	0.797	0.132	10,400	3,600	−3.6
Reduced female hunting, 2011	0.807	0.145	3,800	2,100	−1.6
No female hunt, 2011 level					
- Adult female	*0.815*	0.145	3,100		−0.9
- Juvenile female	0.807	*0.166*		4,100	−0.1
- Adult and juvenile	*0.815*	*0.166*			0.7

The estimated bag size reduction in the female population segment and the population growth rates are also shown. The predicted values of adult and juvenile female survival and population growth rates resulting from a complete hunting ban on females in Danish waters after December 2011 are shown as separate and combined effects (italicised survival rates).

expected from the nature of the bag prior to the two changes in 2004/2005 and 2010/2011. For adult males, the actual bag size after 2004/2005 was much higher than expected when considering the previous seasonal distribution, indicating that hunters compensated for the reduction in season length, maintaining the kill of adult males. After 2011/2012, the male kill was only slightly higher than expected and not significantly different. The actual bag size of juvenile birds after the change in 2004/2005 was markedly lower than expected, indicating that hunters actively avoided shooting juvenile birds of either sex, whereas the change after 2011/2012 complied with the changes expected.

That the actual bag size of adult females generally complied with expected changes while that of males did not most probably relates to the differences in shortening of the season between sexes. Changes in the length of the hunting season and bag size or harvest rate have been found effective for managing game populations in several studies (Heusmann and McDonald 2002; Norman et al. 2004; Fleskes et al. 2007), whereas others suggest that the nature of the information supplied to hunters about the management goals of regulation and the numbers of hunters were the most significant factors in effective management (Pellikka et al. 2005). A clear relationship between changes in season length and bag size may, however, be hard to establish and depend on the original distribution of the bag within seasons. The present study showed that a reduction of ca. 30 % in season length reduced the female bag size by 60 % in 2004/2005, while a reduction of 10 % in season length for males had no effect on the bag size of males. The further reductions in hunting season implemented in 2011/2012 (a further 30 % for adult females and ca. 9 % for adult males compared to season length before 2004/2005) induced significant declines in the bag size of both sexes. These results suggest that with an initial season length of 151 days, a reduction of around 20–25 % seems effective in changing bag size significantly, as this magnitude of reduction apparently leaves no room for hunters to compensate for shortening of the season effectively.

The juvenile bag size also declined markedly following changes in regulation in 2004/2005 especially that of juvenile males, in comparison to what was expected from the closure of hunting in the late season. This was surprising, since the reduction in the open season occurred at the time when the overall bag was dominated by adult birds (Noer et al. 1995; Clausager 2004). The most obvious explanation for this pattern is that hunters avoided shooting at all juvenile birds, due to their inconspicuous dark plumage, which under many hunting situations may be indistinguishable from adult females. Hunters not wishing to risk mistaking juveniles for females may in many cases have adjusted their hunting behaviour to the extent that the juvenile kill was also significantly reduced. Potentially, public focus on the declining development of the eider population and on safeguarding females may have contributed both directly and indirectly, by making more hunters act according to the long-standing ethical rule of shooting males before females, which previously may have been implemented to a lesser or greater extent. Such an explanation follows the predictions of Pellikka et al. (2005), indicating that provision of information to hunters about the motivations behind regulations can be highly effective in contributing to effective management of game populations.

Modelling population effects

Considering that the population parameters included in the population model were from Danish breeding colonies, potential bias arises if these differ from those from the main breeding area of the Baltic-Wadden Sea flyway population in Sweden and Finland from which most Danish wintering birds derive. In the demographic modelling of eider populations, as with other long-lived waterfowl species, adult survival has consistently been shown to be the most sensitive parameter (Nur and Sydeman 1999; Gilliland et al. 2009). In Finland, adult annual survival in eiders has previously been reported to average 0.884 in a long-term study in a local population, showing variation between 0.870 and 0.906 (Hario et al. 2009). However, in the population stronghold of south-east Finland, adult survival has, however, recently been found to be as low as 0.720 as a result of a long-term increase in predation pressure (Ekroos et al. 2012b). In Norway, adult survival has been estimated at 0.85 (Yoccoz et al. 2002), whereas a somewhat higher survival rate of 0.927 has been reported from the southern border of the breeding range in the Netherlands (Kats et al. 2007). In the present study, adult survival was set at 0.842 to obtain long-term population stability. This value is in reasonable agreement with the general pattern, especially considering the recent population decline in this area, which would predict a reduction in average survival in recent years. Although a slight discrepancy between adult survival used in the present model and actual, but unknown, average survival in the overall flyway population may exist, the potential difference is not thought to markedly influence the present estimates of the relative changes in population growth rate in any systematic way.

In modelling the potential effects of reduced hunting, hunting mortality must be seen as either additive to natural mortality or as compensatory, if non-hunted individuals experience higher survival from relaxed density effects (cf. Burnham and Anderson 1984). However, as a long-lived species, the eider, characterised by high adult survival rates, shows less demographic compensation than a short-lived species following perturbations (Peron 2013); hunting mortality in the present modelling was considered completely additive, as confirmed by studies of long-lived geese (Gauthier et al. 2001). Likewise, no density effects were included, mainly because the population is most probably at a level well below the potential carrying capacity, having declined markedly during the past 20 years (cf. Desholm et al. 2002; Ekroos et al. 2012a).

Given these constraints, the simple demographic modelling approach showed that the reduction of hunting of females in 2004/2005 should have a positive effect on the development of the adult female breeding population, theoretically changing the annual population growth rate from −6.3 to −3.6 %, as a result of increased survival of both adult and juvenile females. With the additional reduction in season length in 2011/2012, the growth rate is further expected to increase to −1.6 %. Even though the change in bag size from 2011 to 2012 onwards requires data from more years to substantiate the true nature of the change, the present analyses show that this reduction in the length of the hunting season on females has the potential to further slow the present rate of population decline, all other factors being equal. Although the present analyses do not include density-dependent mortality, if such effects existed, hunters can harvest even more birds without affecting population development. The population model predicted the implemented changes in hunting eider females which would reduce annual population growth rate from −6.3 to −3.1 % after 2004 and to −1.6 % after 2011/2012. Although the primary drivers of the long-term population decline are thought not to be related to hunting (Ekroos et al. 2012a), the reductions in the kill of female eider have the potential at some stage to outweigh the primary causes of the population decline, by minimizing the additive contribution of hunting mortality. The model further predicts that a complete ban on female eider hunting theoretically could change the current negative population trend to one of positive growth of 0.7 % annually, as a result of removal of adult and juvenile female hunting mortality in Denmark. The present model predictions are based on the estimated annual population decline of −6.3 %, which is the best and most recent figure describing overall population development in the Baltic-Wadden Sea flyway population. However, as this estimate encompasses years before and after the implementation of regulated sex-specific hunting in Denmark, we should be prudent about concluding too much from an eider population which may potentially have declined at a somewhat higher, but unknown, rate prior to 2004/2005. Consequently, there is a risk that the population trajectory predicted by the present model is more optimistic than is the reality. However, such a bias does not compromise the relative effect of the implemented hunting restrictions, only the resulting absolute growth rate of the population.

Sustainability

A central question to be addressed is whether the present level of hunting is in accordance with the principles of wise use and sustainability, which implicitly involve assessments of population conservation status. In Europe, this is addressed through the Birds and Habitats Directives (Council Directive 79/409/EEC and 92/43 EEC), which requires Member States to implement a management plan for species of unfavourable status where hunting is thought not to be sustainable (cf. European Commission 2008). As a population showing annual declines of >1 % (European Commission 2006), the Baltic-Wadden Sea eider population qualifies as being of unfavourable conservation status and hunting has probably not been sustainable during the period of the most recent population decline, since estimated annual rates of decline have been of the order of 6.3 % per annum prior to 2004/2005. According to the results of the present study, even after the protective changes implemented in 2004/2005 and 2011/2012, the population showed estimated annual rates of decline of −3.6 and −1.6 %, respectively, insufficient to justify a change in conservation status. Based on the present model predictions, complete cessation of hunting of eider females in this population is required to comply with EU's criteria of sustainability or a management action plan for the species must be implemented.

Management implications and conclusions

The management objective of reducing the hunting bag and mortality of the reproductive female sex in the declining eider population in the Baltic-Wadden Sea flyway was achieved by shortening the hunting season, effectively reducing the female bag size by 82 % and markedly increasing the estimates of annual adult female survival (cf. Table 1).

This significant result was obtained by an effective 30 % reduction in hunting season length and bag changes followed predicted reductions, whereas a 10 % shortening of the male hunting season resulted in lower reductions in bag size than expected. This indicates that relatively substantial reductions in season length are needed in order to obtain effective reductions in the hunting kill, which may otherwise be compensated by the hunters, if season reductions are too small (Sunde and Asferg 2014). A concurrent reduction in the hunting kill of juvenile eiders of both sexes suggests that hunters were reticent to shoot at any non-adult males. Hence, the effect of reducing the hunt of females, of which only adults are easily identifiable to hunters, had the added effect of an unintended reduction in the kill of juvenile birds.

The composite effect of imposing different hunting seasons on male and female eider resulted in the disproportionally larger kill of adult males to adult females in the present study, which would contribute to changes in the overall population sex ratio. With the present skewed sex bias of 75 % males (compared to the 60 % in most eider populations, including this population in the early 1980s (Lehikoinen et al. 2008)), the present changes should tend to return the sex ratio towards such levels. If males continue to be overharvested, the sex ratio may potentially fall below these levels. However, as long as the adult sex ratio does not exceed 1.0 (falling below 50 % males), the difference in kill between the sexes may probably not affect the availability of males to fecund females and affect reproductive success.

As shown in the present study, sex-specific hunting regulations in a dimorphic species potentially provide an effective management tool to safeguard specific segments of populations. Combining such management action with the use of even simple population models not only allows managers to assess the impact of the actions on a population level, which often is the intended goal, but also allows predictions of the potential effects of various managing actions and to test what is needed to, e.g. restore declining populations to desired levels. Implementing sex differentiated hunting has the additional advantage that besides representing a success for managers, it also is of benefit to hunters, who otherwise may face a complete hunting ban on declining quarry populations.

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