# Allocation of body reserves during winter in eider *Somateria mollissima* as preparation for spring migration and reproduction

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## ARTICLE INFO

## ABSTRACT

Capital breeders, such as the eider duck *Somateria mollissima,* accumulate resources before the start of breeding. Eiders preferentially feed on blue mussels *Mytilus edulis* to build up body condition during winter. We explored how body condition and gizzard mass of wintering eiders relate to mussel quality and quantity, winter climate and body condition of females at the breeding grounds. Body condition during winter (defined as scaled body mass index) of eiders increased during winter and the magnitude of the effect depended on age and mussel quality. Gizzard mass of eiders increased during winter with effects of mussel quality, mussel stocks and sex. Body condition in winter of adult females increased from the first half of January to the second half of February on average by 1.5%, equal to c. 96 g. During the same period gizzard mass of adult females increased by 12.2%, i.e., a nearly ten-fold increase compared to that observed in body condition in winter. Body condition of females at the breeding grounds in Finland (defined as body condition at hatching) was significantly positively correlated with gizzard mass in winter, but not significantly correlated with body condition in winter. Thus, eiders allocate body reserves to increase gizzard mass but less so to increase body condition in winter. This can be considered an adaptive migratory strategy of these eiders, whereby large winter (pre-migratory) gizzards increase food processing capacity, making it possible for eiders to arrive at the breeding grounds with superior body condition and a high reproductive potential.

## 1. Introduction

Food resources, climatic conditions and individual characteristics are important determinants of life history in animals (Møller et al., 2010; Sibly et al., 2012; Zhang et al., 2015). Birds require food items of high energy content to fulfill demands for extra energy when preparing for migration or reproduction. For diving ducks, such as the eider *Somateria mollissima*, blue mussel *Mytilus edulis* is important for building up body reserves for reproduction (Laursen and Møller, 2014). Similarly, breeding success depends on the occurrence of specific food items in some seabirds (Frederiksen et al., 2004; Dänhardt and Becker, 2011). Climate affects food availability directly or indirectly, and such changes may influence reproductive success by delaying or advancing availability of different food resources that birds use for raising offspring (Møller et al., 2010; Dunn and Winkler, 2010; Sæther and Engen, 2010). Before breeding, birds invest large amounts of resources to build

up body condition and to restructure organs as preparation for the breeding season (Moreno, 1989; Piersma, 2002; Klaassen et al., 2006). As an example, individual eiders investing in building up large gizzards have superior body condition allowing for greater reproductive effort (Laursen and Møller, 2016).

The mechanistic interactions between food quality, climatic conditions and body mass of birds are rarely studied due to the complexity of such an approach. Here we examine these interactions in eiders of the Baltic/Wadden Sea, a population that has declined considerably during the last two decades (Ekroos et al., 2012a). The eider is considered a capital breeder that builds up parts of its body resources on the wintering grounds and partly near the breeding grounds relying on these resources for subsequent breeding (Meijer and Drent, 1999; Blums et al., 2005). The importance of feeding near the breeding grounds has become clear during recent years, and detailed studies of arctic eider populations point at high local nutrient acquisition before breeding

(Oppel et al., 2010; Sénéchal et al., 2011; Hobson et al., 2015; Jaatinen et al., 2016). Blue mussels play a key role for eiders feeding during winter. The number of eiders increases with the amount of mussel stocks that constitute the main food source during winter in the Wadden Sea (Laursen and Frikke, 2008; Cervencl et al., 2015). Individual eiders with blue mussels in the gizzard have larger body mass than individuals relying on other food items (Laursen et al., 2009; Laursen and Møller, 2016). In addition, long-term changes in the number of breeding eiders at a large Baltic colony were positively related to the amount of mussel stocks at the wintering grounds (Laursen and Møller, 2014). These findings emphasize the importance of blue mussels for building up body condition during winter and spring just prior to the start of reproduction.

Abundance and quality of blue mussels as food for eiders are influenced by winter climate and nutrients (Van Stralen, 1995). The flesh content of mussels is high during cold winters, and the production of eggs (spawn) increases the following spring (Beukema, 1992; Beukema and Dekker, 2007; Waldeck and Larsson, 2013). High nutrient levels increase the amount of phytoplankton and further the amount of mussel stocks (Van Stralen, 1995; Laursen and Møller, 2014; Møller et al., 2015). Although cold climatic conditions have positive effects on mussel stocks, and thus on the feeding conditions of eiders, severe winter conditions may also have a negative effect on the subsequent breeding condition of eiders due to late ice melt in the Baltic Sea (Lehikoinen et al., 2006). During such conditions, eiders have to wait at sea before entering the breeding colonies due to predation risk posed particularly by mammalian predators. While waiting, they use parts of the body stores, and may enter the colony in a poorer condition than in mild winters (Lehikoinen et al., 2006).

The objective of this study was to assess factors that contribute to development of body condition in eiders during winter as preparation for spring migration and successful breeding. As body condition during winter we use 'scaled body mass index' which takes the structural body size of individuals into account (Peig and Green, 2009). Following Peig and Green (2009), we used standardized (reduced) major axis regression, when calculating the scaled body mass index; the magnitude of body condition in winter is thus given without units. For body condition at hatching we use residuals (unitless) from mass-size regressions (Öst and Steele, 2010; for details, see Materials and Methods).We predicted that (1) body condition of eiders in winter increases during winter and is positively correlated with mussel stocks and mussel quality, severe winter climate and individual gizzard mass; (2) the increase in gizzard mass during winter is positively correlated with mussel stocks, mussel quality and severe winter climate; and (3) body condition in winter has positive effects on body condition at subsequent hatching, with potential repercussions for breeding success (Lehikoinen et al., 2006) and subsequent survival (Ekroos et al., 2012b). These predictions were tested using 1210 eiders collected during winter by hunters in the Danish waters, the body condition at hatching of 1033 females measured in a Finnish breeding colony during 2010–2014, mussels collected at 19 sites during 1998–2013 for estimation of flesh quality and at two sites during 1985–2014 for estimation of mussel stocks.

## 2. Materials and methods

### 2.1. Flesh content of blue mussels

Blue mussels were collected during autumn (September–October) at 19 marine sites during 1998–2013 across Danish waters (Fig. 1). At each site, three samples were taken by hand or from ship using a standard grab. The mean number of mussels in each sample was 42 (SE = 1.2). The average water depth at the sites was 2.5 m with a range of 0–15 m. The salinity gradient ranged from 8 to 30‰ depending on year. Flesh content was extracted and dry mass of flesh was recorded to the nearest 0.01 g, the shells were dried and shell mass weighed (see methods described by Baird (1958)). From these data, mussel quality
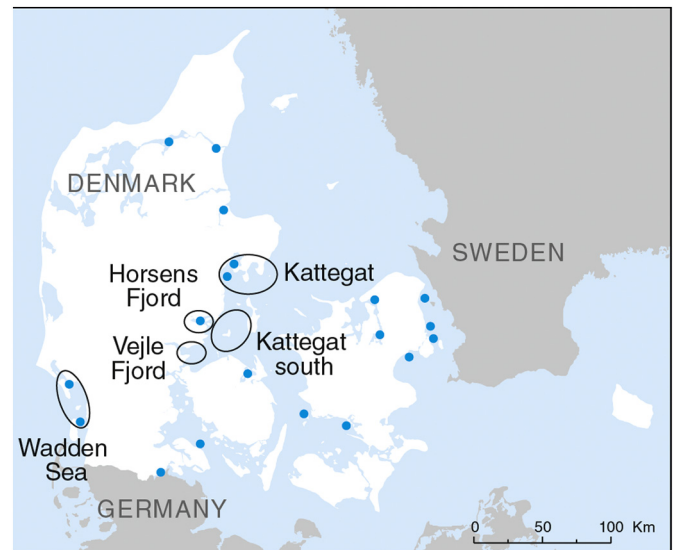


**Fig. 1.** Map of sampling sites in Danish waters during 2010–2014. The dots show sample sites for blue mussel quality (mussel flesh mass/ shell mass), and circles show sample sites for eiders. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

was estimated (flesh weight/shell weight). The reduction in mussel quality during winter (October–March) due to respiration has been estimated for the Baltic Sea by Waldeck and Larsson (2013). As an expression of reduction in mussel quality in the subsequent winter we estimated for each winter the degree sum (°C) from October 1st to March 1st, here termed accumulated winter temperature. We relied on information on surface water temperature provided by the national Danish marine monitoring program NOVANA (Hansen, 2015; J. Carstensen pers. com.) that was related to mussel quality. Statistics for selected variables presented below is given in ESM (Electronical Supplementary Material) Table S1 and temporal trend for mussel quality and accumulated winter temperature together with other variables is given in ESM Table S2.

### 2.2. Mussel stocks

Annual mussel stocks (in metric tons) were estimated for the intertidal zone of the Danish (1986–2007) and Schleswig-Holstein (1998–2015) part of the Wadden Sea during autumn by combining aerial measurements of the size of blue mussel banks (ha) and ground samples of blue mussels on the banks estimating the biomass (wet fresh weight; kg) of blue mussels per m$^2$ (Kristensen and Borgstrøm, 2005, Laursen et al., 2010, Büttger et al., 2012, and updated by B. Diederichs, pers. com.). For 1998–2007, the annual mussel stocks in the two parts of the Wadden Sea are tightly correlated ($r^2 = 0.846$). To estimate the total mussel stocks in the two parts of the Wadden Sea, we estimated the linear regression equation between (1) the mussel stocks in the Danish part (x) and the total mussel stocks for the two parts (y) ($y = 1.3979 \times + 8170.1$), (2) the mussel stocks in the Schleswig-Holstein part (x) and the total biomass for the two parts (y) ($y = 3.1258 \times - 13,157$). These equations are used to estimate missing values for the total mussel stocks during 1986–1997 using eq. (1) and during 2008–2015 using Eq. (2). Data from 2009 to 2014 were used in the current study.

### 2.3. Eider samples and diet of eiders in Denmark

Eiders were collected by hunters during five winters (January 1st - March 4th) 2010–2014 at five large localities situated in the central

parts of the Danish waters and in the Wadden Sea (Fig. 1). Shooting eiders in Denmark has a long tradition, and the birds are used for consumption. The Danish waters including the Wadden Sea constitute the main wintering grounds of the Baltic-Wadden Sea eider flyway population (Noer, 1991; Lehikoinen et al., 2008). The eiders were shot by hunters from motorboats at the feeding grounds in coastal and off-shore waters representing most water depths. We consider the shot eiders to represent a random sample, because the hunters were unaware of the purpose of sampling. Sampling at different water depths and at several locations secured that the samples of eiders were representative of the flyway population at large. Eiders from each hunting bout were labled by locality. The eiders were stored in freezers the day after being shot. Since most food items in the gizzard had shells or exoskeleton there was probably no changes in diet. So the diet analyses reflect the diet obtained by the birds. Later the eiders were processed in the laboratory where information of sex and age were recorded. For aging, 1- to 2-year-old females were classified as juveniles and > 2-year-olds as adults, and 1- to 4-year-old males as juveniles and > 4 year-olds as adults. The following measurements were taken: mass of the entire body (g), length of wing (mm), mass of the empty gizzard (g) and mass of gizzard contents (g). The esophagus and gizzard of 626 eiders (236 females, 388 males and 2 unsexed individuals) were opened and the content was separated into nine categories (*Mytilus edulis, Cerastoderma edule, Ensis directus*, bivalves spp., *Littorina littorea, Hinia reticulate, Buccinum undatum, Carcinus maenas*, and other species) using the methods described in Laursen and Møller (2016). The size of intact items was measured (mm) for mussels and snails as the total (longest) length of shells and for crabs as the width of carapaces. Broken items were identified and measured in 5 mm intervals using a reference collection of intact prey species and size groups.

### 2.4. Date of ice break-up in southern Finland

The date of ice break-up was estimated in southern Finland at Tvärminne Zoological Station (59°50′N, 23°15′E), western Gulf of Finland. The daily ice conditions were assessed from ice maps based on satellite images and daily information from ships. Ice break-up was expressed by two parameters: (1) the date when 50% of the ice cover had melted and (2) the date when ice had completely disappeared. There was a strong positive correlation between the two measurements ($r^2 = 0.95$). We chose the date when 50% of the ice cover had disappeared for the analyses, and calculated the number of days between this date and January 1st for each year.

### 2.5. Female body condition at hatching

The eider population at Tvärminne is well suited for relating female body condition at hatching to that on the wintering grounds, as the entire Finnish eider population winters in Danish waters (Noer, 1991; Lehikoinen et al., 2008). However, eiders from Finland constitute a large part of eiders wintering in Denmark that include birds from the entire flyway population. To examine if breeding success (defined as the total number of ducklings in the end census divided by the total number of recorded breeders (until 1998) or by the sum of brood-caring and solitary adult females in the end census; from 1999 onwards; Lehikoinen et al., 2006) measured at the breeding colony at Tvärminne is representative of breeding success measured in Danish waters, we used a breeding index based on data from the Danish wing survey. In this survey about 1800 eider wings are annually sexed and aged, and a breeding index was estimated (number of young/number of adult females). The wing survey data and the breeding index estimated at the wintering grounds in Denmark are considered representative for the Baltic-Wadden Sea eider population (Lehikoinen et al., 2006, 2008). A comparison between breeding success at Tvärminne, Finland, during 1990–1991 and 1994–2013 and the breeding index obtained from the Danish wing survey (1990–2013) at the main wintering grounds of the

Baltic-Wadden Sea population showed a significant positive relationship (Estimate (S.E.) = 2.75 (1.00); F = 7.53, df = 1,20, $P = .01$), taking year into consideration. This result indicates that breeding success of female eiders at the Tvärminne colony can be considered as representative of the breeding index measured in the eider population at the wintering grounds in Denmark.

Female body condition at hatching was measured during 2010–2014 according to established methodology (Öst and Stele 2010). Females ($N = 1033$, range: 173–248 annually) were trapped at the nests during incubation. Upon capture, females were weighed, the length of the radius-ulna was measured, and incubation stage was estimated by egg floatation. Condition indices were derived as the standardized residuals of a regression of ln-transformed projected weight at hatching (response variable) on ln-transformed radius-ulna length. Indices for 2010–2014 were derived for the pooled data from a longer reference period (1990–2016, $N = 26$ years), and, therefore, mean condition index for the focal five-year period does not equal zero. A female's weight at hatching was estimated by subtracting an estimate of the weight they would be expected to lose during the remaining incubation time from their measured incubation weight. Because females abstain from feeding during incubation, and since the females were captured at different times during their incubation period, the average weight loss was estimated as the slope of the regression of ln (body weight at capture; response variable) on ln (incubation time at capture) and projected hatching date (Öst et al., 2008a). Residuals from mass-size regressions provide a reliable index of body condition in both birds and mammals (Ardia, 2005; Schulte-Hostedde et al., 2005).

### 2.6. Statistical analyses

Sample sizes differed among analyses because not all variables were recorded for all individuals. The first linear mixed model analysis was divided into three steps. First we analysed the body condition of eiders in winter (response variable) in relation to date (number of days after October 1st), age, sex and the interaction between date and sex as predictors, together with locality and year as random effects. Locality and year were included to account for differences in sampling effort among localities and years. By including the interaction between sex and date, we tested explicitly whether the effect of date on body condition in winter differed between males and females. All statistically significant variables ($P < .05$) in the first step of the test remained in the model for the next step in which we included the amount of mussel stocks, mussel quality as reflected by the flesh mass/shell mass ratio, individual gizzard mass and accumulated winter temperature as predictors in order to examine the effect of food, food quality and food processing on body condition in winter. In the third step, nine categories of food items were included into the model, in which all statistically significant variables from the second step were retained, to examine the effect of the specific food items on body condition in winter.

A second linear mixed model analysis was also divided into three steps. First we analysed gizzard mass of eiders (response variable) in relation to wing length, date (number of days after October 1st), age, sex and the interaction of date and sex as predictors, together with locality and year as random effects. Wing length was included in the test to account for differences in body size. By including the interaction between date and sex, we tested explicitly whether the effect of date on gizzard mass in winter differed between males and females. All statistically significant variables in the first step of the test stayed in the model for the next step in which we included mussel quality, mussel stocks and accumulated winter temperature as predictors to examine for the effect of food and food quality on gizzard mass. In the third step of the model (in which all statistically significant variables retained), we included the size of the nine categories of food items to the model and the interactions of the size of food items and sex. The size of the food items was included to examine if they had any effect on gizzard mass of eiders, and if the effects were sex dependent.

In a third linear mixed model, we analysed annual mean female condition indices at hatching during 2010–2014 (response variable) in the breeding population at Tvärminne, southern Finland, in relation to body condition in winter, gizzard mass and day of ice break-up at the breeding grounds as predictors and year and site as random variables. Except for date of ice break-up, the other explanatory variables were measured at the wintering grounds.

Mussel quality is included in step one and two of the statistical analyses, expressed as the flesh to shell mass ratio. Flesh and shell mass can vary independently of each other, which may potentially complicate interpretations of how the ratio relates to body condition and gizzard mass of eiders. We therefore did another, more simplified set of statistical analyses which included (1) body condition of eiders in winter (response variable) in relation to mussel stocks, mussel flesh mass and shell mass as predictors, and (2) gizzard mass of eider during winter (response variable) in relation to mussel stocks, mussel flesh mass and mussel shell mass as predictors. In both analyses a linear mixed model was used with locality included as random effect. The results are presented in ESM Table S3.

We tested for potential multi-collinearity among predictors using variance inflation factors (VIF) (McClave and Sinich, 2003). All VIFs were smaller than three and there were thus no problems of multi-collinearity (McClave and Sinich, 2003). We estimated the magnitude of associations between predictor and response variables using effect sizes estimated as Pearson's product-moment correlation coefficients based on the standard conversion of $F$-statistics to Pearson's $r$ (Rosenthal, 1994). We assessed relationships based on effect sizes according to the criteria listed by Cohen (1988) for small (Pearson $r = 0.10$, explaining 1% of the variance), intermediate (9% of the variance) or large effects (25% of the variance). All values reported are means (SE). All analyses were made with JMP (SAS, 2012).

## 3. Results

### 3.1. Body condition of eiders during winter in relation to food

The first model showed that body condition of eiders during winter increased slightly from an average (SE) of 2288 units (16) ($N = 150$) in the first half of January to 2373 units (10) ($N = 328$) in the second half of February and beginning of March, or an increase by 85 units (or 3.7%; Fig. 2). The body condition in winter for adult females in the first half of January was 2331 units (35) ($N = 43$) versus 2366 units (12) ($N = 242$) in the second half of February and the first days of March, or an increase by 35 units (or 1.5%). During the same period gizzard mass (without food content) of eiders increased from 126.9 g (2.5) to 143.1 g (1.5), or 12.7%. Gizzard mass of adult females increased from 114.4 g (5.8) to 128.4 g (3.0), or by 12.2%. The first step of the model showed a significant positive relationship with October days (Fig. 2) and a significant negative correlation with age (juveniles heavier than adults;
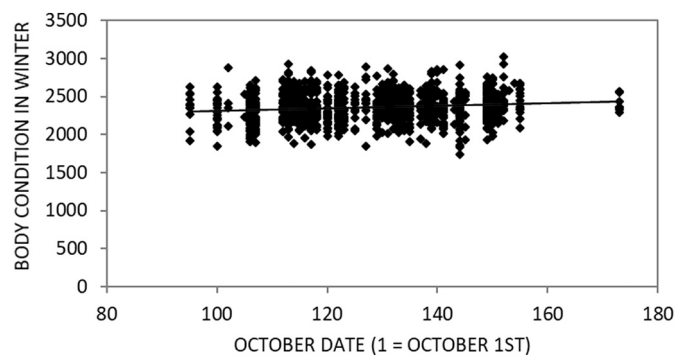


**Fig. 2.** Body condition of eiders in winter (scaled body mass index) collected in Denmark in relation to October days (1 = October 1st). Effect size is 0.23. The regression line is shown for illustrative purposes.

**Table 1**
Final linear mixed model of body condition of eiders in winter (response variable) in relation to October days, age, sex and the interaction between October days and sex, amount of mussel stocks, mussel quality, accumulated winter temperature and nine categories of food items as predictors. Locality and year were included as random effects.

| Variables | F | df | P | Estimate | SE | Effect size |
|---|---|---|---|---|---|---|
| Step 1 | | | | | | |
| October days | 27.253 | 1,1102 | < 0.0001 | 2.064 | 0.395 | 0.16 |
| Age | 52.435 | 1,1102 | < 0.0001 | − 62.087 | 8.574 | 0.21 |
| Step 2 | | | | | | |
| Mussel quality | 18.232 | 1,1102 | < 0.0001 | 2.023 | 0.474 | 0.13 |
| Step 3 | | | | | | |
| Blue mussel | 4.604 | 1505.2 | 0.032 | 60.297 | 28.102 | 0.10 |
| Razor clam | 3.885 | 1563.7 | 0.049 | 77.154 | 39.145 | 0.08 |
| Whelk | 5.825 | 1612.2 | 0.016 | 192.269 | 79.662 | 0.10 |

Table 1). Both variables had intermediate effects.

In the second step of the first model, we examined if body condition of eiders during winter was positively correlated with mussel stocks and mussel quality, severity of winter climate and individual gizzard mass. The results showed that only mussel quality was positively correlated with body condition in winter with a small to intermediate effect (Table 1). No significant correlation with mussel stocks and cumulative winter temperature was found.

In the third step of the first analysis, there were significant positive correlation with the number of blue mussels, razor clam and whelk in the gizzard (Table 1). These effect sizes only accounted for approximately 1% of the variance in body condition in winter.

A statistical analysis of body condition of eiders in winter (response variable) in relation to mussel stocks, mussel flesh mass and shell mass as predictors, showed that only flesh mass of mussels had an positive effect on body condition of eiders (ESM Table S3). A similar result was found in the first model, step two, above.

### 3.2. Gizzard mass in relation to amount and quality of food

In the second model, there were significant positive correlations between gizzard mass and wing length and October days (Table 2), while the interaction between date and sex was not significant ($F = 0.183$, df = 1, 1181, $P = .67$, effect size = 0.01).

In step two of the second analysis, there was a significant positive correlation between gizzard mass and mussel stocks and mussel quality, both having intermediate to large effects (Table 2, Fig. 3). The correlation between gizzard mass and accumulated winter temperature was not significant ($F = 0.031$, df = 1, 986.5, $P = .860$, effect size = 0.01).

In step three of the second analysis, males had 13% longer blue mussels in their gizzards (mean (SE) = 37.39 mm (2.52)) than females

**Table 2**
Final linear mixed model of gizzard mass of eiders (response variable) in relation to wing length, October days, age, sex, the interactions between October days and sex, mussel stocks, mussel quality, accumulated winter temperature, size of nine prey categories and the interactions between the size of food items and sex as predictors. Locality and year were included as random effects.

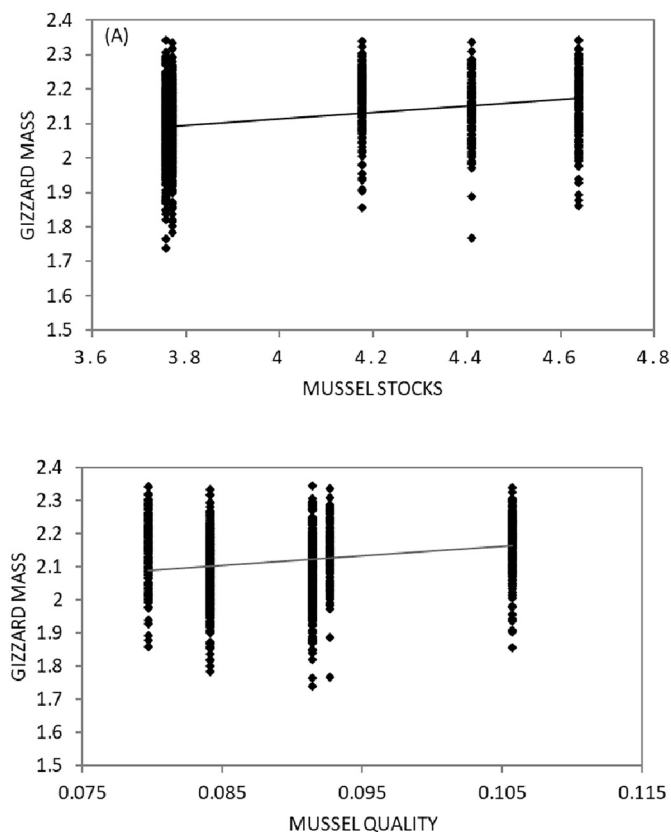| Variables | F | df | P | Estimate | SE | Effect size |
|---|---|---|---|---|---|---|
| Step 1 | | | | | | |
| Wing length | 43.797 | 1,1182 | < 0.0001 | 0.607 | 0.092 | 0.19 |
| October days | 12.085 | 1,1152 | 0.0005 | 0.191 | 0.055 | 0.10 |
| Step 2 | | | | | | |
| Mussel stocks | 18.937 | 1,1036 | < 0.0001 | 11.442 | 2.629 | 0.13 |
| Mussel quality | 45.107 | 1,1188 | < 0.0001 | 601.525 | 89.564 | 0.19 |
| Step 3 | | | | | | |
| Blue mussel size, males-females | 11.927 | 1255 | 0.0006 | 2.203 | 0.664 | 0.21 |

**Fig. 3.** (A) Gizzard mass (log g) of eiders collected in Denmark in relation to mussel stocks in log metric tons (effect size is 0.13), and (B) gizzard mass (log g) in relation to mussel quality (mussel flesh mass/ shell mass) during 2010–2014 (size is 0.19). The regressions lines are shown for illustrative purposes.

(mean = 32.98 (2.64)) (Table 2). In contrast, there were no significant differences between the sizes of prey taken by male and female eiders for other bivalve and snail species (*Cerastoderma edule, Ensis directus, Littorina littorea, Hinia reticulate* and *Buccinum undatum)*. In addition, the random effects of locality and year were non-significant in all three models.

A statistical analysis of gizzard mass of eiders during winter (response variable) in relation to mussel stocks, mussel flesh mass and mussel shell mass as predictors, showed that gizzard mass was positively correlated with mussel stocks, mussel flesh and shell mass (ESM Table S3). A similar result was found in the second model, step two, for mussel stocks and mussel quality in relation to gizzard mass (see above).

### 3.3. Female body condition index at hatching

In the third model, female body condition at hatching was positively correlated with October days, date of ice break-up (number of days since January 1st) and gizzard mass measured at the wintering grounds, with intermediate to large effects (Table 3, Fig. 4). The correlation between body condition in winter on the wintering grounds and female body condition at hatching was not statistically significant, and so body condition in winter was removed from the final model. To this final model we added wing length of eiders during winter in Denmark to examine if the correlation between gizzard mass in Denmark and body condition at hatching in Finland was simply a by-product of structural size of the individuals. However, female body condition at hatching was not correlated with wing length of eiders from Denmark in winter ($F = 0.01$, df = 1,1086, $P = .9266$, estimate (SE) = 0.0208 (0.2252). Thus, the association between gizzard mass in winter and female body

**Table 3**
Final linear mixed model of the annual mean body condition of female eiders at hatching at Tvärminne, southern Finland, during 2010–2014 (response variable) in relation to body condition in winter, gizzard mass, October days and date of ice break-up in southwest Finland, as predictors. Year and site were included as random effects.

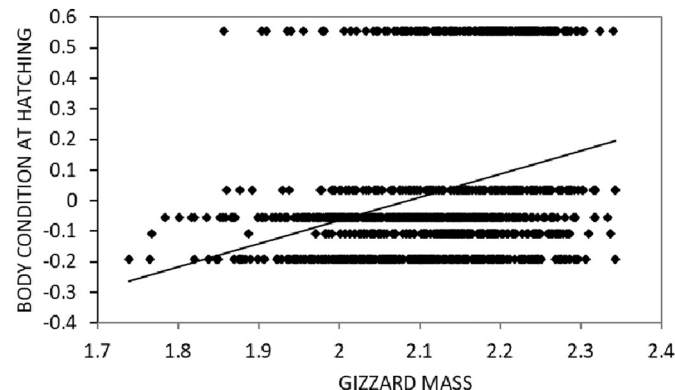| Effect | *F* | df | *P* | Estimate | SE | Effect size |
|---|---|---|---|---|---|---|
| Ice break-up | 839.36 | 1,1188 | < 0.0001 | 3.875 | 0.134 | 0.64 |
| October days | 56.24 | 1,1188 | < 0.0001 | 1.053 | 0.140 | 0.21 |
| Gizzard mass | 8.68 | 1,1188 | 0.0033 | 0.220 | 0.075 | 0.09 |



**Fig. 4.** Body condition of eiders at hatching (annual mean body condition index of females) at Tvärminne, Southern Finland, in relation to gizzard mass (log g) measured at the wintering grounds in Denmark during 2010–2014 (effect size is 0.09). The regression line is shown for illustrative purposes.

condition at hatching was not merely driven by structural size differences among individuals.

### 4. Discussion

#### 4.1. Body stores and mussel quality

The reduction in mussel quality between the start of October and the beginning of March in the Baltic Sea has been estimated to 11–14% in cold winters and 15–19% in mild winters (Waldeck and Larsson, 2013). Compared to the winter temperature regimes used by Waldeck and Larsson (2013), there were two cold winters, two mild winters and one intermediate winter during our study. We used accumulated winter temperature to account for the reduction in quality, but found no significant correlation between this variable and body condition in winter or gizzard mass. According to Waldeck and Larsson (2013), we should expect a negative effect, since cold winters (and lower winter temperatures) should restrict metabolism of mussels during a period when they experience a negative energy balance, resulting in higher mussel quality, i.e., increased relative mussel quality. However, at the breeding grounds there was a positive correlation between later ice break-up and body condition at hatching (Table 3), consistent with the hypothesis of a positive effect of cold winters on eider body condition, mediated by increased blue mussel quality (Waldeck and Larsson, 2013).

#### 4.2. Body condition of eiders in winter

Body condition of eiders increased during winter and was negatively related to age (young birds had better body condition than adults). It is known that eiders increase body mass during winter (Waltho and Coulson, 2015), and we have shown here that this increase is parallel in males and females, with no difference between the sexes.

The body condition in winter of eiders feeding on blue mussels and razor clams is larger than that of individuals feeding on other food

items (such as cockles and crabs) as previously reported for blue mussels from the Danish part of the Wadden Sea (Laursen et al., 2009). However, these effects were small and only accounted for approximately 1% of the variance. Since eiders in the present study were collected from a large part of the main wintering grounds of the Baltic/Wadden Sea eider flyway population (Noer, 1991), we can conclude that these food items in general increase body condition of eiders during winter. Later when females arrive at the breeding grounds, those arriving in better condition lay larger clutches (Öst and Steele, 2010) with a higher probability of hatching (Lehikoinen et al., 2010), their ducklings have higher survival prospects (Bustnes et al., 2002; Öst et al., 2008b), and there is a positive correlation with body condition and female survival (Ekroos et al., 2012b).

Body condition in winter increased with mussel quality (flesh to shell mass ratio), but there was no effect of mussel stocks and accumulated temperature during winter. In contrast, gizzard mass was positively correlated with mussel stocks and mussel quality. These remarkable results indicate that eiders during winter in the Danish waters prioritize the build up of gizzard mass rather than general body condition, with gizzard mass reflecting the ability to exploit food stocks. The functional significance of the size of the gizzard during winter is supported by results showing that individual eiders with large gizzards also had large numbers of blue mussels in the gizzard (Laursen and Møller, 2016). Eider males consumed larger mussels than females, which indicate the presence of sex-specific foraging. In addition, adult females with large gizzards are able to handle larger prey items than females with small gizzards. Finally, females with large gizzards had superior body condition, and, therefore, potentially high reproductive success compared to females with small gizzards (Laursen and Møller, 2016).

The statistical analyses of body condition and gizzard mass during winter rely on mussel stocks and mussel quality measured in the previous autumn. We assume that large mussel stocks and high mussel quality reflext feeding conditions for eiders during winter. Mussels stop growing during autumn, and they are reduced during winter due to predation. However, the magnitude of predation is unknown, although we assume that large mussel stocks during autumn provide better feeding condition for eiders during winter than small mussel stocks. Likewise, high mussel quality provide better feeding condition during winter than poor mussel quality. In the analyses we have included reduction in mussel quality due to respiration during winter, although no measurable effect was found. However, notice the positive effects of ice break up in the Baltic Sea on body condition of female eiders at hatching (Table 3).

### 4.3. Body stores and spring migration

Body condition in winter of adult female eiders increased from 2331 units during the first half of January to 2366 units in the second half of February and the beginning of March. On average, this amounts to 35 units during the stay at the wintering grounds, amounting to a 96 g increase in body mass. The body mass of females at the beginning of the laying period is c. 2500 g (Noer and Christensen, 1996). The mass of one egg is estimated to be 106 g (Cramp and Simmons, 1977), implying that the average increase in body mass during January and February is less than that needed for production of one egg. An increase in female body mass by 200 g during March and April (before the breeding season) required for production of a clutch of c. 4.8 eggs (the average clutch size in southern Finland (Lehikoinen et al., 2006)) equals a body mass of c. 2500 g at the end of April when egg laying starts in Finland (Lehikoinen et al., 2006). In order to achieve that mass, females have to double the rate of increase in body mass during March and April compared to January–February. This indicates that eiders may have to make stop-overs during migration or feed close to the breeding grounds to increase body condition before commencing breeding. Comparison of spring migration of eiders at Falsterbo,

southern Sweden, Ottenby at Öland and Hanko Bird Observatory in southwestern Finland shows that the main spring migration occurs rather quickly (Lehikoinen et al., 2008), so that eiders arrive at Halias in southwest Finland between March 27th and April 10th. The synchronous timing of spring migration across sites indicates that there is relatively few days for stop-over during migration so that eiders probably feed close to or off the breeding grounds for the final increase in body mass, as observed in Denmark (Christensen, 2000), demonstrated in Finland (Hobson et al., 2015; Jaatinen et al., 2016) and in the arctic (Oppel et al., 2010; Sénéchal et al., 2011).

The eider has one of the highest wing-loadings of any flying bird (Rayner, 1988; Guillemette, 1994; Vágási et al., 2016), and they tend, for energetic reasons, to minimize transport of surplus mass when flying, as during migration (Guillemette et al., 2012, 2016). The small increase in body mass at the wintering grounds suggests that the eider has developed a spring migration strategy limited by physiology and food availability. The eider initiates spring migration with a slight increase in general body stores but a considerably enlarged gizzard. By doing so they minimize the load they have to carry over long distances during migration. Such a strategy is supported by Weber et al. (1994) showing that the take-off weight when initiating migration is seldom overloaded. In addition, Hobson et al. (2015) showed by use of isotopes that 50% of the egg yolk derives from feeding at the wintering grounds in the Danish waters, while the rest comes from feeding sites close to the breeding grounds. Using this migration strategy, eiders may resemble other capital breeders such as geese by increasing body stores immediately before reaching the breeding grounds (Chudzinska et al., 2016).

### 4.4. Gizzard mass and breeding condition

In winters when birds shot in Denmark had larger gizzard mass, females breeding in the following spring in Finland had higher body condition at hatching. This effect is likely due to the higher potential to convert gizzard mass into pre-breeding body condition by females initiating spring migration with large gizzards. Thus, a twin study analysing the build-up of body condition during prebreeding at the Åland Islands, Finland, showed a rapid decrease in gizzard mass, and a concomitant increase in body mass expressed as scaled body mass index (Laursen et al., accepted). Futhermore, females with high scaled body mass index had the largest yolk or egg in the oviduct indicating successful reproduction (Laursen et al., 2018). Thus, the results indicate that in years when birds shot in Denmark have large gizzards, females breeding in Finland have better condition at hatching than in years when individuals have small gizzards in winter. In contrast to Lehikoinen et al. (2006), we found a positive relationship between female body condition and date of ice break-up. The reason for this could be that the winters were mild in our study period (2010–2014, mean number (variance) of days for ice break-up = 78.0 (383.3) compared to a 20-year period = 87.6 (682.6) and may remain within the range of winter climate still beneficial for breeding eiders. Severe winters increase mussel stocks and mussel quality (Van Stralen, 1995; Beukema and Dekker, 2007) on the one hand, and on the other very severe winters delay the arrival of eiders at the breeding colonies, and reduce their body condition (Lehikoinen et al., 2006). Females with large gizzards have superior body condition (Laursen and Møller, 2016), and females arriving at the breeding colonies in good condition have on average better breeding success than those arriving in poor condition (Bustnes et al., 2002; Öst et al., 2002; Lehikoinen et al., 2006).

Female eiders in poor condition before the breeding season may give up breeding (Öst et al., 2018), complete breeding but leave ducklings to the care of other females (Kilpi et al., 2001), or successfully breed but being so exhausted that they may avoid breeding in the subsequent breeding season (Waltho and Coulson, 2015). While the prevalence of such 'best-of-a-bad-job'-breeding strategies is unknown in our study, Milne (1974) suggested that 33–40% of females missed

breeding in two specific years. At Tvärminne, SW Finland, the proportion of presumed non-breeding has increased dramatically over the past 15 years, from only ca 5% in 2004 to nearly 50% in 2016 (Öst et al., 2018). Poor feeding conditions also affect the number of non-breeders (Jean-Gagnon et al., 2017).

These results show that the feeding conditions of eiders at the wintering grounds in Denmark have a large effect on the build-up of body condition in the form of gizzard mass. In years when gizzard mass was high in Denmark, breeding females in Finland also had better body condition at hatching. Recently, it has been shown that feeding conditions in Danish waters have strong effects on breeding numbers in a large colony in the western part of the Baltic Sea (Laursen and Møller, 2014). This could indicate that feeding conditions at the wintering grounds in Denmark affect reproductive output in large parts of the Baltic/Wadden Sea population. The results show a disproportionate investment in gizzard growth on the wintering grounds, prepare the female eiders to suitable breeding condition. A similar mechanism is described for another mussel eating bird, the Knot *Calidris islandicay* (Piersma, 2002).

## 5. Conclusions

Eiders wintering in Danish waters belong to the Baltic/Wadden Sea flyway population, which has declined dramatically for more than two decades. Eiders have to build up parts of their body condition during winter for subsequent breeding. There was an increase in body condition over the winter, and the increase in body condition also increased with increasing mussel quality (flesh to shell ratio). The main drivers of increase in gizzard mass were mussel quality and the amount of mussel stocks. The increase in body condition in winter for adult females from the first half of January to the first days of March was only about 96 g (or 1.5%). During the same period, gizzard mass increased by 12.2%. The modest increase in body condition in winter and the large increase in gizzard mass may enhance food intake capacity before spring migration and minimize wing loading across long distances. On the breeding grounds gizzard mass was positively correlated with female body condition at hatching in Finland. Thus, feeding conditions at the wintering grounds in Denmark are important for building up body condition prior to breeding, with potentially important repercussions for population productivity in this species recently listed as endangered in Europe (BirdLife International, 2015).

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.seares.2018.11.005.

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