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Diet of eiders and body condition change from the late 1980s to the mid 2010s

Karsten Laursen^{a,*}, Anders Pape Møller^b

^a Aarhus University, Department of Ecoscience, 8000 Aarhus C, Denmark

^b Ecologie Systématique Evolution, Université Paris-Sud, CNRS, AgroParisTech, Université Paris-Saclay, F-91405 Orsay Cedex, France

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ABSTRACT

Food and foraging decisions are fundamental drivers of the population dynamics of bird species. Eider *Somateria mollissima* was sampled in Danish marine waters during the non-breeding season in 1986–1990 and in 2010–2017 in order to analyze changes in diet and body condition between the two periods. The food items found were among those commonly consumed by eiders. Between the late 1980s and the mid 2010s there was a decrease in the number of blue mussels *Mytilus edulis*, cockles *Cerastoderma edule* and common whelks *Buccinum undatum* in the diet, and an increase in the number of razor clam *Ensis directus*. Blue mussel was the most abundant prey. When present, this prey item occurred almost exclusively in the eiders' digestive tract and was negatively correlated with the numbers of other prey items. Eiders with blue mussels, other bivalves and shore crabs in the gizzard had better body condition than eiders with other food items. Blue mussel was a preferred food item and is important for the build-up of body condition. Body condition increased between the late 1980s and the mid 2010s. We assume that this increase in body condition has occurred in parallel with a decrease in the size of the population of the Baltic/Wadden Sea flyway.

1. Introduction

Food and foraging decisions are fundamental drivers of the population dynamics of birds (Stephens et al., 2007). Diet studies have a long tradition in providing important information on ecology and adaptation to habitats (Waltho and Coulson, 2015). The eider duck *Somateria mollissima* preys upon a large number and diversity of benthic species and other marine organisms, including molluscs, especially bivalves and gastropods, crustaceans, echinoderms, polychaetes and insects, fish including eggs, and plants (references in Waltho and Coulson, 2015), and >130 species have been identified in the diet. Blue mussels *Mytilus edulis* in particular were found in a large proportion of eiders (Waltho and Coulson, 2015), and significant positive relationships have been demonstrated between mussel stocks and abundance of eiders (Laursen et al., 2010; Cervencel et al., 2014), and between mussel stocks and eider numbers at wintering grounds and their subsequent reproduction (Kats, 2007; Waser, 2018; Morelli et al., 2021).

The majority of the Baltic/Wadden Sea eider population winter in Danish waters and in the Wadden Sea (Noer, 1991). The size of this population has decreased considerably during recent decades, which is reflected in the number of breeding as well as wintering individuals

(Ekroos et al., 2012). The underlying causes of this decline are still being investigated, and suggestions for the decline include increased predation at breeding grounds, parasitic infection, thiamine deficiency, decreased nutrient load in marine waters and climate change (Ekroos et al., 2012; Balk et al., 2009; Laursen and Møller, 2014; Morelli et al., 2021). However, other factors may also contribute to this decrease in the eider population. Here we focus on the effects of change in food over time because this mechanism remains poorly researched despite several studies on the diet of eiders (Waltho and Coulson, 2015).

The objective of our study was to compare the diet of eiders during the non-breeding season in the late 1980s and the mid 2010s, which is the period when birds prepare for spring migration through relating diet to body condition. We hypothesised that (i) the diet of eiders changed from the late 1980s to the mid 2010s; (ii) there is a negative relationship between numbers of blue mussel and other food items due to eiders' preference for blue mussels (Waltho and Coulson, 2015); and (iii) body condition of eiders decreased from the late 1980s to the mid 2010s due to reduced amounts of nutrients in marine waters in recent years (Bruhn et al., 2021).

The study was based on information of 1644 eiders sampled in Danish waters during late the 1980s and the mid 2010s.

* Corresponding author.

E-mail address: kl@ecos.au.dk (K. Laursen).

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2. Materials and methods

2.1. Eider samples and study sites

The eiders were sampled during and outside of the open season, the latter sample under special permits from the Nature Agency of the Danish Ministry of the Environment (SN-302-009, SNS-3446-00103, NST-3446-00018, NST-3465-00007). Eiders obtained from each sampling hunt were labelled with locality and date. The eiders were stored in freezers the same day or the morning of the day after being shot. Eiders were sampled in Kattegat and in the Wadden Sea during 1986–1990 (late 1980s) and in 2010–2017 (mid 2010s; Fig. 1). Diet of 1307 eiders was analyzed and body condition was estimated for 1644 eiders (see Appendix 1).

2.2. Body condition and diet

Information on sex and age (juvenile and adult) was recorded according to Cramp and Simmons (1977). We recorded wing length with a ruler to the nearest mm and body mass with a balance to the nearest 100 g. In the sample of eiders from the mid 2010s, wear of wing feathers was recorded. We subsequently estimated scaled body mass index (a unitless index), using wing length as a linear morphological character and body mass following Peig and Green (2009). Wing length was used as a morphological character because it was the only morphological measurement recorded during the late 1980s. Wing feathers become worn due to the length of time after moult and during migration. However, the eiders were sampled within 5–6 months after moult and before the spring migration. Wear of wing feathers was recorded in the sample from the mid 2010s and wear was recorded in 13.9% of the eiders. One individual made these wing measurements in the late 1980s and a

different individual in the mid 2010s. There was a marginal difference between the two samples of 0.7 mm (0.2%). Due to these analyses, we considered wing length a reliable morphological character for estimation of body condition in this study.

The oesophagus, proventriculus and gizzard (hereafter gizzards) were opened and the contents identified and separated into nine categories: blue mussel *Mytilus edulis*, cockle *Cerastoderma edule*, razor clam *Ensis directus*, other bivalve species (mostly carpet shell clam *Venerupis* sp. and ocean quahog *Actica islandica*), periwinkle *Littorina littorea*, draft whelk *Hinia reticulata*, common whelk *Buccinum undatum*, shore crab *Carcinus maenas* and other species. The methods used are described in Laursen et al. (2019). A stereo microscope (x 20 magnification) was used to identify intact prey specimens and broken fragments to species using a reference collection of intact, identified species. The number of umbos, hinges, columnellas and pincers was used to quantify food items. Thus, one columnella, two umbos or hinges and four pincers was considered to derive from one prey item. If the size of these fragments differed, umbos or hinges and pieces were grouped in size classes and counted, under the assumption that they represented individual prey items of different sizes. Due to the large number of broken items we cannot be sure that all fragments belonged to the species named, and thus parts of the items may have belonged to related species. Furthermore, the number of small and soft bodied food items may be underestimated, although we paid special attention to these species to reduce the effects of potential bias.

2.3. Statistical analyses

We used linear ANOVA models with GLM procedure to analyze diet of eiders in relation to period, region and body condition. Pearson correlation analysis was used to estimate the relationship between food items. The following analyses were performed to investigate hypotheses



Fig. 1. Map showing Denmark with the two regions, Kattegat and the Wadden Sea, where eiders were sampled.

(i), (ii) and (iii). For (i), we analyzed whether the number of blue mussels, cockles, razor clams, other bivalves, periwinkle, draft whelk, common whelk and shore crab in the gizzards differed between the late 1980s and mid 2010s. In the statistical models, we included sex, age and region to account for these variables. In the tests, the number of each food item, e.g. blue mussel, was the dependent variable and sex, age, period and region were explanatory variables. For (ii), we analyzed whether the number of blue mussels in gizzards was correlated with other food items (excluding unidentified items) using Pearson correlation. For (iii), we analyzed whether body condition estimated as a scaled body condition index (Peig and Green, 2009) was related to food items in the gizzard. In this model, we tested body condition as the dependent variable in relation to sex, age, period, region and number of eight food items (blue mussels, cockles, razor clams, other bivalves, periwinkle, draft whelk, common whelk and shore crab) as explanatory variables. Sex, age, period and region were included in the model to account for these variables. In the model, non-significant (> 0.05) variables were subsequently excluded. SAS Enterprise Guide 7.1 was used for the statistical analyses (SAS, 2017).

3. Results

3.1. Diet of eider

The diet of eiders in Kattegat and Wadden Sea during the late 1980s and mid 2010s (for all data pooled) showed that blue mussel was the most abundant prey item during the non-breeding season and represented 28.1% of the total number of food items, followed by cockle at 22.9% and razor clam at 20.7% (see Table 1).

3.2. Change in diet between late 1980s and mid 2010s

Blue mussels, cockles, other bivalves and common whelks in the diet of eiders decreased significantly from late 1980s to mid 2010s, while razor clams increased (Table 2). The proportion of eiders with the prey species in the two periods is shown in Fig. 2. The mean number (se) of blue mussels in gizzards decreased from 5.27 (1.53) to 1.35 (0.10) mussels between the two survey periods. Blue mussels were less abundant in gizzards from the Wadden Sea compared to Kattegat (Table 2). The proportion of gizzards with cockles decreased between the two periods from 34.8% to 22.0% and the mean (se) number from 5.21 (0.85) to 0.59 (0.07) individuals. Cockles were most numerous in gizzards from the Wadden Sea (Table 2). Mean (se) number of other bivalves decreased from 0.98 (0.12) to 0.31 (0.03), mostly in gizzards from the Wadden Sea. The proportion of common whelk in gizzards

Table 1

Diet of eiders during the non-breeding season in Kattegat and the Wadden Sea during late 1980s and mid 2010s (data pooled). Prey species are arranged in relation to decreasing proportion of prey species in the diet.

Prey species	Proportion of prey species in the diet	Proportion of eiders with the prey species
Blue mussel <i>Mytilus edulis</i>	28.1	28.8
Cockle <i>Cerastoderma edule</i>	22.9	16.8
Razor clam <i>Ensis directus</i>	20.7	11.2
Periwinkle <i>Littorina littorea</i>	6.5	7.0
Other bivalves <i>Molluscs</i> spp.	5.6	14.2
Draft whelk <i>Hinia reticulata</i>	5.2	3.4
Shore crab <i>Carcinus maenas</i>	4.9	9.9
Other items Spp.	4.0	5.3
Common whelk <i>Buccinum undatum</i>	2.1	3.4

Table 2

Linear ANOVA models with GLM procedure of the relationships between the number of eight food items (blue mussels, cockles, razor clams, other bivalves, periwinkle, draft whelk, common whelk and shore crab) in gizzards of eiders as dependent variable in relation to sex (male and female), age (juvenile and adult), period (late 1980s and mid 2010s) and region (Kattegat and Wadden Sea) as explanatory variables. Food items were $\log_{10} + 1$ transformed. Significant ($P < 0.05$) results are shown in bold font. See Materials and Methods for further explanations.

Variables	F	df	P	Estimate	SE
<i>Blue mussel</i>					
Sex	3.16	1	0.0756	-0.0350	0.0197
Age	0.08	1	0.7761	0.0076	0.0268
Period	19.21	1	<0.0001	-0.1380	0.0315
Region	28.81	1	<0.0001	-0.0546	0.0102
<i>Cockle</i>					
Sex	1.25	1	0.2463	0.0235	0.0202
Age	15.98	1	<0.0001	0.1099	0.0275
Period	14.94	1	<0.0001	-0.1248	0.0323
Region	28.71	1	<0.0001	0.0559	0.0104
<i>Razor clam</i>					
Sex	4.26	1	0.0392	0.0307	0.0149
Age	4.45	1	0.0350	0.0427	0.0202
Period	15.82	1	<0.0001	0.0946	0.0238
Region	26.70	1	<0.0001	0.0397	0.0077
<i>Other bivalves</i>					
Sex	1.26	1	0.2618	0.01305	0.01163
Age	0.50	1	0.4797	0.01117	0.01580
Period	171.85	1	<0.0001	-0.24346	0.01857
Region	173.87	1	<0.0001	-0.07912	0.00600
<i>Periwinkle</i>					
Sex	0.03	1	0.8636	0.0021	0.0012
Age	0.10	1	0.7465	0.0053	0.0162
Period	0.62	1	0.4321	0.0150	0.0191
Region	0.05	1	0.8292	0.0013	0.0062
<i>Draft whelk</i>					
Sex	2.02	1	0.1551	-0.0161	0.0113
Age	3.66	1	0.0561	0.0378	0.0381
Period	0.15	1	0.7015	-0.0069	0.0181
Region	9.05	1	0.0027	-0.0176	0.0058
<i>Common whelk</i>					
Sex	5.22	1	0.0225	-0.0157	0.0069
Age	3.84	1	0.0503	0.0183	0.0094
Period	83.99	1	<0.0001	-0.1007	0.0110
Region	93.83	1	<0.0001	-0.0344	0.0036
<i>Shore crab</i>					
Sex	2.78	1	0.0956	0.01957	0.0117
Age	98.75	1	<0.0001	-0.1585	0.0159
Period	0.10	1	0.7474	0.0060	0.0187
Region	3.98	1	0.0462	0.0121	0.0061

decreased from 8.0% to 4.0% and mean number (se) decreased from 0.42 (0.10) to 0.09 (0.02) common whelks between the two periods. Eiders from Kattegat contained more common whelks than those from the Wadden Sea (Table 2). The number of razor clams decreased between the two periods. However, the proportion of gizzards with razor clams increased from 7.0% to 11.9% between the two periods. Razor clams were most abundant in gizzards from the Wadden Sea (Table 2). Gizzards not containing any food items were found in 55 eiders (11.6%) in the late 1980s and in 85 eiders (10.2%) in the mid 2010s.

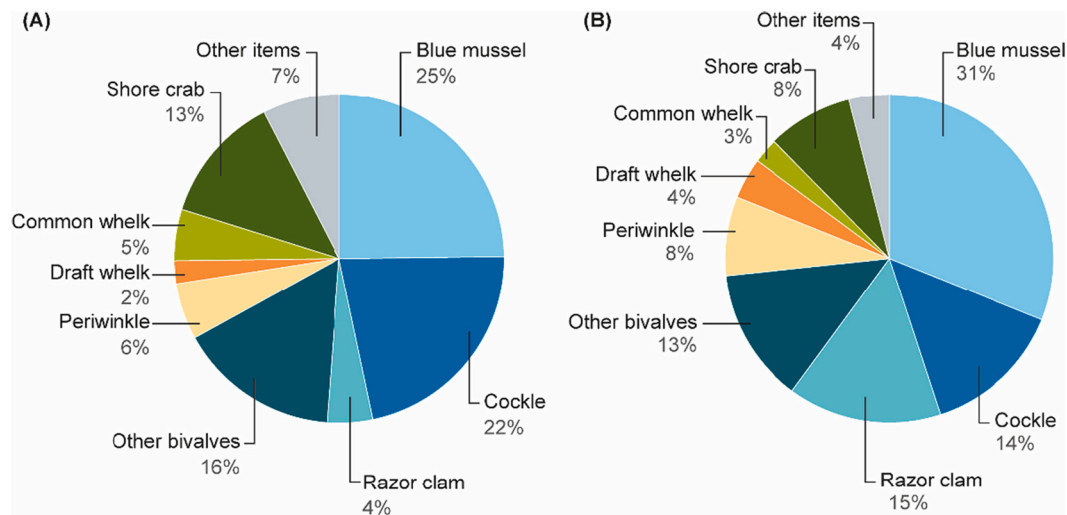


Fig. 2. Overview of the diet of eiders in Kattegat and the Wadden Sea (pooled) during the late 1980s (A) and the mid 2010s (B) shown as the proportion of eiders with the specified prey items.

3.3. Relationship between food items in gizzards

The number of blue mussels in gizzards was significantly negatively correlated with the number of cockles, razor clams, other bivalves, common whelks and shore crabs (Table 3). The number of cockles in gizzards was negatively correlated with the number of common whelk and shore crab. The number of other bivalves was positively correlated with the number of draft whelks and common whelks. Overall, the number of blue mussels in gizzards was negatively correlated with the sum of all other food items (Pearson correlation coefficient = -0.2636 , $p < 0.0001$, $N = 1307$).

3.4. Body condition and period, region and diet

Body condition increased significantly from the late 1980s to the mid 2010s (Table 4). The increase was 3.28% (mean (se): 0.01632 (0.0001) vs. 0.01685 (0.004) no unit of measurement). Furthermore, the body condition was greater in the Wadden Sea than in Kattegat. Body condition increased with the number of blue mussel, other bivalves and shore crab in the gizzards (Table 4).

4. Discussion

4.1. Diet of eider

Six out of seven specific food items taken by eiders in this study were among the ten most common food items exploited by eiders based on 58 studies (Waltho and Coulson, 2015). The seven food items taken were all common benthic species occurring in shallow water of 0–10 m depth (Fenchel, 2006). Only draft whelk was over-represented in gizzards of

Table 3

Pearson correlation coefficients estimated between number of blue mussels, cockles, razor clam, other bivalve, periwinkle, draft whelk, common whelk and shore crab in gizzard of eiders in the non-breeding season in Danish waters (Kattegat and the Wadden Sea) during the late 1980s and the mid 2010s. Numbers were $\log_{10} + 1$ transformed, $N = 1308$. Significant ($P < 0.05$) results are shown in bold font.

Variables	Blue mussel	Cockle	Razor clam	Other bivalves	Periwinkle	Draft whelk	Common whelk
Blue mussel	–						
Cockle	–0.1486	–					
Razor clam	–0.1047	0.0115	–				
Other bivalves	–0.1330	–0.0236	0.0852	–			
Periwinkle	–0.0303	0.0361	–0.0288	–0.0216	–		
Draft whelk	–0.0416	–0.0315	–0.0140	0.0777	0.0476	–	
Common whelk	–0.0578	–0.0754	–0.0402	0.2166	0.0412	0.0531	–
Shore crab	–0.0761	–0.0868	–0.0115	0.0164	0.0055	0.0377	0.0064

Table 4

Final results of a linear ANOVA models with GLM procedure to test relationships between scaled body condition index as dependent variable and sex, age, period (late 1980s and mid 2010s), region (Kattegat and Wadden Sea) and number ($\log_{10} + 1$) of eight food items (blue mussel, cockle, razor clam, other bivalves, periwinkle, draft whelk, common whelk and shore crab) as explanatory variables. Significant ($P < 0.05$) results are shown in bold font.

Variables	F	df	P	Estimate	SE
Period	36.24	1	<0.0001	0.00098	0.00016
Region	9.77	1	0.0018	0.00017	0.00006
Blue mussel	43.89	1	<0.0001	0.00097	0.00015
Other bivalves	11.35	1	0.0008	0.00084	0.00025
Shore crab	3.90	1	0.0484	0.00045	0.00023

eiders in this study. This species is one of the most common marine gastropods in Danish marine waters (Nørrevang and Meyer, 1968).

4.2. Changes in diet

Between the late 1980s and mid 2010s blue mussels, cockles, other bivalves and draft whelks decreased in eider diets, whereas razor clams increased. Mussel stocks have been monitored in the Wadden Sea and in Kattegat (Kristensen and Borgstrøm, 2005; Büttger et al., 2012; Nielsen et al., 2018). In the Wadden Sea annual mussel stocks *Mytilus edulis* were estimated (metric t) for the intertidal zone in the Danish (1986–2007) and Schleswig-Holstein (1988–2015) parts of the Wadden Sea. Due to a positive correlation between the annual mussel stocks in the two parts of the Wadden Sea ($r = 0.92$), mussel stocks were estimated for the Danish part for the years after 2007 using data from Schleswig-Holstein (see

Morelli et al., 2021). In 1986–1989 mussel stocks in the Danish part of the Wadden Sea were estimated to about 28,000 tons, which increased to a maximum level of 127,000 tons in 1994, followed by a decrease to fewer than a hundred tons in 2010–2012. Eiders were collected in the Danish part of the Wadden Sea in 1986–1988 and again in 2011–2012 (see Appendix 1). In these periods mussel stocks decreased from about 40,000 metric tons to about 12,000 metric tons. In the Wadden Sea eider numbers were positively related to mussel stocks (Laursen et al., 2010; Cervencel et al., 2014), and the small numbers of blue mussels in the diet of eiders in 2010–2012 may be a reflection of the small stocks of blue mussels in these years. The decreasing number of blue mussels in gizzards from the late 1980s to the mid 2010s was most pronounced in the Wadden Sea compared to Kattegat (Table 4). In eastern Kattegat, where most eiders in this study were collected, mussel stocks during 2009–2017 were estimated at 60,000–160,000 metric tons (Nielsen et al., 2018). In 2017, the year with the smallest amounts, mussel stocks were estimated to be more than twice as the amount necessary to support consumption by mussel eating birds, including eiders (Nielsen et al., 2018). The finding that mussels in the diet of eiders decreased between the late 1980s and the mid 2010s, and that this decrease was most pronounced in the Wadden Sea, may be a reflection of the abundance of mussel stocks at the two localities.

Razor clams have increased significantly in the Dutch coastal zone since the late 1990s and make up a significant part of the diet of eiders (Tulp et al., 2010). An increase in the number of razor clams was also reported for the north-eastern part of the Wadden Sea, whereas cockles have decreased, although the changes were not statistically significant (Drent et al., 2017). These changes were reflected in the diet of eiders in our study where there was a decreasing number of cockles and an increasing number of razor clams between the late 1980s and the mid 2010s. Both benthic species were mostly taken by eiders in the Wadden Sea compared to Kattegat (Table 2). In Kattegat large synchronous changes in numbers of benthic groups occurred during 1994–2019 without clear trends (Bruhn et al., 2021).

4.3. Correlation between eider food items

Correlation analysis for food items revealed that blue mussel was a preferred food item because this species occurred in relative large numbers and when it occurred, there was negative correlations with the number of other prey items. Further, eiders foraged on at least three groups of benthic organisms. The first group consisted of blue mussels that form banks that occur in patches and are widespread in Danish shallow water areas (Fenchel, 2006). The second group consisted of razor clams, other bivalves, draft whelk and common whelk whose mutual numbers were mostly positively correlated. These species prefer a mixture of sandy and muddy sediments commonly found in the Danish waters (Fenchel, 2006). The third group consisted of cockles that were negatively correlated with the other benthic species and were mostly found in sandy sediment types (Fenchel, 2006). However, this division of benthic species is rough, and species can be found at other sites depending on local conditions. Thus, eiders used a broad range of habitat types as feeding ranges, from mussel banks and a mixture of muddy sediments to sandy sediments. However, in this study eiders preferred to feed on mussel banks and take blue mussels, while other prey species are taken in small numbers randomly or were ignored despite periwinkle, draft whelk and shore crab occurring commonly on mussel banks. Eiders feeding on mussel banks have a higher body mass than eiders feeding on benthic organisms associated with sandy sediments (Laursen and Frikke, 2008). Diet studies reflect the feeding conditions within a few hours or less of when the eiders were sampled. In contrast, body condition is built up over time, probably weeks or months, reflecting feeding conditions during longer periods. Since the abundance of blue mussels was positively correlated with individuals having a high body condition, this result may be an indication that these individuals have been feeding on mussel banks during a relative long

period.

In this study blue mussels were the dominant food item, but other studies have shown different preferences. In the Netherlands the razor clam, *Ensis directus* dominated the diet (Tulp et al., 2010), on Iceland the chiton *Tonicella marmorea* was dominant (Kristjansson et al., 2012), and on Greenland two prey items, the bivalve *Mya eideri* and the polychaete *Pectinarius* spp., made up the largest part of the diet (Merkel et al., 2007). This shows that eiders can specialise on one or more benthic species depending probably on location, season and availability of food.

4.4. Body condition, period, region and diet

Body condition of eiders increased from the late 1980s to the mid 2010s. Due to decreasing amount of nutrients in the Danish waters (Bruhn et al., 2021), we expected that the biomass of benthic organisms, including blue mussels, would decrease between the late 1980s and the mid 2010s, thereby lowering the carrying capacity for eiders and affecting the build-up of body condition of the birds (Laursen et al., 2019). However, a significant increase in body condition was in fact found, which could be related to the number of eiders actually having decreased in the Baltic/Wadden Sea flyway population. This population decrease has lasted more than three decades, probably initiated by decreasing amounts of nutrients in the marine waters in the 1990s, which reduced carrying capacity for eiders and other organisms (Nixon and Buckley, 2002; Philippart et al., 2007; Møller et al., 2015). Decrease in eiders was also caused by predation at the breeding grounds, and during recent years by predation by the increasing population of white-tailed sea-eagles *Haliaeetus albicilla* (Ekroos et al., 2012; Morelli et al., 2021). Density dependent relations of eiders have been described for reproduction and feeding which indicate that the eider population adjusts its numbers in relation to the availability of resources (Cervencel et al., 2014; Gunnarsson et al., 2013; Morelli et al., 2021). However, predation at the breeding grounds in recent years may have decreased the population size of eiders below the carrying capacity at the wintering grounds. If this has happened, it can explain why body condition of eiders has increased in recent years. However, an alternative explanation could be that predation mainly affected eiders with the lowest body condition, which over time could have resulted in a similar result.

A large decrease in mussel stocks was recorded in the Wadden Sea between the late 1980s and the mid 2010s, yet despite this decrease, the body condition of eiders has increased more in the Wadden Sea compared to in Kattegat. One explanation could be that the increasing number of razor clams in the diet has compensated for the decreasing amount of blue mussels taken by eiders. Razor clam was the only food item that increased in the eider diet between the late 1980s and the mid 2010s, and this increase was most pronounced in the Wadden Sea.

Author contribution statement

KL conceived the idea, KL and APM did the lab work, KL conducted the statistical analysis, KL and APM wrote the manuscript and both confirmed the final version.

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Ethical statement

There is no ethical statements to declare.

Data availability statement

The dataset analyzed during the current study are available from the

corresponding author on reasonable request.

Declaration of Competing Interest

There is no conflict of interest to declare.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.seares.2022.102244>.

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