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Original Article

# Determining Baltic salmon foraging areas at sea using stable isotopes in scales—a tool for understanding health syndromes

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Managing fish stocks for species migrating between freshwater and the sea is challenging when ecological information for life stages at sea is poorly known. Oceans offer increased opportunity for growth but also morbidity and mortality. By improving our understanding of foraging at sea we can better identify factors driving stock health and recruitment. We analysed stable isotopes of carbon and nitrogen ($\delta^{13}$C and $\delta^{15}$N) in scales from tagged Baltic salmon (*Salmo salar*) caught at sea over four decades. We found consistently divergent patterns in $\delta^{13}$C and $\delta^{15}$N between the two main basins of the Baltic Sea, which can be used to determine foraging area. Isotope analysis of amino acids revealed differences in source $\delta^{15}$N as the main reason for observed differences between basins. We also analysed isotopes in scales and thiamin concentrations in roe (thiamin deficiency can cause substantial fry mortality) from adult female salmon returning to a river to spawn in 2017 and 2018. Individuals with low thiamin levels were associated with offshore feeding in both basins, suggesting the deficiency syndrome is widespread in the Baltic Sea.

**Keywords:** compound specific isotope analysis, *Salmo salar*, Sweden, thiamin, $\delta^{13}$C, $\delta^{15}$N.

## Introduction

For decades exploitation has been the greatest threat to marine fish populations (Arthington *et al.*, 2016) including diadromous (species that move between freshwater and marine environments) fish at sea (McDowall, 1992). However, there is evidence that large scale ecosystem change due to human activity (climate change and pollution) is increasingly negatively impacting fish populations and stocks (Gobler and Baumann, 2016; Doney *et al.*, 2020). Linking aquatic ecosystem change to population status higher up a food web (particularly larger and mobile predators) is difficult due to the complexity and dynamic nature of ecosystems (DeYoung *et al.*, 2004; Karlson *et al.*, 2020), and further complicated in migrating species because our knowledge on feeding and behaviour of individuals at sea is usually limited.

Advances in animal tracking technology and chemical analysis of tissue (especially hard tissue such as otoliths and scales; Tzadik *et al.*, 2017; Thomas and Swearer, 2019) have greatly improved our understanding of movement and feeding ecology for a few fish species. Many of these are diadromous fish, especially salmonids and eels, which have been focal species partly because of their importance to fisheries, but also because the freshwater phase of their life cycle provides opportunities for easier capture for (non-lethal) sampling or tagging. The ocean environment provides a release from freshwater resource limitation in anadromous fish allowing for a somatic growth and reproductive investment, which would not be possible without migrating. However, it is also associated with high natural and fishing mortality (Jensen *et al.*, 2019), exposure to new (marine) or higher concentrations of diseases (Bakke and Harris, 1998), parasites (Krkošek *et al.*, 2013), and contaminants (Vuorinen *et al.*, 2012) or vitamin deficiencies (Kraft and Angert, 2017).

Baltic salmon are geographically isolated from other Atlantic salmon because they spend their migratory phase in the comparatively small and brackish Baltic Sea. The Baltic Sea environment is well-studied with uniquely long time series data and archived samples from various monitoring programs (e.g. Reusch *et al.*, 2018), which should make it easier to piece together the ecology of Baltic salmon at sea. It is thought that the southern Baltic Proper provides the main feeding ground for many salmon populations, especially from northerly rivers (Jacobson *et al.*, 2020), but extensive use of other regions of the Baltic has been shown (Torniainen *et al.*, 2014, 2017b). Recruitment of the three main prey species, sprat, herring, and sticklebacks (Hansson *et al.*, 2001; Jacobson *et al.*, 2018) have been variable in the Baltic over the last five decades with sprat spawning stock biomass (SSB) peaking in the mid 1990s (c. 1.8 million tons; from a low of c. 200000 tons in the early 1980s) and herring SSB in the Baltic Proper decreasing steadily from c. 2 million tons in the mid 1970s to less than half a million tons in early 2000s. SSB has not been calculated for herring in the Bothnian Sea but catches have increased steadily from c. 20000 tons in the early 1980s to a high of over 120000 tons in 2016 (ICES, 2020). Estimates on stickleback numbers show variability between years but with a general increase from early 2000 to 2015 (Olsson *et al.*, 2019; we could not find estimates for stickleback numbers between 1960 and 2000). Commercial fishing generally, but especially offshore on mixed salmon stocks, has declined and wild smolt production has increased in northern (Bothnian Sea) rivers. However, salmon stocks in rivers flowing into the southern Baltic (Baltic Proper) continue to have low smolt production (Bajinskis *et al.*, 2020). To compensate for the extensive loss of habitat and reduced migration due to hydroelectric power in Sweden, release of salmon smolts has occurred since the 1950s (Karlsson and Karlström, 1994). Smolts that are released are grown in hatcheries, but broodstock are taken from fish caught returning to “natal” rivers from the Baltic to spawn. Annually, a small proportion of released smolt were marked using Carlin tags. Recapture of these individuals, both at sea and on their return to spawn, give information on mortality at sea, growth, and even migration patterns. However, the recapture of an individual at a certain location is not a sure indication of local foraging or resource exploitation in highly mobile individuals.

The Baltic Sea is a semi-enclosed basin with low water exchange with the north Atlantic and high runoff from Baltic countries (Leppäranta and Myrberg, 2009). This has intensified anthropogenic problems such as eutrophication (Andersen *et al.*, 2017), climate change (Räisänen, 2017), and contaminant loading (Sonne *et al.*, 2020) with unknown consequences for health status and recruitment in salmon. Thiamin (vitamin B1) deficiency is documented in the pelagic food-webs and its potential effects on Baltic marine life, including salmon, are well described (Bengtsson *et al.*, 1999). Thiamin is essential for living organisms and plays a central role in energy production in cells (Kraft and Angert, 2017). Female salmon with low thiamin concentrations produce eggs but fry mortality can be over 90% shortly after hatching, which can potentially severely reduce populations (Bengtsson *et al.*, 1999). Thiamin deficiency in salmon occurs sporadically and inconsistently over time and the ultimate cause has not been identified, though it appears that diet plays a role (Hansson *et al.*, 2001; Keinänen *et al.*, 2012, 2018). Salmon health should be related to diet and foraging area so that a better understanding of the migratory phase at sea can reveal ultimate causes of fish condition and morbidity.

Stable isotopes are commonly used to study food web dynamics (Layman *et al.*, 2012) and animal movement (Hobson and Wassenaar, 2018). Elements can occur naturally in stable light and heavy forms. These heavy and light forms can be less or more predictable through a food web or over space and time. Ecological studies can make use of patterns in the occurrence of heavy and light elements (most commonly carbon and nitrogen isotope composition; $\delta^{13}$C and $\delta^{15}$N) to determine the ultimate source of food in a food web, diet partitioning, and trophic position (TP). If the spatial and temporal distribution of isotopes in environmental materials are known, or can be predicted (isoscape), it is possible to compare an individual's isotope value to determine patterns of movement (Bowen, 2010). This has been carried out quite extensively in mammals, birds, and fish (Hobson and Wassenaar, 2018) and has been applied to determine Atlantic salmon movement (MacKenzie *et al.*, 2011) including salmon in the Baltic Sea (Torniainen *et al.*, 2014, 2017a, b). More recently isotope analysis of specific amino acids (AAs; compound specific isotope analysis; CSIA) have refined the use of isotope analysis in ecological studies (Ohkouchi *et al.*, 2017), including animal movement (McMahon and Newsome, 2019; Matsubayashi *et al.*, 2020), since the ultimate nitrogen baseline ($\delta^{15}$N in source AAs) can be separated from the TP estimates calculated from $\delta^{15}$N in trophic AAs (Chikaraishi *et al.*, 2009; Nielsen *et al.*, 2015). This study combined retrospective chemical analyses of archived biological samples from monitoring programs of salmon in the Baltic sea in an attempt to link diet and foraging site information (stable isotope data) with information on their health status (thiamin data); specifically

(i) Analysis of archived scales from Carlin tagged salmon released from 11 Swedish rivers (Mörrum River in the south to Torne River in the north), and caught in four sub-basins of the Baltic Sea (Figure 1) over four decades to investigate if distinct and constant patterns in stable isotopes ($\delta^{13}$C and $\delta^{15}$N) occur. Previous studies have used C, N, and O isotopes in otoliths and scales of salmon returning to natal rivers in the Bothnian Bay and Gulf of Finland (Torniainen *et al.*, 2014, 2017a, b). These fish were shown to either migrate extensively and forage in the southern Baltic or remain in basins closer to their natal rivers. Similarly, we expected to find spatial separation in fish reflected in scale isotope values, but made no predictions on which foraging areas fish originating from different natal rivers exploit (i.e. if fish from northern rivers utilize northern basins more or less than fish from southern rivers).
(ii) Analysis of $\delta^{15}$N in AAs from the archived scales to assessed potential differences in TP (diet) or biogeochemical isotope baselines among regions and decades (i.e. help deciphering the mechanism behind potential differences in $\delta^{15}$N patterns).
(iii) Application of patterns found in the historic dataset to determine most likely sea foraging areas for adult female salmon caught on their river ascent prior to spawning in 2017 and 2018 and relate it to thiamin concentrations. We hypothesized that thiamin deficiency would be primarily associated with fish feeding in the southern Baltic Sea where large scale changes to the ecosystem have been associated with thiamin deficiency in the pelagic ecosystem including M74 incidence in salmon (Majaneva *et al.*, 2020).

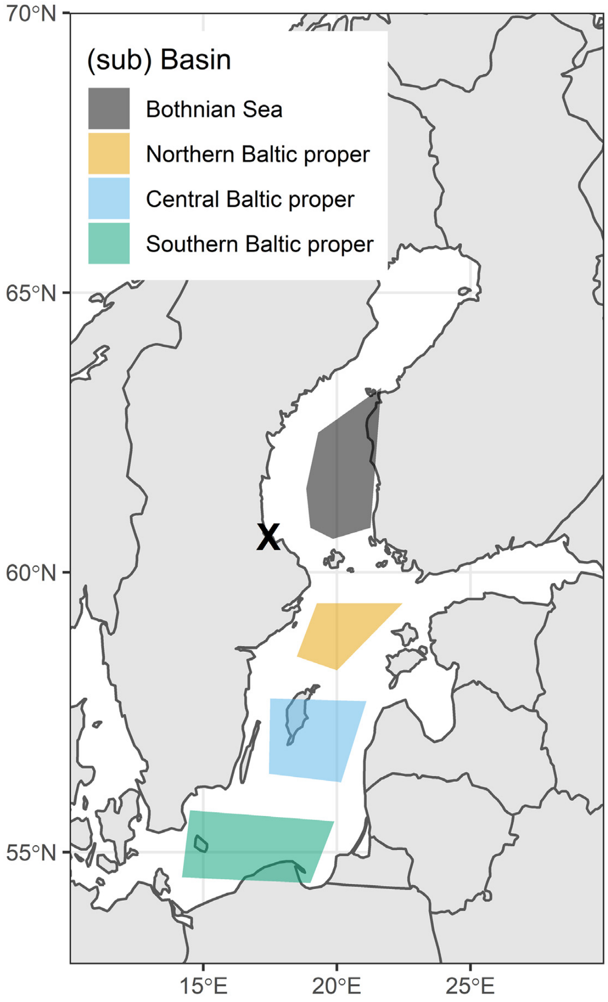

**Figure 1.** Baltic Sea locations from which foraging salmon were sampled 1962–1990 ($n = 40$ per polygon in four sub-basins except northern Baltic proper, where $n = 35$), and location (X) of the Dalälven river where mature returning females were sampled in 2017 and 2018.

## Material and Methods

### Sample collection and preparation; archived scales

Dried scales from tagged salmon caught at sea are archived at the Swedish university of agricultural sciences, with capture and biological data stored in a database. Scales from 155 individuals from 4 years (1962, 1972, 1982, and 1990) spanning four decades and four (sub) basins of the Baltic Sea (Bothnian Sea, Northern, Central, and Southern Baltic Proper, Figure 1) were analysed for bulk carbon and nitrogen and compound specific (AAs) nitrogen isotopes at the stable isotope facility, UC Davis (details below). Scales from fish captured between September and March were used to avoid sampling individuals on their spawning migration and similarly sized and aged fish were selected (based on recorded lengths and age determination from scales). Scales were manually cleaned using a scalpel and rinsed with water. Outer growth rings of 5–10 individual salmon per year and sub-basin were sampled for bulk isotope analysis. More material is needed for analysis of isotopes in specific compounds (here AAs), and we were required to pool individuals from each basin and year to achieve recommended sample weights (~3 mg). In some cases there was no material left after bulk analysis and pooled samples were based on fewer individuals.

### Sample collection and preparation; contemporary fish

As part of the broodstock program females returning to the Dalälven River are captured in permanent traps located at the first migration barrier and stripped of eggs, which are fertilized, hatched, and raised for compensatory release of smolt. Unfertilized eggs were analysed for concentrations of thiamin mono- (TMP) and pyrophosphate (TPP) and non-phosphorylated thiamin (T). Analysis of thiamin was carried out at the Natural Resources Institute, Finland (LUKE) according to Vuorinen *et al.* (2002). Increased mortality (M74) occurs in Baltic salmon fry hatching from eggs with thiamin concentrations lower than 0.6 nmol $g^{-1}$ ww with normal development occurring in fry from eggs with more than 1.6 nmol $g^{-1}$ ww (Amcoff *et al.*, 1999). We prepared scales for isotopes (preparation and analysis as for bulk isotope analysis in archived scales) from 40 female fish returning to the Dalälven River in 2017 ($n = 20$) and 2018 ($n = 20$). Within years we selected ten females with the highest, and ten individuals with the lowest egg T values.

### Stable isotope analysis and TP calculations

Bulk stable isotope analyses were carried out using an elemental analyser interfaced to a continuous flow isotope ratio mass spectrometer (EA-IRMS) at the stable isotope facility, UC Davis. Amino specific N stable isotopes were also measured at UC Davis, using GC-combustion isotope ratio mass spectrometry (GC-C-MRS). Prior to isotope measurements the scale carbonate fraction was removed, proteins hydrolyzed using hydrochloric acid and AAs derivatized (Yarnes and Herszage, 2017). Samples were analysed in duplicate and the mean of two readings per AA were used in further analyses. The stable isotopes are expressed as $\delta$ notation: $\delta$ (‰) $= [(R_{sample/}R_{standard}) - 1] \times 10^3$, where R is the ratio between the heavy and the light isotope $^{13}C$:$^{12}C$ or $^{15}N$:$^{14}N$, and $\delta$ is the deviation from the internationally accepted standard Vienna Peedee belemnite for C and air for N. Fish scales are primarily made up of calcium phosphate (upper mineralized layer) and collagen (underlying plate; Hutchinson and Trueman, 2006), and no fat correction for $\delta^{13}C$ was performed.

TP was calculated from $\delta^{15}N$ in AAs in pooled samples per basin (Bothnian Sea, northern, central, and southern Baltic Proper) and year (1962, 1972, 1982, and 1990). Specifically, TP estimates were based on $\delta^{15}N$ in eight source (unfractionated) and seven trophic AA´s according to Nielsen *et al.* (2015); see Equation (1). To further investigate TP estimates we also used the method based on the trophic AA glutamic acid (Glu) and source AA Phenylalanine (Phe) according Chikaraishi *et al.* (2009); see Equation (2).

$$TP = \frac{\left(\sum(\delta^{15}N_{trophicAA}\right)/7 - \sum(\delta^{15}N_{sourceAA})/8) - \beta}{\Delta trophic - \Delta source} + 1. \quad (1)$$

$$TP = \frac{\left(\delta^{15}N_{Glu} - \delta^{15}N_{Phe}\right) - \beta}{\Delta Glu - \Delta Phe} + 1. \quad (2)$$

$\beta$ is the difference between $\delta^{15}N$ values of trophic and source AAs in primary producers and were set at 2.9 [Equation (1)] and 3.4 [Equation (2)] according to Nielsen *et al.* (2015) and Chikaraishi *et al.* (2009), respectively. $\Delta$ is the trophic discrimination factor (TDF) between trophic and source AAs and were set at 5.9 [Equation (1)] and 7.6 [Equation (2)] according to Nielsen *et al.* (2015) and Chikaraishi *et al.* (2009), respectively.

**Table 1.** Summary of fish lengths, isotope values, and thiamin concentrations (Dalälven River only) for sub-basins and females returning to the Dalälven River. Thiamin amount is free thiamin measured in eggs (Bpr = Baltic proper).

| | $N$ | Mean length ± *SD* (cm) | Mean $\delta^{13}$C ± *SD* (‰) | Mean $\delta^{15}$N ± *SD* (‰) | Mean C:N ratio ± *SD* | Thiamin nmol $g^{-1}$ |
|---|---|---|---|---|---|---|
| Bothnian Sea | 40 | 74.8 ± 12.4 | −16.5 ± 0.5 | 11.1 ± 0.7 | 2.80 ± 0.22 | |
| Northern Bpr | 35 | 73.2 ± 11.7 | −16.5 ± 0.4 | 12.2 ± 0.4 | 2.77 ± 0.17 | |
| Central Bpr | 40 | 77.1 ± 9.6 | −16.3 ± 0.4 | 12.3 ± 0.4 | 2.85 ± 0.14 | |
| Southern Bpr | 40 | 75.2 ± 10.7 | −16.5 ± 0.5 | 12.5 ± 0.6 | 2.85 ± 0.19 | |
| Dalälven high thiamin | 20 | 88.6 ± 6.8 | −17.4 ± 0.4 | 12.1 ± 0.5 | 2.76 ± 0.14 | 4.77 ± 1.71 |
| Dalälven low thiamin | 20 | 86.5 ± 5.9 | −17.8 ± 0.3 | 12.0 ± 0.5 | 2.69 ± 0.07 | 0.54 ± 0.42 |

## Statistical analysis

Graphing and statistical analysis were carried out using the base, tidyverse (Wickham *et al.*, 2019), caret (Kuhn *et al.*, 2020), MASS (Venables and Ripley, 2013), plyr (Wickham, 2011), sf (Pebesma, 2018), rnaturalearthdata (South, 2017), gridExtra (Auguie *et al.*, 2017), SIBER (Jackson *et al.*, 2011), and ggplot2 (Wickham, 2016) packages in R 3.6.2 (R Core Team, 2013).

## Identifying patterns in the isotope ratios of salmon caught in distinct areas of the Baltic Sea

Linear discriminant analysis (LDA) was used to find linear combinations of $\delta^{15}$N and $\delta^{13}$C that could be used to separate fish from different areas of the Baltic Sea. As fish grow their gape size increases allowing them to feed on larger prey (Scharf *et al.*, 2000) that occupy higher positions in food webs, which can result in increasing $\delta^{15}$N with increasing predator body size (Jennings *et al.*, 2008); this should be accounted for prior to LDA. However, our fish were of similar sizes and data exploration revealed no relationship between length and $\delta^{15}$N. Younger fish (1SW) could also potentially cause differences in $\delta^{15}$N due to variable TDF with growth rate (Trueman *et al.*, 2005), and we did find that 1SW individuals had a lower average $\delta^{15}$N value. However, this appears to be due to the 4 individuals caught in the Bothnian Sea having very low $\delta^{15}$N values (the other five 1SW fish caught in the northern Baltic Proper had high $\delta^{15}$N values), and we did not exclude 1SW fish from the data. The complete data set was divided randomly into a training (80% of individuals, $n = 124$) and test (20%, $n = 31$) dataset. The test dataset are treated as unknowns (i.e. origin of capture is unknown). LDA was applied to the larger training dataset to find the best level of between basin separation and within basin similarity. The individuals from the test data set were then classified according to a basin according to their $\delta^{15}$N and $\delta^{13}$C values and based on the analysis from the training dataset. The number of individuals from the test dataset correctly assigned to a basin (prediction accuracy) was evaluated as well as the overall contribution of C and N in separating the groups (loadings). Standard ellipses (Jackson *et al.*, 2011) were calculated and plotted for each sub-basin and year based on individual bulk $\delta^{15}$N and $\delta^{13}$C values.

## Linking thiamin concentration with foraging area

Individuals collected in 2017 and 2018 were assigned to a basin based on their scale $\delta^{15}$N and $\delta^{13}$C values. This was carried out in the same way as for the archived scales, except that all archived scales ($n = 155$) were used as the training dataset and ascending females from 2017 to 2018 ($n = 40$) were the unknown, test data. To check the consistency of predictions we also carried out LDA on Dalälven fish using isotope data from each year (1962, 1972, 1982, and 1990) as training sets and cross checked the results. We could then compare thiamin concentrations in females that had fed in different areas of the Baltic Sea. National monitoring of M74 show that the prevalence of the M74 syndrome was high in 2016 and 2017 but declining in 2018–2020 (Axén *et al.*, 2020). We explored whether thiamin concentrations could be explained by year (2017 and 2018) and isotopes in the 40 returning females using linear models. $\delta^{13}$C and $\delta^{15}$N isotopes, apart from potentially differing between basins due to hydro-geochemical reasons, can give information on individual TP, diet, and food source (pelagic vs. coastal), which could partly explain thiamin concentrations. Continuous predictors were centered to make intercepts meaningful. We began with the fullest model (all predictors and interactions) and discarded predictors using the drop1 function and based on AIC scores until the most parsimonious model was found. Model validation was carried out visually using checks on residuals against fitted values and leverage, quantile plot, and a histogram of residuals.

# Results

A summary of fish length and isotope values can be seen in Table 1, raw data for all individuals is in Supplementary Table S1.

## Patterns in archived scales

One fish (Bothnian Sea) lacked data on length. Mean length (± *SD*) for all fish caught at sea was 75.13 cm ± 11.10. All these fish were 2 sea winters except for nine 1 sea winter individuals, from the Bothnian Sea ($n = 4$) and the northern Baltic proper ($n = 5$). The length of 1 sea winter individuals was within the range of lengths for 2 sea winter fish but mean length (62 cm ± 11) was lower than the mean length of 2 sea winter individuals (76 cm ± 10). $\delta^{15}$N isotopes ranged from 10.23 to 14.36 with fish caught in the Bothnian Sea having consistently lower values (Figure 2). $\delta^{13}$C isotopes ranged from −18.29 to −15.52 with no clear patterns between sea basins. LDA was able to separate fish caught in the Bothnian Sea from the other sub-basins in the Baltic Sea (Figure 3) but could not separate individuals from different basins in the Baltic Proper (northern, central and southern Baltic Proper). In total, two discriminant functions described 97 and 3% of separation. The largest loadings for coefficients of linear discriminants were found for $\delta^{15}$N (Table 2). Overall, the ability of the LDA to correctly assign test individuals to their sub-basins was low (48% accuracy). However, misclassification of individuals between the Bothnian Sea and the Baltic

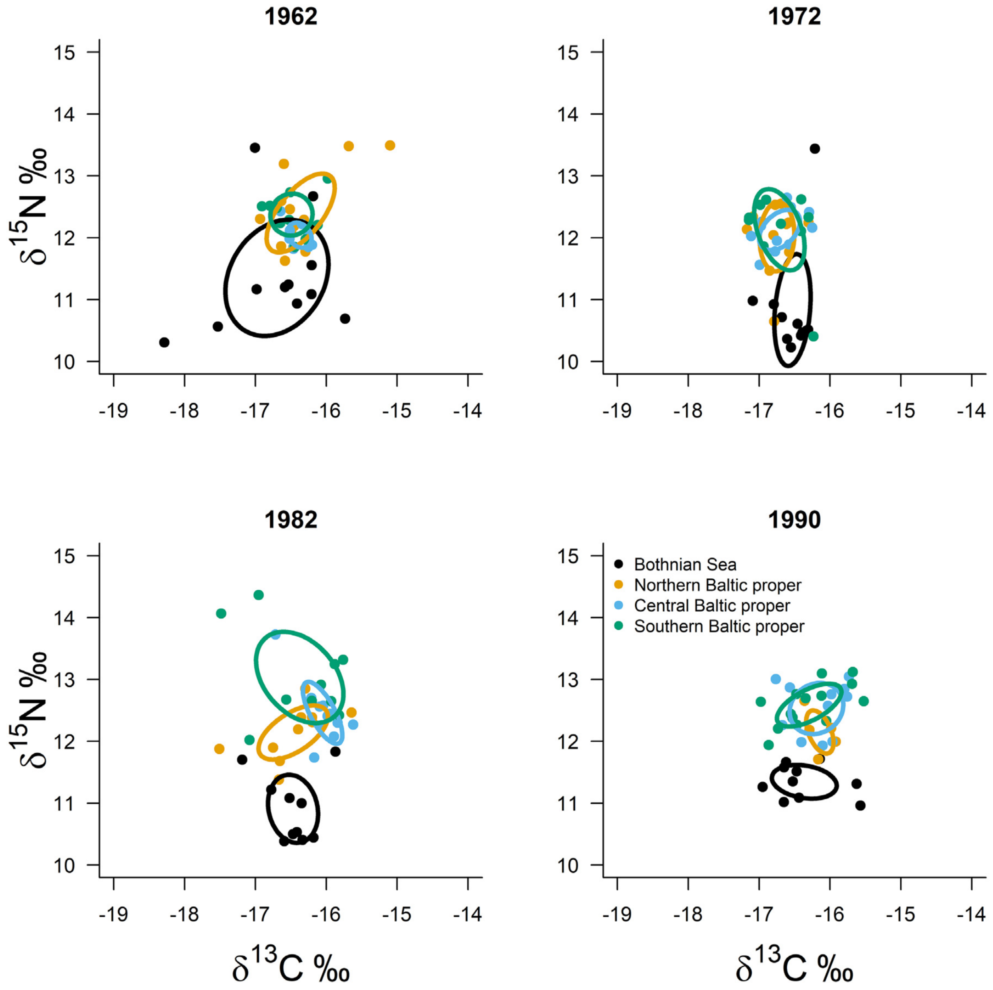

**Figure 2.** Salmon scale standard ellipses for four (sub) basins in the Baltic Sea in 1962, 1972, 1982, and 1990. Ellipses are based on isotope values of $\delta^{13}C$ and $\delta^{15}N$ from 155 individuals (ten per basin and year, except for northern Baltic Proper in 1962 where five individuals were used).

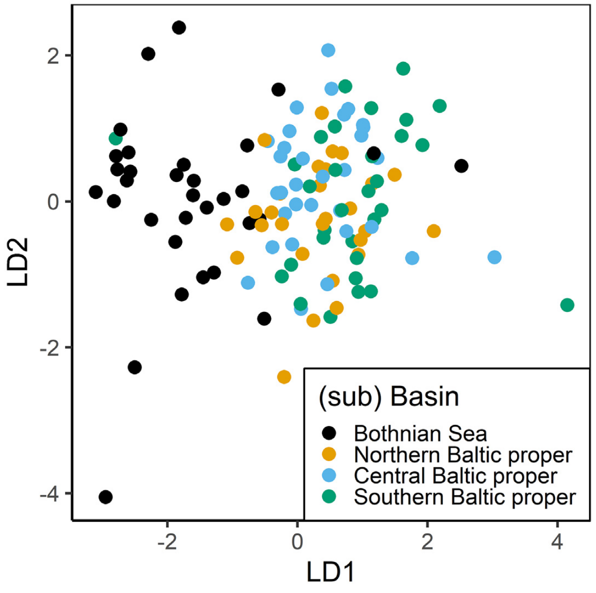

**Figure 3.** Separation of fish from four Baltic Sea sub-basins using LDA based on scale nitrogen and carbon isotopes. See also Table 2.

**Table 2.** Amount of separation achieved between sub-basins for two discriminant functions based on carbon and nitrogen isotopes from salmon scales (1962–1990). The contribution of each isotope to the discriminant functions (loadings) are given. Note larger negative or positive numbers indicate greatest loading.

| Discriminant function | Separation (%) | Loadings | |
|---|---|---|---|
| | | $\delta^{13}C$ | $\delta^{15}N$ |
| LD 1 | 97 | − 0.003 | 1.392 |
| LD 2 | 3 | 1.010 | − 0.112 |

Proper (northern, central, and southern sub-basins) was low with only one individual caught in the Bothnian Sea classified as belonging to the neighbouring sub-basin (central Baltic Proper). No individuals in the test data caught in the Baltic Proper were misclassified to the Bothnian Sea.

## TP from archived scales

Analysis of $\delta^{15}N$ in scale AAs revealed that average $\delta^{15}N$ values in source AAs were consistently ~1–2 ‰ lower in fish caught in the Bothnian Sea compared to fish caught in the Baltic Proper (Figure 4a). However, estimates of TP were similar between basins although a tendency towards decreasing TP over time for both basins could be seen (TP between 3.9 and 4.3 using the Nielsen equation; Figure 4c). TP estimates using the equation by Chikaraishi *et al.* (2009) resulted in values below 4 (Figure 4c), which is low for a large piscivorous fish; but replacing the TDF value (from 7.6 to 6.6) as recommended by Nielsen *et al.* (2015) gave similar, but more ecologically credible estimates.

## Patterns in contemporary scales and thiamin concentrations

Females returning to the Dalälven River in 2017 and 2018 were mostly fish that had spent 2 winters at sea ($n = 37$), but 1 sea winter ($n = 1$) and 3 sea winter fish ($n = 2$) were also included. Returning fish were generally larger than those caught at sea with a mean length of 87.5 cm ± 6.4. $\delta^{15}$N isotope composition ranged from 10.9 to 12.8 and $\delta^{13}$C isotopes ranged from −18.5 to −16.8. Based on the LDA for all salmon caught in the Baltic Sea (above), females returning to the Dalälven River to spawn in 2017 and 2018 were assigned to the Bothnian Sea or the Baltic Proper according to their scale isotope values. Using different decades as test data for predicting foraging area gave similar results, with only two individuals assigned to different basins across four decades (Supplementary Table S2). In total, two-thirds of females ($n = 26$) had spent their last year feeding in the Baltic Proper, and one third in the Bothnian Sea ($n = 14$; Figure 5). Females that produced eggs with low concentrations of non-phosphorylated thiamin (thiamin deficiency) had been foraging in both the Bothnian Sea ($n = 8$ of 14 individuals) and the Baltic Proper ($n = 12$ of 26 individuals). Furthermore, according to our linear model, thiamin concentrations were significantly lower in 2017 (the year with widespread M74) and in individuals with more negative $\delta^{13}$C values across both years. The relationship between thiamin and $\delta^{15}$N was variable across years. In 2017, there was a negative relationship between thiamin concentration and $\delta^{15}$N but in 2018 no relationship was found (Table 3). Visual validation of the final model indicated signs of heteroscedascity. This was most likely because we selected individuals with the highest and lowest thiamin values for both years. Variation was lower in fish with low thiamin concentrations compared to fish with high thiamin values. This could be fixed by transforming the response (we found no differences to results from untransformed data). However, given that main results were unchanged even with transformed data (log) and heteroscedascity was not severe we cautiously interpret the results found on original untransformed thiamin values.

## Discussion

We found that nitrogen isotopes ($\delta^{15}$N) contributed most to spatial partitioning in Baltic Sea salmon (LDA analyses), and that differences between fish from separate basins were consistent over 40 years. Stable isotopes from scales have been used to investigate salmon foraging areas in the Baltic Sea from the 1990s and onwards (Torniainen *et al.*, 2014, 2017a, b) and it is not surprising that we were able to separate individuals into one of two basins over a longer time span in this study. The Bothnian Sea fish have had consistently lower $\delta^{15}$N values since the 1960s, and within basin variation was low enough to allow for accurate predictions of foraging areas. Since $\delta^{15}$N increases in consumers with trophic level, this isotope is generally assumed to be too variable and dependent on individual TP to be useful for partitioning populations geographically. However, CSIA, indicated consistent differences between baseline $\delta^{15}$N entering the food webs in the Bothnian Sea and Baltic Proper. The similarity in fish size over decades and among basins and the derived TP in this study (and generally for spawning salmon) meant this difference could even be measured in bulk isotope analysis on scales—offering a cheap and reliable method to trace sea foraging areas in salmon returning to spawn. However, we note a general increase in baseline $\delta^{15}$N over time in all the basins and anthropogenic change to systems (i.e. through eutrophication) could jeopardize the apparent differences between basins.

We had expected a better level of isotopic separation between the southernmost and northernmost sub-basins in the Baltic Proper and a generally larger role of $\delta^{13}$C in explaining differences among the major basins. In total, two obvious reasons explaining the lack of separation between sub-basins could be that (i) fish move freely and regularly between sub-basins in the Baltic Proper and (ii) there is no obvious partitioning of food webs among the Baltic Proper sub-basins i.e. common isotope baseline (a common temporal $\delta^{13}$C has been shown for mussels from various parts of the Baltic Sea; Ek *et al.*, 2021). Models on ocean circulation show that the Baltic Proper consists of one single, counter clockwise gyre (Placke *et al.*, 2018) suggesting that the $\delta^{13}$C differences between sub-basins is not pronounced. In addition, fish movement patterns in the Baltic Sea are not comprehensively known. It is thought that the southern Baltic Proper provides the main feeding ground for, especially large, salmon (Jacobson *et al.*, 2020) but feeding in other basins, such as the Gulf of Finland or Bothnian Sea have also been demonstrated (Torniainen *et al.*, 2014, 2017a). Without individual telemetry data it is not possible to speculate on whether fish movement or indistinct isotope differences between sub-regions result in the similar isotopes observed from fish within the Baltic Proper.

That $\delta^{15}$N value appear to be unaffected by salmon size or diet probably reflects the relatively uniform length of fish in the study and the poor species diversity of the Baltic Sea with three prey species contributing the bulk of salmon diet (sprat, herring, and sticklebacks; Karlsson *et al.*, 1999; Jacobson *et al.*, 2018). Whilst sprat make up a large proportion of salmon diet in the Baltic Proper, herring becomes increasingly important for larger salmon (i.e. over 60 cm in length; Jacobson *et al.*, 2020). Sprat and herring are primarily pelagic and planktivorous but herring $\delta^{15}$N values are typically more enriched than sprat (herring grow bigger and are also known to feed on nektobenthos at larger sizes; Möllmann *et al.*, 2004). If diet differences between the two areas (i.e. more herring in salmon diet in the Bothnian Sea) were the main reason for differences in $\delta^{15}$N we would expect higher, not lower, $\delta^{15}$N (and derived TP) values in salmon feeding in the Bothnian Sea.

A relatively stable and uniform diet, and limited variation in salmon size in this study, suggest that baseline differences (primary inputs) in $\delta^{15}$N were evident in top consumers and could be used to distinguish foraging areas. Further evidence for this comes from the analysis of $\delta^{15}$N in AAs. This data came from pooled samples and should be interpreted with caution, but generally there were no large differences in salmon's estimated TP between the Bothnian Sea and Baltic Proper. TP estimates are influenced by the TDF used (bulk and CSIA methods) and which AAs are included (CSIA only).

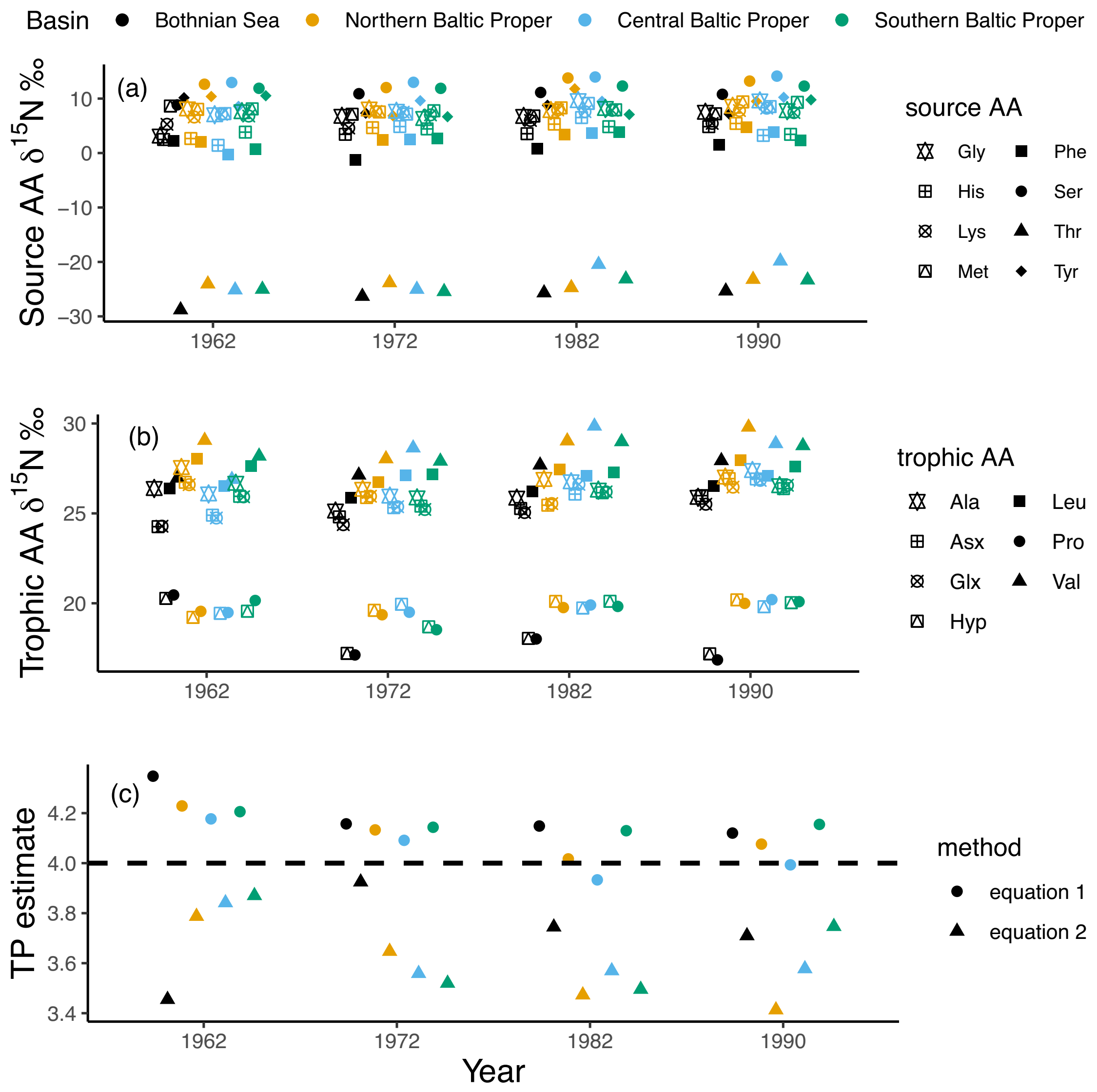

**Figure 4.** $\delta^{15}$N of (a) source and (b) trophic AAs from salmon by (sub) basin and year, and (c) TP estimates based on AAs. Values are from CSIA on single samples per site and year based on a homogenate of scales from (c) A total of ten individuals. In the legends: (a) Gly = glycine, His = histidine, Lys = lysine, Met = methionine, Phe = phenylalanine, Ser = serine, Thr = threonine, and Tyr = tyrosine; (b) Ala = alanine, Asx = Arginine/Asparagine, Glx = Glutamine/glutamic acid, Hyp = hydroxyproline, Leu = Leucine, Pro = proline, and Val = valine; (c) equa 1 = Equation (1) in methods (from Nielsen *et al.*, 2015), equa 2 = Equation (2) in methods (from Chikaraishi *et al.*, 2009). Dashed line in (c) is the ecologically expected minimum TP for a large piscivorous fish in the Baltic Sea (TP 1 = primary producers, TP 2 = primary consumer, and TP 3 = zooplanktivorous fish).

There is no consensus on exact TDF values or which AAs to include in TP calculations. We found that the equation provided by Nielsen *et al.* (2015) gave ecologically reasonable estimates given the Baltic food web and in relation to other studies using bulk isotope methods from muscle tissue and homogenized whole fish (Kiljunen *et al.*, 2008, 2020). However, notable differences were found in source AA $\delta^{15}$N between these two basins, indicating lower bulk $\delta^{15}$N in the Bothnian Sea. That $^{15}$N entering food webs differs between the Baltic Proper and Bothnian Sea is likely due to riverine inputs and physical circulation patterns in the Baltic Sea. Catchments in the northern parts of Sweden and Finland are sparsely populated, and total N inputs and $\delta^{15}$N are comparatively low compared to catchments draining into the Baltic Proper with significant agricultural and sewage inputs (with typically enriched $\delta$15N values; Voss *et al.*, 2005, 2006; Lienart *et al.*, 2021). The Baltic Proper and Bothnian Sea have separate circulation patterns with limited surface water exchange (Jędrasik and Kowalewski, 2019), which can explain the differing $\delta^{15}$N patterns observed between basins. The increase in $\delta^{15}$N in source AAs over time is expected along with increasing eutrophication and was more evident than the temporal pattern for bulk $\delta^{15}$N values, illustrating the value of compound specific isotope analyses.

Salmon is an iconic and important species for angling and commercial fisheries and a lot of attention has been given to

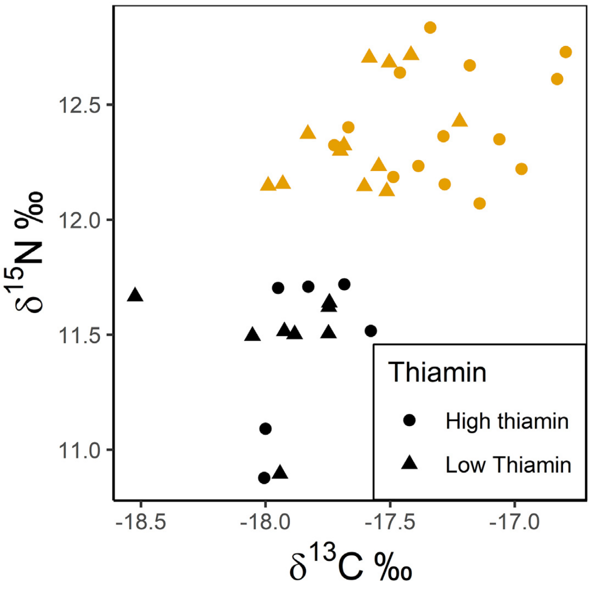

**Figure 5.** Stable isotope values of scales from 40 female spawning fish returning to the Dalälven River in 2017 and 2018. High and low thiamin values are based on free thiamin measured in eggs. Foraging basin was assigned using LDA on scale isotopes from a training set of 155 individuals caught at sea 1962–1990 (black = Bothnian Sea and orange = Baltic Proper).

understanding the cause of thiamin deficiency in Baltic fish (Vuorinen *et al.*, 1997; Karlsson *et al.*, 1999; Keinänen *et al.*, 2018; Majaneva *et al.*, 2020). It is thought that a diet rich in sprat results in a lower supply of thiamin per unit of energy provided (Mikkonen *et al.*, 2011; Keinänen *et al.*, 2012). Thiamin is used up by females during their prespawning fasting and migration period so that free thiamin in eggs is low leading to high fry mortality on hatching (the condition M74). Analysis of fatty acids in salmon have further demonstrated that M74 occurrence is associated with a diet dominated by sprat but not herring (Keinänen *et al.*, 2018). An alternative hypothesis is that herring contain more of the enzyme thiaminase (breaks down thiamin) than sprat (Wistbacka and Bylund, 2008), which could result in lower thiamin levels in salmon that feed preferentially on herring (Wistbacka *et al.*, 2002). We found that lower levels of thiamin were associated with more negative $\delta^{13}$C values in salmon in 2017 and 2018 across both basins. Differences in consumer $\delta^{13}$C can be the result of differences in prey species but sprat and herring (and stickleback) from common foodwebs have similar $\delta^{13}$C values (Mohm, 2018; Kiljunen *et al.*, 2020). Also we found that the proportion of individuals with thiamin deficiency were the same for both basins, but sprat are not as abundant in the Bothnian Sea (Eero, 2012) and make a relatively small contribution to the diet of salmon in this basin, based on stomach content analysis (Karlsson *et al.*, 1999; Hansson *et al.*, 2001; Jacobson *et al.*, 2018). This suggests that differences in the ratio of sprat and herring in the diet were not the main factor resulting in the observed relationship between thiamin and $\delta^{13}$C in our study.

Majaneva *et al.* (2020) found that low concentrations of thiamin in the southern Baltic Proper were related to large-scale abiotic and food web changes that affected nutritional pathways and the supply of thiamin in the pelagic food web. This could be due to a general decrease in thiamin in herring as well as sprat as suggested by Ejsmond *et al.* (2019); Majaneva *et al.* (2020). Offshore pelagic food webs are generally more depleted (negative) in $\delta^{13}$C than littoral/coastal food webs (more negative $\delta^{13}$C values; Fry, 2006) and it is possible that the salmon experiencing thiamin deficiency in our study ate from more pelagic offshore food webs. An alternative explanation is that more negative $\delta^{13}$C values indicate higher reliance on terretrial carbon, reaching the Baltic from riverine inputs (Rolff and Elmgren, 2000). It is not unlikely that a combination of factors determine thiamin levels depending on location and oceanographic conditions (above all the inflow of salt water into the Baltic Sea from the Atlantic; Majaneva *et al.*, 2020) but our results suggest that when thiamin deficiency occurs it is more associated with offshore food webs (Ejsmond *et al.*, 2019; Majaneva *et al.*, 2020) in the Baltic Proper as well as in the Bothnian Sea; with salmon that feed near shore potentially receiving higher amounts of thiamin. Due to the sampling design (low sample size and analysing individuals with the highest and lowest thiamin concentrations), and the range of factors that can influence individual $\delta^{13}$C our speculations on the relationship between $\delta^{13}$C and thiamin should not be overstated. However, it would be interesting to explore thiamin concentrations and multiple isotopes (including bulk sulphur, indicating benthic food sources, and CSIA) in a larger sample of returning salmon.

We show a high level of partitioning between salmon caught in the Baltic Proper and Bothnian Sea based on bulk $\delta^{13}$C and, especially, $\delta^{15}$N isotopes measured in scales. These differences are consistent over time and could be used as a cheap and non-lethal method to indicate foraging location (basin level) of salmon sampled on their return to spawn. Apart from information on diet and TP, this isotope information can be used to link health syndromes in fish to general basins in the Baltic Sea. We show that thiamin deficiency in females returning to the Dalälven River was associated with two major regions of the Baltic Sea, and appears to affect fish that feed in offshore pelagic food webs.

**Table 3.** Results from the linear regression estimating the effects of year (2017 and 2018) and individual isotopes ($\delta^{13}$C and $\delta^{15}$N from scales) on thiamin concentrations measured in eggs. Measurements were taken from female salmon returning to the Dalälven River to spawn. Years are categorical and estimates represent intercepts, isotope estimates are numerical and represent slopes. Continuous predictors were centered so that intercepts are the estimated thiamin concentrations for fish with mean $\delta^{13}$C and $\delta^{15}$N values (i.e. thiamin concentrations of fish with mean isotope values were estimated to be 1.49 nmol g$^{-1}$ in 2017 and 3.59 nmol g$^{-1}$ in 2018).

| **Effect** | **Lower 95% *CI*** | **Estimate** | **Higher 95% *CI*** | **T-value** | ***p*-value** |
|---|---|---|---|---|---|
| Year 2017 | 0.55 | 1.49 | 2.43 | 3.21 | 0.003 |
| Year 2018 | 2.84 | 3.59 | 5.53 | 3.16 | 0.003 |
| $\delta^{15}$N 2017 | − 5.14 | − 2.76 | − 0.37 | − 2.35 | 0.025 |
| $\delta^{15}$N 2018 | − 2.61 | 0.03 | 2.66 | 2.14 | 0.039 |
| $\delta^{13}$C | − 0.85 | 1.63 | 4.09 | 3.61 | 0.001 |

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## Supplementary data

Raw biometric data for individuals (Supplementary Table 1) and results from additional linear discriminant analyses performed for each decade (Supplementary Table 2) are available at the *ICESJMS* online version of the manuscript:

## Data availability

The data underlying this article are available in the article and in its online supplementary material.

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