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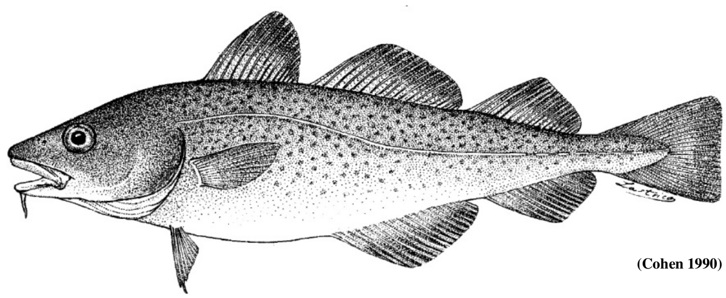
Feeding ecology of Baltic cod assessed by stable isotope analysis



(Cohen 1990)

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LIST OF ABBREVIATIONS

δ	Delta
AB	Arkona Basin
adj	adjusted
BB	Bornholm Basin
C	carbon
cm	centimeter
det	determined
DF	degree of freedom
F	F-value
g	gram
GB	Gotland Basin
GD	Gdansk Deep
GLM	general linear model
ICES	International Council for the Exploration of the Sea
JFT	Jungfischtrawl
L	Linné, Carl von
MS	mean of squares
N	nitrogen
p	p-value
psu	practical salinity units
S	sulfur
SCA	stomach content analysis
SD	subdivision
seq	sequential
SIA	stable isotope analysis
SS	sum of squares
SSB	spawning-stock biomass
TL	total length

ZUSAMMENFASSUNG

Der Ostseedorsch (*Gadus morhua* L.) zählt zu den bedeutendsten kommerziellen Fischarten und ist einer der wichtigsten Prädatoren der Ostsee. Trotz seiner entscheidenden Rolle ist seine Nahrungsökologie noch nicht vollständig verstanden. Die stabile Isotopenanalyse (SIA) ist trotz ihrer zunehmenden Verwendung in Nahrungsnetzstudien noch nicht an kommerziellen Fischarten der Ostsee angewandt worden. Daher wurde sie in dieser Studie genutzt, um die bereits vorhanden Informationen durch Mageninhaltsuntersuchungen (SCA) zu komplementieren. Zu diesem Zweck wurde ein großer Datensatz an Kohlenstoff(C)-, Stickstoff(N)-, und Schwefel(S)isotopenwerten des Top-Räubers Dorsch, der wichtigsten Planktivoren Hering (*Clupea harengus* L.) und Sprotte (*Sprattus sprattus* L.) und anderer pelagischer und benthischer Ostseefischarten ausgewertet. Insgesamt wurden 392 Muskelproben zehn verschiedener Arten untersucht. Diese wurden auf einer zweiwöchigen Fahrt mit dem Forschungsschiff Alkor im April 2014 an insgesamt 19 Stationen in der Kieler Bucht (SD22), des Arkona Beckens (SD24), des Bornholm Beckens (SD25) und des Danziger Tiefs (SD26) genommen. Wie anhand der Ergebnisse von Mageninhaltsuntersuchungen erwartet, zeigte Dorsch einen ontogenetischen Shift in seinen $\delta^{15}N$ Werten. Dennoch war der Shift von benthischer zu pelagischer Nahrung anhand der $\delta^{13}C$ Werte insgesamt schwächer als vermutet. Dies unterstützt die vorherige Hypothese, dass die Bedeutung von benthischer Nahrung für Dorsch aufgrund der verringerten Verfügbarkeit durch zunehmenden Sauerstoffmangel in den Becken abgenommen hat. Kleine Heringe und Sprotten zeigten aufgrund ihrer streng zooplanktivoren Ernährung eine Überlappung in ihren Isotopenwerten, was vorherige Studien bestätigt und deutlich auf eine Nahrungskonkurrenz hinweist. Jedoch zeigten die Heringe, im Gegensatz zu den Sprotten, von denen vermutet wird, dass sie streng zooplanktivor bleiben, einen ontogenetischen Shift, da sie mit zunehmender Größe Nektobenthos fressen. Außerdem verdeutlichen die Ergebnisse dieser Studie, dass es eindeutige räumliche Unterschiede zwischen den isotopischen Baselines gibt. Daher kann eine insgesamte Verschiebung der Isotopenwerte im gesamten Nahrungsnetz des entsprechenden Beckens festgestellt werden. Dies sollte in zukünftigen SIA Studien in der Ostsee, die sich mit Migrationsverhalten beschäftigen, berücksichtigt werden. Außerdem können zusätzliche SIA an Benthos helfen, die Bedeutung benthischer Nahrung und ihre möglichen Auswirkungen auf den Zustand des Dorsches besser zu verstehen.

ABSTRACT

Baltic cod (*Gadus morhua* L.) is the subject of important fisheries and a keystone predator in the Baltic Sea. Despite this important role, the feeding ecology of cod is only incompletely understood. Here, I used stable isotope analysis (SIA), a tool increasingly used in food web studies but surprisingly, not yet for commercial fish species in the Baltic, to obtain a complementary dataset to existing stomach content data (SCA). For this purpose, I analyzed a large set of carbon (C) and nitrogen (N), and a pilot set of sulfur (S) muscle stable isotope data of the top predator cod, the key plankton feeders herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* L.), and other pelagic and benthic fish species of the Baltic. Analyses were based on 392 samples of 10 species from 19 sites covering the Kiel Bight (SD22), Arkona Basin (SD24), Bornholm Basin (SD25), and Gdansk Deep (SD26) that were obtained on a 2-week cruise with the research vessel Alkor in April 2014. As expected from prior stomach content data, cod showed an ontogenetic shift in $\delta^{15}N$ ratios. However, the expected shift in $\delta^{13}C$ ratios from benthic to pelagic diet was overall surprisingly weak. This supports the previous hypothesis that the importance of benthic diet for cod may have decreased due reduced availability of demersal invertebrates as prey for cod due to increasing anoxic condition in deeper water. Confirming previous studies, small herring and sprat displayed a dietary overlap due to a strict zooplanktivor diet, which indicates strong potential for dietary competition. However, herring, in contrast to the presumed strict zooplanktivor sprat, showed an ontogenetic shift because it changes its diet with increasing fish size to nektobenthos. Furthermore, the results of this study demonstrated that there are clear spatial differences in isotopic baselines and therefore an overall isotopic shift in the entire food web between basins of the Baltic, which may be useful for studies in stock mixing and migrations, and which needs to be considered in future SIA studies in the Baltic Sea. Besides, additional SIA of benthos might help to get a better understanding of the importance of benthic prey and its potential consequences for cod's condition.

1. INTRODUCTION

For centuries, cod (*Gadus morhua* L.) is an important fisheries species in the Baltic Sea (Kurlansky 2011) and, hence, of high economical importance. Besides, cod is one of the top predators and hence, plays a key role in the Baltic ecosystem (Rudstam et al. 1994). The Baltic fish communities are rather simple and mainly consist of cod, herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* L.) (Heikinheimo 2011). On top of the food web, cod shapes these communities via top-down control (Rudstam et al. 1994, Möllmann et al. 2009, Casini et al. 2012). As an example, the drastic decline in cod's population in the late 1980s resulted in an increase of its most important prey species herring and sprat. In turn, this led to a decrease in zooplankton abundances which represent the most important part of clupeids' prey (Casini et al. 2012).

Because of the importance of cod, many studies have been conducted to examine its feeding ecology (Zalachowski 1977, Axell 1982, Bagge & Bay 1988, Schulz 1988, Hussy et al. 1998, Pachur & Horbowy 2013), however all carried out through stomach content analysis (SCA). These studies reported the ontogenetic shift in cod's diet from benthic to pelagic prey, however, trophic width of cod and strength of ontogenetic shifts in different basins could not be assessed by SCA. To address these gaps, I used stable isotope analysis (SIA), a method increasingly used to answer ecological questions, to reassess and expand on previous knowledge on herring, sprat and in particular cod feeding ecology.

Both methods have their advantages and disadvantages and complement each other well. As traditional method of choice, SCA allows a detailed view of prey by revealing ingested taxa. However, stomach content data can entail problems regarding the quantification of prey and the detection of temporal and spatial shifts (Renones et al. 2002). Specifically, SCA represents the diet over the last few hours (Cocheret de la Morinière et al. 2003) but only shows a snapshot in time as long as there is no frequent sampling over long periods (Beaudoin et al. 1999). Over the past decades, SIA has emerged as alternative tool. In contrast to SCA, it reflects assimilated food over previous weeks to months (Hobson 1999, Cocheret de la Morinière et al. 2003) and therefore detects general patterns that result from integration over time (Beaudoin et al. 1999). Carbon and nitrogen in particular have been used to elucidate long-time assimilated diet and to provide information about trophic relationships (Minagawa & Wada 1984, Peterson & Fry 1987, Hobson 1999). For example, SIA has been used to identify the presence and pattern of ontogenetic shifts (Cocheret de la Morinière et al. 2003) and general feeding differences between sexes (Bertellotti et al. 2002), as well as spatial differences in feeding ecology (Hebert et al. 1999). Recently, SIA of sulfur has gained in importance, as it is particularly useful for the separation of benthic and pelagic diet (Fry et al. 1982, Mittermayr et al. 2014).

Despite the frequent use in ecological studies, somewhat surprisingly, commercial fish species have rarely been assessed by SIA to date (but see Renones et al. 2002, Sherwood et al. 2007, Matley et al. 2013). This includes cod, herring and sprat in the Baltic Sea, for which no published stable isotope studies exist at present. Here, my goal was to use SIA to obtain a complementary dataset to published stomach content information for Baltic cod, in order to improve understanding of the feeding ecology of this species in the Baltic Sea. For this purpose, I analyzed a large set of C and N, and a pilot set of S muscle stable isotope data of the top predator cod, the key plankton feeders herring and sprat, and other pelagic and benthic fish species of the Baltic. My specific objectives were (i) to get an overview over trophic status and feeding relationships within the fish community based on C and N isotopic data, and to assess (ii) the presence and pattern of ontogenetic shifts and differences between males and females in cod, herring and sprat, (iii) the potential importance of pelagic fishes versus benthic diet for cod, and (iv) the presence of spatial differences in isotopic baselines and feeding ecology of key species between different basins of the Baltic Sea.

2. MATERIAL AND METHODS

2.1 Study area

The Baltic Sea (Figure 1) is a large brackish sea (Rudstam et al. 1994) with a surface area of 415.000 km^2 and a volume of 21.700 km^3 (Jansson 2002). It is a young (about 10.000 years), semi-enclosed water body with a narrow connection to the North Sea (Thulin & Andrushaitis 2003). Influxes of saline and oxygenated water through the Danish straits (Thulin & Andrushaitis 2003) and freshwater inputs from the surrounding countries (Jansson 2002) result in a vertical stratification of the water column which is characteristic for the Baltic Sea (Kononen et al. 1996). It shows a strong west to east gradient with surface salinity levels over 15 psu in the Kattegat and less than 3 psu in the Bothnian Bay (Carlsson 1997).

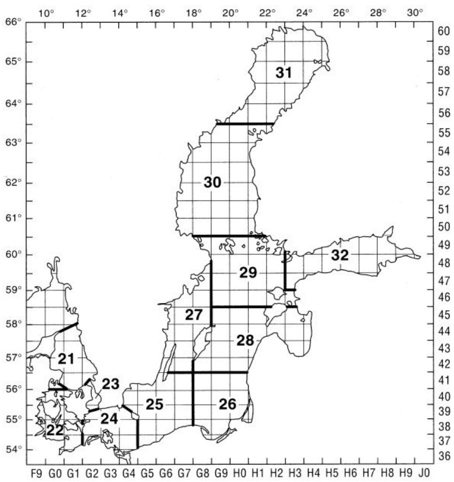

Figure 1. ICES (International Council for the Exploration of the Sea) subdivisions of the Baltic Sea (www.ices.dk)

The Baltic Sea is highly productive and sustains important fisheries (Szefer 2002). Cod, herring and sprat represent the ecological key species and at the same time the most important commercial fish species in the pelagic water body of the Baltic Sea (Sparholt 1994). However, their populations are under strong pressure due to anthropogenic (e.g. overfishing and eutrophication) as well as to atmospheric drivers (e.g. oxygen depletion) (Möllmann et al. 2009). In the 1980s, these circumstances resulted in a drastic ecological reorganization of the entire ecosystem. The Baltic cod population collapsed and its spawning-stock biomass (SSB) decreased from 700.000 tonnes to 100.000 tonnes (Fricke 2007). This subsequently lead to cascading trophic effects in the whole Baltic food web: along with the decline in cod' population, the number of clupeids and, thus, the predator pressure on cod' eggs, increased (Casini et al. 2012). Nevertheless, the stock has recently recovered and SSB has again attained 2000 tonnes (ICES 2014).

2.2 Study organism

The Atlantic cod belongs to the family Gadidae, the cod-like fish (Muus et al. 1999) (Figure 2). It has a protruding upper jaw and a conspicuous barbel on its lower jaw (Cohen et al. 1990). The coloring is brown to green patterned, depending on the substrate of its habitat, with a light lateral line (Muus et al. 1999). Cod can live up to 25 years (Muus et al. 1999) and grow up to 2 meters (Cohen et al. 1990). However, local stocks as the Baltic cod can only reach about 1 meter (Magnussen 2007) due to the less saline water, and mean sizes are even smaller today due to fishing pressure (Svedäng & Hornborg 2014).

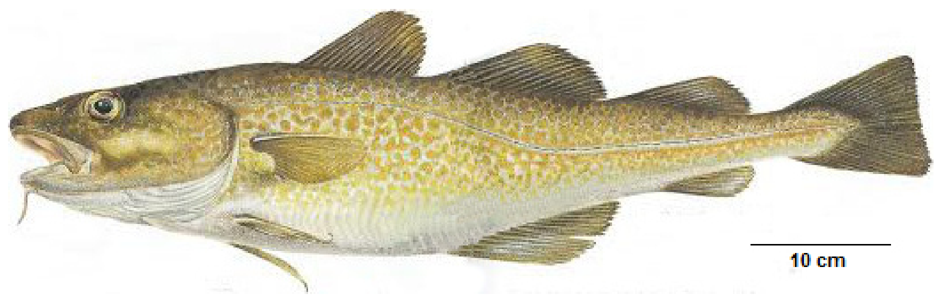

Figure 2. The Atlantic Cod (Muus et al. 1999, drawing by Preben Dahlstrom edited by Author (2014))

Cod is a cold-water fish species and occurs in the North Atlantic from North-Carolina to the Labrador Sea (west) and around Greenland and Iceland. The Atlantic cod is also found from the Bay of Biscay up to the Arctic Ocean along the European cost (including North Sea and Baltic Sea) (Narberhaus 2012). Juveniles usually live in shallow waters, whereas adult live in deeper, colder waters from 150-200 m (Cohen et al. 1990). Larvae feed on plankton, especially on earlier live stages of copepods (Last 1978). Juveniles then become benthic predators and their diet is dominated by crustaceans (Daan 1989). Besides polychaetes and other demersal organisms which play a smaller role in adults' diet, fish become more important, in particular commercial fish species, including young cod (Cohen et al. 1990, Bogstad et al. 1994). Figure 3 shows average stomach contents of cod in the North Sea as percentage weight size class based on stomach content data (Daan 1989).

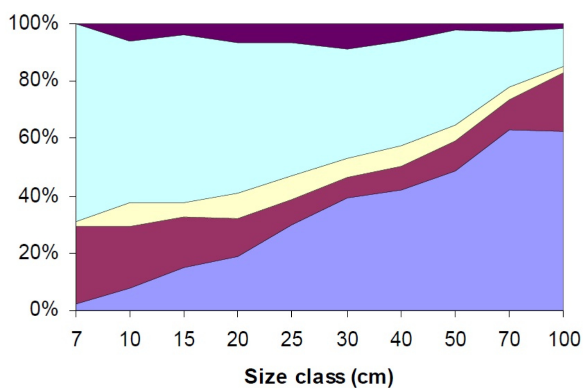

Figure 3. Average stomach contents of cod in the North Sea as percentage weight by size class; rest (■), crustaceans (■), annelids (■), non-commercial fish species (■), commercial fish species (■) (Daan 1989)

In the Baltic Sea, stomach content analysis has revealed that juvenile cods' (< 25cm) diet consist of invertebrates such as *Mysis species*, *Pontopoeira species* and *Bylgides sarsi*. Larger cod (25-35cm) prefer small herring and sprat and also benthic prey especially *Saduria entomon* (Bagge et al. 1994). Within growth, cod's diet (> 35cm) is mainly represented by clupeids (herring and sprat) (Bagge et al. 1994). Cannibalism also plays a role in the Baltic Sea (Cohen et al. 1990). It is thought that the availability and importance of benthic diet for cod decreased after the regime shift in the 1980s (Bagge et al. 1994), however, data to assess this hypothesis are scarce.

Since the reproduction of cod depends on high salinity and oxygen rich water (Wieland & Zuzarte 1991), spawning mainly takes place in the basins of the Baltic Sea: the Bornholm Basin, the Gotland Basin and the Gdansk Deep. Besides, the Kiel Bight and the Arkona Basin are of minor importance (Bagge et al. 1994) (Figure 4).

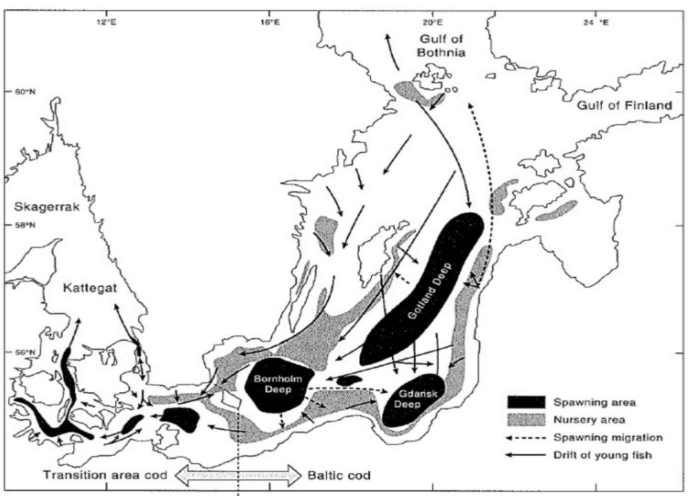

Figure 4. Spawning and feeding areas of cod (Bagge et al. 1994)

2.3 Sampling

Sampling concentrated on the five main spawning areas of cod. All sampling was done on Alkor cruise AL435 in April 2014. In total, 392 samples of 10 species from 19 sites were caught (Table 1, Figure 5). Fish was captured by pelagic trawls ("Jungfischtrawls", JFT) of 0.5 cm mesh size. Sampling was conducted in the Kiel Bight, ICES SD 22 (2 sites), Arkona Basin, ICES SD 24 (3 sites), Bornholm Basin, ICES SD 25 (9 sites), the northern part of

Gdansk Deep, ICES SD 26N (2 sites) and the southern part of Gdansk Deep, ICES SD 26S (3 sites) (Figure 1).

SD	Station	species	size range	$d^{13}C$, $d^{15}N$					$d^{34}S$					Total
				M	F	J	not det.		M	F	J	not det.		
22				**13**	**3**	**3**	**29**	**48**						**48**
	489/KB06			**13**	**3**	**3**	**29**	**48**						**48**
		cod	16,5-23,0	1	1			2						2
		herring	10,5-20,5				10	10						10
		flounder	20,0-32,0	7			2	9						9
		plaice	22,0-38,0				7	7						7
		dab	16,0-30,0				10	10						10
		whiting	13,0-27,0	5	2	3		10						10
24				**51**	**34**	**2**	**6**	**93**				**2**	**2**	**95**
	502/H24			**25**	**24**	**1**	**4**	**54**						**54**
		cod	17,0-46,0	10	9	1		20						20
		herring	18,5-30,5	5	5			10						10
		sprat	9,0-14,5	5	5			10						10
		flounder	23,0-34,0				3	3						3
		plaice	40,0				1	1						1
		whiting	10,0-43,5	5	5			10						10
	515/H21			**19**	**10**			**29**						**29**
		cod	26,0-39,0	7	2			9						9
		herring	10,5-26,5	6	4			10						10
		sprat	8,0-15,0	6	4			10						10
	516/H18			**7**		**1**	**2**	**10**				**2**	**2**	**12**
		cod	10,0			1		1						1
		flounder	19,0-27,0	7				7						7
		fourbeard rockling	32,0				1	1				1	1	1
		*ocean quahog	2,5				1	1				1	1	1
25				**55**	**49**	**5**	**29**	**138**	**12**	**7**	**1**	**2**	**22**	**160**
	530/BB30				**1**			**1**						**1**
		herring	22,5		1			1						1
	531/BB31			**3**	**1**		**1**	**5**				**1**	**1**	**6**
		cod	17	1				1						1
		herring	20,0-23,0	2	1			3						3
		*ocean quahog	3				1	1				1	1	2
	562/BB15			**3**	**1**			**4**						**4**
		cod	17	1				1						1
		herring	20,0-24,0	2	1			3						3
	563/BB24			**7**	**5**	**1**		**13**						**13**
		cod	9,5			1		1						1
		herring	17,5-23,0	2	2			4						4
		flounder	23,0-36,0	5	3			8						8
	564/BB29			**1**	**2**			**3**						**3**
		herring	22,0-23,0	1	2			3						3
	601/BB04			**19**	**19**		**4**	**42**						**42**
		cod	28,0-50,0	9	9			18						18
		herring	16,5-26,5	5	5			10						10
		sprat	9,5-14,5	5	5			10						10
		whiting	40				1	1						1
		coalfish	36,0-40,0				3	3						3
	602/BB04				**2**		**5**	**7**						**7**
		cod	52,0-53,0		2			2						2
		whiting	30				1	1						1
		coalfish	33,0-41,0				4	4						4
	603/BB18						**1**	**1**						**1**
		coalfish	41				1	1						1

	605/BB32			**3**			**18**	**21**	**3**			**1**	**4**	**25**
		cod	11,0-17,0				7	7						7
		flounder	20,0-26,0	3				3	3				3	6
		plaice	25,0-30,0				2	2						2
		fourbeard rockling	16				1	1				1	1	2
		whiting	16,0-27,0				8	8						8
	608/BB42			**19**	**18**	**4**		**41**	**9**	**7**	**1**		**17**	**58**
		cod	7,5-50,0	8	8	4		20	2	2	1		5	25
		herring	10,5-24,5	5	5			10	3	2			5	15
		sprat	8,5-14,5	4	5			9	2	3			5	14
		flounder	20,0-32,0	2				2	2				2	4
26N				**32**	**22**			**54**						**54**
	581/GB80			**21**	**14**			**35**						**35**
		cod	25,0-41,0	11	4			15						15
		sprat	8,5-13,5	5	5			10						10
		flounder	19,0-33,0	5	5			10						10
	584/GB82a			**11**	**8**			**19**						**19**
		cod	27,0-32,0	3				3						3
		sprat	8,5-13,5	5	5			10						10
		flounder	23,0-34,0	3	3			6						6
26S				**40**	**18**	**1**		**59**	**6**	**4**			**10**	**69**
	569/GD59			**24**	**15**	**1**		**40**	**2**	**1**			**3**	**43**
		cod	10,0-54,0	10	8	1		19						19
		herring	20,0-24,0	3	1			4						4
		sprat	11,0-14,0	5	5			10						10
		flounder	22,0-30,0	6	1			7	2	1			3	10
	570/GD60			**1**	**1**			**2**	**1**	**1**			**2**	**4**
		flounder	22,0-31,0	1	1			2	1	1			2	4
	571/GD60a			**15**	**2**			**17**	**3**	**2**			**5**	**22**
		cod	31,0-48,0	15	2			17	3	2			5	22
				191	**126**	**11**	**64**	**392**	**18**	**11**	**1**	**4**	**34**	**426**

Table 1. Sample sizes per ICES subdivision (see Figure 1), sampling site, species, size range [cm], stable isotope analysis element and sex (male, female, juvenile; not determined) obtained during AL 435. *ocean quahog' samples were excluded due to extremely high variances in stable isotope ratios and low sample size of n = 2.

For all species, the weight, measured to nearest g, and total length, rounded to the next lower cm for cod, whiting (*Merlangius merlangus* L.), coalfish (*Pollachius virens* L.), flounder (*Platichthys flesus* L.), dab (*Limanda limanda* L.), plaice (*Pleuronectes platessa* L.), fourbeard rockling (*Enchelyopus cimbrius* L.), and ocean quahog (*Arctica islandica* L.), and to the next lower half cm (sprat, herring) of all individuals was measured. For cod as focus species, single fish data including sex and maturity stage were obtained, and otoliths, fin clips, stomachs and gonad samples were taken. In addition, dorsal white muscle tissue samples were dissected using a biopsy punch (4mm; Stiefel; Durham, USA) or a small knife. Skin or blood was removed to prevent a contamination. Samples were transferred to 2 ml tubes (Sarstedt; Nümbrecht, Germany). Tubes were labeled with a code linking them to the single fish measures described above. All samples were immediately frozen at -20° until further analysis.

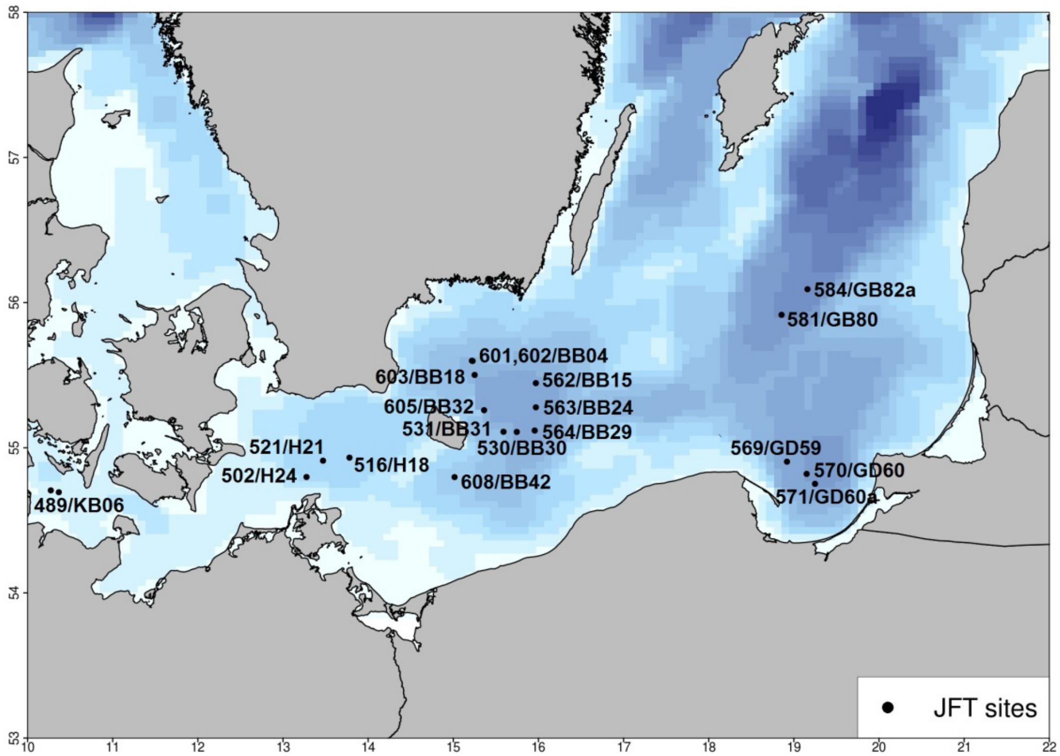

Figure 5. Sampling sites covered during AL 435 with pelagic trawls ("Jungfischtrawls", JFT). Numbers on the y- and x-axis represent degrees N and E, respectively.

2.4 Principle of stable isotope analysis

Chemical elements mostly exist in two or more forms, known as isotopes, which differ in their number of neutrons in the nucleus (Fry 2006). The more massive, so-called "heavier", isotope has an extra neutron and is therefore differently digested and fractionated in comparison to the lighter isotope (Peterson & Fry 1987). These changes in the abundances of isotopes occur in predictable pattern between trophic levels with an enrichment of the heavier isotope (Peterson & Fry 1987). Hence, stable isotope ratios show the assimilated diet in an animal's tissue, based on the principle "you are what you eat" (DeNiro & Epstein 1978, Hobson 1999). Isotopes of carbon (^{13}C / ^{12}C) and sulfur (^{34}S / ^{32}S) indicate food sources of primary producers because of their limited fractionation (0.0-1.0 ‰ enrichment per trophic level (Peterson & Fry 1987)), whereas isotopes of nitrogen (^{15}N / ^{14}N) are enriched from one food step to the next (3.5-5.0 ‰ enrichment per trophic level (Peterson & Fry 1987) and therefore shows an organism's trophic position. The enrichment of ^{15}N is a result of the excretion of the lighter isotope (^{14}N) via urine (Minagawa & Wada 1984, Peterson & Fry

1987). Figure 6 shows the concept of isotopic enrichment of carbon (^{13}C) and nitrogen (^{15}N) over trophic levels.

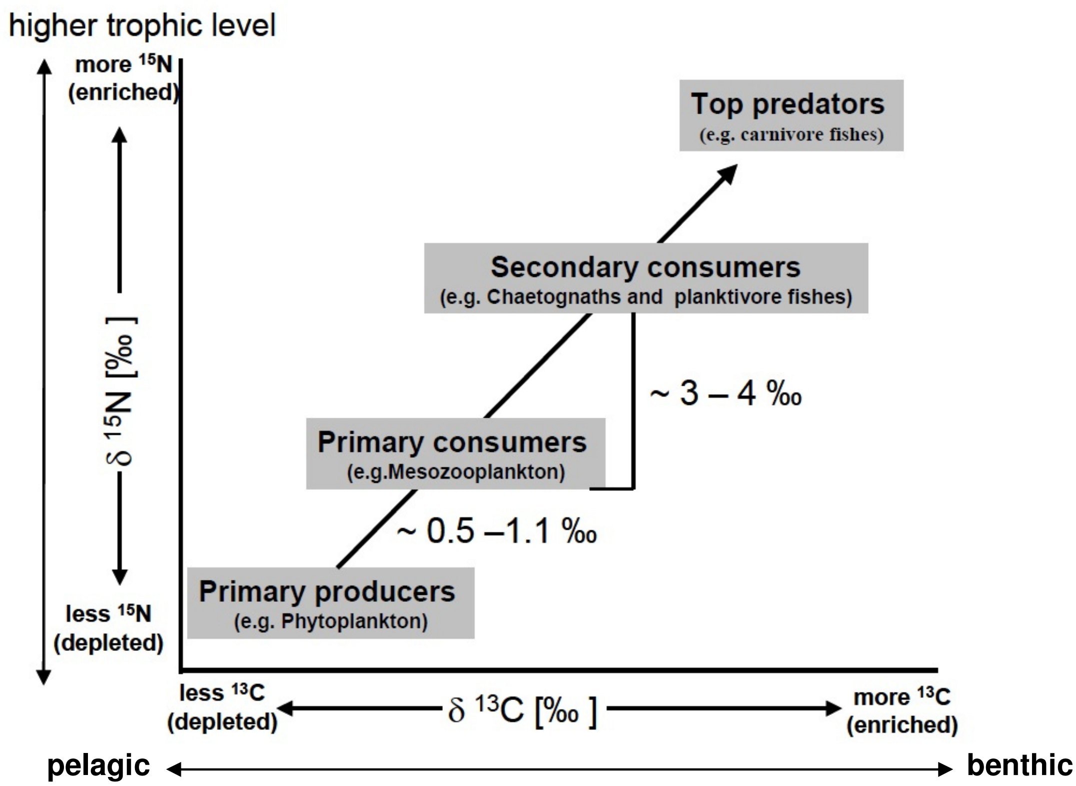

Figure 6. Conceptual scheme of isotopic enrichment per trophic level in marine food pathways using carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) (adapted Agurto 2007).

For all these reasons, SIA is a powerful tool to provide information about trophic relationships in ecological studies (McCutchan et al. 2003), and to gain insights into potential dietary sources of consumers. In addition to its use in feeding ecology studies of fish (Renones et al. 2002, Hadwen et al. 2007, Sherwood et al. 2007, Matley et al. 2013), SIA offers insights into migration behavior in aquatic (Killingley 1980, Hesslein et al. 1991, Dierking et al. 2012) as well as in terrestrial systems (Van der Merwe et al. 1990, Alisauskas & Hobson 1993, Marra et al. 1998).

2.5 Sample preparation and analysis

All samples were freeze-dried to constant mass (freeze-dryer alpha 1-1; Christ GmbH; Osterode am Harz, Germany). Freeze-dried samples were ground to fine powder using a mortar and pestle (75mm, 25ml; Carl Roth GmbH; Karlsruhe, Germany).1.00 ± 0.05 mg of powdered samples were weighted (MC 5 Micro Balanace; Satorius; Göttingen, Germany) into cylindrical tin caps of 5 x 8 mm (Filter Scale SE2F; Sartorius; Göttingen, Germany) which were folded using tweezers. Tin capsules were loaded into flat-bottomed 96-well tissue culture plates (Sarstedt; Nümbrecht, Germany). Open wells in the tray were covered using parafilm until all samples had been added. For shipping, the parafilm was then replaced by an index card underneath the lid to secure the samples in the wells. Stable isotope analysis was then carried out at the Stable Isotope Facility of the University of California (USA). $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios were measured with a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 continuous flow isotope ratio mass spectrometer (IRMS) whereas $^{34}S/^{32}S$ ratios were measured with a Elementar vario ISOTOPE cube interfaced to a 20-22 IRMS (Sercon Limited; Cheshire, UK). Samples were analyzed with standard reference gases (Vienna PeeDee Belemnite (PDB) for carbon, N_2 for nitrogen and SO_2 for sulfur). Analytical precision was 0.2‰ for ^{13}C and 0.3‰ for ^{15}N, ±O.2‰ for ^{34}S.

Stable isotopes are expressed in delta values (δ), defined as the parts per thousand deviation from a standard material (Sherwood et al. 2007):

$$\mathbf{\delta\, X = [(R_{sample}/R_{standard}) - 1] \times 1000}$$

where X is ^{13}C, ^{15}N or ^{34}S and R is the corresponding isotope ratio ($^{13}C/^{12}C$, $^{15}N/^{14}N$ or $^{34}S/^{32}S$).

2.6 Data analysis

For data survey, data evaluation and generation of biplots I used Excel 2007 (Microsoft Corporation; Redmond, USA). MINITAB (Minitab Incorporated; State College, USA) was used for scatterplots, individual value plots, boxplots and statistical analysis. Since my data set was multivariate, ANCOVA type general linear models (GLM) were used to assess the statistical relationship between predictors (explanatory variables (SD, site, sex) and covariates (TL, sex, C/N, TL)) and a continuous response variable ($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$) (MINITAB 14, 2004). Results were considered as significant when $p<0.05$.

3. RESULTS

(i) Trophic status and feeding relationships the Baltic fish community

Figure 7 shows a biplot of mean $\delta^{15}N$ and $\delta^{13}C$ ratios of all sampled individuals per species. High $\delta^{15}N$ values were represented by presumed predators fourbeard rockling ($\delta^{13}C$: -21.3; $\delta^{15}N$: 14.4), whiting ($\delta^{13}C$: -21.1; $\delta^{15}N$: 14.1) and cod ($\delta^{13}C$: -20.9; $\delta^{15}N$: 13.4). They showed intermediate $\delta^{13}C$ ratios suggesting a mixed diet of benthic and pelagic prey. Flatfish dab ($\delta^{13}C$: -20.5; $\delta^{15}N$: 13.4), flounder ($\delta^{13}C$: -21.0; $\delta^{15}N$: 12.8) and plaice ($\delta^{13}C$: -20.3; $\delta^{15}N$: 12.2) had the most benthic $\delta^{13}C$ values and belong due to their lower $\delta^{15}N$ ratios to a lower trophic level in the food web. Interestingly, flounder was characterized by very large variance in stable isotope ratios ($\delta^{13}C$: from -22.7 to -15.3; $\delta^{15}N$: from 10.9 to 16.1), which points to strong individual diet specialization, with some individuals on trophic levels similar to cod and others feeding more than a trophic level lower, and a $\delta^{13}C$ range from values characteristic for benthic feeding to completely pelagic feeding. Coalfish demonstrated a relatively low trophic level with more pelagic $\delta^{13}C$ values ($\delta^{13}C$: -20.7; $\delta^{15}N$: 11.8) followed by presumed plankton feeders herring ($\delta^{13}C$: -21.9; $\delta^{15}N$: 11.5) and sprat ($\delta^{13}C$: -22.4; $\delta^{15}N$: 10.7) displayed the lowest trophic levels in the community with the most pelagic $\delta^{13}C$ values.

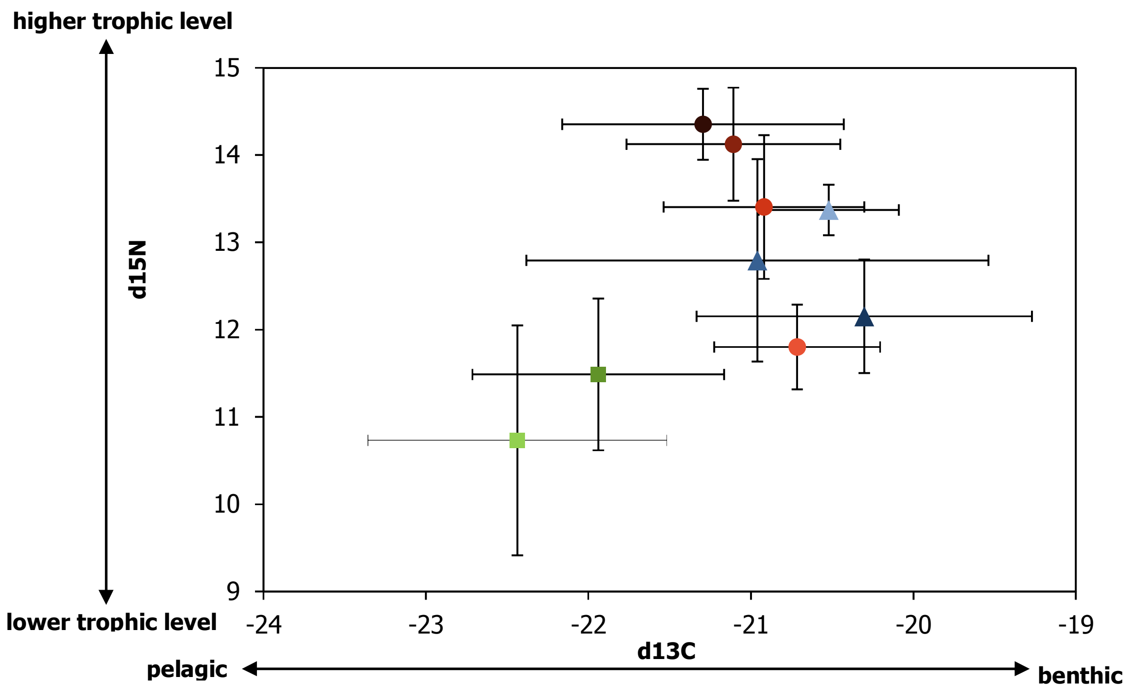

Figure 7. Biplot of mean nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) ratios of all species (combined areas); standard deviation is represented by error bars; clupeids (squares): herring (■), sprat (■); flatfish (triangles): dab (▲), flounder (▲), plaice (▲); cod-like fish (circles): coalfish (●), cod (●), fourbeard rockling (●), whiting (●).

(ii) The presence and pattern of ontogenetic shifts and differences between males and females in cod, herring and sprat

It was highly significant that $\delta^{15}N$ ratios of cod were positively correlated with TL(SD) implying an ontogenetic shift (Figure 8; Table 2). In other words, juvenile cod displayed lower $\delta^{15}N$ ratios indicative of preying on lower trophic levels, and trophic level then increased with size. However, the ontogenetic shift was overall quite weak (less than one trophic level if isotopic enrichment of 3.5-5.0‰ per trophic level is presumed). Male stable isotope ratios were not significantly different from those of females (Table 2).

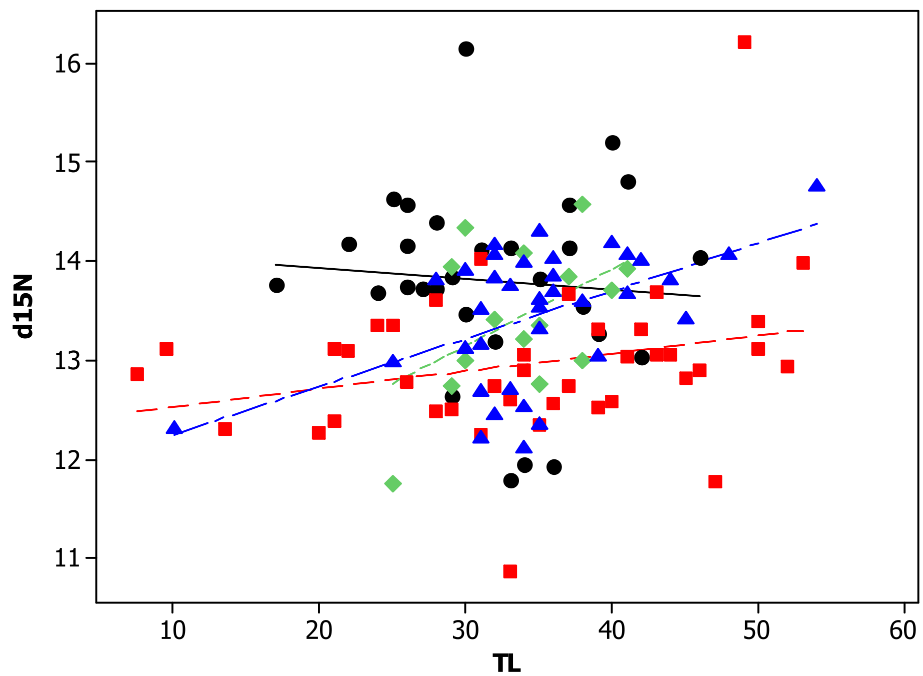

Figure 8. Scatterplot of $\delta^{15}N$ vs. TL for cod per SD; lines represent the regression lines; SD 24–Arkona Basin (●), SD 25–Bornholm Basin (■), SD 26N–Northern part of Gdansk Deep (◆), SD 26S–Southern part of Gdansk Deep (▲); samples of SD22 were excluded due to low sample size of n = 2.

Summary	DF	Seq SS	Adj SS	Adj MS	F	P
SD	3	12.35	3.90	1.30	2.22	0.090
TL (SD)	4	7.80	7.93	1.98	3.38	0.012
Site (SD)	3	2.03	2.16	0.72	1.23	0.303
Sex	2	0.43	0.43	0.22	0.37	0.962
Error	107	62.74	62.74	0.59		
Total	119	85.36				

Table 2. Summary of results of general linear model (GLM) of cod, with $\delta^{15}N$ as response variable,;SD, Site (SD) and sex as explanatory variables; TL (SD) as covariate (non-adj. R^2=26.5%).

The presence and strength of ontogenetic shifts in herring were affected by outliers presumed to be potential migrants. These individuals (encircled in Figure 9 (a) in the color of the basin of emigration) were in further GLMs excluded. Herring then significantly showed a clear ontogenetic shift in its diet (Figure 9 (b); Table 3). Furthermore, stable isotope ratios of nitrogen didn't show any differences between sexes (Table 4).

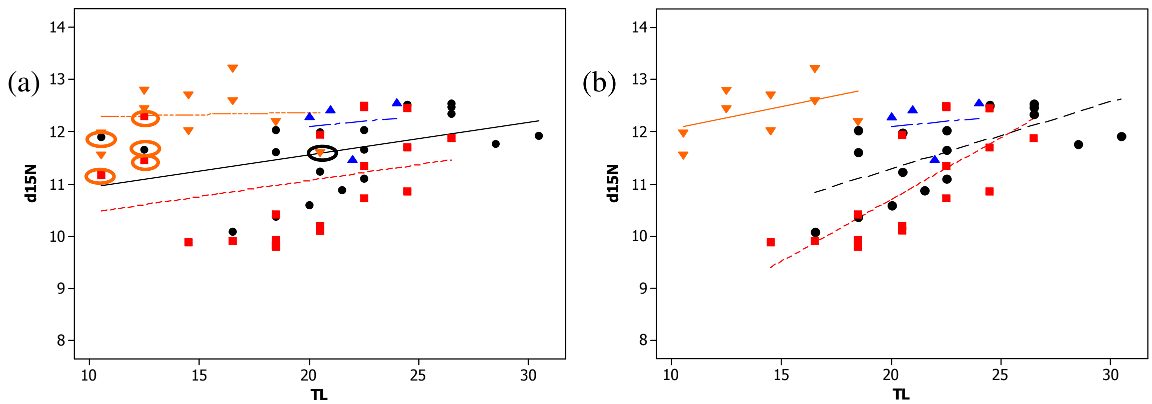

Figure 9. Scatterplot of $\delta^{15}N$ vs. TL with regression lines for herring per SD; SD 22 – Kiel Bight (▼), SD 24–Arkona Basin (●), SD 25–Bornholm Basin (■), SD 26S–Southern part of Gdansk Deep (▲); (a) outliers of SD22, 24 and 25 encircled in the color of the basin of emigration; (b) outliers excluded.

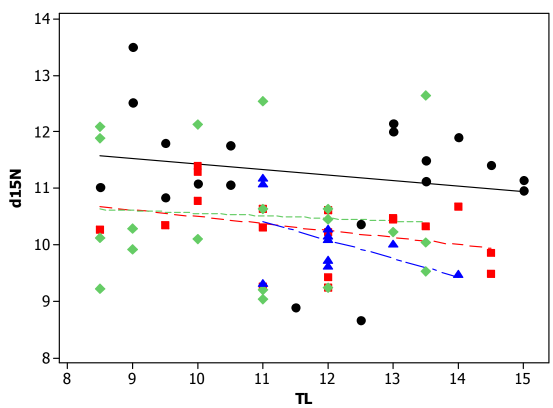

Figure 10. Scatterplot of $\delta^{15}N$ vs. TL with regression lines for sprat per SD; SD 24–Arkona Basin (●), SD 25–Bornholm Basin (■), SD 26N–Northern part of Gdansk Deep (◆), SD 26S–Southern part of Gdansk Deep (▲).

Summary	DF	Seq SS	Adj SS	Adj MS	F	P
TL	1	0.94	8.44	8.44	23.34	<0.001
SD	3	26.04	21.56	7.19	19.88	<0.001
Site (SD)	2	3.02	3.02	1.51	4.18	0.022
Error	41	14.83	14.83	0.36		
Total	47	44.82				

Table 3. Summary of results of general linear model (GLM) of herring, with $\delta^{15}N$ as response variable; SD and Site(SD) as explanatory variables;TL as covariate; excluded explanatory variable due to non-significance: sex (p=0.945) (non-adj. R^2=66.9%).

$\delta^{15}N$ ratios of sprat showed no evidence of an ontogenertic shift (Figure 10; Table 4). This suggests that sprat does not changes its prey with fish size. In contrast to cod and herring, male stable isotope values were significantly different from those of females (Table 4). Males were higher in $\delta^{15}N$ ratios then sprat.

Summary	DF	Seq SS	Adj SS	Adj MS	F	P
TL	1	1.72	1.21	1.21	1.42	0.238
SD	3	12.94	11.68	3.89	4.55	0.006
Site (SD)	3	1.10	1.40	0.47	0.55	0.652
Sex	1	5.09	5.09	5.09	5.96	0.018
Error	58	49.56	49.56	0.85		
Total	66	70.41				

Table 4. Summary of results of general linear model (GLM) of sprat, with $\delta^{15}N$ as response variable; SD and Site(SD) as explanatory variables; TL and sex as covariates (non-adj. R^2=29.6%).

Herring and sprat displayed an isotopic overlap (Figure 11), which is highest between small herring and sprat, suggesting a potential competition between both species for the same prey resources.

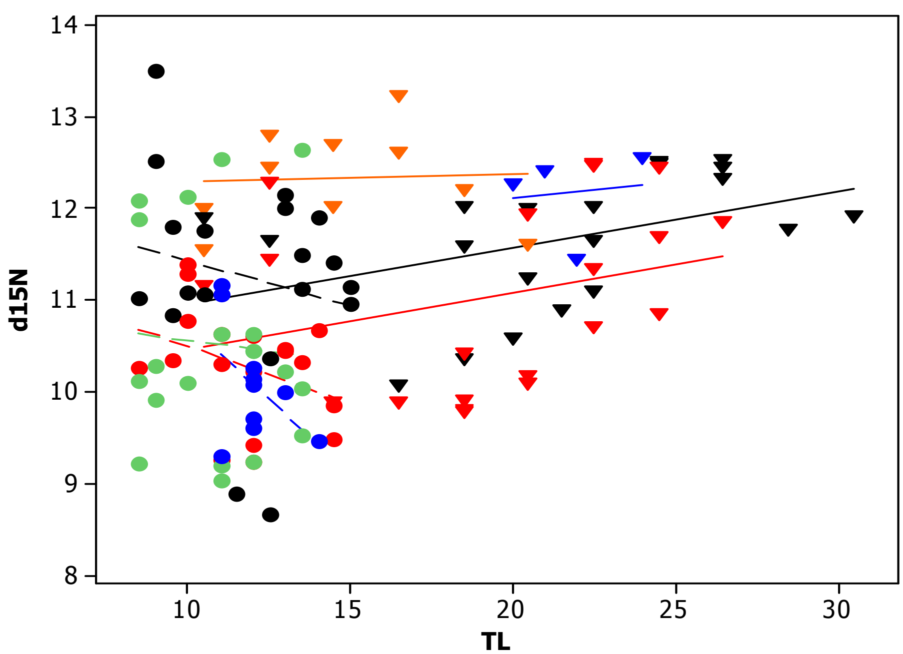

Figure 11. Scatterplot of $\delta^{15}N$ vs. TL with regression lines for herring (triangles) and sprat (circles) per SD; SD 22 – Kiel Bight (▼), SD 24–Arkona Basin (●), SD 25–Bornholm Basin (■),SD 26N–Northern part of Gdansk Deep (◆), SD 26S–Southern part of Gdansk Deep (▲).

(iii) The potential importance of pelagic fishes versus benthic diet as diet for cod

The ontogenetic shift in cod's diet indicated by a correlation of $\delta^{15}N$ ratios with TL (Table 2) is not found in stable isotope ratios of carbon (Table 5). This means that the shift in trophic level (based on nitrogen data) is significant, but the benthic-pelagic shift (based on carbon data) is overall week (Figure 12 (a)). This suggests that there are different carbon sources but they don't differ in their $\delta^{13}C$ ratios, only in two SD (SD24 and SD25).

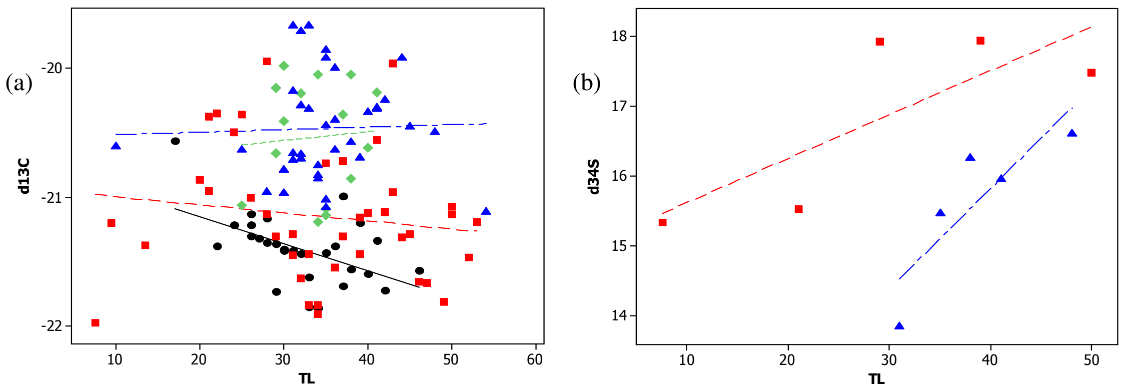

Figure 12. (a) Scatterplot of $\delta^{13}C$ vs. TL; (b) of $\delta^{34}S$ vs. TL; with regression lines for cod per SD; SD 24–Arkona Basin (●), SD 25–Bornholm Basin (■), SD 26N–Northern part of Gdansk Deep (◆), SD 26S–Southern part of Gdansk Deep (▲).

Summary	DF	Seq SS	Adj SS	Adj MS	F	P
TL	1	0.02	0.01	0.01	0.06	0.805
C/N	1	0.49	1.09	1.09	7.68	0.007
SD	3	19.13	17.12	5.71	40.02	<0.001
Site (SD)	3	3.53	3.41	1.14	7.98	<0.001
Sex	2	0.21	0.21	0.11	0.74	0.481
Error	108	15.40	15.40	0.14		
Total	118	38.76				

Table 5. Summary of results of general linear model (GLM) of cod, with $\delta^{13}C$ as response variable, SD, Site(SD) and sex as explanatory variables, and TL and C/N as covariates (non-adj. R^2=60.3%).

In contrast to carbon, it was highly significant that there was a positive correlation of $\delta^{34}S$ ratios with TL for cod in both SD (Figure 12 (b); Table 6). This clear ontogenetic shift in cod's diet (based on sulfur data) suggests a shift from benthic prey (with lower $\delta^{34}S$ ratios) to a diet consisting of pelagic fish (with higher $\delta^{34}S$ values).

Summary	DF	Seq SS	Adj SS	Adj MS	F	P
TL	1	2.72	6.72	6.72	9.95	0.016
SD	1	7.70	7.70	7.70	11.40	0.012
Error	7	4.73	4.73	0.68		
Total	9	15.15				

Table 6. Summary of results of general linear model (GLM) of cod, with $\delta^{34}S$ as response variable; SD as explanatory variable; TL as covariate (non-adj. R^2=68.8%).

Having a look at $\delta^{34}S$ ratios of all species, separation between pelagic and benthic feeding fish species can clearly be seen (Figure 13). The pelagic fish species herring and sprat showed higher ratios and little variability of $\delta^{34}S$ (herring: from 16.9 to 18.4; sprat: from 16.4 to 17.6) which suggests that they are feeding on pelagic prey (plankton). In contrast, the benthic living fourbeard rockling reflected a very low ratio of $\delta^{34}S$ (11.6) referring to benthic living prey. Flounder revealed a less benthic ratio as the rockling (15.1) but showed again a high variance (from 12.6 to 17.7) as it has been already assessed by carbon and nitrogen ratios. Cod also indicated a high variance in $\delta^{34}S$ (from 13.8 to 17.9) presumed to be due to lower $\delta^{34}S$ ratios as juvenile and higher $\delta^{34}S$ ratios as adult.

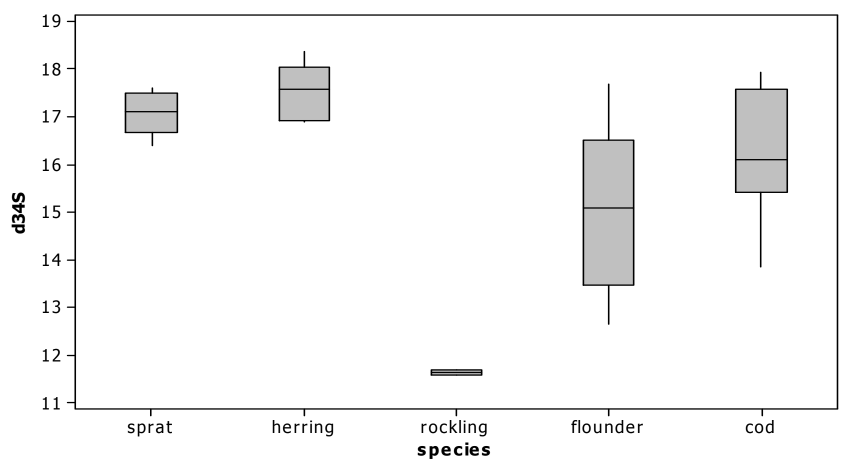

Figure 13. Boxplot of $\delta^{34}S$ per species: sprat, herring, fourbeard rockling, flounder, cod.

(iv) Spatial differences in isotopic baselines and feeding ecology of key species in different basins of the Baltic Sea

$\delta^{13}C$ per SD per species showed significant differences between basins for cod, but not for herring and sprat (Table 5, 7, 8). However, though not significant, the consistency of general trends in spatial patterns between basins for different species (Figure 14) suggested that they were caused by spatial differences in isotopic baselines in the entire food web and not in individual species.

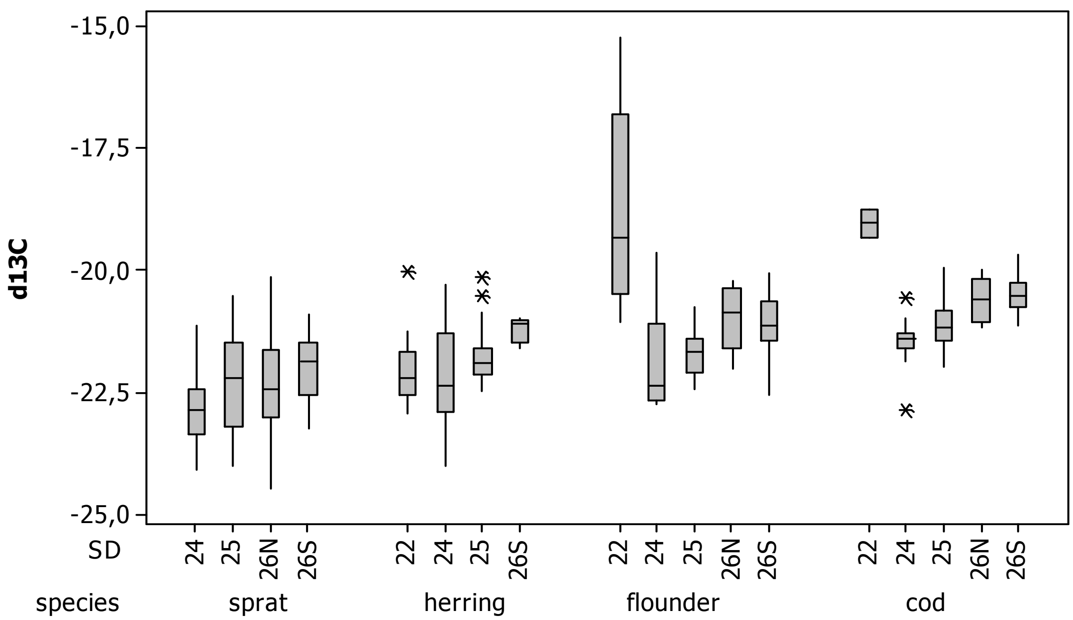

Figure 14. Boxplot of $\delta^{13}C$ per SD per species: sprat, herring, flounder and cod

GLM for carbon were highly significant for spatial differences between SD and sites (SD) for cod (Table 5) This means that there were not only differences between the basins, but also within the basins. As opposed to cod, herring and sprat displayed no spatial differences in $\delta^{13}C$ ratios, either between SD nor between sites(SD) (Table 7, 8).

In contrast to carbon, there were no significant spatial differences in presence in $\delta^{15}N$ ratios between SD or sites(SD) for cod (Table 2). Spatial differences in herring between SD and sites(SD) were whereas highly significant (Table 3). Sprat also showed differences between SD in nitrogen data, but not between sites(SD) (Table 4).

Summary	DF	Seq SS	Adj SS	Adj MS	F	P
Site	5	6.46	6.31	1.26	2.17	0.079
TL (Site)	6	8.63	8.63	1.44	2.48	0.042
Error	35	20.32	20.32	0.58		
Total	46	35.42				

Table 7. Summary of results of general linear model (GLM) of herring, with $\delta^{13}C$ as response variable, Site as explanatory variable, and TL(Site) as covariate (non-adj. R^2=42.6%).

Summary	DF	Seq SS	Adj SS	Adj MS	F	P
TL	1	0.66	0.99	0.99	1.75	0.191
C/N	1	11.15	10.11	10.11	17.87	<0.001
SD	3	7.60	7.59	2.53	4.48	0.007
Site (SD)	3	2.63	2.65	0.88	1.56	0.209
Sex	1	0.09	0.09	0.09	0.16	0.687
Error	58	32.80	32.80	0.57		
Total	67	54.92				

Table 8. Summary of results of general linear model (GLM) of sprat, with $\delta^{13}C$ as response variable, SD, Site(SD) and sex as explanatory variables, and TL and C/N as covariates (non-adj. R^2=40.3%).

4. DISCUSSION

Trophic status and feeding relationships within the Baltic fish community

The isotopic overview over Baltic fish communities agreed well with general knowledge about the feeding guild of most species, but also revealed some surprising aspects. Cod as top predator showed high $\delta^{15}N$ values compared to most other species in the analysis, thus indicating a comparatively high trophic level. This would be consistent with a large importance of fishes in the diet, which confirms previous reports of the importance of herring and sprat, but also young cod, as prey (Cohen et al. 1990, Bogstad et al. 1994). Surprisingly, fourbeard rockling and whiting displayed higher $\delta^{15}N$ ratios than cod. Cohen et al. (1990) described that these species mainly feed benthically (whiting: crustaceans, molluscs, polychaetes; fourbeard rockling: crustaceans), but complement their diet with fish. My results suggest that the fish component of their diet was previously underestimated or has increased since the 1980s. Due to their predation on benthic as well as on pelagic prey, they showed intermediate $\delta^{13}C$ ratios. It was also remarkable that coalfish showed a relatively low trophic level suggesting that it has been overestimated as predator upon fishes reported by Cohen et al. (1990). However, coalfishes were only captured in the Bornholm Basin (SD25) so it might show a higher trophic level in other basins. Lower trophic levels in the food web are represented by flatfishes. Dab demonstrated the highest $\delta^{15}N$ ratios, which corroborates the results of Picton & Morrow (2007) showing that dab not only preys on invertebrates (crustaceans, polychaetes, molluscs, echinoderms), but also on fish (e.g. sand eels). In contrast, plaice presumed to only feed on invertebrates (De Clerck & Buseyne 1989) also showed lower $\delta^{15}N$ ratios than dab. It has been assessed that flounder feeds on benthic fauna (Richard 1994) including small fishes (Cooper & Chapleau 1998). My results showed that flounder demonstrated a very high intrapopulation variance of stable isotopes ratios, from values near cod to values near herring, which would be consistent with the existence of different feeding strategies – concentrating on either benthic, pelagic, or mixed diets. Herring and sprat displayed the lowest $\delta^{15}N$ ratios, which confirms the assumption that they are the main planktivores in the Baltic Sea (Bernreuther 2007). Sprat showed lower $\delta^{15}N$ ratios compared to herring. As reported in previous studies, my results could confirm that sprat is strict zooplanktivor but herring also feeds on nektobenthos and therefore shows higher $\delta^{15}N$ ratios (Möllmann et al. 2004).

Ontogenetic shifts in cod

The high trophic level observed for cod here is consistent with its presumed role as top predator in Baltic systems (see e.g.Rudstam et al. 1994). Previous studies on cod's feeding ecology by SCA showed that juveniles cod's diet consists of invertebrates such as *Mysis sp.*, *Pontopoeira sp.* and *Byglides sarsi* and adult cod mostly feed on herring and sprat, but also *Saduria entomon* plays a role in its diet (Bagge et al. 1994). However, Bagge et al. (1994) also already reported that benthic diet may have decreased in importance due to lower availability following a decline in oxygen levels after the regime shift (see 2.1; Möllmann et al. 2009). For example, there is evidence that benthic invertebrates as *Arctica islandica* were very important before the regime shift but now represent just a small part of cod's prey (Bagge et al. 1994). In a recent analysis of cod stomach contents, clupeids constituted 67% in weight whereby sprat is more important than herring (Pachur & Horbowy 2013) (Table 9). The higher importance of sprat is presumed to be a result of the high increase in sprat stock size after the regime shift (Möllmann et al. 2009). However recent SCA data are too scarce to really assess the strength of this shift. The relatively weak ontogenetic shifts in cod's diet and quite pelagic $\delta^{13}C$ values even in small cod displayed by the results of SIA are suggestive of relatively similar diet of small and large cod. This would confirm the hypothesis that benthic diet have decreased in cod's diet and small cod are forced to start feeding on pelagic prey in earlier life stages.

taxonomic group of prey	Prey category	F [%]	W [%]
Polychaeta	*Bylgides sarsi*	11.9	1.2
Crustacea	Mysidacea gen.spp.	33.8	0.6
	Pontoporeia sp.	9.7	0.9
	Saduria entomon	44.2	13.3
	Crangon Crangon	34.7	3.4
Actinopterygii	*Sprattus sprattus*	51.5	51.4
	Clupea harengus	6.5	14
	Clupeidae gen.spp.	13.1	2.1
	Ammoditydae gen.spp.	1.2	3.8
	Gobiidae gen. spp.	29.1	5.4
	Gadus morhua	2.5	1.7

Table 9. Food composition of cod; F is the per cent frequency of occurrence (prey category with W<0.5 are excluded for the sake of overview; W is the per cent relative wet mass of prey item to the total wet mass of stomach content)(Pachur & Horbowy 2013)

In comparison to other studies using SIA to elucidate the feeding ecology of cod (Sherwood et al. 2007, Matley et al. 2013), the results of this study show the largest ranges for both $\delta^{13}C$ and $\delta^{15}N$ ratios (Table 10), probably caused by spatial differences in this study. This shows the importance of including spatial differences in isotopic analyses. My study was the first to also use of sulfur as indicator for benthic and pelagic prey in Baltic cod. Patterns in $\delta^{34}S$ were much more pronounced than those in $\delta^{13}C$ for the same individuals, which suggests that $\delta^{13}C$ data may underestimate such shift. However, as there was only a pilot dataset of sulfur, more data is needed.

Study	Organism	SIA	d13C range	d15N range	d34S range
Sherwood et al. (2007)	*Gadus morhua*	C	-20.0; -18.0		
Matley et al. (2013)	*Boreogadus saida*	C, N	-21.5; -18.5	13.0; 17.0	
Mohm (2014)	*Gadus morhua*	C, N, S	-22.9, -18.8	10.9; 16.2	13.8; 17.9

Table 10. Summary of all available SIA data for cod. Matley studied the feeding ecology of *Boreogadus saida* (Arctic cod), Sherwood the feeding ecology of *Gadus morhua* in Newfoundland and Labrador Sea.

Ontogenetic shifts in herring and sprat

The overlapping isotopic ranges, and the ontogenetic shift in herring but not in sprat, provided interesting insights into competitive dynamics between these two species. The low stable isotope ratios in carbon and nitrogen of herring and sprat affirm that there are pelagic planktivores (Bernreuther 2007). Möllmann et al. (2004) reported that both species are mainly feeding on calanoid copepods, whereby *Pseudocalanus sp.* is mostly important in herring's diet and *Temora longicornis* in the diet of sprat (Table 11). However, there were differences in the stable isotope ratios of the two clupeid species. Sprat did not show an ontogenetic shift confirming the assumption that sprat is strictly zooplanktivor (Möllmann et al. 2004). Whereas it has been reported by (Arrhenius & Hansson 1994) that herring changes its diet with fish size. Casini et al. (2004) investigated that small herring (<13-15cm) are strict zooplankton feeders, but larger herring (>15-20cm) prey on nektobenthos (Mysidae, amphipods and polychaetes). Corroborating the previous results, the results of SIA reported that herring showed a clear positive correlation of $\delta^{15}N$ ratios with TL indicating an ontogenetic shift. It can also clearly be seen that there is an overlap of stable isotope ratios of sprat and small herring, confirming the previous study of Möllmann et al. (2004) reporting that sprat and small herring are both strict planktivor and therefore feed on the same prey resources implies that they are potential competitors.

	herring		sprat	
prey category	**F[%]**	**W[%]**	**F[%]**	**W[%]**
Pseudocalanus sp.	39.3	33.1	17.5	23.9
Temora longicornis	47.3	15.9	52	44.1
Acartia sp.	28	4.4	34.9	14.2
other plankton	21.9	3.9	-	-
other copepods	-	-	11.7	1.9
Bosnina coregoni maritima	-	-	14.7	8.5
Podon sp.	-	-	8.4	5.5
Evadne nordmanni	-	-	5.3	1.7
Mysidacea	16.2	27	0.1	<0.1
other Macrozooplankton	6.4	3.8	0.8	<0.1
Pisces	0.9	4.1	0	0
Miscellaneous	8.3	7.7	0	0
overlap [%]	43.3			

Table 11. Food composition of herring and sprat; F is the per cent frequency of occurrence; W is the per cent relative wet mass of prey item to the total wet mass of stomach content) (Möllmann et al. 2004)

Due to the regime shift with a drastic increase in sprat stock sizes and decreases in copepod abundances, the intraspecific competition for sprat, as well as interspecific competition for herring has increased dramatically (Möllmann et al. 2004). The overall overlap between large sprat and small herring was found to be over 50 %, 42.3 % between herring and sprat of all sizes (Möllmann et al. 2004). Bernreuther (2007) has also investigated this dietary overlap between the clupeids and its seasonal dependence. So, diet is not only ontogenesis dependent but it is also depending on prey abundance and composition. The change in diet of herring occurs at critical size which is also confirmed by my results. This might be an indication to avoid interspecific competition with sprat (Möllmann et al. 2004).
The sex differences in sprat showed that males displayed higher δ15N ratios than females. This could be a result of different feeding behaviors or of the investment in eggs. The production of eggs could result in a depletion of ^{15}N in tissue of females.

Spatial differences

The observed spatial differences both between basins (cod, herring, sprat), and between sites within basins (cod, herring) provide evidence for the spatial structuring of fish populations both between basins and within basins and thus also ICES management subdivision (see

Figure 1). Specifically, if movement between sites or basins was frequent, there would be no opportunity for isotopic differences to arise, since the latter take months to develop. This finding also entails that potential migrants may be detected based on their isotope values, because they stick out as outliers and seem to belong to another SD due to their stable isotope ratios (as assessed for herring). This is only possible because SIA is a time-integrated method and muscle tissue reflects diet information for a period of several weeks to months (Hobson 1999). Thus, SIA could be used for the assessment of long-term movements and changes in feeding ecology between the basins or even within the basins (sites). Another question concerns the reason for the geographic differences in isotopic baselines. Therefore, additional data of organic matter, producers and primary consumers should be examined in further studies. The advantage of SIA compared to SCA is that spatial differences can be much easier detected. As time-integrated method, SIA would need to resample only twice in contrast to SCA which need to resample many times because you only have one snapshot and you do not know whether differences are a coincidence (e.g., fish sampled at time of unusually high abundance of a prey item, e.g., at a location where a sprat school swam around, cod may contain only sprat, but once the school has moved on, may look totally different). SCA can also entail problems regarding the quantification of prey and the detection of temporal and spatial shifts (Renones et al. 2002) and stomachs are also often empty.

While trying to get a better understanding of cods feeding ecology, it is also important to keep in mind that there are not only spatial differences, but also seasonal differences as obtained by Pachur & Horbowy (2013). The weight proportion of sprat was observed to be higher in winter than in fall and also the cannibalism occurred less in winter than in fall. Recent studies also provide that the food composition of cod yearly changes (Figure 15), suggesting that comparisons of studies of different years and seasons should consider with caution.

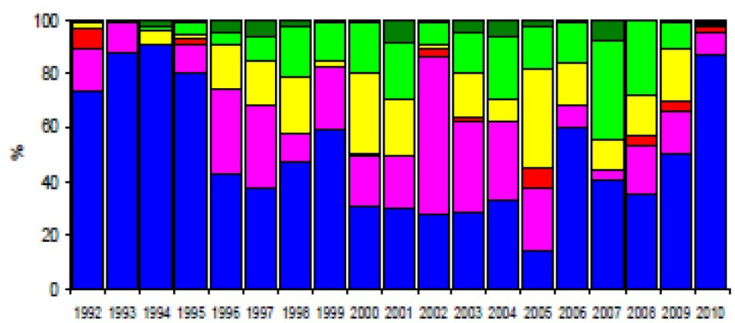

Figure 15. Cod stomach content (1992-2010) of prey items: herring (■), sprat (■), cod (■), other fish (■), *Saduria entomon* (■),other invertebrates (■). SD26. (Patokina 2011)

To sum up, the results of this study confirm previous assumptions on feeding ecology of Baltic fish species assessed by SCA but also provide new information. However, this study also raises questions concerning the temporal changes since the 1980s. For further analyses, it would be interesting to use both methods to get, on the one hand, a close and detailed view of digested prey (taxonomy, quantity) by SCA and, on the other hand, to detect general patterns and to elucidate trophic relationships by SIA. For cod, as focus species, it would be useful to analyze more samples for sulfur stable isotope data and to sample, in context to investigate the importance of benthic and pelagic prey as diet for cod, muscle tissue samples of demersal invertebrates. Furthermore, SIA could be used as tool for future monitoring of Baltic fish stock status to assess changes in large patterns which were a lot more complicated to assess with SCA. This could e.g. include shifts in importance of benthic prey, an increase or decrease in competition between certain species or effects of invasive species moving into foodweb in the future. Another interesting scientific question to address on using SIA concerns the condition of cod which has been reported to be worse although the population has recovered after the regime shift. SIA could help to understand the underlying reasons e.g. oxygen depletion on the sea floor resulting in a low availability of benthos in cod's diet and might be a potential cause for low condition in cod. The results of this study could also be used along with ecosystem models such as Ecopath to validate its assumptions of trophic positions and trophic width (Navarro et al. 2011).

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APPENDIX

SD	station	haul	species	#	TL	δ13C	δ15N	δ34S	Sex	W
22	489/KB06	1	whiting	01W10	13.0	-20.03	14.37		J	
22	489/KB06	1	whiting	01W01	14.0	-19.75	14.82		J	
22	489/KB06	1	whiting	01W08	17.0	-20.18	14.26		J	
22	489/KB06	1	whiting	01W07	21.0	-21.24	13.70		M	
22	489/KB06	1	whiting	01W09	21.0	-20.83	14.92		M	
22	489/KB06	1	whiting	01W05	23.0	-20.74	14.45		M	
22	489/KB06	1	whiting	01W06	24.0	-19.82	15.41		M	
22	489/KB06	1	whiting	01W02	26.0	-20.14	14.71		M	
22	489/KB06	1	whiting	01W03	26.0	-19.91	14.18		F	
22	489/KB06	1	whiting	01W04	27.0	-20.86	14.32		F	
22	489/KB06	2	cod	02C02	16.5	-18.77	14.17		F	32
22	489/KB06	2	cod	02C01	23.0	-19.33	14.82		M	109
22	489/KB06	2	dab	02D10	16.0	-19.81	13.51		not det.	49
22	489/KB06	2	dab	02D01	18.0	-20.70	13.26		not det.	64
22	489/KB06	2	dab	02D06	18.0	-20.43	13.43		not det.	66
22	489/KB06	2	dab	02D02	21.0	-21.12	13.49		not det.	92
22	489/KB06	2	dab	02D04	22.0	-20.85	13.59		not det.	117
22	489/KB06	2	dab	02D07	23.0	-20.71	13.47		not det.	110
22	489/KB06	2	dab	02D05	25.0	-20.07	13.86		not det.	191
22	489/KB06	2	dab	02D08	27.0	-21.04	12.99		not det.	240
22	489/KB06	2	dab	02D09	28.0	-20.29	13.23		not det.	255
22	489/KB06	2	dab	02D03	30.0	-20.22	12.88		not det.	282
22	489/KB06	2	flounder	02F02	20.0	-15.27	10.95		not det.	86
22	489/KB06	2	flounder	02F01	23.0	-20.04	11.87		not det.	334
22	489/KB06	2	flounder	02F06	25.0	-20.91	11.93		M	
22	489/KB06	2	flounder	02F08	31.0	-16.68	10.95		M	
22	489/KB06	2	flounder	02F09	31.0	-16.97	13.20		M	
22	489/KB06	2	flounder	02F03	32.0	-21.06	11.20		M	
22	489/KB06	2	flounder	02F04	32.0	-19.60	12.43		M	
22	489/KB06	2	flounder	02F05	32.0	-19.00	11.87		M	
22	489/KB06	2	flounder	02F07	32.0	-19.35	12.88		M	
22	489/KB06	2	herring	02H01	10.5	-22.15	12.00		not det.	
22	489/KB06	2	herring	02H02	10.5	-22.53	11.56		not det.	
22	489/KB06	2	herring	02H05	12.5	-21.83	12.81		not det.	
22	489/KB06	2	herring	02H06	12.5	-22.50	12.45		not det.	
22	489/KB06	2	herring	02H09	14.5	-21.81	12.71		not det.	
22	489/KB06	2	herring	02H10	14.5	-22.27	12.03		not det.	
22	489/KB06	2	herring	02H11	16.5	-21.26	12.61		not det.	
22	489/KB06	2	herring	02H12	16.5	-20.04	13.24		not det.	
22	489/KB06	2	herring	02H14	18.5	-22.94	12.22		not det.	
22	489/KB06	2	herring	02H17	20.5	-22.56	11.61		not det.	
22	489/KB06	2	plaice	02P01	22.0	-19.69	12.53		not det.	121

22	489/KB06	2	plaice	02P02	22.0	-19.55	13.30		not det.	110
22	489/KB06	2	plaice	02P06	22.0	-20.09	12.00		not det.	96
22	489/KB06	2	plaice	02P04	29.0	-19.75	11.25		not det.	226
22	489/KB06	2	plaice	02P07	31.0	-19.42	11.21		not det.	277
22	489/KB06	2	plaice	02P05	34.0	-19.67	12.80		not det.	402
22	489/KB06	2	plaice	02P03	38.0	-19.55	12.34		not det.	512
24	502/H24	3	sprat	03S08	9.0	-22.62	13.50		F	
24	502/H24	3	sprat	03S17	9.5	-22.39	10.83		M	
24	502/H24	3	sprat	03S05	10.5	-24.06	11.77		F	
24	502/H24	3	sprat	03S18	10.5	-23.18	11.07		M	
24	502/H24	3	sprat	03S06	12.5	-22.89	8.65		F	
24	502/H24	3	sprat	03S12	13.0	-22.23	12.00		M	
24	502/H24	3	sprat	03S02	13.5	-23.27	11.11		F	
24	502/H24	3	sprat	03S11	13.5	-23.60	11.50		M	
24	502/H24	3	sprat	03S13	14.0	-22.14	11.91		M	
24	502/H24	3	sprat	03S01	14.5	-22.64	11.40		F	
24	502/H24	4	cod	04C22	17.0	-20.57	13.76		J	41
24	502/H24	4	cod	04C10	22.0	-21.38	14.19		F	94
24	502/H24	4	cod	04C13	24.0	-21.22	13.69		M	232
24	502/H24	4	cod	04C14	25.0	-22.87	14.62		M	151
24	502/H24	4	cod	04C08	26.0	-21.13	14.16		M	188
24	502/H24	4	cod	04C12	26.0	-21.22	14.57		F	177
24	502/H24	4	cod	04C17	27.0	-21.33	13.73		F	173
24	502/H24	4	cod	04C11	28.0	-21.17	13.73		M	228
24	502/H24	4	cod	04C16	28.0	-21.36	14.40		M	256
24	502/H24	4	cod	04C07	30.0	-21.42	13.46		F	231
24	502/H24	4	cod	04C19	30.0	-21.40	16.15		M	275
24	502/H24	4	cod	04C03	32.0	-21.44	13.19		M	316
24	502/H24	4	cod	04C09	33.0	-21.62	14.14		F	349
24	502/H24	4	cod	04C15	33.0	-21.86	11.79		M	365
24	502/H24	4	cod	04C18	34.0	-21.86	11.95		F	427
24	502/H24	4	cod	04C01	37.0	-21.00	14.57		M	522
24	502/H24	4	cod	04C20	40.0	-21.60	15.21		F	666
24	502/H24	4	cod	04C04	41.0	-21.34	14.81		F	658
24	502/H24	4	cod	04C05	42.0	-21.73	13.04		F	746
24	502/H24	4	cod	04C21	46.0	-21.57	14.03		M	1037
24	502/H24	4	flounder	04F01	23.0	-22.68	13.90		not det.	164
24	502/H24	4	flounder	04F02	32.0	-19.63	13.68		not det.	387
24	502/H24	4	flounder	04F03	34.0	-21.17	11.68		not det.	461
24	502/H24	4	herring	04H01	18.5	-22.26	12.04		M	
24	502/H24	4	herring	04H03	20.5	-23.50	12.00		F	
24	502/H24	4	herring	04H07	22.5	-23.99	11.65		F	
24	502/H24	4	herring	04H08	22.5	-22.38	12.02		M	
24	502/H24	4	herring	04H13	24.5	-21.53	12.51		F	
24	502/H24	4	herring	04H14	24.5	-20.89	12.49		M	

24	502/H24	4	herring	04H16	26.5	-21.28	12.46		F	
24	502/H24	4	herring	04H17	26.5	-21.25	12.34		M	
24	502/H24	4	herring	04H18	28.5	-20.31	11.77		M	
24	502/H24	4	herring	04H20	30.5	-23.39	11.92		F	
24	502/H24	4	plaice	04P01	40.0	-21.61	12.24		not det.	688
24	502/H24	4	whiting	04W01	10.0	-21.39	13.36		M	8
24	502/H24	4	whiting	04W03	16.5	-21.36	15.17		M	35
24	502/H24	4	whiting	04W02	17.0	-21.27	14.51		M	39
24	502/H24	4	whiting	04W04	20.5	-21.39	13.94		M	72
24	502/H24	4	whiting	04W05	27.0	-21.59	14.46		M	173
24	502/H24	4	whiting	04W06	31.0	-21.62	14.40		F	247
24	502/H24	4	whiting	04W07	32.0	-21.85	14.06		F	272
24	502/H24	4	whiting	04W10	39.5	-21.96	12.54		F	600
24	502/H24	4	whiting	04W08	41.0	-21.88	13.85		F	610
24	502/H24	4	whiting	04W09	43.5	-21.49	14.82		F	680
24	515/H21	5	cod	05C09	26.0	-21.31	13.75		M	176
24	515/H21	5	cod	05C05	29.0	-21.74	12.64		M	240
24	515/H21	5	cod	05C07	29.0	-21.37	13.84		F	270
24	515/H21	5	cod	05C06	31.0	-21.42	14.11		M	288
24	515/H21	5	cod	05C02	35.0	-21.43	13.82		M	442
24	515/H21	5	cod	05C01	36.0	-21.38	11.92		M	439
24	515/H21	5	cod	05C08	37.0	-21.69	14.14		F	520
24	515/H21	5	cod	05C03	38.0	-21.56	13.55		M	455
24	515/H21	5	cod	05C04	39.0	-21.20	13.27		M	499
24	515/H21	5	herring	05H10	10.5	-22.57	11.90		F	
24	515/H21	5	herring	05H06	12.5	-22.48	11.65		M	
24	515/H21	5	herring	05H08	16.5	-22.35	10.07		M	
24	515/H21	5	herring	05H04	18.5	-24.01	11.60		F	
24	515/H21	5	herring	05H05	18.5	-22.70	10.36		M	
24	515/H21	5	herring	05H01	20.0	-21.34	10.58		M	45
24	515/H21	5	herring	05H07	20.5	-22.82	11.24		F	
24	515/H21	5	herring	05H11	21.5	-22.00	10.89		F	62
24	515/H21	5	herring	05H03	22.5	-22.94	11.10		M	
24	515/H21	5	herring	05H02	26.5	-21.25	12.54		M	
24	515/H21	5	sprat	05S01	8.0	-22.68	16.41		M	
24	515/H21	5	sprat	05S02	8.5	-23.47	11.01		M	
24	515/H21	5	sprat	05S03	9.0	-22.82	12.51		M	
24	515/H21	5	sprat	05S04	9.5	-22.68	11.81		M	
24	515/H21	5	sprat	05S05	10.0	-23.03	11.07		M	
24	515/H21	5	sprat	05S06	11.5	-22.13	8.88		F	
24	515/H21	5	sprat	05S07	12.5	-21.13	10.37		F	
24	515/H21	5	sprat	05S10	13.0	-23.97	12.14		F	
24	515/H21	5	sprat	05S08	15.0	-22.95	10.97		M	
24	515/H21	5	sprat	05S09	15.0	-23.38	11.13		F	
24	516/H18	6	cod	06C01	10.0	-21.42	13.90		J	

24	516/H18	6	flounder	06F06	19.0	-22.42	14.11		M	69
24	516/H18	6	flounder	06F02	20.0	-20.80	11.82		M	72
24	516/H18	6	flounder	06F16	21.0	-22.67	13.78		M	96
24	516/H18	6	flounder	06F07	23.0	-21.77	12.73		M	113
24	516/H18	6	flounder	06F15	25.0	-22.74	13.68		M	156
24	516/H18	6	flounder	06F11	26.0	-22.52	16.06		M	142
24	516/H18	6	flounder	06F14	27.0	-22.30	12.88		M	171
24	516/H18	6	fourbeard rockling	06Q01	32.0	-21.91	14.07	11.58	not det.	178
24	516/H18	6	ocean quahog	06M01	2.5	-22.06	9.05	12.26	not det.	
25	530/BB30	10	herring	10H11	22.5	-21.53	11.34		F	75
25	531/BB31	11	cod	11C08	17.0	-20.59	13.87		M	43
25	531/BB31	11	herring	11H01	20.0	-22.44	11.19		M	55
25	531/BB31	11	herring	11H02	21.0	-21.96	10.66		F	61
25	531/BB31	11	herring	11H03	23.0	-21.86	11.60		M	68
25	531/BB31	11	ocean quahog	11M01	3.0	-21.95	9.69	15.59	not det.	
25	562/BB15	13	cod	13C21	17.0	-20.58	13.37		M	38
25	562/BB15	13	herring	13H01	20.0	-21.59	10.62		M	51
25	562/BB15	13	herring	13H02	23.0	-22.06	11.30		M	74
25	562/BB15	13	herring	13H03	24.0	-21.95	11.14		F	92
25	563/BB24	14	cod	14C01	9.5	-21.45	14.05		J	10
25	563/BB24	14	flounder	14F05	23.0	-21.45	16.04		M	
25	563/BB24	14	flounder	14F07	24.0	-22.42	13.68		M	
25	563/BB24	14	flounder	14F08	25.0	-21.39	11.61		M	145
25	563/BB24	14	flounder	14F01	27.0	-22.40	13.07		F	263
25	563/BB24	14	flounder	14F04	27.0	-21.39	10.88		M	187
25	563/BB24	14	flounder	14F06	29.0	-21.79	13.02		M	134
25	563/BB24	14	flounder	14F03	31.0	-22.24	12.82		F	346
25	563/BB24	14	flounder	14F02	36.0	-21.53	11.60		F	410
25	563/BB24	14	herring	14H01	17.5	-21.91	11.66		M	42
25	563/BB24	14	herring	14H02	19.0	-21.75	10.20		M	42
25	563/BB24	14	herring	14H03	22.0	-21.90	10.95		F	77
25	563/BB24	14	herring	14H04	23.0	-21.79	11.05		F	79
25	564/BB29	15	herring	15H01	22.0	-21.39	11.62		M	60
25	564/BB29	15	herring	15H02	22.0	-21.81	10.87		F	64
25	564/BB29	15	herring	15H03	23.0	-21.84	11.14		F	75
26S	569/GD59	16	cod	16C21	10.0	-20.61	12.30		J	7
26S	569/GD59	16	cod	16C03	25.0	-20.63	12.98		M	133
26S	569/GD59	16	cod	16C08	28.0	-20.96	13.81		M	187
26S	569/GD59	16	cod	16C10	30.0	-20.97	13.11		M	227
26S	569/GD59	16	cod	16C13	30.0	-20.79	13.90		F	300
26S	569/GD59	16	cod	16C14	31.0	-20.18	12.67		M	243
26S	569/GD59	16	cod	16C01	32.0	-20.70	12.44		M	286
26S	569/GD59	16	cod	16C07	32.0	-19.72	14.17		M	296
26S	569/GD59	16	cod	16C17	32.0	-20.67	13.83		F	269
26S	569/GD59	16	cod	16C18	33.0	-20.32	12.70		F	323

26S	569/GD59	16	cod	16C02	34.0	-20.86	12.52		M	354
26S	569/GD59	16	cod	16C06	35.0	-21.02	13.61		F	457
26S	569/GD59	16	cod	16C15	35.0	-21.08	12.33		F	388
26S	569/GD59	16	cod	16C12	36.0	-20.40	13.84		M	334
26S	569/GD59	16	cod	16C19	36.0	-20.64	13.69		F	433
26S	569/GD59	16	cod	16C09	40.0	-20.34	14.18		M	636
26S	569/GD59	16	cod	16C20	42.0	-20.25	13.99		F	815
26S	569/GD59	16	cod	16C11	44.0	-19.92	13.81		M	595
26S	569/GD59	16	cod	16C16	54.0	-21.12	14.76		F	1655
26S	569/GD59	16	flounder	16F02	22.0	-21.53	14.08		M	112
26S	569/GD59	16	flounder	16F01	23.0	-20.85	13.40	13.73	F	145
26S	569/GD59	16	flounder	16F07	24.0	-20.42	12.08		M	
26S	569/GD59	16	flounder	16F03	26.0	-22.53	14.45		M	
26S	569/GD59	16	flounder	16F04	26.0	-21.32	14.43	14.48	M	
26S	569/GD59	16	flounder	16F06	27.0	-21.13	12.82		M	
26S	569/GD59	16	flounder	16F05	30.0	-20.06	13.33	12.66	M	249
26S	569/GD59	16	herring	16H04	20.0	-20.98	12.27		M	
26S	569/GD59	16	herring	16H01	21.0	-21.08	12.41		F	
26S	569/GD59	16	herring	16H02	22.0	-21.58	11.45		M	
26S	569/GD59	16	herring	16H03	24.0	-21.11	12.55		M	
26S	569/GD59	16	sprat	16S02	11.0	-22.50	11.17		M	
26S	569/GD59	16	sprat	16S03	11.0	-22.16	9.30		M	
26S	569/GD59	16	sprat	16S04	11.0	-21.50	11.07		M	
26S	569/GD59	16	sprat	16S01	12.0	-20.90	10.13		M	
26S	569/GD59	16	sprat	16S05	12.0	-21.55	10.07		M	
26S	569/GD59	16	sprat	16S07	12.0	-23.22	9.61		F	
26S	569/GD59	16	sprat	16S08	12.0	-22.64	10.25		F	
26S	569/GD59	16	sprat	16S10	12.0	-21.89	9.70		F	
26S	569/GD59	16	sprat	16S09	13.0	-21.46	9.99		F	
26S	569/GD59	16	sprat	16S06	14.0	-21.83	9.47		F	
26S	570/GD60	17	flounder	17F02	22.0	-21.23	12.53	15.37	M	99
26S	570/GD60	17	flounder	17F01	31.0	-20.92	12.25	14.82	F	333
26S	571/GD60a	18	cod	18C05	31.0	-20.66	12.19		M	323
26S	571/GD60a	18	cod	18C10	31.0	-20.72	13.15	13.84	F	275
26S	571/GD60a	18	cod	18C14	31.0	-19.67	13.51		M	297
26S	571/GD60a	18	cod	18C13	32.0	-20.29	14.06		M	313
26S	571/GD60a	18	cod	18C15	33.0	-19.67	13.75		M	385
26S	571/GD60a	18	cod	18C11	34.0	-20.75	12.11		M	406
26S	571/GD60a	18	cod	18C12	34.0	-20.83	13.98		M	372
26S	571/GD60a	18	cod	18C04	35.0	-20.44	13.54		M	401
26S	571/GD60a	18	cod	18C08	35.0	-19.86	13.30	15.45	F	391
26S	571/GD60a	18	cod	18C16	35.0	-19.92	14.29		M	442
26S	571/GD60a	18	cod	18C17	36.0	-20.00	14.03		M	438
26S	571/GD60a	18	cod	18C09	38.0	-20.57	13.59	16.24	M	498
26S	571/GD60a	18	cod	18C06	39.0	-20.69	13.03		M	596

26S	571/GD60a	18	cod	18C01	41.0	-20.31	13.67		M	630
26S	571/GD60a	18	cod	18C03	41.0	-20.30	14.06	15.95	M	1002
26S	571/GD60a	18	cod	18C02	45.0	-20.46	13.40		M	834
26S	571/GD60a	18	cod	18C07	48.0	-20.49	14.06	16.60	M	924
26N	581/GB80	21	cod	21C11	25.0	-21.06	11.76		M	123
26N	581/GB80	21	cod	21C02	29.0	-20.16	13.93		M	239
26N	581/GB80	21	cod	21C09	29.0	-20.66	12.74		F	239
26N	581/GB80	21	cod	21C05	30.0	-20.41	12.99		M	267
26N	581/GB80	21	cod	21C10	30.0	-19.98	14.34		M	237
26N	581/GB80	21	cod	21C15	32.0	-20.20	13.41		M	286
26N	581/GB80	21	cod	21C06	34.0	-20.05	14.08		M	209
26N	581/GB80	21	cod	21C07	34.0	-21.19	13.21		M	338
26N	581/GB80	21	cod	21C12	35.0	-21.14	12.76		F	367
26N	581/GB80	21	cod	21C13	35.0	-21.09	13.34		M	367
26N	581/GB80	21	cod	21C14	37.0	-20.36	13.85		F	529
26N	581/GB80	21	cod	21C01	38.0	-20.05	14.58		M	470
26N	581/GB80	21	cod	21C04	38.0	-20.86	12.99		F	523
26N	581/GB80	21	cod	21C08	40.0	-20.62	13.71		M	642
26N	581/GB80	21	cod	21C03	41.0	-20.19	13.93		M	589
26N	581/GB80	21	flounder	21F12	19.0	-22.03	12.34		M	
26N	581/GB80	21	flounder	21F10	22.0	-21.73	11.27		M	
26N	581/GB80	21	flounder	21F08	23.0	-20.81	12.69		M	
26N	581/GB80	21	flounder	21F02	26.0	-20.74	12.98		F	228
26N	581/GB80	21	flounder	21F03	27.0	-20.93	13.07		F	284
26N	581/GB80	21	flounder	21F09	28.0	-20.22	13.86		M	
26N	581/GB80	21	flounder	21F14	29.0	-21.06	11.43		M	
26N	581/GB80	21	flounder	21F05	30.0	-21.93	13.99		F	338
26N	581/GB80	21	flounder	21F06	31.0	-20.96	12.42		F	367
26N	581/GB80	21	flounder	21F04	33.0	-20.32	12.90		F	420
26N	581/GB80	21	sprat	21S07	8.5	-23.43	11.89		M	
26N	581/GB80	21	sprat	21S08	8.5	-24.47	12.08		F	
26N	581/GB80	21	sprat	21S05	10.0	-22.38	12.14		M	
26N	581/GB80	21	sprat	21S06	10.0	-22.69	10.10		F	
26N	581/GB80	21	sprat	21S03	11.0	-22.46	9.19		M	
26N	581/GB80	21	sprat	21S04	11.0	-21.56	10.62		F	
26N	581/GB80	21	sprat	21S01	12.0	-21.36	10.46		M	
26N	581/GB80	21	sprat	21S02	12.0	-21.84	9.24		F	
26N	581/GB80	21	sprat	21S10	13.0	-21.45	10.22		M	
26N	581/GB80	21	sprat	21S09	13.5	-22.75	10.04		F	
26N	584/GB82a	23	cod	23C02	27.0	-20.62	12.35		M	150
26N	584/GB82a	23	cod	23C03	28.0	-20.58	13.23		M	166
26N	584/GB82a	23	cod	23C01	32.0	-21.06	13.00		M	290
26N	584/GB82a	23	flounder	23F05	23.0	-20.55	13.70		M	136
26N	584/GB82a	23	flounder	23F06	25.0	-20.40	13.50		M	158
26N	584/GB82a	23	flounder	23F02	26.0	-21.76	13.08		F	227

26N	584/GB82a	23	flounder	23F04	27.0	-20.26	13.40		M	195
26N	584/GB82a	23	flounder	23F01	31.0	-20.38	12.88		F	406
26N	584/GB82a	23	flounder	23F03	34.0	-21.20	13.09		F	453
26N	584/GB82a	23	sprat	23S03	8.5	-22.41	9.21		F	
26N	584/GB82a	23	sprat	23S04	8.5	-21.96	10.11		M	
26N	584/GB82a	23	sprat	23S09	9.0	-21.92	9.91		M	
26N	584/GB82a	23	sprat	23S10	9.0	-23.09	10.28		F	
26N	584/GB82a	23	sprat	23S05	11.0	-24.01	9.03		F	
26N	584/GB82a	23	sprat	23S06	11.0	-23.87	12.55		M	
26N	584/GB82a	23	sprat	23S07	12.0	-20.15	10.62		M	
26N	584/GB82a	23	sprat	23S08	12.0	-22.81	10.44		F	
26N	584/GB82a	23	sprat	23S01	13.5	-22.83	12.64		M	
26N	584/GB82a	23	sprat	23S02	13.5	-21.34	9.53		F	
25	601/BB04	30	coalfish	30Se03	36.0	-21.40	12.24		not det.	418
25	601/BB04	30	coalfish	30Se01	37.0	-21.09	12.03		not det.	415
25	601/BB04	30	coalfish	30Se02	40.0	-20.93	11.74		not det.	609
25	601/BB04	30	cod	30C18	28.0	-21.14	13.60		M	213
25	601/BB04	30	cod	30C17	31.0	-21.45	12.25		F	292
25	601/BB04	30	cod	30C12	32.0	-21.64	12.74		F	310
25	601/BB04	30	cod	30C19	33.0	-21.44	12.60		M	372
25	601/BB04	30	cod	30C20	33.0	-21.84	10.86		M	342
25	601/BB04	30	cod	30C05	34.0	-21.90	12.89		F	372
25	601/BB04	30	cod	30C03	36.0	-21.55	12.56		F	419
25	601/BB04	30	cod	30C09	37.0	-21.30	13.67		F	502
25	601/BB04	30	cod	30C13	39.0	-21.44	12.52		F	513
25	601/BB04	30	cod	30C24	40.0	-21.12	12.57		M	678
25	601/BB04	30	cod	30C07	42.0	-21.12	13.32		M	660
25	601/BB04	30	cod	30C08	43.0	-20.96	13.05		F	641
25	601/BB04	30	cod	30C23	44.0	-21.32	13.05		M	827
25	601/BB04	30	cod	30C04	45.0	-21.29	12.81		M	760
25	601/BB04	30	cod	30C22	46.0	-21.66	12.89		M	695
25	601/BB04	30	cod	30C10	47.0	-21.66	11.77		F	1077
25	601/BB04	30	cod	30C26	49.0	-21.82	16.21		M	1157
25	601/BB04	30	cod	30C27	50.0	-21.14	13.39		F	1171
25	601/BB04	30	herring	30H10	16.5	-21.42	9.89		F	
25	601/BB04	30	herring	30H08	18.5	-21.78	9.92		F	
25	601/BB04	30	herring	30H09	18.5	-21.60	9.82		M	
25	601/BB04	30	herring	30H01	20.5	-22.15	10.19		M	
25	601/BB04	30	herring	30H02	20.5	-22.47	11.95		F	
25	601/BB04	30	herring	30H07	20.5	-21.81	10.09		F	
25	601/BB04	30	herring	30H05	22.5	-22.04	10.71		F	
25	601/BB04	30	herring	30H06	22.5	-22.43	11.35		M	
25	601/BB04	30	herring	30H03	24.5	-22.14	10.85		M	
25	601/BB04	30	herring	30H04	26.5	-22.10	11.87		M	
25	601/BB04	30	sprat	30S07	9.5	-22.00	10.35		M	

25	601/BB04	30	sprat	30S08	10.0	-21.95	10.78		F	
25	601/BB04	30	sprat	30S05	11.0	-22.24	9.26		F	
25	601/BB04	30	sprat	30S06	11.0	-20.53	10.62		M	
25	601/BB04	30	sprat	30S01	12.0	-21.49	10.21		F	
25	601/BB04	30	sprat	30S02	12.0	-22.93	9.24		M	
25	601/BB04	30	sprat	30S03	13.0	-20.95	10.44		F	
25	601/BB04	30	sprat	30S04	13.0	-21.61	10.46		M	
25	601/BB04	30	sprat	30S09	13.5	-20.90	10.32		M	
25	601/BB04	30	sprat	30S10	14.5	-23.50	9.48		F	
25	601/BB04	30	whiting	30W01	40.0	-22.10	13.48		not det.	555
25	602/BB04	31	coalfish	31Se01	33.0	-20.69	12.35		not det.	308
25	602/BB04	31	coalfish	31Se03	36.0	-19.81	11.03		not det.	482
25	602/BB04	31	coalfish	31Se02	40.0	-21.05	12.06		not det.	630
25	602/BB04	31	coalfish	31Se04	41.0	-20.39	11.82		not det.	640
25	602/BB04	31	cod	31C02	52.0	-21.47	12.94		F	1378
25	602/BB04	31	cod	31C01	53.0	-21.20	13.97		F	1465
25	602/BB04	31	whiting	31W01	30.0	-21.31	14.39		not det.	242
25	603/BB18	32	coalfish	32Se01	41.0	-20.37	11.14		not det.	684
25	605/BB32	34	cod	34C19	11.0	-21.14	13.95		not det.	14
25	605/BB32	34	cod	34C18	12.0	-21.25	13.39		not det.	13
25	605/BB32	34	cod	34C20	12.0	-21.38	13.80		not det.	15
25	605/BB32	34	cod	34C21	12.0	-20.55	14.23		not det.	12
25	605/BB32	34	cod	34C22	12.0	-21.18	13.65		not det.	16
25	605/BB32	34	cod	34C17	16.0	-21.33	13.43		not det.	35
25	605/BB32	34	cod	34C16	17.0	-21.07	13.19		not det.	49
25	605/BB32	34	flounder	34F04	20.0	-21.18	11.75	16.92	M	90
25	605/BB32	34	flounder	34F03	24.0	-21.92	11.23	16.37	M	144
25	605/BB32	34	flounder	34F02	26.0	-21.85	13.50	12.64	M	186
25	605/BB32	34	fourbeard rockling	34Q01	16.0	-20.68	14.64	11.69	not det.	19
25	605/BB32	34	plaice	34P01	25.0	-21.88	12.10		not det.	128
25	605/BB32	34	plaice	34P02	30.0	-21.83	11.76		not det.	242
25	605/BB32	34	whiting	34W08	16.0	-21.60	14.12		not det.	29
25	605/BB32	34	whiting	34W03	18.0	-21.10	13.92		not det.	45
25	605/BB32	34	whiting	34W07	18.0	-21.37	14.14		not det.	50
25	605/BB32	34	whiting	34W05	19.0	-21.45	14.00		not det.	60
25	605/BB32	34	whiting	34W01	20	-21.18	13.57		not det.	62
25	605/BB32	34	whiting	34W04	20.0	-21.31	13.89		not det.	60
25	605/BB32	34	whiting	34W06	20.0	-21.36	13.21		not det.	61
25	605/BB32	34	whiting	34W02	27.0	-21.20	12.78		not det.	192
25	608/BB42	37	cod	37C24	7.5	-21.97	12.86	15.33	J	3
25	608/BB42	37	cod	37C23	9.5	-21.20	13.11		J	6
25	608/BB42	37	cod	37C22	13.5	-21.37	12.29		J	19
25	608/BB42	37	cod	37C19	20.0	-20.86	12.26		M	85
25	608/BB42	37	cod	37C16	21.0	-20.37	13.11		J	73
25	608/BB42	37	cod	37C17	21.0	-20.95	12.38	15.51	F	72

25	608/BB42	37	cod	37C20	22.0	-20.35	13.10		M	91
25	608/BB42	37	cod	37C14	24.0	-20.50	13.34		F	119
25	608/BB42	37	cod	37C10	25.0	-20.36	13.35		M	139
25	608/BB42	37	cod	37C18	26.0	-21.01	12.78		F	148
25	608/BB42	37	cod	37C13	28.0	-19.95	12.48		M	190
25	608/BB42	37	cod	37C05	29.0	-21.30	12.50	17.92	M	249
25	608/BB42	37	cod	37C08	31.0	-21.28	14.02		F	286
25	608/BB42	37	cod	37C06	34.0	-21.84	13.06		M	368
25	608/BB42	37	cod	37C03	35.0	-20.74	12.35		F	366
25	608/BB42	37	cod	37C07	37.0	-20.72	12.73		F	487
25	608/BB42	37	cod	37C04	39.0	-21.16	13.31	17.93	M	565
25	608/BB42	37	cod	37C12	41.0	-20.56	13.03		M	580
25	608/BB42	37	cod	37C01	43.0	-19.96	13.68		F	657
25	608/BB42	37	cod	37C02	50.0	-21.07	13.11	17.47	F	1225
25	608/BB42	37	flounder	37F02	20.0	-21.67	10.86	17.68	M	88
25	608/BB42	37	flounder	37F01	32.0	-20.75	11.60	16.36	M	308
25	608/BB42	37	herring	37H01	10.5	-22.48	11.17	17.56	M	
25	608/BB42	37	herring	37H02	12.5	-22.25	11.46		M	
25	608/BB42	37	herring	37H03	12.5	-22.24	12.30	16.95	F	
25	608/BB42	37	herring	37H04	14.5	-20.86	9.89		F	
25	608/BB42	37	herring	37H05	18.5	-21.94	10.42	17.70	M	
25	608/BB42	37	herring	37H06	18.5	-22.07	9.78		F	
25	608/BB42	37	herring	37H07	22.5	-20.53	12.49		F	
25	608/BB42	37	herring	37H08	22.5	-22.32	12.47	16.88	M	
25	608/BB42	37	herring	37H09	24.5	-21.57	11.69	18.37	F	
25	608/BB42	37	herring	37H10	24.5	-20.13	12.45		M	
25	608/BB42	37	sprat	37S01	8.5	-21.89	10.26	16.93	F	
25	608/BB42	37	sprat	37S02	8.5	-23.20	14.48		M	
25	608/BB42	37	sprat	37S05	10.0	-22.97	11.28		F	
25	608/BB42	37	sprat	37S06	10.0	-23.26	11.39	16.39	M	
25	608/BB42	37	sprat	37S04	11.0	-22.22	10.31	17.60	F	
25	608/BB42	37	sprat	37S07	12.0	-22.27	9.41		F	
25	608/BB42	37	sprat	37S08	12.0	-21.44	10.61	17.10	M	
25	608/BB42	37	sprat	37S09	14.0	-24.01	10.68		M	
25	608/BB42	37	sprat	37S10	14.5	-23.23	9.86	17.40	F	

Appendix 1. Sample list per ICES subdivision (see Figure 1), sampling site, haul number, species, identification number, total length [cm], $\delta^{13}C$ ratio, $\delta^{15}N$ ratio, $\delta^{34}S$ ratio, sex (male, female, juvenile; not determined), weight [g]obtained during AL 435.

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ERKLÄRUNG

Hiermit erkläre ich, dass ich die vorliegende Arbeit selbständig und ohne fremde Hilfe angefertigt und keine anderen als die angegebenen Quellen und Hilfsmittel verwendet habe.

Die eingereichte schriftliche Fassung der Arbeit entspricht der auf dem elektronischen Speichermedium.

Weiterhin versichere ich, dass diese Arbeit noch nicht als Abschlussarbeit an anderer Stelle vorgelegen hat.

Ort, Datum Unterschrift