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Forage fish control population dynamics of North Sea whiting *Merlangius merlangus*

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ABSTRACT: Predator populations are often affected by the abundance of their prey, but pronounced effects on predatory fish have mainly been demonstrated in ecosystems where a key predator depends largely on one key prey species. The North Sea food web has a comparatively high level of complexity with a high diversity of forage fish, and hence strong effects are less likely to occur. However, in the early 2000s within large parts of the North Sea, several forage fish stocks simultaneously suffered from successive years of recruitment failure together with decreasing stock abundances. Whiting *Merlangius merlangus* is a major fish predator in the North Sea ecosystem and is known to be almost exclusively piscivorous. We hypothesised that shortages in forage fish should lead to negative effects on growth or condition of a predator that relies on a few dominant prey fish species. In our study, we combined 6 different North Sea data sets on abundance of forage fish and length-at-age, condition and stomach contents of *M. merlangus* to analyse contrasting periods with high and low forage fish availability. We found a simultaneous decrease in forage fish availability and *M. merlangus* length-at-age in the period from 2000–2007 and a subsequent parallel increase in prey abundance and length-at-age after 2007. In the period of low forage fish availability, mean stomach content mass was on average 60% less than in the reference periods. Additionally, a bioenergetics calculation revealed that even smaller differences in the stomach contents than those observed would have been sufficient to explain the observed differences in length-at-age. Our findings emphasize the need to incorporate predator–prey interactions in assessment models and management strategies.

KEY WORDS: Whiting · Forage fish · Population dynamics · Stomach content analysis · Bioenergetics modelling · Predator–prey relationship

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INTRODUCTION

How and to what extend ecosystems are regulated by bottom-up mechanisms is a fundamental question in ecology (Rindorf et al. 2006, Frederiksen et al. 2007). In marine ecosystems, forage fish represent a major source of food for top predators (Pikitch et al. 2014). Large fluctuations in the abundance of forage fish can significantly influence breeding success of marine birds and mammals (Pomeroy et al. 1999, Rindorf et al. 2000). Likewise, predatory fish populations are influenced by the abundance of their key prey species. In northeast Arctic cod *Gadus morhua* stocks, the first of 4 major stock collapses of its major prey, capelin *Mallotus villosus*, led to a pronounced reduction in average weight-at-age (Mehl & Sunnanå 1991, Gjøsæter et al. 2009). In the Baltic cod stock, a lack of suitable prey led to a substantial

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depression in condition (Eero et al. 2012). Nonetheless, those findings mainly refer to ecosystems characterised by relatively few species and a dominant single predator–prey relationship.

In contrast, the North Sea ecosystem is characterised by a more complex food web structure and a comparatively higher diversity of forage fish consumed by the key fish predators. Hence, decrease in a single prey species stock most likely has less serious consequences for a predator population. Thus, apart from locally restricted or not very pronounced effects (Rindorf et al. 2008, Engelhard et al. 2013, Cormon et al. 2016), evidence for such relationships is rare.

However, in the beginning of the 2000s, several North Sea forage fish stocks (sandeels *Ammodytes* spp., Norway pout *Trisopterus esmarkii*, herring *Clupea harengus* and sprat *Sprattus sprattus*) simultaneously suffered from recruitment failures and subsequent declines in stock sizes (Payne et al. 2009, ICES 2012b). Whiting *Merlangius merlangus* is a key fish predator and an important component of the North Sea ecosystem (Knijn et al. 1993, Greenstreet & Hall 1996, Rindorf 2003). In contrast to other gadoids, *M. merlangus* is a highly selective feeder which is almost exclusively piscivorous at sizes over 25 cm, feeding mainly on *Ammodytes* spp., and on age 0 and 1 groups of *T. esmarkii*, *C. harengus* and *S. sprattus* (Hislop et al. 1991, Knijn et al. 1993). Thus, *M. merlangus* is expected to be more sensitive to changes in a few preferred prey species. In summary, the situation of the North Sea ecosystem in the period 2000–2007 represents an excellent real-world experiment in which to study the reaction of a specialised predator population to changing feeding conditions.

Here we investigated the changes in the North Sea forage fish community that occurred in the early 2000s and the consequences for *M. merlangus*. The period from 2000–2007 was characterised by low prey availability, while in contrast the years after 2007 represent a period of sufficient food supply. Shortages in forage fish should lead to negative effects on condition and/or somatic or reproductive growth of *M. merlangus*. To address this hypothesis, we quantified temporal changes in (1) length-at-age of North Sea *M. merlangus*, (2) forage fish abundance in the North Sea, (3) stomach contents of *M. merlangus* and (4) condition of *M. merlangus* during different feeding regimes. In addition, we estimated the differences in consumption rates and stomach contents that would be theoretically expected if the observed differences in length-at-age were caused solely by lower consumption rates.

MATERIALS AND METHODS

The present study is based on 6 different North Sea data sets. An overview of the spatio-temporal overlap of the different data sources is given in Table 1.

Table 1. Data used in the analyses showing spatial and temporal coverage of the datasets by quarter (Q) and ICES roundfish area (RA; see Fig. 1). The stomach content dataset is composed of 4 different data subsets (a–d); inset table shows their spatio-temporal origin. NS-IBTS: North Sea International Bottom Trawl Survey; YoS: Year of the Stomach; GSBTS: German Small-scale Bottom Trawl Survey; DAPSTOM: Integrated Database and Portal for Fish Stomach Records. Ind.: individual fish

Data	Sources	Data type	Sample type	Sample year	Spatio-temporal coverage Q	RA
Length-at-age	NS-IBTS	Survey	Ind.	1990–2014	1	1–7
Forage fish abundance	NS-IBTS	Survey	Ind.	1990–2014	1	1–7
	Stochastic multi-species (SMS) model	Model	–	1990–2010	1	1–7
Temperature	ICES OcHyd data set	Survey	–	1990–2014	1, 3	1-7
Stomach contents	(a) ICES YoS	Survey	Pooled	1990 and 1991		
	(b) GSBTS	Survey	Ind.	1996 and 1997		
	(c) DAPSTOM	Survey	Ind.	2004–2006		
	(d) IndData	Survey	Ind.	2007 and 2012		
Mass-at-age	NS-IBTS	Survey	Ind.	1990–2014	1	1–7
Liver mass	IndData	Survey	Ind.	2007	3	3, 4
				2012	1	1, 3, 4, 6

Q	1	2	3	4	6
1	a,d		a,d	a,d	a,d
2				a,c	
3	a,d	a,c	a,b,d	a,b,c	
4		a,c		a,c	

Length-at-age of *Merlangius merlangus*

Data on the length-at-age of whiting *M. merlangus* between 1990 and 2014 was obtained from the ICES Database of Trawl Surveys (DATRAS; www.ices.dk/marine-data/data-portals/Pages/DATRAS.aspx) (downloaded 25 Nov 2014). DATRAS contains data collected during the North Sea International Bottom Trawl Survey (NS-IBTS) coordinated by the ICES. The NS-IBTS is a large-scale survey which is based on 1–4 randomly located 30 min GOV (Grande overture vertical) trawl hauls in each statistical rectangle (0.5° latutude × 1.0° longitude) (Fig. 1). A detailed survey description can be found in the 'Manual for the international bottom trawl surveys' (ICES 2012a). The mean length-at-age of *M. merlangus* for a given sex, year and roundfish area (RA) was calculated to evaluate trends over the period 1990–2014. To avoid seasonal bias we used only subsets of the first quarters (Jan–Mar) for the analyses. We compared the mean length-at-age of female and male *M. merlangus* between the periods 1990–1999, 2000–2007 and 2008–2017. For statistical comparisons between the 3 periods, we used the mean length-at-age of the respective RA and year sampled. We used Kruskal-Wallis rank sum tests and adjacent Wilcoxon rank sum tests applying Bonferroni corrections.

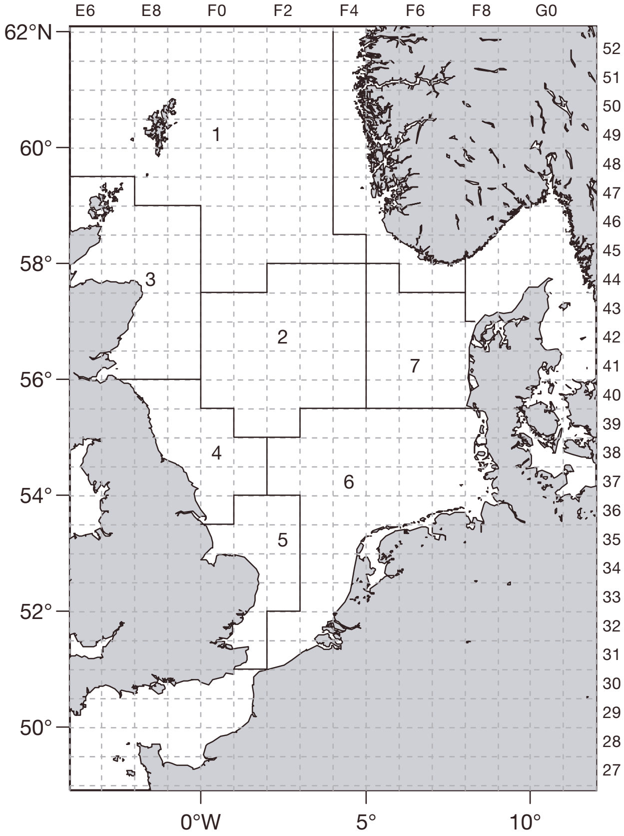

Fig. 1. Study area. Black lines: ICES North Sea roundfish areas (1–7); grey dashed lines: ICES statistical rectangles

Forage fish abundance and temperatures

Forage fish abundance was derived from 2 sources: field and model data. The catch (numbers) per unit effort (CPUE) of forage fish species (*Clupea harengus*, *Sprattus sprattus*, *Ammodytes* spp., *Trisopterus esmarkii*) smaller than 15 cm in total length in first quarters between 1990 and 2014 was extracted from ICES DATRAS. Alternative estimates of annual forage fish abundance were obtained from the output of the 2011 key run (ICES 2011) of an age–length structured stochastic multi-species (SMS) model for the North Sea (Lewy & Vinther 2004). Using the model output acknowledges that catchability of small fish, especially *Ammodytes* spp., is poor for the GOV trawl gear (Fraser et al. 2007) and thus IBTS field data may be biased. We extracted the estimated number of age 1 recruits of *C. harengus*, *S. sprattus*, *Ammodytes* spp. and *T. esmarkii* in the first quarters between 1990 and 2010.

As an annual index of survey abundance, we calculated the mean CPUE of forage fish for the total North Sea from the first quarter IBTS dataset. We first calculated mean CPUE for each forage fish species by RA and year, summed the species-specific means for a given year by RA and finally computed the overall annual mean as an area-weighted mean across RAs, weighted by the number of rectangles in each RA. North Sea temperature data was obtained from the ICES data set on ocean hydrography. Temperatures were averaged for each station within the upper 10 m of the water column. All stations within each statistical rectangle of the North Sea were pooled. RA annual average temperatures were calculated for first and third (Jul–Sep) quarters from statistical rectangles that were sampled continually each year and quarter. Total North Sea mean temperature was calculated using the number of statistical rectangles each RA encompasses as a weighting factor.

Stomach contents

Stomach contents included in this analysis originated from 4 different sources. A summary of stomach samples and the spatio-temporal coverage of samples is given in Table 1. (1) The ICES year of the stomach (YoS) database provided data on *M. merlangus* stomach contents during 1991. Fish stomachs were collected as part of an ICES initiative, and a detailed description of the data collection is given in the manual for the ICES North Sea stomach sampling project in 1991 (ICES 1991, Hislop et al. 1997). (2) Data on *M. merlangus* stomach contents in 1996 and 1997 were obtained from the German Small-scale Bottom Trawl Survey (GSBTS) covering four 10 × 10 nautical mile boxes in the North Sea. A total of 6–8 GOV trawl hauls, each with a target of 30 min towing time within each box were carried out on each of 3 consecutive days per box. A detailed survey description can be found in Ehrich et al. (2007). (3) Data on stomach contents of *M. merlangus* for the period 2004–2006 were derived from the integrated database and portal for fish stomach records (DAPSTOM), which is coordinated by the Centre for Environment, Fisheries & Aquaculture Science (Cefas). A detailed description of the data is given in Pinnegar (2014). (4) Additional stomachs were sampled during 2 North Sea research cruises with the German IBTS standard vessel ('Walther Herwig III') in 2007 and 2012. During both cruises, the IBTS standard GOV trawl was deployed for 30 min. In 2007, fish stomachs were sampled during the GSBTS in July and August. From each haul, if possible, 5 fish of length classes 20–24.9, 25–29.9, 30–34.9, 35–39.9 and >40 cm were immediately frozen at −40°C. In April 2012, *M. merlangus* were caught during a research cruise in the frame of the EU-project VECTORS, with 69 trawl hauls. Where possible, 10 fish of the 2007 sampling scheme length classes were frozen immediately for later analysis. In the laboratory, individual fish total and standard length (1 mm) and body mass (0.01 g) was recorded, as well as sex, gutted weight (0.01 g) and weight of internal organs (0.001 g). Fish that showed signs of regurgitation were registered, and their stomach contents were not analysed to reduce bias introduced by the sampling method. The mass (0.001 g) of the full and empty stomach was recorded as well as the mass of the stomach contents (0.001 g).

Except for 40 stomachs in 2006 samples, all stomachs were taken during the daytime. Time of day is less influential if larger fish prey is consumed, since evacuation times approach or exceed 24 h. Although peak feeding was detected during nighttime, no diel pattern appeared in the stomach content weights in a study of whiting preying on sandeel (Mergardt & Temming 1997).

Since ICES YoS samples were analysed as pooled samples and no information on individual stomach content was available, the same procedure was applied to all other stomach data sets to make them comparable. For each haul and length class of *M. merlangus*, we calculated the average mass of the stomach content (M_{SC}) by pooling the individual samples (Hislop et al. 1991):

$$M_{\text{SC}} = \frac{M_{\text{TOT}}}{N_{\text{F}}} \times \frac{(N_{\text{F}} + N_{\text{SR}} + N_{\text{R}})}{N} \qquad (1)$$

where M_{TOT} is the total stomach content mass of all samples, N is the total number of *M. merlangus* stomachs per haul and size class, N_{F} is the number of stomachs containing food, N_{SR} is the number of stomachs containing only skeletal remains and N_{R} is the number of stomachs with signs of regurgitation. This way of calculating the average stomach content includes the number of stomachs derived from regurgitated whiting in the total number of stomachs containing food. Fish might regurgitate their stomach contents during the process of catching, and by definition, stomachs that show signs of regurgitation were not empty. It is assumed that before regurgitation, regurgitated stomachs contained on average the same mean stomach content as the stomach samples with food (Hislop et al. 1991). We calculated mean M_{SC} for *M. merlangus* for the length classes between 25 and 40 cm because *M. merlangus* are mainly piscivorous at 25 cm and larger (Hislop et al. 1997) and sample size decreased substantially in some subsets for fish larger than 40 cm.

To be able to compare the data from the included size classes, we calculated M_{SC} as percentage of total body mass (M_{SCrel}). Individual body masses of fish were not available from the ICES subset; hence, we calculated the average body mass of each predator size class for all data sets applying the length (L) mass (M) relationship:

$$M(\text{g}) = a \times L\ (\text{cm})^{b}, \qquad (2)$$

where $a = 0.0061$ and $b = 3.067$, based on empirical field data collected during the period 1997–2007 in all quarters throughout the North Sea (Wilhelms 2013). Given that variability in condition during that period was negligible (this study), using a constant length–weight relationship is considered to be justifiable. To assure the representativeness of samples, we only included stomach samples with N of at least 5 per haul and size class for further analysis. The average stomach content per RA was calculated as the weighted mean M_{SCrel} across hauls within a given RA, weighted by the number of stomachs per haul. The year-specific M_{SCrel} was compared on a quarter- and area-specific basis using a Kruskal-Wallis chi-squared test and the adjacent Wilcoxon rank sum test applying Bonferroni corrections. Note that data were not available for all RAs, in all quarters and years (Table 1); however, RA 4 (central-western North Sea) and the third quarter were consistently and repeatedly surveyed.

Condition of *M. merlangus*

Information on length- and mass- at-age of *M. merlangus* in first quarters between 2000 and 2014 was extracted from ICES DATRAS. Prior to that, the body mass of the fish was not recorded individually on a regular basis. To analyse the condition of fish, Fulton's condition factor (k) (Ricker 1975) was calculated as:

$$k = 100 \times \left(\frac{W}{L^3}\right) \qquad (3)$$

where W is the somatic mass (g) and L is the total length (cm) of individual fish. Individual k values were used to compute average k by size class and year. A loess smoother (Cleveland 1979, Cleveland et al. 1992) was fit to the annual time series of k index for each length class to describe the variation in the condition of North Sea *M. merlangus*.

The hepatosomatic index (HSI) was calculated from individual *M. merlangus* samples collected during the 2 research cruises in 2007 and 2012 described above (point 4 in stomach content section), since individual information on the liver masses was available from those fish. Based on forage fish abundance information from the IBTS and the SMS model, 2007 was considered as a year of low food abundance and 2012 as a year with sufficient food supply. HSI (Wootton et al. 1978) was estimated as:

$$\text{HSI} = 100 \times (\text{LW} \times W^{-1}) \qquad (4)$$

where LW and W represent liver and somatic masses (g), respectively. Sex- and length-specific HSI were compared between 2007 and 2012 using Mann-Whitney rank sum tests.

Quantitative relation between growth and food intake

Generalised von Bertalanffy growth models (Pauly 1981) were fitted to first quarter *M. merlangus* length-at-age data from the period 2001–2007 and to length-at-age data from the period 2008–2014 downloaded from ICES DATRAS for females and males, respectively. To check if the observed differences in stomach contents between different periods were sufficient to explain the corresponding differences in length-at-age, we applied a simple bioenergetics model (Temming & Herrmann 2009) which estimates consumption rates (g d^{-1}) as a function of fish weight from the growth parameters of the generalised von Bertalanffy model. The consumption estimates were subsequently transformed into respective stomach contents using information on gastric evacuation rates (see the Appendix for a detailed description of the model). The model accounts for food quality via a parameter for net conversion efficiency (K_3). Food composition of *M. merlangus* in the periods was not significantly different (Lauerburg et al. 2015), thus we used the same K_3 value in both periods. Temperature is indirectly included via the parameter K (catabolic constant) in the model, which represents anabolism (weight loss sensu von Bertalanffy). Parameter K includes both metabolic costs and spawning loss. However, parameter K reflects only the mean conditions during the period covered by the length-at-age data. For our exercise, we used in one scenario the same K value and the same food conversion efficiency (K_3) for both periods, assuming no differences in metabolic cost and prey quality, and estimated the different W_∞ and t_0 values from the length-at-age of whiting in the period 2007–2007 and 2008–2014. These were then translated into corresponding food consumption rates and subsequently into different stomach contents by weight. The calculated theoretical differences in stomach contents between the 2 periods then served as a reference for the interpretation of the field data on stomach contents. Since the ambient temperature of whiting was slightly higher (0.6°C) in the period with poor feeding conditions, we alternatively calculated a second scenario, where we increased the K value of the first period by 4.2%, corresponding to the effect of this temperature increase on metabolic cost, assuming a Q_{10} value of 2 (Brander 1995). Note that the model estimates are not intended to give an accurate picture of the bioenergetics of whiting. A detailed description of the model and parameters used can be found in Tables A1 & A2 in the Appendix.

Length-at-age of *M. merlangus* in relation to forage fish abundance and temperature

The relationships between forage fish abundance and length-at-age of *M. merlangus* and between North Sea temperature and the length-at-age of *M. merlangus* were described using a generalised additive model (GAM) as implemented in the 'gam' package (Hastie 2015) in R v.3.3.0 (R Development Core Team 2016). The average length-at-age of age 2–6 *M. merlangus* from the IBTS data was modelled separately as a function of mean North Sea temperatures in the first quarter, mean temperatures in the third quarter, and forage fish abundance defined as the annual numbers of age 1 prey fish from the SMS model. A loess smooth with a span of 0.75 and a local quadratic fit was used (Hastie 1991, Wood 2006). Temperature, SMS forage fish abundance and *M. merlangus* length-at-age were normalised prior to model fitting:

$$X_{\text{norm}} = \frac{X - \bar{X}}{s} \qquad (5)$$

where X is the annual mean temperature, forage fish abundance or length-at-age, and $\bar{X}$ and s are the mean and standard deviation across the entire time series. Annual mean length-at-age of whiting and annual mean temperatures of first and third quarters and the 3 yr running mean of forage fish abundance were used.

RESULTS

Length-at-age

The mean length-at-age of age 1 female and male *Merlangius merlangus* in the North Sea decreased from 1990 to 2014. The mean length-at-age of both sexes in age classes 2–6 was mainly above the long-term average in the period 1990–1999, followed by significantly lower values from 2000 through 2007 for both sexes. From 2008–2014, mean length-at-age increased again to above long-term average values. Female and male *M. merlangus* from age 2–6 were on average 1.7 and 1.4 cm smaller in the period 2000–2007, compared to 1990–1998. In 2008–2014 compared to 2000–2007, the average length-at-age of 2–6 yr old female and male *M. merlangus* increased by 3 and 2 cm, respectively (Fig. 2, see Tables S1 & S2 in the

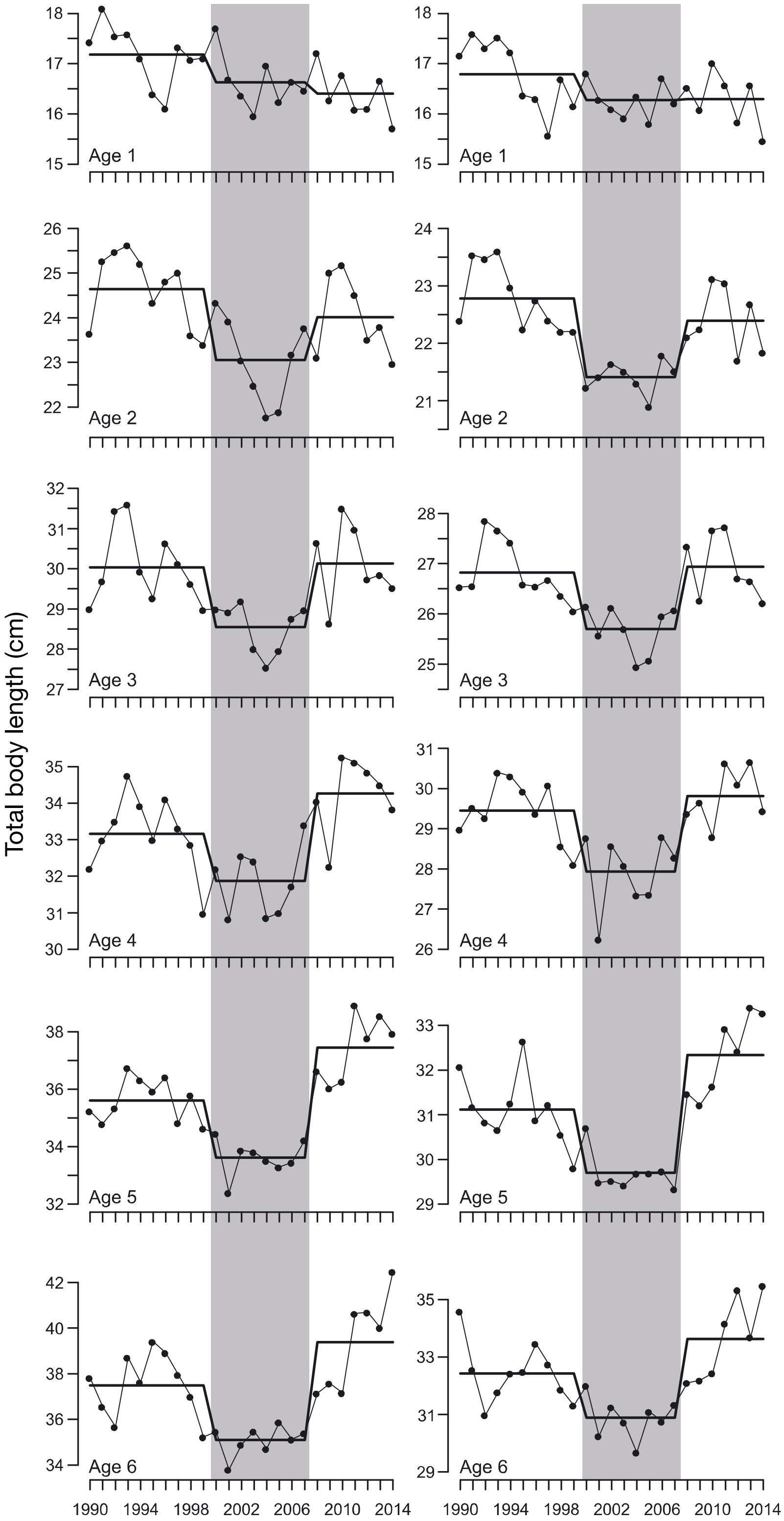

Fig. 2. Mean length-at-age of female (left panels) and male (right panels) North Sea whiting from first quarter North Sea International Bottom Trawl Survey (NS-IBTS) data set provided by the ICES. Shaded area: the period 2000–2007; thick black line: average length-at-age during 1990–1999, 2000–2007 and 2008–2014. Note differences in y-axis scales

Supplement at www.int-res.com/articles/suppl/m594p213_supp.pdf).

Forage fish abundance and North Sea temperatures

The amount of small prey fish available for *M. merlangus* in the North Sea between 1990 and 2014 was below the long-term average for several consecutive years between 2000 and 2007. The mean CPUE of prey in the North Sea was on average 334 ind. h^{-1} (N h^{-1}) in the IBTS time series and on average 296 million recruits of prey fish (age 1 of *Clupea harengus*, *Sprattus sprattus*, *Ammodytes* spp. and *Trisopterus esmarkii*) between 1990 and 2010 in the SMS model output. The patterns of change in the 2 time series of forage fish abundance were similar (Fig. 3). Mean annual forage fish abundance in the period 1990–1999 was 362 N h^{-1} calculated from the IBTS data and 348 million recruits calculated from the SMS model. In 2000–2007, forage fish abundance estimates were 285 N h^{-1} in the IBTS data and 200 million recruits in the SMS model. This represents a reduction by 21 and 42%, respectively. In the years after 2007 the mean forage fish abundance increased again to 353 N h^{-1} (IBTS) and 382 million recruits (SMS model) (Fig. 3). Temperatures within the North Sea showed strong spatial differences between RAs, with lowest winter temperatures and highest summer temperatures in RAs 6 and 7. North Sea temperatures showed divergent trends for first and third quarters analysed. While third quarter temperatures showed an overall increase between 1990 and 2014 (+0.4°C), first quarter temperatures remained almost constant over the observed period (Fig. 4).

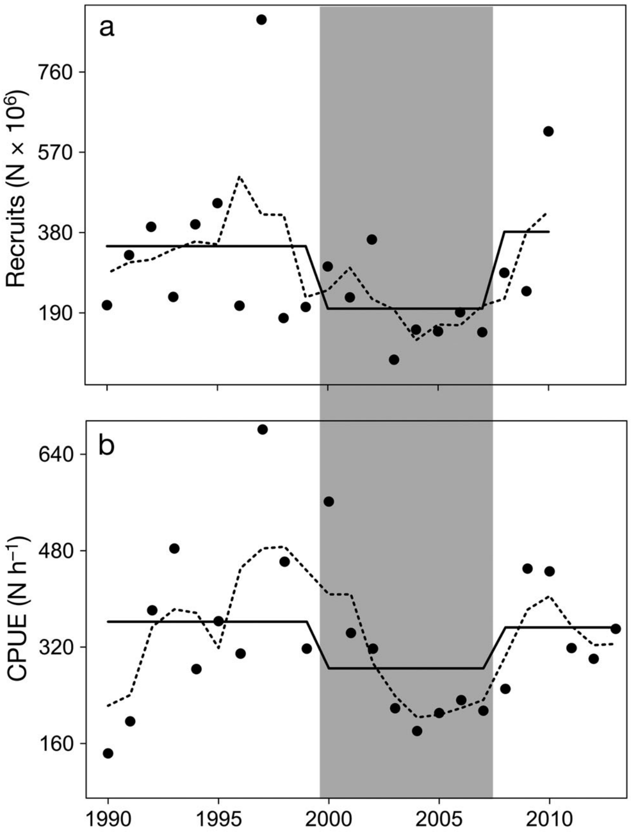

Fig. 3. Forage fish (*Ammodytes* spp., *Trisopterus esmarkii*, *Sprattus sprattus*, *Clupea harengus*) abundance in the North Sea, calculated from the (a) stochastic multi-species (SMS) model and (b) International Bottom Trawl Survey (IBTS) data. Dots: annual means; dotted lines: 3 yr running means; solid line: average length-at-age in the periods 1990–1999, 2000–2007 and after 2007. Shaded area: 2000–2007

Stomach content masses

The average stomach content mass of *M. merlangus* sampled in the period of low prey abundance (2000–2007) was lower compared to samples from the periods of high prey abundance (1990–1999 and 2008–2014) (Fig. 5). To examine spatial and seasonal differences in stomach contents, samples from 1991 (the only year with a full coverage of seasons and regions) were analysed. Stomach contents in first quarter samples were significantly lower compared to the other quarters (χ^2 = 132.5998, df = 3, $p < 0.001$, pairwise Wilcoxon rank sum test with Bonferroni correction Q 1 vs. Q 2–4: $p < 0.001$) and significantly different between the areas sampled (χ^2 = 21.7971, df = 6, $p < 0.01$). Therefore, subsequent between-year comparisons of stomach contents were done separately for each area and quarter.

Stomach contents sampled during first quarters were significantly higher in 2012 compared to 1990 and 1991, except in RA 4. In contrast, the average stomach content mass of *M. merlangus* in all other quarters, with few exceptions, was lower during the period of low mean length-at-age of *M. merlangus* and low forage fish abundance (2000–2007), compared to years when length-at-age and forage fish abundance were high (1990–1998 and 2008–2012) (Fig. 5, Tables 2 & S3).

Condition of *M. merlangus*

Fulton's *k* of *M. merlangus* of size 25–39.9 cm was on average 0.03 g cm^{-3} lower in the period 2000–2007 compared to 2008–2014. This would

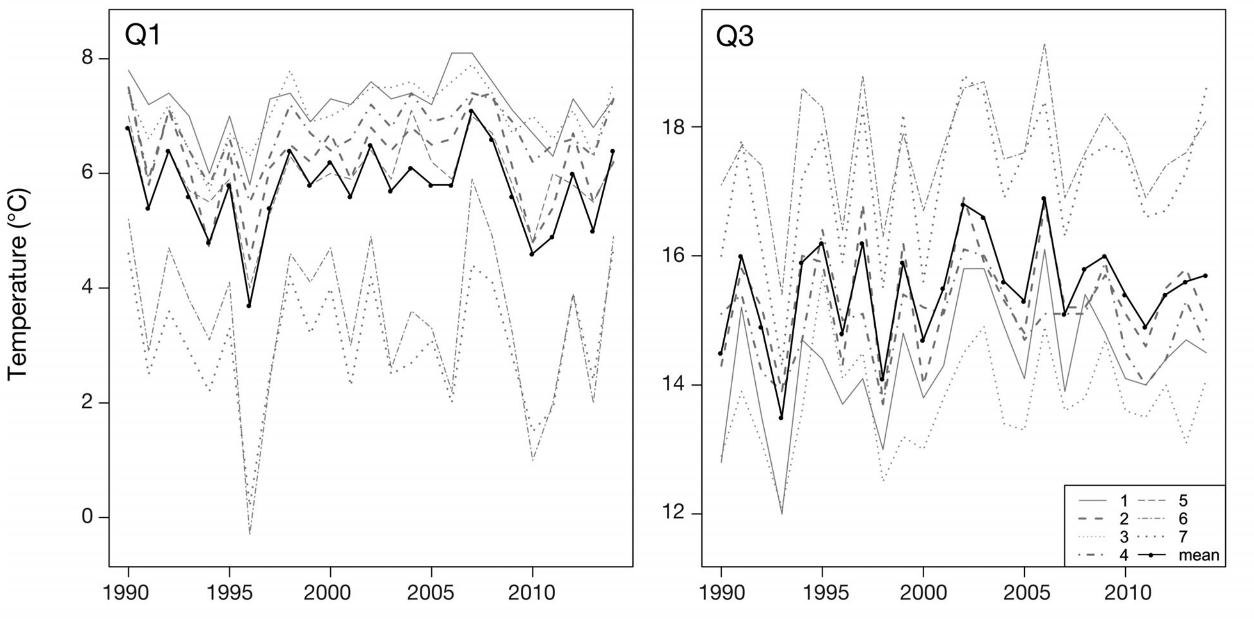

Fig. 4. Average North Sea surface temperatures in first (Q1) and third (Q3) quarters in roundfish areas 1–7 and for the total North Sea (mean) from the ICES Dataset on Ocean Hydrography

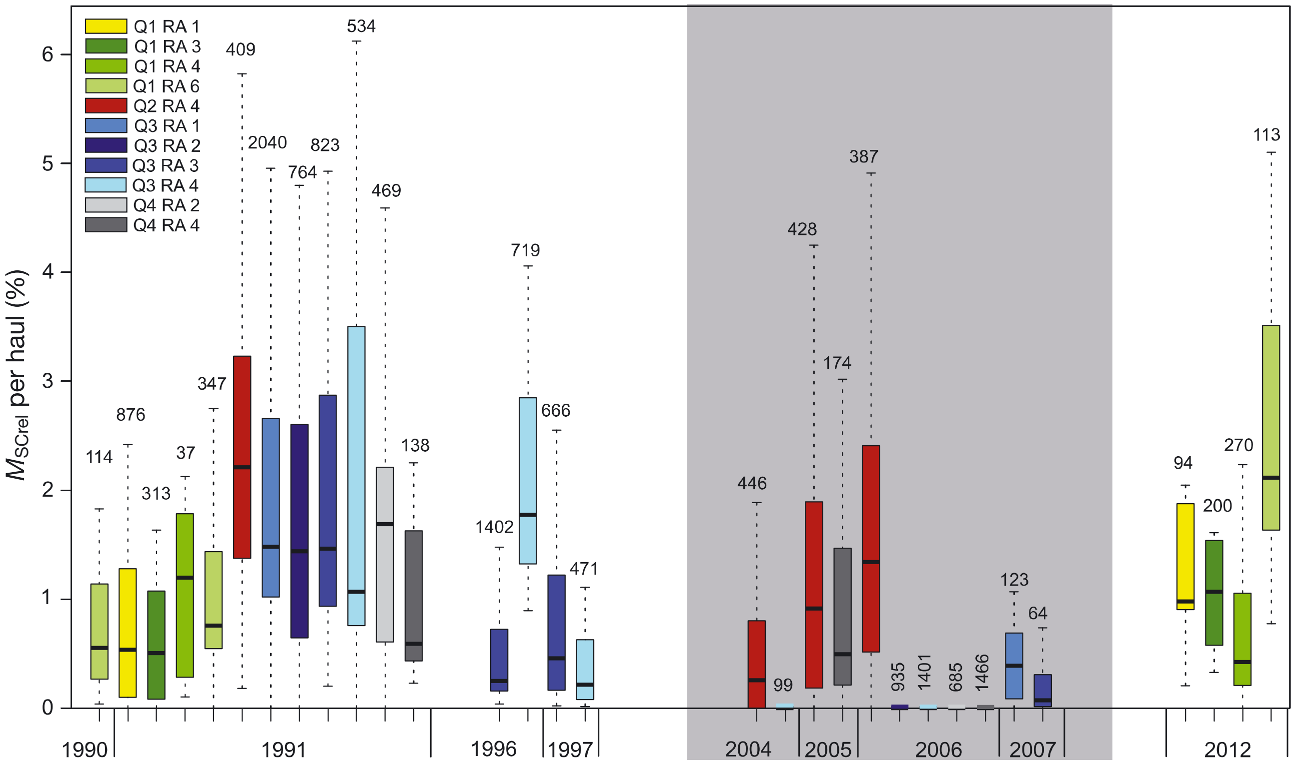

Fig. 5. Average stomach content masses as percentage of total body mass (M_{SCrel}) per haul of North Sea whiting per quarter (Q) and ICES roundfish area (RA) sampled. Shaded area: 2000–2007. Lower and upper ends of the box represent 25 and 75% quartiles, respectively; whiskers mark the most extreme data point, which is no more than 1.5 times the interquartile range from the box. Note that data points beyond the extremes of the whiskers are not shown here. Numbers above boxplots: numbers of stomachs in respective samples

Table 2. Results of the Wilcoxon rank sum tests of the stomach content masses as percentage of the total body mass (M_{SCrel}) of North Sea whiting sampled per quarter (Q), roundfish area (RA) and year; p-values were adjusted using Bonferroni correction

Q	RA	Year	M_{SCrel}		N	χ^2	df	p
			Mean	SD	hauls			
1	1	1991	0.87	1.09	81	5.0	1	<0.05
		2012	1.39	1.06	10			
1	3	1991	0.68	0.71	30	4.4	1	<0.05
		2012	1.26	1.50	16			
1	4	1991	1.10	0.89	5	0.4	1	0.54
		2012	0.80	0.84	20			
1	6	1990	0.76	0.60	13	8.9	2	<0.05
		1991	1.07	0.92	39			
		2012	2.54	1.54	6			
2	4	1991	2.47	1.62	32	40.9	3	<0.001
		2004	0.63	0.87	48			
		2005	1.33	1.56	73			
		2006	1.85	1.89	65			
3	1	1991	2.10	1.84	128	33.7	1	<0.001
		2007	0.48	0.47	22			
3	2	1991	1.94	1.86	59	50.3	1	<0.001
		2006	0	0.00	25			
3	3	1991	1.84	1.24	53	53.6	3	<0.001
		1996	0.57	0.71	34			
		1997	0.77	0.76	44			
		2007	0.18	0.24	12			
3	4	1991	3.46	1.81	27	119.6	4	<0.001
		1996	2.13	1.17	28			
		1997	0.53	0.72	35			
		2004	0	0.00	18			
		2006	0.15	0.68	50			
4	2	1991	1.61	1.18	38	41.3	1	<0.001
		2006	0	0.00	22			
4	4	1991	1.55	2.03	7	50.0	2	<0.001
		2005	0.94	0.97	32			
		2006	0.17	0.66	55			

account for a relatively small difference in body mass: e.g. 12 g in a 33 cm fish (286 vs. 298 g). In the length class 40–49.9 cm, the difference between 2000–2007 and 2008–2014 was 0.1 g cm^{-3}, corresponding to a mass difference of 60 g at a body length of 44 cm (Fig. 6). The median HSI of female and male *M. merlangus* >30 cm was higher in 2012 than in 2007. In 2012, the HSI of 30–34.9 cm females and males was 23%, 15% higher than 2007. The differences in HSI between 2012 and 2007 fish were up to 44% in male *M. merlangus* of 35–39.9 cm and 54% for females of 40–49.9 cm length (Table 3).

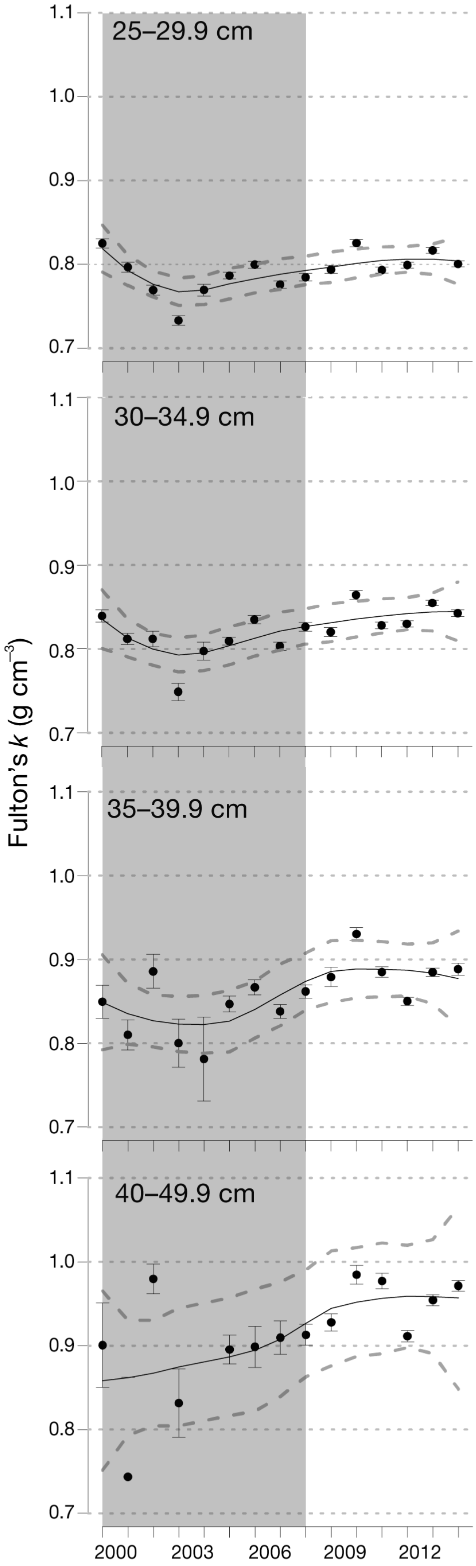

Fig. 6. Annual mean Fulton's *k* of North Sea whiting, calculated from the ICES North Sea International Bottom Trawl Survey (NS-IBTS) data set of the first quarters in 2000–2014. Black lines: fitted loess smoothers; dark grey dashed lines show confidence intervals of the fit. Shaded area: 2000–2007

Table 3. Average liver masses as proportion of the total fish body mass (hepatosomatic index, HSI) of North Sea whiting sampled in 2007 and 2012, and results of the Mann-Whitney rank sum tests (U)

Sex	Fish length (cm)	Median HSI 2007	Median HSI 2012	U	N 2007/ N 2012	p
F	25–29.9	3.76	3.13	5274	99/147	<0.001
F	30–34.9	2.88	3.72	4261	65/219	<0.001
F	35–39.9	2.58	4.36	416	18/120	<0.001
F	40–49.9	2.80	6.10	8	3/42	<0.05
M	25–29.9	2.41	2.44	7208	91/161	>0.05
M	30–34.9	2.10	2.48	2390	45/135	<0.05
M	35–39.9	2.04	3.67	17	8/15	<0.01

Estimated consumption and corresponding stomach contents

The generalised von Bertalanffy growth model fitted to length-at-age data from the North Sea IBTS with a fixed $K = 0.65$ resulted in a mean asymptotic total length (L_∞) of female *M. merlangus* of 37.6 cm (t_0 = −0.48) in the period 2001–2007 and 42.5 cm (t_0 = −0.21) in 2008–2014. Estimated L_∞ of male fish was 32.7 cm (t_0 = −0.77) in 2001–2007 and 35.9 cm (t_0 = −0.55) in 2008–2014. Mean length-at-age for age 2 and older fish was higher for the period 2008–2014 compared to 2001–2007, and the differences increased with age. If the slightly higher value of K = 0.68 is used in the model fits for the period 2001–2007, the resulting L_∞ values are 37.5 cm (t_0 = −0.40) for females and 32.5 cm (t_0 = −0.69) for males. The consumption model (Tables A1–A3) translates these parameter values into the following stomach content differences between the 2 periods: stomach contents were 16.8% higher in the period with high forage fish abundance and growth (females) or 12.9% higher (males) if the same K values (K = 0.65) were used in both periods. If a slightly higher K value (K = 0.68) is assumed to account for warmer temperatures during the period with low forage fish abundance, the theoretical differences in stomach contents are even lower: 7.6% (females) and 3.9% (males). This implies that relatively small differences in mean stomach contents would have been sufficient — all other factors being equal — to generate the observed differences in length-at-age between the 2 periods. In contrast, the observed mean stomach content masses of *M. merlangus* within a size range of 25–40 cm were between 23% (males) and 50% (females) lower in 2007 compared to 2012 (Fig. 7, Tables 4 & A3).

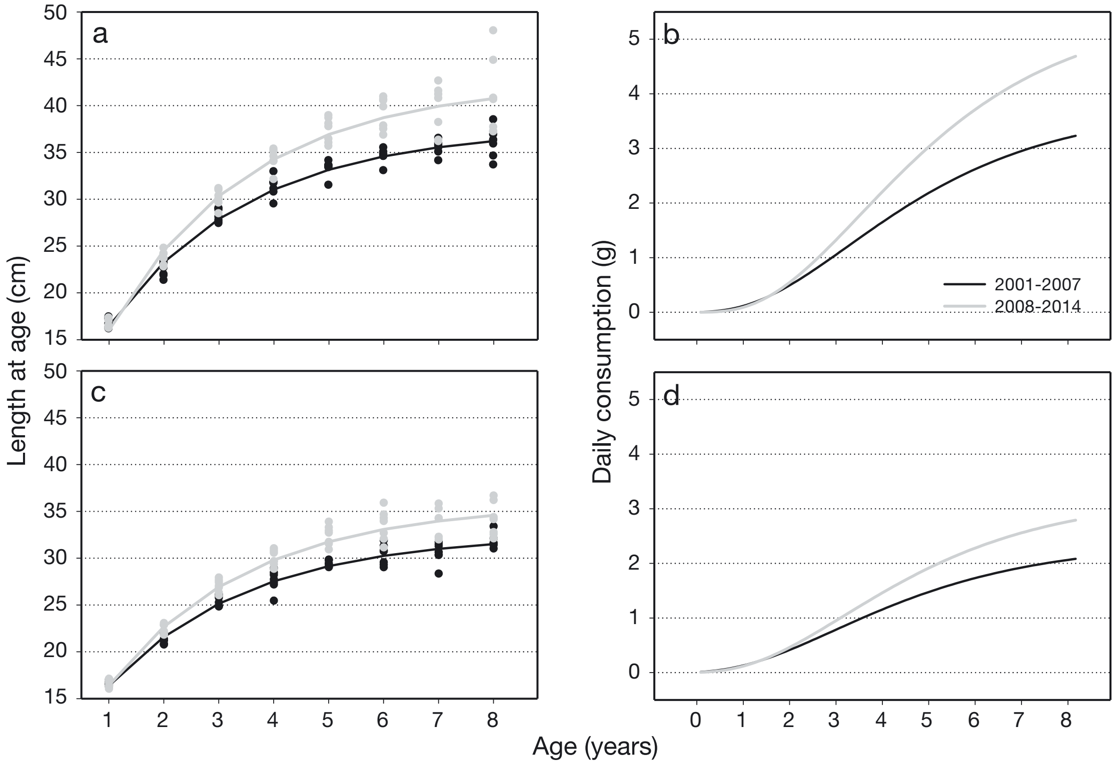

Fig. 7. Length-at-age and estimated von Bertalanffy growth curves of (a) female and (c) male North Sea whiting. Estimated corresponding consumption of (b) female and (d) male whiting (d) from the bioenergetics model (described in the Appendix) for the period 2001–2007 (black) and 2008–2014 (grey) with $K = 0.65$ for both periods

Table 4. Average North Sea whiting stomach content masses expressed as percentage of fish body mass (BM) observed in the field from whiting of total lengths 25–40 cm in comparison to stomach content masses (S) calculated from the bioenergetics model (Temming & Herrmann 2009). Two different scenarios were modelled using the same catabolic constant (K) to estimate consumption from 2001–2007 and 2008–2014 length-at-age data and using a higher K value for 2001–2007 accounting for higher ambient temperatures (see Appendix for detailed description of the model)

	Model output			Field data	
	S (% BM) 2001–2007		S (% BM) 2008–2014	Stomach content mass (% BM)	stomach content mass (% BM)
	K = 0.65	K = 0.68	K = 0.65	2007	2012
Females	0.37	0.41	0.44	0.69	1.39
Males	0.31	0.33	0.35	0.43	0.56

Length-at-age of *M. merlangus* in relation to forage fish abundance and temperature

The length-at-age of *M. merlangus* could not be adequately described by North Sea temperatures in the first and third quarters. Adjusted R-squared of the GAM models were 0.08 and 0.02, respectively. The GAM model using forage fish abundance as an explanatory variable generally fit well (adjusted R-squared: 0.58). Annual mean length-at-age of *M. merlangus* increased linearly with forage fish abundance up to an apparent threshold where it leveled off. However, length-at-age of *M. merlangus* in 2001, a year with moderate forage fish abundance, was much lower than predicted (Fig. 8).

DISCUSSION

Observed changes in the length-at-age of *Merlangius merlangus* were most likely caused by a decline in forage fish abundance in the North Sea. Smaller length-at-age during the period 2000–2007 coincided with changes in 2 other factors that could have influenced the mean length-at-age: size-selective mortality and water temperature. The influence of those factors are evaluated below.

Size-selective mortality and temperature: unlikely candidates for smaller adult length-at-age

Size-selective fishing mortality has been found to cause a decrease in length-at-age and age at maturity in Scotian Shelf haddock *Melanogrammus aeglefinus* (Neuheimer & Taggart 2010) and in the Gulf of St. Lawrence cod stock (Sinclair et al. 2002b). In the North Sea, *Merlangius merlangus* is mainly caught in the mixed demersal roundfish fishery and as bycatch in the Norway lobster *Nephrops norvegicus* (L. 1758), sandeel, Norway pout and flatfish fishery (ICES 2012b). Fishing gears used in mixed demersal fisheries are size-selective, and the growth rates of *M. merlangus* are highly variable

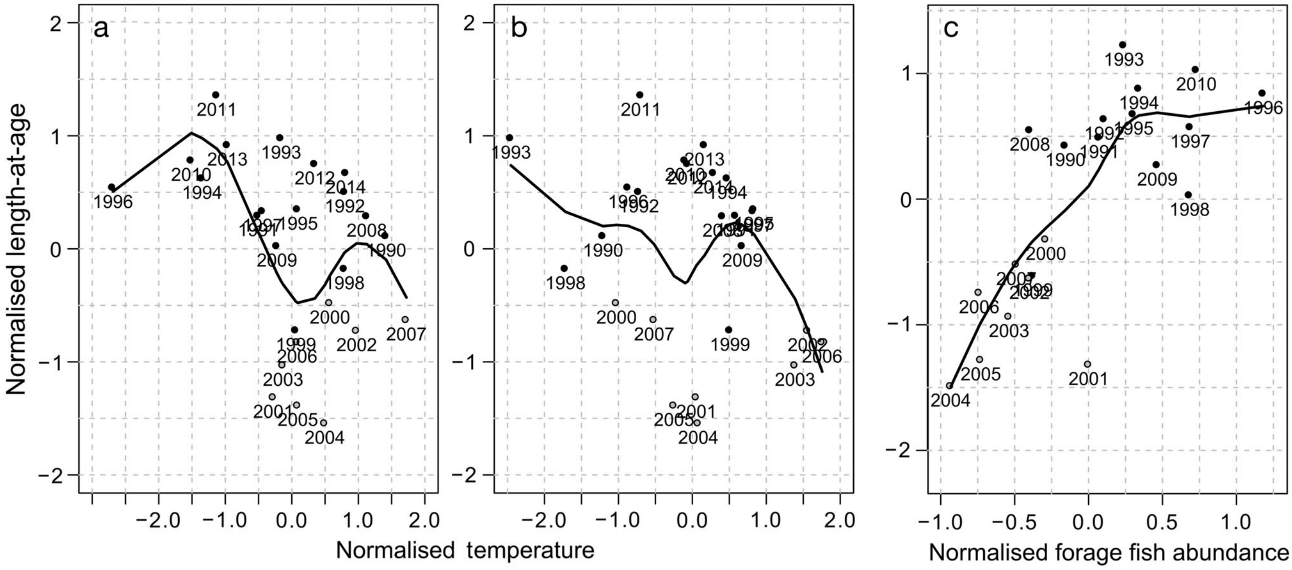

Fig. 8. Annual mean length-at-age of adult North Sea whiting in relation to the annual average of normalised North Sea temperature in (a) the first and (b) third quarters and (c) the 3 yr running mean normalised forage fish abundance. Dots: observed values; line: GAM prediction; grey dots: observations within the period 2000–2007

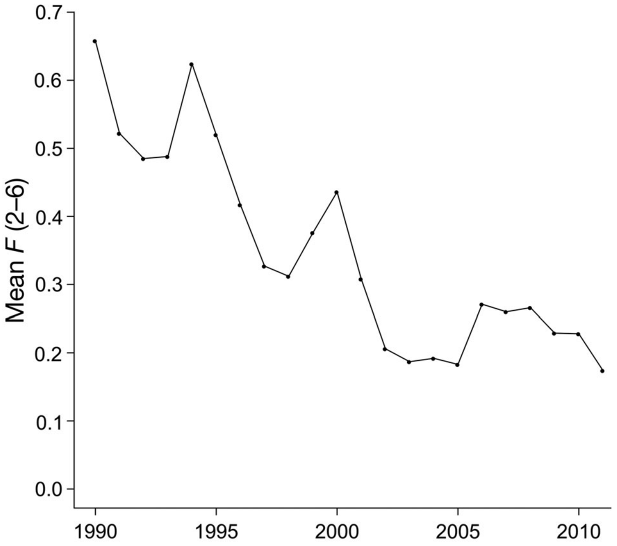

Fig. 9. Time series of the average fishing mortality (*F*) of North Sea whiting ages 2–6 in the North Sea from the ICES Report of the Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak (ICES 2012b)

within a given cohort, implying a high potential for the selective removal of fast-growing individuals and a subsequent decrease in population mean length-at-age (e.g. Sinclair et al. 2002a). However, the pattern in mortality time series of *M. merlangus* is contrary to what would be expected if fishing mortality was the main determinant of changes in length-at-age of the stock. The assessment of *M. merlangus* suggests that fishing mortality (*F*) of age groups 2–6 declined in the period 1990–2012. (Fig. 9, ICES 2012b). In contrast, length-at-age of whiting first declined and then increased again in a period of constantly decreasing *F*.

Temperature alone is also unlikely to be responsible for the observed changes in length-at-age of North Sea whiting, but might have contributed to the changes. The bioenergetics model results demonstrated that even a small difference in temperature between the 2 periods had an effect on energy budgets, and thus, growth. Globally, the North Sea is amongst the most rapidly warming continental shelf seas (Burrows et al. 2011). From 1990 to 2007, the annual mean surface temperature in the North Sea increased continuously by about 0.5°C decade^{-1} (Meyer et al. 2011, Emeis et al. 2015). Decreasing growth rates of Atlantic cod in the southern North Sea has been ascribed to increasing temperatures, since the southern North Sea marks the most southerly boundary of the species' distribution and recent temperatures are at the upper margin of the temperature range that is optimal for cod growth (Jobling 1988, Olsen et al. 2011). However, *M. merlangus* in the North Sea are not at the southern boundary of their distribution, nor are temperatures at the upper limit of their observed temperature range. Within the Black Sea the average temperature experienced by *M. merlangus* ranges from 9–20°C (Shulman & Love 1999). Moreover, in the Irish Sea, the length-at-age of *M. merlangus* was found to be temperature-independent (Gerritsen et al. 2003). Accordingly, our analysis showed that patterns in the temperature time series and whiting length-at-age series are inconsistent with a strong temperature effect on growth. Whiting could have reacted to suboptimal temperatures by spatial displacement, but no significant relationship between temperature in the North Sea and *M. merlangus* spatial distribution has been detected (Kerby et al. 2013). In summary, a negative impact of temperature on the growth of *M. merlangus* cannot account for the observed changes alone.

Divergent pattern in juvenile length-at-age

For juvenile whiting (age class 1), it is most likely that increasing abundances of late-season offspring contributed to a continued decrease in mean length-at-age after the early 2000s. In contrast to the other ages, the mean length-at-age 1 further decreased after 2007, indicating that juvenile length-at-age is influenced by different factors than the older age groups. Theoretically, either a real decrease in growth rates of 0-group *M. merlangus* or a shift in the time of spawning of *M. merlangus* could have caused changes in length-at-age 1. The possible factors resulting in a decrease in growth rates would be the same as for adult *M. merlangus*: water temperature, selective mortality or food resources. The temperature in the North Sea increased from 1990 to 2007 and subsequently decreased slightly (Emeis et al. 2015), whereas the length-at-age 1 of *M. merlangus* remained low until 2014. Thus, it is unlikely that temperature directly caused slower growth in juveniles. Selective mortality of fast growing 0-groups could theoretically have led to the observed decrease in mean length-at-age 1. Size-selective mortality in juvenile fish typically favours larger individuals, since they tend to be more resistant to starvation and less vulnerable to predation (Peterson & Wroblewski 1984). On the other hand, Van der Veer et al. (1997) found that size-selective mortality in juvenile flatfish in the Wadden Sea could actually favour smaller individuals due to predators preying selectively on the larger individuals of the age 0 cohort. Juvenile *M. merlangus* are important prey for adult gadoids, and if these preferred larger 0-groups this might have led to a decrease in size at age 1. However, size-selective mortality requires relatively high predation mortality in the population (Sogard 1997). The stock biomass of cod and *M. merlangus* in the North Sea was decreasing until 2006 (ICES 2012b), leading to lower predation pressure on 0-group *M. merlangus* from gadoids. After 2006, some recovery of cod and *M. merlangus* was observed (ICES 2012b). However, in contrast to the temporal development of the spawning stock biomass of cod and *M. merlangus*, the length of age 1 *M. merlangus* constantly decreased over the observed period. Therefore, size-selective mortality by gadoid predation is unlikely to be the cause of the observed decrease in length-at-age 1. Crustaceans and gobies dominate the diet of *M. merlangus* smaller than 15 cm (Hislop et al. 1991). These prey items are unlikely to result in a growth-limiting factor since both are increasing in abundance in the North Sea due to a release of predation pressure by gadoids (Temming & Hufnagl 2015).

Smaller age 1 fish could alternatively be explained by increasing dominance of late-season cohorts in age class 1 since the beginning of the 2000s. An increasing proportion of late-season cohorts could lead to a smaller length-at-age 1, as recruits originating from later-spawned eggs have less time to grow. A change in the survival patterns of *M. merlangus* offspring could have been induced by a change in the seasonal abundance of zooplankton. According to information contained in the DAPSTOM database (Pinnegar 2014), North Sea *M. merlangus* below the size of 5 cm feed predominantly on planktonic copepods (88% of prey items); in particular, *Calanus* spp., *Pseudocalanus elongatus*, *P. minutus*, *Paracalanus parvus* and *Temora longicornis*. Changes in the zooplankton community can influence the survival of fish larvae and therefore recruitment. Temperature-induced changes in the spatio-temporal distribution of zooplankton led to lower survival of cod larvae in the North Sea (Beaugrand et al. 2003). Zooplankton populations in the southern North Sea are generally characterised by persistently lower availability of *Pseudocalanus* spp., *Calanus finmarchicus*, *Paracalanus parvus* and *T. longicornis* (as well as total copepods) after 2000 compared to the 1990s (O'Brien et al. 2013). Hence, this remains a likely explanation for the decrease in juvenile growth rates in *M. merlangus*, although specific targeted studies are currently lacking.

Forage fish abundance in the North Sea and stomach contents of *M. merlangus*

So far, the most likely explanation for the observed decrease in length-at-age of adult *M. merlangus* is a change in the abundance of forage fish serving as prey for *M. merlangus* in the North Sea ecosystem. *M. merlangus* is a highly selective feeder, which (from a size of 25 cm on) is almost exclusively piscivorous, having less than 20% of non-fish prey in its diet (Hislopet al. 1991). Additionally, *M. merlangus* relies on only a few species, such as *Ammodytes* spp., *Trisopterus esmarkii*, *Clupea harengus* and *Sprattus sprattus* (Knijn et al. 1993, Temming et al. 2007). Thus, changes in the abundance of forage fishes should influence growth rates, as has been demonstrated at a local scale for *M. merlangus* (Engelhard et al. 2013) and for other gadoids in the North Sea (Cormon et al. 2016). Forage fish abundances were below average in the period 2000–2007, but spawning stocks of *Ammodytes* spp., *S. sprattus* and *T. esmarkii* increased thereafter, and the *T. esmarkii* stock produced very strong year classes in 2009 and 2012 (ICES 2012b). The amount of prey available in an ecosystem should generally be reflected by the stomach contents of a predator (Griffiths 1975). Since predator stomach fullness and content composition strongly co-vary with prey abundance in the environment, predator stomachs have been verified as a suitable indicator for prey distribution (Fahrig et al. 1993) and availability (Mills et al. 2007). Thus, low forage fish abundance is also reflected in low stomach contents of *M. merlangus*.

Condition of *M. merlangus*

In contrast to the pronounced changes in growth rates, the observed changes in Fulton's k are surprisingly small (–0.03 to –0.1). Changes in k reflect fitness (e.g. Bolger & Connolly 1989) and local prey availability (Engelhard et al. 2013), and studies on cod in the Gulf of St. Lawrence and the Baltic have revealed more dramatic declines (Lambert & Dutil 1997, Eero et al. 2014). If food supply is insufficient to cover maintenance costs for a prolonged period, the first response will be to use stored energy from the liver (e.g. Marshall et al. 1999), and only if this resource is exhausted will a reduction of muscle tissue be initiated. This suggests that the decline in prey availability for North Sea whiting was less severe and abrupt. However, our data from the period with low prey availability (2007) suggest that the energy stores were severely depleted, as indicated by the low HSI values. The samples in 2007 were taken 1.5 mo after the end of the spawning season in June (Coull et al. 1998), when HSI indices should have recovered to levels above those during spawning (Sağlam & Sağlam 2012). Our samples from 2012 reflect the middle of the spawning period and had significantly higher HSI values than the 2007 samples, suggesting an extended period of limited food supply in the summer of 2007.

Expected differences in consumption and stomach contents

In the period 2008–2014, the stomach contents derived from the growth data were on average 16.8% higher in female and 12.9% higher in male fish compared to respective values for the period 2000–2007. This implies that these rather small differences in stomach contents would have been sufficient — all other factors being equal — to explain the observed growth depression in the period 2000–2007. If the small 0.6°C temperature difference between the 2 periods is explicitly taken into account, the estimated stomach content differences become even smaller (7.6% for females and 3.9% for males). However, the actual stomach content masses from field samples in 2007 were on average 50% (females) and 24% (males) lower than in 2012.

Theoretically, an effect of the different sampling seasons might have contributed to the differences in the observed stomach data. When considering the effect of the quarter on mean stomach content mass, the samples from 1981 and 1991 can serve as a reference since all 4 quarters were sampled during those years. In 1981, *M. merlangus* had higher stomach content masses in the third quarter compared to the first quarter, when *M. merlangus* might reduce their feeding during the spawning period (Hislop et al. 1991). Thus, higher stomach content masses found in 2012 can be considered as an effect of year, rather than season. This finding is confirmed by comparison of the median stomach content masses in 2007 and 2012 with samples from 1991 in the respective quarters and ICES statistical rectangles. *M. merlangus* in 2007 had significantly lower stomach content masses compared to the third quarter stomachs in 1991, whereas *M. merlangus* in 2012 had equal or higher amounts of food in their stomachs than specimen from the first quarter in 1991.

The observed differences in the field data were much larger than the theoretically estimated differences needed to explain the differences in length-at-age. This fact can be explained in 2 ways: either the samples were not a good representation of the overall feeding conditions in the respective period, or whiting had not only reduced growth rates; but employed additional strategies to save energy, such as skipping spawning (Burton et al. 1997) or reducing average activity levels (Auer et al. 2016). There is at least indirect evidence for reduced reproductive output in the period with low food availability from the very low recruitment levels in the same period (see below).

Relationship between forage fish abundance and length-at-age of *M. merlangus*

The predicted relationship between the normalised forage fish abundance and the normalised length-at-age of adult *M. merlangus* from the GAM followed an asymptotic curve. This implies that (1) if prey abundance drops below a certain level, the growth rate of *M. merlangus* decreases and (2) if prey abundance reaches a certain level, the growth rate of *M. merlangus* does not increase any further with more food available. In 2001, this relationship appears not to hold. Whereas the length-at-age of *M. merlangus* was rather low, forage fish abundance was at an average level. This might be due to additional effects of either temperature, *M. merlangus* density or atypical low overlap of the predator and its prey (Temming et al. 2007). However, increasing metabolic costs due to higher temperatures cannot explain the discrepancy in 2001, since the temperature was high compared to e.g. 1990 with equal prey abundance (Emeis et al. 2015). Competition caused by high densities of *M. merlangus* seems to be an unlikely explanation, since in 2001 the spawning stock biomass of *M. merlangus* was not exceptionally high compared to the other years (ICES 2012b). Data on spatial overlap between *M. merlangus* and its prey are not available. Thus, this hypothesis cannot be easily evaluated. However, overall the abundance of forage fish explained much of the variability in the length-at-age of *M. merlangus* in the North Sea. The clear correlation between the length-at-age of *M. merlangus* and the abundance of forage fish in the North Sea might have implications both for the stock recruitment relationship of *M. merlangus* and for multi-species modelling of the North Sea ecosystem. The growth rates and size-at-age of female fish influence the reproductive output.

Smaller females produce fewer offspring and lower growth rates affect the rate at which immature individuals recruit to the spawning stock. In addition, food shortage could have led to reduced egg volumes (Marshall & Frank 1999) or even to skipped spawning (Burton et al. 1997). Thus, lower food availability in the period 2000–2007 might have contributed to the observed minimum in *M. merlangus* recruitment between 2003 and 2007 (ICES 2012b).

Currently applied multi-species models of the North Sea fish community (e.g. SMS) (ICES 2011, Lewy & Vinther 2004) only account for top-down effects of predators on their prey. These might be improved by implementing the relationship between forage fish abundance and growth of whiting documented here. The inclusion of such a bottom-up effect might enhance multi-species model predictions, which can then also serve as a basis for modified reference points of forage fish (sandeel, Norway pout and sprat) that take into account the effects on predator growth and recruitment.

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Appendix

To estimate the expected differences in consumption and mean stomach content of North Sea whiting *Merlangius merlangus* between the 2 periods with contrasting growth, we used a simplified bioenergetics model (Temming & Herrmann 2009). This model estimates consumption (Eq. 3; Table A1) from growth parameters of a generalised von Bertalanffy growth model (Eq. 1; Table A1) using additional constant net conversion efficiency (K_3) and an assumption about the allometric exponent of consumption (m). The estimated consumption can then be transformed into the corresponding mean stomach contents using a feeding model (Eq. 4; Table A1) and information on gastric evacuation (Eq. 5; Table A1). A generalised van Bertalanffy growth function (Eq. 1; Table A1) was fitted to *M. merlangus* first quarter length-at-age data from the period 2000–2007, and to length-at-age from the period 2008–2014, obtained from the IBTS DATRAS for females and males, respectively. Note that 2 different scenarios were modelled: (1) using the same catabolic constant (K) to estimate consumption from 2001–2007 data and 2008–2014 data (K_{eq}) and (2) using a different K value for both periods accounting for higher ambient temperatures in 2001–2007 (K_{diff}). The mean asymptotic total length (parameter L_∞) from both scenarios, for each period and sex was converted into the mean asymptotic mass (M_∞) using Eq. (2) (Table A1). Based on the estimated von Bertalanffy growth parameters in Eq. (3), consumption (ΔC) was estimated.

The average consumption was then converted into the corresponding average feeding rates (Eq. 4). Eq. (4) can be solved for average stomach content (S) to allow for the conversion of the observed differences in consumption into the corresponding differences of average stomach contents using Eq. (5).

Table A1. Equations used to estimate consumption and corresponding stomach contents of *Merlangius merlangus* from length-at-age data. See Table A2 for parameter definitions

No.	Equation
(1)	$L_t = L_\infty \times (1 - e^{-KD(t-t_0)})^{\frac{1}{D}}$, with D = 3(1 – m) (Pauly 1981)
(2)	$M_\infty(g) = a\ L_\infty\ (cm)^b$
(3)	$\Delta C = \frac{1}{K_3} bKM_\infty^{1-m} M_t^m \Delta t$ (Temming & Herrmann 2009)
(4)	$F = RS^B$ (Jones 1974, Temming & Herrmann 2003)
(5)	$R = R'W^C \mathrm{e}^{AT}$ (Temming & Herrmann 2003)
(6)	$S = \left(\frac{\Delta C}{24\ R'}\right)^{\frac{1}{B}}$

Table A2. Parameters used to estimate consumption and corresponding stomach contents of *Merlangius merlangus* from length-at-age data

Eqn.	Parameter	Definition	Value
(1)	L_t	Total length of the fish at time t	
(1), (4)	t	Time	
(1)	t_0	Time at which fish length equals zero	
(1), (2)	L_∞	Mean asymptotic total length	
(1), (3)	K	Catabolic constant	0.65 or 0.68 (this paper)
(1)	D	Parameter of the generalised von Bertalanffy growth function	(Temming & Herrmann 2009)
(1), (3)	m	Allometric exponent of anabolism or consumption term	0.805 (Temming & Herrmann 2009)
(2)	b	Allometric exponent of the length–mass relationship	3.12 (Wilhelms 2013)
(2)	M_∞	Mean asymptotic total body mass	
(2)	a	Scaling factor of the length–mass relationship	0.0042 (Wilhelms 2013)
(3)	ΔC	Consumption in Δt	
(3)	K_3	Net conversion efficiency = growth / food for growth = growth / (food intake − maintenance ratio)	0.6 (Andersen & Riis-Vestergaard 2003, Temming & Herrmann 2009)
(3)	Δt	Time interval	
(3)	M_t	Mean mass of the fish at time t	
(4)	F	Consumption/feeding rate in g h^{-1}	
(4), (5), (6)	R'	Constant of the general gastric evacuation model	0.0093 (Temming & Herrmann 2009)
(6)	S	Average stomach content	
(5)	B	Shape parameter of the general gastric evacuation model	0.49 (Mergardt & Temming 1997, Andersen 1999)
(5)	C	Allometric weight exponent of gastric evacuation	0.306 (Temming & Herrmann 2009)
(5)	A	Temperature coefficient of gastric evacuation	0.075 (Andersen 1999)

Table A3. Detailed results of the consumption (C) and stomach content (S) estimates from the bioenergetics model for average *Merlangius merlangus* body mass of the length classes 25–29.9 cm (157 g), 30–34.9 cm (258 g) and 35–39.9 cm (411 g). Two scenarios were calculated. One with parameter K equal for the periods 2001–2007 and 2008–2014 (K_{eq}) and one scenario with different values for K to account for temperature differences (K_{diff}). See Table A2 for parameter definitions

		Females		Factor	Males		Factor
		2001–2007	2008–2014		2001–2007	2008–2014	
K_{eq}	M_∞	425	627		269	365	
	t_0	−0.48	−0.22		−0.79	−0.57	
	K	0.65	0.65		0.65	0.65	
	C 157 (g d^{-1})	1.70	1.83	1.08	1.57	1.66	1.06
	C 258 (g d^{-1})	2.53	2.73	1.08	2.19	2.33	1.06
	C 411 (g d^{-1})	3.68	3.97	1.08	3.01	3.19	1.06
	S 157 (% BM)	0.33	0.39	1.18	0.28	0.31	1.11
	S 258 (% BM)	0.37	0.44	1.19	0.31	0.35	1.13
	S 411 (% BM)	0.42	0.49	1.17	0.34	0.38	1.12
K_{diff}	M_∞	414	627		263	365	
	t_0	−0.42	−0.22		−0.72	−0.57	
	K	0.68	0.65		0.68	0.65	
	C 157 (g d^{-1})	1.77	1.83	1.03	1.63	1.66	1.02
	C 258 (g d^{-1})	2.63	2.73	1.04	2.28	2.33	1.02
	C 411 (g d^{-1})	3.83	3.97	1.04	3.13	3.19	1.02
	S 157 (% BM)	0.36	0.39	1.08	0.30	0.31	1.03
	S 258 (% BM)	0.41	0.44	1.07	0.33	0.35	1.06
	S 411 (% BM)	0.45	0.49	1.09	0.37	0.38	1.03

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