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Trends in Sandeel Growth and Abundance off the East Coast of Scotland

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Sandeels *Ammodytes marinus* are a crucial forage fish species in the North Sea, transferring zooplankton energy to higher trophic levels. However, there has been a sustained decline in sandeel abundance in the northwestern North Sea since 2000. Here we use field data to analyse year-to-year changes in *A. marinus* growth rate between 1997 and 2009 and assess whether variation in growth rate corresponded with variation in abundance. The signature of the reduction in abundance between 2000 and 2009 was a decline in age 1 sandeels, while no other age class declined. Analysis of age-length data showed that the decline in abundance coincided with a period of low growth. Growth performance indexes were correlated with zooplankton and phytoplankton biomass but not temperature. Further, we observed a significant correlation between larval growth rate and 0-group sandeel length during a period when hatch dates were relatively fixed; suggesting recent changes in length were influenced by food availability.

Keywords: growth rate, length, *Ammodytes marinus*, mortality, fish, abundance

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INTRODUCTION

Ammodytes marinus are lipid rich shoaling fish that form a vital part of the link between zooplankton production and higher trophic levels in the North Sea. *A. marinus*, hereafter sandeels, are essential prey for many birds (Wanless et al., 1998; Furness and Tasker, 2000; Frederiksen et al., 2004; Lahoz-Monfort et al., 2011; MacDonald et al., 2015) and marine mammals (MacLeod et al., 2007). Sandeel dependent seabirds, especially those limited to carrying one fish at a time, are bottom-up limited by abundance (Frederiksen et al., 2007) and highly sensitive to variation in sandeel energy content (Wanless et al., 2005; Rindorf et al., 2016). Length is an indicator of energetic content (Hislop et al., 1991; Wanless et al., 2005), which is influenced by short-term variation in sandeel growth rate (0–2 years) since fish <3 years old dominate the sandeel stock.

No time series on sandeel growth rate exists, although there is evidence of a decline in size; with long-term decreases in the mean lengths of age groups 0, 1, and 2 in the North Sea (Wanless et al., 2004; van Deurs et al., 2014; Howells et al., 2017). Of particular interest to United Kingdom seabird conservationists is the long term decline in 0-group length (Wanless et al., 2004; Howells et al., 2017), as breeding success and survival of many seabird species is sensitive to variation in length and hence energy content of this age class (MacDonald et al., 2015). Changes in 0-group length-at-date decline could be caused by changes in spawning and hatch days, size-dependent larval mortality or larval growth rate (Frederiksen et al., 2011).

A decrease in quality and availability of sandeels' main prey calanoid copepods could have reduced sandeel growth rate between 2000 and 2009. Furthermore, mean calanoid copepod prey size, an indicator of energy value, has declined in the North Sea since the 1980s (Beaugrand et al., 2003). These changes would have reduced sandeel energy uptake if sandeels were handling time limited (van Deurs et al., 2014). Larval growth and subsequent recruitment is likely sensitive to the temporal match between emergence of first feeding larvae and copepod nauplii abundance (Wright and Bailey, 1996). *Calanus finmarchicus* and *Calanus helgolandicus* are the most dominant large copepods in the North Sea, however, it is unclear which of these species has the largest impact on sandeel recruitment success (van Deurs et al., 2009; Régnier et al., 2017). Relationships between sandeel recruitment and the synchrony between sandeel hatch dates and particular copepod species may indicate a prey preference, or simply reflect relative abundance of copepod species.

Sandeel growth is highly seasonal, with the largest increase in size observed between April and June (Winslade, 1974; Bergstad et al., 2002). Growth ceases altogether during winter (Cameron, 1958; Macer, 1966). Marked differences in sandeel growth exist across the North Sea (Boulcott et al., 2007), with fastest growth in Southern United Kingdom waters and off the Norwegian coast (Wright and Bailey, 1993; Bergstad et al., 2002; Boulcott et al., 2007) and slowest growth off Shetland (Warburton, 1982). Many studies have analysed temporal and spatial variation in length at age (Macer, 1966; Baistrocchi, 2003; Boulcott et al., 2007; van Deurs et al., 2014), however, relatively few studies have analysed year-to-year changes in sandeel growth over a lifespan (Bergstad et al., 2002; Rindorf et al., 2016). Significant spatial variation in length-at-age and condition exist (Rindorf et al., 2016), with largest length-at-age positively related to temperature and depth, and asymptotic length and condition positively related to latitude. In the present study we investigate year-to-year changes in sandeel abundance-at-age and length-at age to (1) estimate changes in abundance-at-age in the early 2000s to determine years the stock decreased and what age classes were affected, (2) analyse year-to-year changes in growth rates between 1997 and 2006, (3) assess whether there was a correlation between larval growth rate and 0-group length in June, and (4) assess relationships between growth rates and zooplankton abundances, chlorophyll densities and Sea surface temperature (SST).

MATERIALS AND METHODS

Sampling Methods

Sampling of juvenile and adult sandeels by pelagic trawl has taken place annually off the Firth of Forth between 1997–2003 and 2005–2009 (56° 00′N and 56° 30′N and longitudes 003° 00′W and 001° 00′W, **Figure 1**). In each year, trawling was carried out between 0400 and 1800 h GMT between late May and early July. Surveys covered the main sandbanks, the Wee Bankie, Marr Bank, and Berwick's Bank, prime habitat for sandeels in this area (Proctor et al., 1998; Pedersen et al., 1999). Sampling was undertaken by the FRV *Clupea* for the majority of the study period (1997–2007), before it was replaced by the FRV *Alba Na Mara* (2008–2009).

Sandeel larval sampling was conducted off the east coast by pelagic trawl between 2000 and 2002 (**Figure 2**). Small-scale

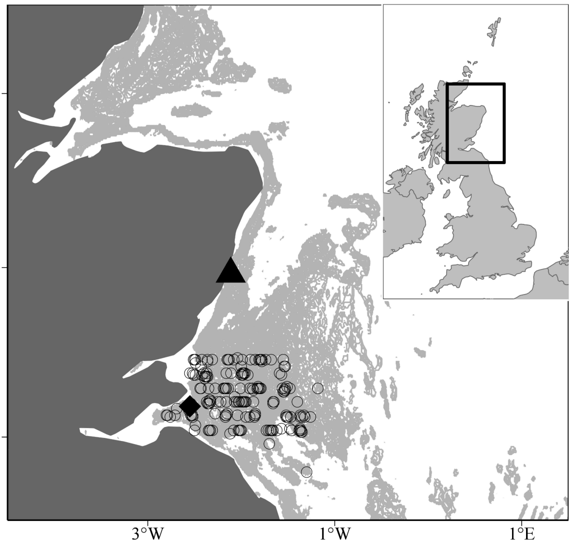

FIGURE 1 | Pelagic trawl locations off the Scottish east coast. Open circles represent pelagic trawl locations. The black diamond and triangle denotes the Isle of May seabird colony and Stonehaven, respectively. The pale grey shaded area indicates water depths between 30 and 70 m, the range of depth sandeels are most commonly found (Wright et al., 2000).

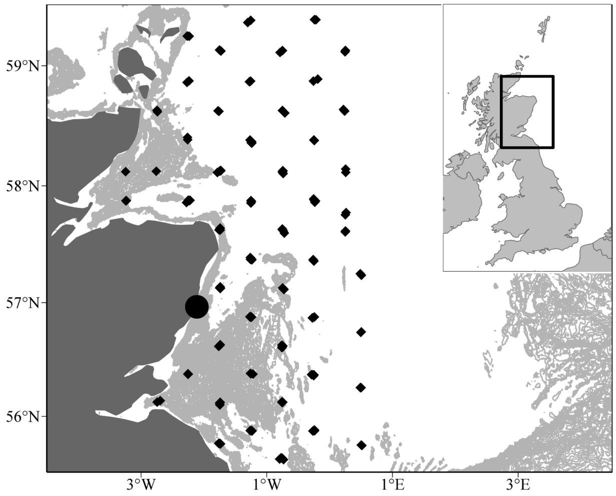

FIGURE 2 | Locations of larval surveys between 2000 and 2002. Larval sampling was conducted at Stonehaven in 2000 and 2001 (circle) and across the northwestern North Sea in 2002 (diamonds).

larval sampling took place at Stonehaven off the northeast coast of Scotland between 2000 and 2001 (56° 57.83′N, 002° 06.74′W, water depth = 45 m). Larvae were sampled with a 100 cm mouth diameter net of 350 m mesh. The net was towed obliquely at a speed of 1 m s^{-1} to within ∼3 m of the seabed depth (45 m). Upon recovery of the net, the whole catch was washed into the cod-end. All sandeel larvae were removed from the catch and identified to species. *A. marinus* was distinguished from the other sandeel species present in the samples (*H. lanceolatus* the Greater Sandeel, and *A. tobianus*) by the absence of dorsal melanophores.

Large scale sampling of sandeel larvae was undertaken in 2002 across the northwestern North Sea by the FRV Scotia between 9 and 23 April (**Figure 2**). An ARIES high-speed sampler (Dunn et al., 1993; mouth area 0.1 m^2, mesh size 200 m) and opening-closing Methot trawl (mouth area 2.25 m^2, mesh size 2 mm) were used to sample small and large sandeel larvae, respectively. All sandeel larvae were extracted from the samples and preserved in 4% formaldehyde. *A. marinus* larvae were measured to the nearest 0.1 mm in standard (notochord) length. A subset of fish was selected for otolith analysis. Daily increments on larval sagitta otoliths were used to calculate sandeel age (Wright, 1993).

In addition, weekly chlorophyll and zooplankton sampling was carried out at Stonehaven between 1997 and 2008, and 1999 and 2013, respectively (**Supplementary Figure S1** and **S2**). Chlorophyll concentration mg m^{-3} was determined by collecting a 10 m integrated hose sample from the surface. To ensure natural "clumping" of chlorophyll in the surface layer would not give a misleading estimation of concentration, the water was mixed before being transferred to bottles. Analysis was done using a spectrophotometer. Timing of the spring bloom was defined as the Julian day at which chlorophyll concentration in the surface layer exceeded 2 mg m^{-3} for five consecutive days (Scott et al., 2006). To determine zooplankton concentration (mg m^{-3}), a 1 m ring net fitted with a 350 μm mesh size net was towed obliquely from a depth within 3 m of the seabed (45 m) to the surface. Plankton were identified to species and dry weight measurements taken. For full details, see Bresnan et al. (2016).

Otolith Analysis

Length-stratified subsamples of juveniles and adults were taken and otoliths were extracted to determine age length keys for each cruise. Total lengths (anterior tip of maxillae to tip of caudal fin) of a random sample of fish were accurately determined to 0.5 cm. A subsample was then removed for age determination. The sequence of annual rings – marked changes in opacity caused by periods of fast and slow growth – formed on sandeel otoliths (ICES, 1995) was used to determine age. These were identified using a microscope under reflected light by experienced readers. **Table 1** shows the number of otoliths collected by pelagic trawling between 1997 and 2009 (excluding 2004 and 2007).

TABLE 1 | The number of sandeels caught and aged from pelagic trawls.

Year	Date	Number of individuals caught	Number of otoliths measured
1997	21st–25th June	731	89
1998	13th–14th June	665	65
1999	2nd–5th July	2290	629
2000	15th, 16th, 18th, and 19th June	2626	842
2001	5th–9th June	5362	1265
2002	15th–20th June	5584	416
2003	14th–17th June	5877	1305
2005	25th–27th May	4759	906
2006	17th–19th June	231	203
2008	13th, 16th June	398	144
2009	13th–15th June	1358	295

Individuals were captured in 1997–2003, 2005–2006, and 2008–2009. No survey took place in 2004, and only six sandeels were measured for length in 2007.

Estimation of Sandeel Abundance

Sandeels are constantly in motion between the sediment and pelagic, and the relative amount in each part is highly variable (Greenstreet et al., 2006, 2010b). This means that the pelagic trawl data cannot be directly used to estimate sandeel abundance. The demersal trawl and acoustic surveys do provide estimates of sandeel biomass in the sediment and water column, respectively (Greenstreet et al., 2006). However, they need to be augmented with pelagic trawl data if one wishes to estimate sandeel length and weight composition. This is because, in contrast to other survey methods, pelagic trawling samples most of the length composition and does not appear to be subject to length-dependent catchability (MacDonald, 2017). Therefore, the estimation of sandeel abundance at a given length, weight, and age requires the integration of demersal, trawl, and acoustic data. Abundance is estimated by first using the sandeel length composition from pelagic trawl data to produce abundance at length, weight and age, then applying correction factors to bring the pelagic trawl biomass-at-age in line with the combined demersal and acoustic estimates of biomass-at-age.

The procedure to estimate sandeel abundance is schematized in **Figure 3**. First, an age-length key was used to estimate the probability of age-given length. Probability distributions of ages for each 5 mm length class were determined using the continuation-ratio logit method for each survey (Kvist et al., 2000; Rindorf and Lewy, 2001; Stari et al., 2010). Then, changes in distribution of age at a given length, as a function of length, were estimated using Generalised Linear Modelling. Fitting was performed using Maximum Likelihood code (Stari et al., 2010). The resultant probability matrices of age-given-length were multiplied by the length frequency of sandeels caught in all trawls to produce an estimate of the abundance at length and age. Then we applied a year-specific weight at length relationship to the matrix of abundance and age and length. This produced a matrix of abundance at age and weight. From this data, we extracted biomass at age. While these biomass-at-age matrices give accounts of biomass caught by trawling, they are not a measure of biomass at the scale of the Firth of Forth sandbanks (**Figure 1**). To obtain the true biomass of sandeels in the study area, correction factors must be applied to biomass-at-age-and-length matrices. Greenstreet et al. (2010a) measured the biomass of Firth of Forth 0-group and 1+

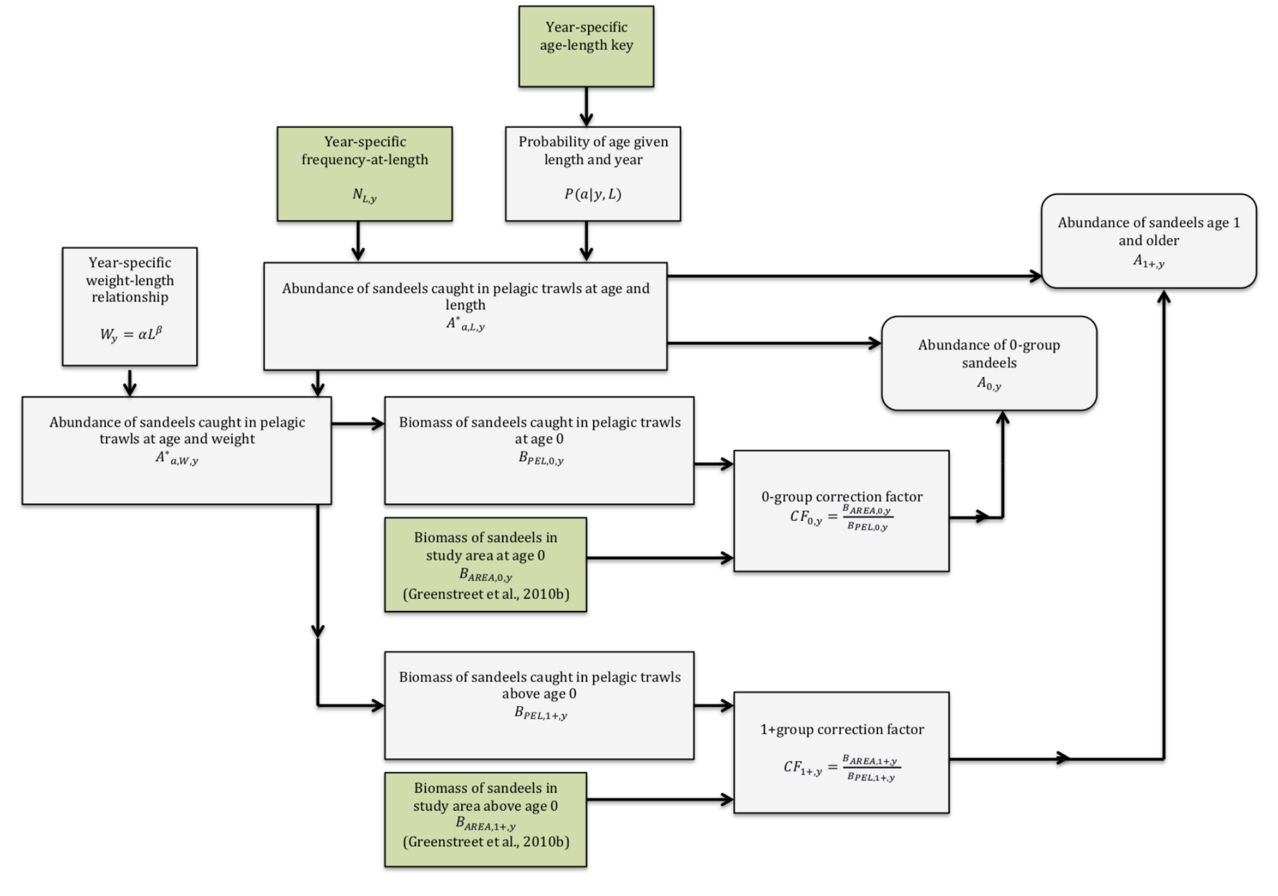

FIGURE 3 | Schematic of the method to estimate sandeel abundance. Input data and modelled data are highlighted in green and grey, respectively.

group sandeels between 1997 and 2009. Correction factors are derived using these estimates and are estimated in the following way:

0-group biomass at year in the pelagic trawl ($B_{PEL,0,y}$) is related to 0-group biomass at year y in the study area ($B_{AREA,0,y}$) using a correction factor ($CF_{0,y}$),

$$CF_{0,y} = \frac{B_{AREA,0,y}}{B_{PEL,0,y}}$$

The biomass of 1+ group sandeels in the study area is found in a similar way, using a correction factor for 1+ group sandeels ($CF_{1+,y}$)

Hence,

$$CF_{1+,y} = \frac{B_{AREA,1+,y}}{B_{PEL,1+,y}}$$

Next, abundance-at-length-and-age matrices of sandeels caught by trawling were multiplied by the appropriate correction factors defined above to give abundance-at-age-and-length of sandeels in the study area. From this, mean length-at-age for a cohort was calculated. Trends in length at age over time were estimated using linear and piecewise regression. Further, estimates of annual mortality rates (year^{-1}) were derived for each combination of age and year. Mortality rates were estimated in the following way. First, we divided the abundance of age class $a + 1$ in year $y + 1$ by the abundance of age class a in year y, which produced an estimate of annual survival rate. Mortality rate is then given by 1− survival rate.

Estimating Growth Rates From Length-at-Age Data

Fish usually grow according to the von Bertalanffy law (von Bertalanffy, 1938), That is, growth rate decreases with time, eventually becoming zero, Interannual variation in growth rates can be directly attributed to environmental changes. This is because the von Bertalanffy equation is derived from first principles on how food and temperature influences ingestion and metabolism.

The standard von Bertalanffy equation is written as

$$L(a) = L_{\infty}(1 - e^{-k(a-a_0)})$$

where $L(a)$ is the length at age (years), L_{∞} is the asymptotic length (cm), k is the rate at which length reaches the asymptotic length (year^{-1}) and a_0, is the age at which length is zero. a_0 is usually treated a fitting parameter and usually does not have any biological meaning. The von Bertalanffy law is limited because it assumes a constant environment over an animal's lifespan. However, due to its simplicity and usefulness in determining animal growth rates over a long time scale, it is widely used in ecology.

Due to the usually negative statistical and biological correlation between k and L_∞ (Pilling et al., 2002; Kimura, 2008) it may be unwise to compare differences in growth to changes in k alone. k is a measure of how quickly a population reaches L_∞ therefore having a high growth rate k may have limited benefits if the asymptotic length L_∞ is low. To account for correlation between k and L_∞, we compare differences in cohort growth rates using the growth performance index ϕ' suggested by Pauly and Munro (1984).

$$\phi' = \log_{10}(k) + 2\log_{10}(L_\infty)$$

Relationships Between Growth and Trophic/Environmental Variables

Growth performance indexes ϕ' for all cohorts were compared with SST, chlorophyll abundance and zooplankton abundance. Mean monthly SST for the post-metamorphic sandeel sampling area (56° 00′N and 56° 30′N and longitudes 003° 00′W and 001° 00′W, **Figure 1**) between 1997 and 2010 was downloaded from the Hadley Centre, United Kingdom Met Office[1]. Chlorophyll and zooplankton samples were taken in Stonehaven (56° 57.83′N, 002° 06.74′W, **Figure 1**) between January 1997 and December 2010, and between January 1999 and December 2010, respectively. For full details on sampling methods, see Bresnan et al. (2016). Copepod abundance was grouped by species and stage.

We investigated relationships between ϕ' and the average chlorophyll concentration (mg m^{-3}) between March and June, the primary sandeel foraging period. This consisted of a linear model that took the form $lm(g_y \sim C_t)$, where g_y is cohort growth performance index ϕ' for sandeels born in year y and C_t is the mean chlorophyll concentration (mg m^{-3}) between year y and year $y + t$.

Similarly, relationships between ϕ' and the concentration of zooplankton species between March and June were explored. This consisted of a linear model that took the form $lm(g_y \sim Z_{i,t})$, where g_y is cohort growth performance index ϕ' for sandeels born in year y and $Z_{i,\,t}$ is the mean biomass concentration (mg m^{-3}) of zooplankton species i between year y and year $y + t$. Relationships between ϕ' and SST were explored using a similar method.

Relationship Between Larval Growth and 0-Group Length

Sandeel larval growth rate in 2000, 2001, and 2002 (sampling locations in **Figure 2**) was estimated by assuming a linear relationship between age a (days) and length l (mm)

$$l(a) = l_0 + ga$$

where g is larval growth rate (mm d^{-1}) and l_0 is larval length at hatch day.

To assess whether larval growth rate and 0-group sandeel length was correlated during the stock decline g was related to 0-group length in June ($L(a) = L(0)$). A significant relationship would provide evidence that a long-term decline in 0-group length at date is being driven by a reduction in growth rate.

Probability of Maturation at Age 1

Maturation occurs in July (Boulcott and Wright, 2008) with length being a major determinant (Boulcott et al., 2007). Quantifying the probability of maturation at age 1 is important since few sandeels mature before age 1 and the stock is primarily composed of fish younger than age 2 (Pedersen et al., 1999). This is possible using a published relationship of probability of maturation given length (crosses and dashed line in **Figure 2**; Boulcott et al., 2007). The probability of maturation, $P(m)$, can be expressed as a logistic equation of the form

$$P(m)(\%) = \frac{100}{1 + e^{m_1(m_2 - L)}}$$

m_1 determines the shape of the logistic curve and m_2 is the length at which 50% of sandeels reach maturity. The model was fitted to maturation-at-length data (crosses in Boulcott et al., 2007), producing parameter estimates of $m_1 = 1.41$ and $m_2 = 10.66$ ($R^2 = 0.996$, $n = 12$).

Mean lengths at age 1 in June are extracted using equation 3 and the corresponding probability of maturation is found using the relationship in Boulcott et al. (2007).

RESULTS

Length Distributions

A total of 33,412 sandeels were measured for length from pelagic trawls between 1997 and 2009. Due to low levels of sandeel detected acoustically in the water column, only six sandeels were caught by pelagic trawl in 2007. This year was therefore excluded from analysis. Annual length distributions revealed a consistent bimodal pattern through the study period (**Figure 4**). Although some distributions appear polymodal, all had 2 main peaks, representing 0-group fish and older fish, with the exception of 2008 when no 0-group sandeels were caught (in 2008 no 0-group otoliths were measured and sampled sandeels were >12 cm).

Sandeel Abundance

Analysis of stock abundance-at-age revealed a decline in 1+ group numbers between 2000 and 2009 ($R^2 = 0.7$, $p < 0.01$, $n = 8$, **Table 2**). This was caused by a decrease in 1-group abundance ($R^2 = 0.63$, $p < 0.02$, $n = 8$). No other age class declined during the study period ($p > 0.05$). On average, 0-group were eight times more numerous than age 1 fish between 2000–2003 and 2005–2006, with 1-group fish being over three times more abundant than 2-group sandeels. Individuals older than age 2 constituted an average of less than 2% of the stock emphasising the importance of young age classes.

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[1] https://www.metoffice.gov.uk/hadobs/hadisst/

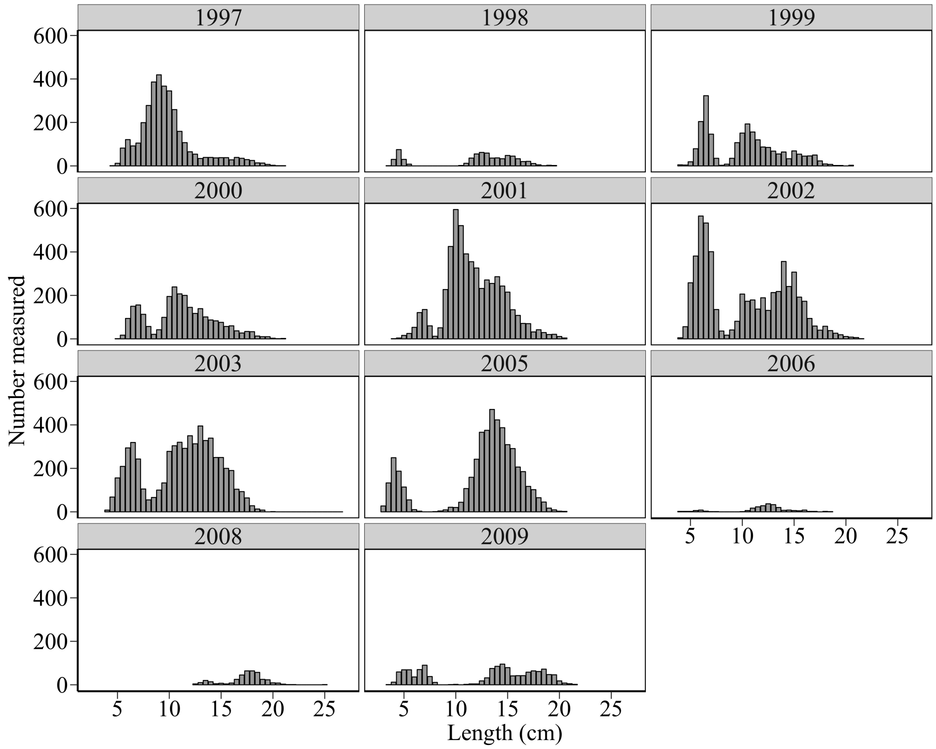

FIGURE 4 | Length frequency distributions (number measured at length) of sandeels in pelagic trawl samples.

There was marked variation in cohort mortality-at-age and mortality-at-year (**Table 2**). For example, between summer 2000 and summer 2001, 0-group and 1-group sandeels suffered annual mortality rates of 24 and 67%, respectively. However, between summer 2005 and the following summer, 0-group and 1-group sandeels suffered much higher annual mortality rates of 99.96% and 95.98%, respectively.

Changes in Growth Rate Between 1997 and 2006

There was a pattern of decreasing length between 1997 and 2005 and increasing length between 2005 and 2009 for most age classes (**Figure 5**). Piecewise linear regression identified break points for several age classes. Significant break points were found for lengths of age 1, age 2, age 5, and age 6 sandeels in 2002, 2005, 2007, and 2005, respectively.

Figure 6 shows von Bertalanffy fits to mean length data. Marked variation in cohort growth trajectories reflected variation in von Bertalanffy growth parameters L_∞ and k (**Figure 7**). There was marked variation in parameters L_∞ and k over the study period. k varied from 0.126 year^{-1} in 2004 to 1.308 year^{-1} in 2006. In biological terms, this meant that sandeels born in 2006 approached their maximum asymptotic length at a rate 10 times faster than individuals born in 2004. An outlier test revealed that the growth parameter k for sandeels born in 2006 was statistically different ($p < 0.02$). The asymptotic length of cohorts (L_∞) varied from 17.95 cm in 1999 to 34.25 cm in 2004. Outlier tests revealed that the asymptotic lengths L_∞ for sandeels born in 2004 were statistically different ($p < 0.0002$). There was a significant relationship between $\log_{10} k$ and $\log_{10} L_\infty$ meaning fast growing sandeels reached lower maximum lengths than slower growing individuals (**Figure 7**). The model of growth performance proposed by Pauly and Munro (1984) (equation 4) provided a good explanation of the data ($\phi' = 2.25 = \log_{10} k + 2\log_{10} L_\infty$, $p < 0.05$, $R^2 = 0.63$). The growth performance index ϕ' ranged from 2.07 for individuals born in 2000 to 2.63 for individuals born in 2006.

Relationship Between Cohort Growth Rate and Temperature and Plankton Biomass

We tested relationships between the growth performance index ϕ' and the biomass concentration of various zooplankton species (**Supplementary Table S1**). Only *C. finmarchicus* Stages C5–6 and *Centropages typicus* Stages C1–6 were significantly correlated with ϕ' for sandeels age 0–2, 0–3, and 0–4 years old ($p < 0.05$).

Significant relationships were also found for Total Copepod Biomass, *Temora longicornis* Stages C1–6, *C. helgolandicus* Stages C5–6, Benthic Larvae, *Acartia clausi* Stages C1–6, Cnidaria, Oithonidae Stages C1–6, but for only 1 or 2 age groupings of sandeel (**Supplementary Table S1**). The strongest correlations were found for *C. finmarchicus* Stages C5–6, *C. typicus* Stages C1–6, Total Copepod Biomass, *T. longicornis*

TABLE 2 | Sandeel abundance (millions) and annual mortality rates (year^{-1}) in the study area by age class and birth year.

	Age 0		Age 1		Age 2		Age 3+
Cohort	**Abundance at age**	**Annual mortality rate between age 0 and 1**	**Abundance at age**	**Annual mortality rate between age 1 and age 2**	**Abundance at age**	**Annual mortality rate between age 2 and age 3**	**Abundance at ages**
Born 1997	NA	NA	NA	NA	NA	NA	3022
Born 1998	NA	NA		NA	4563	0.7533	1381
Born 1999	NA	NA	58516	0.6688	19379	0.526	10458
Born 2000	62560	0.2373	47714	NA	NA	NA	6065
Born 2001	62543	0.8683	8234	−0.074	8840	NA	485
Born 2002	152194	0.8083	29172	NA	NA	NA	2297
Born 2003	80906	NA	NA	NA	3435	0.9944	128
Born 2004	NA	NA	138	0.9598	6	NA	75
Born 2005	255653	0.9996	108	NA	NA	NA	381
Born 2006	333106	NA	NA	NA	12	−17	217
Born 2007	NA	NA	20	−22	453	NA	NA
Born 2008	NA	NA	550	NA	NA	NA	NA
Born 2009	68048	NA	NA	NA	NA	NA	NA

Annual mortality estimates of age 0, age 1, and age 2 sandeels are provided.

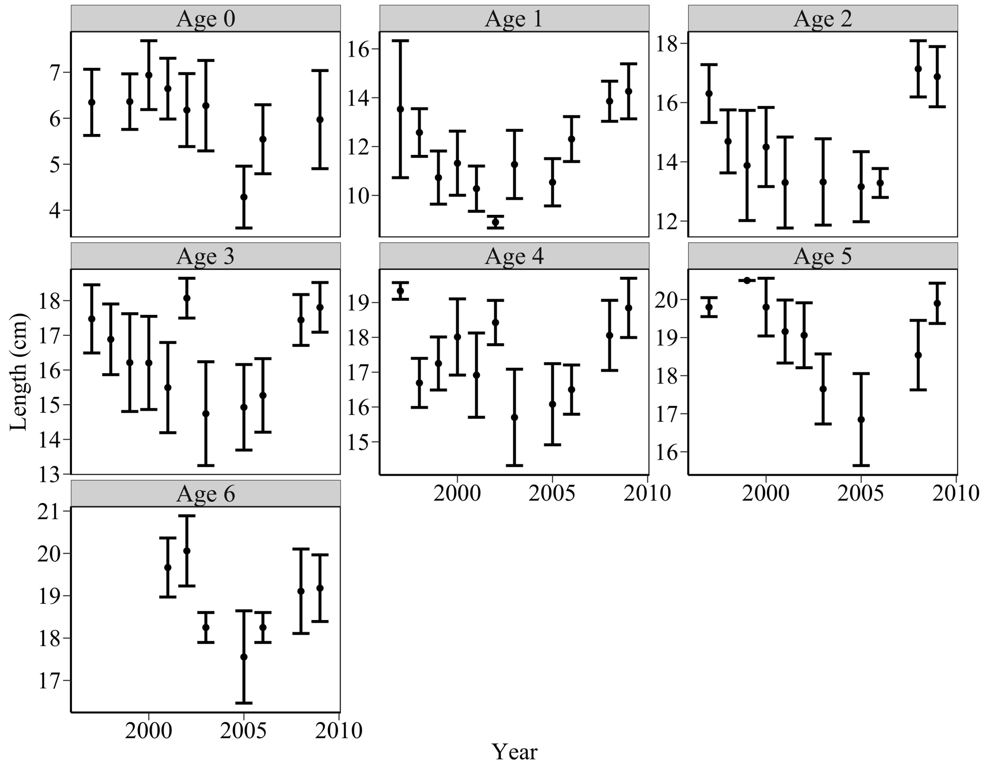

FIGURE 5 | Changes in sandeel mean length at age between 1997 and 2009 off the Firth of Forth (black points), estimated from pelagic trawl data. Error bars indicate ±1 standard deviations. Length at age decreased between 1997 and 2005, and increased between 2005 and 2009.

Stages C1–6, *C. helgolandicus* Stages C5–6 and Benthic Larvae ($R^2 > 0.7$).

There was a significant positive relationship between ϕ′ and mean chlorophyll concentration (mg m^{-3}) during the primary sandeel foraging period for sandeels age 0–3 ($R^2 = 0.35$, $p < 0.05$) and age 0–4 years old ($R^2 = 0.6$, $p < 0.01$). There was no relationship for sandeels age 0–2 years old (**Supplementary Table S2**). No statistically significant relationships were found between ϕ′ and annual or spring SST (March–June) in the study area.

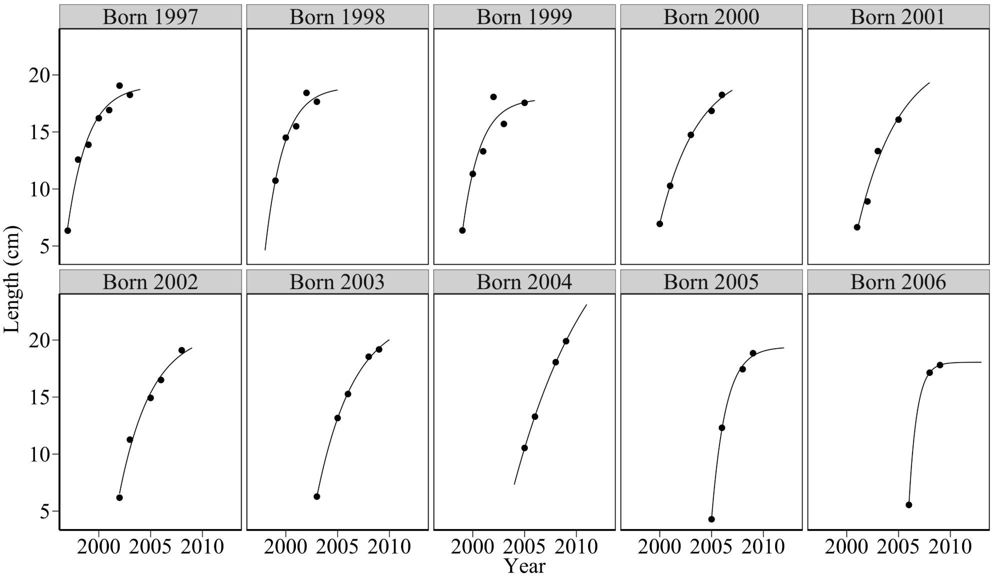

FIGURE 6 | Fitted von Bertalanffy curves for sandeels between 1997 and 2009 off the Firth of Forth. The solid line denotes the von Bertalanffy fit through observed length at age (black points). Marked variation in von Bertalanffy curves indicates corresponding variation in cohort growth parameters k and L_∞ throughout the study period.

Relationship Between Larval Growth and Length of 0-Group Sandeels

Larval length-at-age data revealed marked year-to-year changes in growth rate (**Table 3**). Between 2000 and 2002, larval growth rate ranged from 0.468 mm day^{-1} in 2000 to 0.338 mm day^{-1} in 2002. Metamorphosis dates are estimated by assuming a fixed hatch date and metamorphosis length of 30–55 mm (Cameron, 1958; Macer, 1965; Wright and Bailey, 1996; Jensen, 2001). Tracking forward from median hatch dates between 2000 and 2002 (14th, 17th, and 19th March, respectively), larval growth rates in these 3 years correspond to metamorphosis days of 7th May – 29th June, 19th May – 20th July, and 29th May – 11th August, respectively. Hence, larval phase durations between 2000 and 2002 were 54–107 days, 63–126 days, and 72–145 days, respectively. There was a statistically significant relationship between 0-group length in June (L_0) and larval growth rate (g) between 2000 and 2002 ($L_0 = 4.19 + 5.92g$, $n = 3$, $R^2 = 0.995$, $p < 0.04$, **Figure 8**). A 28% reduction in larval growth rate between 2000 and 2002 corresponded to an 11% decrease in mean length in June.

DISCUSSION

Sandeel abundance in the northwestern North Sea has undergone a sustained decline since 2001 despite the absence of a fishery. Recruitment has been maintained while the number of older sandeels has declined (Heath et al., 2012). Two main factors have been proposed as responsible for the decline in sandeel abundance, increases in overwinter and predation mortality of 0-group individuals (MacDonald et al., 2018). Starvation risk decreases with increasing size (van Deurs et al., 2011); therefore, 0-group length prior to overwintering may correlate with overwinter mortality. Indeed, there is evidence that this is true for the stock off the Firth of Forth (**Table 4**). 0-group length appears to correlate with the cohort mortality rate between the first and second summer (**Table 4**). On a cautionary note, the low mean length recorded in 2005 may be partly due to early sampling (**Table 1**). However, evidence contrary to this is that despite mean lengths in 2001 and 2005 differing by 2.35 cm, surveys were carried out less than 2 weeks apart. Sandeels do not feed in winter and survive on stored energy reserves acquired during a short feeding season (Winslade, 1974; Reeves, 1994). There appears to be little scope for extending the feeding season (Wanless et al., 2004; Boulcott et al., 2007), making energy stores dependent on food availability over a few months. The importance of stored energy reserves for the survival of 0-group fish is highlighted in a paired experimental and field study on rainbow trout *Oncorhynchus mykiss* (Biro et al., 2004). The overwhelming majority of 0-group trout that begin overwintering eventually succumb to starvation, and excluding other forms of mortality, as little as 10% may survive winter (Biro et al., 2004).

In addition to increasing starvation risk, reductions in length are likely to increase predation mortality. Few studies have quantified fish predation on sandeels, even though this is the dominant source of predation mortality (Heath et al., 2009; Reilly et al., 2014). Removals of sandeels and pelagic fish by fish predators are far higher than the combined removals by fisheries and other marine predators (Heath et al., 2009). The fact that sandeel abundance was depressed by the fishery that operated off the Scottish east coast suggests fish predators may have a similar negative effect. Removal of sandeels by haddock alone may in future equate with landings taken at the height of the Danish sandeel fishery, if haddock increase due

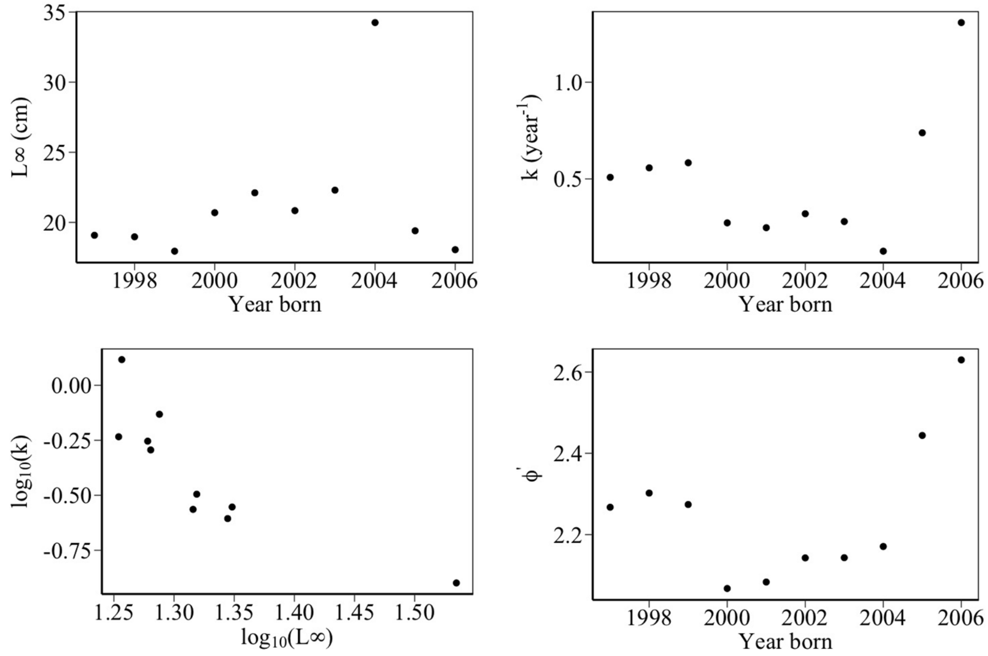

FIGURE 7 | Variation in growth parameters between 1997 and 2009 off the Firth of Forth. The top two panels show changes in growth parameter k and asymptotic length L_∞. k was relatively low between 2000 and 2004 but increased rapidly toward the end of the study period. k ranged between 0.13 and 1.31 year^{-1} over the study period (mean = 0.49 year^{-1}). L_∞ ranged between 18 and 34 cm over the study period (mean = 21.4 cm). This large range was due to the year 2004. Excluding this year, L_∞ ranged between 18 and 22 cm. The bottom left panel shows a significant negative relationship between $\log_{10}(k)$ and $\log_{10}(L_\infty)$, suggesting fast growing sandeels reached lower maximum lengths than slower growing individuals. The bottom right panel shows variation in the growth performance index ϕ', a measure of variation in the growth rates of the different cohorts.

to stricter stock management (Reilly et al., 2014). Clearly, more work is required to quantify the effect of predation on sandeel population dynamics.

To estimate abundance-at-age in a given year, we estimated age composition using pelagic trawl data, then applied correction factors to bring the pelagic trawl biomass-at-age in line with published estimates of combined dredge (for those in sediment) and acoustic (for those in the pelagic) biomass-at-age. Obtaining credible estimates of sandeel abundance-at-age is extremely challenging as fish are constantly in motion between the sediment and pelagic during summer surveys. Four different survey methods are commonly employed to measure sandeel abundance – acoustic, dredge, trawl, and grab surveys (Greenstreet et al., 2006, 2010a,b). However, it is unclear which method is most efficient. For example, grab catchability may be close to 100%, but the area sample is extremely small (0.0961 m^2, Greenstreet et al., 2010b) meaning that, even in prime sandeel habitat, the grab will occasionally catch no sandeels even though individuals may be present in great numbers nearby. An alternative method involves dredging but the dredge is prone to length (MacDonald, 2017) and density dependent catchability (Johnsen and Harbitz, 2013). The pelagic trawl will sometimes fail to capture the largest sandeels because these fish may begin overwintering in the sediment before the survey takes place (Greenstreet et al., 2006). However, the overall degree of length-dependent catchability is considerably weaker in the pelagic trawl than it is in the dredge (MacDonald, 2017).

Sandeel length-at-age declined between 1997 until around 2005, increasing thereafter (**Figure 5**). This pattern was also evident in changes in the growth performance index ϕ' (**Figure 7**). Variation in cohort growth reflected the changes in the abundance of key copepod prey, primarily *C. finmarchicus* Stages C5–6 and *C. typicus* Stages C1–6. This is consistent with evidence that sandeel biomass is determined by bottom-up effects of zooplankton and phytoplankton abundance

TABLE 3 | Results from linear regressions between age (days) and length (mm) for larval *A. marinus* ($l(a) = l_0 + l_g a$). Individuals were caught off the Scottish east coast in 2000, 2001, and 2002.

Year	Hatch length (mm)	Growth rate (mm day^{-1})	R^2
2000	4.62	0.47	0.97
2001	4.71	0.4	0.9
2002	5.65	0.34	0.55

TABLE 4 | Mean length of 0-group sandeels in June and subsequent 1st year annual mortality rate.

Cohort	0-group length (cm)	1st year mortality rate (year^{-1})
2000	6.94	0.2373
2001	6.64	0.8684
2002	6.18	0.8083
2005	4.29	0.9996

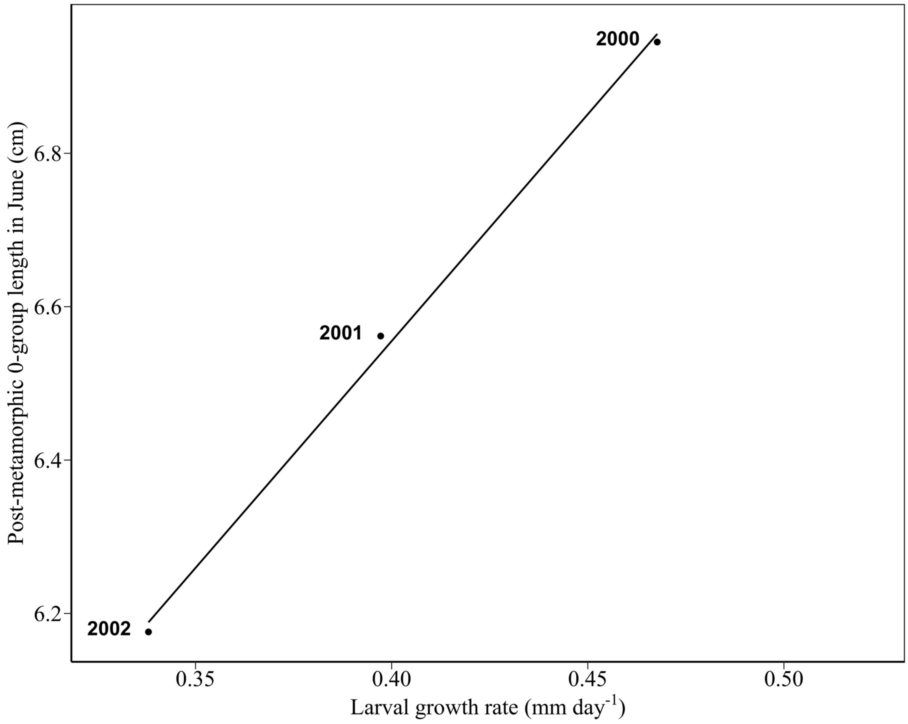

FIGURE 8 | Regression between 0-group length (cm) in June and larval growth rate. The solid line denotes a statistically significant linear relationship through data (black points) (mm d^{-1}) (R^2 = 0.995, $p < 0.04$).

(Frederiksen et al., 2006; Eliasen et al., 2011). Rapid larval growth likely reduces predation and starvation mortality, resulting in strong correlations between sandeel recruitment and abundance of key prey, such as *C. finmarchicus* (van Deurs et al., 2009; Lindegren et al., 2017). In contrast to food, year-to-year changes in temperature did not have a significant influence on variation in growth. This is consistent with the evidence of the lack of direct physiological effects of temperature rises on sandeel (Buckley et al., 1984; Pitois et al., 2012), and United Kingdom fish species in general (Heath et al., 2012).

Changes in 0-group summer length appeared to be driven by changes in larval growth rates between 2000 and 2002 (**Figure 8**). This provides further evidence of a decline in larval growth rate post-2000 (Frederiksen et al., 2011). While changes in differential mortality of larvae could drive a decline in 0-group length, this appears unlikely since larval survival and recruitment increased off the Scottish east coast between 2000 and 2009 (Heath et al., 2012). An increase in larval survival could have been caused partly by decreased food competition stemming from a decline in older sandeels (Lindegren et al., 2017).

The hypothesis of food-driven changes in sandeel growth is also supported by the coincidence of low spring chlorophyll concentration and low sandeel energy values in 2004. The spring bloom did not occur in 2004. Sandeels recovered from seabirds in the summer of 2004 had unexpectedly low energy values, which likely caused catastrophic seabird breeding failures (Wanless et al., 2005). In addition, although no measurements of abundance were taken, changes in seabird breeding output indicated low sandeel availability (Wanless et al., 2005). Larval starvation mortality could have increased if prey abundance was insufficient, specifically older larvae around metamorphosis, which is likely an extremely energy demanding process (Brewster, 1987; Gwak et al., 2003). Sandeels born in 2004 approached their asymptotic length at a slower rate than other cohorts (**Figure 7**), providing evidence of food limitation. Further evidence of bottom-up regulation is that growth rates were lowest for individuals born between 2000 and 2004 (right panels, **Figure 7**), a period when chlorophyll concentration and diatom cell densities were low (Bresnan et al., 2016).

Fish experiencing poor growth conditions tend to have delayed maturation (Berrigan and Charnov, 1994). Indeed, variation in the growth performance indexes ϕ' may account for differences in age-at-maturity across the North Sea (Boulcott et al., 2007). The sandeel stock is dominated by fish younger than age 2 (Pedersen et al., 1999, this study) underlining the importance of early maturation. Therefore, successive years of poor growth, as observed between 2000 and 2004, could decrease stock abundance. Evidence is provided from an experimentally derived probability of maturation-at-length relationship (Boulcott et al., 2007). This probability of maturation-at-length relationship implies that less than 50% of age 1 individuals would have matured between 2001 and 2005 (mean = 36%, **Supplementary Table S3**). In contrast, an average of 80% of individuals matured in other years.

AUTHOR CONTRIBUTIONS

AM, MH, DS, SG, and PB developed the ideas within the manuscript. AM performed the analysis and wrote most of the manuscript. All authors contributed to the interpretation of results and writing of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2019.00201/full#supplementary-material

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