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Investigating trends in the growth of five demersal fish species from the Firth of Clyde and the wider western shelf of Scotland

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ABSTRACT

Demersal fish landings from the Firth of Clyde peaked in 1973, then declined rapidly until the targeted demersal fishery ceased in 2005. The abundance of large fish decreased during this period, and their numbers have not recovered since 2005. We aim to determine whether changing growth rates have contributed to the decline in the abundance of large fish. Bottom trawl survey data from 1980 to 2012 was used to calculate the annual mean length-at-age and time series of von Bertalanffy growth parameters of five demersal species; cod, haddock, whiting, Norway pout and saithe. Two regions were considered: the Firth of Clyde and the neighbouring seas west of Scotland (the western shelf). There have been substantial decreases in the lengths of most age groups of Clyde haddock and whiting due to declines in both asymptotic length and von Bertalanffy growth rate. Lengths-at-age have also declined in western shelf populations, but at markedly slower rates than within the Clyde. Trends in temperature and year class strength tended to contribute little to changes in the growth parameters, so declines in length-at-age have been largely due to other factors. Fishing intensity is greater in the Clyde than western shelf, and the size selectivity of the fisheries differ as more Clyde vessels use *Nephrops* trawling gear. Since trends in growth were also more extreme in the Clyde, it appears as though size-selective fishing may have caused reductions in the lengths of these fish. If the changes in growth are partially due to fishing induced evolution then it may take many generations for the changes to reverse.

1. Introduction

The Firth of Clyde is a large semi-enclosed body of water in the south-west coast of Scotland that has a long history of fishing. Vessels over eight tonnes were prohibited from trawling in the Clyde from 1889 to 1962 in order to protect dwindling fish stocks, particularly herring (Thurstan and Roberts, 2010). The declining seine net fishery for herring lead to the ban on trawling being lifted in 1962 to allow for the exploitation of demersal fish, *Nephrops* and scallops in areas further than three miles from the coast. Landings of demersal fish then increased rapidly, reaching a maximum in 1973 before falling into decline (Hislop, 1986). Trawling within three miles of the coast was permitted from 1984 in an attempt to sustain the high catch levels. Landings then rose in 1985, but continued to decline thereafter (McIntyre et al., 2012). Responding to diminishing demersal fish catches, increasing numbers of fishing vessels began to directly target *Nephrops* during the 1990s. The targeted demersal fishery had stopped by 2005, effectively being replaced by the *Nephrops* fishery. Since 2005 landings of demersal fish have come primarily from the *Nephrops* fishery bycatch.

The Clyde demersal fish community has undergone considerable changes since large vessels began trawling. A recent analysis of bottom trawl survey data over 1927–2009 revealed temporal trends in several community-level length related indices (Heath and Speirs, 2012). They found that the onset of trawling was associated with a steep decline in the mean length of demersal fish, over all species, which decreased from approximately 40 cm in 1960 to an all time low of 20 cm in 2009. Some of the changes were driven by shifts in species abundance. There was an even distribution of species in the period 1920–1959, with thirteen different species – including large predators like spurdog (*Squalus acanthius*) and tope (*Galeorhinus galeus*) – accounting for 95% of the total demersal biomass. Species evenness reached a minimum during 1995–2004, when 95% of the biomass was attributable to only four species, with whiting (*Merlangius merlangus*) alone, accounting for 87% of the biomass. Species evenness has since increased, with the majority of the biomass being distributed among eight different species during 2005–2009. However, it is relatively small species such as Norway pout (*Trisopterus esmarkii*) and poor cod (*Trisopterus*

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minutus) that have begun to contribute more to total biomass, and whiting remains by far the most abundant species. Total demersal biomass in 2009 was approximately equal to the pre-trawling biomass, so demersal fish are still abundant in the Clyde, but few of them are large and the majority are whiting.

The length structure of the Clyde demersal fish community has shown little sign of recovery since the targeted fishery closed, and this may be due to a number of different reasons. If the *Nephrops* fleet is imposing a sufficiently large mortality on the demersal community through discarded bycatch, then the length distribution may become truncated (Jackson et al., 2001; Conover and Munch, 2002). Determining the impact of the *Nephrops* fleet will require investigating the recent discarding practices of the fishery. Additionally, trawling and dredging damage the sea floor, homogenising the habitat and disrupting benthic creatures (Auster and Langton, 1999), many of which are integral components of the diets of demersal fish. Damage to the sea floor may have resulted in large fish migrating from the Clyde to seek out more suitable feeding grounds. Finally, physiological changes in the fish themselves may also be responsible for the continued lack of large individuals. If growth rates have decreased then fish will be relatively small for their age and may never attain a large size. To determine if Clyde fish are indeed growing more slowly, we investigate temporal trends in the mean length-at-age and von Bertalanffy growth parameters of cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*), Norway pout (*Trisopterus esmarkii*) and saithe (*Pollachius virens*). The von Bertalanffy growth model describes length-at-age in terms of an asymptotic length, L_∞, and a growth rate, k. Length-at-age depends on growth history, so changes in growth rate may refer to either changes in length-at-age, which is a combination of L_∞ and k, or to changes in k. To avoid ambiguity, the k notation will be used whenever it is specifically the von Bertalanffy growth rate that is being referred to.

Growth rate is a plastic trait which can vary in response to environmental conditions such as food availability (Overholtz, 1989; Lorenzen and Enberg, 2002) and water temperature (Jorgensen, 1992; Brander, 1995; Daufresne et al., 2009). Surplus energy is used for growth and reproduction, so fish are able to grow more rapidly during periods of high food availability. Food availability for each individual depends primarily upon prey abundance, but also on competition (Ward et al., 2009). Increased competition for food generally decreases its availability to each individual, so fluctuations in year class strength may cause variations in growth (Lorenzen and Enberg, 2002). Water temperature is one of the primary environmental factors that influence growth. Fish from cold regions tend to grow more slowly than those experiencing a warm climate, however they generally live longer and attain larger body sizes (Angilletta et al., 2004). Short-term variation in growth rates may be induced by fluctuations in water temperature, and long term trends of increasing temperature have been shown to decrease the typical maximum lengths of some species (Baudron et al., 2014).

Growth rates have been shown to be modestly heritable with naturally large genetic variability (Gjedrem, 1983; Carlson and Seamons, 2008), so can evolve in response to selective pressures (Conover and Munch, 2002; Enberg et al., 2012). Small fish are more vulnerable to predation than larger individuals as they are easier to swallow and are slower swimmers (Scharf et al., 2000), so within a cohort of young fish, an individual with above average growth rate is more likely to survive predation than its peers. Therefore predation selects for rapid initial growth. Trawling nets employ a wide mesh that is designed to allow small fish to escape (Armstrong et al., 1990), disproportionately increasing the mortality rate of large individuals and generating a selective pressure to oppose that caused by predation (Edeline et al., 2007). If fishing mortality rates are high, and particularly if length distributions are truncated near the mean maturation length, then populations can potentially lose genetic variability in growth rates as fast growing fish are more likely to be caught as juveniles, or after relatively few spawning seasons as adults (Trippel, 1995; Jorgensen et al., 2007). Boldness and competitive ability are often related to growth, so fishing may also select for slow growth by imposing a selection differential on boldness (Biro and Post, 2008). The rate of fishery-induced losses in genetic variability will increase with fishing mortality rate, and relatively isolated populations will be most severely affected (Law, 2000). Growth can therefore evolve in response to fishing, at a pace determined by the heritability coefficient of growth, the fishing intensity, and the reproductive time scale of the species in question. The reversal of changes caused by fisheries induced evolution of growth has been predicted to take as long, or longer, than the initial changes (Law, 2000; Conover et al., 2009).

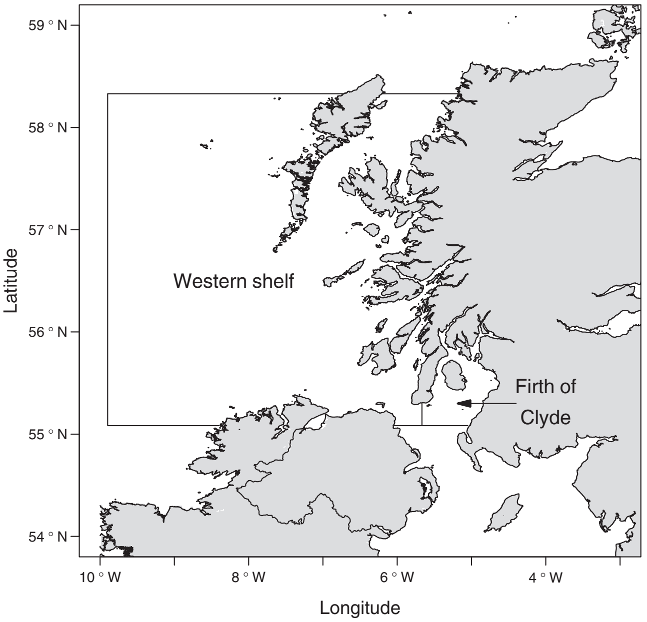

Fig. 1. The Firth of Clyde and western shelf regions.

For our study, age-length distributions for demersal species were derived from bottom trawl survey data (1980–2012) to investigate temporal trends in mean length-at-age and fit von Bertalanffy growth curves to successive cohorts (von Bertalanffy, 1934). We aimed to determine if expected lengths-at-age have changed, and to describe any changes in terms of the asymptotic length, L_∞, and growth rate, k. The L_∞ and k parameters were regressed against sea-surface temperature, estimated year-class strength and time, to determine the extent to which these variables have influenced growth. Significant relationships to temperature or year-class strength would indicate that changes in growth were plastic responses to environmental conditions that ought to revert if conditions were to change back to a prior state. A significant temporal trend may indicate that the growth parameters were responding to some other environmental variables, or that they have been evolving.

Clyde populations were compared to those in the wider west coast of Scotland to determine if any changes in the mean length-at-age and growth parameters of Clyde fish were typical of the wider region or particularly extreme. The two regions considered were the Firth of Clyde and western shelf (Fig. 1). Mixing of the demersal populations between these regions is thought to be limited, as there is evidence indicating that immigration into the Clyde is uncommon (Brander, 1975; Connolly and Officer, 2001); that some populations are resident within the Clyde (Wright et al., 2006); that

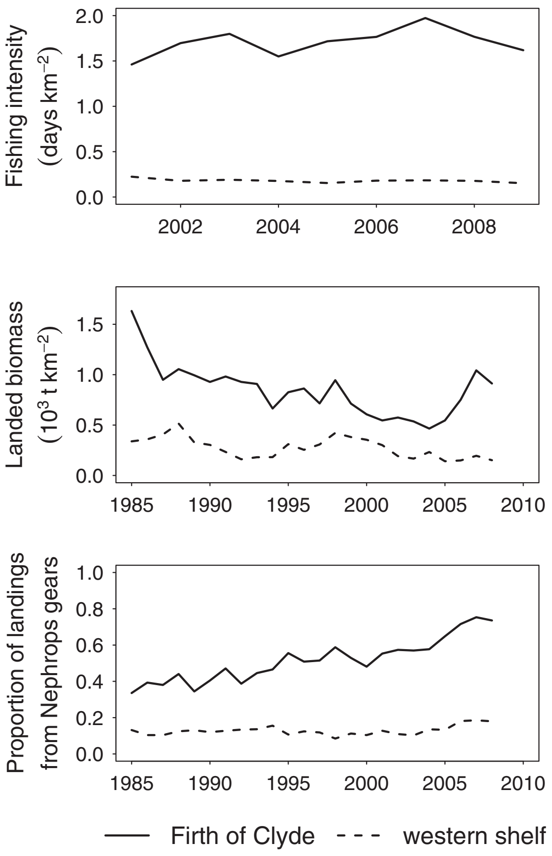

Fig. 2. Differences in the Clyde and western shelf fisheries. Top: annual fishing intensity of UK bottom trawling vessels over 10 m long from 2001 until 2009. Total landings were calculated as the sum of the landed biomass of all species from all demersal and Nephrops trawls. Middle: total landings divided by the area of the region. Bottom: proportion of the total landings caught by *Nephrops* trawls.

Clyde demersal fish tend to spawn within the confines of, or close to, the Clyde (Hislop, 1986); and that the isolation of the Clyde is sufficient for the demersal community to display independent local responses to exploitation, and potentially also to environmental fluctuations (Heath and Speirs, 2012). Regional differences in growth should therefore be examinable with survey data, and may be the result of differences in the local environment. Fishing intensity has been greater in the Clyde than western shelf, and the proportion of vessels that trawl with finer mesh nets to target *Nephrops* has risen steadily in the Clyde and is much greater than in the western shelf (Fig. 2). If fishing has been driving trends in growth then we would expect changes in the Clyde populations to be more severe. Thus, if growth has changed significantly over time then regional comparisons may provide evidence to indicate whether the trends were due to fishing.

2. Materials and methods

2.1. The data

International Bottom Trawl Survey data from the Scottish west coast (SWC-IBTS) were used in this analysis (ICES, 1985). The samples were collected using grande ouverture verticale (GOV) nets and spanned the years 1985–2012. Fisheries Research Services (FRS) demersal trawl survey data were also used, resulting in time series spanning 1980–2012. The bulk of the dataset was length data, which consisted of annual random samples of fish where the total length of each individual had been measured and rounded down to the nearest centimetre. Some of these fish were also aged, by examination of otoliths for annual growth rings, creating a length-stratified age-length data subset. The average annual sample sizes and proportions of the samples that were aged are shown in Table 1. Most of the data had been collected during quarters one and four of the year. To reduce variability in length-at-age, which improves the accuracy of the analysis by creating more distinct peaks in the length frequency distributions, we considered data from quarter one only. We chose quarter one because sample sizes were larger than in quarter four, and there were fewer missing years.

Annual stock assessments of ICES area VIa provide fishing mortality rate estimates for cod, haddock and whiting. However, since ICES area VIa includes both of the regions considered in this paper, these estimates could not be used to evaluate regional differences. We therefore used fishing effort data (Marine Scotland Science, 2016) and landings data collected in the finer spatial scale of ICES statistical rectangles to assess regional differences in fishing activity and size selectivity.

Annual mean summer (June, July and August) sea-surface temperatures were calculated using the Keppel pier, Millport, dataset (University Marine Biological Station, 1949) for the Clyde, and the Hadley Centre HadISST1 dataset (Rayner et al., 2003) for the western shelf. Mean summer temperature was calculated as the mean of mean monthly temperatures based on daily readings. Local temperature data for the years 1988, 1996 and 2003 were missing from the HadISST1 dataset, so the mean summer temperature for these years was assumed to be the average of the mean summer temperature for the preceding and subsequent years.

2.2. Estimating age-at-length

Estimating von Bertalanffy growth parameters requires age-length data, so the age of each individual in the length data was estimated. This was done by analysing the annual length and age-length frequency distributions from the length and age data respectively, using the methods of Martin and Cook (1990) as follows. This method was applied to each year of data individually, so variables are subscripted with y to indicate year. Length-at-age was assumed to be normally distributed such that modelled length frequency distributions consisted of several overlapping normal distributions, each corresponding to a different age class. The probability, $q_y(l|a)$, that an individual is of length l, given its age, a, can then be written as

$$q_y(l|a) = \frac{1}{s_y(a)\sqrt{2\pi}} \int_l^{l+w} \exp\left(-\frac{1}{2}\left(\frac{x - m_y(a)}{s_y(a)}\right)^2\right) dx \tag{1}$$

where $m_y(a)$ and $s_y(a)$ are the mean and standard deviation of length at age a, and w is the width of the length intervals. Upon making this assumption, the length and age-length frequency distributions may be expressed solely in terms of the following parameters.

$$p_y(a) = \text{proportion of fish aged a} \tag{2}$$

$$m_y(a) = \text{mean length of fish aged a} \tag{3}$$

$$s_y(a) = \text{standard deviation of length at age a} \tag{4}$$

Let $p_y(l, a)$ be the probability of a randomly selected fish being of length l and age a. This can be written in terms of Eqs. (2)–(4) as $p_y(l, a) = p_y(a)q_y(l|a)$. The probability of being in length class l is $p_y(l) = \sum_{a=1}^{A_y} p_y(l, a)$, where A_y is the maximum age of fish within the samples. The expected length frequency distribution, $f_y(l)$, can now be written as $f_y(l) = N_y p_y(l)$, where N_y is the total number of sampled fish.

Table 1
The "sample size" columns show the mean number of fish present in the annual samples, with the range shown in parenthesis. The "proportion aged" columns show the proportion of the sampled fish that were aged, averaged over years, with the range in parenthesis. Years without data have been excluded. FC and WS stand for the Firth of Clyde and the western shelf.

Species	Sample size		Proportion aged	
	FC	WS	FC	WS
Cod	29 (3–225)	81 (6–241)	0.921 (0.316–1)	0.769 (0.186–1)
Haddock	141 (1–775)	7404 (989–20716)	0.622 (0.201–1)	0.089 (0.002–0.402)
Whiting	4799 (731–14978)	10396 (1092–29303)	0.056 (0.005–0.461)	0.068 (0.013–0.296)
Norway pout	242 (3–1122)	61548 (1761–145530)	0.169 (0.015–0.865)	0.009 (0.001–0.043)
Saithe	123 (1–699)	84 (2–929)	0.658 (0.133–1)	0.746 (0.100–1)

Let annual age-length keys be defined by $q_y(a|l)$, the probability of age, a, given length, l. Since $p_y(l, a) = p_y(l)q_y(a|l)$, the age-length keys can be written as

$$q_y(a|l) = \frac{p_y(l, a)}{p_y(l)}. \tag{5}$$

Let $n_y(l)$ be the number of fish that were sub-sampled for age in length class l. The expected age distribution of fish from sub-sample $n_y(l)$ is given as $n_y(l, a) = n_y(l)q_y(a|l)$. Thus, the expected length and age-length frequency distributions can both be expressed in terms of Eqs. (2)–(4). The observed length and age-length frequency distributions, $\hat{f}_y(l)$ and $\hat{n}_y(l, a)$, were assumed to follow multinomial distributions, $\hat{f}_y(l) \sim \text{Multi}(N_y, p_y(l))$ and $\hat{n}_y(l = i, a) \sim \text{Multi}(n_y(i), q_y(a|i))$, so that Eqs. (2)–(4) could be estimated by maximum likelihood to yield age-length keys given by Eq. (5). Maximising the likelihood is equivalent to minimising

$$2\sum_{l=1}^{L_y}\hat{f}_y(l)\log\left(\frac{\hat{f}_y(l)}{f_y(l)}\right) + 2\sum_{l=1}^{L_y}\sum_{a=1}^{A_y}\hat{n}_y(l, a)\log\left(\frac{\hat{n}_y(l, a)}{n_y(l, a)}\right) \tag{6}$$

where L_y is the maximum length within the samples (Schnute and Fournier, 1980). Eq. (6) is the objective function that was minimised to estimate $p_y(a)$, $m_y(a)$ and $s_y(a)$.

Minimising Eq. (6) required the parameters to be given some initial values. The initial values of $p_y(a)$ and $m_y(a)$ were calculated directly from the age data. Due to the scarcity of old fish, values of $s_y(a)$ calculated directly from the age data were often underestimated in the older age groups. We assumed that $s_y(a)$ would increase linearly with $m_y(a)$ and fitted linear models, $\tilde{s}(a) = \alpha_0 + \alpha_1\tilde{m}(a)$, where ˜ indicates values calculated from age data from all years combined, to generate more reasonable initial values for $s_y(a)$ in the older age groups. The initial values were then calculated as $s_y(a) = \alpha_0 + \alpha_1 m_y(a)$. In order to acquire physically meaningful estimates, the minimisation procedure constrained the parameters such that $p_y(a)$, $m_y(a)$ and $s_y(a) \geq 0$ and $\sum_{a=1}^{A_y} p_y(a) \leq 1$.

Once the best fitting values $p_y(a)$, $m_y(a)$ and $s_y(a)$ were found, age-length keys could be derived from Eq. (5). The ages of all fish in the length data were estimated by multiplying the observed length frequency distributions through the age-length keys to obtain matrices, $M_{a,l,y} = q_y(a|l)\text{diag}(\hat{f}_y(l))$, in which entries specified the number of individuals at each age and length, after rounding to the nearest whole fish. These numbers at age and length matrices were then transformed to give age-length frequency distributions for cohorts, c, instead of years, $M_{a,l,c}$. Vectors specifying the length, $l_{i,c}$, and age, $a_{i,c}$, $i \in \{1, \ldots, N_c\}$, of each of the N_c sampled fish were extracted from $M_{a,l,c}$ and used to estimate the von Bertalanffy growth parameters.

2.3. Estimating growth parameters

The von Bertalanffy growth model was fitted to the age-length data for successive cohorts

$$l_{i,c} = L_{\infty c}(1 - \exp(-k_c(a_{i,c} - t_{0c}))) + \varepsilon_{i,c}, \quad \varepsilon_{i,c} \sim N(0, \sigma_c^2) \tag{7}$$

assuming that errors were i.i.d. and normal. We used OpenBUGS, via the R package R2OpenBUGS, to estimate the $L_{\infty c}$, k_c and t_{0c} parameters because it produced fewer spurious results than other R functions such as non-linear least squares (nls) and it automatically provided credible intervals for the estimates. Priors for $L_{\infty c}$ and k_c were specified as gamma distributions, and the priors for t_{0c} were normally distributed. The error variances, σ_c^2, were given wide ranging uniform priors. The gamma distribution describes positive variables and provided a sensible choice for the priors, but other less informative priors such as uniform distributions could have been used instead. The parameters for each prior distribution were found by fitting the probability density functions to the range of growth parameter values provided for each species in the online database fishbase.org (Froese and Pauly, 2015). The prior parameter values for each species are shown in Table 2. Three over-dispersed MCMC chains were run simultaneously for each cohort. Convergence was tested for with Gelman and ACF plots, as well as visually with trace plots of the MCMC chains. Simulations were run until convergence was reached, the number of iterations ranged from 1×10^5 to 1×10^7 depending on the pattern of growth of the cohort and the sample sizes, with more data-heavy cohorts requiring a longer run time. Cohorts with growth patterns closely matching von Bertalanffy growth required fewer iterations than those whose growth was more poorly described by the von Bertalanffy curve. The simulations were run on a computer with 8 GB of RAM and four Intel (R) Core (TM) i5-3570 processors, although simulations were run sequentially so that only one of the cores were used. The total run-time taken to generate growth parameter estimates for each cohort for all five species in both regions was approximately two months, however, if all four cores were used then the time taken would have been reduced greatly. The OpenBUGS output consisted of estimates of the growth parameters, $L_{\infty c}$, k_c and t_{0c}, the standard deviation of each parameter, MCMC error and 95% credible intervals.

Table 2
Parameterisation of prior distributions; L_∞ and k were gamma distributed and t_0 was normally distributed.

Species	L_∞		k		t_0	
	Shape	Rate	Shape	Rate	Mean	St. dev.
Cod	13.3	0.12	5.3	27.1	−0.35	0.51
Haddock	27.6	0.40	8.7	36.2	−0.52	0.48
Whiting	15.3	0.33	3.2	9.2	−0.98	1.08
Norway pout	50.9	2.4	8.3	13.9	0.0	1.5
Saithe	26.0	0.22	8.1	55.7	−0.78	0.57

2.4. Trends in mean length-at-age and the growth parameters

The age-length data, $M_{a,l,y}$, estimated following Section 2.2, were used to fit linear models

$$l_j = \beta_{a_j} + \gamma_{a_j} y_j \tag{8}$$

where j indexes individuals. These were independently fitted to each species within each region, to estimate trends in mean

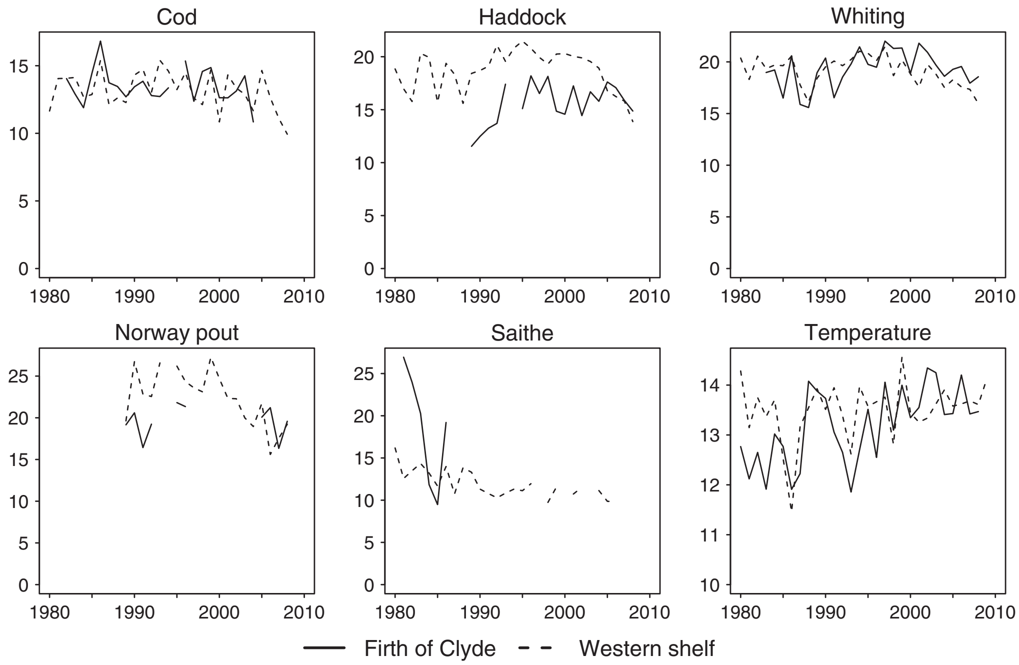

Fig. 3. Time series of estimated log year-class strength (numbers per km^2) for each species, as well as temperature (°C).

length-at-age. Age, a_j, was treated as a categorical variable, so fitting Eq. (8) resulted in separate estimates of β_{a_j} and γ_{a_j} for each age group. The γ_{a_j} terms are the estimated linear rates of change of length within age groups, which were used as a measure of the average annual change in mean length-at-age, and to estimate the total change in mean length-at-age over the time series.

The estimated growth parameters, $L_{\infty c}$ and k_c, were independently regressed against the year of birth of the cohort, Y_c, and against combinations of Y_c, estimated year class strength, $N_{0,c}$, and the mean summer temperature experienced by each cohort during the first three years of growth, T_c,

$$P_c = \delta_0 + \delta_1 Y_c + \delta_2 N_{0,c} + \delta_3 T_c + \delta_4 N_{0,c} T_c \quad (9)$$

where P_c is either $L_{\infty c}$ or k_c. To reduce the impact of poorly estimated growth parameters, these regressions were weighted by the inverse standard deviations of the growth parameter estimates. Parameters were excluded from Eq. (9) using a stepwise AIC procedure, and the interaction term, $N_{0,c}T_c$, was retained only if it was significant ($p < 0.05$). Catchability-at-length estimates for North Sea GOV trawl surveys (Fraser et al., 2007) were used to estimate the actual number of fish in the path swept out by the trawling gear. An abundance-at-age index, $N_{a,c}$, was then created for each cohort by dividing the number of fish at each age – which were in the path of the gear – by the total area swept out during the year that age group was sampled. The year class strength, $N_{0,c}$, was then estimated by fitting a simple survivorship model

$$\log(N_{a,c}) = \log(N_{0,c}) - Z_c a \quad (10)$$

where the gradient, Z_c, denotes estimated mortality rate. Time series of temperature and the estimated log year class strength are shown in Fig. 3.

3. Results

3.1. Age-length data

Annual age-length data sets were generated by calculating the probability of age given length and assigning an age to each individual in the length data. This involved estimating time series of mean lengths, $m_y(a)$, standard deviation of lengths, $s_y(a)$, and the proportions, $p_y(a)$, within each age group, following Section 2.2. The results are summarised in Fig. 4. Comparing the estimated age-length data between regions, it is apparent that age groups four and above, from each of the five species considered, have been relatively poorly sampled within the Clyde. This indicates that the proportion of the Clyde populations that consist of these older individuals is lower than in the western shelf. It may, however, be a consequence of less representative surveys within the Clyde.

3.2. Trends in mean length-at-age

Table 3 shows the results of the linear regressions of length-at-age against time Eq. (8). The changes in mean length-at-age predicted from Eq. (8), and time series of estimated mean lengths-at-age are plotted in Fig. 5.

Mean lengths declined significantly over time in most age groups of Clyde haddock, the exception being age group four. The decreases in length ranged from 5.0 ± 0.6 cm in age group one to 20.0 ± 2.2 cm in age group three during 1985–2011; the mean length of age group five decreased by 9.3 ± 4.7 cm over 2004–2010. Lengths-at-age also declined in western shelf haddock in age groups two and above, but at markedly slower rates than in the Clyde. Decreases in mean length in western shelf haddock ranged from 1.5 ± 0.1 cm to 9.7 ± 0.3 cm during 1980–2011 in age groups two and five respectively.

Declines in mean length were observed in all age groups of Clyde and western shelf whiting, apart from age group five in the western shelf. Decreases in length within the Clyde ranged from 3.7 ± 0.1 cm to 15.1 ± 2.2 cm in age groups one and four during 1980–2011 and 1980–2007 respectively; in the western shelf the decreases in the lengths of these age groups were 2.9 ± 0.1 cm and 4.6 ± 0.2 cm during 1980–2011.

The mean lengths of all age groups of Norway pout from the western shelf have increased significantly over time, by amounts ranging from 0.2 ± 0.01 cm in age group one to 4.6 ± 0.1 cm in age group five during 1990–2011 and 1993–2009 respectively. There were no such increases in the lengths of Clyde Norway pout, in fact, there has been a small but significant decrease

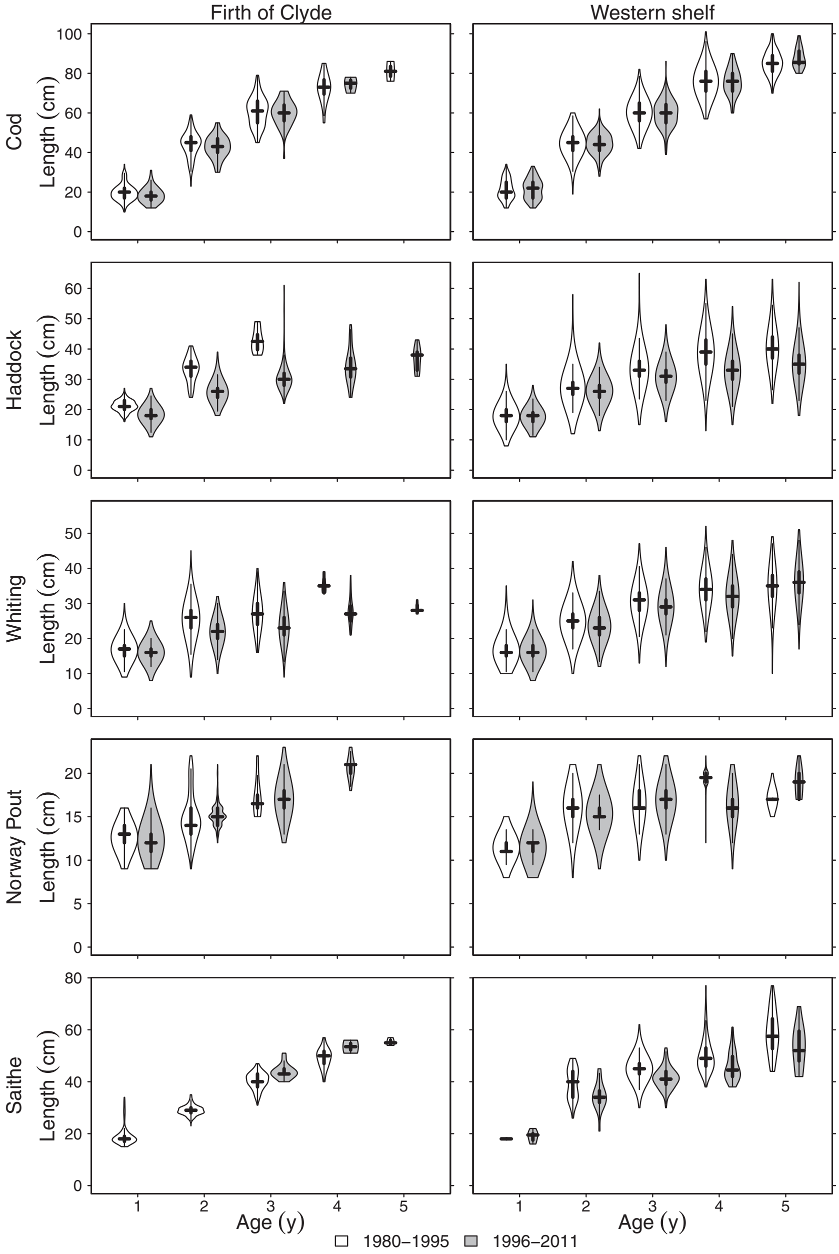

Fig. 4. Violin plots of the estimated age-length data produced from Section 2.2, grouped by periods 1980–1995 and 1996–2011. Horizontal lines indicate median length at age. Thick vertical lines show the interquartile range of length-at-age, and the narrower vertical lines show the range of the data excluding outliers (defined as 1.5 times the interquartile size in either direction). Violins extending beyond the vertical lines indicate the presence of outlying values. Within each period, the width of the violins is proportional to the quartic root of the sample size to indicate proportions at age. Age groups greater than five have been omitted.

of 0.4 ± 0.1 cm in the mean length of age group one during 1990–2011.

Mean lengths of western shelf saithe in age groups two and above declined over time; the largest decrease of 10.5 ± 3.9 cm was observed in age group two during 1980–2011. Most of the data for Clyde saithe were restricted to 1985–1988 (Fig. 5), so long term trends in length-at-age could not be calculated, and consequently the significant trends reported in Table 3 for Clyde saithe should be considered spurious.

3.3. Growth parameters

Fig. 6 shows the von Bertalanffy growth parameters that were estimated by using OpenBUGS to fit the model described in Section 2.3 to the estimated age-length data. The extent to which L_∞ and k changed over the time series was calculated from the output of the regressions against time and shown in Table 4.

3.4. Environmental influences

The growth parameters were regressed against time series of estimated year class strength, average summer temperature over the first three years of growth, and cohort (Fig. 3). The results of these regressions (Table 4) are used in this section to describe how trends in temperature and year class strength may have influenced L_∞ and k.

The growth parameters of Clyde cod did not change significantly over time, so the best fitting models excluded the cohort variable. Temperature and year class strength, however, both appear to influence L_∞, which tended to decrease as the temperature

Table 3
The linear rate of change of mean length-at-age in units of cm y^{-1}, with 95% confidence intervals shown below in parenthesis. Significant trends are indicated in bold. FC and WS stand for the Firth of Clyde and western shelf.

Species	Region	Age 1	Age 2	Age 3	Age 4	Age 5
Cod	FC	−0.067 (−0.171, 0.036)	0.015 (−0.096, 0.126)	−0.062 (−0.183, 0.060)	0.185 (−0.521, 0.891)	3.333 (−1.792, 8.459)
	WS	−0.088 (−0.185, 0.009)	−0.022 (−0.064, 0.020)	−0.045 (−0.099, 0.009)	**−0.143** **(−0.227, −0.059)**	**0.179** **(0.023, 0.335)**
Haddock	FC	**−0.192** **(−0.214, −0.170)**	**−0.424** **(−0.463, −0.384)**	**−0.768** **(−0.853, −0.683)**	−0.222 (−0.551, 0.107)	**−1.550** **(−2.325, −0.775)**
	WS	−0.003 (−0.006, 0.0003)	**−0.048** **(−0.051, −0.045)**	**−0.135** **(−0.139, −0.131)**	**−0.304** **(−0.309, −0.298)**	**−0.312** **(−0.322, −0.303)**
Whiting	FC	**−0.119** **(−0.121, −0.116)**	**−0.232** **(−0.238, −0.227)**	**−0.217** **(−0.237, −0.197)**	**−0.558** **(−0.638, −0.478)**	NA
	WS	**−0.092** **(−0.094, −0.090)**	**−0.128** **(−0.130, −0.125)**	**−0.098** **(−0.102, −0.093)**	**−0.147** **(−0.155, −0.138)**	**0.020** **(0.002, 0.038)**
Norway pout	FC	**−0.017** **(−0.024, −0.010)**	0.011 (−0.0008, 0.022)	−0.006 (−0.069, 0.057)	NA	NA
	WS	**0.0099** **(0.0094, 0.0104)**	**0.0204** **(0.0200, 0.0209)**	**0.026** **(0.025, 0.027)**	**0.052** **(0.046, 0.058)**	**0.290** **(0.283, 0.298)**
Saithe	FC	**−4.873** **(−5.286, −4.460)**	**0.896** **(0.544, 1.248)**	**0.135** **(0.092, 0.178)**	**0.170** **(0.041, 0.298)**	NA
	WS	0.032 (−0.528, 0.593)	**−0.340** **(−0.466, −0.214)**	**−0.142** **(−0.163, −0.122)**	**−0.246** **(−0.310, −0.183)**	**−0.298** **(−0.412, −0.184)**

rose and increase with reducing year class strength. The growth rate of cod in the western shelf increased over time, the best fitting model included temperature and cohort, and temperature explained enough of the variation to make the cohort variable insignificant. The L_∞ parameter decreased over time, the best fitting model included cohort, year class strength, temperature and the interaction term, and all but cohort were significant. However, cohort accounted for a larger decrease in L_∞ than the combination of other variables.

Both L_∞ and k decreased over time in Clyde haddock. The decrease in L_∞ was not explained by trends in temperature or year class strength, but there was a significant relationship between k and year class strength. The predicted increase attributable to year class strength was an order of magnitude lower than the decreases associated with the cohort and temperature variables, and the cohort effect accounted for the largest change. Neither of the growth parameters changed linearly over time in western shelf haddock, and they showed no dependence on the environmental variables. The growth parameters of Clyde whiting did not vary linearly with cohort, and the best fitting models were regressions of L_∞ against temperature, and k against year class strength. Only the rise in year class strength was significant, accounting for about half of the overall change in k. There were no linear relationships between the environmental variables and the growth parameters of western shelf whiting.

Since the growth parameter time series for Norway pout and saithe from the Clyde were sparse, there were no significant relationships with temperature or year class strength. Neither of the growth parameters of Norway pout from the western shelf trend linearly over time, although they both respond to decreases in year class strength, and are balanced by a cohort effect. In each case the largest change in the parameters was due to the cohort effect, which caused decreases in L_∞ and increases in k. The best fitting models for the growth parameters of western shelf saithe included the cohort and year class strength variables, but only the temporal trend in L_∞ was significant.

4. Discussion

4.1. Large reductions in lengths of Clyde fish

Length-at-age has declined in many distinct fish stocks around the world (Pope and Knights, 1982; Swain et al., 2007; Cheung et al., 2012; Audzijonyte et al., 2013; Baudron et al., 2014), and this has now been observed in demersal populations within the Firth of Clyde as well as throughout the Scottish western shelf sea. The rapid declines in the mean length of Clyde haddock in age groups one and above were due to significant declines in L_∞ and k (Table 4); the growth rate decreased steadily throughout the time series, whereas the decrease in L_∞ occurred during 1998–2004 (Fig. 6). Mean lengths-at-age of western shelf haddock declined most rapidly during 1994–2000 (Fig. 5) when k decreased sharply; lengths-at-age were relatively stationary in 1980–1994 as the rise in k was balanced by declining L_∞ values. Long term decreases in both the L_∞ and k values of haddock only occurred within the Clyde population, resulting in the relatively large declines in length. Although linear trends in the growth parameters of Clyde whiting were not significant, L_∞ and k in cohorts from the second half of the time series both tended to be lower than in earlier cohorts, explaining the steady and rapid declines in mean length across all age groups. Decreases in lengths-at-age in western shelf whiting in age groups one to four were due to lower k values in the second half of the time series, as Fig. 6 suggests an increase in L_∞ over time; this increase in L_∞ corresponds to the significant increase in the expected length of age group five. As with haddock, declines in both the L_∞ and k values of whiting only occurred within the Clyde population, explaining the relatively large declines in length-at-age. Increases in the mean lengths of all age groups of western shelf Norway pout appear to have resulted from the rise in k between 1995 and the late 2000s (Fig. 6). There was no such increase in the growth rate of Norway pout from the Clyde, and consequently, no increases in mean lengths-at-age. Decreases in the mean lengths of western shelf saithe in age groups two and above were due to the significant decline in L_∞ (Table 4). The survey data – as well as landings data (Thurstan and Roberts, 2010) – indicate that saithe has become rare in the Clyde since the late 1980s, and the data available for this species was insufficient to analyse long term trends in growth.

Declines in length were much more pronounced in the haddock and whiting populations within the Clyde than in the western shelf region, and the lengths of Norway pout increased in the western shelf while remaining stationary – and actually decreasing in age group one – within the Clyde. This suggests that growth has been changing in response to environmental factors that differ between the two regions, or in response to fishing pressure.

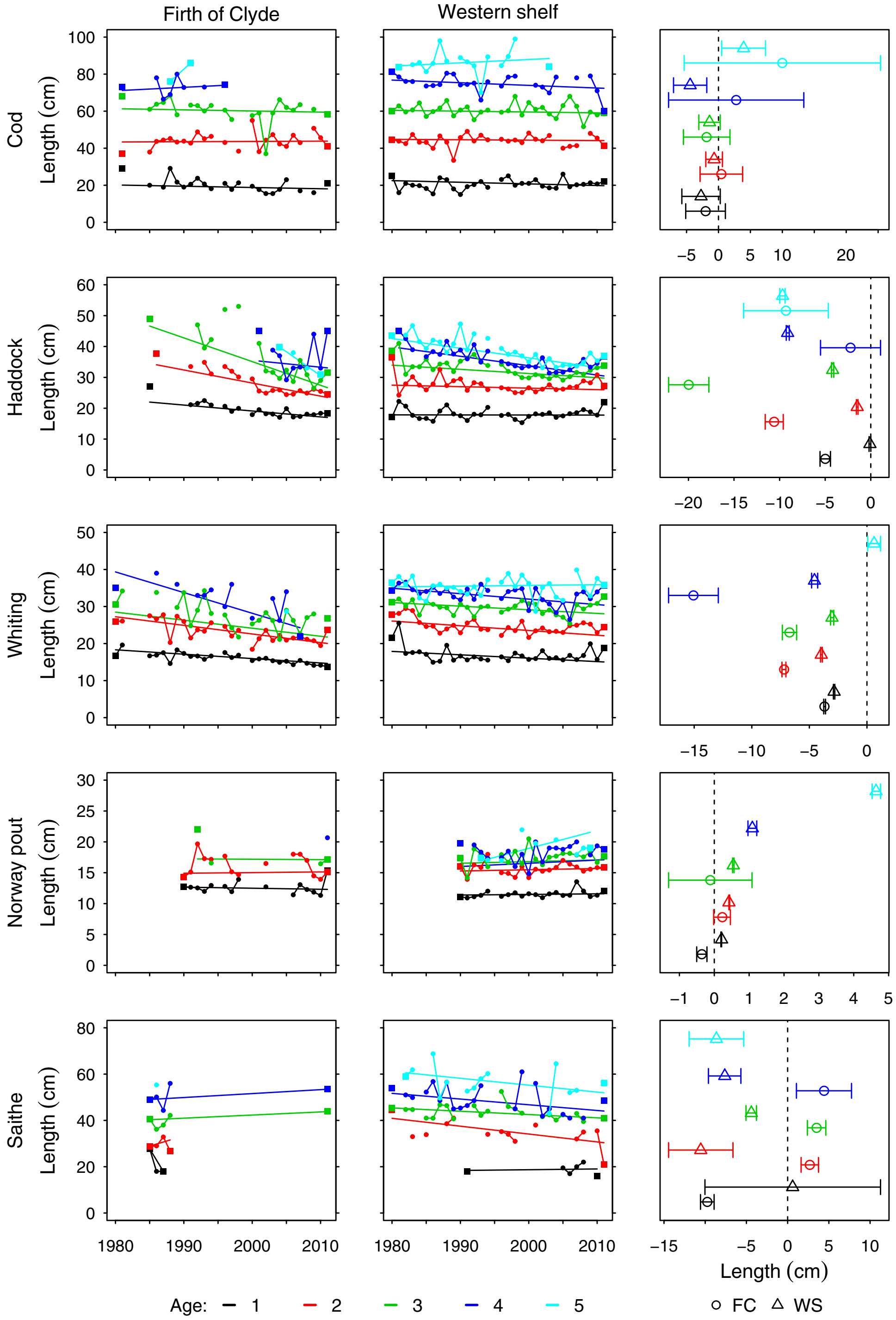

Fig. 5. Points show mean length-at-age, calculated from the estimated age-length data. Square symbols are the estimates corresponding to the first and final years in the time series. Straight lines are regression lines from Eq. (8). Plots in the column to the right show the total change in mean length between the first and final years, with 95% confidence intervals, predicted from Eq. (8). FC and WS stand for the Firth of Clyde and western shelf.

4.2. *Why has growth changed?*

Although changes in L_∞ and k were significantly related to temperature and year class strength in several groups, in most of those cases these two environmental variables only accounted for a small fraction of the observed overall changes. Most of the changes in L_∞ and k were attributable to a cohort effect, so it appears that declines in length-at-age have been due to some other environmental factors or fishing. Growth may vary in response to any environmental fluctuations that induce changes in resource acquisition and allocation (Enberg et al., 2012), but since temperature and food availability have the most direct effects (Nicieza and Metcalfe, 1997), our results imply that large changes in growth have been induced independently of environmental influences. Due to the long term nature of the declines in length, and regional differences in growth trends and the fisheries, we suggest that the changes may have been largely due to over fishing with size selective nets.

Trawl fishing disproportionately targets large individuals as they are unable to escape from the nets, so mean lengths-at-age

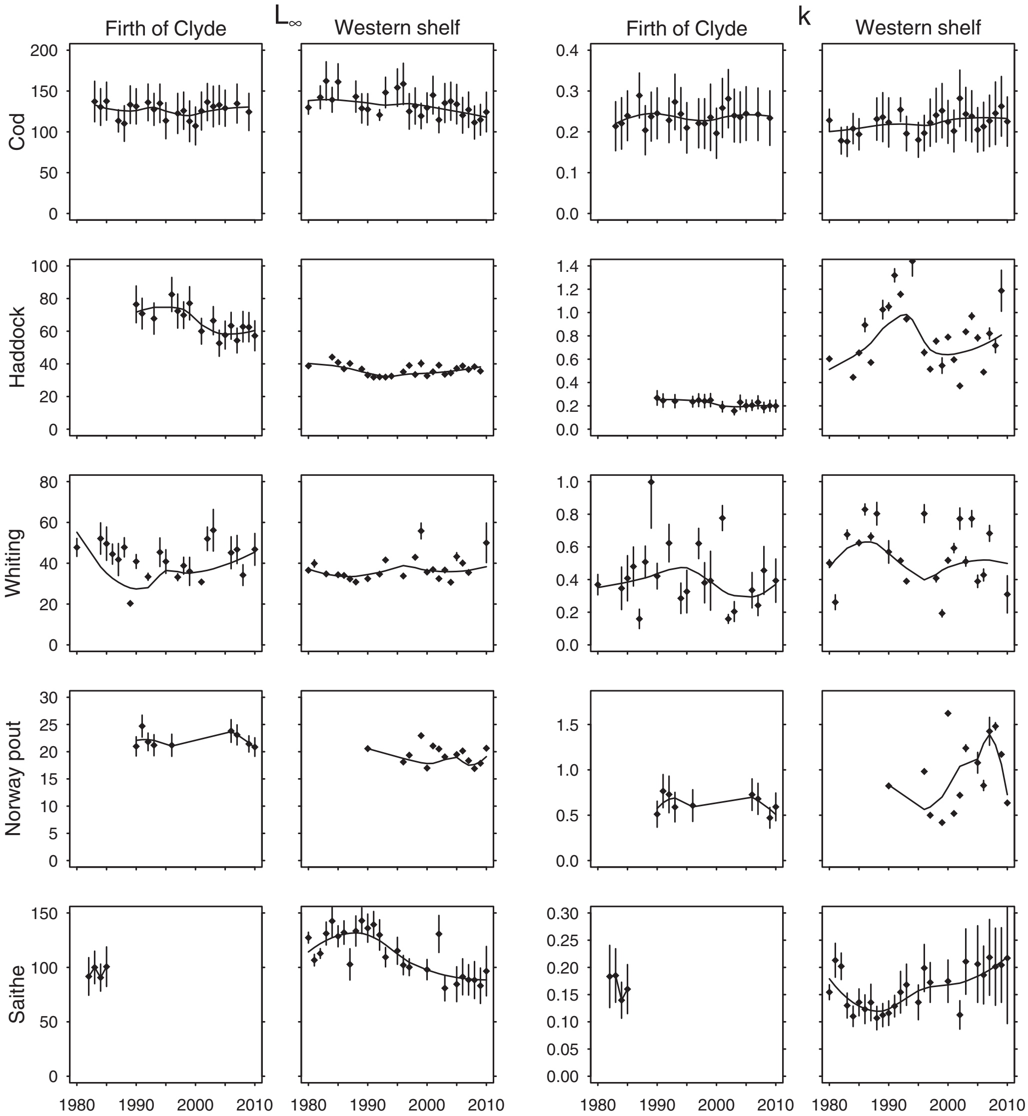

Fig. 6. The estimated mean values and standard deviations of the von Bertalanffy growth parameters, L_∞ (cm) and k (y^{-1}), plotted with loess smoothing curves. Asymptotic lengths in each region are shown in the two columns to the left, and growth rates in the two rightmost columns.

are expected to decline when fishing commences in a region simply because more of the larger fish in each age group are removed from the population. If this were the only effect that fishing had on length distributions then declines in mean length-at-age would be expected to halt as populations approach new steady states under sustained fishing pressure. We have observed steady declines in length-at-age that have occurred over two to three decades, suggesting that the disproportionate removal of large fish has gradually reduced growth rates. The linear declines in length, that were particularly severe in Clyde haddock and whiting, are suggestive of a long term selective pressure favouring small sizes (Law, 2000; Sinclair et al., 2002). This has been observed in other exploited populations (Ricker, 1981; Kirkpatrick, 1993; Law and Rowell, 1993; Haugen and Vollestad, 2001; Sinclair et al., 2002) and through experiments (Silliman, 1975; Walsh et al., 2006; Conover and Baumann, 2009), and can either be caused directly by fishing and environmental fluctuations, or indirectly through several potential secondary responses (Enberg et al., 2012).

When minimum landing sizes are well below L_∞ and a population is heavily fished, large and fast-growing individuals can become increasingly rare. This is because fish that grow quickly to a large L_∞ are more likely to be caught at a young age, so will often have fewer reproductive seasons than slower growing individuals; thus variability in maximum length can be reduced by selection against fish with large L_∞. Since the Clyde is relatively enclosed and the influx of fish from other regions is limited (Brander, 1975; Connolly and Officer, 2001; Wright et al., 2006), genetic variability in growth may have been quickly depleted by intense fishing. It therefore seems likely that decades of size-selective trawl fishing in the Clyde has steadily reduced growth rates and maximum lengths such that the resident fish have evolved to become smaller. Declines in the length-at-age of haddock and whiting were more gradual within the western shelf populations. This can be readily explained by the regional differences in fishing intensity and the selectivity of the fishing gear, which will vary the strength of selection between regions (Law, 2000).

Fishing pressure was much greater in the Clyde than in the western shelf during the 2000s (Fig. 2). The comparatively low fishing intensity in the western shelf will reduce the severity of truncations in length distributions, allowing greater proportions of fast growing fish to survive to adulthood and pass on their genes. This may have resulted in the reduced rates of decline in the length-at-age of western shelf populations. The Clyde *Nephrops* fishery is substantial and trawls with fine 70 mm nets; finer nets catch greater

Table 4

The total changes in L_∞ (cm) and k (y^{-1}) over the time periods shown, predicted from regressing against cohort only, are given with 95% confidence intervals in parenthesis. The "effect" column shows the most informative combination of explanatory variables from Eq. (9). The coefficients and standard errors for these variables, and their expected effect on the growth parameters are shown in the last two columns. The coefficients are rates of change of the growth parameters with respect to cohort, year class strength and temperature, in units of cm y^{-1}, cm 10^{-3} km^2 and cm $^\circ C^{-1}$ for L_∞, and y^{-2}, y^{-1} 10^{-3} km^2 and y^{-1} $^\circ C^{-1}$ for k. Significant changes and linear trends are shown in bold. FC and WS stand for the Firth of Clyde and western shelf.

Group	Parameter	Total change	Effect	Coefficient (SE)	Resulting change
FC cod	L_∞	−1.63	**Year class strength**	**−4.60 (2.00)**	**2.19**
		(−16.43, 13.18)			
1983–2009			**Temperature**	**−7.44 (3.43)**	**−8.86**
	k	0.0067	Year class strength	0.013 (0.0062)	−0.0068
		(−0.0300, 0.0435)			
WS cod	**L_∞**	**−19.66**	Cohort	−0.55 (0.30)	−15.28
		(−36.31, −3.01)			
1980–2010			**Year class strength**	**−18600 (8500)**	**264.72**
			Temperature	**−30.09 (10.35)**	**−20.24**
			y. c. s. × temperature	**1340 (626.6)**	**−253.67**
	k	**0.036**	Cohort	0.00095 (0.00064)	0.027
		(0.0027, 0.0695)			
			Temperature	0.017 (0.015)	0.011
FC haddock	**L_∞**	**−19.47**	**Cohort**	**−0.97 (0.25)**	**−19.47**
		(−30.33, −8.72)			
1990–2010	**k**	**−0.066**	Cohort	−0.0029 (0.0014)	−0.052
		(−0.109, −0.024)			
			Year class strength	**0.0035 (0.0014)**	**0.0037**
			Temperature	−0.026 (0.021)	−0.023
WS haddock	L_∞	−4.11	Cohort	−0.14 (0.084)	−4.11
		(−9.12, 0.90)			
1980–2009	k	0.13	No effect		
		(−0.18, 0.44)			
FC whiting	L_∞	−0.98	Temperature	−3.19 (3.69)	−4.74
		(−14.95, 13.00)			
1980–2010	k	−0.11	**Year class strength**	**−0.00052 (0.00019)**	**−0.058**
		(−0.42, 0.19)			
WS whiting	L_∞	2.05	No effect		
		(−3.85, 7.95)			
1980–2010	k	−0.12	Temperature	−0.15 (0.095)	−0.091
		(−0.39, 0.15)			
FC Norway pout	L_∞	−0.093	No effect		
		(−2.906, 2.721)			
1990–2010	k	−0.053	Cohort	0.016 (0.0066)	0.31
		(−0.265, 0.160)			
			Temperature	−0.21 (0.010)	−0.21
WS Norway pout	L_∞	−1.78	**Cohort**	**−0.18 (0.051)**	**−3.59**
		(−4.82, 1.26)			
1990–2010			**Year class strength**	**−0.00027 (0.000078)**	**0.70**
	k	0.30	**Cohort**	**0.035 (0.014)**	**0.69**
		(−0.45, 1.05)			
			Year class strength	**0.000096 (0.000031)**	**−0.25**
FC saithe	L_∞	4.24	No effect		
		(−33.49, 41.96)			
1982–1985	k	−0.036 (−0.162, 0.090)	Cohort	−0.012 (0.0098)	−0.036
WS saithe	**L_∞**	**−38.13**	**Cohort**	**−1.44 (0.44)**	**−43.12**
		(−57.06, −19.20)			
1980–2010			Year class strength	−40.14 (41.64)	4.35
	k	0.044	Cohort	0.0018 (0.0011)	0.049
		(−0.007, 0.095)			
			Year class strength	0.14 (0.095)	−0.014

proportions of small fish, so 70 mm nets will select for even smaller fish than the 100 mm nets that are used when demersal fish are the main target. The combination of greater fishing intensity and extensive use of 70 mm nets within the Clyde will result in comparatively high mortality rates, particularly in small individuals and small species. Of the five species that we have studied, Norway pout is the smallest, and lengths actually increased across all age groups in the western shelf population. The fishing regime of the western shelf does not seem to be selecting for smaller Norway pout, and may in fact be promoting increased growth rates through some secondary responses (Enberg et al., 2012). The heavy use of *Nephrops* trawling gear within the Clyde, however, appears to have been sufficient to suppress the increase in growth rate observed in Norway pout from elsewhere in the west of Scotland.

Fishing may also have selected for slow growth indirectly, by disproportionately targeting bold and competitive fish that tend to grow more quickly (Biro and Post, 2008), or by selecting for early maturation (Law, 2000). Since growth slows upon maturation, declines in length may also have been indirectly caused by trends in length-at-maturation. The length-at-maturation of Clyde haddock and whiting has been in decline (Hunter et al., 2015), so changing maturation schedules may have contributed to reductions in length. The trends in maturation, however, also appear to have been driven by fishing, so reductions in lengths are likely a combination of direct and indirect effects of fishing. Thus it appears as though trawl fishing in the west coast of Scotland has been selecting for slow growth in demersal species, causing long term reductions in lengths, and that relatively high fishing pressures and extensive use of *Nephrops* trawls has caused this to happen most rapidly in the Clyde.

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