

Growth rate fluctuations of herring in the Celtic Sea: a history of life on the edge

Deirdre Lynch, Jim Wilson* and Maurice Clarke

Marine Institute, Rinvilla, Oranmore, Co. Galway, Ireland.

*Zoology Department, Trinity College, Dublin 2, Ireland.

Contact: deirdre.lynch@marine.ie. Tel. 00 353 91 387 200, Fax: 00 353 91 387 201.

Abstract

The most south-western herring populations in Europe occur in the Celtic Sea, south of Ireland. Biological sampling has been conducted since the 1920s and routinely since 1958. This study collated and analysed these long term data for the first time. Overall results were examined in the context of time series of environmental data and population scale indices of population status. Size at age was low in the 1920s and 1950s, but increased to a peak in the 1970s before declining strongly until recently. Condition factor over time declined, whilst growth rates were greater in the 1960s and 1970s than in the 1980s and 1990s. Further analyses suggest that the changes are influenced by environmental factors, especially the North Atlantic Oscillation sea surface temperature, and the abundance of *Calanus* copepods. The implications of this work, for the rational management of this stock, are discussed.

Keywords: herring, Celtic Sea, size-at-age, condition, environmental data, historical analyses.

Introduction

Atlantic herring, *Clupea harengus* L., in the Celtic Sea, is at the southwestern edge of the species' distribution in the northeast Atlantic. Herring in this area, to the south of Ireland are considered by ICES to comprise a single stock, along with the herring population in Division VIIj (ICES, 2009).

ICES has routinely assessed this herring stock since early 1970s, and biological sampling of the catches has been conducted continuously since 1958 (ICES, 2009) with earlier data available from 1920-1957 (Burd and Bracken, 1965). Spawning stock biomass (SSB) was high in the 1960s, and declined in the 1970s, as fishing mortality (F) increased and recruitment was poor. This collapse led to the closure of the fishery in Divisions VIIg and VIIaS, from 1977 to 1982. The stock rebuilt in the 1980s but not to quite the same level. This rebuilding was due to good recruitments, and was not associated with reduced F. SSB began to decline, again, in the late 1990s and collapsed by 2003. This eventually led to a rebuilding plan, and the stock has since recovered again.

Not alone has the stock displayed strong fluctuations over time, the biological parameters of the herring that comprise the stock have also altered drastically, at least twice in the past century. It is the purpose of this paper to describe these changes in basic biology and to present them in the context of environmental information available for this area.

Materials and methods

The data used for this study derive from biological sampling of the Irish commercial fishery from 1958/1959 – 2006/2007 fishing seasons. In total 2 354 samples were obtained in this time, comprising 354 902 individual length measurements and 108 721 age readings. With the exception of the 2003/2004 season, when length-stratified sampling was employed, age sampling was conducted randomly. The basic sampling protocol has remained almost unchanged since the beginning, though individual fish weight measurements were only collected since 1975. Parameters collected were length (half cm), weight, sex, maturity stage, and age (winter rings).

Assessment of this stock is conducted on a seasonal basis, with a season running from 1st April to 31st March in the subsequent year. These seasons are here described by the earlier year, thus the 1958/1959 season is referred to as 1958. The ageing protocol follows the international convention for autumn spawning herring, whereby a fish termed to be of 2 winter ring, is 3 years of age. To coincide with the assessment season, the last winter ring is only counted in fish caught after the 1st April in a given year.

Data were available as paper records and were entered into an SQL database and mean length and mean weight at age using normal procedures for ICES assessment working groups (ICES, 2009). Mean weight and mean length at age data were used to estimate absolute growth rate, by year class. From the extracted data absolute growth rate was estimated, in terms of mean weight or mean length, by the following equation:

$$I_m = \text{Ln} ((\mu_{y+1} - \mu_y) + 2)$$

Where

- I = increment
- m = weight (g) or total length (cm) measurement
- μ = mean weight or mean length
- Y = year

The log transformation was performed by the addition of 2 to account for apparent negative growth, especially at older ages. This analysis was performed for 1-year age intervals across all fully represented age groups in the catches, and also over the 2-5 winter ring interval. This is because fish of 2-5 winter ring have always been the dominant age groups, in the population (ICES, 2009, Annex 5).

To derive an index of condition of individual cohorts, mean length and mean weight at age data were used. Fulton's condition factor (Ricker, 1975) was applied to mean length and mean weight at age data by cohort.

The Sea Surface Temperature (SST) data used in this study were extracted from a grid dataset (Second Hadley Centre Sea Surface Temperature dataset (HadSST2)). The digital data file was obtained from www.cru.uea.ac.uk/cru/data/temperature (Rayner et al., 2005). North Atlantic Oscillation (NAO) was represented by a dataset containing monthly mean sea-level pressure difference between a station on the Azores and one on Iceland. Here data were used for SW Iceland (Reykjavik) and Ponta Delgada (Azores) and NAO time series was the January values, the NAO winter index; (Hurrell 1995). The NAO is described by Rayner et al. (2005) and the digital data were obtained from the Joint Institute for the study of the Atmosphere and Ocean at www.jisao.washington.edu/data_sets/nao/nao.ascii.

The monthly mean abundance data of both *Calanus finmarchicus* and *Calanus helgolandicus* for ICES Divisions VIIa, VIIg and VIIj from 1958 to 2006 were obtained from the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) through a licence agreement. The total number of samples per month for

each division was also obtained. The monthly mean values provided by SAHFOS from 1958 to 2006 were the average number of organisms (*Calanus finmarchicus* and *Calanus helgolandicus*) in a given month.

To obtain estimates of stock size, exploitation rate and recruitment strength over time, the accepted ICES assessment of the stock (ICES, 2009) was used.

Product Moment Correlation (Fowler et al, 1998) was employed to test the strength of association, and significance, between biological variables on the one hand, and environmental or stock-assessment derived variables (recruitment, fishing mortality and spawning stock biomass) on the other.

Results

Mean length for the main age groups increased above the long term average from the late 1950s, and reached a peak in 1975. After that mean length declined, falling below the long term average again, by the early 1990s. This can be clearly seen in Figure 1. The most recent mean lengths depicted for the main age groups in the catches (2 and 3 ringers) are 5% lower than in 1975. Length at age appears to have been increasing in the 1920s, but had declined to below long term average again by the 1950s. However, it is not possible, from the data available, to determine if mean length underwent an upward cycle between 1930 and 1955, with a peak similar to that observed in 1975. Mean weight data are only available from 1975, and are not presented. However, since 1975, they follow the same trends as for mean length.

Fulton's condition factor displayed a strong decline over time for both dominant age groups. These declines were significant for 2 winter rings (F-statistics, $p < 0.001$, $r^2 = 0.508$, s.e. = 0.0002) and for 3 winter rings also (F-statistics, $p < 0.001$, $r^2 = 0.46$, s.e. = 0.0002). This suggests a decline in overall condition throughout the time series, with the 1999/2000 and 2002/2003 year classes displaying lowest condition factor in the series (Figure 2).

The absolute growth rate in length and weight is presented in Figure 3, over the age interval of 2 to 5 winter rings. When these growth rates were regressed against cohort birth year, declining growth became apparent. These declines were highly significant, both for length (F-statistics, $p < 0.001$, $r^2 = 0.527$, s.e. = 0.097) and weight (F-statistics, $p < 0.001$, $r^2 = 0.374$, s.e. = 0.022). The decline is more marked for mean weight, because weight is a power function of length. There was no significant relationship between absolute growth rate I_m and year class strength, either in terms of length (F-statistics, $p = 0.43$, $r^2 = 0.016$, s.e. = 0.112) or weight (ANOVA, $p = 0.94$, $r^2 = 0.0004$, s.e. = 0.027).

Celtic Sea SST data for September are shown in Figure 4 from 1970/1971 to 2003/2004. September was selected because it was one of the warmest months over the time series, and is considered a good index of temperature throughout the summer. The temperature oscillated from 1970 to 1984. It then became more variable with a strong increase from 1994 onwards. The same trend is apparent as in the Celtic Sea and Irish Sea. Notable peaks in temperature were in the mid 1970s and the late 1990s, with troughs in the 1960s and 1980s. The North Atlantic Oscillation (NAO) winter index fluctuated between positive and negative phases until 1989. The year 1989 is the year with the most positive value and it stayed in the positive phase until 1996. (Figure 5). The abundance of *Calanus helgolandicus* and *Calanus finmarchicus* varied and it was difficult to detect obvious trends. There are a few years where very little sampling was done and there are many null value hauls in the dataset.

The correlation coefficients, and their significance levels, between the environmental parameters (North Atlantic Oscillation, sea surface temperature and the abundance of *Calanus finmarchicus* and *Calanus helgolandicus*) and biological parameters (absolute growth rate in mean length and mean weight, mean

length at age, mean weight at age and condition factor) were investigated and results are shown in Tables 1-3. Relationships displaying significant correlations are shown in Figure 6. All the correlation coefficients were quite low with the maximum value being 0.50. This indicates that at best the correlations were modest. Mean length at age (2 and 3 winter rings) showed significant negative correlations with SST in both the Irish and Celtic Seas. Mean weight at age was found to have positive correlations with the abundance of *Calanus finmarchicus* in the Irish Sea but only for the month of May. This suggests that herring in this area attained larger weight in years where these prey species were more abundant. Very few correlations between *Calanus finmarchicus* abundance and mean size were significant and there were no significant correlations between *C. helgolandicus* and mean size. Absolute growth rate in mean length for 2-5 winter rings was found to have a highly significant, modest and negative correlation with NAO in January. Absolute growth rate in mean weight did not show a significant correlation with NAO but it must be noted that the time series for mean weight was shorter.

There was a significant positive correlation found between Fulton's condition factor and *Calanus finmarchicus* for both 2 and 3 ringers. This points towards better fish condition when prey abundance is higher. However Fulton's Condition Factor shows a significant, negative and weak correlation with sea surface temperature in both the Irish and Celtic Sea. This indicates that high temperatures are associated with a low condition factor. There were no other significant correlations found between the environmental and biological variables.

The relationship between mean length and spawning stock biomass is shown in Figure 7. The maximum mean length was observed when stock was low in the 1970s but mean length is presently at the lowest in the time series and the stock size is as low as it was in the 1970s. This trend is apparent in mean weight also. This suggests that density dependant growth is not a factor at present. It appears from Figure 7 that growth rate decreased since the 1960s when the stock size was high. When the stock size was declining, in the 1970s, growth rate declined markedly. During the period of the stock collapse, the growth rate improved somewhat, and seems to have declined again during the period when the stock recovered.

Discussion

From the data collated and analysed in this project it is clear that growth in herring off the south of Ireland had both low and a high phases in the past 50 years. Historical data (Burd and Bracken, 1965; Farran, 1944) suggest that in the 1920s and 1930s growth was intermediate.

Some scientists have attributed changing growth to density dependence. Melvin and Stephenson (2007) working on George's Bank herring and Oskarrson (2008) on Icelandic summer spawners showed that when SSB was high, growth was low. On the other hand, Watanabe et al. (2008) reported that density dependence was not responsible for changing growth in Japanese herring. In the present study, it is clear, that changes in growth are not density-dependent at the population level, for herring. However, the possibility that density dependence may occur across the entire species assemblage cannot be discounted. A few authors, such as Toresen (1990) and Cardinale and Arrhenius (2000) felt that density dependence, in conjunction with other factors was responsible for the growth changes they examined in Norwegian spring spawning and Baltic herring respectively. The Celtic Sea is a much more complex system than either of those areas (ICES, 2008). Moreover, community-scale density dependence may be difficult to detect.

It is known that autumn spawners tend to be larger at age (Molloy, 1968) in this area. Peak size/weight in the 1970s was associated with an increase in the autumn spawning component. However, there is good evidence that the autumn spawning component was experiencing a change in growth rate at that

time (Harma et al. 2009). Harma et al. (2009) showed that the peaks in size and weight at age in the 1970s are not due to differing relative abundances of autumn and winter spawners. This is an important result because it can be used to discount the effect of variation in spawning components on the apparent growth rate changes.

Fishing mortality has been high and this has led to a stock collapse, when recruitment was low in the 1970s and early 2000s (ICES, 2009). However there is no obvious biological reason why high F would lead to lower growth, especially at low stock size. There was high fishing mortality when growth was increasing in the early 1970s, and when growth was declining in the 1980s and 1990s. Therefore there is no basis to explain changing growth in terms of fishing mortality. However further work is required to investigate if high F may have acted as a selection pressure, to remove fish with a genetic disposition towards faster growth.

The most likely drivers for these fluctuations are likely to be environmental in nature. The strongest influence on growth appears to be the January NAO index, which showed a highly significant ($p < 0.01$) negative correlation with growth rate in length. This indicates that positive NAO is associated with lower growth rate in length over the 42-year period 1958 and 1999.

Increased temperature might be expected to influence growth either positively or negatively, depending on the geographic location of the stock. Hay et al (2001) found that increased food abundance linked to increased temperature led to better growth of a particularly strong year class. In contrast Watanabe et al (2008) stated that high temperatures during winter had a negative effect on the growth of Japanese herring. In this study, sea surface temperature in September showed negative influence on mean length/weight and condition factor, more so in the Irish than in the Celtic Sea. There were fewer significant correlations between SST and growth/condition in the Celtic Sea. There is evidence that increased temperature is associated with reduced size/weight at age and condition, particularly in the Irish Sea.

Calanus helgolandicus abundance was positively correlated with size and weight at age in the Celtic Sea (VIIg) whilst *Calanus finmarchicus* correlated positively in the Irish Sea (VIIa). Perhaps this is explained by the more northern distribution of the latter species. Also, in the Irish Sea, there was a highly significant positive correlation between *C. finmarchicus* and Fulton's condition factor. It is known that the nutritional value for development and growth of fish larvae is lower in *C. helgolandicus* than in *C. finmarchicus* (ICES, 2006). This may explain why higher abundance of the latter species is associated with better condition. Good abundance of *C. finmarchicus* at the larval stage probably leads to the fish having better condition as adults.

Fluctuations in growth and condition have been documented for many herring stocks. However, this study represents the first attempt to understand fluctuations in an oceanic herring stock, at the edge of the species' range in the open north Atlantic. Univariate correlations were used as a first approach to the problem. This approach does not take into account interaction between parameters, or multiple drivers for change, acting together, and further work is required. However the present work does indicate that the explanations for changing growth are environmentally driven, with positive NAO and increased temperature associated with reduced growth in this herring stock.

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Table 1. Correlation coefficients (Corr.), significance levels between NAO (January) and SST (Irish and Celtic Sea) with various biological variables examined. Sample size (n) and degrees of freedom (df) indicated. NS indicates that the correlation was not significant.

Environmental variable	Month	Biological variable	Ages	Years		Corr.	df	Sig	
				Range	n				
NAO	January	Absolute Growth Rate in MW	2/5	1969-1999	31	-0.321	29	NS	
NAO	January	Absolute Growth Rate in ML	2/5	1958-1999	42	-0.442	40	0.01	
NAO	January	Raw mean length at age	year class	2	1960-1999	40	-0.287	38	NS
NAO	January	Raw mean length at age	year class	3	1960-1999	40	-0.400	38	0.05
NAO	January	Raw mean weight at age	year class	2	1975-1999	25	-0.2226	23	NS
NAO	January	Raw mean weight at age	year class	3	1975-1999	25	-0.28301	23	NS
NAO	January	Raw mean length at age		2	1960-1999	40	-0.219	38	NS
NAO	January	Raw mean length at age		3	1960-1999	40	-0.223	38	NS
NAO	January	Raw mean weight at age		2	1975-1999	25	-0.291	23	NS
NAO	January	Raw mean weight at age		3	1975-1999	25	-0.218	23	NS
NAO	January	Fulton's condition factor		2	1972-1999	28	-0.151	26	NS
NAO	January	Fulton's condition factor		3	1971-1999	29	-0.214	27	NS
SST Irish sea	September	Absolute Growth Rate in MW	2/5	1970-2000	31	-0.180	29	NS	
SST Irish sea	September	Absolute Growth Rate in ML	2/5	1970-2000	31	-0.003	29	NS	
SST Irish sea	September	Raw mean length at age	year class	2	1970-2003	34	-0.374	32	0.05
SST Irish sea	September	Raw mean length at age	year class	3	1970-2002	33	-0.367	31	0.05
SST Irish sea	September	Raw mean weight at age	year class	2	1975-2003	29	-0.33571	27	NS
SST Irish sea	September	Raw mean weight at age	year class	3	1975-2002	28	-0.29051	26	NS
SST Irish sea	September	Raw mean length at age		2	1970-2003	34	-0.448	32	0.05
SST Irish sea	September	Raw mean length at age		3	1970-2003	34	-0.464	32	0.01
SST Irish sea	September	Raw mean weight at age		2	1975-2003	29	-0.378	27	0.05
SST Irish sea	September	Raw mean weight at age		3	1975-2003	29	-0.406	27	0.05
SST Irish sea	September	Fulton's condition factor		2	1972-2003	32	-0.357	30	0.05
SST Irish sea	September	Fulton's condition factor		3	1971-2002	32	-0.319	30	NS
SST Cetic Sea	September	Absolute Growth Rate in MW	2/5	1970-2000	31	-0.175	29	NS	
SST Cetic Sea	September	Absolute Growth Rate in ML	2/5	1970-2000	31	-0.011	29	NS	
SST Cetic Sea	September	Raw mean length at age	year class	2	1970-2003	34	-0.42712	32	0.05
SST Cetic Sea	September	Raw mean length at age	year class	3	1970-2002	33	-0.37484	31	0.05
SST Cetic Sea	September	Raw mean weight at age	year class	2	1975-2003	29	-0.31981	27	NS
SST Cetic Sea	September	Raw mean weight at age	year class	3	1975-2002	28	-0.2614	26	NS
SST Cetic Sea	September	Raw mean length at age		2	1975-2003	29	-0.338	27	NS
SST Cetic Sea	September	Raw mean length at age		3	1975-2003	29	-0.355	27	NS
SST Cetic Sea	September	Raw mean weight at age		2	1970-2003	34	-0.435	32	0.05
SST Cetic Sea	September	Raw mean weight at age		3	1970-2003	34	-0.435	32	0.05
SST Cetic Sea	September	Fulton's condition factor		2	1972-2003	32	-0.369	30	0.05
SST Cetic Sea	September	Fulton's condition factor		3	1971-2002	32	-0.319	30	NS

Table 2. Correlation coefficients (corr.) and significance levels (Sig.) between *Calanus helgolandicus* abundance in VIIa and VIIg and various biological variables. Sample size (n) and degrees of freedom (df) indicated. NS indicates that the correlation was not significant.

Environmental variable	Month	Biological variable	Ages	Years			Corr.	df	Sig
				Range	n				
VIIa	May	Absolute Growth Rate in MW	2/5	1971-2000	24	-0.275	22	NS	
VIIa	May	Absolute Growth Rate in ML	2/5	1968-2000	25	0.348	23	NS	
VIIa	May	Raw mean length at age	year class	2	1968-2003	28	0.082	26	NS
VIIa	May	Raw mean length at age	year class	3	1968-2002	27	0.046	25	NS
VIIa	May	Raw mean weight at age	year class	2	1976-2003	23	0.03199	21	NS
VIIa	May	Raw mean weight at age	year class	3	1976-2002	22	-0.16288	20	NS
VIIa	May	Raw mean length at age		2	1968-2006	31	0.113	29	NS
VIIa	May	Raw mean length at age		3	1968-2006	31	0.099	29	NS
VIIa	May	Raw mean weight at age		2	1976-2006	26	-0.011	24	NS
VIIa	May	Raw mean weight at age		3	1976-2006	26	-0.023	24	NS
VIIa	May	Fulton's condition factor		2	1972-2003	26	-0.169	24	NS
VIIa	May	Fulton's condition factor		3	1971-2002	26	-0.291	24	NS
VIIa	September	Absolute Growth Rate in MW	2/5	1971-2000	29	-0.054	27	NS	
VIIa	September	Absolute Growth Rate in ML	2/5	1959-2000	31	-0.120	29	NS	
VIIa	September	Raw mean length at age	year class	2	1967-2003	33	0.176	31	NS
VIIa	September	Raw mean length at age	year class	3	1967-2002	32	0.221	30	NS
VIIa	September	Raw mean weight at age	year class	2	1975-2003	28	-0.005	26	NS
VIIa	September	Raw mean weight at age	year class	3	1975-2002	27	0.025	25	NS
VIIa	September	Raw mean length at age		2	1967-2006	36	0.086	34	NS
VIIa	September	Raw mean length at age		3	1967-2006	36	0.122	34	NS
VIIa	September	Raw mean weight at age		2	1975-2006	31	-0.042	29	NS
VIIa	September	Raw mean weight at age		3	1975-2006	31	0.024	29	NS
VIIa	September	Fulton's condition factor		2	1972-2003	31	0.151	29	NS
VIIa	September	Fulton's condition factor		3	1971-2002	31	0.071	29	NS
VIIg	May	Absolute Growth Rate in MW	2/5	1969-2000	29	0.235	27	NS	
VIIg	May	Absolute Growth Rate in ML	2/5	1958-2000	38	0.265	36	NS	
VIIg	May	Raw mean length at age	year class	2	1960-2003	39	-0.060	37	NS
VIIg	May	Raw mean length at age	year class	3	1960-2002	38	-0.121	36	NS
VIIg	May	Raw mean weight at age	year class	2	1975-2003	27	-0.203	25	NS
VIIg	May	Raw mean weight at age	year class	3	1975-2002	26	-0.276	24	NS
VIIg	May	Raw mean length at age		2	1960-2006	41	-0.176	39	NS
VIIg	May	Raw mean length at age		3	1960-2006	41	-0.135	39	NS
VIIg	May	Raw mean weight at age		2	1975-2006	29	-0.230	27	NS
VIIg	May	Raw mean weight at age		3	1975-2006	29	-0.235	27	NS
VIIg	May	Fulton's condition factor		2	1972-2003	29	-0.187	27	NS
VIIg	May	Fulton's condition factor		3	1971-2002	29	-0.307	27	NS
VIIg	September	Absolute Growth Rate in MW	2/5	1971-2000	28	0.217	26	NS	
VIIg	September	Absolute Growth Rate in ML	2/5	1959-2000	31	-0.051	29	NS	
VIIg	September	Raw mean length at age	year class	2	1965-2003	33	0.250	31	NS
VIIg	September	Raw mean length at age	year class	3	1965-2002	32	0.257	30	NS
VIIg	September	Raw mean weight at age	year class	2	1975-2003	28	0.260	26	NS
VIIg	September	Raw mean weight at age	year class	3	1975-2002	27	0.220	25	NS
VIIg	September	Raw mean length at age		2	1965-2006	36	0.387	34	0.05
VIIg	September	Raw mean length at age		3	1965-2006	36	0.387	34	0.05
VIIg	September	Raw mean weight at age		2	1975-2006	31	0.414	29	0.05
VIIg	September	Raw mean weight at age		3	1975-2006	31	0.363	29	0.05
VIIg	September	Fulton's condition factor		2	1972-2003	30	0.210	28	NS
VIIg	September	Fulton's condition factor		3	1971-2002	30	0.212	28	NS

Table 3. Correlation coefficients (Corr.) and significance levels (Sig) between Calanus finmarchicus abundance in VIIa and VIIg and various biological variables. Sample size (n) and degrees of freedom (df) indicated. NS indicates that the correlation was not significant.

Environmental variable	Month	Biological variable		Years			Corr.	df	Sig
				Ages	Range	n			
VIIa	May	Absolute Growth Rate in MW		2/5	1971-2000	24	0.360	22	NS
VIIa	May	Absolute Growth Rate in ML		2/5	1968-2000	25	0.292	23	NS
VIIa	May	Raw mean length at age	year class	2	1968-2003	28	0.377	26	0.05
VIIa	May	Raw mean length at age	year class	3	1968-2002	27	0.361	25	NS
VIIa	May	Raw mean weight at age	year class	2	1976-2003	23	0.436	21	0.05
VIIa	May	Raw mean weight at age	year class	3	1976-2002	22	0.501	20	0.05
VIIa	May	Raw mean length at age		2	1968-2006	31	0.376	29	0.05
VIIa	May	Raw mean length at age		3	1968-2006	31	0.361	29	0.05
VIIa	May	Raw mean weight at age		2	1976-2006	26	0.461	24	0.05
VIIa	May	Raw mean weight at age		3	1976-2006	26	0.455	24	0.05
VIIa	May	Fulton's condition factor		2	1972-2003	26	0.506	24	0.01
VIIa	May	Fulton's condition factor		3	1971-2002	26	0.528	24	0.01
VIIa	September	Absolute Growth Rate in MW		2/5	1971-2000	29	-0.069	27	NS
VIIa	September	Absolute Growth Rate in ML		2/5	1959-2000	31	-0.075	29	NS
VIIa	September	Raw mean length at age	year class	2	1967-2003	33	0.097	31	NS
VIIa	September	Raw mean length at age	year class	3	1967-2002	32	0.097	30	NS
VIIa	September	Raw mean weight at age	year class	2	1975-2003	28	0.177	26	NS
VIIa	September	Raw mean weight at age	year class	3	1975-2002	27	0.169	25	NS
VIIa	September	Raw mean length at age		2	1967-2006	36	0.193	34	NS
VIIa	September	Raw mean length at age		3	1967-2006	36	0.194	34	NS
VIIa	September	Raw mean weight at age		2	1975-2006	31	0.219	29	NS
VIIa	September	Raw mean weight at age		3	1975-2007	31	0.262	29	NS
VIIa	September	Fulton's condition factor		2	1972-2003	31	0.160	29	NS
VIIa	September	Fulton's condition factor		3	1971-2002	31	0.082	29	NS
VIIg	May	Absolute Growth Rate in MW		2/5	1971-2000	27	-0.074	25	NS
VIIg	May	Absolute Growth Rate in ML		2/5	1958-2000	38	0.272	36	NS
VIIg	May	Raw mean length at age	year class	2	1960-2003	39	-0.182	37	NS
VIIg	May	Raw mean length at age	year class	3	1960-2002	38	-0.253	36	NS
VIIg	May	Raw mean weight at age	year class	2	1975-2003	27	-0.075	25	NS
VIIg	May	Raw mean weight at age	year class	3	1975-2002	26	-0.167	24	NS
VIIg	May	Raw mean length at age		2	1960-2006	41	-0.254	39	NS
VIIg	May	Raw mean length at age		3	1960-2006	41	-0.195	39	NS
VIIg	May	Raw mean weight at age		2	1975-2006	29	-0.178	27	NS
VIIg	May	Raw mean weight at age		3	1975-2006	29	-0.079	27	NS
VIIg	May	Fulton's condition factor		2	1972-2003	29	-0.122	27	NS
VIIg	May	Fulton's condition factor		3	1971-2002	29	-0.210	27	NS
VIIg	September	Absolute Growth Rate in MW		2/5	1971-2000	28	-0.042	26	NS
VIIg	September	Absolute Growth Rate in ML		2/5	1959-2000	31	0.181	29	NS
VIIg	September	Raw mean length at age	year class	2	1965-2003	33	0.108	31	NS
VIIg	September	Raw mean length at age	year class	3	1965-2002	32	0.044	30	NS
VIIg	September	Raw mean weight at age	year class	2	1975-2006	28	0.258	26	NS
VIIg	September	Raw mean weight at age	year class	3	1975-2002	27	0.093	25	NS
VIIg	September	Raw mean length at age		2	1965-2006	36	0.289	34	NS
VIIg	September	Raw mean length at age		3	1965-2006	36	0.247	34	NS
VIIg	September	Raw mean weight at age		2	1975-2006	29	0.371	27	0.05
VIIg	September	Raw mean weight at age		3	1975-2006	29	0.320	27	NS
VIIg	September	Fulton's condition factor		2	1971-2002	30	0.166	28	NS
VIIg	September	Fulton's condition factor		3	1971-2002	30	0.015	28	NS

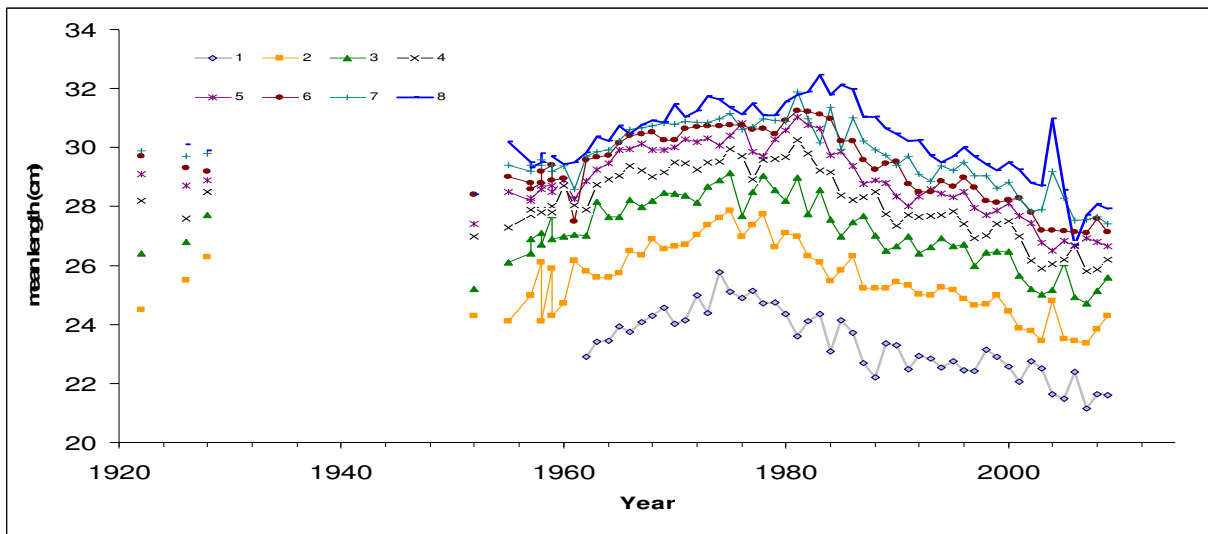


Figure 1. Trends over time in mean length at age. Data in the 1920s are depicted as years though they are groups of years.

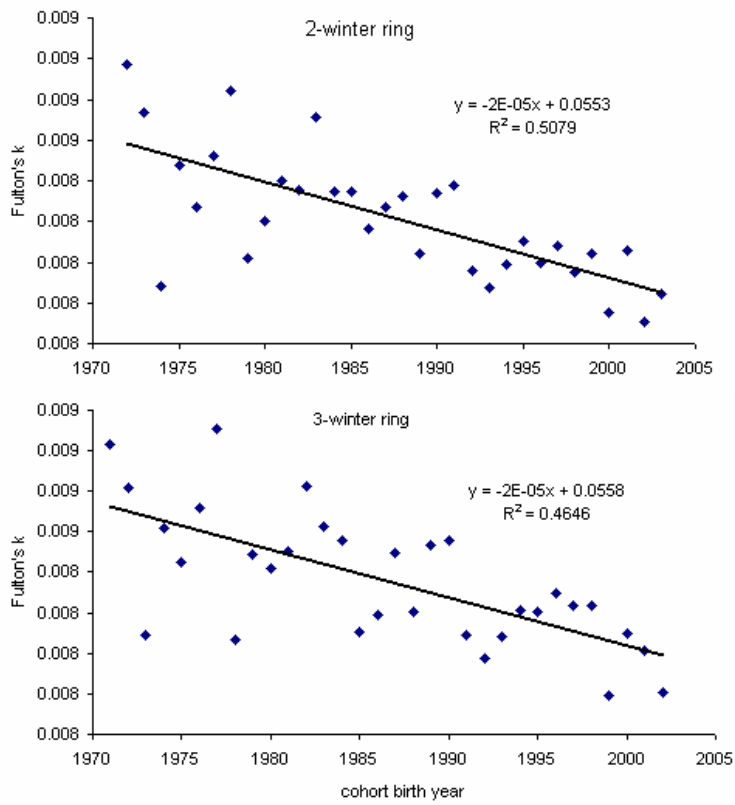


Figure 2. Trends over time of Fulton's condition factor for 2 and 3 winter ring fish.

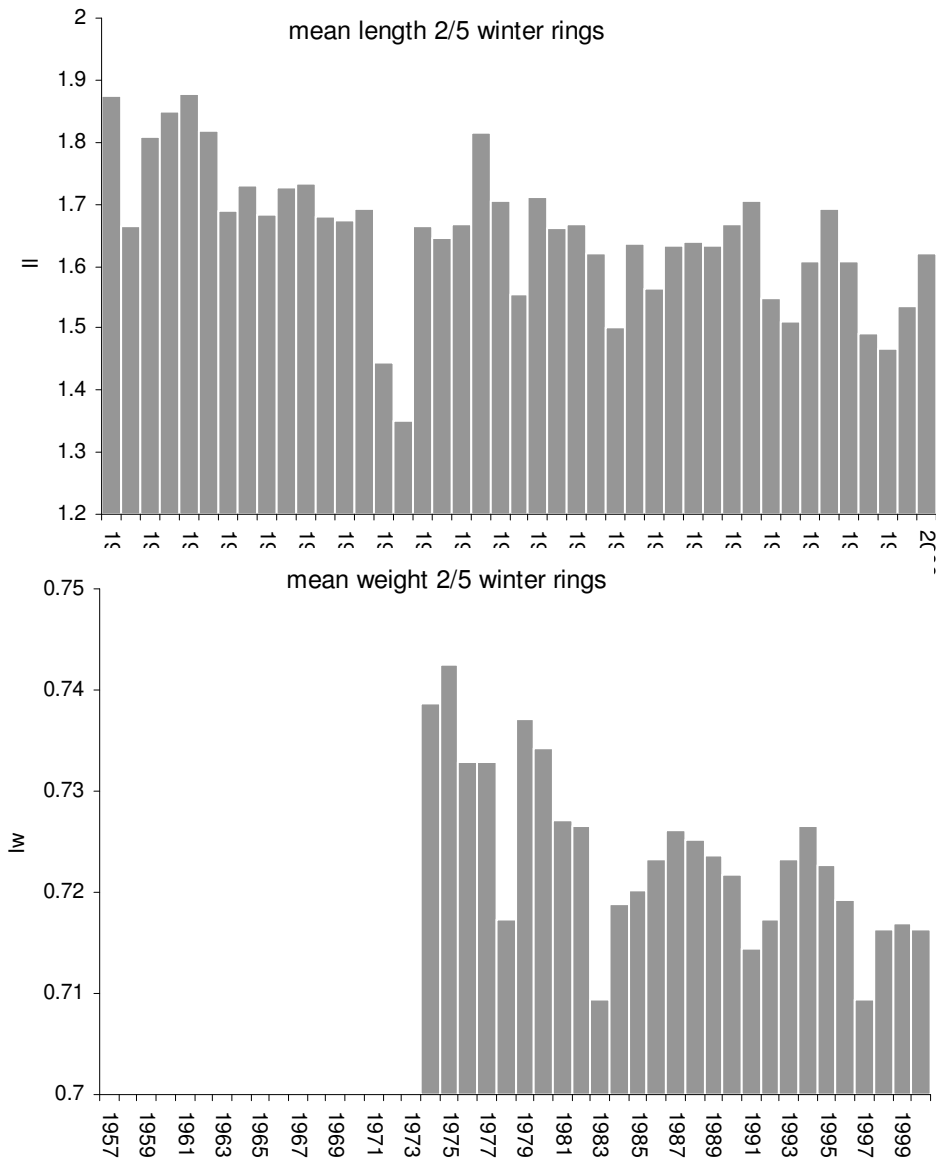


Figure 3. Absolute growth rate in terms of length (l) and weight (lw) for individual cohorts.

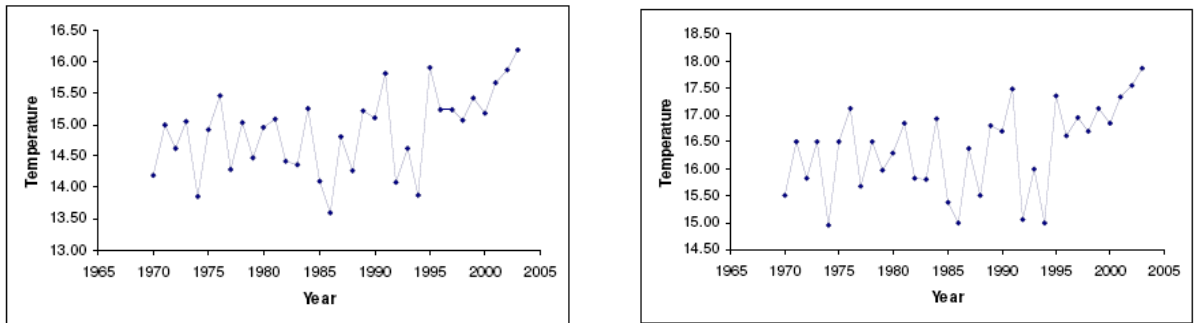


Figure 4. Sea Surface Temperature (SST) for Irish Sea (left) and Celtic Sea (right) by fishing season.

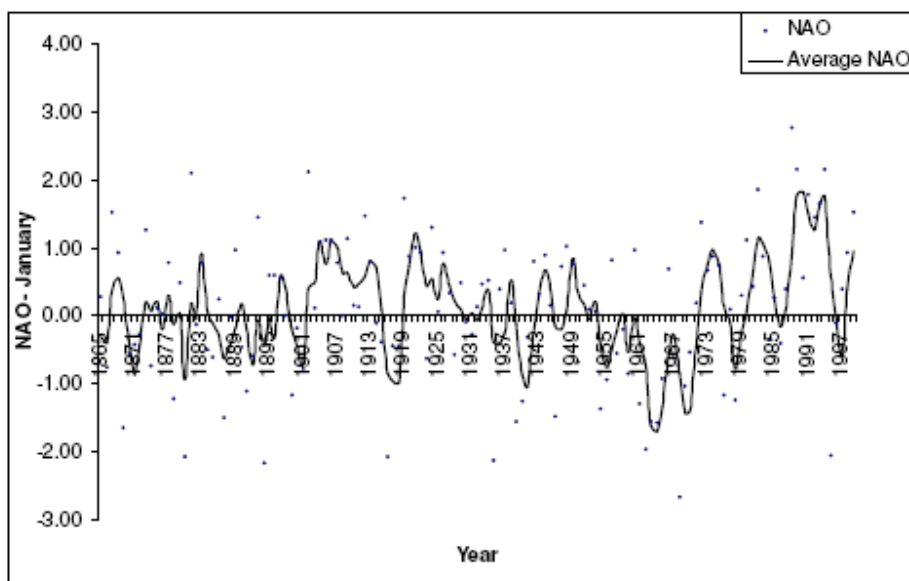


Figure 5. North Atlantic Oscillation (NAO) January index over time, with three year moving average smoother.

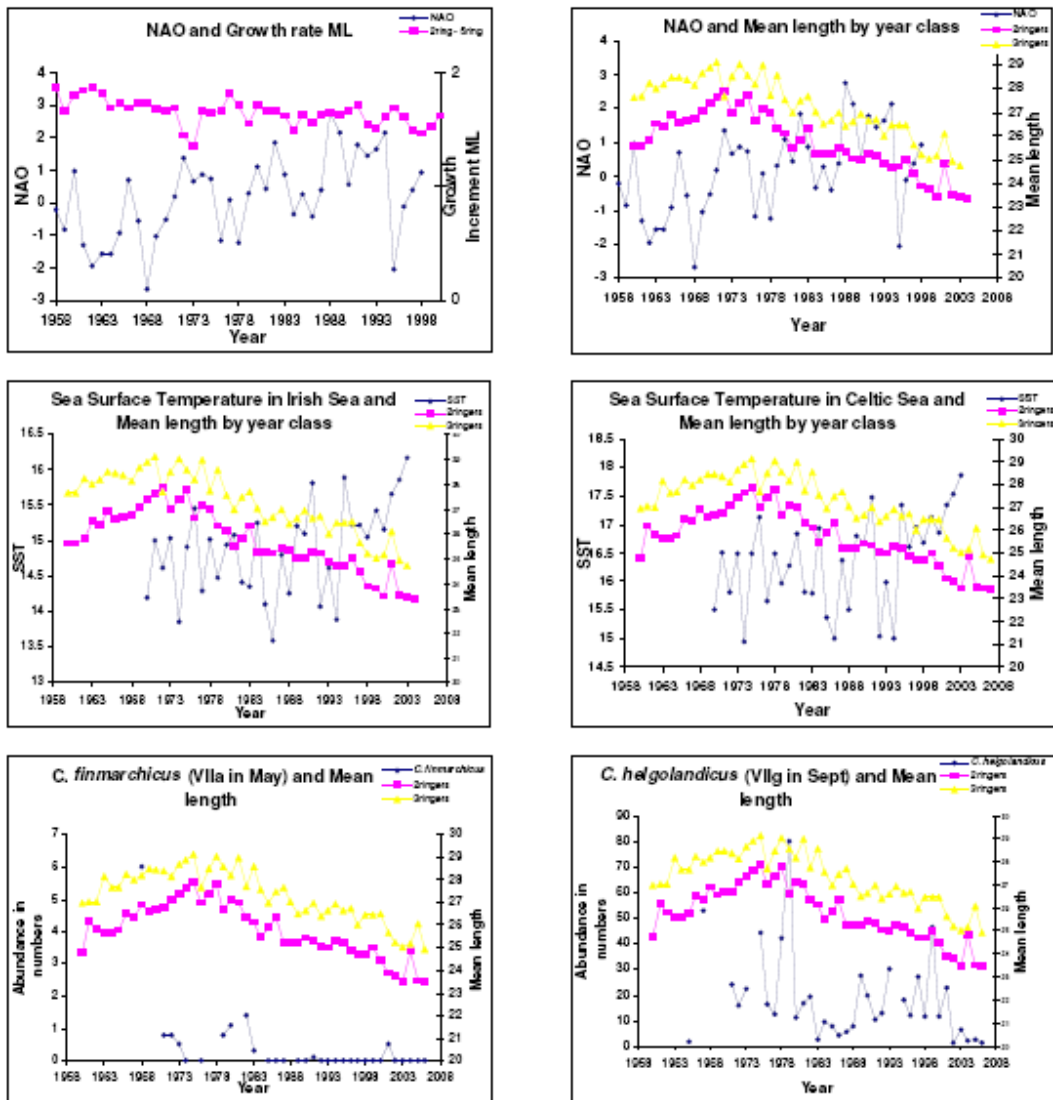


Figure 6. Range of relationships between biological variables and environmental parameters, found to display significant correlations.

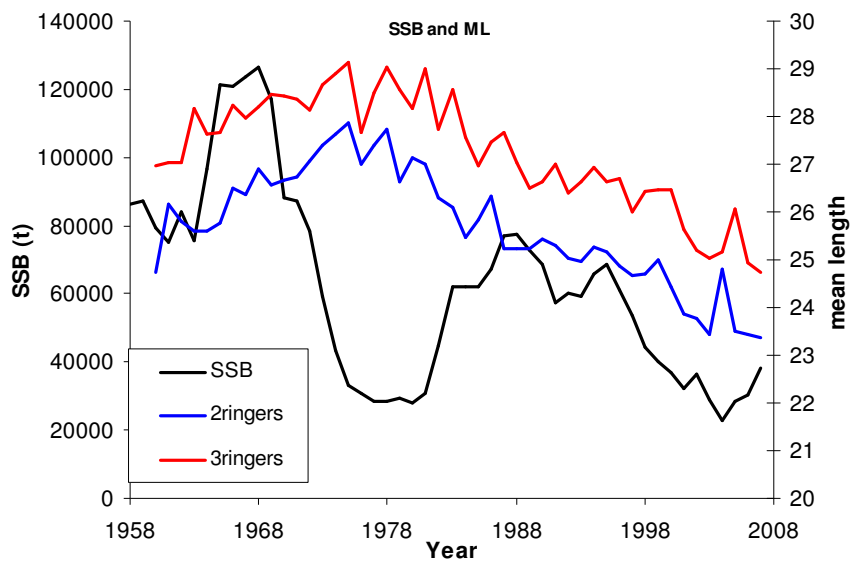


Figure 7. Relationship over time between spawning stock biomass (SSB) and mean length (2 and 3- ring herring).

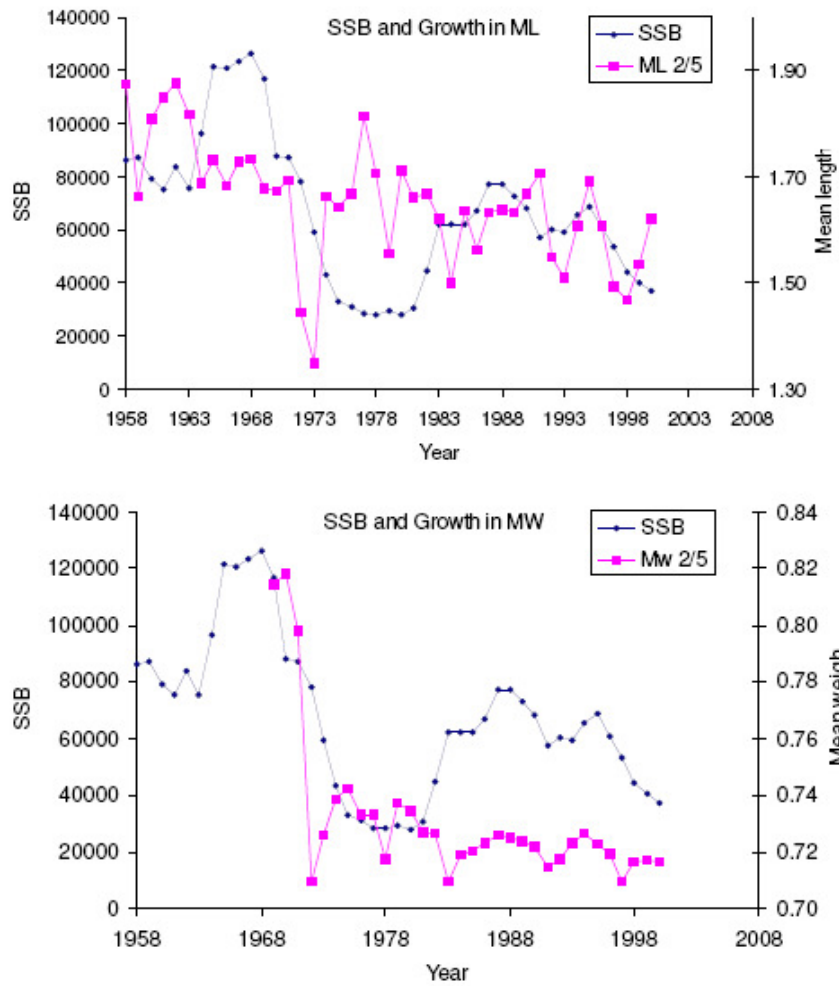


Figure 8. Relationship between spawning stock biomass (SSB) and growth, over 2-5 winter rings, in terms of mean length (ML) and mean weight (MW) over time.