

**The rise and fall of autumn-spawning herring (*Clupea harengus* L.) in  
the Celtic Sea between 1959 and 2009: temporal trends in spawning  
component diversity**

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25    **Highlights**

- 26    ▪ Dynamics of herring populations investigated using a long-term dataset (1959-2009)
- 27    ▪ Herring spawning components were found to have fluctuated greatly over time
- 28    ▪ Celtic Sea autumn-spawners characteristically bigger herring than winter-spawners
- 29    ▪ Marked changes in length- and weight-at-age were also observed
- 30    ▪ However growth changes not explained by the complex and dynamic stock-structure

Abbreviations:

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CS: Celtic Sea

AS: autumn-spawners

WS: winter-spawners

## **Abstract**

Sub-stock components of highly exploited migratory fish species exhibit different life-history traits and can thus show variation in productivity and vulnerability to fishing pressure. Celtic Sea herring comprises both autumn and winter-spawners that are targeted by the same fishery. The current study investigated if the relative abundances of the two components in the Celtic Sea have changed over time, and whether this could explain marked long-term trends in size-at-age. The study utilized a remarkably long time-series of biological data from commercial landings (1959-2009). Based on the maturity state of the gonads at the time of sampling, herring were assigned to seasonal spawning components. Significant temporal variations in spawning component dominance were found, even after potential bias due to fishing history patterns were accounted for. Strong directional changes in the relative proportion of spawning components consisted of autumn spawning herring proportions reaching a peak in the 1990s before drastically declining. Winter spawning herring had lower mean lengths- and weights-at-age than autumn spawning herring. The recent decline in the autumn spawning component did not fully explain the observed decline in size-at-age in the catches, with both spawning components showing similar decreases in mean-size parameters over time. Response of spawning components to environmental changes may have consequences for the fishery, especially in light of the observed influence of temperature on spawning components. Life-cycle diversity in herring stocks may confer resilience to potential climate-induced changes. Therefore, it is suggested that the relative proportions of spawning components should be monitored and diversity should be preserved as part of the management of fisheries for this species, which is characterised by stock complexity.

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55 Keywords: Complex stock structure, Celtic Sea herring, seasonal spawning components,

56 size-at-age, long-term trends.

## 1. Introduction

Ensuring the sustainability of fisheries which exploit a mixture of spawning groups requires cautious management approaches, focusing on the impacts of fishing pressure on sub-stock diversity (Stephenson, 1999). While a suite of techniques are available to accurately identify fish populations and their origin (Cadrin et al., 2005), accounting for complexities in stock structure remains a challenge for fisheries management (Kell et al., 2009; Stephenson, 1999). Although fisheries management measures traditionally focus exclusively on maintaining stock biomass above critical levels, evidence suggests that preserving life-cycle complexity and the behavioural mechanisms which ensure the closure of the life-cycle and survival of future generations are of paramount importance in terms of resilience to stock collapse (Dickey-Collas et al., 2010; Petitgas et al., 2010; Secor et al., 2009).

In an evolutionary context, the reproductive strategies adopted by fish populations can determine their ability to survive and adapt to changing environments (i.e. resistance and resilience). Some species display a large panel of reproductive strategies over the range of their distribution, resulting in the occurrence of sub-stocks with characteristic life-history traits and varying rates of productivity (Bailey, 1997; Brander, 1994; Melvin et al., 2009). When spatial overlap of different sub-stocks exists, a fishery targeting the mixed stocks can have a differential impact on each component (Geffen et al., 2011; Kell et al., 2009). Similarly, changes in stock composition can affect the overall productivity of such mixed fisheries (Kerr et al., 2010). Recent studies, mainly focusing on cod, have highlighted the importance of accounting for underlying sub-stock structure, especially

for the less productive component as overfishing could have important repercussions on the overall spawning diversity of the population, potentially leading to loss of adaptability to environmental changes among other effects (Hutchinson, 2008; Reich and DeAlteris, 2009; Sterner, 2007). A better understanding of biological variation between sub-stock components within the same fishery and of the long-term trends in sub-stock structure can inform the refinement of management plans for heavily-exploited fish populations.

One of the most important pelagic species exploited by fisheries in the northeast Atlantic is the Atlantic herring, *Clupea harengus* L. (Reiss et al., 2009). This “population-rich” species (Sinclair and Iles, 1988) has played a key role in the development of stock structure theories (Cushing, 1969; Hjort, 1914; Iles and Sinclair, 1982; McQuinn, 1997a). The species is characterised by highly variable recruitment over time and phenotypic plasticity (Geffen, 2009), resulting in considerable temporal and spatial stock complexity (Geffen et al., 2011; Melvin et al., 2009; Ruzzante et al., 2006). Timing of spawning in herring populations often acts to isolate sympatric sub-populations (Brophy and Danilowicz, 2002; Brophy and Danilowicz, 2003; Brophy et al., 2006; McPherson et al., 2001). Herring fisheries often exploit a mixture of seasonal spawning components (e.g. Bierman et al., 2010; Clausen et al., 2007; Melvin et al., 2009) thus complicating the assessment and management of exploited stocks.

Herring populations to the south of Ireland, in the Celtic Sea (CS), spawn in several discrete areas along the Irish coast (Breslin, 1998), which is sub-divided within three ICES (International Council for the Exploration of the Sea) Divisions: VIIj, VIIg, and

VIIaS (Figure 1). For assessment and management purposes, CS herring are treated as a single stock unit (ICES, 2010) that encompasses the CS shelf (Figure 1). The discrete spawning stock components are generally mixed throughout most of their life-cycle, on off-shore feeding and overwintering areas, as well as in nursery areas (Brophy and Danilowicz, 2002). Spatio-temporal isolation occurs only for spawning which takes place between late September and February (Breslin, 1998). The CS herring population thus consists of a mixture of autumn-spawners (AS) and winter-spawners (WS). Recently, a decline in size-at-age has occurred, both in the stock and in the catches (Figure 2), but the cause of this decline remains unexplained (ICES, 2010). The phenomenon is not unique to this stock (Cardinale and Arrhenius, 2000; Neuheimer and Taggart, 2010; Toresen, 1990) and warrants further investigation.

Failure to account for underlying stock structure of herring populations that are heavily fished could bias the assessment and potentially lead to ineffective management (Stephenson, 1999). Improved understanding of temporal trends in the relative abundance of spawning components is needed to ensure that management of herring fisheries maintains sufficient spawning diversity and to prevent stock collapse. In light of this, the purpose of the current study was to investigate (1) if the relative abundance of AS and WS components in the CS have changed over time, and if so, (2) whether this could explain the long-term trends in size-at-age observed in the overall population. If the two spawning components display different growth rates, a decline in the faster growing component could explain the observed decrease in overall size-at-age in the fishery. The study utilized data from commercial landings from 1959 to 2009. The use of such a long-

term and unique dataset provided a rare opportunity to track changes in the composition and stock structure of CS herring.

Bio-physical processes in the North-Atlantic basin seem to be mainly influenced by the Atlantic Multi-decadal Oscillation (AMO) which is calculated from de-trended sea surface temperature (SST) anomalies (Kerr, 2000); and by the North Atlantic Oscillation (NAO) which expresses fluctuations in the difference of atmospheric pressure at sea level between the Icelandic low and Azores high (Hurrell et al., 2003). As potential drivers of changes in abundance and distribution of fish populations, the influence of NAO, AMO, local SST and salinity conditions on the relative proportions of the spawning components were also investigated.

## **2. Materials and Methods**

### *2.1 About the database*

#### *2.1.1 Raw data*

Detailed biological and fisheries data have been collected from CS herring commercial landings since 1959. Random samples of 50 or 100 herring were taken from a proportion of landings, primarily caught by mid-water trawls. Sampling effort focused on obtaining spatially and temporally representative samples. Information about the sample, such as the vessel, area, date, location and biological characteristics (i.e. length to the nearest half centimetre interval, weight in grams (only after 1975), sex, maturity stage of the gonads, and age) were recorded.

The CS herring assessment year runs from April 1<sup>st</sup> to March 31<sup>st</sup> the following year (ICES, 2010). Throughout this study, fishing seasons were referred to according to the



year in which the assessment started, so 1959/1960 was referred to as 1959. The standard convention was used to assign fish to age groups using counts of winter rings in otoliths (ICES, 2003). Fish in this stock were given a conventional “birth date” of April 1<sup>st</sup>, and the first translucent winter ring counted on the otolith to age corresponds to its second “birthday”, such that a 1-winter ring herring was classed as a 2-year old.

### *2.1.2 Standardized data*

In each year, monthly sampling effort was affected by the pattern of the fishery. To visually inspect this potential source of bias, the numbers of fish collected in each season in absolute terms (Figure 3a) and as a proportion of the total yearly sampling effort (Figure 3d) were plotted over time. The data were then split into two periods: autumn months (Figure 3b, e) and winter months (Figure 3c, f). Re-sampling was conducted to standardize for sampling effort by randomly selecting a fixed number of fish (n=50) without replacement per unit time (i.e. per month or per season). The re-sampling ensured that any observed fluctuations in the relative proportions would not be driven by sampling effort variability. The relevant models (described below) were also fitted to 100 re-sampled datasets (i.e. iterations). Parameter estimates from these iterations were used to extract the mean values and 95% confidence intervals.

### *2.2 Allocation of fish to spawning components*

The maturity status of herring is assessed using an eight-stage classification system based on Landry and McQuinn (1988) and ICES (2003). Fish were assigned to seasonal spawning components (i.e. AS, WS, or “unknown” (U)) based on the stage of their gonads at the time of sampling. Spawning (stage VI) and spent (stage VII) fish caught

during the autumn period (i.e. September, October and November) were classified as AS, since a fish that has just spawned (i.e. stage VII) is unlikely to have spawned earlier in the season based on historical records of spawning activity in the CS (ICES, 2010; Molloy, 2006). Similarly, stages V (i.e. pre-spawning) and VI fish caught in the winter time (i.e. December, January and February) were classified as WS, as it is unlikely that CS herring would spawn later in the fishing year than during the winter. Fish at other stages of development were classed as U since the timing of spawning could not be reliably predicted.

### *2.3 Statistical analyses*

Statistical analyses of the data were conducted in three stages; firstly two categorical response models (Chi-squared analyses and Generalized Additive Models (GAM)) were fitted to the spawner proportions over time. Secondly, a series of Generalized Linear Models (GLM) were used to establish if the AS and WS components show differences in mean-size at age-3 and over time. Finally, a scenario testing procedure was conducted to examine the relative effect of changes in spawner proportions on the mean-size in the whole population.

#### *2.3.1 Analysis of trends in the relative proportions of spawning components*

##### *2.3.1.1 Preliminary chi-squared analyses*

The dataset was split into months, and each month was analysed separately. The null hypothesis ( $H_0$ ), that the proportion of fish per spawning component remained constant over time was tested. As the most representative months in terms of sampling (i.e.

evenness through time) were November for the autumn season, and January for the winter season (Figure 3), further analyses per ICES Divisions were conducted using data from these two months only. Separate analyses per ICES Division allowed for the investigation of spatial heterogeneity in the relative abundance of the spawning components.

### 2.3.1.2 Multinomial model

#### 2.3.1.2.1 General GAM

A multinomial model was constructed to investigate the temporal dynamics in the proportions of four different categories: AS, WS, and fish collected in autumn and winter that could not be assigned to a spawning component (Ua and Uw respectively). The purpose of fitting a multinomial model was to further investigate the results of the chi-squared analyses by detailed analysis of the inter-annual fluctuations in the proportions of the different spawning categories. Thus, a GAM (using the R-package “VGAM” for Vector Generalized Additive Model; Yee, 2010), with a logit-link and multinomial distribution was fitted to yearly data as follows:

$$\text{Multinomial distribution: } P(y_{s,t} | n_t, p_{s,t}) = \left( \frac{n_t!}{\prod_{s=1}^4 y_{s,t}!} \right) \prod_{s=1}^4 p_{s,t}^{y_{s,t}} \quad (1)$$

$$\text{GAM additive predictor: } \eta_{s',t} = f_{s'}(t) \quad (2)$$

$$\text{Logit link function: } \ln\left(\frac{p_{s',t}}{p_{WS,t}}\right) = \eta_{s',t} \quad (3)$$

where  $y_{s,t}$  is the number of individuals sampled in each category  $s \in \{AS, Ua, Uw, WS\}$  in year  $t$ ,  $n_t$  is the total number of fish sampled in year  $t$ ,  $p_{s,t}$  is the proportion in different categories in year  $t$ , with  $\sum_{s=1}^4 p_{s,t} = 1$ , hence  $s' \in \{AS, Ua, Uw\}$  and WS is the baseline level; and  $f_{s'}(t)$  is a flexible spline function of year. Note that we are primarily interested in the dynamics of the proportions over time, hence the flexible spline function.

The significance of the changes in the proportions by spawning category over time were tested using likelihood ratio tests between the time-varying model above and a model constrained to have constant spawner proportions over time. The maximum log-likelihood for the constant proportion model was given by  $\sum_t \sum_{s=1}^4 y_{s,t} \times \log(\hat{p}_s)$ , where  $\hat{p}_s$  is the estimated constant proportion, and the difference in the degrees of freedom (df) obtained from the estimated df from the time-varying GAM model (can be non-integer) minus 3 (number of free parameters in the constant proportion model).

#### 2.3.1.2.2 *Accounting for changes in fishing patterns*

In the CS, during the 1980s and 1990s, the predominant fishing market for herring was the Japanese roe (i.e. full gonads) market (Molloy, 2006). The roe fishery targeted the spawning grounds more intensively than the fishery that operated over the rest of the time series. A second multinomial GAM was used to investigate the potential effect of the roe fishery, which could introduce a selective bias in our proportions of spawners. The hypothesis that the roe fishery impacted on the spawner proportions in the catches was tested by including an additional binary variable (in the predictor of the GAM) with

yearly values reflecting whether the roe fishery occurred or not in a given year. Likelihood ratio tests were performed between the models including or excluding roe fishery to determine the effect of this variable on the model fit.

#### 2.3.1.2.3 *Potential environmental drivers on spawning composition*

The relationships between the relative proportions of the spawning components predicted by the GAM, and the selected environmental parameters (i.e. NAO, AMO, SST and salinity) were modelled using beta-regressions, as appropriate for proportions (Cribari-Neto and Zeileis, 2010). The two spawning components were analysed separately using the most appropriate model in each case. No collinearity could be detected between any of the environmental variables (Zuur et al., 2010). AIC criteria were used for model selection and variables were systematically removed from the full model based on their significance level calculated using likelihood ratio tests (using the R-package “lmtree”; Zeileis and Hothorn, 2002). The best model was reached when all variables selected showed a significant influence on the response variable, together with an overall best fit of the model.

Local SST and salinity data were downloaded from the ICES website (<http://www.ices.dk/ocean/data/surface/surface.htm>) using the Marsden Square number “181;2” (i.e. the most representative of the CS area, between 55°N-50°N and 5°W-10°W), where data from a total of 84 046 surface stations (<10m. depth) were used. Yearly autumn and winter averages during the period under study (1959-2009) were calculated for SST and salinity values, in order to describe local conditions during spawning. The winter NAO index (i.e. derived for the winter months of December to

March, which exhibit the strongest inter-decadal variability) have been extracted via the Climatic Research Unit (CRU: <http://www.cru.uea.ac.uk/cru/data/nao/> for the years 1959 to 2000; and from <http://www.cru.uea.ac.uk/~timo/datapages/naoi.htm> for 1999-2009). The AMO index, unsmoothed from the Kaplan SST V2, distributed by NOAA/ESRL/PSD1, was downloaded via <http://www.esrl.noaa.gov/psd/data/timeseries/AMO/>. A yearly average of the values from September in a given year to February the following year was calculated for this index to correspond with the timing of our biological data collection.

### *2.3.2 Investigation of size trends within each spawning component*

A primary purpose of our investigations was to establish if the AS and WS components showed differences in mean-length and mean-weight, and if mean-length and weight within each component have changed over time. The total length  $l$  (cm) and total weight  $w$  (g) were modelled as functions of year  $y$ , and spawning component  $s$  within the three different ICES Divisions and for the whole CS, using a GLM. As the response variables were continuous and positive, a gamma-distributed error term was chosen (McCullagh and Nelder, 1989). Spatial area (i.e. whole CS; ICES Division VIIj; ICES Division VIIg; ICES Division VIIaS) and spawning category (i.e. AS, WS, Ua, Uw) were treated as categorical variables (i.e. factors). To remove the potentially confounding effect of temporal changes in age-composition (Sinclair et al., 1982), the analysis was restricted to 2-winter ring herring (3 year-old fish, which were the modal age class in the overall dataset, and first age at 100% maturity (ICES, 2010)). The mean response (i.e. linear predictor of the GLM) for the single age-group was given by

$$l_{i,t,s,a=3} = \alpha_{t,s,a=3} \quad (4)$$

where  $i$  is the individual fish,  $\alpha_{t,s}$  is the average per year  $t$  and by spawning component  $s$ , and  $a$  the age of fish selected in the model.

The significance of the difference between the spawning components in the mean-length through time was established via a likelihood ratio test between the model described by Equation (4) and a constrained version (Equation 5) which combined the spawning components:

$$l_{i,t,s,a=3} = \alpha_{t,a=3} \quad (5)$$

The  $\chi^2$  statistic is obtained from  $-2(\ln(L(5)) - \ln(L(4)))$ , where  $L(5)$  and  $L(4)$  are the maximum likelihood values estimated using the linear predictor in Equation (5) (i.e. the null model of no differences between the spawning components) and Equation (4) respectively. The df are obtained from the number of years times the number of spawning components minus 1.

The same procedure was used for modelling weight at age-3:  $w_{i,t,s,a=3}$ .

### 2.3.3 *The influence of spawning component proportions on trends in mean size*

The final analysis integrated the time series of mean-length and mean-weight with the time series of spawner proportions to establish if changes in the relative proportions of the spawning components could explain the observed trends in size-at-age. Combining the maximum likelihood estimates from the spawner proportions GAM with those from the mean-length or mean-weight GLM provided a prediction of the changes in mean-length or mean-weight over time in the overall catch data. A weighted average is used whereby the mean-length or mean-weight of a spawning component in a given year

(Equation (4) with all ages) was weighted by the proportion of the component present in the year (Equations 1-3), i.e.

$$\bar{l}_t = \frac{\sum_{s=1}^4 \hat{p}_{s,t} \hat{\alpha}_{s,t}}{\sum_{s=1}^4 \hat{p}_{s,t}} \quad (6)$$

A component can be fixed to be an average over time, i.e.  $\hat{p}_{s,t} = \hat{p}_s$  or  $\hat{\alpha}_{s,t} = \hat{\alpha}_s$  while allowing the other to vary. The resulting predictions were compared to the observed average series to determine to what extent the observed changes in size could be explained by changes in the proportions of the spawning components and/or overall changes in mean-size. Different scenarios were tested by altering the constraints. Scenario 1: allowed the relative proportions of spawning components to vary over time (according to the variation in proportions observed in the catches) while mean-length or mean-weight were fixed parameters for the overall population (i.e.  $\hat{\alpha}_{s,t} = \hat{\alpha}_s$ ). Scenario 2: modelled the relative proportions of the four spawning categories as fixed parameters to  $\frac{1}{4}$  each (i.e.  $\hat{p}_{s,t} = \hat{p}_s = 0.25$ ) while mean-length or mean-weight could vary over time (according to the observed trends in overall mean-length and mean-weight observed in the catches). Scenario 3: allowed temporal variability within both parameters. From each scenario, two sub-scenarios were also tested by removing either the AS or the WS component from the model (respectively,  $p_{s=AS,t} = 0$  or  $p_{s=WS,t} = 0$ ), to predict how mean-length and mean-weight would be affected by the complete removal of a particular spawning component (i.e. simulating an absence of spawning diversity within the CS herring stock).



All analyses were performed using the R statistical environment (R Development Core Team, 2009). The significance of the statistical analyses were all tested using the critical value of  $\alpha = 0.05$  (unless otherwise stated).

### 3. Results

The fishery was clearly seasonal, with approximately 90% of the catches taken in autumn and winter (Figure 3). All analyses were restricted to these two main seasons. A total of 126 201 herring have been analysed in this study. Of these, 66 058 were caught in winter and 60 143 in autumn.

#### *3.1 Analysis of trends in the relative proportions of spawning components*

##### *3.1.1 Chi-square analyses*

The null hypothesis ( $H_0$ ), that the ratio of spawning (i.e. AS in autumn months and WS in winter months) to non-spawning (i.e. Ua in autumn months and Uw in winter months) herring in the CS remained constant through time was rejected for each month ( $p < 0.001$ ). The variation in the proportions of the two spawning components also occurred at a finer spatial scale, i.e. in all ICES Divisions ( $p < 0.001$ ).

##### *3.1.2 Multinomial model*

###### *3.1.2.1 General GAM*

The re-sampling procedure was effective at removing the effects of sampling bias (Figure 4a and 4b). Overall fluctuations in the relative abundance of the spawning components appeared less marked once the sample size was kept constant through time (Figure 4b).

The effects of sampling bias were most evident in the trend of the WS component over time. While the model on raw data showed a relatively high proportion of WS during the early period of the study with an overall declining trend, using re-sampled data reversed the pattern, certainly due to an unusually high sampling effort in winter at the start of the time series (Figure 3c).

Over the period of this study (1959-2009), several changes occurred in the composition of the catches with respect to spawning category (Figure 4). Significant variations in the relative proportions of the AS, WS, Ua and Uw components over time confirmed the previous chi-square results (likelihood ratio test:  $\chi^2=331.102$ ,  $df=11.92$ ,  $p<0.001$ ). The AS component showed the strongest directional change in relative abundance over time (Figure 4b). This component exhibited a slight decrease at the beginning of the period of study (1959-1968) and subsequently rose to its highest level in the time series, averaging approximately 40% of the autumn/winter catches by 1990. After this peak-period, the relative abundance of AS declined steadily, and by the early 2000s, their number had dropped considerably to < 10% of the catches, the lowest proportion observed in any of the components during the study period (Figure 4b). The trend in the Ua component was diametrically opposed to the previously described AS one; the relative abundance of that component was high at the beginning and at the end of the time series (in the 1960s-1970s and in the 2000s respectively). It is important to bear in mind that the trends in the Ua component (stages III-V in autumn) partly reflected changes in the relative abundance of winter spawning herring in the autumn fishery as some of these pre-spawning fish may have spawned in winter.

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373 Variability in the WS component was less pronounced than in the AS component,  
374 displaying a slightly bimodal distribution over time: the first peak occurred around 1973,  
375 followed by a slight decrease in the 1990s (coinciding with the AS peak), and a second  
376 peak in the late 1990s (Figure 4b). Once again, the Uw pattern appeared as the negative  
377 reflection of WS, remaining low throughout the time series (proportions <20%), with  
378 maxima at the beginning and at the very end of the period of study, although there was a  
379 higher degree of uncertainty associated with the estimated proportions at the extreme  
380 ends of the time series (as indicated by the larger confidence intervals in figure 4b).

381

382 Spatial heterogeneity in temporal variations in the proportion of spawners was also  
383 highlighted (Figure 5). In each Division, the relative abundance of the AS component  
384 reached a peak in the 1990s (consistent with the analysis of all ICES Divisions  
385 combined); however, the absolute proportion varied between areas (i.e. ~60% of the  
386 catches in Division VIIj; 40% in Division VIIg; only 20% in Division VIIaS). In Division  
387 VIIj, the AS component was always dominant relative to the WS component, except after  
388 2002 (Figure 5a), while in Division VIIaS the WS component was the dominant one  
389 (Figure 5c). In Division VIIg, dominance alternated between the WS and AS components  
390 over the course of the time series (Figure 5b). The WS component displayed a slightly  
391 bimodal trend in all ICES Divisions (consistent with the analysis of all ICES Divisions  
392 combined); this trend was most pronounced in Division VIIg (Figure 5b).

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394 *3.1.2.2 Accounting for changes in fishing patterns*

The binary parameter “roe fishery” did not improve the model fit as the vast majority of the p-values extracted from likelihood ratio tests performed for each re-sampled GAM (n=100 iterations) were non-significant (87 of 100 had  $p>0.05$  and 99 of 100 had  $p>0.01$ ). This confirmed that the observed trends in the spawning components were not merely an artifact of changes in this fishery.

#### *3.1.2.3 Potential environmental drivers on spawning composition*

Some environmental factors, both local and global, exhibited strong relationships with the relative proportions of spawners between 1959 and 2009 (Table 1). However, some unexplained source of fluctuation still remained as the models only explained 48% and 34% (for AS and WS respectively) of variability described in the proportion of spawners through time. Using the AS component as response variable, the best likelihood ratio (Log-likelihood = 32.29, df = 6,  $p<0.001$ ) and lowest AIC value (-52.58) were given by a model including NAO, AMO, averaged autumn SST and mean winter salinity as explanatory variables (Table 1). Using the WS component as response variable, the best likelihood ratio (Log-likelihood = 86.12, df = 6,  $p<0.001$ ) and lowest AIC value (-160.25) were given by a model including the AMO index and averaged autumn SST, while accounting for changes in precision of the model as a function of these two explanatory variables (i.e. an additional fixed dispersion parameter was set to account for rather high heteroskedasticity) (Table 1).

#### *3.2 Investigation of size trends within each spawning component*

Mean-lengths and weights at age-3 of AS and WS components showed a similar decline (Figure 6) to that observed in the un-segregated data (Figure 2). This decline was evident both in the overall CS area and in each ICES Division, but was less pronounced in Division VIIj, where mean-lengths and weights remained relatively constant over the time series (Figure 6c, d). On average, herring in the WS component had a lower mean-length and mean-weight at age-3 than herring from the AS component (mean-length:  $\chi^2=27.176$ ,  $df=146$ ,  $p<0.001$ ; mean-weight:  $\chi^2=592.03$ ,  $df=105$ ,  $p<0.001$ ). Yearly variability implied that the degree of distinction between the spawning components varied over time; the difference between the two components was greatest between the 1980s and 2004 (Figure 6b, d, f, & h).

### *3.3 The influence of spawning component proportions on trends in mean size*

Varying the spawning component structure within the catches produced very slight changes in mean-length and mean-weight of CS herring (Figure 7). The results of scenario 1 showed that when the mean-lengths and mean-weights of each spawning component were held constant over the time series, and the relative proportions of the AS and WS components varied according to the trend observed in the catch data, overall predicted mean-length and mean-weight remained almost constant, with a small peak occurring in the 1990s. This indicates that the dramatic changes in length and weight that are observed in the catches (Figure 2) cannot be explained by variation in the relative abundance of the AS and WS components. When one of the two spawning components was removed from scenario 1, the 1990s-peak either remained (because of AS) or disappeared (flattened with WS), showing the slight contribution of the numerous AS

component to this peak. Scenario 2, which allowed mean-length and mean-weight to vary while the relative proportion of the spawning components remained constant, resulted in mean-length and mean-weight patterns similar to the ones exhibited by the overall CS herring (Figure 7). This corroborated the results from scenario 1, showing that the mean-lengths and weights in the catches over the time series were independent of the relative abundance of the spawning components. Scenario 3 allowed both mean-size and the relative abundance of the spawning components to vary and effectively modelled the real situation. This produced mean-length and mean-weight predictions quite similar to those generated in scenario 2 with slightly lower values between 1960-1970 and between 2000-2009, but higher predicted values in the 1990s. Removing the WS component in scenario 3 had the same effect as removing this component in scenario 2 (not illustrated), with an increase of mean-length and mean-weight predictions between 1980 and 2000. This corresponded to the period when the difference in mean-size between the AS and WS components was most pronounced. Removing the AS component (in scenario 3, as well as in scenario 2) showed the opposite effect with mean-length and mean-weight predictions slightly lower than when the two spawning components were present in the catches.

#### **4. Discussion**

The results of this study revealed annual variations in the relative abundance of the autumn and winter spawning components in landings of Atlantic herring in the CS, from 1959 to 2009, at two spatial scales. Previous studies have highlighted short-term year-to-year variability in the dominance of sympatric herring spawning components (Bierman et

al., 2010; Brophy et al., 2006). The current study describes a directional change over an exceptionally long time series, with an apparent cyclical alternation in the dominant spawning component. Long-term observations of spawning component proportions are more informative than short-term studies in terms of adapting management advice.

When interpreting any time series of commercial catch data, the potentially confounding influence of changes in sampling intensity or fishing patterns due to management restrictions and/or market demands must be considered. The effect of the sampling bias was removed from the analyses by re-sampling procedure. In terms of fishing patterns, the CS herring fishery was fairly consistent for the duration of the time series, with two notable exceptions. As previously described, during the “roe fishery” period of the 1980s-1990s, juveniles and herring without ripening gonads were discarded (i.e. the “Unknown” category in this analysis). Very few studies dealt with the roe fishery impacts on herring populations although this fishing pattern has been present in some other herring grounds, such as in British Columbia (Hay et al., 2008). Hay et al. (2008) found that while Pacific herring spawning patterns are temporally dynamic, no evidence of roe fishery-driven trends could explain these changes. Similarly, accounting for the roe fishery in our multinomial GAM analysis did not explain the pronounced rise and fall of the AS component, nor contribute to the temporal changes in the WS component. In addition, the increase in the strength of the AS component and the first peak in the WS component started in the mid-1970s, before the initiation of the roe fishery.

From 1988 onwards, management measures to protect spawning herring were introduced in the CS in response to European Union fisheries management legislation (Molloy,

2006). A small spawning area is closed to the fishery for 16 days each year, within one of the three ICES Divisions, during the peak spawning time. The closure rotates yearly between the three ICES Divisions, so each spawning area is closed once over a three year period. If these closures were having an impact on the relative numbers of spawning herring in the catches, this should reflect the rolling nature of the closures i.e. occur every three years in each division in turn. In the current study, similar trends in the proportion of spawners were detected in all three ICES Divisions from the 1990s. Overall, it is unlikely that the observed temporal trends in the relative proportions of spawning components are an artifact of changes in sampling intensity or fishing patterns.

There are two mechanisms which could both lead to changes in the dominance of one component relative to the other: either switching of spawning season occurs at the individual level, or productivity of one spawning component relative to the other changes. Variability could also result from a combination of the two processes. A constant level of switching over time with equal levels of exchange between spawning components would result in no changes in the relative strength of the AS and WS components. However, if under certain situations the rate of switching changed, then after several generations of switching between two spawning components, one component would become the dominate one. Alternatively, dominance could alternate between components over the time series because of a change in productivity of a spawning component (e.g. reproductive success, egg and larval survival) relative to the other. Thus, observed changes in the relative strength of the spawning components in the CS do not only imply either spawning season switching or fidelity.



Fidelity of herring populations to spawning area and season has been observed in the northwest (Wheeler and Winters, 1984) and northeast Atlantic (Brophy et al., 2006), confirming that seasonal spawning components may remain discrete over time (Iles and Sinclair, 1982). However, varying levels of spawning season switching have also been reported in short-term studies (Brophy et al., 2006; McQuinn, 1997b). Recent evidence suggests that herring to the west of the British Isles are constituted of a mixture of interconnected spawning groups rather than discrete stocks (Geffen et al., 2011). So far, switching rate has been assumed to be population-dependent. Whether the rate of straying observed in short-term studies reflects a fixed population trait that remains constant over longer time-periods or an adaptive characteristic that may change according to the conditions encountered remains to be established. Further field studies are needed that compare rates of fidelity/exchange both within- and between-populations over short and long time scales.

It is not yet known to what extent the spawning season in migratory fish species such as herring is genetically determined or triggered by a combination of physiological and environmental factors. While some studies investigate differences in spawning herring populations using genetic proxies (Jørgensen et al., 2005; King et al., 1987; McPherson et al., 2003), herring spawning tactics also appear to be influenced by phenotypic variability (Jennings and Beverton, 1991; Winters and Wheeler, 1996). Although it is established that in herring the process of first maturation is triggered by a combination of physiological (size condition of fish) and environmental cues (e.g. January SST: Winters and Wheeler, 1996; photoperiodic cycles: McPherson and Kjesbu, 2011), the relative influence of genetics and environment on herring spawning behaviour (i.e. seasonal

strategy) remains unresolved. The results of this study highlight that the timing of spawning does show directional changes, either due to adaptive selection mechanisms operating on the population or as a result of individual responses to certain external cues.

The observed influence of NAO, AMO, SST and salinity on the relative strength of the components suggests that spawning in one rather than in the other season confers an advantage in terms of energy use and fitness under certain environmental conditions. Surprisingly, AMO was not highly correlated with SST measurements from the CS, possibly due to poor quality of local environmental data (i.e. very discontinuous time series of SST and salinity for the studied period). While SST and AMO would be expected to co-vary, in Irish waters, AMO and NAO fluctuations were reported to only account for 23% and 9% respectively, of interannual variability in local SST (Cannaby and Hüsrevoğlu, 2009).

Environmental fluctuations could operate on any life-stage and could influence various biological processes such as fecundity, larval survival or recruitment to the adult stock (Rijnsdorp et al., 2009). For example, AS herring in the North Sea show less resistance to climate change, in terms of larval survival (Hufnagl and Peck, 2011); and larval survival in cod appears negatively impacted by increasing SST conditions together with negative NAO periods (Lehodey et al., 2006). The spawning ability or reproductive cycle of adult Atlantic herring has often been linked to temperature conditions (Jennings and Beverton, 1991; Winters and Wheeler, 1996). In the western Atlantic, similar alternation in the dominance of AS and WS components is described through modelling (Melvin et al., 2009). It is suggested that warming waters favour AS. Our study showed the opposite

555 pattern in the CS as the peak in the AS proportions in the catches during the 1980s-1990s  
556 coincided with a period of negative AMO (i.e. colder than average SST) together with a  
557 persistent positive NAO phase. In the CS, strong winds (i.e. positive NAO) could favour  
558 mixing of the water column in summer resulting, together with colder and more variable  
559 SST conditions, in better food availability for planktivorous fish such as herring.  
560 Favourable feeding conditions in herring populations are linked to better gonad  
561 development, higher fecundity and improved reproductive success (Engelhard and Heino,  
562 2006; Kennedy et al., 2010; Ma et al., 1998; Óskarsson et al., 2002). Enhanced feeding  
563 during summer, together with colder water temperatures, may trigger earlier spawning.  
564 Indeed, AS (or herring spawning in warmer waters) have been found to exhibit  
565 significantly higher fecundity than WS herring (Blaxter, 1985; Jennings and Beverton,  
566 1991). In another migratory species, the European flounder (*Platichthys flesus*) cooler  
567 temperatures lead to earlier migration and spawning in the English Channel (Sims et al.,  
568 2004). Alternatively, more stormy conditions during winter may have a greater impact on  
569 larval dispersal and survival in the WS than in the AS component as WS herring are at a  
570 more vulnerable stage of development at that time of year. Since the late-1990s, local  
571 SST increased around Ireland (Cannaby and Hüsrevoğlu, 2009; Pinnegar et al., 2002),  
572 coinciding with a reversion to a positive AMO phase. During the same period there was a  
573 drastic reduction of spawning events in autumn and a switch back to WS dominance (or  
574 “retraction” of the spawning strategy to winter months only). When autumn SST were too  
575 warm for herring to spawn, spawning in winter appeared to be favoured (Haegele and  
576 Schweigert, 1985). Similarly, spring-spawning herring in the North Sea are able to  
577 compensate for increasing SST better than the AS component (Hufnagl and Peck, 2011).

Concomitant fluctuations in environmental parameters appear to be linked to the direction and ratio of change in the relative strength of spawning components in herring populations, and act to either enlarge or reduce the spawning season optimal window. According to external forcing, the entire spawning-range window of herring is likely to shift either spatially (Melvin et al., 2009), or temporally (as shown in this study). The relatively low explanatory power of the environmental analyses suggested that the mechanisms underlying the trends in the spawning components are complex and that multiple interactions between fishing related and environmental factors should also be considered. Nevertheless, in a recent physiological modelling approach coupling biological characteristics of North Sea herring with local conditions, Hufnagl and Peck (2011) showed that the timing of spawning was restricted by temperature, food availability and day-length (latitude). Our study further warrants the need for such bio-physical modelling studies, particularly taking into account the CS environment.

Regardless of what is driving trends in the relative proportions of spawners, the loss of a spawning component in a population could impact on the ability of a stock to cope with external forcing (e.g. fishing pressure, changing environmental conditions). Herring in the CS, as in other ecosystems worldwide, have probably adopted different spawning season as one of their survival strategies (Melvin et al., 2009; Sinclair and Tremblay, 1984). However, the abundance of the AS component relative to the WS component in the CS is now at its lowest for the period of this study (from 1959 to 2009). While losing this ability to spawn in different seasons (i.e. their spawning diversity), herring populations' resistance and resilience to changes in environmental conditions and to

fishing pressure, could be considerably impaired (Melvin et al., 2009; Secor et al., 2009). For example, without the ability to spawn in the more clement autumn months, the stock could be vulnerable to recruitment failures; in the North Sea warmer than usual SST coincided with recruitment failures and low larval survival in the AS component (Nash and Dickey-Collas, 2005; Payne et al., 2009). Thus potential loss of sub-stock diversity could contribute to sudden stock collapse as modelled for Canadian cod (Sterner, 2007). The current state of the overall CS stock is considered to be healthy, since it has rebuilt from historically low levels (ICES, 2010). The AS component recovered from the very low levels observed in the 1960's. Therefore the stock may be reasonably robust to fluctuations in the seasonal components and complete loss of a sub-group may be unlikely. Nonetheless, the recent decline in sub-stock diversity signals caution for the future management of the CS fishery.

Previous studies have compared growth difference in seasonal herring populations at the egg, larvae or juvenile stages (Blaxter and Hempel, 1963; Brophy and Danilowicz, 2003; Jones, 1985). The present study highlighted differences in size-at-age between adults from the AS and WS components in CS herring. King (1985) analysed morphological differences among spawning aggregations of herring populations to the west of the British Isles and concluded that (1) the differences between stocks are small, but (2) herring from eastern part of the CS were distinct from neighbouring stocks; these findings are consistent with our results. A recent investigation of herring stock structure to the west of the British Isles showed that the inclusion of length-at-age information with otolith microchemistry data improved classification success (Geffen et al., 2011).

Although AS fish were on average, significantly bigger than WS fish, the groups could not clearly be distinguished based on this single size criterion due to the pronounced yearly variability in size within each component. Jørgensen et al. (2005) encountered a similar overlap in size distributions when trying to distinguish Baltic Sea herring spawners using mean-length characteristics. A meta-analysis on different herring populations in the North Atlantic highlighted that SST was a determinant factor for growth at the species level (Brunel and Dickey-Collas, 2010). However, the AS and WS components in the CS inhabit the same spatial area, thus experiencing the same variations in water temperature. Therefore, more complex mechanisms (e.g. density-dependence at the sub-stock level, genetic constraints) must underlie the observed growth differences between these two spawning components. Although small, the difference in size between AS and WS herring in the CS may have consequences for the effects of fishing on the dynamics of the individual components.

In this study, not only did the relative proportions of spawners vary through time, but their respective size-at-age also fluctuated significantly over time. AS and WS herring displayed similar temporal trends in mean-length and mean-weight, with both spawning components showing a decrease in growth over time from the late 1970s. In addition, the scenario testing analyses showed that complete loss of one spawning component from the CS population could not reproduce the observed decline in growth rates. As there was a time-lag of ca. 5 years between the observed changes in the growth parameters (between 1980 and 1985) and the change in spawning stock composition (between 1985 and 1990), it is possible that the changes in size-at-age of CS herring in the catches led to the

observed changes in the relative proportions of spawners over time (via fishing selection, by acting on the maturation process), rather than the other way round. Finally, the observed size-at-age trends are not attributable to changes in stock structure of CS herring. Other potential factors such as climatic variability coupled with changes in fishing pressure need to be examined.

## **5. Conclusion**

The present study revealed changes in the long-term dominance of seasonal spawning components in CS herring catches which were partly attributed to both local (i.e. averages autumn SST and winter salinities) and global (i.e. the NAO and AMO indices) environmental factors. The seasonal components showed differences in growth, which could lead to differential impact of fishing pressure and selectivity when both components are fished by the same fleet (i.e. during spatially overlapping periods). However, the observed changes in spawner proportions did not explain the recent decline in the overall size-at-age of CS herring catches. While the stock complex or metapopulation may be a more practical unit for stock management, local sub-stocks should be systematically monitored to examine the spawning potential and life-cycle complexity that confers resilience to the stock in the face of changing environmental conditions and to ensure viable local fisheries.

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<http://www.cru.uea.ac.uk/~timo/datapages/naoi.htm> for the last updates (1999-2009).

ICES Local environmental databases for the Celtic Sea:  
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## **Table and figures legends**

Table 1. Results from the two best models selected using beta-regression analyses between AS or WS proportions (as extracted from the multinomial GAM on re-sampled dataset) and environmental parameters (NAO, AMO, SST and salinity). AS and WS were analyzed separately, hence the different environmental variables selected for each model.

Figure 1. Map of the Celtic Sea to the south of Ireland, northeast Atlantic. In the present study, the CS comprises ICES divisions VIIj, VIIg and VIIaS (shaded sea areas). Dark squares represent the main Celtic Sea herring spawning areas (based on highest yearly percentiles of density distribution curves of larval abundance, tracked by larval surveys conducted in the Celtic Sea between 1979 and 1985). Dotted line represents -200 meter depth limit.

Figure 2. Irish-caught Celtic Sea herring mean-length-at-age from 1959 to 2009 (top panel), and mean-weight-at-age from 1975 to 2009 (bottom panel). Bold lines represent the overall mean-length (top panel) and overall mean-weight (bottom panel) trends over time when all ages are gathered.

Figure 3. Sampling effort over time: in terms of numbers of fish collected in each season (a. b. and c.); and expressed as a proportion of the total yearly sampling effort (d. e. and f.). The selected seasons from left to right were all seasons of the year (a. and d.); autumn months (b. and e.); winter months (c. and f.). Autumn and winter data represent 90% of the catch data of CS herring for the period of study (1959 to 2009).

918

919 Figure 4. Comparison of the predictions given by the multinomial GAM analyses fit to a.  
920 the raw proportions of spawning component over time (1959-2009), and b. re-sampled  
921 datasets of 50 fish per season, after averaging 100 re-sampling iterations. Points represent  
922 the observed individual data from 1959 to 2009, and lines show the fitted values for each  
923 spawning component with grey bands highlighting the 95% confidence intervals on the  
924 re-sampled curves.

925

926 Figure 5. Multinomial generalized additive model (GAM) fit to the re-sampled dataset,  
927 predicting the relative proportions of each spawning category per ICES Division (a.  
928 Division VIIj, b. Division VIIg and c. Division VIIaS) over time from 1959 to 2009. No  
929 samples were collected from ICES Division VIIj prior to 1968. Points show the  
930 individual data with colour code associated with the spawning category. Lines represent  
931 AS (black) and WS (grey), while dashed lines are for Ua (black) and Uw (grey). The 95%  
932 confidence intervals appear as grey bands (respectively dark grey for AS and WS; light  
933 grey for Ua and Uw).

934

935 Figure 6. Mean-length in centimetres (left panels) and mean-weight in grams (right  
936 panels) fits of ages-3 AS and WS herring through time for the overall area of study (a.  
937 and b.) and per ICES Divisions (c. and d. Division VIIj; e. and f. Division VIIg; g. and h.  
938 Division VIIaS). Solid and dashed lines represent the average and 95% confidence  
939 intervals, respectively, by spawning component: AS (black), WS (grey).

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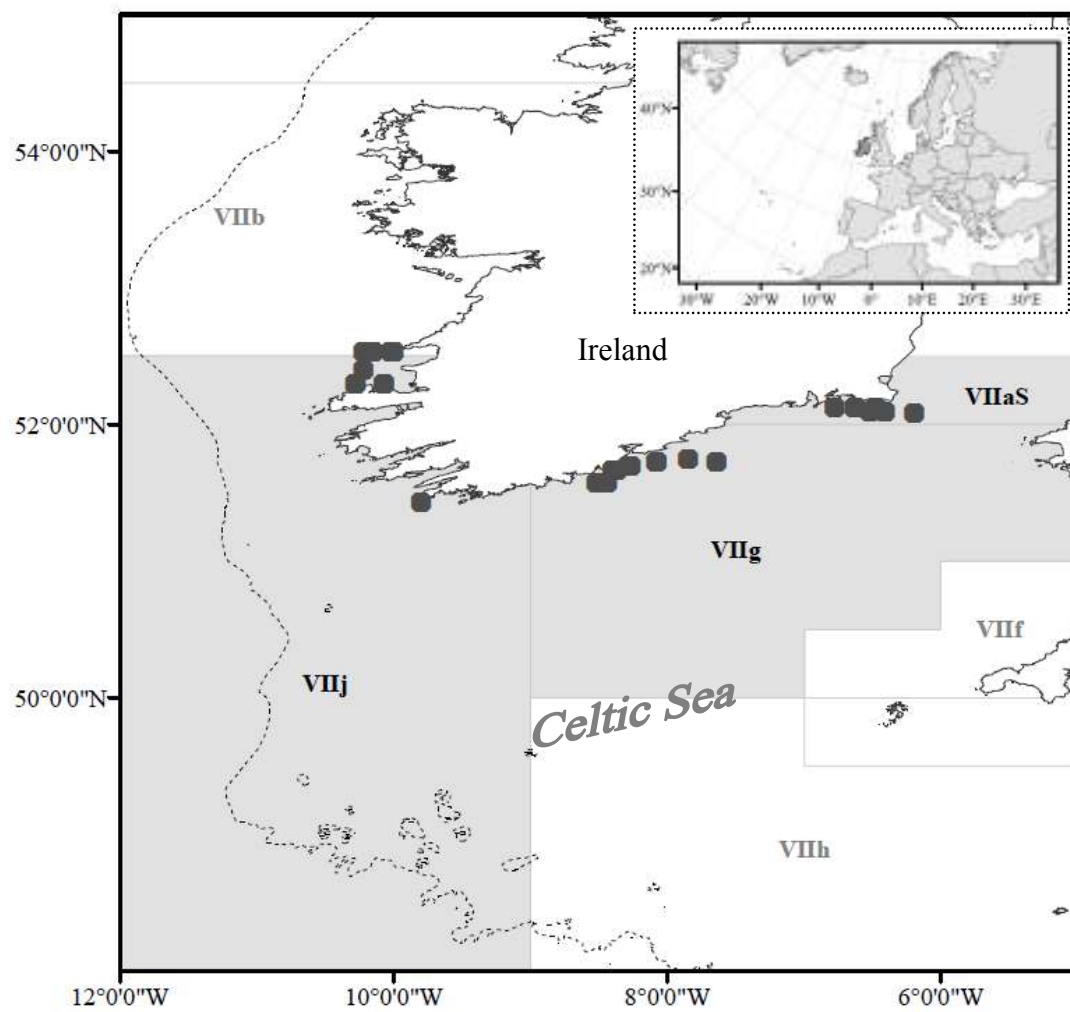
Figure 7. Different scenarios of mean-length in centimetres (top panel) and mean-weight in grams (bottom panel) predictions over time from generalized linear model (GLM) fits, with *Scenario 1*. Relative proportions of spawning-components varying over time and overall mean-length fixed, also when removing WS or AS component from the proportion estimates (dashed lines); *Scenario 2*. Relative proportions of spawning categories fixed to  $\frac{1}{4}$  each, and mean-length varying over time according to the variation observed in the catches (dotted lines); *Scenario 3*. Relative proportions of spawning-components and mean-length varying over time (both according to the variation observed in the catches), also when removing WS or AS component (bold lines). As a basis for comparison, the observed overall mean-length and mean-weight of CS herring over the period of the study are also highlighted (grey stars).



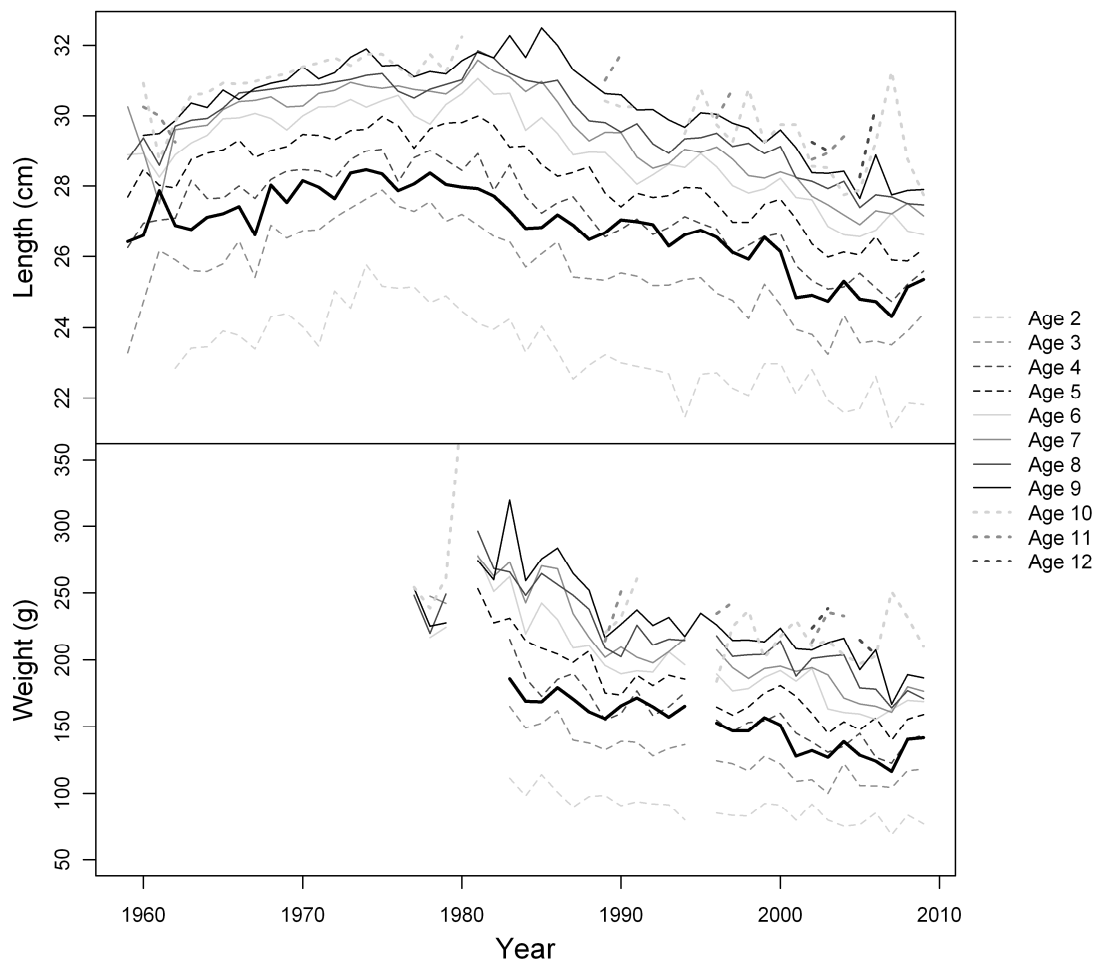
952 Table 1.

	Estimate		Standard error		Z statistics		p-value	
	AS	WS	AS	WS	AS	WS	AS	WS
Intercept	-14.13	4.03	7.87	0.50	-1.80	7.98	0.073	$1.53e^{-15}$
SST (autumn)	-0.22	-0.18	0.10	0.04	-2.29	-4.41	0.022	$1.30e^{-05}$
Salinity (winter)	0.48	-	0.24	-	2.03	-	0.043	-
NAO index	0.18	-	0.08	-	2.37	-	0.018	-
AMO index	-1.59	-1.05	0.46	0.28	-3.46	-3.69	0.0005	0.0002

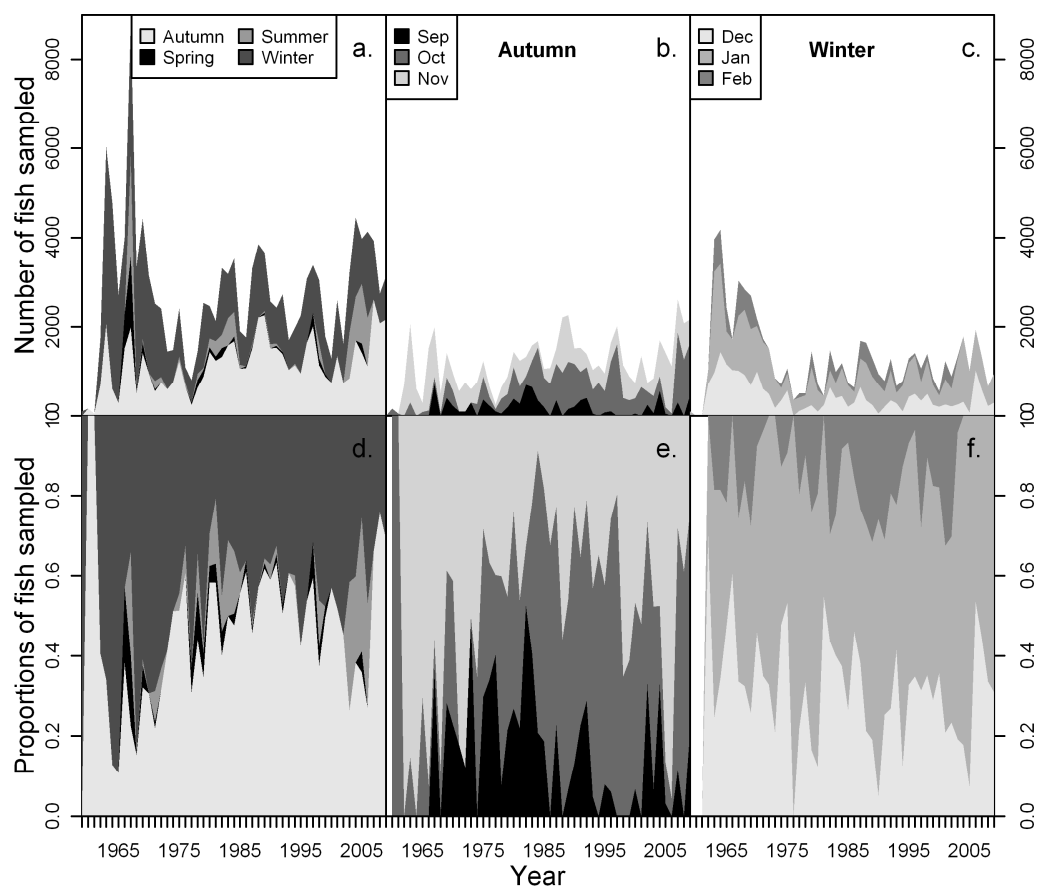
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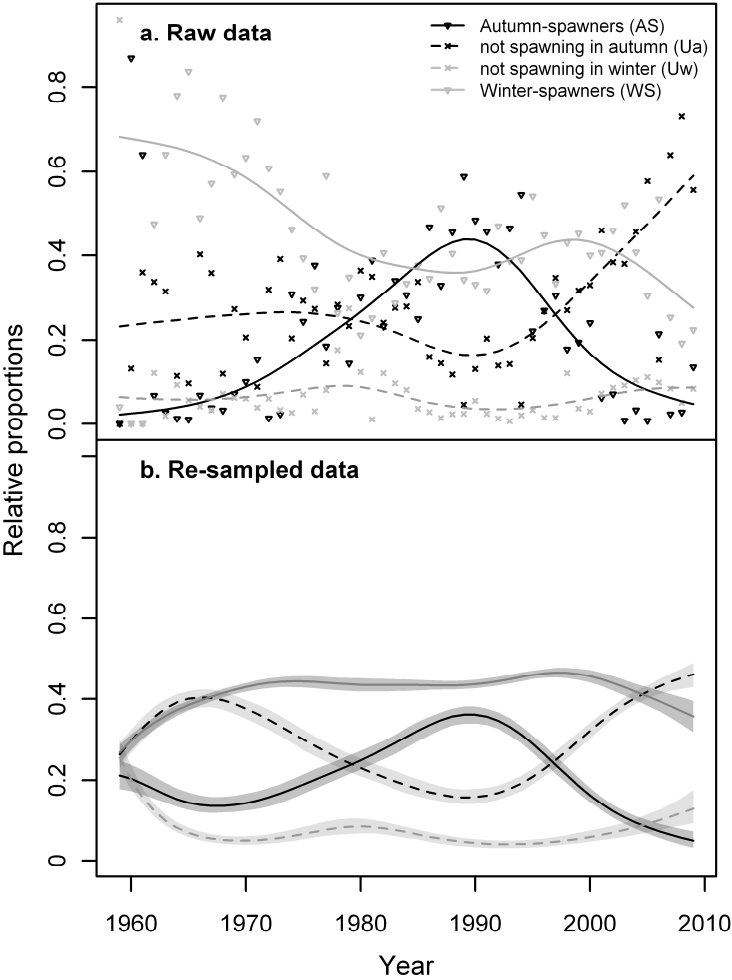


956 Figure 2.

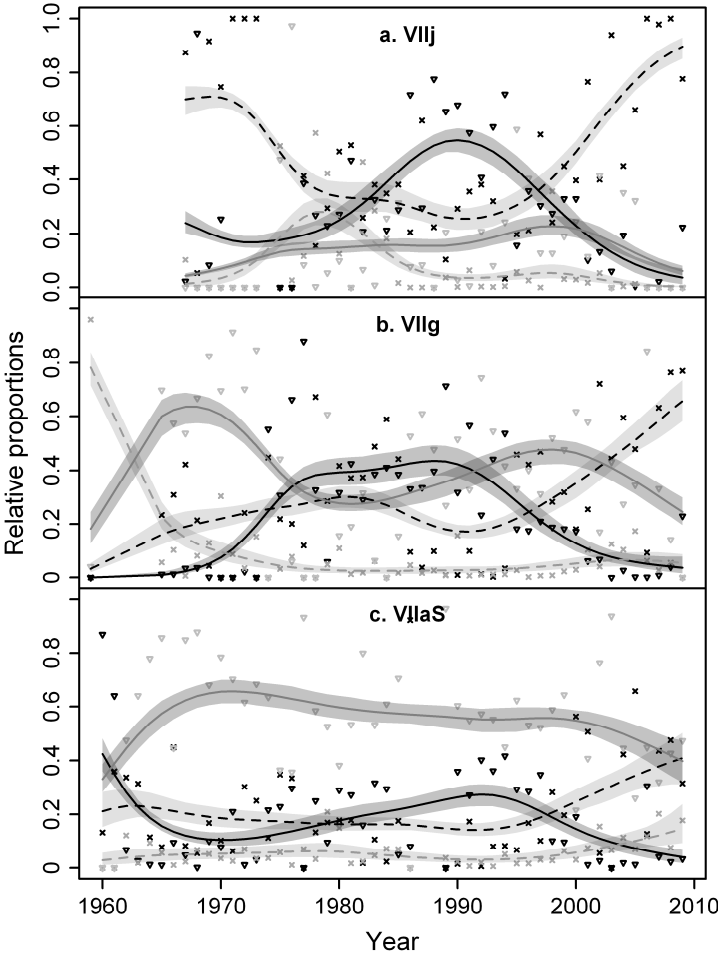


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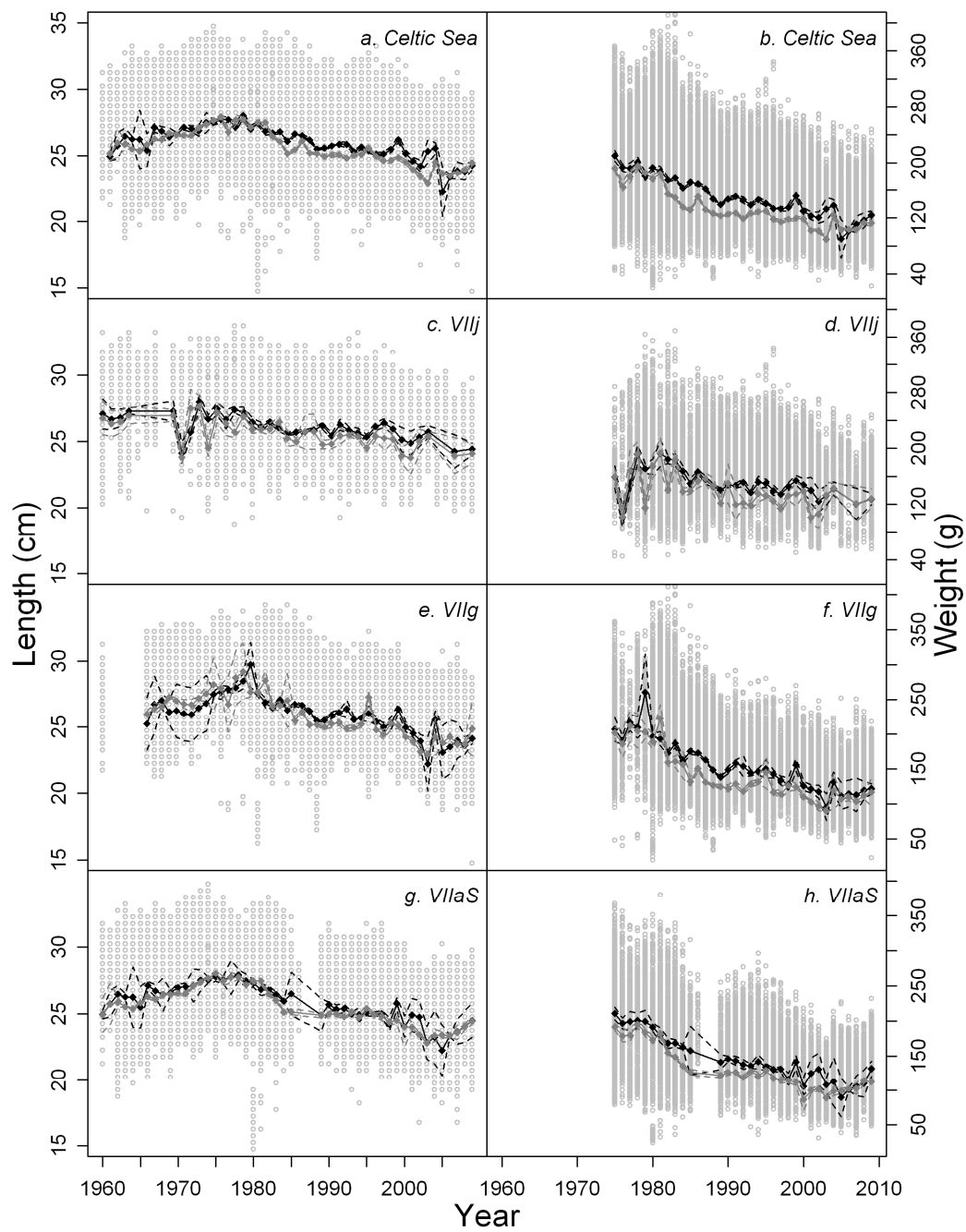




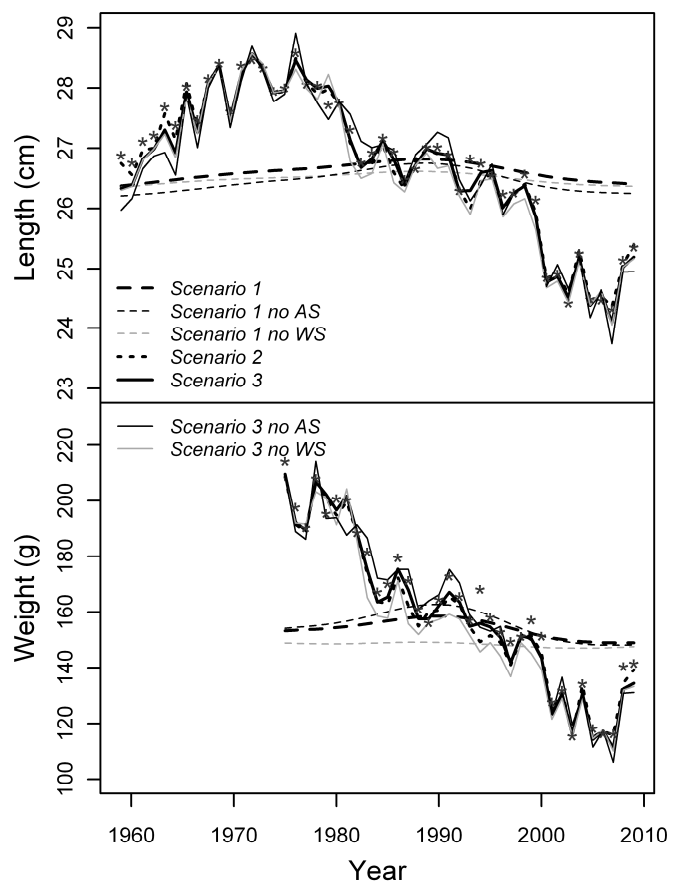
962 Figure 5.



963



966 Figure 7.



967