

Explaining trends in length-at-age of herring using gradient boosting regression trees

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Abstract

Combined effects of environmental change and fishing activity can produce directional trends in size-at-age in exploited fish populations with consequences for stock productivity. Disentangling various potential drivers of such trends is challenging and requires appropriate statistical methods that look beyond correlation and account for deep interactive and non-linear multiplicative effects. Following analysis of correlations with climatic indices (NAO, AMO), this study uses gradient boosting regression trees (GBRTs) to identify the most important variables associated with a marked decline in length-at-age of Atlantic herring (*Clupea harengus*) in the Celtic Sea. The analysis makes use of a comprehensive time-series of biological data (individual lengths, weights and ages) obtained from the commercial fishery (1959-2012). The predominant signal detected by the GBRTs was a non-linear negative relationship between size of Celtic Sea herring and SST; a marked decline in length-at-age 3 occurred above 14.1  C. Associations with indicators of food availability and population size were weak but there was some indication of density dependant growth in the Celtic Sea, particularly at temperatures below 14.1  C. Length-at-age 3 of Celtic Sea herring was not related to trends in fishing mortality. The results suggest that the Celtic Sea herring population, which exists close to the southern limit of the species' distribution, may be particularly vulnerable to impacts of increasing sea temperatures brought about by climate change and a positive phase of the AMO index. The GBRT approach proved effective at identifying the most influential drivers of variability, detecting a non-linear step change and

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examining interactions between large number of explanatory variables.

Keywords: Celtic Sea herring; population dynamics; abundance; supervised machine-learning; gradient boosting regression trees; AMO; NAO; multiple drivers; interactions; effect; growth

1. Introduction

Identifying drivers of change in complex ecological systems and quantifying their effects is a difficult task. Ecological systems are typically influenced by multiple drivers that may combine cumulatively or interactively (Crain et al., 2008) and often exert threshold or non-linear responses (Sugihara & May, 1990; Griffen et al., 2016). These drivers may directly impact the physiology of individual organisms or may exert indirect ecological impacts, for example via trophic interactions (Koenigstein et al., 2016). Attempts to explain biological responses of fish populations using empirical data must therefore look beyond correlation with individual drivers, account for additive and multiplicative effects while considering underlying mechanisms.

In fish populations, biological responses to external pressures are often manifested through changes in growth rate. Directional changes in growth have been observed across many exploited fish populations (Neuheimer & Taggart, 2010; van Walraven et al., 2010; Baudron et al., 2011; Neuheimer et al., 2011) and variously attributed to changes in the physical environment (typically temperature), food availability, population density and the selective effects of fishing (Law, 2000; Conover & Munch, 2002; Swain et al., 2007; Audzijonyte et al., 2016). Declines in growth lead to lower overall productivity via influences on survival, recruitment, fecundity and susceptibility to stock decline (Brander, 2007). This creates an imperative to interrogate temporal change in growth, determine the combined influence of various potential contributing factors and to improve understanding of likely future responses to the combined influence of climate and fishing (Perry et al., 2010).

Investigations of drivers of change to explain biological responses often employ parametric regression models, which can allow for non-linear relationships but given the complexity of ecological system may fail to detect deep interactive effects, nonlinear or abrupt changes. Such methods make assumptions on the distribution of data and often rely on a single

parsimonious model, which imposes limitations on the form of the assumed relationship. These limitations can be overcome by replacing a single model with a collection of simple additive regression models predictions that are averaged to give a more robust estimate of the response. Such methods are called ensemble methods (Hastie et al., 2009). Within ensemble
30 methods, gradient boosting regression trees (GBRT) form a supervised machine learning algorithm, which naturally allows for complex nonlinear interactions between environmental drivers and to produce out-of-bag predictions (Friedman, 2000).

Unlike parametric regression models, GBRTs do not require any assumptions on data distribution, but use an algorithmic model to learn the relationship between the response
35 variable and the covariates and to find patterns. The objective of the algorithmic model is to minimize mean squared error (MSE), by training each successive tree on the errors left over by the collection of earlier trees.

The increased availability of complex environmental datasets has stimulated interest in using machine learning techniques to explain patterns in ecological data (Olden et al., 2008;
40 Peters et al., 2014). These developments are accompanied by ongoing debate about the relative merits of hypothesis-driven versus data-intensive scene (Elliott et al., 2016). However, when carefully applied, machine learning approaches can complement hypotheses-based research to elucidate complex non-linear relationships in ecological systems (Muttill & Chau, 2007; Kelling et al., 2009; Peters et al., 2014). Carefully supervised boosted regression trees
45 are gaining favour in the ecological literature due to their superior predictive ability (Leathwick et al., 2006; Maloney et al., 2012; Escobar-Flores et al., 2013; Franklin et al., 2013; Cameron et al., 2014). For example, Leathwick et al. (2006) demonstrated that boosted regression trees improved predictive performance relative to generalized additive models when applied to the analysis of fish species richness in relation to environmental variables. Previous studies
50 have used the boosted regression trees to gain insight into fish populations and communities response to environmental change via changes in abundance and diversity (Pittman et al., 2009; Trigal & Degerman, 2015; Froeschke & Froeschke, 2016). However, few studies have used this approach to model individual level responses such as growth.

Here, we apply boosted regression trees to investigate a marked decline in herring growth
55 in relation to potential environmental and fishery-related explanatory variables. We present

an approach whereby all variables are chosen based on knowledge of the species' ecology and observed correlations. By doing so we integrate a machine-learning data-driven approach with a hypothesis-driven approach (Peters et al., 2014). Our aims are to: 1) disentangle effects of multiple drivers on herring growth; 2) combine the advantages of a machine learning approach with ecological knowledge to conduct hypothesis-driven analysis; and 3) to demonstrate how GBRT's can be used to identify the relative importance of various exogenous variables in a dynamic system. The advantages of this approach will be illustrated using a unique long time-series of biological data.

2. Materials and methods

2.1. Study area and data

Detailed biological and fisheries data have been collected from herring commercial landings since 1959 as part of Ireland's national fisheries monitoring programme. The data used in this study were from catches originating in the Celtic Sea (CS, ICES divisions VIIJ, VIIg and VIIaS) and the North-West of Ireland (NW, ICES division VIaS) (Figure 1). Samples were primarily from mid-water trawl catches (96% of the total).

From spatially and temporally representative samples of the landings, 50-100 herring were taken and biological characteristics were recorded (length to the nearest half centimetre interval, weight in grams (only after 1975), sex, maturity stage of the gonads and age). Total length of herring was reported to the nearest half centimetre below. To represent the midpoint of the size-class and to ensure consistency with the analyses performed in the assessment of herring (ICES, 2016), 0.25 cm were automatically added to each individual value. Age groups were determined using counts of winter rings in otoliths according to standard ageing protocols. In winter-spawned herring, the first translucent winter ring is formed during the fish's second winter. To account for this, annual counts were converted to ages in years such that a 1-winter ring herring was classed as a 2-year old. In the Celtic Sea, the fishing year conventionally resumes on April 1st so fish from the CS stock are assigned a 'birth date' of April 1st for assessment purpose (ICES, 2016). Fish for which no age estimate were available (e.g., otoliths broken, unreadable, lost) were excluded from further analyses (ca. 3% of the total sample). Fish were assigned to cohorts (c), based on their age in year(s)

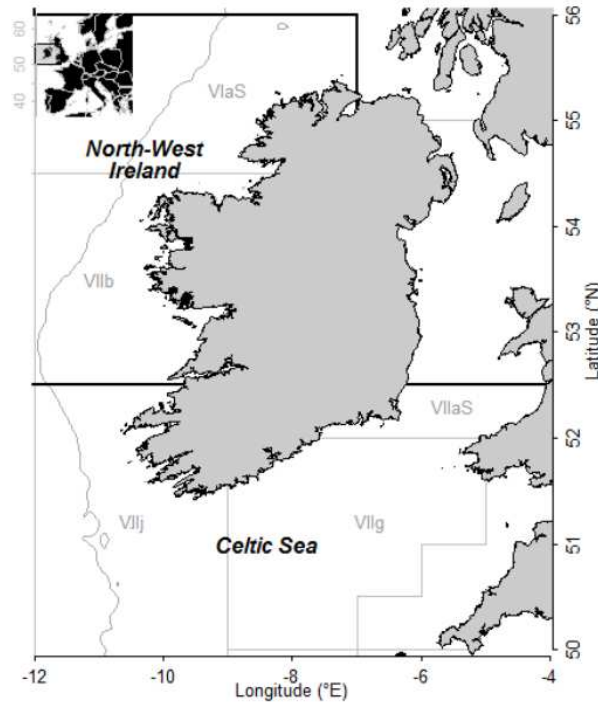


Figure 1: Study area map showing the two Irish herring populations under study: CS for the Celtic sea populations (the ICES divisions VIIa-South, VIIg, VIIj) and NW for the north-west populations (ICES divisions VIIb and VIIa-South)

(a_t) at the time they were caught as follows: $c = t - a_t$. The subsequent analysis was conducted using data from three year old fish because this is the youngest age group that is fully recruited to the fishery and for which samples from the commercial fishery can be assumed to be representative of the population. The final dataset included individual records for 52,582 herring from the CS population and 22,541 herring from the NW population.

To examine temporal trends in fish condition, the mean weight of a 25cm fish was estimated from the length-weight relationship for each year (1975-2012) and area using least squares regression. The relationship between length and weight was modelled as:

$$\ln(W) = a + b * \ln(L)$$

Where W is fish weight in grams, L is fish length in cm and a and b are the parameters of the regression equation. The reference length of 25cm was used because this was the average length of a three year old fish across the time series in both areas.

2.2. *Broad-scale relationships with climatic indices*

As first step in the identification of potential drivers, correlations between herring growth and two broad-scale climate indices were (The Atlantic Multidecadal Oscillation: AMO and
100 the North Atlantic Oscillation: NAO) investigated.

The AMO is an index of fluctuations in Sea Surface Temperature (SST) in the North Atlantic which is linearly detrended to remove the influence of anthropogenic climate change (Enfield et al., 2001). Recent SST observations suggest that the AMO alternates between positive and negative phases at a frequency of 60-80 years (Knight et al., 2006). The in-
105 fluence of AMO on marine ecosystem state is manifested across a broad range of taxonomic groups including some commercial fish species (Edwards et al., 2013). Proximate mechanisms underlying these relationships include the direct effects of temperature, fluctuations in water masses and circulation patterns and changes in food availability (Nye et al., 2014).

The NAO is an index of the difference in sea-level pressure difference between Iceland and
110 either the Azores, Lisbon or Gibraltar. Cyclical fluctuations between positive and negative phases of the NAO are associated with changes in wind patterns, rainfall and temperatures (Rogers, 1997) with reported consequences for fisheries (Lehodey et al., 2006).

General linear models were constructed to determine if the mean length of age 3 herring from the CS and NW populations was associated with the annual mean of the unsmoothed
115 AMO index or the winter NAO index (Dec-March) in the first year after hatching. In 2002, only two observations were available for the NW population; as mean length could therefore not be reliably estimated, this year was excluded from the correlation for the analysis of the NW population. To correct for temporal autocorrelation the significance of the correlations were tested using an adjusted degrees of freedom according to the modified Chelton method
120 (Chelton, 1984; Pyper & Peterman, 1998).

Simulation testing has demonstrated that this approach is robust to Type I error and less prone to Type II errors than methods based on pre-whitening or first-differencing (e.g. ARIMA) (Pyper & Peterman, 1998).

2.3. *Selection of explanatory variables for GBRT analysis*

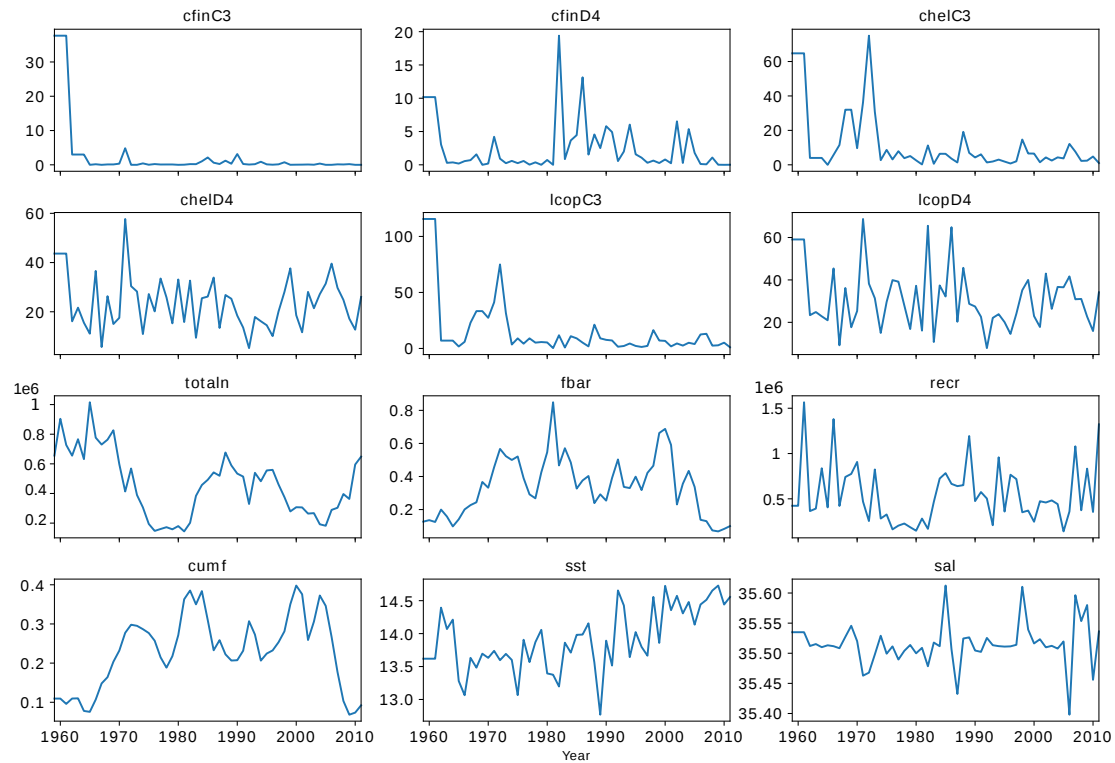
125 While correlation analyses are useful for establishing association between a biological process and climate variability, investigation of relationships with local environmental conditions

is required to build understanding of the mechanism underlying the association (Nye et al., 2014). Here, gradient boosting regression trees (GBRT) were used to identify relationships between growth and various exogenous variables and to determine their relative strength.

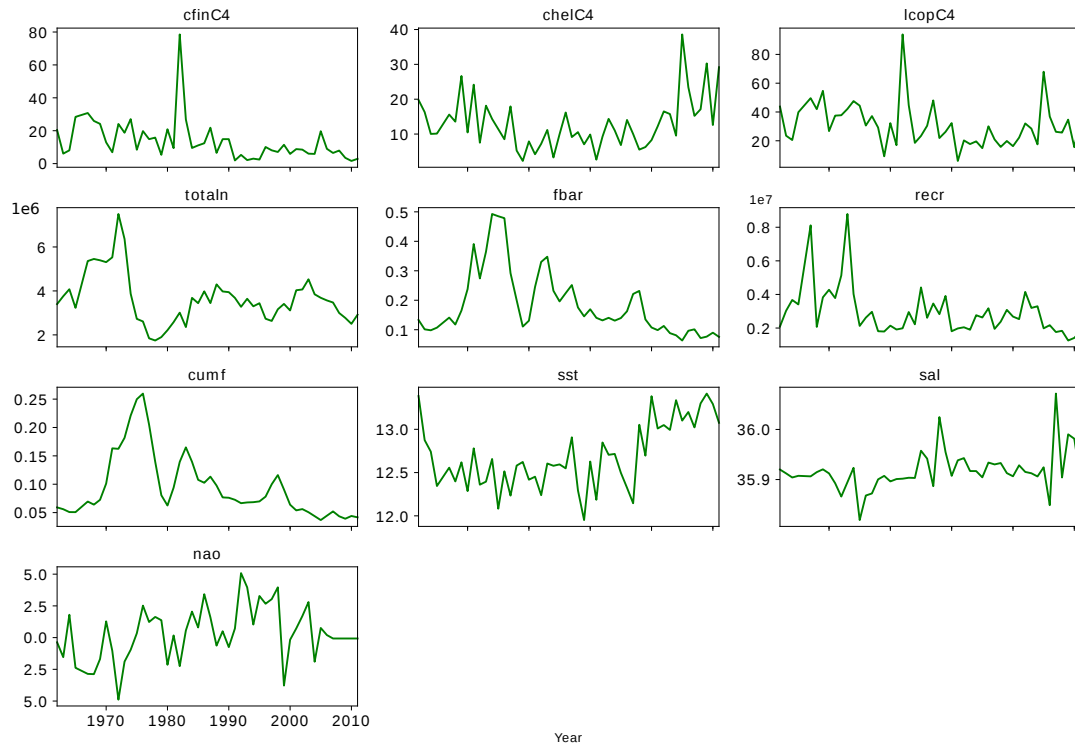
130 Separate GBRT models were constructed for each population to predict fish length based on a set of explanatory variables representing the main drivers likely to contribute to variability in growth of herring (Table 1, Figure 2). The inclusion of the two populations in the analysis facilitates a comparative investigation of their dynamics allowing us to distinguish broad scale change from processes operating locally within the Celtic Sea.

135 The response variable (length-at-age 3) reflects the combined influence of intrinsic and extrinsic factors operating over the entire life of the fish. The first growing season is a particularly important period and conditions during this critical phase can exert a lasting influence on lifetime growth trajectories (Brophy & Danilowicz, 2003; Vincenzi et al., 2008). Variation in juvenile growth is driven primarily by temperature (Ottersen & Loeng, 2000) and feeding conditions (Batten et al., 2016) with some evidence also of density dependence
140 (Casini et al., 2006) and salinity effects (Rajasilta et al., 2011; Berg et al., 2018).

Mean monthly Reynolds Historical Reconstructed SST values (Reynolds et al., 2007) for the Celtic Sea (48.5°N-52.5°N, 12.5°W-4.5°W) and north west of Ireland (52.5°N-56°N, 14.5°W-7.5°W) were included as indicators of the temperature that herring were exposed
145 to during their first growing season (average SST April-August). Calanus copepods are an important food source of juvenile herring (Huse & Toresen, 1996; Pedersen & Fossheim, 2008). Therefore, feeding conditions during the first growing season were described using indices of mean monthly abundance of *Calanus finmarchicus*, *Calanus helgolandicus* and all large copepods from three continuous plankton recorder(CPR) standard areas (C3, C4, D4;
150 (Richardson et al., 2006)). Salinity measurements (Ingleby & Huddleston, 2007) (average April-August) were included to reflect salinity conditions during the first growing season. To test for density dependent growth during the first year, estimates of recruitment from the stock assessment (ICES, 2016) were used as a measure of year-class strength. Total stock size (totalN) in the year of capture was also included as an overall index of the density. Finally, to consider possible selective effects of fishing, estimated fish mortality from the stock
155 assessment summed across all cohorts in year of capture (Fbar) and across each year of life



(a)



(b)

Figure 2: Explanatory variables time series for the Celtic sea (a) and the Northwest (b)

Table 1: Description, temporal resolution, source and accessed date of datasets used as potential variables to explain herring growth variability over time. Spatial resolutions for the local environmental datasets are representative of the latitude and longitude where herring populations are found in the Celtic Sea and off the north-west of Ireland areas. Variables marked with * were excluded due to correlation above 0.8. Abbreviations C3, D4 and C4 refer to standard areas used in the continuous plankton recorder survey (CPR)

abbreviation	variable (unit)	source	website	mean	sd
cfinC3 cfinD4	<i>Calanus finmarchicus</i> in areas C3, D4, C4 (mean abundance in April-August)	Sir Alister Hardy Foundation of Ocean Science CPR survey, in standard areas C3, D4, and C4. DOI 10.7487/2016.109.1.967	https://www.sahfos.ac.uk/	0.45 2.03	0.96 3.71
cfinC4 chelC3 chelD4	<i>Calanus helgolandicus</i> in areas C3, D4, C4 (mean abundance in April-August)	Sir Alister Hardy Foundation of Ocean Science CPR survey, in standard areas C3, D4, and C4. DOI 10.7487/2016.109.1.967	https://www.sahfos.ac.uk/	12.97 10.00 21.22	10.83 14.23 9.98
chelC4 lcpC3* lcpD4*	large copepod in areas C3, D4, C4 (mean abundance in April-August)	Sir Alister Hardy Foundation of Ocean Science CPR survey, in standard areas C3, D4, and C4. DOI 10.7487/2016.109.1.967	https://www.sahfos.ac.uk/	13.61 12.81 28.42	8.10 15.06 13.85
lcpC4* fbar CS,NW reer CS,NW	fishing mortality recruitment (number of 1-ring fish in stock)	(ICES, 2015) stock assessment assessment estimates Table 4.6.2.4	www.ices.dk	31.45 0.33,0.19 520366, 2895939	14.59 0.16, 0.12 271062, 1336270
(cumf) CS,NW	cummulative lifetime fishing mortality - fishing mortality across all cohorts in year of capture			0.23,0.10	0.09,0.06
totalN CS,NW	stock biomass (tonnes)			514972, 3661333	221382, 1277002
sst CS,NW	Reynolds Sea Surface Temperature (C°)	Reynolds Historical Reconstructed SST (2° x 2° resolution) as derived from the Reynolds Optimally Interpolated SST (from the Advanced Very High Resolution Radiometer, AVHRR) and in-situ observations, available from the NASA Jet Propulsion Laboratory (extracted through Hydrax/OpenDAP server), provided by Reynolds, National Climatic Data Center	https://www.esrl.noaa.gov	13.87, 12.70	0.44, 0.38
sal CS,NW	Surface Salinity between 0-400m (PSU)	Met Office Hadley Centre observations datasets, using the "Objective Analysis" of EN3 database (ENSEMBLES: quality controlled in situ ocean temperature and salinity profiles; (Ingleby & Huddleston, 2007)	http://www.metoffice.co.uk , accessed on 14/06/12	35.51, 35.91	0.04, 0.04
month	month, included to account for a month of capture				
(nao) CS,NW		North Atlantic Oscillation	https://www.esrl.noaa.gov/psd/data/correlation/nao.data	-0.09, 0.22	2.25, 2.16

for the age-3 fish (Fcum) were also included as explanatory variables. When missing values are encountered the GBRT model will exclude all data for the corresponding time period. To avoid this, missing values were replaced using forward fill to propagate the previous value forward. The set of explanatory variables was reduced to remove highly correlated variables. As expected, the AMO index was correlated with SST in the Northwest ($r = 0.7, p < 0.05$) and the Celtic Sea ($r = 0.6, p < 0.05$) and so was excluded from this analysis.

2.4. GBRT model specification

Gradient boosting regression trees (GBRT) considers additive models of the following form:

$$F_m(x) = \sum_{m=1}^M \gamma_m h_m(x) \quad (1)$$

where γ_m is a learning rate and $h_m(x)$ are weak learners

GBRT uses decision trees of fixed size as weak learners. Decision trees have a number of abilities that make them valuable for boosting, namely the ability to handle data of mixed type and the ability to model complex functions. GBRT builds the additive model in a forward stepwise fashion:

$$F_m(x) = F_{m-1}(x) + \gamma_m h_m(x) \quad (2)$$

At each stage the weak learner $h_m(x)$ is chosen to minimize the loss function L given the current model F_{m-1} and its fit $F_{m-1}(x_i)$

$$F_m(x) = F_{m-1}(x) + \arg \min_h \sum_{i=1}^n L(y_i, F_{m-1}(x_i) - h(x)) \quad (3)$$

GBRT attempts to solve this minimization problem numerically via steepest descent: The steepest descent direction is the negative gradient of the loss function evaluated at the current model F_{m-1} which can be calculated for any differentiable loss function:

$$F_m(x) = F_{m-1}(x) + \gamma_m \sum_{i=1}^n \nabla_F L(y_i, F_{m-1}(x_i)) \quad (4)$$

Where the step length γ_m is chosen using line search:

$$\gamma_m = \arg \min_{\gamma} \sum_{i=1}^n L(y_i, F_{m-1}(x_i) - \gamma \frac{\partial L(y_i, F_{m-1}(x_i))}{\partial F_{m-1}(x_i)}) \quad (5)$$

This algorithm is similar for regression and classification and only differs in the loss function used.

The accuracy of gradient boosting can be improved by introducing randomization into the procedure through taking randomly selected subsets of training data at each iteration (hence stochastic gradient boosting).

2.4.1. Data splitting by randomisation

For both populations, data were split randomly into two sets: train (50%) and test (50%). A two-part split is a general practice in machine learning, the purpose of which is to test the predictive performance of the model when presented with previously unseen data. In the present analysis, the biological datasets contained 10's of thousands of individual observations each representing an individual fish. However, the environmental datasets had a much lower temporal resolution with most measurements aggregated annually. Therefore, if the data were split randomly at the level of individual both sets very likely would contain individuals from all years and would not include previously unseen combinations of the explanatory variables. Such splitting could lead to overestimation of prediction capability on independent test data and may result in inadequate testing of the power of the model. To address this potential issue, two alternative randomisation approaches were employed at the data-splitting stage and the results were compared: randomisation by individuals (RI) and randomisation by years (RY). The RI data splitting was performed by randomly splitting all individual observations. This is the data splitting approach is generally considered optimum in machine learning as it does not introduce any systematic differences between the test and train datasets. To perform the RY data splitting, individual observations were grouped according to year of capture and years were randomly selected for inclusion in the train and test datasets. Although this may produce systematic differences between the test and train datasets, it ensures that the model is tested using previously unseen combinations of explanatory variables.

A potential drawback of the machine learning approach is that after the model is built

205 using the training dataset, the parameters are optimised based on how well the model performs on the test dataset. Therefore, prediction accuracy for previously unseen data may be overestimated. To perform a more robust test of prediction accuracy a three way split was also performed. The data were split (using the RI splitting approach) into train (50%), test (25%) and validation (25%) sets. The model was built, tested and optimised using the train
210 and validation sets and the models performance was confirmed using the test set.

For the two-part split hyperparameters were tuned using grid search which performs an exhaustive search over specified parameter values for an estimator. Grid search takes a set of possible values for each hyperparameter that should be tuned and evaluates a model trained on each element of the Cartesian product of the sets. It is an exhaustive search that trains
215 and evaluates a model for each possible combination of the hyperparameter values supplied. This algorithm automatically generates the validation sets internally. So there is no need to generate a validation set to select the best model.

For the three-part split the score on the validation set is used instead of the test set. Then one is allowed to tweak the values in the parameters grid to see if values that improve
220 the score can be found. Once there is confidence that the validation score cannot be further improved via parameter tweaking (or feature engineering) one can evaluate the best model on the final test set (only once). It can be the case that the final test score is a bit worse than the validation score. If that's the case the test score is taken as the most realistic evaluation of the true generalization performance of the final model.

225 2.4.2. *Hyperparameters*

Hyperparameter tuning was done manually. As a starting point the learning rate was set as low as possible and the number of iterations as high as computationally feasible (Hastie et al., 2009). The learning rate, which is also called a shrinkage parameter, determines the contribution of each tree to the model. The maximum tree depth which reflects
230 the degree of interaction in the model is usually low. GBRT performs best using fairly shallow trees, so-called tree stumps.

For the RI models the same initial parameters were set for the analysis of the CS and NW datasets, then a grid search was performed on both datasets with a two-part split to give

Table 2: Tuned model parameters. Number of iterations was defined by early stopping (randomised by individuals models only). Subsample rate was 0.75% in all cases. Parameters for 2-part split were defined through grid search, whereas parameters for 3-part split were tuned manually.

Model	splits	Number of iterations	Learning rate	Tree depth
RI CS	2	154	0.10	4
RI CS	3	187	0.05	6
RI NW	2	545	0.01	8
RI NW	3	197	0.05	6
RY CS	2	500	0.005	2
RY NW	2	500	0.005	2

hyperparameters with the highest level of accuracy. These were as following: learning rate
 0.1 and maximum tree depth of 4 for the CS model. For NW model the learning rate was
 0.01 and maximum tree depth was 8. The early stopping technique was used to determine
 when to stop the model training to avoid overfitting. Using early stopping the number of
 iterations required until convergence was 154 for CS and 545 for NW. Grid search was not
 required for a three-part splits, and further tuning of the parameters was done manually.

For the RY models in contrast to the RI models the best performing models (based on
 MSE) were models with the very shallow trees (tree depth of 2 for the both CS and NW)
 and with a learning rate of 0.005. The number of iterations was kept at 500.

The tuned hyperparameters of the final models are shown in Table 2.

3. Results

3.1. Overall trends in length-at-age 3

As previously reported (Harma et al., 2012; Lynch, 2011), mean size at age of of three
 year old herring in the Celtic Sea showed a general increasing trend from 1960-1980 followed
 by a decline from 1981-2012 (Figure 6a). In contrast, temporal changes in length of herring
 from the Northwest of Ireland were less marked but with a slight decline in length between
 1970 and 1980 (Figure 6b).

The mean weight of a 25cm herring over the course of the available time-series was 133.9g
 in the Celtic Sea (1969-2011) and 130.0g (1970-2009) in the Northwest. The temporal trends
 in the mean weight at 25cm indicated that the observed decline in length-at-age did not
 coincide with a decline in condition (Figure 3).

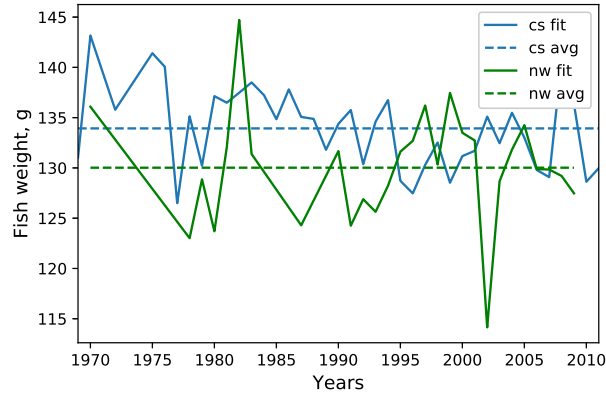


Figure 3: Mean fish weight at 25cm

3.2. Correlation with climate indices

The mean annual AMO index in the first year of life was negatively correlated with mean length-at-age 3 of herring from both the CS ($r = -0.693$, adjusted $df = 13$, $p < 0.001$) and NW ($r = -0.305$, adjusted $df = 25$, $p < 0.05$) populations. There were no significant correlations between mean length and NAO for either population ($p > 0.05$). The decline in size of Celtic Sea herring during the late 1970's and the 1980's coincided with a steady increase in the AMO index and an eventual transition from a negative to a positive phase in the mid-1990's. Earlier increases in the size of Celtic Sea herring during the 1960's and 1970's corresponded with a negative phase of the AMO and a steady decrease until the mid-1970's (Figure 4). In the NW population, mean length-at-age 3 was highest during the negative phase of the AMO in the 1970's, however, after 1980, the inverse relationship between length and AMO was not apparent.

3.3. GBRT model performance

For the RI model the plot of MSE against number of iterations for the test data closely followed that of the train data indicating consistency in model performance across the test and train data. The difference between test MSE and train MSE was slightly greater for the NW than for the CS dataset. For the RY model the MSE for the test data deviated upwards away from the MSE for the train data as number of iterations increased. This indicates some degree of overfitting of the train data. However, the difference between the train and test MSEs remained low (< 1) and prediction to independent data is unlikely to be compromised

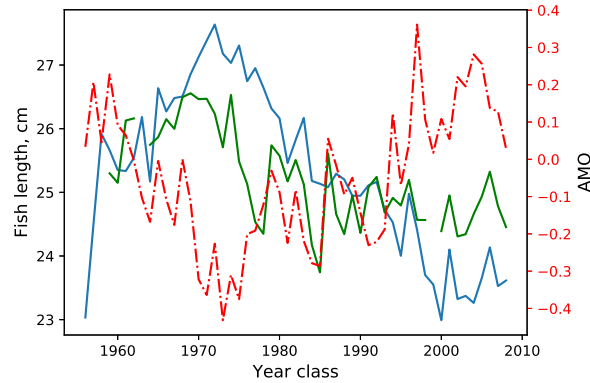


Figure 4: The mean annual AMO index in the first year of life (red) and the mean length-at-age 3 of herring in the Celtic sea (blue) and the Northwest (green)

(Elith et al., 2008). While overfitting is often seen as a problem in statistical modelling, our experience with BRT is that prediction to independent data is not compromised – indeed, it is generally superior to other methods (see e.g. comparisons with GLM, GAM and multivariate adaptive regression splines, Elith et al., 2008; Leathwick et al., 2006). The flexibility in the modelling that allows overfitting also enables an accurate description of the relationships in the data, provided that overfitting is appropriately controlled. This was confirmed by rerunning the RY model ten times, using a different randomised test-train split each time and comparing the output. Neither the predicted relationships between the response and explanatory variables (as reflected in the partial dependence plots) nor the relative influence of the explanatory variables (as indicated by the variable influence plots) showed substantial variation between runs indicating that the model predictions were stable (Figure 5a).

The MSE's and R squared values of all the RI models were lower than those for the corresponding RY models (Table 3, Figure 5). This confirms that splitting at the level of the response variable (RI models) can lead to overestimation of the predictive capability of the model when explanatory variables are measured at a lower resolution than the response. The RY models provide a more robust test of the models' power by ensuring that the train and test sets contained unique combinations of explanatory variables. The R squared values also showed that the models provided a better fit to the data for the CS population (RY model: $R^2 = 18.6$) compared to the NW population (RY model: $R^2 = 9.7$). Overall, percentage explained variability was low. This reflects the high degree of individual variability in size that

Table 3: MSE's and R^2 .

Model	splits	MSE	R^2
RI CS	2	1.27	52.85
RI CS	3	1.31	51.70
RI NW	2	1.55	34.95
RI NW	3	1.64	36.02
RY CS	2	2.46	18.57
RY NW	2	2.29	9.70

could not be accounted for by the explanatory variables, which capture the mean conditions experienced by the population.

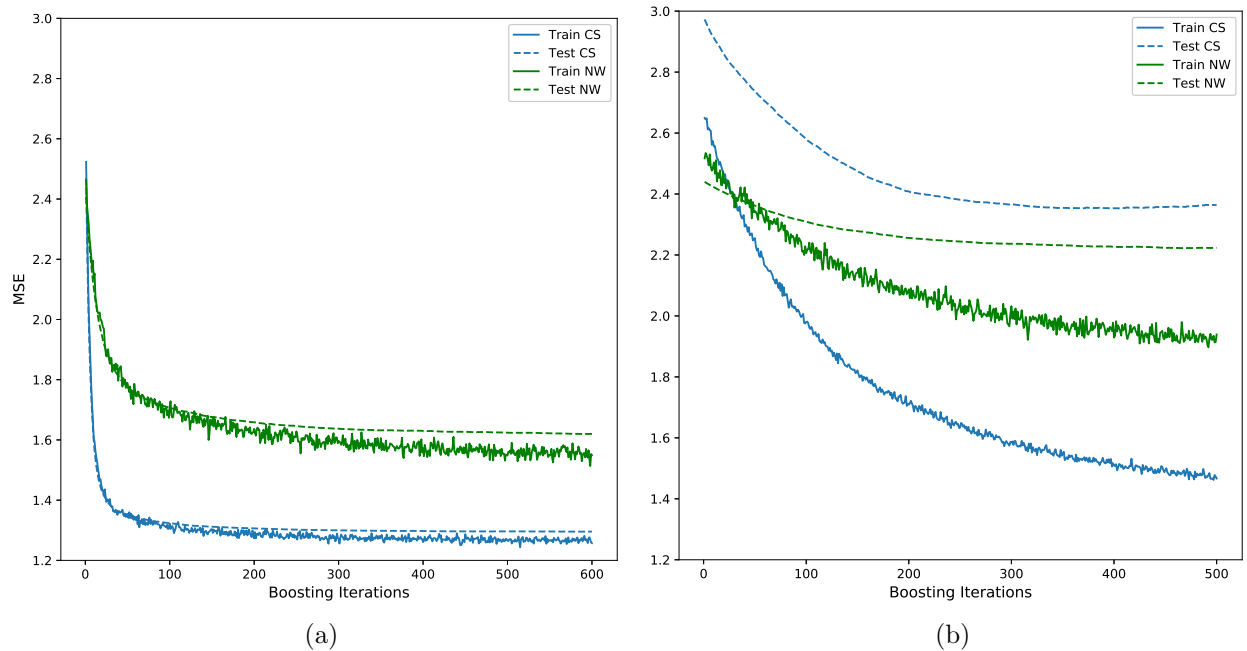


Figure 5: Performance of GBRT models with a two-part split for the CS (green) and the NW (blue). The number of boosting iterations on the x-axis is plotted against MSE on the y-axis. In the RI model the MSE curve for train data closely followed the MSE curve for the test data, although there was a larger gap for the NW (a). In the RY model a gap between train and test data was larger with some evidence of overfit (b)

3.4. Predicted trends in mean length

For the Celtic Sea population, mean length-at-age 3 predicted by the GBRT models followed similar temporal trends to observed mean length-at-age 3 although the models tended to underestimate mean length at the observed peak of the time series (mid 1970's) and overestimate mean length in years when the observed mean length was at its lowest (mid 2000's)

(Figure 6a). For the NW population the models tended to underestimate mean length early in the time series and overestimate it later in the time series (Figure 6b).

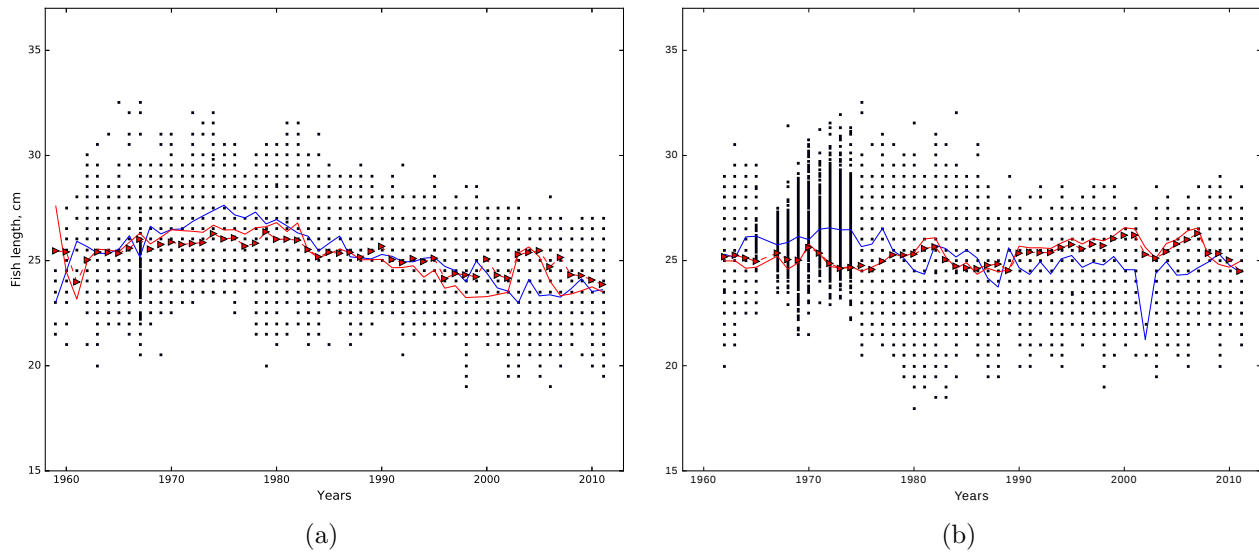


Figure 6: Mean-length of fish at age 3 in centimetres in Celtic Sea (a) and in the north-west of Ireland (b), cm. Measurements are rounded to the nearest 0.5 except for the years 1967 (a) and 1965–1974 (b). Red line is a prediction obtained from RI model and red line with triangles is a prediction from RY model. The blue line represents the observed mean length

3.5. Relative importance of the predictor variables

Figure 7 displays the estimated relative importance of each variable in the GBRT models for the CS and the NW populations. The importance of the predictors varied between the RI and RY models, however, some general trends were apparent. For the CS population, sea surface temperature (SST) in the first growing season was the most important explanatory variable in both the RI and RY models. The high variable influence score indicates that relative to the other variables, SST was selected most frequently for splitting and had the largest influence on predictive power. Variables describing population size (recruitment and total N) and food supply (CPR estimated abundance of *Calanus finmarchicus* or *Calanus helgolandicus*) were also included in the top three most influential predictors, however, their influence was much less marked than that of SST. Other environmental descriptors (salinity, NAO), fishing pressure and month of capture also had only a minor influence on the model predictions for the Celtic Sea population.

For NW population, SST had a much lower influence in the models compared to the Celtic Sea, perhaps reflecting the lower sensitivity of herring to increases in temperature in the cooler waters of the Northwest. According to the RI model, variability in length was most strongly associated with month of capture, reflecting the expected increase in fish size as the year progresses. Capture month was of lesser importance in the RY model but the variable still featured in the top three most influential predictors. Recruitment and fishing pressure also had a strong influence on model predictions for both the RI and RY models. Other environmental descriptors (salinity, NAO), food supply (abundance of *Calanus finmarchicus* and *Calanus helgolandicus*) and total population size were of less importance in the NW models.

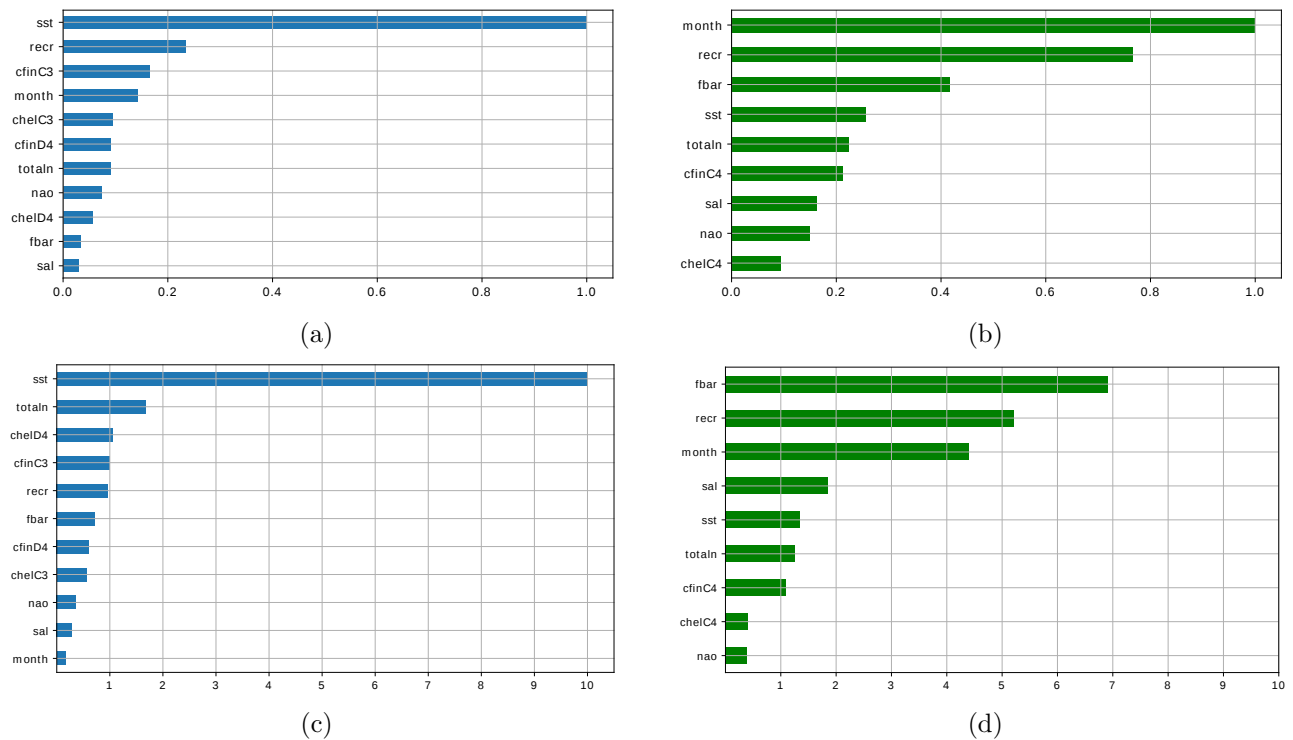


Figure 7: Relative importance of the variables for the CS (a), (c) and the NW (b), (d) populations. RI models (a) and (b) were calculated from one GBRT model, whereas RY models (c) and (d) were based 10 GBRT models

3.6. Partial dependence plots

The partial dependence plots display, for a selection of the more influential predictors, the marginal effects of each predictor on fish length-at-age 3. In general, the RI and RY

models detect similar relationships between the predictors and the response although in some cases the RY model detected much weaker relationships. This may reflect over-fitting of the data when splitting is implemented at the level of the individual (RI model) (Figures 8a and Figure 9a respectively). To avoid over emphasis on outlying data points, interpolations beyond the 9th decile of the variable distribution were disregarded when interpreting the relationships between the predictors and response.

In the CS population SSTs above 14.1°C were associated with a decrease in growth. In the NW population, although SST had a lower influence on model predictions, the partial dependence plot showed a similar trend as in the Celtic Sea with growth decreasing at a lower temperature of 12.8°C.

There was some evidence of density dependence in the CS population; both the RY and the RI models predicted a decrease in length at higher recruitment levels. There was an apparent transition to smaller size when recruitment exceeded ~350,000 individuals. A similar but less pronounced negative relationship between length and total population size (totalN) with an apparent transition to a smaller size when stock size exceeded ~400,000 individuals. The plot of the two-way partial dependence describes the interaction between SST and recruitment (Figure 8a, 8b; when temperatures exceeded 14.1°C the relationship between length and recruitment was weaker. This relationship was not apparent in the partial dependence plot from the RY model (Figure 9a). In the NW population the relationship between length and recruitment was positive suggesting that recruitment and growth may co-vary in response to other conditions that influence both growth and survival (Figure 9b)

Descriptors of food availability during the first growing season were of relatively minor importance in the RI and RY models for both the NW and CS populations and the partial dependence plots did not indicate strong relationships (Figures 8, 9). According to the RY model, length-at-age 3 in the Celtic Sea population was weakly positively associated with the CPR recorded abundance of *Calanus finmarchicus* and *Calanus helgolandicus* at station C3 and with *Calanus helgolandicus* at station D4 while, the relationship with *Calanus finmarchicus* at station D4 was weakly negative (Figure 8a). According to both the RI (Figure 8b) and RY (Figure 9b) models, length-at-age 3 in the NW population was positively related to abundance of *Calanus finmarchicus* at station C4 while there was no detectable

relationship with the abundance of *Calanus helagolandicus*. The two-way partial dependence plots indicated that relationships between length and food availability may be influenced by interactions with other environmental variables. For example, in the CS population, the positive association between length and abundance of *Calanus helagolandicus* (station C3) was more pronounced at higher population sizes (totalN>375,000; Figure 8a). According to the partial dependence plot from the RI model, *Calanus finmarchicus* (station C3) was positively associated with fish length at a lower abundance when temperatures exceeded 14.1°C (Figure 8a). This interaction was not detected by the RY model.

Contrary to expectations, the partial dependence plots from all models suggest a positive association between length and fishing mortality. In the NW populations, there was a pronounced increase in fish length at higher levels of fishing mortality ($F > 0.25$). Although fishing mortality was of much lesser importance in the models for the CS population in this population a positive association with length was also observed.

In both populations there was a positive association between month and fish length, reflecting the expected increase in fish length as the year progresses. In the NW population month and recruitment had an interactive effect; as recruitment levels increased the effect of month on length became less pronounced (Figure 8b).

4. Discussion and conclusions

This study aimed to disentangle the effects of multiple drivers of variability in herring size-at-age from the 1960's, and to identify the most likely causes of observed declines in growth of Celtic Sea herring since the 1980's. The advantages of a machine learning approach were combined with simple correlation analyses and ecological knowledge. The analysis was hypothesis-driven and demonstrated how GBRTs can be used to identify the relative importance of various exogenous variables in a dynamic system. The relationships detected by the GBRT models are complex and interactive and do not necessarily indicate causation. However, many of the observed relationships are consistent with plausible a-priori ecological hypotheses. The GBRT approach proved useful for detecting non-linear relationships and step changes that would have been difficult to detect using traditional parametric approaches. In particular, a marked decrease in length above a threshold temperature was detected. The

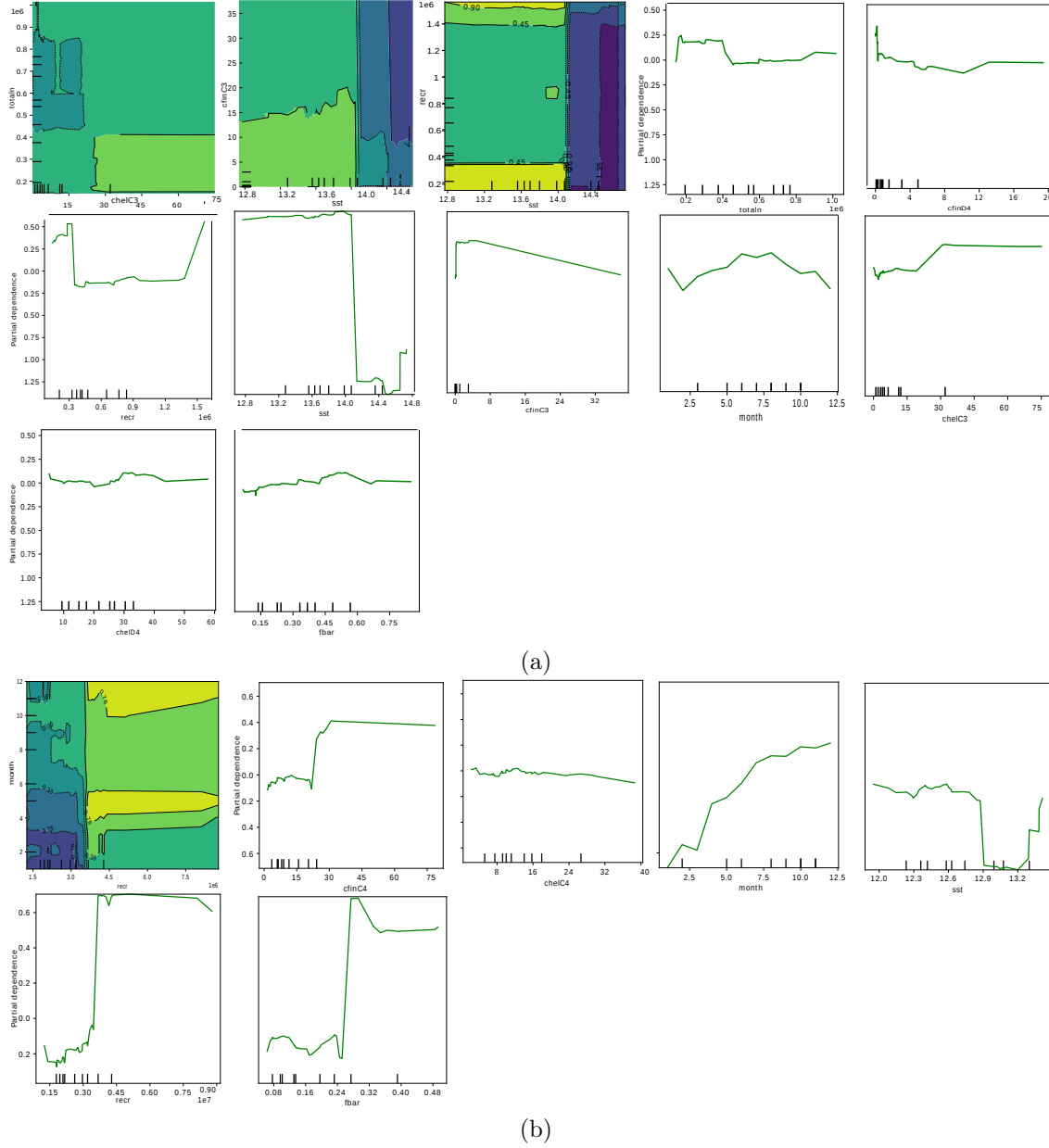


Figure 8: RI partial dependence plots for the CS (a) and the NW (b). One-way partial dependence plots indicate the model predictions after the influence of a predictor marginalizing over all other predictors. Two-way partial dependence plots indicate interaction effect of varying degree. The extreme values for the axes are created using low (0.05) and high (0.95) percentiles. The hash marks on x-axis represent the deciles of the corresponding variable distribution

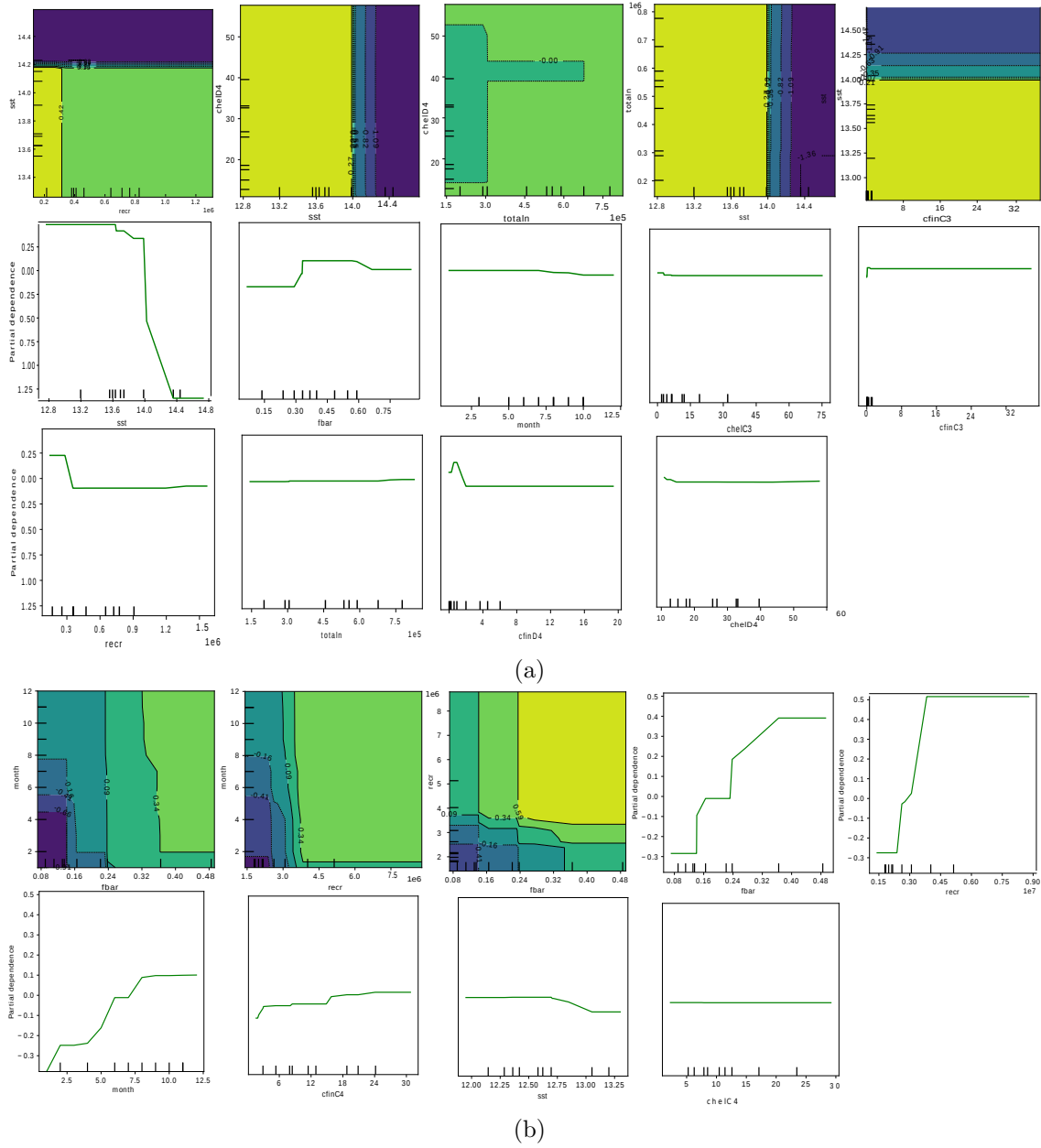


Figure 9: RY partial dependence plots for the CS (a) and the NW (b). One-way partial dependence plots indicate the model predictions after the influence of a predictor marginalizing over all other predictors. Two-way partial dependence plots indicate interaction effect of varying degree. The extreme values for the axes are created using low (0.05) and high (0.95) percentiles. The hash marks on x-axis represent the deciles of the corresponding variable distribution

comparison of the two populations shows both common responses to global drivers and more
390 localised stock-specific relationships.

Length-at-age three was negatively associated with mean AMO in the year after hatch-
ing. The observed negative correlation remained significant after correction for temporal
auto-correlation and is consistent with previous reports of climate driven multi-decadal fluc-
tuations in the distribution and abundance of small pelagic clupeids (Alheit et al., 2014).

395 During a previous warm period, that coincided with a positive phase of the AMO (1930's-
1960's), the abundance of herring in the English Channel (at the southern limits of the
species distribution) decreased and its distribution contracted (Southward et al., 1988) while
abundance of the more northerly Norwegian spring spawning herring population increased
(Toresen & Østvedt, 2000). Concurrent changes in the dynamics of other pelagic clupeids
400 (anchovy, sardine, sardinella and sprat) and similar trends during the more recent warming
period (after the mid-1990's) are indicative of climate driven ecosystem regime shifts that
may be reflected in the AMO signal (Edwards et al., 2013; Alheit et al., 2014). The results
of this study demonstrate that climatic fluctuations may manifest as changes in fish growth
as well as abundance. The association between fish size and AMO was stronger and more
405 consistent in the Celtic Sea than in the Northwest; possibly indicating that the Celtic
Sea population, existing close to the southern limit of the species' distribution, is thermally
limited and more vulnerable to climatic warming than the more northerly Northwest herring
population.

Fluctuations in AMO represent broad-scale environmental change that can affect multiple
410 trophic levels with direct and indirect consequences for fisheries. While the AMO is primarily
an index of SST anomalies, it is also associated with regional fluctuations in precipitation,
wind patterns, ocean circulation wind mixing and stratification (Nye et al., 2014). AMO re-
lated increases in SST can intensify the impact of climate change and directly impact on fish
survival, growth and other physiological processes (Nye et al., 2009). The combined effects
415 of the AMO on temperature, wind patterns and stratification are thought to drive decadal
changes in global phytoplankton abundance (Martinez et al., 2009; Nye et al., 2014), while
temperature changes lead to changes in the distribution of zooplankton, with consequences
for growth of planktivorous fish.(Beaugrand et al., 2009; McGinty et al., 2011). Several inter-

acting mechanisms may therefore underlie observed synchronicities between the AMO signal
420 and pelagic fish populations.

Here, the GBRT modelling approach provided a means to identify the variables that most likely underlie the observed association between the AMO index and herring length-at-age. The low to moderate R squared values associated with GBRT models (9.7-52.8%) reflected the fact that individual variability in length-at-age could not be accounted for by the explanatory
425 variables which were measured with broad temporal and spatial resolution. Nonetheless, predicted mean-lengths from the GBRT models were close to the observed mean lengths for most of the time series (Figure 6) and the observed decline in mean length-at-age 3 in the Celtic Sea population after 1980 was evident in the predictions from both the RY and RI models.

The predominant signal detected by the GBRT models was the negative association between size of Celtic Sea herring and SST during the first growing season (April-August). The relationship with SST was non-linear with a marked decline in length occurring when mean temperature exceeded 14.1°C (Figures 8a, 9a). A similar but much less pronounced step-change occurred at about 13°C in the Northwest population (Figure 8b). At northern lati-
435 tudes, growth of juvenile herring tends to increase with increasing temperature (Husebø et al., 2007). However, experimental studies indicate that the metabolic optimum for the species occurs at around 15-16.1°C with a subsequent decrease in metabolic rate occurring with further increases in temperature (Bernreuther et al., 2013). During the study period, mean temperatures in the Celtic Sea from April-August ranged from 12.7°C-14.7°C. Maximum tem-
440 peratures in August remained below the thermal optimum during colder years but exceeded it in warmer years, reaching highs of above 18°C. As sea temperatures rose due to the combined effect of a positive phase of the AMO and climate change, herring in the Celtic Sea were more likely to encounter temperatures that were sub-optimal for growth and metabolism. In the absence of individual temperature histories, it is not possible to determine if this exposure
445 would be sufficiently frequent or prolonged to produce such a pronounced decline in growth as has been observed in Celtic Sea herring. However, it is plausible that the direct effects of increasing temperature on growth and metabolism could at least partly contribute to the decline.

The results indicate that the Celtic Sea herring population, which exists close to the southern limit of the species' distribution, may respond differently to increasing ocean temperatures than populations at more northern latitudes. In a cross-population examination of weight-length relationships, Brunel & Dickey-Collas (2010) observed that herring growth rates and size at age were positively correlated with mean annual SST while asymptotic weight was negatively correlated. The authors proposed that global warming could lead to higher growth of young age classes, slower growth of older individuals and a shorter lifespan of herring. However, temperature-growth relationships within populations were difficult to resolve; both negative and positive correlations were detected but many were non-significant. In Pacific herring (*Clupea pallasai*) a positive correlation between growth during the first year and SST broke down at higher temperatures and marked reductions in growth were observed in years when mean July-August temperatures exceeded 12.5°C (Batten et al., 2016). In addition, (Watanabe et al., 2008) showed that high temperatures during winter had a negative effect on growth of Hokkaido spring spawning Pacific herring which occupy the southern boundary of the distribution range for that species.

In Atlantic herring populations, predicted positive temperature-growth relationships might not apply when temperatures exceed a certain threshold. This signals caution when extrapolating climate change effects from contemporary field observations and highlights the importance of considering biological responses at distributional extremes.

Changes in the growth of planktivorous fish populations can be mediated by trophic interactions via the influence of environmental processes on plankton abundance (bottom-up control) or due to changes in population density and food-competition (top-down control). Changes in size-at-age have been attributed to density dependence in Baltic Sea (Cardinale & Arrhenius, 2000) and George's Bank (Melvin & Stephenson, 2007) herring populations. In the North Sea, the influence of hydrographic conditions on plankton abundance drives short-term interannual variability in growth of larval and juvenile herring while long-term trends are driven by density dependence (Heath et al., 1997; Shin & Rochet, 1998; Dickey-Collas et al., 2010). In the present study, the GBRT model outputs indicated that herring length-at-age 3 was associated with indicators of food availability and population size. In the Celtic Sea population, these associations were weak and of minor explanatory

importance relative to the temperature effect, particularly when the training/test split was
480 implemented with a yearly resolution (RY model). A negative relationship between length
and recruitment was detected by both the RI and RY models, providing evidence of density-
dependant growth. The two-way partial dependence plot revealed an additional interaction
with SST; at temperatures above 14.1°C fish length did not decline at high levels of re-
cruitment, indicating that the influence of increasing temperatures may over-ride density
485 dependence. Positive relationships with some of the indices of copepod abundance indicated
the possible influence of food availability. In the Northwest population, recruitment was the
second most important explanatory variable in the GBRTs and was positively associated
with fish length. This could arise if growth is independent of density and conditions that
favour high survival during the first year are also favourable for growth.

490 While length and weight at age declined markedly in Celtic Sea herring after the 1980's
there was no concomitant decline in fish condition index (mean weight at 25cm: Figure 3),
suggesting that pronounced changes in feeding conditions have not occurred. This is in
contrast to the situation in the Baltic Sea; declines in weight-at-age of herring during the
1990's coincided with a decrease in condition and both were attributed to increasing densities
495 of pelagic fish and consequent reductions in food availability (Cardinale & Arrhenius, 2000).
Long-term studies have reported climate related shifts in the distribution of zooplankton
species in the Northeast Atlantic with northward movement of temperature species such as
Calanus helgolandicus and declines in boreal species like *Calanus finmarchicus* (Pitois & Fox,
2006). However, the abundance of these calanoid copepods in the Celtic Sea has remained
500 relatively unchanged (Pitois & Fox, 2006; Lauria et al., 2012). In addition, from 1986-2007,
temporal trends in food availability were not linked to biomass of juvenile herring or to climate
indicator (Lauria et al., 2012). It appears unlikely that the availability of calanoid copepods
is a major driver of observed declines in growth of Celtic Sea herring. Nonetheless, it must
be borne in mind that the CPR provides a spatially coarse index of plankton abundance and
505 may not capture localised fluctuations in food availability, particularly within coastal areas
inhabited by young feeding herring.

Intensive fishing is predicted to alter the growth rate of fish populations directly, by
selective removal of large and fast growing individuals from the population or indirectly

through selection for earlier maturation (Heino et al., 2015). Reductions in size-at-age due
510 to the selective effects of fishing have been demonstrated in Atlantic cod *Gadus morhua* in the
Gulf of St Lawrence (Swain et al., 2007). In the present study, fishing mortality contributed
very little to variability in length-at-age 3 of Celtic Sea herring but was a relatively important
explanatory variable in the models describing size variation in the Northwest population. It
was expected that increasing fishing mortality might lead to declines in size-at-age; in fact,
515 length-at-age 3 was positively associated with fishing mortality in both populations. It is
likely that this association indicates temporal concurrence rather than causation; fishing
effort was restricted during the 1980's and 2000's in response to declines in stock biomass
which coincided with declines in size-at-age (ICES, 2016). Overall, the analysis found no
evidence that declines in size at age of Celtic Sea herring are an evolutionary response to
520 fishing.

Due to the nature of the herring fisheries, evolutionary responses to fishing may be rela-
tively minor (Engelhard & Heino, 2004). In Ireland, herring are targeted predominantly by
midwater pair trawls, primarily during the spawning season. Trawls are known to capture
a wide range of length classes (Kuparinen et al., 2009). Length-dependant escapement of
525 Baltic Sea herring from commercial trawls has been demonstrated for fish below 15cm length
(Suuronen et al., 1997). However, escaped fish suffer high rates of mortality (Suuronen et al.,
1996). Herring fisheries target aggregations of spawning or feeding adults (>19cm) which
tend to be spatially segregated from immature fish (Clarke et al., 2010; O'Donnell et al.,
2015). It is plausible that probability of capture for mature herring on the spawning grounds
530 is not strongly size dependant. However, experimental investigation of gear selectivity at
the fishing grounds would be needed to confirm this. The possible contribution of fishing to
declines in size-at-age of Celtic Sea herring could be further interrogated using the approach
of Swain et al. (2007) who related back-calculated lengths-at-age to cohort specific estimates
of fisheries induced selection while controlling for temperature and density related changes
535 in growth.

It is possible that the decline in growth of herring in the Celtic Sea is symptomatic of
broad-scale changes in the pelagic ecosystem. Clupeid fisheries are characterised by variable
abundance. In the past, cyclical changes in herring populations have coincided with alter-

nate changes in sardine (*Sardina pilchardus*) populations, apparently in response to climatic
 540 fluctuations and associated ecosystem change (Southward et al., 1988; Alheit et al., 2014).
 Although sardines occur in the Celtic Sea and are commercially exploited, the stock in this
 area is not assessed and there is no biological data available from scientific surveys or the
 commercial catch (Marine Institute, 2016; ICES, 2017). Available data for adjacent areas do
 indicate recent changes in the growth of sardine. Trends in the mean weight-at-age of sardine
 545 from commercial catches southern Bay of Biscay and Iberian coast (ICES Divisions 8c and
 9a) show an increase in growth since 1990 which coincides with the decrease in growth of
 Celtic Sea herring during the same period (ICES, 2016, 2017) Figure 10. In contrast, mean
 weight-at-age of sardine in survey catches from the rest of the Bay of Biscay (ICES Divisions
 8a, b and d) have declined since 2000 (ICES, 2016, 2017). Without extended growth time-
 550 series, it is not possible to establish if these trends reflect a synchronous response to climatic
 drivers. However, the patterns indicate that closer monitoring of the distribution, growth
 and population dynamics of pelagic clupeids in the Celtic Sea is warranted, particularly as
 new fisheries develop.

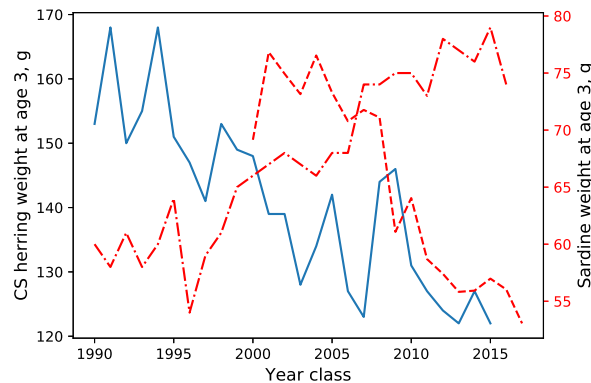


Figure 10: Mean weight-at-age 3 of Celtic sea herring (blue solid line) and sardine in divisions 8c, 9a (red dash-dot line) and divisions 8a,b,d (red dashed line)

In summary, the results of the analysis indicate that the declines in size-at-age of Celtic
 555 Sea herring since the 1980's are most strongly associated with increasing sea temperatures as
 a consequence of climate change and with a positive AMO index. The more stable size-at-
 age trends in Northwest herring may reflect the stock's more northerly distribution and lower
 exposure to metabolically sub-optimal temperatures. The gradient boosting regression tree

approach proved effective at identifying the most influential drivers of variability, detecting a
560 non-linear step change in a biological response to an environmental variable and examining
interactions between explanatory variables.

Analysis was performed:

Platform version: Linux-4.4.0-31-generic-x86i_64-with-debian-stretch-sid

Python version 2.7.11 |Anaconda 2.4.1 (64-bit)| (default, Dec 6 2015, 18:08:32)

565 [GCC 4.4.7 20120313 (Red Hat 4.4.7-1)]

Pandas version: 0.17.1

Matplotlib version: 1.5.1

sklearn version 0.17

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