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Effect of environmental variability on the Atlantic Mackerel (*Scomber scombrus* L.) stock dynamics in the Gulf of St. Lawrence

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

The objective of this study was to assess the effect of environmental variability on the dynamics of the Atlantic mackerel (*Scomber scombrus* L.) stock in the Gulf of St. Lawrence (GSL). We first describe the dominant modes of physical and biological (zooplankton) environmental variability using Principal Components Analyses (PCA) of 40 variables and identify potential environmental regimes during the 1990-2012 period. Two principal modes of variability were identified, a long-term mode (15-20 years) associated with a warming of the GSL and a second mode at higher frequency (5-10 years) describing alternating cold and warm periods. The results also identified a strong link between variations in physical environmental conditions and the abundance, composition and seasonality of zooplankton species known to be important for Atlantic mackerel larvae, juveniles and adults. Moreover, sudden changes in physical environmental conditions and zooplankton dynamics in 1996-1997, 2004 and from 2009 to 2012 were revealed by the analyses. Second, a set of Generalized Additive Models (GAM) was developed to explore the role that these variations in bottom-up processes could play in the control of Atlantic mackerel condition (Fulton's K) and recruitment success (Rs). Optimal GAM including variations in abundance, species composition and phenology of key copepod species such as *Calanus finmarchicus*, *Pseudocalanus* spp. and *Temora longicornis* improved models performance by 40-50% relative to those considering only physical environmental conditions, illustrating the key role of zooplankton dynamics in controlling variations in K and Rs and supporting the match-mismatch hypothesis. Finally, our study showed that large variations in Rs could be caused by varying environmental conditions independently of spawning stock biomass, and they should be considered in the development and application of an ecosystem-based approach to Atlantic mackerel stock management.

Effet des variations environnementales sur la dynamique du stock du maquereau bleu (*Scomber scombrus* L.) du golfe du Saint-Laurent

RÉSUMÉ

Cette étude avait pour objectif d'évaluer l'effet des variations environnementales sur la dynamique du stock du maquereau bleu (*Scomber scombrus* L.) du golfe du Saint-Laurent (GSL). Nous avons décrit d'abord les différents modes de variations de l'environnement physique et biologique à l'aide d'analyses en composantes principales (PCA) appliquées à 40 variables, et identifié des régimes environnementaux distincts durant la période 1990 à 2012. Deux modes principaux de variabilité ont été identifiés, le premier exprimant un réchauffement à long-terme (15-20) du GSL, et un deuxième mode exprimant une alternance à plus haute fréquence (5-10 ans) d'années chaude et froides. Les résultats illustrent également des liens forts entre les variations des conditions physiques et l'abondance, la composition et la phénologie d'espèces de zooplancton importantes pour les larves, les juvéniles et les adultes du maquereau bleu. De plus, des changements abrupts des conditions physiques et de la dynamique du zooplancton ont été identifiés en 1996-1997, 2004 et de 2009 à 2012. En second lieu, un ensemble de Modèles Additifs Généralisés (GAM) a été développé pour décrire le rôle que pourrait jouer les variations interannuelles des processus ascendants décrits ci-dessus dans le contrôle des variations des indices de condition (K de Fulton) et le succès du recrutement du maquereau bleu (Rs). Les GAM considérant les variations de l'abondance, de la composition et de la phénologie d'espèces de copépodes tels que *Calanus finmarchicus*, *Pseudocalanus* spp. et *Temora longicornis* améliorent la performance des modèles de 40-50% par rapport aux modèles ne considérant que l'environnement physique, démontrant l'importance de la dynamique du zooplancton dans le contrôle de K et de Rs et supportant l'hypothèse du "match-mismatch". Finalement, notre étude démontre que de fortes variations du Rs pourraient être déterminées par les fluctuations environnementales indépendamment de la biomasse reproductrice, indiquant que ces effets devraient être considérés dans le développement et l'application d'une approche écosystémique de la gestion du stock de maquereau bleu du GSL.

INTRODUCTION

The Gulf of St. Lawrence (GSL) is the southernmost region with a seasonal ice cover in the northwest Atlantic. It is under the combined influence of the important freshwater runoff from the St. Lawrence River and oceanic Arctic and Atlantic water from the adjacent Labrador and Newfoundland Shelf and its deep slope. In summertime, the water column in the GSL consists of three distinct layers: the surface layer, the cold intermediate layer (CIL), and a deeper water layer. Surface temperatures typically reach maximum values from mid-July to mid-August (Galbraith et al. 2012). During winter, there are only two layers as the surface layer thickens mostly from wind-driven mixing prior to ice formation, and encompasses the CIL (Galbraith 2006). The surface winter layer is near freezing (-1.8 to 0ºC) and extends to an average depth of 75 m and up to 150 m in some places (Galbraith 2006). During spring, surface warming, sea-ice melt waters, and continental runoff produce a lower-salinity and higher-temperature surface layer, below which cold waters from the previous winter are partly isolated from the atmosphere and form the summer CIL. This layer will persist until the next winter, gradually warming up and deepening during summer (Gilbert and Pettigrew 1997; Cyr et al. 2011). The deeper water layer (>150 m) below the CIL originates at the entrance of the Laurentian Channel at the continental shelf and circulates towards the heads of the deep channels without much exchange with the upper layers. The layer from 150 to 540 m is characterized by temperatures between 1 and >7°C and salinities between 32.5 and 35. Interdecadal changes in temperature and salinity of the deep waters entering the GSL at the continental shelf are related to the varying proportion of the source cold–fresh Labrador Current water and warm–salty slope water (Gilbert et al. 2004).

The zooplankton biomass in the GSL is dominated by *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus*, these taxa representing also a dominant component of the total zooplankton abundance during their population growth period in spring and summer while *Oithona* spp and other small taxa dominates numerically in fall and winter (de Lafontaine et al. 1991, Plourde et al. 2002, Plourde et al. 2014). In general, *Calanus* species are transported to shallower areas (depth < 100 m) such as the southern GSL in spring and early summer from the deeper (depth > 100 m) overwintering habitat during their active growth period in surface layers (de Lafontaine 1994, Maps et al. 2011), while smaller species such as *Pseudocalanus* spp and the neritic *Temora longicornis* are likely maintaining local populations (de Lafontaine et al. 1991). Important interannual variations in abundance and dynamics of key species and in zooplankton community structure have been described in different areas of the GSL (Plourde et al. 2001, 2002, 2003, Castonguay et al. 2008, Plourde et al. 2014). However, a comprehensive description of the temporal variability of zooplankton community dynamics and their links to the physical and biological environmental forcing is still lacking. Considering the significant warming trend and the diminishing duration and volume of sea ice observed in the GSL over the last two decades (Galbraith et al. 2014), one must expect profound changes in broad scale zooplankton dynamics and production regime in the region.

The Atlantic mackerel (*Scomber scombrus* L., hereafter mackerel), is an important pelagic fish component of the GSL ecosystem, the southern GSL being historically the main spawning area of the stock (Grégoire et al. 2014). As in many pelagic fish species, the recruitment pattern of mackerel is characterised by the sporadic occurrence of large year-classes (“boomer years”) dominating the stock and the fisheries for several years (Grégoire et al. 2014). Adult mackerel are mainly planktivorous (Grégoire and Castonguay 1989, Darbyson et al. 2003), and several studies conducted in the southern GSL have shown the prominent role of zooplankton in determining the feeding success and growth of mackerel larvae (Ringuette et al. 2002, Castonguay et al. 2008, Robert et al. 2009). These studies identified early stages of *C. finmarchicus*, *Pseudocalanus* spp. and *T. longicornis* as key preys of mackerel larvae, and documented the effect of variations in prey abundance and production on their feeding success, growth, survival and potentially on the recruitment strength of the stock (Runge et al. 1999, Ringuette et al. 2002, Castonguay et al. 2008, Robert et al. 2009). Nonetheless, the mechanism linking mackerel stock dynamics and environment variability are still poorly understood.

The main objective of this study was to assess the effect of environmental variability on the characteristics of the mackerel stock in the GSL. Our analyses were performed within the framework of zooplankton representing a strong link between physical environmental forcing and fish stock dynamics through the match-mismatch hypothesis in which prey availability is function of both zooplankton abundance and timing (Runge 1988, Cushing 1990). First, we characterized the long-term variability of the physical and biological (zooplankton) oceanographic conditions in the GSL using Principal Components Analyses (PCA) to extract the dominant modes of environmental variability and identify potential environmental regimes. Second, we developed a set of Generalized Additive Models (GAM) to identify and quantify the role that variations in bottom-up processes could play in the control of mackerel stock dynamics. Finally, we discuss our results in the context of the general knowledge of the role of abiotic and biotic (zooplankton) environmental conditions on mackerel recruitment, individual condition and overall stock productivity.

METHODS

DATA SOURCES

Abiotic environment and zooplankton indices

A set of 40 variables was assembled to describe the long-term changes in oceanographic conditions in the GSL (see Plourde et al. 2013 for details, Table 1, Appendix 1). Abiotic environmental variables included large-scale climate indices and physical parameters measured at discrete sampling stations over the period considered. Large-scale climate indices (freshwater discharge from the St. Lawrence River, GSL deep water salinity, and Slope Labrador Current volume transport) were used as indicators of the influence of broad-scale atmospheric and oceanographic systems in the region. Physical data collected on an annual basis in the GSL were used to elaborate a set of composite indices in the estuary (SLE), western (wGSL), eastern (eGSL) and the southern (sGSL) regions (see Galbraith et al. 2014). We selected composite indices quantifying the variability in upper (0-150 m) and deep (>150 m) layer water temperature, as well as variations in deep water salinity and winter sea ice using an index combining the seasonal maximum volume and the timing of melt (Plourde et al. 2013).

Variations in biological environmental conditions were described with zooplankton indices extracted from the Rimouski station data series. This site was selected because it represents the longest zooplankton time series in the region (1992-2012). The station is sampled on a quasi-weekly basis from spring to late fall and interannual variations in key zooplankton abundance indices are generally coherent among SLE, wGSL, and sGSL (Plourde et al. 2001, 2014). Two types of zooplankton indices were used. First, mean annual abundance of dominant copepod species/taxa, krill egg abundance (indices of krill abundance, Plourde et al. 2011) and small gelatinous organisms were included (see Table 1). These species/taxa are dominated by copepods, including species for which early stages are important for the feeding of early mackerel larvae and potentially for their growth/survival (Ringuette et al. 2002, Castonguay et al. 2008; Robert et al. 2008, 2009). Late stages of copepods such as *Calanus* species also represent the dominant component in the diet of juvenile and adult mackerel (Grégoire et Castonguay 1989, Darbyson et al. 2003). Other zooplankton taxa could be indicative of variations in environmental forcing in the GSL. The annual average of chlorophyll *a* biomass at Rimouski station was also included in the analyses (Table 1). Second, we developed a set of indices aimed at quantifying changes in the phenology (timing of population development) of copepods using dominant *Calanus* species as indicators (Table 1). We used the maximum abundance of CI-III in early summer and fall as indicative of the timing of the first (G_1) and second (G_2) generations of *C. finmarchicus* as well as their relative importance as indicative of a change in their seasonal production. The relative composition of different overwintering stages of *C. glacialis* and *C. hyperboreus* from August to December was used to describe changes in the phenology of these arctic species in the region.

Atlantic Mackerel stock indices

Abundance indices of the mackerel stock in the GSL from 1971 to 2012 were taken from Grégoire et al. (2013). The spawning stock biomass (SSB), the total biomass, the abundance at age 1 (recruits) used to compute recruitment success (R_s) were obtained from the Sequential Population Analysis (SPA) performed using biological and fishing data obtained on a yearly basis. R_s represented the Ln transformed ratio of the number (× 000') of age 1 individuals during $year_x$ over mature fish during $year_{x-1}$ (Ottersen et al. 2013).

We described variations in individual condition using the Fulton' index (K) (Ricker 1980) determined on fishes captured by commercial fishing (Grégoire et al. 2013). K was averaged over all cohorts to obtain a single population index of the seasonal minimum in condition during spawning in June (K_june) and of the gain in condition during the fattening period using the ratio in K between September and June (K_sept/june).

Competitors' indices

Other planktivorous fish species could compete with mackerel for zooplankton prey and represent a predation threat for early mackerel larvae. Atlantic herring (*Clupea harengus harengus* L.) is an important component of the ecosystem in the southern GSL with feeding preferences overlapping significantly with mackerel (Darbyson et al. 2003). We explored the effect of potential competition for food or predation mortality on early mackerel larvae by including the SSB of spring and fall spawning stocks of Atlantic herring in the southern GSL (NAFO Division 4T) (Table 1) (Leblanc et al. 2012).

DATA ANALYSES

Data standardization

Time series of all environmental and zooplankton variables were standardized by using their annual anomaly. These anomalies were calculated as the difference between the variable's annual value and the variable's average for the reference period; this number was then divided by the reference period's standard deviation. For physical data, anomalies were calculated from the complete time series (1971-2012). For zooplankton, anomalies were calculated for the period the data were available (1992-2012). This approach provided a mean of integrating variables showing different units such as temperature, salinity and ice cover, ensuring with a similar weight in analyses.

Absolute values of the different parameters of the mackerel stock dynamics and Atlantic herring (predator of mackerel larvae, competitors for zooplankton prey) biomass were used.

Principal Component Analyses (PCA)

Our first objective was to describe environmental variability in the GSL and develop a set of indices integrating various environmental indices. Principal Components Analysis (PCA) was chosen in order to reduce this high number of variables to a set of uncorrelated composite variables, and extract the dominant patterns of environmental variability (see Hare and Mantua 2000). Only annual standardized anomalies of the different variables were used in PCA analyses. PCA were run separately for the sets of physical, plankton abundance and zooplankton phenology indices (Table 2). Correlation coefficients were computed among these different sets of indices for the three dominant PCA axes to describe effects of variations in physical environmental conditions on zooplankton abundance and composition and *Calanus* species phenology.

Serial *t*-test Analysis for Regime Shift identification (STARS)

We described the trajectories of different time series by identifying potential shifts and environmental regimes using sequential *t*-test analysis of regime shifts (STARS) (Rodionov 2004). A shift is defined as a sudden transition between two periods (regimes) showing significantly distinct environmental characteristics (de Young et al. 2004). The STARS method determines whether a new observation in a time series represents a statistically significant deviation from the mean value of a regime, and then checks for likely regime shifts between different periods by means of a sequential *t*-test analysis (Rodionov 2004). Temporal autocorrelation was evaluated with the first order autoregressive model (AR1) using the ordinary least square method (OLS) and accounted for before the regime shift detection method was applied (Rodionov 2006). Because we did not know the temporal structure of our time series before the analyses, a conservative cut-off length of 5 years was used in order to detect all potential environmental regimes and shifts. A sensitivity analysis of STARS to variations in cut-off length, Huber parameter (weight given to extreme values in the time series) and correction for temporal autocorrelation are presented in Plourde et al. (2013).

Generalized Additive Models

Biological responses to the environment tend to be non-linear. Bell-shape and skewed responses cannot be capture by Generalized linear models (GLMs), which are limited to *a priori* defined relationships (Yee and Mitchell 1991). GAMs combine parametric and non-parametric terms and are more data-driven than GLMs (Yee and Mitchell 1991), which explain their increasing popularity in fisheries sciences (e.g., Daskalov 1999, Cardinale and Arrhenius 2000, Beare and Reid 2002, Litzow et al. 2014). A set of GAMs was produced in order to quantify the role of bottom-up (physical and biological oceanographic conditions) and top-down (competition for food or predation on larvae) processes controlling the mackerel stock dynamics; i.e., K_june, K_sept/june and R_s. GAMs followed the general formulation:

$$E[y] = a + s(V_i) + \ldots + s(V_n) + \varepsilon$$

where E[y] is the expected value of the response (dependent) variable y, here K_june, K_sept/june or R_s, *a* is the intercept parametric term which represents the mean of the response variable, *s* is the smoothing function based on the thin plate regression spline, V_i are the independent variables and ε the error term. The residuals distribution fitted a Gaussian family with an identity link function. GAMs were fitted in R (v.2.15.2; R Development Core Team 2012) using the "mgcv" package (v.1.7-22, Wood 2012).

We restricted the number of variables and the number of degrees of freedom (edf ≤ 3, k=3) to minimize model over-fitting. Independent variables were selected based on environmental conditions and processes known or hypothesized to influence the characteristics of the fish stock. For each stock variable, we first built a basic GAM using only variables considered in the mackerel stock assessment (R_s, K, SSB). We then applied a forward selection approach to test the effect of PCA axis describing environmental variability. The forward selection was chosen over backward selection because the number of observations (22 to 42) limits the number of variables that can be added to the models. The best models were selected on the basis of the gain in deviance explained (%Dev) relative to the basic model while minimizing the Generalized Cross Validation Criterion (GCV). The GCV behaves and is interpreted as the Akaike Information Criterion (AIC). AIC and GCV are measures of the fit and parsimony of models. Each PCA axis was tested independently to isolate its effect and PCA axes were consecutively added until the Generalized Cross Validation (GCV) increased. GAMs have the same restrictions as linear models for correlated variables and pairs of independent variables showing a correlation coefficient > 0.5 were not used in models. Interactions were considered in model selection and defined by the tensor product smooth (Wood 2006a). The analysis of variance based on the F statistic was used to verify the null hypothesis that the additive structure (without interactions) is better than a model formulated with interactions (Wood 2006b). When the residual deviance was not different between the two models, the model with the additive structure was selected even if its GCV was higher than the model with interactions. This test ensured that the most parsimonious model was selected.

The effect of physical environment conditions (Env) was tested for mackerel population dynamics parameters (K_june, K_sept/june, R_s) for the long (1971-2012) time series because temperature could have (1) a direct effect on individuals physiology and/or (2) an indirect effect mediated by changes in zooplankton (prey) dynamics (Runge 1988). Models constructed with the short time series (1992-2012) allowed the forward selection and comparisons of effect of physical environmental conditions (Env), zooplankton abundance (Plank) and phenology (Pheno).

GAMs with K_june or K_sept/june as independent variable always included total mackerel biomass to consider a possible density-dependent process (basic model). Total biomass was preferred to SSB because cannibalism is common in this species as early as during the late larval stage (Fortier and Villeneuve 1996). Models with K_june were built in order to explore environmental effects of the condition during spawning (seasonal minimum). The effect of environmental variability on K_sept/june was also tested to explain interannual variations in the ‘gain’ in condition (= fattening) over summer. Different combination of Plank and Pheno PCAs were included in order to consider the effect of both food quantity and seasonality.

The basic GAM with R_s as the dependent variable included total biomass because of the potential for within stock density-dependent effects. Because the link between larval feeding success, growth and survival with stock recruitment implies a good timing between food availability and fish larvae peak abundance (match-mismatch, Cushing 1990), different combinations of Plank and Pheno PCAs were considered in each GAMs unless they showed significant correlation between them (Table 3). The potential predatory impact of other planktivorous fishes was considered by testing the effect of herring biomass.

Conditions of application were examined graphically for selected models. We further verified the temporal linear trends of model residuals as function of year using the *gls* function in the *nlme* package (v.3.1-105) in R. Temporal autocorrelation in residuals was tested by the *acf* function implemented in the stats package (2.15.2, R Core Team 2012).

Selected models were validated against models generated with random data. Environmental variables were resampled 1,000 times before calculating principal components (PC score). The generated PCAs were integrated in the models at each iteration and the deviance explained was calculated. A distribution of the deviance explained was plotted to verify if the deviance explained by the selected model is at the higher end of the distribution. Principal components analysis used in the bootstrap loop are computed in the *stats* package in R. All selected models significantly explained more deviance than random data ($p < 0.05$).

RESULTS

PHYSICAL AND BIOLOGICAL ENVIRONEMENTAL VARIABILITY: 1990-2012

The three dominant PCA axes of the physical (Env), zooplankton abundance/composition (Plank) and zooplankton phenology (Pheno) indices revealed several modes of variability (Fig. 1). The PCA1 explained 42-57% of the variability and mainly described long-term changes, and regime shifts in physical conditions (1997, 2011), zooplankton abundance/composition (2004, 2009) and phenology (1997, 2004) (Fig. 1). Figure 2 presents the loadings of the different indices of each PCA. The increase in Env_PCA1 score was mainly driven by the warming of upper and deep waters and by an earlier melt of a diminishing sea-ice cover in the GSL (Fig. 2). The increase in Plank_PCA1 score corresponded to a decrease in chlorophyll *a* biomass and abundance of arctic/cold water copepod species (*C. glacialis*, *M. longa*) accompanied by an increase of the large bodied and lipid-rich *C. hyperboreus* and other small copepod species, including *Pseudocalanus* spp. and *T. longicornis*. (Fig. 2). The increase in Pheno_PCA1 score were mainly driven by an earlier timing of recruitment of G_1 and a smaller body size of *C. finmarchicus* C6f, but also by a positive trend in the importance of *C. finmarchicus* G_2 relative to the G_1 (Fig. 2). A marked decrease in the proportion of C6f in the overwintering population of *C. hyperboreus* was also associated with the increase of Pheno_PCA1.

PCA2s (16-20%) and PCA3s (9-17%) explained a significant proportion of the variability and described variations in environmental conditions occurring at higher frequency with very few regime shifts (Fig. 1). Env_PCA2 and Env_PCA3 mainly represented high frequency variability in sea ice cover, water temperature and in St. Lawrence River freshwater runoff, with a significant decrease in Env_PCA2 score in 2009 reflecting an abrupt decrease of the ice index and an increase in freshwater runoff (Fig. 1, 2). Variability in Plank_PCA2 was caused by a 7-10 year cycle between periods of high (low) abundance of *C. finmarchicus*, *C. hyperboreus* and krill eggs opposed to low (high) abundance of smaller and more neritic taxa such as *Pseudocalanus* spp.and *Acartia*. sp. High frequency variability of *Calanus* species, the small and neritic *T. longicornis* and the mid-water species *Scolecithricella* sp. were the main determinant of Plank_PCA3 values (Fig. 1, 2). Finally, the relative stage proportion of *C. hyperboreus* and *C. glacialis* overwintering stages and positive anomalies in the timing of *C. finmarchicus* G_2 recruitment contributed the most to the pattern of variability of Pheno_PCA2 and Pheno_PCA3 respectively (regime shifts in 1997 and 2009) (Fig. 1, 2).

Regime shifts in physical and biological environmental conditions are synthetized in Figure 3. Abrupt changes in physical environmental conditions (Env_PCAs) accompanied by regime shifts in zooplankton abundance/composition and/or phenology occurred in 1995-1996 and from 2009 to 2012 (Fig. 3). Changes in zooplankton PCAs identified by STARS in 2004 appeared to reflect more gradual changes in oceanographic conditions than a response to a true regime shift (Fig. 1, 3).

A correlation analysis among PCAs previously described indicates that zooplankton dynamics responded to changes in physical oceanographic conditions occurring at different temporal scales (Table 2). A highly significant positive correlation was observed between Env_PCA1 (higher temperature, saltier deep water and less ice) and Plank_PCA1 (lower abundance of cold water species and higher abundance of *C. hyperboreus* and small copepod species) or Pheno_PCA1 (earlier recruitment of G_1 and smaller size of *C. finmarchicus*). Moreover, Plank_PCA2 was negatively correlated with Env_PCA2 (Table 2), suggesting a potential relationship between high abundance of *C. finmarchicus* and *C. hyperboreus* with cold upper layer water, sea-ice index above normal, a warmer and saltier deep water layer, and a lower freshwater runoff from the St. Lawrence River (Fig.1, Fig. 2).

PHYSICS, COMPETITORS, AND MACKEREL STOCK VARIABILITY: 1971-2012

The STARS analysis of the PCAs scores describing the dominant modes of physical environmental conditions (Env) since 1971 revealed marked changes in addition to those described for 1990-2012 (Fig. 4). Env_PCA1 scores were greater than normal (high temperature, low ice conditions) from 1979 to 1985, a period intercalated between years with lower than normal scores (colder water and greater ice index) in 1971-1978 and 1985-1991 (Fig. 2, Fig. 4). A decrease in deep water temperature and salinity, an increase in the St. Lawrence River freshwater runoff, and a decrease in ice cover drove the pattern of Env_PCA2 scores between a period with loadings above the normal (1979-1991: ice cover and deep water temperature/salinity above normal, freshwater runoff below normal) and years (2010-2012) showing the lowest PCA loadings of the time series (ice cover and deep water temperature/salinity below normal, greater freshwater runoff) (Fig. 2, Fig. 4). Env_PCA3 mainly described three regimes driven by variations in freshwater runoff (Fig. 2, Fig. 4).

The STARS applied on time series of Atlantic herring biomass (1971-2012) identified significant changes in potential competitors of mackerel. A collapse of spring spawning herring occurred in 1997 after 15 years of high biomass (Fig. 4). After a period of historically low biomass (1978-1982), fall spawning herring showed two periods of above normal biomass (1983-1994, 2003-2009) separated by years during which the stock was near normal (Fig. 4). Overall, total Atlantic herring biomass showed a stepwise decline driven respectively by the spring (1996) and fall (2010) components (Fig. 4).

Mackerel stock indices showed a relatively stable and long period of high total biomass (and SSB) from 1971 to the mid 1990’s (Fig. 5). SSB sharply decreased in 1992, increased again following the 1999 recruitment event and decreased again from 2007 to 2012 (Fig. 5). No significant regime shift was identified by STARS for R_s characterized by three exceptional recruitment events (1974, 1982, 1999). R_s above the normal were also observed in 2003, 2005 and 2008 (Fig. 5). K during spawning (K_june) significantly decreased in 1985 after a period with high values; the increase observed at the end of the time series (2009) did suggest initiation of a new period of greater K during spawning (Fig. 5). K_sept/june varied over 5-10 year periods between 1983 and 2012 (Fig. 5). Note that the abrupt increase (1986) and decrease (2011) identified by STAR at the beginning or at the end of the time series should be considered with caution because they are based on only 2-3 years of data.

ENVIRONMENTAL EFFECT ON MACKEREL STOCK DYNAMICS

Details of all GAMs investigated and results of the final models with the lowest GCV and greatest gain in deviance explained relative to the basic model are given in Tables 3-4. Descriptions of the best models are provided and illustrated in Figures 6-8. Details about environmental and zooplankton indices strongly associated to PCAs (Fig. 2) and known/potentially important for mackerel were also provided.

Individual condition (K)

The best model for K_june for the 1990-2012 period explained 65.3% of the deviance, a gain of 43.5% relative to the basic run (21.8%) (Table 3). The most significant explanatory variables were Plank_PCA1, followed by Pheno_PCA2 and mackerel total biomass. K_june positively responded to the increase in Plank_PCA1 (increase of *C. hyperboreus, T. longicornis and Pseudocalanus* spp.), to Pheno_PCA2 (phenology of *Calanus* species during spring), and was negatively related to mackerel total biomass (Fig. 6).

Results of models with K_sept/june, representing the gain in K during feeding in summer, were markedly different than those obtained for K_june (Table 3). The best model explained 57% of the deviance in comparison to 10.9% for the basic run considering only mackerel biomass (effect non-significant, Table 3). K_sept/june was negatively affected by an increase in Plank_PCA1 (increase of *C. hyperboreus, T. longicornis* and *Pseudocalanus* spp.) but positively influenced by Pheno_PCA3 (later timing of *C. finmarchicus* G_2 recruitment in summer) (Fig. 7). Although marginally not significant, Plank_PCA2 was selected in the model with its slight positive effect (Fig. 7). Therefore, the model showed that *Pseudocalanus* spp. and *T. longicornis* abundance and late production of *C. finmarchicus* in summer determined the gain in condition (fattening) of mackerel between June and September.

Recruitment (R_s)

The basic models considering only the effect of total biomass on R_s explained the same percentage of deviance for the 1973-2011 and 1990-2011 periods (28.0% and 27.9%) (Table 4). When 2012 was included, the deviance explained by the basic model decreased to 12.4% with a much higher GCV (Table 4). The best model was for the 1990-2011 period and was selected on the basis of ecological significance in addition to our quantitative criteria. It explained 77.6% of the deviance, a gain of 49.7% relative to the basic run (Table 4). Overall, R_s was negatively associated to total mackerel biomass and positively to Env_PCA2 score (low St. Lawrence River freshwater runoff, warm deep water, cold upper layer water and high ice index) (Fig. 8). The third variable selected was Pheno_PCA2 (positive score indicating an earlier development of *C. finmarchicus* G_1 and G_2) showing a dome-shape effect, suggesting that mackerel R_s would not be favoured by neither a very late development nor an extremely early development of *C. finmarchicus* (Fig. 8). The significant and negative correlation between Env_PCA2 and Plank_PCA2 scores suggests that Env_PCA2 could represent a proxy of variations in zooplankton occurring at the same temporal scale, with high abundance of *C. finmarchicus*, *C. hyperboreus* and krill eggs associated with positive Env_PCA scores (Table 2, Fig. 2). Therefore, the best model suggested that R_s was favoured by a combination of high abundance and adequate timing of *C. finmarchicus* occurring at low-to-moderate mackerel total biomass.

The Atlantic herring biomass indices did show a small negative effect on mackerel R_s, but the models including these variables were not selected based on a high GCV and a lower deviance explained (Table 4). The best model obtained when considering 2012 explained 75% of the deviance, and included K in September (Table 4).

Performance of the selected models

The performance of the different models (GAMs) is illustrated in Figure 9. Overall, basic models considering only the effect of SSB did a poor job at predicting long-term and interannual variations of individual conditions in June (seasonal minimum, K_june) or of the gain in condition during summer (K_sept/june) (Fig. 9A-B). For K_june, the selected model assessing the influence of variations in zooplankton abundance, composition and phenology in addition to SSB predicted well the long-term positive trends observed from the early 1990s to the late 2010s as well as the marked interannual variations typical of the time series (Fig. 9A). Similarly, the selected model based on variation in zooplankton dynamics predicted well the 5-6 years cycle in K_sept/june observed from 1990 to 2012 in addition to the sharp decrease occurring from 2003 to 2013 (Fig. 9B).

The basic model relating R_s to SSB predicted the long-term increase in R_s apparent in the observations from 1992 to 2000 and associated to a long-term decrease in SSB initiated during the early 1990s (Fig. 5, Fig. 9C).The selected model considering the effect of variations in zooplankton abundance, composition and phenology did better predicting high-frequency variations in R_s, including the greater values observed from 1995 to 1997 relative to the early 1990s, and the high R_s occurring in 1999 (the last boomer year) and in 2008 (Fig. 9C). On a shorter timescale, R_s varied around the long-term average from 2002 to 2012 with no evidence of a consistent trend (Fig. 9C).

DISCUSSION

Our analyses revealed that variations in physical environmental conditions strongly influence zooplankton abundance, composition and phenology in the GSL at different temporal scales. These variations in physical and biological environmental conditions had significant effects on the individual condition and recruitment success of Atlantic mackerel stock, with variations in zooplankton dynamics showing the stronger impacts on stock parameters. Therefore, variations in bottom-up processes regulating the zooplankton dynamics were important in determining key individual and population parameters of the mackerel stock in addition to the intrinsic stock dynamics (SSB).

PHISICAL AND BIOLOGICAL ENVIRONMENTAL VARIABILITY

Our study provides the first integrated analyses and description of the long-term variations of the environment at the basis of the food web in the GSL by considering indices of physical environmental conditions and zooplankton community structure and dynamics. Principal Components Analysis (PCA) identified different modes of environmental variability with significant correlations between physical and zooplankton PCAs (Fig. 1-2, Table 2). The first PCAs revealed a strong bottom-up effect of a long-term (20 years) warming of upper and deep waters and a decreasing ice coverage resulting in (1) a decrease in abundance of cold/arctic copepod species, (2) an increase in abundance of large-bodied and lipid-rich *C. hyperboreus* and smaller calanoids (*Pseudocalanus* spp., *T. longicornis*), and (3) a change in the phenology of *Calanus* species. The second PCAs described variations occurring at a higher frequency (10-

12 years) of *Calanus* and krill (egg indices) populations (abundance, phenology) opposite to those of smaller copepod species and correlated to variations in sea ice dynamics, water temperature and freshwater runoff. The third PCAs described short-term (5-7 years) variations in abundance of various copepod species and in *Calanus* spp. phenology. These changes in zooplankton community composition and dynamics clearly show that the planktonic production in the GSL is highly sensitive to variations in physical environmental conditions at various temporal scales. Our results suggest that broad scale bottom-up processes dominated the regulation of zooplankton production during the 1990-2012 period.

The three *Calanus* species showed markedly different abundance patterns while all exhibiting phenology changes coherent with a habitat getting warmer. From 1992 to 2012, *C. glacialis* (decrease) and *C. hyperboreus* (increase) showed opposite trends in abundance in response to the warming of upper and deep water layer, whereas abundance of *C. finmarchicus* varied on shorter scales without any evidence for a long-term trend. The environmental conditions prevailing in the GSL and species-specific optimal temperature requirements and life cycle strategy could explain these patterns. The GSL represents the southernmost area with a seasonal sea-ice cover typical of the core habitat of the arctic *C. glacialis*, whereas the temperature regime in the region is either at the higher limit or well within the range of optimal conditions for *C. glacialis* and *C. finmarchicus,* respectively (Helaouët and Beaugrand 2007, Chust et al. 2014). Therefore, *C. glacialis* would be more affected by a warming of the GSL than its congener *C. finmarchicus*. The increase in abundance of the large-bodied *C. hyperboreus*, considered as an arctic species, is somewhat surprising. However, *C. hyperboreus* is more abundant in the GSL than on the adjacent Newfoundland and Scotian shelves (Plourde et al. 2014), probably benefiting from the presence of deep overwintering habitats resembling those along the slope of the Labrador and Newfoundland Shelf where the species is abundant (Head et al. 2003). Due to its larger size, *C. hyperboreus* could potentially have a better capability to overwinter in non-arctic (warmer) regions than *C. glacialis* (Maps et al. 2014). Finally, the change in *C. hyperboreus* phenology observed in our study suggests a switch from a predominant 2-3 year life cycle during cold environmental regimes (see Plourde et al. 2003) to a shorter generation time during warmer periods, potentially resulting in a greater survival and abundance. The phenology of *C. finmarchicus* was also markedly affected by the variations in temperature and sea-ice dynamics with notable changes of the timing and the relative importance of G_1 (spring-summer) and G_2 (fall). Temperature has a well-known effect on the physiology of *Calanus* species, whereas sea-ice dynamics plays a primary role in the control of the timing of onset and amplitude of the spring phytoplankton blooms in seasonally ice-covered regions (Wu et al. 2007).

The warm conditions observed in 2012 across the northwestern North Atlantic, from the Gulf of Maine to the Labrador Shelf, were considered as ‘extreme’ with potential impacts on the northwest Atlantic Shelf ecosystems (Galbraith et al. 2014). In the GSL, these ‘extreme’ warm conditions followed two years (2010-2011) during which water temperature was well above the normal (Fig. 4, Galbraith et al. 2014). However, examination of the first PCA scores obtained from the analysis of the 1971-2012 time series revealed that environmental conditions highly similar to those observed in 2010, 2011, and 2012 occurred 32 years ago in 1980 and 1981 (Fig. 4). Therefore, the warm environmental conditions of 2012 could be considered as extreme but not unique. These two warm ‘events’ were separated by two periods (1984-1990, 1991-1995) characterised by much colder conditions, suggesting the potential for alternating warm and cold environmental conditions overlying a long-term warming trend (Galbraith et al. 2012). Interestingly, water temperature and sea-ice cover reverted to near normal values in 2013, but a few more years of monitoring will be necessary to better characterize the ‘extreme warm event’ of 2012 in its historical context (Galbraith et al. 2014). Consequently, the conditions observed in 2012 (and their effects on the ecosystem) should be considered cautiously if used as a possible window to predict the impact of climate warming on the GSL ecosystem in the future.

The STARS analysis of dominant PCA axes obtained from our set of indices identified several regime shifts in physical environmental conditions and zooplankton dynamics (Fig. 3). Most notably, significant changes occurred in 1996 and 1997 whereas the 2009-2012 period was characterized by several significant changes of various intensity, indicating that the ‘warm’ conditions in 2012 were the culminating point of a warmer event initiated in 2010. However, STARS results should be interpreted with caution. STARS can falsely identify different ‘regimes’ in a sufficiently long time series that is characterised by a gradual long-term trend. Consequently, our regime shift analyses could have identified true regime shift as well as periods with significantly different averages combined with a long-term trend (see Plourde et al. 2013). Additionally, short regimes identified at the end of the time series should be interpreted with caution as the addition of new data could heavily influence the results (see results for the 2010, 2011 and 2012 in Env_PCA1 and Env_PCA2 in Fig. 4). The STARS analyses should therefore be considered as an approach to analyse data in order to objectively describe significant changes in environmental conditions in the GSL. It was not used to only identify ‘pure’ regime shifts per se.

ENVIRONMENTAL EFFECT ON MACKEREL STOCK DYNAMICS

The GAMs revealed that variations in physical and biological environmental conditions had significant effects on fish condition during spawning (K_june), on the level of increase in condition during summer (K_sept/june) and recruitment success (R_s) of Atlantic mackerel in the GSL. For all stock parameters, GAMs incorporating PCAs describing variations in zooplankton abundance, composition and phenology explained a greater deviance of the independent variable than models considering the PCAs of physical environment only, suggesting that feeding success might have a more direct effect on mackerel condition and recruitment success than temperature alone. The high percentage of deviance explained by the final selected GAMs indicates that the three principal PCAs describing different modes of environmental variability did capture elements of bottom-up processes fundamental to mackerel stock dynamics in the GSL. Our results support the conceptual model proposing that copepods act as a strong link between physical environmental variability and fish stock dynamics, a model that could apply particularly well to planktivorous pelagic fish species (Runge 1988). Moreover, our results support in a general way the match-mismatch hypothesis proposing that adequate prey must be abundant enough at the right time to favor feeding success, and consequently individual condition and recruitment success (Cushing 1990). To our knowledge, our study provides for the first time evidences that both zooplankton abundance and phenology, described based on indices at the scale of an ecosystem, are key for pelagic fish stock dynamics.

Coherent with the fact that K_june and K_sept/june must be determined during spring and summer, respectively, different Plank and Pheno PCAs were selected in the optimal GAMs for these variables. The selected GAM selected Plank_PCA1 and Pheno_PCA2 as the most significant variables for K_june (Table 3). Plank_PCA1 had a positive effect on K_june and describes long-term variations in abundance of the large-bodied and lipid-rich *C. hyperboreus*, this species being transported in the southern GSL in spring where it represents a key prey for juvenile and adult mackerel (Grégoire and Castonguay 1989, Darbyson et al. 2003). The significant effect of Pheno_PCA2 suggests that the dynamics (timing, duration) of *Calanus* production in spring, which could be seen as an indicator of the overall seasonal timing of secondary production, is also important in the control of mackerel condition (K_june) (Table 3, Fig. 6). On the other hand, the increase in condition during summer (K_sept/june) was negatively influenced by Plank_PCA1 and positively by Plank_PCA2, these axes describing an opposite effect of large *Calanus* (negative) and a high abundance of *Pseudocalanus* spp. and *Temora* spp. (positive), two smaller copepods taxa that are dominant and actively growing in summer and fall in the southern GSL following the production period of *C. hyperboreus* and *C. finmarchicus* in spring and early summer (Plourde et al. 2014). The selection of Pheno_PCA3 in the final GAM would reflect the significant influence of the timing of *C. finmarchicus* G_2 in late summer and early fall (Fig. 2), which could also act as a proxy of the seasonality in the overall zooplankton productivity late in the season.

In addition to the negative density-dependent effect of high SSB, mackerel R_s was positively affected by Env_PCA2, i.e. by low St. Lawrence River freshwater runoff, cold upper water and high ice index, and by an earlier development of *C. finmarchicus* G_1 and G_2 (Pheno_PCA2) (Fig. 8). The dome-shape effect by Pheno_PCA2 indicates that an optimal timing of zooplankton production might favour mackerel R_s. The negative and significant correlation with Plank_PCA2 suggests that Env_PCA2 could act as a proxy of variations in the abundance of *C. finmarchicus* occurring at the same temporal scale, the eggs and nauplii of this species being some of the few key prey for first feeding mackerel larvae (Table 2, Fig.2) (Ringuette et al. 2002, Castonguay et al. 2008, Robert et al. 2009). Therefore, our results indicate that variations in the abundance and timing of *C. finmarchicus* (and potentially other copepod taxa) would be a key determinant of mackerel R_s, supporting the match-mismatch hypothesis (Cushing 1990).

Our results also indicate that environmental variability is an important determinant of mackerel recruitment in the GSL that could modulate stock productivity. The significant influence of physical and biological (zooplankton) environmental conditions on Baltic Sea herring stocks recruitment support the existence of climate-driven spawning stock- recruitment relationships (Cardinale et al. 2009, Casini et al. 2010, Margonski et al. 2010). Such knowledge could be useful to optimize the management of fish stocks and predict their response to climate change under various exploitation scenarios (Bartolino et al., 2014). Integrating the effect of environmental variability on fish stocks dynamics represent the basis on an ecosystem-based approach of fisheries management.

The fact that mackerel condition in September (K_sept) had to be selected to obtain the best solution for the GAM with R_s when the year 2012 was included in the analysis suggests that our broad-scale zooplankton PCA indices based on the Rimouski station data might not have been representative of the local zooplankton dynamics in the sGSL in 2012. Conditions in the GSL in 2012 were considered as extreme with particularly high summer and fall upper layer water temperature in the sGSL (Galbraith et al. 2014). However, given that mackerel condition was strongly influenced by zooplankton indices (Table 3), condition in September likely reflects the net impact of mackerel feeding conditions during summer in that region.

In conclusion, our analyses identified two dominant modes of environmental variability in the GSL determining changes in zooplankton abundance, composition and phenology, a long-term mode (15-20 years) and a second mode occurring on a shorter time scale (5-10 years. Abrupt changes in bottom-up processes in 1996-1997, 2004 and from 2009 to 2012 were also revealed by our analyses. These variations in bottom-up processes likely play a key role in the control of mackerel individual condition (K) and recruitment success (R_s) with variations in zooplankton dynamics and key copepod species being more important than physical environmental conditions alone. These results also illustrate that the large variations in mackerel stock recruitment in the GSL could be driven by environmental conditions independently of spawning stock biomass suggesting that environmental conditions should be integrated in the management of that stock.

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TABLES

Table 1. List of variables included in the time series analyses.

Name	Description	Period	N	Source
Physical				
Freshwater discharge- St. Lawrence River	Seasonal (Jan-June) freshwater discharge at Québec City	1971-2012	1	Galbraith et al. (2014)
Deep water salinity	Salinity in waters > 150 m	1971-2012	1	Galbraith et al. (2014)
Labrador Current volume transport	Surface (top 200 m) geostrophic transport across Newfoundland and Grand Banks slopes derived from TOPEX/Poseidon altimetry (tract 191, SW Grand Banks)	1992-2010	1	Han G. and Li J. (2008)
Upper layer composite climate index (SLE, nwGSL, NeGSL, sGSL)	Sum of annual anomaly of surface temperature (May-Nov), and in Cold Intermediate layer (CIL) minimum temperature	1971-2012	4	Galbraith et al. (2014)
Deep composite climate index (SLE, nwGSL, NeGSL, sGSL)	Sum of annual anomaly of temperature at 150, 200, 250 and 300 m	1971-2012	4	Galbraith et al. (2014)
Annual Ice Index (SLE, nwGSL, NeGSL)	Sum of annual anomaly of ice volume and timing of ice melting in the GSL	1971-2012	3	Galbraith et al. (2014)
Plankton				
Plankton abundance (Rimouski station)	Annual anomaly of phytoplankton biomass (mg Chla m^{-2}: 0-50 m) and zooplankton species abundance (no ind m^{-2}). Species: *Calanus finmarchicus, C. glacialis, C. hyperboreus, Metridia longa*, krill eggs, *Acartia, Microcalanus, Oithona, Oncaea, Pseudocalanus, Scolecithricella, Temora*, jellies	1992-2012	14	Plourde et al. (2014)
Zooplankton phenology	Annual anomaly in the timing of peak recruitment of CI-III *C. finmarchicus* G_1 and G_2, ratio of max abundance of CI-III *C. finmarchicus* G_2 and G_1, stage composition of overwintering *C. glacialis* and *C. hyperboreus*	1992-2012	10	Plourde et al. (2014)
Atlantic Mackerel				
Total and Spawning biomass (SSB)	Mackerel total and spawning biomass (tons) determined with VPA	1968-2012	1	Grégoire et al. (2013)
Recruitment rate (R)	Ratio of the number of Age 1 individuals and SSB	1973-2011	1	Grégoire et al. (2013)
Individual condition (K)	Mackerel condition (K) in June and September	1973-2011	2	Grégoire et al. (2013)
Competitors				
4T Atlantic herring	Spring, Fall and total herring spawning biomass (tons) in 4T	1978-2012	3	Leblanc et al. (2012)

Table 2. Correlation coefficients among dominant PCAs describing variations in physical environmental conditions (Env), zooplankton abundance (Plank), and phenology (Pheno). Bold: coefficients > 0.50.

	Env_ PCA 1	Env_ PCA 2	Env_ PCA 3	Plank_ PCA1	Plank_ PCA2	Plank_ PCA3	Pheno _PCA1	Pheno _PCA2	Pheno _PCA3
Env_PCA1									
Env_PCA2	0.00								
Env_PCA3	0.00	0.00							
Plank_PCA1	**0.54**	-0.38	0.17						
Plank_PCA2	-0.13	**-0.54**	0.18	0.00					
Plank_PCA3	0.12	0.20	0.03	0.00	0.00				
Pheno_PCA1	**0.71**	-0.14	0.12	**0.67**	0.04	-0.06			
Pheno_PCA2	0.38	0.16	-0.21	-0.19	0.00	0.05	0.00		
Pheno_PCA3	-0.22	0.42	0.24	-0.26	-0.45	-0.02	0.00	0.00	

Table 3. Details of the GAM models testing the effect of environmental variability and mackerel stock parameters on K_june and K_sept/june. Black: basic model. Grey: models not selected. Bold: selected model.

Times series	Model	GCV	DEV	Δ DEV
1973-2012	K_june ~ Maq_Tot_Biom^{ns}	0.00161	4.5	
1973-2012	K_june ~ Env_PCA1** + Maq_Tot_Biom^{ns}	0.00135	24.3	19.9
1973-2012	K_june ~ Env_PCA2^{ns} + Maq_Tot_Biom^{ns}	0.00167	7.5	3.1
1973-2012	K_june ~ Env_PCA3^{ns} + Maq_Tot_Biom^{ns}	0.00163	8.7	4.2
1990-2012	K_june ~ Maq_Tot_Biom*	0.00070	21.8	
1990-2012	K_june ~ Env_PCA1** + Maq_Tot_Biom*	0.00050	49.0	27.2
1990-2012	K_june ~ Env_PCA2^{ns} + Maq_Tot_Biom*	0.00068	31.0	9.2
1990-2012	K_june ~ Env_PCA3^{ns} + Maq_Tot_Biom*	0.00071	28.0	6.2
1990-2012	K_june ~ Plank_PCA1** + Maq_Tot_Biom*	0.00050	49.5	27.7
1990-2012	K_june ~ Plank_PCA2^{ns} + Maq_Tot_Biom^{ns}	0.00077	21.9	0.1
1990-2012	K_june ~ Plank_PCA3^{ns} + Maq_Tot_Biom*	0.00072	31.2	9.4
1990-2012	K_june ~ Pheno_PCA1* + Maq_Tot_Biom^{ns}	0.00058	41.4	19.6
1990-2012	K_june ~ Pheno_PCA2^{ns} + Maq_Tot_Biom*	0.00067	31.4	9.6
1990-2012	K_june ~ Pheno_PCA3* + Maq_Tot_Biom^{ns}	0.00060	43.3	21.5
1990-2012	K_june ~ Pheno_PCA3**	0.00057	41.1	19.3
1990-2012	**K_june ~ Plank_PCA1*** + Pheno_PCA2* + Maq_Tot_Biom***	**0.00038**	**65.3**	**43.5**
1990-2012	K_june ~ Plank_PCA2^{ns} + Pheno_PCA1* + Maq_Tot_Biom^{ns}	0.00064	41.1	19.3
1990-2012	K _june~ Plank_PCA2^{ns} + Pheno_PCA2^{ns} + Maq_Tot_Biom^{ns}	0.00074	31.5	9.7
1990-2012	K_june ~ Plank_PCA2^{ns} + Pheno_PCA3^{ns} + Maq_Tot_Biom^{ns}	0.00066	44.0	22.2
1990-2012	K_june ~ Plank_PCA3^{ns} + Pheno_PCA1* + Maq_Tot_Biom^{ns}	0.00058	50.5	28.7
1990-2012	K_june ~ Plank_PCA3^{ns} + Pheno_PCA2^{ns} + Maq_Tot_Biom*	0.00069	39.7	17.9
1990-2012	K_june ~ HerTotSSB^{ns} + Maq_Tot_Biom^{ns}	0.00067	31.7	9.9
1990-2012	K_june ~ SprHerSSB** + FallHerSSB^{ns} + Maq_Tot_Biom*	0.00054	51.9	30.1
	K_june ~ SprHerSSB^{ns} + Plank_PCA1** + Pheno_PCA2*	0.00051	59.7	37.9
1973-2012	Ksep/Kjun ~ Maq_Tot_Biom^{ns}	0.00545	6.3	
1990-2012	Ksep/Kjun ~ Maq_Tot_Biom^{ns}	0.00319	10.9	
1990-2012	Ksep/Kjun ~ Maq_Tot_Biom^{ns} + Plank_PCA1** + Pheno_PCA2^{ns}	0.00234	48.7	37.8
1990-2012	Ksep/Kjun ~ Maq_Tot_Biom^{ns} + Plank_PCA1** + Pheno_PCA3^{ns}	0.00213	50.5	39.6
1990-2012	Ksep/Kjun ~ Plank_PCA2* + Pheno_PCA3**	0.00218	51.9	41.0
1990-2012	**Ksep/Kjun ~ Plank_PCA1** + Pheno_PCA3* + Plank_PCA2^{ns}**	**0.00194**	**57.0**	**46.1**

p-value of smooth terms are indicated by: ns >0.05; * >0.01; ** >0.001; *** <0.001

Δ DEV is the difference between the model and the basic run

Maq: Mackerel; Tot: total; Spr: Spring, Her: 4T herring, Biom: total biomass; SSB: spawning biomass

Table 4. Details of the GAM models testing the effect of environmental variability and mackerel stock parameters on mackerel recruitment rate (R). Black: basic model. Grey: models not selected. Bold: selected model.

Time series	Model	GCV	DEV	Δ DEV
1971-2011	Rs ~ Maq_Tot_Biom***	1.163	28.0	
1971-2011	Rs ~ Env_PCA1^{ns} + Maq_Tot_Biom***	1.221	29.4	1.4
1971-2011	Rs ~ Env_PCA2^{ns} + Maq_Tot_Biom***	1.202	29.4	1.4
1971-2011	Rs ~ Env_PCA3^{ns} + Maq_Tot_Biom***	1.218	28.5	0.5
1971-2011	**Rs ~ (Env_PCA2 x Maq_Tot_Biom)*** **	**1.087**	**43.1**	**15.1**
1990-2011	Rs ~ Maq_Tot_Biom*	1.052	27.9	
1990-2011	Rs ~ Env_PCA1* + Maq_Tot_Biom**	0.840	52.8	24.9
1990-2011	Rs ~ Env_PCA2* + Maq_Tot_Biom**	0.804	57.3	29.4
1990-2011	Rs ~ Env_PCA3^{ns} + Maq_Tot_Biom**	1.054	38.4	10.5
1990-2011	Rs ~ Plank_PCA2^{ns} + Maq_Tot_Biom*	0.991	48.8	20.9
1990-2011	Rs ~ Pheno_PCA1^{ns} + Maq_Tot_Biom*	1.011	38.3	10.4
1990-2011	Rs ~ Pheno_PCA2^{ns} + Maq_Tot_Biom**	0.991	45.8	17.9
1990-2011	**Rs ~ Env_PCA2*** + Pheno_PCA2** + Maq_Tot_Biom*** **	**0.502**	**77.6**	**49.7**
1990-2011	Rs ~ Env_PCA2^{ns} + Pheno_PCA3^{ns} + Maq_Tot_Biom**	0.887	58.3	30.4
1990-2011	Rs ~ Env_PCA2* + Plank_PCA1^{ns} + Maq_Tot_Biom**	0.820	62.1	34.2
1990-2011	Rs ~ Env_PCA2* + Plank_PCA3^{ns} + Maq_Tot_Biom**	0.884	57.6	29.7
1990-2011	Rs ~ Plank_PCA2* + Pheno_PCA2* + Maq_Tot_Biom**	0.824	66.6	38.7
1990-2011	Rs ~ Plank_PCA2^{ns} + Pheno_PCA3^{ns} + Maq_Tot_Biom*	1.073	50.6	22.7
1990-2011	Rs ~ Plank_PCA3^{ns} + Pheno_PCA3^{ns} + Maq_Tot_Biom*	1.217	32.5	4.6
1990-2011	Rs ~ Plank_PCA3^{ns} + Pheno_PCA2^{ns} + Maq_Tot_Biom**	1.103	47.0	19.1
1990-2011	Rs ~ Plank_PCA1^{ns} + Pheno_PCA2^{ns} + Maq_Tot_Biom**	1.060	48.5	20.6
1990-2011	Rs ~ Plank_PCA1^{ns} + Pheno_PCA3^{ns} + Maq_Tot_Biom*	1.216	33.1	5.2
1990-2011	Rs ~ Plank_PCA2* + Pheno_PCA1^{ns} + Maq_Tot_Biom**	0.792	66.0	38.1
1990-2011	Rs ~ Plank_PCA3^{ns} + Pheno_PCA1^{ns} + Maq_Tot_Biom*	1.126	38.4	10.5
1990-2011	Rs ~ Maq_Tot_Biom* + Her_Tot*	0.878	52.4	24.5
1990-2011	Rs ~ Maq_Tot_Biom* + SprHerBiom^{ns} + FallHerBiom^{ns}	0.973	54.7	26.8
1978-2011	Rs ~ Maq_Tot_Biom*** + SprHerBiom^{ns} + FallHerBiom^{ns}	0.963	47.9	20.0
1978-2011	Rs ~ Maq_Tot_Biom*** + SprHerBiom*	0.902	47.8	19.9
1990-2012	Rs ~ Maq_Tot_Biom^{ns}	1.4425	12.4	
1990-2012	**Rs ~ Env_PCA2* + Pheno_PCA2* + Maq_Tot_Biom*** + Ksept** **	**0.7561**	**75.5**	**47.6**

*p-value of smooth terms are indicated by: ns >0.05; * >0.01; ** >0.001; *** <0.001.*

Δ DEV is the difference between the model and the basic run.

Maq: Mackerel; Tot: total; Spr: Spring, Her: herring, Biom: biomass; SSB: spawning biomass

FIGURES

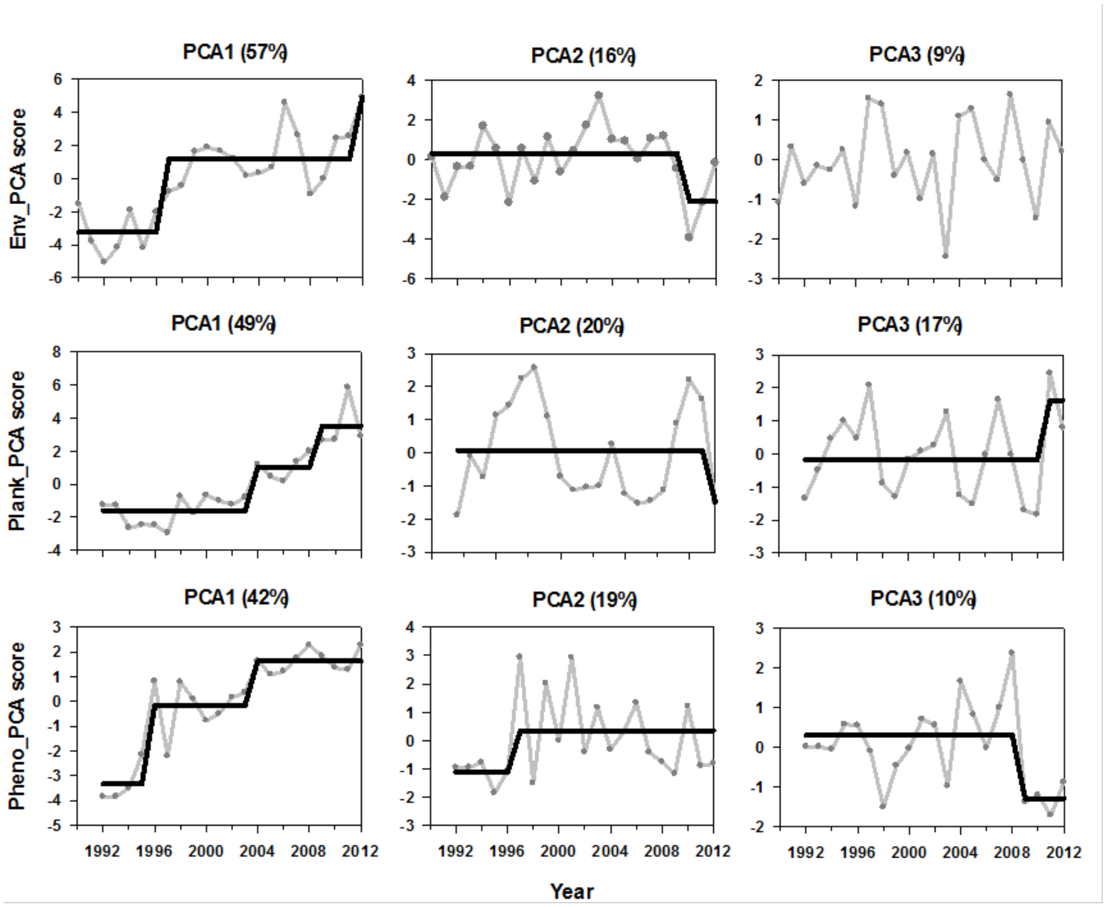

Figure 1: Environmental variability in the Gulf of St. Lawrence from 1990 to 2012. Annual scores (grey) and different periods (black) determined by STARS performed on the first three Principal Components Analysis (PCA) axes of the physical environment (Env, upper panels), zooplankton abundance/composition (Plank, middle panels), and phenology (Pheno, lower panels).The percentage of variations associated with each PCA are shown in brackets above each panel.

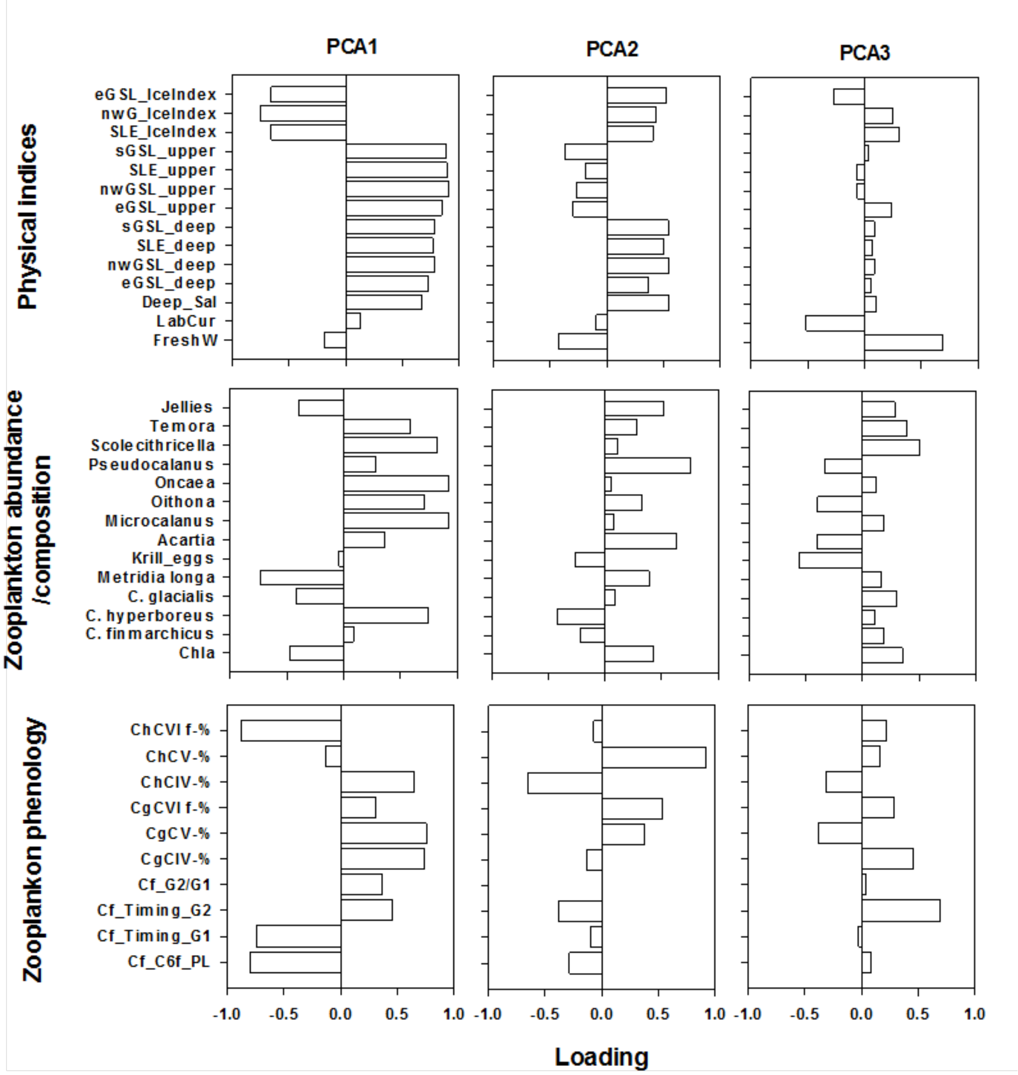

Figure 2: Loadings of different variables on the three dominant PCA axes of physical conditions (upper panels), zooplankton abundance/composition (middle panels), and zooplankton phenology (lower panels). See Appendix 1 for acronyms' description.

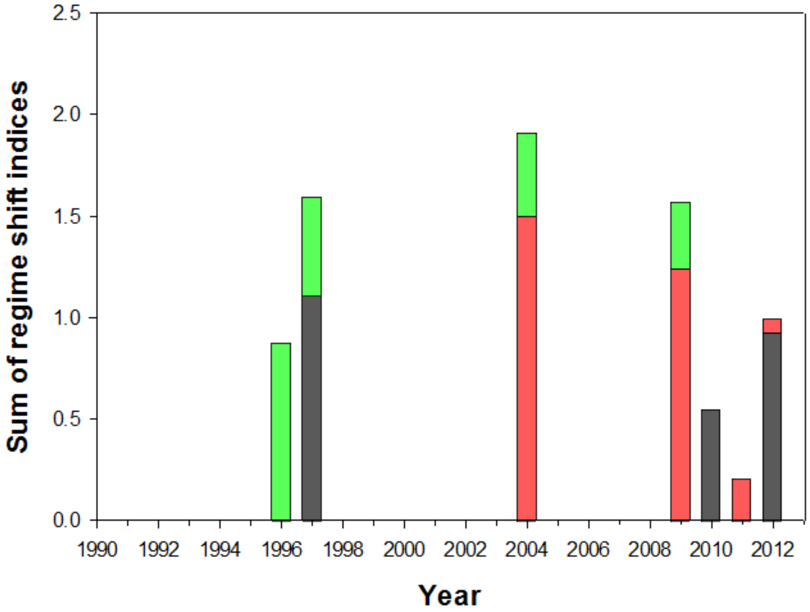

Figure 3: Results of STARS. Sum of regime shifts (absolute value) of the first three PCAs describing variations in the environmental (grey), zooplankton abundance (red) and zooplankton phenology (green).

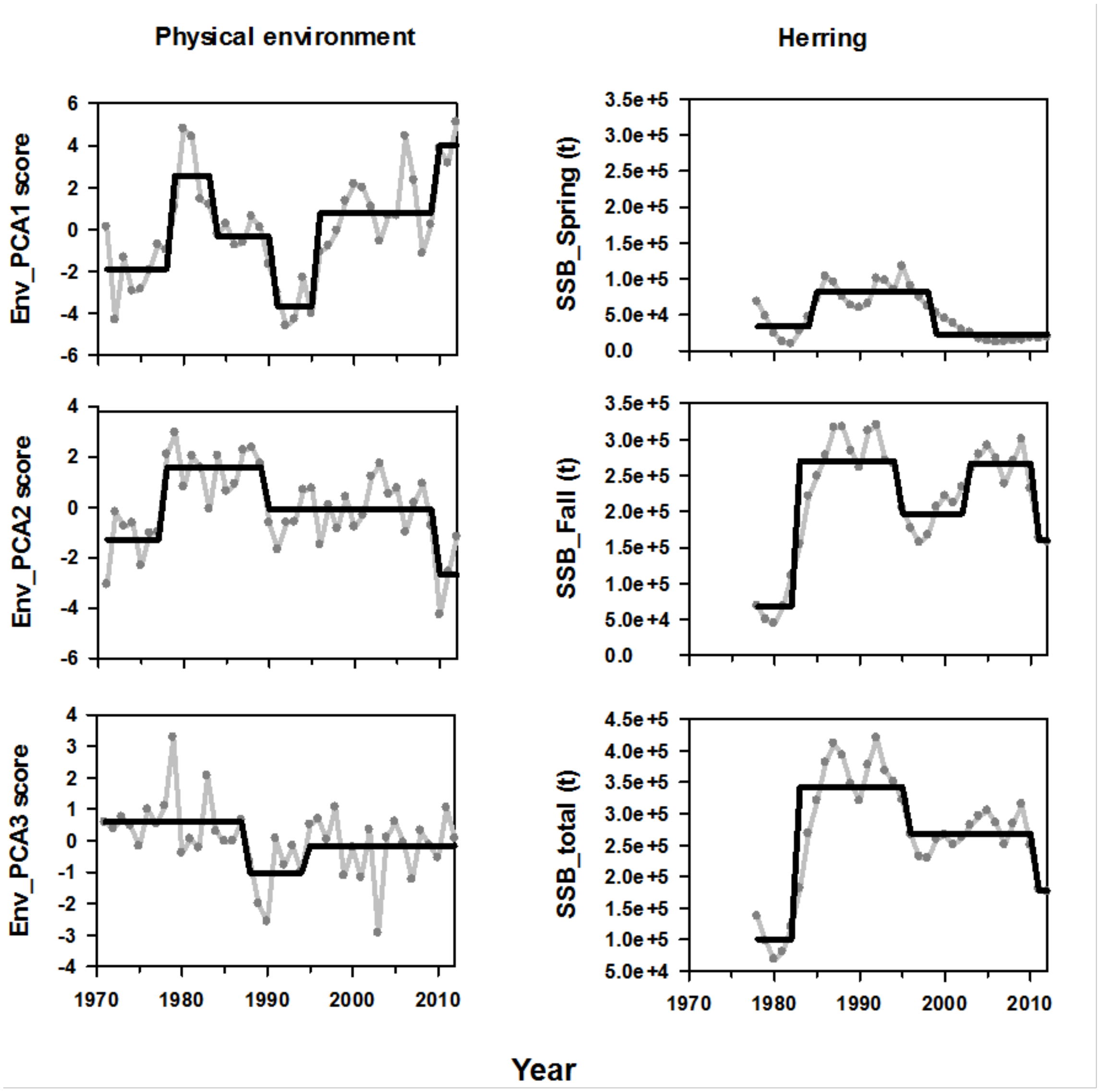

Figure 4. Long-term (1971–2012) variability in physical and biologicals conditions in the southern Gulf of St. Lawrence. Left panels: time series of dominant PCAs performed with a set of physical indices (Env). Right panels: Time series of Atlantic herring spring and fall spawning stock biomass and total spawning biomass (SSB). Grey: time series; Black: different periods (regimes) determined with STARS.

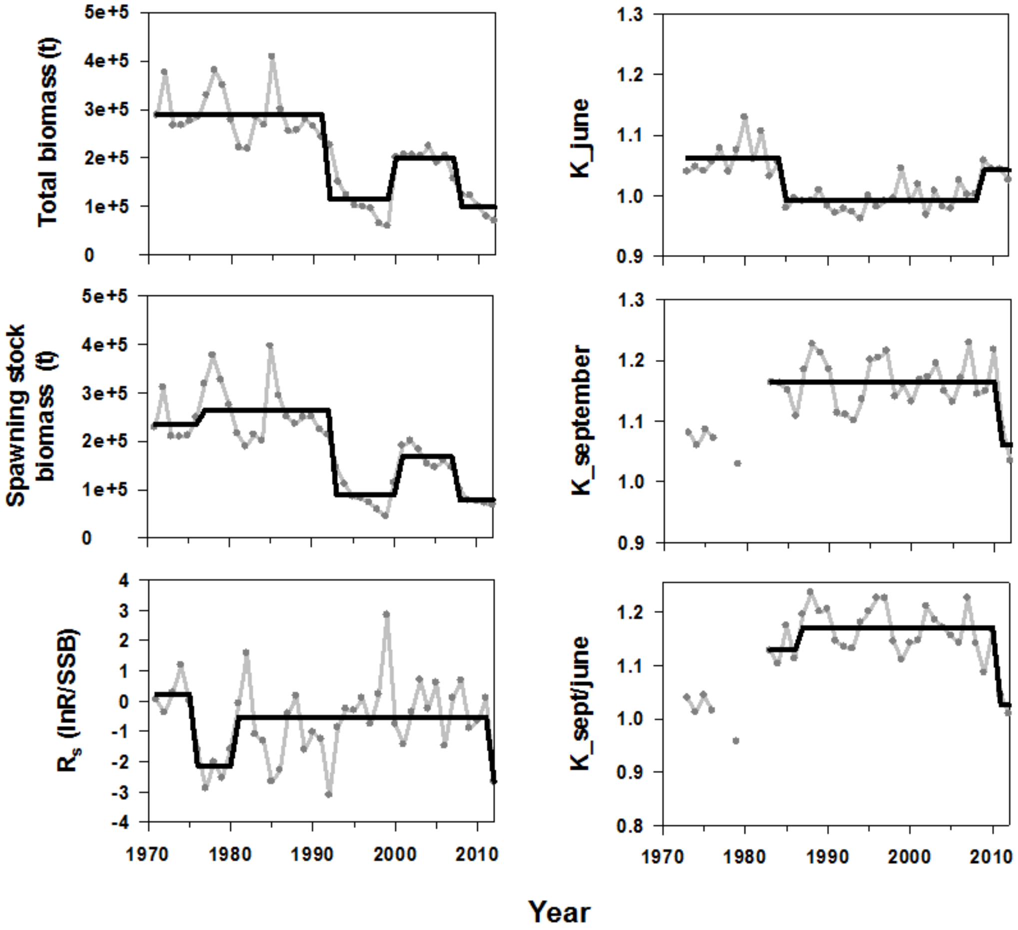

Figure 5. Long-term (1971–2012) variability in Atlantic mackerel stock dynamics. Time series of total biomass (t), spawning stock biomass (SSB) (t), recruitment success (R_S), individual condition (K) during spawning in June (K_june) and in September (K_sept), and the ratio of condition at the end of summer in September and during spawning (K_sept/june). Grey: time series; Black: different periods (regimes) determined with STARS.

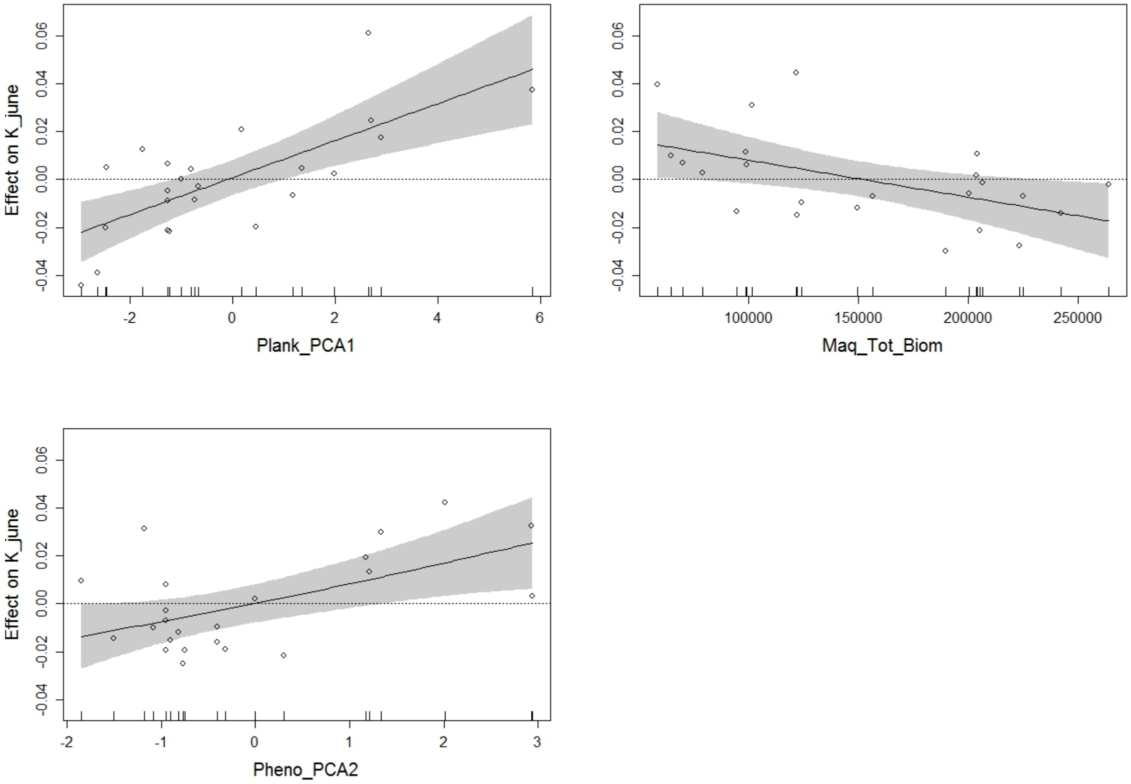

Figure 6: Results of the selected optimal GAM showing the effect of significant environmental PCAs and Atlantic mackerel stock variables on individual condition in June (K_june). Tick marks on the x-axis represent location of data points and open circles represent residuals. The 0 value on the y-axis and the dotted line represent the parametric term of the model (intercept). The solid line represents the main effect of independent variables. The shaded area represents 95% confidence intervals which include the uncertainty around the overall mean.

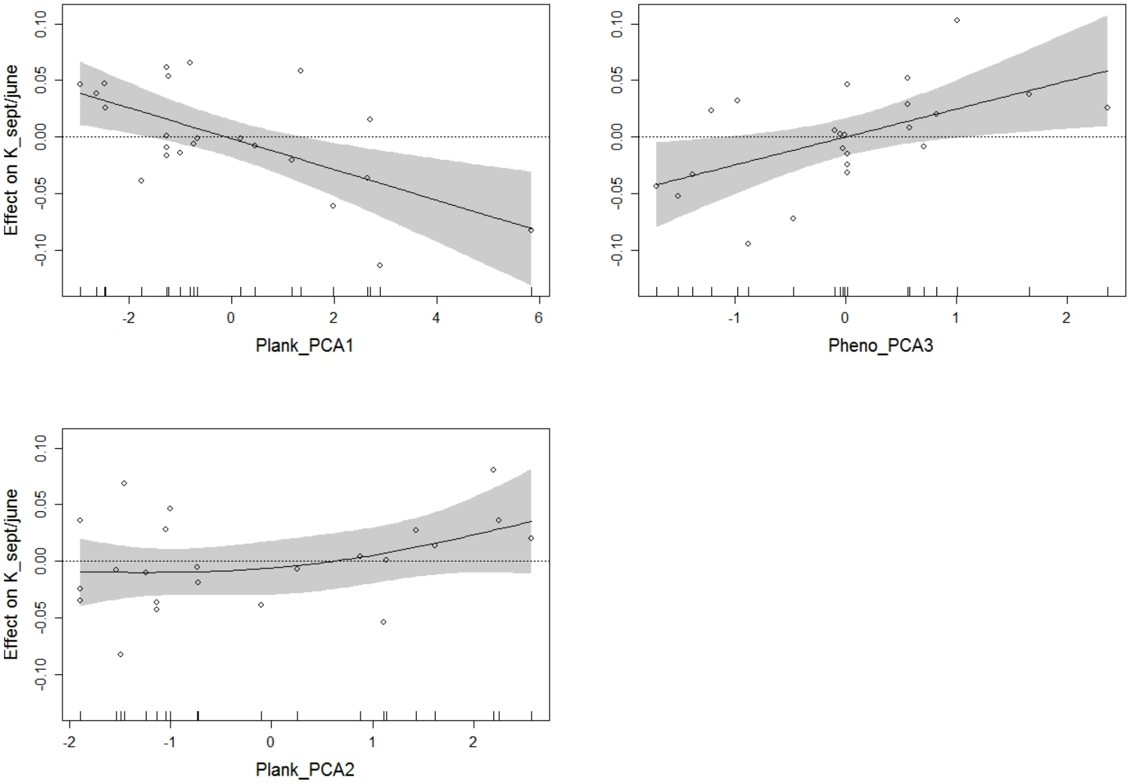

Figure 7. Results of the selected optimal GAM showing the effect of significant environmental PCAs and Atlantic mackerel stock variables on the gain in condition during summer (K_sept/june). Tick marks on the x-axis represent location of data points and open circles represent residuals. The 0 value on the y-axis and the dotted line represent the parametric term of the model (intercept). The solid line represents the main effect of independent variables. The shaded area represents 95% confidence intervals which include the uncertainty around the overall mean.

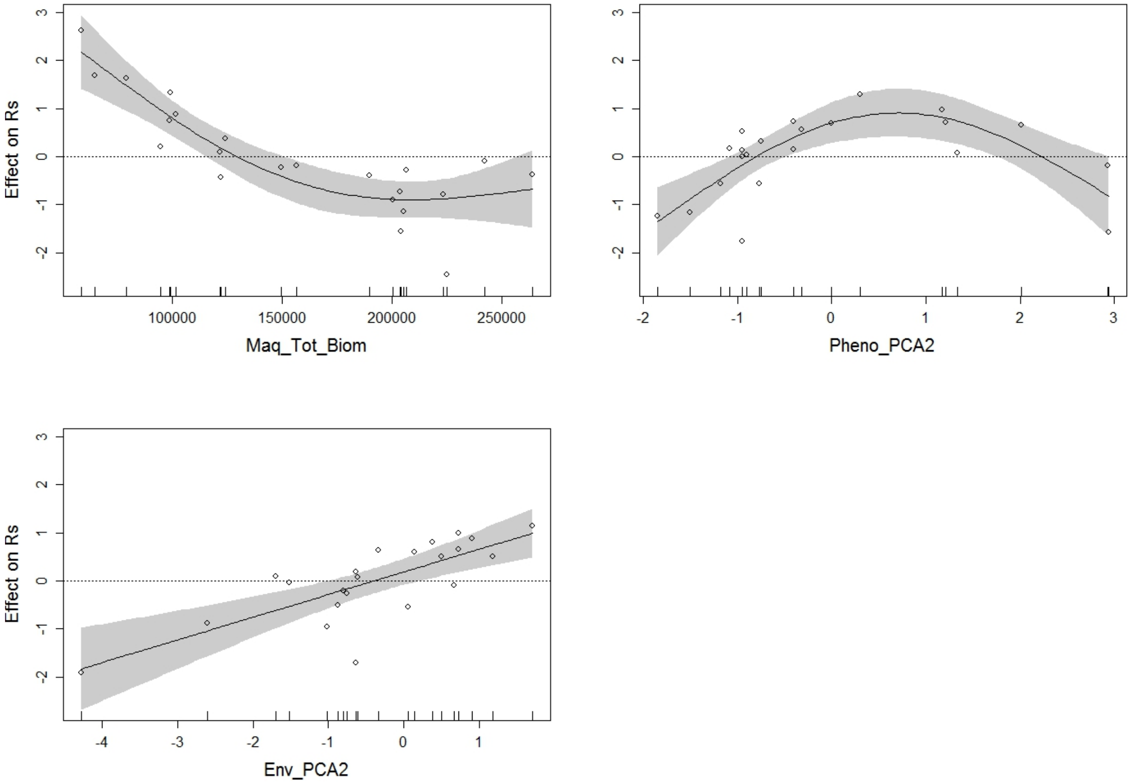

Figure 8. Results of the selected optimal GAM showing the effect of significant environmental PCAs and Atlantic mackerel stock variables on recruitment success (R_s) during the 1990-2012 period. Tick marks on the x-axis represent location of data points and open circles represent residuals. The 0 value on the y-axis and the dotted line represent the parametric term of the model (intercept). The solid line represents the main effect of independent variables. The shaded area represents 95% confidence intervals which include the uncertainty around the overall mean.

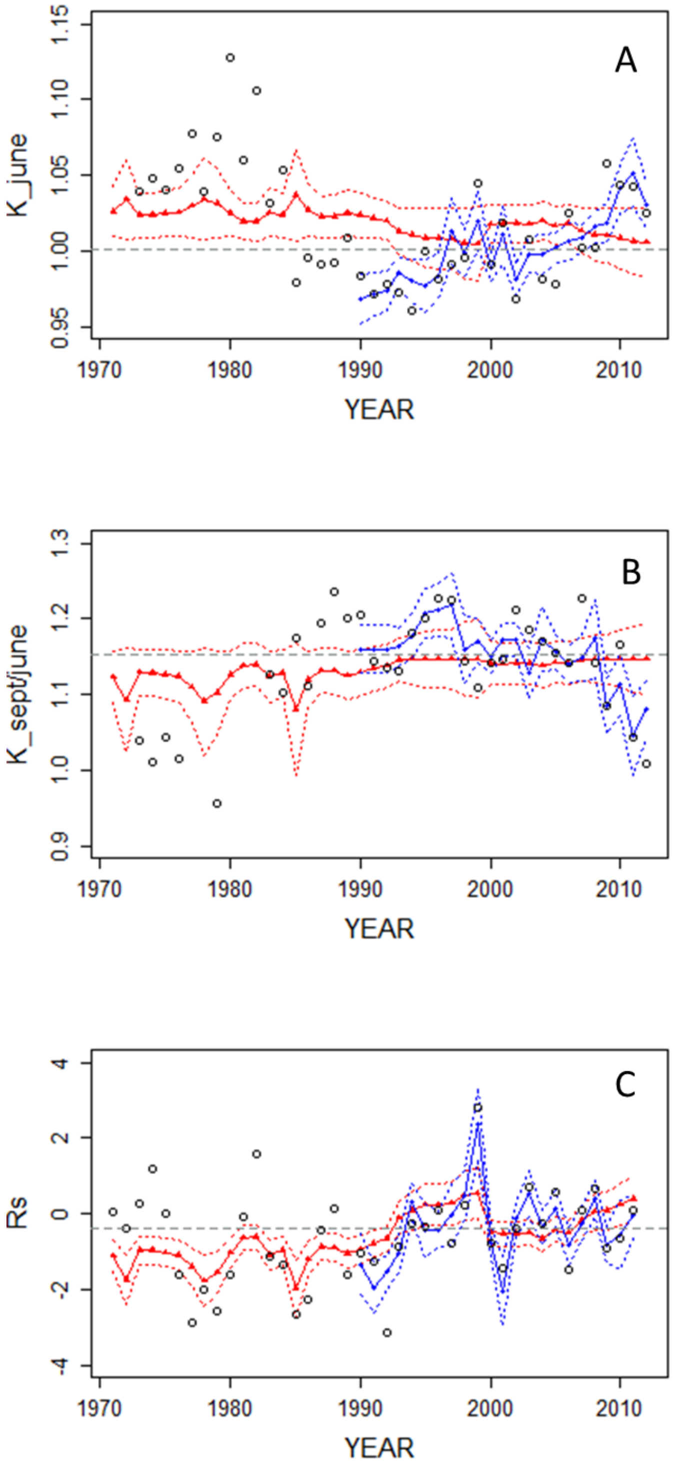

Figure 9. Performance of the selected models relating K_june (A), K_sept/june (B), and recruitment success (R_s) (C) to environmental conditions and stock parameters. Open circles: observed values; red circles: predicted values with basic models based on spawning stock biomass (SSB); blue circles: predicted values with selected models considering environmental variables and SSB. See Tables 2-3 for formulation and statistics associated with each model. Dotted lines: long-term average of observed values (black), and uncertainty (±2 s.d.) around predicted values (red, blue).

APPENDIX 1

List of acronyms used in the text, Tables and figures.

Acronyme	Description
GSL	Gulf of St. Lawrence
SLE	St. Lawrence Estuary
nwGSL	Northwest GSL
eGSL	Eastern GSL
sGSL	Southern GSL
nGSL	Northern GSL
Upper	Upper layer (0-150 m) temperature composite
Deep	Deep layer (> 150 m) temperature composite
Temp	Température
LabCur	Labrador Current volume transport
Sal	Salinity
Freshw	St. Lawrence freshwater outflow
Cf	*Calanus finmarchicus*
Cg	*C. glacialis*
Ch	*C. hyperboreus*
Mlon	*Metridia longa*
Temora	*Temora longicornis*
Biom	Biomass
K	Condition Factor
CVIf	copepodite stage VI female
CIV	copepodite stage IV
CV	copepodite stage IV
PL	Prosome length
Maq	Atlantic mackerel
Her	Atlantic herring
Spr	Spring
Env	Physical environment
Plank	Zooplancton abundance/composition
Pheno	Zoopklankton phenology
STARS	Sequential t-test analysis of regime shift
PCA	Principal components analysis