FISHERIES OCEANOGRAPHY

FISHERIES OCEANOGRAPHY *Fish. Oceanogr. 24:4, 347–363, 2015*

Effect of environmental variability on body condition and recruitment success of Atlantic Mackerel (*Scomber scombrus* L.) in the Gulf of St. Lawrence

STÉPHANE PLOURDE,[1]* FRANÇOIS GRÉGOIRE,[1] CAROLINE LEHOUX,[1] PETER S. GALBRAITH,[1] MARTIN CASTONGUAY[1] AND MARC RINGUETTE[2]

[1]*Fisheries and Oceans Canada, Institut Maurice-Lamontagne, 850, Route de la Mer, Mont-Joli, QC, Canada, G5H 3Z4*
[2]*Fisheries and Oceans Canada, Bedford Institute of Oceanography, 1 Challenger Drive, PO Box 1006, Dartmouth, NS, Canada, B2Y 4A2*

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 described the dominant modes of physical and biological (zooplankton) variability using Principal Components Analyses of 40 variables. Two principal modes of variability were identified, a long-term mode (15–20 yr) associated with a warming of the GSL and a second mode describing alternating cold and warm periods at a higher frequency (5–10 yr). A strong link between physical forcing and the dynamics of zooplankton species known to be important for mackerel was shown. Second, a set of Generalized Additive Models (GAM) was developed to explore how these environmental variations could influence mackerel condition (Fulton's K) and recruitment success (R_s). Optimal GAMs including variations in abundance, species composition and phenology of key copepods improved model performance by 40–50% relative to those considering only physical environmental conditions. The results are consistent with the match–mismatch hypothesis and illustrate the key role of zooplankton dynamics in modulating variations in mackerel K and R_s. Finally, this study showed that large variations in R_s could be caused by varying environmental conditions independently of the influence of stock biomass. Our results strongly indicate that the effect of environmental variability should be considered in the implementation of an ecosystem-based approach to Atlantic mackerel stock management.

Key words: climate change, copepods, Gulf of St. Lawrence, mackerel, recruitment

INTRODUCTION

The Gulf of St. Lawrence (GSL) is the southernmost body of water with a seasonal ice cover in the northwest Atlantic. It is under the combined influence of Arctic and Atlantic water from the adjacent Labrador and Newfoundland shelf and deep slope and the important freshwater runoff from the St. Lawrence River. In summertime, the water column in the GSL comprises three distinct layers: the surface layer, the cold intermediate layer (CIL) and a deeper water layer. Maximum surface temperatures are typically observed from mid-July to mid-August (Galbraith *et al.*, 2012). During the winter, there are only two layers as the surface layer deepens mostly from wind-driven mixing prior to ice formation, and encompasses the CIL (Galbraith, 2006). The deeper water layer (>150 m) is characterized by temperatures between 1 and >7°C and salinities between 32.5 and 35 enter the Laurentian Channel at the continental shelf margin; it circulates upstream in the GSL towards the heads of the deep channels without much exchange with the upper layers (Gilbert, 2004). The region showed a significant warming trend and a diminishing duration and volume of sea ice over the last two decades (Galbraith *et al.*, 2014).

The zooplankton biomass in the GSL is dominated by the planktonic copepods, *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus*. These taxa also contribute most to the total mesozooplankton abundance during spring and summer. The planktonic copepod, *Oithona* spp, and other small taxa numerically dominate in fall and winter (Plourde *et al.*, 2002, 2014). In general, *Calanus* species are transported to shallower areas (<100 m) such as the southern GSL from a

**Correspondence*. e-mail: stephane.plourde@dfo-mpo.gc.ca
Received 21 October 2014
Revised version accepted 1 May 2015

© 2015 John Wiley & Sons Ltd
doi:10.1111/fog.12113

deeper (>100 m) overwintering habitat in spring and early summer while they are actively growing in the surface layer (Maps *et al.*, 2011). Smaller copepod species, such as *Pseudocalanus* spp. and the neritic *Temora longicornis*, maintain local populations in the southern GSL (Plourde *et al.*, 2014). Important interannual variations in abundance and dynamics of key copepod species and zooplankton community structure have been described in different areas of the GSL (Plourde *et al.*, 2001, 2003, 2014). The significant warming trend during the past two decades may have caused profound changes in zooplankton dynamics and production regime in the GSL. However, a comprehensive description of the temporal variability of zooplankton community dynamics and their links to the physical and biological, environmental conditions is still lacking.

The Atlantic mackerel (*Scomber scombrus* L., from now on mackerel) is an important pelagic fish in the GSL ecosystem. The southern GSL is historically the main spawning area of the stock (Grégoire and Beaudin, 2014). As in many pelagic fish species, the recruitment pattern of mackerel is characterized by the sporadic occurrence of exceptionally large year-classes dominating the stock and the fisheries subsequently for several years (Grégoire and Beaudin, 2014). According to the match–mismatch hypothesis, the recruitment of marine fishes would be in large part determined by zooplankton prey availability, a function of both zooplankton abundance and timing (Runge, 1988; Cushing, 1990). Adult mackerel are mainly planktivorous (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). The early stages of *C. finmarchicus*, *Pseudocalanus* spp. and *T. longicornis* are key prey of mackerel larvae and variations in prey abundance and production influence the feeding success, growth, survival and potentially recruitment strength of the mackerel stock (Runge *et al.*, 1999; Ringuette *et al.*, 2002; Castonguay *et al.*, 2008; Robert *et al.*, 2009). While changes in mackerel stock productivity have been associated with variations in physical and biological environmental conditions in the North Sea (i.e., Jansen, 2014), the effects of environmental variability on mackerel stock productivity and the underlying mechanisms involved are still to be determined for the GSL.

The main objective of this study was to examine quantitatively the effect of environmental variability on the characteristics of the mackerel stock in the GSL. The conceptual underpinning for our analyses is that zooplankton represents a strong link between physical environmental forcing and fish stock dynamics (Runge, 1988). Additionally, we hypothesize that availability of zooplankton prey affects mackerel recruitment (Cushing, 1990). To test these hypotheses, we first characterize the long-term variability of the physical and biological (zooplankton) oceanographic conditions in the GSL using Principal Components Analyses (PCA). We develop a set of Generalized Additive Models (GAM) to identify and quantify the extent to which mackerel body condition and recruitment success are related to these variations in bottom-up processes. Finally, we interpret our results in the context of our conceptual hypotheses, the role of environmental conditions in determining mackerel recruitment, individual condition and overall stock productivity and the need to include these environmental linkages in ecosystem-based management approaches in the future.

MATERIALS AND METHODS

Abiotic environment and zooplankton indices

A set of 40 variables was assembled as part of the Atlantic Zone Monitoring Programme (AZMP) to describe the long-term changes in oceanographic conditions in the GSL (Table 1) (see Therriault *et al.*, 1998). 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 atmospheric and oceanographic systems in eastern Canada and northwest Atlantic. Physical data collected annually in the GSL were used to develop a set of composite indices in the lower estuary (SLE), western (wGSL), eastern (eGSL) and the southern (sGSL) regions. We selected composite indices quantifying the variability in upper (0–150 m) and deep (>150 m) layer water temperature, as well as variations in winter sea ice using an index combining the seasonal maximum volume and the timing of melt (see Galbraith *et al.*, 2014).

Variations in biological, environmental conditions were described with chlorophyll *a* and zooplankton indices extracted from the Rimouski station, the longest consistent zooplankton data series available in the GSL (1992–2012). This station located in the SLE is sampled on a quasi-weekly basis from spring to late fall and interannual variations in key zooplankton abundance indices at this station are generally coherent with other sub-regions of the GSL (Plourde *et al.*, 2014). Two types of zooplankton indices were used. First, the mean annual abundance of dominant

Table 1. List of physical and biological environmental indices included in the Principal Component Analyses (PCA).

Name	Description	Period	*N*	Source
Physical				
Freshwater discharge- St. Lawrence River (FreshW)	Seasonal (Jan–June) freshwater discharge at Québec City	1971–2012	1	Galbraith *et al.* (2014)
Deep water salinity (Deep_Sal)	Salinity in waters > 150 m	1971–2012	1	Galbraith *et al.* (2014)
Labrador Current volume transport (LabCur)	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 and Li (2008)
Upper layer (0–150 m) temperature composite (SLE, nwGSL, NeGSL, sGSL)	Sum of annual anomaly of upper layer temperature (May–Nov), and in Cold Intermediate layer (CIL) minimum temperature	1971–2012	4	Galbraith *et al.* (2014)
Deep layer (150–300 m) temperature composite (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	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	Timing of peak recruitment of CI-III *C. finmarchicus* G_1 (Cf_Timing_G1) and G_2 (Cf_Timing_G2), ratio of max abundance of CI-III *C. finmarchicus* G_2 and G_1 (Cf_G2/G1), stage composition (%) of overwintering *C. glacialis* (Cg) and *C. hyperboreus* (Ch), body size of C. finmarchicus CVIf	1992–2012	10	This study

copepod species/taxa, krill egg abundance and small gelatinous organisms were considered (Table 1). These species/taxa include copepods species such as *C. finmarchicus*, *Pseudocalanus* spp and *T. longicornis*, the early stages of which are important in the diet of mackerel larvae (Ringuette *et al.*, 2002; Robert *et al.*, 2008). The late stages of copepods, in particular, *Calanus* species, also constitute the dominant component in the diet of juvenile and adult mackerel (Darbyson *et al.*, 2003). Second, we developed a set of indices aimed at quantifying changes in the phenology of copepods using dominant *Calanus* species as indicators (Table 1). We used the maximum abundance of CI-III in early summer and fall to represent the timing of the first (G_1) and second (G_2) generations of *C. finmarchicus* and the proportion of these stages in the population to indicate a change in its seasonal production cycle. The body size of CVIf was also used as an indicator of potential changes in growth condition of this key species. The relative composition of overwintering stages was used to describe changes in the phenology of *C. glacialis* and *C. hyperboreus*.

Atlantic Mackerel stock indices

Abundance indices of the mackerel stock in the GSL from 1971 to 2012 were taken from Grégoire and Beaudin (2014). The spawning stock biomass (SSB), the total biomass and the abundance at age 1 (recruits) used to compute recruitment success (R_s) were obtained from the Sequential Population Analysis performed using biological and fishing data collected on a yearly basis. R_s represented the Ln transformed ratio of the number ($\times 000'$) of age 1 individuals during $year_x$ over mature fish during $year_{x-1}$ (Ottersen *et al.*,

2013). We described variations in the individual condition using Fulton's 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 while spawning in June (K_june). The gain in condition during the fattening period was represented by the ratio of K in September to K in June (K_sept/June).

Competitors' indices

Atlantic herring (*Clupea harengus harengus* L.) is an important component of the ecosystem in the southern GSL with feeding preferences overlapping significantly with mackerel and also representing a potential predation threat for early mackerel larvae (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) (LeBlanc *et al.*, 2012).

Data analyses

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). We chose to use the complete time series for physical data because we preferred to analyse biological time series data using the same description of the physical environment (see Tables 3 and 4). Examination of the physical variables revealed a similar range of values during the 1971–2012 and 1992–2012 periods (see Galbraith *et al.*, 2014), suggesting that the use of different reference periods would not have a significant effect on the anomaly values. This homogeneous temporal structure of the variables is also evident in the PCA values observed along the complete time series (see Results, Fig. 4). The use of anomalies provided a mean of integrating variables showing different units such as temperature, salinity and ice cover. Absolute values of the different parameters of the mackerel stock dynamics and Atlantic herring biomass were used.

Our first objective was to describe environmental variability in the GSL and develop a set of indices integrating various environmental indices. PCA was selected to reduce this high number of variables to a set of uncorrelated composite variables, from which the dominant patterns of environmental variability can be extracted (Hare and Mantua, 2000). PCA was run separately for the sets of standardized physical, plankton abundance and zooplankton phenology indices (Table 1). Pearson's correlation coefficients were computed for these different sets of indices for the three dominant PCA axes to describe bottom-up effects of physical forcing on zooplankton dynamics.

To attain our second objective, a set of GAMs was performed 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 in controlling mackerel K_June, K_sept/June and R_s. GAMs followed the general formulation:

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

where $E[y]$ is the expected value of the response (dependent) variable y, a is the intercept parametric term that 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 (d.f. ≤ 3, $k = 3$) to minimize model over-fitting. Independent variables were selected based on environmental conditions and processes known or hypothesized to influence mackerel body condition and recruitment success. For each of these stock variables, we first built a basic GAM using only total biomass to consider possible density-dependent processes, this variable being preferred to SSB because cannibalism is common in this species as early as during the late larval stage (Fortier and Villeneuve, 1996). We then applied a forward selection approach to test the effect of PCA axes describing environmental variability. The forward selection was chosen by backward selection because the number of observations (22–42) limits the number of variables that can be added to the models. The optimal models were selected on the basis of the gain in deviance (%Dev) explained relative to the basic model while minimizing the Generalized Cross Validation Criterion (GCV). Each PCA axis was tested independently to isolate its effect, and PCA axes were consecutively added until the GCV increased. Pairs of independent variables showing a correlation coefficient >0.5 were not used in the models (see Table 2). Interactions were considered in the model selection and defined by the tensor product smooth (Wood, 2006a). The analysis of variance

Table 2. Pearson's correlation coefficients among dominant Principal Components Analyses (PCAs) describing variations in physical environmental conditions (Env), zooplankton abundance (Plank), and phenology (Pheno). Bold: coefficients > 0.50.

	Env_PCA1	Env_PCA2	Env_PCA3	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	

based on the F statistic was used to verify that the residual deviance was not different from the additive structure (without interactions) and the model formulated with interactions (Wood, 2006b). When the model with interaction did not perform better than the additive one, 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 mackerel total biomass and physical environmental conditions (Env PCAs) was tested for the 1971–2012 period, whereas models constructed with the zooplankton short time series (1992–2012) also allowed the testing of the effect of zooplankton abundance (Plank) and phenology (Pheno). Different combination of Env, Plank and Pheno PCAs were tested according to the methodological constraints described above to consider the effect of physical environmental conditions, food quantity and seasonality. The potential predatory impact of another planktivorous fish on mackerel R_s was also considered by testing the effect of herring SSB.

Conditions of application were examined graphically for selected models. We further verified the temporal linear trends of model residuals as a function of the year using the'gls' function in the 'nlme' package in R (v.3.1-105; Pinheiro *et al.*, 2012). Temporal autocorrelation in residuals was tested by the 'acf' function implemented in the stats package (2.15.2; R Core Team, 2012). All models respected the conditions of application of homogeneity and normality of residuals. Model residuals were not auto-correlated and showed no temporal trend. The models were validated using a bootstrap approach. The environmental variables were randomly resampled 1000 times to generate random combinations of predictor variables. For each of these random combinations, the principal components were recalculated, the optimal model was refitted and the percentage of deviance was calculated. The percentage of deviance explained by the optimal model obtained with the real data was compared with the distribution of the percentage of deviance obtained with the resampled data. All optimal models significantly explained more deviance than random data ($P < 0.05$).

RESULTS

Physical and biological environmental variability: 1990–2012

The three dominant PCA axes of the physical (Env), zooplankton abundance/composition (Plank) and zooplankton phenology (Pheno) indices revealed two main modes of variability (Fig. 1). Loadings of the

different indices of each PCA are presented in Figure 2. The PCA1 explained 42–57% of the variability and mainly described long-term changes in environmental conditions (Fig. 1). The increase in the Env_PCA1 score was mainly driven by a gradual 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 the Plank_PCA1 score corresponded to a decrease in chlorophyll *a* biomass and abundance of arctic *C. glacialis* and *M. longa* accompanied by an increase in *C. hyperboreus* and other small copepod species, including *Pseudocalanus* spp. and *T. longicornis* (Fig. 2). The increase in Pheno_PCA1 score was mainly driven by an earlier timing of recruitment of G_1 and a smaller body size of *C. finmarchicus* CVIf, 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 frequencies (Fig. 1). Env_PCA2 and Env_PCA3 mainly represented variability in sea ice cover, water temperature and St. Lawrence River freshwater runoff (Figures 1 and 2). Variability in Plank_PCA2 was caused by a 7- to 10-year cycle between periods of high (low) abundance of *C. finmarchicus*, *C. hyperboreus* and krill eggs opposed to low (high) abundance of smaller taxa such as *Pseudocalanus* spp. and *Acartia* sp. High-frequency variability of

Figure 1. Environmental variability in the Gulf of St. Lawrence from 1990 to 2012. Annual scores of 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.

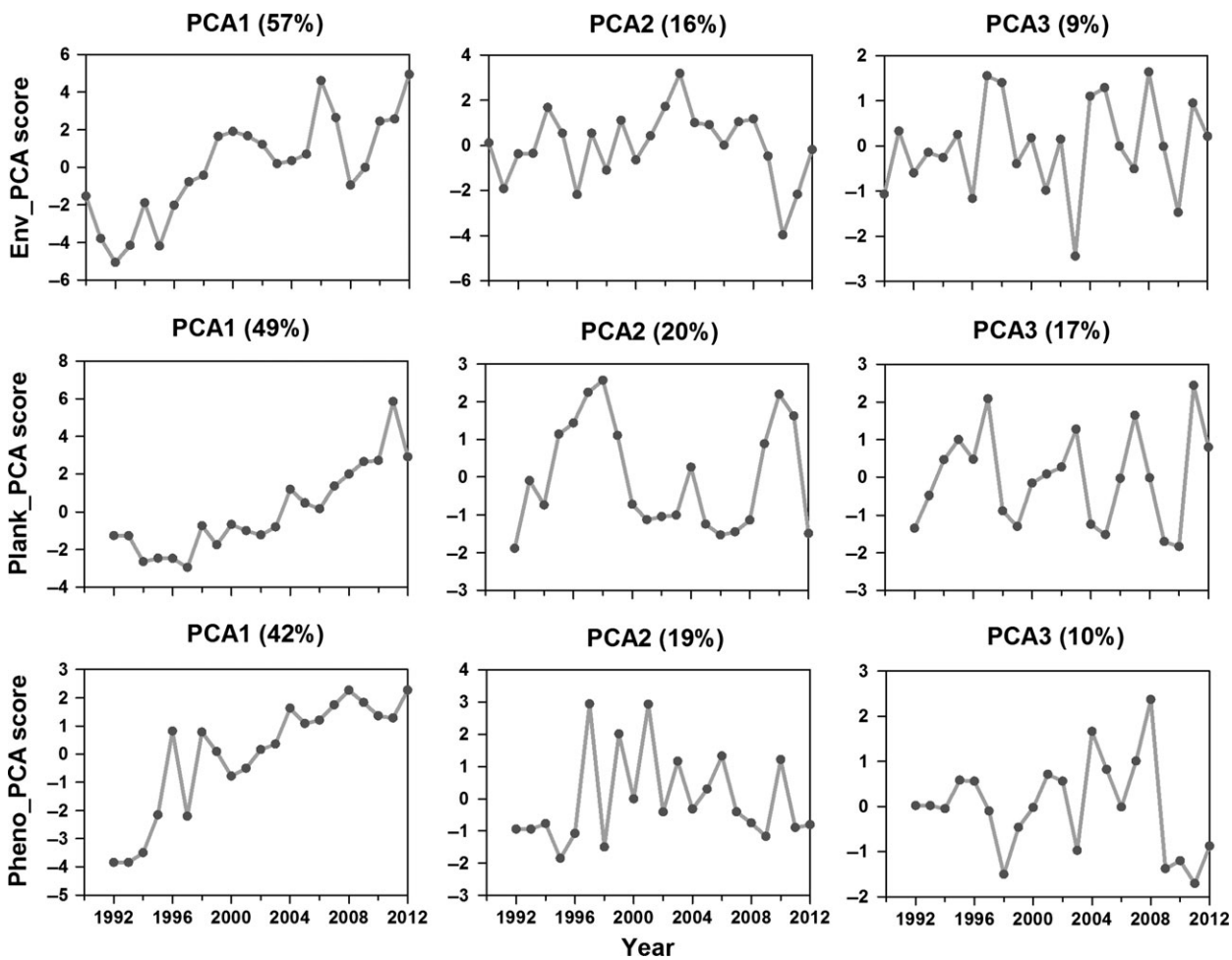
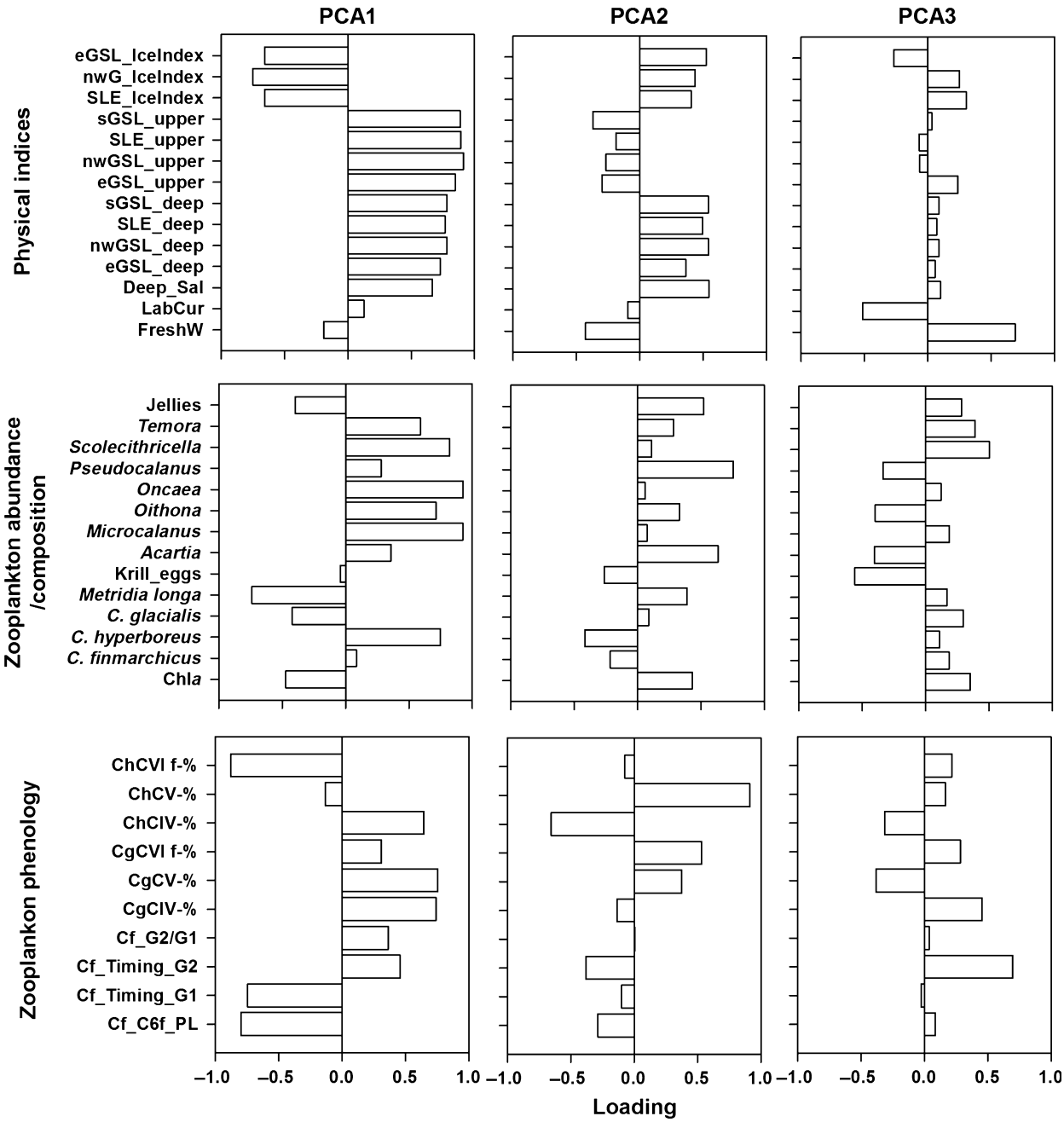


Figure 2. Loadings of different variables on the three dominant PCA axes of physical conditions (upper panels), zooplankton abundance/composition (middle panels), and zooplankton phenology (lower panels). See Table 1 for acronyms' description.



Calanus species, *T. longicornis* and the mid-water species *Scolecithricella* sp. were the main determinant of Plank_PCA3 values (Figures 1 and 2). Finally, the relative stage proportion of *C. hyperboreus* and *C. glacialis* 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 (Figures 1 and 2).

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 strong 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, the strong negative correlation between Plank_PCA2 and Env_PCA2 suggests a potential relationship between the high abundance of C. *finmarchicus* and C. *hyperboreus* with cold upper layer water, a sea-ice index above average, a warmer and saltier deep water layer and a lower freshwater runoff from the St. Lawrence River (Figures 1 and 2).

Physics, competitors and mackerel dynamics: 1971–2012

Env_PCA1 scores were above average (high temperature, low ice conditions) from 1979 to 1985, a period intercalated between years with lower than average scores (colder water and greater ice index) (Figures 2 and 3). Variations in deep water temperature and salinity, in the St. Lawrence River freshwater runoff, and in ice cover drove the pattern of Env_PCA2 scores between a period with loadings above the average (1979–1991) and years (2010–2012) showing the lowest PCA loadings of the time series (ice cover and deep water temperature below average, greater freshwater runoff) (Figures 2 and 3). Env_PCA3 was mainly driven by variations in freshwater runoff (Figures 2 and 3).

Important changes in herring SSB occurred during the 1978–2012 period. The SSB of spring spawning herring steadily decreased between 1995 and 2005 and remained at a near historical low level (Fig. 3). After a period of very low SSB (1978–1982), fall spawning herring showed two periods of high SSB (1983–1994, 2003–2009) separated by years during which SSB was near the average (Fig. 3). Overall, the total herring SSB showed a stepwise decline driven respectively by the spring (mid-1990s) and fall (2010–2012) components (Fig. 3).

Mackerel stock indices showed a relatively stable and long period of high biomass (total and SSB) from 1971 to the mid-1990s (Fig. 4). SSB sharply decreased in 1992, increased again after the 1999 recruitment event and decreased again from 2007 to 2012 to a historical low (Fig. 4). The R_s time series was characterized by three exceptional recruitment events (1974, 1982 and 1999) (Fig. 4). K_June abruptly decreased in 1985 after a period with high values but increased again in 2009 (Fig. 4). K_sept/June varied over 5- to 10-yr periods between 1983 and 2006, much steeply declined between 2007 and 2012 to values only observed in the 1970s (Fig. 4).

Environmental effect on mackerel stock dynamics

The optimal GAM for K_June was for the 1990–2012 period and 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

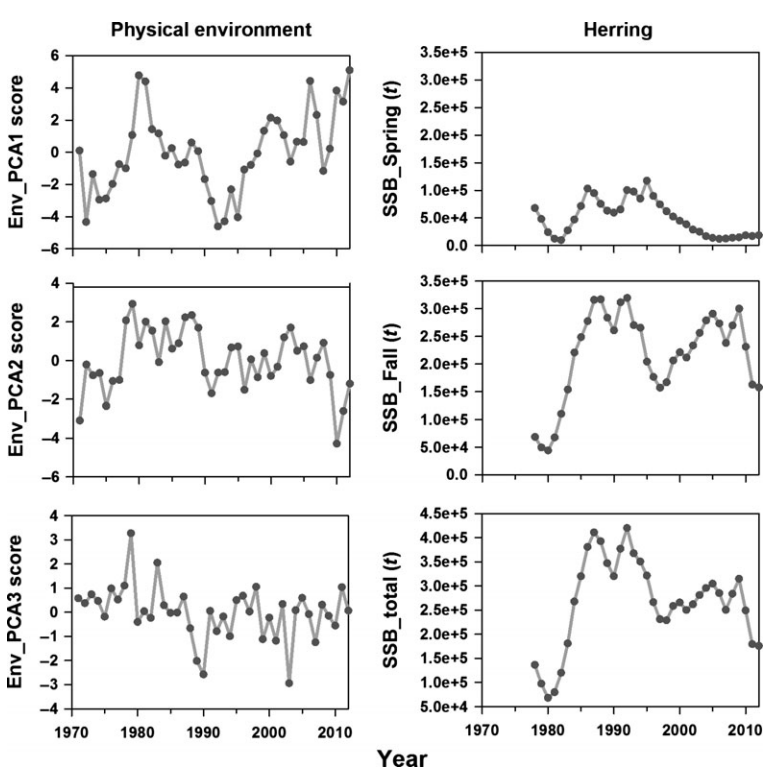


Figure 3. Long-term (1971–2012) variability in physical and biological conditions in the southern Gulf of St. Lawrence. Left panels: time series of dominant Principal Components Analyses (PCAs) performed with a set of physical indices (Env). Right panels: time series of Atlantic herring spring and fall spawning stock biomass and total spawning stoch biomass (SSB).

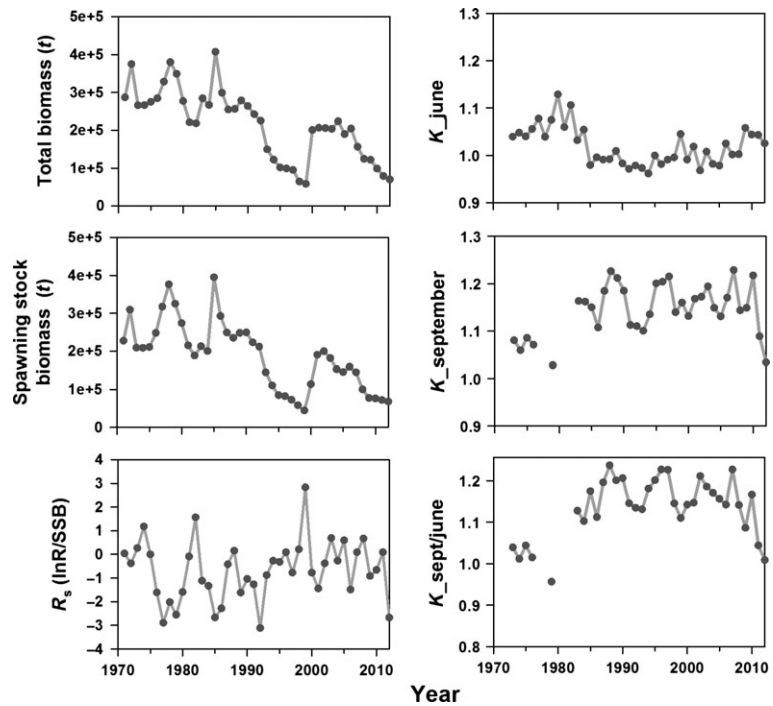


Figure 4. Long-term (1971–2012) variability in Atlantic mackerel stock dynamics. Time series of total biomass (*t*), spawning stock biomass (SSB) (*t*), recruitment success (R_s), individual condition (K) during spawning in June (K_june) and in September (K_sept), and the ratio of condition at the end of summer in September and during spawning (K_sept/June).

Plank_PCA1, followed by Pheno_PCA2 and mackerel total biomass (Table 3). K_june positively responded to the increase in Plank_PCA1 (increase of *C. hyperboreus*, *T. longicornis* and *Pseudocalanus* spp.), to Pheno_PCA2 (an earlier timing of *Calanus* recruitment in spring) and was negatively related to mackerel total biomass (Fig. 5a–c).

Results of models with K_sept/june were markedly different from those obtained for K_june (Table 3). The optimal model explained 57% of the deviance in comparison to 10.9% for the basic GAM considering only mackerel total 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. 6a,c). Although marginally not significant, Plank_PCA2 was selected in the optimal model with its slight positive effect (Fig. 6b). Therefore, this 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.

The basic GAMs considering only the effect of total biomass on R_s explained the same percentage of deviance for the 1971–2011 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 obtained when considering 2012 explained 75% of the deviance, and included K in September (Table 4). The optimal model was for the 1990–2011 period and was selected on the basis of ecological significance as well as 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 with the total mackerel biomass and positively with an Env_PCA2 score (low St. Lawrence River freshwater runoff, warm deep water, cold upper layer water and high ice index) (Fig. 7a,b). 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 either a very late development or an extremely early development of *C. finmarchicus* (Fig. 7c). The strong negative correlation between Env_PCA2 and Plank_PCA2 scores also suggests that Env_PCA2 could represent a proxy for variations in zooplankton occurring at the same temporal scale, with a high abundance of *C. finmarchicus*, *C. hyperboreus* and krill eggs associated with positive Env_PCA scores (Table 2, Fig. 2). The herring SSB 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 explained deviance (Table 4).

Overall, basic models considering only the effect of stock biomass did a poor job at predicting long-term

Table 3. Details of the Generalized Additive Models (GAM) models testing the effect of environmental variability and mackerel stock parameters on K_june and K_sept/june. Normal Black: basic model. Underlined text: models not selected. Bold: optimal 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	K_sept/jun ~ Maq_Tot_Biom^{ns}	0.00545	6.3	
1990–2012	K_sept/jun ~ Maq_Tot_Biom^{ns}	0.00319	10.9	
1990–2012	K_sept/jun ~ Maq_Tot_Biom^{ns} + Plank_PCA1** + Pheno_PCA2^{ns}	0.00234	48.7	37.8
1990–2012	K_sept/jun ~ Maq_Tot_Biom^{ns} + Plank_PCA1** + Pheno_PCA3^{ns}	0.00213	50.5	39.6
1990–2012	K_sept/jun ~ Plank_PCA2* + Pheno_PCA3**	0.00218	51.9	41.0
1990–2012	**K_sept/jun ~ Plank_PCA1** + Pheno_PCA3* + Plank_PCA2^{ns}**	**0.00194**	**57.0**	**46.1**

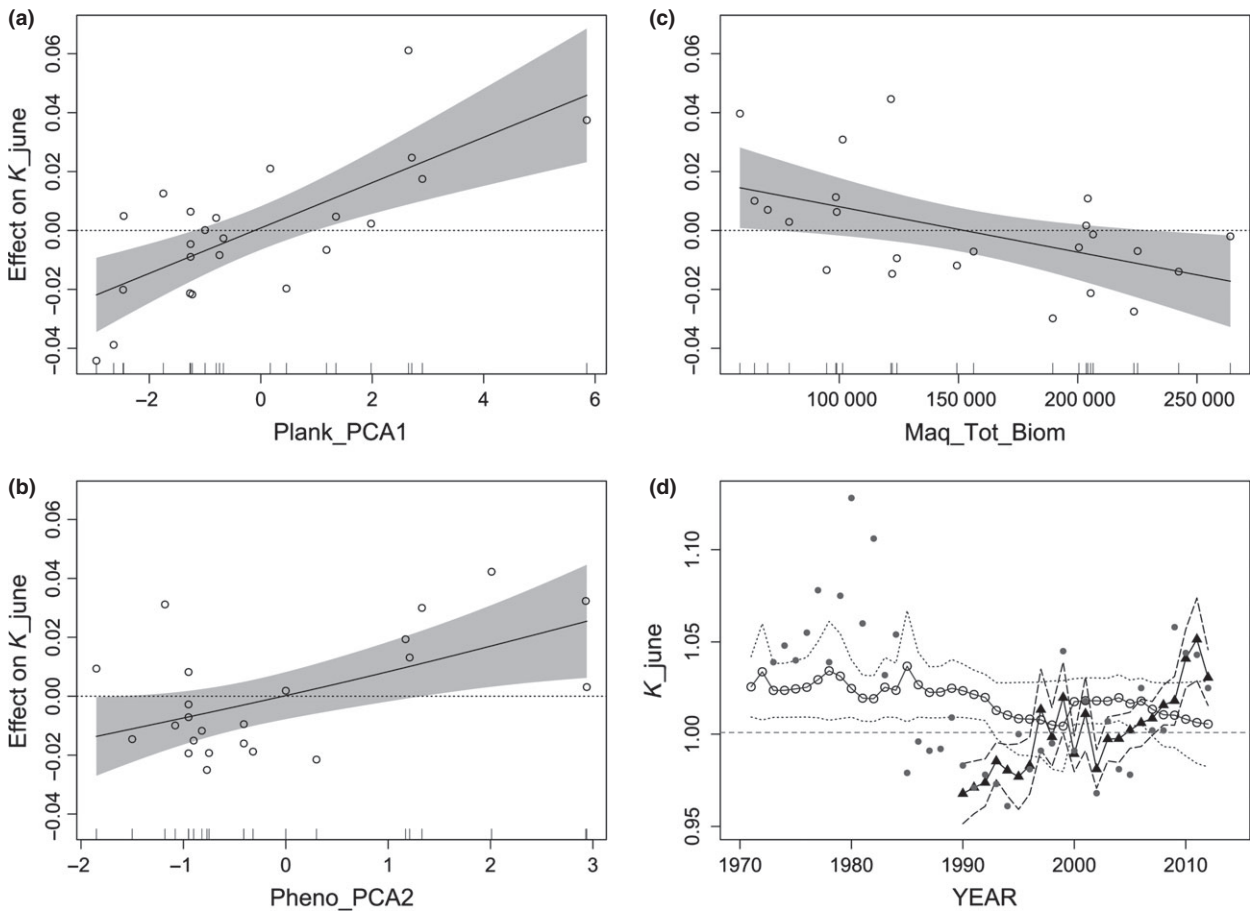
Δ DEV is the difference between the model and the basic run.
Maq, Mackerel; Tot, total; Spr, Spring, Her, 4T herring, Biom, total biomass; SSB, spawning stock biomass.
P-value of smooth terms are indicated by: ns >0.05; *>0.01; **>0.001; ***<0.001.

and interannual variations in K_June, K_sept/June and R_s. For K_June, the optimal model including the influence of variations in zooplankton dynamics in addition to total mackerel biomass predicted well the positive long-term trends observed from the early 1990s to 2011 as well as the marked interannual variations typical of the time series (Fig. 5d). Similarly, the optimal model based on variation in zooplankton dynamics predicted well the 5- to 6-yr cycle in K_sept/June observed from 1990 to 2012 in addition to its abrupt decline occurring from 2007 to 2012 (Fig. 6d). The basic model relating R_s to total mackerel biomass predicted the increase in R_s apparent in the observations from 1992 to 2000 and associated with a gradual decrease in mackerel biomass initiated during the early 1990s (Figures 4 and 7d). The optimal model considering the effect of variations in zooplankton dynamics did better to predict high-frequency variations in R_s, including the high R_s occurring in 1999 (the last strong recruitment year) (Fig. 7d). On a shorter timescale, R_s varied around the long-term average from 2002 to 2012 with no evidence of a consistent trend (Fig. 7d).

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

Figure 5. Results of the optimal Generalized Additive Models (GAM) showing the effect of significant environmental Principal Components Analyzes (PCAs) and mackerel total biomass (Maq_Tot_Biom) on individual condition in June (K_June) (a–c) and performance of the model (d). Panels a–c: tick marks on the *x*-axis represent the 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 and the shaded area represents 95% confidence intervals. Panel d: grey circles denote observed values; open circles: predicted values with basic models based on total stock biomass; black triangles: predicted values with optimal model. See Tables 3 and 4 for formulation and statistics associated with each model. Horizontal grey dashed line: long-term average of observed values. Dotted and long dashed lines: uncertainty (±2 SD) around predicted values of the basic and optimal models, respectively.



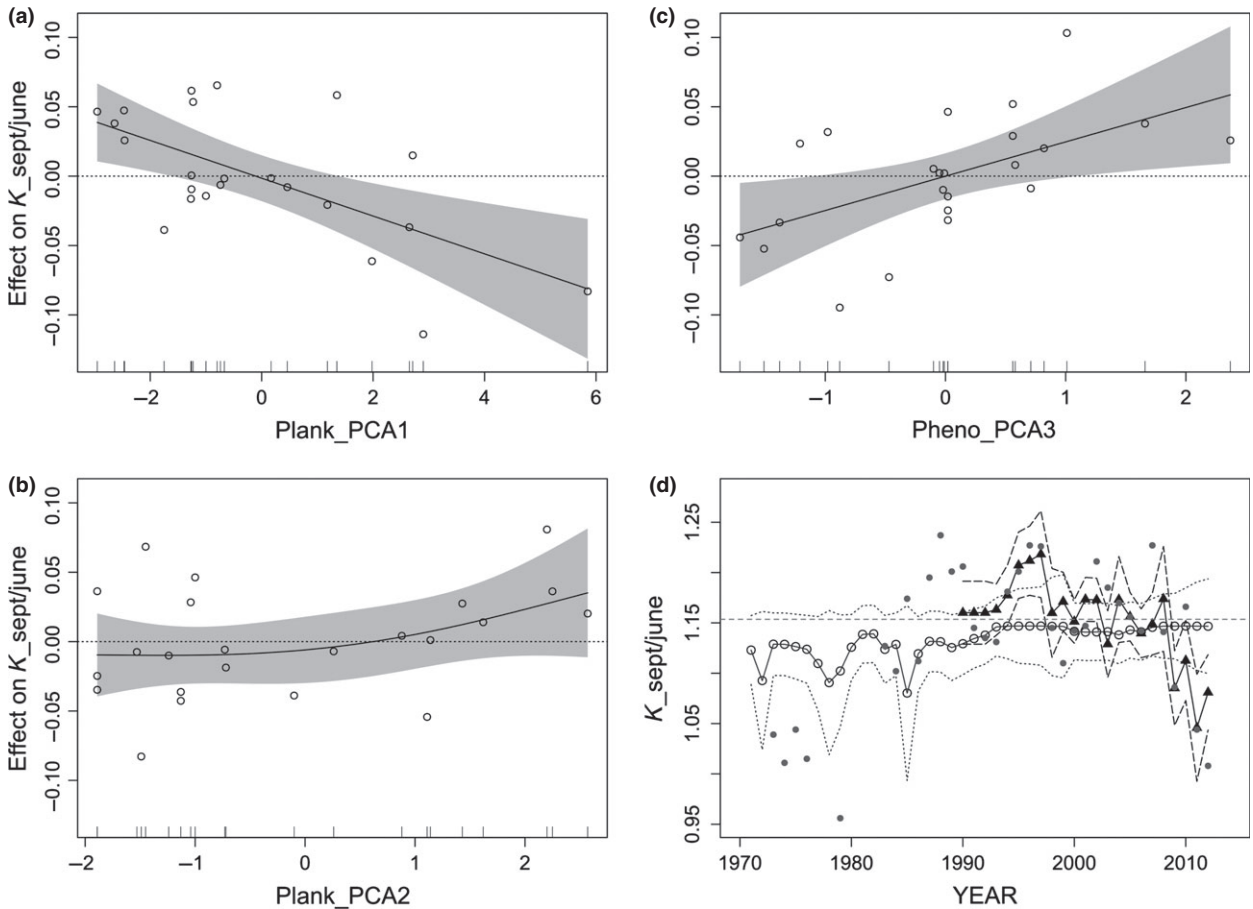
and biological environmental conditions had significant effects on the individual condition (K) and recruitment success (R_s) of the Atlantic mackerel stock, with variations in zooplankton dynamics showing the stronger impacts on stock parameters. Therefore, variations in bottom-up processes were important in determining key individual and population parameters of the mackerel stock in addition to the intrinsic stock dynamics (stock biomass).

Physical and biological environmental variability

Our study provides the first integrated description of the long-term variations of the environment at lower levels of the GSL food web by considering indices of physical environmental conditions and zooplankton community structure and dynamics. PCA identified different modes of environmental variability with strong correlations between physical and zooplankton PCAs (Figures 1 and 2, Table 2). These changes in zooplankton community composition and phenology clearly show that the planktonic production in the GSL is highly sensitive to variations in physical forcing at various temporal scales. Our results suggest that bottom-up processes dominated the regulation of zooplankton production at different time scales during the 1990–2012 period.

Although the three *Calanus* species showed markedly different abundance patterns, all exhibited

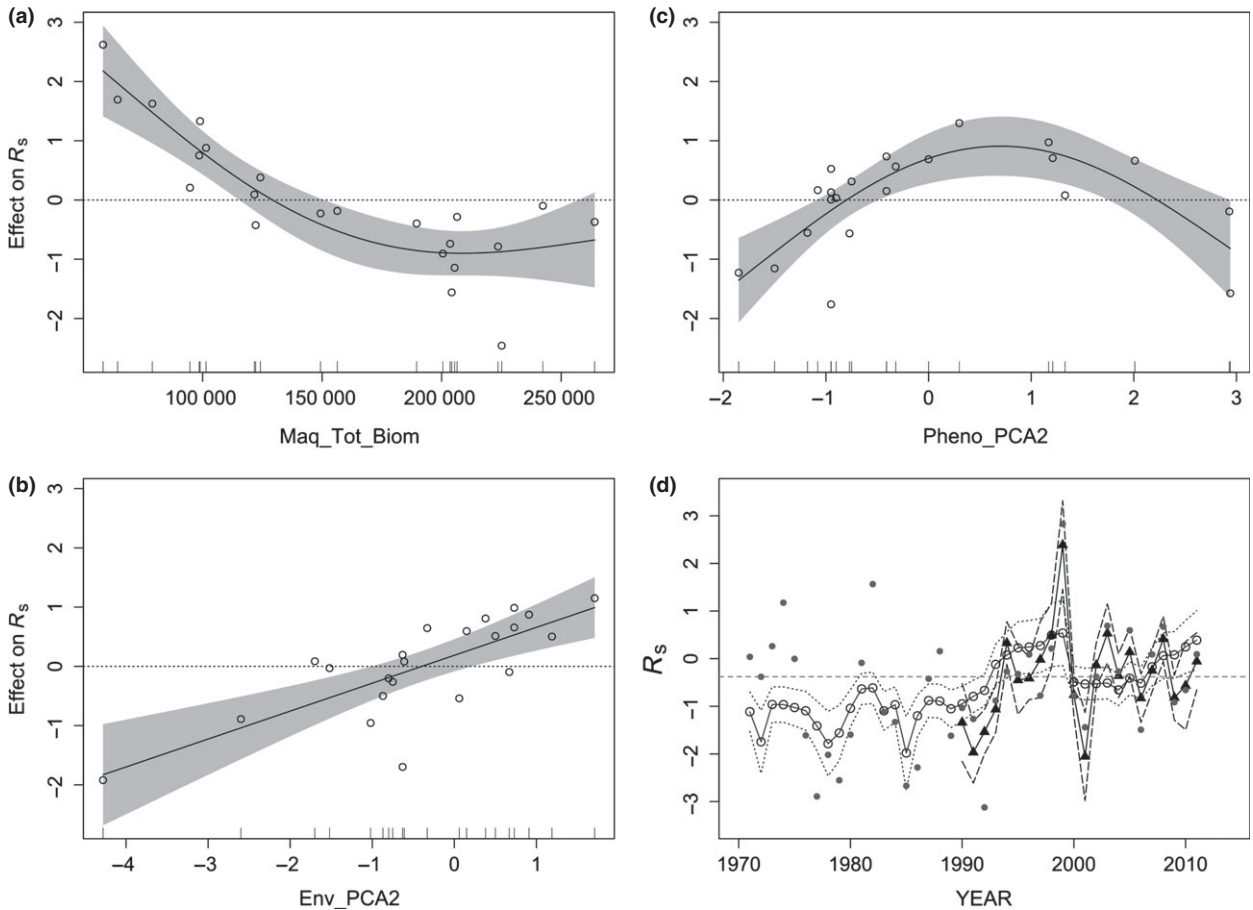
Figure 6. Results of the optimal Generalized Additive Models (GAM) showing the effect of significant environmental Principal Components Analyses (PCAs) on the gain in condition during the summer (K_sept/June) (a–c) and the performance of the model (d). See Fig. 5 legend for layout details.



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 the upper and deep water layer, whereas abundance of *C. finmarchicus* varied on shorter scales without any evidence for a long-term trend. 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 (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 adequate deep overwintering habitats. Owing to its larger size, *C. hyperboreus* could also potentially have a better capability to overwinter in non-arctic (warmer) regions than *C. glacialis* (Maps *et al.*, 2014). The phenology of *C. finmarchicus* was also markedly affected by the variations in temperature and sea-ice dynamics at the scale of 5–10 yr with notable changes in 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 onset and amplitude of the spring phytoplankton blooms (Wu *et al.*, 2007).

The warm conditions observed in 2012 across the northwestern North Atlantic 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 2 yr (2010–2011) during which water temperature was well above the average (Fig. 1, Galbraith *et al.*, 2014).

Figure 7. Results of the optimal Generalized Additive Models (GAM) showing the effect of significant environmental Principal Components Analyses (PCAs) and Atlantic mackerel stock variables on recruitment success (R_s) (a–c) and performance of the model (d). See Fig. 5 legend for layout details.



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 2010–2012 occurred 32 yr ago in 1980 and 1981 (Fig. 3). Therefore, the warm environmental conditions of 2012 could be considered as extreme but not unique. 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.

We chose to use the complete time series for physical data because we wanted to analyse the shorter zooplankton time series (1992–2012) in the context of long-term changes in physical environmental conditions (1971–2012) (Fig. 4). A close examination of the surface (0–150 m) and deep (>150 m) layer temperature composites revealed that similar extreme cold and warm conditions were observed in both the 1971–2012 and 1992–2012 periods (Galbraith *et al.*, 2014). This similarity in physical environmental conditions between the two periods suggests that the use of different reference periods would not have had a significant effect on the anomalies of the physical indices. This similarity also indicates that variations in the zooplankton time series were associated with a range of physical environmental conditions similar to those observed along the long time series.

Environmental effect on mackerel stock dynamics.

The GAMs revealed that variations in physical and biological environmental conditions had significant effects on K_June, K_sept/June and 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 likely has a more direct effect on mackerel K and R_s than temperature

Table 4. Details of the Generalized Additive Models (GAM) models testing the effect of environmental variability and mackerel stock parameters on mackerel recruitment success (R_s). Normal Black: basic model. Underlined text: models not selected. Bold: optimal 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
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* + 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_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* + 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
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**

Δ DEV is the difference between the model and the basic run.
Maq, Mackerel; Tot, total; Spr, Spring, Her, herring, Biom, biomass.
P-value of smooth terms are indicated by: ns >0.05; *>0.01; **>0.001; ***<0.001.

alone. The high percentage of deviance explained by the optimal 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 a 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 favour feeding success, and consequently individual K and stock's R_s (Cushing, 1990).

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 optimal 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 (Darbyson *et al.*, 2003). The significant effect of Pheno_PCA2 suggests that the dynamics (timing, duration) of *C. finmarchicus* 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 K_june (Table 3, Fig. 5). In contrast, K_sept/june was negatively influenced by Plank_PCA1 and positively by Plank_PCA2 (Fig. 6), these axes describing an opposite effect of large *Calanus* (negative) and a high abundance of *Pseudocalanus* spp. and *T. longicornis* spp. (positive), two smaller copepods taxa that are dominant and actively growing in summer and fall in the southern GSL (Plourde *et al.*, 2014). The selection of Pheno_PCA3 in the optimal 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 stock biomass, mackerel R_s was positively affected by Env_PCA2, i.e., by a 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. 7). The dome-shape effect by Pheno_PCA2 indicates that an optimal timing of zooplankton production might favour mackerel R_s. The negative and strong 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).

The fact that 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 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 a 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), K_sept probably reflects the net impact of mackerel feeding conditions during summer in that region.

Our results indicate that environmental variability is an important determinant of mackerel recruitment success in the GSL that could modulate stock productivity. A significant influence of physical and biological (zooplankton) environmental conditions on North Sea mackerel larvae growth and survival and Baltic Sea herring stock recruitment supports the existence of climate-driven spawning stock-recruitment relationships (Cardinale *et al.*, 2009; Casini *et al.*, 2010; Margonski *et al.*, 2010; Jansen, 2014). 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 is central to the ecosystem approach to fisheries management.

While this study shows that bottom-up processes strongly modulate K and R_s of Atlantic mackerel in the Gulf of St. Lawrence, it is important to highlight that the annual mackerel egg survey indicates that the stock is currently near its historical minimum (Grégoire and Beaudin, 2014). The recent stock decline (that started in the mid-2000s) has been caused by fishing mortality levels several times higher than previously sustainable levels. It is possible that the mackerel stock is currently in a situation of recruitment overfishing (DFO, 2014), i.e., the stock may now be at an abundance level where recruitment has been impaired. Hence, in addition to bottom-up processes, the intensive fishery of the past decade may also have had an impact on recent recruitment levels. However, it should be noted that a high R_s was observed in 1999 despite a very low SSB (Figures 4 and 7), suggesting that particular physical and biological (zooplankton) environmental conditions could promote a strong recruitment independently of the influence of SSB.

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 yr) and a second mode occurring on a shorter time scale (5–10 yr). These variations in bottom-up processes likely play a key role in the control of K and R_s of mackerel with variations in key copepod species dynamics being more important than stock biomass or physical environmental conditions alone. These results also illustrate that the large variations in mackerel R_s in the GSL could be driven by environmental conditions independently of stock biomass suggesting that environmental conditions should be considered in the management of that stock.

ACKNOWLEDGEMENTS

We would like to thank the numerous Department of Fisheries and Oceans (DFO) employees that have been and are currently contributing to data and sample collection, analysis and reporting. We thank P. Joly for his dedicated work in sampling at the Rimouski station for more than 20 yr. Suggestions made by D. Duplisea and M. Desgagnés contributed to improve the overall quality of data analyses. We thank P. Ouellet and Yvan Lambert for their comments that contributed to improve this manuscript. Two anonymous reviewers and J. A. Runge also provided suggestions that improved this manuscript. This work was funded by DFO's Aquatic Climate Change Adaptation Services Program (ACCASP).

REFERENCES

Bartolino, V., Margonski, P., Lindegren, M. *et al.* (2014) Forecasting fish stock dynamics under climate change: Baltic herring (*Clupea harengus*) as a case study. *Fish Oceanogr.* **23:**258–269.

Cardinale, M., Möllmann, C., Bartolino, V. *et al.* (2009) Effect of environmental variability and spawner characteristics on the recruitment of Baltic herring *Clupea harengus* populations. *Mar. Ecol. Prog. Ser.* **388:**221–234.

Casini, M., Bartolino, V., Molinero, J.-C. and Kornilovs, G. (2010) Linking fisheries, trophic interactions and climate: threshold dynamics drive herring *Clupea harengus* growth in the central Baltic Sea. *Mar. Ecol. Prog. Ser.* **413:**241–252.

Castonguay, M., Plourde, S., Robert, D., Runge, J.A. and Fortier, L. (2008) Copepod production drives recruitment in a marine fish. *Can. J. Fish Aquat. Sci.* **65:**1528–1531.

Chust, G., Castellani, C., Licandro, P., Ibaibarriaga, L., Sagarminaga, Y. and Irigoien, X. (2014) Are *Calanus* spp. shifting poleward in the North Atlantic? A habitat modelling approach. *ICES J. Mar. Sci.* **71:**241–253.

Cushing, D.H. (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Adv. Mar. Biol.* **26:**249–293.

Darbyson, E., Swain, D.P., Chabot, D. and Castonguay, M. (2003) Diel variation in feeding rate and prey composition of herring and mackerel in the southern Gulf of St Lawrence. *J. Fish Biol.* **63:**1235–1257.

DFO. (2014). Assessment of the Atlantic Mackerel stock for the Northwest Atlantic (Subareas 3 and 4) in 2013. *DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2014/030.*

Fortier, L. and Villeneuve, A. (1996) Cannibalism and predation on fish larvae by larvae of Atlantic mackerel, *Scomber scombrus*: trophodynamics and potential impact on recruitment. *Fish. Bull. US* **94:**268–281.

Galbraith, P.S. (2006) Winter water masses in the Gulf of St. Lawrence. *J. Geophys. Res.* **111:**C06022.

Galbraith, P.S., Larouche, P., Chassé, J. and Petrie, B. (2012) Sea-surface temperature in relation to air temperature in the Gulf of St. Lawrence: interdecadal variability and long term trends. *Deep Sea Res. Part 2 Top. Stud. Oceanogr.* **77–80:**10–20.

Galbraith, P.S., Chassé, J., Gilbert, D.. *et al.* (2014) Physical Oceanographic Conditions in the Gulf of St. Lawrence in 2013. *DFO Can. Sci. Advis. Sec. Res. Doc. 2014/062.* vi + 84.

Gilbert, D. (2004) Propagation of Temperature Signals from the Northwest Atlantic Continental Shelf Edge into the Laurentian Channel. ICES CM 2004/N:7, 12.

Grégoire, F. and Beaudin, L. (2014) Analytical Assessment of the Atlantic Mackerel (*Scomber scombrus* L.) in NAFO Subareas 3–4 in 2013. *DFO Can. Sci. Advis. Sec. Res. Doc. 2014/079.* v + 44.

Grégoire, F., Beaulieu, J.-L., Gendron, M.-H. and Lévesque, I. (2013). The Atlantic Mackerel (Scomber scombrus L.) in NAFO Subareas 3 and 4 in 2011. *DFO Can. Sci. Advis. Sec. Res. Doc. 2013/049.* vi + 130.

Han, G. and Li, J. (2008) Sea level and geostrophic current features from tandem TOPEX/Poseidon-Jason data in the Newfoundland offshore. *Int. J. Remote Sens.* **29:**265–280.

Hare, S.R. and Mantua, N.J. (2000) Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Prog. Oceanogr.* **47:**103–145.

Jansen, T. (2014) Pseudocollapse and rebuilding of North Sea mackerel (*Scomber scombrus*). *ICES J. Mar. Sci.* **71:**299–307.

LeBlanc, C.H., Mallet, A., MacDougall, C., Bourque, C. and Swain, D. (2012). Assessment of the NAFO Division 4T southern Gulf of St. Lawrence herring stocks in 2011. *DFO Can. Sci. Advis. Sec. Res. Doc. 2012/111.* vi + 167.

Maps, F., Zakardjian, B., Plourde, S. and Saucier, F.J. (2011) Modeling the interactions between the seasonal and diel migration behaviors of *Calanus finmarchicus* and the circulation in the Gulf of St. Lawrence (Canada). *J. Mar. Syst.* **88:**183–202.

Maps, F., Record, N.R. and Pershing, A.J. (2014) A metabolic approach to dormancy in pelagic copepods helps explaining inter- and intra-specific variability in life-history strategies. *J. Plankton Res.* **36:**18–30.

Margonski, P., Hansson, S., Tomczak, M. and Grzebielec, R. (2010) Climate influence on Baltic cod, sprat, and herring stock-recruitment relationships. *Prog. Oceanogr.* **87:**277–288.

Ottersen, G., Stige, L.C., Durant, J.M. *et al.* (2013) Temporal shifts in recruitment dynamics of North Atlantic fish stocks: effects of spawning stock and temperature. *Mar. Ecol. Prog. Ser.* **480:**205–225.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. and the R Development Core Team (2012). nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-105.

Plourde, S., Joly, P., Runge, J.A., Zakardjian, B. and Dodson, J.J. (2001) Life cycle of *Calanus finmarchicus* in the lower St. Lawrence Estuary: imprint of circulation and late phytoplankton bloom. *Can. J. Fish Aquat. Sci.* **58:**647–658.

Plourde, S., Dodson, J.J., Runge, J.A. and Therriault, J.-C. (2002) Spatial and temporal variations in copepod community structure in the lower St. Lawrence Estuary, Canada. *Mar. Ecol. Prog. Ser.* **230:**221–224.

Plourde, S., Joly, P., Runge, J.A., Dodson, J.J. and Zakardjian, B. (2003) Life cycle of *Calanus hyperboreus* in the lower St. Lawrence Estuary: is it coupled to local environmental conditions? *Mar. Ecol. Prog. Ser.* **255:**219–233.

Plourde, S., Starr, M., Devine, L. *et al.* (2014) Chemical and Biological Oceanographic Conditions in the Estuary and Gulf of St. Lawrence during 2011 and 2012. *DFO Can. Sci. Advis. Sec. Res. Doc. 2014/049.* V + 46.

R Development Core Team. (2012) R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing.

Ricker, W.E. (1980) Calcul et interprétation des statistiques biologiques des populations de poissons. *Bull. Fish. Res. Board Can.* **191F:**409.

Ringuette, M., Castonguay, M., Runge, J.A. and Grégoire, F. (2002) Atlantic mackerel (*Scomber scombrus*) recruitment fluctuations in relation to copepod production and juvenile growth. *Can. J. Fish Aquat. Sci.* **59:**646–656.

Robert, D., Castonguay, M. and Fortier, L. (2008) Effects of intra- and inter-annual variability in prey field on the feeding selectivity of larval Atlantic mackerel (*Scomber scombrus*). *J. Plankton Res.* **30:**673–688.

Robert, D., Castonguay, M. and Fortier, L. (2009) Effects of preferred prey density and temperature on feeding success and recent growth in larval mackerel of the southern Gulf of St. Lawrence. *Mar. Ecol. Prog. Ser.* **377:**227–237.

Runge, J.A. (1988) Should we expect a relationship between primary production and fisheries? The role of copepod

dynamics as a filter of trophic variability. *Hydrobiologia* **167/168:**61–71.

Runge, J.A., Castonguay, M., de Lafontaine, Y., Ringuette, M. and Beaulieu, J.-L. (1999) Covariation in climate, zooplankton biomass and mackerel recruitment in the southern Gulf of St Lawrence. *Fish Oceanogr.* **8:**139–149.

Therriault, J.C., Petrie, B., Gagnon, J. *et al.* (1998). Proposal for a Northwest Atlantic Zonal Monitoring Program. *Can. Tech. Rep. Hydrogr. Ocean Sci. 194*. vii +57.

Wood, S.N. (2006a) Low-Rank Scale-invariant tensor product smooths for generalized additive mixed models. *Biometrics* **62:**1025–1036.

Wood, S.N. (2006b) Generalized Additive Models: An Introduction with R. London, UK: Chapman and Hall/CRC, pp. 416.

Wood, S.N. (2012) mgcv: Mixed GAM Computation Vehicle with GCV/AIC/REML Smoothness Estimation, R package version 1.7-22.

Wu, Y.S., Peterson, I.K., Tang, C.C.L., Platt, T., Sathyendranath, S. and Fuentes-Yaco, C. (2007) The impact of sea ice on the initiation of the spring bloom on the Newfoundland and Labrador Shelves. *J. Plankton Res.* **29:**509–514.