Fisheries and Oceans Canada
Science

Pêches et Océans Canada
Sciences

Canadian Science Advisory Secretariat (CSAS)

Research Document 2013/129

Quebec region

Ecosystem perspective on changes and anomalies in the Gulf of St. Lawrence: a context in support of the management of the St. Lawrence beluga whale population

Stéphane Plourde, Peter S. Galbraith, Véronique Lesage, François Grégoire, Hugo Bourdages,
Jean-François Gosselin, Ian McQuinn, Michael Scarratt

Fisheries and Oceans Canada
Institut Maurice-Lamontagne
850, Route de la Mer
Mont-Joli, Québec
CANADA G5H 3Z4

May 2014

Foreword

Published by:

Fisheries and Oceans Canada
Canadian Science Advisory Secretariat
200 Kent Street
Ottawa ON K1A 0E6

http://www.dfo-mpo.gc.ca/csas-sccs/
csas-sccs@dfo-mpo.gc.ca

ISSN 1919-5044

Correct citation for this publication:

Plourde, S., Galbraith, P., Lesage, V., Grégoire, F., Bourdages, H., Gosselin, J.-F., McQuinn, I., and Scarratt, M. 2014. Ecosystem perspective on changes and anomalies in the Gulf of St. Lawrence: a context in support of the management of the St. Lawrence beluga whale population. DFO Can. Sci. Advis. Sec. Res. Doc. 2013/129. v + 29 p.

TABLE OF CONTENTS

ABSTRACT IV

RÉSUMÉ V

INTRODUCTION 1

METHODS 1

- DATA SOURCES 1
  - Environmental indices 2
  - Potential fish prey indices 2
  - Beluga whale population and individual indices 3
- DATA ANALYSES 4
  - Data standardization 4
  - Principal Component Analyses (PCA) 4
  - Serial t-test Analysis for Regime Shift identification (STARS) 4

RESULTS 5

- GENERAL ECOSYSTEM CHANGES: 1990-2012 5
- POTENTIAL CHANGES IN BELUGA HABITAT 6

DISCUSSION 7

SUMMARY 11

ACKNOWLEDGEMENTS 12

LITERATURE CITED 12

TABLES 16

FIGURES 19

APPENDIX 28

ABSTRACT

The St. Lawrence beluga whale (*Delphinapterus leucas*) population is at the southernmost limit of the species. In spite of > 30 years protection, there is little or no indication that the population is recovering. The main objective of this study is to characterize long-term changes in the environmental conditions likely to have an impact on beluga population habitat at the scale of the Gulf of St. Lawrence. We used a set of 94 physical and biological parameters to describe different components of the ecosystem. Principal Components Analyses (PCA) were performed to extract the dominant environmental patterns. Shifts in environmental regimes in the time series were identified using sequential t-test analysis of regime shifts (STARS). Our analyses revealed periods during which beluga whale ecosystem parameters changed (late 1990s, mid and late 2000s), such as demersal and pelagic fishes availability and composition, ocean temperature and winter sea ice dynamics. A decrease in the percentage of young beluga in the population and an increase in calf mortality occurred during a period initiated in the late 1990s during which large demersal fish and spring herring biomass was at its lowest and ice coverage was below normal. More recently, years of high calf mortality corresponded to an abrupt decrease in ice cover and duration. The analysis of these environmental parameters over a longer period (1971-2012) revealed that environmental conditions switched from a positive regime, i.e. apparently promoting positive anomalies in beluga population indices, to a predominantly negative regime around 1998, a situation that has worsened since 2009. Our results provide a general ecological context for beluga whale management and suggest that the long-term degradation of suitable prey availability and its winter habitats on the scale of the GSL may explain the population’s lack of recovery.

Perspectives sur les changements et les anomalies dans l'écosystème du golfe du Saint-Laurent : un contexte en support à la gestion de la population de béluga du Saint-Laurent

RÉSUMÉ

Le béluga (*Delphinapterus leucas*) du Saint-Laurent occupe la région située le plus au sud de l'air de distribution de l'espèce. Malgré plus de 30 années de protection, aucune indication de rétablissement de cette population n'est observée. Ce document a pour objectif de décrire les changements à long-terme des conditions environnementales pouvant influencer la population de béluga et son habitat à l'échelle du golfe du Saint-Laurent (GSL) en utilisant un ensemble de 94 variables décrivant différentes composantes de l'écosystème. Des Analyses en Composantes Principales (PCA) ont été utilisées afin de mettre en évidence les patrons dominants de variations environnementales et de la qualité de l'habitat du béluga. Des analyses détectant des changements abruptes des conditions environnementales (STARS) ont également été appliquées afin de mettre en évidence différents régimes environnementaux. Nos analyses ont mis en évidence des périodes (fin de la décennie 1990, milieu et fin des années 2000) durant lesquelles l'écosystème a profondément changé, plus particulièrement au niveau de variables comme la disponibilité de proies potentielles (poissons pélagiques et démersaux), la température de l'eau et la durée et l'amplitude du couvert de glace hivernal. Une diminution de la proportion de jeunes individus dans la population ainsi que des mortalités plus élevées des veaux ont été observées durant une période débutant en 1998 et caractérisée par de très faible biomasse de grands poissons démersaux et de hareng de printemps, ainsi que par des conditions de glace sous la normale à long-terme. De plus, la période de mortalités bien au-dessus de la normale de veaux a été observée durant une période record de très faible couvert de glace. Une analyse de ces variables depuis 1971 a montré que les conditions apparemment associées à des anomalies positives des indices populationnels du béluga ont basculé en 1998 vers un régime semblant défavoriser le béluga, ces conditions s'étant possiblement dégradées de manière encore plus marquée depuis 2009. Nos résultats fournissent un contexte écologique général pour la gestion du béluga et suggèrent que la dégradation à long-terme de son habitat (disponibilité de nourriture, couvert de glace hivernal) à l'échelle du GSL pourrait contribuer à expliquer l'absence de rétablissement de cette population.

INTRODUCTION

The beluga (*Delphinapterus leucas*) is a small odontocete with a circumpolar distribution, and morphologic traits that make it well adapted for living in an ice-covered environment. The population in the Gulf of St. Lawrence (GSL) and its estuary is considered an Arctic relic from the last glaciation, and is at the southernmost limit of the species distribution (de March et al. 2002). This population declined as a result of overharvesting, was afforded full protection from hunting in 1979, and is currently classified as Threatened under the Species at Risk Act. In spite of > 30 years protection, there is no indication that the population is recovering (Hammill et al. 2007).

Various threats to the St. Lawrence Estuary (SLE) beluga population have been identified, including contamination, disturbance, reduced prey availability and quality, and other types of habitat degradation (DFO 2012). However, there has been little consideration given towards threats that could arise from climate mediated changes to the ecosystem, which can profoundly modify habitat, and can be particularly important when dealing with populations at the limit of their distribution range. Features of the habitat that can be particularly important for this ice-adapted species include physical environmental parameters such as water temperature, ice conditions, and prey abundance, availability and quality (see Truchon et al. 2013 for effect of some environmental indices on marine mammal strandings in the SLE).

The main objective of this study was to characterize long-term changes in the environmental conditions in the GSL with an emphasis on physical and biological environmental parameters likely to have an impact on the SLE beluga population. Given the apparent lack of recovery of this population, there are concerns about the quality and amount of habitat available. As a result, we adopted a broad approach encompassing the entire GSL because this species likely uses a vast area of the GSL during its annual cycle (summer and winter habitats) that could impact its population dynamics. We use the term ‘habitat’ in a broad sense as it includes both the physical conditions and potential prey availability at the scale of the GSL. Using a database integrating various components of the GSL ecosystem, including SLE beluga, we first document long-term trends, anomalies or distinct environmental regimes in the physical environment and in different biological components from plankton to demersal fishes. These trends, or distinct environmental regimes, were then examined in the perspective of the changes observed in some of the SLE beluga population indices to characterize the evolution of the SLE and GSL ecosystem in the context of the quality and availability of ‘habitat’ for the SLE beluga population.

METHODS

DATA SOURCES

A set of 94 variables was assembled to describe the long-term changes in environmental conditions in the GSL (see details and references in Table 2). These variables are classified in different categories and aimed at describing different components of the ecosystem, i.e. physical and biological oceanographic conditions, pelagic/forage species biomass and individual condition, and biomass of large and small demersal fish species.

Environmental indices

Climate and physical time series included both large-scale climate indices and physical parameters measured at single stations (see Galbraith et al. 2013 for details). Broad-scale climate indices included the freshwater discharge from the St. Lawrence River as an indicator of continental precipitation variability, and the GSL deep water salinity and Slope Labrador Current volume transport as indicators of the influence of large-scale atmospheric systems on slope water characteristics along the northwest Atlantic shelf (Table 2) (see Greene et al. 2013). Physical data collected on an annual basis in the GSL were used to elaborate a set of indices in different sub-regions of the GSL: estuary (SLE), western (wGSL), eastern (eGSL) and the southern (sGSL) regions (Galbraith et al. 2013, Therriault et al. 1998). These regions are defined based on oceanographic conditions and roughly correspond to NAFO's fisheries management units (4T, 4S, and 4R) (Bourdages and Ouellet 2011). We selected composite indices quantifying the variability in surface (0-125 m) and deep (>150 m) water temperature, as well as variations in winter sea ice using an index combining a measure of quantity (maximum ice volume) and duration (timing of ice melting) (Table 2) (see Galbraith et al. 2013 for details).

Zooplankton indices were extracted from the Rimouski station data series (Table 2) (Plourde et al. 2009, 2011). Rimouski station was selected because it represents the longest zooplankton time series in the region (1992-2012) that also overlaps with the period of beluga and demersal fish monitoring and surveys (see below). Interannual and long-term variations in zooplankton indices at Rimouski station (SLE) were considered representative of the whole GSL, because the large-scale circulation pattern and environmental forcing drives coherent interannual variations in physical and biological oceanographic conditions among SLE, wGSL, eGSL and sGSL (Plourde et al.[1] unpublished data). Two types of zooplankton indices were used. First, mean annual abundance of dominant species/taxa, as well as krill egg abundance and small gelatinous organisms were included (see Table 2). Several of these species/taxa are either important in the food web or indicative of variations in environmental conditions in the GSL. Second, we developed a set of indices aimed at quantifying changes in the phenology (timing of recruitment and population development) of dominant *Calanus* species (Table 2).

Phytoplankton indices were restricted to the annual average of chlorophyll *a* biomass at Rimouski station and abundance of two toxic algae, *Alexandrium tamarense* and *Pseudo-nitzschia seriata,* at the Tadoussac and Ste-Flavie monitoring stations in the SLE (Table 2).

Potential fish prey indices

We included in our analyses time series of abundance and individual condition of some of the potential fish prey of SLE beluga (see Table 2) (Lesage 2014).

Interannual variations in pelagic fish were described using mackerel, herring and capelin (Table 2). The longest available time series are for the Atlantic mackerel (egg survey) and herring (acoustic survey) stock biomass (tons) assessments in 4T (Grégoire et al. 2013a, Leblanc et al. 2012). Atlantic mackerel was included because it is often observed in the SLE and in the wGSL and eGSL despite its historical center of distribution in the sGSL (Grégoire et al. 2013a). The herring spring and fall spawning biomass were considered separately because herring migrating in the SLE spawns in spring and empirical evidence indicates that the spring

---

[1] Fisheries and Oceans Canada, Mont-Joli, QC Canada

spawning component of various herring stocks in the northwest Atlantic is generally decreasing (Auger & Powles 1980, Melvin and Stephenson 2009, Bourne et al. 2013). In the absence of a regular herring stock assessment in 4S and 4R, only 4T herring biomass was included in our data set (Grégoire et al. 2013b). The fact that both spring and fall spawning components showed similar long-term patterns in 4T and 4R (also based on an acoustic survey) suggests that 4T herring is representative of the variability of this species in the region (Grégoire and Beaulieu 2011, Leblanc et al. 2012, Grégoire et al. 2013b). In the absence of a formal stock assessment and extensive commercial fisheries, the dispersion index of capelin (capture probability based on presence/absence) during annual bottom trawl surveys in the GSL was used to describe potential changes in capelin biomass (Table 2) (Grégoire et al. 2013c). However, these data provide only a rough index of biomass because there is also evidence for changes in capelin and herring catch efficiency by bottom trawls as a result of changes in abundance of large piscivorous demersal fish abundance (Mowbray 2002, McQuinn 2009). An individual condition index measured on samples collected by commercial fishermen was used for mackerel (4T) and herring (4T, 4S, 4R) (K index) and 4R capelin stocks (female body length) (see Table 2) (Leblanc et al. 2012, Grégoire and Beaulieu 2011, Grégoire et al. 2013a, Grégoire et al. 2013b).

Interannual variations in demersal fish biomass (kg/tow) were described using data collected during the annual groundfish surveys conducted by DFO in the northern GSL since 1990 (see Bourdages and Ouellet 2011 for details). This group of fish includes seven large demersal species/taxa such as Atlantic cod and redfish and six smaller species/taxa (see Table 2 for a list of species/taxa). Note that several demersal fish taxa were in fact species groups due to a low taxonomic identification of several beluga whale preys. Biomass estimates of commercially exploited and common demersal fish species were adjusted for differences in catching performance between the 1990-2003 and 2004-2012 periods caused by a change in fishing vessel and bottom trawl design (Bourdages et al. 2007). However, biomass estimates of some small demersal fish species/taxa were not adjusted. All small demersal species/taxa were included in the general analyses while a subset of these taxa were selected for the analysis specific to the beluga whale in order to minimize potential bias to our analysis (see below). No individual condition indices for demersal fishes were included at this stage of our exploratory analysis.

Beluga whale population and individual indices

Indices of St. Lawrence beluga population recruitment, mortality and foraging ecology were used to explore for potential association with environmental conditions. Among the indices available, only those where a notable change was observed during the time series were included in the analysis. Specifically, we used the proportion of young (aged 0 and 1 combined) beluga detected during seven aerial photographic surveys of the summer distribution area conducted since 1990 as an index of recruitment (Gosselin et al. 2014, Mosnier et al. 2014). We also used the total number of dead beluga (including calves, which dominated the deaths during some years) found in the SLE and GSL as an index of population mortality (Lesage et al. 2014). Finally, stable carbon isotope signature of beluga muscle for the period 1988 to 2012 was used as an index of the variability in beluga trophic ecology and more specifically, in exploited carbon sources (Lesage 2014).

DATA ANALYSES

Data standardization

Time series were standardized by using an annual anomaly. Annual anomalies were normalized by dividing by the standard deviation of the data over the period considered (here 1990-2012). This approach provided a means of integrating different variables with different units such as temperature, salinity and ice cover, or different fish biomass indices (ex: capelin dispersion index- herring total stock biomass- demersal fish biomass per standard tow), and insuring that all variables had a similar weight in analyses.

Principal Component Analyses (PCA)

A Principal Components Analysis (PCA) was used to examine correlation patterns among variables, reduce the number of variables to a set of uncorrelated composite variables, and extract the dominant patterns of environmental variability to describe large-scale changes in different components of the GSL ecosystem (see Hare and Mantua 2000). Only annual standardized anomalies of the different variables were used in the PCA analyses. PCA were run separately for sets of physical, plankton abundance and phenology, pelagic fish biomass and condition, and demersal fish biomass indices (total of 91 variables, Table 2). Only time series covering most of the 1990 to 2012 period were considered, which corresponds to the period of demersal fish monitoring in the northern GSL (nGSL) and to the time series for beluga aerial surveys. Abundance indices of toxic dinoflagellates were not included in the PCA because the time series was limited to 1994-2011 (Table 2).

A second PCA was performed in an exploratory analysis aimed at identifying environmental variables that are potentially significant to the SLE beluga population. We selected a set of 28 variables: 11 physical indices were considered as indicators of beluga physical habitat, and 17 variables were used as state indicators for potential pelagic (5) and large and small demersal (12) fish prey (biological habitat). We addressed the problem associated with the lack of adjustment of small demersal biomass for the change in sampling gear in 2004 by closely examining each time series. Using results from STARS (see below) on individual time series, we discarded taxa showing only two distinct periods separated by a single change in biomass in 2004. We kept taxa showing a gradual change or several step changes from 2004 to 2012, or similar maximum or minimal values prior to, and after, 2004. This selection minimized the risk of identifying changes solely due to the change of sampling in 2004.

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

Shifts and environmental regimes in time series were identified using sequential t-test analysis of regime shifts (STARS) (Rodionov 2004, 2006). A shift is defined as a sudden transition in physical and biological conditions between two periods (regimes) showing significantly distinct environmental characteristics (de Young et al. 2004). We applied this approach for the first time in the GSL because both physical (ex: cold years in 1990s or warmer years since 2010; Galbraith et al. 2013) and biological (ex: sudden large demersal fish collapse; Bourdages and Ouellet 2011) parameters show patterns similar to the ‘regime’ dynamics observed in other sub-Arctic ecosystems (see 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). Strong autocorrelation (red noise) in the time series can lead to regime shifts being identified incorrectly and needs to be subtracted from the time series by means of filtering procedure before STARS is applied (Rodionov 2006). Red noise was evaluated with the first order autoregressive model (AR1) using the ordinary least square method (OLS) provided with the STARS tool package. After the filtering procedure had been implemented, the regime shift detection method was applied. A Huber parameter (factor for weighing the influence of potential outliers) was defined as 3 and the target significance level set at 0.1. Because the biological time series for the northern GSL is limited to the 1990-2012 period (Table 2) and we did not know the temporal structure of our time series before the analyses, a conservative cut-off length = 5 years was used in order to detect all potential environmental regimes and shifts (see Results). A sensitivity analysis of STARS to variations in cut-off length, Huber parameter and correction for red noise (auto-correlation) revealed small differences in the sum of regime shift indices and in the number of variables showing a significant regime shift (Appendix fig. 1). The consistency in these results indicated that environmental changes identified in our analyses series were robust features.

STARS was performed on all variables or sets of variables synthesized through PCA analysis or simply used individually.

RESULTS

GENERAL ECOSYSTEM CHANGES: 1990-2012

The STARS analysis of a set of 91 variables from 1990 to 2012 identified four periods of intense shifts in environmental conditions and in different components of the ecosystem (Fig. 1). Changes in demersal fish indices occurred in 1993, while several significant regime shifts were detected in environmental (physical and plankton) and pelagic fish time series during the late 1990s, particularly in 1996 and 1997 (Fig. 1). Several regime shifts occurred from 2003 to 2006; while several indices of demersal fish biomass (particularly among small species) showed significant changes in 2004 when fishing gear was changed on the bottom trawl survey, several other regime shifts in environmental (mostly plankton) and pelagic fish indices also occurred in 2004, along with changes in indices of demersal fish biomass in 2003 and in 2005-2006 (Fig. 1). The period when the highest number of variables underwent shifts was from 2009 to 2012 (Fig. 1).

The analysis of the dominant PCA axis of different ecosystem components with STARS detected several modes of variability (Fig. 2, 3). The PCA1 had strong loadings for physical parameters that showed mainly two periods (before and after 1997). The period after 1997 showed evidence of an abrupt change in recent years driven by an increase in surface and deep water temperatures and a reduction in the ice index (see loadings of variables on PCA_env) (Fig. 2). STARS identified significant regime shifts in plankton abundance and phenology indices, with both types of variables showing a significant change between 2003 and 2004 (Fig. 2). Changes in plankton abundance were mainly driven by a decrease in Arctic/cold water shelf species (*C. glacialis*, *M. longa*) and an increase in the large bodied species *C. hyperboreus*; regime shifts identified in zooplankton phenology were mainly driven by changes in the timing of recruitment and body size of *C. finmarchicus* (Fig. 2).

Significant regime shifts were also observed in pelagic fish stock biomass. Loadings of the different variables on the PCA1 indicated a general decrease in mackerel and herring, and an increase in capelin in all regions (dispersion index) (Fig. 3). This change in pelagic fish biomass was accompanied by several positive stepwise changes in condition of pelagic fish of most stocks over the last decade, the notable exception being 4R herring (eGSL) and 4T fall spawning herring (sGSL) (Fig. 3). Finally, the PCA1 of demersal fish biomass showed an abrupt decrease in 1993, the pattern being mainly driven by a decrease in large demersal fish and an increase in several indices of small demersal fish species (Fig. 3).

POTENTIAL CHANGES IN BELUGA HABITAT

The STARS analysis performed on the set of 28 variables describing the ecosystem variability from 1990 to 2012 and potentially contributing more directly to the beluga habitat quality revealed four highly distinct periods of intense changes (Fig. 4), similar to, but better defined, than those previously described with the larger data set (Fig. 1). The physical environment changed in the late 1990s and again from 2009 to 2012. Potential demersal fish prey showed significant changes in 1993, 2004-2006 and 2009-2012 (Fig. 4). Regime shifts in potential pelagic fish prey occurred in 1994-1995, 1998-1999, 2003 and in 2011 (Fig. 4).

The proportion of young beluga detected during the seven aerial photographic surveys of the summer habitat conducted between 1990 and 2012 was examined along with several indicators of physical and biological environmental (Figure 5). The period between 1990 and 1997 was associated with low water temperature and high ice index, and coincided with above normal percentage of young beluga in the population. A positive significant regime shift in the physical environment was observed from the PCA1 analysis to occur between1996 and 1997. The three beluga surveys conducted after this date, which coincided with a period of gradual warming and decrease in ice index, provided consistently lower percentages of young beluga (Fig. 5) (see Appendix fig. 2 for loadings on PCA). The period of lower proportion of young beluga in the population also corresponded with a change to positive anomalies of fish prey PCA1 in 1998-1999 which was driven by a sharp decrease in large demersal fish and 4T spring spawning herring biomass, and an increase in capelin dispersion index and small demersal fish biomass (see Appendix 2 for variables loadings) (Fig. 5). Moreover, a lower proportion of young beluga was also observed during a period of high 4T fall herring described by fish prey PCA2 (see Appendix 2) (Fig. 5) and positive anomalies of pelagic fish condition PCA1 (see Fig. 3 for loadings of variables). These results suggest that the positive anomaly in the proportion of young beluga in the population was associated with high large demersal fish and 4T spring spawning herring biomass with apparently limited direct influence from other variables.

A STARS analysis applied on the annual number of beluga carcasses identified several significantly different periods (Fig. 6). The changes in mortality early in the time series were caused by variations in adult strandings while the significant positive regime shift identified in 2008 was mainly driven by high numbers of calf deaths in 2008, 2010 and 2012 (Fig. 6). There was a general lack of correspondence between toxic algal bloom indicators and death of beluga (ex: 1990s, 2010), although the contribution of an *A. tamarense* bloom to mortalities in 2008 has been suggested based on high toxin levels detected in several potential fish prey and beluga carcasses in the SLE (Starr et al.[2] unpublished data). High calf mortalities in 2010 and 2012 were observed during a period characterized by a highly significant negative regime in ice condition (short duration, low volume/coverage) in the GSL, and, for 2012, high water temperatures (see environment PCA1 and Appendix fig. 2) (Fig. 6). The period of above-normal calf mortalities from 2008 to 2012 also occurred during a regime (2004-2012) of highly reduced large demersal fish and 4T spring herring biomass relative to the 1990s (see fish prey PCA1

---

[2] Fisheries and Oceans Canada, Mont-Joli, QC Canada

and Appendix fig. 2) (Fig 6). Although patterns in beluga deaths in the SLE were not associated with small demersal fish, 4T fall herring biomass and capelin dispersal index (Fig. 6), we note that the highest single value of beluga strandings in 2012 occurred after three years of strongly negative ice conditions, and during a year combining generally low fish prey indicators (fish prey PCA1 and PCA2) (Fig. 6).

The time series of beluga stable carbon isotope signatures was characterized by marked regime shifts in 1995 and 2005 which coincided with changes in surface salinity and potential fish prey availability (Fig. 7). The positive anomaly in beluga carbon isotope ratios observed between 1995 and 2005 corresponded to a regime when biomasses of large demersal fish and 4T fall herring were lower than normal, and when those of small demersal fish and 4T spring herring were higher than normal (see fish prey PCA1 and PCA2, Appendix fig. 2). The negative anomaly observed after 2005 in beluga carbon isotope ratios coincided with a period of positive anomalies in biomasses of small demersal fish, capelin, and 4T fall herring, and occurred during a period of high surface salinity from 2002 to 2010 (Fig. 7). The relatively normal anomaly in stable C isotopes observed from 1990 to 1995 co-occurred with greater than normal large demersal fish and 4T herring biomasses (Fig. 7).

Results from the analyses described above suggest that surface water temperature/ice index, and biomass of large demersal fish and 4T spring herring could potentially be good indicators of more general conditions influencing the SLE beluga population. These variables were examined further to describe the evolution of large-scale ‘physical’ and ‘biological’ habitats of the SLE beluga since 1971. Trawl surveys and monitoring in the SLE and NGL have only been conducted since 1990 (Table 2, Bourdages and Ouellet 2011). However, bottom trawl surveys have been conducted in the sGSL (southern part of 4T) by DFO since 1971 and we were interested to see if longer term changes in the sGSL could be used as a proxy to study changes in the SLE. Overall, long-term changes in large demersal fish stocks in nGSL and sGSL are generally similar, with a massive collapse in stock biomass in the early 1990s followed by an increase in small demersal taxa (Myers et al. 1997, Savenkoff et al. 2007). Therefore, we substituted the nGSL large demersal time series used in our previous analyses (1990-2012) by sGSL time series for this exercise (1971-2012). All four environmental indices showed a sustained negative anomaly (high temperature, short ice season with small coverage, low demersal fish prey biomass) starting in 1996 with unprecedented conditions from 2010 to 2012, resulting in two periods of environmental conditions well below the long-term normal over the last 14 years (Fig. 8). A STARS analysis indicates that these environmental conditions were not observed from 1971 to 1998. High surface temperature/low ice index and lower than normal 4T herring biomass were briefly observed from 1980 to 1984, but large demersal fish indices well above its long-term normal resulted in a short environmental regime characterized by near-normal overall environmental conditions. Before and after this short regime, environmental conditions were characterized by periods of high positive anomalies in 1971-1979 and 1985-1995 (Fig. 8).

DISCUSSION

Our analyses integrating a large array of environmental descriptors of the GSL ecosystem showed distinct periods of intense changes (regime shift) in the physical and biological environment. These shifts separated regimes characterized by different environmental conditions. We were unable to show direct cause and effect, but our analysis has shown that the most recent 5-10 years can be characterized by higher than normal surface water temperatures, lower ice indices and biomasses of demersal fish and 4T spring herring. This appears to have coincided with a decline in the proportion of younger animals in the population and an increase in recent years in beluga mortality mainly driven by calf strandings.

STARS results should be interpreted with care. Firstly, STARS can break down long-term trends into different 'regime' showing significant average values over the time scale considered. Therefore, our regime shift analyses would encompass true regime shift as well as periods with significantly different averages along a long-term, constant trend (see Spencer et al. 2012). Secondly, regime that included the beginning and end of the time series should be considered as indicative of conditions prior to the current analyses or indicators of the future state of the ecosystem (see results for the 2010, 2011 and 2012 in Fig. 1). Our STARS analyses should therefore be considered as a way to synthesize environmental data in order to objectively describe significant changes in the habitat of the SLE beluga whale population, and put various and often discontinuous individual and population variables into a broad ecological context. It was not used to only identify 'pure' regime shifts per se.

The STARS analysis of various dominant axes of a PCA performed on a set of 91 indices identified several regime shifts in environmental conditions in the GSL. However, some of the ecosystem components showed a gradual and constant change following a period of stability indicative of a more constant (intensity and direction) forcing rather than abrupt changes (shift). This pattern suggests that the ecosystem might be in a transitional state as it was observed in PCAs performed with indices of the physical environment, plankton abundance/composition and phenology, and pelagic fish body condition. This coherence among indices suggests a propagation of the environmental signal through the food web typical of a bottom-up effect (Fig. 2, 3) (Greene et al. 2012). PCAs done with demersal and pelagic fish showed changes more typical of abrupt regime shifts potentially resulting from natural processes regulating recruitment and natural mortality (including predation), but also from overfishing (Fig. 3). Various forms of responses in descriptors of marine ecosystems state have been described and have been associated to different dominant modes of environmental forcing (ex: atmospheric vs oceanic) or to inherent characteristics of ecosystem components considered (ex: life history, life span, pelagic vs demersal) (de Young et al. 2004, Spencer et al. 2012, Litzow & Mueter 2014). For example, the abrupt increase in fish prey PCA2 caused by augmenting biomass indices of 4T fall herring and small demersal fish in mid 2000s can be attributed to relatively strong fall herring recruitment events and a sudden increase in small demersal fish following a period of stable indices (Fig. 5) (Leblanc et al. 2012). On the other hand, the continuous increase in fish prey PCA1 from 1990 to 2012 would mainly reflect the continuous decay from 1990 to 1999 of 4T spring herring stock size due to a lack of recruitment and sustained commercial fishing (last boomer year was produced in 1991, Leblanc et al. 2012). Combined with the abrupt collapse in large demersal fish and their lack of recovery potentially due to high predation mortality (Savenkoff et al. 2007, Benoît et al. 2011), the transitional dynamics of 4T spring herring lead to an on-going regime of low biomass of these potential beluga preys (Fig. 5). Therefore, despite the fact that physical and biological indices showed a variety of forms in their responses to large-scale environmental forcing, our STARS analyses nevertheless contributed to identifying distinct periods of environmental conditions in the GSL.

The most recent evaluation of the status of SLE beluga concluded that the population was stable, with a slightly positive outlook (Hammill et al 2007). However, there appears to have been a lower proportion of young beluga in the population during the three aerial photographic surveys conducted in 2000, 2003 and 2009 as compared to surveys done in the 1990s, and a significant increase in the number of calf deaths during the period 2008-2012 (Lesage et al. 2014). These changes coincide with a significant negative anomaly in large demersal fish and 4T spring spawning herring biomass from 1998 to 2012 (Fig. 6, Appendix fig. 2), as well as high surface temperature and the occurrence of the five lowest ice index since 1971, conditions that potentially affected the availability of suitable winter habitat in the GSL (Barber et al. 2001). Additionally, it appears that a very extensive toxic algal bloom in 2008 resulted in high mortality among grey seals, and beluga calves and adults (Starr et al. unpublished data). Thus, it seems that the combined effect of very low large demersal fish and 4T spring herring, and abnormally low ice conditions and high water temperatures since 2006 could have set the stage for a decrease in beluga neonate and adult survival.

It is not known what would be the minimal threshold below which fish biomass, water temperature or ice coverage would begin to affect the dynamics of the St Lawrence beluga population (DFO 2012). The beluga whale is an ice-adapted species that uses particular ice configurations (ice cover 40-90%) as winter habitat, suggesting that variations of adequate ice cover could influence some aspect of its life history as observed in ice-dependent seals species (Barber et al. 2001, Johnson et al. 2005, Friedlaender et al. 2010, Bajzak et al. 2011, Hammill and Stenson 2014). The GSL and SLE are at the southern limit of the seasonal pack ice and showed important interannual variability (Bajzak et al. 2011, Hammill and Stenson[3] unpublished data). The examination of the distribution of ice cover with appropriate characteristics (40-90% coverage) during years of minimal and maximal ice cover revealed that beluga would experience considerable variations in ice conditions and therefore in the availability of suitable winter habitat in the GSL (Fig. 9). The occurrence over the last 7 years of the five lowest annual ice index (duration*volume) recorded since 1971 indicates that ice cover is declining in this area (Fig. 8) (see also Bajzak et al. 2011). Whether, and how, these changes in ice characteristics affect beluga seasonal migration patterns, winter distribution and its overall population dynamics remains uncertain. Ice likely provides shelter against predators and storms. It affects food availability and thus might form an essential part of the beluga habitat. Moreover, decreases in various GSL ecosystem fish components since 1990 are also striking. For example, the large demersal fish biomass in nGSL decreased by 67% during its collapse, a pattern observed in all regions in the eastern Canadian waters (Myers et al. 1997). Likewise, the biomass of 4T spring herring decreased to less than 20% of its historical maximum in the late 1990s (Leblanc et al. 2012). In other regions, spring spawning herring biomass decreased by 75% between 1991 and 1998 in 4R (eGSL) and it has been at 10-15% of its historical maximum since 2008 (Grégoire & Beaulieu 2011). In eastern Newfoundland waters, where spring spawners were historically predominant, autumn spawners have accounted for an increasing proportion of total commercial landings over the past decade (Bourne et al. 2013). In the GSL, the concomitant decrease of spring spawning herring biomass and the collapse of large piscivorous fish (Fig. 2, 3) questioned the proposed trophic cascade hypothesis and pointed toward a key role of climate-driven changes in bottom-up processes regulating recruitment as suggested by the lack of strong recruitment events in spring herring over the last 10-15 years in the GSL (Frank et al. 2005, Greene et al. 2013, Leblanc et al. 2012, Grégoire and Beaulieu 2011, Grégoire et al. 2013b).

In this study we focussed on biomass indices that would provide insights into bottom up processes that may affect beluga in the SLE. Other factors such as top-down processes including natural mortality (mostly predation), competition with other piscivores, e.g. grey, harp and harbour seals and commercial harvesting (identified as secondary threats) were not directly considered (see Benoît et al. 2011, DFO 2012). However, the use of net fish production indices such as total stock biomass (tons) or biomass density (kg/tow) means that competition from

---

[3] Fisheries and Oceans Canada, Mont-Joli, QC Canada

human and other piscivorous predators was implicitly considered in our analyses. Therefore, our analyses made in the context of the beluga population, considered a set of data integrating several factors identified as potentially significant to this beluga population.

Variations in 4T fall herring and small demersal fish biomass, capelin dispersion index, or pelagic fish condition were not associated with patterns in beluga mortality or proportion of neonates in the population, suggesting that they were not first order parameters for the beluga dynamics from 1990 to 2012. In fact, some of these variables appeared inversely related to beluga indices. There could be several reasons to account for these differences. First, adult herring are not resident in the SLE, but based on limited evidence are thought to come from the sGSL (4T) and to enter the SLE in the spring to spawn (Auger & Powles 1980). Thus fall spawning herring may be of little importance for beluga whale at least in its summer habitat. Second, the biomass of small demersal fish species represents only a small fraction (5-6%) of the large demersal fish biomass even after the historical groundfish stocks collapse (Bourdages and Ouellet 2011), indicating that the recent increase in small demersal fish biomass has not compensated for the dramatic loss of large fish biomass and the decrease of spring spawning herring during the 1990s (Savenkoff et al. 2007, Bourdages & Ouellet 2011, Leblanc et al. 2012). Third, the capelin dispersion index determined from the bottom trawl surveys may not reflect an actual increase in population biomass. This may be due to changes in the vertical distribution of both capelin and herring towards deeper habitats in response to the collapse of large piscivorous fish species, (Mowbray 2002, McQuinn 2009). Alternatively, if the capelin dispersion index is a reliable index of its abundance, its apparent inverse association with beluga calf production or beluga mortality suggests that capelin is not a significant component in defining beluga habitat quality. This is in contradiction to historical data on beluga diet, indicating recent consumption of capelin by 50% of the beluga examined (Vladykov 1946). However, the replacement of large demersal fishes and herring by small prey such as capelin has driven the prey field to smaller sizes with potential consequences on the foraging efficiency and overall energy budget (Bowen et al. 2002). Finally, an increase in individual condition as observed in capelin and spring herring would not be sufficient to compensate for the massive decrease in fish biomass described above.

Several fish species commonly observed in beluga whale stomach contents were not included in our analyses because no reliable indicators of their abundance/biomass were available. Sandlance is an important prey species for SLE beluga (Vladykov 1946), but this species is poorly sampled by bottom trawl surveys. The population level of several species characteristics of the upstream portion of the beluga summer habitat in SLE such as the American eel, rainbow smelt and tomcod is considered to be at their historical low (Centre Saint-Laurent 1996). Among them, rainbow smelt and tomcod have shown evidence for decreasing population abundance. Commercial landings of the rainbow smelt south shore population in the SLE markedly decreased and is at 10% of its maximal level since mid-1980s (EREAQ 2008) whereas tomcod abundance has also decreased since the 1980s, and commercial fisheries for this species were closed in the SLE in 1993 (Centre Saint-Laurent 1996). Therefore, evidences point toward a general decline of several potential fish prey located in the upper end of the beluga summer habitat in SLE.

Contemporary data on SLE beluga diet are scarce given that digestive tracts of beluga found dead are often empty. Indirect methods using stable isotope ratios to infer changes in trophic ecology have identified shifts in carbon sources exploited by SLE beluga, suggesting changes in beluga diets or in the characteristics of the ecosystem where they evolve (see Lesage 2014). There may be several causes for the observed decrease in δ^{13}C values of beluga muscle after 2004. However, the increased contribution of a more marine or anadromous/catadromous prey species to the diet, and/or a decrease in a more estuarine or benthic food source is the most likely explanation for the observed change in the beluga isotopic signature (Lesage 2014). Given the varied diet of beluga (Vladykov 1946), the general absence of abundance data for most of these prey in the SLE, and similarity in isotopic signature among several of them, analyses to identify the species responsible for the observed shift in isotopic signature were inconclusive (Lesage 2014). However, a decrease in the contribution to the diet of spring herring originating from the Gulf, and thus from more marine waters, would contribute to enrich the carbon isotope signature of beluga and so, would be contrary to the observed pattern, unless combined with a decline in more ^{13}-C depleted food sources.

The Recovery Plan of St. Lawrence beluga whale identified several threats to the population (DFO 2012). Contaminants, disturbance by human activity, and habitat degradation have been identified as critical threats that have to be diligently addressed to favour population recovery. The Recovery Plan also assumes a constant and non-limiting carrying capacity of the ecosystem, i.e. sufficient availability of adequate physical and biological (ex: food sources) habitats necessary for the population to grow in response to mitigation of critical threats (DFO 2012). Our synthesis analysis provided some insights into general elements identified as knowledge gaps regarding our understanding of factors influencing the SLE beluga population, i.e. diet and energy requirements, critical habitat over a complete seasonal cycle (winter), and impacts of climate change (DFO 2012). Our results indicate that changes in some indices of beluga population dynamics were associated with a decrease in large demersal fish and spring spawning herring biomass that has not been compensated for by the concomitant increase of other potential fish prey or improvements in their body condition (Fig. 5). This observation suggests that the ecosystem might no longer provide conditions necessary to support a beluga population at current levels. The beluga population indices also appeared to be associated to some extent with surface temperature and ice conditions, suggesting a potential impact of variations in the availability of adequate winter habitat on beluga population (Fig. 6). The analysis of these environmental parameters over a longer period (1971-2012) indicates that environmental conditions apparently promoting positive anomalies in beluga population indices switched from a positive regime to a predominantly negative regime around 1998, with measurable impacts on the St. Lawrence beluga whale population (Mosnier et al. 2014). These conditions may have worsened over the last 3-4 years (Fig. 8).

Our results do not diminish the importance of threats identified as critical for the SLE beluga population (DFO 2012). They, however, provide a more general environmental context which is critically important for an understanding of the factors governing beluga population dynamics. The description and understanding of the mechanisms involved in climate-mediated changes in physical and biological environmental conditions possibly contributing to the quality of beluga habitat are important in the wake of the potential future warming of the GSL ecosystem and its adjacent waters (Lavoie et al. 2013). Large-scale environmental conditions potentially detrimental for the fitness of beluga whales could have set the stage for other critical threats to be more harmful (ex: toxic algal blooms, contaminant, and disturbance). The long-term degradation of the winter and biological (food sources) habitat of beluga at the scale of the GSL could also provide a viable hypothesis explaining the lack of recovery of the population despite over three decades of protection (Hammill et al. 2007, DFO 2012).

SUMMARY

- The St. Lawrence beluga whale (*Delphinapterus leucas*) population is at the southernmost limit of the species. In spite of > 30 years protection, there is no indication that the population is recovering.

- A set of 94 time series describing long-term physical and biological (plankton) oceanographic conditions and potential pelagic and demersal fish prey availability between 1990 and 2012 were analyzed using PCA and STARS to identify large-scale significant changes in environmental conditions in the Gulf of St. Lawrence (GSL).
- Analysis revealed three periods (late 1990s, mid and late 2000s) during which significant changes occurred in the general physical and biological (plankton) oceanographic conditions, pelagic fish biomass and condition, and in demersal fish community.
- Analysis revealed that a decrease in the percentage of young beluga in the population and an increase in mortality (calf strandings) occurred during an on-going period initiated in the late 1990s during which large demersal fish and herring biomass was at its lowest and ice conditions was well below normal.
- The period of high calf mortality in 2008, 2010 and 2012 also corresponded to a period of low ice cover and short ice season duration.
- The analysis of these environment parameters over a longer period (1971-2012) suggests that conditions apparently promoting positive anomalies in beluga population indices switched from a positive regime to a predominantly negative regime around 1998, a situation that may have worsened since 2009.
- Our results provide a general ecological context to the beluga whale management and suggest that the long-term degradation of its ‘food’ and winter habitats at the scale of the GSL may explain the lack of recovery of the population

ACKNOWLEDGEMENTS

We would like to thank the numerous Department of Fisheries and Oceans employees that have been and are currently contributing to data and sample collection, analysis and reporting. Their dedication to their work is at the basis of monitoring the biological and physical oceanographic conditions in the Gulf of St. Lawrence and its biological components from pelagic fishes to the beluga whale population. We also thank the several interns and graduate students that have contributed to building this large data set. We are grateful to M.O. Hammill who generously provided comments and suggestions that greatly improved this manuscript.

LITERATURE CITED

Auger, F. and Powles, H. 1980. Estimation of the herring spawning biomass near the Isle Verte in the St. Lawrence Estuary from an intensive larval survey in 1979. Canadian Atlantic Fisheries Scientific Advisory Committee Research Document 80/59. 29 p.

Bajzak, C. E., Hammill M. O., Stenson, G. B., and Prinsenberg, S. 2011. Drifting away: implications of changes in ice conditions for a pack-ice-breeding phocid, the harp seal (*Pagophilus groenlandicus*). Can. J. Zool. 89: 1050-1062.

Barber, D. G., E. Saczuk and P. R. Richard. 2001. Examination of beluga-habitat relationships through the use of telemetry and a geographic information system. Arctic. 54: 305-316.

Benoît, H. P. and Swain, D. 2008. Impacts of environmental change and direct and indirect harvesting effects on the dynamics of a marine fish community. Can. J. Fish. Aquat. Sci. 65: 2088-2104.

Benoît, H. P., Swain, D. P Bowen, D., Breed, G. A., Hammill, M. O., Harvey, V. 2011. Evaluating the potential for grey seal predation to explain elevated natural mortality in three fish species in the southern Gulf of St. Lawrence. Mar. Ecol. Progr. Ser. 442: 149–167.

Bourdages, H., Savard, L., Archambault, D. and Valois, S. 2007. Results from the August 2004 and 2005 comparative fishing experiments in the northern Gulf of St. Lawrence between the CCGS Alfred Needler and the CCGS Teleost. Can. Tech. Rep. Fish. Aquat. Sci. 2750: ix + 57 p.

Bourdages, H., and Ouellet, J.-F. 2011. Geographic distribution and abundance indices of marine fish in the northerm Gulf of St. Lawrence (1990-2009). Can. Tech. Rep. Fish. Aquat. Sci. 2963: VI+ 171 p.

Bourne, C., Mowbray, F., Squires, B., and Croft, J. 2013. An Assessment of Newfoundland East and South Coast Herring Stocks to the Spring of 2011. DFO Can. Sci. Advis. Sec. Res. Doc. 2013/039. v. + 104 p.

Bowen, W. D., Tully, D., Boness, D. J., Bulheier, B. M., Marshall, G. J. 2002. Prey-dependent foraging tactics and prey profitability in a marine mammal. Mar. Ecol. Progr. Ser. 244: 235–245.

Centre Saint-Laurent. 1996. Rapport Synthèse sur l'état du Saint-Laurent. Volume 1: L'écosystème du Saint-Laurent. Environnement Canada- région du Québec, Conservation de l'environnement- et Éditions MultiMondes, Montréal.

de March, B. G. E., Maiers, L. D. and Friesen, M. K. 2002. An overview of genetic relationships of Canadian and adjacent populations of belugas (*Delphinapterus leucas*) with emphasis on Baffin Bay and Canadian eastern Arctic populations. NAMMCO Scient. Publ. 4:17-38.

de Young, B., Harris, R., Alheit, J., Beaugrand, G., Mantua, N. and Shannon, L. 2004. Detecting regime shifts in the ocean: Data considerations. Progr. Oceanogr. 60: 143-164.

DFO. 2012. Recovery Strategy for the beluga whale (*Delphinapterus leucas*) St. Lawrence Estuary population in Canada. Species at Risk Act Recovery Strategy Series. Fisheries and Oceans Canada, Ottawa. 88 pp + X pp.

EREAQ (ÉQUIPE DE RÉTABLISSEMENT DE L'ÉPERLAN ARC-EN-CIEL DU QUÉBEC). 2008. Plan de rétablissement de l'éperlan arc-en-ciel (*Osmerus mordax*) au Québec, population du sud de l'estuaire du Saint-Laurent – mise à jour 2008-2012. Min. Ress. Nat. Faune Québ., Faune Québec. 48 pp.

Frank, K.T., Petrie, B., Choi, J.S. and Leggett, W.C. 2005. Trophic cascades in a formerly cod-dominated ecosystem. Science 308: 1621–1623.

Friedlaender, A.S., Johnston, D.W., and Halpin, P.N. 2010. Effects of the North Atlantic Oscillation on sea ice breeding habitats of harp seals (*Pagophilus groenlandicus*) across the North Atlantic. Prog. Oceanogr. 86: 261–266. doi:10.1016/j.pocean.2010.04.002.

Galbraith, P.S., Chassé, J., Larouche, P., Gilbert, D., Brickman, D., Pettigrew, B.,Devine, L., and Lafleur, C. 2013. Physical Oceanographic Conditions in the Gulf of St. Lawrence in2012. DFO Can. Sci. Advis. Sec. Res. Doc. 2013/026. iv + 92 p.

Gosselin, J.F., Hammill, M. O., Mosnier, A. 2014. Abundance and production estimates based on visual and photographic surveys. DFO Can. Sci. Advis. Sec. Res. Doc. 2014/021. iv + 52 p.

Greene, C. H., Meyer-Gutbrod, E., Monger, B. C., McGarry, L. P., Pershing, A. J., Belkin, I. M., Fratantoni, P. S., Mountain, D. G., Pickart, R. S., Proshutinsky, A., Ji, R., Bisagni, J. J., Hakkinen, S. M. A., Haidvogel, D. B., Wang, J., Head, E., Smith, P., Reid, P. C. and Conversi, A. 2013. Remote climate forcing of decadal-scale regime shifts in Northwest Atlantic shelf ecosystems. Limnol. Oceanogr. 58: 803-816

Grégoire, F., Beaulieu, J.-L., Gendron, M.-H., Lévesque, I. 2013a. 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 p.

Grégoire, F., Beaulieu, J.-L., and McQuinn, I. H. 2013b. The Atlantic herring (*Clupea harengus harengus* L.) stocks of the west coast of Newfoundland (NAFO Division 4R) in 2011. DFO Can. Sci. Advis. Sec. Res. Doc. 2012/121. iv + 70 p.

Grégoire, F., Girard, L., Beaulieu, J.-L., Lussier, J.-F. and Bruneau, B. 2013c. Capelin (*Mallotus villosus*) in the Estuary and Gulf of St. Lawrence (NAFO Divisions 4RST) in 2012. DFO Can. Sci. Advis. Sec. Res. Doc. 2013/023. vi + 90 p.

Grégoire, F., and Beaulieu, J.-L. 2011. Atlantic herring (Clupea harengus harengus L.) on the Quebec North Shore (NAFO Division 4S) in 2010. DFO Can. Sci. Advis. Sec. Res. Doc. 2011/019. vi + 102 pp.

Hammill, M. O., L. N. Measures, J.-F. Gosselin and V. Lesage. 2007. Absence de rétablissement du béluga de l'estuaire du Saint-Laurent. Secr. can. de consult. sci. du MPO. Doc. de rech. 2007/026. 23p.

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 Sen. 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.

Johnston, D.W. Friedlaender, A.S. Torres, L.G. and Lavigne, D. M. 2005. Vartiation in sea ie cover on the east coast of Canada from 1969 to 2002: climate variability and implications for harp and hooded seals. Climate Res. 29: 209-222.

Lavoie, D., N. Lambert, S., Mustapha, B., and van der Baaren, A. 2013. Projections of future physical and biogeochemical conditions in the Northwest Atlantic from CMIP5 Global Climate Models. Can. Tech. Rep. Hydrogr. Ocean Sci. 285: xiv + 156 pp.

LeBlanc, C.H., Mallet, A., MacDougall, C., Bourque, C. et Swain, D. 2012. Évaluation des stocks de hareng de la zone 4T de l'OPANO dans le sud du golfe du Saint-Laurent en 2011. Secr. can. de consult. sci. du MPO. Doc. de rech. 2012/111. vi + 167 p.

Lesage, V. 2014. Trends in the trophic ecology of St. Lawrence beluga (*Delphinapterus leucas*) over the period 1988-2012, based on stable isotope analysis. DFO Can. Sci. Advis. Sec. Res. Doc. 2013/126. iv + 26 p.

Lesage, V., Measures, L., Mosnier, A., Lair, S., Michaud, R. and Béland, P. 2014. Mortality patterns in St. Lawrence Estuary beluga (*Delphinapterus leucas*), inferred from the carcass recovery data, 1983-2012. DFO Can. Sci. Advis. Sec. Res. Doc. 2013/118. iv + 23 p.

Litzow, M.A., Mueter, F.J. 2014. Assessing the ecological importance of climate regime shifts: an approach from the North Pacific Ocean, Prog. Oceanogr., 120: 110-119, doi:

McQuinn, I.A. 2009. Pelagic fish outburst or suprabenthic habitat occupation: legacy of the Atlantic cod (*Gadus morhua*) collapse in eastern Canada. Can J, Fish. Aquat. Sci. 66: 2256-2262.

Melvin, G. D., Stephenson, R. L., and Power, M. J. 2009. Oscillating reproductive strategies of herring in the western Atlantic in response to changing environmental conditions. – ICES J. Mar. Sci., 66: 1784–1792.

Mosnier, A., Doniol-Valcroze, T., Gosselin, J.-F., Lesage, V., Measures, L., and Hammill, M.O. 2014. An age structured Bayesian population model for St. Lawrence Estuary beluga (*Delphinapterus leucas*). DFO Can. Sci. Advis. Sec. Res. Doc. 2013/127. v + 39 p.

Mowbray, F. 2002. Changes in the vertical distribution of capelin (*Mallotus villosus*) off Newfoundland. – ICES J. Mar. Sci., 59: 942–949.

Myers, R. A., Hutchings, J. A., and Barrowman, N. J. 1997. Why do Fish Stocks Collapse? The Example of Cod in Atlantic Canada. Ecol. Appl. 7: 91-106.

Plourde, S., Joly, P., St-Amand, L., and Starr, M. 2009. La station de monitorage de Rimouski : plus de 400 visites et 18 ans de monitorage et de recherche. Bulletin PMZA No. 8, pp 51-55

Plourde, S., Winkler, G., St-Pierre, J-F., Starr, M., and Joly, P. 2011. Long-term seasonal and interannual variations of krill spawning in the lower St. Lawrence estuary, Canada, 1979-2009. J. Plank. Res. 33: 703-714

Rodionov, S. N. 2004. A sequential algorithm for testing climate regime shifts. Geophys. Res. Lett., 31, L09204, doi: 10.1029/2004GL019448.

Rodionov, S. N. 2006. Use of prewhitening in climate regime shift detection. Geophys. Res. Lett., 33, L12707, doi: 10.1029/2006GL025904.

Savenkoff, C., Swain, D.P., Hanson, J.M., Castonguay, M., Hammill, M. O., Bourdages, H., Morissette, L., Chabot, D. 2007. Effects of fishing and predation in a heavily exploited ecosystem: comparing periods before and after the collapse of groundfish in the southern Gulf of St. Lawrence (Canada). Ecol. Modell. 204: 115−128

Spencer, M., Mieszkowska, N., Robinson, L. A., Simpson, S. D., Burrows, M. T., Birchenough, Capasso, E., Cleall-Harding, P., Crummy, J., Duck, C., Eloire, D., Frost, M., Hall, A. J., Hawkins, S. J., Johns, D. G., Sims, D. W., Smyth, T. J., Frid, C. L. J. 2012. Region-wide changes in marine ecosystem dynamics: state-space models to distinguish trends from step changes. Glob. Change Biol. 18: 1270-1281.

Therriault, J.-C., B. Petrie, P. Pépin, J. Gagnon, D. Gregory, J. Helbig, A. Herman, D. Lefaivre, M. Mitchell, B. Pelchat, J. Runge and D. Sameoto. 1998. Proposal for a Northwest Atlantic zonal monitoring program. Can. Tech. Rep. Hydrogr. Ocean Sci., 194: vii + 57 pp.

Truchon, M.-H., Measures, L., L'Hérault, V., Brêthes, J.-C., Galbraith, P. S., and others. 2013. Marine Mammal Strandings and Environmental Changes: A 15-Year Study in the St. Lawrence Ecosystem. PLoS ONE 8(3): e59311. doi:10.1371/journal.pone.0059311.

Vladykov, V.D. 1946. Études sur les mammifères aquatiques. IV. Nourriture du marsouin blanc (*Delphinapterus leucas*) du fleuve Saint-Laurent. Département des pêcheries de la province de Québec. 129 p.

TABLES

Table 1: List of acronyms

Acronyme	Name
GSL	Gulf of St. Lawrence
SLE	St. Lawrence Estuary
nwGSL	Northwest GSL
eGSL	Eastern GSL
sGSL	Southern GSL
nGSL	Northern GSL
Surf	Surface temperature composite
Deep	Deep temperature composite
Temp	Temperature
Sal	Salinity
Cgin	*Calanus finmarchicus*
Cglac	*C. glacialis*
Chyp	*C. hyperboreus*
Mlon	*Metridia longa*
Biom	Biomass
K	Condition Factor
CVIf	Copepodite stage VI female
CIV	Copepodite stage IV
CV	Copepodite stage V
PL	*Prosome length*
Maq	Atlantic mackrel
Her	Atlantic herring
Spr	Spring
Mar	Marlin
STARS	Sequential t-test analysis of regime shift
PCA	Principal component analysis
Sdem	Small demersal fish
Ldem	Large demersal fish

Table 2: List of variables included in the time series analyses

Name	**Description**	**Period**	**N**	**Source**
Physical			**14**	
Freshwater discharge- St. Lawrence	Annual anomaly of seasonal (Jan-June) freshwater discharge at Québec City	1971-2012	1	Galbraith et al. (2013)
Deep water salinity	Annual anomaly of salinity in waters > 150 m	1971-2012	1	Galbraith et al. (2013)
Labrador Current volume transport	Annual anomaly in 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 J. (2008)
Surface composite climate index (SLE, nwGSL, NeGSL, sGSL)	Sum of annual anomaly of temperature (May-Nov), CIL and maximum ice volume	1971-2012	4	Galbraith et al. (2013)
Deep composite climate index (SLE, nwGSL, NeGSL, sGSL)	Sum of temperature anomaly at 150, 200, 250 and 300 m	1971-2012	4	Galbraith et al. (2013)
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. (2013)
Plankton			**26**	
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. (2009), Plourde et al. (2011)
Zooplankton phenology	Annual anomaly in the timing of peak recruitment of CI-III *C. finmarchicus* G1 and G2, ratio of max abundance of CI-III *C. finmarchicus* G2 and G1, stage composition of overwintering *C. glacialis* and *C. hyperboreus*	1992-2012	10	Plourde et al. (2009), Plourde et al. (2011)
Toxic phytoplankton	Abundance of *Alexandrium tamarense* and *Pseudo-nitzschia seriata* at the Tadoussac and Ste-Flavie monitoring stations in the SLE	1994-2011	2	Scarratt and Starr[4] (unpublished data)
Pelagic fish biomass			**6**	
Mackrel biomass 4T	Annual anomaly of mackrel spawning biomass (tons) determined during the egg survey in southern GSL (4T)	1968-2012	1	Grégoire et al. (2013a)
Spring herring 4T	Annual anomaly of spring herring biomass (tons) in 4T	1978-2012	1	Leblanc et al. (2012)
Fall herring 4T	Annual anomaly of fall herring biomass (tons) in 4T	1978-2012	1	Leblanc et al. (2012)
Capelin dispersion index (4T, 4S, 4R)	Annual anomaly of capelin dispersion (probability of being capture per region) index as determined from bottom trawl surveys conducted in the northern GSL from 1990 to 2012	1990-2012	3	Grégoire et al. (2013c)

---

[4] Fisheries and Oceans Canada, Mont-Joli, QC Canada

Name	Description	Period	N	Source
Pelagic fish condition			**8**	
Capelin female body length 4R	Annual anomaly of capelin female body length eGSL	1984-2012	1	Grégoire et al. (2013c)
Mackrel 4T	Annual anomaly of mackrel condition (K) in southern GSL (4T)	1973-2011	1	Grégoire et al. (2013a)
Spring and fall herring 4T	Annual anomaly of herring condition (K) in southern GSL (4T)	1970-2011	2	Leblanc et al. (2012)
Spring and fall herring 4S	Annual anomaly of herring condition (K) in southern GSL (4S)	1984-2010	2	Grégoire and Beaulieu (2011)
Spring and fall herring 4R	Annual anomaly of herring condition (K) in southern GSL (4R)	1970-2011	2	Grégoire et al. (2013b)
Demersal fish biomass			**40**	
Large species/groups in nGSL (4T, 4S, 4R)	Annual anomaly of biomass (kg/tow) of Cod, Flounder, Haddock, Hake, Redfish, Skates, Marlin-Spike	1990-2012	21	Bourdages and Ouellet (2011)
Small species/groups in nGSL (4T, 4S, 4R)	Annual anomaly of biomass (kg/tow) of Lampreys, Lycodes, Lumpfish, Rockling, Sculpins-Cottidae, Snailfish	1990-2012	18	Bourdages and Ouellet (2011)
Large species/groups in sGSL (4T)	Annual anomaly of biomass (kg/tow)of large demersal fish species	1971-2012	not used in PCA	Benoît & Swain (2008), Benoît [5](unpublished data)
TOTAL			**94**	

---

[5] Fisheries and Oceans Canada, Moncton, NB Canada

FIGURES

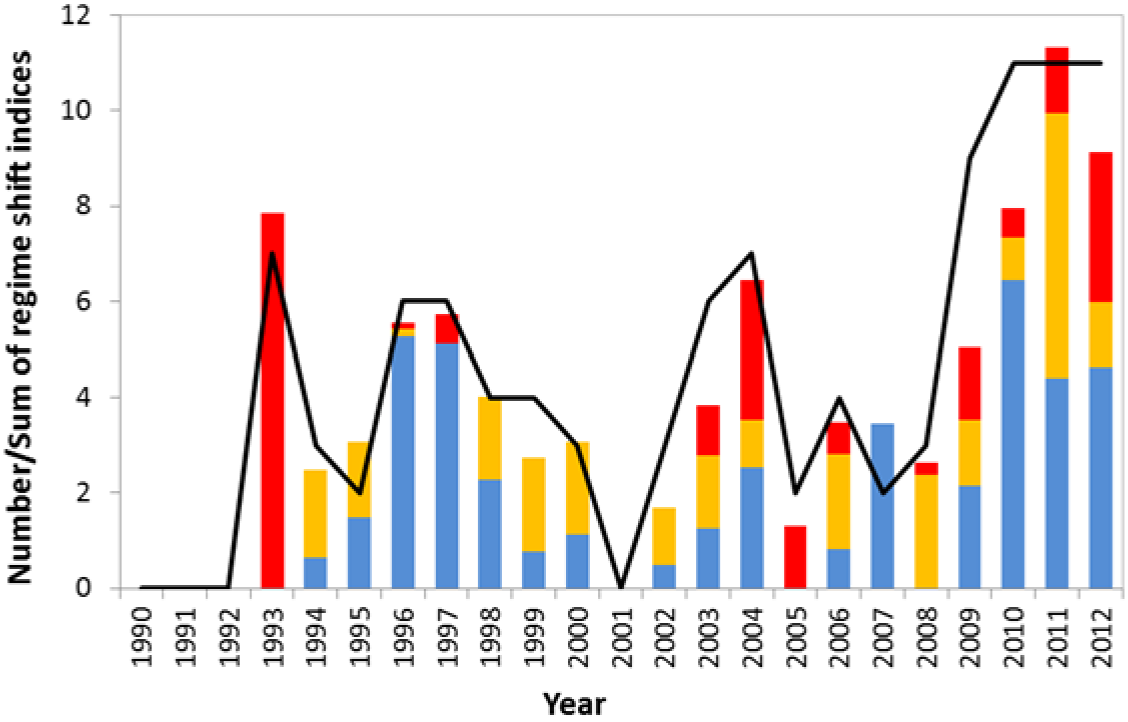


Figure 1: Results of the general regime shift detection method (STARS: target p= 0.1, cut-off length = 5, Huber parameter = 3): number of variables out of the total 91 variables that showed a regime shift (black line), and sum of regime shifts (absolute value) (stacked bars) for the environmental (blue), and potential pelagic (orange) and demersal (red) fish prey.

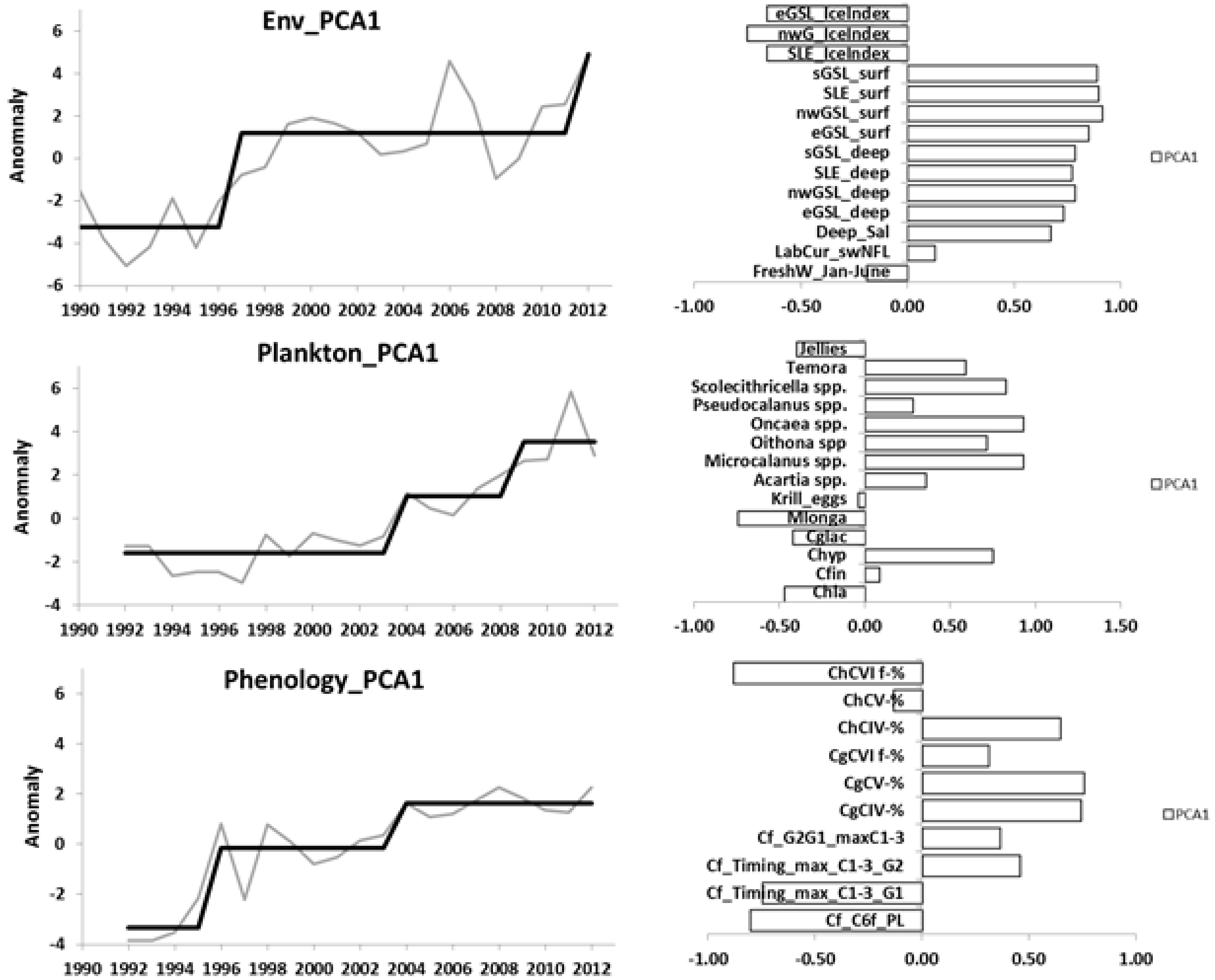


Figure 2: Changes in the physical conditions, and plankton community composition and phenology in the GSL from 1990 to 2012. Left panels: annual anomaly (grey line) and different periods (regimes) (black line) determined by the general STARS analyses performed on Principal Components Analysis axis 1 (PCA1) of physical environment, plankton abundance and zooplankton phenology. Right panels: loadings of individual variables on each PCA.

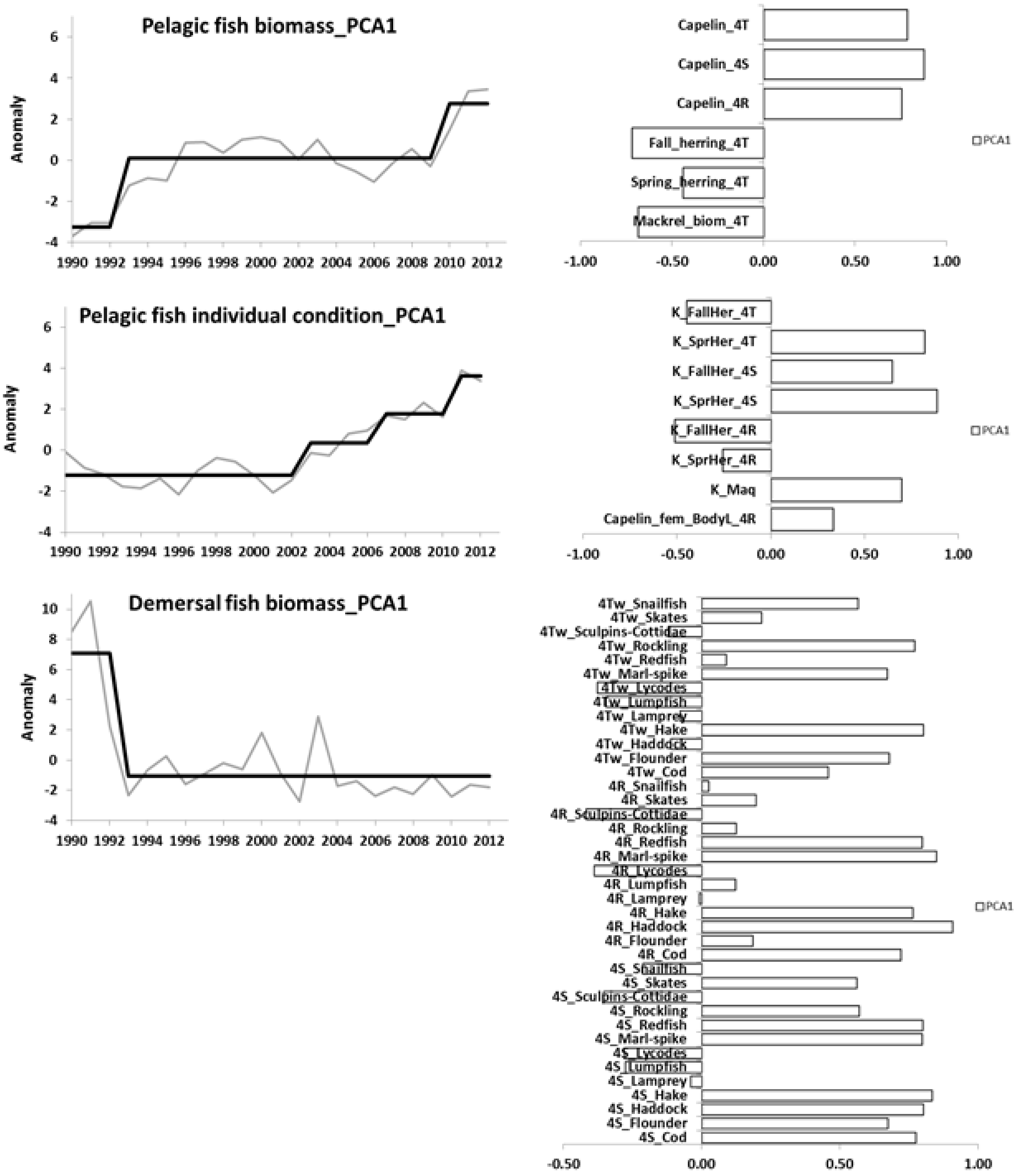


Figure 3: Changes in some pelagic and demersal fish species/taxa biomass indices in the GSL from 1990 to 2012. Left panels: annual anomaly (grey line) and different periods (regimes) (black line) determined by the general STARS analyses performed on Principal Components Analysis axis 1 (PCA1) of pelagic fish biomass and condition, and demersal fish biomass. Right panels: loadings of individual variables on each PCA.

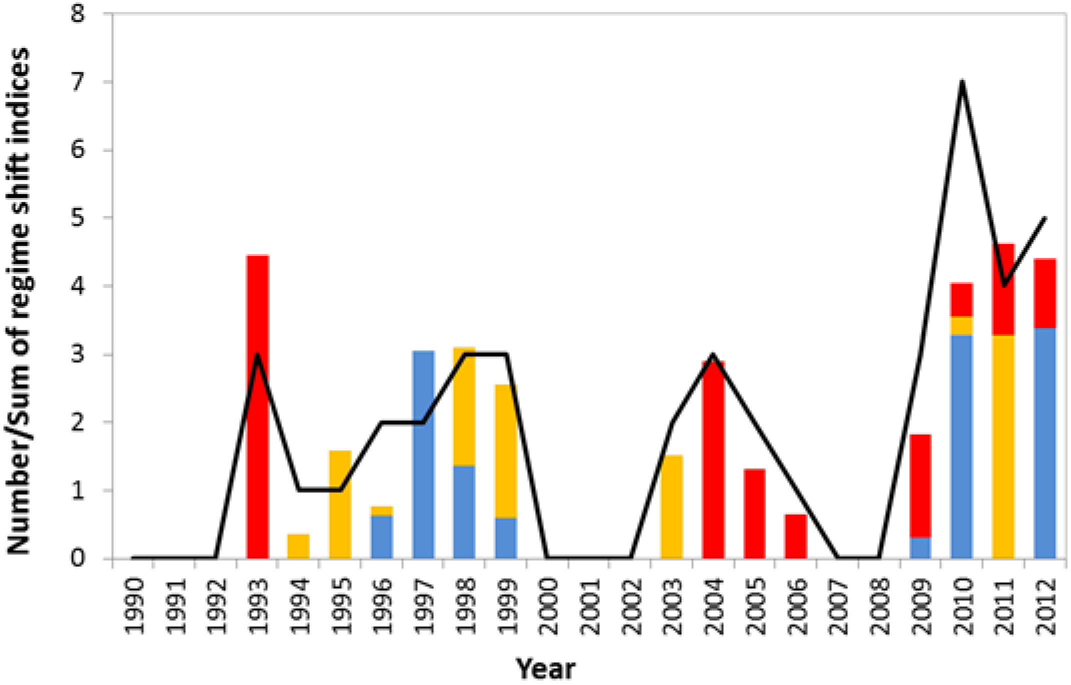


Figure 4: Results of the regime shift detection method (STARS: target p= 0.1, cut-off length = 5, Huber parameter = 3) applied to variables potentially significant for the St. Lawrence beluga whale population: number of variables out of the total 28 variables that showed a regime shift (black line), and sum of the regime shift indices (stacked bars) for the physical environment (blue), and potential pelagic (orange) and demersal (red) fish prey.

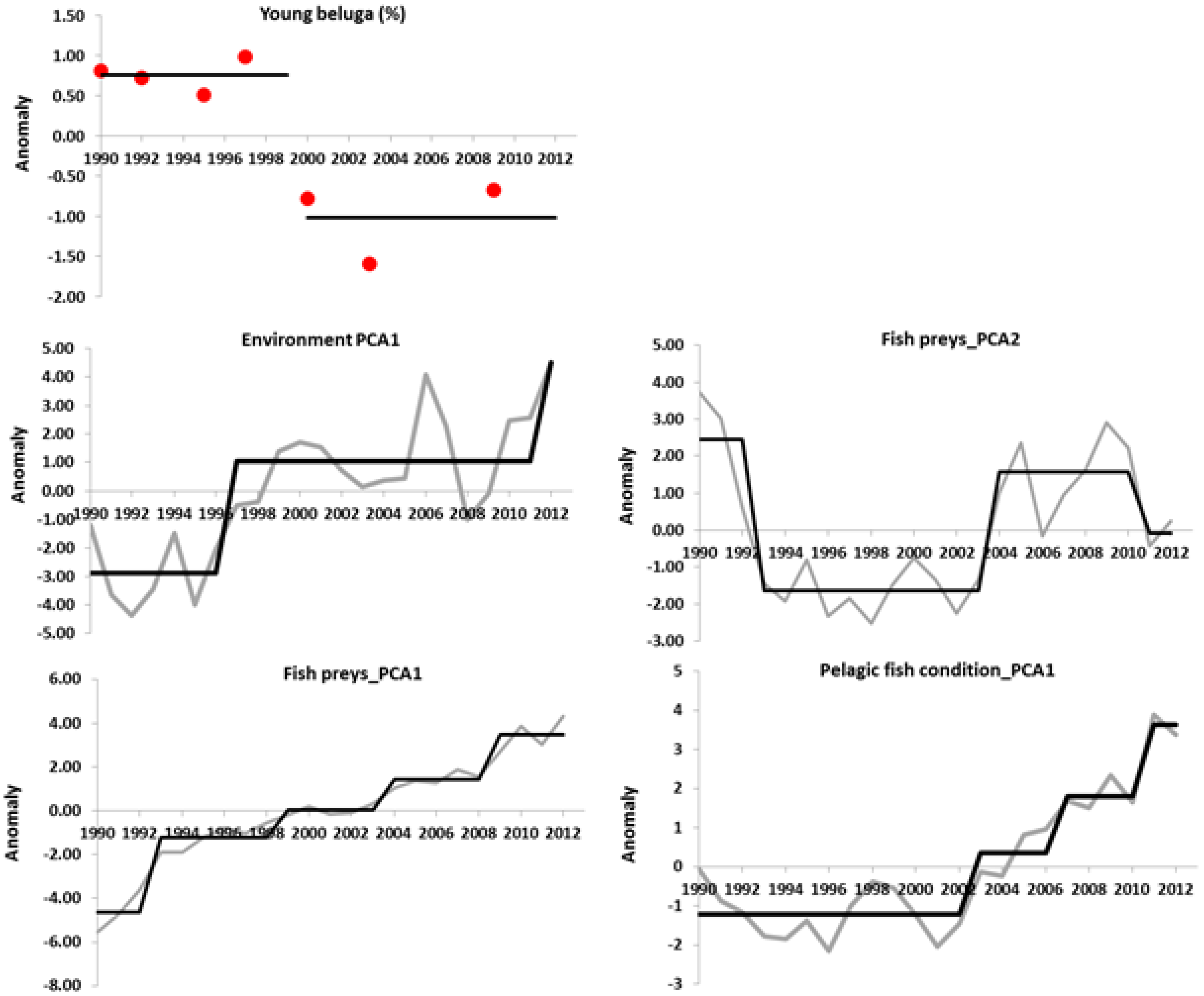


Figure 5: Beluga whale population indices and environmental variations in the GSL. Top panel: percentage (%) of young beluga in the population assessed during photographic aerial surveys in the SLE (red circles) and average (black lines) for periods prior and after 1999. Other panels: annual anomaly (grey line) and regime states (black line) determined by the STARS performed on environment PCA1, potential fish prey PCA1 and PCA2, and pelagic fish condition PCA1 (see titles for variables name). Note that STARS was not performed on the percentage of young in the beluga whale population due to a discontinuous time series. See Appendix fig. 2 for loadings of variables on environment and fish prey PCAs and Figure 3 for pelagic fish condition PCA1.

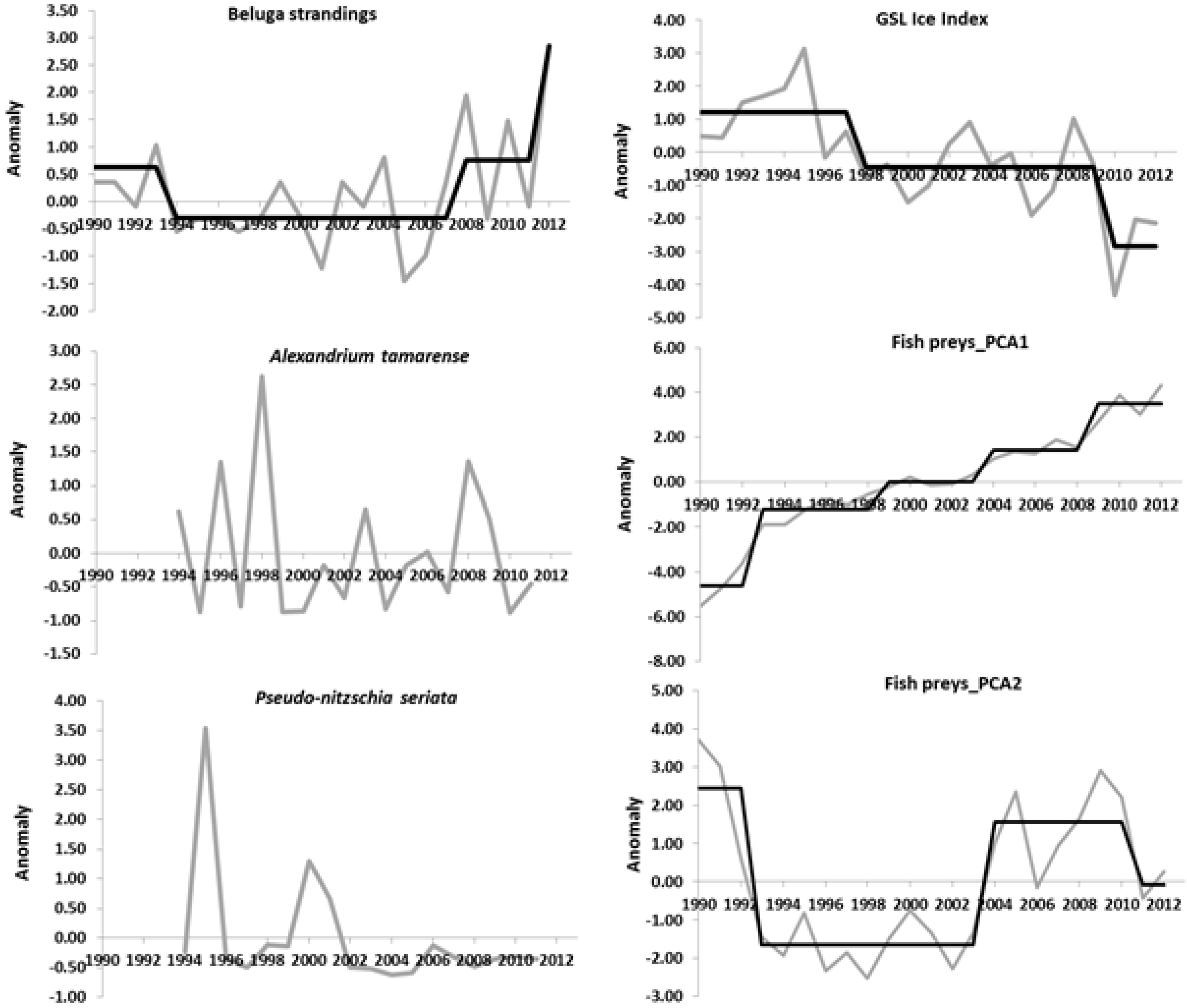


Figure 6: Beluga whale population indices and environmental variations in the GSL. Annual anomaly (grey line) and regime states (black line) determined by the STARS analysis performed on the annual number of dead beluga (calves and adults) , abundance of Alexandrium tamarense and Pseudo- nitzschia seriata, GSL ice index, and potential fish prey PCA1 and PCA2. See Appendix fig. 2 for the loadings of variables on fish prey PCA1 and PCA2.

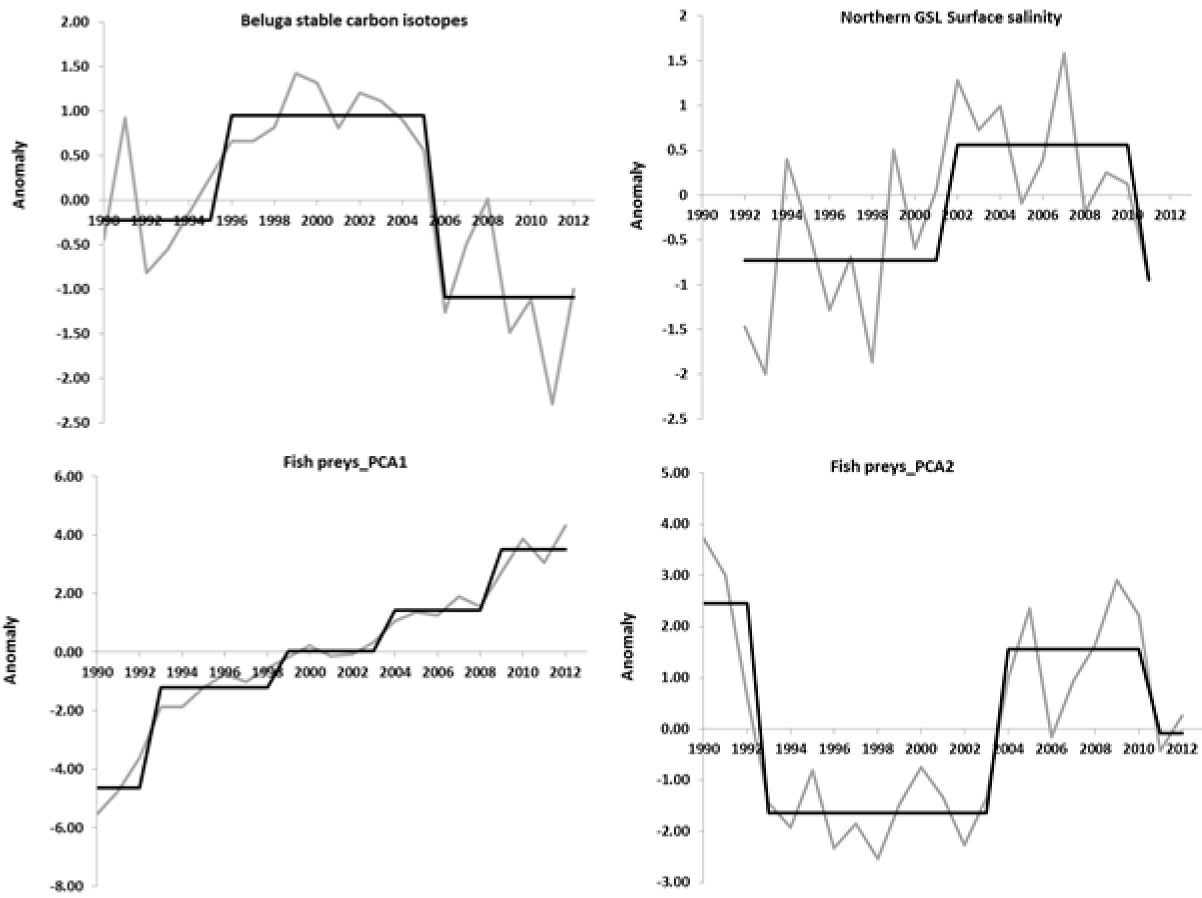


Figure 7: Beluga whale individual indices and environmental variations in the GSL. Annual anomaly (grey line) and different states (black line) determined by the STARS analysis performed on the signature of carbon stable isotopes of beluga whale (top left panel), northern GSL annual surface salinity (top right panel), and PCA1 (lower left panel) and PCA2 (lower right panel) of potential fish prey. See Appendix fig. 2 for the loadings of variables on fish prey PCA1 and PCA2.

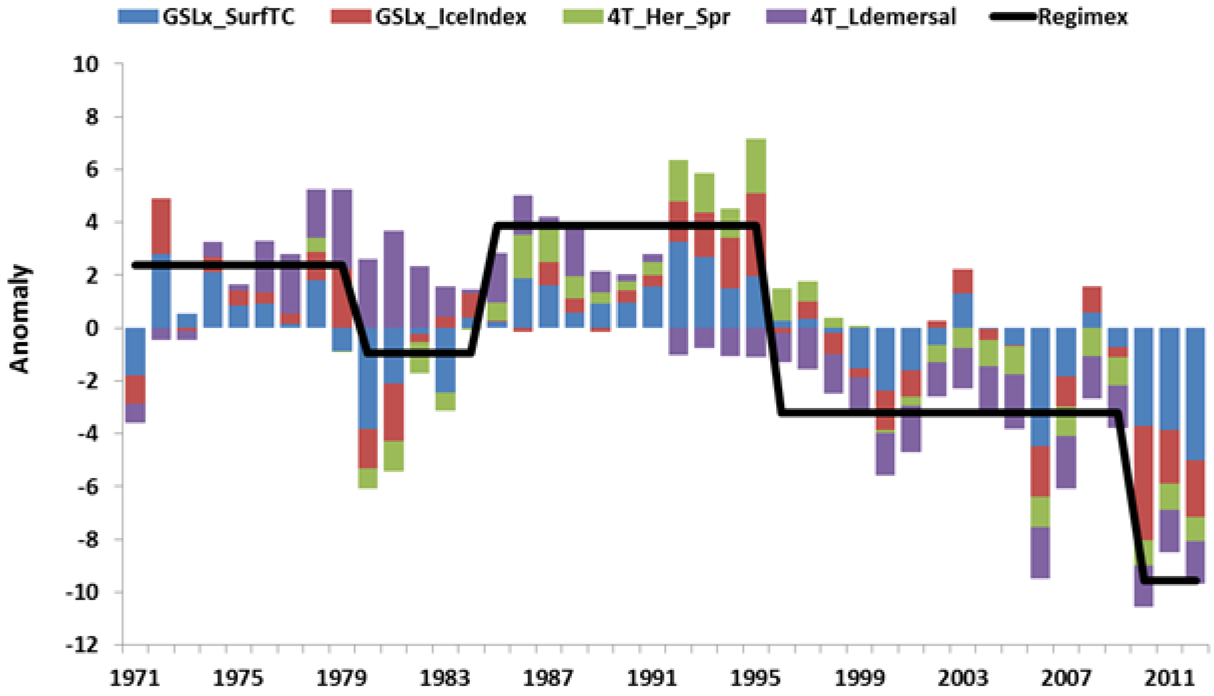


Figure 8: Long-term changes in physical and biological conditions potentially important for the beluga whale habitat. Stacked bars: annual anomaly of physical (surface temperature, ice index) and potential food sources (4T spring herring, large demersal fish). Black line: different environmental regimes separated by shifts determined by the STARS analysis performed on the sum of all anomalies. The sign of the temperature anomaly was changed to reflect its potential negative effect on the beluga whale population as with other variables. Note that the time series of 4T herring begins in 1978.

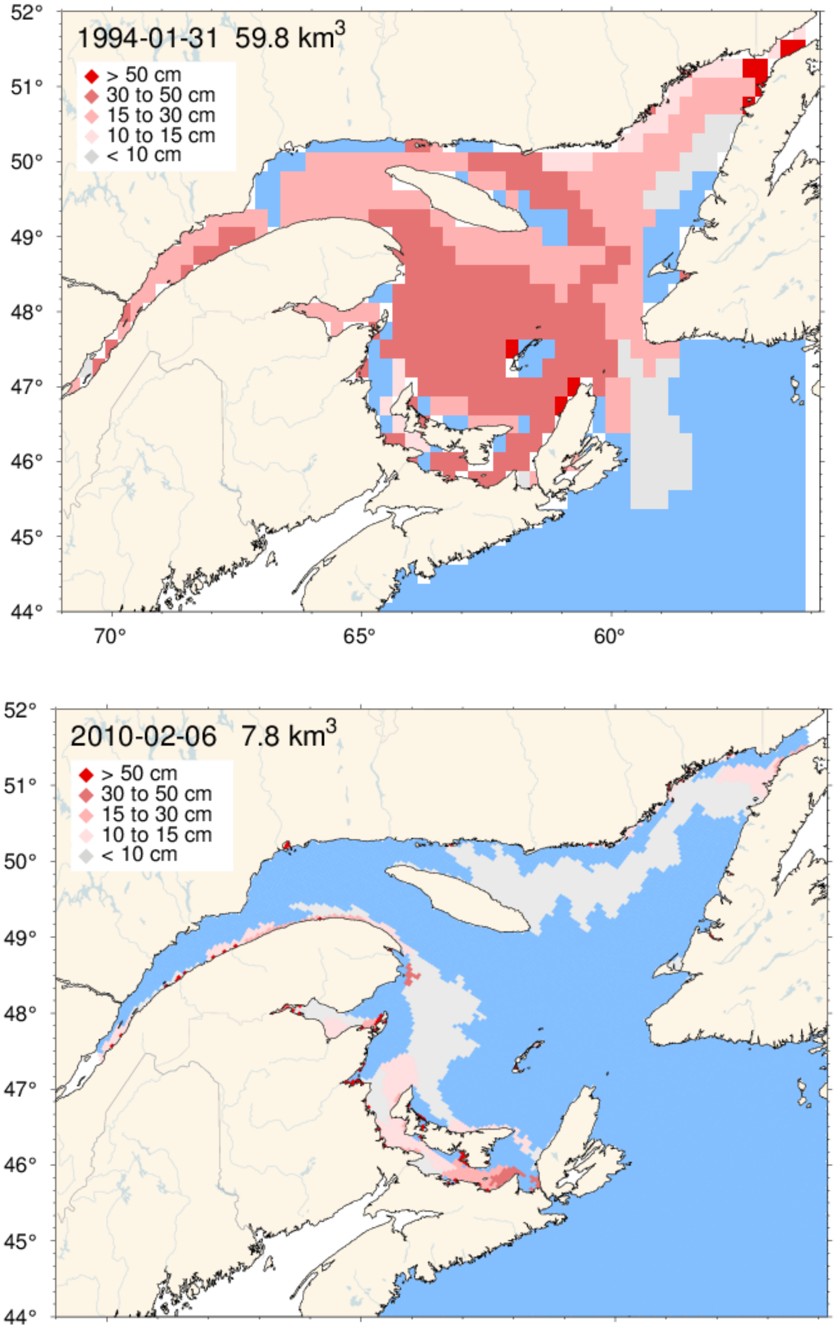
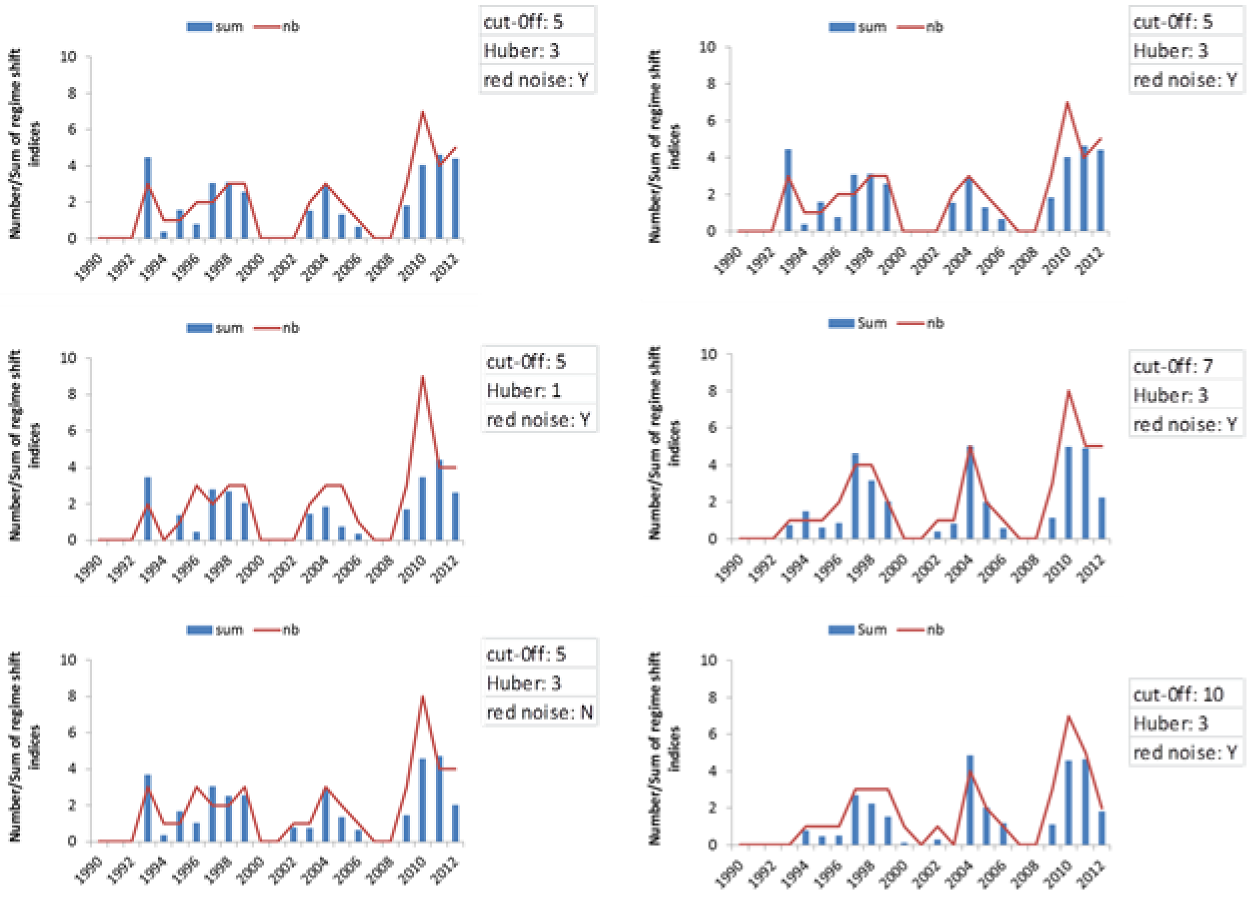
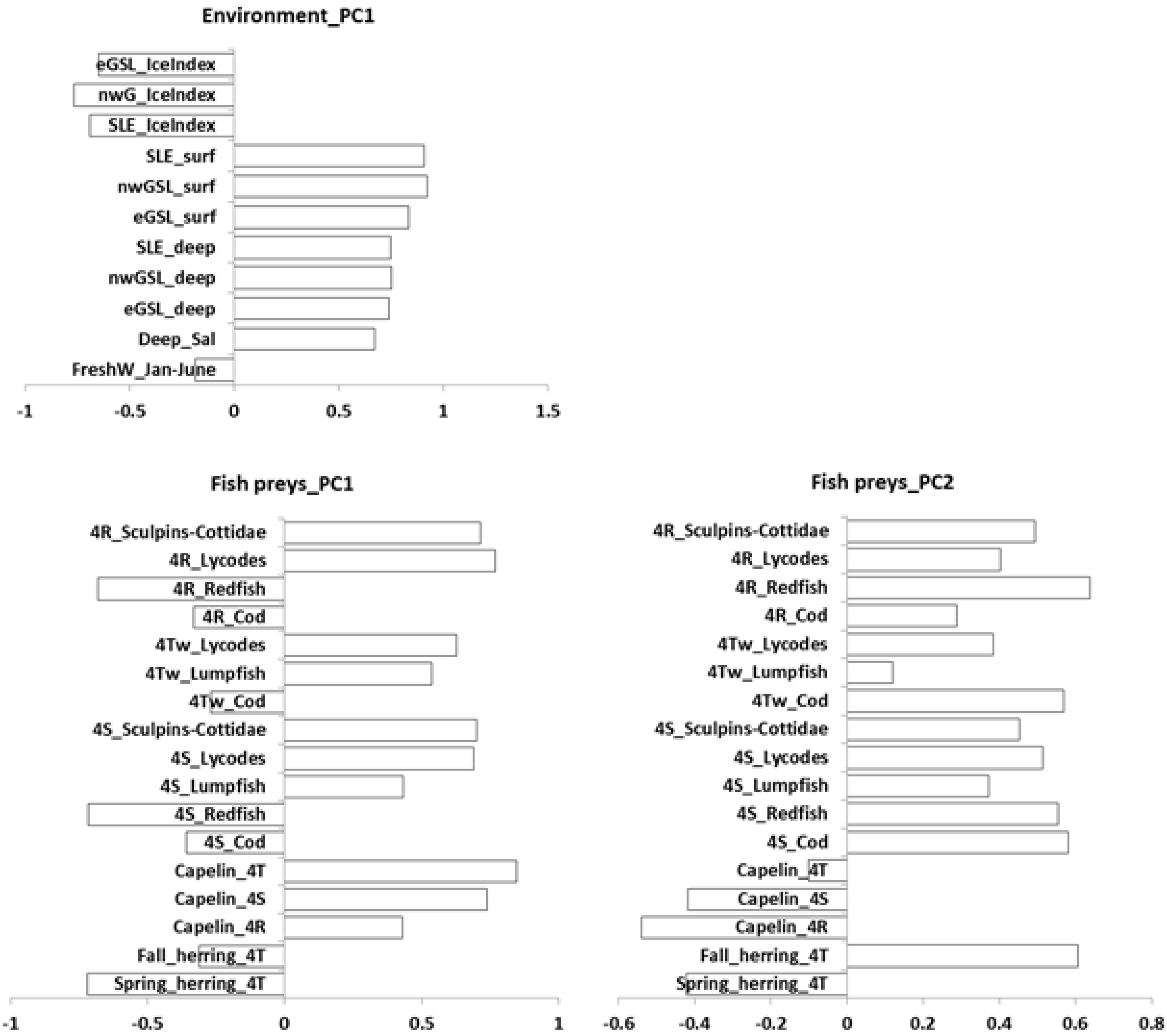


Figure 9: Changes in winter ice conditions in the Gulf of St. Lawrence. Ice distribution and thickness for ice cover > 40% at the seasonal maximum of ice cover in the northern GSL (sum of SLE, wGSL, eGSL) during years of high (upper panel) and low (lower panel) ice cover. Ice volume for regions with ice cover >40% is indicated.

APPENDIX



Appendix figure 1. Sensitivity of the sequential regime shift detection method (STARS: target p= 0.1) to various cut-off lengths (5, 7, and 10 years), Huber parameters (1, 3) and red noise filter (Y: applied; N: not applied). Blue bars: sum of the regime shifts (absolute value). Red line: number of variables that showed a regime shift.



Appendix figure 2. Loadings of variables on environment PCA1 and fish prey PCA1 and PCA2 performed on a set of 28 variables potentially significant for the St. Lawrence beluga whale population.