

Biological regime shifts and changes in predictability

Joachim W. Dippner,¹ Karin Junker,¹ and Ingrid Kröncke²

Received 30 September 2010; revised 5 November 2010; accepted 15 November 2010; published 17 December 2010.

[1] Time series of climate indices and of biomass, abundance, and species number of benthic macrofauna in the southern North Sea are related to each other to investigate the predictability of biological time series in presence of biological regime shifts in 1989/1990 and 2001/2002. The results indicate that a smooth biological regime shift occurred in 1989/1990 caused by positive climate feedback mechanisms. In this case, the benthic community structure remained predictable. In contrast, in 2001/2002 an abrupt biological regime shift caused by a climate regime shift occurred. Here became the biological time series inherently unpredictable. **Citation:** Dippner, J. W., K. Junker, and I. Kröncke (2010), Biological regime shifts and changes in predictability, *Geophys. Res. Lett.*, *37*, L24701, doi:10.1029/2010GL045696.

1. Introduction

[2] Variability in marine ecosystems can be related to climate variability, biological interactions or anthropogenic impacts such as nutrient loading or exploitation. A transition from one dynamic regime to another is called a “regime shift”. The term “biological regime shift” (BRS) is used to describe pronounced changes in abundance and composition of plankton and fish and propagate through several trophic levels [Reid *et al.*, 2001]. Three different types of BRSs (smooth, abrupt and discontinuous) were linked to the linearity or non-linearity of the driving external processes such as climate change or biological interactions [Scheffer *et al.*, 2001]. In this classification, a smooth BRS is characterized by a quasi-linear relationship between driver and response variables [deYoung *et al.*, 2008]. An abrupt BRS is represented by a non-linear relationship between driver and response variable. In a discontinuous BRS, alternative stable states might occur [Collie *et al.*, 2004]. Various BRSs were identified during the last century all over the world [e.g., Beaugrand, 2004; Drinkwater, 2006; Mantua *et al.*, 1997; Peterson and Schwing, 2003; Reid *et al.*, 1998] although no consistent definition exists for BRS [deYoung *et al.*, 2004].

[3] Over the past few decades, climate indices, e.g., the North Atlantic Oscillation (NAO) Index [Hurrell, 1995] were used as drivers to identify the response in marine ecosystems [Drinkwater *et al.*, 2003; Dippner, 2006]. For 1978–1993, atmospheric winter circulation over the North Atlantic, NAO winter index and sea surface temperature (SST) in winter were highly correlated to the time series of benthic macrofauna in the following spring in the southern

North Sea [Kröncke *et al.*, 1998]. SST was also highly correlated to the NAO index. These high correlations and the time lag allowed a successful prediction of the structure of macrofauna communities as demonstrated for 1994–1999 by [Dippner and Kröncke, 2003]. The 2005 update of the time series reveals, however, that since 2000 this correlation and hence the predictability of the structure of macrofauna communities disappeared. Here we show that for the period 1978–2005 two BRSs occurred, in 1989/1990 and 2001/2002. We address the question why the community structure of benthic macrofauna was predictable during the 1989/1990 BRS with a linear model, but not during 2001/2002.

2. Data and Methods

2.1. Benthos

[4] Macrofauna samples were collected in spring 1978 to 2005 in the sublittoral zone off the island of Norderney (southern North Sea) at five different stations located in water depths between 12 m and 20 m using a 0.2 m² van Veen grab. A single grab was taken at each of the five stations. The samples were sieved over 0.63 mm mesh size and fixed in 4% buffered formaldehyde. After sorting, the organisms were preserved in 70% alcohol. Biomass was determined as ash-free dry weight (AFDW) per m². Samples were dried for 24h at 85°C and burned for 6h at 485°C. Species number, abundance and biomass from the five stations were pooled and treated as replicates for the area, since the multivariate comparison had shown no significant difference between the macrofauna communities.

[5] Various methods exist to identify BRSs [Scheffer and Carpenter, 2003; Rudnick and Davis, 2003; Collie *et al.*, 2004; Mantua, 2004]. A necessary condition for a BRS is a significant step in a biological time series. An affirmation of BRS is the occurrence of a bimodal or multimodal frequency distribution of the biological response variable or the existence of a peak in the second time derivative of the time series. These methods were applied to identify BRSs in the time series of macrofauna communities.

2.2. Climate

[6] The following climate data sets were used for the analyses: (1) the Arctic Oscillation (AO) index from 1899–2007 [Thompson and Wallace, 1998] which describes the leading Empirical Orthogonal Function (EOF) of monthly geopotential height anomalies at the 1000 hPa level on the Northern Hemisphere poleward from 20°N, (2) the Atlantic Multidecadal Oscillation (AMO) index from 1856–2009 [Enfield *et al.*, 2001] defined as the monthly SST anomalies in the North Atlantic area weighted from 0°–70°N, (3) the NAO index from 1864–2009 [Hurrell, 1995] defined as the difference between the normalized monthly Sea Level Pressure (SLP) anomalies between Lisbon and Stykkisholmur, (4) SLP anomalies of NH poleward of 30°N from NCEP/

¹Leibniz Institute for Baltic Sea Research Warnemünde, Rostock, Germany.

²Senckenberg, Department for Marine Research, Wilhelmshaven, Germany.

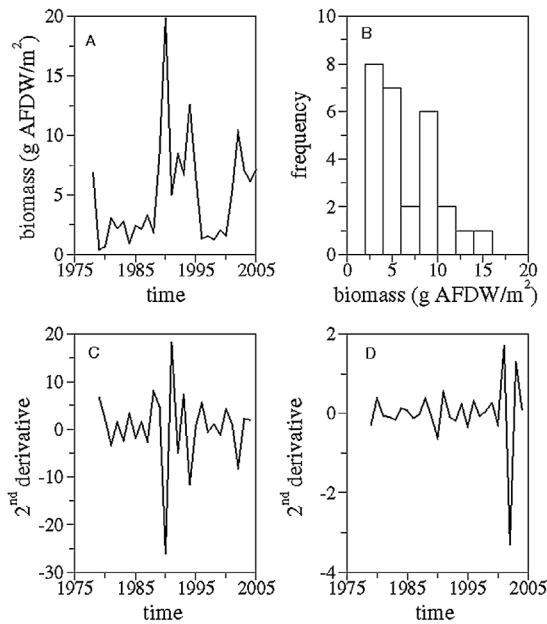


Figure 1. (a) Time series of benthic macrofauna biomass in the southern North Sea; (b) frequency distribution of biomass; (c) 2nd time derivative of biomass time series; (d) 2nd time derivative of abundance time series times 10^{-4} .

NCAR reanalysis [Kalnay et al., 1996] and (5) area averaged monthly SST anomalies (1948–2009) in the southern North Sea (53° – 56° N, 2° W– 9° E) from NCEP/NCAR reanalysis [Kalnay et al., 1996].

[7] Statistical downscaling [von Storch et al., 1993] was used to detect relationships between climate predictors (driver variables) and biological predictands (response variables) by calculating EOFs of the driver and response

variables, by performing a canonical correlation analysis between the leading eigenmodes, and by regressing the benthos time series from the climate driver variable. Composite analysis of SLP fields was performed to analyse changes in climate variability. Using a complex Morlet ($\omega_0 = 6$) mother wavelet, wavelet coherences and phase differences were computed to identify periods of synchronous behaviour between time series [Torrence and Compo, 1998; Jevrejeva et al., 2003].

3. Results

[8] The time series of benthic macrofauna biomass show significant steps in 1989/1990 and 2001/2002 (Figure 1a), a bimodal frequency distribution (Figure 1b), and a strong peak in 1990 and two minor peaks in 1995 and 2002 in the 2nd time derivative of macrofauna biomass (Figure 1c). The 2nd time derivative of macrofauna abundance shows a pronounced peak in 2002 (Figure 1d) whereas the 2nd time derivative of macrofauna species number (not shown) peaks in 1990 as well.

[9] Statistical downscaling was performed for the NAO index as driver variable and for six response variables: the median and mean of macrofauna species number, log abundance and log biomass for the periods 1978–1999, 1978–2005, and 2000–2005. The correlation coefficient r between the regional observations and the cross-validated estimations and Brier-based score skill were used as skill factors and computed for all combinations [Livezey, 1995]. For 1978–1999 (Table 1), highly significant correlations and Brier based score skills indicated a relatively high potential predictability of benthic macrofauna community structure [Dippner and Kröncke, 2003]. For the whole period 1978–2005 only few, and for 2000–2005 no significant correlations and no meaningful skill exist. The same holds for the

Table 1. Correlation Coefficients and the Brier Based Score Skill in Parenthesis Between Climate Predictors and Benthic Macrofauna Predictands for Different Periods^a

Climate Predictor	Benthic Predictand	1978–1999	1978–2005	2000–2005
NAO	Median log abundance	0.73 (0.46)	0.49 (0.17)	0.19 (–)
NAO	Median species number	0.80 (0.61)	0.48 (0.17)	0.38 (–)
NAO	Median log biomass	0.67 (0.42)	0.46 (0.17)	0.72 (–)
NAO	Mean log abundance	0.59 (0.22)	0.40 (0.07)	0.12 (–)
NAO	Mean species number	0.80 (0.58)	0.50 (0.17)	0.13 (–)
NAO	Mean log biomass	0.68 (0.42)	0.47 (0.18)	0.62 (–)
AMO	Median log abundance	0.65 (0.37)	0.13 (–)	0.09 (–)
AMO	Median species number	0.39 (0.07)	0.03 (–)	0.49 (–)
AMO	Median log biomass	0.49 (0.18)	0.16 (–)	0.35 (–)
AMO	Mean log abundance	0.65 (0.38)	0.19 (–)	0.02 (–)
AMO	Mean species number	0.42 (0.09)	0.01 (–)	0.29 (–)
AMO	Mean log biomass	0.45 (0.13)	0.09 (–)	0.62 (0.22)
AO	Median log abundance	0.47 (0.16)	0.36 (0.08)	0.29 (–)
AO	Median species number	0.73 (0.52)	0.52 (0.24)	0.54 (0.01)
AO	Median log biomass	0.53 (0.25)	0.39 (0.12)	0.40 (–)
AO	Mean log abundance	0.38 (0.10)	0.31 (0.06)	0.32 (–)
AO	Mean species number	0.67 (0.41)	0.51 (0.22)	0.50 (–)
AO	Mean log biomass	0.58 (0.29)	0.45 (0.15)	0.36 (–)
NCEP-SST	Median log abundance	0.28 (–)	0.26 (–)	0.57 (–)
NCEP-SST	Median species number	0.56 (0.22)	0.48 (0.17)	0.45 (–)
NCEP-SST	Median log biomass	0.52 (0.25)	0.48 (0.15)	0.55 (0.38)
NCEP-SST	Mean log abundance	0.13 (–)	0.15 (–)	0.59 (–)
NCEP-SST	Mean species number	0.54 (0.19)	0.48 (0.16)	0.50 (–)
NCEP-SST	Mean log biomass	0.44 (0.10)	0.45 (0.13)	0.09 (–)

^aBold numbers mark significant correlations with respect to the 99% confidence level.

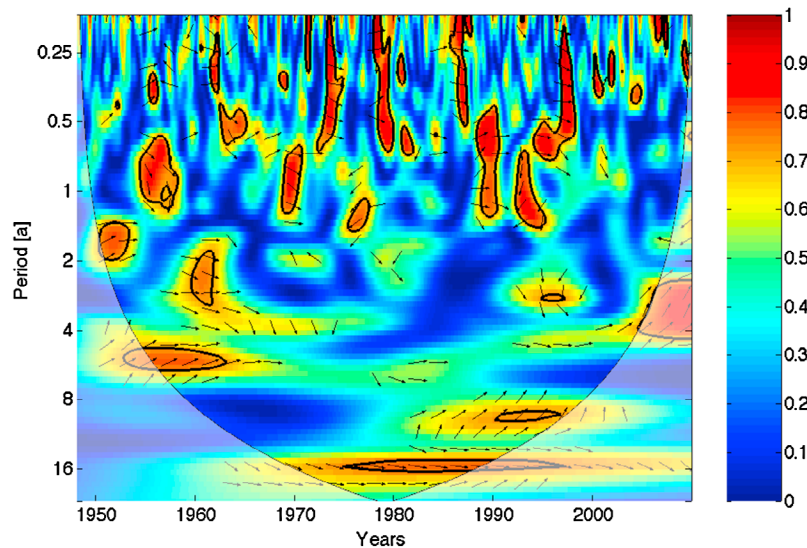


Figure 2. Wavelet coherence and phase between NAO index and NCEP SST in the southern North Sea. Contours are wavelet squared coherencies. The vectors indicate the phase difference between NAO and SST (a horizontal arrow pointing from left to right signifies in phase and an arrow pointing vertically upward means the second series lags the first by 90° , i.e., the phase angle is 270°). The thick black line is the 5% significance level using the red noise model and the thin black line indicates the cone of influence.

AMO, AO, and for the NECP reanalysis SST of the southern North Sea as driver variables (Table 1).

[10] The fact that 2001/2002 BRS was different to the 1989/1990 BRS can be demonstrated by relating the SST to climate time series. The wavelet analysis (Figure 2) shows a significant in phase coherence between NAO index and NCEP SST anomalies for the wavelet period of 14–15 years between the mid 1970s and the end of the 1990s. After ~2000 this coherence disappeared.

[11] A composite analysis of SLP DJFM anomalies (December–March average) north of 30°N shows for the period 1978–1999 a strong zonal orientation, but, a merid-

ional orientation of SLP anomalies over North Atlantic and Eurasia for the period 2000–2009 (Figure 3).

4. Discussion

[12] Two BRSs occurred between 1978 and 2005 in our data sets of benthic macrofauna: the first in 1989/1990 and the second in 2001/2002. In the period 1978–1999, in which the first BRS occurred, statistical downscaling indicated a relatively high potential predictability of benthic macrofauna community structure [Dippner and Kröncke, 2003]. However, since 2001 the correlations between NAO index

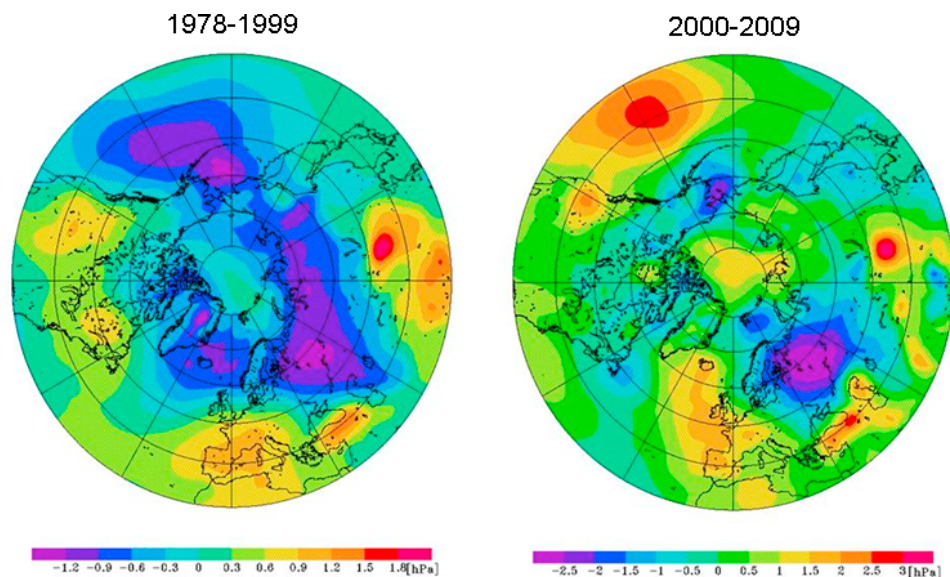


Figure 3. SLP Composite (December–March average) for (left) the period 1978–1999 and (right) the period 2000–2009.

and North Sea SST, macrofauna species number, abundance and biomass diminished indicating the disappearance of potential predictability.

[13] The question remains where the differences in predictability of the two BRSs originated. Here climate variability and climate regime shifts (CRS) will be considered. Defining a CRS as a change in the trend of global mean air temperature [Swanson and Tsonis, 2009], four CRS were identified in the last 100 years: 1910–1920, 1938–1945, 1976–1981, and 2001/2002. Especially the CRS around 1976 [Graham, 1994; Trenberth and Hurrell, 1994] and the CRS around 2000 were well documented [Bond et al., 2003; Peterson and Schwing, 2003].

[14] Often BRSs are directly connected to CRSs, which is consistent with the synchronized incidence of both types of regime shifts, e.g., around 1920 in the North Atlantic [Drinkwater, 2006] and 1976 in the North Pacific [Hare and Mantua, 2000]. However, BRS were observed 1989/1990 in the North Sea [Beaugrand, 2004; Reid et al., 1998, 2001] and in the North Pacific [Bond et al., 2003] although no CRS were documented in this period. This is consistent with the statement of Beaugrand [2004] who mentioned that the change seems more difficult to explain in physical than in biological time series.

[15] From 1976 to 2001, no change in trends occurred in global mean air temperature [Swanson and Tsonis, 2009] or in SST in the North Atlantic and North Pacific. The AMO did not show any change in trend between 1976 and 2001 [Dima and Lohmann, 2007]. This is consistent with the significant wavelet coherence between NAO index and North Sea SST mentioned above. Overall, this period is characterized by a warming caused by an increased heat transport from the tropics to the extra-tropics [Hoerling et al., 2001]. It enhances the amplitude of the NAO and sustains a positive phase. The fact that during this warming no changes in trends occurred, leads to the conclusion that the heat transport to the extra-tropics can be interpreted as a positive feedback mechanism in the terminology of Suarez and Schopf [1988]. The quasi-linear response of the benthic macrofauna communities to this positive feedback indicates a smooth type of BRS which is predictable according to Collie et al. [2004].

[16] The reason for the unpredictability of the 2001/2002 BRS can be found in the simultaneously and globally occurring CRS. Daily SLP fields of the North Atlantic from December to March (DJFM) 1958–2006 were analysed with non-linear cluster analysis Hurrell and Deser [2009]. They identified four patterns: a positive NAO pattern, a negative NAO pattern, a blocking pattern, and a so-called Atlantic ridge pattern. Since 2001, the appearance of the blocking and Atlantic ridge patterns increased. The increase of the number of dominant patterns suggests a shift towards non-linearity in the climate system. The strong meridional orientation of DJFM SLP anomalies during 2000–2009 over the North Atlantic and Eurasia (Figure 3) shows a specific similarity to the blocking and Atlantic ridge pattern. For the period 1978–1999 zonal orientation dominated with no major shift in this period. Hence, we can conclude that the 2001/2002 BRS is caused by a CRS and that the switch from a linear to a non-linear climate system seems to be the reason that the biological system becomes unpredictable. This indicates that an abrupt BRS occurred in 2001/2002 according to the classification of Collie et al. [2004].

[17] For the future, a climate predictor is desirable which allows predictions of biological time series also in presence of CRS. Alternatively, due to the shift towards non-linearity in the climate system, the application of non-linear prediction methods could be a possible solution to overcome the problem of unpredictability. A fundamental understanding of the mechanisms forcing BRSs is a necessary prerequisite for assessing the limits of predictability. This knowledge is particularly important in developing strategies for marine resource management.

[18] **Acknowledgments.** We thank the captains and crews of RV “Senckenberg” for their help with sampling throughout the years. We are indebted to all colleagues for technical assistance in sampling, sample processing, biomass determination, and taxonomic identification. We would like to thank Aslak Grinsted for providing a package for the calculation of wavelet coherences. We are indebted to Eduardo Zorita and two anonymous reviewers for helpful comments. This paper is a contribution to the BONUS+ ERANET Project AMBER (BMBF project 03F0485A) and also a contribution to the Research Centre “Biodiversity and Climate (BiK-F)” funded by LOEWE.

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J. W. Dippner and K. Junker, Leibniz Institute for Baltic Sea Research Warnemünde, Seestr.15, D-18119 Rostock, Germany. (dippner@io-warnemuende.de)

I. Kröncke, Senckenberg, Department for Marine Research, Südstrand 40, D-26382 Wilhelmshaven, Germany.