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Marine Ecosystem Regime Shifts Induced by Climate and Overfishing: A Review for the Northern Hemisphere

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Contents

1. Introduction	304
2. Theoretical Concepts: Regime Shifts and Alternative Stable States	306
2.1 Types of ecosystem responses to external drivers	306
2.2 Resilience and the interaction of multiple drivers	308
2.3 Alternative stable states	309
3. Marine Ecosystem Regime Shifts	310
3.1 Methods for identifying abrupt ecosystem changes	313
3.2 North Pacific	315
3.3 Eastern Scotian Shelf	316
3.4 North Sea	318
3.5 Baltic Sea	321
3.6 Black Sea	323
4. Trophic Cascades	324
4.1 Eastern Scotian Shelf	327
4.2 Baltic Sea	327
4.3 Black Sea	328
4.4 Vulnerability of marine ecosystems to overfishing-induced trophic cascading	329
4.5 Climate-induced changes in trophic control and oscillating control	329
5. Discussion	330
5.1 Synchronicity of timing—Evidence of atmospheric teleconnection	330
5.2 Trophic cascading—The importance of overfishing in triggering ecosystem regime shifts	333
5.3 Interactions of multiple drivers, alternative stable states and the reversibility of ecosystem regime shifts	334
6. Conclusions	339
Acknowledgments	340
References	340

Abstract

Abrupt and rapid shifts in food web and community structure, commonly termed regime shifts, have been increasingly reported for exploited marine ecosystems around the world. Here, we present a review on regime shifts in Northern hemisphere marine ecosystems, most of them using a multivariate approach to statistically analyse time series. We show that rapid shifts occurred in synchrony during the late 1980s/early 1990s, suggesting a common large-scale climate driver and essentially matching times of change in the North Atlantic Oscillation and other atmospheric indices, which modified, for example, the local temperature regimes. We further show that trophic cascades triggered by overfishing and causing a switch of trophic regulation are regularly involved in ecosystem reorganizations. Eutrophication and the introduction of alien species can be important as well, potentially affecting tipping points or the food web structure. Our review highlights how multiple drivers potentially interact in a way that one driver undermines resilience (e.g. overfishing) and the other (e.g. climate change) gives the final impulse for an abrupt change. Further, ecosystem regime shifts can be particularly difficult to reverse when alternative stable states are involved. Understanding the drivers and mechanisms leading to regime shifts is crucial for developing ecosystem-based management strategies and establishing early-warning systems to avoid catastrophic ecosystem changes and achieve a sustainable exploitation of ecosystem services.



1. INTRODUCTION

Sudden and rapid changes in food web and community structure are commonly termed ecosystem regime shifts (Woodward et al., 2010), highlighting the abrupt transition between different states in a complex system. Initially, regime shifts have been described in atmospheric processes on multidecadal time-scales and their effects on the physical environment (Kraberg et al., 2011; Rahmstorf, 1999). They have long been a phenomenon associated with aquatic systems, where environmental and biological drivers can interact to produce alternative equilibria, for instance, as has been widely reported in shallow lake ecosystems for decades (Meerhoff et al., 2012). In biological and fisheries oceanography, the term was originally used based on the observation of a temporal correspondence of climate indices and fish population abundances (Steele, 2004; Wooster and Zhang, 2004). Prominent examples are dominance changes between small pelagic fish populations, such as anchovy and sardine in several regions of the world's oceans (Alheit and Bakun, 2010; Lluch-Belda et al., 1989). More recently, the term ecosystem regime shift has been used to define drastic large time- and space-scale shifts in

abundances of major components of marine biological communities. Climate regime shifts, which signify apparent transitions between differing average climatic characteristics (Bakun, 2005), have been proposed as drivers of these marine ecosystem regime shifts (Hare and Mantua, 2000).

Conceptually, the regime shift theory was further developed during key investigations in freshwater (Scheffer et al., 2001a), on land (May, 1977; Scheffer et al., 2001b) and in coral reef systems (McCook, 1999). These studies pointed towards external drivers other than climate, for example, exploitation and eutrophication, and their interaction. Further, aspects of the nature of regime shifts are discussed, which can be linear or abrupt, or can even be discontinuous when hysteresis is involved (Collie et al., 2004; Scheffer et al., 2001a). Eventually, these developments have resulted in theories on catastrophic regime shifts in ecosystems (Scheffer and Carpenter, 2003) and critical transitions in nature (Scheffer, 2009), addressing the potential existence of alternative stable states in ecosystems. The latter states have important management implications, because restoring regimes considered as favourable may require drastic and expensive management actions (Feld et al., 2011; Scheffer et al., 2001a; Suding et al., 2004), and this could be further complicated by interactions with additional newly emerging stressors (Meerhoff et al., 2012).

Overfishing is seriously affecting the ecosystems of the world's oceans, with about 30% of the world's fish stocks already classified as being overfished (i.e. overexploited, depleted and recovering stocks; FAO, 2010). In addition, over 50% of stocks are considered fully exploited, leaving less than 20% classified as under- or moderately exploited (FAO, 2010). Overfishing or depletion of large predatory fish species, in particular, is a widespread and growing phenomenon (Castle et al., 2011; Myers and Worm, 2003; Peck, 2012; Worm et al., 2006). There is now compelling evidence that changes at the top of the food web can have profound indirect effects on all trophic levels and hence can change the structure and functioning of the whole food web. These trophic cascades have been originally demonstrated for limnic and marine benthic systems, and it was postulated that they may not be widespread in the more fragmented terrestrial and open-ocean pelagic ecosystems (Terborgh and Estes, 2010). However, increasing length of monitoring time series and overfishing as a "natural trophic cascade experiment" has shown the potential of ecosystem reorganization due to overfishing of top-predators (Baum and Worm, 2009).

The goal of this review is to evaluate the importance of climate and overfishing in triggering ecosystem regime shifts in marine systems. For this purpose, ecosystem regime shifts are defined as infrequent and abrupt changes in ecosystem structure and function, occurring at multiple trophic levels and over large geographic scales (Bakun, 2005; Collie et al., 2004; Cury and Shannon, 2004; De Young et al., 2004; Lees et al., 2006). Theoretical concepts about regime shifts and alternative stable states are described in Section 2. In the subsequent sections, prominent regional examples of ecosystem regime shifts and trophic cascades that can cause or pave the way for shifts are given. Finally, in Section 5, the results of this study are summarised to evaluate the potential causes of ecosystem regime shifts and to give recommendations for future research and ecosystem-based management strategies.



2. THEORETICAL CONCEPTS: REGIME SHIFTS AND ALTERNATIVE STABLE STATES

All ecosystems, terrestrial, limnic or marine systems, are exposed to external environmental changes. These can be of climatic origin or directly or indirectly caused by human activities, such as nutrient loading, habitat fragmentation or biotic exploitation. Initially, it was assumed that ecosystems responded to gradual changes in a smooth way: the ability of ecosystems to switch abruptly to a contrasting state was first described in theoretical models (Holling, 1973). More recently, an increasing amount of evidence has shown that this happens also in many real ecosystems, particularly in the aquatic environment (e.g. Bakun, 2005; de Young et al., 2008; Scheffer and Carpenter, 2003; Scheffer et al., 2001a). The occurrence of regime shifts and the potential existence of alternative stable states have important implications for ecosystem approaches to management, which have now evolved to a central paradigm underpinning living marine resource policy (Levin et al., 2009; McLeod and Leslie, 2009). Thus, the study of ecosystem regime shifts, early-warning signals, resilience and alternative stable states and their reversibility is of increasing importance, both ecologically and economically. Before we describe evidence for the existence of these phenomena in the marine realm, we will shortly discuss the theoretical concepts behind them.

2.1. Types of ecosystem responses to external drivers

Theory on regime shifts and catastrophic shifts in nature shows that the response of ecosystems to changing external pressures (e.g. climate, fishing pressure or eutrophication) can vary from smooth to discontinuous (Collie

et al., 2004; Scheffer et al., 2001a). The state of some ecosystems may respond in a gradual and continuous way to external pressure, while other systems display inertia, time lags or hystereses over a range of conditions (Friberg et al., 2011). The latter will respond strongly in a non-linear way when conditions approach a critical level or a threshold (Fig. 1, left panel). Conceptually, different is a situation when the ecosystem response curve shows a so-called backward-folding, implying specific environmental conditions for which the ecosystem has two alternative stable states (Fig. 1, right panel). These states are then separated by an unstable equilibrium (black arrow in Fig. 1) that marks the border between so-called basins of attraction (Holling, 1973).

The potential existence of alternative stable states has profound implications for the response to external drivers (Fig. 1, right panel). It implies that if conditions change sufficiently so that they pass a critical threshold, a “catastrophic transition”, that is, a regime shift occurs. Typically, when monitoring such a system or a variable over time, no obvious change is observed until suddenly an abrupt switch takes place, and hence regime shifts usually occur largely unannounced. Recently, a series of statistical indicators functioning as early-warning signals were described, such as increasing variance or skewness in indicator time series such as population sizes. However, these were mainly tested in ecosystem modelling experiments (Carpenter et al., 2011; Guttal and Jayaprakash, 2009; Scheffer et al., 2009), and empirical evidence is still rare. An even more critical ramification for ecosystem-based management is that restoring the external pressures to values before a

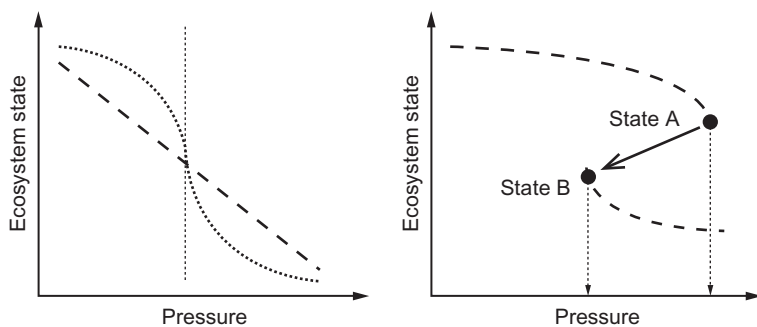


Figure 1 Conceptual diagram showing possible ecosystem responses to external pressures and the development of alternative stable states; left panel shows linear (dashed line) and non-linear (dotted line) changes in ecosystem state—vertical line indicates threshold for the non-linear abrupt case; right panel shows non-linear change with abrupt transition and alternative stable states; arrow indicates an “unstable equilibrium”. After Scheffer et al. (2001a) and Scheffer and Carpenter (2003).

regime shift is often insufficient to restore the biota. Rather, it is necessary to reduce external pressures to far lower values: this hysteresis is a result of a positive feedback in a system and can slow ecological recovery from the alleviation of environmental stress (e.g. [Layer et al., 2011](#)). Restoring systems displaying hysteresis may therefore require far more drastic and expensive management measures ([Suding et al., 2004](#)), and strategies for sustainable management should thus focus on maintaining resilience of the ecosystem or the respective component ([Friberg et al., 2011](#)).

2.2. Resilience and the interaction of multiple drivers

In reality, ecosystems are never fully stable, and stochastic events such as weather extremes or species invasions may cause fluctuations in their state ([Scheffer et al., 2001a](#)). In systems with alternative stable states, the likelihood that the system switches between states (i.e. the occurrence of a regime shift) depends not only on the strength of the perturbation but also on the actual condition of the ecosystem, frequently called “the size of its attraction basin” ([Fig. 2](#)). When this basin is large or deep (equivalent to what is often

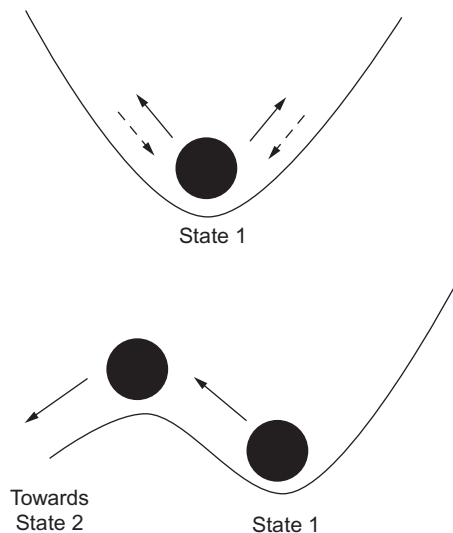


Figure 2 Conceptual diagram of the concepts of resilience and attraction basins; upper panel shows a “resilient” situation with a deep “attraction basin”—pushing the ecosystem state (black ball) by an external driver (black arrow) results in fast return (dashed arrow) to the original state; lower panel shows a situation with “eroded resilience” with a shallow “attraction basin”—the push by an external driver can now change the ecosystem to another state. After [Scheffer et al. \(2001a\)](#) and [Scheffer and Carpenter \(2003\)](#).

presumed to be a “healthy” condition), a substantial external impact would be needed for a regime shift to occur. In contrast, when the basin is small or shallow (i.e. in a “stressed” condition, Fig. 2), even slight perturbations may cause a regime shift—in the theoretical model, the ball is pushed into a different basin of attraction.

The size of the attraction basin is frequently termed its resilience (Holling and Chambers, 1973). This corresponds to the maximum perturbation that a system can stand without causing a shift to an alternative stable state. In a system with alternative stable states, gradually changing conditions may have only minor effects on its state that may not be measurable from mean values, but gradually changing conditions may reduce the resilience of the system and hence make it more fragile so that it can be easily changed by another driver, or a stochastic event, into an alternative stable state. The final push needed to achieve this and hence to trigger a regime shift not only can result from another external driver but can also arise from internal system dynamics (Scheffer et al., 2001a). In reality, an interaction of internal processes (e.g. trophic control; see Section 4) and multiple external stressors (of which some reduce the resilience and others provide the final push) will often cause such a shift. For management, it is thus an important conclusion that, when interpreting causality of regime shifts, there is a tendency to ignore the factors that undermine resilience slowly, for example, eutrophication or global warming (Scheffer and Carpenter, 2003).

2.3. Alternative stable states

It is generally difficult to identify the existence of alternative stable states in natural ecosystems, and usually, experimental work is needed to derive evidence (Scheffer, 2009; Scheffer and Carpenter, 2003). In large ecosystems, experimental manipulation is close to impossible (Ledger et al., 2012; Mintenbeck et al., 2012), but even in marine systems, it is possible to derive indicators of alternative stable states from field data. A first class of indicators includes abrupt shifts or jumps in time series and established methods exist to determine whether such a shift is significant (Hare and Mantua, 2000). However, a significant step-change in a time series does not necessarily prove alternative stable states, as it may simply reflect a stepwise change in an external driver (e.g. a sudden temperature change), or that the external driver has passed a critical threshold but the system has no alternative stable states. A second indicator of alternative stable states is a multimodality of the frequency distribution of states.

These can be investigated not only based on time series but also by exploring spatial distributions (Litzow et al., 2008): ultimately, dual relationships with an external driver may indicate alternative stable states. Tests for multiplicity of regression models are conducted easily using modern statistical methods. All of these methods require large datasets but often have low explanatory power for the generally short and limited ecological datasets that are currently available. Hence, obtaining indications for the existence of alternative stable states from correlational field data is rarely conclusive (Scheffer, 2009; Scheffer and Carpenter, 2003).

3. MARINE ECOSYSTEM REGIME SHIFTS

Regime shifts in marine ecosystems are increasingly reported in the scientific literature, as highlighted in a number of recent special issues (e.g. Bernard et al., 2009) and review articles (e.g. de Young et al., 2004; De Young et al., 2008; Steele, 2004), and a series of statistical methods for their identification have been developed (reviewed by Andersen et al., 2009; Mantua, 2004). Here, we will revisit studies that match the definition of ecosystem regime shifts involving multiple trophic levels, placing emphasis on those that use time series from multiple trophic levels in multivariate statistical analyses, an approach pioneered by the study of Hare and Mantua (2000). Comparable studies using similar methods include the major ecosystem regime shifts reported in the Eastern Scotian Shelf, the North Sea and the Baltic Sea (Figs. 3, 4–7). Major regime shifts have also been described in the past few years for many other regions worldwide, for example, the Japan Sea (Tian et al., 2008), the Mediterranean (Conversi et al., 2010) or the Black Sea (Oguz and Gilbert, 2007; Oguz and Velikova, 2010). Our emphasis will be

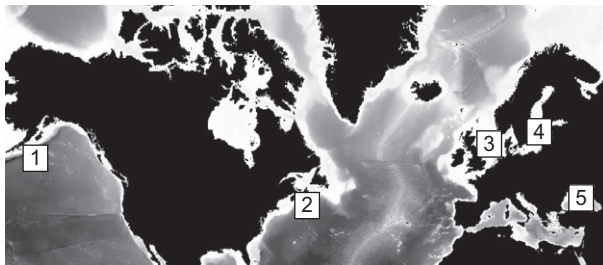


Figure 3 Map of the Northern hemisphere with the ecosystems reviewed in this study. 1, North Pacific; 2, Eastern Scotian Shelf; 3, North Sea; 4, Baltic Sea; and 5, Black Sea. Map drawn with information from the GECO One Minute Grid, version 2.0, <http://www.gebco.net>.

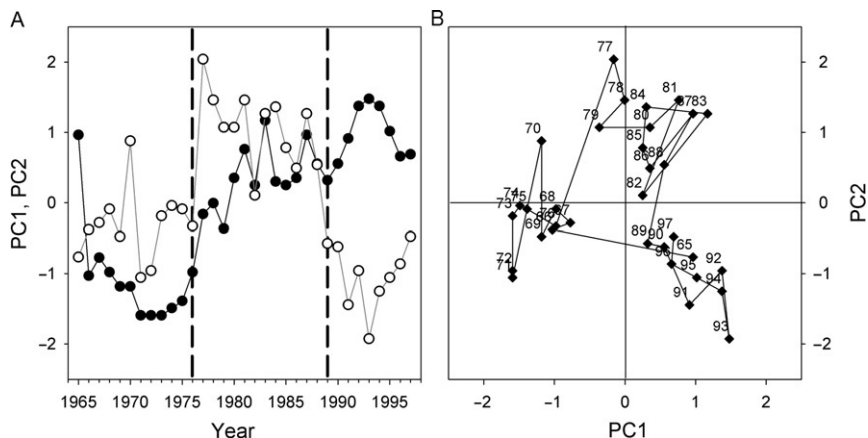


Figure 4 Regime shifts in the North Pacific ecosystem. Temporal trends of principal components (PC1 and PC2) as holistic indicators of ecosystem state from multivariate analyses. (A) PC1 (black dots) and PC2 (white dots) versus time, vertical lines indicate reported regime shifts; (B) phase-space plot of PC1 versus PC2. *Redrawn from Hare and Mantua (2000).*

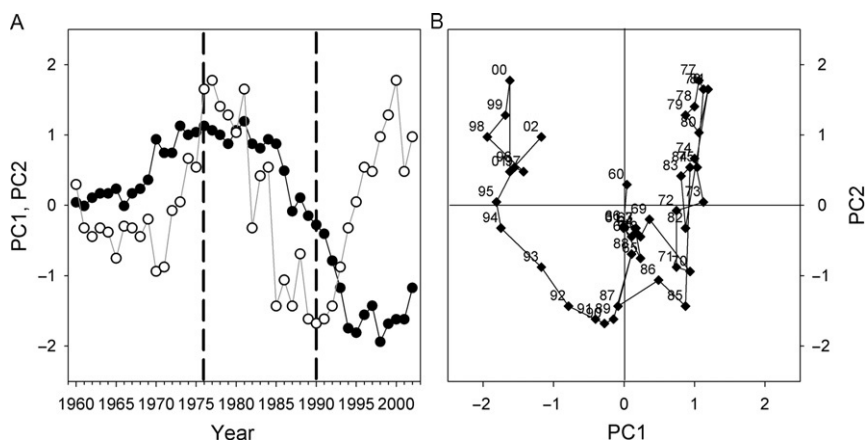
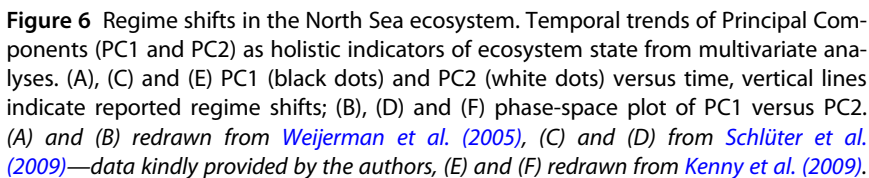


Figure 5 Regime shifts in the Eastern Scotian Shelf ecosystem. Temporal trends of principal components (PC1 and PC2) as holistic indicators of ecosystem state from multivariate analyses. (A) PC1 (black dots) and PC2 (white dots) versus time, vertical lines indicate reported regime shifts; (B) phase-space plot of PC1 versus PC2. *Redrawn from Choi et al. (2005).*

on (i) the timing of the regime shifts, (ii) a description of the changes in the food webs and (iii) the identification of the main drivers of the observed ecosystem changes. We will also compare the timing and characteristics of the regime shifts in the investigated areas, by selecting studies that used comparable methods to



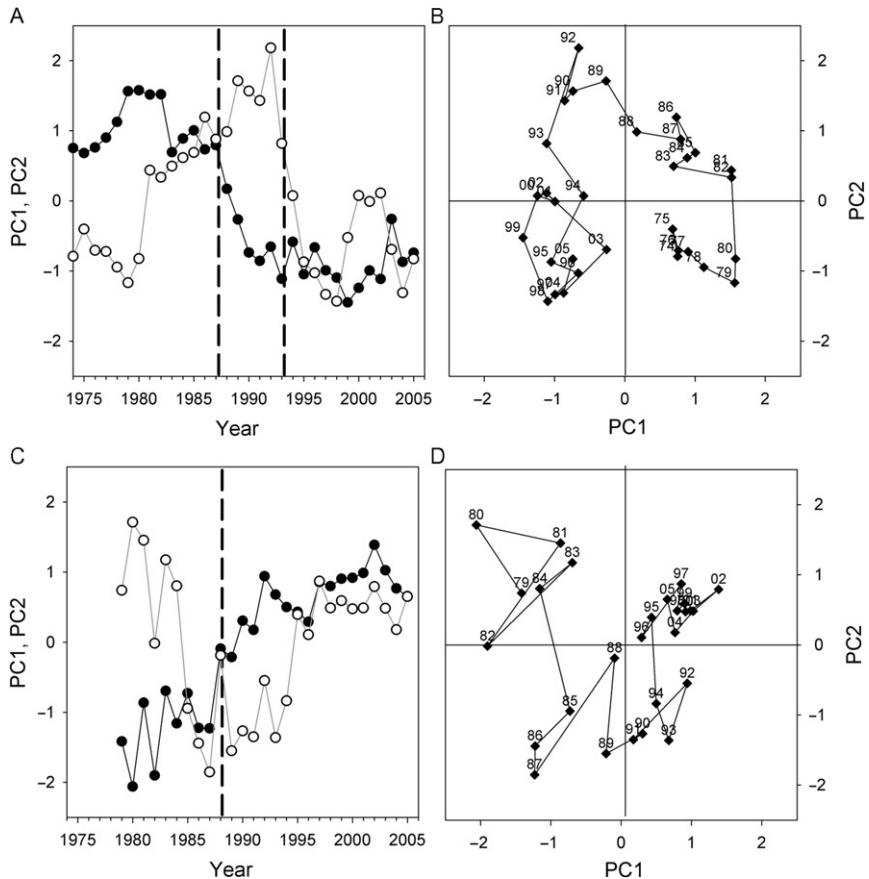


Figure 7 Regime shifts in the Baltic Sea (including The Sound) ecosystem. Temporal trends of principal components (PC1 and PC2) as holistic indicators of ecosystem state from multivariate analyses. (A) and (C) PC1 (black dots) and PC2 (white dots) versus time, vertical lines indicate reported regime shifts; (B) and (D) phase-space plot of PC1 versus PC2. Data kindly provided by Möllmann et al. (2009) (A) and (B) and Lindegren et al. (2010a) (C) and (D).

analyse abrupt changes. This includes the integrated assessment of indicators by ordination, to visualise systemic changes, and discontinuity analysis to identify breaks in single or multivariate datasets. Examples for both approaches are described below briefly.

3.1. Methods for identifying abrupt ecosystem changes

Most of the studies we reviewed used a multivariate approach to analyse ecosystem changes, in which a multitude of variables were collected and, if necessary, averaged over space (if spatially disaggregated) and time (if regularly

spaced temporal data were available) to produce a time-variable matrix. This matrix forms the basis for multivariate ordination techniques that are especially useful for dimension reduction onto only a few axes. Various methods exist and each of them has advantages and limitations. For time series analysis of multiple variables of different kinds, normalised principal component analysis (PCA based on the correlation matrix) is a simple but useful tool that uses an eigenvector technique to decompose the variability in the dataset into new theoretical variables (the principal components or PCs), which are linear but orthogonal composites of the originals. In the graphical representation, the PCs form the new axes and accordingly the objects (here: years) are assigned new coordinates (scores) (\rightarrow phase-space plot of PC1 vs. PC2). When variables and objects are shown in the same biplot graph, the closer two objects (years) are, the more similar they are according to the behaviour of their variables. To illustrate step-like changes, the PC scores can be additionally plotted against time. Further details about the method, the mathematical background and its interpretation can be found in [Rao \(1964\)](#), [Legendre and Legendre \(1998\)](#) and various statistical textbooks.

To identify abrupt changes in data series either in space or in time, various methods, so-called discontinuity analyses, exist that are applicable to single or multivariate data sets. Recently, two different methods were frequently applied in regime shift studies, including most of the studies reviewed below. Unfortunately, these methods tend to find a “shift” in the data series even if only simultaneous long-term trends exist. Thus, they should be always performed in parallel to, for example, ordination techniques that allow visualising gradual changes as well.

Chronological Clustering is a method closely related to the commonly known cluster analysis, with the additional constraint that it can only group sequential samples ([Legendre et al., 1985](#)). It is used for a multivariate dataset from which a similarity matrix needs to be calculated: the “proportional-link linkage algorithm” is then used to agglomerate/group samples in a non-hierarchical solution. Technically, Chronological Clustering is based on a permutation test, for which the significance level and the connectedness level need to be defined by the user ([Legendre et al., 1985](#)).

The sequential regime shift detection method (STARS) is based on a sequential t -test that signals the possibility of a regime shift in real time ([Rodionov, 2004](#)). In addition to its ability to detect shifts in the mean level of fluctuations, it can also identify shifts in the variance, with the latter algorithm being based on a sequential F -test. The code for the method is

written in Visual Basic for Application (Excel) and can be downloaded from <http://www.beringclimate.noaa.gov/regimes/>. The STARS method can be used for many kinds of data (raw data, anomalies, etc.). For multivariate time series, STARS can be applied (1) to each single variable, (2) to all variables or variable groups summing up the resulting regime shift indices for each point in time, and (3) to ordination scores resulting from previously applied dimension reduction techniques (e.g. PCs) and thus indicating overall ecosystem shifts as illustrated by, for example, the first PC-axes.

3.2. North Pacific

In North Pacific ecosystems, evidence for the occurrence of regime shifts began accumulating in the early 1990s and was mainly related to a climatic shift in the mid-1970s. This regime shift was found around 1977, and climate changes (Graham, 1994; Miller et al., 1994) and consequences for the ecosystem (Francis and Hare, 1994; Francis et al., 1998; McGowan et al., 1998) were extensively documented. The first study using multiple environmental time series was provided by Ebbesmeyer et al. (1991), showing a statistically significant “step” change in a composite of these time series in 1976–1977. Subsequently, many additional studies also suggested another although less pervasive regime shift occurred in 1988–1989 (Beamish et al., 1999; Overland et al., 1999; Polovina et al., 1994; Watanabe and Nitta, 1999; Welch et al., 2000).

Hare and Mantua (2000) provided a seminal study on the evaluation of empirical evidence for North Pacific regime shifts during the period 1965–1997, thus including both periods of likely ecosystem changes. They adopted the approach of Ebbesmeyer et al. (1991), in which a diverse array of physical and biological data series is examined, and then assembled 100 physical and biological time series, which are broadly representative for the North Pacific Ocean and Bering Sea ecosystems. Thirty-one physical time series represented atmospheric and oceanic processes, while 69 biological time series covered a wide range of oceanic species from zooplankton to large predators (e.g. salmon and groundfish). The dataset was analysed using PCA to derive the most important modes of variability (i.e. main trends in the multivariate dataset). As in the previous studies performed in the North Pacific, their analysis identified two significant regime shifts in this large marine ecosystem (LME): one in 1976/1977 and the other in 1988/1989 (Fig. 4). This was first done subjectively based on previous ecosystem knowledge, and the authors afterwards quantified and confirmed the steps

between regimes by using the so-called regime-shift analysis (Ebbesmeyer et al., 1991). Indicators of the ecosystem state, the PC1 and PC2 scores, show major step-like changes when inspecting either the score changes over time (Fig. 4A), or the phase-space plot (Fig. 4B). During the late 1970's regime shift, the changes in the physical system included an intensification of the winter-time Aleutian Low, a general cooling of the central North Pacific Ocean and a warming of the coastal Northeast Pacific Ocean and the Bering Sea. As a response, Alaskan salmon populations increased, Alaskan shrimp populations decreased, as did west coast salmon populations and California Current zooplankton abundance. After 1989, the coastal waters in the northern Gulf of Alaska and Bering Sea were cooler in winter, and the temperature of the central North Pacific Ocean increased. Further, the winter and summer Arctic vortex intensified, the winter Aleutian Low weakened and a summer warming occurred throughout the central North Pacific and coastal Northeast Pacific Ocean. Ecological changes included decline in groundfish recruitment in the Bering Sea and the West Coast, Western Alaska, West Coast and British Columbia salmon catches, and increase in Bering Sea jellyfish biomass.

From the loadings of the variables on the first PCs, the Pacific Decadal Oscillation Index (PDO) was strongly related to the regime shifts, the summer PDO to the first shift in 1977, the winter PDO to the second shift in 1988. The PDO is defined as the first principal component of extratropical North Pacific Ocean SST anomalies and describes the large-scale inter-decadal climate variability (Mantua et al., 1997).

The consequences of the changes of the PDO at the end of the 1970s were less evident in the western North Pacific, particularly in the Japan Sea (Tian et al., 2008). However, step changes were also found in the late 1980s for the fish community, including small pelagics. These changes seem to be directly forced by decadal-scale climatic-oceanic variability, such as associated with the Asian Monsoon and the Arctic Oscillation Index (AOI) (Tian et al., 2008), in line with the findings of Hare and Mantua (2000), who describe the regime shifts in the Eastern North Pacific as generally being climate driven and unrelated to overfishing (see also Overland et al., 2008).

3.3. Eastern Scotian Shelf

The Eastern Scotian Shelf off Nova Scotia, Canada contains a resident Atlantic cod (*Gadus morhua*) population that had been subject to heavy exploitation and collapsed during the early 1990s. Despite the cessation of

fishing, it failed to recover for over a decade (Frank et al., 2005). Along with the depletion of the cod stock, a major change in the fish community of the area was observed, with a dominance of smaller pelagic over larger demersal species (Choi et al., 2004). Choi et al. (2005) investigated these changes in the Eastern Scotian Shelf ecosystem in a holistic way using 55 first- and second-order biotic, abiotic and anthropogenic variables over a 43-year period (1960–2002). The 39 first-order indicators of the Eastern Scotian Shelf included the abundance, distribution and composition of finfish, invertebrates, phytoplankton, zooplankton and marine mammals. Abiotic variables included oceanic and atmospheric indicators of ocean climate, while human pressure variables included fishery landings and revenue, area of bottom trawled and the population size of Nova Scotia. Second-order indicators of the Eastern Scotian Shelf (derived from first-order indicators) were related to physiological condition, body size, community composition, metabolic rates and species–area relationships. The dataset was analysed with PCA.

By visual inspection, the analysis clearly revealed a coherent change in the Eastern Scotian Shelf ecosystem in the mid-1970s, but especially the early 1990s (Fig. 5). Variables related to upper trophic levels (such as mean body mass, size–abundance intercept, trawled surface area, groundfish landings, length at age of adults of some groundfish species such as haddock (*Melanogrammus aeglefinus*), cod, pollock (*Pollachius virens*) and silver hake (*Merluccius bilinearis*)) changed abruptly from higher mean values prior to 1990 to generally lower levels in the 1990s. The opposite was true for indicators such as grey seal numerical abundance, human population size of Nova Scotia, total landings and pelagic/demersal ratios, which changed quickly from below to above average after 1990. The multivariate statistical analysis summarised these transitions in the ecosystem into a change in dominance of groundfish versus pelagic/benthic macroinvertebrates in the late 1980s.

Among the lower trophic levels, phytoplankton abundance (Continuous Plankton Recorder (CPR) colour index, diatom and dinoflagellate counts) increased since the 1990s. Decadal changes appeared to be more pronounced in diatoms than dinoflagellates. The key zooplankton species *Calanus finmarchicus* decreased in abundance, while a cold-water species originating from the Gulf of St. Lawrence and the Labrador Current (*Calanus hyperboreus*) increased significantly in the later period.

Further, multivariate analysis revealed a change in ocean climate conditions, indicated by changes in bottom temperatures, cold intermediate layer volume (CIL) and the Gulf Stream frontal position and occurred between

the mid-1970s and late 1980s, and between late 1980s and late 1990s. The first period was characterised by relatively warm bottom waters, low volume of CIL water and a Gulf Stream frontal position close to the shelf. In contrast, the second period displayed cold bottom waters, a high volume of CIL water and a Gulf Stream frontal position distant from the shelf. The reason behind the change to cold conditions appeared to be advection of water along the shelf from both the Gulf of St. Lawrence and southern Newfoundland, augmented by local, atmospherically induced cooling. Similar cold conditions were observed in the near-shore regions of the Eastern Scotian Shelf. In addition to these changes in the thermal regime, important changes in the vertical density gradient were observed, with the highest density difference between 0 and 50 m during most of the 1990s. This increase in water column stability was due to low salinities in the near-surface waters that were advected onto the Shelf from the Grand Banks.

Choi et al. (2005) state that the integrated analyses revealed a “regime shift” experienced by the Eastern Scotian Shelf ecosystem that was characterised by an abrupt transition into a new state during the late 1980s, corresponding with observations made by Link et al. (2002) for the entire northeast U.S. continental shelf ecosystem. They proposed that a suite of indicators representative of environmental change may have preceded the observed biological changes by several years and that fishing cannot account for these changes alone, suggesting interactions between ocean physics, biology and exploitation as the drivers for the observed ecosystem regime shift.

3.4. North Sea

A regime shift in the North Sea since 1987 was first suggested by Reid et al. (2001). Reported ecosystem changes involved an increase in phytoplankton biomass (Reid et al., 1998), a change in zooplankton community structure and organism phenology (Beaugrand and Reid, 2003; Reid et al., 2001), as well as changes in the benthos (Reid and Edwards, 2001). Recent studies additionally show an increase in microalgae, jellyfish, decapod and echinoderm larvae but decrease in bivalve larvae (Kirby and Beaugrand, 2009; Kirby et al., 2009).

Beaugrand (2004) performed a comprehensive study using data from the CPR survey (for phytoplankton and zooplankton) and fish recruitment data for plaice (*Pleuronectes platessa* L.), cod (*Gadus morhua* L.), haddock (*Melanogrammus aeglefinus* L.), herring (*Clupea harengus* L.) and

sole (*Solea solea* L.). This study demonstrated that the regime shift in the North Sea occurred over a longer period, during 1982–1988, although the changes were clustered between 1982–1985 and 1987–1988. Most of the trajectories of the individual ecosystem indicators exhibited stepwise changes, while a few did not change. The timing of the changes between indicators varied strongly and was related to physiological, biological and ecological characteristics of species, to the numerical methods used to identify the shifts and also to the different physical mechanisms by which large-scale hydro-climatic forcing influenced the regime shift. The latter were identified to be the main driver of the regime shift through two mechanisms. Firstly, the increase in sea surface temperature and the change in wind intensity and direction during the late 1970s initiated alterations in the location of a biogeographical boundary along the European continental shelf, being responsible for the regime shift after 1982. Additionally, large-scale hydro-climatic forcing modified local hydro-meteorological variability that affected the North Sea ecosystem directly after 1987.

Weijerman et al. (2005) investigated regime shifts in the North Sea and the Wadden Sea, following the approach of Hare and Mantua (2000). Of the assembled 78 time series from 1970 to 2002, 50 were biological variables comprising multiple trophic levels and representing a very wide range of marine organisms, from phytoplankton to top-predators. The remaining 28 environmental data sets included atmospheric and oceanic variables. Based on four different statistical techniques, they provided evidence of regime changes in 1979 and 1988 (Fig. 6A and B). Characteristic for the first regime shift was a change in phytoplankton composition and an increase in polychaete abundance in the western Wadden Sea. Further changes were a steep decline in the landings of whiting, while the landings of plaice and herring recruitment increased. The late 1980s regime shift included dramatic changes in abundance of several fish species. Non-commercial species such as solenet and scald fish were affected, but so were cod and haddock, and phytoplankton composition changed back to the 1970s situation. Weijerman et al. (2005) identified changes in salinity and weather conditions to initiate the first shift, and temperature to be responsible for the late 1980s changes: hence, ocean climate conditions seemed to be the main drivers of North Sea regime changes.

Similarly, Schlüter et al. (2009) compiled 39 time series for 1975–2004 from the German Bight, a smaller coastal part of the southern North Sea, and analysed them with different ordination techniques (including PCA), the regime shift analysis introduced by Ebbesmeyer et al. (1991), and

Chronological Clustering (Fig. 6C and D). Their results confirm the 1980s North Sea regime shift and also suggest that the German Bight is influenced by long-term modes of variability congruent to atmospheric forcing indices as well. In the German Bight, the shift is driven primarily by temperature, the Gulf Stream index, frost days and Secchi depth. Variables related to the plankton and fish component of the ecosystem appear to be especially responsive to changes in these driving variables. In particular, herring, the dinoflagellate *Noctiluca scintillans*, and, to a lesser extent, the ctenophore *Pleurobrachia pileus* showed increased over time, whereas cod and saithe (*P. virens*) biomass decreased. Generally, the hydro-climatic conditions in the German Bight are highly dynamic, whereas changes in the biological or chemical components, apart from the shift in the late 1980s, appear to be much smoother. Recently, a study focussed on the differences between coastal waters (like the Wadden Sea and the German Bight) and open North Sea regions (McQuatters-Gollop and Vermaat, 2011) showed that hydro-climatic changes in the open North Sea entailed nearly simultaneous responses in the plankton, whereas this was not the case in coastal waters. It was hypothesised that interannual coastal plankton dynamics are less tightly controlled by hydrographic forcing than are those of the open North Sea or display a stronger spatial variation between coastal sectors, in line with the conclusions of Schlüter et al. (2009).

Kenny et al. (2009) identified at least five different eco-hydrodynamic regions through an integrated spatial analysis of the North Sea, demonstrating that the analysis of LMEs without accounting for small-scale differences can be ambiguous. Nevertheless, due to a lack of spatially disaggregated data, especially for important ecosystem components like many fish species or seabirds, they investigated regime changes in the entire North Sea (Fig. 6E and F). Of their 114 selected variables from 1983 to 2003, 19 were hydro-climatic environmental variables. The biological data matrix included 34 plankton species, 14 fish stock assessment metrics, 31 fishing pressure metrics and 17 seabird species. The results show that cod, the key zooplankton species *C. finmarchicus* and Northern Fulmar declined from high values before 1990 to lower values afterwards. Two dominant regimes were identified by STARS: the first before 1993 was characterised by a productive cold-water demersal fin fishery and an increasingly productive pelagic fishery, and a second regime after 1993 was characterised by increased seawater temperature, a decline in the demersal fin fishery, but a still-productive pelagic fishery. The reason for the identification of the shift later than in other North Sea studies is probably related to the shorter time series, which starts in 1983,

because the detection of a shift at the beginning of a time series is technically challenging. However, [Kenny et al. \(2009\)](#) also suggest that the transition in the state of the North Sea ecosystem happened between 1983 and 2003, despite abrupt changes in single variables, for example, *C. finmarchicus* and sea surface temperature. Their analysis supports the interpretation that a temperature increase by 1988 has amplified changes that have been initiated already before, most likely by a combination of gradual warming ([Beaugrand, 2004](#)) and high fishing pressure.

3.5. Baltic Sea

Studies on ecosystem regime shifts in the Baltic Sea were initially focusing on changes in commercially important fish populations, that is, cod, herring and sprat (e.g. [Köster et al., 2003, 2005](#)). Using an ecosystem model (Ecopath with Ecosim, EwE), [Österblom et al. \(2007\)](#) demonstrated that reduced top-down control (seal predation) and increased bottom-up forcing (eutrophication) can largely explain the historical dynamics of the main fish stocks between 1900 and 1980. They identified two major ecological changes: the first, from seal to cod domination, occurred after the 1930s and was caused by a virtual elimination of marine mammals; the second, characterised by a transition from an oligotrophic to a eutrophic state, occurred around 1950. According to their modelling results, eutrophication resulted in a substantial increase in fish production in the Baltic Sea and changed the whole food web.

The best-documented regime shift in the Baltic fish community from empirical data is that from cod to clupeid (i.e. mainly sprat) domination in the late 1980s. It has been explained by not only a combination of overfishing and climate-induced recruitment failure in cod but also increased recruitment of sprat due to warming ([Köster et al., 2003, 2005](#); [MacKenzie and Köster, 2004](#)). Later, it became obvious that the changes in the fish community are merely a component of a larger-scale full reorganisation of the Baltic ecosystem. [Alheit et al. \(2005\)](#) summarised changes on all trophic levels and demonstrated their synchronicity with the regime shift in the North Sea during the late 1980s. Subsequently, multivariate statistical analyses have been conducted for the central Baltic Sea ([ICES, 2008](#)), integrating hydro-climatic, nutrient, phyto- and zooplankton as well as fisheries data, and confirmed a regime shift in the pelagic ecosystem during the late 1980s and early 1990s ([Möllmann et al., 2009](#)). Two regimes (1974–1987 and 1994–2005) were identified by

Chronological Clustering and STARS (Fig. 7A and B), characterised by the opposite patterns in dominance of cod and sprat, as well as the zooplankton species *Pseudocalanus acuspes* and *Acartia* spp. (Möllmann et al., 2008). Further, a change in the dominance of phytoplankton from diatoms to dinoflagellates has been indicated (Wasmund et al., 1998). The central Baltic Sea regime shift occurred in a transition period (1988–1993) characterised by low salinity and oxygen conditions as well as high temperatures and nutrient levels, eventually forcing the biotic part of the ecosystem into a new state (Möllmann et al., 2009). In addition to the physical and chemical conditions, unsustainable cod fishing pressure during the late 1980s contributed to the overall ecosystem changes, accelerating the cod decline and the consequent increase in sprat population, with further indirect changes down the food web (Casini et al., 2008; Möllmann et al., 2008; see Section 4).

Similar multivariate analyses of ecosystem state and development during the past three decades have been conducted for the Sound ecosystem, a narrow strait located between Denmark and Sweden and linking the North and Baltic Seas (Lindegren et al., 2010a). This analysis covered 1979–2005 and included 48 datasets of physical oceanographic and nutrient conditions as well as phytoplankton, zooplankton and fish variables (Fig. 7C and D). Lindegren et al. (2010a) used STARS based on the PC scores and found a similar regime shift timing as in the Central Baltic with major changes occurring between 1987 and 1988. The first regime was characterised by high levels of cyanobacteria, copepods, microzooplankton and molluscs; the new regime showed high levels of flatfish, herring, cod and whiting. This study showed the dominance of atmospheric–oceanographic changes as being the most likely driver of change. Because the Sound is characterised by the absence of commercial trawl fishing and hence by a low fishing mortality, fishing is not the main driver of the ecosystem regime shift here. Consequently, the cod stock in the Sound had recovered to above pre-shift conditions by the mid-1990s, whereas spawning stock biomass (SSB) in neighbouring areas remained in a depleted state. This indicates that this system might be more resilient to changes due to the low fishing pressure and the largely healthy groundfish stock structures.

Multivariate analyses as described above have now been additionally conducted for other Baltic Sea sub-areas such as the Gulf of Riga, the Gulf of Finland, the Bothnian Sea and Bay, as well as a coastal area (Diekmann and Möllmann, 2010). In all ecosystems, pronounced structural changes (i.e. regime shifts) were detected. Although the investigated sub-areas are characterised by different environmental conditions and influenced by either

North Sea water or river run-off and freshwater conditions, the major period of reorganization in the Baltic was invariably found between 1987 and 1989. In several of the systems, abrupt changes were also found during the mid-1990s, probably related to the major North Sea water inflow in 1993 following a long stagnation period. The results of the multisystem analysis suggest that the reorganisation between two ecological states was mainly initiated by changes in atmospheric forcing (Diekmann and Möllmann, 2010), although system-specific drivers might have modulated these effects.

3.6. Black Sea

The Black Sea is a deep, mostly land-locked basin in Eastern Europe linked to the Mediterranean by only narrow straits. It is characterised by a positive water balance and is thus extremely strongly influenced by the drainage basin, which is five times larger than the sea area. Several reorganisations of the Black Sea ecosystem occurred during the past 50 years, and these regime shifts are among the best investigated in the literature. In contrast to the ecosystems discussed above, no multivariate analysis (i.e. PCAs) has been published yet, but Oguz and co-authors (Oguz, 2005; Oguz and Gilbert, 2007; Oguz and Velikova, 2010; Oguz et al., 2006) identified several abrupt and regime-like changes in hydro-climatic variables, nutrients and across all trophic levels from primary producers up to top-predators in the period 1960–2005. They demonstrated the importance of multiple drivers, namely, eutrophication, overfishing, introduction of alien species and food web interactions.

A first major change in the Black Sea food web was the decline of large predatory fish populations due to overfishing and a subsequent progressive increase in small pelagic stocks from the 1960s to the early 1970s. Accordingly, a trophic cascade occurred, leading to decreased zooplankton and increased phytoplankton biomasses (Daskalov et al., 2007; Llope et al., 2011). The period prior to the regime shift is characterised by average warm and mild winters (Oguz, 2005), and by a change from oligotrophic to eutrophic conditions during the first half of the 1970s. However, the effects of eutrophication were mainly restricted to coastal areas, while offshore phytoplankton biomass remained low. Phytoplankton biomass then increased abruptly during the early 1970s as a response to the trophic cascade, favourable climatic influences (indexed by negative NAOI values) and nutrient enrichment from land source. Eutrophication and the development of massive algal blooms further intensified during the 1980s.

A second regime shift in 1988/1989 corresponded to the collapse of the small pelagics due to unsustainable fishing levels. The result of the depletion

of the small pelagic fish stocks was the development of large populations of gelatinous carnivores, firstly, the jellyfish *Aurelia aurita* and then its invasive competitor the ctenophore *Mnemiopsis leidyi*. Heavy *Mnemiopsis* predation on small pelagic fish larvae and food competition with the adults have exacerbated the collapse of small pelagic fishes. Climatically, the mid-1980s and early 1990s were characterised by extremely cold, dry and severe winters (Oguz, 2005) with the coldest sea surface temperatures of the last century. Physical processes driven by climatic cooling and severe winter conditions (e.g. enhanced vertical mixing and stronger upwelling associated with intensification of the cyclonic basin-wide circulation system) resulted in an increased nitrate injection into the surface layer and caused strong spring and summer phytoplankton blooms: increased eutrophication combined with this cooling has resulted in this elevated phytoplankton biomass.

The ecosystem state dominated by gelatinous carnivores and phytoplankton biomass persisted only 5 years followed by markedly varying, transient, oscillatory food web organization during 1991–1996. Since 1997, the gelatinous population decreased and the small pelagic fish stocks continuously recovered because of fishing regulations. Further, another gelatinous ctenophore species, *Beroe ovata*, entered the Black Sea at the end of the 1990s, preying mostly on *Mnemiopsis* (Kideys, 2002; Shiganova, 2004). The tendency of improvement and rehabilitation of the northwestern Black Sea shelf described by McQuatters-Gollop et al. (2008) disagrees with recent findings from Oguz and Velikova (2010). The period following the early 1990s is characterised by intermediate eutrophication and comparably low production but shows a completely different ecosystem structure compared to the pristine system before 1970. The prevailing low zooplankton and fish biomass, moderate *Noctiluca* and jelly biomass (with high interannual variation also between the main species *A. aurita* and *Mnemiopsis*) are indicative of a degraded ecosystem (Oguz and Velikova, 2010). The current state with intermediate productivity can be thus interpreted as an alternative state to the formerly fish-dominated, low-productivity ecosystem at the beginning of the 1960s.



4. TROPHIC CASCADES

In theory, ecosystem regime shifts are caused by the interaction of external and internal sources of population or trophic level variability (Scheffer and Carpenter, 2003). We have shown that external drivers of regime shifts are, to a large degree, climate and overfishing. The large-scale occurrence of

marine ecosystem regime shifts in the Northern hemisphere and the synchrony of their occurrence during the late 1980s/early 1990s suggest a common large-scale climatic driver of ecosystem changes. However, there is also evidence that overfishing plays a crucial role in triggering ecosystem regime shifts, for example, in the Black Sea (Llope et al., 2011). The reorganisation of a food web caused by overfishing involves changes in the trophic cascade and thus in the relationship between bottom-up and top-down control (O’Gorman and Emmerson, 2010).

Trophic cascades can be defined as linear chains of alternating suppression and release between successive pairs of consumer and consumed species (or aggregate groups of species) (Scheffer et al., 2005; Strong and Frank, 2010). This means that predators suppress the abundance of their prey, thereby releasing the next lower trophic level from predation, making the ecosystem essentially top-down controlled. This stands in contrast to the traditional view of bottom-up controlled ecosystems, which was the first paradigm of food web science and dominated the first half of the twentieth century (Elton, 2001; Mulder et al., 2012; Strong and Frank, 2010). Evidence for bottom-up forcing is usually derived by a positive correlation among biomasses of trophic guilds in space or time, and in marine ecosystems, positive correlations between average fisheries yield and primary production can be found (Chassot et al., 2007; Ware and Thomson, 2005).

Figure 8 exemplifies bottom-up regulation of a marine ecosystem (grey circles to the left).

Usually, marine ecosystems have four guilds with overall biomass decreasing from phytoplankton to top-predators (here, piscivorous fish). In a bottom-up control situation, the size of the guild’s biomass depends on the trophic level below, and the suppression of planktivores by piscivores is the “normal situation”. When humans remove the controlling influence of the apex predators, mesopredators increase (Prugh et al., 2009). In marine ecosystems, planktivores hence increase in response to the overfishing-induced depletion of piscivorous species such as cod (Strong and Frank, 2010). The right part of Fig. 8 (black circles) demonstrates the resulting alternating increase and decrease of the trophic guild’s biomasses down to phytoplankton when the ecosystem regulation is changed from a bottom-up controlled situation to a top-down cascade due to overfishing.

Despite the evidence for trophic cascades in many aquatic and terrestrial systems (Terborgh and Estes, 2010), the potential of top-down control in large, open marine systems has been denied until recently (Steele, 1998; Steele et al., 1998). Arguments for this view include high species

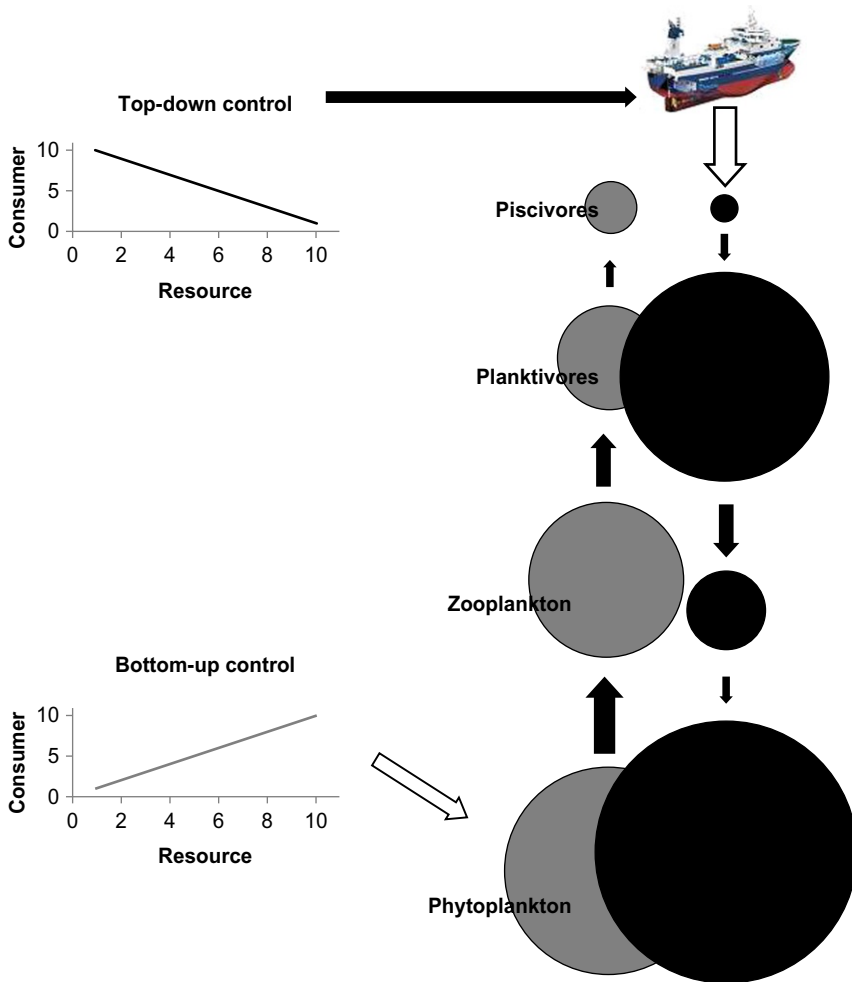


Figure 8 Conceptual diagram showing bottom-up forcing of a marine food chain (grey circles to the left) and trophic cascading induced by overfishing (black circles) where the regulation between trophic levels is changed to top-down control. Graphs at the left-hand side illustrate the correlations between the biomasses of consumers and resources in a top-down or bottom-up controlled ecosystem.

diversity, patchiness in productivity, as well as highly mobile and opportunistic predators (Strong and Frank, 2010). Additionally, the view that recruitment to fish stocks will inexorably generate biomass lost to fishing has dominated (Nixon and Buckley, 2002). However, increasing length of monitoring time series and overfishing as a “natural trophic

cascade experiment” have now shown top-down controls from the upper trophic levels are widespread (Baum and Worm, 2009; Frank et al., 2007; Strong and Frank, 2010; Worm and Myers, 2003). Even more important, now classic examples for trophic cascading over 3–4 trophic levels in LMEs exist, of which we will review the most prominent cases from the Eastern Scotian Shelf, the Baltic Sea and the Black Sea. No community-wide trophic cascade has been published for the North Pacific and the North Sea where ecosystem regime shifts have been reported, but changes in trophic control from top-down to bottom-up have been suggested (Kenny et al., 2009), and indications of trophic cascading between species have been found (Kirby et al., 2009; Lindegren et al., 2010a). After reviewing the three examples of marine trophic cascades, we will return to discuss the main factors affecting the vulnerability of ecosystems to overfishing-induced trophic cascading and the potential of climate to induce changes in trophic control, as well as oscillating controls.

4.1. Eastern Scotian Shelf

The most familiar case of a trophic cascade in a LME has been described for the Scotian Shelf, which had involved four trophic levels and nutrient concentrations (Frank et al., 2005). The trophic cascade was initiated by overfishing of large predators (primarily Atlantic cod) and resulted in increased biomasses of pelagic fish and crustacean species. Further down the food chain, large zooplankton decreased while phytoplankton biomasses increased and eventually depleted nutrient levels. Clearly, the changes in top-predator abundance caused a major reorganisation of the food web through indirect effects of fishing on the lower trophic levels. These ecosystem changes had pronounced social and economic consequences and resulted in the emergence of a new fishery focused on shrimp and crab with a monetary value that exceeds that of the replaced groundfish fishery. Frank et al. (2005) discussed that from an economic perspective this may be an attractive situation, but considering biological and functional diversity as a stabilising force in ecosystems, this may bear strong ecological risks in the face of future natural or anthropogenic perturbations.

4.2. Baltic Sea

Overfishing of cod strongly impacted the Baltic Sea food web leading to an explosive increase of their main prey, the planktivorous fish sprat (*Sprattus sprattus*) (Köster et al., 2003). Trophic cascading was the strongest in summer

when biomass of zooplankton declined, followed by increases in phytoplankton (Casini et al., 2008). In spring, the increased sprat stock only influenced the calanoid copepod *P. acuspes*, while top-down control on other zoo- and the phytoplankton was counteracted by stronger climate-induced bottom-up controls (Möllmann et al., 2008). The strong effect of the uncontrolled sprat stock for the food web as a whole can also be seen by reduced growth due to competition with the planktivorous competitor herring (Casini et al., 2006; Möllmann et al., 2005). The poor condition of the pelagic fish species eventually negatively affected the reproduction of a piscivorous seabird, the common guillemot (*Uria aalge* L.), a further indirect effect of the changes at the top of the food web (Österblom et al., 2006). Overfishing thus contributed to the observed reorganization of the Baltic Sea ecosystem by species interactions and by an interplay between bottom-up and top-down regulation (Möllmann et al., 2009).

4.3. Black Sea

The Black Sea ecosystem has undergone multiple regime shifts under strong anthropogenic forcing such as heavy fishing, eutrophication and invasions by alien species, as well as climate variability (Daskalov, 2003; Oguz and Gilbert, 2007; Oguz et al., 2006). Daskalov et al. (2007) studied time series of five groups of pelagic populations across four trophic levels, that is, phytoplankton, zooplankton, planktivores (gelatinous and fish) and piscivores. Major ecosystem changes were related to overfishing the upper trophic levels of the pelagic food web (Llope et al., 2011). A first event was caused by top-predator depletion and triggered a system-wide trophic cascade involving four trophic levels, nutrients and oxygen in the surface water. The second event was the result of a strong reduction of planktivorous fish, again through overfishing, and an irruption of the alien ctenophore *M. leidyi*. This caused a second system-wide trophic cascade with similar alternating changes in zoo- and phytoplankton, as well as water chemistry. Daskalov et al. (2007) describe the underlying mechanisms by phase-space plots of consumer–resource relationships with the trajectories depending on the delay of the response of the resource to the shift in the consumer. Their conceptual representation also indicates the existence of alternative stable states differing from each other in terms of the trophic control they are under, with collapse and recovery of either the resource or the consumer being unstable intermediate conditions involving hysteresis. According to Llope et al. (2011), the truncated food

web of the Black Sea, initiating a top-down cascade, was further degraded by eutrophication involving bottom-up control. They assume that a more complex food web with viable top-predators might have been more efficient in counteracting the increased productivity in the mid-1980s.

4.4. Vulnerability of marine ecosystems to overfishing-induced trophic cascading

The above examples of trophic cascades in marine ecosystems show that overfishing of top-predators can change food web regulation from bottom-up to top-down control. Not all ecosystems seem, however, to have the same vulnerability to the effect of strong exploitation. [Frank et al. \(2007\)](#) investigated spatial variability in the dominance of bottom-up or top-down control in heavily fished ecosystems of the North Atlantic. Their review spanned 30° of latitude and reported changes mainly involving the two upper trophic levels (piscivorous and planktivorous fish). They showed that in the western Atlantic bottom-up forcing was prevalent in southern areas associated with the Gulf of Maine and the south-eastern continental shelf. Top-down control was observed in most of the other areas from the Western Scotian Shelf to West Greenland. On the eastern side of the Atlantic, the North Sea, Faroe Shelf, south-east Scotland and Bay of Biscay were bottom-up regulated. More northern areas such as Iceland and the Barents Sea appeared to be top-down controlled. The analysis by [Frank et al. \(2007\)](#) revealed a consistent geographic match between the sign of the trophic control and species diversity, as well as with temperature. Bottom-up control seems to dominate in areas with higher species richness, which points towards a greater ability to compensate for the effects of overfishing and hence to prevent a shift to top-down control. Similarly, bottom-up control prevails in warmer areas, which points towards the ability of species to compensate for loss due to exploitation through faster turnover rates. A strong positive relationship is, however, also evident between temperature and species richness, making disentangling the two effects difficult.

4.5. Climate-induced changes in trophic control and oscillating control

Most studies on trophic cascading in marine ecosystems show overfishing to be the responsible external driver, leading to changes in trophic control and inducing ecosystem regime shifts. However, climate can also alter the form of trophic control, with examples coming mainly from the Pacific region. [Litzow and Ciannelli \(2007\)](#) used a 34-year time series of the abundance

of Pacific cod (*Gadus macrocephalus*) and five prey species to show that the sign of trophic control in Pavlov Bay oscillates depending on climate state. Rapid warming during the Pacific regime shift in the 1970s caused switch between bottom-up and top-down control, contributing to the shift from a prey-rich to a prey-poor ecosystem state. This study hence demonstrated that climate-regulated trophic oscillations caused the ecosystem regime shift in Pavlov Bay and the associated Gulf of Alaska. Similarly, [Kirby and Beaugrand \(2009\)](#) showed that temperature can modify predator–prey relationships, a mechanism they call trophic amplification. They claim that this temperature-mediated change in trophic interaction is a major mechanism driving the North Sea regime shift ([Kirby and Beaugrand, 2009](#)).

Oscillations in trophic control have been shown by [Hunt et al. \(2002, 2011\)](#) proposing an oscillating control hypothesis as a mechanism to explain ecological reorganization in the south-east Bering Sea. Here, bottom-up control leads to a population increase, and when the population size is high, biological control, for example, top-down control through cannibalism, is dominating population regulation. Similar changes in the control pattern in relation to Pacific ecosystem regime shifts have been shown for walleye pollock (*Theragra chalcogramma*) in the Gulf of Alaska ([Bailey, 2000](#)). Changes in trophic control from climate-induced bottom-up to top-down control have been shown by [Casini et al. \(2009\)](#) as the mechanism behind the Baltic Sea trophic cascade.



5. DISCUSSION

In this study, we have reviewed ecosystem regime shifts and trophic controls in Northern hemisphere marine ecosystems: we will now consider the synchronicity of the ecosystem changes observed during the 1990s to address the question of whether there is a common large-scale atmospheric driver behind these changes. We will then discuss the importance of overfishing as a driver for ecosystem regime shifts and interactions of multiple drivers and the existence of alternative stable states, leading to the question of the reversibility of ecosystem changes and the resulting management implications.

5.1. Synchronicity of timing—Evidence of atmospheric teleconnection

The data on ecosystem regime shifts observed in the North Pacific, the Eastern Scotian Shelf in the North Atlantic, as well as the North Sea, the Baltic and the Black Sea, demonstrate a strikingly similar timing of regime shifts ([Table 1](#)).

Table 1 Summary of ecosystem regime shift timing (regime shifts during the late 1980s/early 1990s in bold) and the main drivers of change in six Northern hemisphere ecosystems

Ecosystem	Study	Timing	Main driver
North Pacific	Hare and Mantua (2000)	1977 and 1989	Climate
Eastern Scotian Shelf	Choi et al. (2005)	1976 and 1990	Climate, overfishing
North Sea	Beaugrand (2004)	1982–1988; two periods: 1982–1985 and 1988/1989	Climate
	Weijerman et al. (2005)	1979 and 1988	Climate
	Kenny et al. (2009)	1993	Climate, overfishing
Baltic Sea	Möllumann et al. (2009)	1988–1993	Climate, overfishing, eutrophication
The Sound	Lindegren et al. (2010a)	1987/1988	Climate
Black Sea	Oguz and Gilbert (2007)	1973/1974 and 1989	Overfishing, species invasion

[Figure 9](#) summarises the temporal development of holistic indicators of ecosystem change (Principal Component 1 from area-specific PCAs) in order to explore the extent of synchronicity. Although these ecosystems are situated in different areas of the Northern hemisphere and differ strongly in their physical and biological characteristics, major shifts indicated by the comparatively abrupt decrease of PC1 scores have occurred simultaneously during the late 1980s/early 1990s, suggesting strong teleconnections of climate variables.

[Alheit and Bakun \(2010\)](#) propose that the North Atlantic Oscillation (NAO) is the synchronising agent for European aquatic ecosystems: the change of the NAO index from a negative to a positive phase in the late 1980s resulted in a coherent water temperature increase and was associated with regime shifts in the North Sea, the Baltic Sea, the North-western Mediterranean and north and central European lakes. This is also consistent with observations made by [Conversi et al. \(2010\)](#), who analysed and reviewed long-term records of Mediterranean ecological and hydro-climate variables

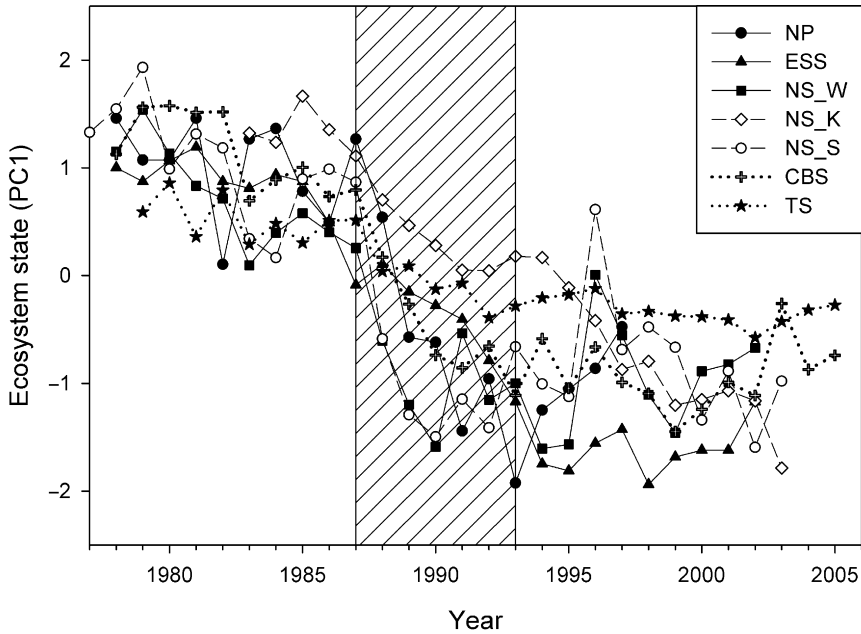


Figure 9 Comparison of the development of ecosystem state indicators (principal component 1—PC1) and reported regime shift timing during the late 1980s/early 1990s (hatched area) in six Northern hemisphere marine ecosystems. NP, North Pacific (Hare and Mantua, 2000); ESS, Eastern Scotian Shelf; NS_W, North Sea (Weijerman et al., 2005); NS_S, North Sea (Schlüter et al., 2009); NS_K, North Sea (Kenny et al., 2009); CBS, Central Baltic Sea (Möllmann et al., 2009); and TS, the Sound (Lindegren et al., 2010a). Data for NP, ESS, NS_W and NS_K were redrawn from publications; data from other studies were kindly provided by the authors.

and found a similar timing of ecosystem regime shifts, that is, in the late 1980s. The study further showed that these changes were related to Mediterranean hydrographic properties, surface circulation and deep-water convection, all triggered by large-scale atmospheric drivers indicated by the NAO, and the Northern hemisphere temperature. Similarly, the AOI and the Monsoon Index over the North Pacific showed abrupt changes and large interannual variability in 1987–1989 leading, for example, to a regime shift in the Japan Sea (Tian et al., 2008). Hence, it is very likely that a main driver of the observed ecosystem changes described here is the large-scale climate variability over the Northern hemisphere. The period of change essentially matches times of change in the NAO and other atmospheric indices at the end of the 1980s, which modified the local temperature regimes (e.g. warming in Northern Europe).

Although regime shifts by definition mean that the observed changes are abrupt, some studies show that it is difficult or impossible to identify single regime shift years, which is also visible by the extended regime shift period (hatched area) in Fig. 9 (e.g. Beaugrand, 2004; Kenny et al., 2009; Möllmann et al., 2009). Two explanations are relevant for this observation. Firstly, lags in response time will occur: this involves to a smaller part time lags in physical oceanic variables induced by oceanic processes, such as Rossby waves, Kelvin waves or advection by mean flows (Overland et al., 2010). More importantly, species respond at different rates to changes in the abiotic environment, for example, plankton species with fast turnover rates will react quickly to an abrupt temperature change. Indicators of stock size for long-lived fish species such as cod have a greater inertia, as temperature effects on, for example, recruitment will only be first visible after a few years (Castle et al., 2011; Peck, 2012; Stenseth et al., 2002). Additionally, abiotic effects on a species may be transmitted through food web interactions (Layer et al., 2010; Olesen et al., 2010), hence displaying an indirect effect on other species or trophic levels (Ottersen et al., 2010). A second major reason for ecosystem regime shifts to occur over an extended period of time is interactive or additive effects of several external drivers. For example, Möllmann et al. (2009) showed that several abiotic conditions (i.e. fishing pressure, temperature, salinity, nutrient concentrations) in the Central Baltic Sea were on extreme levels during a “transition period”, eventually leading to the regime shift.

5.2. Trophic cascading—The importance of overfishing in triggering ecosystem regime shifts

Trophic cascading is caused by a switch of trophic regulation from bottom-up to top-down control at the top of the food web (Woodward et al., 2010). The major examples of trophic cascades in marine ecosystems reviewed here suggest that depletion of predatory fishes due to overfishing (frequently of cod like in the Eastern Scotian Shelf and the Baltic Sea) is a determining factor for ecosystem changes (Table 2). Further, ecosystem vulnerability to exploitation effects depends on the species diversity and on the thermal conditions (Frank et al., 2007). The case of the Black Sea, however, shows that other causes, such as the invasion of alien species, can contribute to trophic cascading. Additionally, studies mainly from the Pacific and the North Sea demonstrate that climatic changes have the ability to induce changes in trophic forcing, and principally, the magnitude and dominance of one or the

Table 2 Summary of trophic cascades that were observed in ecosystems with regime shifts

Ecosystem	Study	Species/trophic levels involved
Eastern Scotian Shelf	Frank et al. (2005)	Demersal fish, pelagic forage fish, large crustaceans, large zooplankton, phytoplankton
Baltic Sea	Casini et al. (2008) , Casini et al. (2009) , Möllmann et al. (2008)	Cod, sprat, zooplankton, phytoplankton
Black Sea	Daskalov et al. (2007) , Oguz and Gilbert (2007)	Pelagic predatory fish, small planktivorous fish, gelatinous plankton, zooplankton, phytoplankton

other control pattern can depend on the climate state and subsequent population development ([Hunt et al., 2002](#); [Litzow and Ciannelli, 2007](#)).

Nevertheless, there is strong evidence that overfishing is a major driver of ecosystem regime shifts in addition to climate, as both external factors are able to change the prevailing trophic control. The effects of climate seem to dominate in the Pacific and the North Sea, where studies of trophic cascading are comparably rare. However, this may be also a bias introduced by a stronger initial focus on climate events ([Beaugrand, 2004](#); [Kirby and Beaugrand, 2009](#); [Reid et al., 2001](#); [Weijerman et al., 2005](#)), while more recent studies increasingly emphasise the role of fishing ([Fauchald, 2010](#); [Kenny et al., 2009](#); [Kirby et al., 2009](#)). From the cases of especially the Eastern Scotian Shelf, the Baltic and the Black Sea, it is clear that overfishing can induce or contribute to the development of regime shifts involving several trophic levels by cascading interactions. Evidence for a synergy of both effects exist from the Baltic Sea ([Möllmann et al., 2009](#)), and from the Scotian Shelf ([Choi et al., 2005](#)), although recently consensus seems to exist that overfishing is the main driver here ([Frank et al., 2011](#)). The Black Sea gives an example that, in interaction with overfishing, invasion of alien species can trigger trophic cascades and influence prey–predator oscillations ([Oguz and Gilbert, 2007](#)).

5.3. Interactions of multiple drivers, alternative stable states and the reversibility of ecosystem regime shifts

It is often assumed that multiple drivers are necessary to cause ecosystem regime shifts ([Bakun, 2005](#); [De Young et al., 2008](#); [Lees et al., 2006](#)). The analysis presented here shows that climate variability is a common

large-scale driver, and seems to be almost solely responsible for the regime shifts in the Pacific and the Sound (Table 1). Even so, a range of other anthropogenic impacts (eutrophication, exploitation, introduction of alien species) are important or even solely responsible for ecosystem change as well, maybe affecting tipping points or affecting the food web structure (Jacob et al., 2011). Eutrophication can contribute to regime shifts as shown for the Central Baltic Sea (Möllumann et al., 2009; Österblom et al., 2007) or the Black Sea (Oguz and Velikova, 2010) but may cause changes in primary production only (Oguz and Gilbert, 2007). Species invasion may also have a role in ecosystem regime shifts, as shown for the alien ctenophore *M. leidyi* in the Black Sea (Oguz and Gilbert, 2007). Invasives can affect the trophic structure and may fill trophic niches formerly occupied by native and sometimes overfished species. Overfishing is clearly important in causing ecosystem regime shifts, and for some of the observed shifts, it is considered to be the most important driver, for example, in the Eastern Scotian Shelf (Frank et al., 2005, 2011) and the Black Sea (Daskalov et al., 2007; Oguz and Gilbert, 2007). In other ecosystems such as the Baltic Sea, overfishing is assumed to have interacted with climate-induced changes (Möllumann et al., 2008, 2009). This seems also to be the case for the North Sea, where more recent studies increasingly emphasise the role of fishing (Kenny et al., 2009; Kirby et al., 2009). In the cases from the Eastern Scotian Shelf, the Baltic and the Black Sea overfishing seem to have contributed significantly to the development of regime shifts and involve several trophic levels by trophic cascading. In contrast, in the absence of intensive fishing, the case study from the Sound exemplifies how at least certain fish stocks can recover relatively rapidly (Lindegren et al., 2010a). Whether this increases the resilience of the ecosystem, in general, for example, by protecting important benthic habitats and organisms, is presently unclear.

Despite the importance of multiple drivers acting in concert with each other (Lees et al., 2006), scientific studies have the tendency to concentrate and postulate the dominance of one single factor inducing regime shifts: interactions between external drivers are rarely investigated. Resilience theory gives a framework for interpreting the interaction of multiple drivers (Scheffer, 2009). Multiple external drivers interact in a way that one undermines resilience (e.g. through fishing) and the other (e.g. abrupt climate change) gives the final impulse for an ecosystem regime shift. For instance, for the Central Baltic Sea, Möllumann et al. (2009) showed that a deterioration of the physical environment through limited inflow of North Sea waters

reduced cod recruitment. Increased fishing pressure as a response to decreasing stock size further undermined the resilience of the stock. Eventually, an abrupt temperature change with positive reactions of some populations, such as sprat, and an even higher fishing pressure on cod caused the regime shift. In contrast to this, the cod stock in the Sound ecosystem was thought to be in a healthy condition in the 1980s (Lindegren et al., 2010a). During a synchronous abrupt change in temperature at the end of the 1980s similar to the one in the Central Baltic, the Sound ecosystem changed drastically: but as cod was not over-fished, no trophic cascade occurred, and the upper trophic levels remained largely unaltered, or recovered rapidly (Lindegren et al., 2010a).

Ecosystem regime shifts can be difficult to reverse if alternative stable states are involved, an important implication for management (Suding et al., 2004). Due to the intractability of experimentation within LMEs, no final mechanistic evidence can be derived neither at present nor for the foreseeable future. Rather indications from empirical correlational data need to be used, and suitable mathematical models developed and applied were possible (Rossberg, 2012).

Identifying jumps in time series is the most frequently applied empirical–statistical approach in detecting alternative regimes and several methods for this exist (e.g. Hare and Mantua, 2000; Legendre et al., 1985; Rodionov, 2004; Solow and Beet, 2005). However, these abrupt changes alone do not provide evidence for the existence of alternative stable states, because they may be caused by a stepwise change in an external driver only. Thus, Scheffer and Carpenter (2003) proposed further indicators that can be obtained from field data, one related to multimodality of the frequency distribution of states. Tests for testing multimodality (bootstrapping) require extensive datasets but often have low explanatory power for the generally short and limited ecological datasets that are currently available. Consequently, multimodality can be often only shown graphically. Further, as with sudden jumps in time series, multimodality does not necessarily imply alternative attractors, as, for example, the driving factor might have also a multimodal distribution. The third possible indicator addresses the relationship of state variables to the control variable. If this relationship is best described by two different functions (e.g. piecewise regression, Threshold GAMs (Ciannelli et al., 2004)), it suggests an underlying hysteresis curve as described for the case of the Baltic Sea. Here, it has been shown that a control of the system due to hydro–climatic variables was replaced by top–down control after a threshold level in sprat abundance was crossed (Casini et al., 2009).

In general, [Scheffer and Carpenter \(2003\)](#) argued that good indications for the existence of stable states can be obtained from field data, but none of the three indicators can be fully conclusive. [Oguz and Gilbert \(2007\)](#) still applied these indicators to time series from the Black Sea covering variables representative for climate, hydrography and various ecosystem components. They found jumps in time series and bimodality related to climate indices, temperature and biogeochemical variables such as dissolved oxygen and hydrogen sulphide concentrations. Sharp transitions and multiple modes were also visible in time series of phytoplankton. For the small pelagic fish stock, two statistically different regression lines for the low and high stock regimes were found, which point to the existence of dual relationships to fishing pressure values. Similar observations were also made for the haddock stock at Georges Bank ([Collie et al., 2004](#)), where two alternate states of high and low haddock biomasses were found for near-constant fishing mortalities.

Alternative stable states in theory develop from positive feedbacks in a system that also causes hysteresis in response to an external driver ([Scheffer and Carpenter, 2003](#)). A suggested feedback explaining the lack of recovery of depleted cod stocks is a so-called predator–prey role reversal or cultivation effect ([Walters and Kitchell, 2001](#)). This effect implies that after the collapse of the top–predator its principal prey, typically a pelagic fish species, increases drastically in stock size and now significantly preys upon eggs and larvae of its former predator: the former prey now controls the predator. This role reversal is believed to be responsible for the hysteresis in the cod stock of the Eastern Scotian Shelf, where the pelagic fish complex is assumed to control the depleted demersal fish component, leading to an ecosystem dominated by pelagics and crustaceans ([Frank et al., 2005](#)). A similar predator–prey role reversal between cod and herring is believed to be responsible for the lack of recovery of the former in the southern Gulf of St. Lawrence ([Swain and Sinclair, 2000](#)). In the North Sea, the herring stock increased after the depletion of the cod stock ([Lindegren et al., 2010a](#)) and through statistical time series modelling, [Fauchald \(2010\)](#) provided indications that herring now controls the North Sea cod stock and prevents its recovery. Further, populations of grey gurnard (*Eutrigla gurnardus*, an early maturing benthic fish species of low commercial value) have increased dramatically ([Floeter et al., 2005](#)). This species now occupies a similar ecological niche as the once dominant cod and has contributed to preventing the recovery of North Sea cod and whiting stocks. In the Central Baltic Sea, the sprat stock exploded after the collapse of the cod stock and is thought to control the cod stock, keeping it in a stable low state ([Casini et al., 2009](#);

Möllmann et al., 2008). One process behind this is a predator–prey role reversal, and the Baltic Sea provides the only case of direct evidence of a predation control. Köster and Möllmann (2000) showed through an extensive field study that sprat at high stock sizes consumes frequently more than the full cod egg production. Additionally, another feedback loop was identified as being potentially responsible for a low stable cod stock in the Baltic: the large sprat stock preys intensively on one of the main zooplanktonic species, the copepod *P. acuspes*, which is a main food item for larval cod. Hence, sprat competes for food with larval cod, likely contributing to cod recruitment failure (Möllmann et al., 2008).

Ecosystems showing regime shifts, especially with cod as a major player being involved, generally give the best evidence for hysteresis in recovery to occur, hence indicating the existence of alternative stable states. Further, for all of these systems, that is, the Eastern Scotian Shelf, the North and the Baltic Sea, positive feedback mechanisms are suggested, which are a prerequisite for alternative stable states to occur. Recently, in two of the systems, which experienced ecosystem regime shifts, signs of recovery of the locally depleted cod stocks are observed. Frank et al. (2011) provide evidence of the transient nature of Eastern Scotian Shelf ecosystem and show that it could be currently returning towards benthic fish species domination. The increased forage fish complex is now in decline, having outstripped their zooplankton food supply and reversing the trophic cascade (Frank et al., 2005). Signs for cod stock recovery exist also for the Eastern Baltic cod stock, generally attributed solely to decreased fishing mortality (Cardinale and Svedäng, 2011) or additionally to improved recruitment (Eero et al., 2011). However, similar internal mechanisms as observed for the Eastern Scotian Shelf may be at work here. Hence, the reversibility of perturbed ecosystems can occur, which is a promising sign for other collapsed fisheries (Frank et al., 2011; Lotze et al., 2011).

The recovery of cod stocks fuels the discussion on the existence of alternative stable states, and their relevance to resource management. In the Baltic, the recent increase in the cod stock size is, on the one hand, interpreted as a sign for the regime shift concept not to be valid (Cardinale and Svedäng, 2011), but, on the other hand, it is suggested that a sufficiently large intervention can reverse ecosystem regime shifts with alternative stable states (Möllmann et al., 2011). Generally, the existence and proof of alternative stable states is not a prerequisite for identifying and understanding regime shifts. However, ignoring the possibility of alternative stable states would not be a precautionary strategy for management of marine resources. When

indications for alternative stable states exist, ecosystems should be managed in a manner that avoids the risk of triggering regime shifts.



6. CONCLUSIONS

Our study shows that multiple drivers such as climate and overfishing interact in triggering ecosystem regime shifts. However, more investigation is needed on a range of potential external drivers and their interaction, and on evaluating the latter with respect to the resilience concept (Mintenbeck et al., 2012). Further, studies addressing the interaction of the external drivers with internal trophodynamics and how these affect the dynamics of the different trophic levels are needed.

The interaction of multiple drivers in causing ecosystem regime shifts clearly shows the need for ecosystem-based approaches to the management of marine resources (McLeod and Leslie, 2009). Among others, the collapse of Eastern Baltic cod during the late 1980s/early 1990s illustrates this need (Möllmann et al., 2011). The stock started to decline with changing climate-induced environmental conditions and subsequent recruitment failure. However, the real collapse was then triggered by overfishing (Eero et al., 2011; Köster et al., 2005). Simulations with a food web model have shown that in hindsight the collapse could have been avoided by adapting fishing pressure to environmental conditions and food web interactions (Lindegren et al., 2009). Further, projections with the same model have shown that for the expected climatic changes it is even more important to be precautionary and adjust future exploitation levels not to endanger the long-term persistence of the stock (Lindegren et al., 2010b).

The essence of the ecosystem approach is considering multiple impacts and stressors, identifying which factors may erode resilience and which have the capability to cause sudden changes, and eventually adapt manageable drivers in order to be precautionary and to avoid potential catastrophic reorganizations in ecosystems (Jacob et al., 2011; Woodward et al., 2010). In the case of highly exploited marine ecosystems as the examples reviewed here, this certainly involves reducing fishing mortality. The extent and duration of the reduction are, however, strongly dependent on the environmental context.

Predicting abrupt regime shifts in complex systems like the ecosystems reviewed here is difficult. However, work in different scientific fields is now suggesting the existence of generic early-warning signals that may indicate for a wide class of systems if a critical threshold is approaching

(Scheffer et al., 2009). The basic rationale behind this family of early-warning indicators lies in the fact that the recovery of a system to equilibrium after a perturbation becomes slower close to a transition (van Nes and Scheffer, 2007). This phenomenon is known as “critical slowing down” (Wissel, 1984) and causes the variance and autocorrelation in the fluctuations of a system to increase prior to a regime shift (Carpenter and Brock, 2006; Held and Kleinen, 2004; Scheffer et al., 2009). In addition, the spatial dynamics of complex systems may also change close to a transition, where alterations in the spatial patterns of variance and correlation of key ecological features may serve as a complementary set of early-warning indicators (Dakos et al., 2010; Donangelo et al., 2010; Guttal and Jayaprakash, 2009). Although the merit of these indicators is that they can be detected across an array of ecosystems and types of transitions (Dakos et al., 2011), their disadvantage is that they require long time series of high resolution for their estimation. At least some ecological time series are now often long enough to apply this technique, but increased monitoring effort on multiple trophic levels is needed in the future to establish early-warning systems to avoid initiating catastrophic ecosystem change.

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REFERENCES

- Alheit, J., Bakun, A., 2010. Population synchronies within and between ocean basins: apparent teleconnections and implications as to physical–biological linkage mechanisms. *J. Mar. Syst.* 79, 267–285.
- Alheit, J., Möllmann, C., Dutz, J., Kornilovs, G., Loewe, P., Mohrholz, V., Wasmund, N., 2005. Synchronous ecological regime shifts in the central Baltic and the North Sea in the late 1980s. *ICES J. Mar. Sci.* 62, 1205–1215.
- Andersen, T., Carstensen, J., Hernandez-Garcia, E., Duarte, C., 2009. Ecological thresholds and regime shifts: approaches to identification. *Trends Ecol. Evol.* 24, 49–57.
- Bailey, K., 2000. Shifting control of recruitment of walleye pollock *theragra chalcogramma* after a major climatic and ecosystem change. *Mar. Ecol. Prog. Ser.* 198, 215–224.
- Bakun, A., 2005. Regime shifts. In: Robinson, A.R., Brink, K. (Eds.), *The Sea. The Global Coastal Ocean: Multiscale Interdisciplinary Processes*, vol. 13. Harvard University Press, Cambridge, MA, USA, pp. 971–1026.

- Baum, J., Worm, B., 2009. Cascading top-down effects of changing oceanic predator abundances. *J. Anim. Ecol.* 78, 699–714.
- Beamish, R., Noakes, D., Mcfarlane, G., Klyashtorin, L., Ivanov, V., Kurashov, V., 1999. The regime concept and natural trends in the production of pacific salmon. *Can. J. Fish. Aquat. Sci.* 56, 516–526.
- Beaugrand, G., 2004. The North Sea regime shift: evidence, causes, mechanisms and consequences. *Prog. Oceanogr.* 60, 245–262.
- Beaugrand, G., Reid, P., 2003. Long-term changes in phytoplankton, zooplankton and salmon related to climate. *Glob. Change Biol.* 9, 801–817.
- Bernard A. Megrey, Jason S. Link, George L. Hunt Jr., Erlend Moksness (2009). Comparative marine ecosystem analysis: Applications, opportunities, and lessons learned. *Progress in Oceanography*, 81, 2–9.
- Cardinale, M., Svedäng, H., 2011. The beauty of simplicity in science: baltic cod stock improves rapidly in a 'cod hostile' ecosystem state. *Mar. Ecol. Prog. Ser.* 425, 297–301.
- Carpenter, S., Brock, W., 2006. Rising variance: a leading indicator of ecological transition. *Ecol. Lett.* 9, 308–315.
- Carpenter, S., Cole, J., Pace, M., Batt, R., Brock, W., Cline, T., Coloso, J., Hodgson, J., Kitchell, J., Seekell, D., Smith, L., Weidel, B., 2011. Early warnings of regime shifts: a whole-ecosystem experiment. *Science* 332, 1079–1082.
- Casini, M., Cardinale, M., Hjelm, J., 2006. Inter-annual variation in herring, *Clupea harengus*, and sprat, *Sprattus sprattus*, condition in the central Baltic Sea: what gives the tune? *Oikos* 112, 638–650.
- Casini, M., Lovgren, J., Hjelm, J., Cardinale, M., Molinero, J., Kornilovs, G., 2008. Multi-level trophic cascades in a heavily exploited open marine ecosystem. *Proc. R. Soc. Lond. B Biol.* 275, 1793–1801.
- Casini, M., Hjelm, J., Molinero, J., Lovgren, J., Cardinale, M., Bartolino, V., Belgrano, A., Kornilovs, G., 2009. Trophic cascades promote threshold-like shifts in pelagic marine ecosystems. *Proc. Natl. Acad. Sci. U.S.A.* 106, 197–202.
- Castle, M.D., Blanchard, J.L., Jennings, S., 2011. Predicted effects of behavioural movement and passive transport on individual growth and community size structure in marine ecosystems. *Adv. Ecol. Res.* 45, 41–66.
- Chassot, E., Melin, F., Le Pape, O., Gascuel, D., 2007. Bottom-up control regulates fisheries production at the scale of eco-regions in European seas. *Mar. Ecol. Prog. Ser.* 343, 45–55.
- Choi, J.S., Frank, K.T., Leggett, W.C., Drinkwater, K., 2004. Transition to an alternate state in a continental shelf ecosystem. *Can. J. Fish. Aquat. Sci.* 61, 505–510.
- Choi, J., Frank, K., Petrie, B., Leggett, W., 2005. Integrated assessment of a large marine ecosystem: a case study of the devolution of the eastern Scotian Shelf, Canada. *Oceanogr. Mar. Biol.* 43, 67–93.
- Ciannelli, L., Chan, K., Bailey, K., Stenseth, N., 2004. Nonadditive effects of the environment on the survival of a large marine fish population. *Ecology* 85, 3418–3427.
- Collie, J., Richardson, K., Steele, J., 2004. Regime shifts: can ecological theory illuminate the mechanisms? *Prog. Oceanogr.* 60, 281–302.
- Conversi, A., Umani, S., Peluso, T., Molinero, J., Santojanni, A., Edwards, M., 2010. The Mediterranean Sea regime shift at the end of the 1980s, and intriguing parallelisms with other European basins. *PLoS One* 5 (5), e10633. <http://dx.doi.org/10.1371/journal.pone.001063>.
- Cury, P., Shannon, L., 2004. Regime shifts in upwelling ecosystems: observed changes and possible mechanisms in the northern and southern Benguela. *Prog. Oceanogr.* 60, 223–243.
- Dakos, V., Van Nes, E., Donangelo, R., Fort, H., Scheffer, M., 2010. Spatial correlation as leading indicator of catastrophic shifts. *Theor. Ecol.* 3, 163–174.
- Dakos, V., Kefi, S., Rietkerk, M., Van Nes, E., Scheffer, M., 2011. Slowing down in spatially patterned ecosystems at the brink of collapse. *Am. Nat.* 177, E153–E166.

- Daskalov, G., 2003. Long-term changes in fish abundance and environmental indices in the black sea. *Mar. Ecol. Prog. Ser.* 255, 259–270.
- Daskalov, G., Grishin, A., Rodionov, S., Mihneva, V., 2007. Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. *Proc. Natl. Acad. Sci. U.S.A.* 104, 10518–10523.
- De Young, B., Harris, R., Alheit, J., Beaugrand, G., Mantua, N., Shannon, L., 2004. Detecting regime shifts in the ocean: data considerations. *Prog. Oceanogr.* 60, 143–164.
- De Young, B., Barange, M., Beaugrand, G., Harris, R., Perry, R., Scheffer, M., Werner, F., 2008. Regime shifts in marine ecosystems: detection, prediction and management. *Trends Ecol. Evol.* 23, 402–409.
- Diekmann, R., Möllmann, C. (Eds.), 2010. Integrated Ecosystem Assessments of Seven Baltic Sea Areas Covering the Last Three Decades. ICES Coop. Res. Rep. No. 302, 90 pp.
- Donangelo, R., Fort, H., Dakos, V., Scheffer, M., Van Nes, E., 2010. Early warnings for catastrophic shifts in ecosystems: comparison between spatial and temporal indicators. *Int. J. Bifurcat. Chaos* 20, 315–321.
- Ebbesmeyer, C.C., Cayan, D.R., McLain, D.R., Nichols, F.H., Peterson, D.H., Redmond, K.T., 1991. 1976 step in the Pacific climate: forty environmental changes between 1968–1975 and 1977–1984. In: Betancourt, J.L., Tharp, V.L. (Eds.), *Proceedings of the Seventh Annual Climate (PACCLIM) Workshop*, April 1990. California Department of Water Resources. Interagency Ecological Studies Program Technical Report 26, pp. 115–126.
- Eero, M., Mackenzie, B., Koster, F., Gislason, H., 2011. Multi-decadal responses of a cod (*Gadus morhua*). Population to human-induced trophic changes, fishing, and climate. *Ecol. Appl.* 21, 214–226.
- Elton, C.S., 2001. *Animal ecology*. University of Chicago Press, Chicago/London 209 pp.
- FAO, 2010. *The State of World Fisheries and Aquaculture 2010*. FAO Fisheries and Aquaculture Department, Food and Agriculture Organization of the United Nations, Rome.
- Fauchald, P., 2010. Predator-prey reversal: a possible mechanism for ecosystem hysteresis in the North Sea? *Ecology* 91, 2191–2197.
- Feld, C.K., Birk, S., Bradley, D.C., Hering, D., Kail, J., Marzin, A., Melcher, A., Nemitz, D., Pedersen, M.L., Pletterbauer, F., Pont, D., Verdonshot, P.F.M., et al., 2011. From natural to degraded rivers and back again: a test of restoration ecology theory and practice. *Adv. Ecol. Res.* 44, 119–210.
- Floeter, J., Kempf, A., Vinther, M., Schrum, C., Temming, A., 2005. Grey gurnard (*Eutrigla gurnadus*) in the North Sea: an emerging key predator? *Can. J. Fish. Aquat. Sci.* 62, 1853–1864.
- Francis, R.C., Hare, S.R., 1994. Decadal scale regime shifts in the large marine ecosystems of the North-East Pacific: a case for historical science. *Fish. Oceanogr.* 3, 279–291.
- Francis, R.C., Hare, S.R., Hollowed, A.B., Wooster, W.S., 1998. Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. *Fish. Oceanogr.* 7, 1–21.
- Frank, K., Petrie, B., Choi, J., Leggett, W., 2005. Trophic cascades in a formerly cod-dominated ecosystem. *Science* 308, 1621–1623.
- Frank, K., Petrie, B., Shackell, N., 2007. The ups and downs of trophic control in continental shelf ecosystems. *Trends Ecol. Evol.* 22, 236–242.
- Frank, K., Petrie, B., Fisher, J., Leggett, W., 2011. Transient dynamics of an altered large marine ecosystem. *Nature* 477, 86–U98.
- Friberg, N., Bonada, N., Bradley, D.C., Dunbar, M.J., Edwards, F.K., Grey, J., Hayes, R.B., Hildrew, A.G., Lamouroux, N., Trimmer, M., Woodward, G., 2011. Biomonitoring of human impacts in freshwater ecosystems: the good, the bad, and the ugly. *Adv. Ecol. Res.* 44, 1–68.
- Graham, N., 1994. Decadal-scale climate variability in the tropical and North Pacific during the 1970s and 1980s—observations and model results. *Clim. Dyn.* 10, 135–162.

- Guttal, V., Jayaprakash, C., 2009. Spatial variance and spatial skewness: leading indicators of regime shifts in spatial ecological systems. *Theor. Ecol.* 2, 3–12.
- Hare, S.R., Mantua, N.J., 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Prog. Oceanogr.* 47, 103–145.
- Held, H., Kleinen, T., 2004. Detection of climate system bifurcations by degenerate fingerprinting. *Geophys. Res. Lett.* 31, L23207.
- Holling, C., 1973. Resilience and stability of ecological systems. *Annu. Rev. Ecol. Syst.* 4, 1–23.
- Holling, C., Chambers, A., 1973. Resource science—nurture of an infant. *Bioscience* 23, 13–20.
- Hunt, G., Stabeno, P., Walters, G., Sinclair, E., Brodeur, R., Napp, J., Bond, N., 2002. Climate change and control of the southeastern Bering Sea pelagic ecosystem. *Deep Sea Res. Pt. II* 49, 5821–5853.
- Hunt, G., Coyle, K., Eisner, L., Farley, E., Heintz, R., Mueter, F., Napp, J., Overland, J., Ressler, P., Salo, S., Stabeno, P., 2011. Climate impacts on eastern Bering Sea foodwebs: a synthesis of new data and an assessment of the oscillating control hypothesis. *ICES J. Mar. Sci.* 68, 1230–1243.
- ICES (2008). Report of the working group on integrated assessment of the baltic sea (WGIIAB). CM 2008/BCC:04.
- Jacob, U., Thierry, A., Brose, U., Arntz, W.E., Berg, S., Brey, T., Fetzer, I., Jonsson, T., Mintenbeck, K., Möllmann, C., Petchey, O., Riede, J.O., et al., 2011. The role of body size in complex food webs: a cold case. *Adv. Ecol. Res.* 45, 181–223.
- Kenny, A., Skjoldal, H., Engelhard, G., Kershaw, P., Reid, J., 2009. An integrated approach for assessing the relative significance of human pressures and environmental forcing on the status of large marine ecosystems. *Prog. Oceanogr.* 81, 132–148.
- Kideys, A., 2002. Fall and rise of the Black Sea ecosystem. *Science* 297, 1482–1484.
- Kirby, R., Beaugrand, G., 2009. Trophic amplification of climate warming. *Proc. R. Soc. B Biol. Sci.* 276, 4095–4103.
- Kirby, R., Beaugrand, G., Lindley, J., 2009. Synergistic effects of climate and fishing in a marine ecosystem. *Ecosystems* 12, 548–561.
- Köster, F., Möllmann, C., 2000. Trophodynamic control by clupeid predators on recruitment success in Baltic cod? *ICES J. Mar. Sci.* 57, 310–323.
- Köster, F., Hinrichsen, H., Schnack, D., St. John, M., Mackenzie, B., Tomkiewicz, J., Möllmann, C., Kraus, G., Plikshs, M., Makarchouk, A., Aro, E., 2003. Recruitment of Baltic cod and sprat stocks: identification of critical life stages and incorporation of environmental variability into stock-recruitment relationships. *Sci. Mar.* 67, 129–154.
- Köster, F., Möllmann, C., Hinrichsen, H., Wieland, K., Tomkiewicz, J., Kraus, G., Voss, R., Makarchouk, A., Mackenzie, B., St. John, M., Schnack, D., Rohlf, N., Linkowski, T., Beyer, J., 2005. Baltic cod recruitment—the impact of climate variability on key processes. *ICES J. Mar. Sci.* 62, 1408–1425.
- Kraberg, A., Wasmund, N., Vanaverbeke, J., Schiedek, D., Wiltshire, K., Mieszkowska, N., 2011. Regime shifts in the marine environment: the scientific basis and political context. *Mar. Poll. Bull.* 62, 7–20.
- Layer, K., Riede, J.O., Hildrew, A.G., Woodward, G., 2010. Food web structure and stability in 20 streams across a wide pH gradient. *Adv. Ecol. Res.* 42, 265–301.
- Layer, K., Hildrew, A.G., Jenkins, G.B., Riede, J., Rossiter, S.J., Townsend, C.R., Woodward, G., 2011. Long-term dynamics of a well-characterised food web: four decades of acidification and recovery in the Broadstone Stream model system. *Adv. Ecol. Res.* 44, 69–117.
- Ledger, M., et al., 2012. Climate change impacts on community resilience: evidence from a drought disturbance experiment. *Adv. Ecol. Res.* 46.
- Lees, K., Pitois, S., Scott, C., Frid, C., Mackinson, S., 2006. Characterizing regime shifts in the marine environment. *Fish Fish.* 7, 104–127.

- Legendre, P., Legendre, L., 1998. *Numerical Ecology*, second ed. Elsevier, Amsterdam, The Netherlands.
- Legendre, P., Dallot, S., Legendre, L., 1985. Succession of species within a community: chronological Clustering, with applications to marine and freshwater zooplankton. *Am. Nat.* 125, 257–288.
- Levin, P., Fogarty, M., Murawski, S., Fluharty, D., 2009. Integrated ecosystem assessments: developing the scientific basis for ecosystem-based management of the ocean. *PLoS Biol.* 7, e1000014.
- Lindegren, M., Möllmann, C., Nielsen, A., Stenseth, N., 2009. Preventing the collapse of the baltic cod stock through an ecosystem-based management approach. *Proc. Natl. Acad. Sci. U.S.A.* 106, 14722–14727.
- Lindegren, M., Diekmann, R., Möllmann, C., 2010a. Regime shifts, resilience and recovery of a cod stock. *Mar. Ecol. Prog. Ser.* 402, 239–253.
- Lindegren, M., Möllmann, C., Nielsen, A., Brander, K., Mackenzie, B., Stenseth, N., 2010b. Ecological forecasting under climate change: the case of Baltic cod. *Proc. R. Soc. B Biol. Sci.* 277, 2121–2130.
- Link, J., Brodziak, J., Edwards, S., Overholtz, W., Mountain, D., Jossi, J., Smith, T., Fogarty, M., 2002. Marine ecosystem assessment in a fisheries management context. *Can. J. Fish. Aquat. Sci.* 59, 1429–1440.
- Litzow, M., Ciannelli, L., 2007. Oscillating trophic control induces community reorganization in a marine ecosystem. *Ecol. Lett.* 10, 1124–1134.
- Litzow, M., Urban, J., Laurel, B., 2008. Increased spatial variance accompanies reorganization of two continental shelf ecosystems. *Ecol. Appl.* 18, 1331–1337.
- Llope, M., Daskalov, G., Royer, T., Mihneva, V., Chan, K.-S., Grishin, A., Stenseth, N., 2011. Overfishing of top predators eroded the resilience of the Black Sea ecosystem regardless of the climate and anthropogenic conditions. *Glob. Change Biol.* 17, 1251–1265.
- Lluch-Belda, D., Crawford, R.J., Kawasaki, T., McCall, A.D., Parrish, R.H., Schwartzlose, R.A., Smith, P.E., 1989. Worldwide fluctuations in sardine and anchovy stocks: the regime problem. *S. Afr. J. Mar. Sci.* 8, 195–205.
- Lotze, H., Coll, M., Magera, A., Ward-Paige, C., Airolidi, L., 2011. Recovery of marine animal populations and ecosystems. *Trends Ecol. Evol.* 26, 595–605.
- MacKenzie, B., Köster, F., 2004. Fish production and climate: sprat in the Baltic Sea. *Ecology* 85, 784–794.
- Mantua, N.J., 2004. Methods for detecting regime shifts in large marine ecosystems: a review with approaches applied to North Pacific data. *Prog. Oceanogr.* 60, 165–182.
- Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M., Francis, R.C., 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bull. Am. Met. Soc.* 78, 1069–1079.
- May, R., 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature* 269, 471–477.
- McCook, L., 1999. Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. *Coral Reefs* 18, 357–367.
- McGowan, J., Cayan, D., Dorman, L., 1998. Climate-ocean variability and ecosystem response in the Northeast Pacific. *Science* 281, 210–217.
- McLeod, K., Leslie, H., 2009. *Ecosystem-Based Management for the Oceans*. Island Press, Washington, DC 368 pp.
- McQuatters-Gollop, A., Vermaat, J., 2011. Covariance among North Sea ecosystem state indicators during the past 50 years—contrasts between coastal and open waters. *J. Sea Res.* 65, 284–292.
- McQuatters-Gollop, A., Mee, L., Raitsos, D., Shapiro, G., 2008. Non-linearities, regime shifts and recovery: the recent influence of climate on Black Sea chlorophyll. *J. Mar. Syst.* 74, 649–658.

- Meerhoff, M., et al., 2012. Environmental warming in shallow lakes: a review of effects on community structure as evidenced from space-for-time substitution approach. *Adv. Ecol. Res.* 46.
- Miller, A., Cayan, D., Barnett, T., Graham, N., Oberhuber, J., 1994. Interdecadal variability of the Pacific–Ocean–Model response to observed heat-flux and wind stress anomalies. *Clim. Dyn.* 9, 287–302.
- Mintenbeck, K., et al., 2012. Impact of climate change on fish in complex Antarctic ecosystems. *Adv. Ecol. Res.* 46.
- Möllmann, C., Kornilovs, G., Fetter, M., Köster, F., 2005. Climate, zooplankton, and pelagic fish growth in the central Baltic Sea. *ICES J. Mar. Sci.* 62, 1270–1280.
- Möllmann, C., Müller-Karulis, B., Kornilovs, G., St. John, M., 2008. Effects of climate and overfishing on zooplankton dynamics and ecosystem structure: regime shifts, trophic cascade, and feedback loops in a simple ecosystem. *ICES J. Mar. Sci.* 65, 302–310.
- Möllmann, C., Diekmann, R., Müller-Karulis, B., Kornilovs, G., Plikshs, M., Axe, P., 2009. Reorganization of a large marine ecosystem due to atmospheric and anthropogenic pressure: a discontinuous regime shift in the central Baltic Sea. *Glob. Change Biol.* 15, 1377–1393.
- Möllmann, C., Blenckner, T., Casini, M., Gardmark, A., Lindegren, M., 2011. Beauty is in the eye of the beholder: management of Baltic cod stock requires an ecosystem approach. *Mar. Ecol. Prog. Ser.* 431, 293–297.
- Mulder, C., et al., 2012. Distributional (in)congruence of biodiversity–ecosystem functioning. *Adv. Ecol. Res.*, 46.
- Myers, R., Worm, B., 2003. Rapid worldwide depletion of predatory fish communities. *Nature* 423, 280–283.
- Nixon, S., Buckley, B., 2002. “A strikingly rich zone”—nutrient enrichment and secondary production in coastal marine ecosystems. *Estuaries* 25, 782–796.
- O’Gorman, E., Emmerson, M., 2010. Manipulating interaction strengths and the consequences for trivariate patterns in a marine food web. *Adv. Ecol. Res.* 42, 301–419.
- Oguz, T., 2005. Black Sea ecosystem response to climatic variations. *Oceanography* 18, 122–133.
- Oguz, T., Gilbert, D., 2007. Abrupt transitions of the top–down controlled Black Sea pelagic ecosystem during 1960–2000: evidence for regime-shifts under strong fishery exploitation and nutrient enrichment modulated by climate-induced variations. *Deep Sea Res. Pt. I* 54, 220–242.
- Oguz, T., Velikova, V., 2010. Abrupt transition of the northwestern Black Sea shelf ecosystem from a eutrophic to an alternative pristine state. *Mar. Ecol. Prog. Ser.* 405, 231–242.
- Oguz, T., Dippner, J.W., Kaymaz, Z., 2006. Climatic regulation of the Black Sea hydro-meteorological and ecological properties at interannual-to-decadal time scales. *J. Mar. Syst.* 60, 235–254.
- Olesen, J.M., Dupont, Y.L., O’Gorman, E., Ings, T.C., Layer, K., Melian, C.J., Troejelsgaard, K., Pichler, D.E., Rasmussen, C., Woodward, G., 2010. From Broadstone to Zackenberg: space, time and hierarchies in ecological networks. *Adv. Ecol. Res.* 42, 1–71.
- Österblom, H., Casini, M., Olsson, O., Bignert, A., 2006. Fish, seabirds and trophic cascades in the Baltic Sea. *Mar. Ecol. Prog. Ser.* 323, 233–238.
- Österblom, H., Hansson, S., Larsson, U., Hjerne, O., Wulff, F., Elmgren, R., Folke, C., 2007. Human-induced trophic cascades and ecological regime shifts in the Baltic Sea. *Ecosystems* 10, 877–889.
- Ottersen, G., Kim, S., Huse, G., Polovina, J., Stenseth, N., 2010. Major pathways by which climate may force marine fish populations. *J. Mar. Syst.* 79, 343–360.
- Overland, J., Adams, J., Bond, N., 1999. Decadal variability of the Aleutian Low and its relation to high-latitude circulation. *J. Climate* 12, 1542–1548.

- Overland, J., Rodionov, S., Minobe, S., Bond, N., 2008. North Pacific regime shifts: definitions, issues and recent transitions. *Prog. Oceanogr.* 77, 92–102.
- Overland, J., Alheit, J., Bakun, A., Hurrell, J., Mackas, D., Miller, A., 2010. Climate controls on marine ecosystems and fish populations. *J. Mar. Syst.* 79, 305–315.
- Peck, M.A., 2012. Intrinsic and extrinsic factors driving match-mismatch dynamics during the early life history of marine fishes. *Adv. Ecol. Res.* 47.
- Polovina, J.J., Mitchum, G.T., Graham, N.E., Craig, M.P., DeMartini, E.E., Flint, E.E., 1994. Physical and biological consequences of a climate event in the central North Pacific. *Fish. Oceanogr.* 3, 15–21.
- Prugh, L., Stoner, C., Epps, C., Bean, W., Ripple, W., Laliberte, A., Brashares, J., 2009. The rise of the mesopredator. *Bioscience* 59, 779–791.
- Rahmstorf, S., 1999. Shifting seas in the greenhouse? *Nature* 399, 740.
- Rao, C., 1964. The use and interpretation of principal component analysis in applied research. *Sabjhyá Ser. A* 26, 329–358.
- Reid, P.C., Edwards, M., 2001. Long-term changes in the pelagos, benthos and fisheries of the North Sea. *Senck. Marit.* 31, 107–115.
- Reid, P., Edwards, M., Hunt, H., Warner, A., 1998. Phytoplankton change in the North Atlantic. *Nature* 391, 546.
- Reid, P., Borges, M., Svendsen, E., 2001. A regime shift in the North Sea circa 1988 linked to changes in the north sea horse mackerel fishery. *Fish. Res.* 50, 163–171.
- Rodionov, S., 2004. A sequential algorithm for testing climate regime shifts. *Geophys. Res. Lett.* 31, L09204.
- Rosberg, R., 2012. A complete analytic theory for structure and dynamics of populations and communities spanning wide ranges in body size. *Adv. Ecol. Res.* 46.
- Scheffer, M., 2009. *Critical Transitions in Nature and Society*. Princeton University Press, Princeton 384 pp.
- Scheffer, M., Carpenter, S., 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends Ecol. Evol.* 18, 648–656.
- Scheffer, M., Carpenter, S., Foley, J., Folke, C., Walker, B., 2001a. Catastrophic shifts in ecosystems. *Nature* 413, 591–596.
- Scheffer, M., Straile, D., Van Nes, E., Hosper, H., 2001b. Climatic warming causes regime shifts in lake food webs. *Limnol. Oceanogr.* 46, 1780–1783.
- Scheffer, M., Carpenter, S., de Young, B., 2005. Cascading effects of overfishing marine systems. *Trends Ecol. Evol.* 20, 579–581.
- Scheffer, M., Bascompte, J., Brock, W., Brovkin, V., Carpenter, S., Dakos, V., Held, H., Van Nes, E., Rietkerk, M., Sugihara, G., 2009. Early-warning signals for critical transitions. *Nature* 461, 53–59.
- Schlüter, M., Merico, A., Wiltshire, K., Greve, W., von Storch, H., 2009. A statistical analysis of climate variability and ecosystem response in the German Bight. *Ocean Dyn.* 58, 169–186.
- Shiganova, T.A., 2004. Interactions between the invading ctenophores *Mnemiopsis leidyi* (A. Agassiz) and *Beroe ovata* Mayer 1912, and their influence on pelagic ecosystem of the Northeastern Black Sea. In: Dumont, H. (Ed.), *Aquatic Invasions in the Black, Caspian and Mediterranean Seas*. Kluwer Academic Publishers, Netherlands, pp. 33–70.
- Solow, A., Beet, A., 2005. A test for a regime shift. *Fish. Oceanogr.* 14, 236–240.
- Steele, J., 1998. Regime shifts in marine ecosystems. *Ecol. Appl.* 8, S33–S36.
- Steele, J., 2004. Regime shifts in the ocean: reconciling observations and theory. *Prog. Oceanogr.* 60, 135–141.
- Steele, M., Forrester, G., Almany, G., 1998. Influences of predators and conspecifics on recruitment of a tropical and a temperate reef fish. *Mar. Ecol. Prog. Ser.* 172, 115–125.
- Stenseth, N., Mysterud, A., Ottersen, G., Hurrell, J., Chan, K., Lima, M., 2002. Ecological effects of climate fluctuations. *Science* 297, 1292–1296.

- Strong, D., Frank, K., 2010. Human involvement in food webs. *Annu. Rev. Environ. Res.* 35, 3.1–3.24.
- Suding, K., Gross, K., Houseman, G., 2004. Alternative states and positive feedbacks in restoration ecology. *Trends Ecol. Evol.* 19, 46–53.
- Swain, D., Sinclair, A., 2000. Pelagic fishes and the cod recruitment dilemma in the northwest Atlantic. *Can. J. Fish. Aquat. Sci.* 57, 1321–1325.
- Terborgh, J., Estes, J.A. (Eds.), 2010. *Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature*. Island Press, Washington 464 pp.
- Tian, Y., Kidokoro, H., Watanabe, T., Iguchi, N., 2008. The late 1980s regime shift in the ecosystem of the Tsushima warm current in the Japan/East Sea: evidence from historical data and possible mechanisms. *Prog. Oceanogr.* 77, 127–145.
- Van Nes, E., Scheffer, M., 2007. Slow recovery from perturbations as a generic indicator of a nearby catastrophic shift. *Am. Nat.* 170, 660.
- Walters, C., Kitchell, J., 2001. Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. *Can. J. Fish. Aquat. Sci.* 58, 39–50.
- Ware, D.M., Thomson, R.E., 2005. Bottom-up ecosystem trophic dynamics determine fish production in the northeast Pacific. *Science* 308, 1280–1284.
- Wasmund, N., Nausch, G., Matthäus, W., 1998. Phytoplankton spring blooms in the southern Baltic Sea—spatio-temporal development and long-term trends. *J. Plankton Res.* 20, 1099–1117.
- Watanabe, M., Nitta, T., 1999. Decadal changes in the atmospheric circulation and associated surface climate variations in the northern hemisphere winter. *J. Climate* 12, 494–510.
- Weijerman, M., Lindeboom, H., Zuur, A., 2005. Regime shifts in marine ecosystems of the North Sea and Wadden Sea. *Mar. Ecol. Prog. Ser.* 298, 21–39.
- Welch, D., Ward, B., Smith, B., Eveson, J., 2000. Temporal and spatial responses of British Columbia steelhead (*Oncorhynchus mykiss*) populations to ocean climate shifts. *Fish. Oceanogr.* 9, 17–32.
- Wissel, C.A., 1984. A universal law of the characteristic return time near thresholds. *Oecologia* 65, 101–107.
- Woodward, G., Benstead, J.P., Beveridge, O.S., Blanchard, J., Brey, T., Brown, L., Cross, W.F., Friberg, N., Ings, T.C., Jacob, U., Jennings, S., Ledger, M.E., et al., 2010. Ecological networks in a changing climate. *Adv. Ecol. Res.* 42, 72–138.
- Wooster, W., Zhang, C., 2004. Regime shifts in the North Pacific: early indications of the 1976–1977 event. *Prog. Oceanogr.* 60, 183–200.
- Worm, B., Myers, R., 2003. Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. *Ecology* 84, 162–173.
- Worm, B., Barbier, E., Beaumont, N., Duffy, J., Folke, C., Halpern, B., Jackson, J., Lotze, H., Micheli, F., Palumbi, S., Sala, E., Selkoe, K., Stachowicz, J., Watson, R., 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science* 314, 787–790.