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DIRECTORATE GENERAL FOR INTERNAL POLICIES  
POLICY DEPARTMENT B: STRUCTURAL AND COHESION POLICIES

FISHERIES

**REGIME SHIFTS  
IN MARINE ECOSYSTEMS:  
HOW OVERFISHING CAN PROVOKE  
SUDDEN ECOSYSTEM CHANGES**

WORKSHOP



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DIRECTORATE GENERAL FOR INTERNAL POLICIES  
POLICY DEPARTMENT B: STRUCTURAL AND COHESION POLICIES

FISHERIES

# ECOSYSTEM REGIME SHIFTS TRIGGERED BY OVERFISHING

## NOTE

### **Abstract**

Marine ecosystem regime shifts occur in synchrony during the late 1980s/early 1990s suggesting a common climate driver. Trophic cascades triggered by overfishing are regularly involved indicating the interaction of multiple drivers. Multiple drivers interact in a way that one undermines resilience (overfishing) and another (climate change) gives the final impulse. Ecosystem regime shifts can be difficult to reverse when alternative stable states are involved. Ecosystem-based management strategies including early warning systems are needed to avoid ecosystem regime shifts.

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## LIST OF ABBREVIATIONS

- CIL** Cold Intermediate Layer
- CPR** Continuous Plankton Recorder Survey
- FAO** Food and Agriculture Organization of the United Nations
- ICES** International Council for the Exploration of the Sea
- NAO** North Atlantic Oscillation
- OCH** Oscillating Control Hypothesis
- PC** Principal Component
- PCA** Principal Component Analysis
- PDO** Pacific Decadal Oscillation

## EXECUTIVE SUMMARY

### Background

Overfishing has been shown to seriously affect the ecosystems of the world oceans. In addition to direct fishing effects on target stocks, ecosystem effects are increasingly reported as a result of unsustainable exploitation levels. There is now compelling evidence that fishing-induced changes at the top of the food web can have profound indirect effects on all trophic levels and hence change the structure and functioning of the whole food web. Such trophic cascades involve a top-down (i.e. consumer) control view on ecosystem functioning, which opposes the traditional bottom-up (resource) control view that existed for marine ecosystems.

Large-scale reorganizations of ecosystems and their food webs, called **regime shifts**, are traditionally considered from a bottom-up perspective. The term regime shift generally describes the abrupt transition between different states in any complex system. Initially, regime shifts have been described in atmospheric processes on multidecadal time-scales and their effects on the physical environment. 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. 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.

Conceptually, the regime shift theory was further developed during key investigations in freshwater, on land and in coral reef systems. These studies pointed toward external drivers other than climate, e.g. exploitation and eutrophication, and their interaction in causing regime shifts. Furthermore, aspects of the nature of regime shifts were discussed, which can be linear or abrupt, or can even be discontinuous when hysteresis is involved. Eventually, these developments have resulted in theories on catastrophic regime shifts in ecosystems and critical transitions in nature addressing the potential of alternative stable states in ecosystems. The existence of alternative stable states has important management implications, because restoring regimes considered as favourable may require drastic and expensive management actions.

### Aim

The general theme of this briefing note is the importance of overfishing in triggering ecosystem regime shifts. For this purpose, ecosystem regime shifts are defined as infrequent and abrupt changes in ecosystem structure and function, occurring at multiple trophic levels and on large geographic scales. The study

- reviews prominent examples of **ecosystem regime shifts** in the North Pacific and the Eastern Scotian Shelf off the East coast of Canada, as well as the North Sea, the Baltic and the Black Sea;
- discusses **trophic cascades** as the phenomenon by which overfishing can cause ecosystem regime shifts using examples from the Eastern Scotian Shelf and the Baltic and Black Seas;

- reviews **alternative stable state theory** and evidence for stable states in the reported cases of marine ecosystem regime shifts;
- presents conclusions on the causes of ecosystem regime shifts with special reference to overfishing;
- makes recommendations for future research and ecosystem-based management strategies.

## Key findings

The **synchronicity in timing** of ecosystem regime shifts over the Northern hemisphere during the late 1980s/early 1990s suggests **a common climate driver**.

Trophic cascades triggered by overfishing are regularly observed, indicating that **multiple external drivers** are usually needed to cause ecosystem regime shifts.

Multiple external drivers interact in a way that one undermines **resilience** (e.g. fishing) and another one (e.g. abrupt climate change) gives the final impulse for an ecosystem regime shift.

Ecosystem regime shifts can be difficult to reverse when **alternative stable states** are involved. Indications for the latter exist from multiple ecosystems.

**Ecosystem-based management strategies** are needed to avoid ecosystem regime shifts and **early warning systems** need to be developed.

## 1. INTRODUCTION

### KEY FINDINGS

- There is now compelling evidence that fisheries-induced changes at the top of the food web can have profound indirect effects on all trophic levels.
- These **trophic cascades**, originally demonstrated for limnic and marine benthic systems, have now also been shown for pelagic systems involving four trophic levels with the most prominent examples from the Scotian Shelf off the Canadian East Coast, the Black Sea, and the Baltic Sea.
- **Ecosystem regime shifts** are drastic large time- and space-scale shifts in abundances of major components of marine biological communities.
- While originally mainly investigated in relation to climate, nowadays **ecosystem regime shifts** are considered to be caused by multiple drivers including overfishing and eutrophication.
- **Ecosystem regime shifts** are here defined as infrequent and abrupt changes in ecosystem structure and function, occurring at multiple trophic levels and on large geographic scales.

Overfishing has been increasingly shown to seriously affect the ecosystems of the world oceans. Presently, ca. 30% of the world's fish stocks are overfished (i.e. overexploited, depleted and recovering stocks; FAO, 2010). Additionally >50% of the stocks are considered fully exploited, leaving only <20% of the stocks to be under- or moderately exploited (FAO, 2010). Especially overfishing or even depletion of large predatory fish species has been evidenced to be a wide-spread phenomenon (Myers and Worm, 2003; Worm *et al.*, 2006).

In addition to direct effects of fishing on target stocks, ecosystem effects are increasingly reported as a result of unsustainable exploitation levels. For example, "fishing down" or "fishing through" the food web has been demonstrated as a result of fisheries targeting increasingly lower trophic level species. The result is a reduction in the mean trophic level (and hence mean size) of fish in the catch and also in the ecosystems (Pauly *et al.*, 1998; Essington *et al.*, 2006). Furthermore, fishing-induced reduction of predatory species at the top of the food webs can have indirect effects on their prey species one trophic level below. For example, collapses of Atlantic cod (*Gadus morhua*) have resulted in increases of their shrimp prey (Worm and Meyers, 2003). Also, fishery-induced depletion of apex predatory sharks off the US east coast has resulted in increases of smaller sharks serving as their prey (Myers *et al.*, 2007).

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" have shown the potential of ecosystem reorganization due to overfishing of top-predators. The most prominent examples for trophic cascades in pelagic systems involving four trophic levels (and hence

zoo- and phytoplankton) have been found for the Scotian Shelf off the Canadian East Coast (Frank *et al.*, 2005), the Black Sea (Daskalov *et al.*, 2007), and the Baltic Sea (Casini *et al.*, 2008).

Despite the increasing evidence for top-down (i.e. consumer) control in marine ecosystems, the traditional view of marine ecosystem functioning is a bottom-up (i.e. resource) control perspective (Verity and Smetacek, 1996; Ware and Thompson, 2005). It is thus no surprise that large-scale reorganizations of ecosystems and their food webs, so-called **regime shifts**, have been originally considered from a bottom-up perspective. The term regime shift generally describes the abrupt transition between different states in any complex system. Initially, regime shifts have been described in atmospheric processes on multidecadal time-scales and their effects on the physical environment (Rahmstorf, 1999; Kraberg *et al.*, 2011). 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 oceans (Lluch-Belda *et al.*, 1989; Alheit and Bakun, 2010). 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 (Bakun, 2005). The term ecosystem regime shift is hence distinct from **climate regime shift** which signifies apparent transitions between differing average climatic characteristics (Bakun, 2005). Not surprisingly, ecosystem regime shifts in marine ecosystems have been usually thought to result from climate regime shifts (Mantua and Hare, 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 toward external drivers other than climate, e.g. exploitation and eutrophication, and their interaction in causing regime shifts. Furthermore, aspects of the nature of regime shifts are discussed which can be linear or abrupt, or can even be discontinuous when hysteresis is involved (Scheffer *et al.*, 2001; Collie *et al.*, 2004). 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 of alternative stable states in ecosystems. The existence of alternative stable states has important management implications, because restoring regimes considered as favourable may require drastic and expensive management actions (Scheffer *et al.*, 2001; Suding *et al.*, 2004).

The general theme of this briefing note is the importance of overfishing in triggering ecosystem regime shifts. For this purpose, **ecosystem regime shifts** are defined as **infrequent and abrupt changes in ecosystem structure and function, occurring at multiple trophic levels and on large geographic scales** (Collie *et al.*, 2004; Cury and Shannon, 2004; deYoung *et al.*, 2004; Bakun, 2005; Lees *et al.*, 2006). In [Chapter 2](#) prominent examples of ecosystem regime shifts in the North Pacific and the Eastern Scotian Shelf off the East coast of Canada, as well as the North Sea, the Baltic and the Black Sea are reviewed. In [Chapter 3](#) trophic cascades are discussed as the phenomenon by which overfishing can cause ecosystem regime shifts. Here the main examples stemming from the Eastern Scotian Shelf and the Baltic and Black Seas are reviewed. Alternative stable state theory and evidence for these in the reported cases of marine ecosystem regime shifts is summarized in Chapter 4. Eventually, in [Chapter 5](#), the results of this study are summarized, to support our conclusions on the causes of ecosystem regime shifts and our recommendations for future research and ecosystem-based management strategies.

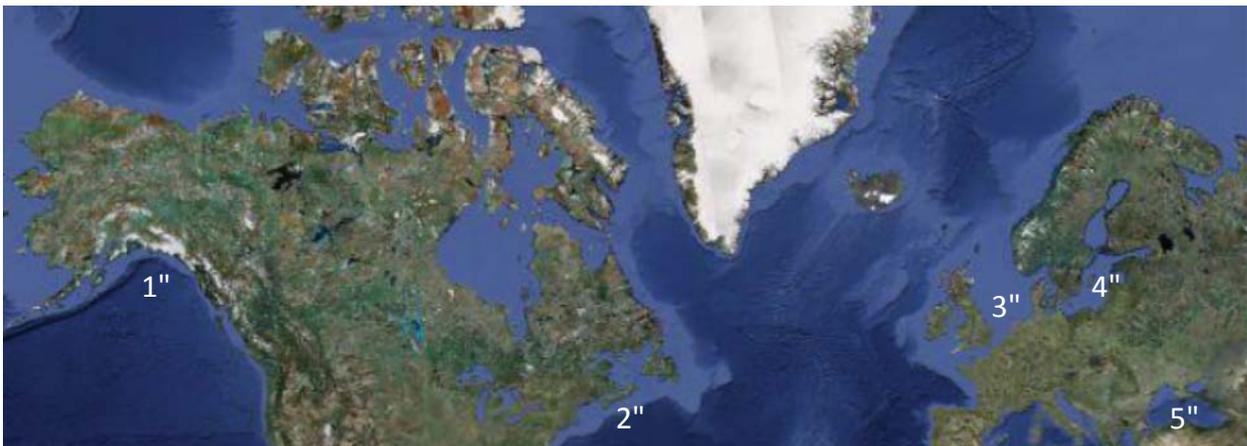
## 2. MARINE ECOSYSTEM REGIME SHIFTS

### KEY FINDINGS

- Major ecosystem regime shifts involving multiple trophic levels are reported from the North Pacific, the Eastern Scotian Shelf, the North Sea, the Baltic Sea and the Black Sea.
- All ecosystem regime shifts show a strikingly similar timing during the end of the 1980s/early 1990s, which points to a common large-scale atmospheric driver.
- All reviewed studies on ecosystem regime shifts report different combinations of drivers including anthropogenic impacts through overfishing and eutrophication, as well as species invasion.

Regime shifts in marine ecosystems are increasingly reported in the scientific literature. A number of special issues and review articles in peer-reviewed journals have been published (e.g. Steele, 2004). Furthermore, a series of statistical methods for identifying regime shifts have been developed (Andersen *et al.*, 2009). Here we specifically review studies that match the definition of ecosystem regime shifts involving multiple trophic levels, given in Chapter 1. Emphasis is placed on studies that use time-series from multiple trophic levels in multivariate statistical analyses, a technique pioneered by the study of Hare and Mantua (2000) for the North Pacific. Comparable studies using a similar approach include the major ecosystem regime shifts reported i.e. in the Eastern Scotian Shelf, the North Sea and the Baltic Sea (Map 1). Major regime shifts also occurred in the Black Sea, where no similar analysis has been published yet. Here, the ecosystem changes are reported based on a major publication considering all trophic levels (Oguz and Gilbert, 2007).

### Map 1: Ecosystems investigated in this study



1 – North Pacific, 2 – Eastern Scotian Shelf, 3 – North Sea, 4 – Baltic Sea, 5 – Black Sea.

**Source:** Google Maps

The review of ecosystem regime shifts in the above listed regions put emphasis on i) the timing of the regime shifts, ii) a description of the changes in the food webs, and iii) the reported main drivers of the ecosystem changes.



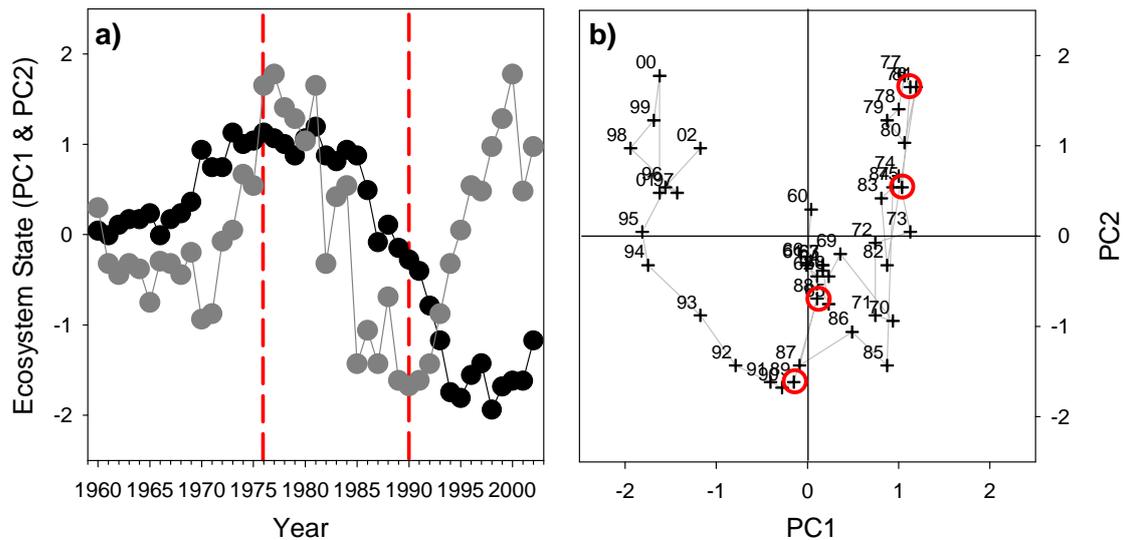
1989, the coastal waters in the northern Gulf of Alaska and Bering Sea were cooling in winter, and the temperature of the central North Pacific Ocean increased. Furthermore, the winter and summer Arctic vortex intensified, the winter Aleutian Low weakened, and a summer warming occurred throughout the central North Pacific and coastal Northeast Pacific Ocean. Ecological changes included declines in Bering Sea groundfish recruitment, Western Alaska chinook, chum, and pink salmon catch, British Columbia coho, pink and sockeye salmon catch, West Coast salmon catches and groundfish recruitment, and increases in Bering Sea jellyfish biomass. The regime shifts in the North Pacific are generally described as climate-driven and being unrelated to overfishing (Hare and Mantua, 2000; Overland *et al.*, 2008).

## 2.2. The Eastern Scotian Shelf

The Eastern Scotian Shelf represents the eastern half of the continental shelf off Nova Scotia, Canada. The resident cod population had been subject to heavy exploitation and collapsed during the early 1990s and, despite the cessation of fishing, it has 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 resulting in 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 ways. They used 55 primary and secondary biotic, abiotic, and human variables over a 43-year period (1960–2002). 39 first-order indicators of the ecology 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 following the approach of Hare and Mantua (2000) using Principal Component Analysis (PCA).

The analysis clearly revealed a coherent change in the Eastern Scotian Shelf ecosystem in the mid 1970s, but especially the early 1990s (Figure 2). 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 of the dominant groundfish species such as haddock (*Melanogrammus aeglefinus*), cod (*Gadus morhua*), pollock (*Pollachius virens*) and silver hake (*Merluccius bilinearis*), estimated metabolic rates) changed abruptly from higher mean values prior to 1990 to generally lower levels in the 1990s. The inverse pattern was found in indicators such as grey seal numerical abundance, human population size of Nova Scotia, specific metabolic rates, landed value/total landings and pelagic/demersal ratios, which changed quickly from below to above average values after 1990. The multivariate statistical analysis summarized these transitions in the ecosystem into a change in dominance of groundfish vs. pelagic/benthic macroinvertebrates in the late 1980s.

On the lower trophic levels, phytoplankton abundance (CPR colour index, diatom and dinoflagellate counts) was found to be higher 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.

**Figure 2: 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) – time-trajectory of PC1 (black dots) and PC2 (grey dots), vertical lines indicate reported regime shifts; b) – phase space plot of PC1 vs. PC2, red circles indicate major transitions.

**Source:** Redrawn from Choi *et al.* (2005)

A further result shown by the multivariate analysis was a change in ocean climate conditions. This was mainly indicated by changes in bottom temperatures, CIL (cold intermediate layer) volume 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 have been observed with the highest density difference between 0 and 50m during most of the 1990s. This increase in water column stability was the result of 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 that the eastern Scotian Shelf ecosystem has experienced a “regime shift” characterized by an abrupt transition into a new state during in the late 1980s. They furthermore argue 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. They suggest an interaction between ocean physics, biology and exploitation to be responsible for the observed ecosystem regime shift.

### 2.3. The North Sea

A regime shift in the North Sea was first suggested to have occurred after 1987 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 as well as decapod and echinoderm larvae but decreases in bivalve larvae (Kirby *et al.*, 2009; Kirby and Beaugrand, 2009).

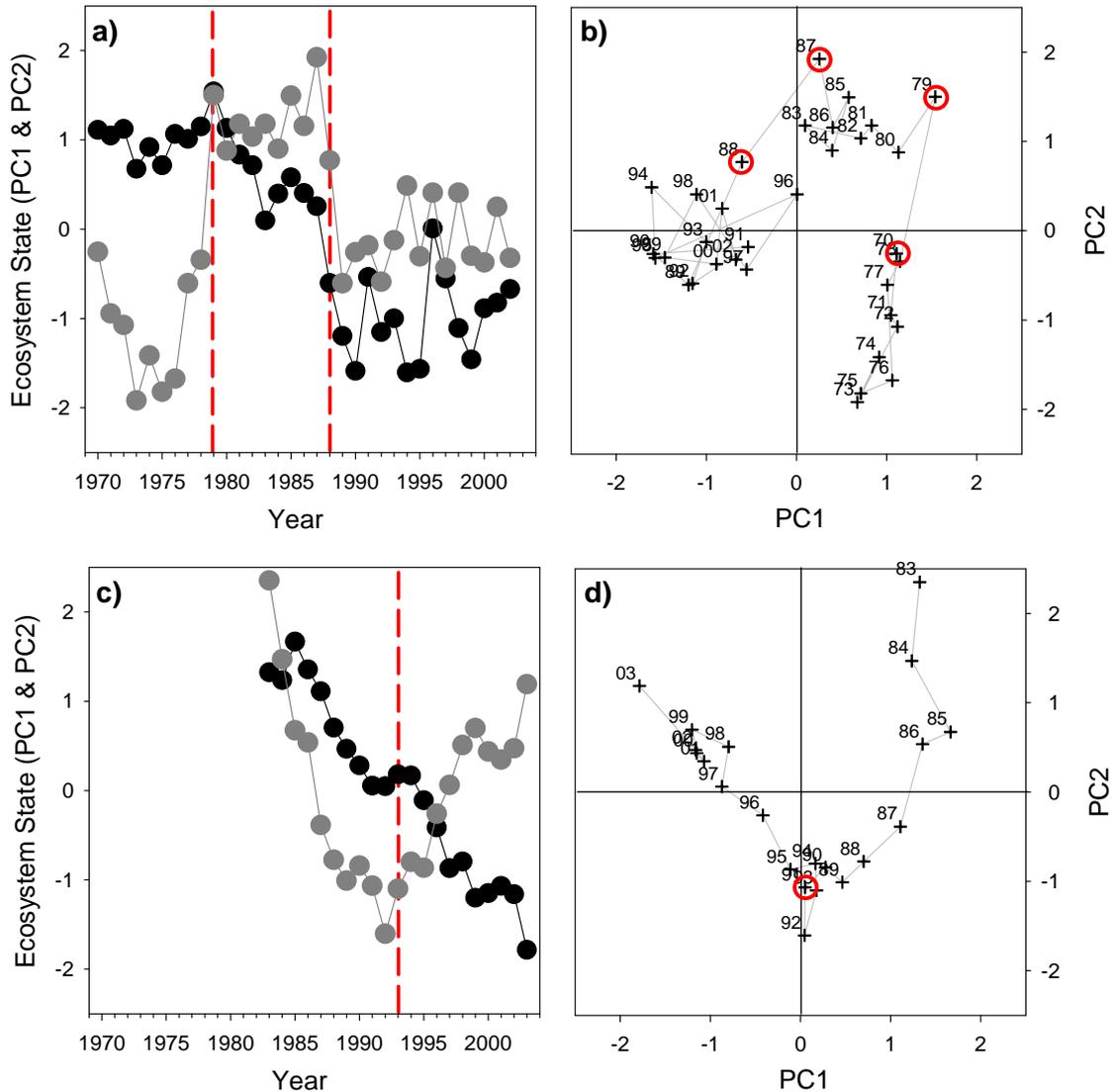
Beaugrand (2004) performed a comprehensive study using data from the Continuous Plankton Recorder (CPR) survey (for phytoplankton and zooplankton) and fish recruitment data for plaice (*Pleuronectes platessa*), cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), herring (*Clupea harengus*) and sole (*Solea solea*). This study demonstrated that the regime shift in the North Sea occurred during a longer period, namely 1982–1988. However, the changes were clustered in two periods, i.e. 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, which is discussed to be 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. First, 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 covering the period 1970 to 2002, 50 were biological comprising multiple trophic levels and representing a very wide range of marine organisms from phytoplankton to top-predators. 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 (Figure 3 a, 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. Especially non-commercial species like solenet and scald fish were affected, but also cod and haddock. 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.

Using a similar multivariate approach, Kenny *et al.* (2009) investigated regime changes in the whole North Sea (Figure 3 c, d). Of their 114 selected variables covering the period 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 *Calanus finmarchicus* and Northern fulmar declined from high values before 1990 to lower values afterwards. Two dominant regimes were identified: a first one before 1993

characterised by a productive cold water demersal fin fishery and an increasingly productive pelagic fishery, and a second regime after 1993 characterised by increased seawater temperature, a decline in the demersal fin fishery, but a still productive pelagic pelagic fishery. Overall Kenny *et al.* (2009) suggest the transition in the state of the North Sea ecosystem between 1983 and 2003, despite single abrupt changes in e.g. *C. finmarchicus* and sea surface temperature. Their analysis supports the interpretation that a temperature increase by c. 1988 has amplified changes that have been initiated already before, most likely by a combination of gradual warming and high fishing pressure.

**Figure 3: Regime shifts in the North Sea ecosystem.**



Temporal trends of Principal Components (PC1 and PC2) as holistic indicators of ecosystem state from multivariate analyses; a) and c) – time-trajectory of PC1 (black dots) and PC2 (grey dots), vertical lines indicate reported regime shifts; b) and d) – phase space plot of PC1 vs. PC2, red circles indicate major transitions.

**Source:** redrawn from Weijerman *et al.* (2005) – a) and b), and Kenny *et al.* (2009) – c) and d).

## 2.4. The Baltic Sea

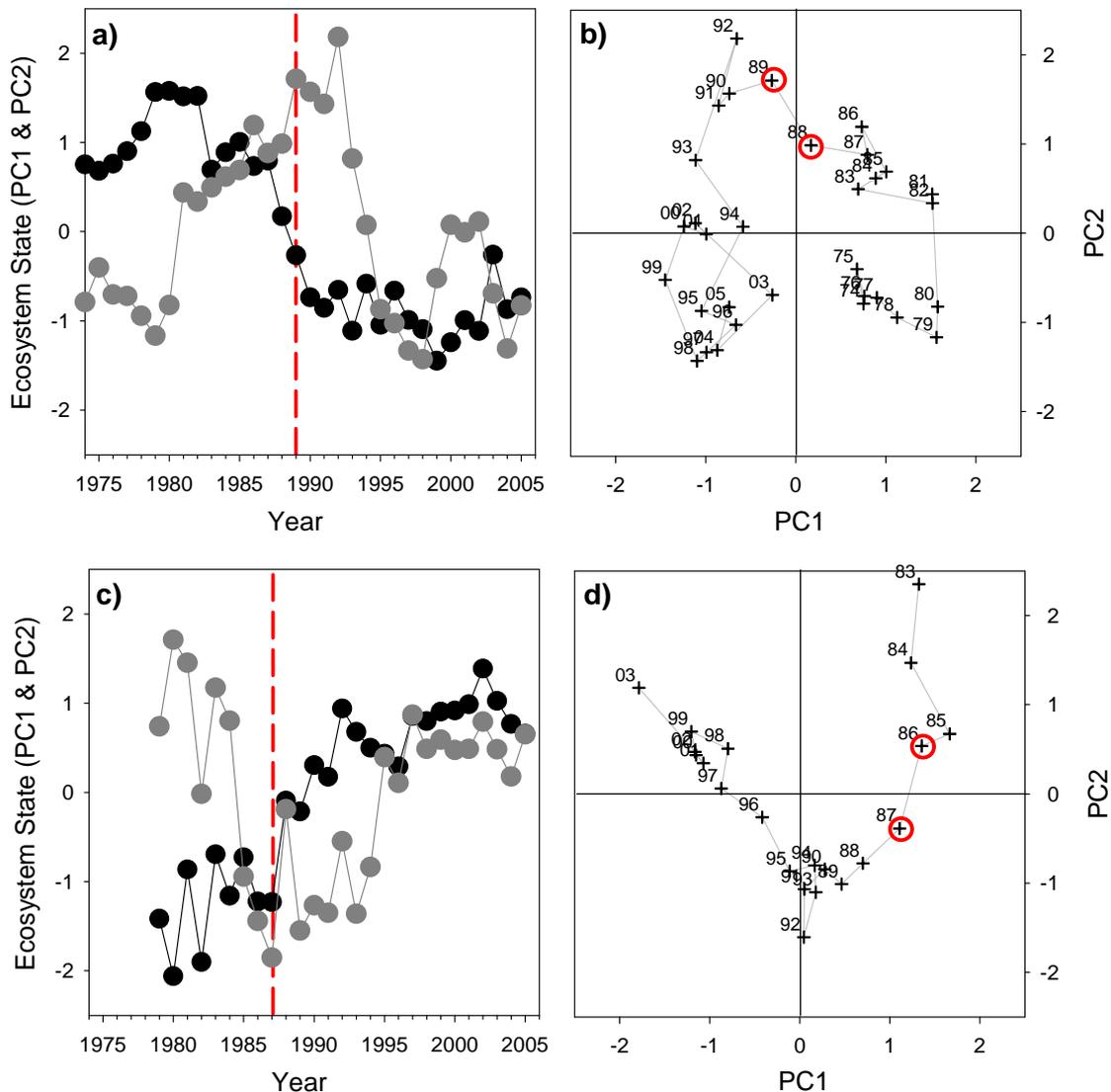
Studies on ecosystem regime shifts in the Baltic Sea have been published only relatively recently. These were mainly focusing on changes in commercially important fish populations, i.e. cod, herring and sprat (e.g. Köster *et al.*, 2003; 2005). Using an ecosystem model (Ecopath with Ecosim, EwE), Österblom *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 in the Baltic Sea between 1900 and 1980. They identified two major ecological changes. The first one, from seal to cod domination, occurred after the 1930s and was caused by a virtual elimination of marine mammals. A second regime shift was characterized by a transition from an oligotrophic to a eutrophic state around 1950. According to their modeling results, eutrophication has resulted in a substantial increase in fish production in the Baltic Sea and has changed the whole food web.

The best documented regime shift in the Baltic fish community is the shift from cod to clupeid (i.e. mainly sprat) domination in the late 1980s. It has been explained by 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 a part of a full reorganization of the Baltic ecosystem. Alheit *et al.* (2005) summarized 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 (Figure 4 a, b), characterized by the opposite dominance of cod and sprat, as well as the zooplankton species *Pseudocalanus acuspes* and *Acartia* spp. (Möllmann *et al.*, 2008). Furthermore, 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) characterized 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, favoring the cod decrease and the consequent increase in sprat population, with further indirect changes down the food web (Casini *et al.*, 2008; Möllmann *et al.*, 2008; see Chapter 3).

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 the North and Baltic seas (Lindegren *et al.*, 2010a). This analysis covered the period 1979–2005 and included 48 datasets of physical oceanographic and nutrient conditions as well as phytoplankton, zooplankton and fish variables (Figure 4 c, d). Lindegren *et al.* (2010a) found a similar regime shift timing as in the Central Baltic with major changes occurring between 1987 and 1988. The first regime was characterized by high levels of e.g. 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 the most likely driver of change. As the Sound is characterized by the absence of commercial trawl fishing and hence of high levels of

fishing mortality, fishing did not appear to be the main driver of the ecosystem regime shift here.

**Figure 4: 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) – time-trajectory of PC1 (black dots) and PC2 (grey dots), vertical lines indicate reported regime shifts; b) and d) – phase space plot of PC1 vs. PC2, red circles indicate major transitions.

**Source:** Möllmann *et al.* (2009) – a) and b), and Lindegren *et al.* (2010a) – c) and d).

Multivariate analyses as described above have now been additionally been 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 characterized by different environmental conditions and more or less 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 presented here suggest that this period of reorganization between two ecological states also occurred in most other Baltic systems,

although with slightly different timing and was mainly forced by changes in atmospheric forcing (Diekmann and Möllmann, 2010).

## 2.5. The Black Sea

Several reorganizations of the Black Sea ecosystem have occurred during the recent 50 years and they are among the best investigated and described ecosystem regime shifts in marine ecosystems. In contrast to the results presented above for the North Pacific and the Scotian Shelf, as well as for the North Sea and Baltic Sea ecosystems, no statistical analysis of multivariate datasets have been published yet. However, Oguz and Gilbert (2007) provide a detailed account of changes on all trophic levels in the period 1960–2000 and demonstrate the importance of multiple drivers.

A first major change in the Black Sea food web was the decline of large predatory fish populations due to overfishing and a subsequent increase in small pelagic stocks during the early 1970s. Accordingly a trophic cascade occurred, leading to decreased zooplankton and increased phytoplankton biomasses (Daskalov *et al.*, 2007; see Chapter 3). The period until the regime shift is characterized 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 such as hypoxia and anoxia were mainly coastal, while offshore phytoplankton biomass remained low. Phytoplankton biomass then increased abruptly during the early 1970s as a response to the trophic cascade. Subsequent continued eutrophication contributed to increasing phytoplankton biomass during the 1980s.

A second regime shift was observed during the 1988/89 and corresponds 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, first the jellyfish *Aurelia aurita* and then its competitor the ctenophore *Mnemiopsis leidyi*. Heavy *Mnemiopsis* predation on small pelagic fish larvae and food competition with the adults has exacerbated the small pelagic collapse. Climatically, the mid-1980s and early 1990s were characterized 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. Together with increased eutrophication this cooling has hence caused increasing phytoplankton biomass.

The ecosystem state dominated by gelatinous carnivores and phytoplankton biomass persisted only five years followed by markedly varying, transient, oscillatory food web organisation during 1991–1996. Since 1997 the gelatinous population decreased and the small pelagic fish stocks continuously recovered because of fishing regulations. Furthermore, another gelatinous ctenophore species *Beroe ovata* entered the Black Sea, preying only on *Mnemiopsis* (Kideys, 2002; Shiganova, 2004). Small pelagics are again controlling the food web as the main top predator of the system, with increased zooplankton declining phytoplankton and gelatinous stocks.



### 3. TROPHIC CASCADES

#### KEY FINDINGS

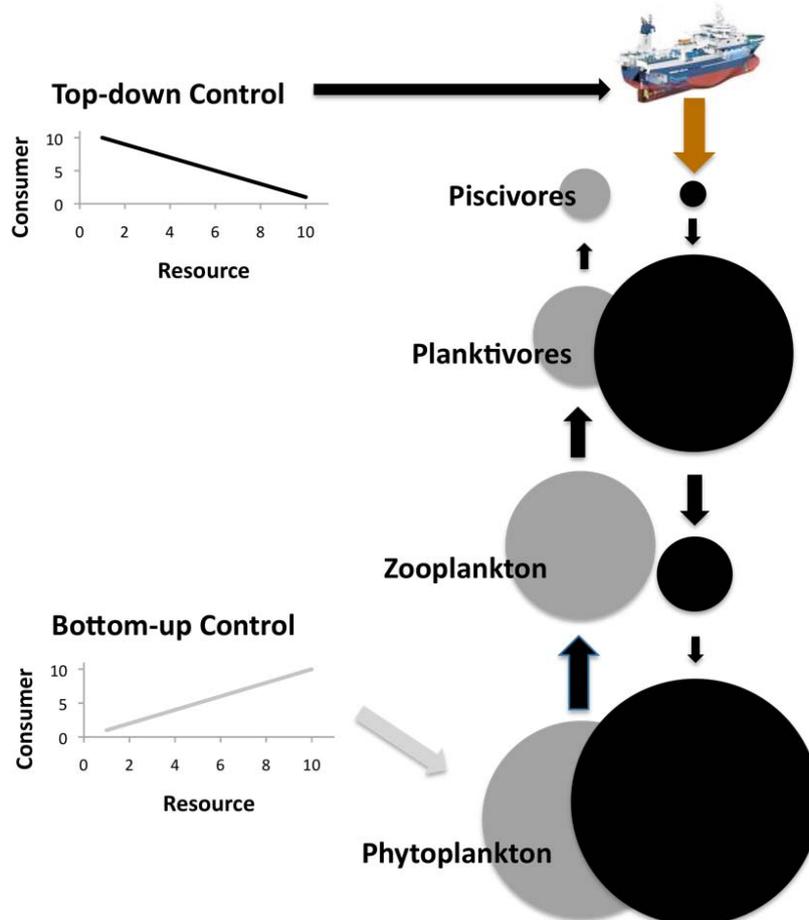
- Trophic cascades are linear chains of alternating suppression and release between successive pairs of consumer and consumed species.
- Major trophic cascades involving four trophic levels are reported from the Eastern Scotian Shelf, the Baltic Sea and the Black Sea.
- Trophic cascades are initiated by a depletion of top-predators and by this changing the trophic control from bottom-up (resource) control to top-down (consumer) control).
- The vulnerability of an ecosystem to a change from bottom-up to top-down control and hence to trophic cascading depends on biodiversity and the thermal regime.
- Changes in trophic control are mainly reported to occur from overfishing, but can also be induced by climate.

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). The analysis presented in Chapter 2 has showed 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 from the cases reviewed in Chapter 2, that overfishing plays a crucial role in triggering ecosystem regime shifts. The reorganization of a food web caused by overfishing is called a **trophic cascade**.

Trophic cascades can be defined as linear chains of alternating suppression and release between successive pairs of consumer and consumed species (Scheffer *et al.*, 2005; Strong and Frank, 2010). Trophic cascades involve a top-down control on the functioning of ecosystems, which is opposed to the traditional view of bottom-up control. Bottom-up control was the first paradigm of food web science and dominated the first half of the twentieth century (Elton, 2001; Strong and Frank, 2010). Usually evidence for bottom-up forcing is derived by a positive correlation among biomasses of trophic guilds in space or time. Evidence for bottom-up relationships in marine ecosystems is given by positive correlations between average fisheries yield and primary production (Ware and Thompson, 2005; Chassot *et al.*, 2007).

Figure 5 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 Figure 5 (black circles) demonstrates the resulting alternating increase and decrease of the trophic guild's biomasses down to the phytoplankton, when the ecosystem regulation is changed from bottom-up to top-down control due to overfishing.

**Figure 5: 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.**



Source: Author

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 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 in upper trophic levels to be widespread (Worm and Myers, 2003; Frank *et al.*, 2007; Baum and Worm, 2009; Strong and Frank, 2010). Even more important, now classic examples for trophic cascading over 3-4 trophic levels in large marine ecosystems exist. Here the most prominent cases from the Eastern Scotian Shelf, the Baltic Sea and the Black Sea are reviewed. No community-wide trophic cascade has been published for the North Pacific and the North Sea where ecosystem regime shifts have been reported. However, changes in trophic control from top-down to bottom-up have been suggested for the North Sea ecosystem as well (Kenny *et al.*, 2009). Additionally, indications of trophic cascading between single species have been shown for the North Sea ecosystem (Kirby *et al.*, 2009; Lindegren *et al.*, 2010a), but are not considered here. After reviewing the main

examples of marine trophic cascades, we 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.

### 3.1. The Eastern Scotian Shelf

The most prominent case of a trophic cascade in a large marine ecosystem involved four trophic levels and even nutrient concentrations (Frank *et al.*, 2005). The trophic cascade was initiated by overfishing of large predators (primarily 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, here the changes in top-predator abundance have caused a major reorganization of the food web through indirect effects of fishing on lower trophic levels. These ecosystem changes had pronounced social and economic consequences and resulted in a fishery on shrimp and crab with a monetary value that exceeds that of the replaced groundfish fishery. Frank *et al.* (2005) discuss that from an economic perspective this may be an attractive situation, but considering biological and functional diversity as a stabilizing force in ecosystems this may bear strong ecological risks in the face of future natural or anthropogenic perturbations.

### 3.2. The Baltic Sea

Overfishing of cod also strongly impacted the Baltic Sea food web leading to an explosive increase of the main cod prey, the planktivorous fish sprat (*Sprattus sprattus*) (Köster *et al.*, 2003). Trophic cascading was strongest in summer where biomass of zooplankton declined, followed by increases in phytoplankton (Casini *et al.*, 2008). In spring, the increased sprat stock only influenced the calanoid copepod *Pseudocalanus 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 and competition of the planktivorous competitor herring (*Clupea harengus*) and the sprat stock itself (Möllmann *et al.*, 2005; Casini *et al.*, 2006). The bad condition of the pelagic fish species eventually negatively affected the reproduction of the piscivorous seabird *Uria aalge* (Österblom *et al.*, 2006), a further indirect effect of the changes at the top-of the food web. Also in the Baltic Sea it is evident that overfishing contributed to the observed reorganization of the ecosystem (Möllmann *et al.*, 2009).

### 3.3. The Black Sea

The Black Sea ecosystem has undergone multiple regimes under strong anthropogenic impacts such as heavy fishing, cultural eutrophication and invasions by alien species, as well as climate variability (Daskalov, 2003; Oguz *et al.*, 2006; Oguz and Gilbert, 2007). Daskalov *et al.* (2007) studied time series of five groups of pelagic populations across four trophic levels, i.e. phytoplankton, zooplankton, planktivores (gelatinous and fish) and piscivores. Major ecosystem changes were related to overfishing the upper trophic levels of the pelagic food web. A first event was caused by top predator depletion and provoked 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, again through overfishing, of planktivorous fish and an outburst of the alien ctenophore *Mnemiopsis*

*leidy*, and caused a second system-wide trophic cascade, displaying similar alternating changes in zoo- and phytoplankton, as well as water chemistry. Clearly, in the Black Sea overfishing was a major driver in causing ecosystem regime shifts.

### **3.4. Vulnerability of marine ecosystems to overfishing-induced trophic cascading**

The above examples of trophic cascading 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 a heavily fished ecosystem in the North Atlantic. Their review spanned 30 degrees of latitude and reported changes mainly involving the two upper trophic levels (piscivores 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, southeast 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 temperature. Bottom-up control seems to dominate in areas with higher species richness, which points towards a higher 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.

### **3.5. 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 which changes trophic control inducing ecosystem regime shifts. However, also climate has been shown to be able to change the 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 is oscillating depending on climate state. Rapid warming during the Pacific regime shift in the 1970s caused an oscillation between bottom-up and top-down control. This shift to top-down control contributed 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 (OCH) as a mechanism to explain ecological reorganization in the south-east Bering Sea. Here bottom-up control through climate leads to a population

increase, and when the population size is high, biological control, i.e. 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 has been shown by Casini *et al.* (2009) as the mechanism for the Baltic Sea trophic cascade.



## 4. REVERSIBILITY OF ECOSYSTEM REGIME SHIFTS

### KEY FINDINGS

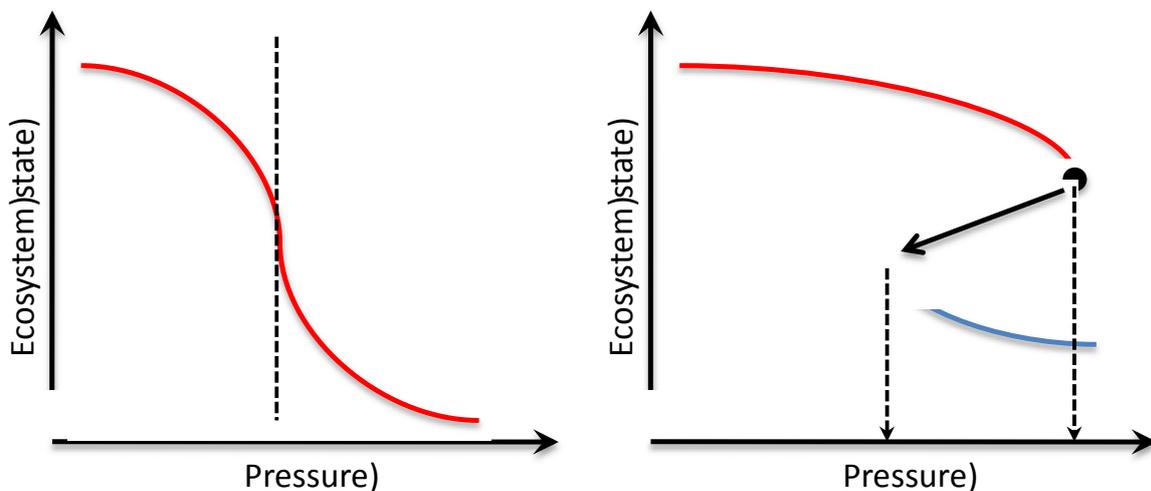
- Ecosystem change can occur in a linear and smooth way, but may also be abrupt involving thresholds in the response to an alternative driver.
- Alternative stable states exist when there is hysteresis in a system, i.e. when it is necessary to reduce the external pressures to lower values than those that have caused the initial abrupt change.
- Resilience can be defined as the maximum perturbation that the system can stand without causing a shift to an alternative stable state. Gradually changing conditions may reduce resilience and hence make it more fragile to other drivers.
- Identification of alternative stable states in natural ecosystems is difficult, but there are several indicators of alternative stable states that can be derived from field data.
- Indications for alternative stable states are found for the Eastern Scotian Shelf, the North Sea, the Baltic Sea and the Black Sea.

The reversibility of ecosystem changes is a critical question for the management of marine resources. Recent developments in the theory of catastrophic shifts and critical transitions in ecosystems have shown that ecosystem regime shifts may not be easily reversible when the system displays alternative stable states (Scheffer, 2009). This would mean that drastic management interventions are needed to reverse change, which is usually costly (Scheffer *et al.*, 2001; Suding *et al.*, 2004). Discussion on stable states in marine ecosystems is usually fueled by the delayed recovery of commercially important fish stocks, mainly cod off the Canadian East coast (Frank *et al.*, 2005; Frank *et al.*, 2011) or the Baltic Sea (Casini *et al.*, 2008; Casini *et al.*, 2009). Usually discussions arise around the question if stable states exist and what are the main drivers of change (Cardinale and Svedäng, 2011; Möllmann *et al.*, 2011). Below we review the theory of alternative stable states and provide evidence for their existence in different ecosystems showing regime shifts.

### 4.1. Types of ecosystem response 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 (Scheffer *et al.*, 2001; Collie *et al.*, 2004). The state of some ecosystems may respond in a continuous way to external pressure, while other systems display inertia over a range of conditions. The latter will respond strongly when conditions approach a critical level or a threshold (Figure 6; 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 (Figure 6, right panel). These states are then separated by an unstable equilibrium (black arrow in Figure 6) that marks the border between so-called “basins of attraction”.

**Figure 6: Conceptual diagram showing possible ecosystem responses to external pressures and the development of alternative stable states.**



Left panel shows linear (blue line) and non-linear (red line) change with abrupt change in ecosystem state – vertical line indicates threshold for the non-linear case; right panel shows non-linear change with abrupt transition and alternative stable states – arrow indicates an “unstable equilibrium”.

**Source:** Author (after Scheffer *et al.*, 2001; Scheffer and Carpenter, 2003)

The potential existence of alternative stable states has profound implications for the response to external drivers (Figure 6 – right panel). It implies that if conditions change sufficiently so that they pass a critical threshold, a “catastrophic transition”, i.e. a regime shift occurs. Characteristically when monitoring a system or a variable no obvious drastic change is observed and hence regime shifts usually occur largely unannounced. More importantly for management of ecosystems is that in case of alternative stable states, restoring the external pressures to values before a regime shift is insufficient, rather it is necessary to reduce external pressures to far lower values. This phenomenon is called hysteresis and is a result of a positive feedback in a system (see below for examples). Restoring systems displaying hysteresis may require drastic and expensive management measures (Suding *et al.*, 2004).

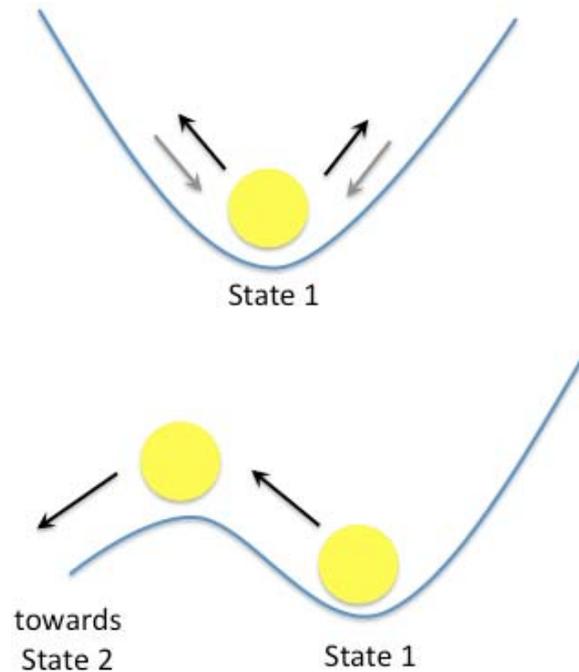
## 4.2. Resilience and the interaction of multiple drivers

In reality ecosystems are never fully stable, and stochastic events such as weather extremes or species invasions may cause fluctuations in ecosystem state (Scheffer *et al.*, 2001). In systems with alternative stable states, the likelihood that the system switches between states (i.e. the occurrence of a regime shift) depends on the strength of the perturbation, but also on the actual condition of the ecosystem, frequently called “the size of its attraction basin” (Figure 7). When the basin is small or shallow (a stressed condition – eroded resilience in Figure 7) only slight perturbations may cause a regime shift, while when the valley is large or deep (a healthy condition) a substantial external impact would be needed for a regime shift to occur.

The size of the attraction basin or the state of the ecosystem is frequently termed its resilience (Holling and Chambers, 1973). It can be defined as the size of the basin around a state, corresponding to the maximum perturbation that the system can stand without causing a shift to an alternative stable state. Importantly, in a system with alternative

stable states, gradually changing conditions may have only small effects on its state. Gradually changing conditions may however 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 changing a system into another stable state and hence triggering a regime shift may result from another external driver, but may also result from internal system dynamics (Scheffer *et al.*, 2001). In reality, an interaction of internal processes (e.g. trophic control; see Chapter 3) and multiple external stressors (of which some reduce the resilience and others provide the final push) will often cause a shift to an alternative stable state. An important conclusion from this is that, when interpreting causality of regime shifts, there is a tendency to ignore the factors that undermine resilience slowly, e.g. eutrophication or global warming (Scheffer and Carpenter, 2003).

**Figure 7: Conceptual diagram of the concepts of resilience and attraction basins.**



The upper panel shows a “resilient” situation with a deep “attraction basin” – pushing the ecosystem state (yellow ball) by and external drivers (black arrow) results in fast return (grey arrow) to the original state; the 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.

**Source:** Author (after Scheffer *et al.*, 2001; Scheffer and Carpenter, 2003)

### 4.3. Alternative stable states

It is generally difficult to explore the existence of alternative stable states in natural ecosystems and usually experimental work is needed to derive evidence (Scheffer and Carpenter, 2003; Scheffer, 2009). In large marine ecosystems experimental manipulation is close to impossible, but it is possible to derive indicators of alternative stable states from field data. A first class of indicators are abrupt shifts or jumps in time series and methods exist to determine whether a shift in a time-series is significant (Hare *and* Mantua, 2000). However, a significant step change in a time series does not necessarily prove alternative stable states, since the shift may simply be due to a stepwise change in an external driver (e.g. a sudden temperature change), or 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 based on time-series but also by exploring spatial distributions. Eventually 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. Hence, obtaining indications for the existence of alternative stable states from field data can never be conclusive (Scheffer and Carpenter, 2003; Scheffer, 2009).

#### **4.4. Evidence for alternative stable states in marine ecosystems**

As discussed above alternative stable states in marine ecosystems are difficult to prove and there can only be indirect evidence (Scheffer and Carpenter, 2003; Scheffer, 2009). The latter can include (i) interactions between external drivers, one of which undermines resilience and another pushes the ecosystem into a new state, (ii) positive feedbacks that drive a system into a new state and keep it stable, and (iii) indicators of alternative stable states according to Scheffer and Carpenter (2003).

##### **4.4.1. Interactions between external drivers**

Although it is frequently stated that multiple drivers are responsible for ecosystem regime shifts to occur (Lees *et al.*, 2006), scientific studies have the tendency to concentrate and postulate the dominance of one single important driver. Hence, interactions between external drivers are rarely investigated. For the Central Baltic Sea, Möllmann *et al.* (2009) show that for one state of the abiotic environment, there are two different ecosystem states, which indicates the existence of alternative stable states. Furthermore, they show that there were potential interactions between external drivers leading to the change. A deterioration of the physical environment through lacking inflow of North Sea waters has reduced cod recruitment and hence undermined the resilience of the stock. Increased fishing pressure as a response to decreasing stock size has furthermore contributed to a reduced cod stock resilience. Eventually, an abrupt temperature change with positive reactions of some populations and an even higher fishing pressure has caused the regime shift.

Confronting the example of the Central Baltic with the ecosystem of the Sound clearly demonstrates the importance of resilience (Lindegren *et al.*, 2010a). Here trawl fishing for cod is banned and hence fishing pressure on the stock is low. When a similar abrupt change in temperature occurred at the end of the 1980s as in the Central Baltic, the Sound ecosystem changed drastically. But since cod was not overfished no trophic cascade occurred, and the upper trophic levels remained largely unaltered (Lindegren *et al.*, 2010a).

##### **4.4.2. Positive feedbacks**

Alternative stable states can develop from positive feedbacks in a system (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. Hence the former prey now controls the predator. This role reversal is discussed to be responsible for the hysteresis in the cod stock of the Eastern Scotian Shelf. Here the pelagic fish complex is assumed to control the depleted demersal fish complex, leading to an ecosystem dominated by pelagics and crustaceans (Frank *et al.*, 2005). A similar predator–prey role reversal between cod and herring has been made responsible for the lack of recovery of cod 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). Through statistical time-series modelling, Fauchald (2010) provided indications that herring now controls the North Sea cod stock and prevents its recovery. Furthermore, populations of grey gurnard *Eutrigla gurnardus* (an early maturing benthic fish species of no 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 (Möllmann *et al.*, 2008; Casini *et al.*, 2009). 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) have shown through an extensive field study that sprat at high stock sizes consumes frequently more than the full cod egg production. Additionally, another feedback loop has been identified as potentially responsible for a low stable cod state in the Baltic. The large sprat stock also preys intensively on one of the main zooplanktonic species, the copepod *Pseudocalanus acuspes*, which is a main food item for larval cod. Hence, sprat compete for food with larval cod which contributes to cod recruitment failure (Möllmann *et al.*, 2008).

#### **4.4.3. Indicators of alternative stable states**

Jumps in time-series is the most frequently applied approach in detecting alternative regimes, even though these jumps alone do not provide evidence for their existence. Oguz and Gilbert (2007) applied several indicators proposed by Scheffer and Carpenter (2003) in order to find indications for stable states in the Black Sea. They applied the approach to abiotic environmental as well as to lower and higher trophic level time-series. 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. Similar indications for alternative stable states are derived from the inspection of pelagic fish biomass time series.



## 5. DISCUSSION

### KEY FINDINGS

- The synchronicity in timing of ecosystem regime shifts over the Northern hemisphere during the late 1980s/early 1990s suggests a common climate driver.
- Trophic cascades triggered by overfishing are regularly observed, indicating that multiple external drivers are usually needed to cause ecosystem regime shifts.
- Multiple external drivers interact in such way that one undermines resilience (e.g. fishing) and another one (e.g. abrupt climate change) gives the final impulse for an ecosystem regime shift.
- Ecosystem regime shifts can be difficult to reverse when alternative stable states are involved. Indications for the latter exist from multiple ecosystems.
- Ecosystem-based management strategies are needed to avoid ecosystem regime shifts, and early warning systems need to be developed.

In this study (i) ecosystem regime shifts in the Northern hemisphere were reviewed, (ii) the occurrence of fishing-induced trophic cascades was evaluated, and (iii) the theory of alternative stable states was discussed and evidence for these in the different ecosystems was reviewed. The results are summarized below and discussed in the light of their importance for the management of marine ecosystems and the resources (a key ecosystem service) they provide to human societies.

First the synchronicity of the ecosystem changes observed during the 1990s will be explored in detail, to address the question of a common large-scale atmospheric driver being responsible for these changes. Afterwards we will discuss evidence that overfishing is an important driver for ecosystem regime shifts. This discussion leads to the question of the reversibility of ecosystem changes and the management implications of this question. We further draw a conclusion concerning future research needs, based on the results of this study.

### 5.1. Synchronicity of timing – evidence for a climate driver

The above review of 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, demonstrates a strikingly similar timing of regime shifts (Table 1). Figure 8 summarizes the temporal development of holistic indicators of ecosystem change (Principal Component 1 from PCA) in order to explore the synchronicity of events. Although these ecosystems are situated remotely all over the Northern Hemisphere and differ strongly in their characteristics such as spatial extend, species composition and biodiversity as well as hydrography, major changes have occurred simultaneously during the late 1980s/early 1990s. This period is obviously characterized by major ecosystem changes around the globe. The timing varies between studies, but it should be kept in mind that an exact selection of a single regime shift year is impossible (see below). Still the synchronicity between the different ecosystems is striking. Furthermore, it should be noted that in three

of the ecosystems (where sufficiently long time-series are available) there are indications of a similar synchronized period during the mid 1970s.

The result of synchronous ecosystem change during the late 1980s is consistent with a study by Conversi *et al.* (2010). These authors analyzed and reviewed long-term records of Mediterranean ecological and hydro-climate variables and find a similar timing of ecosystem regime shifts. The study further showed that these changes were related to Mediterranean hydrographic properties, surface circulation, and deep water convection all triggered by large scale climate, i.e the North Atlantic Oscillation (NAO) and the Northern Hemisphere Temperature. It is hence very likely that a main driver of the observed ecosystem changes is large-scale climate variability over the Northern Hemisphere. The period of change essentially matches times of change in the NAO and the Pacific Decadal Oscillation (PDO) at the end of the 1980s, which modified the local temperature regimes (i.e. warming in Northern Europe).

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

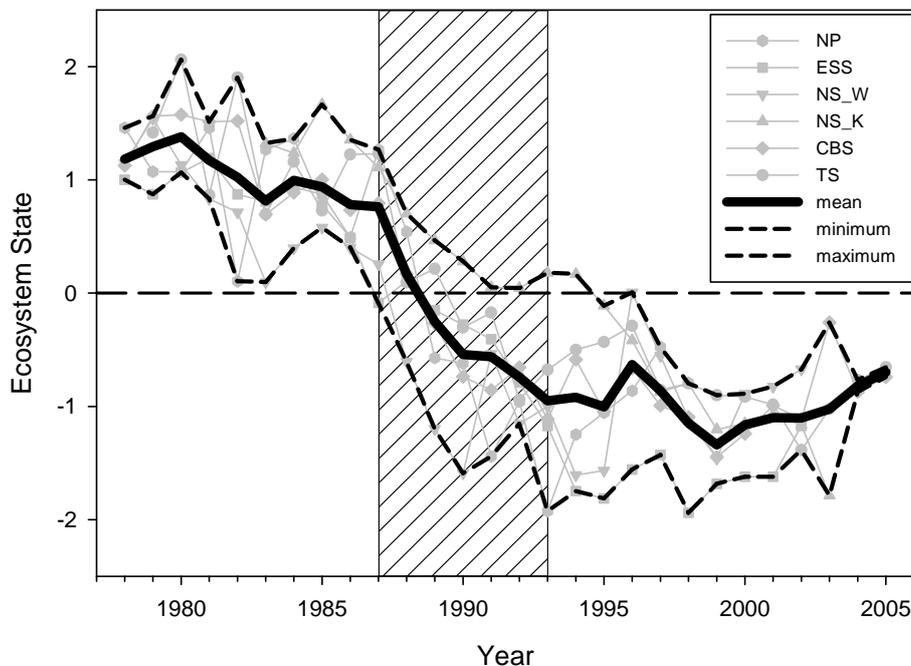
ECOSYSTEM	STUDY	TIMING	MAIN DRIVER
North Pacific	Hare and Mantua, 2000	1977 and <b>1989</b>	Climate
Eastern Scotian Shelf	Choi <i>et al.</i> , 2005	1976 and <b>1990</b>	Climate, overfishing
North Sea	Beaugrand, 2004	1982-88; two periods: 1982-85 and <b>1988/89</b>	Climate
	Weijerman <i>et al.</i> , 2005	1979 and <b>1988</b>	Climate
	Kenny <i>et al.</i> , 2009	<b>1993</b>	Climate, overfishing
Baltic Sea	Möllmann <i>et al.</i> , 2009	<b>1988-93</b>	Climate, overfishing, eutrophication
The Sound	Lindegren <i>et al.</i> , 2010a	<b>1987/88</b>	Climate
Black Sea	Oguz and Gilbert, 2007	1973/4 and <b>1989</b>	Overfishing, species invasion

Some studies clearly show that, although the ecosystem changes have occurred abruptly, it is difficult or impossible to identify single ecosystem regime shift years (e.g. Beaugrand, 2004; Kenny *et al.*, 2009; Möllmann *et al.*, 2009). Two explanations can be given for this observation. First, species can have different response times to changes in the abiotic environment, e.g. plankton species with fast turnover times will respond fast to an abrupt temperature change. Long-lived fish species such as cod will show lagged response time since temperature may affect recruitment and the effect on the stock size will be visible only after a few years (Stenseth *et al.*, 2002). Additionally, abiotic effects on a species may be transmitted through food web interactions, hence displaying an indirect effect on certain species (Ottersen *et al.*, 2010). A second major reason for ecosystem regime shifts to occur in periods, are interactive or additive effects of several external drivers. E.g. 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.

It is generally assumed that multiple drivers are necessary to cause ecosystem regime shifts (Bakun, 2005; Lees *et al.*, 2006; deYoung *et al.*, 2008). 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). But clearly anthropogenic impacts are important or even responsible for ecosystem change as well. Eutrophication can contribute to regime shifts as shown for the Central Baltic Sea (Österblom *et al.*, 2007; Möllmann *et al.*, 2009), but may cause changes only in primary production (Oguz and Gilbert, 2007). Species invasion may also have a role in ecosystem regime shifts, as shown by the invasive ctenophore *Mnemiopsis leidyi* in the Black Sea (Oguz and Gilbert, 2007).

**Figure 8: Comparison of the development of ecosystem state indicators (Principal Component1 - PC1) and regime shift timing during the late 1980s/early 1990s in six Northern hemisphere marine ecosystems.**



Temporal trends of Principal Component1 (PC1) as a holistic indicator of ecosystem state from multivariate analyses; bold line indicates mean of all studies; broken lines indicate minimum and maximum values

**Sources:** NP – North Pacific (Hare and Mantua, 2000), ESS – Eastern Scotian Shelf, NS\_W – North Sea (Weijerman *et al.*, 2005), 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 redrawn from publications; data from other studies kindly provided by authors;

Overfishing is clearly important in causing ecosystem regime shifts and, in some ecosystems, it is considered as the most important driver, e.g. in the Eastern Scotian Shelf (Frank *et al.*, 2005; Frank *et al.*, 2011) and the Black Sea (Daskalov *et al.*, 2007; Oguz and Gilbert, 2007). In other ecosystems such as the Baltic Sea, overfishing is considered to have interacted with climate-induced changes (Möllmann *et al.*, 2008; Möllmann *et al.*, 2009). This seems also to be the case for the North Sea, where initial emphasis has been given to the climate effect (Reid *et al.*, 2001a; Beaugrand, 2004; Weijerman *et al.*, 2005; Kirby and Beaugrand, 2009), while more recent studies increasingly emphasize the role of fishing (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 regime shifts involving several trophic levels by trophic cascading.

## 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. The major examples of trophic cascades in marine ecosystems reviewed here, suggest that depletion of predatory fishes (frequently of cod like in the Eastern Scotian Shelf and the Baltic Sea) due to overfishing is the major cause for ecosystem changes (Table 2). Furthermore, ecosystem vulnerability to exploitation effects depends on the species diversity and on the thermal conditions. 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 other control pattern can depend on the climate state and subsequent population development.

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

ECOSYSTEM	STUDY	SPECIES/TROPHIC LEVELS INVOLVED
Eastern Scotian Shelf	Frank <i>et al.</i> 2005	Demersal fish, pelagic forage fish, large crustaceans, large zooplankton, phytoplankton
Baltic Sea	Casini <i>et al.</i> , 2008, Casini <i>et al.</i> , 2009 ; Möllmann <i>et al.</i> , 2008	Cod, sprat, zooplankton, phytoplankton
Black Sea	Daskalov <i>et al.</i> , 2007; Oguz and Gilbert, 2007	Pelagic predatory fish, small planktivorous fish, gelatinous plankton, zooplankton, phytoplankton

In conclusion, there is strong evidence that overfishing is a major driver of ecosystem regime shifts, in addition to climate. Both external impacts are able to change the prevailing trophic control and hence induce regime shifts. The effects of climate seem to dominate in the Pacific and the North Sea, where studies of trophic cascading are only a few. It remains however to be seen if this is only a bias introduced by a stronger focus of studies on climate events only. As described, for the North Sea initial emphasis has been given to the climate effect (Reid *et al.*, 2001; Beaugrand, 2004; Weijerman *et al.*, 2005; Kirby and Beaugrand, 2009), while more recent studies increasingly emphasize 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 regime shifts involving several trophic levels by trophic cascading. Evidence for a synergy of both effects exist from the Baltic Sea (Möllmann *et al.*, 2009), and initially from the Scotian Shelf (Choi *et al.*, 2005), although recently consensus seem to exist that overfishing is the main driver here (Frank *et al.*, 2011).

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

The results of this study show that multiple drivers are usually involved in causing ecosystem regime shifts (in agreement with previous works of Lees *et al.*, 2006 and deYoung *et al.*, 2008). Here we demonstrate that climate is most likely a common driver among all Northern hemisphere marine ecosystems, but also that overfishing and, to a lower degree, eutrophication and species invasions, are important as well. However, studies on ecosystem regime shifts still frequently favour one factor over the other, and hence the interaction of different external drivers is overlooked (Scheffer and Carpenter, 2003). Resilience theory gives a framework for this interaction. Multiple external drivers interact in a way that one undermines resilience (e.g. fishing) and another (e.g. abrupt climate change) gives the final impulse for an ecosystem regime shift.

Ecosystem regime shifts can be difficult to reverse if alternative stable states are involved. Alternative stable states are caused by positive feedbacks for which indications exist in marine ecosystems. Due to the intractability of experimentation within large marine ecosystems, no final evidence can be derived. Rather indications from empirical data need to be used. Several cases indicate alternative stable states in the marine ecosystems reviewed above, however a final conclusive decision on their existence cannot be derived. Nevertheless, ecosystems showing regime shift, especially with cod as a major player being involved, give the best evidence for hysteresis in recovery to occur. Furthermore, for all of these systems, i.e. 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, but generally attributed to decreased fishing mortality (Cardinale and Svedäng, 2011; 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 good sign for other collapsed fisheries (Frank *et al.*, 2011).

Recovery of cod stock fuels the discussion on the existence of alternative stable states as for Baltic cod. Here the recovery of the cod is on the one hand interpreted as a sign for the regime shift concept to not be valid (Cardinale and Svedäng, 2011). On the other side it is suggested that the Baltic case shows that a sufficiently large intervention can reverse ecosystem regime shifts with alternative stable states (Möllmann *et al.*, 2011). It should be said that the existence of alternative stable states is not a prerequisite for identifying and understanding regime shifts in general. Alternative stable states are generally difficult to demonstrate in large marine ecosystems. Although there is no conclusive proof yet of the existence of alternative stability, 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, the possibility should be accounted for and ecosystems should be managed in a manner that avoids the risk of regime shifts.

#### **5.4. Economic and social impacts of ecosystem regime shifts**

This study has shown that overfishing, in combination with other external drivers such as climate and species invasion, can change entire food webs with respect to structure and function, i.e. can cause ecosystem regime shifts. These reorganizations of the ecosystem however may feedback on the fisheries, with important negative economic and social impacts. Usually collapses of commercially and hence also socially important fish stocks were part of the observed ecosystem regime shifts. Well known are the examples of cod in the North-west Atlantic off Canada (Myers *et al.*, 1997; Hutchings, 2000), but also in the North Sea (Cook *et al.*, 1997) and the Baltic Sea (Köster *et al.*, 2005). These collapses caused severe reductions in the revenues of the respective fisheries and fishing communities (Lindegren *et al.*, 2009). However, these collapses may also have unexpected consequences, as observed on the Eastern Scotian Shelf. Here the trophic cascading has produced a new fishery regime in which the inflation-adjusted, monetary value of the increased shrimp and crab landings (a consequence of the groundfish, mainly cod collapse) far exceeds that of the groundfish fishery it replaced. From an economic perspective, here a more attractive situation has evolved, which may however on the long-term bear ecological risks (Frank *et al.*, 2005). A further example shows that cascading effects of overfishing can indirectly cause the termination of century-long fisheries including its negative social consequences. Myers *et al.* (2007) show that overfishing of large Atlantic sharks of the US coast cascaded down the food web resulting in the depletion of bay scallops, the target of a historically important coastal fishery.

An intensively discussed feature of ecosystem regime shifts which can also feedback on the fisheries and have economic and social consequences are jellyfish outbreaks. Many fish compete with jellyfish for the same zooplankton prey, and fish are also predators of jellyfish, with benthic and reef fish species ingesting polyps, and pelagic fish species eating ephyrae and small individuals (Purcell and Arai, 2001). However, the widespread overexploitation of fish stocks may open ecological space for jellyfish (Richardson *et al.*, 2009). Hence, major jellyfish outbreaks have followed overexploitation and collapse of a locally dominant, small filter-feeding fish stock (e.g. anchovy, sardine or herring) in situations where another rapidly responding, similar fish species is not available as an adequate replacement. Examples come from the northern Benguela upwelling system,

where intense fishing decimated sardine stocks and jellyfish now dominate (Lynam *et al.*, 2006), and off Japan where the giant Nomura jellyfish has occurred following the collapse of the local sardine population (Kawasaki, 1993). Most likely here the collapse of the sardine stocks lowered the predation pressure on jellyfish and increased their available food resources (Bakun and Weeks, 2006). Other examples are explosions in abundances of ctenophores as described for the Black Sea following the collapse of anchovy, a similar event in the Caspian Sea (Daskalov *et al.*, 2007), and a decade-long increase in jellyfish abundance in the Bering Sea following a decline in herring (Brodeur *et al.*, 2008). The available evidence shows that increasing jellyfish abundances have been observed now for many ecosystems and have been in addition to overfishing attributed to eutrophication (Purcell *et al.*, 2001) and climate change (Lynam *et al.*, 2004; Purcell, 2005; Brodeur *et al.*, 2008; Molinero *et al.*, 2008; Gibbons and Richardson, 2009), or combinations of all drivers (Lynam *et al.*, 2011).

Of great concern with respect to jellyfish outbreaks and their consequences on local fisheries is a permanent jellyfish domination. A self-enhancing feedback loop, which is similar to the concept of positive feedbacks in establishing alternative stable states described in Chapter 4.4.2, would act to promote the jellyfication of an ecosystem and may keep it in a difficult to reverse jellyfish-dominated state. In such a case jellyfish become established so strongly that it may be impossible for fish stocks to recover to preexploitation levels, even if commercial fishing is reduced (Richardson *et al.*, 2009). A recent study furthermore suggests major shifts in microbial structure and function associated with jellyfish blooms (Condon *et al.*, 2011). Jellyfish outbreaks are discussed to result in a large detour of carbon toward bacterial CO<sub>2</sub> production hence and away from higher trophic levels. This effect may lower fisheries production and amplify a potential jellyfish-dominated ecosystem state. While final evidence for such a stable state difficult to derive (see Chapter 4.3), the jellyfish example shows that unwanted ecological states resulting from ecosystem regime shifts (and their negative economic and social implications) need to be avoided by insightful and precautionary management.



## 6. CONCLUSION

This 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. Furthermore, 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). The collapse of Eastern Baltic cod during the late 1980s/early 1990s also 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 (Köster *et al.*, 2005; Eero *et al.*, 2011). Simulations with a food web model have shown that in hindsight the collapse could have been avoidable by adapting fishing pressure to environmental conditions and food web interactions (Lindegren *et al.*, 2009). Furthermore, 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). For example, a fishing mortality of  $F=0.3$  (corresponding to the actual EC management plan, EC 2007) could be too high if the hydrographic conditions will deteriorate, as predicted by up-to-date climate change scenarios (BACC, 2008), and therefore fishing mortality would need to be reduced as well.

The essence of the ecosystem approach is considering multiple impacts/stressors, identifying which factors may erode resilience and which have the capability to cause sudden change, and eventually manage in order to be precautionary and to avoid potential catastrophic reorganizations in ecosystems. In the case of highly exploited marine ecosystems such as the Eastern Scotian Shelf, the North Sea, Baltic Sea and the Black Sea, this certainly involves reducing fishing mortality. But with how much and for how long is strongly dependent on the environmental context. Therefore, fishery pressure should be adapted to ecosystem conditions, in order to avoid stock collapses and the need for expensive interventions.

The value of ecosystem-based management approaches and ecosystem knowledge in general (not necessarily only related to regime shift theory) lies additionally in reducing uncertainty in present day single-species approaches. Gårdmark *et al.* (2011) showed how strong the uncertainty is in the case of the state of Eastern Baltic cod. However, they also provide ways to reduce this uncertainty and present indicators for the state of the environment directly developed out of the knowledge derived from regime shift studies on the Baltic ecosystem. These indicators comprise stock specific biological indicators (such as stock structure; predator and prey biomasses), indicators of ecosystem development and trends in the physical environment known to affect cod recruitment. An analysis of these shows indications for changes in the abiotic environment for Eastern Baltic cod, which have however not significantly affected the biological environment of the stock yet. Indicator systems of this kind are fundamental elements of every ecosystem approach and in our view crucially needed for a future sustainable resource management.

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 (Held and Kleinen, 2004; Carpenter and Brock, 2006; 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 complimentary set of early-warning indicators (Guttal and Jayaprakash, 2009; Dakos *et al.*, 2010; Donangelo *et al.*, 2010). 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. However, ecological time-series are now long enough to apply this technique. Additionally increased monitoring effort on multiple trophic levels is needed to establish early-warning systems to avoid catastrophic ecosystem change.



**DIRECTORATE GENERAL FOR INTERNAL POLICIES**  
**POLICY DEPARTMENT B: STRUCTURAL AND COHESION POLICIES**

**FISHERIES**

**ECOSYSTEM SHIFTS IN THE BALTIC SEA**

**NOTE**

**Abstract**

This note presents the main changes in ecosystem structure and functioning in the Baltic Sea, and identifies the processes leading to ecosystem shift. Overfishing, eutrophication and climate changes, acting at both higher and lower level of the food web, have been the main external pressures that drove the shift. Reduced fishing pressure and anthropogenic nutrient emissions may reverse the shift, but the current hydro-climate conditions, the newly established biological and chemical processes, and the expected future climate change could hamper the realization of this goal.

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## LIST OF ABBREVIATIONS

**DIN** Dissolved inorganic nitrogen

**DIP** Dissolved inorganic phosphorus

**HELCOM** Helsinki Commission

**ICES** International Council for the Exploration of the Sea

**SMHI** Swedish Meteorological and Hydrological Institute

**SD** ICES Subdivision

**SSB** Spawning stock biomass



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## EXECUTIVE SUMMARY

Several marine and terrestrial ecosystems have experienced dramatic changes in the past few decades, often referred to as regime shifts. Nowadays, regime shifts are defined mainly on the basis of changes in the ecosystem as a whole and are typically characterized by infrequent and abrupt changes in ecosystem structure and function, occurring at multiple trophic levels and on large geographic scales. In different regions, the observed ecosystem shifts have been attributed to overfishing, eutrophication, pollution, climate changes, or a combination of the diverse pressures.

One of the potential consequences of a regime shift is the establishment of new biological and/or physical internal mechanisms that could tend to maintain the new state, even when the pressures that originally triggered the shift have ceased. In this case the two states are defined as 'alternative stable states' and under these circumstances the return to the previous state could be seriously hindered.

Multi-level ecosystem changes, and their potential to shift the ecosystem into alternative states, have evidently large implications for the management of the exploited resources and ecosystem conservation.

The Baltic Sea has experienced large changes in the biological and physical components during the past few decades. The characteristic low salinity of the Baltic Sea implies that the marine species inhabiting this region are at the border of their distribution range and therefore experience a strong physiological stress. Therefore even small changes in the external pressures (such as fishing, eutrophication or climate variations) may strongly impair their populations. The low biodiversity of this system also implies that there are very few key trophic links and that, therefore, changes at one trophic level may propagate through the whole food web. The enclosed nature of the Baltic, with only reduced water exchanges with the North Sea and a water residence time of around 20-25 years, makes this area acting as a sink for anthropogenic nutrient and pollutant emissions.

The aims of this note are:

- to present the main biotic and abiotic changes occurred in the Central Baltic ecosystem during the past 40 years, and
- to identify the relative importance of the external drivers for the observed shifts, as overfishing, eutrophication and climate changes

Moreover, the potential reversibility of the ecosystem shift will be discussed, along with the management actions that should be implemented to trigger such a reversal. The note ends with recommendations for the future management of fisheries and other anthropogenic activities.

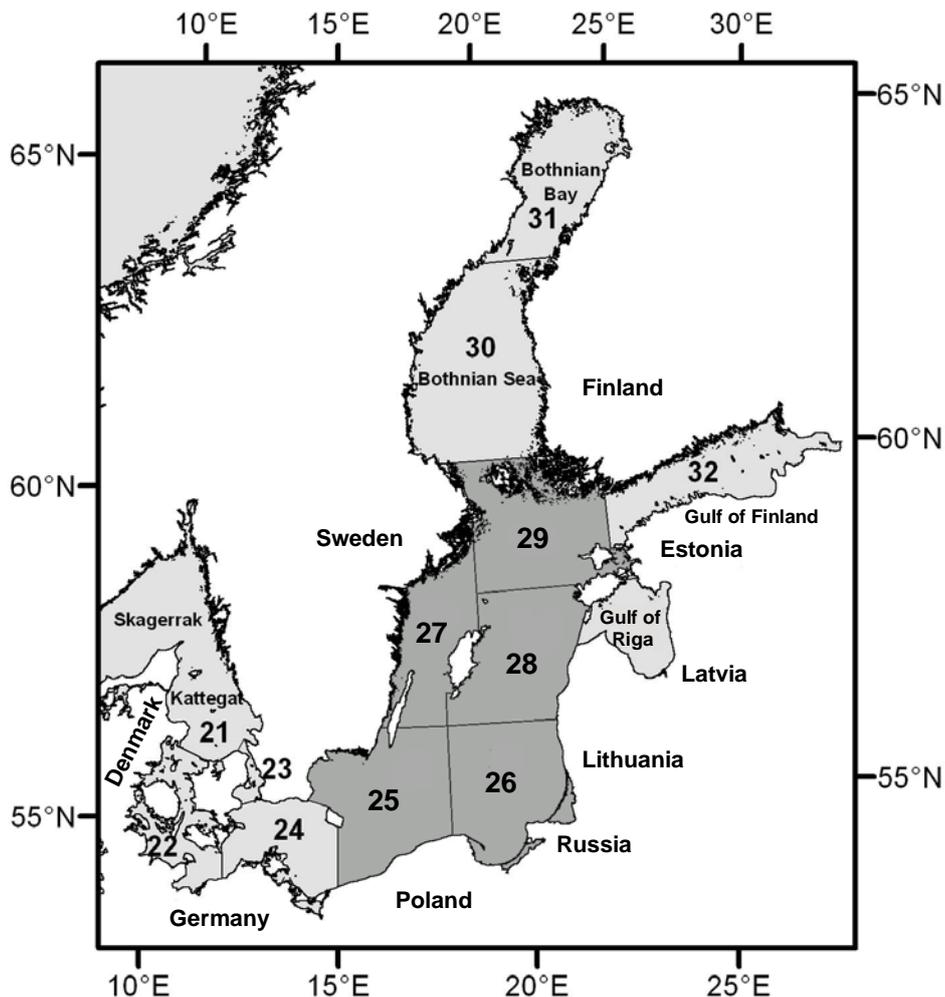


## 1. INTRODUCTION

This report mainly focuses on the Central Baltic, corresponding to the ICES Subdivisions (SDs) 25-29 (Map 1). This is the Baltic Sea area with the higher amount of available information on ecosystem conditions and changes. This is also where the most important commercial fisheries are concentrated and the area of intense eutrophication symptoms, and it is therefore of major importance when analysing the effect of overfishing versus other external pressures on the ecosystem. However, other regions of the Baltic Sea are also taken into consideration when necessary for comparison and completeness. The Western Baltic Sea (SDs 22-24) is also a very important fishing region, but information on its ecosystem is currently being collated for analyses and is thus not treated here.

The information provided here is based on data for the last four decades, because stock assessment data for the three main commercial species in the Baltic Sea (cod *Gadus morhua*, herring *Clupea harengus*, and sprat *Sprattus sprattus*) are available only during this period. However, data extending further back in time are also taken in consideration and discussed when necessary for the understanding of the more recent situation.

**Map 1: Map of the Baltic Sea. The dark grey area corresponds to the Central Baltic.**



Source: Author





## 2.1. Biological ecosystem development

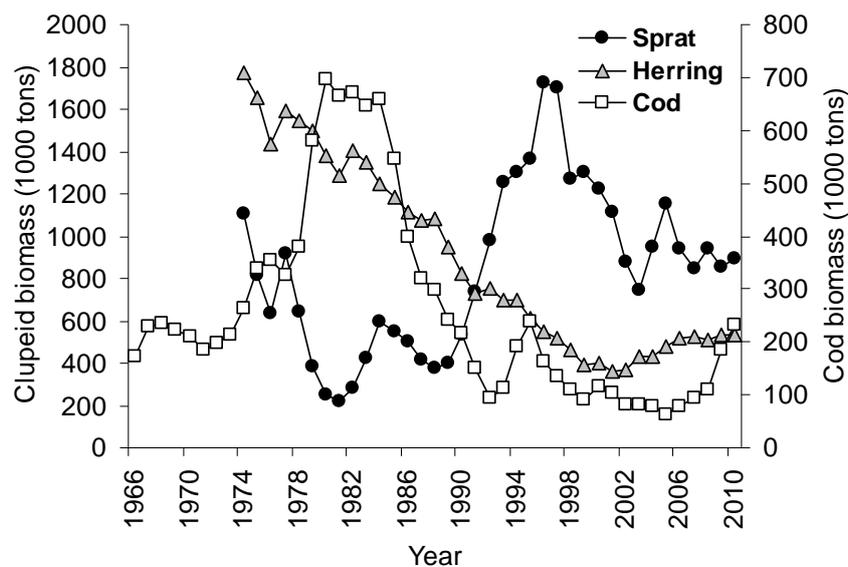
### 2.1.1. Aquatic mammals

In the past 40 years the cod (*Gadus morhua*) has been, together with men, the main top-predator in the open Baltic Sea. In the early 20<sup>th</sup> century the dominant top-predator in the Baltic were marine mammals, such as seals (gray seal *Halichoerus grypus*, ringed seal *Phoca hispida* and common seal *Phoca vitulina* seals) and harbour porpoises (*Phocoena phocoena*), which drastically decreased afterwards due to human activities, like hunting and toxic pollutants (Österblom *et al.*, 2007; MacKenzie *et al.*, 2002).

### 2.1.2. Fish

Concerning commercial fish species, analytical stock assessment has started to provide stock development information from 1966 for cod and from 1974 for herring and sprat (ICES, 2011). A common way to present the state of the stock is by estimating the biomass of fish old enough to spawn, i.e. the spawning stock biomass (SSB).

**Figure 2: Time-series of cod, sprat and herring spawning stock biomass**



Source: Data from ICES (2011)

The Baltic cod stock was relatively low until mid 1970s, grew very high in the mid 1980s, and decreased afterwards eventually reaching lasting very low levels. In the last three years the cod population has shown signs of recovery (ICES, 2011; Figure 2).

The sprat stock since the 1974 has shown an inverse pattern, first decreasing in the early 1980s and then increasing considerably from the early 1990s. Since the mid 1990s the sprat stock has been fluctuating at high levels, both in terms of abundance and biomass (ICES, 2011; Figure 2).

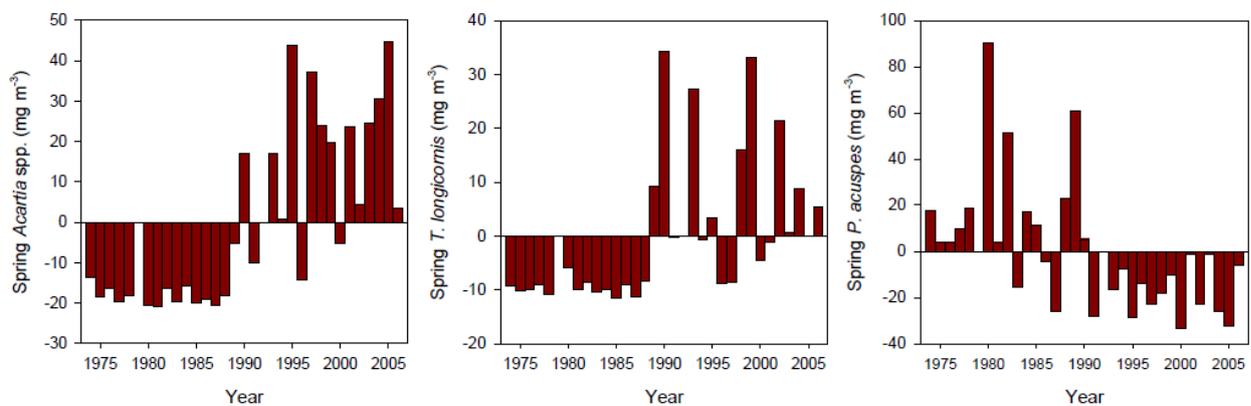
The herring stock has constantly decreased since the mid 1970s, even though the decrease was much more evident in terms of biomass than abundance (ICES, 2011; Figure 2).

### 2.1.3. Plankton

Zooplankton, which is the major prey for sprat and cod larvae and one of the main preys for herring, has shown changes in total biomass and species composition (Möllmann *et al.* 2008; Casini *et al.*, 2008, 2009). The general main shifts have been a decrease of the copepod *Pseudocalanus* spp. and an increase of *Temora longicornis* and *Acartia* spp. The cladoceran species also decreased in the open sea (ICES, 2010, Figure 3). The shift occurred in the late 1980s-early 1990s.

At the community level (total biomass) the zooplankton has decreased since the early 1990s (Casini *et al.*, 2008).

**Figure 3: Time-series of the main zooplankton species in spring (spawning period for cod, sprat and herring). Left panel: *Acartia* spp.; central panel: *Temora longicornis*; right panel: *Pseudocalanus acuspes***



Source: ICES (2010)

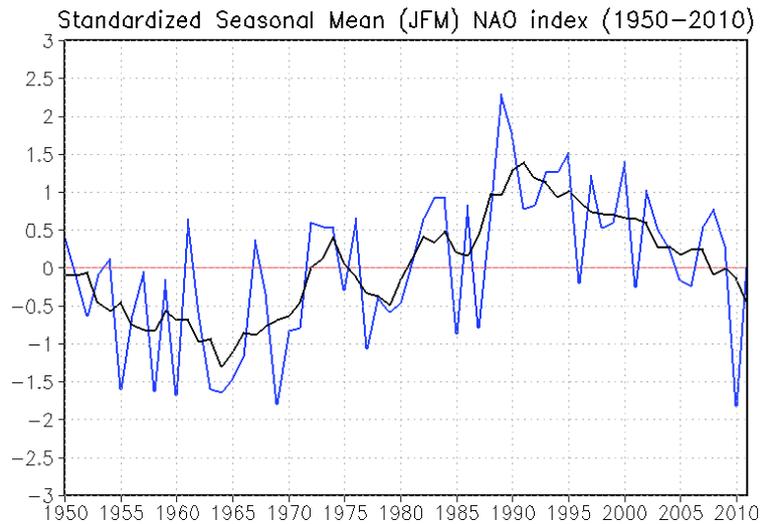
Phytoplankton, main food for zooplankton, often measured and reported as chlorophyll *a* concentration, has generally increased after the early 1990s (Casini *et al.*, 2008).

## 2.2. Abiotic ecosystem development

### 2.2.1. General climate index

The climate mode dominating the Northern hemisphere is the North Atlantic Oscillation (NAO). High NAO values correspond generally to increased strength of westerly winds, increased precipitation and milder temperatures over the Northeast Atlantic, including the Baltic Sea. NAO index was low in 1950-1980s, whereas it has been high afterwards (Figure 4).

**Figure 4: Time-series of NAO winter index**

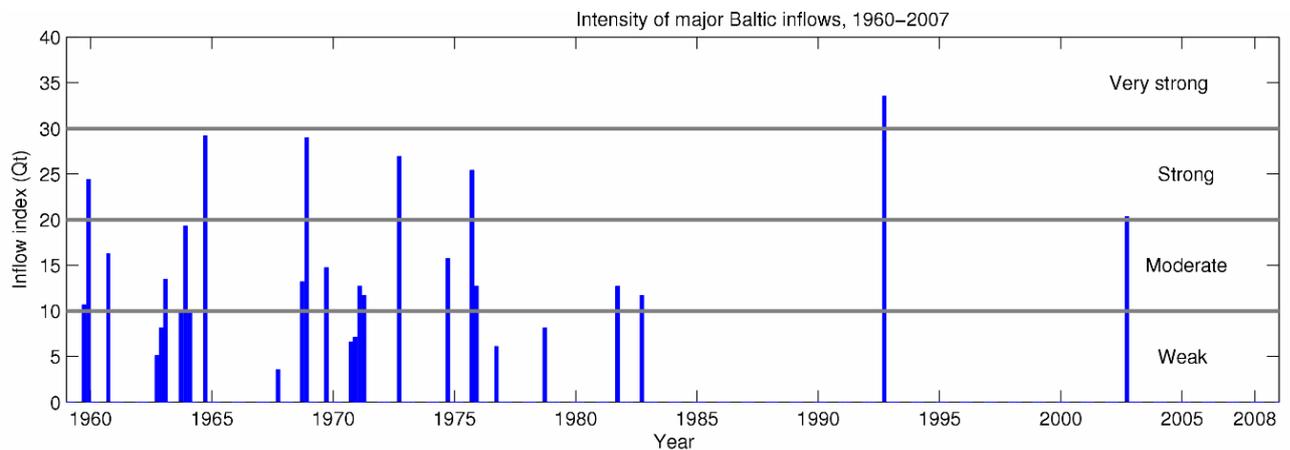


Source: NOAA Climate Prediction Center

**2.2.2. Water inflows from the Kattegat (eastern North Sea)**

The frequency of water inflows from the Kattegat decreased since the 1970s. This has been related to changes in the global climate influencing wind strength and direction, precipitation and river runoff in the Baltic region. Since the mid 1980s a stagnation period has occurred in the Central Baltic with very limited intrusions of salty and oxygen-rich waters from the Kattegat (Figure 5).

**Figure 5: Time-series of water inflows from the Kattegat to the Baltic Sea**



Source: SMHI (2008)

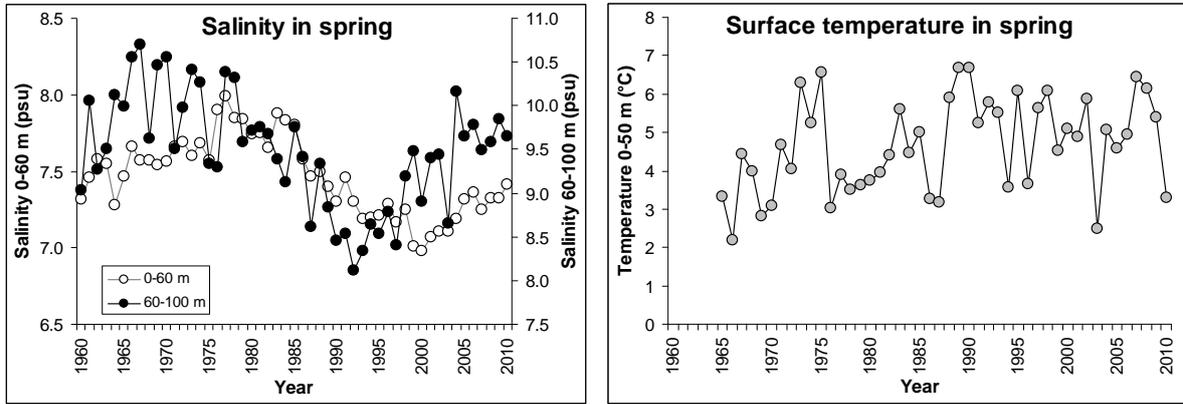
**2.2.3. Salinity and temperature**

During the last 50 years, surface salinity has been high in the late 1970s-early 1980s, but has decreased steadily until the late 1990s, when a slight increase started to occur. Deep salinity was at its highest in the 1960s and 1970s, dropped in the 1980s and showed a strong increase afterwards reaching, in the 2000s, levels almost similar to the 1960s (Figure 6).

Surface salinity is mainly driven by precipitation and runoffs, whereas deep water salinity is principally affected by saltwater inflows from the Kattegat.

The temperature at the upper layer has slightly increased during the past four decades, with several years of consecutive high temperatures in the past 20 years.

**Figure 6: Time-series of surface salinity (above halocline), deep salinity (below halocline), and surface temperature**

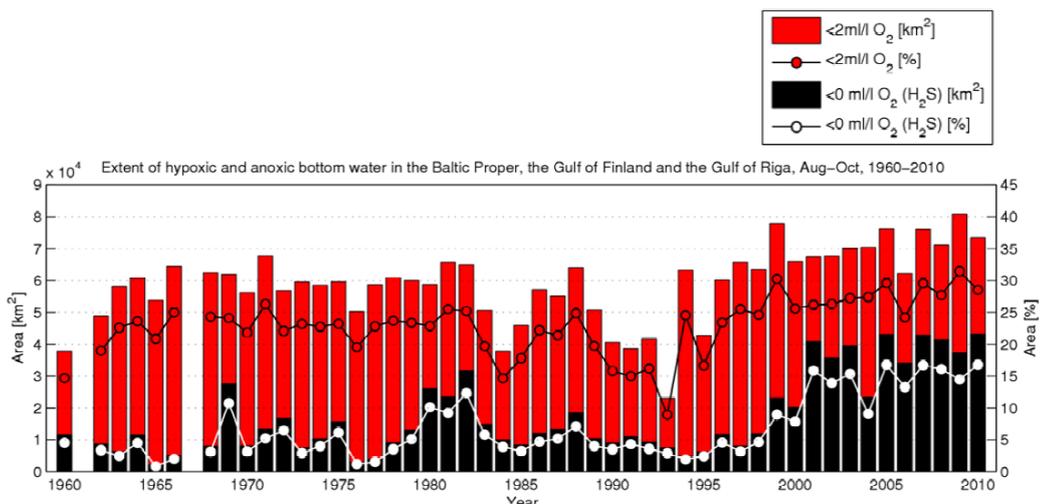


Source: Data from SMHI SHARK database, and Hansson and Omstedt (2008)

### 2.2.4. Oxygen

The extent of the anoxic (oxygen concentration <0 ml/l) and hypoxic (oxygen concentration <2 ml/l) bottoms have varied. However, the anoxic waters extent has markedly increased since the mid 1990s (Figure 7). Low oxygen concentrations are mainly due to scarce water inflows from the Kattegat and high levels of bacterial activity decomposing the organic matters falling on the sea bottom.

**Figure 7: Time-series of anoxic and hypoxic areas (these values include the Gulf of Finland and Gulf of Riga)**



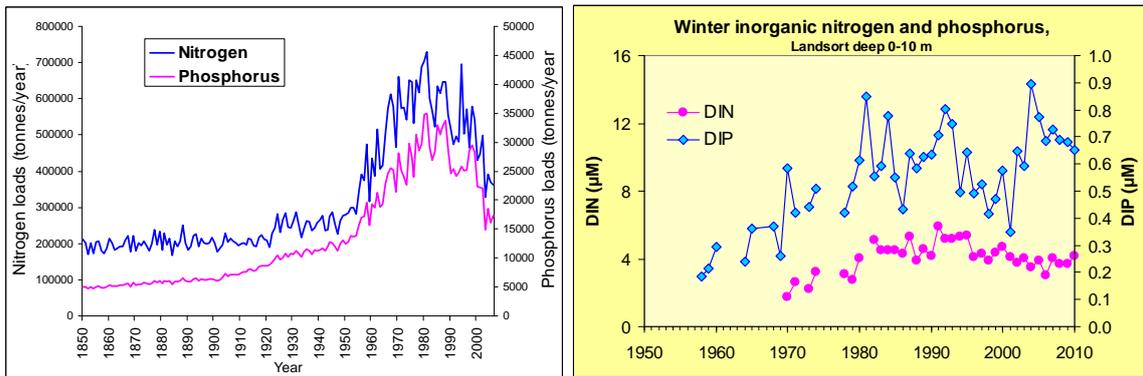
Source: SMHI (2010)

### 2.2.5. Nutrients' loads and concentration

Nutrient loads, after a strong increase during the second half of the 20<sup>th</sup> century, have shown a sign of decrease since the early 1980s, possibly due to the emission regulations put into force (HELCOM, 2007).

Inorganic nutrients (DIN: dissolved inorganic nitrogen; DIP: dissolved inorganic phosphorous), which together constitute the fraction usable by phytoplankton, have increased during the past decades. However, although DIP has continued to increase also in the latest years, DIN seems to have levelled off or even decreased after the mid 1990s (Figure 8).

**Figure 8: Time-series of nutrients' loads and concentrations**



Source: Baltic Nest Institute

Source: Ulf Larsson (Stockholm University)

### 3. MECHANISMS OF ECOSYSTEM SHIFT

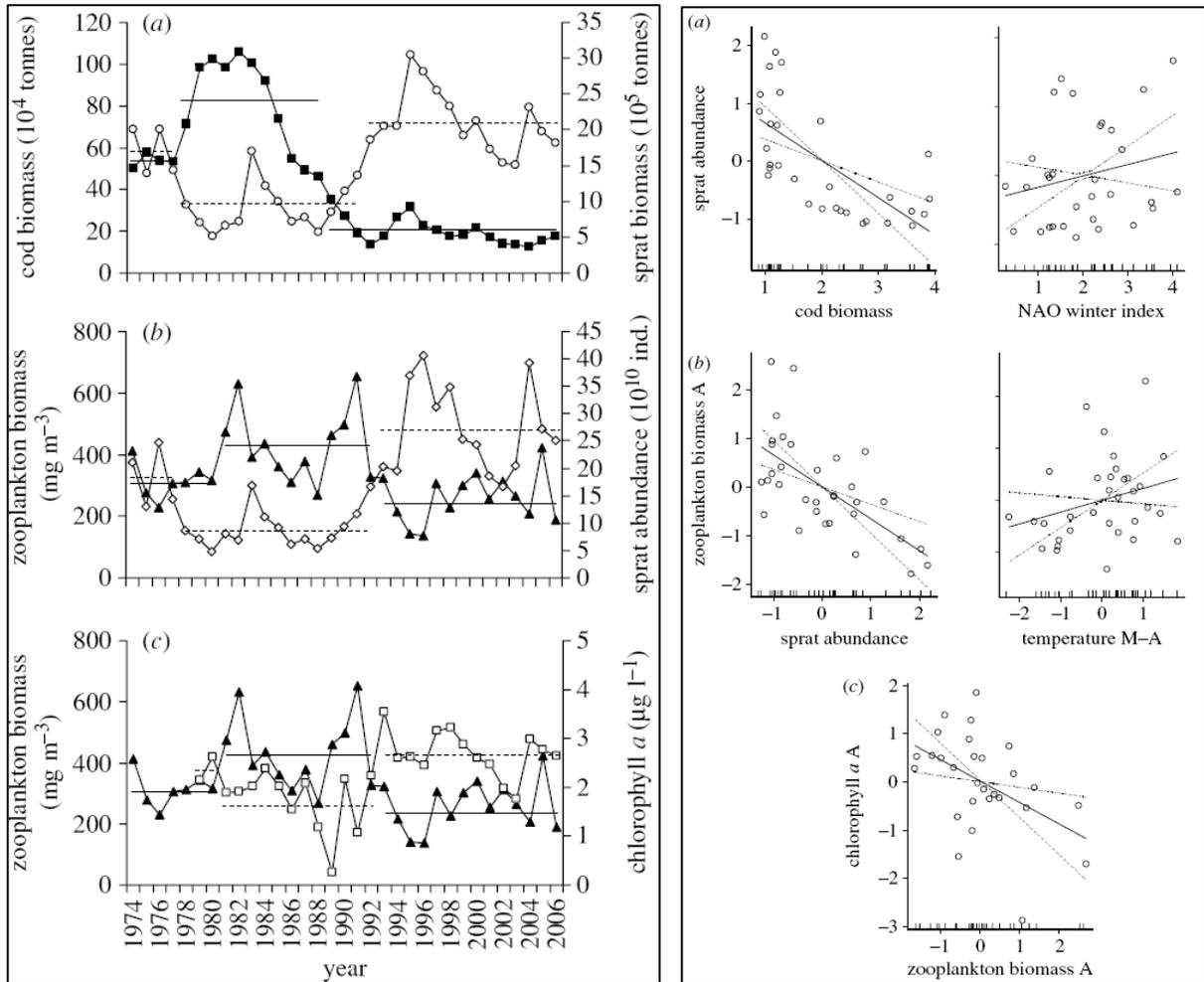
#### KEY FINDINGS

- The **cod** stock collapse is related to **overfishing** and **hydro-climate conditions**, especially decreased salinity and increased extent of hypoxic bottoms. Hypoxic bottoms are partly a result of high nutrient levels causing **eutrophication**. **Historical data** suggest that the relative strength of the main drivers of cod stock may have changed during the past hundred years.
- The **sprat** stock increase is mainly due to **low cod predation**. **Temperature** has also had a positive effect on **egg survival**, and on the development of the main **zooplankton** prey for sprat larvae.
- Herring stock has decreased mainly because **high fishing mortality**, **eutrophication**, **low salinity** and **competition with sprat**.
- **Predation by seals** and **other aquatic mammals** could have an impact on cod, herring and sprat as suggested by modelling studies. However, fishing pressure and hydro-climate conditions seem to be main drivers, at least for cod stock dynamics.
- **Total zooplankton biomass** in summer has **decreased** due to an increased **sprat stock**. Beside the sprat top-down control on zooplankton, the decrease in **salinity** has also negatively contributed to the decline of the main **zooplankton prey for cod larvae** and **herring**.
- **Phytoplankton increase** is related to an increase in **nutrient concentrations** and, in some areas, due to **low zooplankton biomass**.
- **Top-down control (predation)** is very strong, at least down to the zooplankton level. At the phytoplankton level top-down control is intertwined with **bottom-up (nutrient)** and **hydro-climate** effects.
- Cod stock variations in the open Central Baltic have caused multiple **ecosystem changes** also in **coastal areas and adjacent systems** as the Gulf of Riga.

Marine ecosystems are typically considered to be bottom-up driven, i.e. nutrients and physical features drive the primary productivity of the system (phytoplankton), and in turn, the productivity and biomass of the higher trophic levels (zooplankton, fish, aquatic mammals, birds). This is usually manifested as a series of positive relationships between trophic levels. However, when a system is heavily perturbed at the apex of the food web, for example due to hunting or fishing, this perturbation can cascade down the lower trophic levels with a series of top-down regulation driven by predation, a process called trophic cascade. This is usually manifested as a series of negative relationships between adjacent trophic levels. Trophic cascades are potentially particularly strong in systems with a low number of species, like the Baltic Sea, where there are only few key interlinkages between trophic levels (Figure 9).

Hydro-climate and eutrophication pressures affect all the biotic component of the ecosystem, and may therefore either reinforce or weaken the top-down regulation. When hydro-climate and eutrophication pressures act on the top of the food web, their effect may reinforce or even trigger the trophic cascade.

**Figure 9: Illustration of the trophic cascade in the Central Baltic**



Source: Casini *et al.* (2008)

Hereafter the strength of top-down control on the key components of the Central Baltic ecosystem will be analysed versus bottom-up control and hydro-climate pressures. The changes in the Central Baltic ecosystem will be discussed in relation to fishery, climate and eutrophication.

### 3.1. The fish dynamics

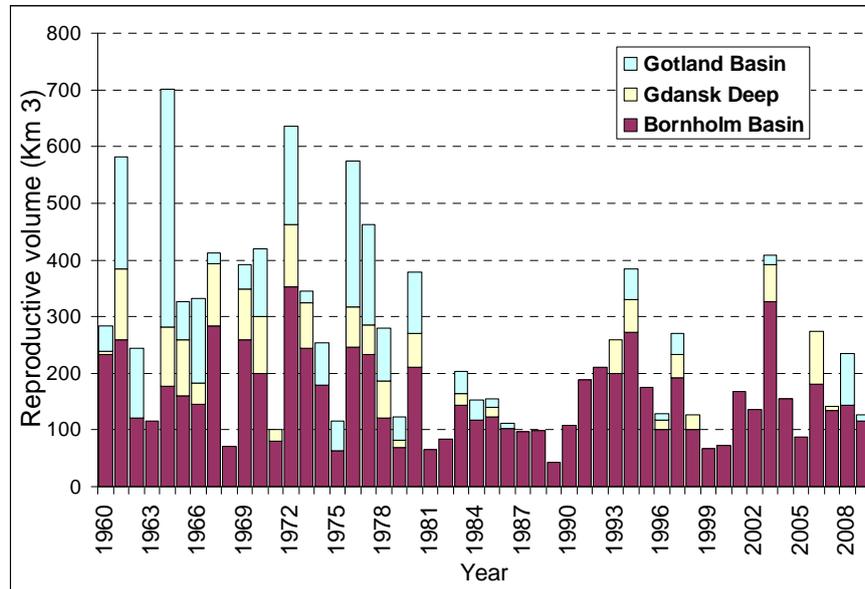
#### 3.1.1. Cod

Cod stock development is directly related to all the external pressures: fishing, hydro-climate and eutrophication.

The cod stock reached the highest level in the early 1980s, corresponding to relatively low fishing mortality and good recruitment conditions (favourable conditions for egg and larval survival) some years earlier. Good conditions for egg survival in the 1970s are indicated by the high cod reproductive volume (water volume in which cod eggs may survive, corresponding to salinity > 11 psu and oxygen > 2 ml/l) (Figure 10). Good conditions for

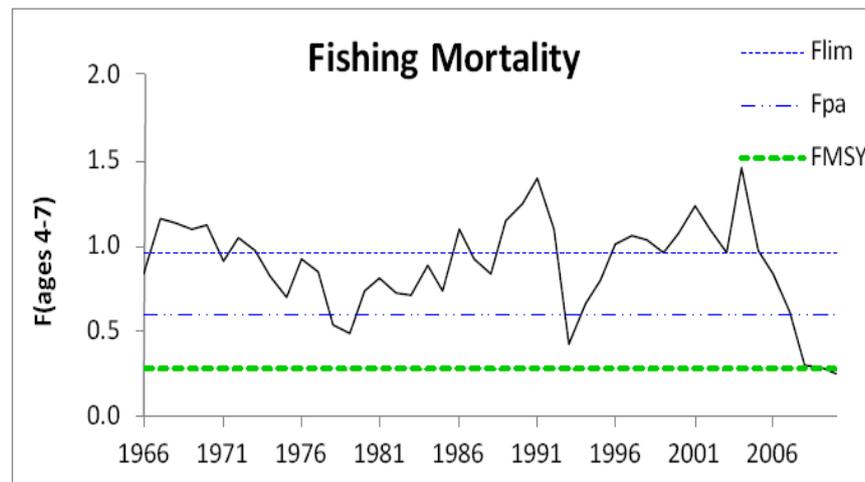
larval survival are indicated by the high abundance of the main prey for cod larvae, the copepod *Pseudocalanus acuspes* (Figure 3).

**Figure 10: Reproductive volume of Baltic cod in the main spawning areas (see Chapter 1 for the time-series of salinity and oxygen conditions)**



Source: Maris Plikshs (Fish Resources Research Department, Latvia)

**Figure 11: Cod fishing mortality.  $F_{pa}$  correspond to the precautionary fishing mortality reference point that should not be exceeded to avoid overexploitation of the stock.  $F_{msy}$  is the fishing mortality that would maximise yield in the long term**



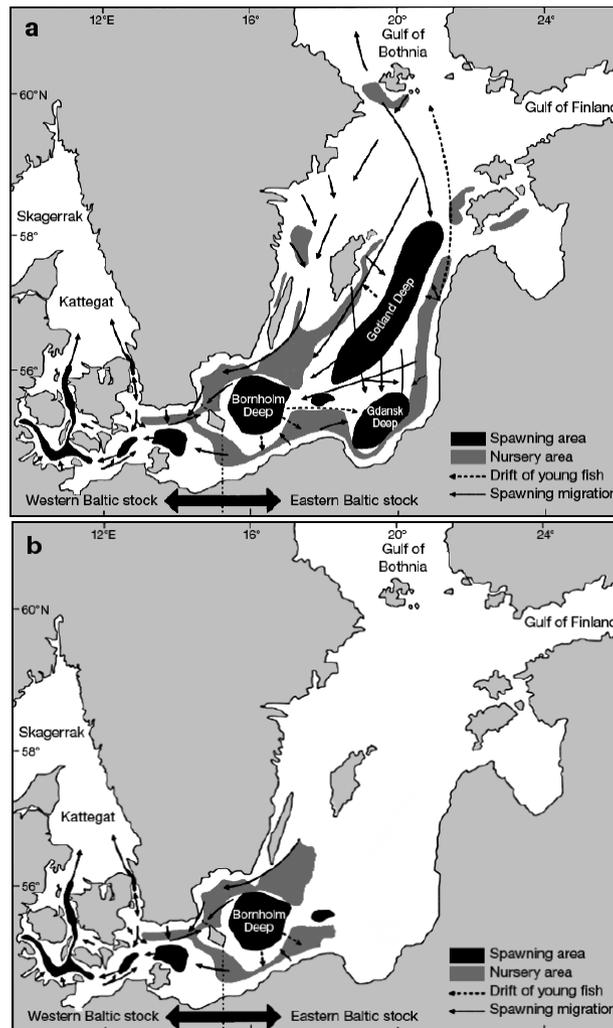
Source: ICES (2011)

After the mid 1980s the cod stock collapsed due to overfishing (fishing mortality above the biological reference limits for several years, Figure 11) and adverse abiotic conditions, as indicated by a strong decrease in cod reproductive volume. The decrease in reproductive volume is attributable to the decrease in salinity and increase in anoxic/hypoxic sea bottoms, the latter being an effect of eutrophication and lack of water inflows from the Kattegat.

Corresponding to the collapse, the cod stock has also progressively reduced its range of distribution, concentrating after mid 1980s in the southern areas of the Central Baltic where it can still find suitable conditions for reproduction (Figure 12).

The cod stock has started to show a sign of recover in recent years, corresponding to a strong decrease in fishing mortality (ICES, 2011; Cardinale and Svedäng, 2011). This further stresses the strong negative impact of fishing on the cod stock.

**Figure 12: Illustration of the spawning areas of Baltic cod in the 1970s-early 1980s (left panel) and 1990s-2000s (right panel)**

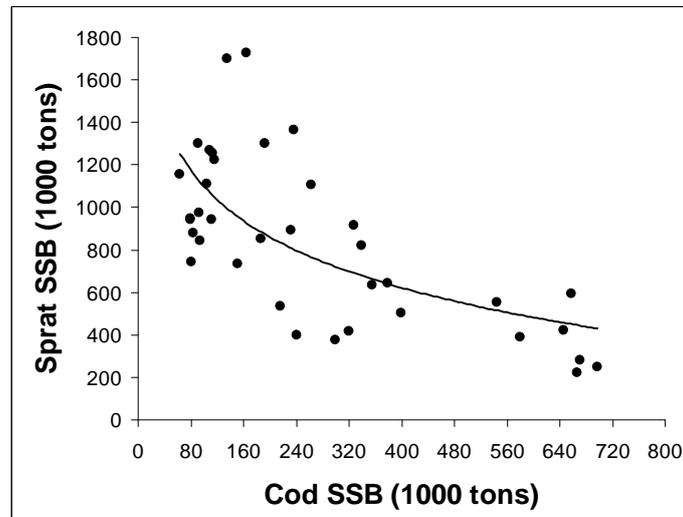


Source: Cardinale and Svedäng (2011)

### 3.1.2. Sprat

The sprat stock increase since the early 1990s is mainly related to the decrease of the cod stock and hydro-climate conditions.

Sprat is the main fish prey for cod and, in general, a high cod stock keeps the sprat stock low by top-down control (ICES, 2011). On the other hand, during periods of low cod biomass, the sprat is released from cod predation and its stock size increases (Casini *et al.*, 2008). During the last three decades, following the collapse of the cod stock, the sprat stock increased fourfold, shifting the Central Baltic from being cod-dominated to being sprat-dominated (Figure 13).

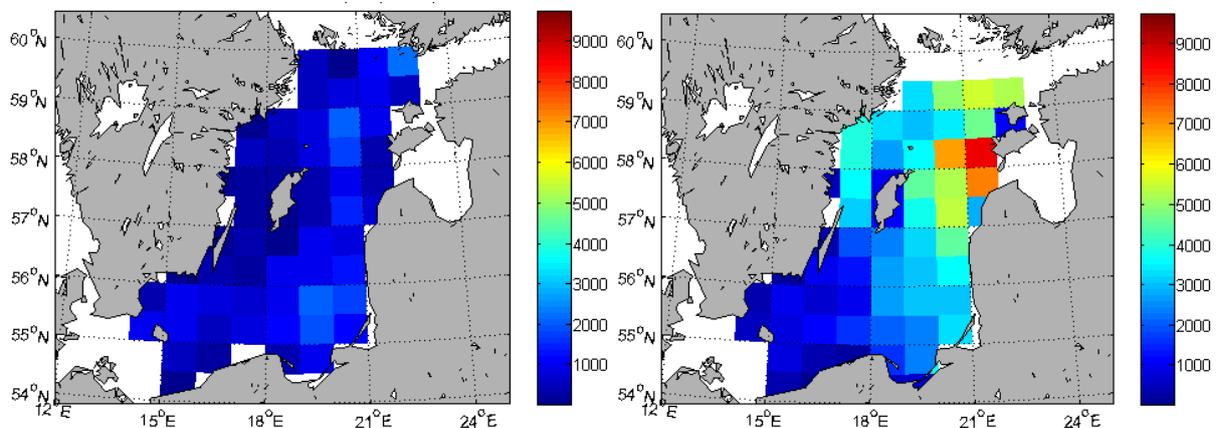
**Figure 13: Relation between cod and sprat stocks**

Source: Data from ICES (2011)

The increase in sprat stock after the early 1990s has also been favoured by high frequency of mild spring temperature (MacKenzie and Köster, 2004) which supports sprat egg production and survival (Nissling, 2004), larval growth (Baumann *et al.* 2008) as well as the development of the main prey for larval sprat, the copepod *Acartia* spp. (Voss *et al.*, 2003; Alheit *et al.*, 2005).

Fishing mortality was low at the moment of the sprat outburst, likely favouring the increase of the sprat stock (ICES, 2011). The increase of the sprat stock has produced a significant decrease in the sprat individual body weight and condition (Casini *et al.*, 2006, 2011; ICES, 2011), although without evident consequences on the stock dynamic.

Corresponding to its outburst, the centre of distribution of the sprat stock has moved towards northern areas (Figure 14) where the cod predation mortality has become negligible after its collapse.

**Figure 14: Distribution of sprat abundance in the 1980s (left panel) and in the period 1990s-2000s (right panel)**

Source: Casini *et al.* (2011)

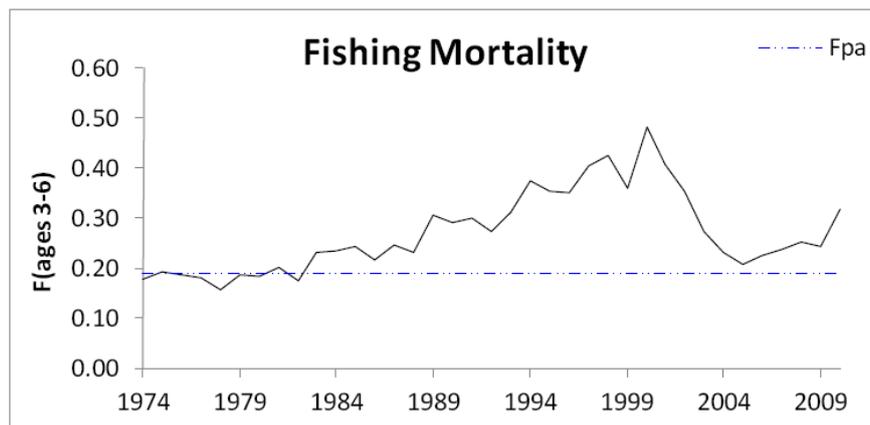
### 3.1.3. Herring

The decrease of the herring stock during the past four decades is due to the synergetic effects of high fishing pressure, eutrophication-related degradation of coastal spawning grounds and competition with sprat.

Fishing pressure has been above the safe biological limits since the early 1980s (ICES, 2011; Figure 15), whereas the eutrophication of the coastal areas has reduced the amount of macro-vegetation that is the preferred spawning substrate for herring (Cederwall and Elmgren, 1990).

The strong decrease in herring SSB is also due to the drop in the mean individual body weight own to increased competition with the increased sprat stock and salinity decrease, both affecting the main zooplankton prey for herring, the *Pseudocalanus acuspes* (Casini *et al.* 2010).

**Figure 15: Herring fishing mortality. Fpa corresponds to the precautionary fishing mortality reference point that should not be exceeded to avoid overexploitation of the stock**



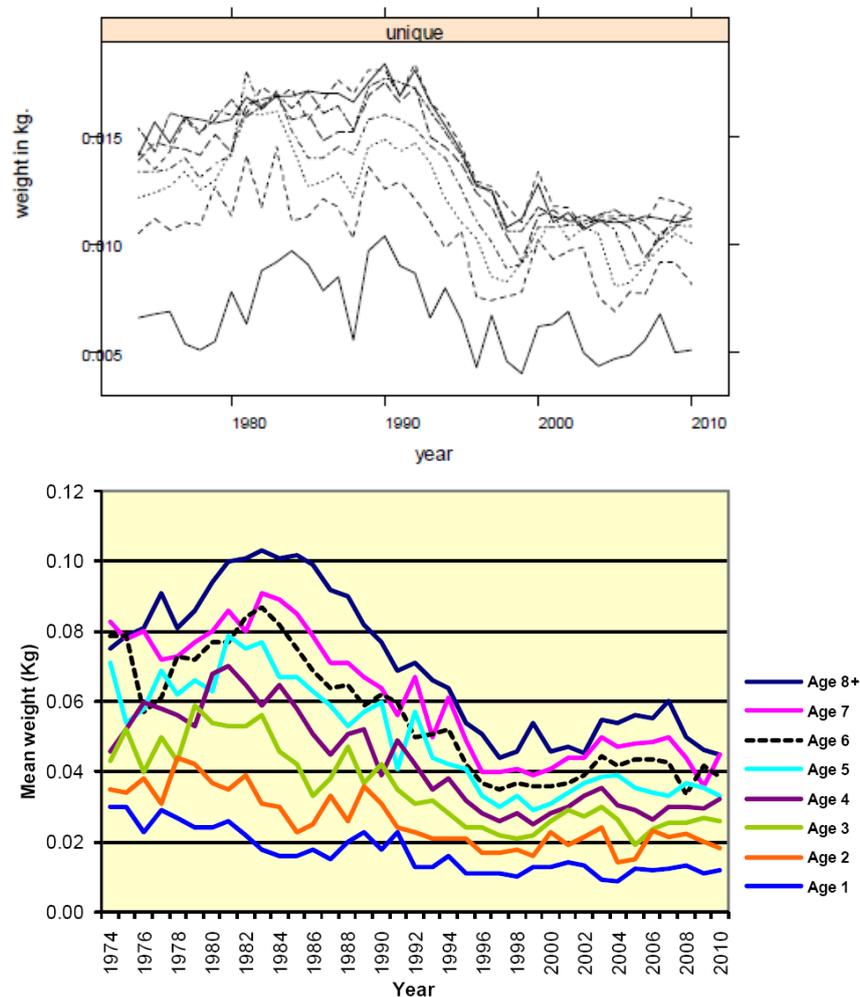
Source: ICES (2011)

### 3.1.4. Sprat and herring growth

Sprat and herring body growth is heavily affected by density-dependent factors. The drastic increase of the sprat population in the early 1990s caused an abrupt decrease in both herring and sprat mean weights (Cardinale and Arrhenius, 2000; Casini *et al.*, 2010) (Figure 16) and condition (Möllmann *et al.*, 2005; Casini *et al.*, 2006, 2011), caused by the strong intra- and inter-specific feeding competition.

The decrease in herring growth, however, could have been initiated by a decrease in salinity and bottom oxygen, affecting respectively one of the main prey items for herring, the copepod *Pseudocalanus* spp. (Casini *et al.*, 2010), and the abundance of zoobenthic prey for larger herring (Flinkman *et al.*, 1998).

**Figure 16: Sprat (upper panel) and herring (lower panel) mean weight at specific ages**



Source: ICES (2011)

### 3.1.5. Indirect effects of trophic cascades on other fish species

Stickleback population has noticeably increased in the northern areas of the Central Baltic (Eriksson *et al.*, 2011) partly due to the decrease of cod and the contraction of its distribution into the southern Baltic areas. The sticklebacks' increase however started some years later than the cod collapse and thus other factors have certainly also been involved.

There are indications that high sprat stock size may induce the M74 syndrome in Baltic salmon (*Salmo salar*). When the sprat stock is high, an unbalanced salmon diet constituted by sprat may induce this reproductive disorder, manifested as mortality of salmon offspring during the yolk-sac fry phase caused by thiamine deficiency in the eggs (Mikkonen *et al.*, 2011).

## 3.2. The plankton dynamics

### 3.2.1. Zooplankton

The zooplankton species composition has changed during the past four decades (see Chapter 1, Figure 3) from being dominated by the *Pseudocalanus acuspes* (with affinity for high deep water salinities) to being dominated by *Acartia* spp. and *Temora longicornis* (with affinity for higher surface temperatures). This shift in species composition has therefore likely been triggered by hydro-climatic changes (Möllmann *et al.*, 2008). However, the decrease in *Pseudocalanus acuspes* has also been caused by sprat predation pressure since this plankton is one of the main preys for sprat (Möllmann *et al.*, 2008; Casini *et al.*, 2010). After the early 1990s deep water salinity increased at high levels, but *Pseudocalanus acuspes* did not, confirming the strong top-down pressure of sprat. The abundance of cladocerans has also diminished likely due to sprat predation pressure (Casini *et al.*, 2008, 2009).

At the community level, i.e. when considering the total zooplankton biomass, top-down regulation seems to be stronger than hydro-climatic pressure (Figure 9), the latter mostly altering zooplankton species composition.

Herring, on the other hand, does not seem to influence the open sea zooplankton (Casini *et al.*, 2008), probably because of the omnivorous nature of the bigger individuals and the coastal distribution of the strictly zooplankton-feeding smaller herring. However, the generally lower stock abundance of herring, if compared to sprat, during the past three decades could also partially explain the lower impact of herring on zooplankton resources in this period.

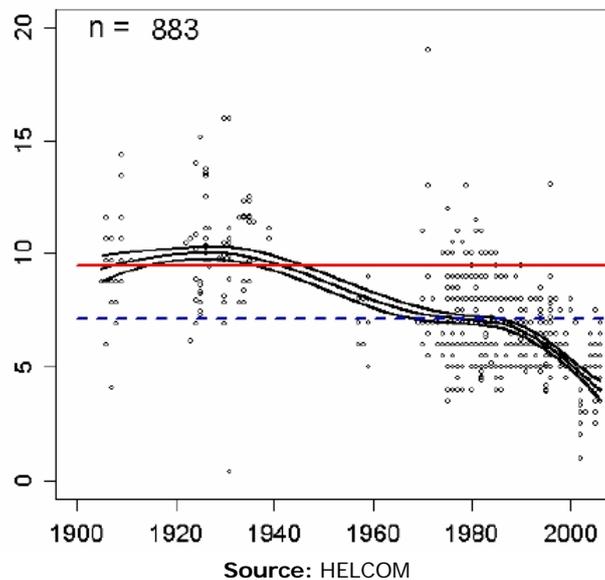
### 3.2.2. Phytoplankton

In the Central Baltic the phytoplankton biomass (as indicated by chlorophyll *a* concentration) has followed sprat population development. It means that high sprat stock, by reducing zooplankton, may reduce also its predation pressure on phytoplankton (Casini *et al.*, 2008). Similar patterns have also been observed in the Gulf of Riga, where an increase in herring stock size has depressed the local zooplankton biomass.

Secchi depth (the depth of the photic zone) is often taken as indicator of phytoplankton biomass, with the rationale that higher phytoplankton concentration would lead to a decrease in water transparency and thus a decrease in the secchi depth. Long-time series of secchi depth show that there has been a decrease in the last century (Figure 17), indicating a positive effect of nutrient loads and concentration. However, without sprat or zooplankton long-time series it is not possible to understand the long-term interplay between top-down and bottom-up control in phytoplankton dynamic.

The fast decline of the secchi depth after the late 1980s (Figure 17) matches temporally with the increase of the sprat stock, and occurs in a period of constant or slightly decreasing nutrient concentration. This could confirm the effect of sprat which, decreasing the summer total zooplankton biomass, allows phytoplankton to proliferate.

**Figure 17: Time-series of summer secchi depth (meters) in the northern area of the Central Baltic (red line: reference condition by HELCOM Eutro Pro; blue dotted line: target value)**



### 3.3. Effects of trophic cascades on adjacent ecosystems

There are indications that the offshore decrease of the cod stock after the mid 1980s may have caused cascading effects on the coastal food web. At high stock sizes, the cod spreads its spatial distribution into the northern and coastal areas of the Baltic Sea. Conversely, at low stock size, the cod reduce its spatial distribution concentrating into the southern open sea areas. The near disappearance of cod from the northern coastal areas seems to have been one of the reasons of the fast increase of the three-spined sticklebacks which, by controlling the mesograzers, has caused an increase of the filamentous algae in coastal areas (Eriksson *et al.*, 2011).

The occurrence of cod seems also to affect the whole ecosystem of the Gulf of Riga. At high stock size, in fact, the cod colonize the Gulf of Riga triggering a trophic cascade that decreases the local herring stock, increases the zooplankton biomass and diminishes the phytoplankton density (Michele Casini, preliminary analyses).

These two examples show that the cod stock, when at high levels, may control also the food web of coastal and semi-isolated ecosystems reducing the local algal biomass.

### 3.4. The historical perspective

Historical reconstructions of Baltic cod stock development have also been performed. These reconstructions show that at the beginning of the 20<sup>th</sup> century the cod population was also relatively low, and that the high population size of the mid 1970s-early 1980s was an extraordinary situation during the last hundred years (Eero *et al.*, 2011).

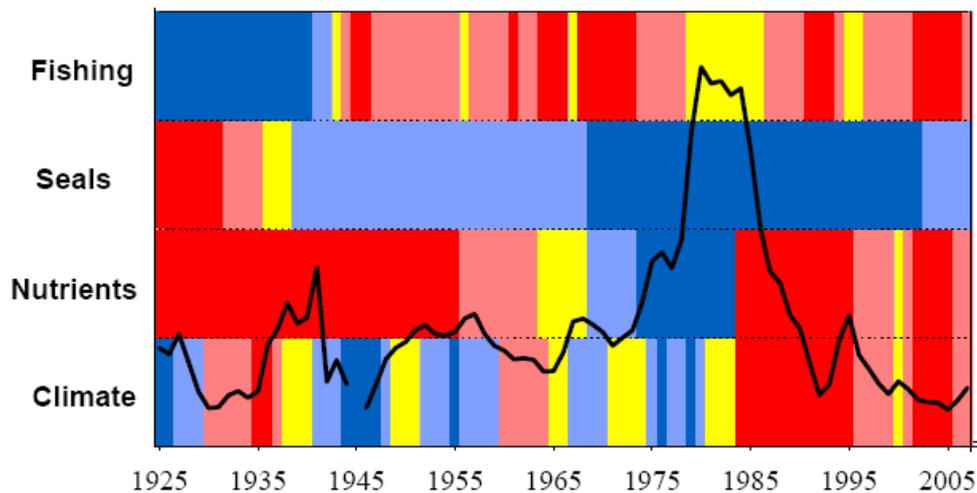
The low population at the beginning of the 20<sup>th</sup> century was likely due to the combined effects of high seal predation and low nutrient concentration. Around the middle of the 20<sup>th</sup> century the start of a more industrialized fishery kept the cod stock low. The drastic increase in cod stock in the late 1970s-early 1980s was due to a temporarily low fishing

mortality, slightly increased nutrient concentration and good hydro-climatic conditions, intertwined with very low seal predation. The collapse of the early 1990s was instead due to a combination of long-lasting high fishing pressure, high nutrient levels and worsened hydro-climate conditions (Figures 18 and 19).

This provides evidence that the dynamics of the cod stock has been driven by different pressures in different time periods. It also confirms that increased nutrient levels may have a positive effect on the system at first (by increasing system general productivity), but when the nutrient levels increase too much (often associated to anthropogenic emissions) this has negative effects on the system by producing anoxic areas.

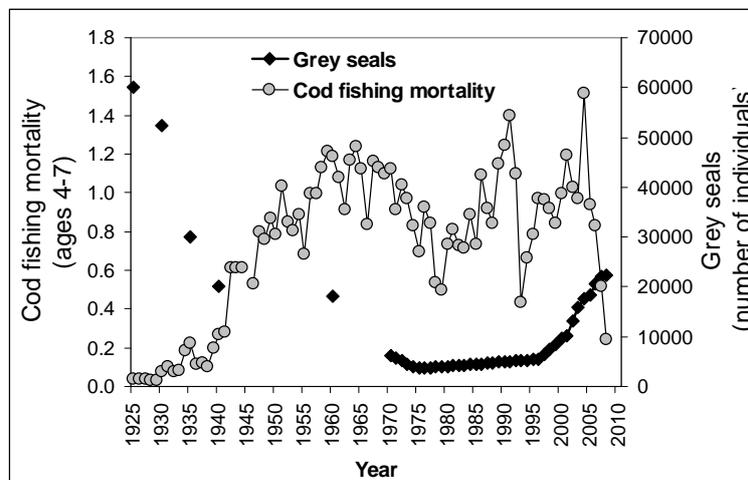
Historical reconstructions of the Baltic sprat and herring stocks are currently lacking.

**Figure 17: Changes in hydro-climate conditions, nutrient concentration, seal abundance and fishing mortality compared to cod SSB development. The colours represent beneficial (blue), neutral (yellow) and detrimental (red) conditions for cod**



Source: Eero *et al.* (2011)

**Figure 19: Changes in cod fishing mortality and grey seals' abundance over hundred years**

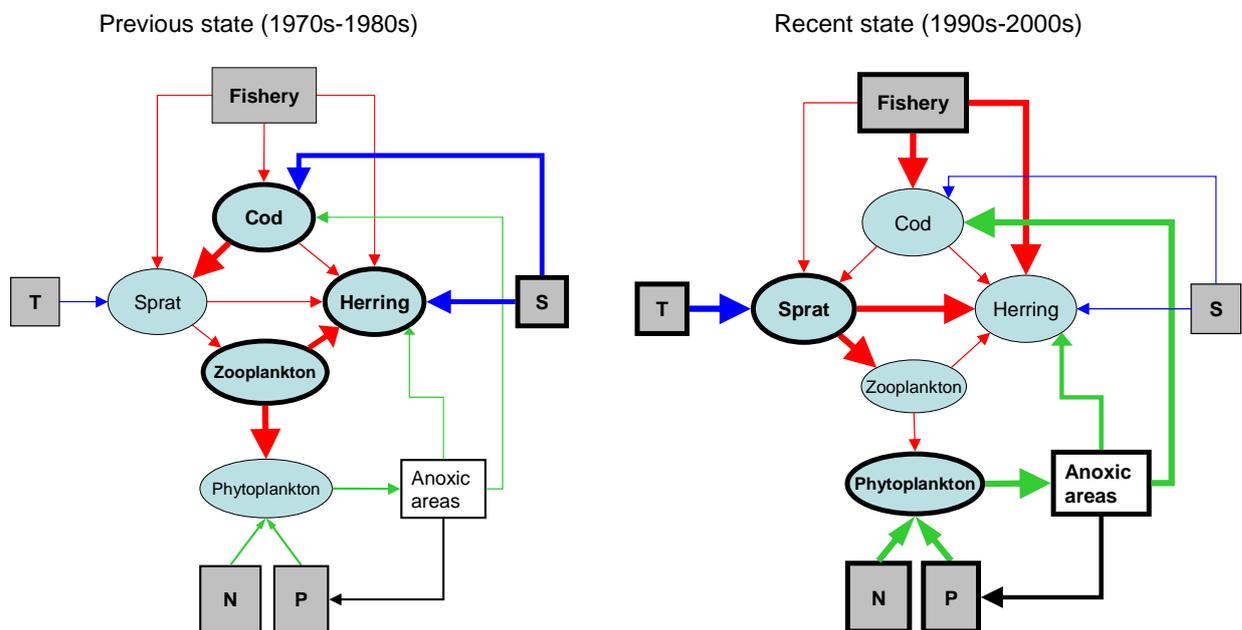


Source: Data from MacKenzie *et al.* (2011)

### 3.5. Conceptual models of the ecosystem shift

The conceptual simplified representation of the ecosystem shift, along with the strength of the pressures and controls is illustrated in Figure 20. This represents the shift observed in the early 1990s, and does not take therefore account of the changes occurred previously, such as the drastic decrease of seals. The nutrients' emissions were very high already in the previous state (before the early 1990s), but the nutrients' concentration in the water was significantly lower then in the recent state.

**Figure 20: Simplified conceptual model of the structure and functioning of the Central Baltic ecosystem. Bold arrows indicate the strength of the control, leading to the current state of different ecosystem components (also in bold). Thin arrows indicate the processes that are currently weak. Red=top-down; Green=bottom-up; Blue=hydro-climate. (N=nitrogen and P=phosphorus; T=temperature and S=salinity)**



Source: Author



## 4. SHIFTS IN ECOSYSTEM FUNCTIONING

### KEY FINDINGS

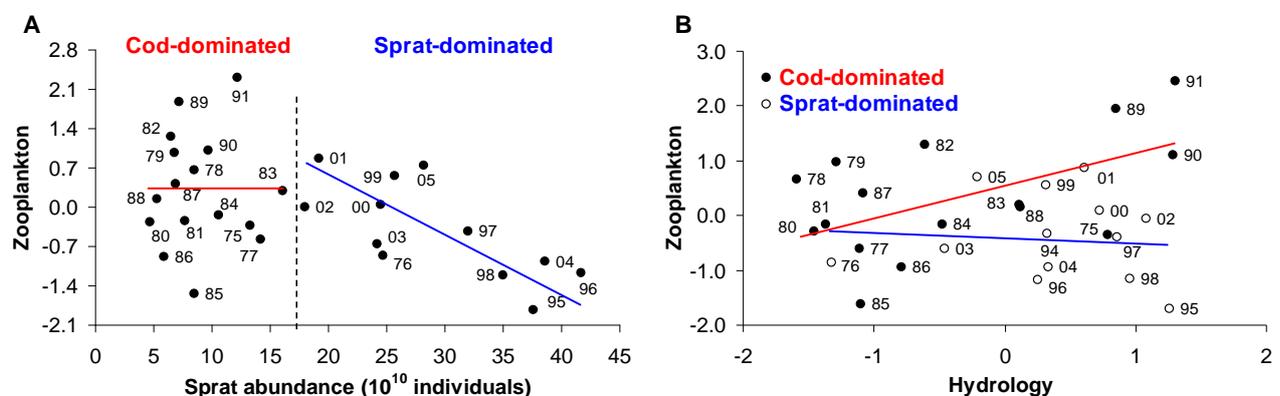
- The way the ecosystem functions has changed at the beginning of the 1990s. **Zooplankton** and **herring body growth**, which were mainly controlled by hydro-climate conditions, became controlled by **top-down mechanisms** and **competition with the sprat stock**.
- This change is related to the **increase of the sprat population** which has decoupled zooplankton from hydro-climate conditions.
- This emphasizes the crucial importance of the **predator cod** in maintaining **ecosystem function and resilience**.

### 4.1. Threshold in the regulation of zooplankton and fish growth

Apart from the general concurrent effects of bottom-up, hydro-climate, and top-down regulation, it has been shown that the relative strength of these different regulatory mechanisms of ecosystem functioning can vary in the Central Baltic (Casini *et al.*, 2009, 2010).

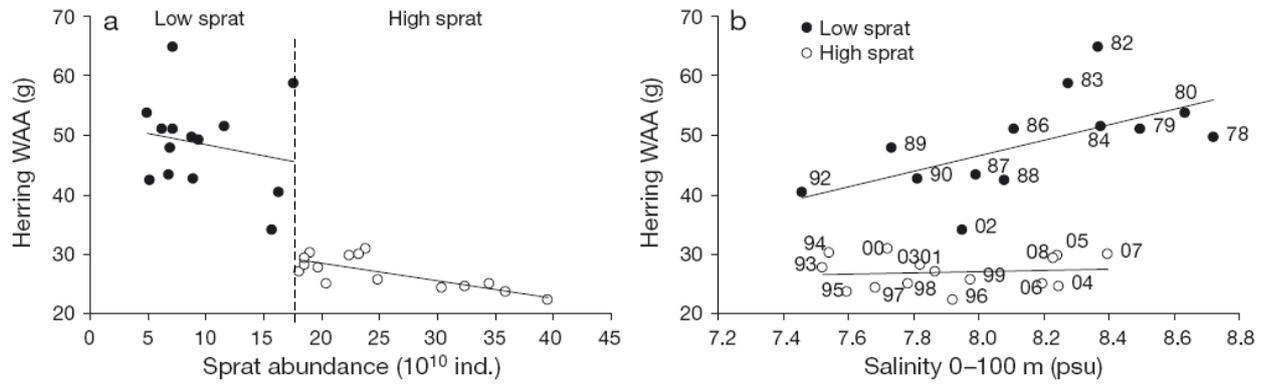
When the cod stock is high, keeping low the sprat stock, zooplankton and herring growth are regulated by hydro-climate conditions (e.g. salinity). On the other hand, when the cod stock is low, the resulting high sprat stock decouples zooplankton and fish growth from the hydro-climate circumstances. In this case, the sprat stock becomes the main regulator of zooplankton and herring growth through top-down control, reinforcing the general strength of the trophic cascade (Figures 21 and 22). This emphasizes the importance of large predatory fish, as cod, in the maintenance of ecosystem functioning and resilience.

**Figure 21: Changes in ecosystem functioning, illustrated as the shift in the main regulatory process of zooplankton**



Source: Modified from Casini *et al.* (2009)

**Figure 22: Changes in ecosystem functioning, illustrated as the shift in the main regulatory process of herring mean body weight.**



**Source:** Modified from Casini *et al.* (2010)

## 5. REVERSIBILITY OF THE ECOSYSTEM SHIFT

### KEY FINDINGS

- The **cod stock may recover** quite quickly at relatively high levels if the **fishing mortality is kept at low levels** (as set by the EU management plan).
- Feedback loops between sprat and cod may theoretically slow down the full cod recovery. However, at the moment the **strength** of these **'vicious circles'** are **not enough understood**.
- The conditions of **oxygen deficiency** tend to **maintain the eutrophicated state** of the Baltic releasing phosphorus from the sediments, and creating another **'vicious circles'** at the lower trophic levels. This is also **detrimental for the cod stock recovery**.
- **Eutrophication** (human-induced high and frequent phytoplankton blooms) will decline if the **nutrient inputs** are **reduced**. A recover of the **cod stock**, and the subsequent decrease of the sprat stock, may further **weaken the eutrophication symptoms**.
- The reversal of the ecosystem state is possible in the **short- and medium-term (2-15 years)** provided that **cod fishing mortality is kept low** and **nutrient inputs** continue to be **reduced**. This would also weaken the strength of the feedback loops.
- However, **ecosystem reversal** is **hampered** if the **climate change** prognoses, anticipating further increase in temperature and decrease in salinity, are correct. In this case, in the **long-term**, full lasting ecosystem recovery might be not possible.
- **Reversing back the ecosystem state** has the potential **risk** to open a niche for **jellyfish outbreaks**.
- The **effects on aquatic birds**, with a decrease in their main food (sprat) could be **negative**.
- The envisaged **decrease in nitrogen** could favour the proliferation of **cyanobacteria**, if phosphorous is not reduced at the same time.

The reversibility of the ecosystem shift depends on the potential occurrence of biological and/or chemical feedback loops. These feedback loops are processes that tend to maintain the ecosystems in a determined state even though the external pressures (fishery, nutrient inputs, hydro-climate) that originally triggered the shift return to the original state. In this case we speak of "vicious circles" that will obstacle ecosystem recovery.

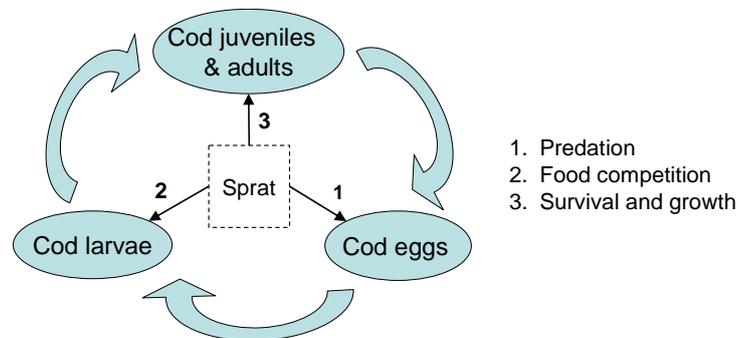
### 5.1. Feedback loops in the sprat/cod interaction

High cod stock is very effective in controlling sprat stock via predation pressure. In turn, a high sprat stock could potentially influence cod recruitment via predation on cod eggs (Köster and Möllmann, 2000) and competition with cod larvae for zooplankton resources,

especially the copepod *Pseudocalanus acuspes* (Möllmann *et al.*, 2008; Casini *et al.*, 2009). This “vicious cycle”, strengthened when the sprat abundance is high, may possibly contribute to cod recruitment failure even in periods of favorable hydro-climatic conditions for cod recruitment (Casini *et al.*, 2009). Therefore, a high sprat stock may decouple cod recruitment from abiotic forcing and tend to maintain the food-web in a new stable state (Möllmann *et al.*, 2008; Casini *et al.*, 2009). Moreover at high sprat stock sizes the size composition of the sprat stock changes, providing insufficient food of the most suitable size for juvenile cod to grow and reproduce (Van Leeuwen *et al.*, 2008). All these prey-to-predator feedback loops could partially explain the lack of cod recovery after the early 1990s (Figure 23).

However, beside these ecological feedback loops, it must be kept in mind that cod recruitment is also strongly affected by the parental stock size and age-structure, heavily shaped by fishing (Cardinale and Arrhenius, 2000b).

**Figure 23: Schematic representation of the potential feedback loops between cod and sprat**



Source: Casini *et al.* (2011b)

## 5.2. Feedback loops in the nutrients/oxygen relation

High nutrient concentrations (phosphorus and nitrogen), by enhancing primary production, enhance also the bacterial oxygen consumption in the deep waters, since bacteria consume oxygen to decompose the organic matter that falls on the sea bottom. In turn, oxygen deficiency causes a release of the accumulated phosphorus from the sediments, bringing it back into the system. This “vicious circle” tends to maintain high nutrient concentrations in the water even when the nutrient inputs from land and atmosphere decrease, stabilizing the eutrophicated state (Österblom *et al.*, 2007). This is what is happening in the Baltic, where despite a reduction of the nutrient inputs (Chapter 1, Figure 8), the nutrient concentration in the water (specifically phosphorus) has not declined. This process tends to keep high the primary production and enhance phytoplankton blooms (especially the phosphorus-limited cyanobacteria), in turn worsening the deepwater oxygen conditions and reducing the extension of cod spawning grounds (Hansson and Rudstam, 1990).

### 5.3. Can the ecosystem shift reverse?

#### 5.3.1. *Short and medium-term perspective*

In the latest few years the cod stock has shown signs of a relatively quick recover. This occurred in correspondence of a robust decrease in fishing mortality, made possible by 1) the EU cod management plan (EC, 2007) setting a target fishing mortality at 0.3 intertwined with 2) a severe reduction in Polish fishing quotas, accompanied by improved control and enforcement schemes, after years of misreporting and black landings (EC, 2008). This demonstrates that keeping fishing pressure low enough, the cod stock increases, potentially stabilizing at relatively high levels.

A lasting recovery of cod to the very high levels of the early 1980s is however likely unfeasible if the currently adverse hydro-climate conditions (low water inflows from the Kattegat) and eutrophication symptoms (large areas of oxygen-depleted bottoms) will not improve. In this case, the northern spawning grounds would be hardly usable by cod, limiting its reproductive success and its further increase in stock size.

At low and moderate population sizes, cod tend to concentrate in the southern Baltic and therefore its impact on sprat, currently inhabiting mainly the northern Baltic areas, could be minor. Therefore, a strong lasting reverse of the trophic cascade (decrease in sprat with all the following direct and indirect effects) would be difficult to take place if all the pressures (fishery, hydro-climate and eutrophication symptoms) will not act in the same direction promoting the cod stock. To trigger a reversal of the trophic cascade, the cod must be able to reduce the sprat stock below the abundance threshold capable to control zooplankton.

In the short and medium terms, the reversal of the trophic cascade can be more or less strong depending on the cod stock size and the consequent degree of spatial overlap with the sprat stock. If the cod stock continues to increase, its predation pressure will be able to erode the sprat stock step by step in more northern areas, in this way progressively weakening the potential prey-to predator feedback loops mechanisms.

This would also reduce the frequency and intensity of phytoplankton blooms and partly weaken the nutrients/oxygen feedback loop. The effects of a robust cod stock increase on lower trophic levels could be quite fast (few years). However, in order for the top-down control of phytoplankton to be really effective, the decrease in nutrients' emission should continue (HELCOM, 2007). The main target should be especially the reduction in phosphorus (Håkansson *et al.*, 2010), since 1) phosphorus is released from anoxic sediment and 2) phosphorus is the limiting nutrient for the toxic cyanobacteria.

#### 5.3.2. *Long-term perspective*

Climate change prognoses indicate that the Baltic Sea will experience a decrease in salinity and increase in temperature in the next hundred years (HELCOM, 2007b). This would imply even harder environmental conditions for cod whose persistence in the Baltic could be hampered if eutrophication symptoms will not be radically reduced. To allow the persistence of cod in this potentially harsh future environment, fishing mortality would also likely need to be further reduced from the current value of 0.3. On the other hand, these conditions could be favorable for sprat (low predation pressure and increased recruitment)

potentially worsening the water quality. In general however, a decrease in salinity would have large consequences on all the Baltic organisms, not only on cod, and the general effect at the ecosystem level is hard to predict.

The effect of further increase in seals, and potentially other mammals, on the fish community is also hard to predict, especially due to the multiple ecological interactions within the fish community. However, in the scenario of climate change (decrease in salinity and increase in temperature), the predation pressure of seals on cod would be an additional pressure hampering the cod stock. The investigations so far performed trying to estimate the predation effect of seals on fish have not provided congruent results. Therefore, to reliably foresee the effect of increased mammal predation on the fish community is currently not possible.

#### **5.4. Risk of ecosystem reversal**

A reduction in the sprat stock, especially if accompanied by an increase of water temperature, could potentially open a niche for the proliferation of jellyfish which could feed on both sprat and cod eggs and compete with cod larvae and sprat for planktonic food (Haslob *et al.*, 2007).

A reduction of the sprat stock could be disadvantageous for certain seabird species which are specialised sprat-feeders (Hjernquist and Hjernquist, 2009).

The decrease in nitrogen, especially when coupled with increased water temperature, could favour the blooms of the nitrogen-fixing cyanobacteria (including toxic species) which instead are limited by phosphorus concentration (Håkansson *et al.*, 2010). Therefore a decrease in phosphorus must also be implemented at the same time.

## 6. CONCLUSIONS AND RECOMMENDATIONS

### KEY FINDINGS

#### Actions for ecosystem recovery

- **Fishing pressure on cod** should be **kept low** (at least as low as set by the EU management plan).
- **Fishing pressure on herring** should be **reduced**.
- **Cod fishing pressure** should be **adaptive** to the **hydro-climate conditions** to keep the cod stock size high. For example, an expected future decrease in salinity should be tackled with a further decrease in cod fishing mortality.
- **Anthropogenic nutrient inputs**, both **nitrogen and phosphorus**, should be **reduced**.
- **Biomanipulation** has been proved successful in lakes. However in the Baltic the effectiveness of an **artificial reduction of the sprat stock** (by increasing sprat fishing mortality) needs **further investigations**.

#### Expected effects

- In the **current hydro-climate conditions**, the **cod stock may recover** quite quickly at relatively high levels if the fishing mortality is kept low.
- **Recovery of the cod stock** and **decrease in nutrient emissions** would contribute to decrease the intensity and frequency of **algal blooms** and **to diminish the extent of oxygen-deficient areas**.
- **Improved oxygen conditions** will enhance the **demersal macrofauna**, food for cod and herring, and increase the size of suitable **spawning areas for cod and herring**.
- A **low sprat stock** would **improve the growth rate of sprat and herring**.
- A **low sprat stock** would further **enhance the herring stock** and **reduce the salmon M74 syndrome**.
- **Recovery of the cod stock**, when coupled with an **expansion of its distribution**, would also **enhance coastal macroalgae**, which are **crucial habitat** for the reproduction of several coastal species, and **decrease phytoplankton density in adjacent areas** as the Gulf of Riga.

#### Potential external hindlers

- **Hydro-climate changes** may **aid or counteract** the management actions.
- The effective **reduction of Baltic nutrients** level may require longer periods of oxygen-rich **deepwater inflows** from the Kattegat.
- Future **climate change long-term projections** anticipate a decrease in salinity and increase in temperature and precipitations, which may **hinder the ecosystem recovery** in the long run.

#### Potential risks

- The **potential risks** of ecosystem reversal are: **jellyfish proliferation, decline of some seabird species**, and increase of summer **cyanobacterial blooms**.

The Central Baltic ecosystem shift that occurred around the early 1990s has been caused by the combined direct and indirect effects of overfishing, eutrophication and hydro-climate changes.

The fishery has affected:

- Cod negatively, triggering the trophic cascade which resulted in sprat increase, total zooplankton decline and contributing to the increase of the phytoplankton blooms' intensity and frequency. The trophic cascade propagated also to coastal areas and adjacent ecosystems as the Gulf of Riga.
- Herring negatively, both directly through increased mortality and indirectly through increased competition with sprat.

Eutrophication has affected:

- Cod negatively, by reducing its spawning grounds.
- Phytoplankton positively, by increasing the strength and frequency of their blooms.
- Herring negatively, by reducing the coastal habitat suitable for spawning.

Hydro-climate changes have affected:

- Sprat positively, with increased temperature.
- Cod and herring negatively, with decreased water inflows from the Kattegat and increased precipitation, both acting to reduce the oxygen levels and salinity.

The human restraint of the first two anthropogenic pressures (fisheries and eutrophication) will most likely help reversing back the state of the Central Baltic.

The cod fishing pressure should be kept low (EC, 2007), in this way reversing the cod-mediated trophic cascade with favorable effects for herring and increased zooplankton predation pressure on phytoplankton.

On the other hand, very little can be done about general climate changes, driving water inflows, precipitations, salinity and temperature (apart from dampening the temperature increase induced by greenhouse gases). Therefore, the target cod fishing mortality should be also set considering the hydro-climate conditions, which means that it should be adaptive (Lindegren *et al.*, 2009). If the prognoses of decreased future salinity are correct, then a fishing mortality of 0.3 could be too high for cod and should be decreased further. In this case the Baltic cod could also run the risk to lose its currently high commercial importance.

A shift back to a real oligotrophic state is a more complicated matter. Given that more nutrients are now in circulation, repeated deep water inflows that give longer periods of deep water oxygenation are needed together with a reduction of nutrient emissions. However, the policy of nutrient inputs' reduction should be continued (HELCOM, 2007), directly dampening phytoplankton blooms and enhancing cod reproductive possibilities. A decline of phosphorous, along with nitrogen, is necessary to avoid the risk of cyanobacterial proliferation.

The risks associated with a sprat decrease (proliferation of jellyfish and decrease of some seabird species) should be first evaluated.

An alternative way to try increasing more rapidly the cod stock could be through the artificial thinning of the sprat stock, which could weaken the potential prey-to predator feedback loops (Casini *et al.*, 2009). This kind of biomanipulation has been sometimes proved efficient in lakes, but before considering its application in the Baltic further studies on the strength and nature of these feedback loops must be done.





DIRECTORATE GENERAL FOR INTERNAL POLICIES  
POLICY DEPARTMENT B: STRUCTURAL AND COHESION POLICIES

FISHERIES

# ECOSYSTEM SHIFTS IN THE BLACK SEA

## NOTE

### **Abstract**

This note reviews the evidence of ecosystem shifts, explains the underlying mechanisms, and elaborates on the adaptive management approaches to sustain resilient ecosystems and fisheries in the Black Sea. Ecosystem shifts cascading down the food web were registered during the 1970s and 1990s. Overfishing and stock collapses are recognised as triggering factors associated synergistically with climate, eutrophication, and alien invasion. A successful management strategy would build on robust knowledge base, ability to learn and adapt to uncertainty and change, and cooperation of flexible institutions in multi-level governance systems.

This document was requested by the European Parliament's Committee on Fisheries.

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## LIST OF ABBREVIATIONS

- ALPI** Aleutian Low Pressure Index
- ATC** Alternating Trophic Controls
- DG MARE** Directorate-General for Maritime Affairs and Fisheries of the European Commission
- EAF** Ecosystem Approach to Fisheries
- EAWR** East Atlantic West Russia index
- EU** European Union
- GFCM** General Fisheries Commission for the Mediterranean
- NAO** North Atlantic Oscillation
- NGO** Non-Governmental Organisation
- PDO** Pacific Decadal Oscillation
- SSB** Spawning Stock Biomass
- SST** Sea Surface Temperature
- STECF** Scientific, Technical and Economic Committee for Fisheries



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## EXECUTIVE SUMMARY

### Background

Once described by Aristotle as healthy and dominated by various marine predators, the Black Sea ecosystem had experienced, by the late 20th century, anthropogenic impacts such as heavy fishing, cultural eutrophication and invasions by alien species. Severe fisheries collapses, harmful algal and jellyfish blooms, benthic communities loss, and extensive upper shelf hypoxia have had dramatic consequences for the natural ecosystems and socio-economic systems depending on them. Initially most changes were attributed solely to cultural eutrophication. Recent research has demonstrated that several fundamental factors including climate forcing, trophic interactions and anthropogenic influences (overfishing, eutrophication, and invasive introductions) acting synergistically have contributed to the major changes.

The Black Sea is a deep, semi-enclosed basin in eastern Europe. The surrounding land area supports intensive human activities and has experienced profound economical and societal changes in the formerly communist countries. The Black Sea drainage basin is five times more extensive than the sea area, which makes it very sensitive to distant anthropogenic activities. Climate affects the Black Sea via atmospheric transfer and river inflow. The latter has been demonstrated as a significant factor for the overall water balance and basin-scale circulation, as well as nutrient loading from human activities in surrounding land. The physical environment of the Black Sea has a major influence across the food web at different time scales and has been shown to be influenced by the Atlantic climate through cross-Europe atmospheric teleconnections.

The food web in the Black Sea is relatively simple and effects of both resource (bottom-up) and predation (top-down) have been identified. Major effects of predators at top and middle trophic levels have been found to drive system-wide trophic cascades in the Black Sea. The overfishing of pelagic top predators in the 1970s, of planktivorous fish in the 1990s and the unintentional introduction with ships' ballast water of the comb jelly (ctenophore) *Mnemiopsis leidyi* resulted in cascading changes in zoo- and phytoplankton and disturbed the structure and functioning of the entire pelagic food web.

### Aim

Simultaneous alterations in abundance of fish and other marine populations, such as trophic cascades and regime shifts, are related to the degree of structural and functional reorganization of ecosystems. These highly non-linear phenomena are driven through feedback processes and are often triggered by external perturbations such as climate or fishing.

The aim of this note is to provide a comprehensive review of evidence, data, and analyses of ecosystem shifts in the Black Sea. It explores influences of overfishing and trophic cascades as primary triggers of such shifts, develops explanatory models based on the food web theory, and discusses other possible causes for the changes, such as climate, eutrophication and invasive introductions. The note describes the consequences of ecosystem shifts on the marine environment and on the Black Sea fisheries, and comments on the potential reversibility of ecosystems shifts. It elaborates on the possible ways of managing of regime shifts and developing of an adaptive governance system, which would enable to sustain resilient ecosystems and fisheries.

## Key findings

Ecosystem regime shifts cascading down from top-predators to primary producers and affecting water quality were registered during the 1970s and 1990s. The first shift followed the depletion of top predators from the 1950-1970, after which the ecosystem stabilized at low abundance of top predators, high abundance of planktivores, low zooplankton biomass and high phytoplankton biomasses during the 1970s and 1980s. The second shift was associated with the collapse of planktivorous fish and outburst of the invasive *M. leidy*, which resulted in a second system-wide trophic cascade, with similar alternating effects on zoo- and phytoplankton, and on water chemistry.

Fishing is a structuring factor affecting not only fish stocks, but the whole ecosystem and can be responsible for the system shift to unhealthy states. Overfishing and stock collapses of pelagic predators before 1970 and of planktivorous fish in 1990s, are recognised to trigger cascading ecosystem shifts. The changes at the top of the food web were related to a major rearrangement of the whole ecosystem, with feedbacks between different components shifting the marine environment from a state characterized by variable fish fauna and clear water to a turbid one with frequent blooms of algae and jellyfish, bottom hypoxia and localized production of hydrogen sulphide.

Regional and global climate change, eutrophication, and invasive species are also synergistically involved in ecosystem shifts. They are related to other external (fishing) and internal (trophic interactions) factors in complex multi-causal way, where all factors interact through non-linear feedbacks contributing to development of alternate regimes and the shifts between them. The outburst of the invasive *M. leidy* and its consequences for fish stocks illustrate how both food web interactions and external factors, in this case anthropogenic introduction, may affect ecosystem structure and functioning, and drive an ecosystem shift.

An important question from a theoretical, practical, and management perspective is whether regime shifts are reversible. The analyses of the shifts in the Black Sea prove that complex marine ecosystems undergoing structural alternations are unlikely to recover to their exact previous states, but will rather adapt to the immediate local conditions. Some components, however, mainly in the base of the food web (phytoplankton biomass, oxygen content), have been subject to partial recoveries, and the overall state on the marine environment in the recent decades have improved due to the reduction of the nutrient load, partial control over *M. leidy*, and positive climatic changes. Stocks and catches of small planktivorous fish recovered to intermediate levels, but large valuable species like turbot, bonito and bluefish are still very scarce comparing to historical abundances. Partial recovery, therefore, is not a stable objective, and further changes (e.g. an unfavourable climate or alien species) may drive the system into the next catastrophic loop. Regime shifts and factors behind them are known to exhaust systems' resilience and, the aim of management must be to restore the ecosystem to a balanced state with the potential to provide sustainable use of its essential goods and services. Recovery of a resilient ecosystem should mean restoring all important components (including top-predators) into the new desirable state: reducing the anthropogenic impact, normalizing species interactions, buffering trophic cascades, increasing biodiversity and improving environmental quality. Such a state of the ecosystem would provide strategic benefits, such as a clean marine environment, abundant and diverse fish stocks and sustainable economic activities (e.g. fishing, tourism), to a range of stakeholders and society as a whole.

Current management practices based on conventional science are often insufficient to deal with complex issues such as ecosystem regime shifts, and recovery and management procedures fail when essential explanatory models are missing. A better strategy would be to extend the scope of possible hypotheses by challenging the existing paradigms and adding new knowledge, concepts and models in order to resolve the complex phenomena being observed. Management of complex adaptive systems would benefit from the combination of different knowledge systems, such as interdisciplinary research, social-economic analyses, and practitioners' experience including traditional knowledge. Successful management must continuously test, learn, and modify its activities and understanding for coping with change and uncertainty in complex systems. The ongoing fusion between ecology, fisheries science and socio-economics would lead to further development of management that is proactive and adaptive.

An adaptive governance framework relies on the collaboration of a diverse set of stakeholders operating at different social and ecological scales. The sharing of management power and responsibility can involve multiple institutional linkages among user groups or communities, from local to international levels. In the specific example of the environmental and fisheries management in the Black Sea area, the involved institutions must cooperate at national level (e.g. governmental and private institutes and agencies, NGOs), regional level (e.g. Black Sea Commission, prospective Fisheries Commission), and broader international scale (e.g. EU STECF, DG MARE, EU Parliament, GFCM).

Even if resolving ecosystem complexity and implementing a successful ecosystem management system may seem a much more difficult task than traditional single-species management, the state of aquatic living resources and habitats is of such importance that this challenge must be taken up by the involved stakeholders and the society.



## 1. INTRODUCTION

Once described by Aristotle (in the 4th century BC, 2001) as healthy and dominated by various marine predators, the Black Sea ecosystem had experienced, by the late 20th century, anthropogenic impacts such as heavy fishing, cultural eutrophication and invasions by alien species. Severe fisheries collapses, harmful algal and jellyfish blooms, benthic communities loss, and extensive upper shelf hypoxia have had dramatic consequences for the natural ecosystems and socio-economic systems depending on them (Zaitsev, 1993, Mee *et al.*, 2005, Daskalov *et al.*, 2008). Initially most changes were attributed solely to cultural eutrophication (Zaitsev, 1993; Bologna *et al.*, 1995). Recent research (Daskalov *et al.*, 2007, Oguz and Gilbert, 2007, Llope *et al.*, 2010, Oguz and Velikova, 2010) has demonstrated that several fundamental factors including climate forcing, trophic interactions and anthropogenic influences (overfishing, eutrophication, and invasive introductions) acting synergistically have contributed to the major changes.

The Black Sea is a deep, semi-enclosed, basin in eastern Europe. It is linked to the Mediterranean by the narrow straits of Bosphorus and Dardanelles (Map 1). The surrounding land area supports intensive human activities and has experienced profound economical and societal changes in the formerly communist countries. That the Black Sea has undergone dramatic environmental changes in recent decades underlies its importance as a 'natural laboratory' for studying marine ecosystem dynamics (Daskalov *et al.*, 2007, Oguz and Gilbert, 2007, Mee *et al.*, 2005)

**Map 1: Location of the Black Sea**



Source: Author

The Black Sea is the world's largest meromictic basin consisting of two water layers separated by a permanent pycnocline (Sorokin, 2002). This density boundary effectively limits the vertical exchange between the oxygenated upper layer – influenced by the atmospheric and fluvial processes – and the almost completely isolated anoxic deep water. Despite its more than 2,000 m depth, most of the biological activity (apart from bacteria) is hosted within the upper 100–150 m.

The Black Sea is characterized by a positive water balance that results in a net outflow into the Mediterranean. With a drainage basin five times more extensive than the sea area (Ludwig *et al.*, 2009) it works as a virtually isolated ecosystem, and is sensitive to distant anthropogenic activities. Climate affects the Black Sea via atmospheric transfer and river

inflow. The latter has been demonstrated as a significant factor for the overall water balance and basin-scale circulation (Oguz *et al.*, 1995), as well as nutrient loading from human activities in surrounding land. The Danube River provides about 70% of the freshwater inflow. Thirty-three and 56% of the phosphorus emissions are estimated to be derived from agriculture and urban settlements, respectively; only 8% is considered to be of natural origin (Kroiss *et al.*, 2005). The physical environment of the Black Sea has a major influence across the food web at different time scales (Daskalov, 2003) and has been shown to be influenced by the Atlantic climate through cross-Europe atmospheric teleconnections (Polonsky *et al.*, 1997; Oguz *et al.*, 2006).

The food web in the Black Sea is relatively simple and effects of both resource (bottom-up) and predation (top-down) have been identified. Major effects of predators at top and middle trophic levels have been found to drive system-wide trophic cascades in the Black Sea (Daskalov *et al.*, 2007). The overfishing of pelagic top predators in the 1970s, of planktivorous fish in the 1990s and the unintentional introduction with ships' ballast water of the comb jelly (ctenophore) *Mnemiopsis leidyi* resulted in cascading changes in zoo- and phytoplankton and disturbed the structure and functioning of the entire pelagic food web (Daskalov *et al.*, 2007; Oguz and Gilbert, 2007).

Simultaneous alterations in abundance of fish and other marine populations, such as trophic cascades and regime shifts, are related to the degree of structural and functional reorganization of ecosystems. These highly non-linear phenomena are driven through feedback processes and are often triggered by external perturbations such as climate or fishing.

The aim of this note is to provide a comprehensive review of evidence, data, and analyses of ecosystem shifts in the Black Sea. It explores influences of overfishing and trophic cascades as primary triggers of such shifts, develops explanatory models based on the food web theory, and discusses other possible causes for the changes, such as climate, eutrophication and invasive introductions. The note describes the consequences of ecosystem shifts on the marine environment and on the Black Sea fisheries, and comments on the potential reversibility of ecosystems shifts. It elaborates on the possible ways of managing regime shifts and of developing an adaptive governance system, which would enable to sustain resilient ecosystems and fisheries.

The situation in the Black Sea is particularly worrisome given the weaknesses of current controls on fisheries harvests and the failure of countries around the shores of the Black Sea to adopt an effective international fisheries management system. Understanding the mechanisms of ecosystem shifts is essential for successful resource and environmental management, and the amelioration and recovery of deteriorated fish stocks and ecosystems.

## 2. THE NOTIONS OF ECOSYSTEM SHIFTS AND TROPHIC CASCADES

### KEY FINDINGS

- Complex marine ecosystems are believed to exist in internally consistent dynamic states, which have been termed stable states and dynamic regimes
- Ecosystem shifts are radical changes between alternate states; the established regimes persist long enough; they encompass multiple biological components on large (at least regional) spatial scale
- Some shifts are triggered by disproportionately small changes in the conditions until a critical threshold is passed, then the system requires substantially stronger driving force to recover at the initial state
- Trophic cascades exert strong, indirect, top-down effects on two or more trophic levels perturbing ecological structure and function
- The most obvious trophic cascades in large marine ecosystems result from elimination of whole functional groups of top predators.

### 2.1. Ecosystem regime shifts

Complex marine ecosystems are believed to exist in internally consistent dynamic states, which have been termed stable states and dynamic regimes (Mayer and Rietkerk, 2004). Switches between persistent alternative regimes are called regime shifts (Scheffer and Carpenter, 2003), and they can be driven by both external forcing (climate change, alien invasions, eutrophication, overfishing) and by internal perturbations of the ecosystem's structure and function, e.g. species replacements, trophic cascades, distributional alterations (Mayer and Rietkerk, 2004; Bakun, 2005). The notion of regime shifts in marine science has been initially evoked by the observed alternation of major sardine and anchovy populations (Schwartzlose *et al.*, 1999). Two issues have been discussed by the researchers: synchrony of alternative regime related to global climate patterns and switches in domination between sardine and anchovy (replacement) and their causes. Bakun (2005) formulated the ecosystem regime shift in the sea to confine with three criteria: 1. the shift must be radical i.e. a large change between alternate states; 2. the established regime must persist long enough; 3. the shift encompasses multiple biological components on large (at least regional) spatial scale. Some shifts are triggered by seemingly small changes in the drivers until a critical threshold is passed, after which the system requires a substantially stronger forcing to recover to its initial state, an effect referred to as hysteresis (Scheffer and Carpenter, 2003).

Some ocean shifts are exclusively explained by climate. Such are the ocean wide transitions in the North Pacific (Hare and Mantua, 2000; Alheit and Niquen, 2004; Grebmeier *et al.* 2006, Overland *et al.* 2008). These shifts were detected synchronously on a multitude of biotic and abiotic indices such as various climate indices of temperature, atmospheric pressure e.g. Pacific Decadal Oscillation (PDO), Aleutian Low Pressure Index (ALPI), invertebrates, fish, marine mammals and birds (Hare and Mantua, 2000; Lees *et al.*, 2006; Grebmeier *et al.*, 2006). North Pacific shifts are related to global climate

changes in the North Pacific such as reflected by the PDO and thus ecosystem changes are considered to be externally (climate) driven (Hare and Mantua, 2000; Grebmeier *et al.*, 2006; Overland *et al.*, 2008).

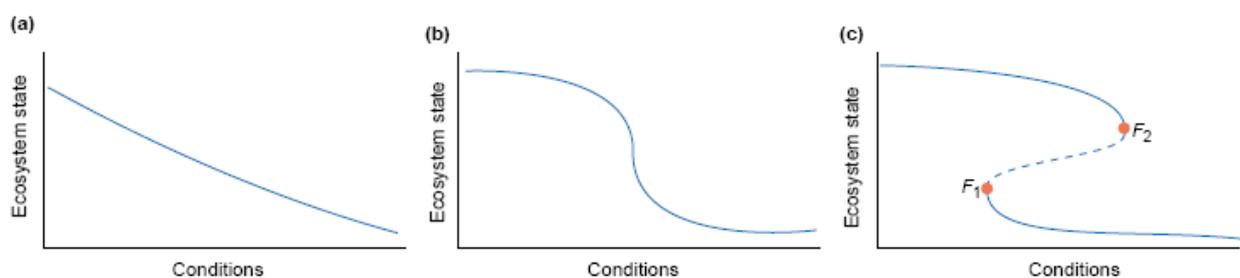
Many of the reported regime shifts are observed to happen over the same periods in remote marine areas, suggesting a global-scale synchrony that can be explained by teleconnections between global atmospheric patterns such as the North Atlantic Oscillation (NAO, Alheit *et al.*, 2005; Alheit and Bakun, 2010), and the Pacific Decadal Oscillation (PDO, Alheit and Bakun, 2010). Synchrony in regime shifts has been observed in many European marine ecosystems such as the North Sea, the Baltic, the Mediterranean and the Black Sea (Alheit *et al.*, 2005, Oguz and Gilbert, 2007, Casini *et al.*, 2008; Molinero *et al.*, 2008; Möllmann *et al.*, 2009; Llope *et al.*, 2010).

### Box 1: Characteristics of ecosystem regime shifts

#### Ecosystem regime shifts are:

1. Abrupt and radical: the system state responds with a change which is disproportionately large relative to the change in conditions. The change in the ecosystem state on the y-axis is much bigger than the change in conditions on the x-axis in the area of the sudden or discontinuous shifts (embedded Figure b and c).
2. Long lasting: the established regime must persist long enough - much longer than the shift period
3. Encompass multiple ecosystem components, populations, trophic levels and environmental conditions
4. Extend over large spatial scale - the boundaries of the given ecosystem (e.g. lake, continental shelf, sea)
5. Involve non-linearity, thresholds (tipping points) and hysteresis. Typical regime shifts are triggered by disproportionately small changes in the conditions until a critical threshold is passed, then the system requires substantially stronger driving force to recover at the initial state, a process referred to as hysteresis (embedded Figure c).

#### Smooth (a), abrupt (b) and discontinuous (c) shifts



Source: Scheffer and Carpenter (2003)

Ecosystem regime shifts could be triggered by external factors like climate or fishing (Lees *et al.*, 2006) but the mechanisms of change are explained mainly by internal transformations of various ecosystem components and processes (e.g. Carpenter, 2003). Ecosystem shifts between alternate states have been described in many terrestrial and aquatic systems (e.g. reviews in Mayer and Rietkerk, 2004; Terborgh and Estes, 2010). In marine areas ecosystem shifts are documented in a variety of systems including intertidal areas (Paine, 2010), coral reefs (e.g. Hughes *et al.*, 2003), shelf seas open ocean and

semi-enclosed seas (Daskalov, 2002; Frank *et al.*, 2005; Möllmann *et al.*, 2009; Essington, 2010)

## 2.2. Trophic cascades

A common mechanism involved in ecosystem shifts is the trophic cascade which can exert strong, indirect, top-down effects on two or more trophic levels perturbing ecological structure and function (Box 1; Pace *et al.*, 1999; Terborgh and Estes, 2010). In the marine environment, trophic cascades are more pronounced in coastal and benthic systems (Estes and Duggins, 1995; Pinnegar *et al.*, 2000), but are believed to be less common in the open ocean (Micheli, 1999; Cury *et al.*, 2003). Recently, more cases of system-wide trophic cascades have been reported in large marine ecosystems (Essington, 2010). Predation and fishing have both been shown to be potentially important in driving trophic cascades (Parsons, 1992; Daskalov *et al.*, 2007; Essington, 2010) but parasites and pathogens can also be strong drivers in some occasions (Menge, 1995, Pinnegar *et al.*, 2000).

In diverse and resilient systems, species may alternate in abundance without causing major alterations in ecosystem structure or function (e.g. species composition and diversity, diet and energy transfer; Cury and Shannon, 2004). However, most large marine ecosystems have already been subject to exploitation and other human-driven disturbances for a long time (Jackson *et al.*, 2001), and their virgin diversity, structure and trophic hierarchy have been substantially altered. Many top predators and large marine mammals have fared particularly poorly under intensive fishing. In such situations, prey fish and invertebrate species are released from predatory control and increase in numbers, resulting in fisheries targeting and then eliminating them in turn. Often, the end result is that the dominant position at the top of the food web is occupied by non-edible gelatinous species such as jellyfish, as recently seen in the Black Sea and Caspian Sea, the northern Benguela and other exploited systems (Richardson *et al.*, 2009).

Predation by fish is considered to be a substantial factor in marine food webs (Bax, 1998), but processes strongly regulated by the physical environment, such as recruitment could in fact be more important in determining differences in fish abundance (Cury *et al.*, 2005). Much of the predation by fish is of a generalist nature, such that there is great overlap in diet between species, and hence scope for one species to replace another in ecological terms. Many fish are prey to a range of predators and, under such circumstances, extensive reductions across predator species must take place before increases in prey densities are likely (Polunin and Jennings, 1998). At the same time, if several species can fulfil similar predatory roles, then the magnitude of predation on certain species or functional groups is expected to be greater per preyed-upon individual than when only one or two specialist predator species are involved, assuming recruitment and other controls on the predator populations are similar. Such a situation indicates that top-down controls by generalist predators exist, but that they have more chance to influence prey populations when several functionally similar predators increase or decrease substantially in abundance (Pinnegar *et al.*, 2000). Indeed, the most obvious trophic cascades in large marine ecosystems have resulted from elimination of whole functional groups of top predators (Daskalov, 2002; Frank *et al.*, 2005; Myers *et al.*, 2007).

**Box 2: Definitions, terms and examples associated with trophic cascades (after Pace *et al.* 1999)**

- Trophic cascades result in inverse patterns in abundance or biomass across more than one trophic link in a food web. For a three-level food chain, abundant top predators result in lower abundances of midlevel consumers and higher abundance of basal producers. In this case, removing a top predator would result in a greater abundance of consumers and fewer producers.
- The trophic cascade concept arose from the observations and experiments of field ecologists who observed the powerful organizing force that alternative predatory regimes could instill in the marine intertidal zone and in lakes.
- Particular terms are often used in association with trophic cascade. For example, 'top-down' control means regulation of lower food web components by an upper-level predator. The contrasting term 'bottom-up control' describes regulation of food web components by either primary producers or the input of limiting nutrients to an ecosystem.
- Although trophic cascades might be transitory, trophic interactions can also be strong and might stabilize systems in an 'alternate state'. Thus, trophic cascades can induce dramatic shifts in both the appearance and properties of ecosystems.

### 3. ECOSYSTEM SHIFTS AND TROPHIC CASCADES IN THE BLACK SEA

#### KEY FINDINGS

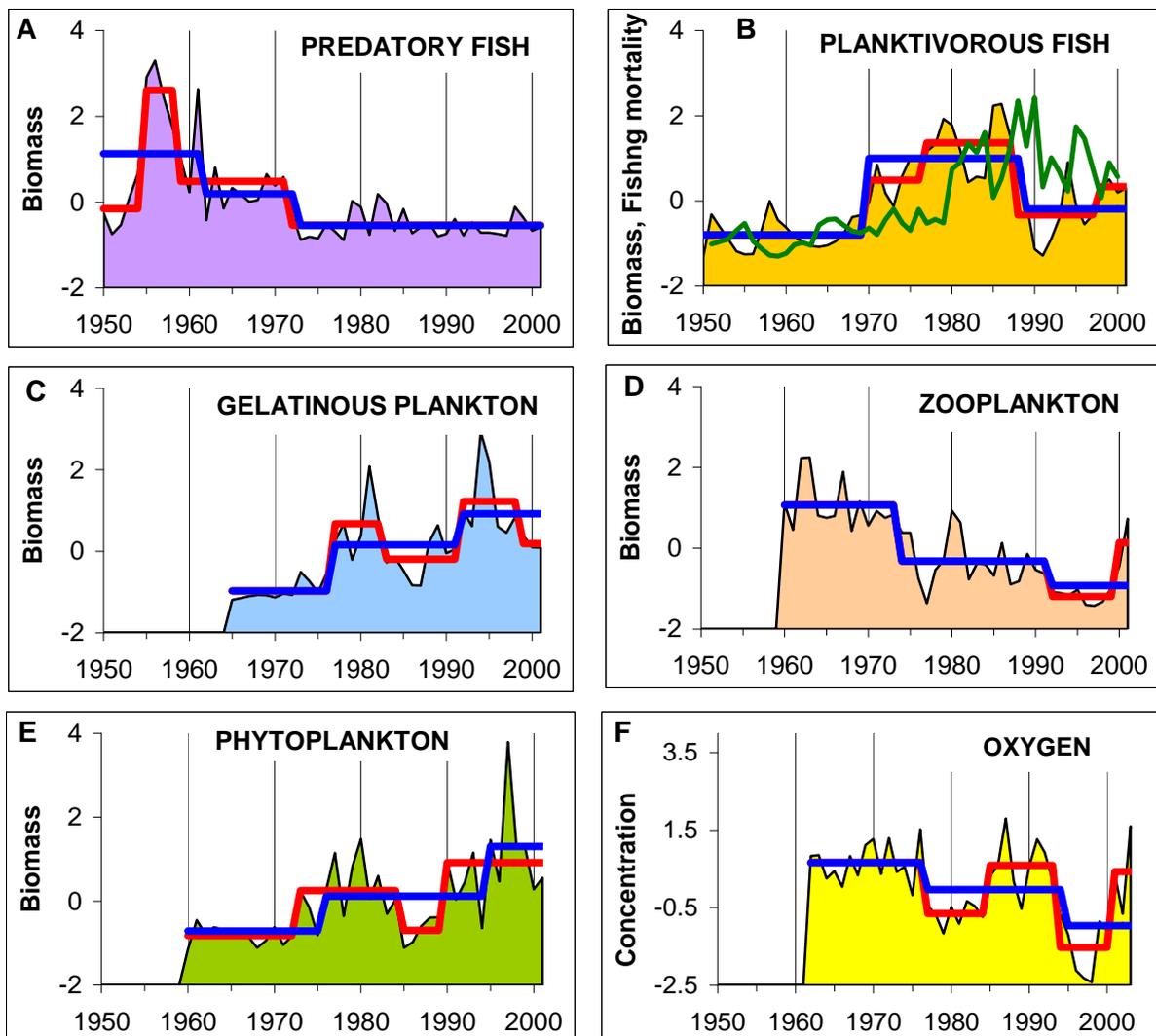
- The ecosystem shifts in the Black Sea have been driven by trophic cascades triggered by overfishing of, initially, pelagic top predators and, later, of planktivorous fish that became evident from counter trends at four trophic levels.
- The first regime shift followed the depletion of top predators from the 1950-1970, after which the ecosystem stabilized at low abundance of top predators, high abundance of planktivores, low zooplankton and high phytoplankton biomasses during the 1970s and 1980s.
- The second regime shift was associated with the collapse of planktivorous fish and outburst of the invasive *M. leidy*, which resulted in a second system-wide trophic cascade, with similar alternating effects on zoo- and phytoplankton, and on water chemistry.
- The changes at the top of the food web were related to a major rearrangement of the whole ecosystem, with feedbacks between different components shifting the marine environment from a state characterized by variable fish fauna and clear water to a turbid one with frequent blooms of algae and jellyfish, bottom hypoxia and localized production of hydrogen sulphide.

The Black Sea is the first large marine ecosystem where ecosystem shifts cascading over the whole trophic pyramid have been found (Daskalov, 2002). The ecosystem shifts are apparently driven by trophic cascades triggered by overfishing of, initially, pelagic top predators and, later, of planktivorous fish, that became evident from counter trends at four trophic levels (Figure 1). The dataset used in elucidating this comes from long-term international monitoring and has been used and referred to in several studies already (Prodanov *et al.*; 1997, Daskalov, 2002, 2003; Daskalov *et al.*, 2007). Data were collected in the open sea as well as over the shelf, where most of the biomass of the different trophic groups of the Black Sea is distributed (Simonov *et al.*, 1992). Data from different areas of the Black Sea show consistent trends and are representative of the main biological populations (Daskalov *et al.*, 2007).

Two major shifts were detected, both associated with important perturbations of the upper levels of the pelagic food web (Figure 1; Daskalov *et al.* 2007). The first event was related to depletion of top predators, which provoked a system-wide trophic cascade involving four trophic levels, nutrients and oxygen. Pelagic piscivores had declined by the early 1970s (Figure 2). The large population of dolphins which previously consumed some 500 000 t of fish annually (mainly sprat *Sprattus sprattus*, and anchovy *Engraulis encrasicolus*) diminished about tenfold through overexploitation (Sirotenko *et al.*, 1979; Öztürk, 1996). Before 1970, the fishery targeted mainly large, valuable, migratory species, the most abundant being the bonito (*Sarda sarda*), and slightly less of the Black Sea mackerel (*Scomber scombrus*) and bluefish (*Pomatomus saltatrix*, Figure 3). Large migratory predators such as bluefin tuna (*Thunnus thynnus*) and swordfish (*Xiphias gladius*) were also regularly reported in the catch statistics. During the regime of high abundance, top predators were controlled mainly by the abundance and availability of their

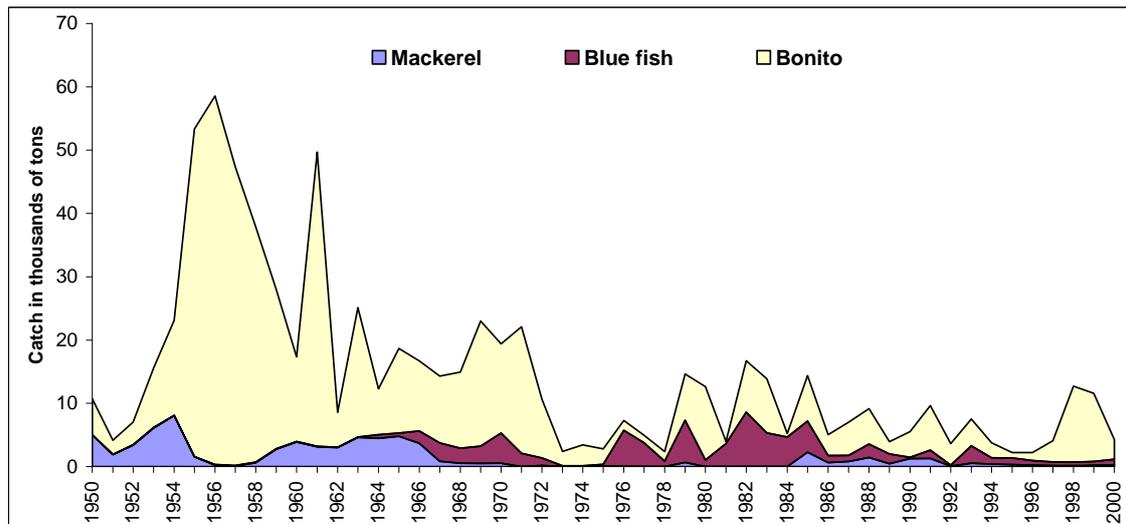
food. Later, they were depleted by heavy fishing, releasing the predation pressure on planktivorous fish, which themselves increased rapidly after 1970 (Figure 1B). As a response to increased planktivory by fish, zooplankton populations declined from 1973 (Figure 1D). Subsequently, consumption of zooplankton increased even more because of an outburst of jellyfish, *Aurelia aurita*, in the early 1980s, reaching more than 1 kg of biomass per m<sup>2</sup> (Shushkina and Musaeva, 1983, Figure 1C).

**Figure 1: Stepwise cascading shifts at four trophic levels in the Black Sea (data are standardized to zero mean, unit variance). A. Pelagic predatory fish; B. Small planktivorous fish, Fishing mortality (green line); C. Gelatinous plankton; D. Zooplankton; E. Phytoplankton; F. Oxygen. Shifts in the mean are detected using cut-off lengths of 15 (blue line) and 7 years (red line). All time-series data are presented as relative anomalies with mean = 0 and variance = 1 in order to allow better comparison of trends**



Source: Author (after Daskalov *et al.*, 2007)

**Figure 2: Catch of predatory fish in the Black Sea (catch in the Bosphorus area is excluded)**



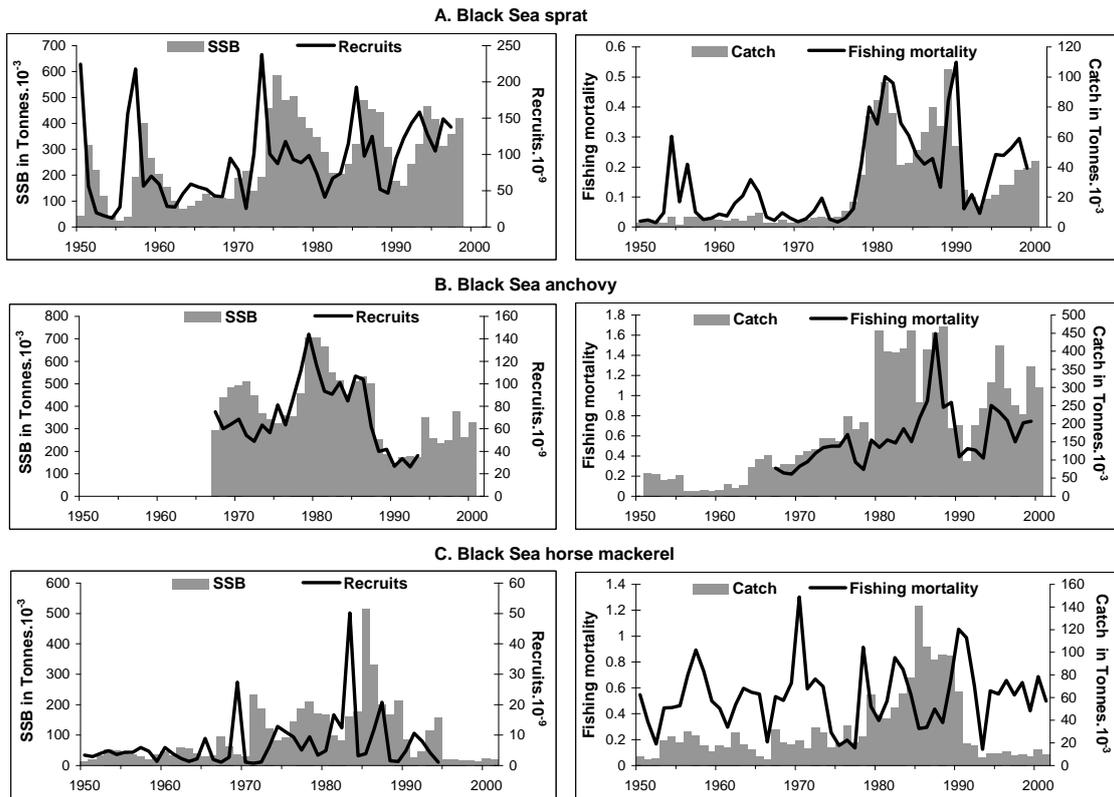
Source: Author

**Figure 3: Bluefish is the most voracious pelagic predatory fish in the Black Sea at present as well as a very valuable catch**



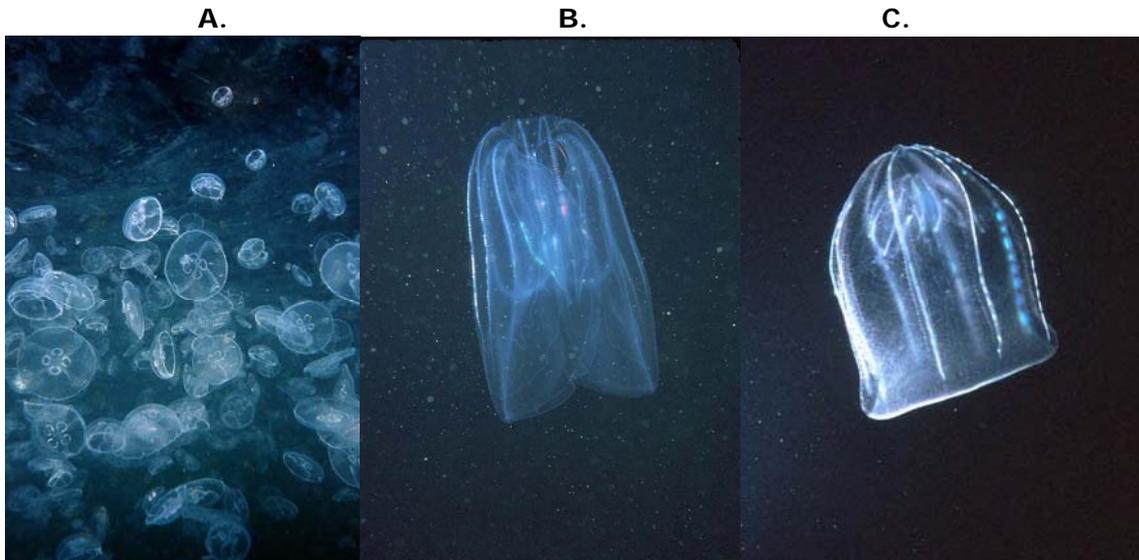
Source: L. Klissurov © <http://www.klissurov.dir.bg>

**Figure 4: Time series of recruitment, Spawning Stock Biomass (SSB), catch, and fishing mortality of: A. sprat, B. anchovy, and C. horse mackerel**



Source: Author (after Daskalov *et al.*, 2007)

**Figure 5: Gelatinous plankton in the Black Sea: A. Jellyfish *Aurelia aurita*; B. Comb jelly *Mnemiopsis leidyi*, and C. Comb jelly *Beroe ovata***



Source: L. Klissurov © <http://www.klissurov.dir.bg>

The second major shift happened in the early 1990s. The increase in biomass and catch of small pelagic fish during the 1970s and 1980s promoted the expansion of powerful trawl and purse seine fishing fleets and a steady increase in fishing effort (Gucu, 1997). Maxima of catch and fishing mortality were recorded in the late 1980s parallel to the decrease in exploited biomass following recruitment failures in the previous years (Figure 4). Sharp reductions in biomass and catch in the early 1990s were described as stock collapses (Daskalov *et al.*, 2008). After 1990, fishing effort decreased because of a scarcity of fish, and stocks started to recover. By the late 1980s the jellyfish *A. aurita* was replaced in its dominating position by the exotic ctenophore, *M. leidyi*, (Figure 5) which developed in similar large quantities ( $\sim 2 \text{ kg/m}^2$ ; Shushkina and Vinogradov, 1991) and further depleted the zooplankton biomass (Figure 1D). Phytoplankton responded to the decline in zooplankton by increasing to a new maximum in biomass after 1995 (Figure 1E). Oxygen concentration in surface coastal waters was relatively high during the period 1962–1970, corresponding to a low biomass of phytoplankton, then dropped after 1974 in response to increased oxygen demand attributable to respiration and decomposition of the surplus of algal biomass and detritus in the water (Figure 1F). The increased phytoplankton biomass also resulted in enhanced uptake of nutrients and a reduction of concentrations in surface waters (Daskalov, 2002). The frequent phytoplankton blooms and the bulk of unutilized algal biomass degraded water quality, which was characterized by low transparency and high concentrations of detritus, leading to hypoxia and the production of hydrogen sulphide (Daskalov, 2003; Mee *et al.*, 2005). After 1996, the standing stock of gelatinous plankton decreased, followed by a reverse cascade – a recovery in zooplankton and a decrease in algal biomass between 1998 and 2000 (Figures 1C, D). Surface oxygen concentration dropped between 1991 and 1997, but later recovered in response to a fall in algal biomass (Figure 1F).

Trophic cascades are the proposed mechanism driving regime shifts in the Black Sea (Daskalov *et al.*, 2007). Daskalov and his co-workers (2007), using statistical techniques, detected two major shifts between three different regimes in the Black Sea and developed a conceptual model explaining their causes, with important perturbations of the upper levels of the pelagic food web. The first regime shift followed the depletion of top predators from the 1950s to the early 1970s, after which the ecosystem stabilized at low abundance of top predators, high abundance of planktivores, low zooplankton biomass and high phytoplankton biomasses during the 1970s and 1980s. The second regime shift was associated with a collapse of planktivorous fish and an outburst of the alien *M. leidyi*, which resulted in a second system-wide trophic cascade, with similar alternating effects on zoo- and phytoplankton, and on water chemistry. That second event did indeed verify the initial trophic cascade hypothesis of Daskalov (2002). In its third state, during the 1990s, the ecosystem was characterized by low abundance of planktivorous fish, but high biomass of gelatinous organisms, and even lower zooplankton and higher phytoplankton biomass than during the 1980s. Minor reverse shifts in the mid-1980s and after 2000 also supported the cascade hypothesis illustrating partial hysteretic return to initial states (Figure 1; Daskalov *et al.*, 2007). The changes at the top of the food web were related to a major rearrangement of the whole ecosystem, with feedbacks between different components shifting the marine environment from a state characterized by variable fish fauna and clear water to a turbid one with frequent blooms of algae and jellyfish, bottom hypoxia and localized production of hydrogen sulphide.



## 4. TROPHODYNAMIC MECHANISMS OF REGIME SHIFTS

### KEY FINDINGS

- The food web theory hypothesizes that top-down (consumer) and bottom-up (resource) controls compete for dominance at each trophic link. Top predators only experience resource limitation, but they regulate the abundance of their prey and, at each successively lower trophic level, populations are alternately either regulated in a dominantly bottom-up (underexploited) or top-down (overexploited) manner.
- Changes in consumers are followed by changes in resource, with longer, shorter or no time lags. When resource populations are plotted against consumers they form a quasi-rectangular non-linear pattern, which suggests different forward and return paths characterising hysteretic systems.
- Positive feedback tends to amplify the underlying processes and thus result in a much bigger effect than presumed by the strength of the driving force. Negative feedback on the contrary tends to smooth changes and thus regulate system interactions.

Regime shifts create important problems to fisheries management because of the difficulty of distinguishing between the impacts of fishing and natural variability, aside from the generally insufficient understanding of the underlying processes. Developing explanatory concepts and models is crucial for fostering of viable ecosystem science and providing better advice for management.

System-wide regime shifts in the Black Sea can be explained by the food web theory. This hypothesizes that top-down (consumer) and bottom-up (resource) controls compete for dominance at each trophic link. Top predators only experience resource limitation, but they regulate the abundance of their prey and, at each successively lower trophic level, populations are alternately either regulated in a dominantly bottom-up (underexploited) or top-down (overexploited) manner (Hairston *et al.*, 1960; Fretwell, 1977). Therefore, the impact of top predators cascades down the trophic pyramid, generating Alternating Trophic Controls (ATC) at each level and, ultimately, regulating primary production (Hairston and Hairston, 1993; Daskalov *et al.*, 2007).

The first radical shift (~1970) in the Black Sea took place when top predators were eliminated and the system switched from a configuration with four trophic levels to one with three, namely high zooplanktivore (top level), low zooplankton and high phytoplankton (Daskalov, 2002). In such a system, zooplanktivores are bottom-up controlled and indirectly forced by enrichment (Rosenzweig, 1971; Daskalov, 2002). The shift in the 1990s was not a switch in trophic dominance (top-down to bottom-up control, or vice versa), but rather a dominant top-down control on zooplankton being changed from fish-dominated (selective feeding) to ctenophore-dominated, unselective feeding by *M. leidyi*, leading to even more evident cascading changes (Figure 1). The removal of the top level in an ATC-structured web may result in several possible indirect effects. The first and most obvious is a straight trophic cascade that produces inverse, alternating changes in abundance down the trophic pyramid. The new dominant groups proliferate because of weakened consumer control and compensatory growth (Ives and Cardinale, 2004). Also, they are allowed to proliferate by the increase in basal productivity, sometimes eutrophication, i.e. bottom-up control (see also Figure 8D).

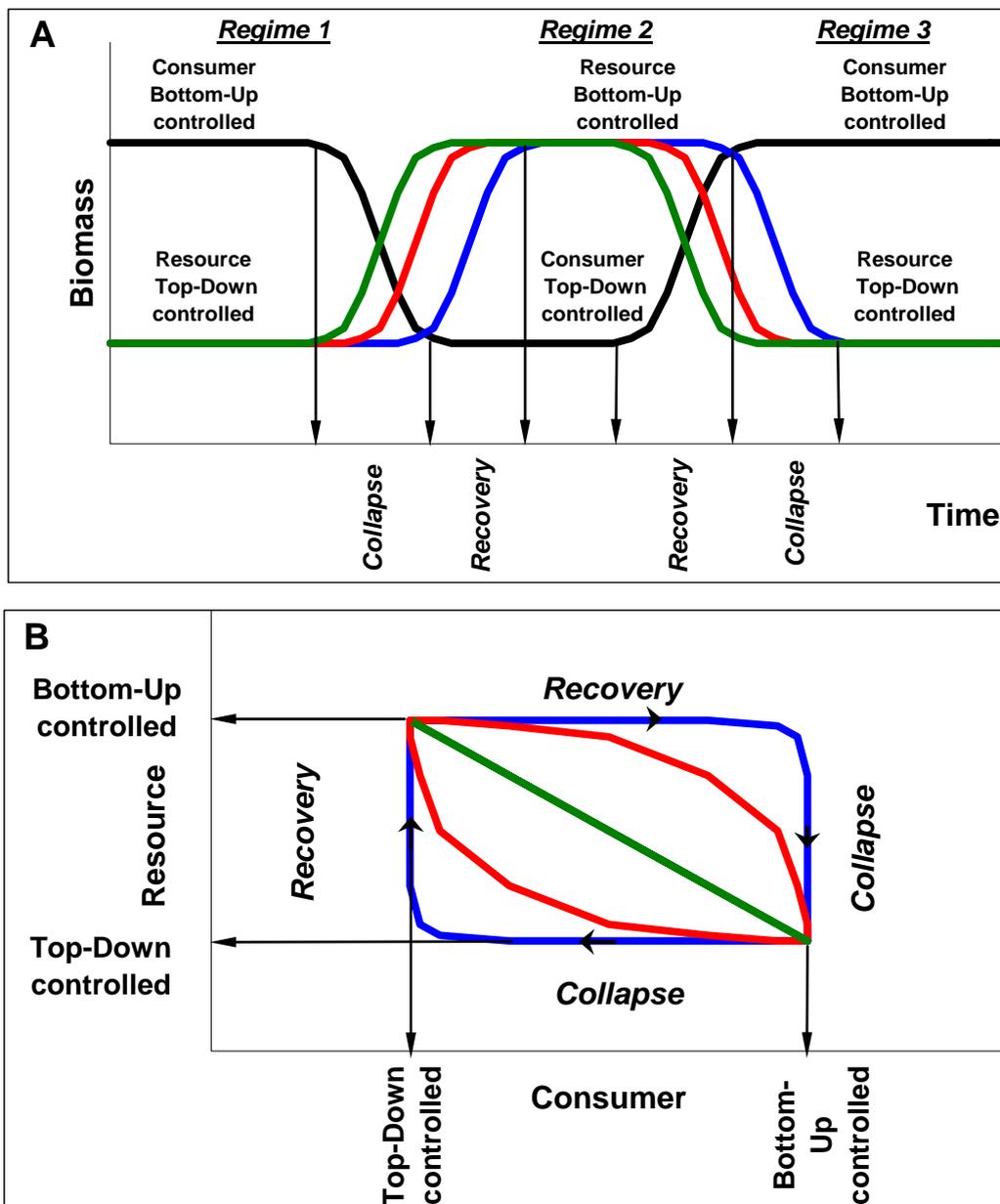
## 4.1. Conceptual model of ecosystem shifts in the Black Sea

In order to explain the causality behind the shifts, Daskalov and co-authors developed a mechanistic conceptual model (Figure 6, Daskalov *et al.*, 2007). The plots allow us to observe the co-evolution of consumer/resource populations over subsequent regimes. The trajectories of consumer and resource populations over time show that changes in consumers are followed by changes in resource, with longer, shorter or no time lag (Figure 6A). When resource populations are plotted against consumers (so called phase space plot, Figure 6B) they form a quasi-rectangular non-linear pattern, which suggests different forward and return paths characterising hysteretic systems. The angles indicate quasi-stable regimes, and sides parallel to the axes indicate regime shifts (Figure 6B).

According to the hypothesis of Hairston and co-workers (Hairston *et al.*, 1960; Hairston and Hairston, 1993), food web populations are controlled alternatively by consumption (top-down control) or by production and availability of resources (bottom-up control). When applying this theory to Black Sea data we can define alternative regimes of, respectively, consumer and resource populations (Figure 6). Populations are top-down controlled when their productivity is low and/or they are heavily exploited by consumers, so the consumption/production ratio (also referred to as ecotrophic efficiency, Pauly *et al.*, 2000) is high and tends towards 1. As a result, top-down-controlled populations sustain relatively low biomass (resource in regime 1 on Figure 6A). Populations are bottom-up controlled when they are only lightly exploited and/or productivity is high, in which cases the ecotrophic efficiency is low and the standing stock biomass relatively high (consumer in regime 1 on Figure 6A, Hairston and Hairston, 1993). In such systems, a switch to an alternative regime is driven by overexploitation of the consumer population (regime 2 on Figure 6A). In most cases overexploitation (including overfishing) is attributable to a combination of low productivity (poor recruitment and slow somatic growth) and sustained heavy fishing or predation, resulting in a rise in exploitation mortality (~ecotrophic efficiency) and ultimately biomass collapse (see also Chapter 5.1). The return to initial states (regime 3 on Figure 6) follows a different path (hysteresis, Figure 6B) and leads to recovery of consumer biomass, which subsequently suppresses the resource biomass at a lower level. The response of the resource population is delayed by some reaction time (that may be related to the resource population generation time). The trajectory in the phase space (Figure 6B, Figure 7,) is pronouncedly non-linear (rectangular) when the change in the resource (response variable) follows the change in the consumer (driver variable). Alternatively, the resource population may respond simultaneously or with minor delay, which would result in a linear or crescent pattern of the phase space trajectory, respectively (Figure 6B).

The conceptual model was tested by plotting consumer (as drivers) against resource (response) as phase space plots (Figure 7). A decrease or an increase in consumers have provoked a reciprocal response in the resources, indicating switches in trophic control at consecutive trophic levels (Figure 7). Low-resource/high consumer regimes indicating dominant top-down control are characterized by little variability of the resource and great variability in the consumer, and vice versa. The degree of non-linearity depends on the delay (time lag) in the response of the resource to a shift in consumers, so that delayed responses (longer reaction time) result in bent rectangular trajectories, swifter or simultaneous responses – in smooth or linear trajectories, respectively (Figure 6). Trajectories of the apex trophic groups (fisheries, fish) tend to show strongly bent patterns (Figure 7A, E) and those of the basal groups – smoother patterns (Figure 7C, D, G) that imply that the reaction time of the response may be related to the population generation time.

**Figure 6:** Sketch of alternating regimes in consumer and resource populations: **A.** State space representation: both consumer (solid black line) and resource (blue, red, and green lines depending on the reaction time) can hold alternatively either bottom-up or top-down controlled stable regimes and switch between them, shifts are referred as collapse and recovery. **B.** Phase space representation: the sides of the rectangle represent regime shifts (collapse or recovery). Consumer/resource relationship may follow quasi-rectangular (blue line), crescent (red line) or linear (green line) trajectories depending on the delay of the response in resource to the shifts in consumers (simultaneous and slightly delayed response are shown with green and red lines respectively in panel A, see text for explanation)

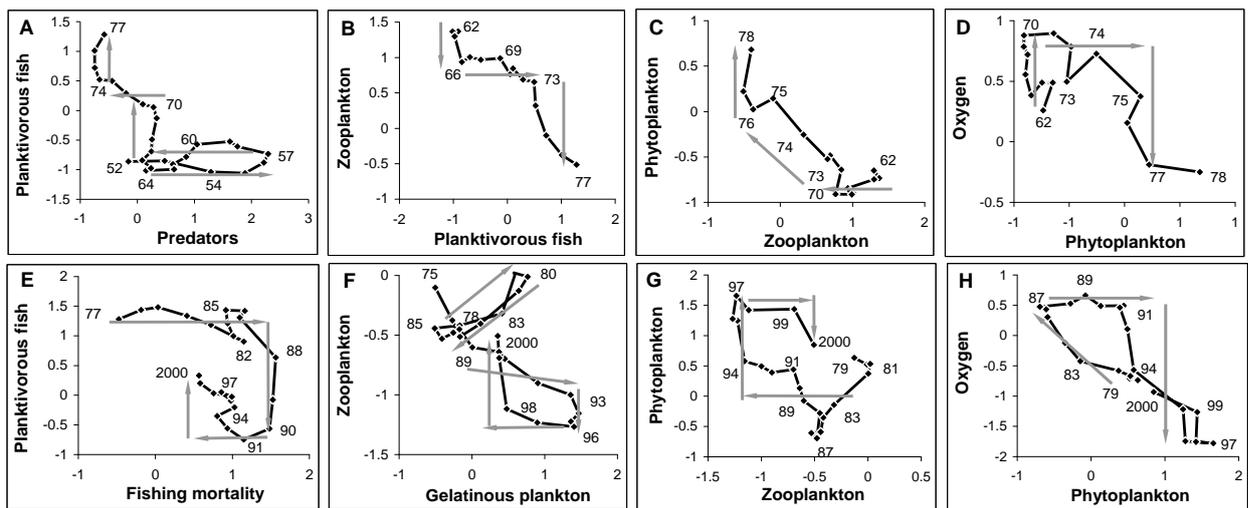


Source: Author (after Daskalov *et al.*, 2007)

Two of the criteria defining a regime shift are the formation of distinct stable states and hysteresis (i.e. a return to the previous state through a different path, see Box 1). The cause of establishing and sustaining persistent new regimes is recognized to be the shift in

trophic control (ATC) and a trophic cascade following disturbance of the upper trophic levels. Tendencies of a return to a previous state are found by examination of reverse cascades which occurred in the mid-1980s and 2000s. The first reversal was detected as a decrease of gelatinous plankton (*A. aurita*) and phytoplankton, and an increase in oxygen (Figure 1). Hysteretic loops are most clear at the basal levels, where the oxygen increased between 1983 and 1987 as a response to the decrease in phytoplankton in the years 1980-1983 (Figures 1F, 7H), and in the phase plot of zooplankton against phytoplankton (Figure 7G). The recovery did not continue long, and in the 1990s, the gelatinous biomass dominated by *M. leidy* burgeoned, leading to a further decrease in zooplankton and planktivorous fish. The second recovery was related to an increase in planktivorous fish and a decrease in *M. leidy* by the late 1990s, leading to a subsequent increase/decrease/increase in zooplankton/ phytoplankton/ oxygen (Figures 1 and 7), and showed evidence of hysteresis at all levels from fish to oxygen (Figure 7E, F, G, H). This corresponded to a general (although limited) improvement of the environmental quality (Kideys, 2002).

**Figure 7: Phase space plots of consumer (driver) against resource (response), illustrating the ecosystem regime shifts of the 1970s (A, B, C, D) and 1990s (E, F, G, H). Standardized data from Fig. 1 are used. Numbers on the plots are years**



Source: Author (after Daskalov *et al.*, 2007)

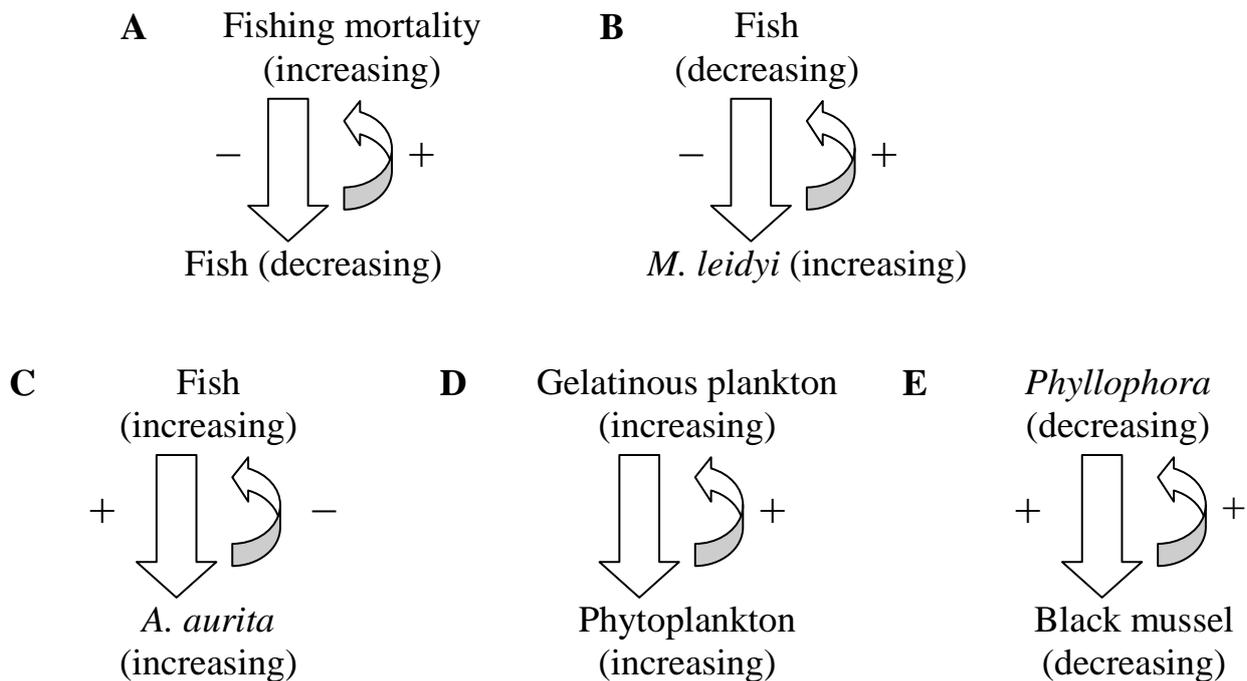
## 4.2. Feedbacks effects

Structural/functional transformations related to regime shifts often involve positive (amplifying) and negative (regulatory) feedbacks and interactions between fast and slow processes (Scheffer and Carpenter, 2003; Mayer and Rietkerk, 2004). Positive feedback tends to amplify the underlying processes and thus result in a much bigger effect that presumed by the strength of the driving force (Box 1). Negative feedback on the contrary tends to smooth changes and thus regulate system interactions.

When overfishing of a single fish stock is involved, regime shifts (stock collapse followed by recovery) can be explained by increased catchability of schooling fish at low stock densities, or depensation (reduced recruitment at low spawning stock), both leading to higher fishing mortality at low stock levels and further biomass reduction (Jones and Walters, 1976; Mullon *et al.*, 2005). In such a situation, the negative effect of fisheries is

self-enforced (positive feedback; Figure 8A) and the collapsed stock is usually trapped at a low level (Daskalov *et al.*, 2008).

**Figure 8: Feedback mechanisms in the Black Sea. Straight block arrows are direct effects and looped arrows are feedback effects. Direct effects are positive when they lead to a change in response consistent with the change in the driver (i.e. an increasing driver leads to an increasing response), and negative in the opposite case (i.e. an increasing driver leads to a decreasing response). Feedback effects are positive when leading to amplification of the existing direct effects, and negative when reducing the strength of direct effects, or can even invert them.**



Source: Author (after Daskalov, 2008)

The leading factor for the explosion of *M. leidy* in the early 1990s is now recognised of being the overfishing of planktivorous fish stocks (Daskalov *et al.*, 2007, Oguz *et al.*, 2008). Favourable conditions for the outburst were created then by decreased zooplanktivory resulting in surplus zooplankton production (Grishin *et al.*, 1994). The ctenophores are particularly efficient when food density is high (Sørnes and Aksnes, 2004). In subsequent years, *M. leidy* overexploited the zooplankton, and led fish stocks to a food deficiency that strengthened the low biomass state of the stocks (positive feedback; Figure 8B). An example of negative feedback was the alternating pattern between sprat and jellyfish *A. aurita* in the 1980s (Figure 8C; Daskalov, 2003). Initially, the growing fish population selectively reduced large zooplankton, leading to a compensatory increase of small zooplankton, and creating favourable trophic conditions for *A. aurita* (Daskalov, 2002). Consequently, both large and small zooplankton decreased under the combined predation of fish and jellyfish, creating conditions where the planktivorous sprat was outcompeted by *A. aurita*. As a result, the relationship between sprat and *A. aurita* was inverted and they started to fluctuate out of phase (Daskalov, 2003). Therefore, it seems that although the major depletion of zooplankton could be attributed to gelatinous predators, changes in zooplanktivory are usually initiated by zooplanktivorous fish, which are more active and better at searching for prey. Farther down the food pyramid, the

outburst of gelatinous plankton indirectly favoured blooms of phytoplankton (through a trophic cascade) which, unchecked by the depleted zooplankton population, ended as detritus and decomposed. The recycled organic matter provided a bottom-up enrichment for the gelatinous plankton organisms, which are not controlled by predators (positive feedback; Figure 8D). The massive algal blooms and organic matter in the Black Sea reduced water transparency and deprived macrophytobenthos from light, leading to its mortality (Daskalov, 2003). The destruction and decomposition of the vast fields of red macroalgae (*Phyllophora* sp.) reduced the oxygen supply of the associated benthic communities and led to hypoxia and mortality of associated sessile organisms, notably the black mussel. Destruction of the fields of filter-feeding mussels created a positive feedback loop (Figure 8E), which is still keeping the previously abundant and diverse northwestern Black Sea shelf in a turbid and unproductive phase (Mee *et al.*, 2005). Such developments suggest that regime shifts affect ecosystem function, implying major changes in productivity, consumption, production of detritus and nutrient regeneration, and leading to system-wide effects such as plankton blooms, turbidity and hypoxia (Bologa *et al.*, 1995; Daskalov, 2003). Anoxic conditions and the accumulation of organic matter on the seabed led to anoxic bacterial production and a release of hydrogen sulphide that further contributed to flora and fauna kills and a loss of ecosystem function (Daskalov, 2003; Mee *et al.*, 2005).

Overfishing of planktivorous fish has been hypothesized to cause regime shifts involving feedbacks on three trophic levels and water clarity in Norwegian fjords, as well as in the Black Sea (Aksnes *et al.*, 2004; Aksnes, 2007). Aksnes *et al.* (2004) found that different fjords were dominated by either fish (clear water) or jellyfish (turbid), and that abundance of planktivorous fish was inversely related to light absorbance. The mechanism hypothesized to explain these findings was a trophic cascade in which jellyfish replaced fish and suppressed zooplankton, leading to blooming algal production. The increased algal blooms and organic matter then reduced visibility and negatively impacted the ability of fish as visual predators to find food. Therefore, the development of dominant jellyfish populations initially triggered by removal of fish later sustained turbid conditions that did not allow fish to recover. Aksnes (2007) applied this hypothesis to explain the fish–jellyfish shift in the Black Sea. Turbidity may also have affected predatory fish (e.g. bonito), whose migration routes have changed greatly since the 1970s: subsequently, bonito have been avoiding the turbid northwestern shelf waters of the Black Sea that were previously used as a preferred foraging area (Daskalov *et al.*, 2008).

## 5. ALTERNATIVE EXPLANATIONS: CLIMATE, EUTROPHICATION, INVASIVE SPECIES

### KEY FINDINGS

- Regional and global climate change, eutrophication, and invasive species are also synergistically involved in ecosystem shifts. They are related to other external (fishing) and internal (trophic interactions) factors in complex multi-causal way, where all factors interact through non-linear feedbacks contributing to development of alternate regimes and the shifts between them.
- Overfishing and collapses happen when declining stocks are confronted with overcapacity of a fishing fleet or burgeoning fishing effort (e.g. through better efficiency/technology), because of the inability of fishery management to forecast and adapt rapidly to changes in fish stocks.
- A four levels structured food web (including abundant top-predator) may be able to support a higher nutrient load and then be more resilient against anthropogenic eutrophication.
- The outburst of the invasive *M. leidy* and its consequences for fish stocks illustrate how both food web interactions and external factors, in this case anthropogenic introduction, may affect ecosystem structure and functioning, drive an ecosystem shift.

The explanations presented in Chapter 4 mainly describe effects of changes in fish and fisheries on the trophic flows, structure and functions of the food web. Alternative (and often complimentary) explanations have been proposed in several studies indicating that climate, eutrophication and alien species are possible drivers of regime shifts in the Black Sea (Daskalov, 2002, 2003; Mee *et al.*, 2005; Daskalov *et al.*, 2007; Oguz and Gilbert; 2007; Oguz and Velikova, 2010).

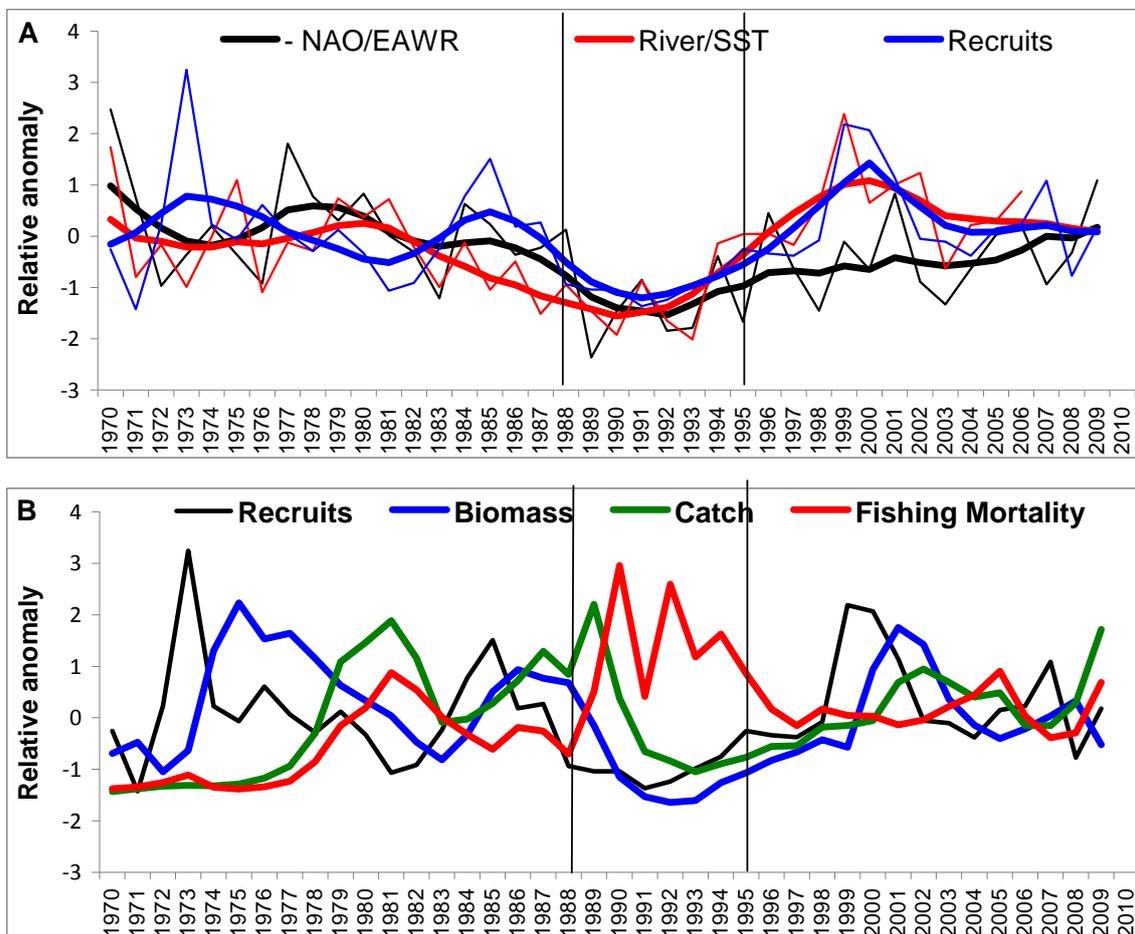
### 5.1. Climate as a driver of regime shifts

Although a climatic connection is assumed in most of the studies of regime shifts (e.g. Lees *et al.*, 2006), the origin and mechanisms by which climatic shifts affect the ecosystem remain not entirely clear (Bakun, 2005; Overland *et al.*, 2006). When climate and multiple biological components are affected, it is natural to assume that the climate shift is the driving force of ecosystem transition, although usually the amplitude of the biological response seems greater than the possible climatic drivers could cause (Hare and Mantua, 2000; Bakun, 2005).

Long-term variations in climate and hydrological indices have been found to correlate with several biological time-series in the Black Sea (Daskalov 2003; Oguz *et al.*, 2006). Sea temperature, river run-off, wind and atmospheric pressure are among the variables linked to biological productivity. The local Black Sea climate seems to be strongly affected by Atlantic climate (Oguz *et al.*, 2006; Llope *et al.*, 2010) as exemplified by the North Atlantic Oscillation (NAO). NAO index is estimated as the difference in normalized sea level pressures between Lisbon (Portugal) and Reykjavik (Iceland). NAO is known to oscillate between distinctive positive and negative regimes. A positive winter NAO index is

associated with cold and dry air masses in southern Europe and the Black Sea region, since the westerly winds take a more northwards direction. Conversely, a negative NAO index implies milder winters, with warmer air temperatures and less dry/more wet atmospheric conditions over the Black Sea due to the more direct effect of the west winds over the region (Oguz *et al.*, 2006). Negative NAO years are therefore associated with greater run-off and higher temperatures (Polonsky *et al.*, 1997; Oguz *et al.*, 2006).

**Figure 9: Climate and overfishing: A. Correlations between Atlantic influence (black line) presented as the composite between North Atlantic Oscillation (NAO) and the East Atlantic West Russia index (EAWR), Black Sea climate index (red line) presented by a composite of the River Danube run-off and Sea Surface Temperature (SST), and sprat recruits (blue line); B. Time series of sprat recruits, biomass, catch, and fishing mortality. The period of overfishing and stock collapse is delineated with vertical lines. All time-series data are presented as relative anomalies with mean = 0 and variance = 1 in order to allow better comparison of trends**



Source: Author

Oguz and Gilbert (2007) distinguished between warm and cold climate regimes and attributed major ecosystem shift in the 1990s mainly to the switch from cold to warm climate (together with other factors such as eutrophication, overfishing, and *M. leidy* invasion). Llope and co-authors (2010) applied sea temperature and NAO as statistically significant explanatory variables in their models of regime shifts in the Black Sea. NAO was found to affect biological productivity in relation with the nutrient input (phosphorus):

namely negative NAO values had a strong effect on productivity when the levels of phosphorus were high (Llope *et al.*, 2010). This relation is explained by the effects of NAO on precipitation and river run-off that enhances phosphorus input in the sea (also reported by Daskalov, 2003)

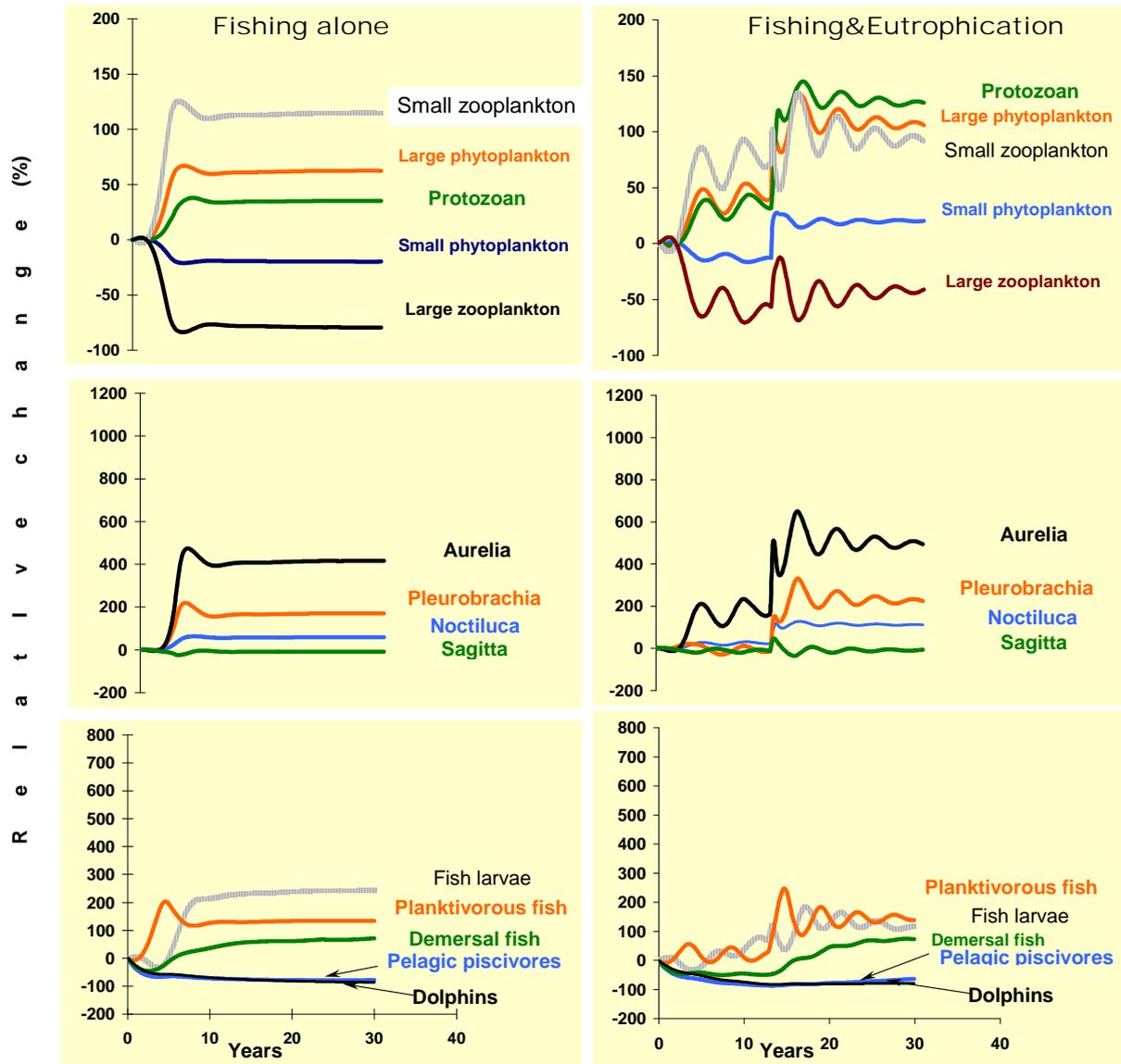
Stock collapses in the Black Sea are good examples of how climate and overfishing interact. In most cases, overfishing occurs when stock abundance decreases often associated with a negative climatic influence (Figure 9). Overfishing and collapses happen when declining stocks are confronted with overcapacity of a fishing fleet or burgeoning fishing effort (e.g. through better efficiency/technology), because of the inability of fishery management to forecast and adapt rapidly to changes in fish stocks. Environmental degradation (e.g. eutrophication and bottom hypoxia) can worsen the conditions for recruit survival leading to stock collapse, as in the case of Black Sea turbot in the late 1980s (Prodanov *et al.*, 1997; Daskalov, 2003). In the example presented on Figure 9A sprat recruitment is associated with both Black Sea and Atlantic climates indexed by the SST/River composite and NAO/EAWR composite respectively. Figure 9B shows how changes in sprat recruitment e.g. the drop in 1988 is followed by a drop in the biomass due to persistent high catch which resulted in overfishing - record values of fishing mortality and stock collapse in the early 1990s.

## 5.2. Cultural eutrophication as a driver of regime shifts

The Black Sea has been a subject of intense cultural eutrophication which peaked in the 1970-1980s (Zaitsev, 1993; Bologna *et al.*, 1995). Eutrophication also can be suspected as an important driver of regime shifts. Indeed, Oguz and Gilbert (2007) related the shifts in phytoplankton to changes in the nitrogen load from the River Danube. They found abrupt transitions between 3 states (low, medium and high) of the phytoplankton biomass in 1973-1974 and 1984-1985. It is worth mentioning that Oguz and Gilbert (2007) have used a different phytoplankton biomass data set referring to the central Black Sea, from the one presented in this study (Figure 1E). Further, Oguz and Velikova (2010) analysed a rich data set from the northwestern Black Sea and emphasized on the importance of nutrient control as a main driver of ecosystem changes. They found that conditions for phytoplankton abruptly shifted from nitrogen to phosphorus limitation after the decline in anthropogenic phosphate load by 1990, that severely reduced phytoplankton production and led to a catastrophic collapse of the entire food web. Oguz and Velikova (2010) described 3 main ecosystem regimes: pre-eutrophic (prior to 1970), eutrophic (1980s) and post-eutrophic (after 1993). They concluded that in the present regime the prevailing phosphate limitation maintained a low-energy, trophically inefficient food web structure characterized by heterotrophic phytoplankton and gelatinous zooplankton, and warned that this recent regime is very different from the pristine ecosystem structure, and recovery of pre-eutrophic conditions may be impossible.

Eutrophication has also been evoked as the main driver in benthic system shifts characterised by the decline of benthic macroalgal (e.g. red macroalgae *Phylophora* fields) and filter-feeder (blue mussel) communities and consequent hypoxia, hydrogen sulphide production and mass mortality of benthos over extended shelf areas (Zaitsev, 1993; Daskalov, 2003; Mee *et al.*, 2005). In these processes a two stage trophic cascade (black mussel - phytoplankton) and a quasi-mutualistic feedback between filter-feeders and macroalgae via water clarity is involved as described in Chapter 4.2.

**Figure 10: Results from simulations with the dynamic food web model Ecosim: A. Changes due to fishing mortality forcing: "Fishing alone", B. Changes due to fishing mortality and eutrophication forcing: "Fishing&Eutrophication "**



Source: Author (after Daskalov, 2002)

Daskalov (2002) simulated the eutrophication effects in his food web model (Figure 10). Forcing by eutrophication has only increased the amplitude of the trends in abundance at different trophic levels, but their directions were still controlled by predation. These patterns are also confirmed by time-series data (Figure 1). In the mid-1980s, when the nutrient enrichment of anthropogenic origin was at its highest levels (Daskalov, 2003; Oguz and Gilbert, 2007), biomass peaked mainly in the bottom-up controlled groups such as phytoplankton, planktivorous fish and jellyfish. Meanwhile, top-down controlled groups such as zooplankton, oxygen and surface phosphate concentration decreased (Daskalov, 2002; Daskalov *et al.*, 2007). Further increases in phytoplankton in the 1990s were probably top-down driven (by the drop in zooplankton resulting from the proliferation of *M. leidy*), because nutrient input decreased over that period (Daskalov, 2003; Oguz and Gilbert, 2007). The strong correlation ( $r = 0.7$ ; Daskalov *et al.*, 2007; Figure 1) between non-adjacent bottom-up controlled trophic levels, e.g. between phytoplankton and gelatinous plankton, implies synchrony of trophodynamic effects. Bottom-up forcing,

however, seems to act only within the framework of an established ATC structure, whereas transformations in the food web structure should rather be attributed to top-down effects (Daskalov, 2002). Rearrangement of the ATC structure may lead to a decrease in the efficiency of trophic transfer. In a three-level system, the base level (phytoplankton) is only weakly controlled by grazing and can still force the system from below through burgeoning algal and detrital production (a consequence of underexploitation by grazers). Therefore, a reduction from a four- to a three-level system may create conditions for autocatalytic bottom-up forcing, which will not contribute to increased productivity of zooplankton and fish, but will rather be channelled into the microbial/jellyfish loop (Grishin, 2001, see also Figure 8D).

Increase in nutrient loading was simulated in the modelling study by Llope and co-authors (2010) resulting in a pronounced change in the control over phytoplankton biomass switching from top-down (by zooplankton consumption) to bottom-up (by nutrient enrichment). Llope and co-authors (2010) further speculated that a 4-levels structured food web (including abundant top-predator) would be able to support a higher nutrient load and then be more resilient against anthropogenic eutrophication.

### 5.3. Invasive species as drivers of regime shifts

The outburst of the invasive ctenophore *M. leidyi* and its consequences for fish stocks in the Black Sea illustrates how both food web interactions and external factors - in this case anthropogenic introduction - affect ecosystem structure and functioning. In the 1980s, the system was dominated by small planktivorous fish (anchovy, sprat) and the native jellyfish *A. aurita*. After 1985 the jellyfish *A. aurita* was replaced by *M. leidyi* which was introduced with commercial ship ballast waters. *M. leidyi* is thought to be present in the Black Sea since 1982 (Zaitsev and Mamaev, 1997), but its population only exploded in 1990 when decreased zooplanktivory by overfished stocks created a favourable trophic condition of surplus zooplankton productivity to be used by the burgeoning *M. leidyi* population (Grishin *et al.* 1994, Bilio and Niermann 2004). Therefore, the *M. leidyi* bloom seems to have been triggered by a fish stock collapse, and indeed such a scenario is confirmed by the timing of the shifts in fish and *M. leidyi* (Figure 1). The fast development of *M. leidyi* in subsequent years led to a massive decline in zooplankton biomass, strong competition for food, and a further decrease in fish stocks. Fish stocks were affected mainly by food competition through decimation of the food zooplankton. Although fish larvae are part of the diet of *M. leidyi*, they represent only a very small contribution (Tsikhon-Lukonina *et al.*, 1992), and their consumption can hardly lead to fish recruitment failure. The newly introduced exotic predatory ctenophore *B. ovata* was hypothesized to contribute to the regulation of *M. leidyi* and to lead to a recovery of fish stocks (Kideys, 2002). However, sprat and anchovy stocks started to recover after the decrease in fishing pressure, when *M. leidyi* were still abundant. Our analyses indicate that although the major effects on zooplankton could be related to predation by gelatinous plankton, changes in zooplanktivory were initiated by changes in abundance of zooplanktivorous fish. The leading factor for fish stock collapse is now recognised to be the overfishing, whilst the outburst of *M. leidyi* was an associated factor decimating the zooplankton food resources available to fish larvae (Daskalov *et al.*, 2007, Oguz *et al.*, 2008).



## 6. ECOSYSTEM SHIFTS - A CHALLENGE FOR FISHERIES MANAGEMENT

### KEY FINDINGS

- The successful application of the Ecosystem Approach to Fisheries (EAF) requires better quantitative knowledge of the effects on ecosystem dynamics resulting from the removal of large quantities of predators and prey, and of the various environmental factors which strongly influence ecosystem structure, functioning and integrity.
- Regularity of regimes-like oscillations (e.g. decadal, bi-decadal) would make long-term assessment easier. Quasi-regular long-term cycles have been observed in several major stocks, being explained mainly by fluctuating climatic conditions. The development of harvest strategies in low and high abundance regimes needs to be a research priority in future.
- Expected duration of a recovery plan will be significantly influenced by the duration of unfavourable and favourable regimes, and by the differing probabilities of good recruitment within each regime. In some scenarios the recovery can be much longer than the unfavourable regime itself, especially if the probability of good recruitment is relatively low.
- An important question from a theoretical, practical, and management perspective is whether regime shifts are reversible. The analyses of the shifts in the Black Sea prove that when following structural changes, complex marine ecosystems are unlikely to recover to their exact previous states, but will rather adapt to the immediate local conditions.

The trigger for regime shifts in the Black Sea ecosystem appears to have been overfishing and the collapse of stocks of pelagic predators before 1970, and of planktivorous fish in 1990. Consequently, fisheries for pelagic predatory fish vanished in most of the Black Sea, and one species – mackerel *Scomber scombrus* – disappeared from the Black Sea altogether (Daskalov, 2002). In the 1990s, anchovy, sprat, and horse mackerel catches dropped by a factor of six (Daskalov *et al.*, 2008), causing estimated losses of US\$16.8 million from the anchovy fisheries alone (Knowler, 2005).

Despite the relatively good knowledge of fish stock dynamics (e.g. Prodanov *et al.*, 1997), the management of fisheries in the Black Sea has not been able to assure their smooth and predictable development. Instead there has been a series of crises, a loss of valuable resources, economical ineffectiveness and overall ecosystem degradation.

Recently an obligation to consider the impacts of fishing on marine ecosystems has been widely accepted by both the public and decision-makers. The Ecosystem Approach to Fisheries (EAF) has been developing to account for all major ecosystem components and their interactions in order to assist the sustainable management of the fisheries (Browman and Stergiou, 2004; Garcia and Cochrane, 2005). The successful application of the EAF requires better quantitative knowledge of the effects on ecosystem dynamics resulting from the removal of large quantities of predators and prey, and of the various

environmental factors which strongly influence ecosystem structure, functioning and integrity.

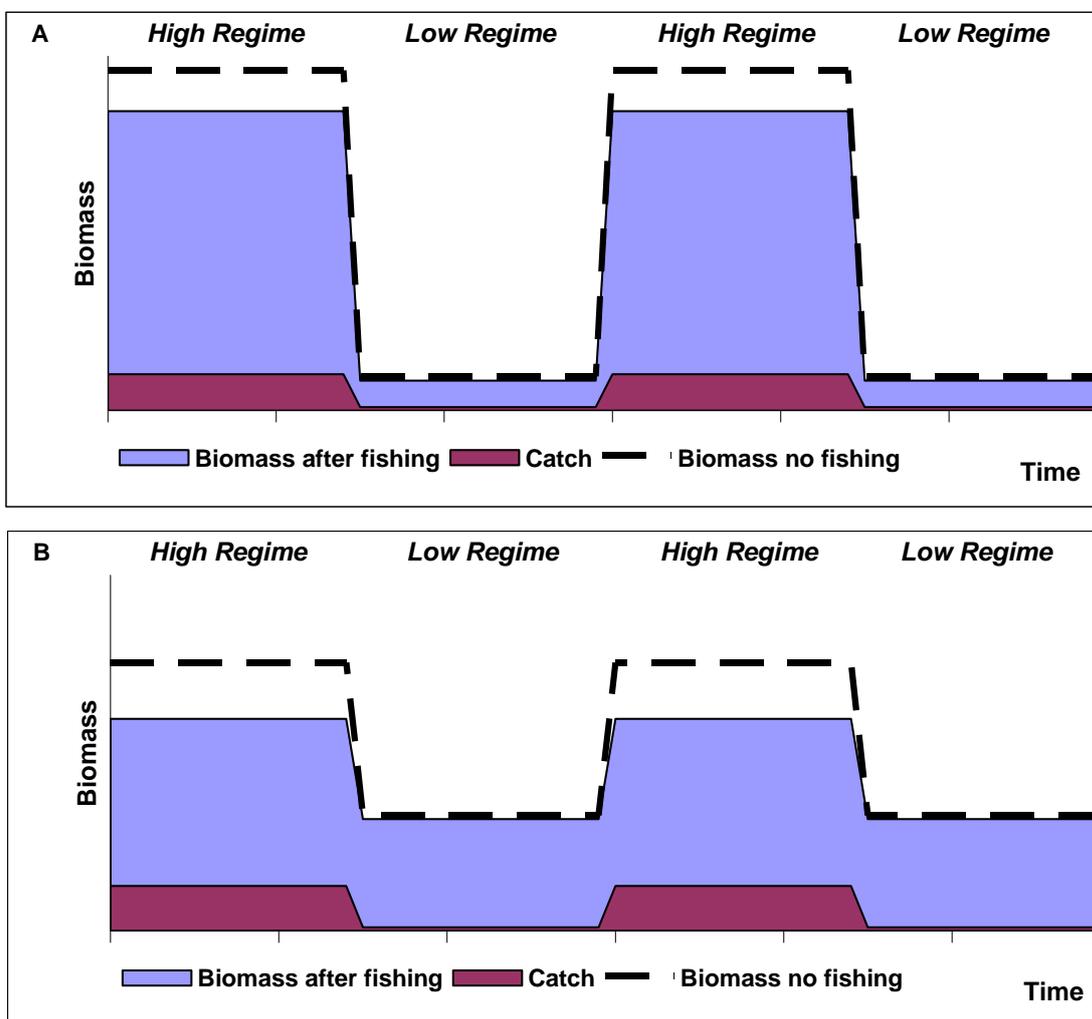
Understanding the indirect effects of overfishing, including trophic cascades, on the structure and function of marine ecosystem is crucial for the application of an EAF (Pauly *et al.*, 2002; Daskalov *et al.*, 2008). Some authors have expressed scepticism about widespread occurrences of trophic cascades in large marine ecosystems (Jennings and Kaiser, 1998; Micheli, 1999; Pinnegar *et al.*, 2000; Cury *et al.*, 2003). After the classic examples reported from kelp forests and benthic ecosystems (Estes and Duggins, 1995; Pinnegar *et al.*, 2000), more cases were discovered from large marine ecosystems, including both pelagic and benthic subsystems and their related fisheries (Daskalov, 2002; Frank *et al.*, 2005, 2006; Myers *et al.*, 2007; Daskalov *et al.*, 2007; Essington, 2010). A common feature of these cascades is the elimination of whole functional groups of top-predators: pelagic predators in the Black Sea (Daskalov, 2002), predatory gadoids (Frank *et al.*, 2005, 2006), and large piscivorous sharks (Myers *et al.*, 2007) along the east coast of North America. These cases tend to confirm the conclusions and predictions of hypotheses concerning the fishing down of marine food webs (Pauly *et al.*, 1998; Jackson *et al.*, 2001). More studies on non-commercial species and on indirect effects will help to elucidate the role and mechanisms of trophic cascades, but reversing the trends in overexploitation and declining abundance of top marine predators must certainly be one of the targets of implementing an EAF.

Regime shifts create important problems to fisheries management because of the difficulty of distinguishing between the impacts of fishing and natural variability, aside from the generally insufficient understanding of the underlying processes. All these factors generate substantial uncertainties. Fréon *et al.* (2005) advocated a two-level management strategy that would combine conventional fisheries management to deal with short-term variation, with a long-term management strategy (e.g. regulating fleet capacity and investment cycles) to account for decadal changes. For managing fisheries under scenarios of fluctuating fish abundance, Polovina (2005) based on model simulations by MacCall (2001) proposed the application of regime-specific harvest rates in which management responses are related to the timing of periodic regime shifts. The harvest rates can be determined when there are indications of a new (more or less productive) regime. I developed an illustrative example of the Polovina's (2005) approach where two hypothetical regimes - with high and low stock abundance, respectively are harvested with constant or regime specific harvest rates (Figure 11). In Figure 11A a constant harvest rate of 12% is applied to the stock in both high and low regimes. The resulting biomass of the stock then varies about 10 times. In the second case (Figure 11B) specific harvest rates are applied: 21% in the high regime and 3% in the low regime leading to lesser variation of the stock biomass between the high and the low regimes (about 2 times). The second option yielded about 35% increase in the average catch. In practice a provisional stepwise approach to changing harvest rates until the productivity level of a new regime has been established could yield better results.

As productivity regimes can affect different species synchronously in opposite ways, single-species management systems are less satisfactory than those that consider the dynamics of alternating resources. For example, sprat (*Sprattus sprattus*) and cod (*Gadus morhua*) have fluctuated out of phase in the Baltic in recent decades, with consequences for associated species such as herring (*Clupea harengus*). For these reasons, multispecies models seem to provide a more balanced approach to assessment of Baltic stocks (Köster *et al.*, 2003). De Oliveira (2006) investigated different harvesting strategies in the South African fishery for sardine (*Sardinops sagax*) and anchovy (*Engraulis encrasicolus*), and concluded that management procedures designed under the assumption of out-of-phase

sinusoidal trends in species abundance could be more effective than traditional modelling approaches. However, the performance of proposed management procedures deteriorates rapidly as the amplitude of fluctuations in abundance increases. Some degree of regularity of the regimes (e.g. decadal, bi-decadal) would certainly make long-term assessment easier. More or less regular long-term fluctuations have been observed in several major stocks, being explained mainly by fluctuating hydroclimatic conditions (Klyashtorin, 1998; Schwartzlose *et al.*, 1999; Daskalov, 2003). Bakun (2001) described a hypothetical mechanism that may synchronize fish abundance to long-term climate variations. However, regimes and their consequences are still difficult to predict. The development of harvest strategies in low and high abundance regimes needs to be a research priority in future.

**Figure 11: Illustrative example of applying two alternative harvest strategies A. Constant harvest rate of 12%, and B. regime specific harvest rates of 21% over the High regime, and - 3% over the Low regime**



Source: Author

An important question from a theoretical, but also a practical, management perspective is whether regime shifts are reversible. Can systems recover to their previous states? Although top predators have not yet recovered in the Black Sea, the 1980s fisheries partially replaced them by exploiting planktivorous fish, finally driving those stocks to virtual collapse (Figure 1; Daskalov *et al.*, 2008). Instead of recovery to the previous state of high zooplankton and low phytoplankton, this provoked an outburst of *M. leidy*, which

further strengthened the cascade through zoo- and phytoplankton. In the new conditions, a return to the previous state (i.e. that prevailing in the 1960s) was not possible. Since 2000, the *M. leidy* population has stabilized, planktivorous fish have partially recovered and *B. ovata* (a predator of *M. leidy*) entered the pelagic food web. The conclusion is therefore that when structure changes, complex systems are unlikely to recover to their previous state, but will rather adapt to the immediate local conditions. Recent improvements, however, suggest some potential for ecosystem recovery as exemplified by the reverse cascades detected in the mid 1980s and 2000s (see Chapter 4.1).

Modelling studies by Llope *et al.* (2010) demonstrated that increased productivity could be more efficiently handled by a more complex (including viable top-predators) and therefore more resilient system. For that reason, a recovery of the previous 4-levels vertical architecture by rebuilding the top-predators could improve the system's ability to counterbalance fluctuations driven by climate or eutrophication at the base of the food web.

Caddy and Agnew (2004) presented a detailed review of designing and implementing plans for restoring fish stocks and their environment, taking into account ecosystem and regime-shift considerations. They noted that in addition to overfishing, environmental fluctuations or ecological changes can radically affect the possibilities of stock rebuilding from collapses and that regime shifts may have controlling influence on the span of the recovery period. In their paper they reviewed several cases of important long-term fluctuations in stock abundance and catches and commented that while recruitment is limited (due to a low productivity regime), and managers are waiting for favourable conditions for natural rebuilding, stocks should be maintained under the lowest rate of exploitation feasible (in order to sustain a viable reproductive capacity), so as to profit from stock rebounds when the favourable arrives. Caddy and Agnew (2004) carried out a simulation study that confirmed that the expected duration of a recovery plan will be significantly influenced by the duration of unfavourable and favourable regimes, and by the differing probabilities of good recruitment within each regime. In some scenarios the recovery can be much longer than the unfavourable regime itself especially if the probability of good recruitment is relatively low.

## 7. CONCLUSIONS AND RECOMMENDATIONS

The Black Sea ecosystem has proven to be very fragile, especially when stressed simultaneously by several factors (heavy fishing on several species, nutrient discharge, invasive species). Regime shifts and anthropogenic pressure have eroded the ecosystem resilience and created undesirable environmental and social conditions such as depleted fisheries, harmful algal blooms, perturbed biodiversity and ecosystem functions. Building and maintaining resilience is likely to be the most pragmatic and effective way to manage complex ecosystems, followed by the development of adaptive management practices applied by governance structures that are capable of interacting at ecological, social and economic levels (deYoung *et al.*, 2008). Therefore, any attempt to restore the system to a more desirable and resilient state would necessarily require deliberate consideration of the main anthropogenic impacts as well as complex system phenomena such as trophic cascade and regime shifts, but accordingly recovery through new configurations of the ecosystem will require management to adapt consistently.

### Box 3: Elements of an adaptive governance framework for social-ecological systems

**Embracing uncertainty and change.** A well functioning social-ecological system must develop resilience for dealing with external change, such as climate effects, evolving market demands, or changes to economic subsidies and government policies. A resilient social-ecological system could make use of disturbances as opportunities to transform into more desired states whereas vulnerable systems might be overwhelmed by such events.

**Building knowledge and understanding of resource and ecosystem dynamics.** Supporting resilience requires an understanding of ecosystem processes and functions. The knowledge of complex systems and phenomena such as regime shifts is growing, but still needs to be translated from academic monographs to management applications. Management of complex adaptive systems would benefit from the combination of different knowledge systems, such as interdisciplinary research, social-economic analyses, and practitioners' experience including traditional knowledge.

**Developing management practices that measure, interpret and respond to ecological feedback.** Successful management must continuously test, learn, and modify its activities and understanding for coping with change and uncertainty in complex systems. The ongoing fusion between ecology, fisheries science and socio-economics would lead to further development of management that is proactive and adaptive.

**Supporting flexible institutions and social networks in multi-level governance systems.** An adaptive governance framework relies on the collaboration of a diverse set of stakeholders operating at different social and ecological scales. The sharing of management power and responsibility can involve multiple institutional linkages among user groups or communities, from local to international levels. In the specific example of the environmental and fisheries management in the Black Sea area, the involved institutions must cooperate at national level (e.g. governmental and private institutes and agencies, NGOs), regional level (e.g. Black Sea Commission, prospective Fisheries Commission), and broader international scale (e.g. EU STECF, DG MARE, EU Parliament, GFCM).

Source: Modified and amended after Hughes *et al.* (2005)

Recognizing that fishing influences not only fish stocks but also ecosystems is essential for modern ecosystem-based fisheries management. Given the present situation largely characterized by overfished stocks and a degraded environment, management must aim to restore the ecosystems to balanced states with the potential to provide sustainable use of their essential goods and services. Partial recovery is not a stable objective, and further changes (e.g. an unfavourable climate or alien species) may drive the system into the next catastrophic loop. Recovery of a resilient ecosystem should mean restoring all important components into the new desirable state (Gundarson *et al.*, 2002): reducing the anthropogenic impact, normalizing species interactions, buffering trophic cascades, increasing biodiversity and improving environmental quality. Such a state of the ecosystem would provide strategic benefits, such as a clean marine environment, abundant and diverse fish stocks and sustainable economic activities (e.g. fishing, tourism), to a range of stakeholders and society as a whole. Current management practice based on conventional science is often insufficient to deal with complex issues such as ecosystem regime shifts and recovery. Even sophisticated procedures would fail when essential explanatory hypotheses are missing, and management is based on under- or mis-specified models (Peterson *et al.*, 2003). A better strategy would be to extend the scope of possible hypotheses by challenging the existing paradigms and adding new knowledge of the phenomena being observed. Even if resolving ecosystem complexity and implementing a successful ecosystem management system may seem a much more difficult task than traditional single-species management, the state of aquatic living resources and habitats is of such importance that this challenge must be taken up by the involved stakeholders and the society.



DIRECTORATE GENERAL FOR INTERNAL POLICIES  
POLICY DEPARTMENT B: STRUCTURAL AND COHESION POLICIES

FISHERIES

# MANAGEMENT RESPONSES TO REGIME SHIFTS IN MARINE ECOSYSTEMS

NOTE

## Abstract

Regime shifts are relatively abrupt changes in a marine ecosystem that lead to a persistent change in the state of that ecosystem. Human influence on the environment is one factor that has led to marine regime shifts. This note reviews appropriate management responses to regime shifts in marine ecosystems. Recommendations are made to improve our understanding and monitoring of regime shifts and the management of marine ecosystems.

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## LIST OF ABBREVIATIONS

- AO** Arctic Oscillation
- EA** Ecosystem Approach
- EAF** Ecosystem Approach to Fisheries
- EAFM** Ecosystems Approach to Fisheries Management
- EBF** Ecosystems Based Fisheries
- EBFM** Ecosystems Based Fisheries Management
- ENSO** El Niño Southern Oscillation
- FAO** Food and Agriculture Organisation of the United Nations
- FRCC** Fisheries Resource Conservation Council
- GOOS** Global Ocean Observing System
- NAFO** North Atlantic Fisheries Organization
- PDO** Pacific Decadal Oscillation

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## EXECUTIVE SUMMARY

### Background

This study will review the present state of our understanding of regime shifts in the ocean in the context of fisheries management of marine ecosystems. The review will build upon our understanding of regime shifts as they have been observed in many different marine ecosystems, from the tropics to high-latitudes and from the coast to the open ocean. Regime shifts have been identified in all parts of the ocean, at scales from the coral reef to the basin scale of the North Pacific. A regime shift is a relatively abrupt transition from one persistent ecosystem state to another. The change from one state to another can occur within months or years and the ecosystem can stay in the newly established state for many years. The shifts can have very different characteristics and different drivers. There is quite often a preconditioning phase in which the resilience of the ecosystem is degraded. Resilience, an important characteristic of an ecosystem, is the ability of an ecosystem to maintain its state even if disrupted. The greater the resilience, then the greater the disturbance that an ecosystem can absorb without changing state. The resilience of marine ecosystems around the world has declined because of human impacts on the ocean including fishing, climate change and ocean acidification. Overfishing has been shown to directly cause regime shifts, where the disturbance is very intense. Even if the disturbance is not so great, overfishing can degrade resilience such that a regime shift may occur at a later time.

### Aim

The aim of this study is to provide guidance as to how to improve fisheries management in the face of regime shifts. Key characteristics leading to regime shift will be identified. Our understanding of regime shifts, the potential for their occurrence and their impact on marine ecosystems leads to several clear recommendations for the improvement of marine ecosystem management. The note will present approaches to improve awareness, detectability and management, through adaptation and mitigation.

### Key recommendations

There are several different possible actions that should be considered for improved understanding and management of marine ecosystems. We need better monitoring of the ocean conditions associated with regime shifts and an improved understanding of the dynamics and characteristics of regime shifts. Improved awareness of regime shifts should lead to changes in the management of marine ecosystems.

**The ecosystems approach to fisheries should be implemented.** We have sufficient knowledge and information to develop and apply the ecosystems approach to management. Fisheries management in particular must move beyond the single species approach. While some consideration of ecosystem connections is now part of much fisheries management, in practice such inclusion is quite limited and qualitative. Fisheries management plans should directly address issues of ecosystem impact and connectivity.

**Resilience must be included in any ecosystems management strategy.** While a difficult concept, resilience is a fundamental characteristic of marine ecosystems. Its enhancement also fits well with one of the goals of the ecosystems approach, to minimize the impact of human activities on ecosystems.

**There should be greater international coordination of the study of regime shifts and the development of monitoring strategies to identify regime shifts.** Because regime shifts can occur at many different scales, from the local and regional to the basin-scale and perhaps global, it is important that we develop internationally coordinated approaches to the study of and monitoring of marine ecosystems.

**Fisheries management should include consideration of regime shifts and their potential to disrupt ecosystem structures, patterns and distributions as presently observed.** Regime shifts can lead to changes in the function of marine ecosystems and also the distributions of marine organisms. Such changes can disrupt planning based upon a view of the ocean as a fixed and static system. The key characteristics of the regime shifts are well enough known to be included in the large-scale ocean management.

## 1. INTRODUCTION

### KEY FINDINGS

- The development of the concept of **regime shifts** has improved our understanding of how marine ecosystems change.
- **Resilience** is an important aspect of ecosystem function that strongly influences the likelihood of the occurrence of a regime shift.
- **Human activities** in the ocean are generally **disruptive**, leading to a decline in resilience and thus an increase in the potential for regime shifts.

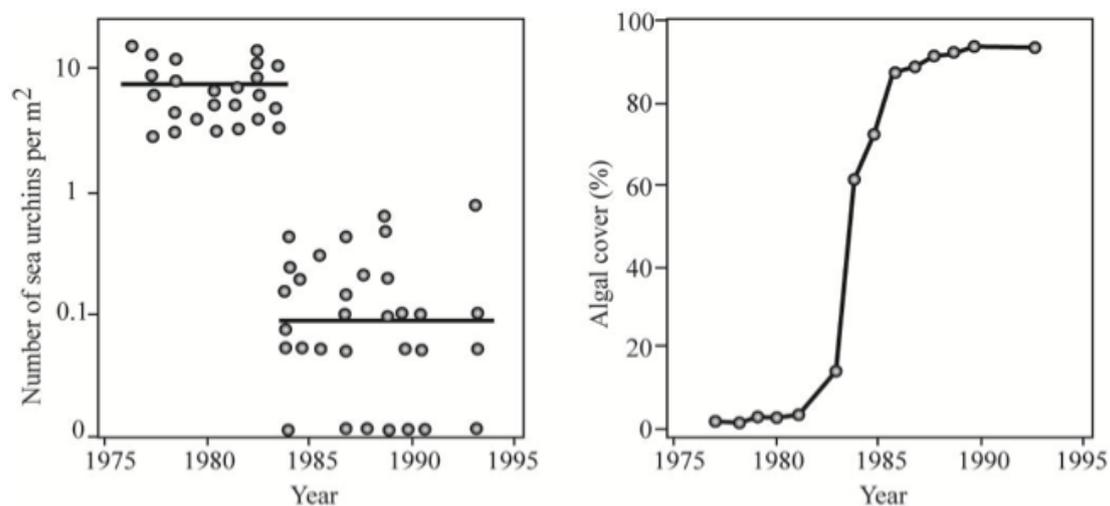
The concept of regime shifts in the ocean is relatively recent, dating back just a few decades (Isaacs, 1976; deYoung *et al.*, 2004). Our developing understanding of regime shifts is tied to our growing awareness of the complexity of the ocean and that ocean stability is less common than was previously thought. Much of our understanding of the ocean, going back to the founding of oceanography in the late 19<sup>th</sup> century, was tied to intermittent cruises that would sample the ocean at widely separated distances with quite limited instrumentation and sampling capability. From these limited measurements developed a rather incomplete view of the ocean. Our perspective on the ocean has since changed with dramatic improvements in our observational capability and the extension of our observational data sets. The instrumentation that we now have allows us to observe many different aspects of the ocean, including the physical, biological and chemical properties of the ocean from quite small to very large spatial scales. For example Argos floats continuously sample the world's oceans on a weekly basis (reference) and have near-continuous satellite imagery from the entire oceans. But perhaps most importantly we now have long time series, spanning many decades, from many different areas around the world, illustrating the shifting behaviour of ocean ecosystems.

Ocean sediments have revealed regime shifts over very long time scales. Baumgartner *et al.* (1992) showed that there have been fluctuations in sardines and anchovies going back two millennia. These records, and others (Chavez *et al.*, 2003), show that there are global scale fluctuations of sardine and anchovy stocks. The mechanism underlying these fluctuations remains uncertain (Alheit and Bakun, 2010) but their existence, first identified almost two decades ago, demonstrated the occurrence of natural, large scale fluctuations in fish stocks at periods from decades (Chavez *et al.*, 2003) or longer. These data showed two important things: first that there is such variability, and second that fish populations can vary, and do so on large spatial scales, even in the absence of human influence.

Further evidence for regime shifts in the ocean also began to accumulate from studies at relatively small spatial scales. Coral reefs in different locations showed dramatic changes following anthropogenic influences that degraded these systems and made them vulnerable because of a reduction in their resilience. The shifts in Caribbean reefs took place after many years of human impact from overfishing on the reefs and eutrophication of coastal waters and degradation of coastal habitat from development. The particular trigger in the Caribbean was a species-specific pathogen that caused mass-mortality of the sea urchin *Diadema antillarum* during the early 1980's. Urchin densities crashed to less than 1% of their original level, triggering a regime shift in the reef community as it became overgrown with brown fleshy algae that expanded because they were no longer subject to such intense grazing pressure (Hughes, 1994). This shift is closely tied to reductions in fish populations from overfishing, with a reduction in fish predation on

urchins that enabled the initial growth of the sea urchin populations. It is not only the collapse of the urchins that is of concern but the impact on the reef itself by the imbalance of an urchin dominated system in which the urchins bio-erode the reef at a rate faster than it can accumulate (Hughes *et al.*, 2005). The dramatic changes in the reef, which are quite visible, and the short time-scale over which the shift takes place (1-2 years), has made them relatively straightforward to document and understand (Figure 1). The new state, after the shift, has persisted in some areas for over twenty years. As noted above, the shift is preceded by a pre-conditioning phase in which human influence on the reef waters reduces the resilience of the ecosystem.

**Figure 1: The Caribbean coral regime shift illustrated by changes on Jamaican reefs. (a) Collapse of populations of the sea urchin *Diadema antillarum* resulting from a pathogen outbreak. (b) Resulting increase in macro-algal cover at 7 m depth.**



Source: deYoung *et al.* (2008)

The existence of regime shifts has been accepted for a much longer time in the terrestrial ecological community (Folke *et al.*, 2004). The demonstration of regime shifts in temperate lakes has been more straightforward (Scheffer, 1997) because of the relative ease with which they can be studied, because of the clarity of the shifts that are observed there, and because they are amenable to experimental study (Carpenter, 2003). The two regimes most commonly considered in these lakes are the clear-water and turbid-water regimes. In clear-water, phosphorous inputs, phytoplankton biomass and the recycling of phosphorous from sediments are all relatively low. In the turbid-water regime, all these variables are high but so too are toxic cyanobacteria, anoxic events and fish kills. In clear-water conditions, higher aquatic plants form on the bottom, stabilize sediments, and provide habitat for fish. These plants may be lost with the shift to very high phytoplankton abundance through shading. With the loss of the bottom plants, waves more easily suspend sediment and phosphorous recycling supports the phytoplankton and helps to support the turbid-water state. The role of fish can be demonstrated by experimentally removing the herbivorous fish and allowing the bottom plants to recover (Schroeder *et al.*, 2005). The mechanisms in deep-water lakes are different but the shift from clear to turbid water is similar (Carpenter, 2003).

Ecosystem resilience was first defined by Holling (1973) as the magnitude a disturbance can experience before it shifts into a different state. He defined engineering resilience as a measure of the rate at which a system approaches steady state after a perturbation, that

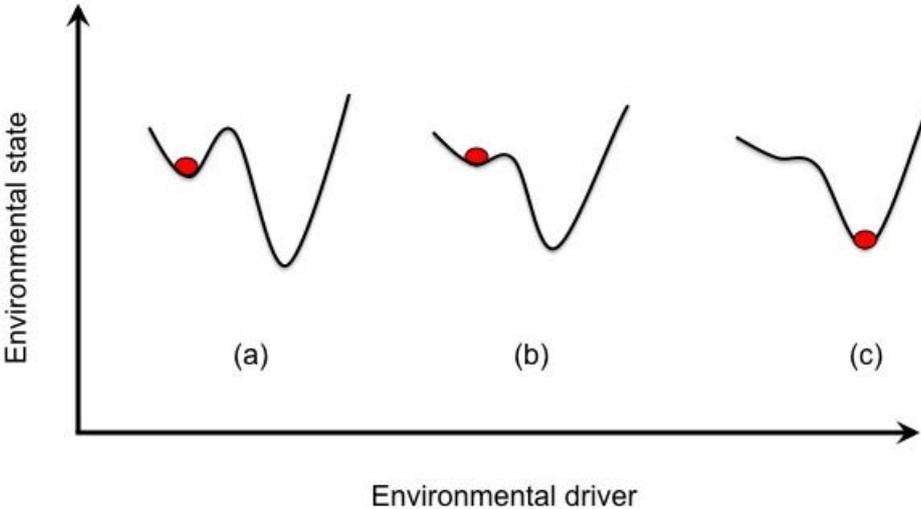
is the speed with which it returns to equilibrium. He later suggested (Holling, 1996) that engineering resilience is less useful as a measure in ecosystems that have multiple stable states or that are driven to multiple stable states. Here we shall follow Folke *et al.* (2004) and define resilience as the capacity to absorb disturbance and reorganize while undergoing change yet retaining essentially the same function, structure, identity and feedbacks. Resilience is a measure of the systems ability to self-organize, or reorganize in response to an external disturbance, and yet maintain the same, or a very similar, overall function.

Marine ecosystems are not static and the issue of regime shifts raises the question of how to define the state of such a complex and complicated system and also the issue of equilibrium dynamics. Mathematically the shift from one equilibrium state to another can be defined but it is increasingly recognized that it may be very difficult to define an equilibrium state with limited data. An equilibrium state may not persist for long enough to enable sufficient measurements to enable easy identification. The assumption of equilibrium dynamics has been inherent to marine studies for so long (Caddy, 1996) that its departure has left many with the challenge of how to describe the particular state of an ecosystem.

One approach to understanding the transition between states (Scheffer and Carpenter, 2003) is to think about how the reduction of resilience influences the stability of the marine ecosystem. Resilience provides stability to the ecosystem. With greater resilience, the ecosystem will undergo less change in response to a disturbance or an external stimulus. For example, a resilient ecosystem (illustrated in Figure 2a) would be a coral reef system that is dominated by coral and not subject to human impacts. Such a system is in a relatively stable position. Small disturbances can disrupt it but resilience will ensure that the system stays in much the same functional state, returning to its initial state following a disturbance. A large disturbance, e.g. a change associated with changing climate, could shift the coral reef ecosystem a new state.

As human impacts on the coral reef system accumulate, resilience declines and the ecosystem is more susceptible to disturbance (Figure 2b). Degredation of the coral reef ecosystem comes from overfishing, coastal eutrophication from runoff containing fertilizers, bleaching from increased ultra-violet radiation and ocean acidification tied to increased carbon dioxide in the atmosphere. The reef may remain in the same state as resilience declines until a disturbance large enough to shift the ecosystem appears. As resilience declines so too does the size of disturbance necessary to cause a shift. A disturbance could be a hurricane, causing damage to the reef from which it is no longer able to recover or a disease that causes a population collapse of the sea urchins allowing the algae to take over (Figure 2c). Once in this new state, it can be difficult for the ecosystem to return to the original state because the characteristics and dynamics of the marine ecosystem have changed. Simply restoring the external environmental conditions, or removing the disturbance that caused the shift, will not ensure the return to the original state. This is another feature often associated with regime shifts; they are not simply reversible.

**Figure 2:** For the figure at the left, before resilience declines, there is a barrier between the two ecosystem states and only very large perturbations would cause a shift between one stable state and another. As resilience declines (b), perhaps because of human influence on the ecosystem, so the barrier between the two states declines. The barrier between states becomes so low (c) that only relatively weak perturbations can lead to a shift to an alternative stable state and return to the original state, in this particular example, is unlikely.



Source: Author

## 2. DETECTION OF REGIME SHIFTS

### KEY FINDINGS

- Regime shifts have been detected in **all parts of the world's oceans**.
- Regime shifts can **encompass all aspects of the ocean ecosystem**, from nutrients to plankton to fish.
- The detection of regime shifts requires **good data and careful analyses** as there is the potential for false identification.

The examples in the introduction reveal some of the variation inherent to marine regime shifts. They vary in complexity, in spatial and temporal scales, in the amount of data available, in the type of ecosystem and in many other ways. So regime shifts can exhibit quite different characteristics. These differences will be important in determining our ability to observe and detect them, to predict them (if that is at all possible) and to manage them. To begin, let us consider the challenge of detection. How easily, how reliably and how quickly is it possible to identify a regime shift? We will review some of the general aspects of this challenge focusing on a few different examples to illustrate the issues of detection.

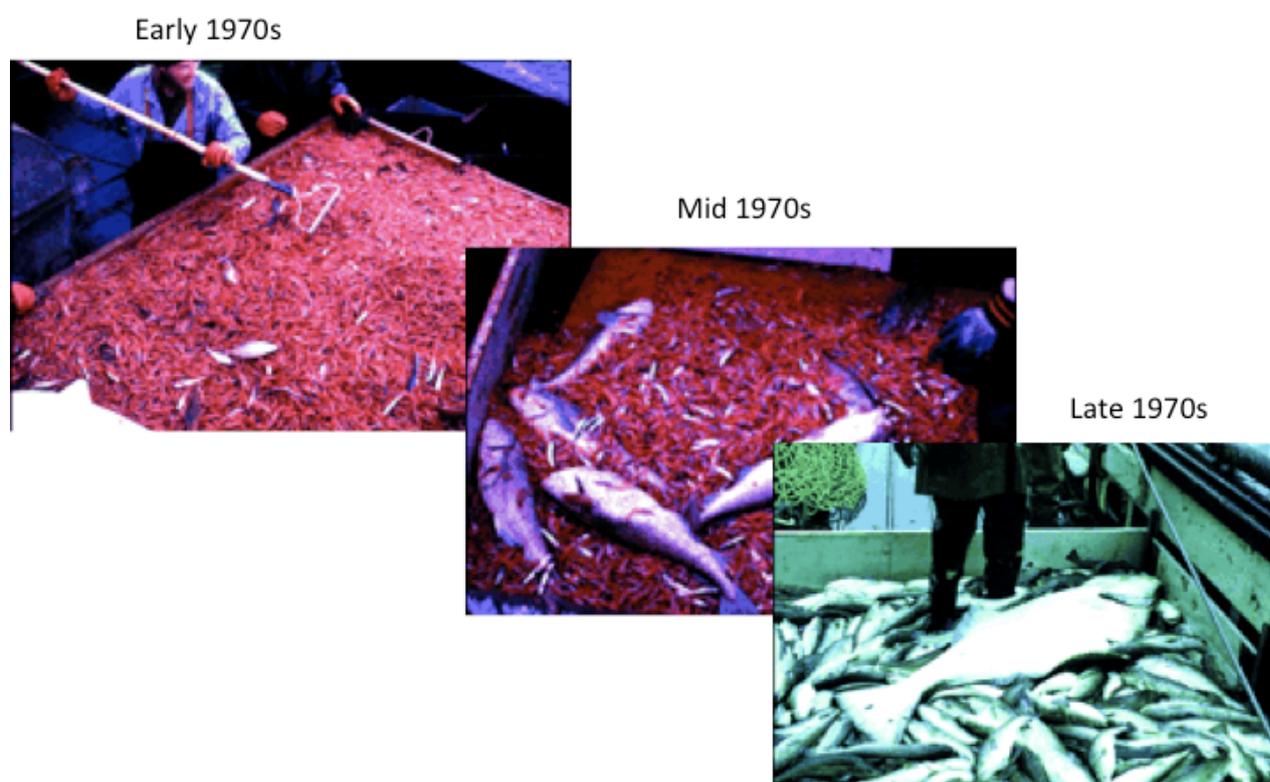
We will structure our review by considering external forcing, the drivers, and the response of the ecosystem itself. This distinction allows us to consider how the forcing agents, such as physical climate forcing or human overfishing, directly influence the biological ecosystem. We will then review three quite different systems: coral reefs, the North Pacific and the North Sea, to see how they differ, exploring the characteristics of the regime, the temporal and spatial scales, our potential for detection and prediction and the management options. In this section we will limit our discussion to the issues of characterization, scaling and detection. In later sections we will discuss prediction and management.

The demonstration of regime shifts in the North Pacific (Hare and Mantua, 2000) stimulated many others to investigate such shifts in the ocean. Many of the initial ocean studies arose out of exploratory data analysis of long-time series looking for correlations and patterns among the many variables that make up an ecosystem description. The Pacific study was particularly challenging, and its success therefore quite important in supporting the concept, because of the complexity and scale of the observed ecosystem shift. The observed shifts take place over a spatial scale of roughly 10,000 km with relatively rapid (a few years) and persistent (many years) shifts in many different components of the Pacific including phytoplankton, zooplankton and fish assemblages (deYoung *et al.*, 2004). Indeed some aspects of the shift are so apparent that they can be demonstrated with a few photographs (Figure 3). There was a shift from a highly productive benthic community of commercially important shrimp and crab to a similarly productive gad population in much of the Bering Sea and the Gulf of Alaska (Anderson and Piatt, 1999). The physical and biological times series provide compelling evidence for strong physical forcing of the ecosystem and the variables brought together clearly show abrupt changes in the marine ecosystem state (Figure 4).

The drivers of the North Pacific regime shift are quite complex, associated with differing aspects of the North Pacific climate system (Overland *et al.*, 2010). The response in the

North Pacific is found throughout the ecosystem, from phytoplankton and zooplankton all the way to fish and mammals (Figure 5). The dynamics of the North Pacific regime shifts appear to be primarily bottom up with relatively little impact of direct human intervention through fishing. The drivers of regime shifts in the Caribbean coral reefs are primarily anthropogenic, including fishing and eutrophication but do also include triggers associated with parasite influences on sea urchins. The response is a shift from a coral to an algal dominated coastal ecosystem. The shifts observed in the North Sea are primarily driven by with changes in ocean climate associated with global warming but are also linked to interannual variability in the North Atlantic tied to the North Atlantic Oscillation and the influence of fishing and overfishing. The response in the North Sea appears to be a combination of bottom up, tied to climate change, and top down, tied to overfishing (see Table 1).

**Figure 3: Changes in species composition of catches in a small mesh bottom trawl in Pavlof Bay, Alaska, through the regime shift of the mid-1970s. The change in the regime is obvious from a period dominated by invertebrates to one in which pelagic fish dominate.**

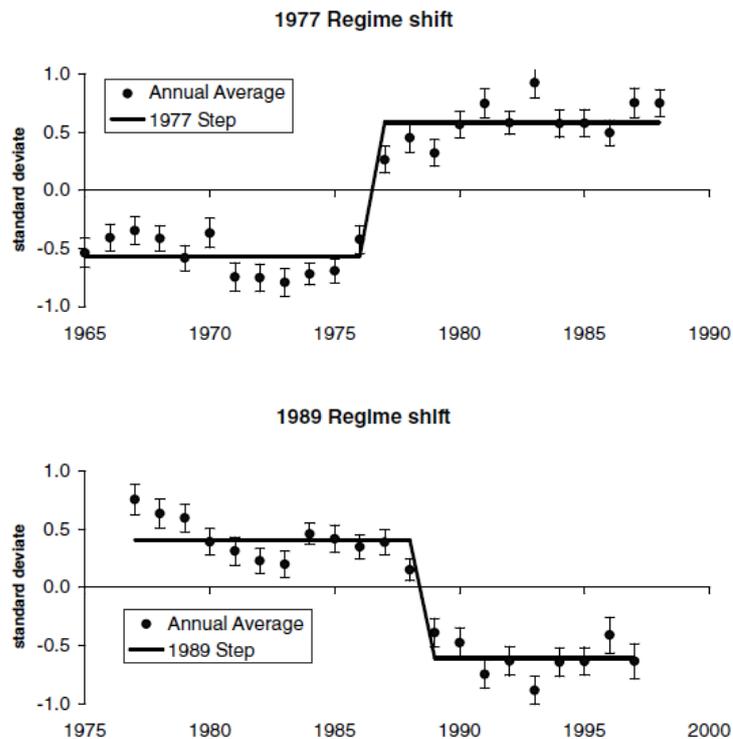


**Source:** Alverson (1992)

The time scales of the different ecosystem responses are often related to the spatial scales. For the North Pacific, spatial scale of the forcing is at the basin scale and while the response is observed over the whole basin as well, many of the response characteristics, such as those in the California Current and in the Gulf of Alaska are more regionally observed, at spatial scales of 1,000 to 2,000 km. The drivers show variability at interannual periods from a few years to a decade. The shift in the response takes place over a few years while the persistence appears to last many years, certainly as long or longer than a decade based upon recent observations (Overland *et al.*, 2006). In coral reef systems, the time scale for the erosion of the resilience is tens of years. The forcing of the regime shift, by a hurricane or the arrival of a parasite, can take place within a year or two. The shift happens quickly, in less than two years, but the persistence is much longer,

for decades at least. The spatial scales of the drivers and the response are tied to those of the reef itself, from 10 to 100 km. The North Sea drivers occur at very large spatial scales, at the basin scale or larger in terms of climate, while the ecosystem response is at the scale of the Northwestern shelf, including parts of the Norwegian Sea and the Bay of Biscay. The erosion of resilience has taken place over several decades. The time scale of the shift is very similar for the response and the drivers and while we know that the persistence of each is quite long, we probably do not know the persistence of the response as the shift is still ongoing. Given the direct link to anthropogenic forcing, we might expect the persistence of the response to be fairly closely tied to that of the driver (Beaugrand *et al.*, 2003).

**Figure 4:** The indices, designed to represent the North Pacific marine ecosystem are made up of one hundred or more variables which are normalized so that they can be combined together. These plots show the resulting composite time series. The step passes through the mean standard deviate within each regime. The standard error of the 100 time series is illustrated for each year.



Source: Hare and Mantua (2000)

In general, regime shifts are most commonly found by exploratory analyses of observations rather than by controlled experimentation (Schroder *et al.*, 2005). The detection of a regime shift is an example of a problem in numerical analysis, looking for a change in a system, in this case a relatively abrupt shift in a marine ecosystem. Most scientific studies (*cf.* Anderson *et al.*, 2009) have looked for evidence of past regime shifts through analysis of existing oceanographic time series. Once identified the challenge is to develop an understanding or a model of the regime shift. Identification of a regime shift through numerical analysis is not always convincing since the observed patterns, like correlations found by comparing time series, may be accidental.

**Table 1: Characteristics of regime shifts in five different marine ecosystems. The drivers and the responses have different values and considerations for each of the characteristics of the regime shift – time, space, detection, prediction and management – that are considered.**

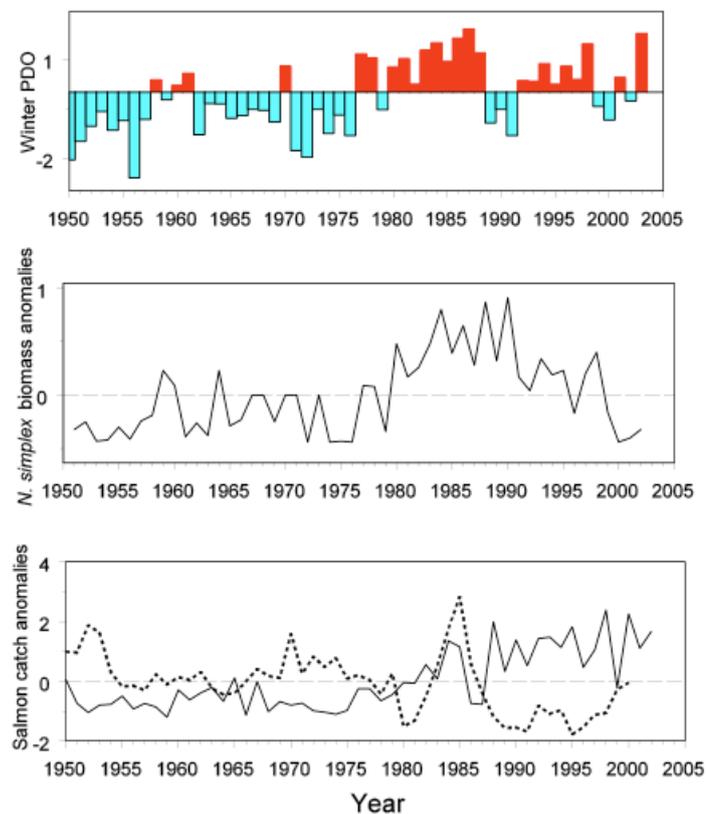
	Regions					
	North Pacific		Coral - Jamaica		North Sea	
	Drivers	Response	Drivers	Response	Drivers	Response
<b>Regime Shift Characteristics</b>	Complex physical climate (AO, PDO, ENSO)	Phyto-Zooplankton to fish and mammals	Fishing Eutrophication Parasites	Algal, coral, fish dynamics	Ocean climate (circulation and temperature) related to NAO and fishing	Phytoplankton to mammals
<b>Time scale</b>	Shift: 1-5 years Persistence: 20 years	Shift: 1-5 years Persistence: > 10 years	Parasite (Trigger): 1-2 years Erosion of resilience (10 year)	Shift: 1-2 years Persistence: 10-20 years	Shift and 1-5 years (NAO) Oceanic persistence – 10 years Erosion of resilience – 10 years - fishing	Shift: 1-5 Years Persistence: > 10 years
<b>Spatial scale</b>	10,000 km (basin)	1,000-2,000 km (regional)	10-100 km	10-100 km	2000 km (fishing, oceanic) to 10,000 km (atmospheric)	Up to 1000s km
<b>Detection</b>	2 years	3-5 years	< 1 year	1-5 years	5 years	1-5 years
<b>Prediction</b>	Little skill	Follows from detection and persistence	Erosion fishing impact is predictable Trigger – no	Little skill, probabilistic	Physical shifts are predictable, erosion to effects of fishing	Follows from detection, via Geographic shifts predictable
<b>Management</b>	Not possible	Adaptive fisheries management after detection - adaptation	Marine management of resilience and trigger >> prevention	Not possible (limited erosion of resilience from fishing)	Climate – only at the large scale; fishing erosion can be regulated	Fishing management after detection

Source: Author

What data should be used for the analysis of a regime shift in the ocean (Ibañez and Beaugrand, 2008)? Three different types of data are typically considered: meteorological, physical oceanographic and biological oceanographic data. For a broader analysis, social and economic data could also be considered. It is often a challenge to find time series covering the full period of interest that are both complete and of sufficient quality. Some of the necessary time series are only a few decades in length, often with critical gaps. Few data sets extend beyond sixty years (the end of the second world war), even fewer date back to the 19<sup>th</sup> century. Thus we are often limited by the length of the time series in looking for processes that can persist for decades. One of the problems in fisheries data is that very little of the data is collected independently. While the quality of oceanographic data collected within a fishery can be very high, the confounding of the data and the activity of the fishery can lead to bias that makes interpretation of the results quite difficult (Rotherham *et al.*, 2007). All these issues, and problems, with the data need to be considered in the analysis.

**Figure 5:** Example of northeast Pacific ecosystem conditions since 1950, illustrating the regime shift of the late 1970s.

(a) Winter (January-February-March mean) Pacific Decadal Oscillation (PDO) index. (b) Biomass anomalies for the euphausiid *Nyctiphanes simplex* in the California Current System as an indicator of plankton biomass. (c) Pacific salmon catch anomalies for pink salmon *Oncorhynchus gorbusha* (solid line) in southeast Alaska (lagged 1 year to match year of entry into the ocean) and Chinook salmon *O. tshawytscha* (dotted line) in Washington, Oregon and California (lagged 3 years to match year of ocean entry). Whereas the PDO shows a series of mostly above average values since the late 1970s, which includes substantial interannual variability (a), the biological time series clearly show changes from the first half of the record, with the euphausiid biomass index showing negative anomalies until the late 1970s after which the anomalies are positive for more than a decade. The salmon catch data show a somewhat later shift, with a decline in the catches of Chinook by the mid-1980s roughly coincident with an increase for pink salmon.



**Source:** The North Pacific Marine Science Organization at <http://www.pices.int/publications/> from records compiled by the North Pacific Anadromous Fish Commission, as makes salmon data available [special\\_publications/NPESR/2005/npesr\\_2005.aspx](http://special_publications/NPESR/2005/npesr_2005.aspx)

The most common technique in regime shift analysis is that used by Hare and Mantua (2000) in their analysis of the North Pacific time series. They took about a hundred different time series, normalizing each one by the variance so that they could be combined together. The result (Figure 4) is a time series of an index made up of many different variables. At each point in time one can calculate the standard error to help in the

determination if any observed shifts are statistically significant. Such an approach is quite straightforward with the biggest challenge being the selection of the variables. It is possible, however, for this approach to produce false positives (Solow and Beet 2005, Overland *et al.*, 2006) because of the low-frequency characteristics of oceanographic data. It can be shown that if you apply this approach to different time series with the low-frequency characteristics (long period) typical of oceanographic data then it is possible, depending upon the time series, to produce abrupt transitions even if there is none present and that the characteristics of the transition will change simply by choosing different time series. For the North Pacific time series, Anderson *et al.* (2009) showed that using a very different approach confirms the presence of the shift so the North Pacific result is not an artifact. The North Pacific shift can be clearly seen in individual physical and biological time series and there is general agreement that the analysis approach of Hare and Mantua (2000) does work for this particular problem. In general, no matter what technique is applied, it is possible that random time series, brought together, can demonstrate a false positive (Rudnick and Davis 2003). Careful statistical analysis and proper and conservative interpretation of the data themselves are necessary to minimize the potential for such mis-diagnosis.

In reviewing approaches to the determination of a sudden change in a system, which could be ecological or economic, Anderson *et al.* (2009) note that most of the techniques are commonly known in statistical analysis. Depending on the field of study these changes can have many different names such as regime shift, abrupt change, tipping point, break point or ecological threshold. Essentially all these different labels apply to the same phenomenon. Application of these techniques requires careful consideration of the data and attention to limitations of the technique itself.

Principal component analysis, or empirical orthogonal functional analysis, involves bringing together the time series to look for the basis functions that underlie the variance structure of the data (Jolliffe, 2002). More robust than a simple linear combination of the time series, this approach also allows for statistical analysis of the resulting functions that are found to determine when a truly meaningful pattern is found. It is still necessary to conduct statistical analysis of the resulting time series to determine if the shift or jump is statistically significant. Hare and Mantua (2000) also applied this technique to confirm their results. One limitation of this technique is that it can only be applied to linear problems, although there is an extension of the technique that can be applied to non-linear ones (Hsieh, 2009).

Common to many of the mathematical approaches is the need to look at a change in the mean of the time series, looking for a change in the mean state (Mantua, 2004). It is also possible to look at higher statistical moments, such as the variance or the skewness since it is not only the mean that can change (Rodionov, 2005). There is no fundamental difference in the approach to analyzing the variance rather than the mean. Most of the analyses that have been conducted to date have been on the mean rather than the variance.

No matter the technique applied, most regime shifts cannot be identified until after they have begun. The time lag between the shift and its identification will depend on the availability of data, the strength of the shift and its complexity. A shift such as observed in the coral reef systems is relatively easy to identify because it is so dramatic. Identification will be more difficult, and we can expect that it would be relatively delayed, in systems such as the North Pacific, where the shift can take many different forms, occurs over such large scales, and includes so many different ecosystem components. The North Pacific shifts were not identified until several years after they took place (Overland *et al.*, 2008).

But what about prediction of a regime shift? In the absence of a forecast model, of which there are few to none, is it possible to identify a regime shift before it occurs? Recent work suggests that variance and skewness may be indicators of a coming shift (Guttal and Jayaprakash, 2008; Biggs *et al.*, 2009). While it has yet to be applied in practice, two different model simulations have shown that the variance of key ecosystem variables rises in advance of a transition. Not all components of the ecosystem, not all variables will show the change in variance, or change at the same rate. The idea is that there are slowly changing variables, such as human developments in coastal system, that are pushing the system towards a shift, but there are fast variables, such as nutrient recycling, that respond to the slow changes more quickly and exhibit changes on much shorter time scales, and hence demonstrate increased variance as the system slowly moves towards a regime shift in response to the slowly changing driver. Separating out the dynamics of the slow and fast variables, and the driver and response dynamics is crucial for this predictor to be effective.

Carpenter and Brock (2006) used a simplified model of phosphorous and lake sediment to show that the variability in the phosphorous increased in advance of the shift in the lake dynamics, in advance of a regime shift. They note that lake phytoplankton variability is observed to increase in lakes before a regime shift and that such an increase in variability could be a useful indicator of a coming shift. They found that the variance was a predictor of the shift by as much as ten years. Guttal and Jayaprakash (2008) found that skewness could provide as much as five years early warning. Biggs *et al.* (2009) used a simplified model of fish interaction in which there were two controllable variables, fishing pressure (which could be reduced quickly) and shoreline development (which could only be gradually adjusted). They found large changes in the variance, skewness and kurtosis associated with the regime change but the changes in the indicators before the shift were difficult to identify as tied to the shift. In their model, the impact of the shift could be mitigated by adjusting the quick variable (fishing) but not with the slow variable (shoreline development). They also find that skewness can vary in the absence of a regime shift and thus that false positive identification of a shift is possible if care is not taken.

Another potential advantage in exploring the statistics of individual variables is their potential for identifying regime change that is a result of increased external forcing rather than reduced resilience. Guttal and Jayaprakash (2008) show that the skewness works as a predictor even if the regime change is a result of an increase in the amplitude of the driver rather than a decline in the resilience of the ecosystem. In this sense skewness, and perhaps other statistical indices, are relatively robust predictors.

It appears that the timing of the shift, from one state to another, determines the potential for statistical prediction of a coming regime shift. The skewness and variance increase as the ecosystem approaches the transition state. Thinking back to Figure 2 and the balls, as the resilience declines, the steepness of the well also declines and at the same time the curve will demonstrate more asymmetry as it becomes wider thus allowing for asymmetry in the temporal dynamics of the ecosystem indices, if the environmental forcing is strong enough to push the ecosystem from one side of the well to another. As the resilience decreases and this well flattens out, the potential for a given amount of forcing to generate this asymmetry, or skewness, increases. But if the transition happens very quickly there may simply not be enough time for the ecosystem to demonstrate this behaviour and the ecosystem will appear to have jumped from one state to another before the statistical character has had time to change. In such a case, none of the statistical markers (variance, skewness, kurtosis) will provide a useful forecast of the coming shift.

There is much to be learned about the structural dynamics of ecosystems and their behaviour as they move from one state to another. While prediction appears possible even in the absence of an understanding of the dynamics associated with a regime shift, it is unlikely that confidence in such predictions will be high unless we can provide some explanation of the behaviour that we appear to see tied to the statistical indices. While simpler models of ecosystems clearly have limitations, they do nonetheless provide useful tools for the assessment of particular characteristics of nonlinear ecosystem function. Controlled experimentation, which is possible numerically, is very difficult in the field and not at all possible for historical data.

### 3. CHARACTERISTICS RELATED TO PREDICTABILITY AND CONNECTIONS TO FISHERY COLLAPSES

#### KEY FINDINGS

- The **prediction of a regime shift is difficult** and unlikely in general but is possible in some particular situations.
- Fishing can cause the **decline in ecosystem resilience** that enhances the potential for the development of a regime shift.
- After a regime shift, the **marine ecosystem may not return to its original state** and even if it does the process can take a long time, decades or longer.

While prediction of a regime shift appears possible, so far this has not been demonstrated nor has such a prediction been used in fishery planning or management. There have, however, been several different fisheries in which a regime shift has taken place associated with a fishery collapse. So we can look at how regime shifts influence fisheries and how fisheries influence regime shifts. How have these collapses developed and in particular what has been the role of anthropogenic forcing, through overfishing or some other environmental influence, on the collapse? Once we have identified the issues linking regime shifts and fisheries we will explore the implications for management in the next section.

Perhaps the most dramatic fisheries collapse in recent decades is the near-disappearance of the Northern cod (*Gadus morhua*) on the Newfoundland shelf and the associated collapse of the groundfish stocks on the Canadian continental shelves of the Northwest Atlantic (Kurlansky, 1998). While there is little doubt that overfishing was the proximate cause for the fishery collapse (Hutchings and Myers, 1994), there is also general agreement that poor environmental conditions influenced the productivity and distribution of the stock and played a role in the decline (Rose *et al.*, 2000, Colbourne and Anderson, 2003). Nearly twenty years after the collapse there has been no real recovery of the different stocks of groundfish, and cod in particular remains at very low levels (Hutchings and Ranglely, 2011). Bundy *et al.* (2008) applied a mass balance model to show that the near complete removal of groundfish in this region led to a trophic cascade which shifted with a notable increase in forage species (including capelin, herring and shrimp). The particular forage species that increase does change around the region but there is a clear pattern of changing ecosystem structure. Indeed there is now talk of a substantial seal cull to 'rebalance' the ecosystem (FRCC, 2011). On the eastern Scotian Shelf, Frank *et al.* (2005) show that the trophic cascade extends from top predators, through forage species down to zooplankton, phytoplankton and nutrients. Overfishing in the Northwest Atlantic was so extreme that it forced a regime shift, changing the fundamental character of the ecosystem.

The Black Sea offers an example in which human influence has reached nearly every level of the ecosystem. Over the past thirty years there has been a collapse of the predatory fish stocks (Daskalov, 2002), an invasion and widespread expansion of the ctenophore *Mnemiopsis leidyi*, and phytoplankton blooms that have led to hypoxia and the loss of benthic communities (McQuatters-Gollop *et al.* 2008). It is generally accepted that eutrophication, from runoff, was the primary driver, together with fishing, of the shift in the Black Sea that began more than thirty years ago. In recent years, there has been

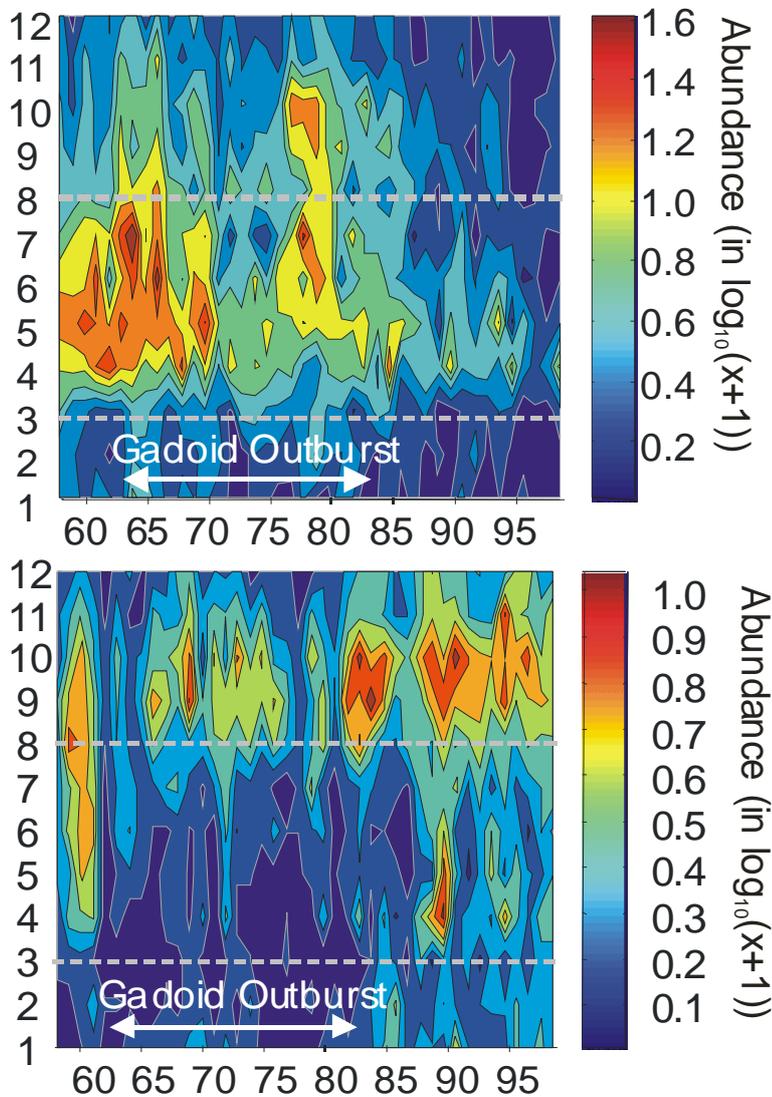
some improvement, notably with an increase in the ratio of diatoms within the phytoplankton community, a decrease in the number of algal blooms, in the overall phytoplankton abundance and in the area of hypoxia (McQuetters-Gollop *et al.*, 2008). While the changing human impact on the Black Sea has been the primary driver there, McQuetters-Gollop *et al.*, (2008) show that climate change, in particular the cooling of the winter of 2001, and the overall decline of phytoplankton abundance that has taken place associated with overall global warming (Behrenfeld *et al.*, 2006) have also been influential. While the regime shift was driven anthropogenically, the recovery from it does appear to have an environmental component.

The Baltic Sea has undergone a number of transitions over the past one hundred years. As with many semi-enclosed seas, depressed oxygen levels tied to eutrophication have shifted the structure of the Baltic in which the narrow straits at Denmark control stratification and salinity. Cod (*Gadus morhua*), herring (*Clupea hareng*) and sprat (*Sprattus sprattus*) are the dominant fish in this species-poor sea which has a mixture of marine and freshwater species. Over the past century there have been large changes in the relative abundance of mammals (seals), demersal fish (cod) and pelagics (herring and sprat). A century ago the Baltic was an oxygen-rich, clear water system favourable to cod (and clupeids) that were the primary prey for seals (Österblom *et al.*, 2007). With developing land use going back more than a century, agricultural fertilizer substantially added to the nutrients (Hoffmann *et al.*, 2000), leading to a fairly dramatic decline in oxygen in the deepwaters of the Baltic in the early 1950s (Österblom *et al.*, 2007). It is the shift from the oligotrophic to the eutrophic state that is the primary regime shift in the Baltic fundamentally changing the condition for fish in the Baltic. The other changes that we have seen lay on top of this fundamental shift. Cod were able to expand in spite of poor hydrographic conditions in the 1960s and 1970s, because of reduced seal predation, but overfishing in the early 1980s dramatically reduced cod abundance. Present management plans call for a shift in the exploitation targets (MacKenzie *et al.*, 2011), with the removal of spawner biomass targets and a shift to exploitation targets rather than limits. It remains to be seen if these management changes together with other conditions that appear to be changing favourably (declining eutrophication and low predation from seals) will permit cod to recover in abundance.

Determination of a regime shift can require not only careful consideration of the variables to be analysed but also attention to the treatment of the variables. Thus two researchers, working with the same data set, can appear to come to quite different conclusions. For the North Sea, analysing for the total abundance of Calanoid copepods – *Calanus finmarchicus* and *Calanus helgolandicus* – Taylor (2002) was unable to find any evidence for a regime shift. Starting with the same data, but looking at the individual species and looking at changes in species abundance through the year, Beaugrand (2004) was able to clearly demonstrate two different regime shifts that took place centered around 1982-1985 and 1987-1988 (Figure 6). The total number of copepods is not a good marker because the abundance of *Calanus finmarchicus* decreases while the abundance of *Calanus helgolandicus* increases (Beaugrand, 2003; Reid *et al.*, 2003). Although many variables, from phytoplankton diversity to fish abundance, did show a step-wise change, a marker of a regime shift, not all indicators or components of the ecosystem demonstrated such a change. Beaugrand (2004) argues that the change in the North Sea was a result of large-scale, hydro-meteorological changes. In essence warming on the European shelf, through the late 1970s and 1980s, led to a change in the species composition in the North Sea. Cold water copepods (i.e. *Calanus finmarchicus*) declined in relative abundance and warm water copepods (i.e. *Calanus helgolandicus*) increased in relative abundance. One might think that these organisms, which are similar in size and appear to offer quite similar predator-prey roles within the ecosystem, are so similar that this shift would have no

ecological influence, but there is actually a significant difference in the annual development cycle of these two organisms. The peak in abundance of *C. finmarchicus* occurs in the spring while that for *C. helgolandicus* occurs late in the fall. This shift changes the timing of food that will be available for fish larvae. The survival of young cod in the North Sea depends on the abundance, seasonal timing and size composition of their prey (Brander, 2010). Beaugrand (2003) notes that the period when *C. finmarchicus* is dominant corresponds to the period of the gadoid outburst, when gadoids abundance increased dramatically in the North Sea. Changes in conditions since the late 1950s have resulted in increased survival and good recruitment of cod throughout the 1960s and 1970s and then a progressive decline over the past 30 years (Beaugrand *et al.*, 2003).

**Figure 6:** Abundance in the North Sea region of two key zooplanktoners (a) *Calanus finmarchicus* and (b) *Calanus helgolandicus*. The data are from the continuous plankton recorder. The period of the gadoid outburst, when cod and other gadoids greatly increased in abundance is shown.



Source: Beaugrand *et al.* (2003)

In biological oceanography the balance between top-down and bottom-up effects has long been debated, with the new concept of wasp-waist systems added to the discussion (Hunt and McKinnell 2006). Here the focus is on how anthropogenic forcing at the top of the ecosystem (e.g. through fishing removals) competes with bottom up influences through such effects as coastal habitat degradation or the addition of agricultural fertilizers leading to eutrophication. The Baltic Sea and the Black Sea show two regions in which both these effects are at play at once, with each influencing the observed shifts that have taken place there. In general, though, it would be useful if we could understand how far we might expect these drivers to propagate through a trophic foodweb. It is only by disrupting marine ecosystems, as we have across the planet, over the past century, that we are able to see how marine ecosystem will respond to strong forcing at the top and the bottom end of the food chain. Frank *et al.* (2005) in a review of the North Atlantic show that either temperature or species richness reveals the extent to which ecosystems are either top-down or bottom-up. Species richness generally increases with temperature so either temperature or species richness seems to work. Of course in some systems, the ecosystem is neither and there is the potential for interplay between the two effects. This is particularly relevant to fisheries management since it suggests that the resilience to top-down effects, e.g. from fishing predation, could be assessed, through a determination of species richness. This would provide a marker to determine the susceptibility to marine ecosystem effects associated with fishing.

## 4. IMPLICATIONS FOR MANAGEMENT

### KEY FINDINGS

- **Classical fisheries management**, with a focus on the population dynamics of a single species, **is inadequate** to respond to regime shifts.
- The **Ecosystems Approach to Fisheries (EAF)** is a necessary improvement required for fisheries management.
- The **enhancement of resilience** should be a central goal of fisheries and ocean management.

The management of fish resources has been undergoing a period of dramatic shift from its post-war growth phase to the relatively recent changes following a sequence of fishery collapses. Many of the collapsed fisheries were, apparently, being managed properly following modern principles of single species management (Hutchings *et al.*, 2010), yet still the collapses took place. These collapses have led many to question the fundamental principles of single species management. Quite provocatively, Worm *et al.* (2006) have pessimistically described the present state of fisheries management, noting the remarkable percentage of managed fisheries in decline and assessed as overfished. They forecast that the fisheries are declining at such a rate that commercial fisheries will collapse by 2048. While accepting the dismal state of many fish stocks, and the challenges faced by fisheries managers, there has been much criticism of such apocalyptic pronouncements, both because of the underlying scientific approach to the discussion (Hilborn, 2006), and the particular forecast itself (Longhurst, 2007; Daan *et al.*, 2011).

Classical fisheries management, which developed in the 1950s and 1960s, was built primarily on population models of single species (Hilborn and Walters, 1991). The initial success of the single species modeling spurred great interest in their application to fisheries management, since they were able to demonstrate many dynamical characteristics of populations subject to fishing mortality. They also seemed to be ideal models for fisheries management because relatively few measurements were required, or so it seemed, for their application. Unfortunately fisheries managers relied too heavily on such models with too little consideration of their limitations, both in the sense of the data used to setup and verify the models but also the features of the fishery and the ecosystem that were not included in the model.

Fisheries management has over the past few decades begun to pay at least some qualitative attention to the environment and in some cases explicitly include multi-species interaction. There has been a growth in awareness of the limitations of the models being used in fisheries management and a substantial expansion in our ability to observe and model other aspects of the fishery ecosystem. These developments have led to the Ecosystem Approach to Fisheries - EAF (FAO 2003). While there is general agreement that a new approach to fisheries management is needed, and that some form of ecosystem approach is necessary (Pikitch *et al.*, 2004), there still remains much disagreement as to what is included and indeed even what to call it (with an alphabet soup of names including EBFM, EAF, EAFM, EA and others *cf.* Ward *et al.*, 2002). The EAF has two fundamental goals, first to minimize human impact on marine ecosystems, recognizing that degradation of the ecosystem is itself bad but that such impact also has unintended consequences for other human use. The second goal of the EAF is to account for the requirements of other

components of the ecosystem in management. Some argue that all components of the ecosystem and human use (e.g. fisheries, mining, recreational use, transportation etc.) should be managed together, while others suggest that such complete ecosystems approaches are too complicated and impractical, and that the focus should be on fisheries and the inclusion of ecosystem issues to ensure consideration of ecosystems services in the management of a single or perhaps multiple species.

Some countries are much further ahead in the development of the EAF, notably Norway and the USA, and perhaps Australia, Canada, Iceland and South Africa (*cf.* the report card assessment by Pitcher *et al.* (2010)). While these countries have begun to move ahead, none of them have a fully operational management strategy. In most cases, in practice, the EAF is applied on a fishery by fishery basis and is not fundamental to the development of all fishery management plans. Thus it remains a rather haphazard and occasional development. In Canada, for example, while there have been recommendations for expanded application of the ecosystem approach (*cf.* FRCC, 2007) only components of the approach have been generally applied and no fishery fully follows the ecosystem approach. Nonetheless these developments in fisheries management already bring many of the issues tied to regime shifts in the ocean to the attention of fisheries managers and force their consideration.

The complexities of ecosystems, and the character of regime shifts, add to the uncertainty of fisheries management. So, regime shifts are just one of the characteristics of ecosystem behaviour that are used to support the case for the development of an ecosystem approach to fisheries. They are an extreme outcome of the complex interactions that make up marine ecosystems; however, even without regime shifts there would be good reason to move towards the EAF. But regime shifts do make a compelling case for ecosystem based management both in that it should enable possible prevention of regime shifts and for adaptation if one should develop. For prevention, the central issue is to enhance resilience, which is also associated with one of the fundamental goals of the ecosystems approach to fisheries, to minimize anthropogenic influences on marine ecosystem. Enhancement of resilience will help to minimize the potential for regime shifts and is particularly important given the growing number of ways in which we are degrading or affecting marine ecosystems. Climate change (Brander, 2010) and ocean acidification (Denman *et al.*, 2011) are just two of the most obvious trends leading to change in the ocean. There is a lot of evidence for changing biogeographic patterns tied to climate change, e.g. the North Sea shifts leading to a regime shift (Beaugrand, 2004), and coral reef systems around the globe have been influenced by the growing acidification of the oceans. While it is clear that the ocean will continue to acidify in the coming decades, and it is expected to negatively influence marine organisms, the extent of the impact remains uncertain (Denman *et al.*, 2011).

Awareness of regime shifts is the first step in adaptive management and is typically a component of the EAF. It does require more than a simple openness to the idea. In practical terms it means that there should be active programs to ensure that adequate data is being collected from the ecosystem and also that analysis takes place with the explicit goal of looking for regime shifts. Active research programs should underlie both components of this strategy since for many regions we have little understanding of the possible form regime shifts might take and therefore little awareness of how we should, or could, effectively monitor ocean conditions. In those systems where the time-series are short it may be several years, or longer, before it is possible to identify a regime state or shift. Adaptation requires determining how the character or productivity of marine management regions may have changed. For a simple biogeographic shift, it could be that there are winners in one region (where fish appear) and losers in another region (from

which the fish have moved). Such a situation could lead to an increase in catch in one zone, and a decrease in another. As an example on the eastern Scotian Shelf in the early 1990s there was an influx of capelin and snow crab, likely from across the Laurentian Channel and the Grand Banks. The spread was tied to the cold-water conditions of the early 1990s, which also led to the redistribution of cod during this same period (deYoung and Rose, 1993; Rose *et al.*, 2000). Fisheries managers for the Scotian Shelf saw the influx of a species not seen before as an anomaly, and rather than treat it as a shift leading to the development of a longer-term management plan, they setup a fishery with the explicit goal of fishing out the 'invading' species.

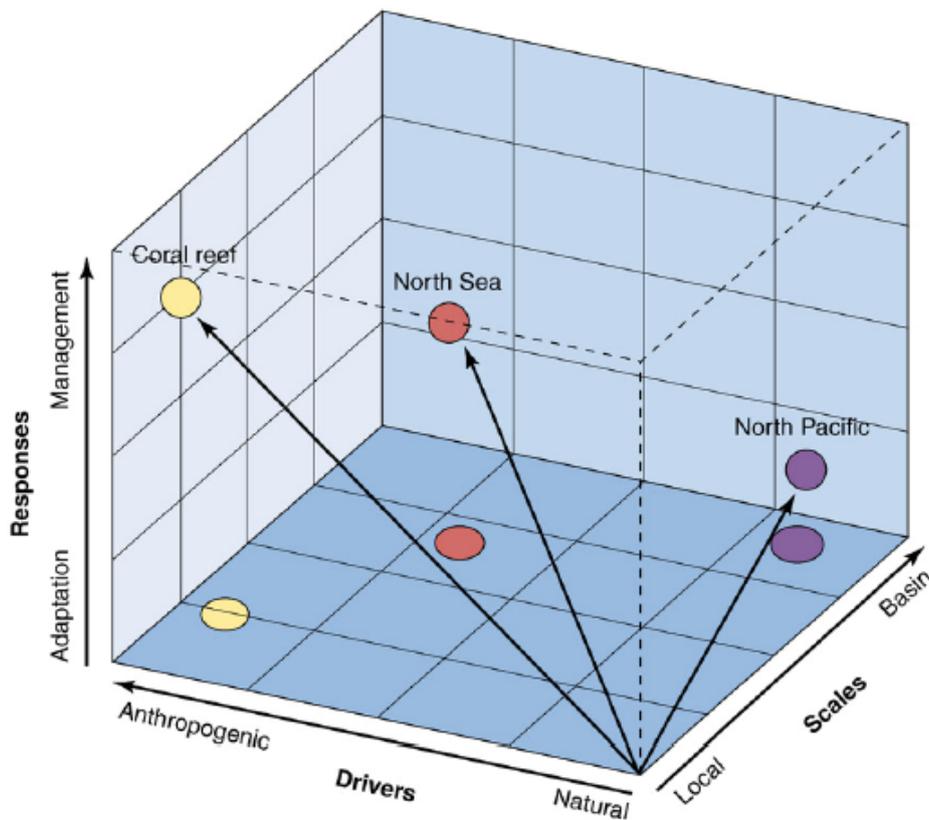
If the regime shift includes a change, either a decrease or an increase in productivity, then this too could involve either a positive or negative management response. Two issues will determine the management challenge of decision making, the confidence associated with the regime shift assessment and the impact or scale of the change (see Figure 7). Thus decision making should be tied to a risk assessment in which risk is tied to the probability times impact. For regime shifts, the convolution is built on the confidence times the degree of the change or shift. The greater the confidence and the greater the size or impact of the shift then the more compelling will be the case for a change in management. If the confidence is low and the change is also seen to be small then the case for a changing the management strategy will be weak.

What are the long-term effects of overfishing on the marine ecosystem? Even in the absence of a regime shift the impacts of overfishing, accumulated over many years, are now clearly seen to be much greater than was previously thought. Hutchings (2000) found that 5–15 years after declines of 50 and 80%, gadid and other non-clupeid populations, on average, have increased marginally or not at all. It may be that some shorter lived species, such as herring or capelin, can bounce back more quickly, but stocks such as the Northern cod in the Northwest Atlantic have exhibited recovery times that are many times the average age of the fish (Hutchings and Rangeley, 2011). Overfishing thus poses two direct threats, the potential for very long-term declines of a stock, and the possibility of a regime shift that will influence other ecosystem services.

Adaptive management is aimed at integrating existing interdisciplinary information into dynamic models that attempt to make predictions about the impacts of alternative policies (Walters 1997). For marine fisheries, various simulation studies have examined what constitutes an optimum adaptive management strategy for resources that undergo regime shifts. One possible approach is through the application of regime-specific harvest rates (King, 2005; Polovina, 2005). Simulation work has demonstrated the value of this approach, particularly for short-lived species (species with life spans shorter than the duration of the adverse conditions) (McCall, 2001). The most effective approach is to set such rates as part of a decision-rule framework, associated with timeframes for a management response that is triggered when there are indications that a regime shift has occurred. The first step in such a response is the identification of a regime shift. A provisional stepwise approach to changing harvest rates could be applied in which, for example, harvest rates decline given the uncertainty of the shifting state of the ecosystem, until the productivity level of a new regime has been verified. Simulation work indicates that improved management results could be achieved even if the switch in harvest rates did not coincide with the regime switch but lagged by the age of recruitment to the fishery of the given resource (Miller and Munro, 2004). This is useful because, in addition to delays in recognizing the shift, the implementation of any management action can often be delayed by scientific uncertainty, stakeholder pressure or institutional resistance (Schertzer and Prager, 2007).

**Figure 7: Phase space for drivers and responses of regime shifts.**

Regime shifts can be differentiated based upon their spatial scales (local or basin), their drivers (natural to anthropogenic) and the potential for human responses (from adaptation to management). The three regime shifts discussed in Chapter 2 are plotted in this three-axis system. Plotting regime shifts in this phase space differentiates those shifts, which are naturally driven, and for which there are few management options (the North Pacific) from those which are much more influenced by human activity and for which management options do exist (coral reefs). The North Pacific is an example of a regime shift that is almost exclusively naturally driven, the corals almost exclusively anthropogenically driven and the North Sea a combination of the two drivers.



Source: deYoung *et al.* (2008)

Alternatively, assuming that regime shifts are fundamentally decadal to multi-decadal events, a two-level management strategy has been suggested (Fréon *et al.*, 2005) combining a conventional single-species management to deal with short-term fluctuations with a long-term ecosystem management strategy (e.g. driving fishing fleet capacity and investment cycles). Because the response of long-lived marine species, such as cod, to regime shifts is likely to be slower or lagged compared to the response of short-lived species, such as anchovy, maintaining an appropriate age structure in spawning stock biomass should be a major management goal to develop resilience to regime shifts (King, 2005). Where shifts involve a change in dominance between species, such as the anchovy and sardine fluctuations that are observed in both the Atlantic and the Pacific (Schwartzlose *et al.*, 1999), management procedures designed under the assumption of out-of-phase sinusoidal trends in species abundance are more effective than are traditional modeling approaches (de Oliveira, 2005), particularly if the fisheries interact. Such approaches have not yet been implemented and appear to be strongly sensitive to the amplitude of regime cycles (de Oliveira, 2005).

## 5. ECOSYSTEM RESILIENCE AND OVERFISHING AND IMPLICATIONS FOR INTERNATIONAL PLANNING

### KEY FINDINGS

- The **definition and measurement of resilience** will be necessary to ensure effective management.
- Regime shifts could **lead to the large-scale redistribution of marine species** and this potential should be considered in fisheries management and international planning.

### 5.1. Ecosystem resilience and links to overfishing

The importance of resilience for the stability and maintenance of ocean ecosystems is now clear. For many years, it was assumed, with little evidence, that the impact of overfishing was limited to the targeted species and also that variability in the marine ecosystem was unlikely to influence fish stocks in a way that would strongly influence fish catches. We know now that none of these assumptions are correct (Folke *et al.*, 2004).

The possibility of a regime shift should encourage management of marine ecosystems that is geared toward developing resilience, understood as the capacity of a system to absorb disturbance and reorganize itself while undergoing change so as to retain essentially the same function, structure, identity and feedback mechanisms (Folke *et al.*, 2004). The significant erosion of ecosystem resilience caused by regime shifts has similarly dramatic consequences on social systems that depend on these ecosystem resources (Scheffer *et al.*, 2001a). Thus, building resilience into both social and ecological systems through adaptive management should be the ultimate objective of management under regime shifts (Hughes *et al.*, 2005).

One challenge to the management of resilience will be to measure it. While there are some general scientific approaches to assessing resilience, they may not be practically applicable as management tools. One such scientific approach is to fit a dynamical model and then determine the response characteristics of the ecosystem (Carpenter *et al.*, 2001). Such a modeling effort requires substantial scientific effort and a large amount of data to set and constrain the model. A more straightforward, but somewhat more qualitative and limited approach, is to monitor indices of the ecosystem, such as the phosphorous turnover rate or measures of the human impact by looking at land-use indices. For fisheries, one can assess the species removals or some aspect of ecosystem robustness, e.g. oxygen levels in the water column. The challenge with an index is to know how to relate the index to the state of resilience.

### 5.2. Implications for international planning

Regime shifts also have implications for international agreements, such as those dealing with transboundary stocks. At present, such agreements generally assume that the geographic patterns of movement and distribution of the species under consideration are fixed (Miller and Munro, 2004). However, forecasts of climate change (IPCC, 2007) suggest that climatically driven biogeographical shifts will become more common and, as a result, fixed management zones defined by the historical oceanography might no longer be

viable. Consideration of the possibility of a regime shift would enable, and require, some consideration of adaptive structures (including changing management zones) in future agreements that would operate if a regime shift were to take place (Wilson, 2002).

Several different aspects of regime shifts have implications for international agreements. Not only do some regime shifts cut across international boundaries, indeed most of them do, but the response of a shift within one ecosystem can have implications for adjacent ecosystems. The efforts to define large marine ecosystems (*cf.* Botsford *et al.*, 1997) their practical application has yet to be realized as ocean ecosystems influence each other, particularly at long time scales. The most obvious management problem is that agreements for large-scale international management, such as the NAFO arrangements for dealing with trans-boundary stocks are imperfect, and are designed based upon existing distributions of fish and fisheries. Changes in the distribution patterns of fish and fishing associated with regime shifts may occur at time scales, perhaps a few years or a decade, that is faster than we are able to develop institutional arrangements to manage the changes. It would therefore be sensible to consider such issues in the design and arrangement of institutional systems for fisheries management.

It is not only in the impact and the management of regime shifts that international issues become important. The measurement and detection of regime shifts also requires international coordination. The development of integrated observation systems within national boundaries and in international waters, such as the Argos program (Roemmich *et al.*, 2004), needs to be expanded to include more measurements of the biological and biochemical characteristics of the ocean enabling us to better assess the ecosystem status. There remain challenges with developing sensors for making the needed measurements, and also with securing the funding to setup and coordinate an integrated, international ocean ecosystem observational program.

## 6. RECOMMENDATIONS FOR IMPROVED FISHERIES MANAGEMENT

### KEY FINDINGS

- Given that most regime shifts will only be identified after they take place, **fisheries management will often be forced to adapt to the shifts that occur rather than actively managing them.**
- Fisheries management plans must **include both short-term (tactical) and longer-term (strategic) considerations.** Presently, strategic planning, in which the goals of the management plan are laid out, is typically uncommon or ignored in practice.
- **International coordination** is necessary to ensure the development of basin and global scale scientific studies that will lead to an improved understanding of and ability to detect regime shifts.

In general, for the management of the impacts of regime shifts, past attention has focused on preventing particular perturbations rather than enhancing the stability of the ecosystem. Building and maintaining resilience of desired ecosystem states is likely to be the most pragmatic and effective way to manage ecosystems in the face of increasing environmental change, followed by the development of flexible, adaptive management practices arising out of governance structures that are capable of interacting at ecological, social and economic levels and at multiple temporal and geographical scales (deYoung *et al.*, 2008). In some cases, such as the North Pacific, there may be few options for species specific management actions in advance of the shift because of our inability to forecast the shift or its trajectory but, once detected, different management options should be considered.

There are several different specific actions that should be considered given our awareness of the scale and impacts of regime shifts. The ecosystems approach to fisheries should be implemented. While there are some who argue that we lack the data or understanding to properly develop this approach, it seems clear that we know enough for some version of the approach (Tallis *et al.*, 2010). We certainly do not yet have enough understanding or information to fully manage all aspects of the marine ecosystems, including all the biological, social and economic components but we certainly know enough to do a much better job than we do at present, even if that means beginning with an incomplete ecosystems approach (Lester *et al.*, 2010).

One important goal for management should be the inclusion of resilience as an important consideration in fisheries management. Excessive focus on the status of individual species has been associated with too little attention on the integrated ecosystem of which fish are a part. Although resilience is a difficult concept to develop and measure, at the simplest level, simply minimizing human impact on the marine ecosystem should be seen as benefiting fisheries through the enhancement of resilience. We should work on the development of quantitative measures of resilience (Fischer *et al.*, 2010), but beginning by working with semi-quantitative, or qualitative, measures would still be an improvement over ignoring it altogether.

Fisheries plans should be both strategic and tactical. Few fisheries plans are explicitly defined and even fewer include both strategic (longer-term) and tactical (shorter-term) considerations. Much of fisheries management is responsive with little consideration of the longer-term implications of decisions, either in the sense of the impact on the ecosystems, or on the social and economic structures that make up the fisheries. Without the longer-term perspective, fisheries management decisions in the face of change are purely reactive. Regime shifts do require adaptive management but also pressure us to plan strategically both to minimize the need for adaptation and to guide us should a regime shift take place.

There should be more coordinated international scientific study of marine ecosystems to ensure that we are investigating the marine ecosystems at the geographic scales at which the shifts occur. We know from many different studies, e.g. studies of the Pacific shifts (Hare and Mantua, 2000; deYoung *et al.*, 2004), that regime shifts can take place at the basin scale of the ocean. New programs such as BASIN (Wiebe *et al.*, 2009), a recently funded North Atlantic program funded under 7th Framework Programme of the European Union, provide a good example of such an international effort that seeks to understand ecosystem dynamics at the basin scale.

Ecosystem observation programs, such as the Global Ocean Observing System (GOOS), need to include measures of marine ecosystems, beyond the physical component of the marine ecosystems. The data from these and other measurement programs should be made easily available to ensure the widest possible perspective on the state of the marine ecosystem. Too often in the past data has been difficult to access. This has been particularly true for data collected by harvesters within the fishery. Public sharing of data on a public resource is necessary to ensure that our perspective is broad enough that we can detect changes in the ecosystem as soon as is possible.

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