Journal of Marine Systems 167 (2017) 78–92

Contents lists available at ScienceDirect

Journal of Marine Systems

journal homepage: www.elsevier.com/locate/jmarsys

A retrospective view of the development of the Gulf of Bothnia ecosystem

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ARTICLE INFO

Article history:
Received 24 March 2016
Received in revised form 25 November 2016
Accepted 27 November 2016
Available online 29 November 2016

Keywords:
Eutrophication
Food webs
Long-term changes
Multivariate analysis
Baltic Sea
Gulf of Bothnia

ABSTRACT

We analysed long-term monitoring data from 1979 to 2012 in the Gulf of Bothnia, the northernmost extension of the Baltic Sea, to examine changes in the summer food web structure, and to reveal the factors causing the observed changes. Of the two sub-basins in the Gulf of Bothnia, the Bothnian Sea is more dynamic in its hydrography and food web structure than the Bothnian Bay, due to the variable influence of the more eutrophic and more saline Baltic Proper. Variation in deep-water intrusion from the main Baltic Proper, and its effect on salinity and stratification, had a clear effect on the phyto- and zooplankton communities in the Bothnian Sea. Probably due to this intrusion, the nutrient status in this basin has also changed in terms of nitrogen limitation, with subsequent class- and genus-level changes in phytoplankton community composition. The migration of cod to the Bothnian Sea during the 1980s had profound effects on the herring population, but cascading effects affecting the basis of the food web were not obvious. In contrast to a more pronounced interplay of both top-down control and bottom-up nutrient limitation of the Bothnian Sea, the Bothnian Bay food web was mostly driven by hydrography and climate, and major changes were observed in the basis of the food web. Community changes were observed in both basins in the Gulf of Bothnia throughout the entire time period. Human influence considerably affects both the basis of the food web and its very top, where man has replaced the natural top predators. Though the eutrophication status of the Gulf has been rather stable, the results indicate that the potential symptoms should be surveyed specifically in the Bothnian Sea, and that management of Baltic herring stocks requires an understanding, and thus monitoring, of the entire food web.

1. Introduction

Long-term oceanographical observations are essential for evaluating possible changes in ecosystems, following their recovery, and observing natural and/or anthropogenic causes behind ecosystem changes. Monitoring has been conducted in the Baltic Sea for decades, which enables the analysis of long-term trends in this highly dynamic ecosystem. Consistent time series data is also essential for improving models of physical-biogeochemical-ecological ocean dynamics (Ducklow et al., 2009). Recent studies of the Baltic Sea time series have discussed the potential causes for long-term changes in single ecosystem components such as phytoplankton and zooplankton (Suikkanen et al., 2013), important indicators of water quality such as Secchi depth (Dupont and Asknes, 2014), and several physical, chemical and biological parameters (Lennartz et al., 2014). All these studies reveal the strength of long-term data. However, food web analyses with physical and chemical data are scarce, as data sets of different food web compartments with similar quality are not always available. Whole-ecosystem analysis using long-term data could reveal both resource-based bottom-up effects and cascading food web effects, which act simultaneously. The subject of our study is the ecosystem of the Gulf of Bothnia in the Baltic Sea. It was selected as our target area as it is a physically highly dynamic system with high river inflow and variable winter regimes, and a number of species living at the very margins of their adaptive capability. Furthermore, the ecosystem properties of the Gulf of Bothnia are not as well-known as those of the more southern parts of the Baltic Sea.

The Gulf of Bothnia is the northernmost extension of the Baltic Sea (Fig. 1). It covers approximately 30% of the total Baltic Sea area. The Gulf of Bothnia can be considered an independent entity due to the combination of its specific characteristics. It is the most Arctic of all Baltic Sea subareas because of its northern location, and the least marine due to its distance from the Danish Straits, i.e. the connection to the North Sea and high riverine freshwater inflow. The two sub-basins of the Gulf of Bothnia, the northern Bothnian Bay and the southern Bothnian Sea, are separated by the narrow and shallow Quark area (Fig. 1). Only a limited number of organisms have adapted to living in the harsh northern conditions, leading to low a biodiversity of macro-organisms in the Bothnian Bay specifically (Elmgren and Hill, 1997). Here, the biota is a mixture of freshwater and brackish water species.

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http://dx.doi.org/10.1016/j.jmarsys.2016.11.020
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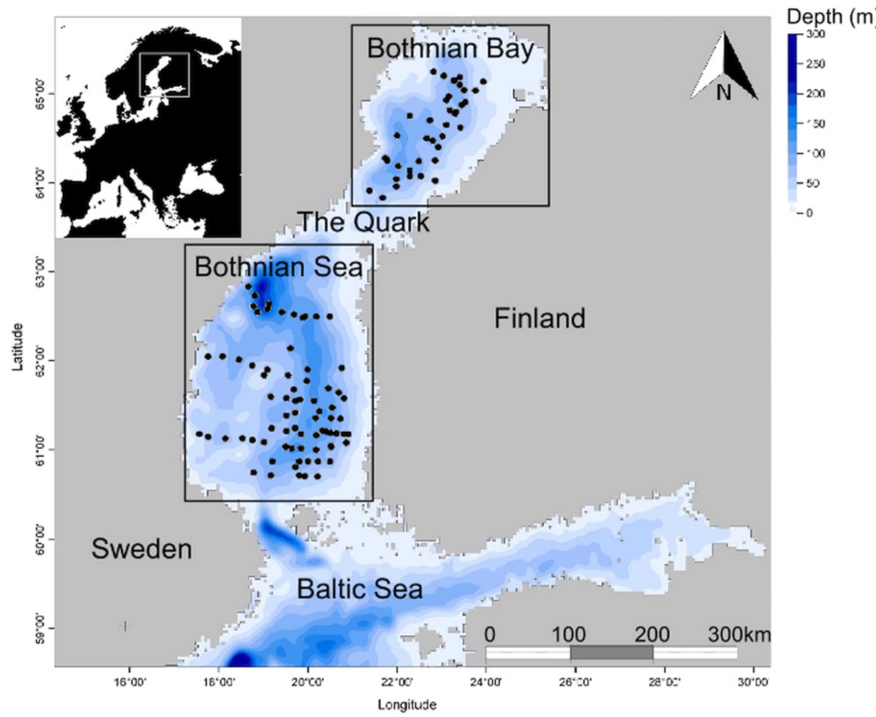

Fig. 1. Bathymetric map of the Gulf of Bothnia. The sampling stations in the Bothnian Bay and the Bothnian Sea are marked in both basins.

The species composition in the Bothnian Sea is closer to that of the Baltic Proper. However, the analysis by Elmgren and Hill (1997) shows that functionally the Bothnian Sea is similar to the Baltic Proper, and that most functional groups are also present in the Bothnian Bay though brackish water species are partly replaced by freshwater species.

The Gulf of Bothnia has no permanent salinity stratification due to southern sills, which prevent the intrusion of saline deep water into the Gulf from the Baltic Proper (Fig. 1). In the absence of a permanent halocline, deep-water layers and sediment remain nearly normoxic, which has a stabilising effect on benthic animal communities and basin-wide nutrient dynamics. The Bothnian Bay has very low algal production and it is mainly phosphorus-limited in comparison with the higher production capacity and temporal nitrogen limitation of the Bothnian Sea (Sandberg et al., 2004, Tamminen and Andersen, 2007). However, Elmgren (1984) also demonstrates a reduced flow of autochthonously produced carbon in the Bothnian Sea compared with the Baltic Proper. Terrigenous organic carbon originating from the catchment area is important as an energy and nutrient supply to the Gulf of Bothnia ecosystem, specifically in the Bothnian Bay (Sandberg et al., 2004). Consequently, the ecosystem structure in these northern Baltic basins is skewed towards bacteria-microbial loop-dominated carbon flows (Wikner and Andersson, 2012).

The variability in the Baltic Sea ecosystem is due to both human influence and natural factors. Österblom et al. (2007) showed how drastic these changes have been over the past century. They conclude that the large regime shifts, i.e. critical transitions between alternative stable states, are based on anthropogenic causes, although climate has also contributed to the changes observed. As early as the end of the 1980s, Rapport (1989), using a combination of ecosystem stress indicators including nutrients and biotic composition, found signs of 'ecosystem distress' in all spatial scales in the Gulf of Bothnia. In Rapport (1989), ecosystem distress symptoms already included early signs of eutrophication in coastal areas, a reduction in species diversity, and increased dominance by opportunistic species.

We aim to investigate changes in the Gulf of Bothnia during a 34-year period (1979–2012). In addition to the top-down control pathways (Österblom et al., 2007, Rudstam et al., 1994), we also cover the lower parts of the food web in as much detail as possible, and include hydrographic and nutrient parameters. The goals of our analysis are to examine 1) how the physical environment and nutrient status in the two basins has changed, 2) how these changes are reflected in the summer food web structure, 3) whether the changes are due to local factors or large-scale phenomena, and 4) how top-down control of the lower food web levels is compared to bottom-up limitation by nutrients.

2. Materials and methods

2.1. Study area

The Gulf of Bothnia is geographically divided into two sub-basins: the northern basin referred to as the Bothnian Bay or sometimes as the Bay of Bothnia, and the southern Bothnian Sea (Fig. 1). The Bothnian Bay and the Bothnian Sea cover areas of ca. 37,000 km^2 and 65,000 km^2, respectively. These two sub-basins are separated by the shallow (20-m) Quark, and their circulation patterns are rather isolated with only minor current systems crossing the Quark (Myrberg and Andrejev, 2006). As their hydrography and ecology define them as clearly distinguishable from each other (Myrberg and Andrejev, 2006), the two sub-basins can be analysed as separate units. A full account of the basic physics of the area is given in Leppäranta and Myrberg (2009).

Most of our data originates from regular monitoring stations in the open Gulf of Bothnia. We selected stations with appropriate monitoring data and a depth of >60 m from the Bothnian Sea (a total of 79 stations) and the Bothnian Bay (a total of 38 stations) (Fig. 1). The sampling area is very close to the combined Swedish and Finnish Exclusive Economic Zone in the Bothnian Sea, but somewhat wider than that in the Bothnian Bay. The sampling stations were expected to represent the same water mass in each area, and all available monitoring data collected was included in the analysis. Fish were sampled from the entire Gulf of Bothnia.

2.2. Data sets

Sampling period, depth, method and analyses for each parameter are given in Table 1. The time series data from 1979 to 2012 [excluding