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Otolith biochronology as an indicator of marine fish responses to hydroclimatic conditions and ecosystem regime shifts



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ABSTRACT

Sclerochronological studies based on hard structures of marine organisms are valuable tools—both for reconstructing past climate conditions and for predicting future impacts of environmental changes on marine resources. Existing archives, which house millions of fish otoliths (ear stones) constitute an excellent basis for such research; but, they remain underutilized. The objective of this project was to identify the factors that influence the annual growth patterns of the European flounder (*Platichthys flesus*) based on an analysis of otolith increments. We applied linear mixed models to develop a 74-year long chronology that reflects the inter-annual variations in flounder growth rates using otolith samples collected from 1957 to 2016 in the southern part of the Baltic Sea, which is considered to be highly vulnerable to global climate change. By analyzing the widths of otolith increments we revealed the existence of common environmental factors that influence fish growth. Using a mixed modeling framework, we incorporated a recent method to identify the optimal time window for climatic factors and showed that the most significant effect of the mean Baltic Sea Index occurs during August–December, while mean sea surface temperature is most significant from April–June. Change point analysis on the developed chronology identified major alterations occurred in flounder growth in 1988, 1992 and 2006. This result is in accord with published studies on regime shifts in the Baltic Sea ecosystem. This paper reports information concerning the response of the commercially important European flounder to the changing environment that may support future ecosystem-based management of fish stocks. Moreover, the results also highlight the potential for applying biochronological techniques to identify rapid regime shifts in marine ecosystems.

1. Introduction

Ocean temperatures have increased substantially in recent decades and are projected to rise further during the 21st century under all investigated scenarios (IPCC, 2014). It is assumed that warming will lead to various alterations in ocean hydrology, such as increase in sea level, greater stratification of the water column or more intense storm systems (Hoegh-Guldberg and Bruno, 2010). The future consequences of these changes for the functions and structures of ecosystems are still highly uncertain—especially for marine systems, where long-term biological data are scarce (Poloczanska et al., 2013). Our understanding of how organisms respond to changes in climatic conditions could be extended through sclerochronological studies based on the hard structures of marine organisms (Morrongiello et al., 2012). This technique is a valuable tool both for reconstructing past climate conditions (Reynolds et al., 2016) and for predicting future environmental impacts on marine resources (Rountrey et al., 2014).

Fish population dynamics are often driven by climatic variations

(Mackenzie et al., 2007). Because current practices and fish stock assessment models may be inadequate for projected environmental conditions (Hoegh-Guldberg and Bruno, 2010), the management strategies of these marine resources will need to be modified (Brander, 2007). The form of such modifications will depend on the sensitivity of each species to ecological changes (Rowland et al., 2011). Such sensitivity can be measured by net growth response, which reflects the direct and indirect impacts of environmental parameters on population over time in an integrated manner (Rountrey et al., 2014). For these purposes, biochronologies based on the annual increments of otoliths (which are hard structures located in the inner ears of fish) may be used as proxies of somatic growth changes over time (e.g., Black et al., 2013; Rountrey et al., 2014; Izzo et al., 2016). In fisheries science, hundreds of thousands of otoliths are used annually to estimate the age of individual specimens (Campana and Thorrold, 2001). These methods have the potential to provide information concerning past ecological responses at unprecedented temporal and spatial scales (Morrongiello et al., 2012).

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Biochronological approaches have been successfully applied to a wide range of species and regions to deliver long-term data on fish responses to environmental factors. These studies have primarily used dendrochronological methods (e.g., Matta et al., 2010; Gillanders et al., 2012; Black et al., 2013; Ong et al., 2016), mixed models (Izzo et al., 2016; Morrongiello and Thresher, 2015; Morrongiello et al., 2011; Weisberg et al., 2010) and Bayesian techniques (Helser et al., 2012) to reveal a variety of relationships between fish growth and external drivers, quantifying sources of year-to-year variability or long-term trends. However, investigations of developed biochronologies in the context of their potential to detect periods of rapid changes in environmental conditions, such as ecosystem regime shifts, are still rare. Currently, term regime shifts is typically defined as infrequent and abrupt alterations in the whole ecosystem structure and function, occurring at multiple trophic levels and on large geographic scales (Möllmann et al., 2009). Regime shifts can cause losses of ecological and economic resources with important management implications (Möllmann et al., 2009). Such reorganization have been described in many marine ecosystems, including North Pacific (e.g. Hare and Mantua, 2000), Black Sea (e.g. Daskalov, 2002) or North Sea (e.g. Alheit et al., 2005) and have been explained mainly as a results of climatic forcing, anthropogenic impacts or combination of both causes (Möllmann et al., 2009).

Development of robust methodologies for detecting previous regime shifts is considered the first step for prediction of this phenomena in the future and for adaptation of management policies to possible consequences of these rapid reorganizations of ecosystems (Kraberg et al., 2011). To our knowledge, such detection of past ecosystem alterations, using formal statistical analyses of fish otolith biochronology, have thus far been conducted only for Pacific ocean perch (*Sebastes alutus*) in the Bering Sea region. This study presented the significant influence of the 1976–1977 regime shift on fish growth (van der Sleen et al., 2016). Faced with a developing network of marine biochronologies (Reynolds et al., 2016), and because often other ecological time series are insufficient, the suggested approach may provide hints for future research regarding both species' sensitivity to rapid ecosystem alterations (Izzo et al., 2016) and identification of past abrupt ecosystem regime shifts.

The objective of this study was, first, to develop a multidecadal biochronology for the commercially important European flounder (*Platichthys flesus*) in the southern Baltic Sea based on archived otoliths (using samples collected from 1957 to 2016) and, subsequently, to investigate relationships between fish growth patterns and selected hydroclimatic factors. To identify the best predictor and optimal time window for climatic signals, we applied a state-of-the-art exploratory “sliding window” approach. Moreover, we conducted statistically-based analyses of fish growth phase transitions to investigate whether the developed otolith biochronology was suitable for detecting discontinuities in ecosystem states. We compared the results with information from other studies concerning regime shifts in the function and structure of the Baltic ecosystem to validate the change points defined using the biochronology.

2. Materials and methods

2.1. Study area

The Baltic Sea, located in Northern Europe, is one of the largest brackish-water basins in the world (415 200 km²). The functioning of this semi-enclosed sea is highly impacted by climate variability (Mackenzie et al., 2007; Möllmann et al., 2009). Because the Baltic Sea's only connection with the Atlantic Ocean is through the Danish Straits, the hydrological situation within the Baltic depends mainly on water mass exchanges with the North Sea (Lehmann et al., 2002). The area of this study was located in southern Baltic Sea—mainly the Bornholm Basin, Eastern Gotland Basin and the Gdansk Deep (Fig. 1).

2.2. Study species

The European flounder (*Platichthys flesus*) is the most common and commercially important flatfish in the Baltic Sea, with yearly international landings of up to 15,000 tons. It is distributed throughout the Baltic Sea except in the eastern portion of the Gulf of Finland and in the Gulf of Bothnia (Nissling and Dahlman, 2010). Baltic flounder can be divided into two types: demersal (“bank flounder”) and pelagic (off-shore) spawners. The demersal spawners produce small, heavy eggs that develop along the bottoms of shallow banks and coastal areas in the northern part of the Baltic. The pelagic spawners are distributed in the southern and the deeper eastern parts of the Baltic Sea and spawn at a depth of 40–80 m (Nissling and Dahlman, 2010). This study focused on flounders caught in the southern part of the Baltic Sea; consequently, most were assumed to be pelagic spawners. However, there is no clear geographic boundary between the demersal and pelagic types. During spawning, the demersal and pelagic types travel into shallower and deeper areas, respectively, but they probably mix during the feeding season (Florin and Höglund, 2008). Flounders from the southern Baltic spawn from March to May/June (Aro, 1989). After spawning, they migrate toward feeding grounds in the shallow coastal waters. Flounder can live up to 20 years (the oldest fish in this study), but most live to no more than 10 years.

2.3. Otolith measurements

Studies that use annual increments of otoliths to reconstruct or predict fish growth assume that there is a relationship between fish length and otolith radius (Campana, 1990). This assumption was tested for European flounder within our study area using a group of 755 individuals caught between 1977 and 1992 (Draganik and Kuczyński, 1993). Because there was a high reported correlation between fish length and otolith radius ($R = 0.98$), we were able to assume that there was a strong relationship between fish somatic growth and otolith growth.

We used otoliths from flounders sampled in the southern Baltic Sea from 1957 to 2016. We usually chose symmetric otoliths, but when symmetric otolith was not available or it was broken, an asymmetric one was used (20 samples). The otoliths were placed in horizontal rows concave side down, anterior end uppermost and embedded in epoxy resin. We sliced them into 0.4-mm-thick transverse sections through the primordium and along the dorsolateral plane using an automatic precision cut-off machine (Struers Accutom-50). The otolith slices were etched with 1% hydrochloric acid and stained with a solution of neutral red. We viewed all samples using reflected light at 32 × magnification. Otolith images were acquired using a stereo microscope (Leica M 205C) with a digital camera (Leica DFC 450).

We analyzed a total of 518 otolith images using ObjectJ (an ImageJ plugin). Increments were marked along the polynomial axis perpendicular to the annual rings from the nucleus to the dorsal edge of each otolith and the distances between them were measured (4725 measurements in total). Measurements of the first and last ring widths were excluded because they showed incomplete growth (Fig. 2).

2.4. Environmental predictors

Environmental predictors were derived from Baltic Sea physics reanalysis data of the Swedish Meteorological and Hydrological Institute (SMHI) available at the Copernicus-Marine Environment Monitoring Service (CMEMS, 2016) and from Extended Reconstructed Sea Surface Temperature (ERSST v4) model data (Huang et al., 2015). The reanalysis products for the physical conditions in the Baltic Sea were combined by SMHI using the 3D Ensemble Variational scheme in the High-Resolution Operational Model for the Baltic (HIROMB) circulation model. The product provides data at a 3-nautical-mile grid (5.5 km) scale. The ERSST v4 is a global monthly sea surface tempera-

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