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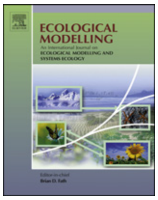

Ecosystem flow dynamics in the Baltic Proper—Using a multi-trophic dataset as a basis for food–web modelling

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ABSTRACT

The Baltic Proper is a semi-enclosed, highly productive basin of the Baltic Sea with a low biodiversity, where only a few key species drive the system's dynamics. Recently, an ecosystem regime shift was described having pronounced changes at all trophic levels, driven by changes in fishery and climate and leading to a food–web reorganisation. An Ecopath with Ecosim Baltic Proper food–web model (BaltProWeb) was developed to simulate and better understand trophic interactions and their flows. The model contains 22 functional groups that represent the main food–web components. BaltProWeb was calibrated to long-term monitoring data (1974–2006), covering multiple trophic levels and is forced by fisheries and environmental drivers. Our model enables the quantification of the flows through the food–web from primary producers to top predators including fisheries over time. The model is able to explain 51% of the variation in biomass of multiple trophic levels and to simulate the regime shift from a cod dominated to a sprat dominated system. Results show a change from benthic to more pelagic trophic flows. Before the reorganisation macrozoobenthos was identified as an important functional group transferring energy directly from lower trophic levels to top predators. After the regime shift, the pelagic trophic flows dominated. Uncertainties and limitations of the modelling approach and results in relation to ecosystem-based management are discussed.

1. Introduction

It is the flow of energy that drives the cycles of materials (Odum, 1953). In marine ecosystems several environmental and anthropogenic factors, such as temperature, salinity and fisheries may affect the dynamics of trophic flows. Such induced changes in the food–web structure and function may affect system productivity (i.e., primary production, growth or recruitment), interactions (i.e., food preferences, trophic control) or diversity (non-native species invasions and species extinction), which further may results into state changes of the system. Such a system state is often characterized by certain dominating trophic interactions and associated with state-specific energy paths (Scheffer et al., 2001; Daskalov, 2002; Collie et al., 2004; Heymans et al., 2007).

Recently, in the late 1980s, an ecosystem regime shift was also described for the Baltic Proper (BP) (Alheit et al., 2005; Möllmann et al., 2009). The BP is the central basin of the brackish, semi-enclosed Baltic Sea with gradients in salinity and temperature and also low biodiversity. The regime shift in the BP was associated with pronounced changes and reorganisations within and across the trophic levels of zooplankton and fish (Alheit et al., 2005; Möllmann et al., 2009). In particular, the zooplankton community changed from the dominance of the copepod *Pseudocalanus sp.* to *Temora* sp. and *Acartia* spp., most probably due to climate-related effects (Möllmann et al., 2003). Further, changes in the hydrography and fishing pressure affected the reproductive success and abundance of the major fish species, resulting in a change of dominance from piscivorous cod (*Gadus morhua*) to planktivorous sprat (*Sprattus sprattus*) (Köster et al., 2003). This caused a further decrease in the biomass of the sprat prey *Pseudocalanus sp.* Möllmann et al. (2009) suggest that internal predator-to-prey (P2P) feedback-loops possibly stabilized the new regime.

To better understand such an ecological phenomenon tools are needed, for example food–web models, to quantify the flows and simulate the system's behaviour. In general, food–web models have been built: (a) to answer ecological questions (Arias-Gonzalez et al., 1997; Arreguın-Sanchez and Manickchand-Heileman, 1998; Coll et al., 2007; Sánchez and Olaso, 2004), (b) to quantify flows and food–web structure (Shannon et al., 2000, 2003, 2004; Mackinson et al., 2003; Bradford-Grieve et al., 2003; Coll et al., 2006a; Tomczak et al., 2009), (c) to assess fisheries and environmental impacts (Bundy and Pauly, 2001; Harvey et al., 2003; Hansson et al., 2007; Bundy and Fanning, 2005; Guénette et al., 2006), (d) to undertake ecological network analysis (Coll et al., 2006b; Heymans and

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Baird, 2000; Heymans et al., 2007; Tomczak et al., 2009) and (e) to evaluate fisheries management strategies (Bundy, 2004; Okey and Wright, 2004; Walters et al., 2008).

Previously, differing modelling approaches have been applied in the Baltic Sea (i.e., multivariate autoregressive model – Lindegren et al., 2009; multispecies virtual population analysis – Vinther et al., 1998; Vinther, 2002; extended survival analysis – Darby and Flatman, 1994; biogeochemical modelling – Reed and Gustafsson, 2011; Savchuk and Wulff, 2009, as well as the food–web mass-balanced approach – Jarre-Teichmann, 1995; Sandberg et al., 2000; Sandberg, 2007; Tomczak et al., 2009; Harvey et al., 2003). Here, we base our work on the Ecopath with Ecosim (EwE) food–web model by Harvey et al. (2003), with substantial extensions and improvements in the model structure and an enlarged calibration dataset spanning multiple trophic levels. The dynamic model of Harvey et al. (2003) was constructed to analyse "the food–web and fisheries interactions" and included 15 functional groups. The model focused on fish stocks and aggregated ecosystem components (i.e., zooplankton and benthos). Moreover, their model was calibrated only to fish and fisheries data and was, besides fishing mortality, forced only by one environmental factor – cod reproductive volume (see for definition Plikshs et al., 1993). With their model structure and forcing they focused on interactions at higher trophic levels, but could not simulate the food–web dynamics described for example by Möllmann et al. (2009).

Our overall aim is to construct an ecosystem model for the Baltic Proper to quantify the flows and simulate the effect of multiple drivers and food–web interactions. This study will explore what type of trophic interactions and external multiple drivers (fisheries and environmental factors) are needed to reasonably simulate the observed dynamics and reorganisations of the food–web flows between year 1974 and 2006. In particular, we will address (i) the temporal changes in the energy flows (ii) the trophic controls between certain functional groups of the food–web; and (iii) the role of fisheries using ecosystem resources. This will lead towards a more comprehensive tool for ecosystem-based management of the Baltic Proper.

2. Material and methods

2.1. Area of study

The Baltic Sea environmental conditions are characterized by (i) a horizontal salinity gradient from 10 PSU in the South-West to 6 PSU in the North-Eastern part of the Baltic Proper (ICES, 2008b), (ii) high riverine inflows (Wulff et al., 2001) and (iii) irregular major inflows of saline water from the North Sea, leading to a permanent pycnocline that partly contributes to deep-water hypoxia (Conley et al., 2002, 2009). Our model aims to describe the food–web dynamics of the Baltic Proper (Fig. 1) from Bornholm to the Åland islands, excluding the Gulf of Finland and Gulf of Riga (ICES Sub-Divisions (SD) 25–29, without the Gulf of Riga). The maximum basin depth is 400 m and the model is covering an area of 2.4×10^5 km^2. During the last century, high nutrient loads from land have led to an eutrophication status of the BP with typical eutrophication-related symptoms, such as massive cyanobacteria blooms in summer and widespread deep-water anoxia (Bianchi et al., 2000; Conley et al., 2002).

Fisheries have heavily exploited the BP fish resources, by taking out 0.5–1 million tonnes of fish annually since the early 1960s (Thurow, 1997). Landings of the main commercial fish stock, the Eastern Baltic cod (*G. morhua*), increased dramatically at the beginning of the 1980s and collapsed in the early 1990s (ICES, 2008a,b). During the last three decades the cod biomass declined severely and remained low (Horbowy, 1996; ICES, 2008a,b). Small pelagic fish, i.e., sprat and herring, have dominated the catches during the last 20 years (ICES, 2008a). Herring biomass declined continuously since the 1970s (ICES, 2008a,b), while sprat biomass increased sharply in the 1990s. The fisheries assessment and management advice are given by the International Council for the Exploration of the Sea (ICES). Here, we used the ICES assessments (ICES, 2008a) from the following stocks in the ICES Sub-Divisions (SD): for cod SD 25–29, for herring SD 25–29:32 excluding the Gulf of Riga, and for sprat SD 22–32.

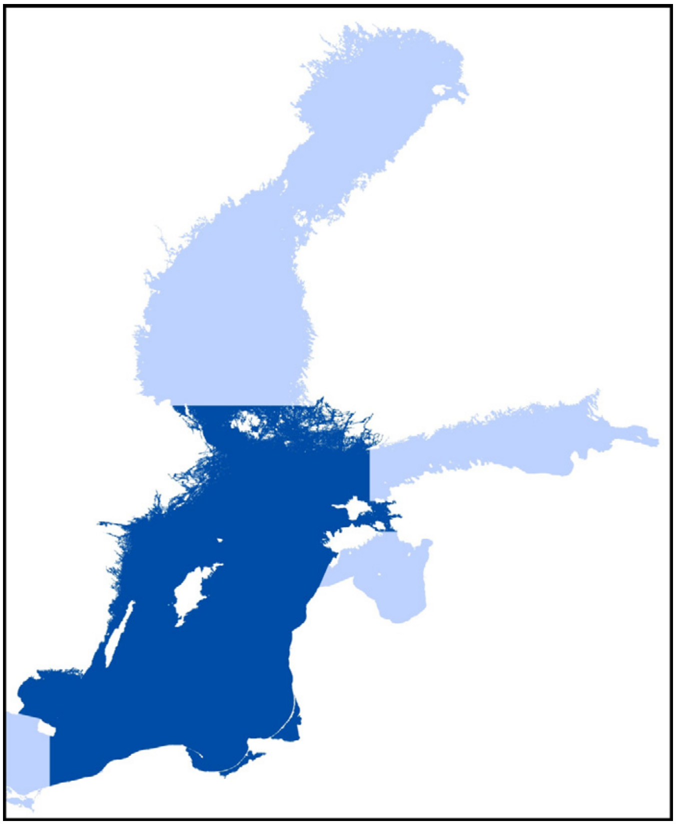

Fig. 1. The Baltic Proper study area (dark).

2.2. Mass-balance model

The EwE software (Ver. 5.1 Pauly et al., 2000; Christensen and Walters, 2004) was used to describe the BP food–web. The basic equation of Ecopath represents a mass-balance for each trophic group *i* in a system of *n* trophic groups,

$$B\left(\frac{P}{B}\right)_i = \sum_j B_j\left(\frac{Q}{B}\right)_j \mathrm{DC}_{ij} + Y_i + E_i + \mathrm{BA}_j + B_i\left(\frac{P}{B}\right)_i (1 - \mathrm{EE}_i) \qquad (1)$$

where: B_i is the biomass of group *i*; P_i is its total production; DC_{ij} – the proportion of trophic group *i* in the diet of group *j* and Q_j is the total food consumption of group *j*. EwE divides the production (P) of a functional group, into (i) biomass consumed by its predators ($\sum(B_j(Q/B)_j \times \mathrm{DC}_{ij})$); (ii) exports from the system both by fishery (Y_i) and net migration (E_i); (iii) biomass accumulation in the ecosystem (BA_i); and (iv) other mortality or mortality not captured by the model ($1 - \mathrm{EE}_i$), where EE_i is the ecotrophic efficiency of the group *i*, i.e., the proportion of annual productivity (P/B) consumed by predators within the system combined with the proportion of the productivity exported out of the ecosystem (i.e., by fishing activity) (Christensen and Walters, 2004). Under these mass-balance conditions, the annual production rate $(P/B)_i$ is considered to be equivalent to total mortality (Z) (Allen, 1971).