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Long-term shifts in marine ecosystem functioning detected by inverse modeling of the Helgoland Roads time-series

Kai W. Wirtz[a,*], Karen Wiltshire[b]

[a]Institute for Coastal Research, GKSS Research Centre, Max-Planck-Str. 1, 21501 Geesthacht, Germany
[b]Biologische Anstalt Helgoland, Alfred Wegener Institute for Polar and Marine Research, P.O. Box 180, 27483 Bremerhaven, Germany

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Abstract

Over the past decades, the North Sea ecosystem has been subjected to long-term variations of key natural as well as anthropogenic factors. Decadal trends in eutrophication or of the North Atlantic climate system presumably led to changes in extensive ecosystem variables such as algal biomasses or nutrient concentrations. These are investigated in great detail as part of few monitoring programmes such as the long-term time-series at Helgoland Roads (HR) within in the German Bight. In order to study the more relevant changes in ecosystem functioning as a response to external forcings and to assess the endogenous dynamics of the system, a new combination of modeling methods is proposed. The approach is based on a comprehensive marine food-web model, the European Regional Seas Ecosystem Model (ERSEM) together with an inverse modeling procedure. After integrating the HR time-series together with other environmental data relevant to the German Bight, long-term trends in the calibrated functional characteristics are unequivocally revealed. Apparently, the ecosystem evolves using a small number of distinct regulation modes, as reflected by a sequential timing of transitions in single ERSEM parameters. Typical transition times are estimated to be about 3–6 years. The most prominent shifts are observed for the maximal growth rates of all phytoplankton groups, several diatom growth parameters and for the specific nitrification rate. While for many sites within the North Sea including HR, significant alterations in nutrient and biomass levels were repeatedly reported in the early 1980s, major internal adaptations detected by the inverse method accumulate during the late 1960s and mid-1990s. Hence, one has to differentiate between the long-term evolution of standing stocks and the evolution of ecophysiological traits. First indications of the subtle influence of North Atlantic climate on the southern North Sea ecosystem are discussed. The study also illuminates several limitations together with potential improvements of marine ecosystem models.

Keywords: Adaptation; Inverse modeling; Helgoland roads; Ecosystem structure; ERSEM; Monte Carlo method

* Corresponding author.
E-mail addresses: wirtz@gkss.de (K.W. Wirtz), kwiltshire@awi-bremerhaven.de (K. Wiltshire).

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1. Introduction

1.1. Long-term trends in the North Sea ecosystem

Marine ecosystems are sensitive to a variety of external forcings whereby often physical controls, such as hydrodynamics including stratification, solar energy input or temperature are often most prevailing. In many areas, in particular coastal seas, the human use of the marine environment constitutes a second group of predominating influences with fishing or riverine nutrient inputs as prominent examples (Lozan et al., 1994). In the North Sea region, many of those anthropogenic, biochemical and abiotic controls together with their consequences on single species and entire food-webs have been monitored over several decades (Colijn, 1998), some documented observations even going back to the 19th century. All these data sets show both sudden or steady regime changes, unevenly distributed among different areas, periods and indicators. It is, however, still much under debate as to what extent and by which processes the North Sea ecosystem has responded to external signals, or evolved through endogenous dynamics under anthropogenic pressure in the second half of the 20th century (Philippart and Cadee, 2000; Reid et al., 2003).

Hence, one of the greatest challenges facing the coastal sciences with regard to global change is the integration of existing monitoring information into a higher system framework such as ecosystem modeling. In this paper we integrate the Helgoland Roads long-term data set into the European Regional Seas Ecosystem Model (ERSEM) with an inverse modeling procedure in order to pinpoint shifts in the system in terms of internal functioning.

Already Radach (1998) undertook a detailed statistical analyses for addressing long-term trends on an ecosystem level in the southern North Sea. Using an extensive time-series of physical, biochemical and biological parameters measured at Helgoland Roads (see Section 1.2) he defined an index which aggregates all these different parameters into a single number. The time course of this index reveals smooth changes during the 1960s and 1970s followed by an abrupt shift in biomass and nutrient concentration levels at the end of the 1970s, in particular with regard to higher abundances in heterotrophic nanoflagellates. This modification of phytoplankton succession might reflect changed N/P ratios due to eutrophication as well as alternating hydrographic regimes, possibly triggered by the North Atlantic Oscillation (NAO). However, the flagellate-related shift may also in part be artificial as in the early 1980s the set of monitored flagellate species was enlarged (Wiltshire and Dürselen, 2004).

There are further examples of ecological changes within the greater North Sea region which are in general agreement with a major shift around 1980: Heyen et al. (1998) reported that winter abundances of selected zooplankton species show greatest increments and decrements in the early 1980s compared to the 1970s and early- to mid-1990s. A similar timing of larger alterations in biomass levels was also found for benthic heterotrophs in the coastal zone of the southern German Bight (Kröncke et al., 1998). In this region, the abundance of the bivalve *Nucula nitidosa* also shows most steep changes in mid-1970s and mid-1980s (Rachor, 1990), in synchrony with algae and copepod biomasses in the southern North Sea according to Heath et al., 1999. Only Allen et al. (1998), analysing a time-series which started at 1954, found major shifts at a distant station in the central part of the Irish Sea already in the preceding period, i.e. the mid-1960s and mid-1970s.

1.2. The Helgoland Roads long-term time-series

In 1962, a long-term pelagic monitoring program observing nutrients, salinity and plankton species composition at Helgoland (54° 11N, 7° 54E) was initiated by the Biologische Anstalt Helgoland (Hickel et al., 1993; Hickel, 1998).

Surface water samples where taken usually before 9 am on working days. The temperature was measured immediately. After mixing and subsampling, the phytoplankton samples were preserved using Lugols solution and counted daily following the Utermöhl method to species level. Salinity and macro-nutrients were subsequently measured in the laboratory employing the methods described in Grasshoff et al. (1983).

Covering more than 12 different state variables for about 14,000 measurement days the Helgoland Roads (HR) time-series can be regarded as one of the most