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Detecting changes to the functioning of a lake ecosystem following a regime shift based on static food-web models

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ABSTRACT

Ecosystem management requires a large base of knowledge regarding the main factors of the components in the system, the relationship between them and their relationships with the external forces that affect ecosystem behavior. In many cases, this knowledge is not always available. Therefore, analyzing previous events and determining the effects they had on the ecosystem can provide insights regarding the factors that caused the changes and their continuing effect on the ecosystem. This task is not simple, due to a large variability of factors in the ecosystem and the difficulty in identifying them. Based on the Ecopath approach, we developed a means for analyzing the Lake Kinneret ecosystem by comparing two mass balance models representing two very different periods. The first model is based on the period of 1990–1993, prior to a regime shift that occurred in the ecosystem and the second model is based on 2006–2010, a period characterized by unstable behavior in the ecosystem. Examining the differences between the two models allowed us to map changes in the ecosystem and to identify the changes and the ecosystem components affected by the regime shift. Using the results we demonstrate the potential of providing management recommendations regarding Lake Kinneret's ecosystem and fishery.

1. Introduction

One of the main goals of ecosystem research, especially following a regime shift, is to recognize the changes in the ecosystem after a shift has occurred. The usual state in nature is one of populations fluctuating around some trend or stable average. However, occasionally this stability is interrupted by an abrupt shift to a dramatically different regime (Scheffer and Carpenter, 2003).

The ability to recognize the impact of a regime shift can be a major factor in understanding and managing an ecosystem (Folke et al., 2004). It is very important to have a clear understanding of the causes for the regime shift, especially for the purpose of management, in order to try to prevent the occurrence of future dramatic changes in the ecosystem. Although it is of great importance to identify a regime shift and the effect on the ecosystem, it is not always practical, or possible, to constantly monitor all necessary ecosystem processes and variables. While it is relatively easy to detect and identify general phenomena like large changes to phytoplankton populations or fishery yield, it is far more difficult to determine and predict the processes that lead to such events. As a result, the nature of regime shift in a variety of ecosystems has been the subject of a number of studies involving modeling (Samhouri et al., 2010; Scheffer, 2009), which focused mainly on identifying indicators that can detect a regime shift prior to its occurrence.

Ecosystem models constructed using the Ecopath with Ecosim (EwE) software (Christensen et al., 2005) are popular and widely considered to be an appropriate tool for the analysis of food webs (Coll et al., 2009; Coll and Libralato, 2012). Ecopath is software used for constructing ecosystem models, which allows the user to summarize and view species interactions within an ecosystem (Christensen and Walters, 2004). Both the direct and the indirect effects of changes to species composition in the ecosystem can be explored and effects on the overall functioning of the ecosystem can be estimated (Heymans et al., 2004). Furthermore, one

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of the strengths of this approach lies in its application to a broad field of theories that are useful in ecosystem studies, e.g. thermodynamic concepts, information theory, trophic level description and network analysis (Xu et al., 2011). Coll et al. (2009) presented several cases in which comparisons between Ecopath models of the same ecosystem, based on different time periods, were used to study changes that occurred over time. In all cases a regime shift occurred in the ecosystem, and the models were used to identify the tipping points or to provide directions to events that could have led to the occurrence of these tipping points. Additional examples include Heymans et al. (2004), who identified significant changes in the northern Benguela (Namibia) ecosystem structure and in its trophic functioning since the 1970s, namely a shift from a pelagic to a demersal-dominated ecosystem. Neira et al. (2014) compared models created based on data sampled in 1992 and 1998 in the South Humboldt, SH, (Central Chile) ecosystem. Their results suggest that the SH ecosystem experienced at least two different environmentally distinct periods in the last three decades. Bundy (2004) compared models of the Eastern Scotian shelf (North Atlantic) before and after the collapse of the Atlantic cod fishery and explored the changes that took place in the ecosystem's structure. She demonstrated a shift from benthic-feeder dominance to pelagic-feeder dominance and an increase in piscivory. Downing (2012) used the comparison method to compare variability over time of a part of the ecosystem of Lake Victoria, sampled during several time periods, in order to identify the shifts in the lake caused by stocking Nile perch (*Lates niloticus*) and Nile tilapia (*Oreochromis niloticus*).

In the present study, we use the same approach and compare between two distinct time-periods in order to identify the effect a regime shift had on Lake Kinneret's (Sea of Galilee) ecosystem, which underwent significant changes over the past 25 years (Gal and Anderson, 2010; Zohary et al., 2014; Zohary and Ostrovsky, 2011). The lake is very important as it is one of the country's main freshwater resources, thus maintaining a stable ecosystem is a prime objective of the resource managers. However, over the past 25 years, Lake Kinneret has undergone a plethora of transformations that have impacted most of the lake's food web. At the high trophic levels, one of the most significant developments was the dramatic decrease in fish catch in general, and in the yield of Galilee tilapia (*Sarotherodon galilaeus*), the most economically important fish, in particular. In 2008, the annual catch reached an all-time low of 8 tons, compared to annual catches of over 300 tons several years earlier (Shapiro, 2009). The decreasing fish catch is obviously just a symptom of the numerous processes that have led to the lake's current state. At the lower tropic levels, a long-term record dating back to the 1960s indicates that *Peridinium gatunense*, an armored dinoflagellate, dominated the phytoplankton of Lake Kinneret until the mid-1990s, with a relatively stable spring bloom. However, since 1994 these blooms have become irregular, failing to develop during 10 out of the past 16 years (Zohary et al., 2012). Furthermore, the predatory zooplankton of the lake underwent a regime-shift during the mid-1990s, in tandem with the observed changes in the phytoplankton population (Gal and Anderson, 2010).

The goal of the present study was to find the effect of the regime-shift that occurred during the mid-1990s in Lake Kinneret's ecosystem by comparing Ecopath models from two different periods of time. Comparison of the outputs of the two models provided a means for identification of the ecosystem components that underwent changes.

2. Materials and methods

2.1. Study area

Lake Kinneret is a warm, monomictic lake located in the northern part of Israel (Fig. 1). Its maximum depth is 45 m and its mean depth is 24 m. The lake covers an area of 168 km^2 and its residence time is approximately 9 years. The lake stratifies for about 9 months a year (March-December), during which the hypolimnion becomes anoxic and H_2S enriched. The main inflow to the lake is from the Jordan River, which is situated at the northernmost part of the lake, providing on average 70% of the total annual inflow (Gal et al., 2003). For the period of 1976–2009, the average annual recharge from rain, runoff and river inflow to the lake was 581 mcm (Weinberger et al., 2012). Due to annual fluctuations in rainfall and in annual water extraction from the lake, the water level has varied between −208.90 and −214.87 m over the last four decades. As a result, the littoral zone varies in its position; and can shift by hundreds of meters where the shores slope gently (mainly in the

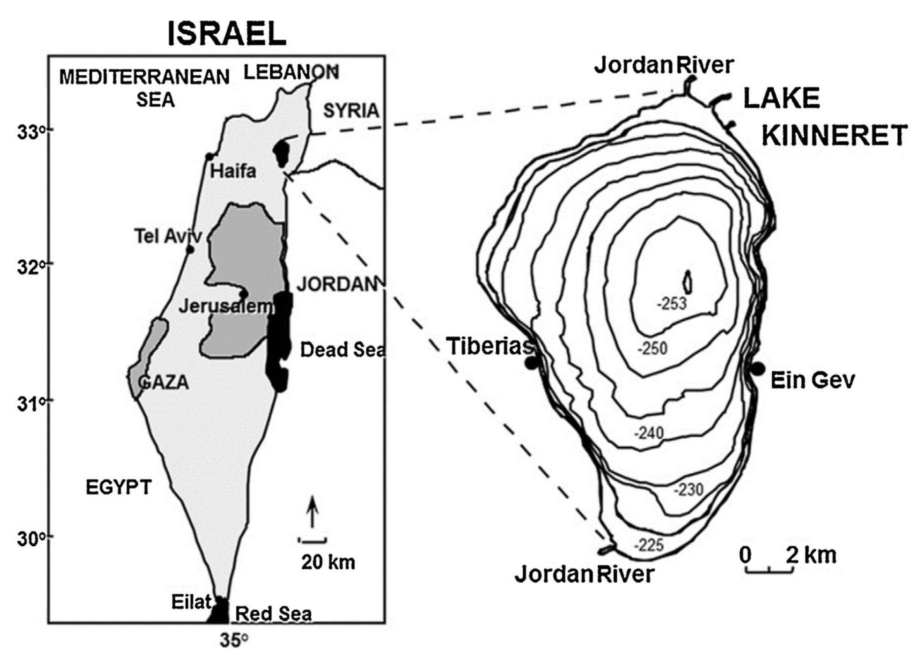

Fig. 1. Lake Kinneret and its location in Israel (reproduced from Parparov and Gal, 2012).