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Quantifying the ecological stability of a phytoplankton community: The Lake Kinneret case study

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ABSTRACT

The widely used term "stability" has multiple meanings and is rarely quantified in limnological studies. The main objective of this study was to develop an approach for quantifying the stability of a phytoplankton community using Lake Kinneret as a case study. It is a first attempt of calculating an index of stability for each of the five main taxonomic groups of the Kinneret phytoplankton (Bacillariophyta, Chlorophyta, Cryptophyta, Cyanophyta and Dinophyta), and for the entire community. A simple statistical approach to calculate the stability index was devised, using phytoplankton wet-weight biomass as the parameter being manipulated. The period 1970–1979 was selected as a reference period. The following stability indices were established and applied (each at three time scales): (1) a stability index for each of five main taxonomic groups; (2) a combined index of the stability, aggregating the stabilities of the individual taxonomic groups and (3) a stability index of entire community based on total phytoplankton biomass. The dynamics of these indices during 1969–2011 were examined. Destabilization of the community structure was triggered by an increase in the variability of Bacillariophyta biomass shortly after the reference period, in 1981–1983. Only 10 years later, the community destabilization become associated with progressively increasing biomass of Cyanobacteria. Dinophyta were the last to destabilize in the mid 1990s. Despite notable changes in the community structure, the total phytoplankton biomass remained relatively stable. Therefore, in 1969–2011 the stability index based on total phytoplankton biomass was higher than the combined index based on the stabilities of the individual taxonomic groups. Only weak relationships were found between the stability index values and potential driving forces (lake water level fluctuations and nutrient loads). While this approach was applied to Lake Kinneret, the concept presented is not lake specific and could be applied to other lakes.

1. Introduction

The term "stability" is widely used in the field of ecology (Holling, 1973; Ludwig et al., 1997; Umnov, 1997; Alimov, 2003). Ecologists traditionally interpret an increase in changes to the structural and functional characteristics of ecological units, as a decline in the stability of those units. Theoretical and mathematical ecologists have used the Lyapunov stability to describe the dynamics of ecological units (e.g. populations, communities or ecosystems). The use of Lyapunov stability, a mathematical concept taken from the world of physics, has however, limited implementations for hierarchically organized, multiple connected ecological units (Justus, 2008). Depending on the actual ecological situation under investigation, there are hundreds (sometimes, incompatible) definitions of ecological stability in the ecological literature (Rykiel, 1985; Lehman and Tilman, 2000; Donohue et al., 2013). Grimm and Wissel (1997) distilled many of those definitions into only three fundamental properties of ecological stability: (1) the ability to stay essentially unchanged (constancy), (2) the ability to return to the reference state after a temporary disturbance (resilience) and (3) persistence through time (persistence).

Qualitatively, stability is the ability of a system to maintain its functioning without changing the internal structure in spite of external perturbations (Rykiel, 1985; Reynolds, 2006). Drastic, obvious changes in the structure of an ecological unit (e.g., disruption of regularity of succession of the producer species) could be qualitatively ranked as destabilization of the ecological unit. How large were the observed changes? Which criteria should be applied in order to diagnose the stability state of an ecological unit? Different stability properties (e.g., resistance and/or resilience)

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are progressively becoming the object of management of natural resources (Holling, 1973; Ludwig et al., 1997; Groffman et al., 2006; Parparov and Gal, 2012). Therefore, the need to quantify stability and its relationships with various driving forces is growing.

According to the "ecological checklist" concept (Grimm and Wissel, 1997), the following stages are necessary in order to proceed to any quantitative definition of stability:

1. *Determining the ecological unit of interest* (e.g., population, community or ecosystem). Stability of hierarchically organized ecological units is an emergent property: separate populations could be ranked as unstable, while higher hierarchical levels (e.g., community of those populations) may seem stable.
2. *Selecting a set of state variables*: Dynamic behavior of any ecological unit could be described using different state variables (e.g., species density or biomass), which may lead to contradicting stability estimates. For instance, Rahel (1990) showed that a phytoplankton population could be ranked as "unstable" based on the temporal dynamics of its biomass. However, when the presence/absence of individual species was examined, the same population could be described as being "stable".
3. *Establishing a reference state* is a key stage in the quantification of ecological stability. Innis (1975) and Ulanowicz (1978) postulated the existence of a "non-disturbed", *reference*, state of the ecological unit. However, defining the reference state is not straight forward as there is no clear definition for it. Two possible ways of establishing a reference state are (1) to define a steady state expected to occur under optimal conditions (i.e. a potential state), or (2) to employ a state of the community that existed in the past and was considered non-disturbed, or minimally disturbed (Grimm and Wissel, 1997; Donohue et al., 2013). Similarly to other stages of quantification of ecological stability (e.g., the choice of state variables), selection of the reference state depends on the object of the study, researcher interest, objectives of management and available information.
4. *Establishing the relevant temporal and spatial scales*. This stage contributes to the balancing of the requirements of temporal and spatial resolution with the needs of the concrete task. Ecological units might look unstable on a seasonal scale and be highly stable on a decadal scale (Rahel, 1990).
5. *Disturbance*. At this stage, the researcher should establish the relationship(s) between the changes to stability and "driving forces" responsible for these changes. For instance, destabilization of lake ecosystems is traditionally associated with eutrophication, as a result of an increase in nutrient loads (Smith and Schindler, 2009), or drastic changes to lake morphometry (Gal and Anderson, 2010; Jeppesen et al., 2015). However, in many cases, especially related to disruptions of the species succession of aquatic organisms, those driving forces could be unknown.

Any quantitative, operational, definition of stability (i.e. *stability index*) should be represented by a mathematic formula, combining the current and reference values of the selected variable. Accordingly, it would then be possible to define a point (or points) in time at which *destabilization* event(s) of the ecological unit occurred. This point would coincide with the period during which the stability index values fall outside the limits of the reference state.

Changes to an ecological unit could be quantified via monitoring of the changes to its structural characteristics (e.g., biomass). Known examples of destabilization of ecological units associated with structural changes include for example shifts in the proportion of different types of primary producers (phytoplankton versus macrophytes) in shallow lakes (Scheffer et al., 1993), or in the phytoplankton (Zohary, 2004; Zohary et al., 2014b) and zooplankton community structure in Lake Kinneret (Gal and Anderson, 2010). Drastic changes in the variability and regularity of the dynamics of primary producers and zooplankton in Lake Sevan, and disappearance of several species, clearly illustrated plankton community destabilization (Parparov, 1990).

There are different approaches to quantifying ecological stability: from relatively simple (Umnov, 1997; Alimov, 2003), to complicate calculations using techniques of canonical or/and principal component analysis (Roelke et al., 2007; Goberville et al., 2011; Donohue et al., 2013).

The *ecological distance* between the current state of an ecological unit and its state during a predefined reference period can be used as a tool for quantifying stability associated with structural changes. The ecological distance allows characterization of the changes in abundance or relative composition of the ecological unit with a single statistic (Kindt and Coe, 2005; Greenacre, 2008). The valuation of the increase of the distance beyond the limits of the reference state is a quantitative measure of the structural changes of the ecological unit, and thus of stability, i.e., the greater the ecological distance, the lower the stability.

The main objective of this study was to develop an approach for quantifying the stability of a phytoplankton community. Lake Kinneret was used as the case study. In order to quantify stability, phytoplankton wet-weight biomass was used as the parameter characterizing the Lake Kinneret phytoplankton community. A reference state during which the phytoplankton community was considered least disturbed was selected. The following stability indices were established and applied (each at three time scales): (1) a stability index for each of five main taxonomic groups; (2) a combined index of the stability, aggregating the stabilities of the individual taxonomic groups and (3) a stability index of the entire community based on total phytoplankton biomass. The lake monitoring program provided a long-term record (1969–2011) of phytoplankton biomass (5 taxonomic groups and total), as well as insights into the phytoplankton community dynamics (Serruya, 1978; Berman et al., 2014; Yacobi et al., 2014a; Zohary et al., 2014b), and thus allowed quantification of the stability of this community. The data collected as part of the monitoring program indicated that over the past two decades the phytoplankton community structure (species composition) underwent large changes. These changes were interpreted as indications of ecosystem destabilization (Roelke et al., 2007; Gal et al., 2009; Zohary et al., 2014b). In addition, relationships between potential environmental factors and stability indices were examined. Analysis of long-term dynamics of the developed stability indices provided a detailed description of the evolution of the Lake Kinneret phytoplankton community over the last four decades and an assessment of the role of several taxonomic groups in its destabilization.

Structurally, ecological communities consist of ecological units of different hierarchical levels. For example, a phytoplankton community consists of sub-communities of several taxonomic groups. Hence, any community is a lower hierarchical level in relation to some higher level(s). The phytoplankton community, for example, is a lower level of the plankton community, which in turn is a lower level of seston. Quantitatively, the biomass of the community is an additive quantity: it is equal to the sum of biomasses of the individual sub-communities, and hence of all the populations comprising the community. However, stability of the community is not an additive quantity and should not be an arithmetic sum of stabilities of its sub-communities (Webster, 1979; Justus, 2008). In this study, it was hypothesized that the stability index of the entire phytoplankton community (based on total phytoplankton biomass) should be higher than the combined stability index aggregating stabilities of the individual taxonomic groups.