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ECOSYSTEMS

Quantifying Ecological Stability: From Community to the Lake Ecosystem

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Abstract

We performed a methodological study aimed at extending our previously developed approach to quantify the ecological stability of biotic communities and an entire ecosystem, using Lake Kinneret as a case study. The ecological stability of the biotic communities (phytoplankton and zooplankton) of Lake Kinneret was estimated using two different aggregating schemes. The first scheme used the combined stability index, based on the combined indices of the individual phytoplankton (SI $[\mathrm{Comb}]_{\mathrm{P}}$) and zooplankton ($\mathrm{SI}[\mathrm{Comb}]_{\mathrm{Z}}$) taxonomic groups. The total community stability index was calculated based on the total abundances of these communities. The stability of the entire ecosystem was estimated for two sets of ecosystem state variables, a lake ''trophic state'' set and a ''water quality'' set, which provided considerably different estimates of the lake ecosystem stability. Good agreement between the results of this study and qualitative estimates of Lake Kinneret stability validates the suitability of this approach to estimate the stability of different ecological units.

Key words: ecological stability; phytoplankton community; zooplankton community; aquatic ecosystem; Lake Kinneret; sustainable management.

Introduction

The terms ''ecosystem,'' ''stability,'' and'' management'' are widely used in modern hydroecology, though these terms are poorly defined and the relevant literature ''…is bedeviled with loose terminology and multiple definitions'' (Walker and others 2002). The definitions of ''ecosystem'' vary widely: from ''an assemblage of biotic and abiotic compartments'' (Jax 2006) to ''…a whole whose parts include all living and nonliving processes or objects'' (McLeod and Leslie 2009). Although conceptually correct, this range of definitions hinders the development of an *operational* definition of an ecosystem, that is, what parameters should be selected as *ecosystem variables*, and at what space and time scales?

The definition of ''stability'' is not much better. How should the stability of an ecological unit be defined and evaluated? Historically, stability was first formally defined by Lyapunov (sensu Justus 2008). The Lyapunov stability, however, offers limited implementations for hierarchically organized and multiply connected ecological units. Furthermore, the Lyapunov concept does not provide a quantitative estimate of stability (that is, an ''index of stability''). The structural and functional properties of ecological units (for example, communities and/or ecosystems) are principally distinct

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from non-living systems, and therefore their stability should be described in specific ''ecological stability'' terms. However, an ecological unit in a given time interval might have different stability estimates for different sets of ecosystem variables. Furthermore, there are hundreds of, often, incompatible definitions of ecological stability in the literature (Rykiel 1985; Lehman and Tilman 2000; Walker and others 2002; Donohue and others 2013). Grimm and Wissel (1997) distilled many of the definitions of ecological stability (hereafter referred to as ''stability'') into three fundamental properties: (1) the ability to stay essentially unchanged (constancy), (2) the ability to return to the reference state after a temporary disturbance (resilience), and (3) the ability of an ecological system to exist through time (persistence).

Diagnostics of an ecological unit stability status (that is, stable/non-stable) is of principal importance to managers because non-stable systems are non-manageable, at least theoretically (Milsum 1966). Therefore, sustaining stability is a key objective of sustainable management (Walker and others 2002; Groffman and others 2006), which means that stability should be an input to the management objective function. Consequently, stability should be estimated in measurable terms, that is, it should be quantified. There are a number of approaches to quantify ecological stability: from relatively simple ones (Umnov 1997; Alimov 2003) to rather complicated calculations that use techniques of eigenvalue and principal component analysis as well as mathematical models (Harte 1979; Ives and others 2003; Roelke and others 2007; Gsell and others 2015). The approach based on statistical properties of the ecological units was applied for establishing the relationships between stability and biological diversity. In some of those studies, temporal stability was defined as a proxy for ecological unit variance (Tilman 1999; Ives and others 2003). The ecological distance of the current state of the ecological unit from a predefined relative reference state (the existence of such a ''non-disturbed'' reference state was postulated by Innis (1975) and Ulanowicz (1978)) is one of the relatively rarely used proxies of stability (for example, Tett 2015). Different metrics are used for estimating this distance: the difference between nutrient concentrations (Carpenter and others 2001), Mahalanobis generalized distance (Goberville and others 2011), and Euclidean and non-Euclidean metrics (Donohue and others 2013), among others.

Recently, Parparov and others (2015) developed and employed a simple statistical approach to quantify the stability of the Lake Kinneret phytoplankton community based on Grimm and Wissel's (1997) ''ecological checklist.'' Conceptually, this approach defined stability of an ecological unit as the inverse of the *Euclidean Distance* between the unit current state and some predefined ''reference'' state. The phytoplankton stability was quantified using a set of stability indices calculated for the individual taxonomic groups, their combined value, and the total algal biomass. The results of the study corresponded well to the qualitative estimates of the stability status of the lake phytoplankton (Zohary and others 2014c). This newly developed approach provided a way to perform a quantitative comparison between the stability of the various groups and a means for identifying stable and unstable periods.

The main objective of this study was to test the underlying hypothesis that the approach developed for the quantification of the ecological stability of the producer community is applicable for the estimation of the stability of other ecological units and of the entire ecosystem. We applied this approach to the quantification of the stability of the consumer (zooplankton) community of Lake Kinneret and to two different sets of lake ecosystem state variables that define the lake ecosystem in relation to its trophic status and water quality.

Materials and Methods

Site Description

Lake Kinneret is a subtropical lake located approximately 210 m below mean sea level. The *trophic status* of the lake has been classified as meso-eutrophic with a mean annual primary production of 650 g C m^{-2} (Yacobi and others 2014; Zohary and others 2014c).

The Lake Kinneret phytoplankton community consists of five major taxonomic groups: Bacillariophyta, Cryptophyta, Chlorophyta, Dinophyta (the dominating group), and Cyanophyta. An annual spring bloom of the dinoflagellate *Peridinium gatunense* was a prominent biological feature of the lake until 1994, but since then the lake has exhibited uncharacteristic phytoplankton succession patterns, including the first-ever bloom of a potentially toxic, N_2-fixing, cyanobacteria *Aphanizomenon flos-aquae* (in 1995), and the lack of *Peridinium* blooms (Zohary and others 2014c).

The zooplankton community of Lake Kinneret can be divided into three major taxonomic groups: Cladocera, Copepoda, and Rotifera (Gal and Hambright 2014). During the period of 1970–2011, the zooplankton density dynamics followed the dynamics of the Copepoda, the numerically dominating group, whose density and percentage of the total zooplankton abundance declined from a mean value of 247.5 ind l^{-1} (59.8%) during 1970–1979 to 115.4 ind l^{-1} (49.2%) during 1990–1999, maintaining a similar level during the period 2006–2011.

Berman and others (2014) and Zohary and others (2014a, b, c) concluded that after the mid-1990s (in comparison with 1970–1990), the lake ecosystem was destabilized due to the changes in the phytoplankton succession patterns, the increased variability of the annual mean biomass of the phytoplankton groups, and the trend of declining dinoflagellate annual biomass. Progressively increasing lake water level fluctuations were considered as a key driving variable of these changes. The zooplankton community also underwent a shift in the mid-1990s (Gal and Anderson 2010): its population abundance decreased to very low levels in 1993, from which it recovered only in 2003 (Gal and Hambright 2014). The decrease in zooplankton abundance between 1980 and 1993 has been linked to intensified fish predation pressure (Hambright 2008), though the interactions were likely more complex and led to the changes that were observed on all trophic levels (Gal and others 2013; Ofir and others 2016).

One of the objectives of the Lake Kinneret water resources management is sustaining the water quality of the lake within limits corresponding to the state observed during 1969–1992 (Parparov and Gal 2012). Lake *water quality*, with regard to the conservation of the lake ecosystem, has been quantified using the Composite Water Quality Index (CWQI, Parparov and Hambright 2007). An analysis of the CWQI dynamics indicated a trend of water quality deterioration during the period 1978–2011(Parparov and others 2014) due to increase of salinity and increase of Cyanophyta abundance.

Basic Definitions

In this article, we defined *ecological stability* as *constancy*, that is, the ability of an ecological unit to sustain its state within predefined limits. We also used the following basic definitions (Grimm and Wissel 1997; Jax 2006; Muller and others 2015):

- *Ecological units* all those units that are subject to ecological research and comprise more than one organism. The most basic and widely used types of ecological units are ''population,'' ''community,'' and ''ecosystem'';
- *Community* an assemblage of populations of different species in space and time. The most basic types of limnetic communities are phytoplankton, zooplankton, and zoobenthos;
- *Ecosystem* an assemblage of biotic communities together with their abiotic environment in space and time;
- *State variables* the variables used to describe the state of an ecological unit (for example, biomass or density for the communities; Secchi depth, nutrient and chlorophyll 'a'' concentration for the ecosystems). Each state variable corresponds to one of the coordinates of the underlying *state space*.

Ecological Units Under Investigation

In this study, we explored a number of *ecological units* of Lake Kinneret (Table 1) intensely investigated as a part of ongoing monitoring program since 1969 (Sukenik and others 2014). These units included the phytoplankton community, the zooplankton community, and the entire ecosystem. For this study, the *phytoplankton community* was characterized by the biomass of each algae group separately and the total sum of their biomass (TotB), all from the upper 10 m of the water column. The *zooplankton community* was characterized by the individual group densities and the total sum of their densities (TotZoo).

To examine the ecosystem as a whole, we used two different sets of state variables that represent two separate approaches used to define the lake ecosystem. The first, the trophic set of variables consisting of Secchi Depth (S), and the concentrations of total nitrogen (TN), total phosphorus (TP), and chlorophyll (Chl). These variables provide the means for calculating the lake Trophic State Index (TSI, Carlson and Simpson 1996) used to determine the lake trophic status, the regulation of which is a major target of the European Union natural water resources management (WFD 2000). The TSI was calculated as follows (based on Carlson and Simpson 1996):

$$\mathrm{TSI} = (\mathrm{TI[S]} + \mathrm{TI[Chl]} + \mathrm{TI[TN]} + \mathrm{TI[TP]})/4 \qquad (7)$$

where

$$\mathrm{TI[S]} = 60 - 14.41 * \mathrm{Ln(S)} \qquad (8)$$

$$\mathrm{TI[Chl]} = 9.81 * \mathrm{Ln(Chl)} + 30.6 \qquad (9)$$

$$\mathrm{TI[TP]} = 14.42 * \mathrm{Ln(TP)} + 4.15 \qquad (10)$$

$$\mathrm{TI[TN]} = 14.43 * \mathrm{Ln(TN)} + 54.45 \qquad (11)$$

Table 1. The Elements of the Ecological Unit Stability Quantifying

	Ecological units			
	Biotic communities		Lake ecosystem	
	Phytoplankton	Zooplankton	Trophic state	Water quality
State variables (SV_i)	Biomasses of the algae groups and their sum (TotB)	Densities of the zooplankton groups and their sum (TotZoo)	S, TN, TP, Chl	S, TN, TP, Chl, TSS, B[Cyano], B[Dino], TotZoo
Reference period	1970–1979			
Temporal and spatial scales	Annual mean average for 0–10 m depth in the period from 1970 to 2011 For zooplankton, from the entire water column or down to thermocline depth			
Ecological distance	Standardized ecological distance $EuD_i = ABS\left(\frac{SV_i - Ref(SV)_i}{STD(SV)_i}\right)$ (1) $AggrEuD = \sqrt{\sum (EuD)_i^2}$ (2)			
Stability index (SI),	$SI = \frac{1}{1+EuD_i}$ (3)			
Combined stability index	$SI[Comb] = \frac{1}{1+AggrEuD}$ (4)		$SI[Comb] = \frac{1}{1+AggrEuD}$ (4)	
Total community stability index	$SI[TotB] = \frac{1}{1+EuD[TotB]}$ (5)	$SI[TotZoo] = \frac{1}{1+EuD[TotZoo]}$ (6)		
Lower stability level (LSL)	The LSL value was defined as the 5th percentile of the stability index values time series during the reference period.			
Normalized SI, SI/LSL	Stable state of the ecological unit: (SI/LSL) > 1 Non-stable state of the ecological unit: (SI/LSL) < 1			
Driving variables	Lake water level fluctuations, nutrient (TN & TP loads)			

S = Secchi depth; TN, TP, Chl, and TSS = concentrations of total nitrogen, total phosphorus, chlorophyll a, and seston, respectively; B[Cyano] and B[Dino] = biomasses of Cyano- and Dinophyta.

and S, Chl, TN, and TP represent the annual mean values of Secchi Depth and the concentrations of chlorophyll, total nitrogen, and total phosphorus, respectively, all from the upper 10 m of the water column.

The second set of variables is the *water quality* set of the state variables consisting of S, concentrations of TN, TP, Chl, and seston (TSS), the biomasses of Cyanophyta and Dinophyta and total zooplankton density. This set corresponds to the water quality system, aimed at the conservation of the Lake Kinneret ecosystem as a key source of drinking water (Parparov and others 2014).

Calculating the Stability Index of the Ecological Units

The approach used to calculate the stability index was described in detail in our previous publication (Parparov and others 2015). The main elements of this approach based on the ''ecological checklist'' concept (Grimm and Wissel 1997) are summarized in Table 1.

To calculate the ecological unit stability, a reference period was defined based on the assumption that the variability of the driving and the state variables (estimated as the coefficient of variance) during this period was relatively small and corresponded to their ''natural'' or ''normal'' variability. The set of the state variables corresponding to the ''reference period'' uniquely defines ''reference state,'' therefore we used these two terms as synonyms. The lower and upper natural variability limits of each driving and state variable were defined as the 5th and 95th percentiles during the reference period. The changes to the state of the investigated ecological units were studied based on the temporal variations in the annual mean of the driving and state variables (for example, the lake water level and Secchi depth; *see* Table 1) in relation to the respective mean values obtained for the reference period. The reference period selected was 1970–1979, as explained in the Results.

The *stability index* values were defined (equations (1) and (3) in Table 1) as an inverse function of the standardized Euclidean Distance (EuD_i) of the state variable, SV_i (for example, biomass or nutrient concentration), from the respective reference state ($RefSV_i$) at a given point in time *t* (Kindt and Coe 2005; Greenacre 2008).

The stability of the *biotic communities* was quantified by comparing the stability indices using two different aggregating schemes. The first scheme used the combined stability index (SI [Comb]), which was calculated based on the combined stability indices of the individual phytoplankton ($SI[Comb]_P$) and zooplankton ($SI[Comb]_Z$) taxonomic groups (equation 4 in Table 1). The combined stability index characterizes the stability of a community associated with the changes to the abundance of the individual taxonomic groups. It was calculated based on the sum of the Euclidian distance for individual taxonomic groups. The second scheme used a total community stability index, calculated based on the total abundance of phytoplankton (SI[TotB]) and zooplankton (SI[TotZoo], equations 5 and 6 in Table 1).

The stability of the entire lake ecosystem was estimated using indices calculated (equation 4; Table 1) for the ''Trophic State'' and ''Water Quality'' sets of the state variables (SI[Comb]TS and SI[Comb]WQ, respectively). To establish possible relationships between ecosystem stability and lake water quality and trophic status, the values of SI[Comb]WQ and SI[Comb]TS were compared with the values of the aggregated water quality (CWQI) and the Trophic State Index (TSI).

To determine the stability status of an ecological unit and to allow a direct comparison between the stability index values of different ecological units, the SI values were normalized to a lower stability limit (LSL). The LSL value was defined as the 5th percentile of the stability index values calculated for the reference period. Note that the upper stability level of any stability index is unity, that is, SI values cannot exceed unity; therefore, the ''upper stability limit'' is irrelevant. The LSL-normalized values of the stability indices that were larger than unity indicated that the ecological unit is stable, while the values smaller than unity indicated a non-stable status of the ecological unit: the population, the entire community, or the ecosystem. In this article, further considerations were based mostly on the LSL-normalized (hereafter ''normalized'') stability index values.

The results of our previous study showed that the decadal scale indicates the main features and trends concerning stability quantification. Therefore, in order to test our approach, we examined the main features of the temporal dynamics of the 10-year mean of the state and the driving variables and the normalized stability indices during four decadal periods: 1970–1979 (reference period), 1982–1991, 1992–2001, and 2002–2011. The fluctuations in the lake water level and the nutrient (TN and TP) loads were considered the major *driving factors*, potentially responsible for the destabilization of the biotic communities and the lake ecosystem (Gal and others 2009; Parparov and Gal 2012; Zohary

Table 2. The Coefficients of Variability of the Driving and State Variables in Different 10-year Periods

	Period of observation			
	1970–1979	1982–1991	1992–2001	2002–2011
Driving variables				
Water level, below −208.0 m	0.26	0.33	0.48	0.35
TN load	0.24	0.10	0.26	0.20
TP load	0.18	0.13	0.18	0.31
State variables				
S	0.10	0.08	0.10	0.07
TN	0.24	0.10	0.26	0.20
TP	0.18	0.13	0.18	0.31
TSS	0.09	0.19	0.20	0.18
Total algae biomass[1]	0.14	0.11	0.26	0.32
Biomass of cyanophyta[1]	0.34	0.56	0.47	0.21
Biomass of dinophyta[1]	0.17	0.17	0.43	0.53
Total zooplankton density	0.17	0.27	0.32	0.21
Chl	0.25	0.24	0.45	0.40

Water level, below −208.0 m was used to avoid the negative values of the lake water level
[1] Square root transformed values

and others 2014b). The Mann–Whitney *U* test (Zar 1998) was applied to test the significance of destabilization events, that is, the hypothesis that the normalized SI decadal average are smaller than unity ($n = 10$, $P < 0.05$, $U_{\mathrm{crit}} = 23$)

The lack of quantitative criteria posed a challenge for validating our approach. We, therefore, view qualitative estimates of the Lake Kinneret ecosystem stability status (Berman and others 2014; Zohary and others 2014b) an important criterion for validation of our approach.

Results

The Reference Period

Defining the reference period is not straightforward as there is no clearly defined approach for its definition. Two possible ways of defining a reference period are (1) to define the steady state expected to occur under optimal conditions (that is, a potential state) or (2) to employ a state of the community that existed in the past and was considered minimally disturbed (Grimm and Wissel 1997; Donohue and others 2013). We used the decadal dynamics of the ecological units and their stability as an argument for establishing the reference period. The coefficients of variation (an indirect stability estimate) in 1970–1979 and 1982–1991 were similar. However, 1970–1979 was selected as the reference period for all the ecological units because during this period, the variability of lake water level (key driving variable), TSS, and the Cyanophyta biomass was lower compared to the rest of the study period (Table 2). Another period, (for example, 1992–2001), being selected as the reference period, would have a much wider range of variability for most of the driving and state variables (Table 2), and thus limited sensitivity to the stability changes in comparison with 1970–1979.

The Changes to the Biotic Communities Structure

Despite the continued dominance of the dinoflagellates, their mean biomass decreased from 4.7 mg l^{-1} in 1970–1979 to 3.41 mg l^{-1} in 2002–2011 (Figure 1A). Concurrently, the mean biomass of the other groups increased, especially that of Chlorophyta (from 0.34 to 0.81 mg l^{-1}) and Cyanophyta (from 0.17 to 0.60 mg l^{-1}). In spite of these large changes, the overall mean decadal total algal biomass varied much less throughout the same period, ranging between 5.20 and 5.70 mg l^{-1} (Figure 1).

In contrast to the phytoplankton, the zooplankton total density decreased from 414 ind l^{-1} in 1970–1979 to 230 ind l^{-1} in 1982–1991, mainly due to the drop in the Copepoda and Rotifera abundance (Figure 1B). In the latter two decades (1992–2001, 2002–2011), the total zooplankton density somewhat recovered reaching an annual average of approximately 277 ind l^{-1}.

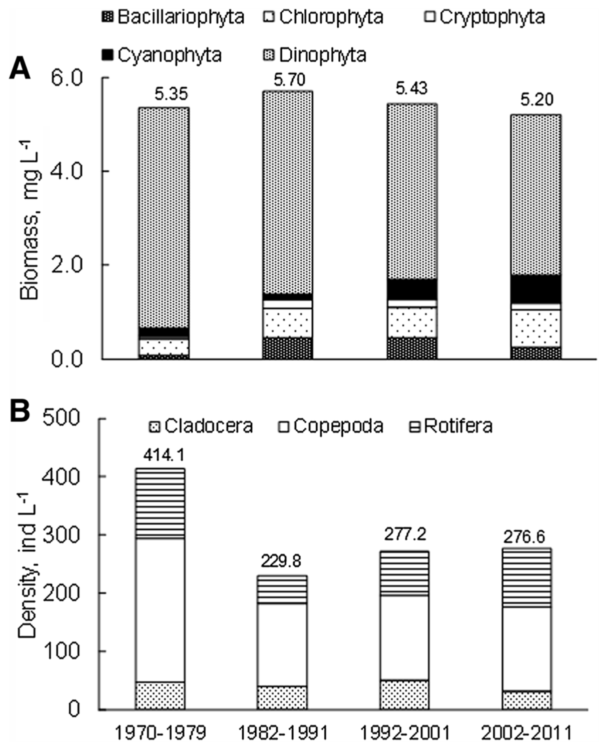

Figure 1. The dynamics of the 10-year annual average values of the Lake Kinneret phytoplankton biomass (**A**) and zooplankton densities (**B**). The numbers above the stacked columns represent the values of the total phytoplankton biomass and total zooplankton density.

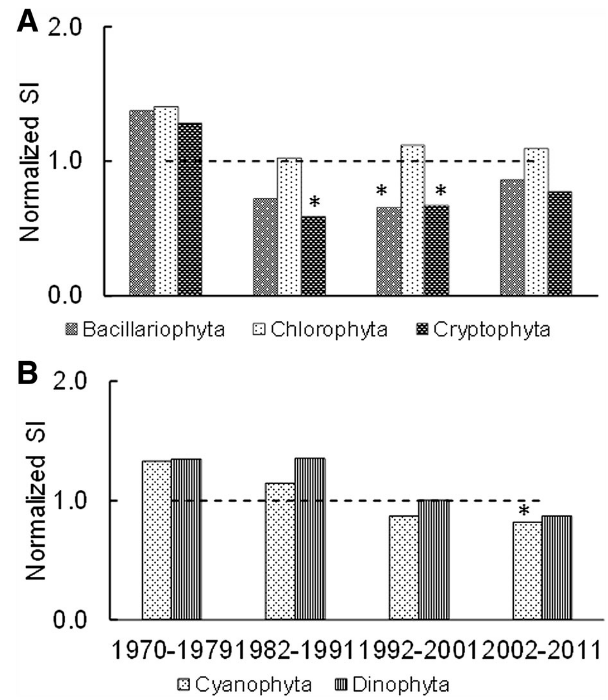

Figure 2. The dynamics of the phytoplankton individual group stability indices (10-year annual average values): **A** Bacillariophyta, Chlorophyta, and Cryptophyta; **B** Cyanophyta and Dinophyta. The *horizontal dashed line* indicates the value of the normalized stability index equal to unity, and thus separates the stable and non-stable states of the ecological unit. *Asterisks* above column indicates values significantly smaller than unity (at $P < 0.05$).

The Dynamics of the Stability Indices of the Biotic Communities

The Bacillariophyta and the Cryptophyta were the first algae groups that exhibited destabilization due to an increase in their biomass. Their individual group normalized stability indices decreased below unity in the early 1980s, that is, just after the reference period (Figure 2A). The normalized stability index of Cyanophyta exhibited values on average lower than unity starting from the early 1990s, whereas the Dinophyta was the last to indicate destabilization, in 2002–2011 (though the Dinophyta decadal stability index insignificantly differed from unity, Figure 2B).

The decrease in the zooplankton stability was caused by a drop in the Copepoda and Rotifera abundance (Figures 1B, 3). Nevertheless, on average, the Cladocera and the Rotifera normalized stability indices exceeded unity, that is, they were within the ''natural'' stability limits for almost the entire duration of the study. Stability index of Copepoda on average was smaller than unity in 1982–2011 (though, insignificantly).

The dynamics of the combined phytoplankton stability index values indicated that the phytoplankton structure destabilized ($SI[Comb]_P < 1$) just after the reference period, that is, starting from the early 1980s (Figure 4A). In contrast, the dynamics of the total biomass stability index (SI[-TotB]) did not indicate a destabilization of the phytoplankton: despite a considerable decrease in the SI[TotB] from the mid-1990s, the normalized SI[TotB] values exceeded unity, on average, in each decadal period (Figure 4A). During the entire period of 1970–2011, $SI[Comb]_P$ was lower than SI[TotB].

We compared the $SI[Comb]_P$ dynamics obtained for two different reference periods: 1970–1979 and 1992–2001 for estimating the effect of the reference period selection on the calculation of the stability index. Selection of 1992–2001 as the reference period would have resulted in contrasting results for the phytoplankton combined stability index dynamics, in relation to the selected 1970–1979 reference period (Figure 4B).

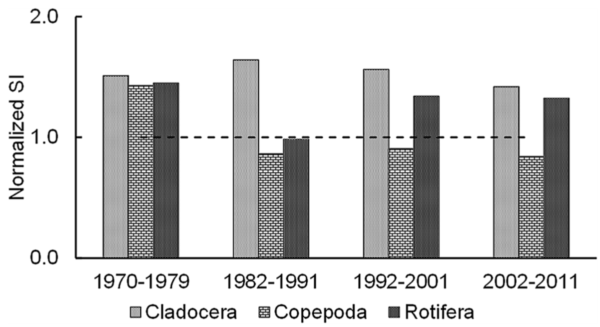

Figure 3. The dynamics of the zooplankton individual group stability indices (10-year annual average values). See Figure 2 for other designations.

As opposed to the phytoplankton, the dynamics of the zooplankton combined stability index (SI $[\mathrm{Comb}]_Z$) and the total density stability index (SI [TotZoo]) were similar (Figure 4C). The normalized decadal $\mathrm{SI}[\mathrm{Comb}]_Z$ and SI[TotZoo] average values decreased after the reference period, though this decrease, as well as the differences between these stability indices, was insignificant and their values were close to unity.

Ecosystem Stability Indices Calculated for the Trophic and Water Quality Sets of the State Variables

The value of the Lake Kinneret Trophic State Index, TSI, during the period 1970–2011 ranged within the limits of natural variability (44.3–53.0, Figure 5A). These values were close to the limits of the ''mesotrophic'' state [$30 < \mathrm{TSI} < 50$, Carlson and Simpson (1996)]. In contrast, lake water quality (as CWQI) deteriorated after 1992 from ''good'' ($60 < \mathrm{CWQI} < 80$) to ''intermediate'' ($40 < \mathrm{CWQI} < 60$) (Figure 5B).

The dynamics of the normalized SI[Comb]TS (Figure 5C) indicated a gradual decrease from 1.34 during the reference period to 1.01 in 2002–2011, mostly due to increased variability of TN and Chl (Table 2). Thus, although the trend of decreasing values, the lake trophic state remained within its stability limits (SI[Comb]TS > 1). The SI [Comb]WQ decadal dynamics (Figure 5C) indicated, however, lake ecosystem destabilization starting from 1982 to 1991. From this period, the normalized SI[Comb]WQ on average was lower than unity and gradually decreased from 1.23 during 1970–1979 to 0.71 during 1992–2001 and remained at that level through to 2002–2011. The destabilization of the WQ set was caused mostly by the destabilization of the Cyanophyta and Dinophyta populations, whereas ''pure'' ecosystem variables, such as Secchi Depth and TSS, remained relatively stable.

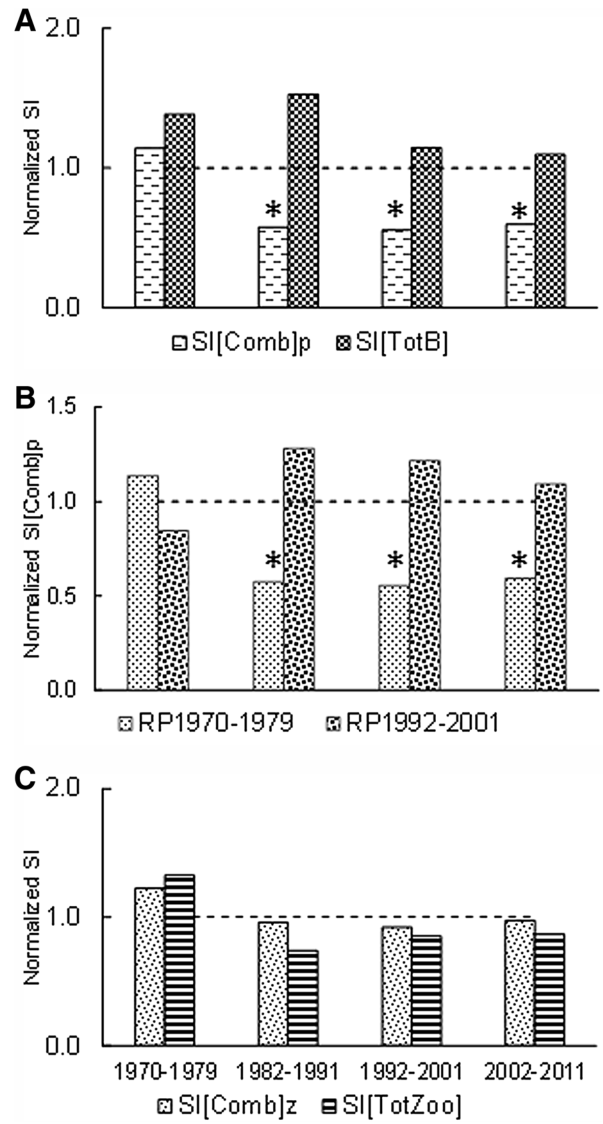

Figure 4. The dynamics of the normalized stability indices (10-year annual average values) of the biotic communities: the combined stability index (SI[Comb]), calculated based on the individual taxonomic group abundances, and SI[Tot], calculated based on the total abundances. **A** Phytoplankton, **C** zooplankton. **B** The dynamics of the combined stability index of phytoplankton (SI[Comb]P) calculated for two different reference periods (RP): 1970–1979 and 1992–2001. See Figure 2 for other designations.

The stability indices for most of the ecological units, except phytoplankton total community stability (SI[TotB]) and the trophic state associated stability (SI[Comb]TS) indicated a destabilization of the communities and entire ecosystem with values decreasing below the stability limits during 1992–

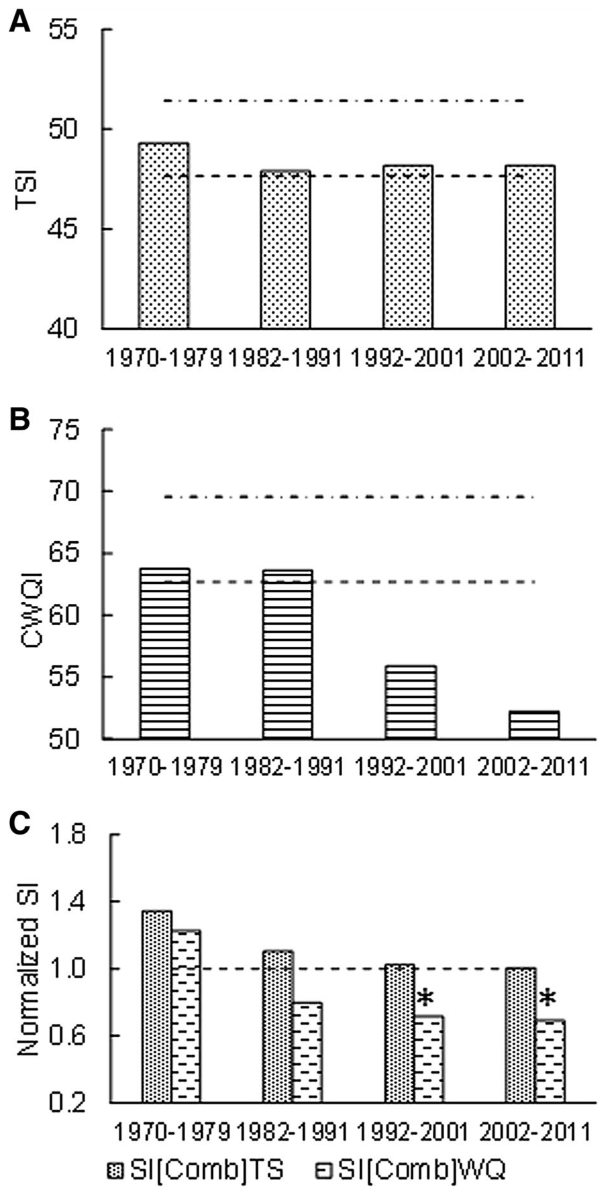

Figure 5. The dynamics of the 10-year annual average values of Lake Kinneret trophic state index, TSI, (**A**) and combined water quality, CWQI (**B**). The *horizontal dashed lines* represent the natural variability limits obtained as 5th and 95th percentiles of time series in 1970–1979. **C** The dynamics of the normalized combined stability indices (10-year annual average values), calculated for the trophic and WQ sets of state variables. The *horizontal dashed line* indicates the value of the normalized stability index equal to unity, and thus separates the stable and non-stable states of the lake ecosystem. See Figure 2 for other designations.

2001 (that is, normalized SI < 1, Table 3). Both SI[TotB] and SI[Comb]TS remained within their stability limits (that is, the respective normalized SI values exceeded unity).

The Relationships between the Ecological Unit Stability and the Potential Driving Variables

The lake water level progressively decreased below its lower natural variability limit (−210.8 m, Figure 6A), with increasing variability (Table 2). The nutrient loads, did not show, on average, any temporal trends and were inside of their ''natural variability'' limits (Figure 6B, C). On the decadal scale, a decrease in the values of the driving variables from reference state values was accompanied by a decrease in stability of almost all the ecological units (except SI[TotB], Figure 7). The phytoplankton structure (estimated as (SI[Comb]$_p$) was relatively more destabilized than other indices. Similarly, the stability of the water quality set (SI[Comb]WQ) exhibited low stability values (<1), whereas the trophic set (SI[Comb]TS) remained within its stability limits.

Discussion

The prime objective of this study was to verify the approach we developed, and applied, for quantifying stability, of an aquatic primary producer community. To test the validity of the approach, we tested it on additional aquatic ecological units including the entire ecosystem. Decision about the plausibility of the new approach should be made based on a comparative analysis with other case studies. The direct comparison of our results with the results of other case studies runs into problem, mainly because of the large range of definitions of stability and the lack of published stability index calculations for different ecological units. Therefore, we applied qualitative and intuitive estimates as the criterion for the validation of the approach (Harte 1979; Tilman 1996; Justus 2008). The results of our study and our conclusions regarding the destabilization of the phytoplankton structure corresponded with available qualitative estimates. Furthermore, there was a match between our estimated relative stability of the lake trophic status and the destabilization of the lake ecosystem as regards to its water quality with previous qualitative estimates. We consider this correspondence as indirect validation of our approach for quantifying the stability of the biotic communities and of the ecosystem.

Compared to other approaches, our approach is relatively simple when it comes to calculations. Calculation of the stability index (equations 1, 3) are much simpler than more complex calculations such as those suggested by Harte (1979), or the

Table 3. Normalized Stability Indices of the Lake Kinneret Ecosystem and Its Biotic Communities (10-year average values)

Time intervals	Phytoplankton		Zooplankton		Trophic set	WQ set
	SI[Comb]p	SI[TotB]	SI[Comb]z	SI[TotZoo]	SI[Comb]Tr	SI[Comb]WQ
1970–1979	1.14	1.39	1.22	1.30	1.34	1.23
1982–1991	0.57	1.52	0.96	0.72	1.10	0.80
1992–2001	0.56	1.14	0.92	0.90	1.02	0.71
2002–2011	0.59	1.10	0.97	0.87	1.01	0.69

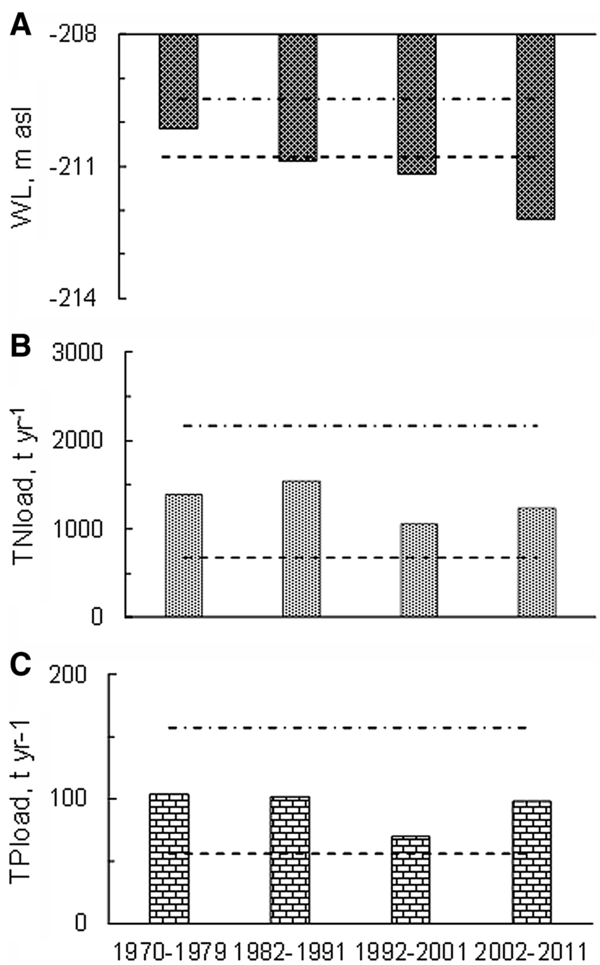

Figure 6. The dynamics of the decadal average values of the potential driving variables: lake water level (**A**), TN (**B**), and TP loads (**C**). The *horizontal dashed lines* represent the natural variability limits obtained as 5th and 95th percentiles of the 1970–1979 time series.

modifications of the Mar1 model by Gsell and others (2015). Our approach does not require the use of complicated mathematical techniques (for example, eigenvalue and/or wavelet analysis) or assumptions regarding the character of the interrelationships between the community components. Nevertheless, this approach allowed us to provide a quantitative estimate of the stability status of different ecological units, which makes it a useful tool in the context of stability management of lake ecosystems.

The validation of the stability quantification approach is strongly affected by its subjectivity at all stages of the quantification (Rykiel 1985), starting from the definition of stability. Traditionally (Harte 1979; Holling 1996; Justus 2008), ecological stability (resistance and/or resilience) was defined as a measure of the reaction of an ecological unit to perturbations. This definition requires establishing a relationship between the recorded changes in an ecological unit structure and/or functioning and the magnitude of the perturbation (''cause-effect relationships''). However, identification of the perturbation itself based on monitoring data might be an unsolvable task. This is well known for the phytoplankton and zooplankton communities, for which the reasons for, and the mechanisms of, the changes in structure are poorly investigated (Reynolds 2006; Sommer 2012). The definition of ecological stability we used, namely constancy, is apparently independent of a specific perturbation (Justus 2008). Nevertheless, the analysis of the long-term stability index data (Figure 7), together with the implementation of ecological modeling, should enable researchers to establish the functional relationships between the stability index and the perturbations that affect the ecological unit, and thus its resistance and resilience (Cottingham and Schindler 2000; Ives and others 2003; Gal and Anderson 2010; Gal and others 2013; Gsell and others 2015).

The effect of subjectivity is mostly obvious at the stage of the selection of the state variables. More specifically, how to distinguish between ecosystem and non-ecosystem state variables? In this study, the set characterizing the lake trophic status (TS set) consisted of ''pure ecosystem'' variables, integrating major biogeochemical cycles (TN and TP) and light-dependent bioproductive processes (S

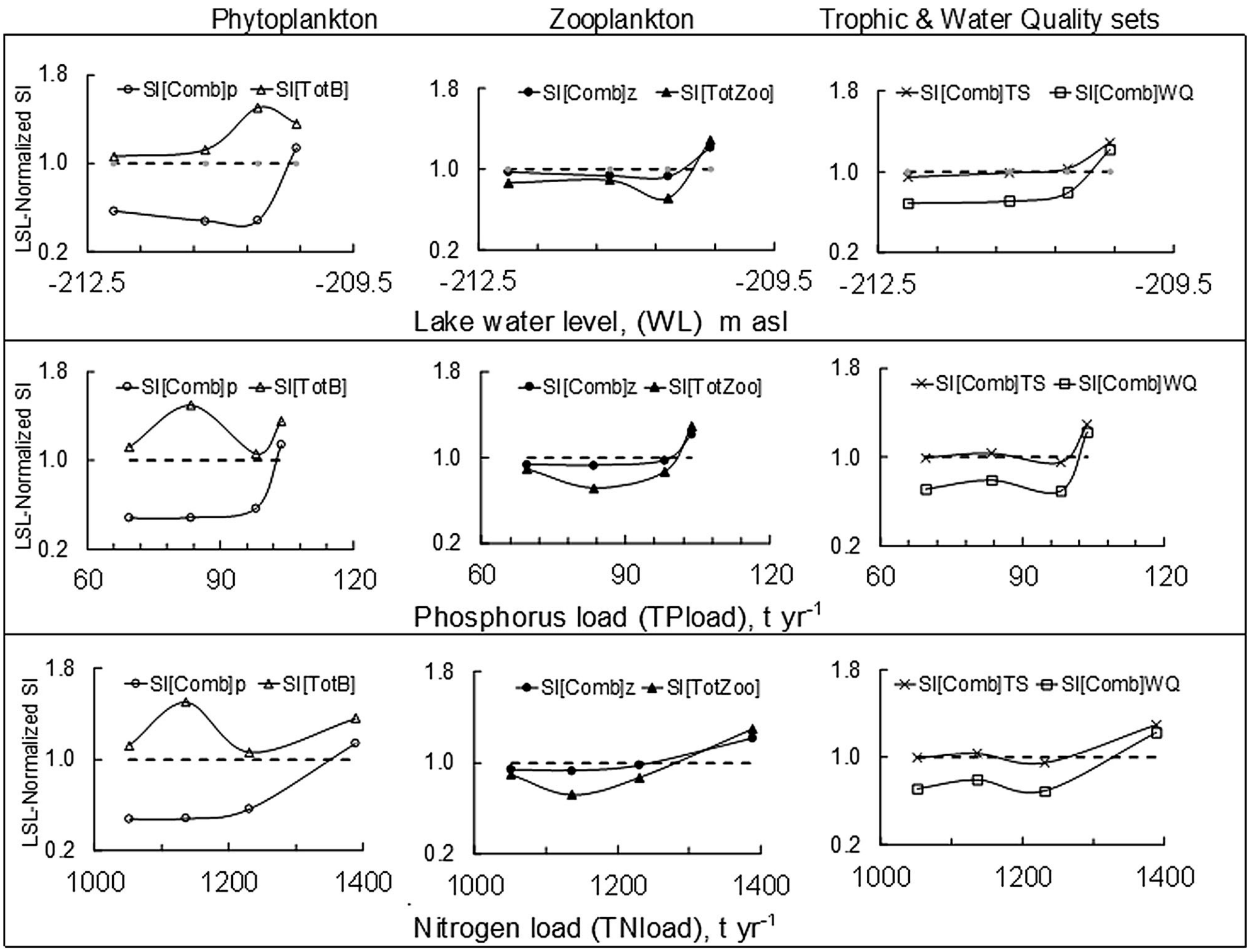

Figure 7. Scatter plots of the relationships between the decadal average values of the stability indices and the potential driving variables. The *right points* in each plot correspond to average for the reference state values. The *horizontal dashed line* indicates the value of the normalized stability index equal to unity, and thus separates the stable and non-stable states of the ecological unit.

and Chl). In order to characterize water quality, the TS set was supplemented with the variables from different hierarchical levels: abundance of algal populations (Cyanophyta and Dinophyta) and community (zooplankton). The selection of such, an apparently eclectic, set of variables was dictated by the management policy. The policy established for Lake Kinneret required the conservation of the lake ecosystem within predefined trophic state limits *as well as* the conservation of the main producer abundance. We have shown (Parparov and others 2015) that the documented changes to the phytoplankton structure, namely, the increase in Cyanophyta and decrease of Dinophyta biomass, through a complex network of interactions should significantly affect the detrital food web and its availability for zooplankton, hydrooptical field, microbial loop (Berman and others 2010), and thus the entire ecosystem functional properties. Therefore, in this case study, biomass of Cyanophyta and Dinophyta should be considered as ecosystem state variables.

The TS and WQ sets provided considerably different estimates of lake ecosystem stability (Table 3; Figure 5C). The trophic status of the Lake Kinneret ecosystem remained relatively stable throughout 1970–2011, despite a gradual decrease of the normalized decadal average SI[-Comb]TS: from 1.29 to 0.95 (Figure 5C). This result is in-line with the qualitative estimate of the trophic state of the lake ecosystem made by Zohary and others (2014c) and Yacobi and others (2014). At the same time, from the point of view of the lake water quality, the lake ecosystem has been destabilized since the 1980s (Figure 5C). The drop in ecosystem stability indicated by the SI[Comb]WQ dynamics (Figure 5C), together with the lake water quality deterioration, requires remedial measures such as regulation of lake water level and/or of the nutrient loads (Gilboa and others 2014). However, the effectiveness of possible remedial measures may be restricted due to the non-stable state of the ecosystem. The comparison between the long-term dynamics of the two combined ecosystem stability indices (SI[Comb]TS and SI[Comb]WQ) highlighted the importance of the selection of the set of ecosystem variables and its feedbacks with the diagnostics of the ecosystem stability status, and thus with the management policy. This comparison also emphasizes the relativity of the concept of ecosystem stability: the estimation of the stability of an ecosystem is pointless without a clear definition of ''What the Ecosystem Is'' (Grimm and Wissel 1997; Carpenter and others 2001).

We have shown how the reference state selection can have a large impact on the results of the stability quantification (Figure 4B). Calculations carried out with 1970–1979 as a reference period indicated considerable destabilization of the phytoplankton structure during 1982–2011. However, if 1992–2001 was selected as the reference period, the phytoplankton structure during almost entire study period remained stable. What of these, mutually exclusive, the phytoplankton stability estimates is ''correct''? According to the qualitative estimates, 1992–2001 was a period of drastic community structure changes, including the intensification of the Cyanophyta vegetation and the appearance of potentially toxic, N_2-fixing cyanobacteria (Zohary and others 2014c). Therefore, this time interval was not selected as the reference period. This example highlights the role of the reference state selection and illustrates the importance of the qualitative estimates in validation of the stability quantification results.

The stability of biotic communities has been intensely investigated using statistical approaches and model (MAR1) simulations (Doak and others 1998; Lehman and Tilman 2000; Ives and others 2003; Gsell and others 2015). These authors showed that communities should be more stable than their individual components (populations). Our data on the phytoplankton stability confirmed this statement: the values of the total community stability index were systematically higher than its combined stability (SI[TotB] > SI[Comb]$_P$, Figure 4A). Earlier, Parparov and colleagues (Parparov and others 2015) interpreted the discrepancies between the dynamics of the two stability indices as evidence of the emergence principle, that is, the existence of an internal mechanism that allows the sustaining of relative constancy (and thus the stability) of the total algal biomass. Are the revealed discrepancies common in a wider spectrum of ecological units? Comparison of the dynamics of the zooplankton stability indices: SI[Comb]$_Z$ and SI[TotZoo], apparently do not confirm to the generality of this suggestion: the SI [Comb]$_Z$ values were very close to the values of the total community stability index (SI[TotZoo], Figure 4C). We did not find any published data that would allow a comparison of our results with other case studies.

The absence of sufficient available data documenting the long-term dynamics of the biotic communities prevented us from comparing between different case studies. Implementation of this developed approach to existing databases, such as the Naroch Lakes (Belarus, Winberg 1985), Lake Tahoe (Goldman 2008), Balaton (Hainal and Padisak 2008), and Oneida Lake (Rudstam and others 2016), would considerably improve the plausibility of this approach and our understanding of the quantified stability.

Concluding Remarks

In this methodological study, we applied a previously developed simple statistical approach to the quantification of the ecological stability of different ecological units in Lake Kinneret ecosystem. These included the primary producer (phytoplankton) and consumer (zooplankton) communities, and the entire ecosystem.

For the first time, the stability of the biotic communities was quantified using two different aggregating schemes: the combined stability index characterizing the stability of a community associated with the changes to the abundance of the individual taxonomic groups. The second scheme used a total community stability index, calculated based on the total abundance of phytoplankton (SI[TotB]) and zooplankton (SI[TotZoo]). The total community stability of the producer (phytoplankton) remained unaffected by the drastic changes to its structure, while the combined stability of the phytoplankton underwent considerable destabilization. At the same time, the total community stability of the consumer (zooplankton) decreased simultaneously with the changes in its composition.

Our approach was also used to estimate the lake ecosystem stability with two sets of state variables associated with the lake trophic status, calculated as TSI, and water quality, calculated as CWQI. A comparison between the long-term dynamics of the two combined stability indices highlighted the importance of the selection of the set of ecosystem state variables. The selection of the state variable affects the diagnostics of the status of ecosystem stability, and thus its interrelation with water resources management policy.

Our results correspond to the reported qualitative estimates of the ecological stability of these ecological units in the lake. We therefore conclude that this simple statistical approach might serve as a practical tool for the solution of fundamental and applied tasks concerning understanding of possible mechanisms for managing ecological stability of different ecological units.

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