Alternative states in the phytoplankton of Lake Kinneret, Israel (Sea of Galilee)

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SUMMARY

1. Through analyses of a 34-year record of phytoplankton, zooplankton and physico-chemical parameters from Lake Kinneret, Israel, we show that distinct and persistent phytoplankton assemblage states occurred from winter to summer.
2. The most obvious characteristic of these states was the presence or absence of a spring bloom of the dinoflagellate, *Peridinium gatunense*.
3. Analyses of the data within the framework of the alternative states model revealed a possible complex triggering mechanism, and system hysteresis.
4. A change in zooplankton biomass and body size coincident with changes in predation pressure associated with the collapse of the Kinneret Bleak, *Acanthobrama terraesanctae*, fishery appeared to be the 'slow changing' variable in the context of the alternative states model. Alternative phytoplankton states were only possible after this variable crossed a threshold in 1993–94, following the collapse of the fishery.
5. When alternative states were possible, some physicochemical parameters and the structure of the zooplankton assemblage appeared to control which phytoplankton state emerged in a given year. In years without a *P. gatunense* bloom, important physicochemical parameters in winter included low NO_3 loading, high water temperature, high water level, a deeper thermocline, low transparency, high concentrations of NO_3 and Cl in the epilimnion, and low concentration of epilimnetic total phosphorus. In addition, the cladoceran *Chydorus sphaericus* and adults of the copepod *Mesocyclops ogunnus* were observed in winter in years without a bloom.
6. Zooplankton biomass and body size of some taxa have recovered since the 1993–94 collapse of the fishery, yet incidence of both phytoplankton states in Lake Kinneret was still possible. Within the framework of the alternative states model, this suggests that the slow changing variable threshold where alternative states became possible is different from the threshold where alternative states will no longer be possible. In other words, the system is characterised by a hysteresis.

Keywords: alternate states, distinct, hysteresis, persistent, threshold

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Introduction

The concept that distinct community structures occur in the same environment (see Lewontin, 1969; Holling, 1973; May, 1977), often referred to as alternative stable states, is important to our understanding of the factors

that govern ecosystem structure and function. Such alternative states are characterised by positive feedbacks, which result in persistent community structure through many generations. Factors that influence the incidence of alternative states are not always well understood. Knowledge of such factors is of particular interest in the more applied fields of ecology, e.g. conservation biology, and human and ecological risk assessment, where management aim to prevent undesirable ecosystem states (Roelke, 2000; Roelke & Buyukates, 2001, 2002; Van Dolah, Roelke & Greene, 2001; Buyukates & Roelke, 2005).

Alternative stable states occur in a variety of systems, including lakes. For example, some shallow lakes alternate between dominance by phytoplankton and submerged aquatic vegetation (Scheffer *et al.*, 1993; Jeppesen *et al.*, 1997; Bayley & Prather, 2003), while others switch between dominance by cyanobacteria and algae (Scheffer, Rinaldi & Kuznetsov, 1997; Scheffer, 1998; Carpenter, Lathrop & Brock, 1999; Carpenter *et al.*, 2001). Various factors regulate the incidence of alternative states in lakes. For example, the amount of phosphorus stored in sediments and available in the water column, the ratio of the euphotic zone depth to the mixing depth, the degree of hydraulic flushing, water depth, sediment resuspension and herbivory are all thought to impact the incidence of alternative states.

But factors that influence the incidence of alternative states are not always understood. In modelling studies of plankton (and plant) systems, it was shown that the initial assemblage structure under certain disturbance regimes controlled which one of the alternative states would occur, although the process could only be described using a complex basin boundary diagram where some regions were chaotic (Huisman & Weissing, 2001; Roelke, Augustine & Buyukates, 2003). While this model was completely deterministic, the behaviour of the model was so sensitive to initial conditions that realistically it was undeterminable. In other words, predicting which of the alternative states would occur in a real-world setting would be impossible.

Lake Kinneret, Israel, might be another aquatic ecosystem characterised by alternative states. In this lake, however, the alternative states may be different from those previously described for other, usually shallower, lake systems. Briefly, during the period from 1969 to 1993 seasonal succession in the phytoplankton of Lake Kinneret showed remarkable consistency that was characterised by a large spring bloom dominated by the dinoflagellate, *Peridinium gatunense* Nygaard (note that detailed records were not kept prior to 1969), and annual dynamics that in many aspects were predictable (Pollingher & Berman, 1977; Pollingher, 1981, 1986; Berman, Yacobi & Pollingher, 1992; Berman *et al.*, 1998; Zohary, 2004). In fact, the lake was described as having 'one of the best known and attested examples of year-to-year similarity in abundance, distribution and composition of the phytoplankton' (Reynolds, 2002). This predictable annual pattern ceased in 1994 after the collapse of the Kinneret Bleak fishery, *Acanthobrama terraesanctae* Steinitz, and has not returned (see Zohary, 2004). The lake now experiences years in which there is either no spring bloom of *P. gatunense* or the spring bloom of the dinoflagellate is extreme, with peak densities often higher than observed in the previous 25 years (Fig. 1; also see Zohary, 2004).

Having found no relationships between the incidence of *P. gatunense* blooms with other biological and physicochemical characterisations of Lake Kinneret when using conventional statistics (correlation and principal component analyses, and non-metric multidimensional scaling, results not shown), we
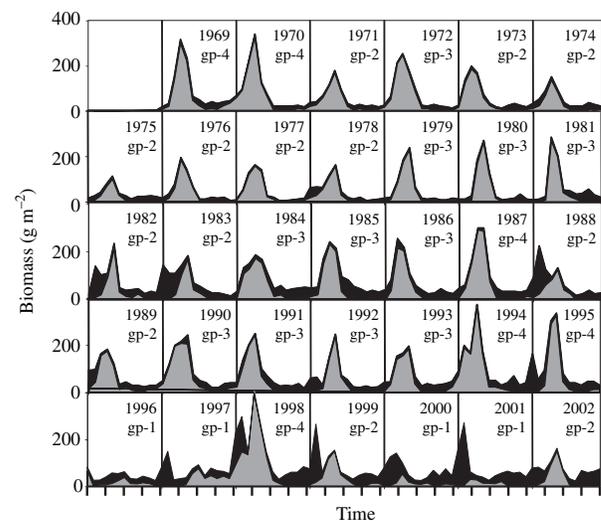

Fig. 1 Recurring blooms of the dinoflagellate *P. gatunense* (grey) in Lake Kinneret (biomass of all other phytoplankton shown in black), which after 1994 became much less predictable (modified from Zohary, 2004). Years were classified based on the extent of the *P. gatunense* bloom, where group 1 (gp-1) was formed by grouping the no-bloom years, and groups 2, 3 and 4 (gp-2 to gp-4) were formed by grouping years where the spring *P. gatunense* bloom was small, intermediate and large, respectively.

explored the data using a more complex approach where we hypothesised that patterns in the Lake Kinneret phytoplankton were indeed characterised by alternative states. We first compared the phytoplankton assemblage structures during years when *P. gatunense* blooms occurred and years when they did not, where the focus was on persistence of distinct assemblages. Using the framework of the alternative states model, we then investigated likely triggering mechanisms that led to no-bloom or bloom years, and looked for evidence of system hysteresis. We accomplished these tasks using the 34-year record of plankton and water chemistry from Lake Kinneret. Our findings shed new light on an ecosystem that has been the focus of intense study for nearly four decades (see Serruya, 1978; Hambright & Hershcovitch, 1998).

Methods

Long-term, time-series data from Lake Kinneret

A long-term monitoring programme of Lake Kinneret, initiated in 1969, has generated a continuous record of a suite of physical, chemical and biological parameters for the lake and its Jordan River inflow. From this extensive record, we selected data on phytoplankton, zooplankton and the fishery, and on parameters that are known to influence, directly or indirectly, plankton assemblage structure and population dynamics. These parameters that characterised Lake Kinneret in various ways were: *hydrological*, i.e. lake level, inflow from the Jordan River, and loading of ammonium (NH_4), nitrate (NO_3), dissolved organic nitrogen (DON), total dissolved phosphorus (TDP), total phosphorus (TP), and sulfate (SO_4); *chemical concentrations* in lake water, i.e. NH_4, NO_3, nitrite (NO_2), DON, TDP, TP, SO_4, and chloride (Cl); and *physical*, i.e. thermocline depth, Secchi depth, the ratio of euphotic zone depth to mixing depth, and temperature.

The lake water-quality data (chemical, biological and most physical parameters) were collected at one- or two-week sampling intervals for a period of 34 years, and at several depths from a single station. For the purposes of this research, we integrated the water-column phytoplankton or zooplankton biomass data over the depth of the mixed layer, and used averages for the upper 10 m for the chemical and temperature data. Regarding the phytoplankton, rare taxa were removed from the data by eliminating species that never exceeded 5% of the total phytoplankton biomass, or that only appeared in less than 5% of the total number of observations. Our resulting data arrays for phytoplankton (74 genus- and species-level identifications), zooplankton (35 categories based on species and life stages), and the physicochemical environment (20 parameters) consisted of 1057 lines of data. Methods used to collect and process samples for determination of these parameters were described elsewhere (see Serruya, 1978; Zohary, 2004).

Distinct and persistent assemblages: the use of non-parametric discriminant analysis, 1969–2001

To explore whether the bloom and no-bloom (post-1994) years in Lake Kinneret represented distinct and persistent phytoplankton assemblages, we looked more closely at the phytoplankton composition after removal of *P. gatunense* cell numbers from total cell counts. Because distinctness and persistence are characteristics of alternative states (Lewontin, 1969; Holling, 1973), we assumed that if this remaining phytoplankton assemblage was persistently different between no-bloom and bloom years, then analyses of potential triggering mechanisms and ecosystem hysteresis within the framework of the alternative states model would be justified. We further assumed that causative relationships could be inferred if the zooplankton and/or physicochemical data were also distinct between no-bloom and bloom years.

To quantify the 'distinctness' of phytoplankton and zooplankton assemblages, and the physicochemical environment, we used discriminant analyses. Since our data sets did not meet the assumptions of multivariate normality and the homogeneity of variance-covariance matrices, we used a non-parametric discriminant analysis. Briefly, we chose the k-nearest neighbour method (k-NN) with three nearest neighbours to estimate the *a posteriori* probabilities of classification of observations into their predetermined groups. The k-NN method produces a classification criterion based on the Mahalanobis distances estimated from the pooled covariance matrix. Under the k-NN method an observation is assigned to the same group as its k-nearest neighbours. To evaluate the classification accuracy we obtained *a posteriori* probability error-rate estimates using the cross validation option (leave-one-out method) (Huberty, 1994;

Khattree & Naik, 2000). These *a posteriori* probability error-rate estimates refer to the proportion of observations in a group that are misclassified. Non-parametric discriminant analyses were performed using the SAS 9.12 statistical software (SAS Institute, Cary, NC, U.S.A).

Our approach was to use non-parametric discriminant analyses to ascertain if predetermined groups were indeed distinct, then to investigate the persistence of the distinct groups by repeating the analyses throughout the course of a season. To accomplish this, a year (or full season) was defined based on the timing of autumn destratification, leading to winter holomixis. For Lake Kinneret, advanced destratification typically begins at the end of October and early November. Consequently, we defined here the start of a season as November and the end in October of the following year.

For each of the data arrays, phytoplankton, zooplankton and physicochemical parameters, we predetermined four groups for the non-parametric discriminant analyses. Group 1 was formed by combining the no-bloom years, i.e. no significant spring (March to May inclusive) population of *P. gatunense*, which were 1996, 1997, 2000 and 2001. Groups 2, 3 and 4 were formed by combining years where the spring *P. gatunense* bloom was small, medium and large, respectively (see classification of years in Fig. 1).

Not all of the data were entered into the non-parametric discriminant analyses at once. Instead we employed a 'running' two-month window that shifted through the season. For example, the first analysis used data from November–December from all of the years in the record, the second analysis used data from December–January, and so on, until the end of a season where the analysis used data from September–October from all years. This enabled us to discern during which periods of the season assemblages were undistinguishable and when they were distinct. We chose a two-month window based on the rate of phytoplankton population overturn in Lake Kinneret. This resulted in five to eight lines of data for each year of the data record being entered into the non-parametric discriminant analysis.

Output from non-parametric discriminant analyses included the number of cases that were correctly classified into their *a priori* group designation, as well as the number of cases that were incorrectly classified into an *a priori* group designation. For each group, we then calculated 'distinctness' by subtracting the percent of cases that where incorrectly classified from the percent of cases that where correctly classified. Thus, a value of 100 represented a period of the season where groups (or a group) were absolutely distinct from each other (i.e. no misidentifications).

Distinct and persistent assemblages: the use of non-parametric discriminant analysis, 1994–2001

Another set of non-parametric discriminant analyses were conducted on each data array using only information from 1994 to 2001 inclusive, a period starting after the lake crossed an important system–level threshold (discussed below). For this set of analyses, we only defined two groups because we had fewer data available for group determination. Group 1 was the same composite of no-bloom years as before (1996, 1997, 2000, 2001), when no significant spring population of *P. gatunense* occurred, and group 2 was a composite of years (1994, 1995, 1998, 1999, 2002) when a spring *P. gatunense* bloom did occur, regardless of size.

Important taxa and lake conditions, use of indicator species analysis and parametric discriminant analysis

In parametric discriminant analysis, the absolute value of the discriminant function coefficients can be used to evaluate which variables contribute most to trends revealed along the discriminant functions. Unfortunately, the output of the non-parametric discriminant analysis did not include the discriminant function coefficients. So, using this statistic alone did not allow us to determine which taxa and physicochemical parameters contributed most to the distinctness of no-bloom and bloom years. To compensate for this, we relied on two other statistical tests, an indicator species analysis and parametric discriminant analysis.

To elucidate phytoplankton and zooplankton taxa that were probably important during no-bloom and bloom years, we used indicator species analysis [the indicator value method (IndVal); Dufrêne & Legendre, 1997]. We ran this analysis on each of the data subsets used in our non-parametric discriminant analyses. The indicator value (IV_{ij}) for species i in group j was computed as follows:

$$IV_{ij} = A_{ij} \times B_{ij} \times 100$$

where A_{ij} was the proportion of the abundance (biomass) of species i in group j relative to the abundance (biomass) of species i over all groups (a measure of specificity), and B_{ij} was the relative frequency of species i in group j (a measure of fidelity). Indicator values, as percentages, ranged from 0% (no indication) to 100% (perfect indication). A maximum IV is obtained for those species in which all of their records occurred in only one group (i.e. maximum specificity, $A_{ij} = 1$) and were present in all of the sampling units within that group only (i.e. maximum fidelity, $B_{ij} = 1$). The indicator value of species i was the largest value of IV_{ij} observed over all groups j. The statistical significance of the IV for each species was tested using 1000 random Monte Carlo permutations. The P value obtained was the proportion of randomised trials with indicator values equal to or exceeding the observed indicator values (McCune & Mefford, 1999). In this study, a significance value of $P < 0.05$ was used. Indicator species analyses were run using PC-ORD for windows 4.14 (MjM Software Design Gleneden Beach, OR U.S.A).

To elucidate physicochemical parameters that were probably important during no-bloom and bloom years, we repeated our previous non-parametric discriminant analysis procedure using parametric discriminant analyses (SPSS). The results were remarkably similar. In fact, for our analyses of the post-1994 physicochemical parameters the results were identical. Consequently, we assumed that the parameters with heavier weightings in the parametric tests (highest absolute values of the discriminant function coefficients) were equally important in the non-parametric tests.

Causative mechanisms

Of all the documented catchment and in-lake events for Lake Kinneret (see Serruya, 1978; Hambright & Hershcovitch, 1998; Zohary, 2004), two coincided with the onset of unpredictable seasonal succession patterns. These were the collapse of the *A. terraesanctae* fishery in 1993 (Hambright & Shapiro, 1997; Ostrovsky & Walline, 2001), and hydrological changes in the peat soils of the Hula Valley, upstream of Lake Kinneret in 1994 (Hambright & Zohary, 1998). While it was hypothesised that changes to the amounts and

composition of trace metals and/or chelators arriving from the Hula Valley may have contributed to the changes in phytoplankton observed in Lake Kinneret (Berman *et al.*, 1998), there were no routine measurements that allowed for testing of this hypothesis, and it was left for future investigation. On the other hand, the fishery collapse was well documented and its potential impact on the food-web was debated (Hambright & Shapiro, 1997). To explore potential triggering mechanisms and ecosystem hysteresis within the framework of the alternative states model, we investigated data addressing fishery yields, and zooplankton biomass and body size.

Results

Distinct and persistent assemblages, 1969–2001

Our non-parametric discriminant analyses revealed that the phytoplankton assemblage, which involved both dominant and less abundant taxa, was distinct in years with a bloom of *P. gatunense* from that in
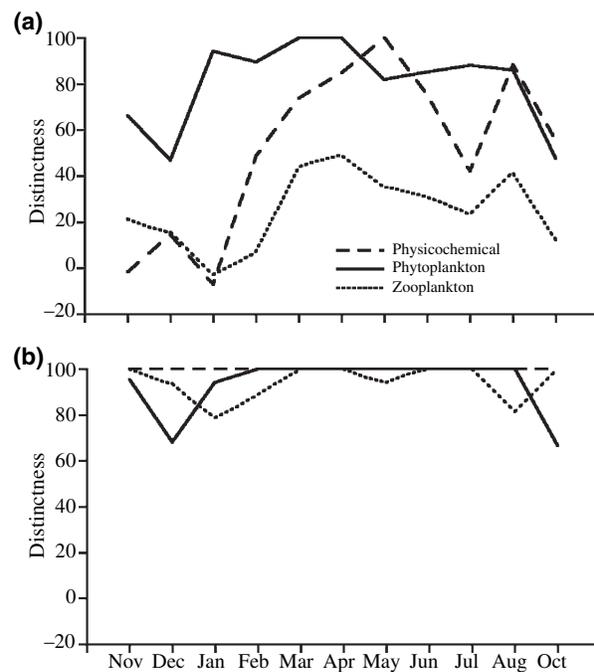

Fig. 2 Non-parametric discriminant analyses for the phytoplankton, zooplankton and physicochemical parameters. When the full data record was included in the analyses, 1969–2001 (a), only phytoplankton assemblages showed persistent distinctness, which spanned January to May inclusive. However, when only data from 1994–2001 (b) were used in the analyses, phytoplankton and zooplankton assemblages, and physicochemical parameters showed persistent distinctness.

no-bloom years (Fig. 2a). Furthermore, the 'distinct-ness' of no-bloom years was persistent because it spanned the period from January to May inclusive (Fig. 2a). The phytoplankton assemblages that occurred during years where there was a spring *P. gatunense* bloom (groups 2, 3 and 4) were not distinct from each other (results not shown).

When data from the entire zooplankton and physico-chemical records were analysed using the non-parametric discriminant analyses, the predetermined groups were not distinct during the period from November to May inclusive (Fig. 2a). In other words, zooplankton assemblages and physicochemical parameters were not significantly different during no-bloom and bloom years at this time of year. The physicochemical parameters eventually became dis-tinct, but only for the May–June period. Zooplankton assemblages were never distinct.

Distinct and persistent assemblages and environmental conditions, 1994–2001

A different picture emerges, however, when only data from 1994 through 2001 were considered in the analyses. For these latter years, the phytoplankton during no-bloom years and bloom years was again persistently distinct. However, then the environ-mental conditions were distinct for the entire year, and zooplankton assemblages were distinct at differ-ent times of the year. Zooplankton first became distinct during the early-winter months (November–December), well before the period when the phyto-plankton assemblage diverged. Zooplankton then became persistently distinct beginning in March and extending into the summer months (Fig. 2b).

Characteristics of the distinct no-bloom and bloom years

We relied on the results from our indicator species analyses to infer which phytoplankton and zooplank-ton taxa were important during no-bloom and bloom years. During the January–February period, when the phytoplankton first became distinct, a suite of green algae and a dinoflagellate species characterised the assemblage during no-bloom years. The green algae were *Oocystis* spp., *Coelastrum microporum* Naegeli, *Tetraedron minimum* (A Braun) Hansgirg, and *Scene-desmus* spp., and the dinoflagellate was *Peridiniopsis cunningtonii* Lemmermann (Fig. 3). Phytoplankton
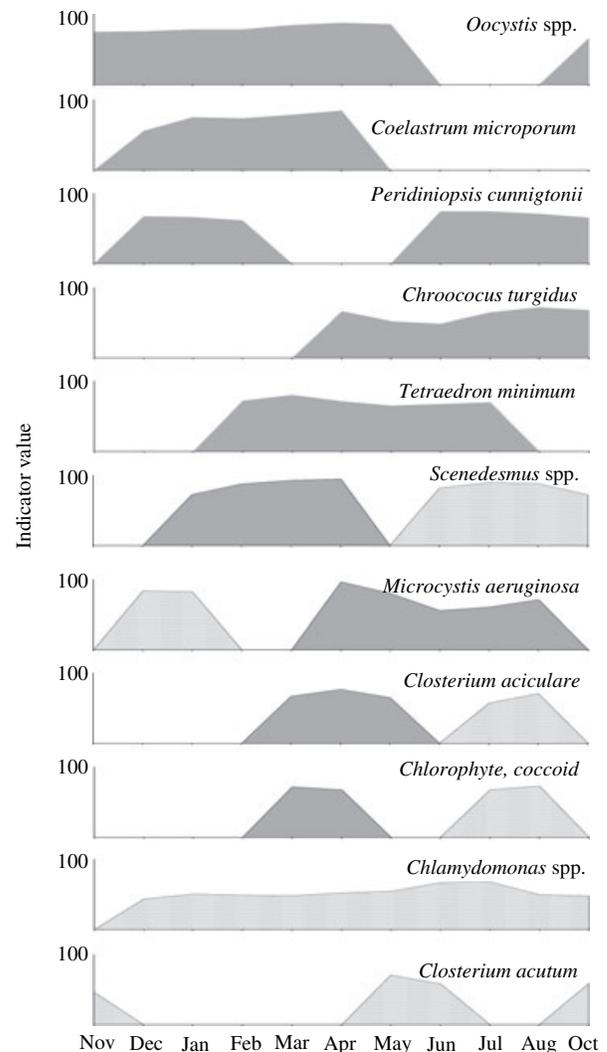

Fig. 3 Indicator species analyses of phytoplankton assemblages. Species were indicators of no-bloom years (dark grey), bloom years (light grey), and sometimes both (but at different times of the year, and during different years, see main text).

that characterised bloom years at this season included the cyanobacteria *Microcystis aeruginosa* Kuetz and species of the green alga *Chlamydomonas*.

Some of the taxa were indicators of both no-bloom and bloom years at different times of the year. This does not mean that a taxon was an indicator for both no-bloom and bloom states in the same year, however. To clarify, we focus on *M. aeruginosa* in Fig. 3: either *M. aeruginosa* was an important indicator species during no-bloom years late in the year (spring and summer months), or it was an important indicator species during bloom years early in the year, i.e. winter months. Note that during no-bloom years, the

importance of *M. aeruginosa* was significant well after the time of year when distinct phytoplankton assemblages emerged. During bloom years, however, *M. aeruginosa* was an important species just before distinct phytoplankton assemblages emerged.

During November–December, before distinct phytoplankton assemblages emerged, zooplankton taxa characteristic of no-bloom years included the cladoceran *Chydorus sphaericus* Mueller and the adult stage of the copepod *Mesocyclops ogunnus* Onabamiro (Fig. 4). Starting from the March–April period and persisting through the summer months, zooplankton taxa characteristic of no-bloom years included the cladocerans *Diaphanosoma brachyurum* Lieve and *Bosmina longirostris cornuta* Jurine, the adult stage of the copepod *Thermocyclops dybowskii* Landé, and juvenile and naupliar stages of cyclopoid copepods. Taxa
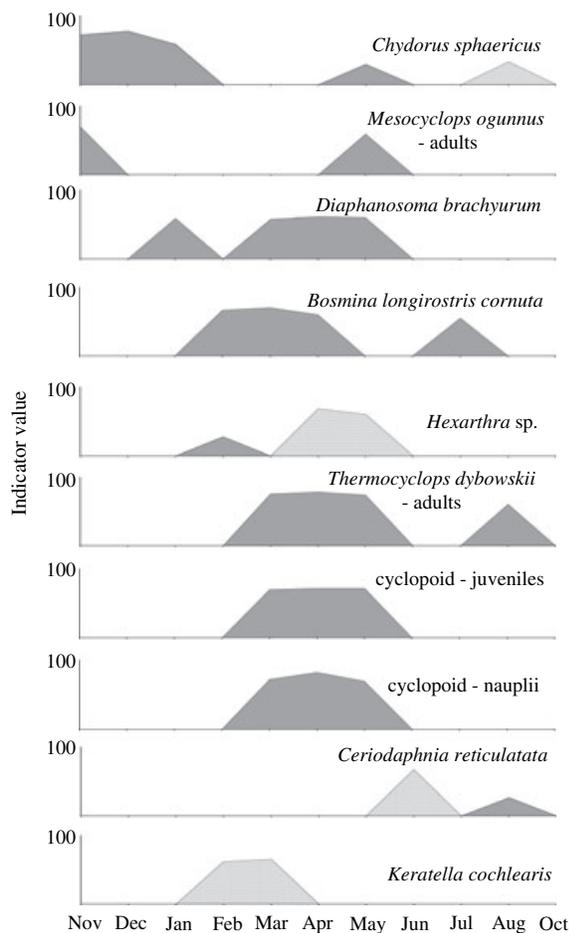

Fig. 4 Indicator species analyses of zooplankton assemblages. Zooplankton taxa were indicators of no-bloom years (dark grey), bloom years (light grey), and sometimes both (but at different times of the year, and during different years, see main text).

characteristic of bloom years during this time included the rotifers *Hexarthra* sp. and *Keratella cochlearis* Gosse, and the cladoceran *Ceriodaphnia reticulata* Jurine.

The discriminant function coefficients from our parametric analyses reflected those physicochemical parameters that more strongly influenced the distinctness of no-bloom and bloom years. For example, from January to April (a period corresponding to the emergence of distinct phytoplankton states) environmental conditions indicating no-bloom years included lower loading of NO_3 from the Jordan River, higher epilimnetic temperature, higher concentrations of NO_3 and of Cl, lower epilimnetic concentrations of TP, higher water levels, greater depths of the thermocline, and shallower Secchi depths (Fig. 5).

Possible causative mechanisms

In 1993–94 the Kinneret Bleak, *A. terraesanctae*, fishery collapsed (Fig. 6a) as a result of a change in the size structure of the fish population. Large individuals became extremely rare, while the abundance of smaller individuals increased by an order of magnitude due to unusually successful reproduction and survival of the young-of-year in 1992/3 (Hambright & Shapiro, 1997; Ostrovsky & Walline, 1999). This reproductive success was attributed to an extreme increase in water level during the exceptionally rainy winter of 1991/2 following a series of drought years and artificial draw-down of the water level. Coincident with this fishery collapse was a very low zooplankton biomass and a decrease in the average body size of many taxa (Fig. 6b,c).

Discussion

When using conventional statistics, the assumption that correlation implies causation has often been used to elucidate relationships between forcing factors and ecosystem response. However, conventional statistics might fail to discover significant relationships when the system response to a forcing factor is nonlinear (see Dwyer & Perez, 1983; Ellner & Turchin, 1995; Pascual & Caswell, 1997; Pascual & Ellner, 2000). In other words, poor correlation in these cases would not necessarily discount causation. Rather, it might be that more complex models are needed to elucidate relationships. One such model encompasses the
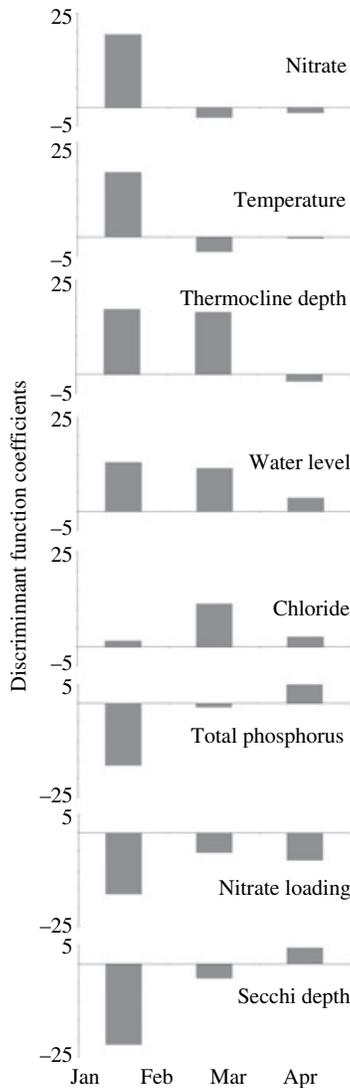
Fig. 5 Parametric discriminant analyses of physicochemical parameters. For this figure only the period between January and April is shown, which corresponded to the period when distinct phytoplankton assemblages emerged. Positive discriminant function scores meant the parameter was strongly weighted for no-bloom years, and negative scores meant the parameter was strongly weighted for bloom years.

Fig. 6 Fishery yields of the Kinneret Bleak, *A. terraesanctae* (updated from Hambright & Shapiro, 1997), and changes to zooplankton biomass and taxon-specific body mass for selected zooplankton. As a result of intense fishing pressure, the mean body size of the Kinneret Bleak decreased. Eventually, the fishery collapsed in 1993–94 (a). Coincident with the reduction in fish body size and collapse of the fishery, zooplankton biomass decreased (b). This decrease came about through shifts in community composition, where smaller taxa emerged as dominants (data not shown), and decreases in body mass of specific taxa (c). Fishery data are courtesy of Jamie Shapiro, Israel Fisheries Department.

concept of alternative states (Scheffer *et al.*, 1997; Scheffer, 1998; Carpenter *et al.*, 1999, 2001), where critical thresholds must be crossed before incidence of alternative states is possible. When data encompass periods before and after a crossing of a threshold, correlations between system response and forcing factors can be poor indeed.

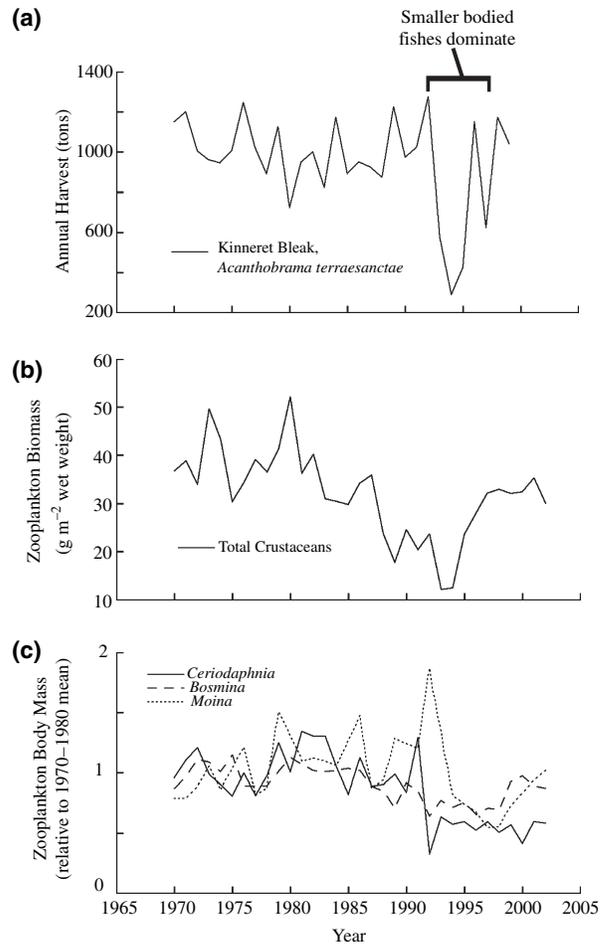The phytoplankton assemblages, comprising dominant and non-dominant taxa, that characterised succession from January to the summer months during no-bloom years were distinct from the assemblages during bloom years. While it was difficult to determine the positive feedbacks that allowed these different states to persist, there are some factors that are more likely than others. For example, because Lake Kinneret is 43 m deep, unlike the shallow lake systems where other distinct and persistent states have been described, the role of interactions between the water-column and sediment is reduced. In other words,

factors that impacted the persistence of these states in Lake Kinneret probably resided in the water-column.

A potential factor contributing to the persistence of the distinct states might have been *P. gatunense* populations in the water-column. For example, *P. gatunense* blooms are known to influence food web structure, population dynamics and productivity in Lake Kinneret through mechanisms relating to quantity and quality of food, allelopathy and sequestration of nutrients (Hadas & Pinkas, 1995; Zohary *et al.*, 2000; Hambright, Blumenshine & Shapiro, 2002; Vardi *et al.*, 2002). Furthermore, temporal correlations linking spring and summer phytoplankton biomass that involved *P. gatunense* blooms were observed in Lake Kinneret (see Berman *et al.*, 1998). The absence of *P. gatunense* blooms might also be important, where factors relating to quantity and quality of food, allelopathy and sequestration of nutrients are relaxed, thereby allowing a different seasonal succession trajectory to emerge. Additional research is needed that targets potential positive feedbacks that lead to persistence of these distinct phytoplankton states.

What might have triggered the incidence of these distinct phytoplankton states? While *P. gatunense* might have impacted the persistence of the states, it was unlikely to influence which state occured in a given year. The distinctness we observed in the phytoplankton assemblage was apparent by the January–February period, before the intensification of spring *P. gatunense* blooms. In addition, November–December *P. gatunense* population density accounted for little of the variation in the January–February *P. gatunense* population density (analyses not shown), i.e. population densities during the period of destratification did not appear to influence the incidence of blooms. Finally, our analyses using conventional statistics (correlation and principal component analyses, and non-metric multidimensional scaling, results not shown) failed to reveal which physicochemical and biological factors influenced *P. gatunense* blooms.

When we focussed only on the period spanning 1994–2001, however, correlative relationships were apparent, and they involved physicochemical parameters and zooplankton taxa where linkages between biota and the physicochemical environment, and food web interactions could be envisaged. For example, Serruya & Pollingher (1972) argued that high NO_3 loading enhanced the development of *P. gatunense* blooms, so it is not surprising that our analyses revealed higher NO_3 loading as a characteristic of bloom years. Similarly, Sukenik *et al.* (2002) observed allelopathic interactions between *M. aeruginosa* and *P. gatunense*. Therefore, it is not unexpected that *M. aeruginosa* was an important indicator species during bloom years prior to the time of year when *P. gatunense* blooms intensify (but not concurrently with *P. gatunense*).

In our analyses, years with blooms were characteristic of higher NO_3 and lower TP concentrations during the time of year when the distinct phytoplankton states emerged. It is likely that our analyses showed multiple species of green algae as important indicators of the no-bloom state, because green algae are known to compete well under these conditions (Sommer, 1989; Reynolds, 1994; Roelke, Cifuentes & Eldridge, 1997; Roelke, Eldridge & Cifuentes, 1999; Roelke *et al.*, 2004). Regarding *P. gatunense*, Berman *et al.* (1984) observed that during blooms the bulk of assimilated nitrogen was derived from NO_3, whereas for other species it was mostly derived from NH_4, thus in no-bloom years more NO_3 remained in the water. In addition, high epilimnetic TP concentrations were typically associated with *P. gatunense* blooms (Berman *et al.*, 1992), so it is not surprising that in our analyses TP concentrations were lower during no-bloom years.

Years without blooms were also characterised by higher temperature and lake level at the time of year when the distinct phytoplankton states emerged. Higher winter temperature probably gave a competitive advantage to the green algae, with their faster growth rates. Higher water levels meant that the lake rose and inundated dried areas, which perhaps impacted the process of *P. gatunense* excystation. Indirect and hitherto unresolved impacts of higher water level were also possible.

Finally, through selective grazing processes and the stoichiometry of consumer-driven nutrient recycling, zooplankton strongly influence the composition and succession trajectories of phytoplankton (Sommer *et al.*, 1986; Sterner, 1989; Hansen, Bjornsen & Hansen, 1994; Elser & Urabe, 1999). While the suggestion that the winter-time abundance of the cladoceran *C. sphaericus* and the copepod *M. ogunnus* influenced the incidence of no-bloom and bloom years seems plausible, the specifics of the interaction remain to be elucidated.

It will require much experimentation to evaluate the nature of the triggering mechanism for no-bloom and

bloom years, which may involve interaction between several mechanisms, such as those mentioned above. The enticing question from our analyses of the Kinneret data, however, is why did we observe potential causative relationships in the 1994–2001 data subsets, but not when we analysed the entire data record? In other words, was a mechanism at play that negated the effect of processes influencing the incidence of no-bloom years prior to 1994?

There were many human-induced changes that occurred in the Kinneret catchment and the lake in recent history (see Serruya, 1978; Hambright & Hershcovitch, 1998; Zohary, 2004), which included manipulations of the hydrology, lake water level, nutrient loading and fishery practices and management. Most of these changes did not coincide with the observed changes in the plankton, however (i.e. from 1994 onward). The exception was the change in the dominant fishery. While fishery yield data also correlated poorly with *P. gatunense* population density, the timing of the fishery collapse coincided with the occurrence of distinct and persistent states in the phytoplankton assemblage.

We now focus on the collapse of the *A. terraesanctae* fishery, and potential cascades that might have occurred in the zooplankton assemblage. We interpret our findings in the framework of the alternative states model. We selected this model as a conceptual framework because of the occurrence of system hysteresis, which is a signature of systems behaving according to the alternative states model (Scheffer *et al.*, 1997; Scheffer, 1998; Carpenter *et al.*, 1999, 2001).

The dominant fishery in Lake Kinneret harvesting *A. terraesanctae*, collapsed in 1993–94 (Fig. 6a) as a result of a change to the size structure of the fish population due to long-term overexploitation. That is, large individuals disappeared, while small fish became much more abundant (Hambright & Shapiro, 1997; Ostrovsky & Walline, 1999, 2001). How might this reduction in the body size of *A. terraesanctae*, which accounts for 30–60% of the total zooplanktivory in Lake Kinneret (Blumenshine & Hambright, 2003), have impacted the phytoplankton? Coincident with increased fishing pressure on the Kinneret Bleak population, the biomass of the zooplankton declined (see Fig. 6b). Contributing to this decline were reductions in the mean body mass for most crustacean taxa (see Fig. 6c). Such changes are consistent with known impacts of increasing fish predation pressure on

zooplankton (Brooks & Dodson, 1965; Carpenter, Kitchell & Hodgson, 1985; Hambright & Hall, 1992). Moreover, there is substantial evidence of cascading effects of such changes at the zooplankton level to phytoplankton (Reynolds, 1994; Persson, 1997; Drenner & Hambright, 1999, 2002; Matveev, 2003).

To put all the potential mechanisms together, we refer to a hypothetical alternative states model tailored to Lake Kinneret (Fig. 7). The curved lines in the figure represent no-bloom and bloom years. A 'slow changing' variable is shown on the *x*-axis and 'fast changing' variables are shown on the *y*-axis. For Lake Kinneret, the slow changing variable seems to involve shifts in grazing pressure exerted on the phytoplankton as a function of changes in the abundance and body size of zooplankton. The fast changing variables seem to involve several winter-time physicochemical parameters and some zooplankton taxa. Using this framework, it can be seen that moderate variation in the physicochemical parameters and zooplankton assemblage structure (a shift from Z-PC$_B$ to Z-PC$_{NB}$, Fig. 7) would only influence the incidence of alternative states when the slow changing variable (*x*-axis) places the system in region Y of the model. In other
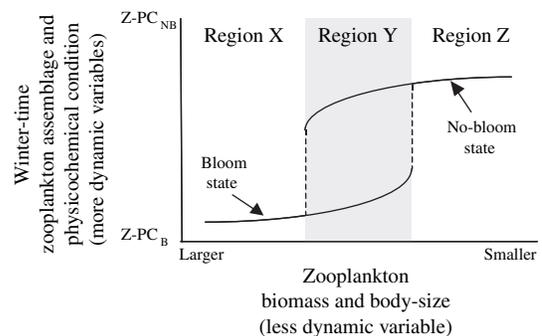

Fig. 7 Alternative states model tailored for Lake Kinneret (see Scheffer, 1998; Carpenter *et al.*, 2001). Two alternative states of the system are described, no-bloom and bloom years. Incidence of alternative states are governed by two variables. The first variable involves zooplankton biomass and body size (the 'slow changing' variable, *x*-axis). When the system is characterised by greater zooplankton biomass and large zooplankton (region X of model) only bloom years are possible. Similarly, when the system is characterised by very low zooplankton biomass and small zooplankton (region Z of model) only no-bloom years are possible. Only at intermediate values of zooplankton biomass and body size (region Y) are the alternative states possible. When the system is in region Y, the second variable influences which state, no-bloom or bloom, will emerge in a given year. This second variable involves variation in winter-time zooplankton assemblage structure and some physicochemical parameters (the 'fast changing' variables, *y*-axis).

words, in the latter years of the Kinneret record (post-1994), the shift in biomass and body size of the zooplankton assemblage made it possible for the incidence of alternative states. Prior to the collapse of the Kinneret Bleak fishery, incidence of alternative states was not possible because the system was in region X of the model. Interpreting the data within the framework of an alternative states model also provides an understanding of why statistical analyses encompassing the full data record failed to output significant relationships between physicochemical and biological factors with incidence of no-bloom years. Lake Kinneret shows hysteresis in that zooplankton biomass has increased and some of the taxa have regained their former body size (Fig. 6b,c), yet incidence of alternative states still occurs.

To summarise, we observed distinct and persistent states in the phytoplankton assemblages of Lake Kinneret that corresponded with no-bloom and bloom years of the dinoflagellate *P. gatunense*. Using conventional statistics, we were unable to determine factors that impacted which phytoplankton state would emerge in a given year (results not shown). Within the framework of the alternative states model, however, we were able to elucidate potential triggering mechanisms, which were a function of wintertime physicochemical conditions and zooplankton assemblage structure, and zooplankton biomass and body size. System hysteresis was observed in that the biomass and body size of some key zooplankton taxa recovered, but no-bloom and bloom years still occurred in the lake. While the anomalous no-bloom years in Lake Kinneret can be explained within the framework of the alternative states model, we have not supported this idea through experimentation, which is a future research goal.

Acknowledgments

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