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Predicting the impact of Lake Biomanipulation based on food-web modeling - Lake Kinneret as a case study

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Abstract

Biomanipulation is a tool for decision makers use to achieve desirable management goals. In lakes, one of the most common goals is the improvement of water quality, an objective that can be achieved mainly by reducing the amount of phytoplankton in the water. Although it is a very clear goal that is achievable by using actions that affect the phytoplankton biomass, experience shows that primary biomanipulation goals are rarely achieved. A biomanipulation program was conducted in Lake Kinneret over a 12-year period with the goal of improving water quality by reducing the population of the dominant fish species in the lake. However the biomanipulation failed to achieve the goal and the program was stopped. We used Ecopath with Ecosim (EwE) scenarios to examine the effect of biomanipulation on the ecosystem. The results of these scenarios show that biomanipulation actions, such as those used in the lake, indeed fail to improve water quality; furthermore, they will actually increase the amount of phytoplankton in the water and decrease water quality. The development of the method described in the present article provides managers with the means to evaluate the effect of biomanipulation on an ecosystem. This method enables researches to conduct a pre-action analysis of the planned measures and examine whether the goal can be achieved, saving money and time and preventing damage to the ecosystem.
Introduction

Over the past 30 years it has been recognized that stocking or removing certain fishes from lakes (i.e., biomanipulation) can have an important influence on the food-web structure and the resulting water quality. Biomanipulation is increasingly used as a lake restoration technique, largely because the ability to enhance water quality and support fish populations is important to a variety of lake users (Mehner et al., 2002). Biomanipulation, in aquatic ecosystems, involves the manipulation of fish populations for the purpose of inducing a consumer-mediated trophic cascade in the food-web that will in turn influence water quality (Jeppesen et al., 2012). This technique can be integrated with other biomanipulation approaches, such as introducing or enhancing the herbivorous fish biomass in order to control the macrophytic biomass (Rowe and Champion, 1994).

Although biomanipulation research has contributed substantially to our understanding of lake foodwebs, the successful application of these techniques is not a "one size fits all" approach. In a review of biomanipulation research, Mehner et al. (2002) discussed the factors affecting food-web complexity and the success of various biomanipulation efforts. They made the following observations: (1) nutrient recycling by aquatic organisms contributes to bottom-up impacts on lake productivity, but the magnitude of these impacts varies greatly between lakes; (2) the complexity of food-web interactions is enhanced by size-dependent interactions and bottom-up impacts on lake productivity, but the magnitude of these impacts varies greatly between fishes and can limit our ability to predict the outcome of a biomanipulation event successfully; (3) it is important to consider the temporal and spatial scales of biomanipulation research – repeated interventions may be necessary to maintain the desired outcome in the lakes; and, (4) a correct balance between piscivorous, planktivorous, and benthivorous fishes is needed in order to achieve the desired biomanipulation outcome, but it can be a challenge due to a general lack of quantitative assessment. When practical, the removal of undesirable fishes seems to have a larger impact on water quality than stocking of piscivorous fishes. A synthesis of biomanipulation studies involving 39 lakes that varied in size, between 0.18 and 2,650 hectares and with a mean depth of 23 m, showed that changes in phytoplankton biomass and water transparency as a result of biomanipulation were most successful in small, shallow lakes smaller than 25 hectares and with a mean depth of < 3 m (Drenner and Hambright, 1999). Changes in water quality were also influenced by the type of
biomanipulation implemented. Approximately 90% of the studies that implemented partial
fish removal succeeded in improving water quality. Other approaches had varying levels of
success: (1) elimination and restocking of fish (67%), (2) partial fish removal together with
piscivore stocking (60%), (3) elimination of fish (40%), and (4) piscivore stocking (27%).
Moreover, approximately 15% of the studies that used biomanipulation techniques were
unsuccessful in enhancing water quality for at least 1 year (Drenner and Hambright, 1999).
Although the mechanisms responsible for these changes can vary, evidence suggests that in
lakes dominated by benthivorous fishes (e.g., common carp) more than 50% of the turbidity
can be caused by sediment resuspension (Meijer et al., 1994). Reducing the number of
benthivorous fishes in the lake can also indirectly reduce algal biomass, since it triggers a
shift to the clear, macrophyte-dominated state characteristic of many shallow lakes (Hubert
and Quist, 2010). Yet not all the studies that used biomanipulation met with success or
produced stable ecosystems. Burns et al. (2013) summarized 50 years of biomanipulation
attempts in several lakes in New Zealand and concluded that in some lakes biomanipulation
has indeed resulted in a better water quality in the short term (< 5 years), but that in the long-
term the results of biomanipulation must be accompanied by reductions in nutrient loading,
achievable only via an integrated management program that will consider both the direct and
the indirect impacts of each step of a proposed biomanipulation program on the whole lake
ecosystem.

A long term biomanipulation program was implemented in Lake Kinneret, Israel, between
1994 and 2006, based on the trophic cascade hypothesis and with the aim of preventing
deterioration and improving water quality. The plan aimed to decrease the number of
Mirogrecs terraeasantae (locally known as Lavunn), with the final goal of both decreasing the
predation pressure on the zooplankton and making it possible for the remaining fishes to
"benefit" from more food, thus enabling them to reach commercial size in a better physical
state. Beyond that, reducing the predation pressure of the Lavnum on the zooplankton would
revive and increase the zooplankton population and thus allow them to graze on more
phytoplankton. This, it was assumed, would improve the quality of the water in Lake
Kinneret (Gasith and Zohary, 2006). In the framework of the program, quantities of between
300 and 900 tons of Lavnum were removed from the lake annually between 1994 and 2006.
Most of them were not used commercially, but were buried in nearby landfills after their
removal from the lake. Despite the ongoing removal program, another collapse of the
Lavnum’s commercial fishing occurred in 2004/5, and the fish caught were of sub-
commercial size (Hambright, 2008). The unsuccessful biomanipulation of Lake Kinneret as well as the results of biomanipulation programs conducted in different lakes in New Zealand emphasize the need for a tool that will enable managers to determine the likely outcomes of biomanipulation on the ecosystem.

The dynamic simulation modelling tool Ecosim has the ability to simulate future management scenarios and analyze the impact of different variables on the ecosystem. Ecosim, a component of the Ecopath with Ecosim software package (www.ecopath.org), expands Ecopath’s capabilities and allows the exploration of temporal impacts of fishing and environmental factors. It enables users to change fishing mortality or fishing effort over time, enabling the exploration of fishing options and changes in ecosystem functioning. It also dynamically responds to changes in fishing mortality and biomass, enabling the creation of dynamic simulations at the ecosystem level from the primary parameters of a baseline Ecopath model (Christensen et al., 2000; Walters et al., 1997).

Christensen and Walters (2004) used Ecosim to search for alternative exploitation patterns, setting different sustainability objectives and optimizing for profit, value and conservation in the Gulf of Thailand. Coll et al. (2009) summarized several cases where an Ecosim model was used to analyze policy optimization and management; most of the scenarios focused mainly on the aspect of fisheries management. Heymans et al. (2009) used the time dynamic model to explored alternative policy options for the northern Benguela ecosystem. Heymans et al. (2016) summarized the use of models in several aspects including management context, specifically using the concept of ‘key runs’ for ecosystem-based management.

In the present study, we used Ecopath with Ecosim (EwE) to analyze the effect the biomanipulation program had on Lake Kinneret’s ecosystem. We used an Ecopath model that was previously used to study the lake’s food-web (Ofir et al., 2016). In the current study we developed a time-dynamic model (Ecosim) based on the Ecopath model, which was calibrated using lake data for the time-period of 1996-2012. We compared simulations that included or excluded biomanipulation strategies in order to evaluate the impact of the biomanipulation on the ecosystem. This was done by running and comparing 10-year simulations.
Methods

Study area

Lake Kinneret (with alternative names as Sea of Galilee and Lake Tiberias), the largest freshwater body in the Middle East, is a mono-mictic subtropical lake located at ~210 m altitude, i.e., below mean sea level. It has a surface area of approximately 167 km² and a watershed of 2730 km². The main inflow is from the Jordan River, which contributes on average 70% of the total inflow (Gal et al., 2003), while the main outflow, until recently (2014), was pumping into Israel’s National Water Carrier. The lake’s water level represents the balance between inflows, evaporation and withdrawals for water supply, while direct rain plays an insignificant role (Rimmer and Givati, 2014). Details regarding the basic limnology of Lake Kinneret can be found in (Zohary et al., 2014). Since the establishment of Israel’s National Water Carrier (1965), the main uses of the lake have been drinking and irrigation supply (the lake supplies 30% of the total national demand for drinking water). As a consequence of these uses, the most critical management issues Lake Kinneret’s resource managers face are the progressively increasing portion of cyanobacteria among the algal biomass (Zohary, 2004) and the gradual increase in water salinity. Due to the lake’s importance to Israel and the need to manage the ecosystem, there is an ongoing monitoring program that has been operating since 1969, which includes the maintenance of an extensive long-term database that contains the data of more than 100 hydrological, meteorological, chemical and biological variables, some collected weekly and others fortnightly at five stations and at several depths (Sukenik et al., 2014). The highly detailed ecological monitoring system in Lake Kinneret enables researches to use the lake as a model for a wide spectrum of management studies (Gal et al., 2009; Gal et al., 2014; Gilboa et al., 2014; Parparov and Gal, 2012). In this study, we use these data for the period of 1990-2012 in order to complement and test the model simulations.

Model structure

We constructed a time-varying food-web model of Lake Kinneret’s ecosystem using Ecopath with Ecosim (ver. 6.4) (Christensen et al., 2000; Coll et al., 2009). The model was designed to focus on the upper trophic levels in order to provide a means for identifying major changes to the ecosystem functioning and analyze the influence of biomanipulation. The model includes 26 groups that represent all the important components of the lake’s food-web (Ofir
et al., 2016). The phytoplankton include all the species of importance in the lake, divided into 7 groups (Aphanizomen, Aulacosira, Microcystis, Peridinium, Debarya, nanoplankton, as well as nanoplankton 2, a group that included all the rest of the phytoplankton species), each composed of a combination of several species. The zooplankton are divided into three functional groups (predatory, herbivorous and micro-zooplankton). The fish in the model mainly include the commercial fish species in the lake, with some additions that are important to the food-web structure. While most groups included only one general age group, three groups of the fishes that are stock in the lake, included multiple life stages, known as multi-stanza in the software (i.e., division into several age periods), in order to address the stocking of these species into the lake taking into account that the fingerling come from outside the lake. We incorporated bacteria, detritus and birds into the model as well in order to simulate the complete food-web. The birds, namely Cormorants (Phalacrocorax carbo), nest around the lake and feed on the fish during the winter months. The fishing effort in the lake was separated into purse seine and trammel fishing, according to records obtained from the Fisheries Department. The model was set in yearly units of t km$^{-2}$ and in measurements of wet tons, and all the data were transformed accordingly.

**The dynamic model**

The time-dynamic model (Ecosim) was linked to the mass-balance model (Ecopath) and derived all the necessary food-web parameters from it in order to conduct the simulations over time. In this study we used an Ecopath model based on the time period of 1990-1995 (Ofir et al., 2016). A time-series of data for the period of 1996-2012 was then provided as input to Ecosim in order to calibrate the model and evaluate the model’s results.

**Input data**

Our time-series data input to the model included phytoplankton and zooplankton biomass extracted from the Kinneret Limnology Laboratory (KLL) database and fishing effort. Cormorant biomass data were based on Nature and Parks Authority (NPA) reports. Additionally, Ecosim simulations are mainly calibrated to a time-series of biomass or catch data, or to estimates of how the fishing effort impacts the fish populations over a certain time-period (e.g., the total fishing mortality of a functional group). Thus, the time-series input data also included catch data. The commercial catch and relative fishing effort data were obtained from the Israel Fisheries Department (J. Shapiro, unpublished data) and (Shapiro, 2006). We improved the diet matrix in the basic food-web model using ongoing researches that analyses stomach contents of silver carps (J. Shapiro, unpublished data).
The user can define the status of the time-series data input to the model as forcing or non-forcing data. When the forcing option is used the model results have fit the data better but skip the calibration process, and therefore the forcing data are normally used only for the lower tropic levels (Watters et al., 2003). Mackinson et al. (2009) showed that using all the existing data (the primary production and low tropic groups biomass) improves the model’s forecasting capability. Accordingly, in this study we forced the model with phytoplankton biomass, the data of the fingerling stocking the Cormorant biomass and the fishing effort (Table 1). For all remaining groups we did not force the model and therefore the observed dynamics in the model outcome are a result of the model simulation. Simulated values of the catch were compared to the available time-series data as part of the model’s calibration process.

Table 1 – Time-series data used for the Lake Kinneret Ecosim model

<table>
<thead>
<tr>
<th>Data time-series</th>
<th>Units</th>
<th>Time period</th>
<th>Model Group</th>
<th>Forced/ Not forced</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cormorant biomass</td>
<td>(t km² y⁻¹)</td>
<td>2003-2012</td>
<td>Cormorant (Phalacrocorax carbo)</td>
<td>Forced</td>
<td>Nature and Parks Authority (NPA)</td>
</tr>
</tbody>
</table>
| Fingerling stocking    | (t km² y⁻¹) | 1996-2012   | • Silver Carp (Hypophthalmichthys molitrix)  
• Mugilids (Liza ramada, Mugil cephalus)  
• Sarotherodon galilaeus | Forced             | Dept. Fisheries                          |
| Zooplankton biomass    | (t km² y⁻¹) | 1996-2012   |                                   | Not forced         | KLL                         |
| Phytoplankton biomass  | (t km² y⁻¹) | 1996-2012   |                                   | Forced             | KLL                         |
| Fishing effort         | Relative to 1995 | 1996-2012 | • purse seine  
• trammel | Forced             | Dept. Fisheries                         |
| Commercial catch       | (t km² y⁻¹) | 1996-2012   |                                   | Not forced         | Dept. Fisheries                         |

Calibration procedure
The procedure for Ecosim model calibration is well explained by Heymans et al. (2016). The procedure is based on statistical correlation between the model output and the data, taking into
account the impact of fishing, changes in predator-prey dynamics (also called the vulnerability settings), possible changes in primary production, or all of the above. Therefore, the parameters that obtain the lowest AIC (Akaike Information Criterion) provide the combination that fits the model to the data best while using the smallest number of parameters to do so (Akaike, 1974).

The combination of parameters tested included:

1. Baseline - the model run without fishing and with no changes in vulnerabilities (the availability of the prey to the predator) or to the phytoplankton biomass forcing.
2. Baseline and changes in vulnerabilities.
3. Baseline and changes in vulnerabilities and in the phytoplankton biomass forcing.
4. Catch.
5. Catch and phytoplankton forcing.
6. Catch and changes in vulnerabilities.
7. Catch and changes in vulnerabilities and phytoplankton biomass forcing.

In order to fit the time-series to the model we used the Stepwise Fitting Procedure Plug-in (Scott et al., 2016). The standalone plug-in automatically provides Ecosim with alternative hypothesis testing, as described above.

**Sensitivity analysis**

Ecosim allows the user to test the sensitivity of the model output to the basic inputs to the model (Biomass, P/B, Q/B and EE) using a Monte-Carlo (MC) routine, which runs the model with combinations of different input data values. Using this routine we ran 2500 simulations of different combinations of parameter values within the range of the confidence levels of the data provided to the model in the pedigree, i.e, the defined range of confidence provided as input to the Ecopath model, as described in Ofir et al. (2016). The confidence level was determined based on the source of the data. The biomass of the phytoplankton, zooplankton and cormorants and the fish catch were based on data from monitoring programs, so the confidence in these parameters was high, while the P/B and Q/B were calculated using different models and thus had lower confidence levels. The output of the MC routine and simulations were 2500 different balanced Ecopath models that in turn served as the basis for the Ecosim simulations of the lake for the years 1996-2012. The output was used to check the sensitivity of the different fish groups to potential changes in model parameters. We assumed that a limited sensitivity of the model output to the changes in the parameter values increases the confidence in the output of the management scenarios.
The management scenarios

As Ecosim is a time-dynamic model it allows the user to evaluate the possible outcome of potential management scenarios, such as changes in stocking policy, fishing regulations, etc. In order to analyze the potential effects of removing Lavnun from the lake on the ecosystem we created a 10 year biomanipulation scenario from 2013-2022 that included several basic assumptions:

1) The stocking effort of St. Peter’s Fish (*Sarotherodon galilaeus*), Mugilids (*Liza ramada, Mugil cephalus*) and Silver Carp (*Hypophthalmichthys molitrix*) remain at the same level as it was in 2012; 2) Lavnun fishing increase over the period of the simulation (2013-2022) to an annual catch of 500 tons, a value higher than the catch in 2007-2012 but lower than the catch during the biomanipulation program that took place in the lake between 1994 and 2006; 3) In order to obtain this amount of catch there will be a doubling of the fishing effort, mainly through purse seine fishing. These scenarios were based on the 2012 conditions in the lake. Consequently, stocking rates, fishing effort, phytoplankton, zooplankton and Cormorant biomasses were also set to the 2012 levels. In order to identify the changes that occurred following the implementation of various management steps, we created a scenario called the “base scenario”, which assumed that there would be no changes over the course of the simulation period. We therefore maintained the 2012 conditions, including fishing effort and fish stocking, for the duration of the base scenario. The results of the management scenario were then compared to the base scenario. We analyzed the changes in biomass and the catch of all the groups in the model in order to determine the impact of the management steps.

Results

A model of the lake’s food-web was created as part of the output from Ecopath, defining the trophic level of all the components and the linkages between all the functional groups (Fig. 1). The Lavnun fish, group no. 14 in the model, has one of the highest trophic levels, with a large biomass compared to the rest of the fish groups. As a consequence, removing the Lavnun could potentially have a big impact on the lake’s ecosystem.

Comparing model output with data

In order to evaluate the results of the time dynamic model we compared them to the data that we used in the time-series, which was part of the calibration process. The model was forced with fishing effort and we use the commercial fish catch estimate with what the model predict as a means for evaluating model output. The model generally successfully captured the reported catches, with a number of exceptions. For the Barbel and Carpio there was a good correlation between the simulated and actual catches and in the observed trends (Fig. 2A, B). The Muglides and Silver Carp don’t reproduce in the lake and their fingerlings are stocked every year, though the stocking of Silver carp fingerlings was stopped in 2015. The model successfully simulated both the actual catch and long-term trends in the Muglides but was less accurate in simulating the silver-carp (Fig. 2C,D). The model reproduce the catches and trends of the most valuable
species in the lake, *S. galilaeus*, with the exception of 1997 and 2005 (Fig. 2E). *Oreochromis aureus* (Fig. 2F) and Zilli (Fig. 2G) are groups of tilapia with very low market value and the motivation to catch them is low. Though the model reproduced the observed trends, the actual catches were over-estimated by the model during part of the simulation period, with differences of ±0.045 Ton/km² and -0.04 Ton/km² on average, for O. aureus and Zilli, respectively (Fig, 2F,G). The Lavnun’s catch dynamics, which are the main focus of this study, were successfully reproduced by the model and the results show a good fit between the model output and the data, with the exception of the period of 2001-2002 (Fig. 2H).
Figure 2 – A comparison between the model results and the catch data of fishes for the time period of 1996-2012. Where: A) Barbel, B) Carpio, C) Muglides, D) Silver Carp, E) *Sarotherodon galilaeus* (S.G), F) *Oreochromis aureus*, G) Zilli, H) Lavnun. The SS is presented on the right top box of the group.

### Statistical evaluation

As part of the examination of the model, a statistical evaluation regarding the model’s level of adjustment to lake data was conducted using the Stepwise Fitting Procedure Plug-in ([Scott et al., 2016](#)). The results can be described in two stages. The first stage is the output of the fitting procedure, which provides an indication of the best way to fit the model to the data, and the second is the correlation between model results and the data for each individual group. In stage one we used the output of the Stepwise Fitting Procedure to fine-tune the combination of parameters that provide the lowest AIC value. The best combination that provided the lowest AIC value was achieved by using Fishing (catch) and allowing the model to change 4 vulnerabilities (Table 2). As the number of vulnerabilities the model changed increased, the sum of squares (SS) value decreased but the AIC increased, providing a worse solution of the
parameter values. The optimum set of parameter values provided results of an AIC of 25.12 AIC and a SS of 203.79.

The second stage included checking the SS results for the different groups. The SS was calculated by the model for every group as the difference between the model’s results and the data input in the time series. While differences are often visually obvious (Fig. 2), calculating the SS values provides a quantitative estimate of the similarities or differences. For example, the Lavnun had a SS of 10.17, which reflects a good fit to the data and a high reliability for using the model in Lavnun scenarios. On the other hand, the group of Oreochromis aureus had a high SS value (112.35), suggesting a poor correlation between the simulated and lake-based data, and therefore the reliability of using the model for Oreochromis aureus is low.

Table 2. Part of the Stepwise Fitting Procedure results. Where K is the number of runs, V is the vulnerabilities (the predator-prey dynamics), SS is the calculated sum of squares, AIC is the Akaike Information Criterion and AICc is the small-sample-size corrected version of AIC.

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<tr>
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<th>K</th>
<th>SS</th>
<th>AIC</th>
<th>AICc</th>
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</table>
Monte-Carlo simulations

We ran 2500 Ecosim Monte-Carlo (MC) simulations in which we varied the initial biomass values and inputed parameter values. The MC simulations resulted in limited changes to the model outcome for all the groups for which a high level of confidence in the data existed (Fig. 3). For example, a high level of confidence exists for data associated with the Lavun, the main topic of this research (Fig. 3J). As a result, the simulated biomass throughout all the MC simulations varied by no more than 4 Tons (max to min) per year, which represent up to 13% of the annual biomass. The outcomes for the zooplankton groups (Fig. 3K, L) showed good results, with a difference of no more than 2 Tons per year. In contrast, groups with a higher level of uncertainty associated with their data, for example the Mugilids, showed large variations in the MC simulations, reaching a difference of 14 Tons per year, which represents almost 100% of the best-fit solution. In two cases (Mugilids and Silver carp) there was an increase in variability over time. For example, the variability in the Muglides’ (Fig. 3D) biomass increased from 1 Ton in the first year to almost 15 tons in the last year of the simulation, representing ±50% of the biomass. Nevertheless, the observed trend in the base run, for all groups, was echoed by the results of the MC simulations, even those that had large variations due to low confidence levels.
Figure 3. The output of the MC simulations for the biomass of several fish and zooplankton groups. The grey area represents the 5-95 percentile range of the simulated biomass for all MC simulations. The black line represents the best fitted model result. Where: A) Catfish, B) Barbel, C) Carpio, D) Muglides, E) Silver Carp, F) S.G (Sarotherodon galilaeus) – natural reproduction, G) stocked S.G H) Oreochromis aureus, I) Zilli, J) Lavnum, K) Zooplankton – predatory, L) Zooplankton – herbivores.

Management Scenarios

The relationship between the Lavnum and other types of fish – most of the fishes in the lake were not influenced by the changes to the Lavnum’s biomass (fig. 4). This is mainly because their food sources don’t overlap with the Lavnum’s food sources. For example, the Sarotherodon galilaeus (represented by a green line in Fig. 4) shows an almost flat line, meaning that the change in the biomass of the Lavnum had almost no impact on the Sarotherodon galilaeus. However, the absences of Lavnum in the lake had a big impact on the Silver carp, with an increase in biomass of more than 2.5 fold, compared to the difference between the scenarios (Fig. 5). The silver carp is a non-endemic species that has been stocked in the lake since 1969. In general, the reduction in the Lavnum population had a small positive influence on the biomass of most fish groups.
Figure 4. A comparison between the two scenarios (deducting the culling scenario output from the base scenario output) regarding the changes in the biomass of the fishes in the lake relatively to 2011. The output was calculated by reducing the result of the management scenario from the base scenario and converting the outcome to relative change.

Figure 5 – Relative differences in fish biomass (the average of all the scenario years in a relative scale).

The changes in the Lavnum population led to changes in the zooplankton population. Model results suggest an increase in the predatory zooplankton biomass, concurrent with the decline in the Lavnum biomass. The increase in predatory zooplankton...
enhances the predation pressure on the herbivorous zooplankton and microzooplankton, leading to a decline in their biomass (Fig. 6). At the end of the 10-year simulation, the model predicts an increase of approximately 9% in the predatory zooplankton biomass and a decrease of approximately 8% in the herbivorous zooplankton biomass. It should be noted, however, that though the rate of change in the biomass slowed, it did not stabilize over this period, and it is possible that the changes may continue over time. Predatory zooplankton is the main food source for the Lavnnun, and a decrease in the amount of Lavnnun will lead to an increase in predatory zooplankton.

Figure 6 – Expected changes in the biomass of three zooplankton groups. The output was calculated by reducing the result of the management scenario from the base scenario and calculating the relative change.

**The influence of Lavnnun reduction on phytoplankton biomass**

The model results indicated an inverse relationship between the Lavnnun biomass in the lake and the phytoplankton biomass (Fig. 7). An examination of the model results shows that as the amount of Lavnnun decreases, the phytoplankton biomass increases. This change in phytoplankton biomass between the two scenarios is mainly due to an constant increase in the *Peridinium* biomass, which reached a level of more than 16% during the simulation years.
Figure 7. A comparison between the two scenarios of changes in the biomass of the phytoplankton groups following the changes in the biomass of the Lavun. The output was calculated by reducing the result of the "culling" scenario from the base scenario and converting the result to a relative scale.
Discussion

Biomanipulation is a tool that decision makers use in order to achieve goals in ecosystem management. A biomanipulation program was conducted in Lake Kinneret (Israel) between 1996 and 2006 in which almost 1000 Tons of Lavun was removed from the lake every year. It was, however, difficult to determine whether the program’s goals were achieved and therefore the program was stopped in 2006. In order to demonstrate the ability of food-web models to help in the planning process of biomanipulation, we used this past experience at Lake Kinneret and tested the possible effect any future Lavun removal could have on the ecosystem.

In order to test the quality of fit of our model to the data, we used a recently developed fitting tool for Ecosim (Scott et al., 2016). However, there is a difference in the SS (sum of squares) values of the various groups that reflects the difference between the model output and the data. In the Lavun group, for example, the correlation is very high throughout the entire period, with the exception of 2002 (Fig. 2H). This is probably due to the impact of the low lake level on the Lavun’s habitats and on its ability to reproduce in the lake. These processes are not simulated by the model and thus this phenomenon was not captured in the model results. The model successfully captured the S. galilaeus’ temporal dynamics, with the exception of 1997 and 2005 (Fig. 2E). This is most probably a result of the changes in the lake level (2-3 years before 1997 and 2005), which affected the habitats and the nesting of this fish (Ostrovsky et al., 2014), a phenomenon that the time dynamic model couldn’t reproduce (Ofir, 2015).

Oreochromis aureus has a low market value and the motivation to catch this fish is very low. Thus, probable due to the lack of demand for this fish, there was a relatively large discrepancy between the model output and the actual catch data, a phenomenon that the model couldn’t predict. It is worth noting that in all cases in which the model did not successfully simulate the trends, it was the result of factors that are not simulated by the model.

All model parameters suffer from a degree of uncertainty that may affect model performance and outcome when testing management scenarios. We tested the impact of the uncertainty associated with the model’s parameters by conducting 2500 Month Carlo simulations based on the range of uncertainty defined for each parameter (the Ecopath pedigree table). The results of all the biomass simulations of the fish groups show that the range of change in the Lavun biomass is narrow, with a maximum change of 12% from the basic model results (Fig. 3J). This output increases the confidence when using the model for Lavun scenarios. That is also the case for Sarotherodon galilaeus, one of the most commercially important species in the lake.
and the focus of much effort to maintain and increase their biomass in the lake. This model can be used in the future to examine biomanipulation plans that involve *S. galilaeus*. This, however, is not the case for all fish groups, as there are groups with large differences between the MC simulations, like the Muglides (Fig. 3D). Their biomass changed by approximately 50% over the range of the MC simulations, indicating a higher sensitivity to some of the parameters compared to other groups.

In order to test the potential effect of future biomanipulation plans, including the removal of Lavnun from the lake, we compared two scenarios. Biomanipulation actions are sometime used in order to improve the conditions of the target fish. In Lake Kinneret the target fish is the *Sarotherodon galilaeus* (St. Peter fish), which has a high market value and is one of the main target species for fishing, and so one of secondary goals of the aforementioned plan was to improve its biomass.

The absence of Lavnun in the lake had a big impact on the silver carp, with more than a 2.5-fold increase between the scenarios (Fig. 5). The silver carp is a non-endemic species that is stocked in the lake every year since 1969. The silver carp can't reproduce in the lake and so its biomass and catch depend on the number of fingerlings stocked in the previous years. However, the growth and development of the fingerlings are very much dependent on the condition of the lake and the availability of the food sources. Shapiro, in unpublished data (2014), showed that the fish stocked in the lake during recent years were in part a hybrid silver carp whose main food source is zooplankton, information that contradicts the common knowledge regarding the herbivorous diet of the silver carp in the lake (*Shapiro, 1985; Spataru and Gophen, 1985*). This new knowledge was used to improve the diet matrix in Ecopath, resulting in the conclusion that the removal of Lavnun will increase the amount of zooplankton and thus lead to an increase in the biomass of the silver carp. Increasing the biomass of the silver carp was not one of the goals of the biomanipulation program, and it does not contribute to water quality or to the income of the fishermen (the silver carp has a low market value).

In the Ecopath diet matrix the zooplankton is the main food source for the Lavnun, and therefore large changes in the Lavnun population are expected to have an impact on the zooplankton. Scenario results demonstrate a decrease in the herbivorous zooplankton biomass during the years following the removal of the Lavnun from the lake (Fig. 6). Over this same period there was an increase in predatory zooplankton biomass, suggesting an increased
predation by predatory zooplankton on herbivorous zooplankton. And indeed, model results suggest a 9% increase in predatory zooplankton biomass and a decrease of 8% in Herbivorous zooplankton biomass during that period. This is expected, given the nature of the interactions between the Lavnu and these two zooplankton groups; the main food source of the Lavnu is the predatory zooplankton and the main food source of the predatory zooplankton is the herbivorous zooplankton. Therefore, as seen in Figure 6, reducing the Lavnu biomass will lead to an increase in the predatory zooplankton and a decrease in the herbivorous zooplankton (a group that consumes phytoplankton).

The removal of the Lavnu resulted in an increase of over 16% in the amount of phytoplankton in the lake (Figure 7), mainly in the Peridinium, during the simulation years. This is most likely a result of reducing the amount of Lavnu, which in turn increases the biomass of the zooplankton and allows fishes to consume more zooplankton and less phytoplankton. The results indicate an inverse relationship between the Lavnu and the phytoplankton. Intense fishing pressure on the Lavnu resulted in a rise in the biomass of the phytoplankton in the lake over time (Fig. 7), probably due to a change in the predation over time.

By combining part of model results regarding the zooplankton, with a decreased predation pressure on the predatory zooplankton, the subsequent increased predation pressure on the herbivorous zooplankton and the increase in phytoplankton biomass, we get an explanation of the effect that reducing Lavnu biomass have on the ecosystem. The results describe a phenomenon known in ecological literature as intraguild predation (Polis et al., 1989), described in length in previous studies as a "food-web triangle". The partners in this triangle are the Lavnu, the predatory zooplankton and the herbivorous zooplankton. In tandem to the predatory-prey interactions between the groups, competitive relationships exist as well. The Lavnu and the predatory zooplankton compete for the herbivorous zooplankton, and the latter group competes with the Lavnu for phytoplankton. The results of removing the primary predator of this triangle are often unpredictable because of the specific traits of these relationships. These relationships and the results of removing the Lavnu were evaluated in previous studies with similar results (Makler-Pick et al., 2011a; Ofek et al., 2010), and are thus used to model the indirect influences of the Lavnu on the zooplankton and phytoplankton.

The results of the current model, which describes the relationship between the Lavnu, the zooplankton and the phytoplankton, are consistent with previous modeling efforts (Makler-Pick et al., In prep) that were based on a very different modeling approach, namely DYRESM-CAEDYM (Makler-Pick et al., 2011b).
Removing the Lavnun from the lake is an option that needs to be evaluated in light of the desired goals. If the goal is to improve the quality of the lake’s water by reducing the amount of phytoplankton in the water, it can clearly be seen from the results of this model that this goal has not been achieved. Moreover, the secondary goal of improving the biomass of the *Sarotherodon galilaeus* was also not achieved. Therefore, this biomanipulation plan should not take place in Lake Kinneret.

In order to develop the abilities of this method for future biomanipulation plans it is necessary to complete the missing data in the basic food-web model (like: fish biomass, part of the P/B and Q/B parameters) and to run the Monte Carlo sensitive analysis on future simulations to check the uncertainty around the results.

**Conclusions**

In many lakes and water resources biomanipulation actions are performed in order to achieve particular goals that will also increase the benefits that can be obtained from ecosystem services. However, in many cases the results of these actions do not meet the goals, and unexpected results are occur in the ecosystem, leading to the reevaluation or even the discontinuation of the program and culminating in a loss of time and money.

The results of the present research emphasize the importance of using food-web models as planning tools for any biomanipulation plan. It is not only important when determining the goals, but it is also necessary for assessing the influence of the chosen actions on the ecosystem. Using the biomanipulation performed in Lake Kinneret during 1994-2006 as an example, we have shown that using the model to execute a scenario that tests the proposed biomanipulation plan could lead to the understanding that this biomanipulation action will not result in the desired outcomes and another strategy must be considered.

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