

# Comparison of Three Modelling Frameworks for Aquatic Ecosystems: Practical Aspects and Applicability

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## Research Article

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# Abstract

Freshwater ecosystems are under multiple stressors and it is crucial to find methods to better describe, manage, and sustain aquatic ecosystems. Ecosystem modelling has become an important tool in integrating trophic relationships into food webs, assessing important nodes using network analysis, and making predictions via simulations. Fortunately, several modelling techniques exist, but the question is which approach is relevant and applicable when? In this study, we compare three modelling frameworks (Ecopath, Loop Analysis in R, STELLA software) using a case study of a small aquatic network (8 nodes). The choice of framework depends on the research question and data availability. We approach this topic from a methodological aspect by describing the data requirements and by comparing the applicability and limitations of each modelling approach. Each modelling framework has its specific focus, but some functionalities and outcomes can be compared. Predictions of Ecopath's Mixed Trophic Impact plot and the Loop Analysis models are in agreement for groups at higher trophic levels, but not for lower trophic levels. This suggests that further comparisons are needed of networks of varying resolution and size. Generally, when data are limiting, loop analysis can provide qualitative predictions, while the other two methods provide quantitative results, yet rely on more data.

## Introduction

Ecosystem modelling has greatly evolved over the past decades with several software frameworks available to scientists and resource managers (Geary et al. 2020). Ecosystem models have been used as a tool to integrate ecosystem components with processes (e.g., trophic interactions) into a representative model. Here, we focus on network-based trophic models in which the components of a system are described in terms of nodes (e.g., species or functional groups) and their trophic interactions (e.g., diet matrix) (Jordán and Scheuring 2004; Belgrano et al. 2005). These are simplified versions of an ecosystem, focusing on connecting consumer(s) with the resource(s) (e.g., predator-prey interactions). These interactions can be based on presence-absence (i.e., connectance web) or weighted (quantitative) connections (Woodward et al. 2005). Each model has limitations and assumptions, under which the question of interest can be examined, which necessarily means that there is no perfect model. However, depending on data availability (e.g., quantitative vs qualitative), there are considerations on which modelling approach is most suitable for the research question in a context-dependent way.

Our objective is to compare three commonly used but rarely compared modelling frameworks (Ecopath, STELLA, Loop Analysis) using a case study of a general lake model. We discuss the data requirements and the potential of incorporating social systems (e.g., socio-ecological models). It is imperative to apply interdisciplinary, system-level thinking to the complex problems facing society today (Richmond 1993; Saviano et al. 2019). As aquatic ecosystems are under increasing anthropogenic pressure and their biodiversity is threatened globally (Dudgeon et al. 2019; Sala et al. 2000), the need to better describe and understand these systems is urgently needed.

First, we provide a brief overview of the modelling frameworks. In Table 1, a summary table was compiled describing several practical aspects of the three frameworks and their main references. Then, we discuss the preliminary model outcomes using a case study of a freshwater lake by comparing the STELLA and Loop Analysis models to the Ecopath model.

Table 1

Summary table of practical aspects and the main references for the three modelling frameworks (Ecopath, STELLA, Loop Analysis). (1) Christensen et al. 2005; (2) Steenbeek et al. 2016; (3) Heymans et al. 2014; (4) isee Exchange 2021; (5) Levins

1974

|   | Ecopath  | STELLA  | Loop Analysis       |
|---|--|---|---------------------|
| <b>Software framework</b>                 | Ecopath with Ecosim (EwE)<br>(1)   | isee systems or R package (StellaR)   | R                   |
| <b>Cost</b>                               | free   | license cost  | free                |
| <b>Programming</b>                        | NA for basic use (runs in MS .NET). Extensions available with other programs (2) | visual programming  | R                   |
| <b>Main focus</b>                         | ecological / ecosystem modelling   | system dynamics   | ecological networks |
| <b>Static/Dynamic</b>                     | static (Ecopath)<br><br>dynamic (Ecosim and Ecospace)                            | dynamic   | dynamic             |
| <b>Qualitative/Quantitative</b>           | quantitative   | quantitative  | qualitative (5)     |
| <b>Mathematical background</b>            | ODE (ordinary differential equations)  | ODE   | ODE                 |
| <b>Number of groups (aquatic systems)</b> | 6-68 (3)   | <10   | 2<                  |
| <b>Parameters</b>                         | biomass, production, consumption, ecotrophic efficiency, catches, diet matrix    | stocks (e.g., biomass), flows (processes), converters (rates), connectors (cause-effect relationship) | diet matrix (+/-)   |
| <b>Simulation</b>                         | temporal (Ecosim) and spatial (Ecospace)   | temporal  | temporal            |
| <b>Databases (online repository)</b>      | EcoBase  | isee Exchange (4)   | NA                  |

## Ecopath

Ecopath with Ecosim (EwE) is a comprehensive modelling framework initially developed in the early 1980s, based on the theoretical approach by Polovina (1984a; 1984b), and since then, continuously improved with various extensions and specific functionalities (Christensen et al. 2005; Steenbeek et al. 2016). It has three major parts: *Ecopath* (static, mass-balanced system); *Ecosim* (time-dynamic simulation); and *Ecospace* (spatial and temporal simulation) (Christensen et al. 2005). Its online data repository (EcoBase) holds over 200 freely accessible models (Colléter et al. 2013). The objective of these trophic models is to address general ecological questions (e.g., food web network analysis, D'Alelio et al. 2016; Adebola and de Mutsert 2019; Rahman et al. 2019) and to investigate more complex issues (e.g., fisheries management, policy options, Mackinson and Daskalov 2007; Kao et al. 2014).

# STELLA

STELLA (Systems Thinking, Experimental Learning Laboratory with Animation) is a visual programming software developed in 1985 (Richmond et al. 1987). The idea behind the creation of STELLA was to approach problems requiring "*systems thinking*" by utilizing four building blocks (*stock, flow, connector, converter*) (Richmond 1994). The program applies numerical simulation by solving ordinary differential equations (ODE), although only to 2-digit-precision (Cellier 2008). Complex socio-economic models have been integrated using STELLA, such as the World3 model on global sustainability (Meadows et al. 1974; Meadows et al. 2004). As an icon-based dynamic modelling and simulation tool, it has been used in education with interdisciplinary applications in environmental systems (Deaton and Winebrake 1999; Ford 2010). Recently, an extension to R open-source framework was developed (Naimi and Voinov 2012).

## Loop Analysis

Loop analysis is a qualitative method, that uses signed digraphs to illustrate networks of interacting variables, where the figures show two types of connections: arrows ( $\diamond$ ) for positive and circle-head links (-o) for negative effects (Levins 1974; Puccia and Levins 1985). This technique gives the opportunity to represent the structure of linkages of the variables and the patterns of their variations (Dambacher and Ramos-Jiliberto 2007; Bodini and Clerici 2016). This qualitative modelling approach provides a method that is useful where species and their natural history are well-known, but not quantified (Dambacher et al. 2003). Using the qualitative modelling framework of loop analysis, one can analyze pathways and feedbacks in the system, making predictions about the response of variables to perturbations. For example, these can be the addition (increased biomass) or deletion (decreased biomass) of other nodes. Based on feedbacks and pathways, one can qualitatively specify the direction of change. For getting these predictions, loop analysis uses differential equations (Bodini 2000; Bodini and Clerici 2016; Fábíán 2021).

## Data And Methods

### Data

Lake Balaton is a large (596 km<sup>2</sup>), shallow (3.25 m average depth), freshwater lake located in Hungary (Istvánovics et al. 2008). A freshwater lake model was created with 8 general functional groups and fishing pressure added, in three modelling frameworks: Ecopath, STELLA, and Loop Analysis. For Lake Balaton, our model ecosystem, an Ecopath model described in Bíró (2002) was taken as baseline. Functional groups were aggregated (Producers = Phytoplankton, Periphyton, Benthic algae; 7 fish species grouped into 'Other Fishes') to be more general. These functional groups are purposefully very general for simplicity and to provide the basis for the methodological comparison. In the next section, we describe the creation of each of the models.

### Ecopath Model

Diet matrix (Appendix A), biomass data (Appendix B-1, Appendix D), and fishing yield (Weiperth et al. 2014) were updated to recent values using literature data from 2000-2020 (manuscript in preparation). 8 nodes describe this lake system, of which six are aggregate functional groups and two nodes are for the main fish species in the lake

(Figure 1). In both Ecopath models, total biomass is comparable across trophic levels (measured in t/km<sup>2</sup>/year). Total primary production decreased significantly over the two time periods (changing from eutrophic to oligotrophic state, Bernát et al. 2020), being the main ecological difference between the earlier (Bíró 2002) and this newer Ecopath model. Pre-balance (PREBAL) diagnostics (Link 2010) were run to check the model's compliance with basic ecological principles (Appendix B-1) and the Mixed Trophic Index (MTI) was obtained (Appendix C, Figure 3). The MTI table is used to compare with the loop analysis predictions.

## Stella Model

The STELLA model was created in *isee systems* software (Figure 2). We used the same input data (as in Ecopath) for the stocks (biomass of functional groups), flows (diet matrix, annual fishing yield), and converters (mortality) (Appendix D). The model was parametrized starting from the bottom up (i.e., producer stock and output flows, then invertebrate stocks and flows, fishes, and finally detritus), ensuring that the relative contribution of diet groups is accurately represented. Some additional assumptions had to be made in order to be able to run the model: 1) production input is constant (oligotrophic state), 2) natural mortality at 18°C (average annual water temperature) was retrieved for *Sander lucioperca* and *Abramis brama* from FishBase (and their average taken for OFish), 3) for invertebrates, natural losses at the stock outflows were estimated to be highest for Zooplankton (75%), and lower for Mollusca (40%) and OBI (25%) (to balance inflows and outflows), 4) living to non-living flows are unknown (not parametrized) and are not connected to detritus (otherwise the detritus stock would accumulate these), except for producers. Further settings are the following: time step (DT = 1 year), Runge-Kutta 2 integration method.

## Loop Analysis Model

The Loop Analysis model was created in R software (R Development Core Team 2020). We used MASS 7.3–51.5 and nlme 3.1–148 R packages for the analyses (Venables and Ripley 2002; Pinheiro et al. 2013). For simulating sign predictions, we used the R code in Bodini and Clerici (2016). The figure was created with GVEdit Graph File Editor For Graphviz version: 1.02 and Graphviz version: 2.38 (Ellson et al. 2004). For making the community matrix, Ecopath model's diet matrix was used. The community matrix got a 1 (-1) value where in the diet matrix was a prey-predator (predator-prey) relationship. 0 means there is no trophic connection between two groups. The diagonal terms of the community matrix are self-effects of system variables, represented in signed digraphs as links connecting variables with themselves. These links are self-dampening (circle-headed) with self-limiting growth rate, except detritus, because self-limitation was considered only for living groups (Table 2).

Table 2

**Community matrix of the Loop Analysis model.** Direct trophic interactions are represented in such a way that the elements in the rows impact the elements in the columns. The values can be - 1, 0, or 1. Self-dampening (diagonal elements) is only for living groups.

|             | Pike | OFish | Bream | Mollusca | OBI | Zooplankton | Producers | Detritus | Fishing |
|-------------|------|-------|-------|----------|-----|-------------|-----------|----------|---------|
| Pike        | -1   | -1    | -1    | 0        | 0   | 0           | 0         | 0        | 1       |
| OFish       | 1    | -1    | 0     | -1       | -1  | -1          | -1        | -1       | 1       |
| Bream       | 1    | 0     | -1    | -1       | -1  | -1          | 0         | -1       | 1       |
| Mollusca    | 0    | 1     | 1     | -1       | 0   | 0           | -1        | -1       | 0       |
| OBI         | 0    | 1     | 1     | 0        | -1  | 0           | -1        | -1       | 0       |
| Zooplankton | 0    | 1     | 1     | 0        | 0   | -1          | -1        | -1       | 0       |
| Producers   | 0    | 1     | 0     | 1        | 1   | 1           | -1        | 0        | 0       |
| Detritus    | 0    | 1     | 1     | 1        | 1   | 1           | 0         | 0        | 0       |
| Fishing     | -1   | -1    | -1    | 0        | 0   | 0           | 0         | 0        | -1      |

We followed the routine described in Bodini and Clerici (2016) to get the predictions for our network. The loop formula is used for calculating the equilibrium value of the variables following a perturbation, so it can be deduced how does the abundance of a certain variable change (Bodini 2000):

$$\frac{\delta x_j}{\delta c} = \frac{\sum_{i,k} \left[ \frac{\partial f_i}{\partial c} \right] \times [p_{ji}^{(k)}] \times [F_{n-k}^{(comp)}]}{F_n}$$

On the left side,  $x_j$  is the variable with the equilibrium value being calculated and  $c$  is the changing parameter (e.g., mortality, fecundity, abundance). On the right side,  $f$  is the growth rate,  $\partial f_i / \partial c$  designates whether the growth rate of the  $i^{\text{th}}$  variable is increasing or decreasing (positive or negative input, respectively),  $p_{ji}^{(k)}$  is the pathway connecting the variable to the changed biomass variable (where the perturbation enters the system),  $F_{n-k}^{(comp)}$  is the complementary feedback, which buffers or reverses the effects of the pathway and  $F_n$  designates the overall feedback of the system, which is a measure of the inertia of the whole system to change (Bodini 2000, Bodini and Clerici 2016). See also Puccia and Levins (1985) for the discussion of the correspondence between matrix algebra and loop analysis.

A perturbation on variable  $j$  (in this case the perturbation is the increase in the biomass of  $j$ ) has a net effect (the sum of the direct and indirect effects) on variable  $i$  given by the  $j - i^{\text{th}}$  element of the inverse community matrix  $[A]^{-1}$  (see Levins 1974; Puccia and Levins 1985b; Raymond et al. 2011). The sign of the coefficients of  $[A]^{-1}$  gives the direction of the expected changes for the variables (Bodini and Clerici 2016). To make predictions, we used a routine that randomly assigns numerical values from a uniform distribution to the coefficients of the community matrix (these coefficients belong to the links of the signed digraph). This was performed  $100 * N^2$  times, where  $N$  is the number of variables in the system. Matrices satisfying the asymptotic Lyapunov criteria were accepted and inverted. The routine of Bodini and Clerici (2016) calculated predictions for the probabilities based on the

percentage of positive and negative signs and zeroes in the inverted matrices. They defined a set of rules to make a final table of predictions only from signs (Appendix E, Bodini and Clerici, 2016).

Using this routine, we obtained the matrix of predictions (Appendix E), and the version with directions only (Table 3). Table 3 was turned into a graph with the Graphviz software for better visualization (Figure 4). For direct comparability with Ecopath's MTI, we used the directions of predictions.

Table 3

Table of predictions by Loop Analysis, only with directions, used for comparison of Loop Analysis and Ecopath's Mixed Trophic Impact plot.

|             | Pike | OFish | Bream | Mollusca | OBI | Zooplankton | Producers | Detritus | Fishing |
|-------------|------|-------|-------|----------|-----|-------------|-----------|----------|---------|
| Pike        | +    | -     | -     | +        | +   | +           | -         | 0        | 0       |
| OFish       | 0    | +     | -     | -        | -   | 0           | -         | +        | +       |
| Bream       | 0    | -     | +     | 0        | 0   | 0           | +         | -        | +       |
| Mollusca    | 0    | 0     | 0     | +        | -   | -           | 0         | -        | 0       |
| OBI         | 0    | 0     | 0     | -        | +   | -           | 0         | -        | -       |
| Zooplankton | 0    | 0     | 0     | -        | -   | +           | 0         | -        | 0       |
| Producers   | 0    | +     | -     | 0        | 0   | 0           | +         | -        | 0       |
| Detritus    | 0    | +     | +     | 0        | 0   | 0           | -         | +        | +       |
| Fishing     | -    | 0     | 0     | 0        | 0   | 0           | 0         | 0        | +       |

## Results And Discussion

The STELLA and Loop Analysis models were compared to the Ecopath model (which is the most comprehensive framework).

## Comparison: Ecopath And Loop Analysis

The predictions of the Mixed Trophic Impact plot from Ecopath (Figure 3) could be compared with the predictions of Loop Analysis (Figure 4). The MTI quantifies how an infinitesimal increase of any of the impacting groups (rows) is predicted to have on the impacted groups (columns) (Christensen et al. 2005), while loop analysis gives qualitative predictions. The advantage of an MTI plot is also to highlight interactions (and system components) whose importance otherwise might not have been realized (Ulanowicz and Puccia 1990). MTI provides not only a plot but a matrix with values too. Based on the quantitative MTI plot (Appendix C), we defined a threshold to find the links where the change in the biomass of the impacted groups was almost zero. First, we ranked the absolute values in the rows, then in the columns of each group of the network, after this step, we selected from these two ranked tables the first and second-ranked values. We sorted these values and rounded the lowest of them to one decimal to get the threshold. We transcribed the values of the MTI table in the  $[-0.1, 0.1]$  interval to "0", then the values under (above) this interval to "-" ("+") sign. Using this method, we made a comparable matrix (Appendix F)

to the directions of the Loop Analysis predictions (Table 3). Then, we made a summary table with 1 and 0 numbers, where 1 (0) means the signs in that point is (not) the same in the Loop Analysis and in the MTI tables.

We calculated the percentage of identical signs (= % of sign-agreement) in the full matrices (overall sign agreement), and in their rows and columns. For the calculations, we excluded the self-effects due to methodological differences between MTI and Loop Analysis. MTI predicts self-limiting growth (negative effect), so if a group's abundance or biomass increases, it will not increase infinitely. In contrast, in the prediction matrix of Loop Analysis, the affecting groups are increasing as the representation of the perturbation. The sign-agreement in the rows show which group's *impact* is the most predictable. In the columns, we find which group's *response* to the perturbation of the others is most predictable. The overall sign-agreement was 63.9% (Appendix G). The impact of Fishing was the most similar (87.5%) in Loop Analysis and MTI. Furthermore, Pike, Mollusca, and OBI groups showed relatively high (75%) sign-agreement in their rows. The lowest predictability of a group's impact was for OFish (37.5%) and Producers (50%) and Detritus (50%) (Appendix G). For the columns, OFish showed the highest similarity (100%), and the responses of Pike were the most predictable (75%) (Appendix G).

Figures 3 and 4 show that the high percentage of sign-agreement does not mean that it has an impact. For example, the increase of Fishing has no effect on most groups (only weak negative impact on pike in Loop Analysis), even so the predictions of MTI and Loop Analysis are in this row very similar. 76% of the directed predictions in the Loop Analysis are equal to the predictions of MTI table (Figure 4).

We were interested if there is any correlation between the sign-agreement (%) of MTI and Loop Analysis and the trophic level of the groups or the number of top-down / bottom-up connections. The Pearson's correlation coefficients showed negative correlation between the sign-agreement (%) and the number of trophic levels connected to the groups ( $r = -0.7$ ) and the number of top-down connections ( $r = -0.61$ ).

## Comparison: Ecopath And Stella

Simple dynamic changes can be visualized (graphical and numerical outputs) in the STELLA model, for example, one could easily double the predation rate of pike on bream, which would change system dynamics. However, such predictions from the STELLA framework are not as comprehensive as Ecopath's MTI, therefore we did not compare them with each other. When focusing on trophic connections between the living groups, we found it possible to recreate Ecopath's trophic structure with our simple assumptions, meaning that the predicted biomass magnitudes are meaningful and comparable to Ecopath's biomass values shown in Figure 1. For example, for fishes, biomass ( $t/km^2/year$ ) in the steady-state are comparable between the two frameworks (Bream: 16.88, OFish: 17.34 in STELLA at the end of the simulation; and Bream: 14.03, OFish: 16.64 in Ecopath). The STELLA model initially overestimated the biomass of pike, therefore an additional fixed loss of  $2.4 t/km^2/year$  was subtracted. The primary production is constant, which represents the overall production in the lake during an oligotrophic state (minor interannual deviations are negligible as long as the lake remains in an oligotrophic state). Ultimately, trophic efficiency (called "ecotrophic efficiency" in Ecopath, which is the proportion of the production utilized in the system (e.g. accumulating or moving onto higher trophic levels)) in our model was estimated to be high for producers (~90%) and invertebrates (~70%), and lower for fish and zooplankton (~20-30%) (meaning that primary production and invertebrates are readily consumed, while zooplankton and fish species are mainly lost via natural mortality and diseases), following best practices detailed in Heymans et al. (2016). For the invertebrate groups, both models showed deviation from the expected value (Ecopath gave high values for the Mollusca group

(Appendix B-1), and STELLA predicted high values for the Zooplankton group 17.77 vs the input of 9.7 t/km<sup>2</sup>/year in Ecopath. This difference probably comes from the simplicity of processes (*flows*) of the STELLA model at the second trophic level.

Fath et al. (2007) discuss the applicability of STELLA numerical simulation as an input to an Ecopath model. To test this, we plugged in the biomass results from the end of numerical simulation (when steady state was reached) into Ecopath (all other settings remained the same as in the original Ecopath model), resulting in comparable PREBAL diagnostics to the original Ecopath model (Appendix B-2). While the Ecopath framework allows for some uncertainty if data is limited (e.g., the software can estimate one input parameter per group), the STELLA model needs to be fully parameterized in order to run, which in some cases leads to inevitable oversimplification of the system (e.g., omission of living to detritus flows due to lack of quantitative data).

## Conclusion

In our freshwater lake case study, we found that the predictions of the MTI and the Loop Analysis models are in good agreement. If data is limiting (qualitative), loop analysis can be used. We found negative correlation between predictability with these two methods and the number of trophic levels connected to the groups and the number of top-down effects. The groups' impact on others is highly predictable at the higher trophic levels, and possibly of the groups with the highest biomass, except the primary producers. Also, the responses to the increase of other groups were most similar in the case of the higher trophic levels. Fábíán (2021) found such consistency in the case of three food webs: there was high similarity between the predictions of dynamic simulation and of Loop Analysis. The lowest predictability of a group's impact was for the highly aggregated groups (e.g., OFish has 7 fish species with varying diets), so we speculate that the resolution of the food web would influence the predictability of the changes. In general, the resolution of the food web can influence many other aspects of network analysis (e.g., Martinez et al. 1993; Giacomuzzo and Jordán 2021).

Our findings agree with Fath et al. (2007), suggesting transferability between the two frameworks, STELLA and Ecopath. Our recommendation is, that when a system is well documented with quantitative data and the processes are clear, STELLA models can be a great way to better understand the system as a whole (Power et al. 1995; Gertseva et al. 2004; Xuan and Chang 2004), to highlight important feedback loops (Richmond 1994; Hayes 2012), and even to raise awareness about an environmental problem (Jørgensen and De Bernardi 1997; Jørgensen and De Bernardi 1998), and educate the public with its interactive interface (iSee Exchange 2021). Cellier (2008) details further advantages and disadvantages of using the STELLA software for dynamic modelling. Due to the details of parametrization, STELLA is best applicable for small networks (<10 nodes).

Both frameworks, Loop Analysis and STELLA can be used to complement an existing Ecopath model, for example, if time/spatial dynamics predictions are needed, but Ecosim/Ecospace models are not yet available. A limitation of our study is that we only used one small network. It would be important to check our methods using several networks (of different size, resolution, etc.). Discrepancies between quantitative and qualitative approaches are not surprising and expected to some extent (e.g., less detail and/or information loss is inevitable in qualitative methods compared to quantitative methods). However, not every research question requires numerically parametrized models. For example, it can be qualitatively shown that the effect on an external factor (e.g., aquaculture) negatively impacts certain groups (primary producers, zooplankton, and deposit-feeders), and positively impacts predators and scavengers (Forget et al. 2020). Modelling is thus important to bring out complex, network-level interactions, which might not be evident simply from single parts. The challenge now is to extend

these modelling frameworks to social-ecological systems (Martone et al. 2017; Niquil et al. 2021; Rodriguez et al. 2021).

## Declarations

### *Ethics approval and consent to participate*

Not applicable

### *Consent for publication*

Not applicable

### *Availability of data and materials*

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

### *Competing interests*

On behalf of all authors, the corresponding author states that there is no conflict of interest.

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### *Authors' contributions*

V.F. performed the loop analysis modeling and the statistical analysis. She wrote the paper.

K.P. performed the Ecopath and STELLA modeling. She wrote the paper.

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## Figures

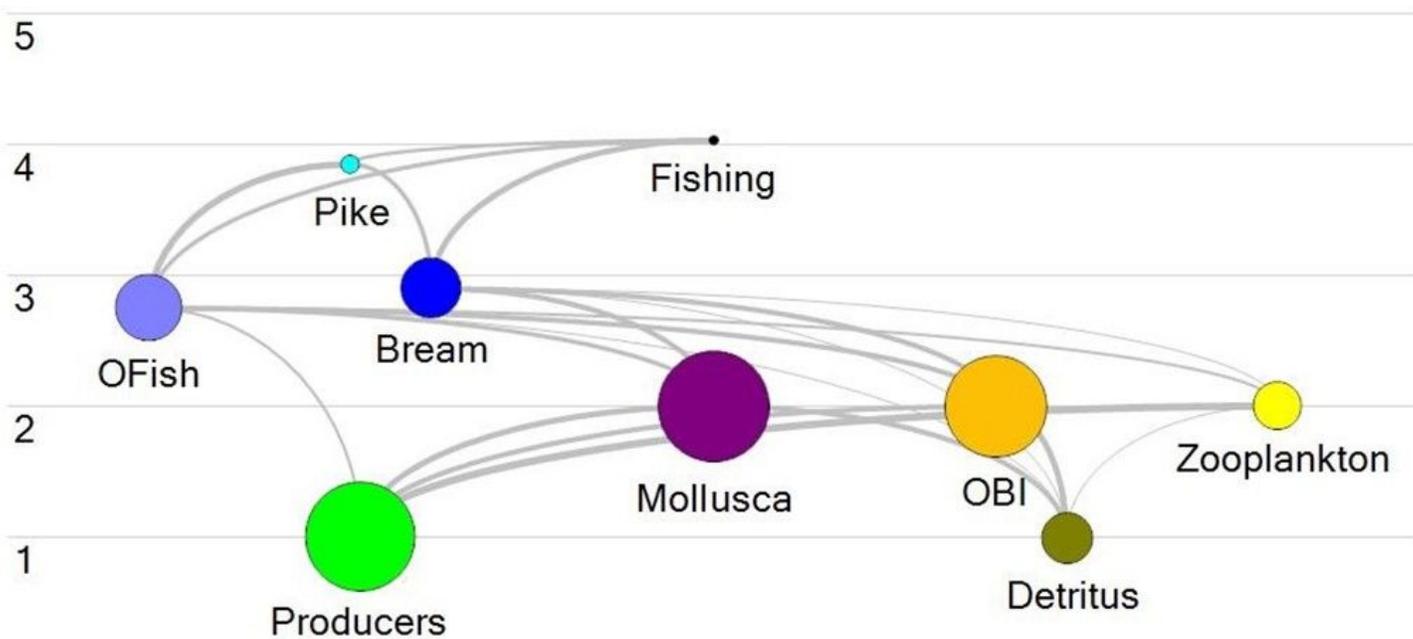


Figure 1

**Trophic structure of the Ecopath model (based on Bró(2002) aggregated and modified with recent data).** The model contains eight nodes and fishing pressure. Six nodes are aggregate functional groups (Detritus, Producers, Zooplankton, OBI = Other Benthic Invertebrates, Mollusca, OFish = Other Fish Species), and two nodes represent the main fish species in the lake (Bream = *Abramis brama*, Pike = *Sander lucioperca*).

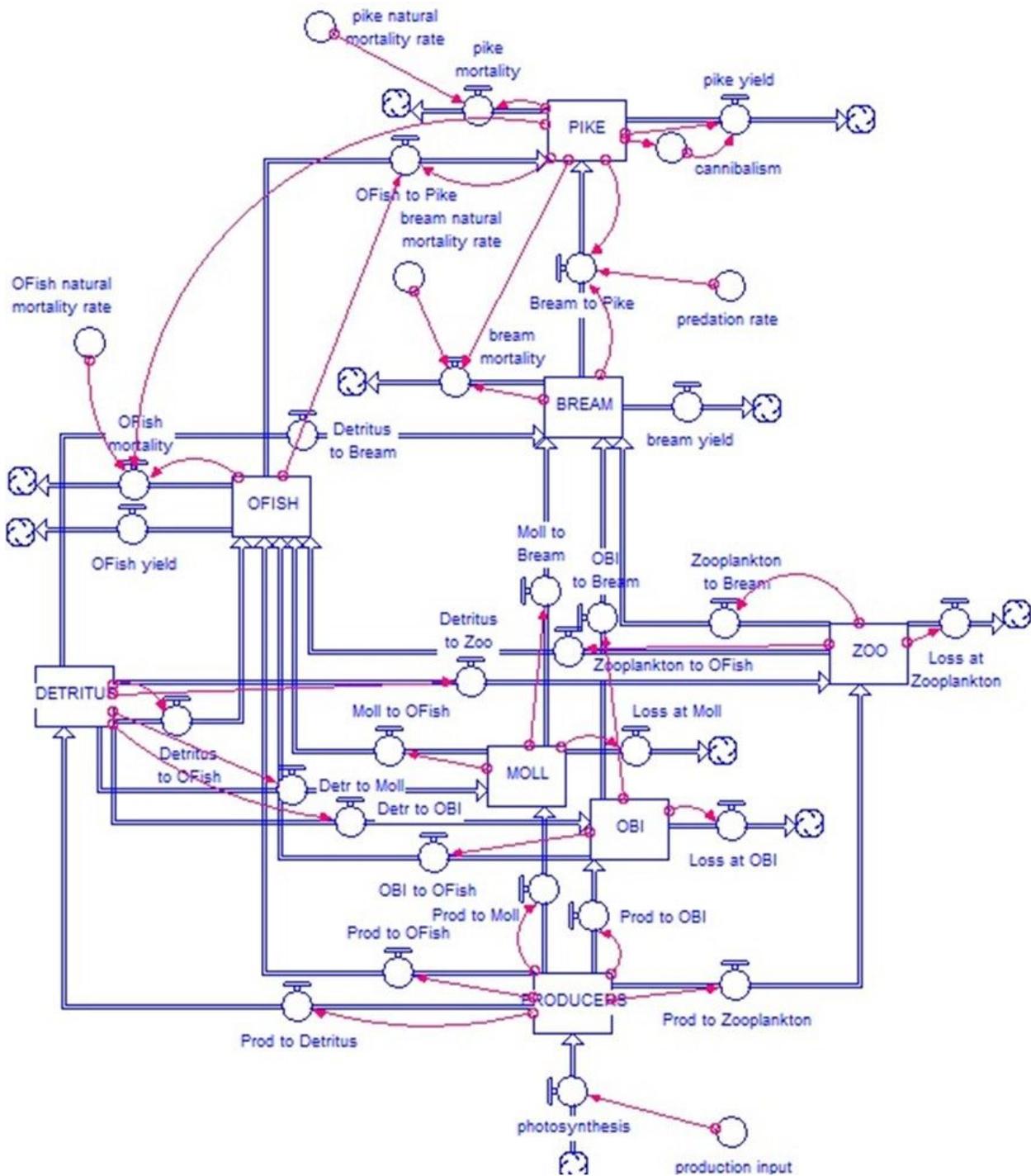
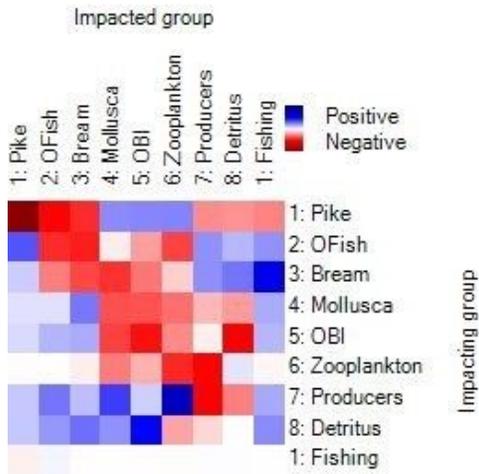


Figure 2

STELLA model with 8 stocks (biomass of functional groups), flows (trophic interactions, fishing yield, and other losses), and converters (natural mortality). Model parameters and equations are found in Appendix D. STELLA symbology: stock (rectangle), flow (double lines with the arrow indicating direction), converter (circle), connector (red arrow).



**Figure 3**

**Mixed Trophic Impact plot.** MTI plot showing positive (blue), negative (red), and neutral (white) combined direct and indirect trophic impacts between the 8 functional groups and fishing pressure. Darker color indicates a stronger effect of the impacting group on the impacted group.

**Figure 4**

**Prediction graph of the loop analysis model.** Blue arrows indicate positive effect, red lines show negative effect, and black lines highlight those effects that are different from Ecopath's MTI plot. As an example, if the biomass of group 1 increases, then the biomass of groups 4, 5, and 6 will increase, groups 2 and 3 will decrease. Self-effects are omitted from the graph. Nodes 1-8 are coded the same as in the MTI plot (Figure 3), and 9= Fishing.

## Supplementary Files

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