ORIGINAL ARTICLE

Comparison of three modelling frameworks for aquatic ecosystems: practical aspects and applicability

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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. The predictions of Loop Analysis as compared to Ecopath's Mixed Trophic Impact plot are in good agreement at the top and bottom trophic levels, but the middle trophic levels are less similar. 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.

Keywords Aquatic ecosystem · Ecopath · Loop Analysis · STELLA

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 & 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),

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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.

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 (Colléter et al., 2013) holds over 200 freely accessible models (to date). The objective of these trophic models is to address general ecological questions (e.g., food web network analysis, Adebola & de Mutsert, 2019;

D'Alelio et al., 2016; Rahman et al., 2019) and to investigate more complex issues (e.g., fisheries management, policy options, Kao et al., 2014; Mackinson & Daskalov, 2007).

STELLA

STELLA (Systems Thinking, Experimental Learning Laboratory with Animation) is a visual programming software developed in 1985 (Richmond et al. 1985). 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, 2004). As an icon-based dynamic modelling and simulation tool, it has been used in education with interdisciplinary applications in environmental systems (Deaton & Winebrake, 1999; Ford, 2010). Recently, an extension to R open-source framework was developed (Naimi & Voinov, 2012).

Table 1 Summary table of practical aspects and the main references for the three modelling frameworks (Ecopath, STELLA, Loop Analysis)

	Ecopath	STELLA	Loop analysis
Software framework	Ecopath with Ecosim (EwE) (1)	isee systems (5) or R package (StellaR) (6)	R (9)
Cost	free	license cost	free
Programming	*NA* for basic use (runs in MS.NET). Extensions available with other programs (2)	visual programming	R
Main focus	ecological / ecosystem modelling	system dynamics	ecological networks
Static/Dynamic	static (Ecopath) dynamic (Ecosim and Ecospace)	Dynamic	dynamic
Qualitative/Quantitative	quantitative	quantitative	qualitative (10)
Mathematical background	ODE (ordinary differential equations)	ODE	ODE
Number of groups** (aquatic systems)	6–68 (3)	< 10 (7)	< 24 (11)
Model input	biomass, production, consumption, ecotrophic efficiency, catches, diet matrix	stocks (e.g. biomass), flows (processes), converters (rates), connectors (cause-effect relationship)	Jacobian / community matrix ($\pm$)
Model output	graphical and tabular	graphical and tabular	tabular
Simulation	mass-balance (Ecopath), temporal (Ecosim)*, spatial–temporal (Ecospace)*	mass-balance (steady-state), temporal	equilibrium change (12)
Databases (online repository)	EcoBase (4)	isee Exchange (8)	CRAN (13)

(1) Christensen et al., 2005; (2) Steenbeek et al., 2016; (3) Heymans et al., 2014; (4) Colléter et al., 2013; (5) Richmond, 1985; (6) Naimi & Voinov, 2012; (7) Fath et al., 2007; (8) isee Exchange, 2021; (9) R Development Core Team, 2020; (10) Levins, 1974; (11) Novak et al., 2011; (12) Ortiz & Wolff, 2008; (13) Dinno, 2018; * not compared in this study; ** Approx. nodes for ecological networks, but the number of nodes are dependent on the system being modelled

Loop Analysis

Loop Analysis is a qualitative model (Levins, 1974), that 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 feedback 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 feedback and pathways, one can qualitatively specify the direction of change. For getting these predictions, Loop Analysis uses differential equations (Bodini, 2000; Bodini & Clerici, 2016; Fábián, 2021).

Data and methods

Data

Lake Balaton is a large (596 km^2), 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 (Fig. 1). In both Ecopath models, total biomass is comparable across trophic levels (measured in t/km^2/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
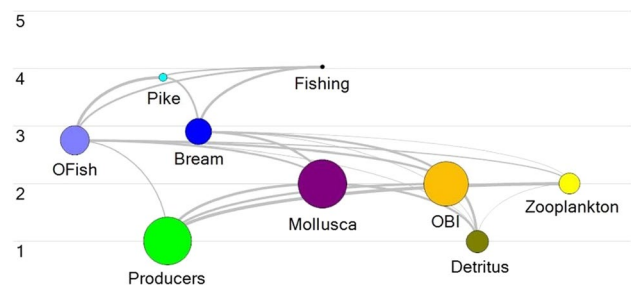

Fig. 1 Trophic structure of the Ecopath model (based on Bíró (2002) aggregated and modified with recent data). The model contains eight nodes and fishing pressure. Six nodes are aggregate functional groups (Detritus, Producers, Zooplankton, OBI = Other Benthic Invertebrates, Mollusca, OFish = Other Fish Species), and two nodes represent the main fish species in the lake (Bream = *Abramis brama*, Pike = *Sander lucioperca*)

Index (MTI) was obtained (Appendix C, Fig. 3). The MTI table is used to compare with the Loop Analysis predictions.

STELLA model

The STELLA model was created in *isee systems* software (STELLA, 2021; Fig. 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 analyzes (Pinheiro et al., 2013; Venables & Ripley, 2002). For simulating sign predictions, we used the R code in Bodini and Clerici (2016). Optionally, a signed digraph figure can be created
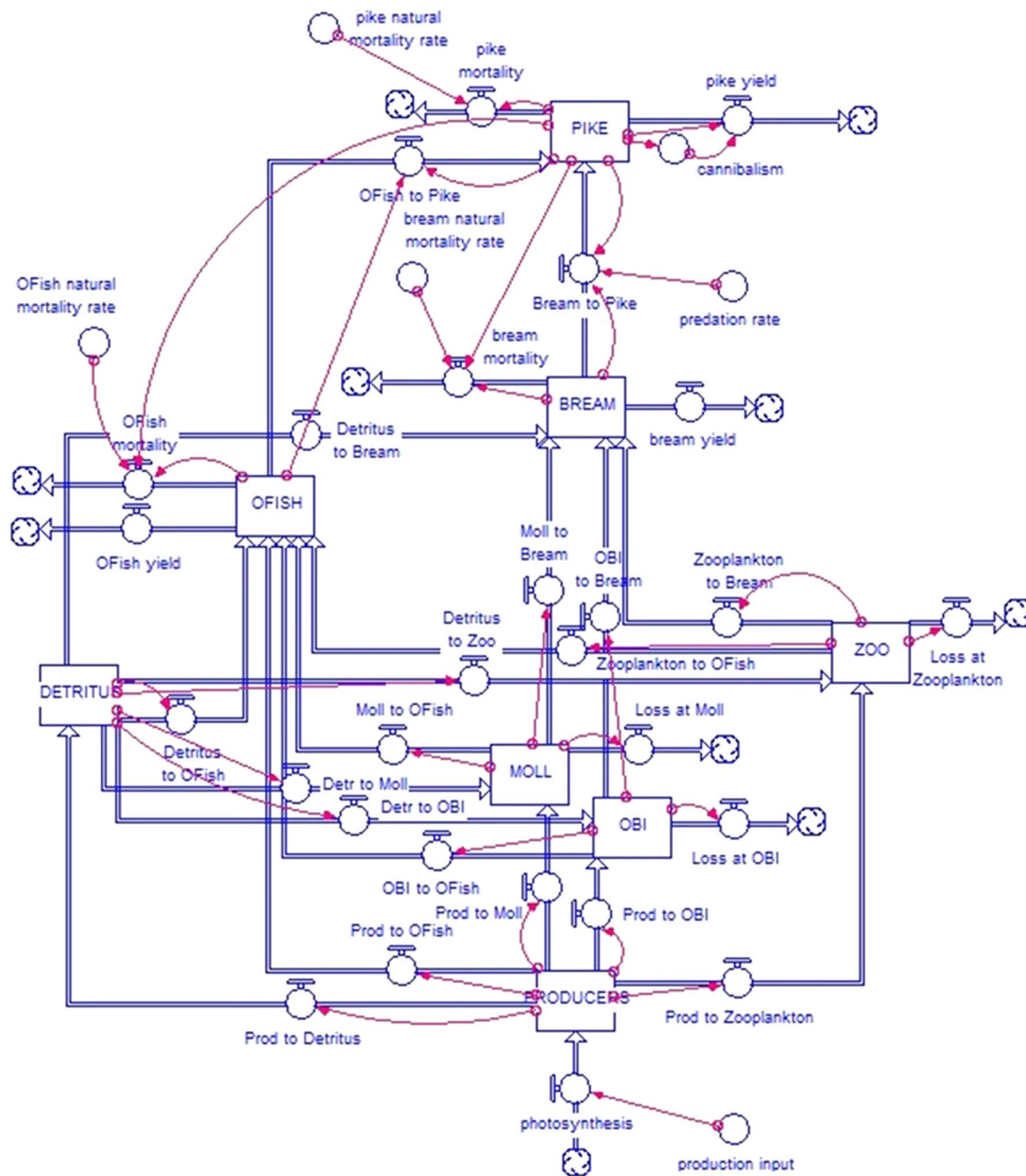
Fig. 2 STELLA model with 8 stocks (biomass of functional groups), flows (trophic interactions, fishing yield, and other losses), and converters (natural mortality). Model parameters and equations are found in Appendix D. STELLA symbology: stock (rectangle), flow (double lines with the arrow indicating direction), converter (circle), connector (red arrow)

using GVEdit Graph File Editor For Graphviz version: 1.02 and 2.38 (Ellson et al., 2004), but was not applied here. 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 with self-limiting growth rate, except detritus, because self-limitation was considered only for living groups (Table 2).

We followed the routine described in Bodini and Clerici (2016) to get the predictions for our network (Table 3). The loop formula is used for calculating the equilibrium value of the variables following a perturbation, so it can be deduced how the abundance of a certain variable change (Bodini, 2000):

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) are 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

Table 3 The output of Loop Analysis. The percentage of positive (A), and negative (B) responses, and the table of predictions (C) are presented. The frequency of positive ("+") effects in the inverted matrices defines the sign of predictions: "-"=0–24%, "?-"=25–39%, "0*"=40–59%, "?+"=60–74%, "+"=75–100%, finally "0" means no change (where 100% of the values were 0). The percentage of + predictions were used for comparison of Loop Analysis and Ecopath's Mixed Trophic Impact table

A	%	Pike	OFish	Bream	Mollusca	OBI	Zooplankton	Producers	Detritus	Fishing
	Pike	92.99	16.68	33.19	68.12	67.64	68.15	27.84	42.48	55.59
	OFish	53.55	93.39	23.91	41.46	40.37	40.17	34.23	68.43	72.16
	Bream	51.09	28.57	87.87	43.03	44.79	43.90	85.03	35.78	73.00
	Mollusca	47.78	41.64	49.91	92.68	26.51	25.93	41.79	33.23	40.91
	OBI	48.58	43.66	48.65	25.47	93.15	26.13	42.08	33.96	41.73
	Zooplankton	49.73	44.06	49.31	25.95	27.11	92.97	41.04	35.05	42.44
	Producers	51.89	72.23	22.76	54.75	54.57	53.86	90.37	15.51	46.74
	Detritus	52.71	59.67	81.12	53.44	53.90	53.95	28.70	94.43	90.22
	Fishing	4.53	48.31	48.98	50.82	50.80	50.09	48.49	48.96	92.32
B	%	Pike	OFish	Bream	Mollusca	OBI	Zooplankton	Producers	Detritus	Fishing
	Pike	7.01	83.32	66.81	31.88	32.36	31.85	72.16	57.52	44.41
	OFish	46.45	6.61	76.09	58.54	59.63	59.83	65.77	31.57	27.84
	Bream	48.91	71.43	12.13	56.97	55.21	56.10	14.97	64.22	27.00
	Mollusca	52.22	58.36	50.09	7.32	73.49	74.07	58.21	66.77	59.09
	OBI	51.42	56.34	51.35	74.53	6.85	73.87	57.92	66.04	58.27
	Zooplankton	50.27	55.94	50.69	74.05	72.89	7.03	58.96	64.95	57.56
	Producers	48.11	27.77	77.24	45.25	45.43	46.14	9.63	84.49	53.26
	Detritus	47.29	40.33	18.88	46.56	46.10	46.05	71.30	5.57	9.78
	Fishing	95.47	51.69	51.02	49.18	49.20	49.91	51.51	51.04	7.68
C	predictions	Pike	OFish	Bream	Mollusca	OBI	Zooplankton	Producers	Detritus	Fishing
	Pike	+	–	?–	?+	?+	?+	?–	0*	0*
	OFish	0*	+	–	0*	0*	0*	?–	?+	?+
	Bream	0*	?–	+	0*	0*	0*	+	?–	?+
	Mollusca	0*	0*	0*	+	?–	?–	0*	?–	0*
	OBI	0*	0*	0*	?–	+	?–	0*	?–	0*
	Zooplankton	0*	0*	0*	?–	?–	+	0*	?–	0*
	Producers	0*	?+	–	0*	0*	0*	+	–	0*
	Detritus	0*	0*	+	0*	0*	0*	?–	+	+
	Fishing	–	0*	0*	0*	0*	0*	0*	0*	+

$$\frac{\delta X_j}{\delta C} = \frac{\sum_{i,k} \left[\frac{\delta f_i}{\delta C}\right] \times \left[P_{ji}^{(k)}\right] \times \left[F_{n-k}^{(comp)}\right]}{F_N}$$

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 ith 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 & 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 $j - i$th element of the inverse community matrix $[A]^{-1}$ (see Levins, 1974; Puccia & Levins, 1985; Raymond et al., 2011). The sign of the coefficients of $[A]^{-1}$ gives the direction of the expected changes for the variables (Bodini & 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 A in Bodini & Clerici, 2016) which is what we applied in this study (Table 3). Using this routine, from stable matrices we obtained the simulated tables of percentages of ± and 0 and the table of predictions generated from the tables (Table 3).

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 Mixed Trophic Impact plot from Ecopath (Fig. 3A) could be compared with the predictions of Loop Analysis (Fig. 3B). The MTI quantifies how an infinitesimal increase of any of the impacting groups is predicted to have on the impacted groups (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 & Puccia, 1990), including direct and indirect interactions (e.g. competition) in the system (Christensen et al., 2005). For the MTI, a net impact matrix is constructed of all system components in which the element q_{ij} indicates the net impact of i upon j. Specifically, the net impact (q_{ij}) will equal the difference between g_{ij} (the amount that i serves as a prey item for j) and f_{ji} (the detrimental impact the consumer i has on the resource j). Also, the indirect effects are taken into account (if i has an effect on j, and j influences k, then there is an indirect pathway between i and k), see Ulanowicz & Puccia, 1990. Fishing pressure is regarded as "predator", and for detritus $g_{i,j}$ is set to zero. MTI values fall within the range of -1 to + 1, inclusive. The MTI routine based on the net impact matrix by Ulanowicz and Puccia (1990) is automatically implemented in Ecopath and the MTI plot (and numerical values) can be accessed under the Ecopath output tab.

For the correlation, 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.

We found a positive correlation between the percentage of positive predictions in Loop Analysis (LA + (%)) and the quantitative values of MTI (r = 0.62, Fig. 4). According to both methods, the groups with the most positive impact on

Fig. 3 Mixed Trophic Impact plot **A** and Loop Analysis predictions **B**. The plots 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
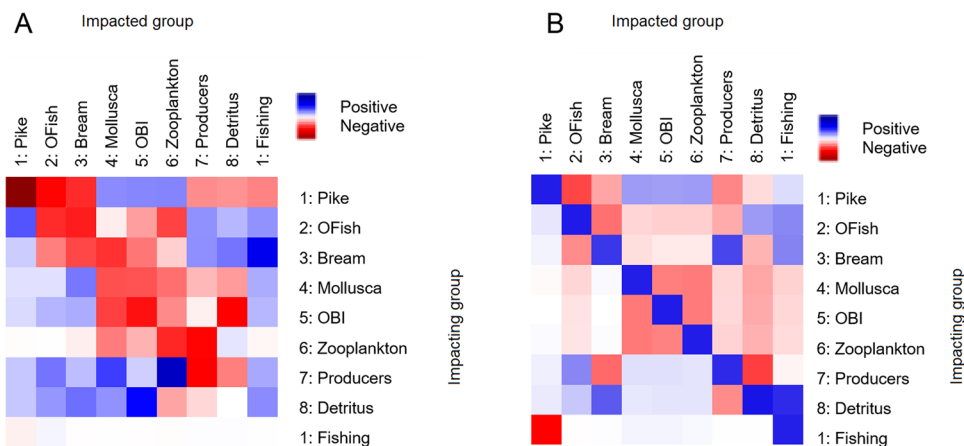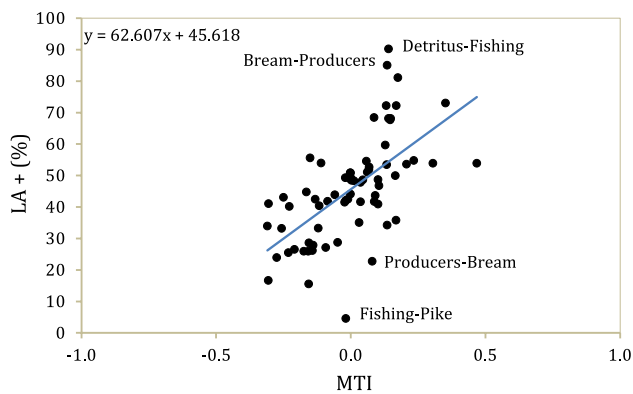
Fig. 4 Correlation between the Mixed Trophic Impact (MTI) and the percentage of positive responses in Loop Analysis (LA +)

others are Producers and Detritus (Fig. 3). The strongest negative impacts in Loop Analysis matched those of the MTI plot (i.e., Pike-OFish, Producers-Detritus; Fig. 3). The predictions of Loop Analysis as compared to the outcome of the MTI are in good agreement at the top and bottom trophic levels, but the middle trophic levels (e.g., OBI) are less similar. Most of the directions of predictions are similar, but their strength in the MTI plot is stronger (Fig. 3). The quantitative method results in stronger strength of impacts (Fig. 3A) as compared to the qualitative method (Fig. 3B). The difference between the qualitative and quantitative methods is apparent if we observe the Fishing-Pike effect. Fishing has a single-step direct negative impact on the group Pike (Figs. 1 and 4B), while in the quantified network the interaction strength makes the effect more subtle (Fig. 3A). Some of the visibly outlier points of the network (e.g., Detritus-Fishing, Bream-Producers, Producers-Bream, Figs. 3–4) are nodes that represent the most distant groups within the network (having the most trophic steps between them), which means that their predictability is most difficult due to pathway redundancy (Ulanowicz, 1980; Ulanowicz & Puccia, 1990).

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 Fig. 1. For example, for fishes, biomass (t/km²/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/km²/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/km²/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 output of Ecopath's MTI plot and the Loop Analysis model are in good agreement. Since Loop Analysis relies only on network topology (assuming no knowledge of interaction strengths in the input; Novak et al., 2011), and Ecopath needs more details of the network (quantitative interaction strength; Ulanowicz & Puccia, 1990), MTI can provide more robust results. Bondavalli et al. (2009) present a hybrid approach, based on a quantitative model of a low-resolution lagoon (7 nodes), in which the net impact matrix was amended with an additional variable (capturing exchanges between the ecosystem components

and the surrounding environment), after which the loop analysis procedure was performed. The resolution of the food web can influence many aspects of network analysis (e.g., Martinez et al. 1991; Giacomuzzo & Jordán, 2021). The connectance of the network influences the proportion of correct predictions, thus the reliability of predictions diminishes as network size and connectance increase (Novak et al., 2011). As the number of groups increases within a network, the predictability of Loop Analysis decreases due to pathway redundancy (Ulanowicz, 1980; Ulanowicz & Puccia, 1990), thus it is best recommended for small networks (< 24 nodes, Novak et al., 2011).

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 (Gertseva et al., 2004; Power et al., 1995; Xuan & Chang, 2014), to highlight important feedback loops (Hayes, 2012; Richmond, 1994), and even to raise awareness about an environmental problem (Jørgensen & De Bernardi, 1997, 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 dynamics predictions are needed, but Ecosim models are not yet available. A limitation of our study is that we only used one small network. It would be important to compare these 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). In general, data availability (e.g., lack of information on nodes or on interaction strength) influences food web properties and sampling effects need to be taken into consideration (Berlow et al., 2004; Goldwasser & Roughgarden, 1997). However, not every research question requires numerically parametrized models. For example, it can be qualitatively shown that the effect of 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).

Appendix A

See Fig. 5

Appendix B-1,Bb-2

See Figs.6 and 7

Appendix C

See Table 4

BREAM(t) = BREAM(t—dt) + (OBI__to_Bream + Zooplankton__to_Bream + Moll_to__Bream + Detritus__to_Bream—Bream_to_Pike—bream_yield—bream__mortality) * dt.

INIT BREAM = 14.

OBI__to_Bream = OBI*0.4

Zooplankton__to_Bream = ZOO*0.1

Moll_to__Bream = MOLL*0.4

Detritus__to_Bream = 2.

Bream_to_Pike = (BREAM/PIKE)*predation_rate.

bream_yield = 0.03.

bream__mortality = (BREAM*bream_natural__mortality_rate)*PIKE.

DETRITUS(t) = DETRITUS(t—dt) + (Prod_to_Detritus—Detritus__to_Bream—Detritus__to_OFish—Detr_to_Moll—Detr_to_OBI—Detritus_to_Zoo) * dt.

INIT DETRITUS = 10.

Prod_to_Detritus = PRODUCERS*0.1

Detritus__to_Bream = 2.

Detritus__to_OFish = DETRITUS*0.1

Detr_to_Moll = DETRITUS*0.06.

Detr_to_OBI = DETRITUS*0.09.

Detritus_to_Zoo = DETRITUS*0.015.

MOLL(t) = MOLL(t—dt) + (Prod_to_Moll + Detr_to_Moll—Moll_to__Bream—Moll_to_OFish—Loss_at_Moll) * dt.

INIT MOLL = 56.

Prod_to_Moll = PRODUCERS*0.3

Detr_to_Moll = DETRITUS*0.06.

Moll_to__Bream = MOLL*0.4

Moll_to_OFish = MOLL*0.2

Loss_at_Moll = MOLL*0.40.

OBI(t) = OBI(t—dt) + (Prod_to_OBI + Detr_to_OBI—OBI__to_Bream—OBI_to_OFish—Loss_at_OBI) * dt.

INIT OBI = 44.

Prod_to_OBI = PRODUCERS*0.2

Detr_to_OBI = DETRITUS*0.09.

OBI__to_Bream = OBI*0.4

PREY \ PRED	Pike	OFish	Bream	Mollusca	OBI	Zooplankton	Data Source
Pike	0.05						(1)
OFish	0.65						(2)
Bream	0.3						(3)
Mollusca		0.25	0.4				(4)
OBI		0.35	0.4				(4)
Zooplankton		0.15	0.1				(5)
Producers		0.15		0.6	0.4	0.9	NA
Detritus		0.1	0.1	0.4	0.6	0.1	NA
(1)	Specziár, A., 2011. Size-dependent prey selection in piscivorous pikeperch Sander lucioperca and Volga pikeperch Sander volgensis shaped by bimodal prey size distribution. *Journal of Fish Biology* , *79* (7), pp.1895-1917.						
(2)	Inlcudes 7 fish species: *Alburnus alburnus* (Bíró, P. and Muskó, I.B., 1995. Population dynamics and food of bleak (*Alburnus alburnus* L.) in the littoral zone of Lake Balaton, Hungary. Hydrobiologia, 310(2), pp.139-149.); *Aspius aspius* (Krpo-Ćetković, J., Hegediš, A. and Lenhardt, M., 2010. Diet and growth of asp, *Aspius aspius* (Linnaeus, 1758), in the Danube River near the confluence with the Sava River (Serbia). Journal of Applied Ichthyology, 26(4), pp.513-521.); *Cyprinus carpio* (Specziár, A., Tölg, L. and Bíró, P., 1997. Feeding strategy and growth of cyprinids in the littoral zone of Lake Balaton. Journal of Fish Biology, 51(6), pp.1109-1124.); *Esox lucius* (https://www.fishbase.org/TrophicEco/FoodItemsList.php?vstockcode=272&genus=Esox&species=lucius); Percidae (Rezsu, E. and Specziár, A., 2006. Ontogenetic diet profiles and size-dependent diet partitioning of ruffe *Gymnocephalus cernuus* , perch *Perca fluviatilis* and pumpkinseed *Lepomis gibbosus* in Lake Balaton. Ecology of Freshwater Fish, 15(3), pp.339-349.); *Rutilus rutilus* (Specziár, A., Tölg, L. and Bíró, P., 1997. Feeding strategy and growth of cyprinids in the littoral zone of Lake Balaton. Journal of Fish Biology, 51(6), pp.1109-1124); *Silurus glanis* (https://www.fishbase.se/TrophicEco/FoodItemsList.php?vstockcode=303&genus=Silurus&species=glanis)						
(3)	Specziár, A., Tölg, L. and Bíró, P., 1997. Feeding strategy and growth of cyprinids in the littoral zone of Lake Balaton. *Journal of Fish Biology* , *51* (6), pp.1109-1124.						
(4)	Includes general estimates for the diet of the abundant *Dreissena polymorpha* (Kumar, R., Varkey, D. and Pitcher, T., 2016. Simulation of zebra mussels (*Dreissena polymorpha*) invasion and evaluation of impacts on Mille Lacs Lake, Minnesota: An ecosystem model. Ecological Modelling, 331, pp.68-76.) and other molluscs (Makhutova, O.N., Protasov, A.A., Gladyshev, M.I., Sylaieva, A.A., Sushchik, N.N., Morozovskaya, I.A. and Kalachova, G.S., 2013. Feeding spectra of bivalve mollusks Unio and Dreissena from Kanevskoe Reservoir, Ukraine: are they food competitors or not?. Zoological Studies, 52(1), pp.1-10.). OBI (Other Benthic Invertebrates) includes general estimates for detritivores and efficient shredders (e.g., *Gammarus pulex, Asellus aquaticus*), having more detritus in their diet.						
(5)	General estimate.						

Fig. 5 Diet matrix values and data sources used in the Ecopath model

OBI_to_OFish = OBI*0.35.

Loss_at_OBI = OBI*0.25.

OFISH(t) = OFISH(t—dt) + (Prod_to_OFish + Moll_to_OFish + OBI_to_OFish + Detritus__to_OFish + Zooplankton_to_OFish—OFish_to_Pike—OFish__mortality—OFish_yield) * dt.

INIT OFISH = 16.6

Prod_to_OFish = PRODUCERS*0.07.

Moll_to_OFish = MOLL*0.2

OBI_to_OFish = OBI*0.35.

Detritus__to_OFish = DETRITUS*0.1

Zooplankton_to_OFish = ZOO*0.15.

OFish_to_Pike = (OFISH/PIKE)*0.32.

OFish__mortality = OFISH*PIKE*OFish_natural__mortality_rate.

OFish_yield = 0.018.

PIKE(t) = PIKE(t—dt) + (Bream_to_Pike + OFish_to_Pike—pike_yield—pike_mortality) * dt.

INIT PIKE = 1.63.

Bream_to_Pike = (BREAM/PIKE)*predation_rate.

OFish_to_Pike = (OFISH/PIKE)*0.32.

pike_yield = 0.011 + (PIKE*cannibalism).

pike_mortality = 2.4 + (PIKE*pike_natural__mortality_rate).

PRODUCERS(t) = PRODUCERS(t—dt) + (photosynthesis—Prod_to_Moll—Prod_to_OBI—Prod_to_Zooplankton—Prod_to_OFish—Prod_to_Detritus) * dt.

INIT PRODUCERS = 53.3

photosynthesis = production_input.

Prod_to_Moll = PRODUCERS*0.3

Prod_to_OBI = PRODUCERS*0.2

Prod_to_Zooplankton = PRODUCERS*0.33.

Prod_to_OFish = PRODUCERS*0.07.

Prod_to_Detritus = PRODUCERS*0.1

ZOO(t) = ZOO(t—dt) + (Prod_to_Zooplankton + Detritus_to_Zoo—Zooplankton__to_Bream—Zooplankton_to_OFish—Loss_at__Zooplankton) * dt.

INIT ZOO = 9.2

Prod_to_Zooplankton = PRODUCERS*0.33.
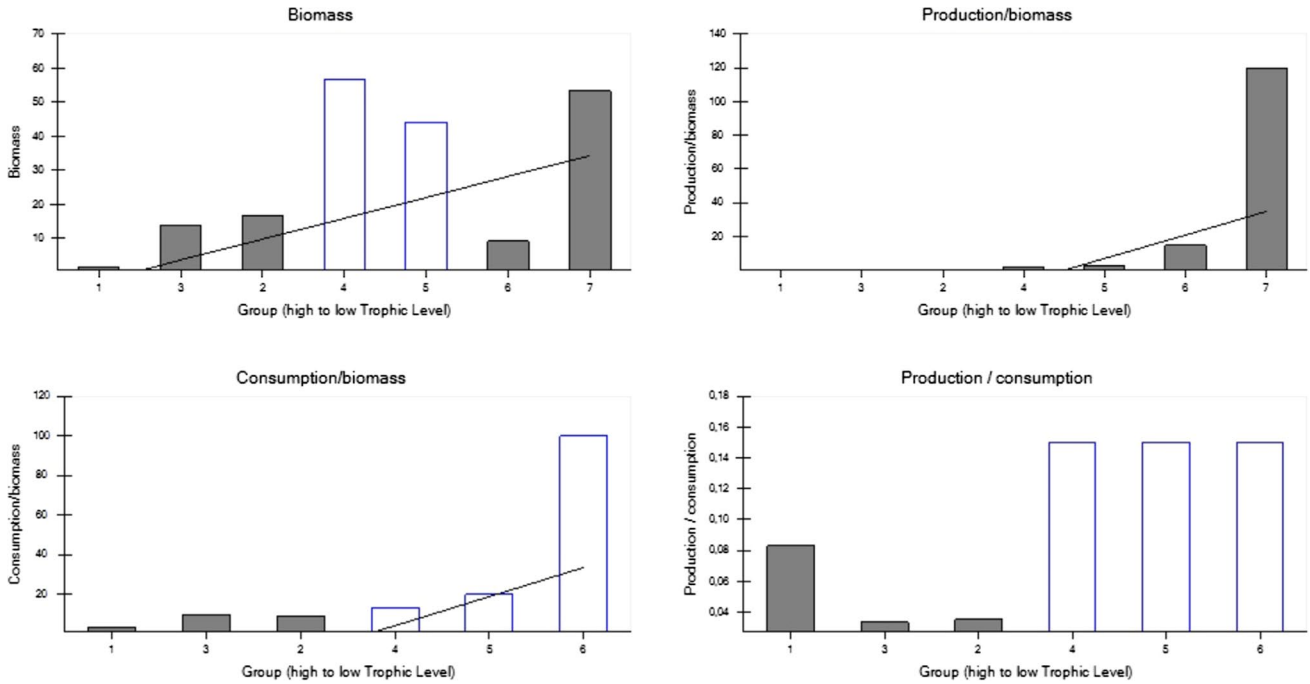
Detritus_to_Zoo = DETRITUS*0.015.

Fig. 6 PREBAL diagnostics obtained from Ecopath (Link, 2010). Groups are 1=Pike, 2=OFish, 3=Bream, 4=Mollusca, 5=OBI, 6=Zooplantkon, 7=Producers. Blue bars indicate values estimated by the model (e.g., biomass data was not feasible to estimate from survey data). Biomass for Mollusca is estimated by Ecopath to be high and Zooplankton biomass (based on survey data) is low. Biomass data were obtained from the best available data from years 2000–2020 for Lake Balaton, Hungary (modified from Bíró, 2002)
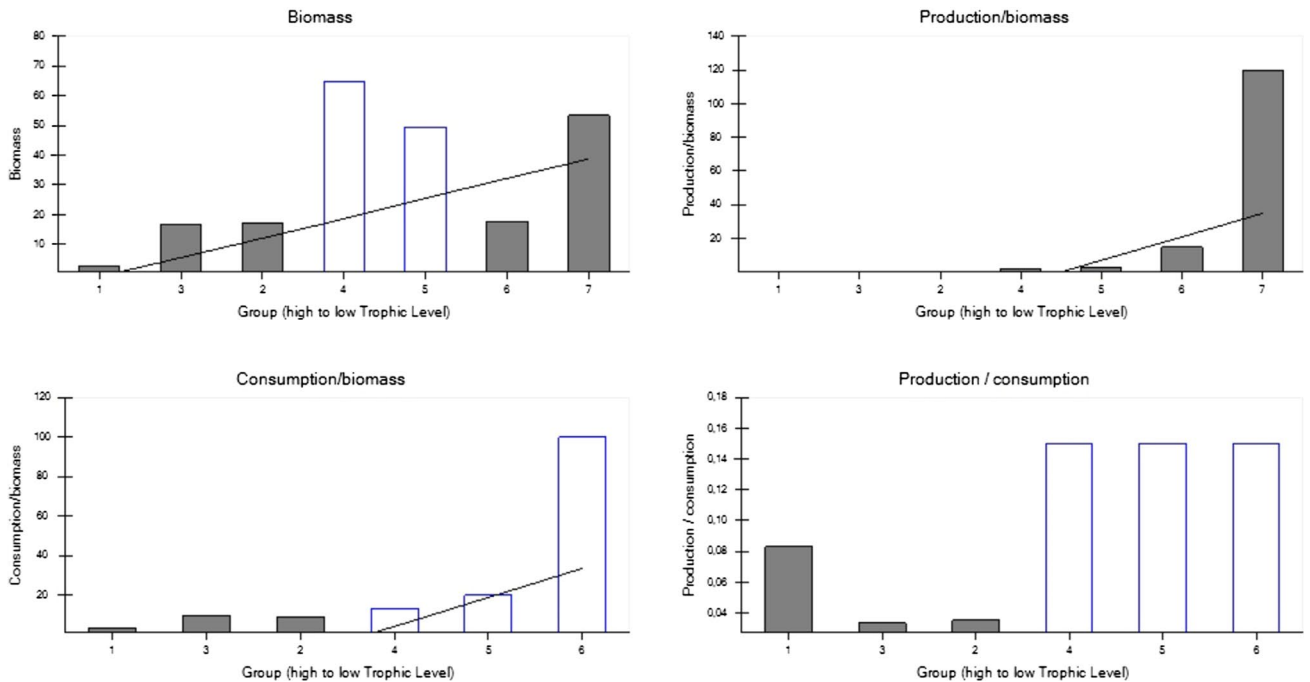
Fig. 7 PREBAL diagnostics obtained from Ecopath based on the biomass numerical simulation output from STELLA (all other settings remained the same). The diagnostics are comparable to the original Ecopath model

Table 4 Mixed Trophic Impact (MTI) table obtained from Ecopath in numeric format (the equivalent of Fig. 3). 1–8 are coded the same as in the MTI plot (Fig. 3), and 9 = Fishing

Impact-ing group	Impacted group								
	1	2	3	4	5	6	7	8	9
1	−0.617	−0.306	−0.257	0.14	0.146	0.148	−0.14	−0.132	−0.151
2	0.207	−0.258	−0.275	−0.023	−0.117	−0.228	0.135	0.0867	0.132
3	0.0617	−0.155	−0.222	−0.25	−0.165	−0.0587	0.135	0.168	0.352
4	0.0361	0.0364	0.165	−0.212	−0.209	−0.174	−0.0856	−0.121	0.101
5	0.0449	0.0908	0.101	−0.232	−0.289	−0.142	−0.0181	−0.31	0.0871
6	−0.0032	−0.00075	−0.0202	−0.158	−0.0926	−0.263	−0.305	0.031	−0.0109
7	0.0677	0.169	0.0798	0.234	0.0582	0.468	−0.313	−0.156	0.105
8	0.0679	0.128	0.175	0.133	0.305	−0.11	−0.0486	0	0.14
9	−0.0183	0.0116	−0.0024	−0.001	−0.0023	−0.0039	0.00255	0.00186	−0.0011

Zooplankton__to_Bream = ZOO*0.1
Zooplankton_to_OFish = ZOO*0.15.
Loss_at__Zooplankton = ZOO*0.75.
bream_natural__mortality_rate = 0.32.
cannibalism = PIKE*0.001.
OFish_natural__mortality_rate = 0.285.
pike_natural__mortality_rate = 0.25.
predation_rate = 0.15.
production_input = 53.3

Appendix D. STELLA model equation layer

INIT [group name] indicates the initial biomass (t/km^2/yr), which are the same as in the Ecopath model (e.g., INIT ZOO = 9.2 t/km^2/yr). Constant values are set for production input, natural mortality rates, and fishing yield. Others are expressed as rate of change: e.g., "Bream_to_Pike = (BREAM/PIKE)*predation_rate" means that the amount of biomass transferring from Bream to Pike is a function of the Bream to Pike ratio, multiplied by the predation rate. "PIKE(t) = PIKE(t—dt) + (Bream_to_Pike + OFish_to_Pike—pike_yield—pike_mortality) * dt" is the difference equation describing the dynamics of the pike stock, where inflow = (Bream_to_Pike + OFish_to_Pike); outflow = (pike_yield—pike_mortality), at each time step (dt). These equations are represented in the STELLA symbology layer (Fig. 2.).

Authors' contributions VF. performed the Loop Analysis modelling and the statistical analysis, prepared manuscript text and figures. KP. performed the Ecopath and STELLA modelling, prepared manuscript text and figures.

Availability of data and materials The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

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

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