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A Modelling Approach for the Management of Invasive Species at a High-Altitude Artificial Lake

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Abstract: The ecosystem structure of a Mediterranean high-altitude artificial lake (Aos Springs, Northwest Greece) was assessed and quantified using the Ecopath with Ecosim model. The artificial lake was created in 1990 for hydroelectric production and the fish fauna has been enriched across years due to deliberate or accidental fish stockings, as well as the introduction of the invasive pumpkinseed (*Lepomis gibbosus*), which may cause adverse effects on aquatic ecosystems and their biota. The model considered 20 species/taxa groups with biological data gathered during 2021–2022 from field surveys, interviews with recreational anglers and literature. The results revealed that the artificial lake of Aos is a resilient ecosystem to unexpected events with low intensity of fisheries exploitation. The biomass of the introduced invasive species *Lepomis gibbosus* is low, due to the low biomass level of its diet, Chironomidae and zoobenthic organisms as well as other fish species.

Keywords: trophic model; Ecopath with Ecosim; *Lepomis gibbosus*; artificial lake of Aos; Greece



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1. Introduction

Reservoirs are unique and changing inland water habitats because they were created by humans in places where none previously existed, yet they retain all the ecological characteristics of the systems from which they originated (rivers, springs). It is worth noting that Directive 2000/60 EC examines these systems (Artificial Water System) individually. Significant changes in the bio-community occur in these systems during their evolution. At the initial stage, these modifications are expected to result from changes in ecological traits (creation or modification of habitats exploited by native species), as well as from anthropogenic interventions related to the deliberate or accidental introduction of species into the new ecosystem [1,2]. Deliberate anthropogenic intervention in the form of enrichment of the ecosystem with commercially valuable species has been or is being practised worldwide, while the need to control undesired species is becoming more apparent [1].

Ecopath with Ecosim (EwE) models have been implemented to quantify, depict and evaluate the anthropogenic impacts on freshwater food webs and to assess the suitability of specific management activities [3], taking into consideration the interspecific interactions of all organisms. Similar approaches have been also applied to other natural lakes in Greece for managing invasive species (Lake Volvi: [4] and Lake Trichonis: [5]) to evaluate the ecological role of the invasive species at the ecosystem level.

Herein, an EwE model was applied to the high-altitude artificial lake of Aos (hereafter ALA) to quantify the energy flows and investigate the trophic interactions among species/taxa groups within the food web. This marks the first instance of an ecosystem-based mode being utilised for this purpose. The studied system was characterised by the absence of professional fishery, and of commercially important fish species. In addition,

non-native fish species, such as the pumpkinseed *Lepomis gibbosus* (Linnaeus, 1758) [6] and Prussian carp *Carassius gibelio* (Bloch, 1782) [7] have been introduced into the ecosystem, which is considered highly detrimental to aquatic biodiversity [8]. The purpose of the present study focused, through the EwE methodology, on integrating all the available information for the studied ecosystem derived from recent and historical field surveys and personal interviews with recreational anglers. This is crucial information for data-poor systems where fisheries data are regularly underestimated, similar to other European freshwaters [4].

2. Materials and Methods

2.1. Study Area

Aoos River stands as one of the largest rivers in the Western Balkans, stretching over a length of 260 km, with an average annual discharge of 70.4 m³/s and a maximum flow at the Albania-Greece border reaching 125.5 m³/s (estimated during 1951–1988). The average annual runoff is recorded at 1638 hm³, while the July runoff alone amounts to 50 hm³. The total drainage basin covers an area of 6710 km², with 2154 km² located within the Greek region.

ALA, characterised as “alpine-type” ecosystem, located at an altitude of 1343 m, covers a surface area of 11.5 km², with a capacity of 260 × 10⁶ m³, up to 80 m of depth (Figure 1). The system is oligotrophic, characterised by seasonality in the water temperature, which ranges from 4 °C, in winter, to 26 °C, in summer [9]. Oxygen levels fluctuate from 7.79 mg/L in August to 11.12 mg/L in March, while saturation levels range from 95.7% in December to 110.3% in June. Its limnological characteristics shift from monomictic in the absence of ice formation to dimictic under ice-bound conditions [10]. During the summer, the water column is thermally stratified, with layers forming at depths ranging from 5 to 15 m [10]. Nitrate and total phosphorus maintain consistent levels from January to October, doubling or tripling in quantity during November and December (nitrate: 0.09–0.35 mg/L, total phosphorus: 0.01–0.32 mg/L). During the studied period, the order of magnitude of nitrates and phosphates appears to be at similar levels compared to an earlier study and the climatic conditions lay within the average range [9].

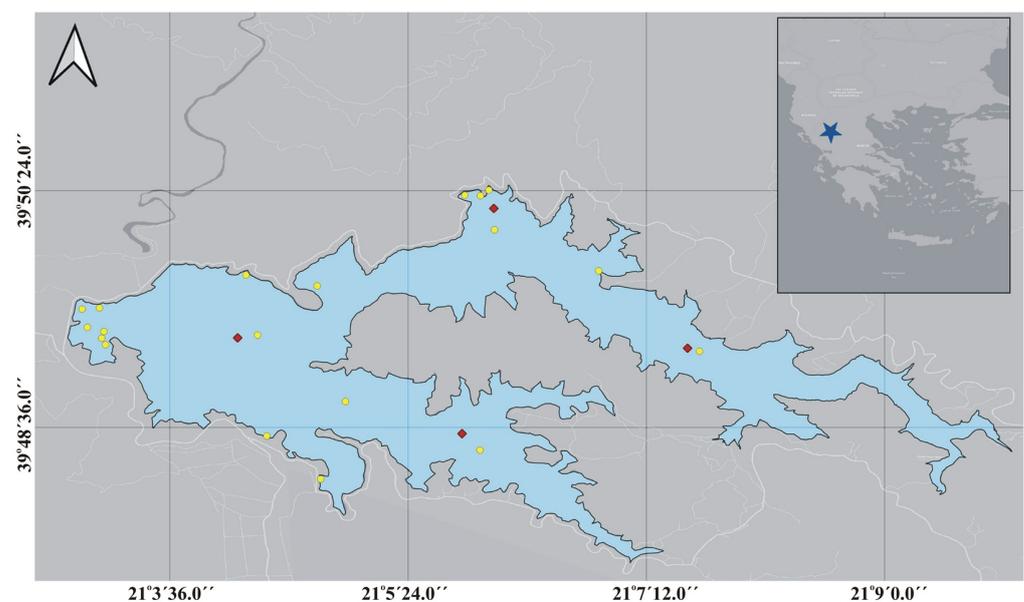


Figure 1. Sampling stations for the in situ sampling in the studied ecosystem. Yellow points indicate sampling stations with multi-mesh gillnets and red points stations for sampling of phytoplankton and zoo-plankton. Blue star indicates the location of the study area in relation to Greece.

2.2. Interview Survey

From July 2021 to May 2022, an interview survey was conducted in person with recreational anglers operating in the ALA to reveal their expert fisher knowledge. This methodology offers the advantage of providing “in situ” information. The interviews were conducted privately with each angler to avoid influences from their coworkers and were conducted by the same individual to minimise sample bias. Anglers were informed before starting the questionnaire that participation was voluntary and that any information that may be used to identify them would be kept confidential. Each questionnaire included questions related to the frequency of the fishing activity (expressed by the number of fishing days per season), whether species are overfished, the presence of invasive species, the frequency of stocking events, species extinctions, and demographic features of anglers. A total number of 35 recreational anglers filled out the questionnaire.

2.3. Model Parameterisation

The Ecopath module of EwE software (version 6.2.0x.62) [11–13] was implemented to quantify the trophic structure of the ALA (11.2 km²) in 2022. The methodology is detailed and presented in Appendix A. A total of 20 species/taxa groups (Table A1) were included in the model: one group for phyto- and zooplankton, Chironomidae, zoobenthos, detritus, nine groups for fish and one group for decapod species and three groups for aquatic birds which prey on fish in the area exclusively or occasionally. Table A1 in Appendix B presents a full description of the groups and the data sources utilised to parameterise the model, while Table A2 in Appendix B shows food composition by species group B.

Biomass values were expressed as t × km⁻² wet weight and flow as t × km⁻² × yr⁻¹. Biomasses for producers, zooplankton, Chironomidae and zoobenthic organisms were estimated based on seasonal field sampling conducted in nine sites during 2021–2022 (Figure 1). A total of 25 species were identified in phytoplankton community, categorised into 6 groups [10]: cyanobacteria (4 species), chlorophyceae (6 species), diatoms (10 species), chrysophyte (2 species), dinoflagellate (2 species), and euglenophyceae (1 species). During the spring, the predominant genus in the Aaos River is *Asterionella*, while in summer and autumn, the most abundant genus is *Cyclotella* [10]. Biomass of the phytoplankton was estimated through sampling at 2 m from the surface. Seasonal Chlorophyll- α concentrations were quantifying spectrophotometrically [14]. The estimation of phytoplankton biomass followed the assumption that at the euphotic layer of 10 m, the ratio of the carbon to Chlorophyll- α is 40 and of the carbon to phytoplankton wet weight is 0.1 [15]. Zooplankton consists of copepods, cladocerans, and rotifers [10]. During spring, the abundance of cladocerans, predominantly belonging to the *Bosmina* genus, is increasing accompanied by a less predominant increase in copepods, particularly of calanoida type. In July, the abundance of cladocerans depicts a gradual decrease compared to May but remains at relatively high levels. The presence of *Bosmina* sp. was minimal at all stations and persisted this way until September. The abundance of copepods decreased in July while an increase in the concentration of rotifers was observed compared to the spring months [10]. Zooplankton were sampled using vertical hauls with a conical net with mesh size of 100 μ m covering the whole water column. The biomass was estimated as dry weight and then converted to wet weight (dry weight to wet weight ratio: 0.2), according to [16]. Biomass for top predators specifically aquatic birds was estimated from the records of the Management Body (N2KGR1310002) during 2021–2022.

The estimation of the biomass for the fish species was based on Catch Per Unit of Effort (CPUE) estimates [17,18], which are frequently used in ecosystems with limited data [19], where CPUE data often constitute the sole source of information. In the present study, CPUE was estimated from seasonal, experimental samplings conducted during July 2021–May 2022, using Nordic-type benthic multi-mesh gillnets set (Figure 1). This methodology is used for monitoring freshwater fish fauna at a pan-European level in accordance with the European Directive 2000/60/EC and provides qualitative and quantitative data concerning species composition and abundance per m² [20,21]. The average catch

per unit of fishing effort (kg/m^2) from all four seasonal samplings was used to estimate approximately the annual biomass of fish species or taxa groups per surface area (as t/km^2), having considered the lake's surface.

No biomass estimates were feasible for European eel (*Anguilla anguilla* (Linnaeus, 1758)), Danube sturgeon (*Acipenser gueldenstaedtii* Brandt and Ratzeburg, 1833), Rainbow trout (*Oncorhynchus mykiss* (Walbaum, 1792)), Balkan brook trout (*Salmo farioides* Karaman, 1938) and Noble crayfish (*Astacus astacus* (Linnaeus, 1758)). These species were rarely caught by recreational anglers, according to their statements, over the last decade. Consequently, their biomass was estimated by the model setting ecotrophic efficiency values at 0.99 indicating that most of their production was used in the system [22]. This approach helped mitigate the risk of overestimating fish abundance and the resulting impact [23]. The P/B and Q/B ratios for both fish and invertebrates were estimated using empirical equations [24] or obtained from the existing literature expressed as annual rates (Table A1 in Appendix B). For certain species or taxa groups, with limited available data, input parameters such as DC (trophic level), P/B, and Q/B were incorporated from previously developed Ecopath with Ecosim (EwE) models for Greek lakes.

Fishing activities were incorporated into the model through shore-based recreational fishing because vessel-based professional and recreational fishery is prohibited by law. As recreational fishing exhibits high selectivity for fish size, no discard quantities were included in the model.

2.4. Ecosystem Indicators and Sensitivity

The ecological robustness of the model structure and parameterisation was assessed using PREBAL diagnostics [25]. These diagnostics evaluate the biomass slopes and production-to-consumption ratios among taxa at increasing trophic levels [25]. Additionally, models with catches deviating by $\pm 50\%$ were adjusted to investigate the potential impact of catch data uncertainty, particularly related to illegal fishing, on the model parameterisation and ecosystem structure. Furthermore, a sensitivity analysis was conducted to gauge the effects of gradual changes in input parameters for specific groups on the ecological efficiency of all the groups [26]. This analysis serves as a straightforward indicator of the uncertainty associated with the model's initial parameters [26].

3. Results

3.1. Sensitivity Analysis

To achieve mass balance, adjustments were made to the input parameters of species/taxa groups under the following conditions: (a) when EE values were greater than 1, (b) when P/Q values fell below 0.5 and (c) when Q/B values aligned with the physiological characteristics of each species/taxa. This typically meant low Q/B values for species/taxa at lower trophic levels and high Q/B values for top predators. The resulting food composition matrix lay within the range of values estimated in prior research (Table A2 in Appendix B).

The PREBAL diagnostics revealed that there was a 5–10% decline in biomass values with rising trophic levels. Notably, detritus biomass was found to be in a similar order of magnitude as primary producers. Additionally, P/B, Q/B, and R/B ratios exhibited a consistent decline with increasing TL (with the exception of aquatic birds). The analysis further indicated that altering the value of one input parameter within a group had a more pronounced impact on the other parameters within the same group but generally had minimal or negligible effects on other groups. Modifying catches by $\pm 50\%$ depicted no discernible impact on the output parameters of the model or the structure of the food web. All groups remained balanced even when catches were increased by 50%. Apart from the indices linked to catches, such as total catch, gross efficiency, and some mixed trophic impacts, all other indices exhibited values that closely resembled those of the original model.

3.2. Food Web Structure

In the food web of the ALA (Figure 2), most species and taxa groups exhibited low biomass values, while detritus was estimated to have a high biomass. The TLs of the various groups ranged from 1 (for detritus and phytoplankton) to 3.88 (for aquatic birds) (Figure 2 and Table 1). Out of the 20 groups of organisms considered, 14 exhibited EE values exceeding 0.5, indicating that their production was either fully utilised within the ecosystem or exported as catches. The majority of the system's biomass, production, and consumption were attributed to low-trophic level groups, specifically phytoplankton, zooplankton, Chironomidae, and zoobenthic organisms (Table 1). Excluding the low trophic level groups, Common carp (*Cyprinus carpio* Linnaeus, 1758), Prussian carp (*Carassius gibelio* (Bloch, 1782)) and Aaos' Chub (*Squalius* sp. Aaos (Linnaeus, 1758)) accounted for the highest proportion 39.5% of the ecosystem's production. Zoobenthic and zooplankton organisms represented over 96.2% of the lake's consumption flows. Among the species/taxa groups, those ranked as keystones in the ecosystem (K-S) included *C. carpio*, Chironomidae, the lower TL species/taxa groups, pelicans, and to a lesser extent *C. gibelio*, and *Squalius* sp. Aaos (Table 1). Aquatic birds (all three groups) and *A. anguilla* had omnivory values above 0.4 (Table 2), while groups with intermediate to low trophic levels (such as *C. carpio*, *L. gibbosus*, and *A. astacus*) had OI with low values (close to or less than 0.25). The majority of the system's biomass, production, and consumption came from low trophic level groups, including phytoplankton, zooplankton, Chironomidae, and zoobenthic (over 80% in each case) (Table 2).

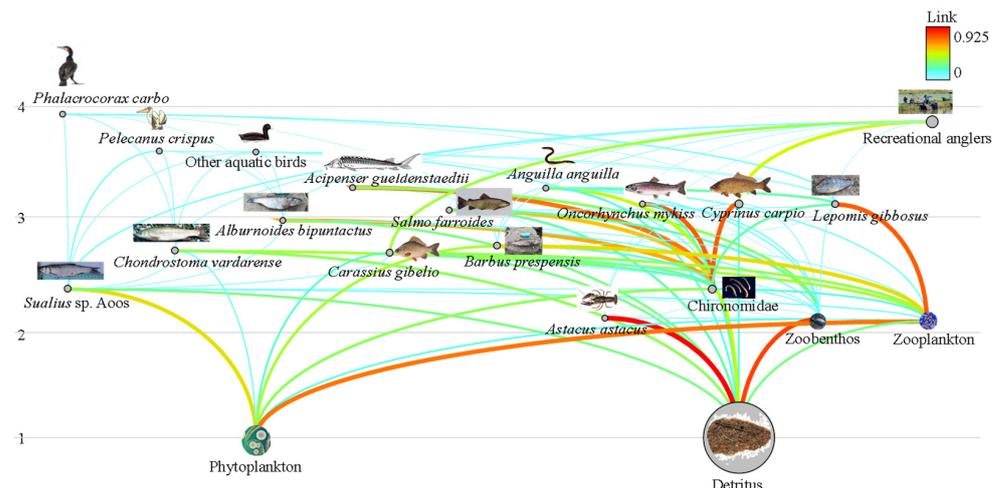


Figure 2. Food web structure in the artificial lake of Aaos, 2021–2022. The size of the circles represents proportionally the biomass per each species group, lines show the energy links between these species' groups and colour lines illustrate the intensity magnitude of these flow rates.

The trophic flows per trophic level in the ALA were 1.3 to 2.3 times higher in the food web of the primary producers than in the detritus-based one (Figure 3), the mean transfer efficiency depicted a significant reduction (>85%) passing from flows in TL II and TL III towards TL III and TL IV. In contrast, the highest values were observed between TLI and TLII for both primary production and detritus-based trophic paths (Figure 3).

3.3. Ecosystem Approach

The combined direct and indirect trophic impacts revealed that the indirect effects were scattered throughout the ALA's trophic web, evaluating the relative importance of top-down and bottom-up food web regulation. In particular, *L. gibbosus* was positively impacted by the lower trophic level species/taxa and negatively by the top predators. Mixed trophic impacts were limited for the recreational fishery on each species/taxa group, whereas detritus exhibited a positive impact, especially in the medium trophic level groups and phytoplankton in the low trophic level groups (Figure 4).

Table 1. Numerical input (in italics) and output estimated parameters for the model of the artificial lake of Aaos, 2021–2022. TL: trophic level estimates, B: biomass ($t \times km^{-2}$), P/B: production rate (yr^{-1}), Q/B: consumption rate (yr^{-1}), EE: ecotrophic efficiency, OI: omnivory index, K-S: keystone-ness index (K-S), P/Q: production/consumption ratio (yr^{-1}), F/Z: exploitation rate, R/A: respiration/assimilation ratio, TST: total system throughput $t \times km^{-2} \times yr^{-1}$, and catch from recreational anglers ($t \times km^{-2} \times yr^{-1}$).

C	Functional Groups	TL	B	P/B	Q/B	EE	OI	K-S	P/Q	F/Z	R/A	TST	Catch
1	<i>Phalacrocorax carbo</i>	3.9	0.0109	0.205	109.45	0.000	1.032	-0.341	0.002		0.998	1.193	
2	<i>Pelecanus crispus</i>	3.6	0.0125	0.105	177.82	0.000	0.859	-0.209	0.001		0.999	2.230	
3	Other aquatic birds	3.6	0.0130	0.171	69.34	0.000	0.836	-0.587	0.002		0.997	0.901	
4	<i>Acipenser gueldenstaedtii</i>	3.3	0.0065	0.200	1.10	0.990	0.004	-1.277	0.182	0.990	0.773	0.007	0.001
5	<i>Salmo fariooides</i>	3.1	0.0159	0.400	23.90	0.990	0.285	-0.910	0.017	0.990	0.979	0.380	0.006
6	<i>Anguilla anguilla</i>	3.3	0.0163	0.390	4.00	0.990	0.390	-1.223	0.098	0.990	0.878	0.065	0.006
7	<i>Oncorhynchus mykiss</i>	3.1	0.0316	0.400	2.70	0.990	0.185	-1.495	0.148	0.990	0.815	0.085	0.013
8	<i>Squalius</i> sp. Aaos	2.3	0.3050	1.500	8.50	0.950	0.348	-0.358	0.162	0.297	0.797	2.592	0.125
9	<i>Chondrostoma vardarensis</i>	2.7	0.2154	1.500	10.50	0.950	0.298	-0.656	0.124	0.134	0.845	2.261	0.038
10	<i>Cyprinus carpio</i>	3.1	0.3702	0.780	6.65	0.950	0.159	-0.243	0.251	0.911	0.686	2.462	0.564
11	<i>Alburnoides bipunctatus</i>	3.0	0.0918	2.270	8.5	0.950	0.266	-0.673	0.267	0.150	0.666	0.781	0.031
12	<i>Carassius gibelio</i>	2.7	0.3485	0.632	8.7	0.950	0.292	-0.316	0.192	0.727	0.760	3.032	0.423
13	<i>Barbus prespensis</i>	2.7	0.2152	0.370	10.4	0.950	0.289	-0.765	0.036	0.393	0.956	2.238	0.031
14	<i>Lepomis gibbosus</i>	3.1	0.1960	1.360	7.5	0.950	0.004	-0.684	0.181	0.046	0.773	1.470	0.013
15	<i>Astacus astacus</i>	2.1	0.0193	6.520	26.09	0.990	0.082	-2.021	0.250	0.937	0.688	0.503	0.001
16	Chironomidae	2.3	0.1830	17.255	62.50	0.969	0.185	-0.024	0.276		0.655	11.440	
17	Zoobenthos	2.1	0.3800	4.500	26.00	0.835	0.076	-0.589	0.276		0.784	9.880	
18	Zooplankton	2.1	0.4338	60.00	240.0	0.454	0.052	-0.211	0.173		0.687	104.10	
19	Phytoplankton	1	2.9700	250.0		0.109	0.000	-0.489	0.250			742.50	
20	Detritus	1	29.699			0.062	0.079					1597.000	

Table 2. Ecological indicators associated with community energy and structure, nutrients cycling and information indices, in the artificial lake of Aaos, 2021–2022.

Parameters	Value	Units
Sum of all consumptions	152.913	t/km ² /year
Sum of all exports	657.289	t/km ² /year
Sum of all respiratory flows	88.946	t/km ² /year
Sum of all flows into detritus	702.477	t/km ² /year
Total system throughput	1601.625	t/km ² /year
Sum of all production	775.885	t/km ² /year
Estimated total net production	742.500	t/km ² /year
Total primary production/total respiration (Pp/R)	8.348	
Community energetic and structure	653.554	t/km ² /year
Net production	109.023	
Total primary production/total biomass (Pp/B)	0.004	
Total biomass/total throughput (TB/TST)	6.810	t/km ² /year
Total biomass (except detritus)	7.102	
Total transfer production	1.252	t/km ² /year
Total fisheries catch	2.863	
Mean trophic level of the catch (TLC)	35.460	t/km ² /year
Primary production (pp) required to sustain fishery (from pp) (PPR) ($t \times km^{-2} \times yr^{-1}$)	21.310	t/km ² /year
Primary production (pp) required to sustain fishery (from pp + det) (PPR) ($t \times km^{-2} \times yr^{-1}$)	0.0008	
Net production (fishing production/net productivity)	15.870	t/km ² /year
Network flow indices	3.886	
Finn’s cycling efficiency (without detritus)	52.860	t/km ² /year
Finn’s cycling index (% without detritus)	1.346	
Finn’s cycling efficiency (including detritus)	2.140	
Finn’s cycling index (% of total throughput)	2.143	
Mean Finn’s path length	2.111	
Finn’s mean path length (without detritus)	0.236	t/km ² /year
Finn’s mean path length (with detritus)	0.322	
Connectance index		
System omnivory index (SOI) (% of total throughput excluding detritus)		

Table 2. Cont.

Parameters		Value	Units
Information indices	Total system overhead (Flowbits)	3817	
	Overhead (Ci, %)	53.380	
	Total system capacity (Flowbits)	7151	

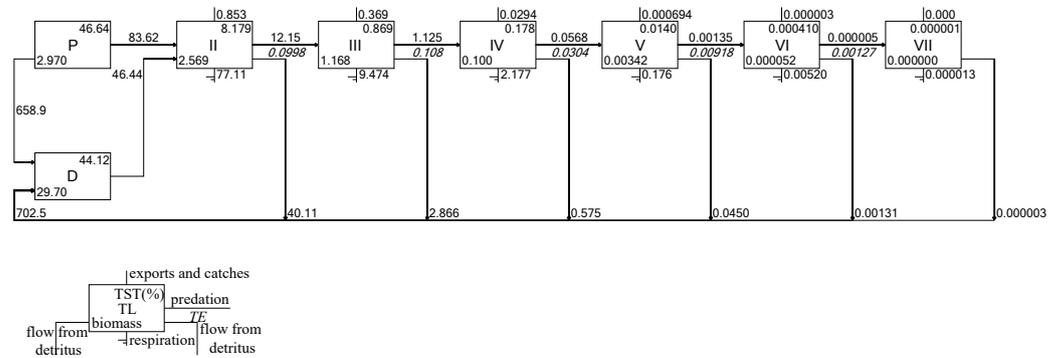


Figure 3. Flow diagram per trophic level for two food chains, primary producers (P) and detritus (D) (both with TL = I), of the artificial lake of Aaos, 2021–2022. TE is the transfer efficiency.

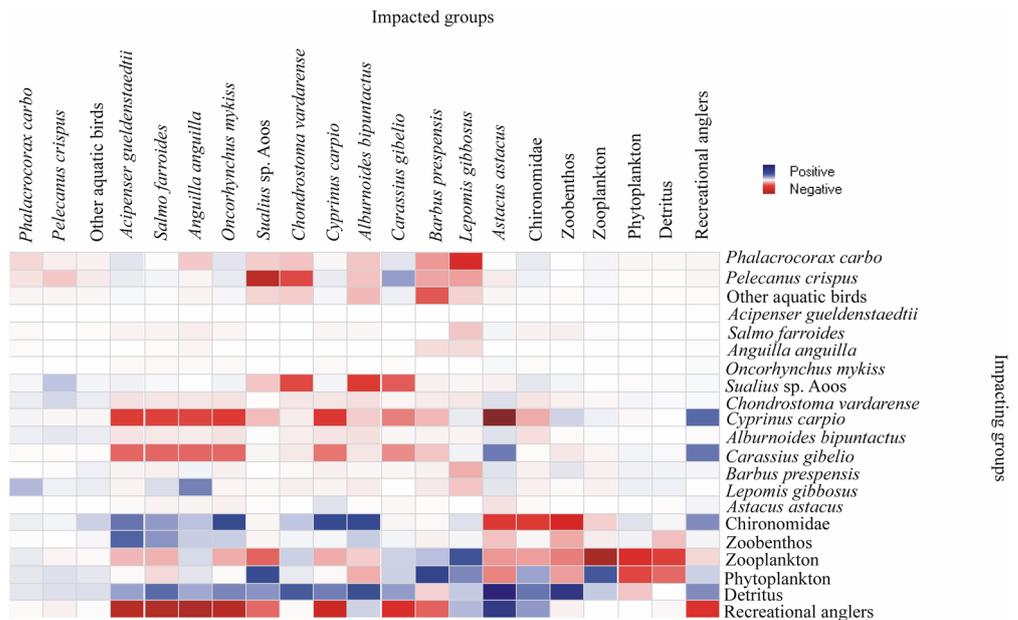


Figure 4. Mixed trophic impact (MTI) chart of the artificial lake of Aaos, 2021–2022. Negative (red bars) and positive (blue bars) effects are comparable between groups.

4. Discussion

This study employs a food-web modelling approach that integrates in situ surveys, expert judgments, and historical archive information. The developed model allows for the quantification of both challenging to measure indirect effects of the food web structure and the direct effects of fisheries on the target species through mortalities. The implementation of an EwE model in the ALA revealed a relatively simple food web structure, with bottom-up control as the dominant pattern. An examination of the keystone species and ecosystem mass flows underscored the importance of lower trophic level groups to the higher trophic levels. The low EE of detritus (0.058) suggests that the entire food web does not efficiently utilise the detritus resource. Given that higher trophic levels exhibited low ecological efficiency, phytoplankton is the dominant source of biomass flow to detritus from trophic levels I and II, accounting for approximately 80% of total biomass flow.

Due to bottom-up control, a significant portion of the production from low trophic level groups was lost as it became incorporated into the bottom sediments of the lake. This phenomenon may account for the relatively low average transfer efficiency (7.88%) observed in the lake's ecosystem when compared to other lake systems. In comparison to other freshwater systems [4,5] and displaying nearly identical values to some African tropical lakes [27], the ecosystem exhibited limited flow renewal as indicated by the low Finn's value and an exceptionally low gross fisheries efficiency (0.00022). The high P/R and the low EE values for both phyto- and zooplankton suggest that these taxonomic groups acted more as a sink than a link to higher trophic level groups [27]. Consequently, a substantial accumulation of organic matter in the bottom layers of the lake was anticipated.

The positive influence observed from detritus and phytoplankton on all higher trophic groups further supports the dominance of bottom-up control. Except for detritus, all functional groups exhibited a negative impact on themselves, likely resulting from intra-group competition for the same resources [26]. The mixed trophic index analysis depicted inter-specific relationships revealing widespread indirect effects of prey relationships on all TLs within the ALA's food web. This emphasises how crucial it is to adopt a management strategy within the framework of the food web and take multi-species mortality assessment into account when re-evaluating the state of stock assessments [4].

The high-altitude ALA exhibited a high level of ecosystem stability, as seen by its ability to revert to a stationary state following a short-term disturbance. This was confirmed by the high values of overhead (53.38%) and TST, when compared with EwE estimates in other lakes worldwide (e.g., Awassa: [6], Malawi: [28], Brazil: [29]) and in Greece (Lake Volvi: [4], Lake Trichonis: [5]). The high maturity stage of the ecosystem can be attributed to the elevated values of overhead, representing a substantial reserve of energy [30], as well as the broad feeding spectrum in the diet (SOI: 32.5%) a low biomass/total throughput ratio and a high connectance index. These factors support the coexistence of species and enhance the ecosystem's resilience to environmental stress [31], which are indices of the lake's robust ecological status. These values are consistent with those estimated in mature natural and man-made freshwater ecosystems worldwide (for review see Table 5 in [4]). It is worth noting that the relationship between maturity and stability has been a subject of debate [32]. The existence of a bacterial microbial loop, which can operate as a vital source of energy for the planktonic food chain [33] and hence improve overall ecosystem maturity, is one potential factor influencing ecosystem maturity [34]. It is crucial to take into account the possibility that this could cause respiration estimates to be underestimated [23]. The presence of a microbial loop that can control a system's high maturity phase [34] is vital for supporting the energy needs of planktonic groups. This highlights the importance of managing and protecting the lake from external influences such as pollution and water regulation, all of which have the potential to disrupt the system's dynamics.

The successional development of the ALA is clear through the increased recycling of nutrients within the ecosystem, and its construction. From the time of the lake's construction in 1991 to the present day, the ecosystem has progressively accumulated significant reserves to withstand external disturbances, as evidenced by the high Finn's cycling index relative to mean path length values [35]. Towards the observed ecosystem stability in the system, it is worth noting that certain non-endemic fish species, including *C. gibelio*, *C. carpio*, and *L. gibbosus*, have been introduced into the ecosystem. Some of these species are listed among those severely impacting global biodiversity [6] and the local aquatic fauna. For instance, *L. gibbosus* is considered an invasive species [36], which was dispersed, survived, and reproduced in various locations, spanning a wide range of habitats and occurrences. It has also been associated with the decline in fish, gastropod, and other invertebrate populations. However, when compared to other fish species (such as *Squalius* sp. Aaos, *C. carpio*, *C. gibelio*, and *Barbus prespensis*), the biomass of *L. gibbosus* is low. This is likely due to the low biomass level of Chironomidae and zoobenthic, and other fish species as food sources. The fact that the *L. gibbosus* and other intermediate–low trophic level species/taxa groups exhibited low trophic plasticity (SOI less than 0.25), explains the

dispersal of trophic interactions between different groups of animals [37]. On the contrary, ALA favours consumer groups with significant dietary adaptability, as indicated by the high value of the dietary specialisation index (SOI: 0.325).

The indirect effects were spread across all trophic levels of the trophic web, as evidenced by the intensity of the interspecific interactions between lake organisms and the values of the mixed trophic index (MTI) (Figure 4). The pumpkinseed, which holds an average position in the trophic web of the lake ecosystem flows, received inbound energy flows from lower trophic levels while losing energy to top predators. The model also revealed that lower trophic levels (phyto- and zooplankton) have a beneficial effect on pumpkinseed survival, but top predators of fish (e.g., *A. anguilla*) and waterfowl had a relatively negative effect. These factors most likely explain the invading species' quick reaction in the ecosystem, owing to the presence of food from lower trophic levels and the concomitant absence of higher predators that would regulate its proliferation.

5. Conclusions

This ecosystem-based approach for the ALA has enabled us for the first time to depict the trophic flows between species/functional groups present in the system and the trophic flows between them. Primary producers and detritus were two significant energy sources that defined the food web of the artificial lake, which was a resilient system to extreme perturbations. The projected interspecies linkages and direct and indirect interactions between species could help re-evaluate fishery management practices by giving a better knowledge of the mechanisms underlying the ecosystem's structure and function.

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Appendix A

The Ecopath module of the EwE program based on the equilibrium of energy flows and biomass for each species/taxa group (version 6.2.0.62) [11–13] calculates the ecological path. Two linear equations are used to guarantee the energy balance within each group: one sets food consumption equal to each group's production, respiration, and unassimilated food; the other sets species/taxa group production equal to each group's predator consumption, export from the system (for example, fisheries yield), and natural mortality (see [26] for more information). The input parameters are biomass (B_i), consumption rate (Q/B), production rate (P/B), which is equivalent to the total mortality rate [11], and species diets (diet matrix DC_{ij} as a fraction of prey i in the diet of predator j). Additionally, the input parameters are exports EX_{ik} from various fishing activities (k) (including by-catch and discards) and the unassimilated food ratio (UN_i) for each group n . The growth efficiency (P/Q), respiration rate (R/B) by

group, and the production proportion that is either exported or used by predators inside the system (referred to as eco-trophic efficiency, EE) are often calculated using the model.

When the following conditions are satisfied, the model reaches equilibrium: With the exception of the fast-growing groups, all groups have EE values less than 1, P/Q values greater than 0.10 and smaller than 0.35, and R/B values consistent with the group’s metabolism that is, high values for small organisms and top predators [18]. While the input parameters included biomass (Bi), production rate (P/B), consumption rate (Q/B), dietary preferences (diet matrix DC_{ij}), and exports EX_{ik} from various fishing activities, including by-catch and discards, the missing parameter for nearly all incorporated groups was EE_i, which was estimated by the program.

The model’s structure was evaluated, and the following ecological indices and analyses were computed to produce artificial metrics that might be useful for contrasting with alternative models: The species/taxa group that are affected by fisheries can be estimated using the following methods: (a) analysis of the various sources of mortality for each species; (b) Mixed trophic impact (MTI) analysis [38], which shows the species with low biomass but significant ecological roles; (c) Keystoneness analysis (K-S) [39], which highlights species of low biomass but significant ecological roles; (d) a simplified diagram showing the biomasses and trophic fluxes that are combined to form primary producers and detritus (Lindeman spine: [40–42]); (e) transfer efficiency (TE) [43] that quantifies the energy transferred between the trophic levels TLs [24] and (f) total system throughput (TST) that is the sum of all the flows (consumption, export, respiration, detritus), which represents the size of the studied ecosystem [24].

The estimation of the following parameters was used to determine the maturity of the system: (a) primary production/respiration ratio (Pp/R), where values close to 1 are indicative of a mature system, whereas values outside of this range indicate immaturity and eutrophication; (b) primary production/biomass ratio (Pp/B), which is expected to decrease with system maturity; (c) R/A respiration to assimilation ratio, which is expected to be close to 1, although it will typically be lower but still positive for organisms at lower trophic levels; and (d) system biomass/throughput, which is expected to increase with system maturity. Additionally, estimates were made for ecological indicators like gross efficiency (GE: catch/net p.p.), information indices like system overhead and ascendancy, and network indices like Finn’s cycling index (FCI): [44] and system omnivory index (SOI): [37]. Low gross efficiency indicates low exploitation or overexploitation of the top predators. GE assesses fisheries catches as a function of primary production. The food web’s fraction of recycled flows, or FCI, is displayed [44]. Mature ecosystems are characterised by high values of this indicator. A more weighted indicator of the food web’s connectivity is the SOI. The food chain is more interconnected the greater the SOI. Higher values indicate more resilient systems [45]. System overhead and ascendancy [44] indicate a system’s resilience to unforeseen disruptions and the energy that an ecosystem has stored up, respectively. To examine the direct and indirect effects of fishing on the ecosystem, the mean trophic level of the captures (TLc) was computed [46]. The primary production required (PPR) to maintain the fishery [47] in relation to the primary production in the system (i.e., PPR/PP, also known as PPR%) was also computed for the landings and discards.

Appendix B

Table A1. Main equations and/or references used for basic input parameters (biomass (B), production over biomass (P/B), and consumption over biomass (Q/B)) of the Ecopath model developed for the artificial lake of Aaos, 2021–2022.

Species/Taxa Groups	Description	Reference
Cormorants (<i>Phalacrocorax carbo</i>)		
B	Estimated from the records of the Management Body (N2KGR1310002) (2021–2022)	[48,49]
P/B	Empirical equations based on [50]	[4,51,52]

Table A1. Cont.

Species/Taxa Groups	Description	Reference
Q/B	Empirical equations	[4,29,51–54]
Diet	Diet composition	[4,51–54]
<i>Pelicans (Pelecanus crispus)</i>		
B	Estimated from the records of the Management Body (N2KGR1310002) (2021–2022)	[48,49]
P/B	Empirical equations based on [50]	[4,51,52,55]
Q/B	Empirical equations	[4,51,52,55]
Diet	Diet composition	[4,51,52,55]
Other aquatic birds (<i>Anas</i> spp., <i>Ardea cinerea</i> , <i>Aythya</i> spp., <i>Calidris</i> spp., <i>Cygnus olor</i> , <i>Egretta</i> spp., <i>Fulica atra</i> , <i>Gallinago gallinago</i> , <i>Mergus serrator</i> , <i>Numenius arquata</i> , <i>Platalea leucorodia</i> , <i>Pluvialis</i> spp., <i>Phoenicopterus ruber</i> , <i>Podiceps</i> spp., <i>Recurvirostra avocetta</i> , <i>Tachybaptus ruficollis</i> , <i>Tadorna tadorna</i> , <i>Tringa</i> spp., <i>Vanellus vanellus</i>)		
B	Estimated from the records of the Management Body (N2KGR1310002) (2021–2022)	[48,49]
P/B	Empirical equations based on [50]	[51,52]
Q/B	Empirical equations	[4,51,52,55]
Diet	Diet composition	[4,51,52,55]
<i>Acipenser gueldenstaedtii</i>		
B	Due to the low quantities of the species biomass was estimated from the model	E = 0.99
P/B	Z = F + M	[56]
Q/B	Empirical equations	[56,57]
Diet	Diet composition	[56]
Fisheries catches	Data reported from interviews of local shored-based recreational anglers (2021–2022)	
<i>Salmo farioides</i>		
B	Due to the low quantities of the species biomass was estimated from the model	E = 0.99
P/B	Z = F + M	[56]
Q/B	Empirical equations	[56,57]
Diet	Diet composition	[56]
Fisheries catches	Data reported from interviews of local shored-based recreational anglers (2021–2022)	
<i>Anguilla anguilla</i>		
B	Due to the low quantities of the species biomass was estimated from the model	E = 0.99
P/B	Empirical equations based on [50]	[56]
Q/B	Empirical equations	[56,57]
Diet	Diet composition	[58,59]
Fisheries catches	Data reported from interviews of local shored-based recreational anglers (2021–2022).	
<i>Oncorhynchus mykiss</i>		
B	Due to the low quantities of the species biomass was estimated from the model	E = 0.99
P/B	Z = F + M	[56]
Q/B	Empirical equations	[56,57]
Diet	Diet composition	[56]
Fisheries catches	Data reported from interviews of local shored-based recreational anglers (2021–2022)	
<i>Squalius</i> sp. Aaos		
B	Estimated from seasonal samplings in the artificial lake of Aaos (2021–2022)	
P/B	Empirical equations based on [50]	[56]

Table A1. Cont.

Species/Taxa Groups	Description	Reference
Q/B	Empirical equations	[56,57]
Diet	Diet composition	[56]
Fisheries catches	Data reported from interviews of local shored-based recreational anglers (2021–2022)	
<i>Chondrostoma vardareense</i>		
B	Estimated from seasonal samplings in the artificial lake of Aaos (2021–2022)	
P/B	$Z = F + M$	[56]
Q/B	Empirical equations	[56,57]
Diet	Diet composition	[56]
Fisheries catches	Data reported from interviews of local shored-based recreational anglers (2021–2022)	
<i>Cyprinus carpio</i>		
B	Estimated from seasonal samplings in the artificial lake of Aaos (2021–2022)	
P/B	$Z = F + M$	[4,60,61]
Q/B	Consumption/Biomass	[4]
Diet	Diet composition	[58]
Fisheries catches	Data reported from interviews of local shored-based recreational anglers (2021–2022)	
<i>Alburnoides bipunctatus</i>		
B	Estimated from seasonal samplings in the artificial lake of Aaos (2021–2022)	
P/B	$Z = F + M$	[56]
Q/B	Consumption/biomass	[56,57]
Diet	Diet composition	[56]
Fisheries catches	Data reported from interviews of local shored-based recreational anglers (2021–2022)	
<i>Carassius gibelio</i>		
B	Estimated from seasonal samplings in the artificial lake of Aaos (2021–2022)	
P/B	$Z = F + M$	[4,62,63]
Q/B	Consumption/biomass	[4,59]
Diet	Diet composition	[58,64]
Fisheries catches	Data reported from interviews of local shored-based recreational anglers during (2021–2022)	
<i>Barbus prespensis</i>		
B	Estimated from seasonal samplings in the artificial lake of Aaos (2021–2022)	
P/B	$Z = F + M$	[56]
Q/B	Consumption/biomass	[56,57]
Diet	Diet composition	[56]
Fisheries catches	Data reported from interviews of local shored-based recreational anglers (2021–2022)	
<i>Lepomis gibbosus</i>		
B	Estimated from seasonal samplings in the artificial lake of Aaos (2021–2022)	
P/B	$Z = F + M$	[56]
Q/B	Consumption/biomass	[56,57]
Diet	Diet composition	[56]
Fisheries catches	Data reported from interviews of local shored-based recreational anglers (2021–2022)	
<i>Astacus astacus</i>		

Table A2. Cont.

Code	1	2	3	4	5	6	7	8	9
8	0.025	0.100	0.025	0.000	0.000	0.000	0.000	0.000	0.000
9	0.025	0.050	0.025	0.000	0.000	0.000	0.000	0.025	0.000
10	0.020	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
11	0.020	0.025	0.025	0.000	0.000	0.000	0.000	0.025	0.000
12	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.050	0.000
13	0.010	0.005	0.020	0.000	0.000	0.050	0.000	0.000	0.000
14	0.100	0.020	0.025	0.000	0.050	0.200	0.000	0.000	0.000
15	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000
16	0.000	0.000	0.070	0.700	0.550	0.400	0.750	0.045	0.200
17	0.000	0.000	0.010	0.290	0.200	0.100	0.100	0.005	0.050
18	0.000	0.000	0.000	0.000	0.000	0.100	0.000	0.100	0.350
19	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.500	0.100
20	0.000	0.000	0.000	0.000	0.200	0.150	0.150	0.250	0.300
Inputs Total	0.800	0.800	0.800	0.000	0.000	0.000	0.000	0.000	0.000
Code	10	11	12	13	14	15	16	17	18
1	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
2	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
3	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
4	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
5	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
6	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
7	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
8	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
9	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
10	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
11	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
12	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
13	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
14	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000
15	0.050	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
16	0.750	0.600	0.200	0.140	0.200	0.015	0.100	0.010	0.000
17	0.050	0.100	0.050	0.000	0.050	0.010	0.050	0.010	0.000
18	0.000	0.050	0.315	0.500	0.750	0.050	0.150	0.050	0.050
19	0.000	0.000	0.160	0.350	0.000	0.000	0.300	0.130	0.700
20	0.150	0.250	0.250	0.000	0.000	0.925	0.400	0.800	0.250
Inputs Total	0.000	0.000	0.025	0.000	0.000	0.000	0.000	0.000	0.000
Total	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

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