

Article

Assessing the Fisheries and Ecosystem Structure of the Largest Greek Lake (Lake Trichonis)

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Abstract: An Ecopath with Ecosim (EwE) modeling approach was used to explore the ecological structure of the largest lake in Greece (Lake Trichonis). Until the mid-1990s, the lake was receiving a high level of pollution and the fishing pressure was intense, while since the early 2000s, fisheries and other human pressures gradually declined. Nowadays, the lake's fisheries mainly target *Atherina boyeri* due to the absence of market demand for the other fish species in the lake, resulting in a low overall fisheries pressure on the fish stocks. The model was built with data collected through: (a) field samplings, (b) in-depth targeted interviews of professional fishermen and (c) historical archive information. The model considered 22 functional groups, while fishing activities were represented by three classes according to the used gears. The outputs of the model revealed that the ecosystem is dominated by low trophic level species (also identified as keystone species), indicating the significance of bottom-up control in the regulation of food web processes. Ecological indicators depicted that the lake's ecosystem is mature and resilient to external disturbances. The methodological approach used in this study was shown to be helpful for studies addressing ecosystem structure, in particular with limited data availability.

Keywords: trophic model; Ecopath with Ecosim; fisheries; fishermen ecological knowledge; Lake Trichonis



Citation: Petriki, O.; Moutopoulos, D.K.; Tsagarakis, K.; Tsionki, I.; Papantoniou, G.; Mantzouni, I.; Barbieri, R.; Stoumboudi, M.T. Assessing the Fisheries and Ecosystem Structure of the Largest Greek Lake (Lake Trichonis). *Water* **2021**, *13*, 3329. <https://doi.org/10.3390/w13233329>

Academic Editors: Pedro Segurado and Francisca Aguiar

Received: 11 October 2021

Accepted: 18 November 2021

Published: 24 November 2021

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1. Introduction

Habitat loss and degradation, species invasions, pollution, overexploitation and climate change have raised concern for the management of freshwater ecosystems and the protection of the life that they support (e.g., [1–3]). Within this framework, the Ecopath with Ecosim (EwE) methodology gained attention by providing a useful tool for depicting freshwater food webs and evaluating the impacts of anthropogenic stressors on specific groups of organisms or the whole ecosystem [4]. Among others, EwE models have been developed for quantifying the impact of fisheries management strategies, such as changes in fisheries regulations and enhancement of fish stocks on the aquatic community. Therefore, their use aims to determine the appropriateness of particular management actions [5] and establish more effective and feasible strategies by incorporating interspecific interactions of all involved organisms and their habitat.

Although EwE models have been applied to a wide variety of ecosystems (i.e., open sea, coastal areas, estuaries, lakes, rivers) worldwide [6], their application in freshwater ecosystems and especially in lentic European water bodies remains scarce (Ijsselmeer in Netherlands: [7], Lake Aydat in France: [8], Lake Volvi in Greece: [9]).

In the present study, the EwE methodology was applied to Lake Trichonis (Western Greece) in order to: (a) synthesize all the available information on biota and fisheries to quantify the energy flows and characterize the structural and functional aspects of the ecosystem, (b) investigate trophic interactions among the various compartments of the food web, (c) quantify the possible impact of fishing on the overall function of the whole ecosystem. The model was developed based on data collected from past and recent field surveys (from published and grey literature), while fisheries-related information was also derived from expert fishermen knowledge (EFK) through personal interviews. This information is crucial, especially for data-deficient systems, such as European freshwaters, where fisheries data are frequently misreported and underestimated [9].

2. Materials and Methods

2.1. Study Area

Lake Trichonis (Latitude: 38°33′0.59″ N, Longitude: 21°33′8.99″ E) is a Mediterranean warm, monomictic, deep lake with a mean depth of 30.5 m and a maximum depth of 57.0 m [10]. It is the largest natural lake in Greece (surface area: 98.6 km², catchment area: 421 km², altitude 15 m.a.s.l.). The lake exhibits a long period of thermal stratification [11], and has been classified as oligotrophic to mesotrophic [12–14]. Excess water outflows to Lake Lysimachia through a narrow superficial long canal (2.8 km) located at the western part of the lake. Until the mid-1990s, the fishing pressure in the lake was intense and the lake was receiving a high level of pollution, while since the early 2000s, fisheries and other human pressures gradually declined [15,16].

The lake belongs to the Greek State and fisheries exploitation is conducted by an association of local fishermen. Thirty years ago, fisheries exploitation was conducted with artisanal fishing gears, mainly set nets (i.e., trammel and gill nets) and gears targeting specific fish species, such as eel traps, long lines or pots, and small trawl-type gears, which were used seasonally. Total landings (and fishing effort, i.e., the number of licensed fishermen) in the lake substantially increased from 1989 to more than 500 t annually in 1998 [16].

Nowadays, fishing is regulated by the National Law “Fisheries Code” (Law 420/70) and Laws 1740/87 and 2040/92. According to the official data (of 2019) registered by the Fisheries Department of the Regional Unit of Etoloakarnania, 35 vessels were licensed to fish in Lake Trichonis. However, only three of them were allowed to fish the big-scale sand smelt, *Atherina boyeri* Risso 1810, with an encircled towed net. The rest are small-sized vessels equipped with benthic nets and longlines. The technical characteristics of the fishing vessels and the demographic features of the professional fishermen are shown in Table A1. In particular, the vessels using the encircled towed net were the largest in length (>9 m), horsepower (>130 HP) and draft (4–5 m), and their age ranged from 5 to 24 years (Table A1, in Appendix A). Almost 65% of the fishermen were over 60 years old (Table A1, in Appendix A).

According to the Presidential Decree No. 99 (Government Gazette 94/24-4-2003), fishing of *A. boyeri* in Lake Trichonis is carried out with (i) gill nets (with a minimum mesh size of 8 mm) up to 200 m long per vessel at depths greater than 12 m and (ii) encircled towed nets (with a maximum length of up to 150 m, a height up to 30 m and a minimum mesh size of 6 mm) complemented with the use of light (up to 3 electric lamps with maximum light intensity of 1500 lm), at depths greater than 35 m. The owners of the three professional fishing vessels that target *A. boyeri* operate exclusively on the lake and declare their fishing production on a monthly basis to the local fishing administration. According to the aforementioned Decree, the use of towed fishing gears is prohibited during March–April and from 15 June to 20 July of each year, while fishing is banned for all species during March–April due to National Law to allow species reproduction.

2.2. Interview Survey

From March 2019 to May 2020, an on-the-spot interview survey, to provide “in situ” information, was conducted on the local professional fishermen operating in Lake Trichonis in order to reveal their EFK. Interviews were: (a) carried out in Greek, (b) held privately, as one-to-one sessions, to prevent influences from their colleagues, (c) carried out by the same person, ensuring that questions were presented identically to minimize sampling bias and (d) took place around fishermen’s mooring/landing sites, frequently on board their own vessel before/after going out fishing, to minimize disruption to their fishing routines. Prior to completing the questionnaire, fishermen were informed that their participation was not mandatory and that any personal data, which could lead to their identification, would remain confidential.

Each questionnaire included four basic pillars of questions based on issues related to the: (a) fishing strategy (i.e., technical characteristics of the gears used, target, by-catch and discarded species and quantities per gear and season), (b) degree of dependence on fisheries (effort data expressed as the number of fishing days per season), (c) personal opinion (i.e., problems encountered by professional fishermen in fishing activity, presence/absence of species overfishing, invasive species, frequency of stocking events, and species extinctions), and (d) demographic features of fishermen. Annual catches were estimated from the daily species catch multiplied by the number of fishing days for each fisherman interviewed. Efforts were made to contact and interview all the professional fishermen who held a professional fishing license. However, only the owners of the three vessels that target *A. boyeri* with an encircled towed net and 10 more vessel owners out of the 35 licensed ones participated in the survey.

2.3. Ecopath Model

The Ecopath module of EwE software (version 6.2.0.62) [17–19] was implemented to describe the trophic structure and function of the food web of Lake Trichonis. This methodology is based on the balance of energy flows and biomass for each functional group, which represents one or more species with similar ecological and trophic functions. The energy balance within each group is ensured through two linear equations: one that sets food consumption equal to production, respiration, and unassimilated food of each group and another that sets the production of the functional group equal to predator consumption, export from the system (e.g., fisheries yield) and natural mortality (see [20] for details).

The input parameters are biomass (B_i), production rate (P/B), which is equal to total mortality rate [17], consumption rate (Q/B), species diets (diet matrix DC_{ij} as a fraction of prey i in the diet of predator j), exports EX_{ik} by different fishing activities (k) (including by-catch and discards), and the unassimilated food ratio (UN_i) for each group i . The production’s fraction that is either utilized within the system by predators or exported (termed Ecotrophic Efficiency, EE), the growth efficiency (P/Q) and the respiration rate (R/B) by group are usually estimated by the model.

The model’s balance is achieved when the following criteria are met: (i) EE values are smaller than 1 for all groups, (ii) P/Q values are higher than 0.10 and smaller than 0.35 for all groups, except the fast-growing ones, and (iii) R/B values are consistent with the metabolism of the group, i.e., high values for small organisms and top predators [18]. For almost all incorporated groups, EE_i was the missing parameter and was estimated by the software program, while the input parameters were biomass (B_i), production rate (P/B), consumption rate (Q/B), dietary preferences (diet matrix DC_{ij}) and exports EX_{ik} by different fishing activities including by-catch and discards.

2.4. Functional Group Definition

A total of 22 functional groups (Table 1) and three fishery compartments were included in the model. All autotrophic and heterotrophic species were either aggregated into functional groups considering their ecological traits (i.e., diet, predators, life history

traits and habitat preferences) or, due to their commercial importance, were represented individually. Specifically, those groups were: one group for phyto- and zoo-plankton, benthic invertebrates, detritus and discards, respectively; 14 groups for fish species; and three groups for aquatic birds that prey on fish exclusively (great cormorants) or occasionally (pelicans and other aquatic birds). The grouping of fish species (the fish species that have been reported in the lake are provided in Table A2 in Appendix A) was based on similarities of their diets, their ecology and fishing pressure that is imposed on them following [9]. According to the above, the fish species were categorized into the following groups: (a) piscivorous, in which fish represents more than 75% of total ingested biomass, (b) omnivorous, whose diet includes at least 25% of plant and 25% of animal material, (c) small size benthic, (d) gobies, (e) introduced fish species and (f) Mugilidae. In particular, the group of piscivorous included the Siluridae family (i.e., Aristotle's catfish *Silurus aristotelis* Garman, 1890, and Wels catfish *Silurus glanis* Linnaeus, 1758); the omnivorous included species Vardar bitterling *Rhodeus meridionalis* Karaman, 1924, Peloponnese chub *Squalius peloponensis* (Valenciennes, 1844), Tench *Tinca tinca* (Linnaeus, 1758), Stymphalia minnow *Pelagius stymphalicus* (Valenciennes, 1844); the small size benthic fish group included Trichonis blenny *Salaria economidisi* Kottelat, 2004, and Trichonis spined loach *Cobitis trichonica* Stephanidis, 1974; the gobies group included species Western Greece goby *Economidichthys pygmaeus* (Holly, 1929), Trichonis dwarf goby *Economidichthys trichonis* Economidis & Miller, 1990, and Caucasian dwarf goby *Knipowitschia caucasica* (Berg, 1916); and the introduced fish group included species Topmouth gudgeon *Pseudorasbora parva* (Temminck & Schlegel, 1846) and Eastern mosquitofish *Gambusia holbrooki* Girard, 1859. The group of Mugilidae included, according to professional fishermen, the Striped grey mullet *Mugil cephalus* Linnaeus, 1758 and Thinlip grey mullet *Chelon ramada* (Risso, 1827). The species that participated as separate functional groups consisted of the European eel *Anguilla anguilla* (Linnaeus, 1758), *A. boyeri*, Trichonis rudd *Scardinius acarnanicus* Economidis, 1991, Prussian carp *Carassius gibelio* (Bloch, 1782), European carp *Cyprinus carpio* Linnaeus, 1758, Acheloos roach *Leucos panosi* (Bogutskaya & Iliadou 2006), and Albanian barbel *Luciobarbus albanicus* (Steindachner, 1870). The Hellenic Minnow roach *Tropidophoxinellus hellenicus* (Stephanidis, 1971), a species without commercial value but with a large abundance in the lake, was also included as a separate group.

2.5. Model Parameterization

A detailed description of the groups and the data sources used to parameterize the model are listed in Table A3 in Appendix A, whereas diet composition per functional groups is shown in Table A4 in Appendix A.

Fishery components incorporated in the model were disaggregated into: (a) encircled towed net for the licensed fishing vessels that target *A. boyeri*, (b) small-mesh size nets for catching *A. boyeri*, and (c) benthic gillnets and bottom longlines.

Biomass values were expressed as $t \cdot km^{-2}$ wet weight and flows as $t \cdot km^{-2} \cdot year^{-1}$. Biomasses for producers and zooplankton were estimated based on monitoring data of seasonal sampling conducted in nine sites in 2019. Phytoplankton biomass was estimated by samples taken at 2 m depth (from surface). Seasonal Chlorophyll- α concentrations were determined spectrophotometrically [21]. Estimation of phytoplankton biomass was performed assuming a euphotic layer of 10 m, carbon to Chlorophyll- α ratio of 40 and carbon to phytoplankton wet weight ratio of 0.1, according to [22]. Zooplankton were collected with vertical hauls of a conical net (mesh size 100 μm) covering the whole water column. Their biomass was first determined as dry weight and, afterwards, transformed to wet weight (dry weight to wet weight ratio: 0.2), according to [23].

Biomass estimations for fish species were based on Catch Per Unit of Effort (CPUE) estimates. CPUE data are often used as an index of relative abundance, assuming proportionality between CPUE and fish abundance [24,25]. This proportionality is particularly important in data-poor ecosystems [26], where CPUE data are often the only form of data available to assess temporal evolution and patterns of distribution and abundance of exploited populations. In the present study, CPUE estimations resulted from: (a) monthly monitoring of encircled towed net (two out of the three licensed vessels) during May 2019–2020 (except for March–April due to temporal prohibition), (b) the quantification of the qualitative information (i.e., landings and discards, and fishing effort information) provided by fishermen expert knowledge and (c) seasonal (conducted during February–November 2019) experimental samplings using Nordic type benthic and pelagic multi-mesh gillnets throughout the lake [27]. In total, 87 benthic multi-mesh Nordic type gillnets (30×1.5 m length * height each, mesh size range: 5–55 mm) and 20 pelagic (6×27.5 m length * height each, mesh size range: 6.25–55 mm) were used. These gillnets were set at dusk and lifted by dawn in different depth zones. The biomass values of omnivorous fishes, small-size benthic species, gobies and the introduced fish species were estimated from seasonal sampling with benthic and pelagic Nordic gillnets (set throughout the whole horizontal and vertical area of the lake). This type of gillnet and the methodology described in [27] provide qualitative and quantitative data regarding species composition and abundance per m^2 , which are considered as representative of the fish fauna structure [28]. Therefore, this particular methodology is widely applied for monitoring fish fauna in lake ecosystems at a pan-European level according to the implementation of the European Directive 2000/60/EC. The average catch per unit of fishing effort (kg/m^2) from all 4 seasonal samplings was used to estimate the approximate annual biomass of these functional groups (as t/km^2). The biomass of the aforementioned functional groups could not be estimated from the fishermen's knowledge because, due to their small size, they are not usually caught by their selective fishing gear and in the cases that they are, they are totally discarded due to their negligible commercial value.

No biomass estimations were feasible for the groups of *T. hellenicus* because the species is totally discarded, and benthic invertebrates due to the high variation of the available data. Therefore, their biomass estimations were assigned to the model, setting ecotrophic efficiency values at 0.85 for *T. hellenicus* (considering that although it is a discarded catch and fishermen do not target this species, it is caught at the same intensity as *A. boyeri* due to its preference for the pelagic zone), and at 0.95 for the second group, as it was considered that most of its production was used in the system [4]. In this way, the possibilities of overestimating pelagic fish abundance and effects were reduced [29]. The P/B and Q/B ratios for fish and invertebrates were estimated using empirical equations [30] or taken

from the literature and expressed as annual rates (Table A3 in Appendix A). For some functional groups, for which relative information was lacking, the input parameters (DC, P/B, Q/B) were also integrated from previously built EwE models for similar systems (for details, see Table A3 in Appendix A).

2.6. Model Quality and Sensitivity

The pedigree routine was used to evaluate the data sources and assess the quality of input parameters. The pedigree index in EwE may fluctuate between 0 and 1, with values near 1 indicating that the model is constructed with data obtained from studies conducted locally. Lower values indicate that the used data were derived from other models or were extrapolated from other systems [30]. The PREBAL [31] diagnostics were used to assess whether the model structure and parameterization were ecologically robust. These tools assess the slopes of biomass and production and consumption ratios across taxa of increasing trophic levels [31]. In addition, in order to test if the uncertainty in the catch data (i.e., illegal fishery) could have a significant effect on the model parameterization and ecosystem structure, we additionally constructed models with $\pm 50\%$ catches and explored their results. Finally, we performed a sensitivity analysis to evaluate the impact of gradual changes in the input parameters of a group on the EE of all the groups, as a simple measure of the uncertainty of the initial parameters of the model [32]. This analysis was performed by a previous version of the software (v5), as it is not currently available in EwE v6.

2.7. Ecosystem Indicators and Model Summary Statistics

To evaluate the model's structure and to provide synthetic measures that might be useful for comparison with other models, the following analyses and ecological indices were performed and calculated: (a) analysis of different sources of mortality for each functional group; (b) Mixed Trophic Impact (MTI) analysis [33], which allows the estimation of the direct and indirect impacts of fisheries upon the functional groups; (c) Keystoneness analysis (K-S), which highlights the species of low biomass but of high importance in the ecosystem [34]; (d) an analysis and a simplified representation of the trophic flows and biomasses aggregated into primary producers and detritus trophic webs (Lindeman spine: [35–37]); (e) transfer efficiency (TE) [38] that quantifies the energy transferred between the trophic levels TLs [30]; and (f) Total System Throughput (TST) that is the sum of all the flows (consumption, export, respiration, detritus) and quantifies the whole ecosystem size [30].

System maturity was determined through the estimation of: (a) Primary Production/Respiration ratio (Pp/R), with values close to 1 characterizing a system as mature, whereas higher and lower values indicate system immaturity and eutrophication; (b) Primary Production/Biomass ratio (Pp/B) that is expected to decrease as a system matures; (c) R/A respiration to assimilation ratio that is expected to be close to 1, while it will tend to be lower, but still positive, for organisms at lower trophic levels; and (d) System biomass/Throughput that is expected to increase with system maturity. Ecological indicators such as Gross Efficiency (GE: catch/net p.p.), network indices (i.e., Finn's Cycling Index—FCI: [39]; System Omnivory Index—SOI: [40]) and information indices (i.e., System overhead and ascendency) were also estimated. GE measures fishery catches as a function of primary production, with low gross efficiency indicating low exploitation or exploitation of the top predators. FCI shows the percentage of flows recycled in the food web [39] with high values characterizing the mature ecosystems. SOI is a more weighted measure of how connected the food web is. Specifically, the higher the SOI, the more connected the food web. System overhead and ascendency [41] reflect a system's strength when it is under unexpected perturbations and the energy in reserve of an ecosystem, respectively, with the higher values characterizing more resilient systems [41].

To analyze the direct and indirect impacts of fisheries on the ecosystem, except for the estimation of the group mortalities and the MTI analysis, the mean trophic level of the catches (TLc) was calculated [42]. Moreover, the Primary Production Required (PPR)

to sustain the fishery [43] relative to the primary production in the system (i.e., PPR/PP, hereafter PPR%) was also calculated for the landings and discards.

3. Results

3.1. Interview Results

3.1.1. Encircled Towed Net Fishery

The fishing effort (fishing days) of the vessels that had a license for targeting *A. boyeri* with the encircled towed net (three vessels) was very high during August–February (from 20 to 24 fishing days/month), while it was significantly reduced in June and July and zero in March–April, during the *A. boyeri* fishing ban season. The intensity of the fishing effort per vessel was 190 days for 2019 and according to the statements of the professional fishermen ranged around an average value of 200 fishing days per year. The overwhelming percentage of the encircled towed net fishery's production (~80%) derived from the production of *A. boyeri* and, to a lesser extent, from other species (Table 2).

Table 2. Species composition (%) of the commercial, by-catch and discard ratios used in the model based on board and interview surveys conducted in professional fishing vessels in Lake Trichonis, 2019.

Species	Encircled Towed Net	Small Mesh Net	Bottom Nets and Longlines
<i>Commercial</i>			
Big scale sand smelt	82.60	75.00	
<i>By-catch</i>			
European carp	0.30		3.00
Acheloos roach	2.70		32.80
Prussian carp	0.54		7.50
Trichonis rudd	1.40		30.00
Wels catfish	0.10		2.00
European eel	0.01		0.50
Albanian barbel	1.80		0.30
Mugilidae	0.30		14.00
Other fish species	0.25		9.90
<i>Discards</i>			
Hellenic Minnow roach	10.00	25.00	

The estimated monthly production of *A. boyeri* per fishing vessel ranged from 2.5 to 8.5 t, depending on the month as a result of a daily catch of 160 to 350 kg. In 2019, the annual total fishery production for *A. boyeri* was estimated slightly over 160 t and the production of the by-catch and the discards was estimated at approximately 20 and 8 t. The amount of the by-catch species fluctuated seasonally with their contribution to the total encircled towed net catches ranging from 5%, during winter months, to 15% during summer. By-catch consisted principally of *L. panosi*, *S. acarnanicus*, *L. albanicus* and to a lesser extent of *S. aristotelis*, *C. gibelio* and other fish species (Table 2). The discarded catch, which amounted to an average of 10%, consisted entirely of *T. hellenicus*, which had no commercial interest and was discarded before landing on the fishing vessel.

3.1.2. Artisanal Fishery

Local fishermen are targeting *A. boyeri* for up to 80% of the total artisanal catches on an annual basis, as it is the only species that ensures a good market price, and occasionally other species (mainly carps during spring and summer and eels during winter). Therefore, professional fishermen mainly use gillnets for *A. boyeri* (mesh size 8 mm bar length) throughout the fishing period (up to 150 fishing days per year) and only occasionally, mostly during summer, nets with wider mesh sizes and longlines for targeting other species (mainly for self-consumption) (Table 2).

As mentioned, *A. boyeri*'s fishing activity is defined by the presidential decree 99/Government Gazette 94/24-4-2003 and is carried out with gillnets of a fixed length per commercial vessel (up to 200 m long). According to interviews with professional fishermen, the daily fishery production from this fishing gear ranged from 15 to 50 kg per day, while

there have been days when the production reached 100 kg per fishing vessel. Apart from *A. boyeri*, discarded catches of *T. hellenicus*, which have no commercial value, were caught at a rate ranging from 5% to 30%, depending on the season. Both the fishery production of *A. boyeri* (with an average estimate of 30 kg per day and fishing vessel) and the discarded catches (estimated as 25% of the total catch) of this particular gear were incorporated in the model. The fishing effort with this gear was estimated at 150 days for all 30 registered vessels. Therefore, for incorporation in the model, the catches of the other species were estimated as an average catch of 2.5 kg per day and vessel (based on fishermen statements) multiplied by the active number of fishing days (150 fishing days per year) and the number of active vessels.

The intensity of the fishing effort concerning the occasional fishing of species other than *A. boyeri* during the year showed seasonal variability. The fishing activity was higher in spring and summer (around 20 fishing days per month), where there was an increased demand for fish, and lower in autumn and winter. Professional fishermen used cotton benthic nets with a mesh size of 50 mm to 100 mm for *S. acarnanicus* and with a mesh size of 24 mm to fish *L. panosi*. During summer, fishermen mainly targeted *C. carpio* with 70 mm cotton nets, while occasionally (less than 10% of the total number of fishing days), they used bottom longlines with a hook of size No7 for eel fishing using *A. boyeri*, *L. panosi* or worms as bait. In autumn and winter, fishing with nets was low (around 10 fishing days per month) and targeted mainly *L. panosi*, while during the period January–February, fyke nets were used to fish eels.

The duration of the fishery was around 12 h for each fishing day. In Table 2, the species composition (%) caught by benthic gillnets and to a lesser extent by bottom longlines are presented.

3.1.3. Problems and Perspectives in Lake Fishery

The main problem reported by fishermen regarding their financial dependence on fisheries was the lack of market demand for lake fish species. All interviewed fishermen stated that they sell their total catches in retail except those of *A. boyeri* that were sold in wholesale to intermediaries who finally sell it mainly in Agrinio and to a lesser extent in Aetoliko, Patra and Preveza. The decline in lake fish market demand was mainly recorded after 2000. As fishermen typically stated, while in the 1990s a professional fisherman managed to sell all his daily production, currently, he hardly manages to retail 20% of the respective production. Based on their opinion, the financial crisis of the last decade in combination with the increase in operating costs, contributed to the acceleration of the departure from the profession. The lack of commercial interest in lake fish species is also reflected in the reluctance of all the professional fishermen to embark on subsidy/modernization programs for their fishing vessels, which may also result from either a lack of interest in inland fisheries subsidies or in the complex process that needs to be followed.

The lack of market demand regarding lake fish species (except for *A. boyeri* whose value was/is particularly low (~1–2 euros/kg)) resulted in a reduction in fishing pressure in the lake fish stocks, which is also reflected in the statements of professional fishermen. Thus, all the fishermen who participated in the survey stated that they do not consider that there is a problem of fish stocks overfishing, as they did not observe significant reductions in the production of several species, such as *C. carpio*, *C. gibelio*, *L. albanicus*, *L. panosi*, *T. tinca* and *S. aristotelis*. However, they reported a significant presence of non-commercially important species, such as *S. acarnanicus*.

Among the common problems faced by the professional fishermen in Lake Trichonis, based on their statements, was the illegal fishing conducted in the canal connecting the lake with Lake Lysimachia. The fyke nets and gillnets used for illegal fishing activities were set in a way that did not allow the free movement of species such as *A. boyeri*, *A. anguilla*, *M. cephalus*, *C. carpio*, etc. However, despite the aforementioned challenges, all the fishermen of the lake stated that they did not intend to retire from fishing activities in the near future, and/or to replace/modernize their fishing vessels.

The positive statements reported by the fishermen regarding the condition of the lake included the absence of amateur fishermen and polluters. Regarding the latter, they stated that they have observed an improvement in the water quality over the last 20 years, which is probably due to the reduction in the permanent population of the lakeside communities and the subsequent decrease in agricultural activities in the watershed that impacted the lake through their runoff. The fishermen also stated that they had not noticed any problems from the presence of introduced fish species. They also stated that no stockings with commercial species had been conducted in the lake, which is in contrast to the practices conducted in Lake Lysimachia where stockings with mullets take place regularly.

The most crucial proposal of the fishermen for improving the lake's fishery production was the intensification of policing, especially in the overflow channel and the removal of the existing illegal fishing gear, especially during the reproductive period when many species migrate (autumn and winter). According to fishermen, these actions would enhance the lake's fish stocks, mainly those of *A. boyeri*, *M. cephalus*, *C. carpio* and maybe *D. larvax*. The fishermen who had a fishing license for targeting *A. boyeri* using encircled towed nets expressed the opinion that it would be more cost-effective to ban fishing of the species in February instead of the current ban in summer (15 June to 20 July). They claimed that they would benefit from the increased market demand during summer, while the ban in winter would result in a 3-month period free of fishing pressure, which would allow species reproduction.

3.2. Model Structure

3.2.1. Ecological Indicators

The estimated Pedigree index of the presented model was equal to 0.633. To obtain mass balance, we adjusted the value of the input parameters of the functional groups exhibiting EE values higher than 1. The final diet composition matrix remained within the same range as that reported from past diet studies in the lake (Tables A3 and A4 in Appendix A).

The PREBAL diagnostics (Figure A1 in Appendix A) showed that the parameterization was ecologically sound. The range of biomass values was about 6 orders of magnitude, with a slope of (log scale) 5–10% decline with increasing trophic level; detritus biomass was on the order of Primary Producers; P/B, Q/B, and Respiration/B were decreasing with increasing TL (except for aquatic birds).

The sensitivity analysis showed that the effect of altering the value of an input parameter of a group was higher on the rest of the parameters of the same group, but usually low (or none) on the other groups. Modifying catches by $\pm 50\%$ had no apparent effect on the model parameterization and food web structure; all groups were balanced, even when catches increased by 50%, while for decreased catches, only the discards turned out to be unbalanced. In addition, all indices had values very close to the original model, with the exception of the ones directly related to catches (Total catch, Gross efficiency and some Mixed Trophic Impacts).

The TLs of groups ranged from 1 (i.e., for detritus and phytoplankton) to 3.68 (for piscivorous fish) (Table 1). The EE values for 12 groups of organisms were higher than 0.5 and, thus, their production was either consumed within the ecosystem or exported from it in terms of catches or discards. Aquatic birds (all three groups) and *A. anguilla* exhibited omnivory values higher than 0.5 (Table 1), whereas intermediate-low trophic-level groups (i.e., zooplankton and *C. carpio*) showed low values of OI (close or less than 0.1).

The food web of Lake Trichonis (Figure 1) exhibited low biomass values for most functional groups, whereas high biomasses were estimated for detritus, phytoplankton, benthic invertebrates, *A. boyeri* and *T. hellenicus*. Low-trophic-level groups (i.e., phytoplankton, zooplankton and benthic invertebrates) contributed the most to Total System Throughput (TST), biomass, production and consumption of the system (over 80% in each case) (Table 1). By excluding the low-trophic-level groups, the highest production of the ecosystem was consumed by *T. hellenicus* (39.5%) and *A. boyeri* (34.6%) and to a lesser

extent by *L. panosi* (5.9%), *L. albanicus* (5.2%) and *S. acarnanicus* (3.0%). More than half of the consumption flows in the lake (56.2%) were derived from benthic invertebrates and zooplankton (Table 1). Great cormorants, other aquatic birds, benthic invertebrates, zooplankton, *A. boyeri* and omnivorous fish species were the functional groups ranking high in terms of importance as keystones in the ecosystem (K-S) (Table 1).

The flow diagram per integer trophic level (TL) in the form of the Lindeman spine (Figure 2) showed that the flows in Lake Trichonis were greater in the food chain of the primary producers than in the detritus-based one. The mean Transfer Efficiency (TE) for the primary producer-supported food chain (5.05%) was almost equal to the detritus-based food web (5.03%). Transfer efficiency was high for low trophic levels and decreased towards higher trophic levels with the mean TE exhibiting significant reduction (>75%) for the flows between TL III-TL IV and TL IV-TL V, while maximum values were observed between TLII and TLIII for both primary production and detritus-based trophic paths (Figure 2).

Ecological indicators related to community structure, cycling of nutrients and information theory are shown in Table 3. The Pp/R and Pp/B values were high (3.045 and 61.257, respectively). Primary Production Required (PPR) by fisheries both from primary producers and detritus-based food chain was $325.57 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$, whereas the footprint of the fisheries (i.e., the ratio of the PPR to the total primary production used in the system) reached 15.9% of the total ecosystem impacts, with the remaining amount of impacts disaggregated to natural and interspecies interactions.

Table 3. Ecological indicators related with community energetic and structure, cycling of nutrients and information indices, Lake Trichonis, 2019.

	Parameters	Value	Units
Community energetic and structure	Sum of all consumptions	1501.874	$\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$
	Sum of all exports	4.280	$\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$
	Sum of all respiratory flows	811.660	$\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$
	Sum of all flows into detritus	2149.288	$\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$
	Total system throughput	4467.102	$\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$
	Sum of all production	2775.940	$\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$
	Estimated total net production	2471.305	$\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$
	Total primary production/total respiration (Pp/R)	3.045	
	Net production	1659.645	$\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$
	Total primary production/total biomass (Pp/B)	61.257	
	Total biomass/total throughput (TB/TST)	0.009	
	Total biomass (except detritus)	40.343	$\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$
	Total transfer production	5.033	
	Total fisheries catches (landings + discards)	4.280	$\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$
	Mean trophic level of the catch (TLc)	2.529	
Network flow indices	Primary production (pp) required to sustain fishery (from pp) (PPR) ($\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$)	194.660	$\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$
	Primary production (pp) required to sustain fishery (from pp + det) (PPR) ($\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$)	325.570	$\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$
	Net production (fishing production/net productivity)	0.002	
	Finn's Cycling efficiency (without detritus)	6.388	$\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$
	Finn's Cycling Index (% without detritus)	0.347	
	Finn's Cycling efficiency (including detritus)	297.880	$\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$
	Finn's Cycling Index (% of total throughput)	6.669	
	Mean Finn's path length	5.474	
	Finn's mean path length (without detritus)	2.250	
	Finn's mean path length (with detritus)	5.109	
Information indices	Connectance Index	0.283	$\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$
	System Omnivory Index (SOI) (% of total throughput excluding detritus)	0.269	
	Total system overhead (Flowbits)	13,748.000	
	Overhead (Ci, %)	80.012	
	Total system capacity (Flowbits)	17,182.000	

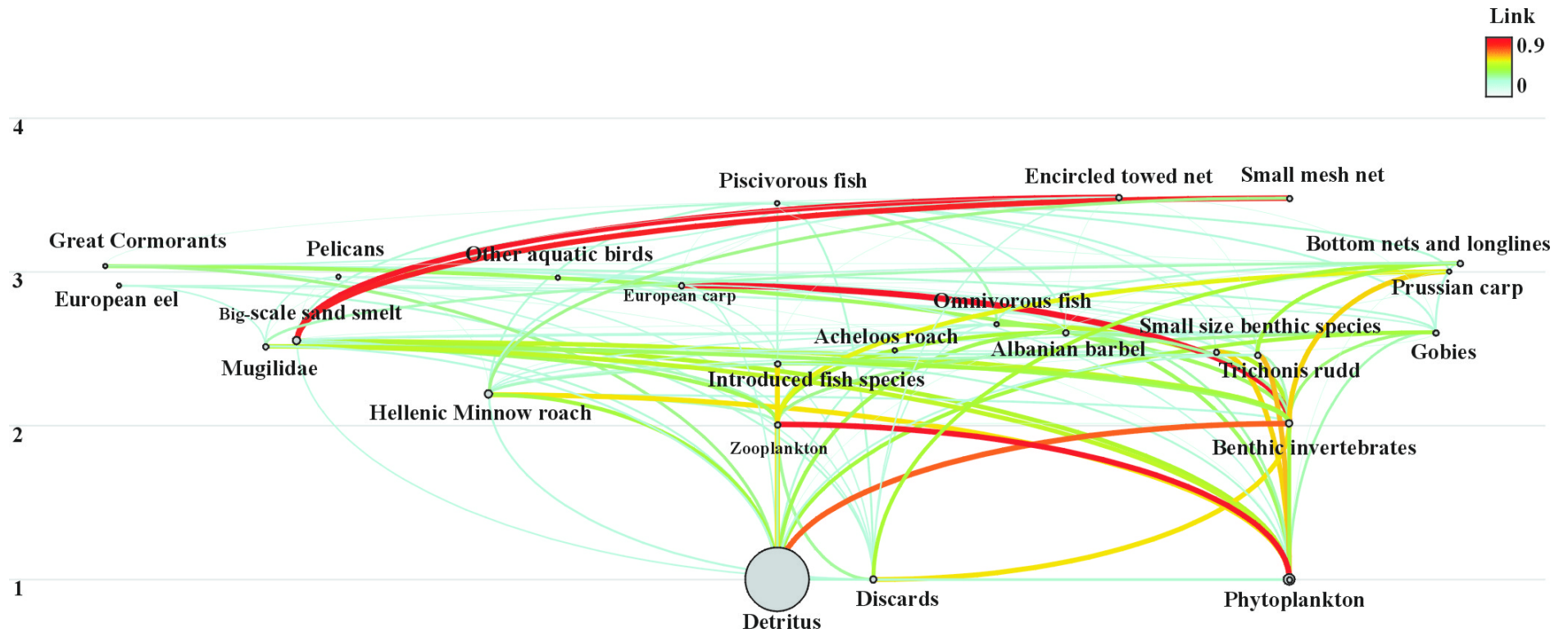


Figure 1. Food-web structure in Lake Trichonis 2019. Circle size proportionally represents the biomass of each functional group and lines indicate the trophic links between functional groups. Color of the lines illustrate the magnitude of the flow rates. Numbers on the left side indicate the trophic food web levels.

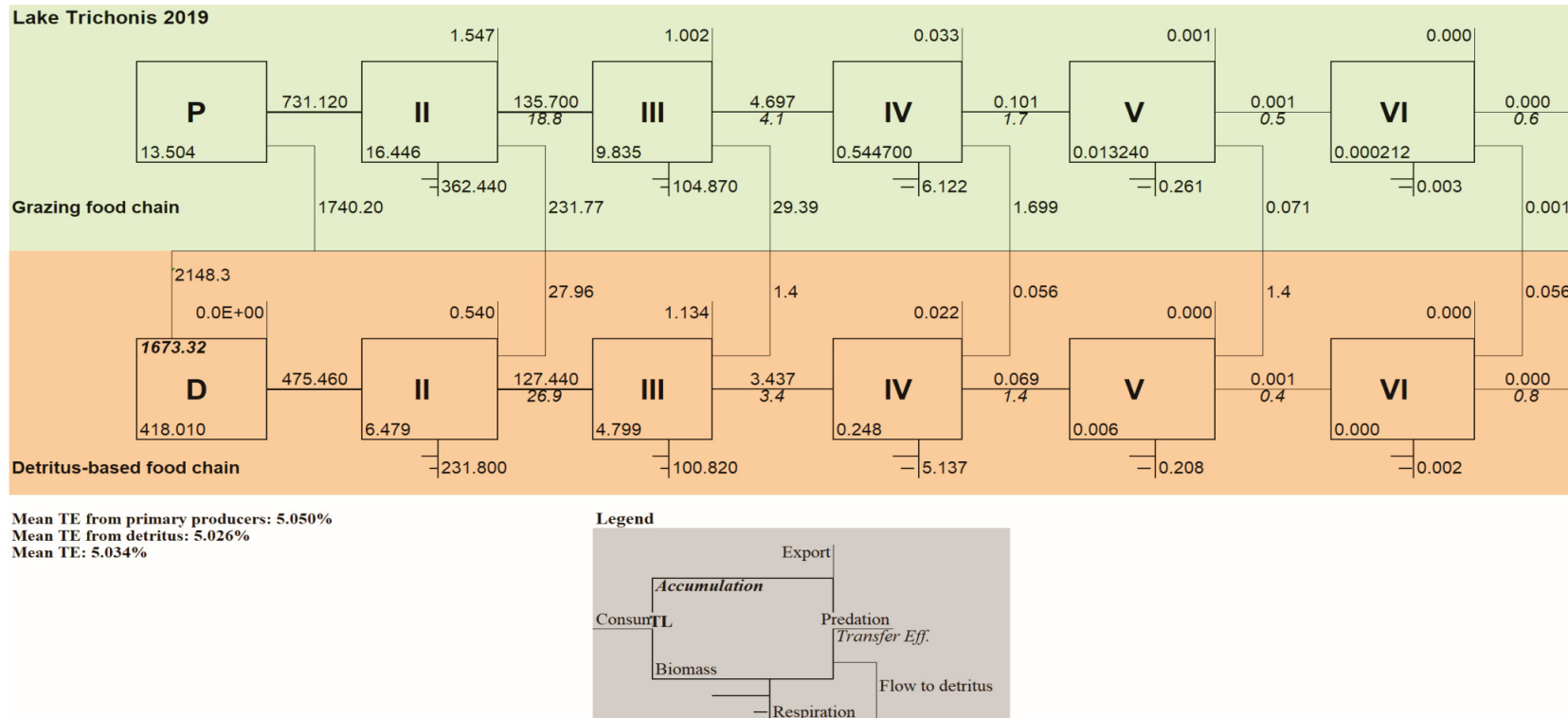


Figure 2. Flow diagram per integer trophic level (TL) in the form of the Lindeman spine for two food chains, primary producers (P) and detritus (D) (both with TL = I), Lake Trichonis, 2019. TE is the transfer efficiency. Numbers in the lines indicate the flows and those within the boxes indicate the biomasses.

3.2.2. Fisheries Indicators

The composition (%) of the catches per species and fishing gear are shown in Table 2. *A. boyeri* contributed 78% to the fisheries catches for all fisheries combined, while the other commercial fish species = 16% and discards = 12%, with most of the discards derived from encircled towed nets (Figure 3).

The exploitation rate (fishing mortality/total mortality) imposed by the fisheries was high for *A. boyeri*, *A. anguilla* and *C. carpio* (Figure 3). Predation mortality due to high intraspecific competition was higher than 50% for the low functional groups (zooplankton and benthic invertebrates) and for *T. hellenicus*, *C. gibelio* and small benthic fish (Figure 3).

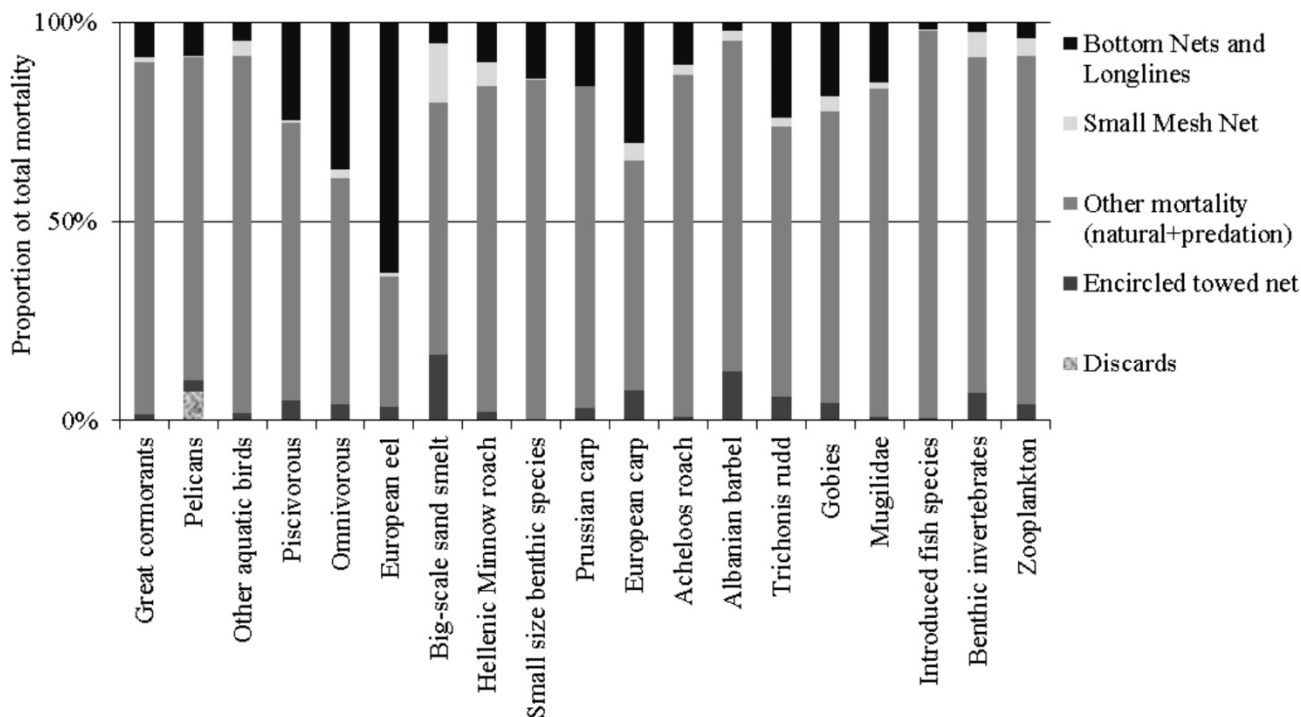


Figure 3. Disentangling mortality components (other mortality caused by predation and natural mortality) and fishing mortality imposed on each functional group by different fishery types in Lake Trichonis, 2019.

Mixed trophic effects/impacts are depicted in Figure 4. The combined direct and indirect trophic effects evaluate the relative importance of the top-down and bottom-up control of the food web. Fishing generally exhibited a moderate effect on the species caught, with the exception of targeted *A. anguilla*, due to its extremely low biomass in the lake. The impact from the encircled towed nets was high for *A. boyeri* and to a lesser extent for *T. hellenicus* (discard), whereas the impact of the artisanal fishery was high for *A. anguilla* using longlines, and for *C. carpio*, *S. acarnanicus*, piscivorous and omnivorous species using benthic gillnets (Figure 4). In contrast, both the encircled towed nets and the passive small-size nets that target *A. boyeri* had a positive effect on the small-size benthic species and *T. hellenicus*. In contrast, detritus had mostly positive effects on the other functional groups, especially on the medium-trophic-level groups.

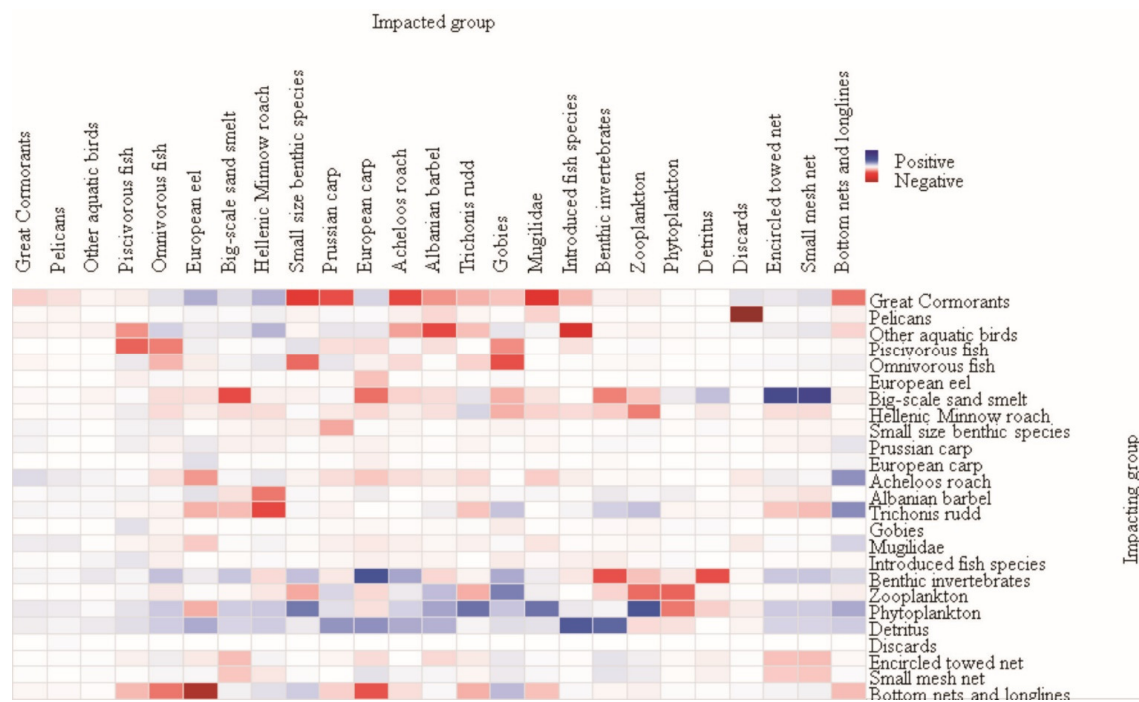


Figure 4. Mixed trophic impact (MTI) chart in Lake Trichonis, 2019. Negative (red bars) and positive (blue bars) effects are comparable between groups.

4. Discussion

The present study is based on a food web modelling approach used for seven situ surveys, expert judgement and historical archive information, in order to provide valuable insights into the ecosystem function of the largest lake in Greece (Lake Trichonis). The developed model allowed the quantification of the direct impacts of fisheries on the target species through mortalities and also their indirect effects via the food web structure, which are otherwise difficult to assess.

4.1. The Importance of Expert Fishermen Knowledge (EFK)

Expert fishermen knowledge (EFK), despite its potential biases [44], has been gradually gaining attention, as it provides quantitative information [45] that can be incorporated in ecosystem-based models [46] to evaluate changes in the ecosystem structure and function [47]. Moreover, EFK frequently highlights several management issues that call for an urgent reassessment of management practices. In the present study, EFK was used to portray the fisheries status and potentially correct the inherent limitations of the catch and effort official records. The latter are frequently underestimated, due to misreported and/or non-declared production by professional fishermen (for taxation reasons) and illegal fishing [48,49]. This may encourage the use of the EFK in relevant studies especially in areas with a lack of available data, giving a boost to their management and protection efforts.

4.2. Socio-Economic Approach of Lake Fisheries

The fishing fleet in Lake Trichonis presents a similar operating pattern to that observed in other lakes in Greece (e.g., Lake Volvi: [49]). Most fishing vessels are small with the basic equipment adapted to the characteristics of inland fishing (closed area, short distances compared to offshore fishing, shallower depths).

More than 85% of the lake's fishery production came from *A. boyeri* caught mainly by encircled towed nets and to a lesser extent by gillnets. The once commercial species of the lake, which were, according to the statements of the fishermen, the fisheries' targets 25 years ago (i.e., *S. acarnanicus*, *L. panosi*, *S. aristotelis*), have nowadays little commercial

interest. It is noteworthy that, in some cases, the amount of by-catches with the encircled towed nets was almost similar to that of the *A. boyeri* (200 kg). However, those catches were thrown back to the lake due to a lack of commercial interest.

The age distribution of fishermen revealed that most of them were aged and that their profession tends to be abandoned (the fact that only 10 registered fishermen were active and willing to participate in the survey reflects the reduced fishing exploitation of the lake). The aging of the lake's professional fishermen was also reported in a similar study conducted 20 years ago, where it was estimated that the percentage of active fishermen over 60 years old was around 40% [50]. Although, in the last 20 years, the fishing fleet of the lake has been modernized owing to engines (from 17.8% rowing boats in Trichonis in 1997, to 5.5% in 2019), the problem of fishermen aging is alarming for the future of the lake's fishery. This is observed not only in the fisheries of the inland waters of Greece (Lake Volvi: [49]), but also in those of the country's coastal zone [51,52], and generally in the coastal Mediterranean fisheries.

The uncertain future of fisheries is exacerbated by the reluctance of young people to become fishermen, which reflects the lack of a long-term sustainable fisheries strategy [53]. According to their statements in the framework of the present and previous studies [50], from the 1960s until the end of 1990, there were about 50 active fishing vessels, while at the time this study was conducted (i.e., in 2019), there were active, part-time, about half. Such a reduction in fishing activity has also been reported in other parts of southern Europe (Galicia, Catalonia: [54]) and is a potential explanation for the chronic shortage of young people in the European fishing industry ([55]). In addition, it is common among fishermen to declare fishing as their main occupation, despite the fact that they are employed in the agricultural sector or in other professions (e.g., taxi drivers, employees). This reinforces the lack of stakeholder involvement in decision making as indicated by the absence of a commonly accepted fisheries cooperative. The percentage of fishermen that are exclusively occupied in the fisheries of inland waters is significantly smaller than the respective coastal fisheries (~40%: [56]) or individual areas such as Amvrakikos Bay (45%: [57]).

4.3. Lake Ecosystem Structure

According to Odum's [58] theory of ecosystem development, an important trend in ecosystem successional development is the increase in the amount of nutrients and energy recycled (or entrapped) within the ecosystem. The food web of Lake Trichonis was characterized by two important energy sources: primary producers and detritus. Ecosystems that depend on detritus as an energy source are characterized by increased plasticity and resilience. Regarding the primary producers (i.e., phytoplankton)-based food web, an important part of the biomass and production of the low-trophic-level groups was not assimilated in higher trophic levels and was exported, by being incorporated into the lake's bottom sediments. The dependence on detritus probably maintains system stability and resilience (i.e., the ability to return to previous conditions after a short disturbance) by providing a high source of reserved energy as indicated by the high values of overhead [59]. The dominance of bottom-up control is also supported by the positive impact exhibited from detritus and phytoplankton to all upper groups. All functional groups, apart from detritus, exhibited a negative impact on themselves. This is probably an effect of the within-group competition for the same resources [32]. The mixed trophic impact analysis showed widespread indirect impacts on all TLs of the Lake Trichonis food web, either due to the negative impact of the professional fishery on the commercial fish groups or due to interspecific prey relationships. This revealed the need to shift toward a multispecies mortality assessment for the re-evaluation of stock assessment status and, thus, towards management in a food web context [60]. The detritus neutral response observed in the studied lake has also been identified in many lakes worldwide [4,61], including Lake Volvi in Greece [9].

The lake was also characterized by a simple structured food web (TB/TST: 0.009, and SOI: 0.269) as almost all biomass was concentrated in the first two trophic levels

(approximately 95%), with low biomass transfer values between the various trophic levels. The reduction in transfer efficiency from the trophic levels TL I and TL II upwards has also been observed in other lake ecosystems [61]. Mass flows in the ecosystem and keystone species analysis also indicated the importance of low-trophic-level groups in relation to the higher-trophic-level ones. Particularly, the fact that phytoplankton and detritus had a positive effect on various functional groups, as depicted by the MTI, highlights the significance of bottom-up processes in the regulation of the food web [61]. This is also confirmed by the high keystone-ness of the lower-trophic-level functional groups of the lake (i.e., phytoplankton and zooplankton). The value of the Finn Cycling Index (6.669), which represents the fraction of the total flows that is recycled [39], fell within the limits estimated in other models (Pantanal lakes, Brazil: [62]) and was relatively low, highlighting the low energy recycling flow.

The evaluation of the model's robustness based on the bioenergetic indices estimated for Lake Trichonis, and compared with other EwE models implemented in freshwater systems worldwide, showed very low value of gross efficiency of the fisheries (0.002), almost similar to the values estimated for some African tropical lakes. The large accumulation of organic matter in the bottom layers may be explained by the high production/respiration values (3.045) and the low EE for both phytoplankton and zooplankton, implying that these resources were a 'sink' and not a 'link' to higher trophic levels [63]. However, the fact that the model developed in this study represented annual budgets does not allow for full verification of this explanation and provides a topic for future studies and analyses.

Overhead (80.012%) and the total capacity of the system were high, compared to other lake ecosystems (Awassa, Ethiopia: [63], Malawi: [64], Pantanal, Brazil: [62]) and almost close to another large Greek lake (Lake Volvi: [9]). These estimates are indicative of the high maturity and resilience of the ecosystem, suggesting that the food web of Lake Trichonis has the capacity to absorb recurrent perturbations and withstand external disturbances. The high maturity stage of Lake Trichonis was also indicated by the low total biomass/total throughput ratio (0.009 year^{-1}), the high estimates of connectance index ($0.283 \text{ t*km}^{-2}*\text{year}^{-1}$) and the existence of high zooplankton biomass [65], whose values lay within the corresponding ones estimated in mature natural and human-made freshwater ecosystems around the world. In contrast, the low value of primary production/biomass (Pp/B) and the primary production/respiration (Pp/R) ratios suggested that the lake is still an immature ecosystem in a developing stage. Nevertheless, the relationship between maturity and stability has been a controversial issue [66] and bioenergetic indices should be considered with caution, because this phenomenon might be attributed to the absence of data concerning the bacteria microbial loop. The latter acts as an essential energy source for the planktonic food chain [61], thus enhancing ecosystem maturity [58]. However, on the other hand, it may lead to an underestimation of the respiration estimates [4]. The potential presence of a microbial loop that determines the high maturity phase of a system [61] could support the source of energy for the planktonic groups. This enhances the need for the lake's management and protection from external impacts, such as pollution and water regulation, all of which could potentially alter its dynamics.

4.4. Lake Fisheries Aspects

The fishing pressure in the lake is very low, which is reflected in the model estimates. The low average trophic level of the catches (2.529) was attributed to the predominance of the low trophic level species *A. boyeri* in the fisheries catches. The discards (approximately 15% of the total catches) were mainly the result of the encircled towed nets catches of *T. hellenicus* that were released before transporting to fishing vessels due to the lack of market demand for the species. The zero discarded quantities of the other commercial species indicated the high selectivity of the fishing gear used. This has also been observed in the second largest Greek natural lake, Lake Volvi [9].

The total catch from the fisheries of the lake was estimated to be almost 300 t per year (282 t). *A. boyeri* represented 75% of the total catch and was principally caught (85%) by

encircled towed nets followed by benthic small-sized nets. The species composition of the catches was in line with the statements of the professional fishermen and the landings data reported in the late 1990s. Fishery records of *A. boyeri* in Lake Trichonis during 1988–1999 exhibited that annual catches often exceeded 500 t annually [67], with the stock being underexploited according to the estimation of exploitation level (0.35). Additionally, the fishing pressure on the remaining species of the lake was also low, based on both the results of the model and the fishermen's knowledge, who stated the absence of overfishing for most target species. As already mentioned, although fishermen's ecological knowledge must be used with caution as they may miss or forget information [44], in our study, licensed fishermen provided accurate catch estimates, because the interviews were anonymous and they were not able to be traced for tax purposes.

The outputs of the model revealed a competitive relationship between professional fishermen and aquatic birds, which impacted the fish stocks through predation mortality. Aquatic birds–fisheries interactions are an important issue in Greek wetlands, where large populations of aquatic birds, mainly great cormorants whose population have increased dramatically over the past few decades, due to species' protection and the availability of food, compete with local fishermen for the same limited fisheries resources [68].

The fishermen's knowledge revealed two key points in the fisheries' management of the lake. The first concerns the intensification of the patrolling controls on the overflow canal in order to extirpate the illegal fishery and the second, the replacement of the fishing ban of *A. boyeri* during summer. Regarding the first, these gears are set in the canal arbitrarily, providing easy and free of cost catches for the illegal fishermen while causing economic damage to the professionals as they prevented the free movement of fish. Removing those gears will allow fish movements between Lakes Trichonis and Lysimachia that will help the enhancement of Trichonis fish stocks. This agrees with the suggestions previously made by [16,69] who refer to the reconnection of the lakes as “the umbilical cord of supply and renewal”. Additionally, the free movement of the fish between the lakes and the Acheloos River is one of the commitments that the country has undertaken concerning the application of the EU regulation 1100/2007 regarding the protection of *A. anguilla* stocks that was imposed after their generalized collapse in all European waters [70].

Regarding the fishing of *A. boyeri*, fishermen expressed the view that a temporary reshuffle of the species summer fishing ban either to February or to September would be more cost-effective for the local economy without unbalancing its sustainable exploitation. The summer closure (15 June–20 July) limits the lake's fishermen economic return during a period with high market demand for the species, which cannot be balanced during the other period of the year. Since the implementation of the temporal fishing ban (PD 99/2003), the accumulated fishing experience of the fishermen has formed the belief that the scope and duration of the temporal closures do not bring the best result in the relationship of “stock sustainability-optimal economic exploitation”. This view was also stated by fishermen 30 years ago [16]. It is worth noting that the temporal closure is the least economically expensive management measure compared to others proposed, such as increasing the mesh size of the encircled towed nets and the reduction in the light intensity of this gear. Therefore, a study re-evaluating the temporal fishing closure of the encircled towed net fishing in Lake Trichonis would be particularly useful in order to contribute to the sustainable management of the species stock and, consequently, maintain the economic returns of the professional fishermen.

Regarding other management issues, ways for the utilization of the discarded *T. hel- lenicus* quantities should also be investigated as they could contribute to the development of the local economy, aiming to boost the income of professional fishermen while managing sustainably natural resources.

5. Conclusions

The present study provides useful insights into the function and structure of the food web of the largest Greek lake, Lake Trichonis, and key information of the lake's fishery

that is lacking for most European freshwater systems. Significant information regarding the above came from the professional fishermen's knowledge, proving that it can be a useful source of ecological data, specifically when there is a lack of relevant studies. The lake's food web was characterized by two important energy sources: primary producers and detritus. The lake is a mature system with high resilience to external disturbances. The estimated direct and indirect interactions among fisheries, commercial and discarded species and interspecies relationships, which provide an improved understanding of the processes that underlie the structure and function of the ecosystem, could aid in reassessing fishing management practices.

Author Contributions: Writing—original draft preparation, O.P. and D.K.M.; writing review and editing, K.T., I.T., G.P., I.M. and R.B.; modeling, D.K.M.; conceptualization D.K.M. and M.T.S.; funding acquisition, M.T.S. All authors have read and agreed to the published version of the manuscript.

Funding: This research was supported by the research project "ANATHALLOI" "Development of management tools for marine and freshwater ecosystems" MIS 5002500, funded by Greece and the European Regional Development Fund under the Operational Programme "Competitiveness, Entrepreneurship and Innovation, NSRF 2014–2020".

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: The data and the detailed questionnaire presented in this study are available on request from the corresponding author.

Acknowledgments: The authors wish to express their gratitude to fisherman Nikos Zarkadas for his assistance in the fieldwork.

Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

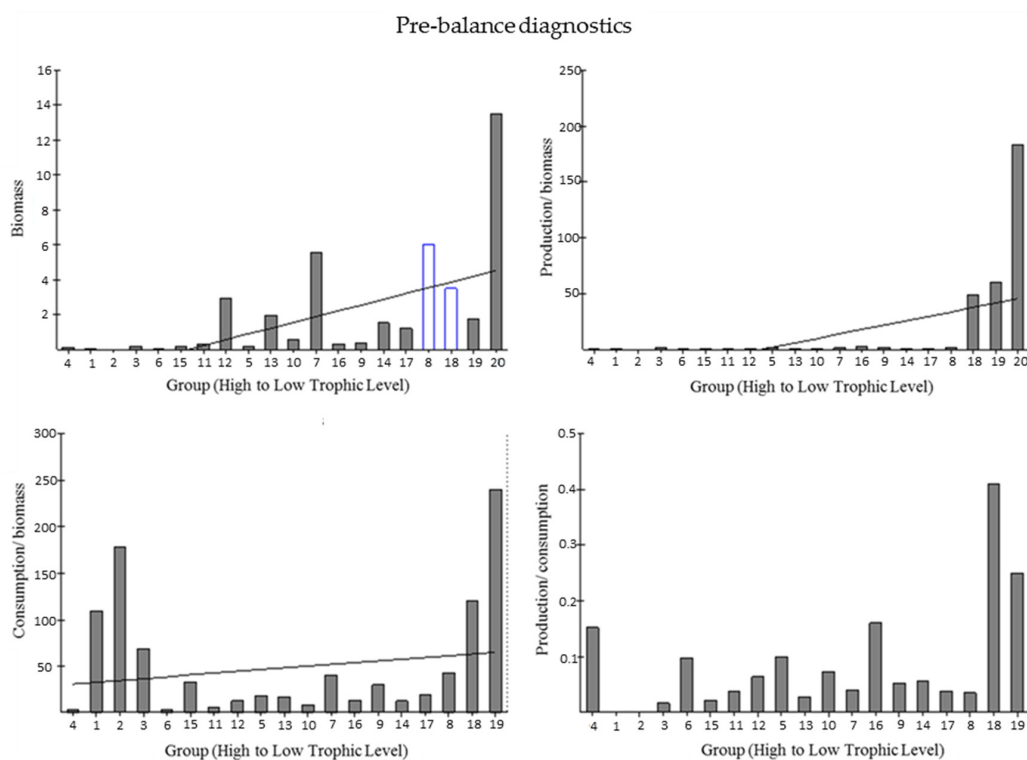


Figure A1. PREBAL diagnostics [31] of the model developed for Lake Trichonida (2019). The group numbering on the x-axis is according to Table 1. Blue bars in biomass graph indicate the biomass values estimated by the model as this was not feasible from the surveys (see Materials and Methods).

Table A1. Technical characteristics of the fishing vessels in Lake Trichonis and demographic features of the local fishermen. Bold values indicate the vessels that fish with encircled towed net.

Vessel Length (m)	N	%	Engine Power (HP)	N	%
3–5	16	45.71	2–5.9	3	8.33
5–7	11	31.43	6–9.9	8	22.22
7–9	4	11.43	10–19.9	9	25.00
9–11	1	2.86	20–49	6	16.67
11–13	1	2.86	50–80	4	11.11
13–15	2	5.71	>130	4	11.11
Rowing vessel	2	5.56	Vessel Material		
Fisher age (year)			Plastic	5	16.67
20–39	4	23.5	Wood	16	53.33
40–59	2	11.8	Polyester	14	46.67
>60	11	64.7	Vessel age (year)		
Vessel depth (m)			0–4	8	22.9
1–2	21	60.0	5–9	16	45.7
2–3	8	22.9	10–14	5	14.3
3–4	3	8.6	15–19	1	2.9
4–5	3	8.6	20–24	3	8.6
			25–29	1	2.9
			30–35	1	2.9

Table A2. Fish species which had been reported in Lake Trichonis and caught by benthic (B) and pelagic (P) gillnets during the seasonal (Wi, winter; Sp, spring; Su, summer; and Au, autumn) samplings of 2019.

Family/Species	Wi	Sp	Su	Au
Anguillidae				
<i>Anguilla anguilla</i> (Linnaeus, 1758)	-	-	-	-
Atherinidae				
<i>Atherina boyeri</i> Risso, 1810	B/P	B/P	B/P	B/P
Blenniidae				
<i>Salaria fluviatilis</i> (Asso, 1801)	-	-	-	-
<i>Salaria economidisi</i> ¹ Kottelat, 2004	B/P	B	B	B
Cobitidae				
<i>Cobitis trichonica</i> ¹ Stephanidis, 1974	B	B	B	B
Cyprinidae				
<i>Barbus peloponnesius</i> ¹ Valenciennes, 1842	-	-	-	-
<i>Carassius gibelio</i> ² (Bloch, 1782)	-	B	-	-
<i>Cyprinus carpio</i> Linnaeus, 1758	-	-	B	-
<i>Luciobarbus albanicus</i> ¹ (Steindachner, 1870)	B/P	B	B	B
<i>Pelagus stymphalicus</i> ¹ (Valenciennes, 1844)	-	B	B	-
<i>Pseudorasbora parva</i> ² (Temminck & Schlegel, 1846)	B	-	B	-
<i>Rhodeus meridionalis</i> ¹ Karaman, 1924	B	B	B	B
<i>Leucos panosi</i> ¹ Bogutskaya & Iliadou, 2006	B/P	B/P	B/P	B/P
<i>Scardinius acarnanicus</i> ¹ Economidis, 1991	B/P	B/P	B/P	B/P
<i>Squalius peloponensis</i> ¹ (Valenciennes, 1844)	-	-	-	-
<i>Telestes pleurobipunctatus</i> ¹ (Stephanidis, 1939)	-	-	-	-
<i>Tinca tinca</i> (Linnaeus, 1758)	-	-	-	-
<i>Tropidophoxinellus hellenicus</i> ¹ (Stephanidis, 1971)	B/P	B	B/P	B/P
Gobiidae				
<i>Economidichthys pygmaeus</i> ¹ (Holly, 1929)	B	-	-	-
<i>Economidichthys trichonis</i> ¹ Economidis & Miller, 1990	-	-	-	-
<i>Knipowitschia caucasica</i> (Berg, 1916)	-	-	-	-
Moronidae				
<i>Dicentrarchus labrax</i> (Linnaeus, 1758)	-	-	-	-
Mugilidae *				
unidentified	P	-	-	-
Poeciliidae				
<i>Gambusia holbrooki</i> ² Girard, 1859	-	-	-	-
Siluridae				
<i>Silurus aristotelis</i> ¹ Garman, 1890	-	B	B	B
<i>Silurus glanis</i> Linnaeus, 1758	-	-	-	-

¹: Endemic of Greece or Balkans [71], ²: Introduced fish species, * Probably *Mugil cephalus* Linnaeus, 1758.

Table A3. Main equations and/or references used for basic input parameters (Biomass (B), Production over Biomass (P/B), Consumption over Biomass (Q/B), Diet (D)) of the ecopath model developed for Lake Trichonis, 2019.

Functional Groups	Description	Reference
Cormorants (<i>Phalacrocorax carbo</i>)		
Biomass	Average value of the bird specimens that were present during the years 1984–2014. It was estimated considering the birds that live in the wider area, the size of the lake and the birds; number that an area may potentially have per day.	[68,72]
Production/Biomass	Empirical equations. Corrections were made according to Opitz ([73]) considering the temperature differences between the area where the data came from and the study area.	[74,75]
Consumption/Biomass	Empirical equations.	[62,74–77]
Diet	Diet composition.	[75,78,79]
Pelicans (<i>Pelecanus crispus</i>)		
Biomass	Average value of the bird specimens that were present during the years 1984–2014. It was estimated considering the birds that live in the wider area, the size of the lake and the birds' number that an area may potentially have per day.	[68,72]
Production/Biomass	Empirical equations. Corrections were made according to Opitz ([73]) considering the temperature differences between the area where the data came from and the study area.	[74,75]
Consumption/Biomass	Empirical equations.	[74–76]
Diet	Diet composition.	[75,78,79]
Other aquatic birds (<i>Anas acuta</i>, <i>Anas crecca</i>, <i>Anas penelope</i>, <i>Anas platyrhynchos</i>, <i>Anas strepera</i>, <i>Ardea cinerea</i>, <i>Aythya ferina</i>, <i>Aythya fuligula</i>, <i>Calidris alpine</i>, <i>Calidris minuta</i>, <i>Cygnus olor</i>, <i>Egretta alba</i>, <i>Egretta garzetta</i>, <i>Fulica atra</i>, <i>Gallinago gallinago</i>, <i>Mergus serrator</i>, <i>Numenius arquata</i>, <i>Platalea leucorodia</i>, <i>Pluvialis apricaria</i>, <i>Pluvialis squatarola</i>, <i>Phoenicopterus ruber</i>, <i>Podiceps cristatus</i>, <i>Podiceps nigricollis</i>, <i>Recurvirostra avocetta</i>, <i>Tachybaptus ruficollis</i>, <i>Tadorna tadorna</i>, <i>Tringa erythropus</i>, <i>Tringa nebularia</i>, <i>Tringa tetanus</i>, <i>Vanellus vanellus</i>)		
Biomass	Average value of the bird specimens that were present during the years 1984–2014. It was estimated considering the birds that live in the wider area, the size of the lake and the birds' number that an area may potentially have per day.	[68,72]
Production/Biomass	Empirical equations. Corrections were made according to Opitz ([73]) considering the temperature differences between the area where the data came from and the study area.	[74,75]
Consumption/Biomass	Empirical equations.	[62,74–77]
Diet	Diet composition per species.	[75,78,80]
Piscivorous fish species (<i>Silurus glanis</i>, <i>Silurus aristotelis</i>)		
Biomass	Biomass was estimated from monthly samplings of commercial encircled towed net fishery (data of fishing production and fishing effort) in the lake (2019).	
Production/Biomass	$Z = F + M$	[81–83]
Consumption/Biomass	Empirical equations.	[84]
Diet	Diet compositions estimated in the lake by previous studies and in other lake' ecosystems.	[83,85]
Fisheries catches	Data reported from encircled towed net fishery, benthic gillnets and longlines fisheries were derived from monthly, seasonal sampling and interviews of local fishermen, respectively, during the model's reference period (2019).	
Omnivorous fish species (<i>Pelagus stymphalicus</i>, <i>Rhodeus meridionalis</i>, <i>Squalius peloponensis</i>, <i>Tinca tinca</i>)		
Biomass	Biomass was estimated from seasonal samplings in the lake (2019) with benthic and pelagic Nordic type gillnets.	
Production/Biomass	$Z = F + M$	[86,87]
Consumption/Biomass	Empirical equations.	[84,88]
Diet	Diet composition estimated in other lakes.	[89,90]

Table A3. Cont.

Functional Groups	Description	Reference
Fisheries catches	Data reported from encircled towed fishery, benthic gillnets and longlines fisheries were derived from monthly, seasonal sampling and interviews of local fishermen, respectively during the model's reference period (2019).	
European eel (<i>Anguilla anguilla</i>)		
Biomass	Biomass was estimated from monthly samplings of commercial encircled towed net fishery (data of fishing production and fishing effort) in the lake (2019).	
Production/Biomass	Empirical equations. Corrections were made according to Opitz ([73]) considering the temperature differences between the area where the data came from and the study area.	[89]
Consumption/Biomass	Empirical equations.	[84]
Diet	Diet composition estimated in other lakes.	[91,92]
Fisheries catches	Data reported from encircled towed net fishery, benthic gillnets and longlines fisheries were derived from monthly, seasonal sampling and interviews of local fishermen, respectively, during the model's reference period (2019).	
Big-scaled sand smelt (<i>Atherina boyeri</i>)		
Biomass	Biomass was estimated from monthly samplings of commercial encircled towed net fishery (data of fishing production and fishing effort) in the lake (2019).	
Production/Biomass	$Z = F + M$	[68]
Consumption/Biomass	Empirical equations.	[84]
Diet	Diet compositions estimated from seasonal samplings conducted in 2019 and previous studies in the lake.	[10,93]
Fisheries catches	Data reported from encircled towed net fishery, benthic gillnets and longlines fisheries were derived from monthly, seasonal sampling and interviews of local fishermen, respectively, during the model's reference period (2019).	
Hellenic Minnow roach (<i>Tropidophoxinellus hellenicus</i>)		
Biomass	Due to the fact that the species is totally discarded estimations were made from the model	$E = 0.95$
Production/Biomass	Empirical equations. Corrections were made according to Opitz ([73]) considering the temperature differences between the area where the data came from and the study area.	[89]
Consumption/Biomass	Empirical equations	[84]
Diet	Diet composition estimated by seasonal samplings in the lake (2019).	
Fisheries catches	Data reported from encircled towed net fishery, benthic gillnets and longlines fisheries were derived from monthly, seasonal sampling and interviews of local fishermen, respectively, during the model's reference period (2019).	
Small size benthic species (<i>Cobitis trichonica</i>, <i>Salaria economidisi</i>)		
Biomass	Biomass was estimated from seasonal samplings in the lake (2019) with benthic and pelagic Nordic type gillnets.	
Production/Biomass	$Z = F + M$	[89,94]
Consumption/Biomass	Empirical equations.	[84]
Diet	Diet composition estimated for the lake in previous studies.	[94]
Fisheries catches	Data reported from encircled towed fishery, benthic gillnets and longlines fisheries were derived from monthly, seasonal sampling and interviews of local fishermen, respectively, during the model's reference period (2019).	
Prussian carp (<i>Carassius gibelio</i>)		
Biomass	Biomass was estimated from monthly samplings of commercial encircled towed net fishery (data of fishing production and fishing effort) in the lake (2019).	

Table A3. Cont.

Functional Groups	Description	Reference
Production/Biomass	$Z = F + M$	[95,96]
Consumption/Biomass	Consumption/Biomass.	[84]
Diet	Diet composition estimated in other lakes.	[91,97]
Fisheries catches	Data reported from encircled towed fishery, benthic gillnets and longlines fisheries were derived from monthly, seasonal sampling and interviews of local fishermen, respectively, during the model's reference period (2019).	
European carp (<i>Cyprinus carpio</i>)		
Biomass	Biomass was estimated from monthly samplings of commercial encircled towed net fishery (data of fishing production and fishing effort) in the lake (2019).	
Production/Biomass	$Z = F + M$	[98,99]
Consumption/Biomass	Consumption/Biomass.	[84]
Diet	Diet composition estimated in other lakes.	[91]
Fisheries catches	Data reported from encircled towed fishery, benthic gillnets and longlines fisheries were derived from monthly, seasonal sampling and interviews of local fishermen, respectively, during the model's reference period (2019).	
Albanian barbel (<i>Luciobarbus albanicus</i>)		
Biomass	Biomass was estimated from monthly samplings of commercial encircled towed net fishery (data of fishing production and fishing effort) in the lake (2019).	
Production/Biomass	$Z = F + M$	[100]
Consumption/Biomass	Consumption/Biomass.	[84]
Diet	Diet compositions estimated from seasonal samplings conducted in 2019 and previous studies in the lake.	[101]
Fisheries catches	Data reported from encircled towed fishery, benthic gillnets and longlines fisheries were derived from monthly, seasonal sampling and interviews of local fishermen, respectively, during the model's reference period (2019).	
Acheloos roach (<i>Leucos panosi</i>)		
Biomass	Biomass was estimated from monthly samplings of commercial encircled towed net fishery (data of fishing production and fishing effort) in the lake (2019).	
Production/Biomass	$Z = F + M$	[102]
Consumption/Biomass	Consumption/Biomass.	[84]
Diet	Diet composition estimated by seasonal samplings in the lake (2019).	
Fisheries catches	Data reported from encircled towed fishery, benthic gillnets and longlines fisheries were derived from monthly, seasonal sampling and interviews of local fishermen, respectively, during the model's reference period (2019).	
Trichonis rudd (<i>Scardinius acarnanicus</i>)		
Biomass	Biomass was estimated from monthly samplings of commercial encircled towed net fishery (data of fishing production and fishing effort) in the lake (2019).	
Production/Biomass	$Z = F + M$	[103]
Consumption/Biomass	Consumption/Biomass.	[84]
Diet	Diet compositions estimated from seasonal samplings conducted in 2019 and previous studies in the lake.	[104]
Fisheries catches	Data reported from encircled towed fishery, benthic gillnets and longlines fisheries were derived from monthly, seasonal sampling and interviews of local fishermen, respectively, during the model's reference period (2019).	

Table A3. Cont.

Functional Groups	Description	Reference
Gobies (<i>Economidichthys pygmaeus</i>, <i>Economidichthys trichonis</i>, <i>Knipowitschia caucasica</i>)		
Biomass	Biomass was estimated from seasonal samplings in the lake (2019) with benthic and pelagic Nordic-type gillnets.	
Production/Biomass	$Z = F + M$	[105–107]
Consumption/Biomass	Consumption/Biomass.	[84]
Diet	Diet consumption estimated from other lake ecosystems.	[16,105]
Fisheries catches	Data reported from encircled towed fishery, benthic gillnets and longlines fisheries were derived from monthly, seasonal sampling and interviews of local fishermen, respectively, during the model's reference period (2019).	
Mugilidae (<i>Mugil cephalus</i>, <i>Chelon ramada</i>)		
Biomass	Biomass was estimated from monthly samplings of commercial encircled towed net fishery (data of fishing production and fishing effort) in the lake (2019).	
Production/Biomass	$Z = F + M$	[108,109]
Consumption/Biomass	Consumption/Biomass.	[84]
Diet	Diet compositions estimated in other lake' ecosystems.	[110]
Fisheries catches	Data reported from encircled towed fishery, benthic gillnets and longlines fisheries were derived from monthly, seasonal sampling and interviews of local fishermen, respectively, during the model's reference period (2019).	
Introduced fish species (<i>Pseudorasbora parva</i>, <i>Gambusia holbrooki</i>)		
Biomass	Biomass was estimated from seasonal samplings in the lake (2019) with benthic and pelagic Nordic type gillnets.	
Production/Biomass	Empirical equations. Corrections were made according to Opitz ([73]) considering the temperature differences between the area where the data came from and the study area.	[111,112]
Consumption/Biomass	Consumption/Biomass.	[84]
Diet	Diet compositions estimated in other lake' ecosystems.	[113,114]
Fisheries catches	Data reported from encircled towed fishery, benthic gillnets and longlines fisheries were derived from monthly, seasonal sampling and interviews of local fishermen, respectively, during the model's reference period (2019).	
Benthic invertebrates		
Biomass	Estimated by the model.	
Production/Biomass	A mean value was estimated from other models developed in temperate and oligotrophic lake ecosystems where oligochaetes was the dominant group.	[64]
Consumption/Biomass	A mean value was estimated from other models developed in temperate and oligotrophic lake ecosystems where oligochaetes was the dominant group.	[64]
Diet	Diet estimations were based on relevant estimates used in models developed for similar ecosystems.	[115–118]
Zooplankton		
Biomass	Biomass was estimated by seasonal samplings in the lake during the model's reference period (2019).	
Production/Biomass	The empirical equation $\text{Log}(P/B) = -0.73 - 0.23 \times \log(w)$ was used; $CF = 1.12$, where w is the average dry weight of the dominant zooplankton groups and CF is a correction factor for calibrating the logarithmic values. The average dry weight was estimated at 2132 μg /specimen and based on the sampling the dominant group in winter was the bivalve and in all seasons the copepods at 56% (Cladocera 38%) and Rotifers (7%).	[63,115,116]

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