1 **Title:** The Effect of Anthropogenic and Environmental Factors in Coupled
2 Human-Natural Systems: Evidence from Lake Zürich

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4 **Running Head:** Factors Affecting Coupled Human-Natural Systems
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6 by

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The Effect of Anthropogenic and Environmental Factors in Coupled Human-Natural Systems: Evidence from Lake Zürich

Abstract: Exploiting a rich dataset including both individual fishing activities and ecology, we study how eutrophication and climate warming influence plankton biodiversity in Lake Zürich and the consequent effects on fishers' behavior and fishery yield. Our analysis indicates that changes in the fishery of Lake Zürich were driven by complex dynamic interactions between fishing efforts, environmental conditions and lake ecosystem ecology. Results show that nutrient levels and climate warming have both direct and indirect dynamic and non-linear effects on both fishers' behavior and lake productivity. Ecological factors such as plankton abundance and diversity affect the dynamics of fish population, which, in turn, influences fishing effort. The analysis highlights the importance and the interdependence of ecological-human linkages in aquatic ecosystems.

Keywords: lake, management, plankton, biodiversity, fish catch, nutrient pollution, temperature.

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Recommendations for Resource Managers

- This model estimates and simulates the effects of temperature and nutrients on the ecology and the management of a commercial lake fishery.
- Natural and anthropogenic factors have both direct and indirect effects on fishing intensity and the dynamics of lake productivity.
- In the long term, increasing phosphorus has negative impacts on the plankton of the lake; higher nitrogen has positive impact on zoo-abundance, but a negative impact on zoo-richness; higher temperatures have positive effects on phytoplankton.
- Considerable heterogeneity exists in both in lake ecology at different habitats (top versus bottom of the lake) and behavioral response (pelagic nets versus demersal nets) to environmental fluctuations.

1. Introduction

The overlapping of social and natural environment creates complex interactions between human and natural systems in multi-trophic fish communities (Vogt et al., 2006). In complex ecological systems, a system approach to fisheries is important to gain insights into the interactions between ecology and management (Garcia and Cochrane, 2005; Doyen et al., 2017). Significant progress has been made evaluating the nature of such interactions (e.g., Liu et al., 2007). Yet, much remains to be done understanding the integration of ecological and social systems and the underlying mechanisms connecting human behavior and the natural environment in the assessment of the dynamics and management of aquatic ecosystems. Indeed, previous literature has highlighted the need to identify better the linkages and feedbacks between human activities and the ecology of freshwater ecosystems (e.g., Beard et al., 2011). This issue becomes even more important when

the presence of anthropogenic and environmental factors play an important role in determining how such systems respond to human-induced or environmental changes (Turner et al., 2003) as freshwater ecosystems are affected by pollution and climate change (Arlinghaus et al. 2002). Of special interest are the direct and indirect effects on lake ecology and fishers' behavior and their dynamic interactions on ecosystem functioning. This paper aims to address these issues in the context of a lake ecosystem and the management and productivity of the local fishery with an application to Lake Zürich in Switzerland.

Our paper investigates how anthropogenic and natural factors (nutrient pollution and temperature) influence different trophic levels of a lake ecosystem and the consequent effects on fishers' behavior and fishery production. Our empirical analysis analyzes the dynamics of different trophic levels in a freshwater body, a lake, coupling plankton ecology and its biodiversity, measured by plankton evenness and richness, and human exploitation of fish. We develop and estimate a dynamic model of the lake ecosystem and its interactions with fishing effort and fish catch. In a multi-trophic ecosystem, our integrated model evaluates the feedback effects induced by anthropogenic and natural factors on fishing efforts on lake ecology and plankton productivity (e.g., as fish feed on zooplankton which in turns prey on phytoplankton). We also investigate the economic and ecological effects of biotic (e.g., competition, predation) and abiotic (e.g., eutrophication and climate) changes on the biodiversity and ecosystem functioning of a lake and their linkages with fish catch.

Our analysis is applied to Lake Zürich in Switzerland. The availability of good ecological and economic data makes the analysis of Lake Zürich a great case study of lake ecology (Pomati et al., 2012, 2015). This paper contributes to the literature on the economics and management of fisheries. It presents a refined analysis of lake ecosystem dynamics, providing new insights on the role of spatial heterogeneity (Smith and Wilen, 2003; Smith et al., 2008) as well as dynamic interactions between management and natural systems (e.g., Turner et al., 2003; Liu et al., 2007; An, 2012). We document the presence of much heterogeneity in the fishery of Lake Zürich, heterogeneity being driven by complex interactions between fishing efforts, environmental conditions and lake ecosystem ecology. Temperate lakes in Switzerland have been subject to environmental forcing (climate warming and eutrophication / re-oligotrophication) and changes in plankton biodiversity

(Monchamp et al., 2018, 2019). Our analysis of Lake Zürich is relevant and has broad implications for all peri-alpine and temperate lakes in Europe and worldwide (Spears et al., 2017). We show how fishing efforts vary in response to both environmental and ecological changes. In particular, we document how adjustments in fishing efforts vary significantly between pelagic nets and demersal nets. Our research stresses the presence of heterogeneity both in lake ecology at different habitats (top versus bottom of the lake) and behavioral response (pelagic nets versus demersal nets) to environmental fluctuations. Further, we examine the effects of long-term changes in temperature, phosphorus and nitrogen on the dynamics of lake ecology, which in turn affect the production of ecosystem services. We evaluate how fishing effort and environmental conditions interact with lake ecology to affect the productivity of lake fishery.

In summary, our investigation is a timely and topic and Lake Zürich is an excellent case study of how the interplay between human-induced environmental changes and human behavior affect ecosystem services. Our analysis documents the role of feedbacks and their role in the dynamic adjustments of an ecological system in response to changes in environment conditions and management.

2. Conceptual Model

Consider an ecological system involving multiple species. The state of the ecosystem is represented by the vector $y_t = (y_{1t}, y_{2t}, \dots, y_{Kt})$ where y_{kt} is the k -th state (biotic) variable at time t , $k = 1, \dots, K$. The state variables can measure the biomass of a particular species; and it can reflect a global characterization of the ecosystem (e.g., its biodiversity). The ecosystem changes over time. Its dynamics is represented by the state equation

$$y_t = f(y_{t-1}, z_t), \quad (1)$$

where z_t is a vector of environmental factors affecting the ecosystem at time t and y_{t-1} denotes the vector of state variables observed in the previous period. Equation (1) is a first-order difference equation representing the evolution of the ecological system. It allows for an arbitrary number of species as well as general dynamic interactions across species. For example, consider the case where y_{it} is the biomass associated with the i -th

species. Under differentiability of $f = (f_1, \dots, f_K)$ in (1), having $\frac{\partial f_i}{\partial y_{j,t-1}} < 0$ and $\frac{\partial f_j}{\partial y_{i,t-1}} < 0$ means that species i and j compete with each other, each species having a negative dynamic effect on the other. Alternatively, having $\frac{\partial f_i}{\partial y_{j,t-1}} < 0$ and $\frac{\partial f_j}{\partial y_{i,t-1}} > 0$ correspond to a predator-prey relationship where species j (the predator) has a negative effect on species i (the prey) while the prey $y_{i,t-1}$ supports the predator y_{jt} . Finally, situations where $\frac{\partial f_i}{\partial y_{j,t-1}} > 0$ and $\frac{\partial f_j}{\partial y_{i,t-1}} > 0$ correspond to mutualism where each species helps the survival of the other.

We consider the case where equation (1) takes the form

$$y_t = g(y_{t-1}, z_t) - h_t \quad (2)$$

where $h_t = (h_{1t}, \dots, h_{Kt}) \in H$ denotes harvest, H being the feasible set for h_t with $0 \in H$.⁶ Having $h_t = 0$ in (2) reduces to the special case of a natural ecosystem. More generally, when y_{kt} is the biomass of the k -th species, then h_{kt} denotes the harvest rate (or catch) for the k -th species at time t . In this case, having $h_t \neq 0$ in (2) represents an ecosystem under active management. We are interested in studying lake management and its implications for the productivity and ecology of the lake.

The production function for catch is defined as

$$h_t = h(e_t, y_{t-1}, z_t), \quad (3)$$

where e_t denotes fishing effort at time t . Note that fishing effort is typically measured by number of boats, the amount of gear deployed (e.g., number of nets or traps), or the frequency of fishing activities (e.g., fishing days) (Stewart et al., 2010). The production function in (3) allows harvest h_t to be affected by effort e_t , ecological states y_{t-1} and environmental factors z_t .

The two key management decisions are fishing effort (denoted by the vector e) and harvest h . Let the feasible set for e be F and the feasible set for h be H , with $e \in F$ and $h \in H$. When present, regulations impose restrictions on lake management and influence the feasible sets F and H . For example, reducing the length of

⁶ Equation (1) assumes that the state vector y_t is measured at the end of period t . In this context, h_t (the catch at time t) affects the states at time t .

the fishing season would reduce effort and make F smaller. Or implementing fishing quotas would limit harvest and restrict the feasible set H .

The analysis of management decisions involves decision rules for both effort and harvest. Such decision rules can only depend on the information available to decision makers. Typically, decision makers have imperfect information about lake ecology. The imperfect information can involve both the state variables y_t and the environmental variables z_t in equation (1). Let $y_t = (y_{at}, y_{bt})$ and $z_t = (z_{at}, z_{bt})$, where $(y_{a,t-1}, z_{at})$ are observed at time t while $(y_{b,t-1}, z_{bt})$ are not. Not being observed at time t , the variables $(y_{b,t-1}, z_{bt})$ are treated as random variables with a given (subjective) distribution conditional on the information available to the decision maker at that time. For example, a common situation is for fish stock not to be observed directly, in which case fish stock would be an unobserved variable in y_{bt} .

Lake management depends on the objective of the managers/policy-makers. Denoting the unit prices of effort e_t by q_t , then the total cost of fishing effort at time t is $q_t e_t$. Consider the case of a manager/policy-maker who wants to maximize discounted expected future net benefits, where the present value of future net benefit is $\sum_{t \geq 0} \beta^t [B_t - q_t e_t]$, where $\beta \in (0,1)$ is a discount factor, B_t denotes the benefit obtained from the ecological system at time t and $q_t e_t$ is the associated management cost. Assume that the benefit function at time t is $B_t = B_t(h_t)$. Using equations (2) and (3), the management of the lake ecosystem can be represented by the solution of the stochastic dynamic programming problem given by Bellman equation

$$V_t(y_{t-1}, \cdot) = \text{Max}_{h_t \in H, e_t \in F} \{B_t(h_t) - q_t e_t + \beta E_t[V_{t+1}(g(y_{t-1}, z_t) - h_t, \cdot)]\};$$

$$h_t = h(e_t, y_{t-1}, z_t), \quad (4)$$

where $V_t(y_{t-1}, \cdot)$ is the value function and E_t is the expectation operator over the random variables $(y_{b,t-1}, z_{bt})$ based on the information available at time t . Equation (4) is a dynamic programming formulation under imperfect state information, where the states $y_{b,t-1}$ are not observed and are treated as random variables with a given subjective probability distribution (Bertsekas, 1976, pp. 111-158). The solution to equation (4)

gives the harvest decision rule $h_t^*(y_{a,t-1}, \cdot)$ and the effort decision rule $e_t^*(y_{a,t-1}, \cdot)$.⁷ Note that these decision rules can change over time. As such, they can capture the effects of seasonality or of changes in ecological and climate conditions.

The above discussion has important implications. If $B_t(h_t)$ measures the social benefit of the ecosystem, then the optimization in (4) corresponds to an efficient allocation of resources. As such, (4) provides useful guidance to assess the efficiency of ecosystem management. But there are situations where the ecosystem may not be efficiently managed. This can arise under two scenarios. First, in the presence of externalities, private benefit can differ from social benefit. In the case where $B_t(h_t)$ measures the private benefit of the ecosystem (as opposed to its social benefit), then equation (4) would be privately optimal but socially inefficient. Second, there are scenarios where poorly assigned property rights would affect the evaluation of the opportunity cost of future benefit. In such case, the decision rules $h_t^*(y_{a,t-1}, \cdot)$ and $e_t^*(y_{a,t-1}, \cdot)$ in (4) would lead to inefficient outcomes. In either case, this can motivate a search for policy interventions and/or management schemes leading to more efficient allocations. Policy interventions could take the form of pricing policy that affect current decision rules so as to internalize current and future social benefits. Or they could involve active management of the ecosystem to move it in the direction of efficient outcomes. For example, this could take the form of regulatory constraints that restrict the feasible sets F and H in (3) and (4) (e.g., the case of harvest ban or harvest quotas). Such regulatory constraints could induce private management to be consistent with efficiency. But they could also reduce the prospects for management adjustments to economic changes.

Let $b_t = \partial B_t / \partial h_t$ denote the marginal benefit at time t . This includes as special case the situation where h_t are market goods and b_t are the market prices of h_t . Then, the solution to equation (4) gives the harvest decision rule

$$h_t = h_t^*(b_t, q_t, y_{a,t-1}, z_{at}) \quad (5a)$$

and the effort decision rule

⁷ Note that the decision rule $h_t^*(y_{a,t-1}, \cdot)$ and $e_t^*(y_{a,t-1}, \cdot)$ associated with (4) holds under a finite horizon (Bertsekas, 1976). It can also apply under an infinite planning horizon.

$$e_t = e_t^*(b_t, q_t, y_{a,t-1}, z_{at}). \quad (5b)$$

In addition, letting $g = (g_a, g_b)$, we have $g_a(y_{t-1}, z_t) = E_t[g_a(y_{t-1}, z_t)] + \epsilon_t$ where ϵ_t is a random variable with mean 0. Then, given $h = (h_a, h_b)$ and using equation (2), the states y_{at} at time t can be written as

$$y_{at} = y_{at}^*(b_t, q_t, y_{a,t-1}, z_{at}) \equiv E_t[g_a(y_{t-1}, z_t)] - h_{at}^*(b_t, q_t, y_{a,t-1}, z_{at}) + \epsilon_t. \quad (5c)$$

Equations (5a), (5b) and (5c) identify the factors affecting the ecological system and its management. These factors include benefit b_t , cost q_t , the ecological state $y_{a,t-1}$ and the environmental variables z_{at} . These equations provide the basis for the empirical dynamic analysis presented below.

3. Empirical Application to Lake Zürich

The conceptual analysis presented in the previous section is now applied to the ecology of Lake Zürich in Switzerland. Lake Zürich is a deep sub-Alpine lake subject to thermal stratification in summer and turnover in winter, which however has been decreasing over the past decades due to climate warming. It has a surface of 90 km^2 , an altitude of 405 m and a maximal depth of 143 m . In the twentieth century, sewage led to over-fertilization of the lake, contributing to algal blooms that adversely affected the fish stock and compromised the use of the lake water. Over the last few decades, Lake Zürich has been under active management by local and Swiss authorities. This includes conventional wastewater treatment since 1955 and a phosphorus removal program since 1965, leading to decreases in lake P load (re-oligotrophication).

As described below, recent studies on Lake Zürich have revealed important and peculiar ecological changes in the lake plankton communities over the past three decades, principally induced by climate warming and re-oligotrophication. An increase in thermal stability of the water column, reduced deep mixing (Livingstone 2003; Posch et al. 2012) and reduction in phosphorus inputs combined with warming-mediated enhancement of resource heterogeneity has co-occurred with a change in phytoplankton community diversity (Pomati et al. 2012) and compositional turnover (Anneville et al. 2004; Matthews and Pomati 2012; Pomati et al. 2015). Overall, the phytoplankton data suggested potential changes in the ecological mechanisms driving the

dynamics of plankton communities (Pomati et al. 2015; Pomati et al. 2017). This makes Lake Zürich a great case study of a lake changing due to human activities with potential dynamics affecting ecosystem services.

Lake Zürich hosts commercial fishery, whose activities are also regulated by Swiss cantonal authorities. In order to limit fishing intensity, the number of commercial fishing permits is closed, implying that the number of full-time fishermen has varied little over the last few decades. Regulations also limit the number and size of fishing nets. Two types of nets are commonly used. Pelagic nets, mostly used in summer that are easier to operate and are used to target mainly whitefish (*Coregonus sp.*). Demersal nets that are used in deeper water, mostly in winter, to target also whitefish. Demersal nets are also used in summer to fish for perch (*Perca fluviatilis*) in the littoral areas.⁸ As noted above, fishing efforts can be affected by regulations (e.g., regulations can make efforts less sensitive to market conditions).

3.1. Data

Our analysis examines the determinants of lake ecology, with an application to Lake Zürich in Switzerland. The investigation studies the factors affecting three sets of variables: the dynamics of lake ecology as represented by the state variables y_t , the amounts of effort e_t and the harvest represented by fish catch h_t . The explanatory variables include output price b_t , cost q_t , environmental variables z_t , and lagged values reflecting dynamics.

We exploit two sets of data. From the department of Hunting and Fishing of Canton Zürich we have monthly data on the catch and effort for each of the twelve commercial fishers operating on Zürich Lake in the period 2003-2012. For catch we have the biomass for 28 species; however, the largest part of the catch is composed by white fish (*Coregonus sp.*) with an annual average share of 55 percent of the total catch, with roach (*Rutilus rutilus*) 23 percent, perch (*Perca fluviatilis*) 15 percent, and pike (*Esox lucius*) 4 percent as other relevant commercial species. The number of nets used by the fishing firms measures effort. Fishers use three types of nets: one demersal net that is 2.5 m high, with an annual average share of 76 percent of the total

⁸ In general, Pelagic nets have the following dimensions: length: 90 m, height: 10 m, with mesh size between 40 to 50 mm from September through November. Demersal nets have the following dimensions: length: 90 m, height: 2.5 m, with mesh size between 26 and 35mm.

number of nets used, one type of pelagic nets, 23 percent, and very few demersal nets that are 5m high are also used (less than 1 percent), which does not give us enough power to estimate the productivity related to this net type. We drop observations for firms using nets of the latter type. Also, two fishers are excluded because of the poor quality of the data they reported over the years.

In addition, we have monthly data on the chemistry, physics, and plankton for the lake for the period 1977-2012, collected in the center of the lake (in front of Thalwil) as part of the monitoring program by the Zürich Water Supply Company (WVZ). Details about these data and data collection can be found in Pomati et al. (2012, 2015).⁹ For this study, we used average values of chemistry, physics, and plankton biodiversity / abundance over the water column. As in previous studies (Pomati et al., 2012) we used water temperature (°C), PO₄ (µg L⁻¹), NO₃ (µg L⁻¹), phytoplankton biomass (µg L⁻¹), evenness (relative biomasses of species – Pielou's index), and richness (num. of species), zooplankton abundance (counts m²) and richness (num. of species) for statistical analysis and modelling. Water temperature, PO₄ and NO₃ are included in the environmental variables z_{at} as they are expected to affect the dynamics of lake ecology.

Finally we have monthly price data for fuel of the type used by fishers, i.e., unleaded gas 95 octane, reported at the average price for the Zürich area.¹⁰ For output price we have a price index for fresh fish also observed at the cantonal level. Summary statistics are presented in Table 1. Variables exhibit considerable variation, which allows us to identify the Lake fishery and ecological relationships. In particular, focusing on the forcing variables, we notice that water temperature and PO₄ show a much larger variation than NO₃. Finally, notice that using temperature also allows us to control for environmental seasonality.

⁹ Sampling of physical and biological variables occurred at 14 depths, from bottom to top. Zooplankton counts were obtained by plankton net-collection in the same location and at same date of the other parameters. Phytoplankton was sampled with Nokin bottle, fixed in lugol, and identified and counted under an inverted microscope after sedimentation in chambers.

¹⁰ Data from the office of statistics of Zürich, www.stadt-zuerich.ch/zik.

3.2. Lake Fishery

As noted above, we consider the case where $y_t = (y_{at}, y_{bt})$ where y_{at} are the state variables that are observed while y_{bt} are states that are unobserved. In our case, we have observations on four state variables $y_{at} = (y_{1t}, y_{2t}, y_{3t}, y_{4t})$: phytoplankton biomass (y_{1t}), phytoplankton richness (y_{2t}), zooplankton abundance (y_{3t}), and zooplankton richness (y_{4t}). These variables provide important information on the ecological state of the lake at time t . However, we also have one unobserved state variable y_b , the fish stock biomass. In other words, we do not have data on fish biomass and thus our observation of the state of the lake is incomplete. Nevertheless, our analysis presented in section 2 allows for incomplete state information and provides the basis for our empirical analysis.

Using equation (5c), the dynamics for y_{at} is represented by the specification

$$y_{at} = f_{at}(b_t, q_t, y_{a,t-1}, z_{at}). \quad (6)$$

Equations in (6) capture lake dynamics of the observable states y_a under general conditions.¹¹ We also investigate the determinants of effort e_t . From equation (5b), the effort decision rule is

$$e_t = f_{et}(b_t, q_t, y_{a,t-1}, z_{at}) \quad (7)$$

where $(b_t, q_t, y_{a,t-1}, z_{at})$ are factors affecting effort. In our analysis, we have two effort equations, $e_t = (e_{1t}, e_{2t})$, where e_{1t} is demersal nets, and e_{2t} is pelagic nets, reflecting that efforts vary with lake depth.

Finally, we investigate the determinants of fish catch h_t . We specify the fish catch equation as follows

$$h_t = f_{ht}(e_t, y_{a,t-1}, z_{at}). \quad (8)$$

Equation (8) includes the factors $(e_t, y_{a,t-1}, z_{at})$ as determinants of catch. Note that this includes the effects of effort e_t . With effort being determined in equation (7), equation (8) relates to the harvest decision rule h_t^* in (5a) as follows: $h_t^*(b_t, q_t, y_{a,t-1}, z_{at}) = f_{ht}(f_{et}(b_t, q_t, y_{a,t-1}, z_{at}), y_{a,t-1}, z_{at})$. This shows that the factors (b_t, q_t) can affect fish catch but only through the effort equation (7). In addition, $(y_{a,t-1}, z_{at})$ can have two effects on catch: direct effects captured in equation (8), and indirect effects through adjustments in e_t as

¹¹ Note that we explored introducing additional lags $(y_{a,t-2}, y_{a,t-3}, \dots)$ in equation (6). In our application, we found that using $y_{a,t-1}$ in (6) provided a good empirical representation of ecological dynamics.

captured by equation (7). The nature and magnitude of these direct and indirect effects are evaluated below. Potential concerns regarding the endogeneity of effort decisions and potentially omitted variables are addressed in the following section.

4. Empirical Analysis

Equations (6)-(8) provide the basis for our empirical analysis. Note that we do not have strong a priori information on the effects of environmental/ecological factors on lake ecology and its management. Phytoplankton Richness and Evenness, and Zooplankton Richness are used as proxies for plankton biodiversity. Plankton biodiversity is supposed to influence fish stock biomass through trophic cascade effects, with influences on energy and biomass fluxes in the food-web and eventually on fish growth and demography (Carpenter et al., 1985; Cadier et al., 2019; Barbier et al., 2019). Specifically, plankton biodiversity is expected to influence fish stock biomass, as an ecosystem service, via three mechanisms (Drake, 2003). These are: 1/ higher probability to include species of greatest productivity or palatability for fish larvae in a community that is more rich in species (sampling effect); 2/ more diverse communities should be able to use resources more completely, assuming that species differ in resource requirements, therefore increasing energy transfer through the food-web (niche complementarity effect); 3/ certain species help or allow other species to grow by modifying the environment in a favorable way (physical/chemical aids), which again might increase edible or high nutrition food for fish and/or increase energy transfer in the food-web (facilitation effect). .

Although there is evidence that biodiversity enhances ecosystem productivity (e.g., Hooper and Vitousek, 1997; Tilman et al., 1997; Norberg, 2004; Hillebrand and Matthiessen, 2009; Cardinale et al., 2012; Brooks et al., 2016), the magnitude and direction of such effect on stock biomass are not clear. By affecting the fish stock, plankton diversity influences indirectly fishers behavior in equation (7), and catch in equation (8). Phytoplankton Biomass and Zooplankton Abundance can affect fish stock because they proxy water quality

(algal blooms), the former, and food availability, the latter.¹² Both factors can influence directly the dynamics of fish population and thus, indirectly, fishing effort and catch. Our approach allows us to estimate the net effect of biodiversity on the lake fishery, where plankton diversity and biomass (or abundance) determine, through ecological interactions and the final perceived ecosystem state, the effort decision and fish catch. Finally, because fish stock in the next period is determined by how much fish biomass is extracted, we include in our analysis the total fish catch (of all species) aggregated over all fish firms operating on the lake at each time point.

Given that effort decisions are endogenous (as reflected in equation (7)), ordinary least squares (OLS) estimation of the catch equation (8) is subject to possible endogeneity bias. We address this issue by estimating the model using an instrumental variable approach, which involves estimating the catch equation (structural equation) and two equations for the fishing effort using a two-stage least square (2SLS) estimator.¹³ This requires instruments that can generate consistent estimates of the parameters. The required conditions are: 1/ all parameters must be identified; 2/ the instrument must be orthogonal to the error terms; and 3/ the instruments must not be weak. As explored below, we consider the following candidates for instruments: fuel price and fish price index. Market prices are exogenous variables that determine effort decisions, equation (7). Thus, market prices and fuel price are excluded from the structural equation and enter only as instruments in the effort equations. The empirical specification also includes individual fixed effects to control for the unobserved ability of the fishers or other potentially omitted variables varying systematically across fishers. Finally, in the analysis presented below, all variables are measured in natural logs.¹⁴

¹² We also considered using zooplankton biomass instead of zooplankton abundance. The estimation, discussed later in the paper, gave qualitatively similar results to those obtained using abundance, but the zooplankton biomass data contained several missing values and outliers. Given the poor quality of the zooplankton biomass data, we decided to use zooplankton abundance.

¹³ Ordinary least squares (OLS) and two-stage least square (2SLS) are standard methods used in empirical analysis. Readers can refer to Kennedy (2003) or Wooldridge (2015) for discussion of these methods. The 2SLS method involves estimating a linear regression of the fishing effort on the instrumental variables, defined in section 4.1, and covariates, and saving the predicted fishing effort values. In the second stage, the outcome, harvest, is regressed on the predicted outcome variable from the first stage, fishing effort, and covariates. Notice that using 2SLS we estimate effort decisions and thus our analysis does not suffer from econometric problems of endogeneity and inconsistent coefficients for fishing effort that are found in previous literature (see Gordon 2015 for an overview).

¹⁴ This means that each parameter can be interpreted as an elasticity, i.e. as the percentage effect of a 1 percent change in the corresponding explanatory variable.

4.1. Estimating the Factors Affecting Fishery Management

The catch equation (8) is estimated using the following specification

$$h_{it} = \alpha_1 e_{it}^{Demersal} + \alpha_2 e_{it}^{Pelagic} + \mathbf{y}_{t-1} \mathbf{d} + \delta z_t + \mu_i + \epsilon_{it}, \quad (9)$$

where h_i denotes total harvest (catch) for the i -th firm, $\mathbf{y}$ is a vector of phyto/zooplankton biomass (abundance), evenness and richness, $\mathbf{d}$ is a vector of parameters to be estimated, while z denotes water temperature and μ_i denotes the intercept specific to the i -th fish firm.¹⁵ The empirical specification for the fishing effort equations is

$$e_{it}^{Demersal} = \beta_1 b_t + \beta_2 w_t + \beta_3 z_t + \beta_4 e_{it-1}^{Demersal} + \beta_5 e_{it-1}^{Pelagic} + \beta_6 h_{t-1} + \mathbf{y}_{t-1} \mathbf{g} + \sigma_i + \eta_{it}, \quad (10)$$

$$e_{it}^{Pelagic} = \gamma_1 b_t + \gamma_2 w_t + \gamma_3 z_t + \gamma_4 e_{it-1}^{Demersal} + \gamma_5 e_{it-1}^{Pelagic} + \gamma_6 h_{t-1} + \mathbf{y}_{t-1} \mathbf{k} + \theta_i + v_{it}, \quad (11)$$

where b_t and w_t denote price of fresh fish and fuel at time t , respectively, h_t is total harvest aggregated for all firms operating in the lake, $h_t = \sum_i h_{it}$; σ_i and θ_i are firm-specific intercepts for the i -th fish firm. Although no data exists on fish stock biomass or abundance for Lake Zürich, there is anecdotal evidence that while fish stock was abundant for most years of our sample period, it was low in the period around the year 2005 (personal communication of the Department of Fishing and Hunting, Canton Zürich, Switzerland). Indeed, the data show that total catch was lower around 2005 than for the rest of the sample period even though effort was still relatively high (figure 1). It is possible that the (unobserved) stock had different effects on catch and fishing effort in the period of low stock than in the period when stock was high. For instance, stock may not be a limiting factor in the period when it is high, but it is in the period when stock is low. In those instances, density-dependent factors may also play a role. To account for these potential effects we augment the specification for (9)-(10) with a series of interaction terms of phytoplankton biomass and richness, and zooplankton abundance and richness, and aggregate total harvest with a dummy variable that takes value equal to one in the period 2004-2006, and zero otherwise: $\mathbf{y}_{t-1} \cdot Low$, where $Low = 1$ in 2004-2006 and $Low = 0$ otherwise. This allows for stock effects to be different in periods of low vs. high fish abundance.

¹⁵ Although we have access to catch by species, because nets cannot effectively select individual species, we decided to model total catch and a function of fishing effort and natural/ecological factors.

Results

Equations (9)-(11) are estimated using a two-stage least square (2SLS) estimator. Results are presented in Table 2 where 2SLS estimates can be compared to OLS estimates obtained only for the equation for Total Catch. For the 2SLS model, estimates for the first stage are also presented. The second column shows 2SLS estimates where environmental/ecological variables enter in the catch equation, but do not include variables on plankton diversity.¹⁶ However, the first stage results show that these variables are correlated with the choice of fishing nets, especially pelagic nets. This might be explained by the diversity of plankton forms, relative to their abundance, not being a direct factor affecting growth and behavior of fish, while it may signal turnover in seasonal species that impact on Lake Zürich water quality (Anneville et al. 2004). This specification implies that biodiversity might affect directly stock biomass and only indirectly the catch of the fishing firms. Furthermore, plankton and demersal species are linked via direct and indirect mechanisms. Fish larvae feed on zooplankton, which migrates vertically in the water column to avoid predation during the day. Plankton therefore affect the pelagic food-web, whose functioning and efficiency determines how much energy and biomass reaches high levels of the trophic chain (Carpenter et al., 1985; Cadier et al., 2019; Barbier and Loreau, 2019). Phytoplankton affects both zooplankton standing biomass due to trophic interactions, and the quality of fish habitat: non-edible phytoplankton biomass is degraded by heterotrophic bacteria causing anoxia in the hypolimnion, which has strong impacts on fish ecology (Vonlanthen et al., 2012). The F -statistics of the first stage equations indicate that the instruments are relevant, while the Hansen- J -statistic indicates the validity of the exclusion restrictions for the instruments. Notice that output price measured by the cantonal fish price index is not statistically significant. This probably reflects the fact that fishers respond to local and regulatory conditions more than fish market conditions as mentioned above. Overall, results show that, as expected, effort has positive and statistically significant effects on total catch. The analysis reveals that marginal productivity, i.e., how total catch changes when an input changes, is higher for demersal than pelagic nets. Indeed, a one

¹⁶ Preliminary analysis indicated that variables measuring plankton diversity are not significant determinant of total catch. Thus, to avoid oversaturating the model we removed them from the list of regressors.

percent increase in the use of demersal nets is associated with an increase of catch by 0.21 percent, while the same increase in pelagic net use leads to a 0.11 percent increase in individual catch. In general, demersal and pelagic nets target different fish species.

Our preferred econometric analysis, the estimation using the 2SLS, shows strong and statistically significant effects of plankton on both catch and effort. Through interactions with the stock level, Table 2 also documents that these effects are often nonlinear. Lagged nets also have statistically significant effects on effort, showing the presence of dynamics in effort. The coefficients of phytoplankton biomass and zooplankton abundance are statistically different from zero indicating that these ecological components influence catch. Phytoplankton biomass in the previous month has a negative effect on contemporaneous catch. The effect becomes less negative in the period when stock was low.¹⁷ Large phytoplankton biomass negatively influences lake pelagic food webs. High biomass is often related to the dominance of algal species that are non-edible (and sometimes toxic) to zooplankton, preventing the flow of mass and energy through the food-web and anoxia (due to microbial degradation of phytoplankton biomass) below the lake surface water layer (thermocline) (Posch et al., 2012). Algal blooms degrade the environment in which fish thrive and reproduce, which could decrease both the fish stock available in the next period (thus depressing catch) and fish diversity (Vonlanthen et al., 2012). Also, stress and organ damage induced by cyanobacterium *Planktothrix rubescens*, abundant in Lake Zürich (Posch et al., 2012), may reduce weight and fitness as noted in whitefish (Ernst et al., 2006), which composes the majority of catch in Lake Zürich. These effects are clearly dependent on density of fish populations. Indeed, when fish stock is high the water quality effect is stronger. A significant coefficient when stock is low corroborates the existence of different effects due to density-dependence factors, but the two effects partially offset each other while still showing a negative effect of phytoplankton biomass on firm catch.

Zooplankton abundance in the previous month has a positive and strongly significant effect on contemporaneous catch. This appears reasonable because higher zooplankton abundance indicates higher food

¹⁷ Notice that to the effect of plankton on harvest in the period when the stock is obtained by adding the coefficient on the contemporaneous variable and the coefficient specific to when the stock was low. For instance, for phytoplankton biomass, the effect is given by summing -0.331 and 0.301, which gives an effect equal to -0.030.

availability for fish, which translate in higher stock biomass during that season. The overall effect turns slightly negative in the period of low stock (-0.003). However, the positive-strong effect in the high stock period may be because with higher fish density, and stronger competition for available resources, increasing food availability is highly beneficial. As expected, temperature is positively correlated with catch and fishing effort. Indeed, warmer temperature can increase fish biomass due to a positive effect on metabolism and growth rate (e.g., Brown et al., 2004; Duffy et al., 2016), but it also can increase fish activity and feeding behavior and thus catchability (e.g., Albanese et al., 2004; Stoner, 2004; Linløkken and Haugen, 2006). This result confirms findings of positive effects on catchability of water temperature in prior economic studies (e.g., Massey et al., 2006). Aggregate harvest for the Lake in the previous period affects the availability of current stock. It is expected that larger harvest would decrease stock availability and thus depress individual fish catch. This is indeed revealed by a negative and significant coefficient for lagged aggregate harvest, -0.228. When the stock is considered to be low the impact of aggregate harvest on individual catch is negligible, 0.071. In other words, when fish population is small increasing harvest for the whole lake has basically no impact on fish stock and thus the productivity of the individual fishing firm. In Lake Zurich there is a positive relationship between richness and productivity as expected by literature (Cardinale et al., 2012) and as was shown in previous papers (Pomati et al., 2012; Pomati et al., 2015). Richness co-variates also with an increase in dominance by the toxic cyanobacterium *Planktothrix rubescens* (Pomati et al., 2012; Yankova et al., 2017). These relationships are very important in the model and likely determine the outcome of the statistical correlations. This is however inevitable because it belongs to history of the system, but it resembles trends in plankton biodiversity of other peri-alpine and temperate lakes of the same region (e.g., Spears et al., 2007). This suggests that our findings might have some general applicability.

Results for the first stage reveal two interesting findings. First, it appears that ecological factors are important determinants of the decision of how many nets fishers use. Plankton biomass/abundance, evenness and richness affect the dynamics of fish population, which, in turn, influences the effort decisions, equation (7). Our empirical analysis shows that these are statistically significant factors for the choice of net use. Second, the

effect that lake ecology has on the number of nets fishers use is not uniform, but it influences different net types in different ways. This may imply that different depths of the lake have different ecological properties and dynamics that are reflected on the choice of different net types.

The heterogeneity of lake Zürich depths and its importance for the maintenance of both ecological productivity and diversity of plankton has been shown previously (Pomati et al., 2012; Posch et al., 2012; Pomati et al., 2017). With respect to the commercial fishery, the ecological variables have less effect on the number of demersal nets used than pelagic nets. Zooplankton abundance has a statistically significant effect showing that larger availability of Zooplankton of one percent decreases the number of Demersal Nets used by a half percent. Under the assumption that larger zooplankton leads to higher fish biomass, the negative sign suggests substitutability between nets and fish stock. Phytoplankton Richness and Evenness have opposite effects. The former decreases the use of demersal nets by almost 1.2 percent, while the latter has a positive effect, although it is marginally significant. Phytoplankton Biomass and Zooplankton Richness have no effect on the use of Demersal Nets. However, they do affect the choice of Pelagic Nets. Since it proxies water quality (algal blooms), larger Phytoplankton Biomass may reduce water transparency especially in the littoral zone of the lake, inducing fishermen to put more effort in positioning nets in the pelagic zone. Notice that Demersal Nets are used in the winter time, while Pelagic Nets are mostly used in the summer when also phytoplankton biomass is higher. Phytoplankton and Zooplankton Richness negatively impact the amount of Pelagic Nets used. The negative coefficient is consistent with the explanation that larger biodiversity, proxied by plankton richness, requires a smaller number of nets to be used because its positive effect on fish availability. Such effect is quite large, especially for Phytoplankton Richness given that a one percent increase allows fishers to use 4.5 percent less pelagic nets to keep catch constant. Lastly, when more fish is caught over the entire lake, which reduces fish stock, a larger effort is necessary for the individual fisher to haul the same level of harvest.

4.2. Estimating the Factors Affecting Lake Ecology

Now that we established a relationship between lake ecology and commercial fishery, we investigate how lake ecology is influenced by natural and anthropogenic factors, such as Temperature and nutrients (Phosphorous and Nitrogen). This involves estimating equations (6). The dependent variables in (6) are phytoplankton biomass, phytoplankton richness, zooplankton abundance and zooplankton richness. The explanatory variables include environmental variables such as water temperature, phosphorous and nitrogen. Equation (6) also includes lagged dependent variables capturing the dynamics of lake ecology.

Our empirical model for the ecology of the lake is based on the structure of the trophic levels depicted in Figure 2. This simple nutrient-phytoplankton-zooplankton-fish model is a standard paradigm in lake food-web ecology (Stomp et al. 2011, Sommer et al. 2012), and has been adjusted to match previously established links between plankton richness and productivity in lake Zürich (Pomati et al. 2012). The empirical specification for the dynamics of the lake ecology is represented by the system of equations

$$y_{a1,t} = \lambda_{1,0} + \lambda_{1,1} h_t + \lambda_{1,3} y_{a2,t} + \lambda_{1,4} y_{a3,t} + \lambda_{1,5} y_{a1,t-1} + \mathbf{z}_t \mathbf{r} + \xi_{1,t}, \quad (12)$$

$$y_{a2,t} = \lambda_{2,0} + \lambda_{2,1} h_t + \lambda_{2,2} y_{a2,t-1} + \mathbf{z}_t \mathbf{r} + \xi_{2,t}, \quad (13)$$

$$y_{a3,t} = \lambda_{3,0} + \lambda_{3,1} h_t + \lambda_{3,2} y_{a3,t-1} + \mathbf{z}_t \mathbf{r} + \xi_{3,t}, \quad (14)$$

$$y_{a4,t} = \lambda_{4,0} + \lambda_{4,1} h_t + \lambda_{4,2} y_{a4,t-1} + \mathbf{z}_t \mathbf{r} + \xi_{4,t}, \quad (15)$$

$$y_{a5,t} = \lambda_{5,0} + \lambda_{5,1} h_t + \lambda_{5,2} y_{a1,t} + \lambda_{5,3} y_{a2,t} + \lambda_{5,4} y_{a4,t-1} + \mathbf{z}_t \mathbf{r} + \xi_{5,t}, \quad (16)$$

where $\mathbf{y}_a = \{\text{Phyto-Biomass, Phyto-Evenness, Phyto-Richness, Zoo-Abundance, Zoo-Richness}\}$ and

$\mathbf{z}_t = \{\text{Temperature, Temperature squared, PO}_4, \text{NO}_3, \text{PO}_4 \times \text{Temperature}\}$ and $\mathbf{r} = (r_1, r_2, r_3, r_4, r_5)$ is a vector of parameters. As we are estimating a system of equations, there are potential efficiency gains from using a system estimator.

Results

We estimate equations (12)-(16) using a Generalized Method of Moments (GMM) estimator¹⁸ with standard errors consistent to arbitrary heteroscedasticity and autocorrelation (see Hayashi, 2000; Baum et al., 2007; Schaffer, 2010). The estimates of the dynamics of lake ecology are presented in Table 3. We find that phytoplankton biomass is negatively correlated to zooplankton (grazers) abundance (Table 3, column 1). This suggests the presence of a predator-prey relationship between phytoplankton and zooplankton, relationship that was not explored in previous work on Lake Zürich (Pomati et al. 2012). However, this effect does not appear in the dynamics of Zoo-abundance (column 4), i.e., the coefficient for phytoplankton biomass is not statistically different from zero. Lagged aggregate catch has a positive effect on Zoo-abundance. This seems reasonable because removing fish from the lake reduced predation on zooplankton. A negative correlation between Phytoplankton richness and biomass was also expected because the peak of biomass production is general associated with blooming of only few species (Posch et al. 2012). Phytoplankton Biomass is negatively correlated with Richness and not correlated with Evenness. Aggregate catch in the previous month does not seem to be correlated with plankton, but we find evidence of a predator-prey interaction with Zooplankton Abundance.

Using these estimates for the ecological model, we can obtain some insights on the short-run effects of changes of environmental and anthropogenic factors on plankton. Water temperature has a positive effect on Phytoplankton Biomass, 0.64.¹⁹ This is plausible because increasing temperature correlate with higher light intensity as a resource, and leads to stronger and more stable stratification of the lake water column, which concentrates phytoplankton in the lake epilimnion (Pomati et al. 2012, Posch et al. 2012). Water temperature has also a positive effect on Phytoplankton Evenness; a 1 percent increase in temperature seems to induce a 0.46 percent increase in evenness, while it is mildly positively correlated with Phytoplankton Richness, 0.17

¹⁸ The Generalized Method of Moments (GMM) estimation method is a general econometric method that deals with endogeneity issues in multiple equation systems (e.g., Stock and Watson, 2003).

¹⁹ This is calculated taking the derivative of the estimated equation of Phytoplankton Biomass with respect to temperature: $-3.391 + 0.531 * 2 * \text{Temperature} + 0.541 * \text{PO}_4$, evaluating variables at their sample mean.

percent.²⁰ However, we find virtually no statistically significance correlation between water temperature and Zooplankton Abundance or Richness.

Phosphorous has a negative and significant effect only on Phytoplankton. This effect is stronger for the biomass and it depends on water temperature. The effect is smaller for Phytoplankton Richness, 0.15 percent, while larger for Phytoplankton Richness, -0.59 percent. Generally, a negative effect of PO₄ on phytoplankton productivity is uncommon and not expected in general terms, being phosphorus the main limiting factor for algal growth in freshwaters and the driver of eutrophication processes. This result is probably driven by the peculiar history of Lake Zürich, which has undergone a temporal stable decrease in PO₄ over the past four decades without a significant decrease in algal biomass. This is primarily because the lake has become dominated by the cyanobacterium *Planktothrix rubescens*, who is able to exploit the limited available resources better than the other algae and persists through most winters without large decay of biomass (Pomati et al., 2012; Posch et al., 2012).

Plankton can also be influenced by available nitrogen (Table 3). Zooplankton abundance is positively correlated to NO₃ levels in Lake Zürich. This effect is rather strong; a 1 percent increase in the concentration of NO₃ leads to a 1.55 percent increase in Zooplankton Abundance. Instead, we find that nitrogen is negatively correlated with Phytoplankton Biomass and plankton Richness, for both Phyto- and Zooplankton. This effect is stronger for zooplankton than for phytoplankton. These results are consistent with analyses performed previously on the same dataset (Pomati et al. 2012). Finally, Table 3 shows that lagged dependent variables are all statistically significant, showing the presence of important dynamics in lake ecology. The implication of these dynamics is further explored below.

²⁰ This is calculated taking the derivative of the estimated equation of Phytoplankton Evenness and Phytoplankton Richness with respect to temperature: $-7.205 + 1.535 * 2 * \text{Temperature} + 0.448 * \text{PO}_4 = 0.46$, and : $-0.945 + 0.260 * 2 * \text{Temperature} + 0.0231 * \text{PO}_4 = 0.17$, and evaluating variables at their sample mean.

5. Implications for commercial fisheries under environmental change

Our empirical analysis describes how the production of the commercial lake fishery is influenced by plankton biodiversity and how the latter is affected by temperature and nutrient gradients, which are in turn shaped by human activities (e.g. eutrophication and climate change). Results clearly reveal that natural and anthropogenic factors have both direct and indirect effects on both lake ecology and fishers behavior. Our results confirm previous findings with regards to the environmental drivers of phytoplankton and zooplankton richness (Pomati et al., 2012) and highlight some environmental factors that are important for plankton productivity. They also provide empirical evidence that there are detectable and significant dynamics in both plankton community and fishers behavior. This implies that changes in temperature and nutrient concentrations can have contemporary effect on fishery production; but they have also longer term effects associated with lagged responses of the lake ecosystem and the fishing industry.

We use the estimated model for the commercial fishery, equations (9)-(11), and lake ecosystem, equations (12)-(16), to uncover what are the dynamics effects of changes in temperature and nutrient pollution on the ecology and the commercial fishery of Lake Zürich. To do this, we simulated time paths for the lake ecosystem variables and the commercial fishery under selected scenarios representing changes in water temperature and nutrient concentrations. Starting from the sample average for all variables, the variables were simulated until they reached a steady-state long run equilibrium. To evaluate the sensitivity of the results, a stochastic simulation was performed using the bootstrapping method proposed by Krinsky and Robb (Krinsky and Robb, 1986) with 5000 replications, based on the empirical distribution of the estimated parameters reported above. The simulated long run results are presented in Figure 3 under three sets of scenarios: 1/ changes in temperature; 2/ changes in phosphorus; and 3/ changes in nitrogen. Figure 3 shows the long run effects of environmental changes on three variables: demersal nets, pelagic nets, and total catch. Each plot in Figure 3 shows the simulated response of the specific outcome variable, number of Demersal and Pelagic Nets, and Total Catch (dark-tick line) due to changes in the forcing variables, Temperature, Phosphorous, and Nitrogen, based on the estimated models for the lake fishery (9)-(11) and ecology (12)-(16). The plots also

show the 95% confidence interval of the simulated values (thin lines). The simulated long run results for all endogenous variable (including means and standard errors) are reported in table 4. Such effects capture the full extent of potential future changes in temperature and nutrient loading in a small fishery.

We report the effects of changes in environmental conditions going from 50% decrease to a 50% increase in each variable (temperature, phosphorus and nitrogen). The 0% change corresponds to the baseline long run equilibrium obtained by keeping water temperature and nutrient concentrations at the observed sample mean. Departures from the baseline show how changes in temperature and nutrients affect the long run performance of the lake. Figure 3 shows the sensitivity of the lake fishery to changes in water temperature (left panels), phosphorous (central vertical panels), and nitrogen (right panels). The thick lines indicate the simulated long run means and the thinner lines the 95% confidence interval of the simulated steady-states.

Figure 3 reveals interesting results. First, the bottom three panels document the long run effects of environmental changes on total catch. They show that the steady-state catch is an increasing function of all three factors: temperature, phosphorus and nitrogen. However, note that the magnitude of these positive effects can differ a lot. Results in Table 4 show that the effects of temperature on catch tend to be relatively small, as they vary from -5% for a 50% decrease in Temperature to +5% for a 50% increase. In the short run, warmer temperatures also have a positive direct effect on catch and fishing effort, which translate into positive indirect effects on catch (Table 2, last three columns). In the long-run, indirect effects result from the fact that warmer temperatures have also positive effects on plankton richness (Figure 4 and Figure 5), which increase fish biomass, as noted by Duffy et al. (2016). The effects of changes in phosphorous on catch are also of relatively small magnitudes. However, Figure 3 shows that the long run effects of nitrogen on catch are much larger: they vary from -25% for a 50% decline in nitrogen to +24% for a +50% increase. Such results stress the importance of controlling for nitrogen in the management of lake fishery.

Second, the central horizontal panels in Figure 3 report the long run effects of environmental and anthropogenic influence on Pelagic Nets. Again, they show that the steady-state number of pelagic nets is an increasing function of all three factors: temperature, phosphorus and nitrogen. The magnitudes of these effects

differ across factors. While the effects of temperature and phosphorus on pelagic nets tend to be relatively small, the long run effects of nitrogen are found to be a larger magnitude. This result indicates that the large effects of nitrogen on catch reported above are due mostly to effort adjustments in pelagic nets. This suggests that the effects of environmental changes on catch are driven in large part by induced adjustments in fishing effort.

Third, the top panels in Figure 3 reports the effects on demersal nets. They show that such effects differ significantly from pelagic nets. While higher temperatures increase long run demersal nets (like pelagic nets), phosphorus and nitrogen have opposite effects: higher phosphorus and higher nitrogen tend to lower the number of demersal nets (unlike pelagic nets). And from Figure 3, the long run negative effects of nitrogen on pelagic nets are very strong. This result documents the presence of significant heterogeneity in lake ecology (top versus bottom of the lake) and behavioral response (pelagic nets versus demersal nets) to environmental shocks.

Fourth, Figure 3 shows environmental effects on catch (the bottom panels) are always in the same direction as their effects on pelagic nets (the central horizontal panels). But this property does not hold for demersal nets. This indicates that the effects on catch are dominated by pelagic nets. In addition, Figure 3 shows that the magnitude of factor effects is much larger for Pelagic than Demersal Nets; especially for nutrients concentration. For instance, for phosphorous the effects on Pelagic Nets use range between -38% to +44%; for Demersal Nets use is nonlinear and ranging between 3% to 5% increase. Nets use is especially sensitive to fluctuations in nitrogen: between plus/minus 130% for Demersal and plus/minus 35% for Pelagic Nets, respectively, with respect to the baseline.

This evidence suggests that anthropogenic conditions have different effects on top part versus bottom part of the lake. Epi versus hypo-limnion represent very different environments with different food-webs and responses to environmental/anthropogenic changes (Jeppesen et al., 1997). Our empirical analysis shows that plankton richness has significant effect on nets use, especially for Pelagic Nets, implying that larger richness requires a smaller number of nets to be used because its positive indirect effect on fisherman behavior. While Figure 3 shows that an increase in temperature, nitrogen or phosphorus has each positive long term effects on

total catch, these results hide much heterogeneity about the effects of environmental changes on lake ecology. Figure 4 reports the long term effects of temperature, nitrogen and phosphorus on the ecology of Lake Zürich. Again, each plot shows the simulated response of the specific outcome variable, Phytoplankton Richness, Evenness, and Biomass (dark-tick line) due to changes in the forcing variables, Temperature, Phosphorous, and Nitrogen, based on the estimated models for the lake fishery (9)-(11) and ecology (12)-(16). The plots also show the 95% confidence interval of the simulated values (thin lines). We find that overall increasing nitrogen or phosphorus each have negative impacts on Phytoplankton Richness and Phytoplankton Biomass. However, temperature can have the opposite effects. That is, higher temperatures tend to increase both Phytoplankton Richness and Phytoplankton Evenness, while we do not see a strong long-term effect on Phytoplankton biomass. Figure 4 also illustrates the complexity of these effects, as the impact of the increased temperature is found to be non-linear. Indeed, decreasing temperature also increases Phyto-Richness and Evenness.

Figure 5 reports the long term effects of temperature, nitrogen and phosphorus on the zooplankton in Lake Zürich. Again, each plot shows the simulated response Zooplankton Abundance and Richness, due to changes in the forcing variables, Temperature, Phosphorous, and Nitrogen, as well as the 95% confidence interval of the simulated values. Figure 5 shows that increasing temperature has positive impacts on zoo-abundance and zoo-richness. But increasing phosphorus has opposite effects: higher phosphorus decreases both zoo-abundance and zoo-richness. Indeed, higher phosphorous concentrations are correlated with lower phytoplankton richness. In the context of our study this implies that, as phosphorous concentration increases, a larger number of Pelagic Nets was used to compensate for loss of water and littoral habitat quality. This appears also from the fact richness' effect on Demersal Nets use is smaller (Table 2, last two columns). That may be why the use of those nets is not particularly sensitive to fluctuations in phosphorous. Changes in phosphorous point to the same conclusions. And Figure 5 shows that the long run impact of higher nitrogen on lake zooplankton is mixed: positive on zoo-abundance and negative on zoo-richness.

6. Concluding Remarks

This paper has presented an analysis of the interplay between ecological and management factors affecting the functioning and productivity of a lake ecosystem, with an application to Lake Zürich. Our results show the crucial role of biodiversity, nutrient concentration (particularly nitrogen) and temperature on fishery production. These effects are nonlinear and dynamic. Overall, we find that temperature, nitrogen and phosphorus each contribute to higher total catch, although with different strengths. But these effects are complex and involve the determinants of fishing efforts as well as the dynamics of lake ecology. Adjustments in fishing efforts in response to plankton diversity vary significantly between pelagic nets and demersal nets. This indicates the presence of heterogeneity both in lake ecology (top versus bottom of the lake) and behavioral response (pelagic nets versus demersal nets) to environmental changes. We find that, as far as total catch is concerned, the effects of pelagic nets dominate. Our analysis also documents the role of the lake ecology and its dynamic effects on lake productivity. It shows that, in the long term, increasing nitrogen or phosphorus has each negative impacts on the phytoplankton of the lake; but higher temperatures have positive effects on the phytoplankton. We also find that higher phosphorus has negative impacts on the zooplankton of the lake; but the impact of higher nitrogen on zooplankton is mixed: it has positive impact on zoo-abundance, but a negative impact on zoo-richness. These results reflect the complex dynamics of lake ecology: plankton biomass and abundance affect the dynamics of fish population, which, in turn, influences fishing efforts and fish catch, with environmental factors playing a role in every part of the ecosystem. Our analysis shows how fishing efforts, environmental conditions and lake ecology interact with each other as they affect the functioning of a lake ecosystem and its productivity.

This analysis highlights the importance to understand feedbacks mechanisms when examining how exogenous changes in biodiversity affect economic outcomes. As such, our analysis of Lake Zürich is a great case study documenting the presence of complex dynamic interactions between ecological and economic factors relevant in the evaluation and management of a lake ecosystem. This documents the presence of much heterogeneity about the effects of environment factors on lake ecology. This heterogeneity reflects complex

dynamic interactions between fishing efforts, environmental conditions and lake ecology Overall, our results suggest that, although marginal productivity is higher for Demersal Nets than for Pelagic Nets, the fact that the use of Pelagic Nets is extremely responsive to changes plankton richness makes it such that increasing temperature and nutrient concentrations lead to higher long run catch. This result applies despite the fact that the more productive fishing effort respond negatively to increases of nutrient concentrations. To our knowledge, there are no other studies that approach the issue of lake fisheries with the same goal and approach as our study. The conclusions of our case study are rooted in the history of the lake studied, which is similar to many other deep lakes in temperate regions, but might not be applicable universally. Therefore, more research is needed to explore the ecology and economics of lakes and other ecosystems as they respond to environmental changes.

Author Contributions

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Design of the work; acquisition, analysis, and interpretation of data; drafting and revising the work; final approval of the version to be published; agreement to be accountable for all aspects of the work in ensuring that questions related to the accuracy and integrity of any part of the work are appropriately investigated and resolved.

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References

- Albanese, B., Angermeier, P.L. and Dorai-Raj, S., 2004. Ecological correlates of fish movement in a network of Virginia streams. *Canadian Journal of Fisheries and Aquatic Sciences*, 61(6), 857-869.
- An, L., 2012. Modeling human decisions in coupled human and natural systems: review of agent-based models. *Ecological Modelling*, 229, pp.25-36.
- Anneville, O., Souissi, S., Gammeter, S. and Straile, D., 2004. Seasonal and inter-annual scales of variability in phytoplankton assemblages: comparison of phytoplankton dynamics in three peri-alpine lakes over a period of 28 years. *Freshwater Biology*, 49(1), 98-115.
- Arlinghaus R., Mehner T. & Cowx I.G., 2002. Reconciling traditional inland fisheries management and sustainability in industrialized countries, with emphasis on Europe. *Fish and Fisheries* 3, 261–316.
- Barbier, M. and Loreau, M., 2019. Pyramids and cascades: a synthesis of food chain functioning and stability. *Ecology letters*, 22(2), 405-419.
- Baum, C. F., M. E. Schaffer, and S. Stillman, 2007. ivreg2: Stata module for extended instrumental variables/2SLS, GMM and AC/HAC, LIML, and k-class regression. Boston College Department of Economics, Statistical Software Components S425401. Downloadable from <http://ideas.repec.org/c/boc/bocode/s425401.html>.
- Beard Jr, T.D., Arlinghaus, R., Cooke, S.J., McIntyre, P.B., De Silva, S., Bartley, D. and Cowx, I.G., 2011. Ecosystem approach to inland fisheries: research needs and implementation strategies. *Biology Letters* 7, 481–483
- Bertsekas, D.P. 1976. *Dynamic Programming and Stochastic Control*. Academic Press, New York.
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. and West, G.B., 2004. Toward a metabolic theory of ecology. *Ecology*, 85(7), 1771-1789.
- Brooks, E.G.E., Holland, R.A., Darwall, W.R.T. and Eigenbrod, F., 2016. Global evidence of positive impacts of freshwater biodiversity on fishery yields. *Global ecology and biogeography*, 25(5), pp.553-562.
- Cadier, M., Andersen, K.H., Visser, A.W. and Kiørboe, T., 2019. Competition–defense tradeoff increases the diversity of microbial plankton communities and dampens trophic cascades. *Oikos*.
- Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., Mace, G. M., Tilman, D., Wardle, D. a., Kinzig, A. P., Daily, G. C., Loreau, M., Grace, J. B., Larigauderie, A., Srivastava, D. S., and S. Naeem, 2012. Biodiversity Loss and Its Impact on Humanity. *Nature* 486, 59–67.
- Carpenter, S., Kitchell, J. and Hodgson, J., 1985. Cascading trophic Interactions and lake productivity. *BioScience*, 35(10), pp.634-639.
- De Laender, F.; Ashauer, R.; Baird, D. J.; Berger, U.; Eisenhauer, N.; Grimm, V.; Hommen, U.; Maltby, L.; Meliàn, C. J.; Pomati, F.; Roessink, I.; Rohr, J. R.; Radchuk, V.; Brink, P. J. Van den. 2016. Re-Introducing Environmental Change Drivers in Biodiversity-Ecosystem Functioning Research. *Trends in Ecology and Evolution* 12: 905-915.
- Doyen, L., Béné, C., Bertignac, M., Blanchard, F., Cissé, A.A., Dichmont, C., Gourguet, S., Guyader, O., Hardy, P.Y., Jennings, S. and Little, L.R., 2017. Ecoviability for ecosystem-based fisheries management. *Fish and fisheries*, 18(6), pp.1056-1072.
- Drake, J.M., 2003. Why does grassland productivity increase with species richness? Disentangling species richness and composition with tests for overyielding and superyielding in biodiversity experiments. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 270(1525), pp.1713-1719.

- Duffy, J.E., Lefcheck, J.S., Stuart-Smith, R.D., Navarrete, S.A. and Edgar, G.J., 2016. Biodiversity enhances reef fish biomass and resistance to climate change. *Proceedings of the National Academy of Sciences*, 113(22), 6230-6235.
- Ernst, B., Hoeger, S.J., O'Brien, E. and Dietrich, D.R., 2006. Oral toxicity of the microcystin-containing cyanobacterium *Planktothrix rubescens* in European whitefish (*Coregonus lavaretus*). *Aquatic toxicology*, 79(1), 31-40.
- Garcia, S.M. and Cochrane, K.L., 2005. Ecosystem approach to fisheries: a review of implementation guidelines. *ICES Journal of Marine Science*, 62(3), pp.311-318.
- Gordon, D.V., 2015. The endogeneity problem in applied fisheries econometrics: A critical review. *Environmental and Resource Economics*, 61(1), pp.115-125.
- Hayashi, F., 2000. *Econometrics*. Princeton University Press.
- Hillebrand, H. and Matthiessen, B., 2009. Biodiversity in a complex world: consolidation and progress in functional biodiversity research. *Ecology letters*, 12(12), pp.1405-1419.
- Hooper, D. U. and P. M. Vitousek, 1997. The effects of plant composition and diversity on ecosystem processes. *Science* 277 (5330), 1302-1305.
- Kennedy, P., 2003. A guide to econometrics. MIT press.
- Krinsky, I. and Robb, A.L., 1986. On approximating the statistical properties of elasticities. *Review of Economics and Statistics*, 715-719.
- Linløkken, A. and Haugen, T.O., 2006. Density and temperature dependence of gill net catch per unit effort for perch, *Perca fluviatilis*, and roach, *Rutilus rutilus*. *Fisheries Management and Ecology*, 13(4), 261-269.
- Liu, J., Dietz, T., Carpenter, S.R., Alberti, M., Folke, C., Moran, E., Pell, A.N., Deadman, P., Kratz, T., Lubchenco, J. and Ostrom, E., 2007. Complexity of coupled human and natural systems. *Science*, 317(5844), pp.1513-1516.
- Livingstone, D. M. 2003. Impact of Secular Climate Change on the Thermal Structure of a Large Temperate Central European Lake. *Climate Change* 57, 205–225.
- Matthews, B.; Pomati, F. 2012. Reversal in the Relationship between Species Richness and Turnover in a Phytoplankton Community. *Ecology* 93, 2435–2447.
- Monchamp, M.E., Spaak, P., Domaizon, I., Dubois, N., Bouffard, D. and Pomati, F., 2018. Homogenization of lake cyanobacterial communities over a century of climate change and eutrophication. *Nature Ecology & Evolution*, 2(2), p.317.
- Monchamp, M.E., Spaak, P. and Pomati, F., 2019. High dispersal levels and lake warming are emergent drivers of cyanobacterial community assembly in peri-Alpine lakes. *Scientific reports*, 9(1), p.7366.
- Norberg, J., 2004. Biodiversity and ecosystem functioning: a complex adaptive systems approach. *Limnology and Oceanography*, 49(4part2), pp.1269-1277.
- Pomati, F., B. Matthews, J. Jokela, A. Schildknecht, and B. W. Ibelings, 2012. Effects of re-oligotrophication and climate warming on plankton richness and community stability in a deep mesotrophic lake. *Oikos* 121 (8), 1317-1327.
- Pomati, F., C. Tellenbach, B. Matthews, P. Venail, B. W. Ibelings, and R. Ptacnik, 2015. Challenges and prospects for interpreting long-term phytoplankton diversity changes in lake Zürich (switzerland). *Freshwater Biology* 60 (5), 1052-1059.

- Pomati, F., Matthews, B., Seehausen, O., and B.W. Ibelings, 2017. Eutrophication and Climate Warming Alter Spatial (Depth) Co-Occurrence Patterns of Lake Phytoplankton Assemblages. *Hydrobiologia*. 787(1), 375-285.
- Posch, T., Köster, O., Salcher, M. M., and J. Pernthaler, 2012. Harmful Filamentous Cyanobacteria Favoured by Reduced Water Turnover with Lake Warming. *Nature Climate Change* 2, 1-5.
- Schaffer, M.E., 2010. xtivreg2: Stata module to perform extended IV/2SLS, GMM and AC/HAC, LIML and k-class regression for panel data models. <http://ideas.repec.org/c/boc/bocode/s456501.html>.
- Smith, M.D., J. Zhang, and Coleman, Felicia C. 2008. Econometric modeling of fisheries with complex life histories: Avoiding biological management failures, *Journal of Environmental Economics and Management*, Volume 55, Issue 3: 265-280
- Smith, M.D., J. E. Wilen. 2003. Economic impacts of marine reserves: the importance of spatial behavior, *Journal of Environmental Economics and Management*, Volume 46, Issue 2: 183-206.
- Sommer, U.; Adrian, R.; De Senerpont Domis, L.; Elser, J. J.; Gaedke, U.; Ibelings, B. W.; Jeppesen, E.; Lüring, M.; Molinero, J. C.; Mooij, W. M.; van Donk, E.; Winder, M. 2012. Beyond the Plankton Ecology Group (PEG) Model: Mechanisms Driving Plankton Succession. *Annual Review of Ecology, Evolution and Systematics* 43, 429–448.
- Spears, B.M., Fitter, M.N., Jeppesen, E., Huser, B.J., Ives, S., Davidson, T.A., Adrian, R., Angeler, D.G., Burthe, S.J., Carvalho, L. and Daunt, F., 2017. Ecological resilience in lakes and the conjunction fallacy. *Nature ecology & evolution*, 1(11), p.1616.
- Stewart, K.R., Lewison, R.L., Dunn, D.C., Bjorkland, R.H., Kelez, S., Halpin, P.N. and Crowder, L.B., 2010. Characterizing fishing effort and spatial extent of coastal fisheries. *PloS one*, 5(12), p.e14451.
- Stock, J.H. and Watson, M.W., 2003. Introduction to econometrics (Vol. 104). Boston: Addison Wesley.
- Stomp, M.; Huisman, J.; Mittelbach, G. G.; Litchman, E.; Klausmeier, C. 2011. Large-Scale Biodiversity Patterns in Freshwater Phytoplankton. *Ecology* 92, 2096–107.
- Stoner, A.W., 2004. Effects of environmental variables on fish feeding ecology: implications for the performance of baited fishing gear and stock assessment. *Journal of Fish Biology*, 65(6), 1445-1471.
- Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. and Siemann, E., 1997. The influence of functional diversity and composition on ecosystem processes. *Science*, 277(5330), 1300-1302.
- Turner, B.L., Matson, P.A., McCarthy, J.J., Corell, R.W., Christensen, L., Eckley, N., Hovelsrud-Broda, G.K., Kasperson, J.X., Kasperson, R.E., Luers, A. and Martello, M.L., 2003. Illustrating the coupled human–environment system for vulnerability analysis: three case studies. *Proceedings of the National Academy of Sciences*, 100(14), pp.8080-8085.
- Vogt, R.J., Romanuk, T.N. and Kolasa, J., 2006. Species richness–variability relationships in multi-trophic aquatic microcosms. *Oikos*, 113(1), pp.55-66.
- Vonlanthen, P.; Bittner, D.; Hudson, a G.; Young, K. a; Müller, R.; Lundsgaard-Hansen, B.; Roy, D.; Di Piazza, S.; Largiader, C. R.; Seehausen, O., 2012. Eutrophication Causes Speciation Reversal in Whitefish Adaptive Radiations. *Nature*, 482, 357–62.
- Wooldridge, J.M., 2015. Introductory econometrics: A modern approach. Nelson Education.
- Yankova, Y., Neuenschwander, S., Köster, O. and Posch, T., 2017. Abrupt stop of deep water turnover with lake warming: drastic consequences for algal primary producers. *Scientific reports*, 7(1), p.13770.

Table 1: Summary statistics of the economic and ecologic variables.

Variables	N. Obs.	Mean	S.D.	Min	Max
Total Catch (kg)	1,029	995.763	714.359	0	3,902.9
Number of Demersal Nets	1,032	199.357	172.811	0	900
Number of Pelagic Nets	1,032	58.942	71.382	0	310
Fuel Price (Swiss Francs)	1,032	1.617	0.171	1.29	1.98
Fish Price (Price Index)	942	99.845	2.327	94.7	104.6
Phytoplankton Biomass ($\mu\text{g L}^{-1}$)	384	1,178.957	0.409.835	533.432	2,363.382
Phytoplankton Richness (num. of species)	384	44.763	4.929	33	56
Phytoplankton Evenness (relative biomasses of species – Pielou’s index)	384	0.554	0.189	0.246	1.230
Zooplankton Abundance (counts m^2)	384	1,275,996	809,762.6	321,109	3,900,838
Zooplankton Richness (num. of species)	384	15.180	2.525	11	21
Water Temperature ($^{\circ}\text{C}$)	384	8.116	2.229	3.82	11.68
Phosphorous PO_4 ($\mu\text{g L}^{-1}$)	384	23.225	3.881	14.97	31.93
Nitrogen NO_3 ($\mu\text{g L}^{-1}$)	384	659.559	57.901	494.11	739.81

Table 2: Estimated Model of Fishing Behavior.

Variables	OLS Total Catch	2SLS Total Catch	First Stage	
			Demersal Nets	Pelagic Nets
Demersal Nets	0.231*** (0.043)	0.214** (0.086)		
Pelagic Nets	0.149*** (0.017)	0.112*** (0.037)		
Phytoplankton Biomass (t-1)	-0.373*** (0.135)	-0.331*** (0.12)	0.181 (0.206)	1.168*** (0.303)
Zooplankton Abundance (t-1)	0.375*** (0.095)	0.366*** (0.109)	-0.561*** (0.177)	0.0827 (0.23)
Phytoplankton Richness (t-1)	0.19 (0.385)		-1.170** (0.563)	-4.453*** (0.731)
Phytoplankton Evenness (t-1)	0.0147 (0.122)		0.395* (0.205)	0.958*** (0.319)
Zooplankton Richness (t-1)	0.203 (0.258)		0.225 (0.34)	-1.615*** (0.464)
Aggregate Harvest (t-1)	-0.243* (0.127)	-0.228* (0.119)	-0.117 (0.193)	1.142*** (0.299)
Phytoplankton Biomass (t-1)×Low	0.334** (0.158)	0.301** (0.123)	-0.196 (0.215)	-0.663* (0.357)
Zooplankton Abundance (t-1)×Low	-0.399*** (0.104)	-0.369*** (0.11)	0.431** (0.19)	0.578** (0.252)
Phytoplankton Richness (t-1)×Low	-0.173 (0.417)			
Phytoplankton Evenness (t-1)×Low	-0.171 (0.155)			
Zooplankton Richness (t-1)×Low	-0.0141 (0.308)			
Aggregate Harvest (t-1)×Low	0.385** (0.15)	0.299* (0.154)	-0.507* (0.274)	-0.351 (0.381)
Temperature	0.152 (0.172)	0.256* (0.147)	0.575*** (0.22)	0.634 (0.41)
Demersal Nets (t-1)			0.208*** (0.06)	-0.0242 (0.055)
Pelagic Nets (t-1)			-0.0707** (0.031)	0.296*** (0.051)
Gasoline			-1.099** (0.555)	2.135** (0.832)
Fish Price Index			-0.588 (2.26)	0.524 (3.472)
<i>F</i> -statistic (<i>SW F</i> -stat)			9.64	17.51
Hansen- <i>J</i> statistic		4.118		
p-value		0.533		
Observations	623	589	589	589
R-squared (centered and partial)	0.993	0.789	0.444	0.615

Notes: Standard errors and statistics robust to heteroscedasticity and autocorrelation. Triple ***, double ** and single * asterisks denote significance at 1, 5, and 10 percent levels, respectively. Standard errors in parentheses. *SW* denotes the *Sanderson-Windmeijer* multivariate *F*-statistic of excluded instruments; Low is a dummy variable taking value equal to 1 when the stock was in the low period, e.g., 2004-2006. Estimates obtained using *ivreg2* in STATA 15.1.

Table 3: Estimates of the ecological model.

Variables	Phytoplankton Biomass	Phytoplankton Evenness	Phytoplankton Richness	Zooplankton Abundance	Zooplankton Richness
Intercept	21.22*** (2.751)	12.20*** (1.854)	4.627*** -0.542	-2.294 (5.851)	3.649*** (1.282)
Phytoplankton Biomass				0.132 (0.19)	-0.06 (0.048)
Zooplankton Abundance	-0.446*** 0.141				
Phytoplankton Richness	-0.724** (0.305)				0.583*** (0.2)
Phytoplankton Evenness	0.084 (0.137)				-0.09 (0.064)
Phytoplankton Biomass (t-1)	0.297*** (0.057)				
Phytoplankton Richness (t-1)			0.453*** -0.026		
Phytoplankton Evenness (t-1)		0.338*** 0.031			
Zooplankton Abundance (t-1)				0.170*** (0.047)	
Zooplankton Richness (t-1)					0.221*** (0.046)
PO ₄	-1.655*** (0.334)	-1.223*** (0.179)	-0.201*** -0.048	-0.37 (0.695)	-0.202 (0.136)
NO ₃	-0.22 (0.317)	-0.516** 0.201	-0.167*** -0.057	1.550*** (0.298)	-0.373*** (0.078)
Water Temperature	-3.391*** (1.21)	-7.205*** 0.851	-0.945*** -0.216	0.188 (1.896)	-0.675 (0.519)
Water Temperature squared	0.531** (0.236)	1.535*** 0.153	0.260*** -0.037	0.026 (0.308)	0.210** (0.102)
PO ₄ × Water Temperature	0.541*** (0.16)	0.448*** 0.093	0.0231 -0.029	0.042 (0.307)	0.001 (0.059)
Aggregate Catch (t-1)	0.0459 (0.056)	-0.0335 0.046	-0.0221* -0.012	0.338*** (0.053)	0.009 (0.019)
N. of parameters	47				
N. of moments	60				
Hansen-J statistic	12.692				
p-value	0.4618				
N. obs.	383				

Notes: Estimates were obtained using a Generalized Method of Moments (GMM) estimator. GMM is a general estimation model where the estimated parameters are those that provide the best fit to a system of multiple equations, with each equation satisfying the condition that a sample moment equals zero (e.g., Stock and Watson, 2003). Triple ***, double ** and single * asterisks denote significance at 1, 5, and 10 percent levels, respectively. Heteroscedasticity-autocorrelation robust standard errors in parentheses. Estimates obtained using `gmm` in STATA 15.1.

Table 4: Long-Run values achieved by ecological and economic variables, in logs, for simulated changes in Temperature, Phosphorous (PO₄), and Nitrogen (NO₃).

Temperature	-50%	-40%	-30%	-20%	-10%	Baseline	10%	20%	30%	40%	50%
Phyto-Richness	3.652 (1.261)	3.538 (1.289)	3.514 (1.31)	3.465 (1.326)	3.441 (1.345)	3.481 (1.38)	3.567 (1.398)	3.669 (1.441)	3.809 (1.457)	3.985 (1.495)	4.186 (1.573)
Phyto-Evenness	-0.346 (3.125)	-0.702 (3.143)	-1.18 (3.177)	-1.443 (3.258)	-1.462 (3.238)	-1.345 (3.495)	-1.276 (3.582)	-0.884 (3.725)	-0.368 (3.825)	0.205 (4.004)	1.037 (4.185)
Phyto-Biomass	6.483 (6.729)	6.636 (7.001)	6.875 (7.162)	6.825 (7.321)	7.021 (7.231)	6.861 (7.475)	6.867 (8.005)	6.873 (8.148)	6.991 (8.576)	6.823 (8.777)	6.867 (9.212)
Zoo-Abundance	13.094 (6.21)	13.198 (6.336)	13.163 (6.428)	13.559 (6.689)	13.701 (6.911)	13.891 (6.975)	13.769 (7.331)	14.098 (7.617)	14.315 (8.01)	14.405 (8.2)	14.684 (8.758)
Zoo-Richness	2.395 (2.201)	2.353 (2.235)	2.334 (2.308)	2.293 (2.312)	2.278 (2.362)	2.353 (2.412)	2.4 (2.453)	2.561 (2.603)	2.666 (2.687)	2.899 (2.788)	3.069 (2.851)
Demersal Nets	5.462 (8.522)	5.629 (8.558)	5.391 (8.703)	5.199 (8.82)	5.203 (9.123)	5.178 (9.34)	5.473 (9.417)	5.449 (9.655)	5.582 (10.07)	5.801 (10.141)	5.719 (10.7)
Pelagic Nets	4.342 (24.413)	5.391 (24.762)	5.147 (24.817)	5.849 (24.931)	6.824 (25.382)	6.37 (26.08)	6.228 (26.842)	6.424 (27.167)	6.291 (28.023)	5.363 (28.499)	5.413 (29.364)
Total Catch	9.464 (4.55)	9.628 (4.642)	9.502 (4.629)	9.747 (4.733)	9.843 (4.676)	9.96 (4.878)	9.974 (4.912)	10.12 (5.071)	10.247 (5.105)	10.288 (5.162)	10.394 (5.392)
Phosphorous	-50%	-40%	-30%	-20%	-10%	Baseline	10%	20%	30%	40%	50%
Phyto-Richness	4.02 (1.355)	3.912 (1.369)	3.833 (1.379)	3.682 (1.359)	3.601 (1.375)	3.481 (1.38)	3.387 (1.372)	3.269 (1.36)	3.184 (1.381)	3.046 (1.403)	2.951 (1.364)
Phyto-Evenness	-0.449 (3.458)	-0.557 (3.447)	-0.845 (3.421)	-0.998 (3.456)	-1.239 (3.454)	-1.345 (3.495)	-1.563 (3.492)	-1.789 (3.448)	-2.087 (3.438)	-2.217 (3.507)	-2.356 (3.46)
Phyto-Biomass	7.686 (7.673)	7.512 (7.611)	7.142 (7.556)	6.93 (7.784)	6.97 (7.525)	6.861 (7.475)	6.567 (7.55)	6.617 (7.691)	6.472 (7.641)	6.224 (7.62)	6.076 (7.552)
Zoo-Abundance	14.471 (7.135)	14.299 (7.102)	14.037 (7.049)	14.221 (7.083)	13.866 (7.036)	13.891 (6.975)	13.706 (7.156)	13.684 (7.209)	13.264 (6.957)	13.237 (6.98)	13.172 (7.233)
Zoo-Richness	3.035 (2.412)	2.927 (2.447)	2.756 (2.456)	2.571 (2.439)	2.477 (2.422)	2.353 (2.412)	2.228 (2.408)	2.066 (2.4)	1.966 (2.366)	1.823 (2.416)	1.685 (2.368)
Demersal Nets	5.362 (9.478)	5.22 (9.44)	5.222 (9.385)	4.955 (9.272)	5.403 (9.183)	5.178 (9.34)	5.276 (9.183)	5.128 (9.171)	5.521 (9.002)	5.343 (8.988)	5.42 (9.112)
Pelagic Nets	3.977 (25.998)	4.006 (26.334)	4.254 (26.16)	5.788 (26.086)	5.471 (25.857)	6.37 (26.08)	6.699 (26.497)	7.867 (25.707)	7.643 (25.664)	8.661 (26.414)	9.192 (25.79)
Total Catch	9.704 (4.845)	9.661 (4.861)	9.696 (4.791)	9.953 (4.893)	9.907 (4.91)	9.96 (4.878)	9.97 (4.902)	10.047 (4.778)	10.001 (4.798)	10.163 (4.93)	10.293 (4.84)
Nitrogen	-50%	-40%	-30%	-20%	-10%	Baseline	10%	20%	30%	40%	50%
Phyto-Richness	4.572 (1.215)	4.432 (1.258)	4.128 (1.282)	3.956 (1.282)	3.731 (1.335)	3.481 (1.38)	3.289 (1.417)	3.04 (1.452)	2.797 (1.487)	2.625 (1.528)	2.376 (1.588)
Phyto-Evenness	1.453 (2.996)	0.978 (3.125)	0.303 (3.139)	-0.244 (3.304)	-0.804 (3.33)	-1.345 (3.495)	-1.932 (3.542)	-2.532 (3.686)	-3.166 (3.837)	-3.738 (4.011)	-4.338 (4.158)
Phyto-Biomass	11.662 (6.919)	10.636 (6.835)	9.499 (7.078)	8.588 (7.301)	7.938 (7.552)	6.861 (7.475)	5.847 (7.789)	5.029 (8.145)	4.232 (8.416)	3.045 (8.593)	2.193 (9.134)
Zoo-Abundance	7.301 (6.97)	8.384 (6.83)	9.918 (7.09)	11.271 (6.807)	12.425 (7.061)	13.891 (6.975)	15.086 (7.081)	16.365 (7.394)	17.645 (7.453)	19.04 (7.526)	20.339 (7.699)
Zoo-Richness	4.019 (2.418)	3.743 (2.394)	3.348 (2.419)	3.073 (2.414)	2.714 (2.409)	2.353 (2.412)	2.058 (2.484)	1.678 (2.463)	1.28 (2.543)	1.019 (2.56)	0.649 (2.571)
Demersal Nets	12.072 (9.135)	10.947 (9.137)	9.416 (9.317)	7.861 (9.149)	6.793 (9.103)	5.178 (9.34)	3.946 (9.082)	2.477 (9.526)	1.033 (9.61)	-0.18 (9.668)	-1.579 (10.157)
Pelagic Nets	2.206 (24.475)	1.754 (24.501)	4.125 (24.707)	4.022 (24.872)	5.332 (25.982)	6.37 (26.08)	6.956 (26.694)	8.41 (27.739)	9.641 (27.957)	9.767 (28.976)	10.861 (30.488)
Total Catch	7.48 (4.57)	7.77 (4.673)	8.598 (4.756)	8.929 (4.64)	9.414 (4.746)	9.96 (4.878)	10.434 (4.867)	10.928 (5.161)	11.356 (5.109)	11.877 (5.236)	12.339 (5.531)

Figure Legends

Figure 1: Aggregate monthly data for Total Catch and number of nets used by type, Demersal and Pelagic, for the commercial fishery of Lake Zürich.

Figure 2: Graph depicts the relationships between trophic levels of Lake Zürich where fishing firms are the top predators. There is no direct link between Biodiversity, measured by Phytoplankton and Zooplankton Richness and Harvest. With reference to the theoretical model, individual Fishing Harvest is denoted by h_i , Fishing Effort (net use) is e_i , Fish Stock is y_b , y_a denotes a vector of the Phyto/Zooplankton variables, while Temperature, Phosphorous, and Nitrogen are denoted by z .

Figure 3: Long run effects on lake fishery measured by the number of demersal and pelagic nets and total catch in response to changes in water temperature (left-top/bottom), phosphorous (center-top/bottom), and nitrogen (right-top/bottom). The thick lines indicate the mean while the thinner lines the 95% confidence interval of the simulated Long-Run values (steady-states) obtained using the estimated models for the lake fishery (9)-(11) and ecology (12)-(16) and bootstrapping with 5000 repetitions. Values for outcome variable are in logarithmic scale.

Figure 4: Long run effects on lake Phytoplankton in response to changes in water temperature (left-top/bottom), phosphorous (center-top/bottom), and nitrogen (right-top/bottom). The thick lines indicate the mean while the thinner lines the 95% confidence interval of the simulated Long-Run values (steady-states) obtained using the estimated models for the lake fishery (9)-(11) and ecology (12)-(16) and bootstrapping with 5000 repetitions. Values for outcome variable are in logarithmic scale. Phyto = phytoplankton.

Figure 5: Long run effects on lake Zooplankton in response to changes in water temperature (left-top/bottom), phosphorous (center-top/bottom), and nitrogen (right-top/bottom). The thick lines indicate the mean while the thinner lines the 95% confidence interval of the simulated Long-Run values (steady-states) obtained using the estimated models for the lake fishery (9)-(11) and ecology (12)-(16) and bootstrapping with 5000 repetitions. Values for outcome variable are in logarithmic scale.

Lake Fishery