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Fishing triggers trophic cascade in terms of variation, not abundance, in an allometric trophic network model

Silva Uusi-Heikkilä, Tommi Perälä, and Anna Kuparinen

Abstract: Trophic cascade studies often rely on linear food chains instead of complex food webs and are typically measured as biomass averages, not as biomass variation. We study trophic cascades propagating across a complex food web including a measure of biomass variation in addition to biomass average. We examined whether different fishing strategies induce trophic cascades and whether the cascades differ from each other. We utilized an allometric trophic network (ATN) model to mechanistically study fishing-induced changes in food web dynamics. Different fishing strategies did not trigger traditional, reciprocal trophic cascades, as measured in biomass averages. Instead, fishing triggered a variation cascade that propagated across the food web, including fish, zooplankton and phytoplankton species. In fisheries that removed a large amount of top-predatory and cannibalistic fish, the biomass oscillations started to decrease after fishing was started. In fisheries that mainly targeted large planktivorous fish, the biomass oscillations did not dampen but slightly increased over time. Removing species with specific ecological functions might alter the food web dynamics and potentially affect the ecological resilience of aquatic ecosystems.

Résumé : Les études de cascades trophiques reposent souvent sur des chaînes alimentaires linéaires plutôt que sur des réseaux trophiques complexes, ainsi que sur des mesures de la biomasse moyenne, plutôt que des variations de la biomasse. Nous étudions la propagation de cascades trophiques à travers un réseau trophique complexe en intégrant une mesure de la variation de la biomasse en plus de la moyenne de cette dernière. Nous tentons de déterminer si différentes stratégies de pêche induisent des cascades trophiques et si ces dernières diffèrent les unes des autres. Nous utilisons un modèle de réseau trophique allométrique (RTA) pour étudier de manière mécaniste les modifications induites par la pêche de la dynamique du réseau trophique. Différentes stratégies de pêche ne déclenchent pas de cascades trophiques réciproques traditionnelles, telles que mesurées par la biomasse moyenne. La pêche déclenche plutôt une cascade de variations qui se propage dans tout le réseau trophique, incluant des espèces de poissons, de zooplancton et de phytoplancton. Dans les pêches qui prélèvent une grande quantité de poissons cannibales et prédateurs de niveau supérieur, les oscillations de la biomasse commencent à diminuer après le début de la pêche. Dans les pêches qui ciblent principalement de grands poissons planctonivores, les oscillations de la biomasse ne s'atténuent pas, mais augmentent plutôt légèrement au fil du temps. Le retrait d'espèces ayant des fonctions écologiques précises pourrait modifier la dynamique des réseaux trophiques et avoir une incidence sur la résilience écologique des écosystèmes aquatiques. [Traduit par la Rédaction]

Introduction

The widespread importance of trophic cascades ("indirect species interactions that originate with predators and spread downward through food webs" sensu Ripple et al. 2016) has become increasingly recognized since they were first identified as primary determinant of community structure and ecosystem dynamics (Hairston et al. 1960; Paine 1980; Pace et al. 1999). Cascades are typically defined as effects that alter the density, biomass or productivity of a population or community across more than one link in the food web (Carpenter et al. 1985; Carpenter and Kitchell 1993; Pace et al. 1999). Cascade studies historically relayed on simple, linear food chains comprising functional groups (producers, herbivores, predators) rather than a web of species (Ripple et al. 2016; Shanafelt and Loreau 2018). However, nature is more commonly constructed of complex food webs rather than chains; thus, the three- or four-level cascades (Fig. 1*a*) may not realistically represent a complex food web within which the food chains are embedded (Persson 1999; Krause et al. 2003; Heath et al. 2014). The

alteration of one species can spread throughout the food web via interactions that connect the species (Fig. 1*b*). These interactions are not limited to typical predator–prey interactions, as in a classic trophic cascade concept, but those can be competitive or other indirect interactions (e.g., Borer et al. 2005, 2006). Complex food web models have been used to study the effects of human activities, such as fisheries regulation or ocean acidification, on food web properties but not to directly study human-induced trophic cascades (Kaplan et al. 2010; Ainsworth et al. 2011). The majority of trophic cascade studies utilize simplified food webs that consist of only few species (e.g., reviewed in Strong 1992; Schmitz et al. 1997; Shurin et al. 2002; Finke and Denno 2004; Schmitz et al. 2004; Liu et al. 2018; Fig. 1*a*), and only a minority of studies utilize complex food webs consisting of a high number of species (e.g., Bascompte et al. 2005; Frank et al. 2005; Myers et al. 2007; Fig. 1*b*).

Trophic cascades can vary by ecosystem type, initial perturbation magnitude, and the choice of response variables (Ripple et al. 2016). They are typically measured as density, biomass, or productivity

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Fig. 1. (*a*) A theoretical food chain in a food web. Plots inside the nodes demonstrate reciprocal changes in the abundances of consumers in the presence and absence of fishing. Vertical line indicates when fishing was started. The colours of the nodes refer to different trophic levels. Fishing decreases the abundance of a top consumer (Consumer 4), the abundance of its prey (Consumer 3) increases and the abundance of Consumer 3's prey decreases. This illustrates a reciprocal trophic cascade (in terms of abundance) caused by fishing. (*b*) When exploring a segment of a food web, the reciprocal trophic cascade is no longer visible. The top consumer (Consumer 4) predates on two trophic levels and partly on the same species as the Consumer 3. While the abundance of the Consumer 3 increases, the abundance of its prey species can either increase or decrease owing to the feeding preferences of Consumer 3 and the feeding interactions between Consumer 4 and Consumer 2. Because of indirect interactions, traditional reciprocal trophic cascades can be difficult to detect in complex food webs. The nodes and interactions are based on the Lake Constance food web.
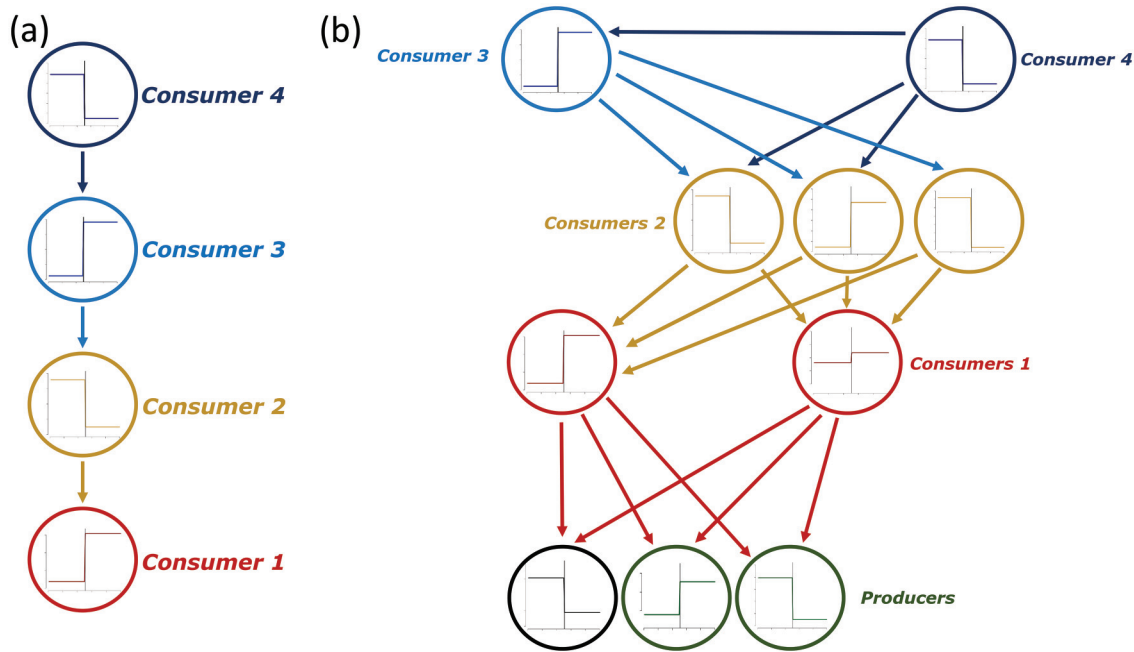
averages. Measures of variation or oscillation have been less studied (but see Halpern et al. 2005; Long et al. 2011; Shanafelt and Loreau 2018 in linear food chains or relatively simple food webs), although changes in the variation of density or productivity can be also important. Increased variation is known to destabilize food webs and decrease populations' resistance, resilience, and reactivity to disturbances, such as human exploitation and changing environmental conditions (Pimm 1984; Bascompte et al. 2005; Ives and Carpenter 2007; Shackell et al. 2010; Arnoldi et al. 2016). In this study, we explore trophic cascades propagating across a food web using both a traditional measure of average biomass densities and a less used measure: biomass variation (measured as the relative amplitude of biomass oscillation). When studying a complex food web, it is not straightforward to detect the traditional reciprocal effect, particularly in terms of variation, as in studies focusing on linear food chains (Fig. 1). Therefore, we explore whether removal of high trophic level predators can alter biomass variation and whether this effect can propagate across the food web (Fig. 1*b*).

Intensive removal of a top consumer from an ecosystem by modern harvesting practices can lead to disturbances in cascading trophic interactions (Frank et al. 2005; Shackell et al. 2010). For example, fishing typically removes enormous amounts of top predators and consequently lower trophic levels are released from predation. Although fisheries exploit top predators, and this could lead to significant changes in top-down processes, the evidence of fisheries-induced trophic cascades remain unequivocal. Some studies demonstrate a clear traditional (reciprocal) trophic cascade of up to four trophic levels induced by fishing (Frank et al. 2005; Daskalov et al. 2007; Andersen and Pedersen 2010; Gasche and Gascuel 2013), while others provide no evidence of fisheries-induced trophic

cascades (Reid et al. 2000; Steele and Collie 2004). The effect of predatory species, exploited for example by fisheries, on ecosystem stability also remains controversial. Some studies show that removing predators or consumers from the ecosystem stabilizes (i.e., decreases variance) lower trophic levels (Halpern et al. 2005; Long et al. 2011), while others demonstrate a destabilizing effect (Post 2013; Britten et al. 2014) or no effect (Valone and Balaban-Feld 2019). Most of these studies are based on empirical data and are confounded by various environmental effects (e.g., Frank et al. 2005; Daskalov et al. 2007). Modeling studies focusing on the mechanistic understanding of the effect of fisheries on trophic interactions are rare (but see Andersen and Pedersen 2010). Here, we investigate whether fishing can trigger trophic cascades utilizing a deterministic modeling approach, which excludes changes in biomass in response to any other external disturbance and (or) environmental fluctuation. By doing so, we are able to pinpoint the observed changes directly to fishing. We also studied the effects of different fishing gear on food web dynamics after adding environmental stochasticity in the model. The life-history-structured food web model (allometric trophic network, ATN; Boit et al. 2012) that we use allows us to increase the mechanistic understanding of food web dynamics and trophic interactions (see also de Roos 2020). Our model system is North European, alpine Lake Constance, as the ATN model has been parameterized and validated for this ecosystem (Boit et al. 2012; Kuparinen et al. 2016).

With the ATN model, we primarily focus on simulating two different fisheries. Large-mesh fisheries reduce mainly the abundance of large planktivorous fish from the system while the small species and individuals can escape (refer to online Supplementary Fig. S1[1]).

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[1]Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2021-0146.

Small-mesh fisheries, on the other hand, target mainly smaller piscivorous and cannibalistic fish species (Supplementary Fig. S1[1]). Hence, small-mesh fisheries reduce the biomass of higher trophic level predators more intensively than large-mesh fisheries. We study whether the two different fishing gear trigger trophic cascades in terms of biomass densities (abundance cascade) and in terms of biomass variation (variation cascade). Here, variation refers to the amplitude of biomass oscillation within taxa over time and variation cascade refers to the extent to which changes in oscillations (caused by fishing) propagate across the food web to the unfished species. Theoretical and empirical research have demonstrated both stabilizing and destabilizing effect of apex predators on ecosystems (Sterner et al. 1997; Halpern et al. 2005; Long et al. 2011). Approaching this question from a complex food web perspective, we can evaluate the role of two different species from different trophic levels and with different feeding links in controlling community dynamics and stability. Fishing-induced trophic cascades altering ecosystem functions and destabilizing the food web may be harmful for the fisheries and ultimately reduce the resilience of the entire ecosystem (Scheffer et al. 2001).

Materials and methods

ATN model

To study whether the different fishing strategies trigger a trophic cascade in the Lake Constance (LC) food web, we used an ATN model, which has been parametrized and validated for the LC ecosystem (Boit et al. 2012) and modified by Kuparinen et al. (2016) to better address the life-history structure of fishes. The network consists of two fish species: planktivorous whitefish (*Coregonus lavaretus*) and piscivorous perch (*Perca fluviatilis*) and their five different life-history stages (larvae, juvenile (one-year-old), two-year-old, three-year-old and ≥four-year-old). Whitefish population is largely dependent on stocking (i.e., release of hatchery-reared larvae; Eckmann et al. 2007). In addition to fish, the food web consists of detritus, six basal producers (five algal and one autotrophic picoplankton species), one heterotrophic bacterium feeding on detritus, 12 primary consumers feeding on producers, out of which six are also secondary consumers (e.g., *Daphnia* and cyclopoid copepods), and one secondary consumer (a large carnivorous *Leptodora*). Altogether, the LC food web consists of 30 functional trophic guilds (Supplementary Table S1[1]) and 133 feeding interactions among the guilds.

Biomass densities are described through relative carbon densities ($\mu g C \cdot m^{-3}$). The daily biomass dynamics across an annual 90-day growth season are modelled through a set of ordinary differential equations (ODE), which include saturating functional responses that regulate predator-prey interactions and intraspecific predator interference (Supplementary Table S2[1]). Basal production is controlled by a logistic growth model with a shared community carrying capacity for all the producers. In phyto- and zooplankton communities, biomass densities are determined by the intrinsic growth rates of phytoplankton species, competition among the species, the carrying capacity of the environment, and the consumption rate (i.e., at what rate individuals of a particular species are consumed by a predator). In fish, fishing mortality also affects their biomass densities. If fish are not caught by the fisheries or consumed by a predator, the biomass passes on to the next life-history stage at the end of each 90-day growth season. During the growth season, the mature fish also allocate a portion of their biomass gained from consumption to reproduction. At the end of each growth season, the biomass densities of younger fish turn from their current life-history stage to the next age-dependent stage (guild). Species' body sizes determine their metabolic rates and feeding interactions based on empirical studies except when more directly measured metabolic rates are available (Boit et al. 2012). More detailed description of the ATN model is presented below. Functional guilds (i.e., nodes in the food web) along with their feeding links and node properties are given in Supplementary Table S1[1]. Parameters for the ATN model are given in Supplementary Table S2[1].

Our ATN model system dynamics are divided into two parts. In the first part, the food web dynamics for year Y are simulated in continuous time during the "growth season". This part includes the producer growth, consumer and fish feeding, maintenance of organism's bodily functions, and the allocation of portion of adult fish biomass for reproduction as well as the removal of fish biomass by fishing. These dynamics are modelled as a system of ODEs. The second part of the system dynamics is called "reproduction and ageing", and it consists of the birth of new fish larvae and the transfer of fish biomass to the next life stage for year $Y + 1$.

Growth season dynamics

The core biomass dynamics of species or groups of functionally similar species (i.e., guilds, denoted by their index i; see Supplementary Table S1[1] for detailed guild information) within the growth season of year Y are described by a set of ODEs. The biomass of guild i and its derivative with respect to time are denoted by $B_{Y,i}(t)$ and $\dot{B}_{Y,i}(t)$, respectively, where $t \in [0, t^{end}]$. The vector of all guild biomasses is denoted by $\boldsymbol{B}_Y(t)$. The length of the growth season is 90 days, and thus we set $t^{end} = 90$. For notational simplicity, we omit the year Y and time t from the description of the growth season dynamics.

Producer guild ($i \in \{1, \ldots, 6\}$) dynamics are driven by their intrinsic (logistic) growth and the feeding subjected to them by their herbivore predators. The ODE for the biomass of producer guild i during the growth season is

$$(1) \qquad \dot{B}_i = \overbrace{r_i B_i G_i(\boldsymbol{B})(1 - s_i)}^{\text{gain from producer growth}} - \sum_j \frac{\overbrace{x_j y_{ji} B_j F_{ji}(\boldsymbol{B})}^{\text{loss to consumer } j}}{e_{ji}}$$

where r_i is the mass-specific intrinsic growth rate of producer i (Boit et al. 2012); $G_i(\boldsymbol{B}) = 1 - \left(\sum_{j=\text{producers}} c_{ij} B_j \right) \Big/ K$ is the limiting factor in the logistic growth model of the producers, and it includes producer competition coefficients c_{ij} and carrying capacity coefficient K shared by all autotrophs. In our deterministic simulations, $K = 540\,000$ was constant. In our stochastic simulations, however, the carrying capacity varied from year to year, and we randomly drew K each year from the normal distribution $N(\mu_K, CV_K \mu_K)$, where $\mu_K = 540\,000$ and for the coefficient of variation $CV_K \in \{0.01, 0.025, 0.05, 0.075, 0.1, 0.15, 0.2, 0.25\}$, eight different levels were tested: s_i is the fraction of exudation; x_i is the mass-specific metabolic rate of consumer i based on allometric scaling; y_{ij} is the maximum consumption rate relative to metabolic rate of guild i feeding on guild j; e_{ji} is the assimilation efficiency describing the fraction of ingested biomass lost by egestion. $F_{ij}(\boldsymbol{B})$ is the consumer and fish guilds' normalized functional response to prey guilds densities

$$(2) \qquad F_{ij}(\boldsymbol{B}) = \frac{\omega_{ij} B_j^q}{B0_{ij}^q + d_{ij} B_i B0_{ij}^q + \sum_{l=\text{resources}} \omega_{il} B_l^q}$$

where ω_{ij} is the relative prey preference of consumer guilds i feeding on resource guilds j; $q = 1.2$, which forms a relatively stable version of the Holling type II functional response (Williams and Martinez 2004); $B0_{ij}$ is the half saturation constant of resource guilds j feeding on species j; d_{ij} is the coefficient of intraspecific feeding interference of species i while feeding on guilds j.

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Consumer guild (including bacterial detritivores; $i \in \{7, \ldots, 20\}$) dynamics consists of the maintenance of bodily functions, gains from feeding on their prey, and losses due to getting fed on by their predators, and the ODE is

$$(3) \qquad \dot{B}_i = - \overbrace{f_m x_i B_i}^{\text{maintenance loss}} + \overbrace{f_a x_i B_i \sum_j y_{ij} F_{ij}(\boldsymbol{B})}^{\text{gain from resources}} - \overbrace{\sum_j \frac{x_j y_{ij} B_j F_{ji}(\boldsymbol{B})}{e_{ji}}}^{\text{loss to consumer } j}$$

where f_m is the fraction of assimilated carbon respired by maintenance of basic body functions; and f_a is the fraction of consumed carbon used for production of consumers' biomass under activity $(1 - f_a$ is respired).

The fish guilds have indices 21–30 so that whitefish have odd and perch have even indices. The growth season dynamics of the larval and juvenile fish guilds ($i \in \{21, \ldots, 24\}$) are identical to the consumers' dynamics, i.e.:

$$(4) \qquad \dot{B}_i = -f_m x_i B_i + f_a x_i B_i \sum_j y_{ij} F_{ij}(\boldsymbol{B}) - \sum_j \frac{x_j y_{ji} B_j F_{ji}(\boldsymbol{B})}{e_{ji}}$$

The adult fish guilds ($i \in \{25, \ldots, 30\}$) have no predators in our model, and they allocate a portion of the biomass gained from consumption to reproduction. We use $\dot{B}_i^+$ to denote the rate of biomass allocation to reproduction by adult fish guild i during the growth season. The biomass allocation is determined by the consumption gains $\mathscr{g}_i = f_a x_i B_i \sum_j y_{ij} F_{ij}(\boldsymbol{B})$ and the maintenance losses $\ell_i = f_m x_i B_i$. We use a piecewise function

$$(5) \qquad \dot{B}_i^+ = \begin{cases} P_i I_i \cdot \dfrac{\mathscr{g}_i^2}{2\ell_i}, & \mathscr{g}_i < \ell_i \\[2mm] P_i I_i \cdot \left(\mathscr{g}_i - \dfrac{1}{2}\ell_i \right), & \mathscr{g}_i \geq \ell_i \end{cases}, \quad i \in \{25, \ldots, 30\}$$

to enforce impaired reproduction when the maintenance losses are greater than the consumption gains. Here, P_i denotes the proportion of mature biomass in adult fish guild i, and I_i is a parameter controlling how much gets invested into reproduction. The proportion of mature biomass in the two, three-, and ≥four-year-old whitefish and perch guilds are 5%, 50% and 95%, respectively, and the corresponding investment parameter values are 10%, 15% and 20%. The biomass allocated to reproduction is not available for growth and is thus considered in the ODE modelling the biomass of adult fish guild i

$$(6) \qquad \dot{B}_i = -f_m x_i B_i + f_a x_i B_i \sum_j y_{ij} F_{ij}(\boldsymbol{B}) - \dot{B}_i^+ - E S_i B_i$$

Furthermore, to determine the amount of accumulated biomass allocated to reproduction by adult fish guild i, B_i^+, we add eq. 5 to the system of ODEs.

In our simulations the adult fish are also subjected to fishing. The last term in eq. 6 describes the rate of fishing mortality, and it consists of the length-dependent selectivity of the fishing gear, S_i, and the fishing effort, E (Supplementary Figs. S1, S2[1]).

The simulation starts at year $Y = 1$, and the initial biomass vector $\boldsymbol{B}_1(0)$ consists of the biomasses at the system's equilibrium and the initial value for $B_{Y,i}^+ = 0, \forall i \in \{25, \ldots, 30\}, \forall Y$. The system of ODEs is then solved for the growth season.

Reproduction and ageing

After the growth season of year Y, the accumulated biomass allocated to reproduction $B_{Y,i}^+(t^{\text{end}})$ by the adult fish guild i translates to initial larvae biomass for the next year's growth season. The initial biomass of the larvae for year $Y + 1$ for a given fish species is the sum of the larvae produced by the different adult life-stages of that fish species, i.e.:

$$(7) \qquad B_{Y+1,i}(0) = \sum_{a=2}^{4} B_{Y,i+2a}^+(t^{\text{end}}) + h_{Y+1,i}, \quad i \in \{21, 22\}$$

where h is the amount of stocked fish larvae (200 units for whitefish, 0 units for perch). The initial biomasses of the juveniles (age 1), and the two first adult life stages (ages 2 and 3) for year $Y + 1$ are the biomasses of the previous life stages at the end of the growth season of year Y

$$(8) \qquad B_{Y+1,i}(0) = B_{Y,i-2}(t^{\text{end}}), \quad i \in \{23, \ldots, 28\}$$

The oldest life stage (age 4+) consists of the 4-year-old fish and all the older fish, and thus the initial biomass of the 4+ group for year $Y + 1$ is a sum of the 4+ and 3 group biomasses at the end of the growth season of year Y:

$$(9) \qquad B_{Y+1,i}(t^{\text{init}}) = B_{Y,i}(t^{\text{end}}) + B_{Y,i-2}(t^{\text{end}}), \quad i \in \{29, 30\}$$

Fisheries simulation

We first simulated the ecosystem dynamics without fishing until it had started oscillating regularly around its equilibrium state. We then recorded the next 50 years of the system dynamics. Next, we applied fishing for 160 years. The first 10 years under fishing were discarded as they roughly represent the transient dynamics from one equilibrium state (no fishing) to another (with fishing), and we wanted to compare the dynamics of the two equilibrium states.

We mainly focused on two different, yet common, fishing strategies. Large-mesh fisheries targeted the largest fish. The selectivity in large-mesh fisheries was one for a 30 cm fish and negligible for fish smaller than 15 cm and larger than 45 cm (Supplementary Fig. S1[1]). Large-mesh fisheries has been suggested to follow good fisheries management as it catches the large adult fish and allows small juveniles and immature individuals to escape (Armstrong et al. 1990). Unlike large-mesh fisheries, small-mesh fisheries targeted the small fish. The selectivity was one for a 20 cm fish and negligible for fish larger than 30 cm (Supplementary Fig. S1[1]). Small-mesh fisheries have been suggested to promote sustained production by allowing a higher proportion of the spawning biomass to remain in the stock (Wolff et al. 2015). We also simulated fisheries that caught even smaller fish than small-mesh fisheries and even larger fish than large-mesh fisheries (Supplementary Fig. S2[1]). In our simulations, the instantaneous fishing effort (E) was set to 0.75/90 days for both fisheries. Additionally, more moderate fishing effort levels ($E = 0.5/90$ and 0.25/90 days) were tested. Finally, in addition to reporting results based on the deterministic model we explored the results after adding stochasticity (varying CV_K) in the model (explained above in section on Growth season dynamics). We simulated 100 replicates of each level of CV_K, fishing effort and fishing gear.

Our LC ATN-model produces oscillating biomass time series. To study whether fishing can trigger an abundance cascade, we calculated changes in average biomass (i.e., average of the biomass oscillation) across growth seasons, guilds, and trophic levels in the food web in the absence and in the presence of large- and small-mesh fisheries. Variation cascade was demonstrated by visualizing biomass oscillation among guilds and trophic levels and by calculating and comparing the amplitude of oscillation in the absence and presence of large- and small-mesh fisheries. All comparisons were conducted utilizing the growth season average biomass values.

To quantify the biomass time series, we fitted a modified sinusoidal function of the form

Fig. 2. Changes in the biomasses caused by large-mesh fisheries of (*a*) whitefish life stages and their prey, (*b*) perch life stages and their prey, and (*c*) zooplankton prey of adult whitefish and their prey. Changes in the biomasses caused by small-mesh fisheries of (*d*) whitefish life stages and their prey, (*e*) perch life stages and their prey, and (*f*) zooplankton prey of adult whitefish and their prey. Numbering on horizontal axes refers to fish life stages (0 = larva, 1 = juvenile, 2 = two-year-old, 3 = three-year-old, 4 = ≥four-year-old). Prey species for each guild are listed in Supplementary Table S1[1]. Increase in juvenile to ≥four-year old whitefish prey biomass densities are identical because these whitefish guilds feed on the same prey (i.e., *Daphnia*, cyclopoid copepods, and *Leptodora*).
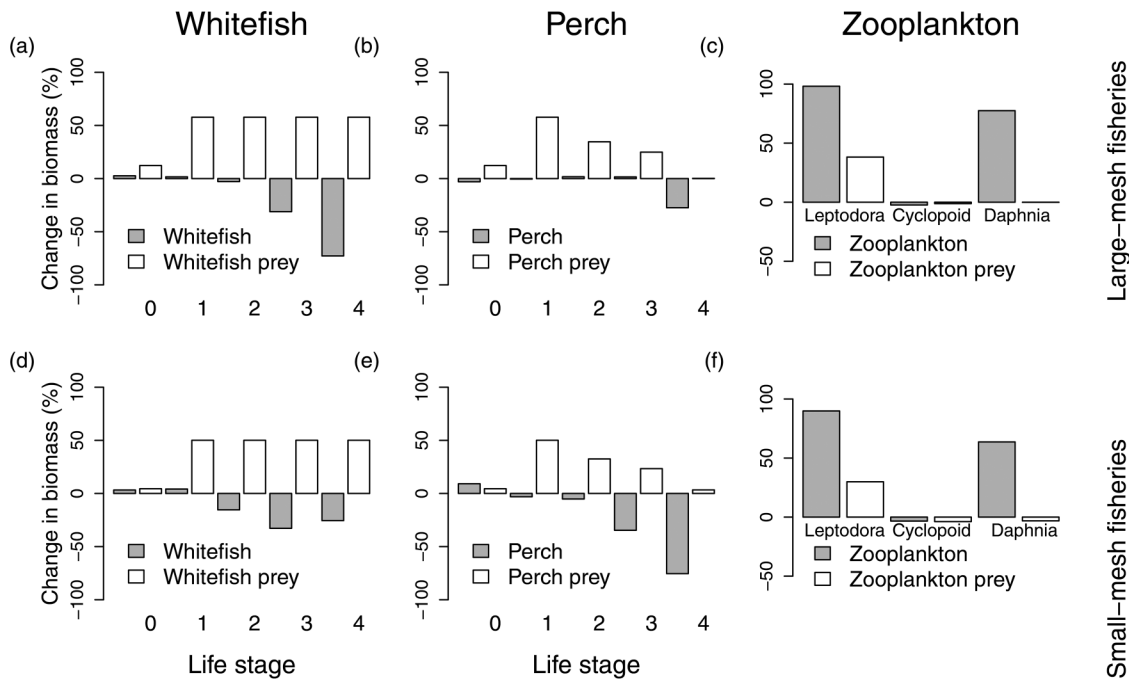
$$(10) \qquad f(t) = \mu + A_{max} e^{-\frac{\log(2)}{\lambda}(t-t_0)} \sin[\omega(t-t_0) + \varphi]$$

that allowed for the amplitude to increase or decrease in time. The abundance cascade was examined using the mean, μ, and the variation cascade using the maximum amplitude, A_{max}. The relative amplitude was calculated by dividing A_{max} with μ. The decreasing or increasing nature of the oscillation was determined by the sign of the half-life, λ. For the noisy biomass time-series produced by the stochastic simulations such a smooth and regular function fits poorly, and thus a moving coefficient of variation with a window of 10 years (five years was also tested and the results were quantitatively the same) was used to capture the trends in the variation after fishing was started.

Results

Abundance cascade

The most significant difference between the large-mesh and small-mesh fisheries was that due to targeting different-sized fish the former primarily reduced the biomass densities of the largest, three- and ≥four-year-old, whitefish (Figs. 2*a*, 2*b*), while the latter reduced also the biomass densities of the adult perch (Figs. 2*d*, 2*e*). Although the decrease in adult whitefish biomass densities in both fisheries led to a substantial increase in the biomass densities of whitefish prey species (particularly in *Daphnia* and *Leptodora*; Figs. 2*a*, 2*d*), the pattern was only seen cascading down one feeding link as the biomass densities of the prey of *Daphnia* and *Leptodora* (one of which is *Daphnia*) either remained unaltered or even increased (Figs. 2*c*, 2*f*). Reductions in adult perch biomass densities did not increase the biomass densities of their prey species at the same extent than reductions in adult whitefish densities (Figs. 2*b*, 2*e*). Three- and ≥four-year-old perch are piscivorous and their diet consists mostly of larval and juvenile fish (Supplementary Tables S1, S3[1]), whose biomass densities

did not increase much under either of the fishing scenarios. This is likely because of the balancing effect of reduced reproductive output in perch. The lack of a substantial increase of whitefish larvae and juveniles is a result of very low natural reproduction of whitefish (which is maintained mainly by stocking).

Although the traditional, reciprocal abundance cascade appears to be present when fisheries remove whitefish (as the biomass densities of two of their prey species increase), the cascading effect does not propagate throughout the food web. There were no substantial changes in the biomass densities of zooplankton species, other than *Leptodora* and *Daphnia* (Supplementary Figs. S3*a*, S3*c*[1]), or in the biomass densities of phytoplankton species (Supplementary Figs. S3*b*, S3*d*[1]) caused by either large or small-mesh fisheries.

Variation cascade

Although fisheries did not trigger an abundance cascade (as it only went down one link and did not propagate across the food web), it did trigger a variation cascade measured by the relative amplitude of the biomass density oscillation. Here, we look at the variation cascade in terms of altered oscillation within taxa instead of reciprocal cascade, where variation would increase and then decrease from one trophic level to another. In large-mesh fisheries, the amplitude increased among fish guilds targeted by fisheries as well as among fish guilds that were not, and among zoo- and phytoplankton species (Table 1). Biomass oscillation induced by large-mesh fisheries across trophic levels did not show any sign of dampening even after 150 years of fishing but, in fact, slightly increased over time (Fig. 3). This was indicated by negative half-life values.

Small-mesh fisheries, on the other hand, reduced biomass oscillation across trophic levels (Fig. 4). The relative amplitude that was used to quantify biomass oscillation was lower in small-mesh fisheries compared to large-mesh fisheries (Table 1). In

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Table 1. Relative (%) and absolute amplitude as a measure of oscillation among fished and non-fished guilds, zooplankton (all species combined; Supplementary Table S1[1]), and phytoplankton (all species combined; Supplementary Table S1[1]) in the absence and presence of large- and small-mesh fisheries.

	Trophic level	Before fishing		After fishing	
		Relative	Absolute	Relative	Absolute
Large-mesh	Fished guilds	5.77	4805	10.40	5484
	Non-fished guilds	7.85	4552	8.59	5059
	Zooplankton	4.40	4276	5.00	4764
	Phytoplankton	2.70	7649	3.24	9149
Small-mesh	Fished guilds	5.53	3612	4.42	1752
	Non-fished guilds	4.75	3615	2.41	1588
	Zooplankton	4.40	4276	2.21	2120
	Phytoplankton	2.70	7649	1.49	4244

Note: Notice that the two fisheries targeted different fish species, and therefore the values are different in the absence of fishing between the fishing gear among fished and non-fished guilds.

Fig. 3. Biomass oscillation caused by large-mesh fisheries in (*a*) fish life stages targeted by fishing (primarily three- and ≥four-year-old whitefish and ≥four-year-old perch), (*b*) fish life stages not targeted by fishing, (*c*) zooplankton (all species combined; Supplementary Table S1[1]), and (*d*) phytoplankton (all species combined; Supplementary Table S1[1]). Fishing started after 50 years and continued for 150 years. Vertical dotted lines indicate when fishing was started. Notice different scales on *y* axes.
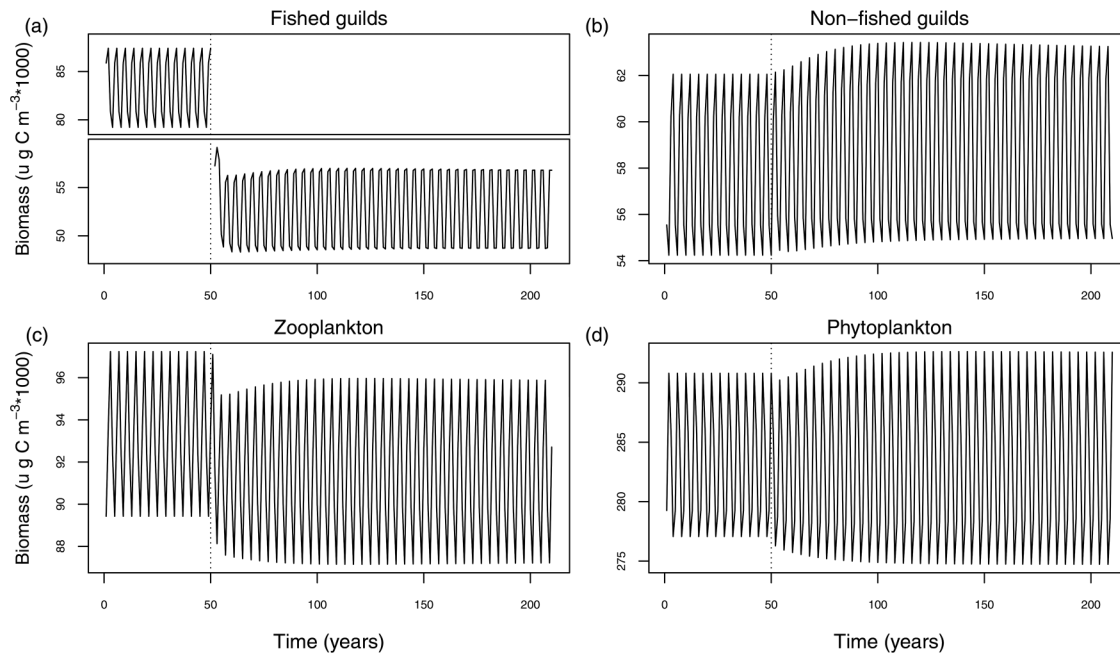
addition, half-life values were positive (ranging from 54.2 to 55.6 years), which indicate that oscillation dampened during the 150-year fishing period.

The oscillation increased over time when fisheries targeted even larger fish than large-mesh fisheries (Supplementary Fig. S4; Table S4[1]) and decreased when fisheries targeted on average smaller-sized fish than small-mesh fisheries (Supplementary Fig. S5; Table S4[1]).

The oscillation patterns were not substantially affected by a more moderate fishing effort level $E = 0.5$ (Supplementary Figs. S6, S7[1]). At a low effort level ($E = 0.25$), the differences in oscillation patterns between the two fisheries were not as pronounced as in high fishing efforts (Supplementary Figs. S8, S9[1]) and became similar to the oscillation in the absence of fisheries.

Low levels of environmental stochasticity (CV < 0.05) did not alter the oscillation pattern: fishing increased biomass variation in large-mesh fisheries and decreased variation in small-mesh fisheries, particularly at high ($E = 0.75$) and more moderate ($E = 0.5$)

fishing effort levels (Fig. 5). However, under high levels of environmental stochasticity the pattern disappeared and even led to increased variation in small-mesh fisheries among fish life stages targeted by fishing (Fig. 5). With a low to moderate level of environmental stochasticity (0.01 ≤ CV ≤ 0.05) the moving coefficient of variation of the biomass timeseries shows clear downward trend for small-mesh (and tiny-mesh fisheries) among fish guilds targeted by fisheries (Supplementary Fig. S10[1]), whereas an increase is visible for the large-mesh net fishery (Supplementary Fig. S10[1]). Among the fish guilds not targeted by fisheries, zooplankton, and phytoplankton only a slight decrease can be seen for the small-mesh (and tiny-mesh fisheries; Supplementary Figs. S11–S13[1]). Higher levels of environmental stochasticity mask or break the oscillatory patterns and any changes in their amplitude.

Discussion

We showed that, independent of the fishing gear (i.e., large-mesh or small-mesh), fishing did not trigger an abundance

Fig. 4. Biomass oscillation caused by small-mesh fisheries in (*a*) fish life stages targeted by fishing (primarily two-, three-, and ≥four-year-old whitefish and three- and ≥four-year-old perch), (*b*) fish life stages not targeted by fishing, (*c*) zooplankton (all species combined; Supplementary Table S1[1]), and (*d*) phytoplankton (all species combined; Supplementary Table S1[1]) in the absence and in the presence of small-mesh fisheries. Fishing started after 50 years and continued for 150 years. Vertical dotted line indicates when fishing was started. Notice different scales on *y* axes.
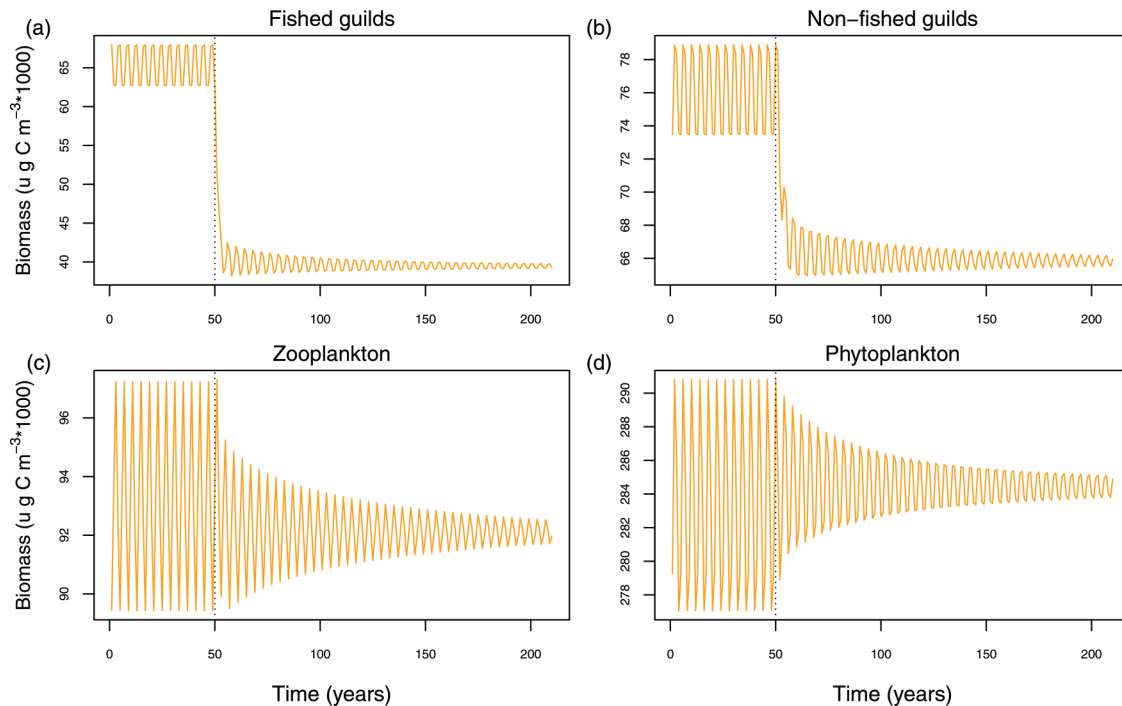
cascade (Fig. 2). However, both large-mesh and small-mesh fisheries triggered a variation cascade, which propagated across the food web. Because our model consists of a complex food web, not of a simple food chain, it is difficult to demonstrate a wide top-down cascade, where, for example, the removal of piscivorous fish increases the abundance of the smaller fish (larvae and juveniles of whitefish and perch) they prey upon, which would then reduce the zooplankton biomass. The lack of a reciprocal trophic cascade is at least partly caused by the food web structure: consumers can feed on different trophic levels, not only on the one directly below them. However, we demonstrated variation cascade in both fisheries by showing that a change in biomass oscillation propagated throughout the food web after the human-induced disturbance (i.e., fishing). In small-mesh fisheries, the biomass oscillation started to decrease within two decades after fishing was started at each trophic level (Fig. 4), whereas in large-mesh fisheries the biomass oscillation increased and did not seem to dampen even after a century (Fig. 3).

Abundance cascade

Removing adult whitefish from the ecosystem led to an increase in the abundance of their prey species *Daphnia* and *Leptodora*. These two species are the most consumed prey among adult whitefish while cyclopoid copepods, whose abundance slightly decreased (Fig. 2c), are less consumed prey (i.e., biomass gain from *Daphnia* and *Leptodora* was higher than biomass gain from cyclopoid copepods; Supplementary Table S3[1]). Fisheries-induced changes in the abundance of *Daphnia* and *Leptodora* did not cascade further down the food web (Figs. 2c, 2f). There are three likely explanations for this. First, *Leptodora*'s main prey species is *Daphnia* and fishing substantially increased the abundance of *Daphnia*. *Leptodora* occur at relatively low densities in LC; thus, they cannot consume *Daphnia* by large quantities. Second, *Daphnia* is a generalist (i.e., it preys unselectively on 16 zoo- and phytoplankton species from various

trophic levels; Supplementary Table S1[1]) and consequently has a high connectivity in the food web. This type of feeding diversity and omnivory has been suggested to buffer against abundance cascade (Bascompte et al. 2005; Borer et al. 2005). Furthermore, it highlights *Daphnia*'s role as an intermediate consumer in the food web. The final explanation for the lack of abundance cascade propagating across the food web is that in our model phytoplankton is very abundant; thus, no matter how much *Daphnia* feed on a zooplankton species that feed directly on phytoplankton (for example *Ciliata*; Supplementary Table S1[1]), *Daphnia* cannot substantially reduce the abundance of these ciliated protozoa.

Interestingly, the one-trophic-level effect was not as clear among perch and its prey. Unlike planktivorous whitefish, adult perch feed mostly on fish larvae and juveniles (Supplementary Table S3[1]). While the abundance of whitefish larvae was not altered substantially, the abundance of perch larvae increased when fishing targeted adult perch (in small-mesh fisheries). The increase in perch larvae biomass densities was likely caused by reduced predation by adult perch. Observing the biomass densities at the beginning of the growth season revealed that the densities of perch larvae increased by 22.7% (and whitefish larvae by 7.32%) in the presence of small-mesh fisheries. Even though removal of large perch might lower the overall reproductive output (although this ultimately depends on the biomass adults are able to allocate to reproduction), it simultaneously reduces predation upon fish larvae, hence initially increases their biomass densities (see also de Roos 2020).

The lack of abundance cascade propagating through the food web might not be surprising given that food webs are complex and as the complexity increases, the top-down effects might be less easy to distinguish (Mougi and Kondoh 2016) or may be counteracted by other indirect responses. Food webs that deviate from a linear food chain include interactions within a guild (e.g., competition) or among trophic levels (e.g., omnivory) and may show reduced cascade strength due to weaker and more diffuse

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Fig. 5. Analysis of the change in the biomass variation caused by fishing as a function of the environmental noise level. The vertical axis shows the coefficient of variation of biomass under fishing relative to the pre-fishing coefficient of variation. Values above (below) 100% (dashed black line) indicate cases where fishing increased (decreased) biomass variation. The rows represent three different values of fishing effort E. Each column is constructed for the combined biomass of a given group (fished guilds, non-fished guilds, zooplankton, and phytoplankton). Blue, red, yellow, and magenta lines represent different fishing gears: tiny-mesh net, small-mesh net, large-mesh net, and giant-mesh net, respectively. The points represent eight different environmental noise levels tested, characterized as the coefficient of variation of the autotroph carrying capacity K (0.01, 0.025, 0.05, 0.075, 0.1, 0.15, 0.2 and 0.25). The results are averages of 100 replicate runs with randomly generated normally distributed environmental noise. The case with the least environmental noise (0.01) is very similar to the deterministic case, and even with moderate noise levels of up to to 0.1, the results are quantitatively similar. Increasing the noise level further masks or completely breaks down the oscillatory pattern and the differences between the pre-fished and fished periods start to vanish.
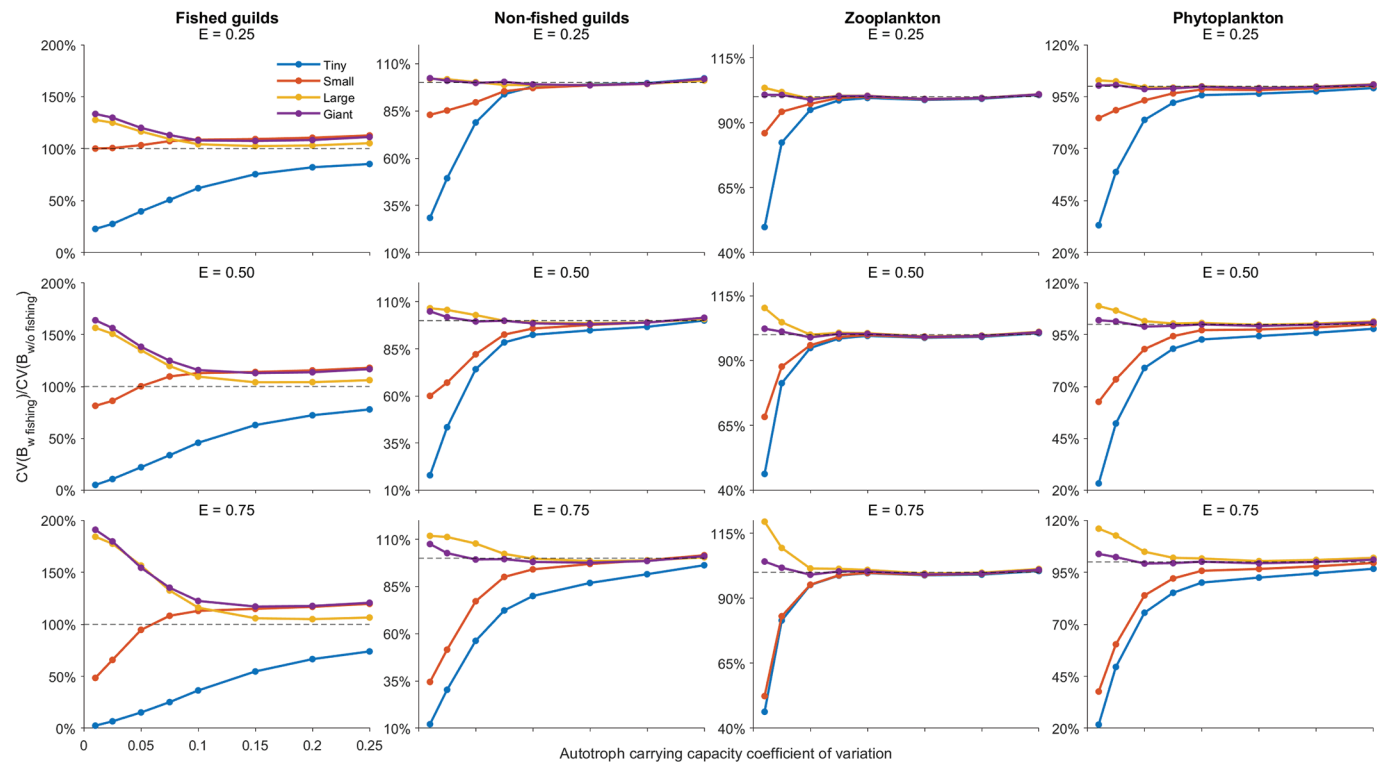

interactions among trophic levels (Fagan 1997; Leibold et al. 1997; Agrawal 1998). Furthermore, large diversity can stabilize the system and may influence the potential cascading effects of fishing (Frank et al. 2007; Baum and Worm 2009; but see Borer et al. 2005; O'Connor and Bruno 2009). Diverse systems are expected to have a high degree of redundancy of ecological function between species. Therefore, if some species are depleted, either by fishing or by increased predation pressure, other species will be able to occupy their niche and consequently avoid or dampen the trophic cascade. Finally, many trophic cascade studies are confounded by the issue of scale: a smaller study scale and short time scales favor the detection of trophic cascades (Sommer 2008). For example, mesocosm experiments have provided strong evidence for the prevalence of top-down control while single-lake studies have provided mixed evidence (e.g., Persson 1999; Polis 1999). Our study system fulfils the above-mentioned criteria (large study scale (in comparison to microcosm or mesocosm experiments), long time scale, and complex food web) suggesting that trophic cascades propagating across a food web might not be easily detected.

The complex nature of a food web compared to a food chain is illustrated in Fig. 6. When examining a random food chain detached from the food web, one could rather easily detect fisheries triggering an abundance cascade (Fig. 6a). The biomass of adult (three- and ≥four-year-old) perch decreases and the removal of these predatory guilds leads to an increase in larval fish biomass. This is accompanied by a decrease in the biomass densities of cyclopoid

copepods (Cyc), which are an important prey for fish larvae (Table S3[1]). This, in turn, coincides with an increase in the biomass densities of medium-sized *Ciliata* (Cil3) on which cyclopoid copepods feed. However, taking a broader look into a segment of the food web (notice that not all links are presented), the complex interactions are revealed (Fig. 6b). For example, despite the increase in larval fish biomass, the abundance of *Daphnia* (Cru) increases, not decreases, because fish larvae feed significantly less on *Daphnia* compared to cyclopoid copepods (Supplementary Table S3[1]) although fishing induces an increase in larval gain (biomass gained from the prey) from *Daphnia* because of its increased biomass density. The substantial increase of *Daphnia* is mainly caused by a simultaneous decrease in the biomass densities of adult whitefish, who also feed on *Daphnia* (not shown in Fig. 6). The decrease in cyclopoid copepods and large rotifer (Asp) biomass densities correspond with an increase in the densities of medium-sized *Ciliata* (Cil3), while the biomass densities of another medium-sized *Ciliata* species (Cil4) remain less altered. Similarly, although the two *Ciliata* prey on same species (Supplementary Table S1[1]), only the biomass densities of Cil3 increase. This is likely caused by the lowered predation pressure (decreased gain) by cyclopoid copepods. This segment of a food web is already more complex than a linear food chain even though it only displays less than 20% of the feeding links in the LC food web.

Fig. 6. (a) A randomly selected food chain of the Lake Constance (LC) food web. (b) A segment of the LC food web. Plots inside the nodes demonstrate changes in the biomass densities of a particular species in the presence and absence of small-mesh fisheries. Vertical line indicates when fishing was started. The colors of the nodes refer to different trophic levels (Supplementary Table S1[1]). The abbreviations of the species are explained in the text and in Supplementary Table S1[1]. The thickness of the arrows illustrates changes in feeding-link biomass gain (from feeding on prey) caused by small-mesh fisheries (solid arrow = gain increased, dotted arrow = gain decreased).
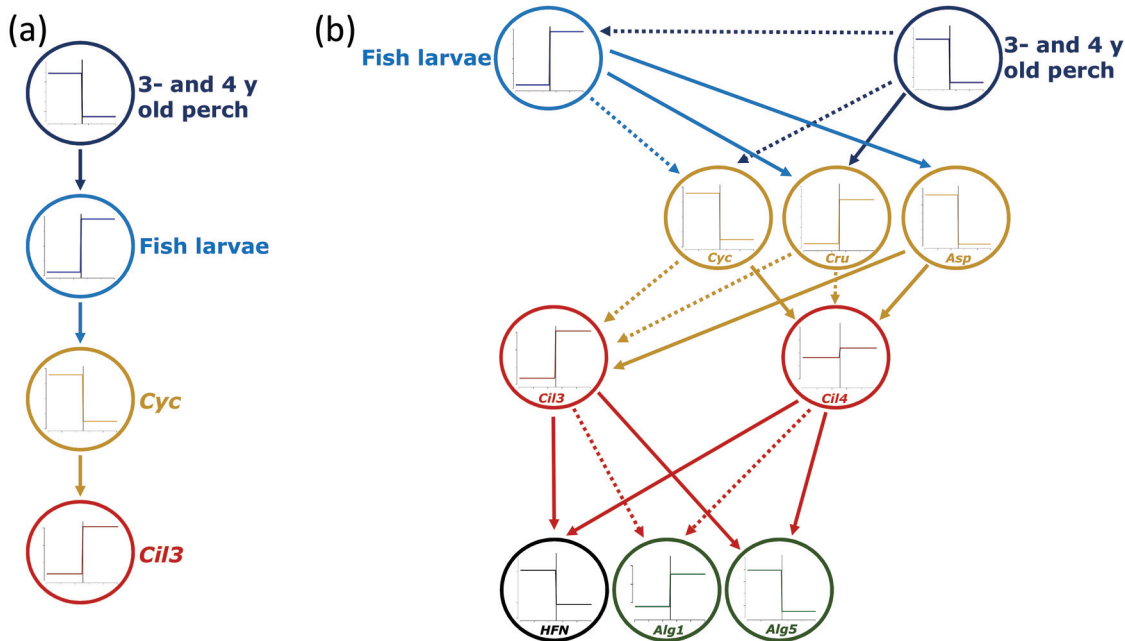
Variation cascade

While we found no evidence of fisheries-induced abundance cascade, a more unconventional method of measuring trophic cascade provided a strong signal: both fishing strategies changed biomass variation across trophic levels in the food web. Fishing is a great disturbance for the ecosystem, and it has been shown to increase density fluctuations among harvested populations (Hsieh et al. 2006; Anderson et al. 2008; Kuparinen et al. 2016) and even propagating down the food web (Kuparinen et al. 2016), likely owing to the removal of old and large individuals known to stabilize population dynamics. Indeed, in the large-mesh fisheries, biomass oscillation increased, albeit not as much as it decreased in small-mesh fisheries, potentially destabilizing the ecosystem. At least theoretically, variation cascade propagating across the food web can destabilize the entire ecosystem and lead to the loss of its resilience (Scheffer et al. 2001). Even though we cannot generalize these results across lakes or marine ecosystems with different environmental characteristics, we can illuminate the complexity of natural food webs and their potential responses to fisheries.

Interestingly, in small-mesh fisheries, the biomass oscillation decreased when fishing was started and continued to decrease over time. This might suggest that despite triggering a variation cascade, not all fishing strategies are equally harmful for the ecosystem. While large-mesh fisheries mainly removed the largest whitefish from the system (Fig. 2a), small-mesh fisheries distributed fishing mortality more widely across species and body sizes (Fig. 2d). It has been suggested that the ecosystem resilience can be improved by balanced exploitation (i.e., more moderate fishing mortality across a range of species and sizes; Law et al. 2012; Law et al. 2015). In their modeling study, Rochet and Benoît (2012) showed how fishing can amplify oscillation in the biomass flow. They also showed that when fishing was targeting the largest fish, the oscillations appeared at lower fishing intensity and had wider amplitude (see also Zhang et al. 2013). Similarly, we showed that in large-mesh fisheries, which targeted the largest whitefish,

oscillations increased over time. It has also been suggested that fishing on several trophic levels can dampen the abundance cascade (Andersen and Pedersen 2010).

Small-mesh fisheries removed large piscivorous perch from the ecosystem and thus increased the abundance of whitefish and perch larvae, particularly at the beginning of the growth season. Fish larvae appeared to be the key guilds stabilizing the ecosystem. Although one would intuitively think that the largest and oldest fish are the apex predators in this system because they are at the top of the food web and do not have natural predators, the newborn larvae have a more generalist foraging strategy and prey at different trophic levels. For example, a four-year-old whitefish feeds on only three zooplankton species (*Daphnia*, *Leptodora*, and cyclopoid copepods), whereas a whitefish or a perch larva feeds on two different *Ciliata* species and four different rotifer species (Supplementary Table S1[1]). Thus, the niche width of a larval fish is broader than that of an adult fish. Indeed, generalist-dominated systems are suggested to be more stable than specialist-dominated ones (Oksanen et al. 2001). Although it is known that apex predators play a key role in community dynamics and ecosystem stability (Rooney et al. 2006; Estes et al. 2011), it was rather surprising that these important predators in the LC system appeared to be the smallest fish larvae. Indeed, when we added perch larvae into the system in the presence of large-mesh fisheries, the biomass oscillation dampened over time (Supplementary Fig. S14[1]).

While it is known that some fishing strategies (e.g., balanced harvesting) can stabilize populations, demonstrations of fishing-induced variation cascades propagating across food webs are rare. Empirical studies focusing on fishing-induced abundance cascades do not provide direct evidence of variation cascades whether a clear abundance cascade is demonstrated (e.g., Frank et al. 2005; Gasche and Gascuel 2013) or not (Reid et al. 2000). Although many of these studies are based on relatively long-term data (e.g., Reid et al. 2000; Frank et al. 2005), not many of them have utilized a measure to study long-term temporal oscillation patterns. Daskalov et al. (2007) demonstrated that intense fishing

in the Black Sea triggered system-wide trophic cascades and decreased consumer control changed the amplitude of the trends significantly. However, the changes in variance did not match the changes in mean values and were either increasing or decreasing, depending on the trophic level (Daskalov et al. 2007). Kuparinen and colleagues showed that fishing can increase variation at different trophic levels even long after fishing has ceased (Kuparinen et al. 2016) but they did not explore how species' ecological functionalities could further affect the variation cascade pattern, neither did they look into any mechanistic explanation for the pattern or the effect of environmental stochasticity. A recent modeling study came up with a general theory for stability changes with the addition or removal of trophic levels in a linear food chain (Shanafelt and Loreau 2018). A species at the top of a food chain had highest stability and a species just under the top of a food chain had lowest stability. Hence, removing a top predator could destabilize the food chain more than removing a primary or secondary consumer. Our results, on the other hand, demonstrate a slightly different pattern: removing the largest and oldest top predators had an ecosystem stabilizing effect likely due to the increase in other key predator guilds in the system (i.e., whitefish and perch larvae). To understand the mechanisms behind variation cascade, it is important to separate fish life stages into their own guilds as they differ in their growth, metabolism, and energy allocation, and most importantly consume different prey than adults (van Leeuwen et al. 2013; de Roos 2020).

Our results are based on a validated food web model, but they remain somewhat theoretical as we cannot validate the results using empirical data from LC owing to the lack of long time series data across taxa and theoretical fishing simulations. Adding low levels of environmental stochasticity to the model did not change the oscillation patterns caused by different types of fisheries (Fig. 5, Supplementary Figs. S10–S13[1]). However, the oscillation patterns were either broken or masked by high levels of stochasticity (Fig. 5, Supplementary Figs. S10–S13[1]) as virtually any pattern can be masked with high enough levels of environmental noise. Our results are based on a single food web model parametrized for a freshwater system, and the generality of our findings, for example, on to marine systems, needs to be verified in future studies by constructing and parametrizing an ATN model to other aquatic food webs. Modeling of biomass flows within a complex aquatic food web is one tool we can use to better understand fisheries-induced trophic cascades, but other methods based on empirical data should be used to complement and verify these results. While the food web model we used certainly would benefit from further development (e.g., addition of abiotic factors or overwintering mortality), our results provide insights on how removing biomass of fish species with different ecological functions could affect the variability in the food web dynamics differently.

Conclusions

In the coming decades, there will be an urgent need to understand how human disturbances (e.g., removal of large amounts of fish by fishing and introduction of new species) alter aquatic food webs, their productivity, and resilience. Forecasting when, under what conditions and how trophic cascades may occur will help us to anticipate, prevent and potentially reverse the cascading effects of fishing or other human activities. We exemplified that detecting fisheries-induced trophic cascades can be challenging when approaching them from a complex food web perspective. We also propose a novel concept and measure to study trophic cascades, a measure that could describe ecosystem stability (Shanafelt and Loreau 2018). Instead of focusing on cascading effects measured only as average biomass densities, it can be useful to measure those also as biomass variation (e.g., using coefficient of variation in time series data). The response of ecosystem to disturbance and ecosystem stability are of crucial importance for managing the natural

resources, protecting aquatic ecosystems and aiming towards ecological resilience.

Data availability statement

Data are available in the Dryad Digital Repository: doi:10.5061/dryad.rn8pk0p9c.

Acknowledgements

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