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Title: Limited effects of size-selective harvesting and harvesting-induced life-history changes on the temporal variability of biomass dynamics in complex food webs

Year: 2023

Version: Published version

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Please cite the original version:

Nonaka, E., & Kuparinen, A. (2023). Limited effects of size-selective harvesting and harvesting-induced life-history changes on the temporal variability of biomass dynamics in complex food webs. Ecological Modelling, 476, Article 110150. https://doi.org/10.1016/j.ecolmodel.2022.110150

Ecological Modelling 476 (2023) 110150

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

Limited effects of size-selective harvesting and harvesting-induced life-history changes on the temporal variability of biomass dynamics in complex food webs

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ARTICLE INFO

Keywords:
Allometric trophic network (ATN) model
Ecological networks
Size-selective fishing
Fisheries-induced evolution
Niche model
Temporal variation

ABSTRACT

Harvesting has been implicated in destabilizing the abundances of exploited populations. Because selective harvesting often targets large individuals, some studies have proposed that exploited populations often experience demographic shifts toward younger, smaller individuals and become more sensitive to environmental fluctuations. The theory of consumer–resource dynamics has been applied to address the impacts of harvesting in simple modular food webs, but harvested populations are embedded in a complex food web in nature. In addition, exploited populations have been shown to undergo trait evolution or phenotypic changes toward early maturation at smaller sizes. Using an empirically derived complex food web model, Kuparinen et al. (2016. *Fishing-induced life-history changes degrade and destabilize harvested ecosystems*. Scientific Reports: 6, 22,245) demonstrated that exploited fish populations and other ecosystem properties increased variability due to harvesting and harvesting-induced life-history evolution in the absence of environmental fluctuations. In the present study, we examined a large set of simulated complex food webs to attest the generality of the findings in Kuparinen et al. (2016). We found that harvesting both increased and decreased temporal variability of fish biomass dynamics, especially in food webs with intrinsically oscillating dynamics, while the vast majority of the food webs did not experience destabilization. We also elucidated the large impacts of the shape of functional responses on food web structure, energy flow, and changes in temporal variability caused by harvesting. Our results suggest that the destabilizing or stabilizing effects of harvesting and harvesting-induced evolution importantly depend on the shape of functional responses in dynamical models of complex food webs and that food webs with intrinsically oscillating dynamics are more prone to changes in temporal variability caused by harvesting and harvesting-induced evolution.

1. Introduction

Size-selective harvesting, which preferentially removes individuals of certain sizes, has been implicated to result in phenotypic and potentially evolutionary changes in life-history traits related to survival and reproduction in exploited populations (Ernande et al., 2004; Heino et al., 2015; Kuparinen and Festa-Bianchet, 2016). It imposes high mortality and strong selection pressure typically on older and larger individuals and thus can truncate size structure (Barnett et al., 2017; Hsieh et al., 2006). The theory of life-history evolution predicts greater investment in reproduction and early maturation to evolve in populations undergoing high mortality in adults or equally across all life stages (resulting in smaller body size at maturity; Charlesworth, 1994; Law, 1979; Reznick and Ghalambor, 2005). As a consequence, populations experiencing high mortality in adults may consist more of younger and smaller individuals with higher reproductive capacities (Reznick et al., 1990; Stearns, 2000) and metabolic rate (Auer et al., 2018). The possibilities of fisheries-induced evolution (FIE) have been demonstrated by laboratory experiments of size-selective harvesting (Conover and Munch, 2002; Therkildsen et al., 2019; Uusi-Heikkilä et al., 2017) and indicated by a diverse array of species in the wild (Allendorf and Hard, 2009; Darimont et al., 2009; Heino et al., 2015; Jorgensen et al., 2007; Kuparinen and Festa-Bianchet, 2016). Over the last several decades, reductions in the body sizes of fishes have been

Abbreviations: ATN, Allometric trophic network; FIE, Fisheries-induced evolution.

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https://doi.org/10.1016/j.ecolmodel.2022.110150
Received 12 June 2022; Received in revised form 5 September 2022; Accepted 19 September 2022
Available online 8 December 2022
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observed in exploited populations in response to size-selective fishing (Devine et al., 2012; McClenachan, 2009; Olsen et al., 2004).

Evolutionary and plastic changes in life-history traits could modulate population growth rate, interaction strength, and energy flow up through food chains. Therefore, size-selective harvesting could alter the stability of populations (Bronikowski et al., 2002; Cameron et al., 2013) and of consumer–resource interactions (McCann, 2012; Rip and McCann, 2011). A modeling study by Kuparinen et al. (2016) showed that fishing-induced changes in life-history traits magnified temporal variation of intrinsic fish biomass dynamics and of other organisms over and above fishing even after fishing ceased, using an empirically parameterized bioenergetic food web model of a well-studied lake ecosystem. Although the notion that fishing often increases temporal variability of exploited fish populations appears to prevail (Anderson et al., 2008; Hsieh et al., 2006), the theory of consumer–resource interactions suggests that fishing could potentially either destabilize or stabilize fish populations through altered energy flow due to elevated metabolic rate and increased mortality of consumer populations (McCann, 2012; Rip and McCann, 2011). The generality of the effects of fishing and FIE on fish population dynamics suggested by existing studies remains unknown, albeit such information is highly relevant to sustainable management of fisheries ecosystems. Comprehensive empirical investigations are virtually impossible due to the lack of long-term fisheries and survey data that include not only measurements on relevant traits of focal species but also monitoring of the key prey species and the entire ecosystem dynamics. A complementary approach is to apply bioenergetic food web models, such as the one used by Kuparinen et al. (2016), to a large set of computer-generated ("synthetic") realistic food webs that encompass a wide variety of network structures. This is the path we take in the present study.

We investigated how typical it would be for fishing and fisheries-induced life-history trait changes (hereafter FIE; these changes can be evolutionary or plastic responses) to increase temporal variabilities of food web dynamics and examined the associations between food web structure and responses to fishing and FIE in a large set of synthetic food webs. To this end, we used a recently developed composite model by Nonaka and Kuparinen (2021) which adds stage structure to fish populations in synthetic food web topologies stochastically generated by the niche model (Williams and Martinez, 2000). The dynamical model uses the allometric trophic network (ATN) approach (Bland et al., 2019; Boit et al., 2012; Brose et al., 2006; Glaum et al., 2020a; Hale et al., 2020; Martinez et al., 2006; Martinez, 2020; Williams et al., 2007; Williams and Martinez, 2004), which utilizes allometric scaling relationships for parameterizing vital rates, predator–prey interactions, and energy flow. We simulated deterministically without external forcing the scenarios for fishing with (F-FIE) and without FIE (fishing only; F-O) on an identical set of food webs along a gradient of the shape of the functional responses of consumers. Functional responses describe how the consumption rate of a predator varies across prey density and have critical effects in models of population dynamics. The parameter, the so-called Hill exponent (q in Eq. (2) below), shifts the shape of functional responses from type II (hyperbolic) to III (sigmoidal), along which the dynamical stability of consumer–resource interactions increase (Murdoch and Oaten, 1975; Uszko et al., 2015). Type III functional response promotes prey persistence at low prey densities through reduced predator consumption rates presumably owing to changes in prey and predator behaviors (e.g., prey hiding in refugia or predators forming search image on more abundant prey, adaptively foraging, or switching prey). It substantially influences the dynamical stability of ATN models (Martinez et al., 2006; Williams and Martinez, 2004). We classified food webs by types of responses to the F-FIE and F-O scenarios and measured food web structure and energy flow to compare food webs that showed different types of temporal dynamics and responses.

2. Methods

2.1. Life-history structured allometric trophic network model (ATN)

The methods for generating food webs and the parameterization of the ATN are fully described in Nonaka and Kuparinen (2021; Fig. 1a). All the simulations were run in MATLAB with Statistical Toolbox and Parallel Computing Toolbox Release 2020b (The Mathworks, Inc., Natick, Massachusetts, United States). The code is available in the Dryad Digital Depository (https://datadryad.org/stash/dataset/doi:10.5061/dryad.z612jm6bk). Briefly, the model was built on the niche model (Williams and Martinez, 2000) with an extension to add life-history stages to a subset of "trophic species." A trophic species consists of one or more taxa that share the same sets of predators and prey (Cohen et al., 1990; Havens, 1992). Some of the trophic species were grouped based on niche overlap to form a stage-structured population. The minimum overlap between feeding ranges to be qualified as consecutive stages of the same stage-structured fish taxon was set to 20% based on a literature survey (Nonaka and Kuparinen, 2021). Relative body masses are assigned to the terminal stages of stage-structured species and invertebrates based on the short-weighted trophic levels (Williams and Martinez, 2004) in accordance with the theory of allometric predator–prey body mass ratio (Brose et al., 2006). We used the von Bertalanffy isometric growth curve (Wootton, 1998) to define the masses of younger stage classes (Table 1). Because of this way of parameterization, the final predator–prey body mass ratios deviated from the theoretical mass ratio, but the shape of the distribution conformed to the empirical data (Brose et al., 2006, see the online appendix for Nonaka and Kuparinen 2021). It originally calculates body sizes (lengths) of fish as a function of age (Pauly 1980, Froese & Binohlan 2000), while we used ontogenetic stages instead because age and stages are practically related in many fishes (e.g., perch, white fish) and in our model (see below the use of the Leslie matrix).

We applied the ATN to the food webs to simulate population biomass dynamics (Brose et al., 2006). The population dynamics of the species and life-history stages in the food web were described by a set of ordinary differential equations (ODE), which encoded the rates of biomass changes during a growing season. The population dynamics within the food webs were formulated as a multispecies consumer–resource model (Yodzis and Innes 1992; Brose et al., 2006; Boit et al., 2012; Bland et al., 2019), which was originally developed by Yodzis and Innes (1992) and has been further developed and analyzed by a number of studies (Bland et al., 2019; Boit et al., 2012; Brose et al., 2006; Glaum et al., 2020a; Hale et al., 2020; Martinez et al., 2006; Martinez, 2020; Williams et al., 2007; Williams and Martinez, 2004). Our parameterization followed the standard procedure for ATN models published elsewhere (Bland et al., 2019; Brose et al., 2006; Nonaka and Kuparinen, 2021). The population dynamics were encapsulated in the following equations.

$$\frac{dB_i}{dt} = \overbrace{g_i\left(1 - \sum_{j\in autotrophs} \frac{B_j}{K}\right)B_i}^{\text{logistic growth of autotrophs}} - \overbrace{\sum_{j\in\ consumers} x_j y_{ji} B_j \frac{F_{ji}}{e_{ji}}}^{\text{loss to grazing}} \tag{1}$$

$$\frac{dB_i}{dt} = \underbrace{-f_m x_i B_i}_{\text{metabolic loss}} + \underbrace{\sum_{j\in resources} f_a x_i y_{ij} B_i F_{ij}}_{\text{dietary intake("gain")}} - \underbrace{\sum_{j\in consumers} x_j y_{ji} B_j \frac{F_{ji}}{e_{ji}}}_{\text{loss to predation}} - \underbrace{F_{\max} S_{stage} B_i}_{\text{loss to selective fishing}} . \tag{2}$$

Here, B_i was the biomass of species i, g_i was the intrinsic growth rate of autotroph i, K was the carrying capacity, x_i was the metabolic rate of consumer i, y_{ij} was the maximum consumption rate relative to metabolic rate, e_{ij} was the assimilation efficiency of predator i eating prey j, f_m was the fraction of assimilated carbon lost for maintenance, and f_a was the fraction of assimilated carbon that contributes to biomass growth (see Table 2a for parameter definitions and values). F_{max} (maximum fishing intensity) and S_{stage} (stage-specific harvesting selectivity) together

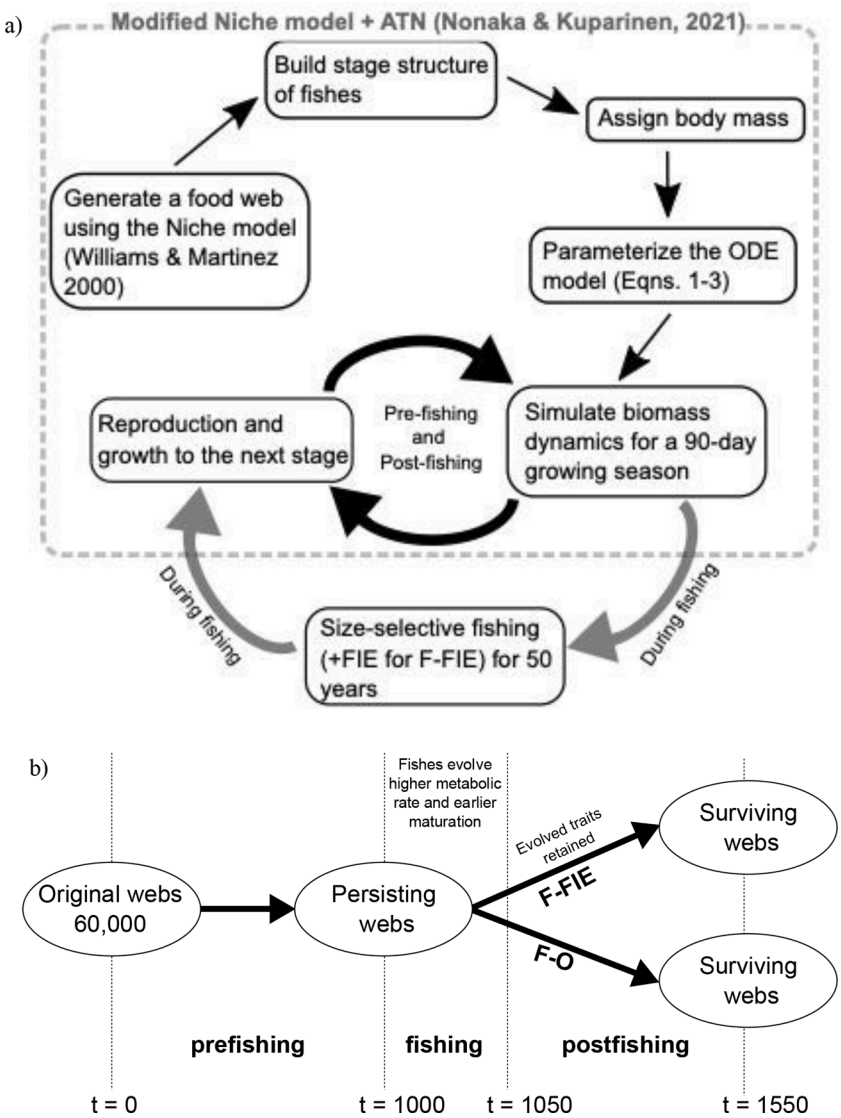

Fig. 1. a) A conceptual diagram of the model. This paper added selective fishing and fisheries-induced phenotypic changes (FIE) to the model developed by Nonaka and Kuparinen (2021) to analyze their impacts on fish food web dynamics. b) Simulation design. Persisting webs were the webs reached to the end of the pre-fishing period, all the nodes of persisting species/fish stages were connected in one network, no invertebrates were without predators, and at least one fish with 3 or more stages remained. F-FIE=fishing and fisheries-induced evolution. F-*O* = fishing only.

determined the proportion of biomass removed by fishing (see*2.2 Implementing fishing andfisheries-induced evolution*). F_{ij} was the functional response of consumer *i* when dealing with prey *j* (Bland et al., 2019; Boit et al., 2012):

$$F_{ij} = \frac{\sum_{l \in resources} \frac{\omega_{ij}}{\omega_{il}} B_j^q}{B_{0_{ij}}^q + \sum_{k \in consumer} \left(c_{kj} p_{ik} B_k B_{0_{kj}}^q \right) + \sum_{l \in resources} \left(\frac{\omega_{il}}{\sum_{l \in resources} \omega_{il}} B_l^q \right)} \quad (3)$$

ω_{ij} was the diet preference parameter, and we assumed that fishes preferred fish to invertebrates and invertebrates to basal species as food items if they were included in their diets (Table 2a; Nonaka and Kuparinen 2021). ω_{ij} was normalized by the sum of preferences toward all resources eaten by *j* to obtain relative preference. Likewise, we assumed that invertebrates preferred invertebrates over fish and basal species (Table 2a). $B_{o_{ij}}$ was the half saturation constant of consumer *i* eating prey *j*, which was the density of *j* at which *i* achieved half its maximum consumption rate (Table 2a; Williams, 2008). The Hill exponent *q* of the functional response was varied between 1.05 and 1.65 by an increment of 0.15. This range was chosen because $q = 1$ and $q = 2$ correspond to type II and III functional responses, respectively, and because past ATN studies used *q* between 1.2 and 1.5 (see *4.2. The effect of q (Hill exponent of functional responses) and the choices of q by previous studies*; Williams and Martinez 2004b, Martinez et al., 2006). The second term in the denominator encoded interference competition between consumer *i* and *k* which shared the fraction p_{ik} of resource *j* at an intensity specified by the coefficient c_{kj} (Table 2a). We assumed only intraspecific interference competition and no interspecific or between-stage interference competition for this study (i.e., $c_{kj} = 0$ for $k \neq i$; see *4.4. Limitation of the model* in Discussion). Each year consisted of a 90-day growing season (90 time-steps in the ODE Solver) followed by a non-growing season where surplus energy (dietary intake minus all the losses in Eqn (2)) was allocated to growth and reproduction. The proportion allocated to reproduction increased linearly with stage and was none (0) for the first stage and 0.2 (I_{max}) for the terminal stage with an equal increment between stages (Table 2a; Kuparinen et al., 2016, Nonaka and Kuparinen 2021). Fish in the terminal stage additionally reproduced in exchange for 30% of their biomass (Roff, 1992; Wootton, 1998). The fraction of mature individuals of fish at each life stage was determined by a logistic function which specified that 50% of individuals were mature halfway to the terminal stage (Table 1). We used the Leslie matrix to shift the majority of somatic biomass to the next stage via growth and to convert it to new recruitment via reproduction at the terminal stage (Table 1). A fraction, a_h, of a stage class remained in the same stage to reflect variation in growth (Table 2a). There was no gain or loss of biomass between consecutive growing seasons (i.e., no winter mortality).

Table 1
Model components.

Model component	Formulation	Sources and notes
Body mass at stage h (The von Bertalanffy isometric growth curve)	$W_h = W_\infty(1-e^{-\kappa(h-h_0)})^3$, where $\kappa = \frac{3}{v}$ $h \in \{1,\ldots,v\}$ v = terminal stage class of the fish $\left(\frac{W_v}{W_\infty}\right) = 0.9$	Pauly (1980), Froese & Binohlan (2000), Bland et al. (2019) The value of h_0 is obtained by solving the equation for h_0 with W_h= 0 and W_v from the predator-prey body mass ratio.
The fraction of mature fish at each stage	$P_{mature} = 1/(1+e^{-3(h-h_{50})})$ h_{50} = the stage at which 50% of individuals are mature	Kuparinen et al. (2016) We assume h_{50} occurs halfway through to the terminal stage.
Investment to reproduction	$I = (h - - 1)(I_{max}/(v-1))$ I_{max} = maximum investment = 0.2	Kuparinen et al. (2016)
The Leslie matrix to model growth and reproduction by the terminal stage between growing seasons	$\begin{pmatrix} B_{i,1} \\ B_{i,2} \\ B_{i,3} \\ \vdots \\ B_{i,v} \end{pmatrix}_{t+1} = \begin{pmatrix} a_1 & 0 & 0 & 0 & b_v \\ b_1 & a_2 & 0 & 0 & 0 \\ 0 & b_2 & a_3 & 0 & 0 \\ 0 & 0 & \ddots & \ddots & 0 \\ 0 & 0 & 0 & b_{v-1} & a_v \end{pmatrix} \begin{pmatrix} B_{i,0} \\ B_{i,1} \\ B_{i,2} \\ \vdots \\ B_{i,v} \end{pmatrix}_t$ b_h = the proportion of biomass in stage h to be shifted to stage $h+1$ (or to stage 1 for $h = v$), a_h = the proportion of biomass in stage h to remain in the same stage	Modified from Bland et al. (2019) Younger reproducing stages reproduce through surplus energy, which is accounted for separately. Terminal stages reproduce through surplus energy and in exchange for biomass.
Stage-specific harvesting selectivity	$S_{stage} = 1/(1+e^{-2(h-v/2)})$, for $h > 1$ $S_{stage}(h=1) = 0$	Kuparinen et al. (2016)

We generated 60,000 networks of 60 nodes (S_0) and connectance (C) equal to 0.15, which is a commonly used value of connectance in ATN models (Berlow et al., 2009; Bland et al., 2019; Dunne et al., 2002; Martinez et al., 2012), with error tolerance at 0.025 (i.e., webs with C between 0.1475 and 0.1525 were accepted) containing between 2 and 6 fishes (N_{fishes}) with at least 3 and up to 5 stages ($Nstage_{min}$, $Nstage_{max}$; Table 2b). Taxa with trophic level (Th_{fish}) > 2 were eligible to become a fish node (i.e., need to include at least one non-basal species in diet). We then ran the ATN on each network from random initial biomasses uniformly distributed between 0.1 and 100 μgC/L. Taxa were considered extinct when the biomass was less than 10^{-6} μgC/L or "invalid" if the biomass surpassed 10^{12} μgC/L. This occurred because the terminal stage could accumulate large biomass over time (70% of biomass remained in the last stage) and some food webs allowed it to become very large. At the end of each growing season, fishes that retained only older stages, but not younger ones, for more than 10 years were removed as extinct. Food webs were regarded as persistent if simulations lasted for 1000 years, all the nodes of persisting species were connected in one network, no invertebrates were without predators, and at least one fish with 3 or more stages remained ("the qualifying criteria"). We refer to these selected webs as "persisting webs" below (Fig. 1b).

2.2. Implementing fishing and fisheries-induced evolution (F-FIE and F-O scenarios)

On the persisting webs, we implemented two scenarios: (1) fishing and associated fisheries-induced life-history evolution (F-FIE) and (2) fishing only (F-O) (Fig. 1b). Following Kuparinen et al. (2016), we set stage-specific fishing selectivity (S_{stage}) to vary by stage, starting with zero in the first stage (Table 1). For example, for a fish species with 5 stage classes, S_{stage} is 0, 0.27, 0.73, 0.95, and 0.99 for stage-classes 1, 2, 3, 4, and 5, respectively. Non-fish trophic species were not subjected to fishing. Fishing effort (instantaneous fishing mortality rate, F_{max}) was set at 0.5, as motivated by the empirical rate from Lake Constance used by Kuparinen et al. (2016). We imposed fisheries-induced changes in life histories, namely the onset of maturity and stage-specific metabolic rate, to investigate their effects on fish biomass dynamics. As in Kuparinen et al. (2016), during the fishing period, the age at 50% maturity in fishes was advanced by 0.5% per year (younger and smaller size at maturity) and fishes' metabolic rate was increased by 10^{-4} per year (Andersen and Pedersen, 2009; Audzijonyte et al., 2013a; Darimont et al., 2009; Kuparinen et al., 2016). We assumed that evolutionary recovery from fishing was very slow (Conover et al., 2009; Enberg et al., 2009; Jorgensen et al., 2007; Kuparinen and Merilä, 2007; Law, 2000; Law et al., 1989), so that fishes retained the life-history traits attained at the end of the fishing period unchanged during the post-fishing period. We first ensured that the biomasses of the species in the persisting webs settled at dynamic equilibria (stable or stable oscillations) and then subjected the fish populations to fishing and FIE for 50 years followed by 500 years of no fishing (F-FIE scenario). In the F-O scenario, no FIE was imposed during the fishing period (Fig. 1). The model was run for a long post-fishing period to observe the dynamics beyond the transients after fishing ceased.

2.3. Determining the temporal variability of fish biomass dynamics

Coefficients of variation (CV) were calculated as the standard deviation of $log_{10}(biomass)$ divided by the absolute value of the mean across time for each fish stage. The maximum CV among stages was used to characterize the temporal variability of the fish biomass dynamics of a food web. We used the maximum, not the mean, to better capture the sensitivity of population fluctuations. CVs were calculated separately for the pre-fishing period from time step 901 to 1000 (CV_{pre}) and for the post-fishing period from time step 1451 to 1550 (CV_{post}) or from the last 50 time steps if the fish populations went extinct before the end of simulations.

To address the main question regarding the additional effects of FIE more directly, we classified the simulated food webs by their responses to the F-FIE and F-O treatments. Because a set of identical food webs were subjected to the two scenarios, we considered their differential responses as isolated effects of FIE. We categorized the food webs into a 5 × 5 contingency matrix. (For the definitions of the response categories, see Table 3). The combinations of responses were further classified into "consistent" (same responses to F-FIE and F-O), "higher destabilization in F-FIE", or "higher destabilization in F-O". For the webs that were either "destabilized" or "stabilized" (hereafter refers to webs that increased and decreased temporal variability, respectively) consistently between the two scenarios, the levels of changes in temporal variability between F-FIE and F-O were quantitatively compared and assigned one of the three categories above (Table 3).

Table 2

a. Parameter definitions and values used in this study for the allometric trophic network (ATN) model.

Parameters	Definition	Value	Sources or remarks
Z	Body mass ratio	$10^{2.6}$ for fish predators and prey $10^{1.15}$ for invertebrate predators and prey	Brose et al. (2006)
g_i	Autotroph intrinsic growth rate for i	Randomly drown from $0.8 < N(0.9, 0.5) < 1$	Bland et al. (2019)
K	Autotroph carrying capacity	540 $\mu gC/L$	Boit et al. (2012); Bland et al. (2019)
x_i	Mass specific metabolic rate of i	0 for autotrophs $0.314M_i^{-0.15}$ for invertebrates $0.88M_i^{-0.11}$ for fish	Bland et al. (2019); de Castro & Gaedke (2008); Killen et al. (2007, 2010)
y_{ij}	Maximum consumption rate of i eating j	4 for fish 8 for invertebrates	Brose et al. (2006); Boit et al. (2012)
e_{ij}	Assimilation efficiency of i eating j	0.95 when j is a fish 0.75 when j is an invertebrate 0.45 when j is an autotroph	Kelso (1972); Elliott (1976), Gavoni et al. (1986); Yodzis and Innes (1992); Brose et al. (2006)
f_m	Fraction of assimilated carbon respired for maintenance of basic bodily functions	0.05	Modified from Bland et al. (2019); Boit et al. (2012)
f_a	Fraction of assimilated carbon that contributes to growth	0.5	Modified from Bland et al. (2019); Boit et al. (2012)
q	Hill exponent of functional response (Eqn. (3))	Varied between 1.05 and 1.65 by an increment of 0.15	Williams & Martinez (2004); Martinez et al. (2006)
ω_{ij}	Prey preference (relative to toward autotrophs)	When i is a fish, 500 times toward fishes 200 times toward invertebrates When i is an invertebrate, 100 times toward invertebrates	Fishes do not eat much autotrophs in temperate and northern regions (Gonzalez-Bergonzoni et al. 2012; Vejříková et al. 2016). Fish needs to eat fish to grow fast and large (Post 2003; Juanes et al. 2002). The values are calibrated to achieve little consumption of autotrophs by fishes with animal prey in the diets.
$B_{o_{ij}}$	Half saturation density of i eating j	1.5 $\mu gC/L$ when an invertebrate i eats j 15 $\mu gC/L$ when fish i eats fish j 20 $\mu gC/L$ when fish i eats omnivore j 150 $\mu gC/L$ when fish i eats small herbivores j (more than 50 times smaller than the fish in body mass) 15 $\mu gC/L$ when fish i eats large herbivores j (not as much smaller than the fish in body mass)	Tonin (2011); Martinez et al. (2012); Bland et al. (2019) See Fig. 1 in Bland et al. (2019) Herbivores are organisms whose diets consist of autotrophs for more than 70% (Bland et al., 2019).
c_{ij}	Consumer interference competition coefficient of i eating j	Randomly drawn from $0 \leq Exp(\lambda = 5) \leq 0.5$ when k is an invertebrate 3×10^{-4} when fish k eats fish j $10^{-4}$when fish k eats omnivore j 1 when fish i eats small herbivore j $10^{-4}$when fish k eats large herbivore j	Tonin 2011; Martinez et al., 2012; Bland et al., 2019 See Fig. 1 in Bland et al. (2019) All interspecific interference competition for feeding on prey j, (c_{kj}), was set to zero (i.e., $c_{kj} = 0$ for $k \neq i$; intraspecific (within-node) interference competition only).
p_{ij}	the fraction of resources of consumer i shared with consumer j	(the number of prey i shares with j)/the number of i's prey	Bland et al. (2019)
$1 - I$	Fraction of biomass invested to growth	1 for the first stage class 0.8 for the last stage class	Kuparinen et al. (2016) I = investment to reproduction (Table 1)
P_{mature}	Probability of reaching maturation at stage h, $h = 1, 2, \ldots, n$	0 for the first stage class $(1 + e^{-3(n-n_{50})})^{-1}$ for higher stages, where $n_{50} = \frac{n}{2}$ is the stage at which 50% of the individuals become mature	Kuparinen et al. (2016)
a_h	Fraction of biomass staying in the same stage	0.05 for $h = 1, \ldots, n-1$ 0.7 for $h = v$	Fish in the terminal stage reproduces by converting 30% of total biomass to offspring regardless of surplus energy.
b_h	Fraction of biomass moving to the next stage	$1 - a_h$	*i.e.*, $b_v = 0.3$
L	Number of days in a growing season	90	A typical length of a growing season in northern temperate regions (Kuparinen et al., 2016; Bland et al., 2019)
$Th_{extinct}$	Extinction threshold	10^{-6} $\mu gC/L$	When biomass goes below this value, the population is considered extinct
$Th_{explode}$	Explosion threshold	10^{12} $\mu gC/L$	When biomass exceeds this value, the population is considered no longer sustainable.
$h_{50}IncRate$	The rate of advances in stage at 50% maturity	5×10^{-3}per year	Kuparinen et al. (2016) and citations thereof.
$metIncRate$	The rate of increase in metabolism	10^{-4}per year	Kuparinen et al. (2016) and citations thereof.
F_{max}	Maximum fishing intensity	0.5 (50% of fish biomass in target stages is harvested)	Kuparinen et al. (2016)

(*continued on next page*)

Table 2 (*continued*)

b. Parameter definitions and values used in the modified niche model to generate food webs (Nonaka and Kuparinen 2021).

Parameter	Definition	Value used	Sources or remarks
S_0	Number of species	60	
C	Connectance (proportion of realized links (L) out of all possible, L/S_0^2)	0.15	Berlow et al. (2009); Martinez et al. (2012); Bland et al. (2019) Dunne et al. (2002) compiled empirically measured connectance and reported that it ranged between 0.03 and 0.3.
C_{error}	Error tolerance on connectance	0.025	Bland et al. (2019)
N_{fishes}	The number of stage structured fish species	Between 2 and 6	Reasonable numbers of naturally cooccurring fish species in a community
Th_{fish}	A node at the trophic level > Th_{fish} can become a fish stage	2	The diet of fishes should include non-autotrophs (trophic level of pure herbivores is 2)
OL_{min}	Minimum overlap of niche ranges between consecutive stages of a fish	0.2	In terms of the fraction of the union of the two feeding ranges
$Nstage_{max}$	The maximum number of stages a fish species can have	5	Reasonable maximum numbers of fish stages
$Nstage_{min}$	The minimum number of stages a fish species should have	3	Reasonable minimum numbers of fish stages

2.4. Quantifying food web structure and energy flow

We used common network metrics in complex food web studies to quantify the basic structures of food webs (Table 4; Dunne, 2009; Gross et al., 2009; Williams and Martinez, 2008) and food web energetics by measuring the slopes of biomass spectra and the amounts and variation of energy influxes gained by fishes. Because we wanted to compare the food web structure before and after the fishing period (but not during the fishing period due to difficulties with removing transient dynamics), we measured these quantities with regard only to persisting species (i.e., "filtered" by the ATN dynamics) in the last 25 years of both the pre-fishing and the post-fishing periods (or the last 25 years before collapse). The slopes of biomass spectra were obtained by fitting a linear model with biomass in trophic levels as the response variable and body mass as the explanatory variable (Trebilco et al. 2013, Woodson et al. 2018). The model output the gain metrics containing the pairwise "gain" term (energy influxes) of the biomass rate equations Eqns. (1) and (2) integrated over a growing season. We took the mean across $log_{10}(gain)$ in the last 100 years of the pre-fishing and post-fishing periods (or minimum of 25 years before collapse) to calculate CVs, skewness (here skewness is invariant to scaling and shifting of distributions), and total sum across incoming links for all the fish stages.

Table 3
Classification of fish biomass dynamics in this study.

Within each scenario (F-FIE or F-O)	
Stable (i.e., not temporally variable)	$CV < 0.05$
Unstable, oscillating	$CV > 0.05$
Destabilization by fishing (and FIE)	$(CV_{post} - CV_{pre}) > 0.05$
Stabilization by fishing (and FIE)	$(CV_{pre} - CV_{post}) > 0.05$
(De)stabilization after fishing or not	
No change in temporal variability	$abs(CV_{post} - CV_{pre}) < 0.05$
Stabilization by fishing (and FIE)	$(CV_{pre} - CV_{post}) > 0.05$
Destabilization by fishing (and FIE)	$(CV_{post} - CV_{pre}) > 0.05$
Collapsed during or after fishing	No fish with intact stage structure remained in these periods
Contingency table (Fig. 3)	
Qualitative comparisons (No change, Collapse/during fishing, Collapse/after fishing)	
Consistent (blue)	Same qualitative responses to F-FIE and F-O (in the diagonal)
Higher destabilization in F-FIE (orange)	F-FIE caused greater destabilization than F-O in the destabilization hierarchy*
Higher destabilization in F-O (green)	F-O caused greater destabilization than F-FIE in the destabilization hierarchy*
Quantitative comparisons (Destabilized, Stabilized)	
Consistent (blue)	$abs(CV_{post,F\text{-}FIE} - CV_{post,F\text{-}O}) < 0.05$
Higher destabilization in F-FIE (orange)	$(CV_{post,F\text{-}FIE} - CV_{post,F\text{-}O}) > 0.05$
Higher destabilization in F-O (green)	$(CV_{post,F\text{-}O} - CV_{post,F\text{-}FIE}) > 0.05$

* Destabilization hierarchy: Collapse/during > Collapse/after > Destabilized > No change > Stabilized.

3. Results

3.1. Temporal variability of fish biomass dynamics

The proportion of persisting and qualified webs increased with q, while the proportion of oscillating qualified webs generally decreased (Fig. 2a). Food webs with stably oscillating biomass dynamics were rare. Almost the same number of food webs reached the end of simulations (i.e., 1550 years) in the F-FIE and F-O scenarios.

The distributions of CVs of energy gain by fishes were highly skewed to the right, and the frequency rapidly and continuously declined toward larger CVs. Categorizing simulated time series with CV > 0.05 as temporally variable (i.e., "unstable") best matched visual inspection of subsets of the time series (Fig. S1). The distributions of absolute differences between CV_{pre} and CV_{post} were wide but mostly concentrated near 0 (Fig. S2). The absolute differences greater than 0.05 appeared the most

Table 4
Network metrics used in this study and their definitions.

Name	definition
num_spp	Number of trophic species (nodes)
link_dens	Link density (L/S = total number of links/total number of nodes)
prop_fish_stages	Proportion of fish stages
prop_inverts	Proportion of invertebrates
prop_basal	Proportion of basal species
prop_intermed	Proportion of intermediate species (species that have both predators and prey)
prop_top	Proportion of top species (species that do not have predators)
prop_herbiv	Proportion of herbivores (feed only on basal species)
prop_cannib	Proportion of cannibals (including inter-stage cannibals)
prop_omniv	Proportion of omnivores (species that feed on prey at different trophic levels)
GenSD	Standard deviation of generality (the number of prey)
VulSD	Standard deviation of vulnerability (the number of predators)
max_TL	Maximum trophic level
ShPath_avg	Average shortest path
max_TL_fish	Maximum trophic level of fish
bm_spectra_slope	Slope of biomass spectra
fish_energy_influx	Total amount of energy influxes into fishes
gain_skew	Skewness of the distribution of normalized energy influxes to fishes
gain_CV	Coefficient of variation of normalized energy influxes to fishes

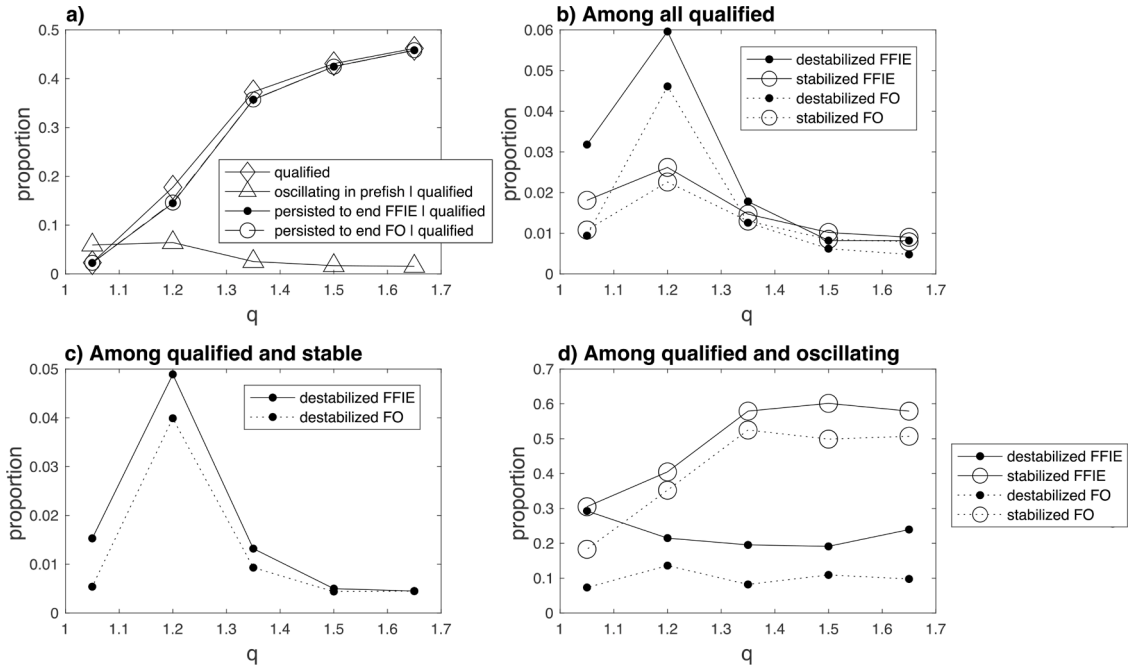

Fig. 2. a) The proportions of qualified webs (i.e., reached 1000th year) containing at least one oscillating fish stage and of surviving webs (i.e., reached 1550th year), from the F-FIE and F-O scenarios. b) The proportions of destabilized (filled circle) and stabilized (open circle) webs among all the qualified webs. c) The proportions of destabilized webs that were stable in the pre-fishing period. d) The proportions of destabilized and stabilized webs that were oscillating in the pre-fishing period.

adequate to indicate differences in temporal variability in comparisons with visual inspection (Fig. S3). Hence, we categorized food web dynamics as either "stable" (CV_{pre}, $CV_{post} < 0.05$) or "unstable" (i.e., oscillating) (CV_{pre}, $CV_{post} > 0.05$) and determined that fishing (and FIE for F-FIE) increased the variability of the dynamics if ($CV_{post} - CV_{pre}$) > 0.05 and reduced if ($CV_{pre} - CV_{post}$) > 0.05 (Table 3).

The majority of webs did not change temporal variability before and after the fishing period. The proportions of the webs that became more (destabilized) or less (stabilized) temporally variable were hence small but notably peaked at $q = 1.2$ (Fig. 2b). The peak was dominated by food webs that were stable prior to fishing (Fig. 2b, c). Among the oscillating webs, the proportions of stabilized webs increased with the values of q up to 1.35, after which they stayed similar, while the proportions of destabilized webs remained roughly constant (Fig. 2d). The proportions of food webs that changed temporal variability, either increased or decreased, were greater under the F-FIE than the F-O scenario across all the values of q examined, indicating additional effects of FIE on the temporal variability of food web dynamics.

Among the webs with oscillating dynamics, the proportions of the webs that were more negatively affected or more destabilized by F-FIE than by F-O were higher than those affected more by F-O than by F-FIE at lower values of q (Fig. 3). At higher values of q, the two became similar. For stable webs, most webs exhibited no change in both scenarios (Fig. S4). This result mirrored the above finding that FIE had additional effects on the temporal variability of food web dynamics beyond the effects of fishing alone at lower values of q.

3.2. Food web structure and energy flow

The modified niche model generated food webs with a wide variety of network structural properties (Fig. S5). The values of the network structural metrics of the persisting food webs also showed high variation (Fig. 4). The mean trend almost monotonically increased or decreased along with q, and the patterns were similar among stabilized, destabilized, and unchanged webs in both the pre-fishing and post-fishing periods (Fig. 4a-o). As q increased, the persisting webs contained more species, more links, proportionally more intermediate and invertebrate species, and correspondingly proportionally fewer fishes and basal species. The patterns of the proportions of cannibals and omnivores and of maximum trophic levels reflected the compositional change (i.e., more fish stages). The destabilized and stabilized food webs on average had slightly lower proportions of basal species and slightly higher proportions of fishes that occupied marginally higher trophic levels than did the webs whose temporal variability not change before and after fishing (Fig. 4c,o).

The mean trend for the slopes of biomass spectra increased with increasing q, indicating that the shapes of biomass pyramids became less bottom heavy as q increased (Fig. 4p). The total energy gained by the fishes also increased with q (Fig. 4q). These increasing patterns together with increasing patterns of maximum trophic levels suggested that the food webs channeled more energy toward the top of the food chains (mostly fishes) with increasing q. The variation in the energy flow along each link into fishes (a proxy for interaction strength) increased with q (Fig. 4s), and an increasing number of these links became more concentrated at smaller values (greater positive skews; Fig. 4r) as q increased. These indicated that, when q was high, the food webs contained higher proportions of weaker feeding links on average.

In the post-fishing period, food webs contained fewer species and links and experienced changes associated with these compositional changes (Fig. 4). The mean trends of the slopes of biomass spectra increased slightly (Fig. 4p) and the skewness and variation of energy fluxes into fishes declined modestly (Fig. 4r, s) at low to intermediate values of q for the stabilized and destabilized webs. Hence, fishing caused the food webs to have lower proportions of weak interactions and less bottom-heavy biomass pyramids at low to intermediate values of q. The patterns were very similar for the F-O scenario (Fig. S6).

4. Discussion

4.1. Limiting effects of fishing and FIE on the temporal variability of complex food webs

Kuparinen et al. (2016) demonstrated that, using an empirically parameterized model without external forcing, increased temporal variability of fish abundances due to fisheries-induced phenotypic changes could remain even after fishing stopped. In the current study,

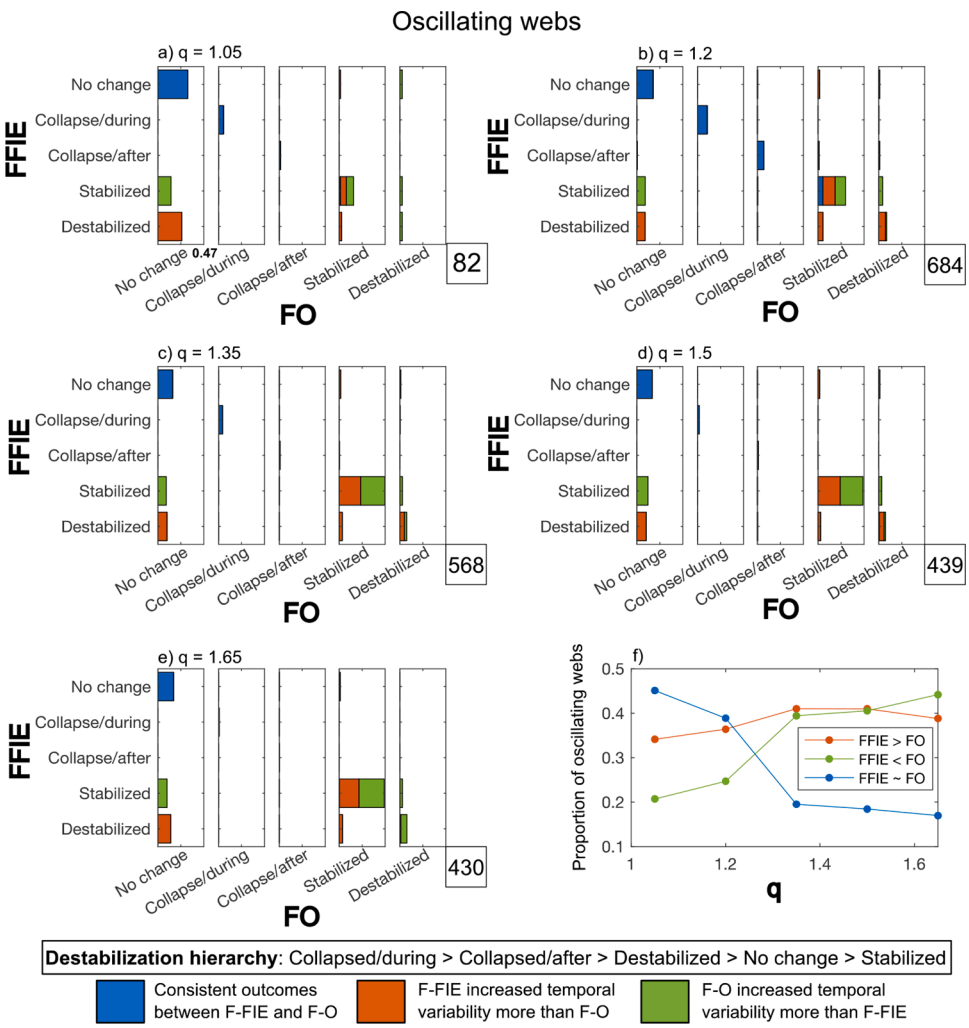

Fig. 3. a-e) The responses of identical food webs to the F-FIE and F-O scenarios for oscillating fish biomasses during the pre-fishing period were classified into the contingency matrices (for stable food webs see Fig. S4). The responses from F-FIE are listed along the vertical axis, and those from F-O are along the horizontal axis. The colored bars indicate the proportions of webs whose responses fell in the categories (the proportion goes up to 0.47 in all columns). The total number of food webs is shown at the bottom right corner. In the diagonal, F-FIE and F-O led to consistent responses in the first three categories (No change, Collapsed during fishing, Collapsed after fishing). In the Stabilized and Destabilized categories, the responses were further classified quantitatively with the same color scheme. f) The proportions of oscillating webs at five values of q on which FIE had an additional destabilizing effect (orange) and an additional stabilizing effect (green).

we examined their result in a large number of food webs with various topologies and observed that phenotypic changes caused by size-selective fishing infrequently increased or decreased but predominantly neither the temporal variability of fish biomass dynamics from the pre-fishing to the post-fishing period. The principle of energy flux (Gellner and McCann, 2016; McCann, 2012; Rip and McCann, 2011) can help explain the patterns of temporal variability in fish abundance. It predicts that an increase in energy flux to a consumer, relative to its loss term (relative energy flux), makes the population dynamics more temporally variable (or less stable) and the consumer–resource biomass ratio less bottom-heavy. Based on this principle, we can expect that, in the absence of environmental fluctuations, fishing and FIE could reduce the variability of fish populations if an increase in the loss term through fishing mortality and elevated metabolism reduce relative energy influx to the consumer. Likewise, we can expect that they could increase variability if energy influx to the consumer increases due to increased metabolic demands or higher resource availability mediated by trophic cascades or compensatory growth of prey. Finally, we can also expect that changes in gain and loss may be insufficient or that greater loss balances out increased gain, causing not much net changes in temporal variability. Our results appear to support the latter possibilities the most.

In our study, the vast majority of food webs had stable biomass dynamics before and after fishing. Food web theory, which encompasses the principle of energy flux, that has been developed by McCann and others Gellner and McCann, 2016; McCann, 2012; McCauley et al., 2018; Nilsson et al., 2018; Rip and McCann, 2011) states that along the gradient of increasing energy flux (or decreasing energy loss) to a consumer a food web can transition from a non-excitable (never oscillates) to an excitable state (possible to oscillate), when the largest eigenvalue of the community matrix (the Jacobian matrix of the dynamical equations, Eqns. (1)-(3) turns from real to complex, before exhibiting sustained oscillations. In the stable food webs we observed, fishing and FIE presumably did not alter the food web structure or dynamics enough to bring them into the parameter region of sustained oscillations (Borrelli et al., 2015). Our result does not seem unrealistic as intrinsically oscillating populations, either exploited or not, appear uncommon in nature (Kendall et al., 1998; Shelton and Mangel, 2011). Instead, studies have pointed out the importance of environmental fluctuations interacting with nonlinear population dynamics perturbed by harvesting to destabilize the abundances of exploited populations (Anderson et al., 2008; Cameron et al., 2016).

We observed that changes in temporal variabilities of fish biomasses occurred more often in food webs already oscillating prior to fishing and that those webs were more likely to reduce, rather than increase, temporal variability. The oscillating food webs were in excitable states (i.e., the largest eigenvalue of the community matrix was complex), where slight shifts along the energy flux gradient due to fishing and FIE could alter biomass variability qualitatively or quantitatively. The reason for reduced temporal variability could be that it is more likely for fishing and FIE to perturb the system to move toward a more stable state (by removing energy or pruning less stable modules), while it is less likely for perturbations to bring systems upward the instability gradient. Nonetheless, temporal variability increased in some oscillating webs because the systems collapsed or reorganized possibly to channel greater

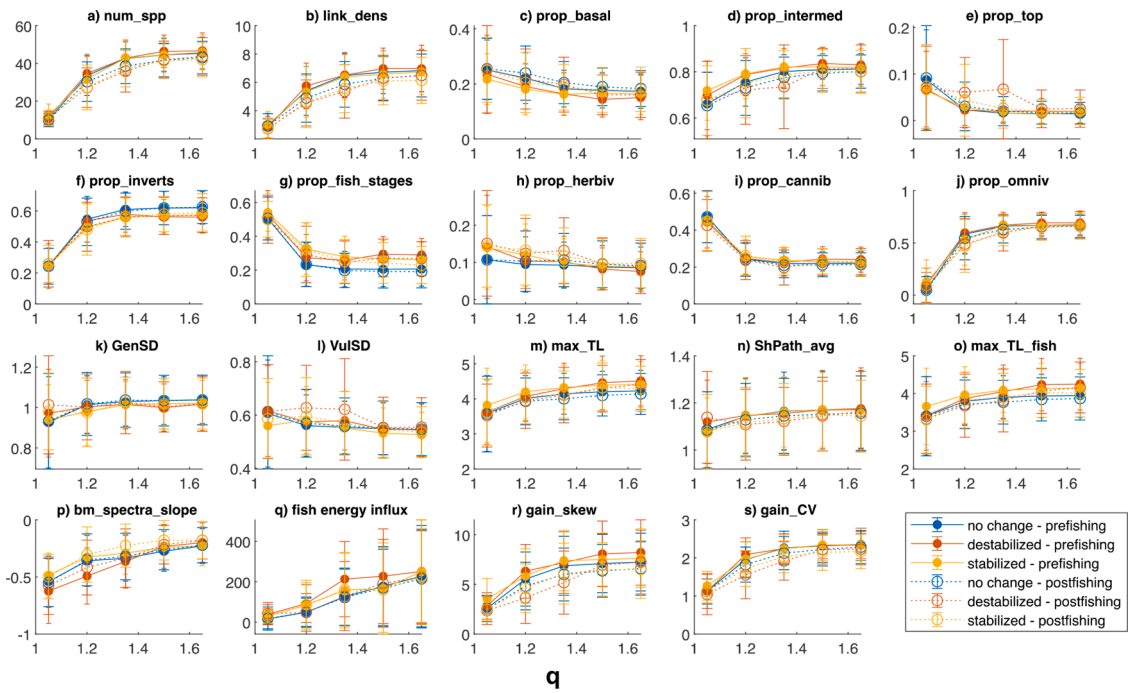

Fig. 4. (top three rows, a-o) The measures of network structure for food webs that were destabilized (red), stabilized (orange), or neither (no change; blue) across the values of q (x-axes) examined for the F-FIE scenario from the pre-fishing (solid line with filled circles) and post-fishing period (dashed line with open circles). (bottom row; p-s) Measures related to energy flow in the food webs. The more negative the slopes of biomass spectra, the more bottom-heavy the biomass pyramids. Fish energy influx refers to the total amount of incoming energy into fishes. gain_skew and gain_CV capture the distribution and variation, respectively, of energy flow toward fishes along each feeding link, considered as indicators of interaction strength. The definitions of the network metrics are in Table 4. The error bars demarcate 1 SD. Similar patterns were observed for the F-O scenario (Appendix S3).

energy up in remaining food chains.

To isolate the effects of FIE from fishing, we classified each food web based on its responses to the two treatments (F-FIE and F-O; Fig. 3). The result indicated that additional negative effects (increased variability or collapse) of FIE predominated at lower values of q. At $q \leq 1.2$, the food webs were relatively unstable, and extra perturbations from FIE brought about more temporal variability. As q increased, the food webs became progressively more stable, and FIE was equally likely to exacerbate or alleviate the effects of perturbation by fishing (Rip and McCann 2011; McCann 2012; Gellner and McCann 2016). We speculate that, when q was low, food webs probably had to have high stability conferred by food web structure to persist through the pre-fishing period. The fraction of persisting webs was smaller when $q \leq 1.2$ (Fig. 2a), and larger fractions of these webs consistently responded to both F-FIE and F-O (i.e., not sensitive to FIE; Fig. 3f). When q was higher, stability conferred by food web structure was probably not as crucial for persistence (more discussion regarding q below). A higher fraction of the oscillating webs was differentially perturbed by F-FIE and F-O at higher q possibly because of weaker stability-inducing network structure and consequently higher sensitivity to perturbations (Fig. 3f).

4.2. The effect of q (Hill exponent of functional responses) and the choices of q by previous studies

We found that the proportion of destabilized food webs peaked at $q = 1.2$ (Fig. 2b), and these webs were predominantly stable in biomass dynamics prior to fishing. As described above, the stable food webs with $q = 1.2$ seemed to be located along the energy flux gradient closer to the region of sustained oscillation than were those with lower or higher q (i.e., likely to go through the discontinuity in stability when perturbed). At $q = 1.05$, probably only webs that were far from the region of sustained oscillation by having stability-inducing structure attained stable dynamics. At higher q, stability conferred by the sigmoidal functional responses likely largely contributed to the stable dynamics. Oscillating food webs did not show a peak at $q = 1.2$ (Fig. 2d) presumably because oscillating webs were already in the excitable state. The parameter q determines the shape of functional responses (Eqn. (3)) and critically affects the stability and dynamics of consumer–resource models, including those using the ATN approaches (Brose et al., 2006; Hunsicker et al., 2011; Koen-Alonso and Yodzis, 2005; Williams and Martinez, 2004a). Existing empirical data support various values of q from 1 to above 3 (Rosenbaum and Rall, 2018; Uszko et al., 2015), but accurately estimating it using empirical data is challenging (Uszko et al., 2020). Among ATN modeling studies, popular values for q are 1 (i.e., Type II) and 1.2 (e.g., Bland et al., 2019; Boit et al., 2012; Curtsdotter et al., 2018; Glaum et al., 2020b; Kuparinen et al., 2016; Quévreux and Brose, 2018; Schneider et al., 2012), while no sensitivity analyses were usually provided with respect to this parameter. Some other studies sampled values from a plausible range between Type I and Type II functional responses (e.g., Curtsdotter et al., 2011; Kalinkat et al., 2013; Schneider et al., 2016), but they did not report which values of q prevailed in the persisted simulation runs that were subsequently analyzed.

Previous ATN studies appear to have justified q being slightly above 1 to enhance the stability of the models and facilitate complex food web research. Martinez and others (Martinez et al., 2006; Williams and Martinez, 2004b) specifically investigated the effects of q on the persistence of complex food webs and cogently demonstrated that a seemingly modest increase from 1 to 1.2 achieved about a 20% increase in persistence. Boit et al. (2012) presented a successful application of the ATN approach to an empirical system, Lake Constance, with $q = 1.2$. Although their ATN model fitted well to high-quality empirical data from the lake, q was not directly estimated with the data. Kuparinen et al. (2016) adopted the same parameter values from Boit et al. (2012) and concluded that fisheries-induced trait changes in exploited fish

populations of Lake Constance magnified the variability of their abundances. Based on our results, the particular choice of q in Kuparinen et al. (2016) may have been responsible for the observed increased variability in fish dynamics. Post-hoc analyses of their model showed that destabilization could be observed with q between 1.1 and 1.25 (unpublished results). Furthermore, the shapes of functional responses could vary among predator–prey pairs (Smith and Smith, 2020), but the majority of implementations of ATN in literature used a uniform value of q, including our study. Given the large impact of functional responses on predator–prey dynamics, the generality of conclusions regarding stability and persistence of species in complex food webs from studies that used only one value of q in the absence of reliable estimates without providing sensitivity analysis on the parameter may be limited (e.g., Bland et al., 2019, Glaum et al., 2020b; Hale et al., 2020; Sentis et al., 2021). Uncertainty also surrounds other parameters in the ATN models. Given the large number of input parameters, it is not feasible to fully explore the sensitivities of the parameters of the ATN models. The allometric parameters were refined as more data became available since the original formulation by Yodzis and Innes (1992; Brose et al., 2006). Although our results are subject to the same criticism, we focused our investigation on the effects of q on food web stability.

The key advantage of the ATN approach is to anchor the parameterization of the models of complex species interactions on established allometric and other known relationships regarding physiological, life-history, demographic, and species-interaction traits through a relatively limited number of assumptions (Brose et al., 2006; Brown et al., 2004; Rooney et al., 2007; Yodzis and Innes, 1992). The ATN models contain parameters for which general allometric relationships are not known or there are no good estimates available. These include half-saturation constant (B_0), predator interference (c), q, and diet preference (ω). Conceptually, the ATN models are useful as virtual mesocosms of complex food webs and a convenient heuristic tool. As in empirical mesocosm studies, making inferences to realistic contexts is a challenge—rigorous estimation and prudent choices of parameter values and careful, though limited, sensitivity analyses are warranted.

4.3. Food web structure and responses to fishing and FIE

The variations in measured food web metrics were very large (Fig. 4 for F-FIE, Fig. S6 for F-O). Clearly, many more food webs were needed to narrow the ranges, but it was computationally prohibitive. Nonetheless, many of the food web metrics steadily increased or decreased in their means with q, indicating the parameter's monotonic influence on food web structure and energy flow. With increasing q, the number of nodes (species or fish stages) and link density increased, and the structure of food webs became more intermediate- or invertebrate-dominated. Similarly, the total energy gained by fishes increased, food chains became longer, and the shapes of biomass pyramids became less bottom heavy (i.e., the slopes of biomass spectra became less negative) with increasing q. Despite increased complexity and shifts in food web structure, many more food webs persisted to the end of the pre-fishing period with the majority exhibiting stable fish biomasses with higher q. One explanation could be that increasing proportions of weak interactions in the food webs with increasing q enhanced stability of the food webs, as indicated by the skewness and CVs of fish energy gains. This was likely realized because of the increased complexity (more nodes and links) of the food webs and species (or fish stages) having more interaction links on average (higher link density).

It was not possible to discern differences in structure among food webs that responded differently to the F-FIE and F-O scenarios. The mean trends suggested that the food webs that changed temporal variability had proportionally slightly more fishes and contained longer food chains (i.e., higher maximum trophic levels) than did the webs whose variability did not change before and after fishing (Fig. 4). It was a straightforward consequence of fishing targeting larger fishes that such food webs were more affected by fishing. In the post-fishing periods, although food webs on average lost weak interactions (as indicated by lower skewness and CVs of fish energy gains) and showed less bottom-heavy biomass pyramids, the majority did not change the level of temporal variability before and after fishing. This implies that the relationships between food web structure and stability are not robust (Tang et al., 2014) or are very difficult to disentangle with a modest number of replicated food webs.

4.4. Limitations of the model

The changes of life-history towards attaining higher metabolic rates and reproductive capacity earlier in life in our model implicitly mimic evolution towards smaller body size, a phenomenon that has been observed in multiple exploited fish populations (Devine et al., 2012; McClenachan, 2009; Olsen et al., 2004). Despite this assumption, fishes at all stages in our model advanced from stage to stage at the same rate and interacted with the same set of predators and prey as in the pre-fishing period. Our objective was to investigate the generality of the findings by Kuparinen et al. (2016) in a wider set of food webs, so we decided to keep the assumption of an unchanging food web structure despite decreasing fish body sizes. Rewiring of trophic interactions is an important consideration for food web modeling dealing with FIE and climate change (Audzijonyte et al., 2013b). However, it is difficult to implement changes in food web topology as body size shrinks under the current formulation of the model (because trophic relationships in the initial input food web determine body masses).

As in Kuparinen et al. (2016), mass-specific metabolic rates of fishes were assumed to increase by a small percentage every year during the fishing period to match the assumption of shrinking body size under FIE. This was based on the inverse relationship between body size and mass-specific metabolic rate, which has been documented both interspecifically and intraspecifically (Brown et al., 2004; Huang et al., 2013; Jerde et al., 2019; Killen et al., 2010). Furthermore, Auer et al. (2018) reported rapid evolution of higher standard metabolic rates (SMR) in response to high predation mortality in adults in Trinidadian guppy populations, which was argued to be a good model system to inform about FIE in exploited populations (Reznick and Ghalambor, 2005). In contrast, no difference in SMR was reported between size-selectively and randomly harvested experimental populations of zebra fish (*Danio rerio*) (Uusi-Heikkilä et al., 2015) and between early and late maturing genotypes of salmonid species (Åsheim et al., 2021; Prokkola et al., 2022). In experimental studies, feeding rate and activity levels, which are known to be positively related to SMR (Cooke et al., 2007), declined in response to harvesting treatments (Pauli et al., 2019; Walsh et al., 2006). Bold, fast growing, and active individuals are found more prone to be fished out, leaving less active and shy ones behind (Arlinghaus et al., 2017; Biro and Post, 2008; Claireaux et al., 2018; Redpath et al., 2010). On the other hand, individuals with higher swimming capacities and stamina may be more capable of escaping certain fishing gear types (Crespel et al., 2021; Hollins et al., 2018; Killen et al., 2015). Vulnerability to fishing is likely context dependent, as growth and food intake rates depend on not only SMR but also environmental conditions including temperature and food availability (Bouffet-Halle et al., 2021; Hollins et al., 2018). Given this uncertainty, we decided to retain the original scheme of Kuparinen et al. (2016) and assumed the inverse intraspecific allometric relationship between body mass and mass-specific metabolic rate to simulate FIE. This implementation resulted in higher rates of metabolic loss and dietary intake in Eqn (2) (i.e., x increased). These increased loss and gain rates probably balanced out to some extent and may explain partially why most of the food webs did not change temporal variability.

We used the same rates of increases in metabolic rate and maturation as in Kuparinen et al. (2016) and similarly assumed that evolution halted after fishing ended but did not reverse during the post-fishing period. The rates of evolution were assumed to be small (Table 2a) as fitness-related traits often show low heritability (Law, 2007). Selection

imposed by fishing is considered much stronger than is natural selection (Darimont et al., 2009; Fugère and Hendry, 2018; Hutchings and Fraser, 2008; Law, 2000), and reversals of FIE are thought to be slow or difficult (Allendorf and Hard, 2009; Conover et al., 2009; Enberg et al., 2009; Kuparinen and Merilä, 2007; Walsh et al., 2006). We simulated the post-fishing period for 500 years to merely observe dynamics beyond transients.

Instead of externally imposing trait changes, FIE can also be modeled more mechanistically through endogenously arising natural selection (Forestier et al., 2020). Quantitative genetics methods (McPeek 2017) or adaptive dynamics (Dieckmann and Law, 1996; Geritz et al., 1998) could be used to model trait evolution. Furthermore, as fished populations may potentially coevolve with other species in the community, FIE could cascade up or down the food chains (Wood et al., 2018) with smaller taxa lower in the chains possibly evolving faster (Barraclough, 2015). Hence, in our study, selection was disconnected from species interactions, changes in community dynamics due to fishing did not feedback to evolutionary dynamics, and predator-prey coevolution was neglected. These are important challenges to move the field forward in future FIE research. It will increase model complexity substantially and obtaining reliable estimates for an increased number of parameters will be difficult. Our approach requires simpler assumptions and many fewer parameters than such mechanistic models but still can incorporate empirically supported patterns (e.g., harvested fish becoming smaller) and hypotheses or predictions from theory (e.g., higher mass-specific metabolic rates in smaller organisms). It will be informative to compare results from these two approaches in future studies.

Classifying time series into categories (stable vs. unstable, temporal variability changed or not) according to CV involved subjective judgement because of numerical errors and continuous distributions of CV or difference between CVs (Fig. S1-S3). We visually assessed a large subset of simulated time series and selected cutoff at 0.05 because it gave the most consistent results to our visual assessments (Fig. S1, S3). It also allocated sufficient food webs to each category. Because it is not feasible to obtain analytical expression of eigenvalues for the system of Eqns. (1)–(3), numerically computing eigenvalues will encounter a similar issue.

We assumed no interspecific and inter-cohort interference competition. Interference competition can stabilize consumer dynamics in some consumer–resource models by reducing energy uptake rate by consumers, but at the same time it could decrease energy loss from predation in prey species (i.e., increase in net energy gain) to induce oscillation in prey (McCann 2012). The strength of interference competition could arise from consumers themselves or from prey behavior in response to increasing consumer densities (Kondoh, 2003; McCann, 2000), for which no allometric theory based on body size or predator–prey mass ratio has been developed. The abovementioned study on Lake Constance by Boit et al. (2012) chose reasonable parameter values based on their expert knowledge on the system. We initially used the same parameter values as in previous studies (Bland et al., 2019; Boit et al., 2012; Kuparinen et al., 2016), but only a very small number of oscillating food webs persisted. We decided to retain only intraspecific interference competition coefficients to have a reasonable number of webs with oscillating dynamics. Consequently, our model does not speak to how common intrinsically oscillating food webs might be in nature.

5. Conclusions

Our aim was to investigate the generality of the magnifying effect of fishing and FIE on food web dynamics in realistic, synthetic food webs. We found that the majority of the food webs did not change temporal variability in abundance before and after the fishing period in our model. Although food webs with oscillating fish biomass dynamics were rare, those oscillating prior to fishing were more prone to increased as well as decreased temporal variability by FIE than those with stable dynamics. The frequencies of food webs that changed temporal variability varied across the shape of functional responses (q). Lastly, the generality of the conclusions regarding complexity and stability of food webs from studies that use the ATN approach without testing the sensitivity to the shape of functional responses could be limited.

Funding

This study was funded by the Academy of Finland (project grant 317495 to A.K.), Natural Sciences and Engineering Research Council of Canada (NSERC; Discovery Grant to A.K.) and the European Research Council (COMPLEX-FISH 770884 to A.K.).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

The code to generate food webs and run the ATN biomass dynamics has been published with our previous publication https://datadryad.org/stash/dataset/doi:10.5061/dryad.z612jm6bk.

Acknowledgements

The authors thank Sara Hocevar for providing comments on an earlier version of the manuscript and the Language Services of the University of Jyväskylä for proofreading. The present study reflects only the authors' view; the funders are not responsible for any use that may be made of the information it contains.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2022.110150. Simulated data used to produce the results and figures are available from the first author.

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