A modified niche model for generating food webs with stage-structured consumers: The stabilizing effects of life-history stages on complex food webs

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Abstract

1. Almost all organisms grow in size during their lifetime and switch diets, trophic positions, and interacting partners as they grow. Such ontogenetic development introduces life-history stages and flows of biomass between the stages through growth and reproduction. However, current research on complex food webs rarely considers life-history stages. The few previously proposed methods do not take full advantage of the existing food web structural models that can produce realistic food web topologies. 2. We extended the niche model by Williams & Martinez (2000) to generate food webs that included trophic species with a life-history stage structure. Our method aggregated trophic species based on niche overlap to form a life-history structured population; therefore, it largely preserved the topological structure of food webs generated by the niche model. We applied the theory of allometric predator-prey body mass ratio and parameterized an allometric bioenergetic model augmented with biomass flow between stages via growth and reproduction to study the effects of a stage structure on the stability of food webs. 3. When life-history stages were linked via growth and reproduction, fewer food webs persisted while persisting food webs tended to retain more trophic species. Topological differences between persisting linked and unlinked food webs were small to modest. Temporal variability of biomass dynamics and slopes of biomass spectra were lower in the linked food webs than the unlinked ones, suggesting that a life-history stage structure enhanced stability of complex food webs. 4. Our results suggest a positive relationship between the complexity and stability of complex food webs. A life-history stage structure in food webs may play important roles in dynamics of and diversity in food webs.

Introduction

A large body of research in the last several decades has investigated potential factors that can promote the structural and dynamical stability of complex food webs and their constituent populations. These factors include hierarchically ordered feeding), characteristic predator-prey body mass ratios (Brose *et al.* 2006), allometric degree distributions of feeding links (Otto *et al.* 2007), compartmentalization (Stouffer & Bascompte 2011), weak interaction links including weak omnivory and reduced predation pressure at low densities

(, pairwise negative correlation between interaction strengths , and self-regulation (e.g., cannibalism, intraspecific interference,), among others (reviewed by). More recently, studies have started incorporating different types of interactions in complex food webs (multiplex or multi-layer networks;) to account for multiple types of ecological interactions, such as mutualisms and parasitism, in which organisms simultaneously engage in natural communities.

A ubiquitous feature of natural systems is that almost all organisms grow in size during their lifetime and switch diets, trophic positions, species interacting with, and habitats as they grow . Such ontogenetic development introduces life-history stages and flows of biomass between the stages through growth and reproduction to food webs, collectively forming complex multi-layer ecological networks. Studies have shown that ontogenetic diet shifts have far-reaching effects on competitive and predator interactions, population dynamics, and community structure in small food web modules . The persistence of consumers can be enhanced in life-history structured communities through biomass overcompensation in consequence of ecological asymmetry between different stages (e.g., juveniles are better competitors than adults;). Such asymmetry, however, can also be expected to destabilize populations by inducing cohort cycles or alternative stable states without a predator . Research on how these effects in small food web modules may scale up to an entire complex food web is still in its infancy, and so are the tools to generate life-history structured complex food webs in a biologically justifiable manner.

Studies have reported the mixed effects of including a stage structure on the stability of complex food webs . Rudolf & Lafferty (2010) found that, using static topological models of food webs, structural robustness to species removal was lower with a stage structure than without. They pointed out that species might be more sensitive to resource loss when ontogenetic stages were sequential resource specialists. Bland et al. (2019) used population dynamical models of complex food webs and showed that non-stage-structured food webs lost twice as many consumer taxa as stage-structured webs, while the variability of biomass dynamics did not differ. Mougi (2017) also used similar population dynamical models and concluded that species persistence (the fraction of species persisting in a food web) increased as the proportion of stage-structured species increased in the food webs and that the effect was more pronounced in food webs with a greater number of species and interactions. More studies are needed to elucidate the role of a stage structure on persistence and stability and how it may come about in complex food webs.

Rudolf & Lafferty (2010) and Bland et al. (2019) used the niche model (Williams & Martinez 2000) to generate network topologies and split a node into stages to create a stage-structured taxon (nodes represent taxa, and interacting taxa are connected by links in ecological networks). The niche model has a demonstrated ability to produce many observed structural properties of empirical food webs despite its simplicity and has been the most widely used food web structural model. Splitting a node, as in Rudolf & Lafferty (2010) and Bland et al. (2019), can nontrivially modify the food web topology generated by the niche model, likely compromising the desirable properties of the food webs. Therefore, it is unclear how realistic the modified food webs in these studies would still have remained after new nodes and links were added to incorporate a life-history structure. Firstly, minimizing the alteration of the network topology generated by the niche model is desirable because it is capable of producing realistic food web topology and because food web data resolved to life-history stages to verify the topology of food webs with stage-structured taxa are currently very scarce. Secondly, the niche model generates a “trophic species,” which is a functional group defined to consist of one or more taxa (e.g., species, genus, ontogenetic stages) that share the same sets of predators and prey . Life-history stages of a species are distinguished for their distinct ecological roles, at least partly by their characteristics related to feeding, so that a life-history stage can be considered as a whole trophic species (not a fraction of it). Based on these interpretations and the observation that ontogenetic diet shifts are widespread in nature (Werner & Gilliam 1984), a plausible alternative approach is to instead group nodes generated by the niche model to assemble a stage-structured taxon. This approach would allow preserving mostly the original topologies of the food webs from the niche model. No study has investigated this approach before.

We took the grouping approach to introduce a stage structure into complex food webs. Following Bland et al. (2019), we applied the allometric trophic network (ATN) model of biomass dynamics to the stage-structured food webs on which we linked stages by biomass flow via growth and reproduction. We motivated the food webs studied here from aquatic communities at temperate and northern latitudes. It is well established that consumer-resource interactions are hierarchically structured largely by body size in aquatic communities because of the indeterminate growth of fishes and gape-limited predation . We found that food webs with stage-structured consumers tended to be less dynamically variable and supported a greater number of species than food webs with non-stage-structured consumers.

Materials and Methods

Introducing life-history stage-structured consumers to the food webs generated by the niche model

We built on the original niche model by Williams & Martinez (2000; Box 1) and incorporated an additional algorithm to construct life-history structured consumers by grouping trophic species based on the extent of overlap between feeding ranges. As organisms grow in size during their ontogeny, they experience changing competition, predation, and energetic demands and may shift diets to maintain positive growth and minimize mortality (Werner & Gilliam 1984). Ontogenetic diet shifts among life-history stages within a species are widely observed in nature (Werner & Gilliam 1984, Werner 1986), with diet ranges overlapping at various degrees . Diet overlap is negligible in the case of diet shifts associated with habitat shifts (e.g., riverine vs. marine) or metamorphosis (e.g., aquatic vs. terrestrial), nested when organisms add larger prey to the diet as they grow in size, or partially nested because smaller prey are successively dropped from diet for energetic or mechanical reasons . We applied this concept to construct food webs with consumers with a life-history stage structure.

After obtaining food webs from the niche model (Box 1), we assigned two measures of trophic position, the short-weighted trophic level (T) and the prey-averaged trophic level ($T2$), to each taxon . The short-weighted trophic level is the average of shortest trophic level ($T1$) and the prey-averaged trophic level (Williams & Martinez 2000, 2004). The shortest trophic level is equal to 1 + the shortest chain length from a basal species to the consumer, and the prey-average trophic level is equal to 1 + the mean trophic level of all the consumer's resources (Williams & Martinez 2004). An integer (N_{fishes}; Table 1) was uniformly randomly drawn from an interval between the desired minimum and maximum numbers of stage-structured taxa. We assumed that they were fishes (assume no stage structure in autotrophs and invertebrates) and that fishes fed on at least one non-basal taxon (i.e., $T2 > 2$). To create a stage-structured fish taxon, we first selected a species with the highest $T2$ (a "focal taxon") that was greater than 2 (Th_{fish}), indicating that this taxon ate at least one non-basal taxon (Fig. 1 and Fig. A1 for an extended graphical example). We then identified taxa whose feeding range maxima fell within the range of the focal taxon with the overlap of the two feeding ranges greater than a specified minimum overlap (OL_{min}) of the union of the two and whose niche value was smaller than and closest to the focal taxon's niche value, to become the next lower stage. This stage became the next focal taxon, and we repeated the steps until either the specified maximum number of stages ($\text{Nstage}_{\text{max}}$) had been assigned or taxa whose range maxima fell in the range of the focal taxon with sufficient overlap ran out. When a focal taxon did not have any overlapping taxa to choose from to form the minimum number of stages ($\text{Nstage}_{\text{min}}$), this taxon was disqualified and another taxon was chosen in the same way as the current focal taxon if other choices for the previous focal taxon were available. If it was impossible to find the minimum number of stages for the first focal taxon, it (but not the other ones that had been subsequently considered) was reclassified as a taxon without a stage structure and classified as an invertebrate. This occurred when a focal taxon happened to have a small feeding range so that no range optima fell in the range. The multiple taxa (nodes) selected in this procedure collectively made up one stage-structured fish taxon and were removed from the pool of available taxa. We then chose another focal taxon with the next highest$T2$ from the remaining taxa and repeated the steps. We repeated these procedures until the chosen number of fishes had been created or taxa with suitable range overlaps had run out. If the minimum number of stage-structured taxa could not be created, the food web was discarded. Predation of lower stages by higher stages within a stage-structured taxon was interpreted as cannibalism. Cannibalism within a stage and cannibalism of higher stages by lower stages (very rare) were removed (cannibalism in non-structured taxa was kept). Taxa that were not identified as autotrophs nor fishes were identified as invertebrates (non-structured consumers). Therefore, nodes in the network represented autotrophic trophic species, invertebrate trophic species, or life-history stages of a fish. Hereafter, a node or a taxon refers to a non-stage-structured species (invertebrates and autotrophs) or a fish stage (Fig. 2). A species refers to an autotrophic species, an invertebrate species, or a fish species that consists of three or more life-history stages, while a stage refers to a fish life-history stage.

Coupling stage-structured food webs and biomass dynamics in the allometric trophic network (ATN) framework

To simulate deterministic population dynamics of the species, we employed a bioenergetic model in the allometric trophic network (ATN) framework developed by Brose et al. (2006) and expanded by Bland et al. (2019) to food webs with stage-structured fishes (see Brose et al. 2006 for a complete description). Consequently, we used many parameter values and sub-models used in their work.

Body mass: In this framework, body mass plays integral part in determining bioenergetic parameter values . More specifically, the rates of metabolism and maximum consumption are approximated by means of body-mass scaling relationships (Yodzis & Innes 1992). We calculated relative masses of the taxa based on the short-weighted trophic position (T) in accordance with the theory of allometric predator-prey body mass ratio (Brose et al. 2006). We set the body mass ratio (Z) of fish predators and their prey to $10^{2.6}$ and of invertebrate predators and their prey to $10^{1.15}$ (; Table 1b). The function, body mass, $M = \ Z^{T-1}$, was used to define the body masses of invertebrates and the terminal stages of stage-structured fishes. Hence, the body masses were relative to those of autotrophs whose body masses were defined to be equal to 1 (Brose et al. 2006; Bland et al. 2019). As in Bland et al. (2019), to model the well-known pattern of fish growth with time, we used a von Bertalanffy isometric growth curve to define the body masses of lower stages (Table 2). We assumed that the individuals of terminal stages reach 90% of their asymptotic weight (Bland et al. 2019). Although body masses in lower stages no longer strictly conformed to the allometric body mass ratios, the median ratios from our model fell near the modes of the empirical distributions (Fig. 3 in Brose et al. 2006; Figure A2).

Dynamical model: The population dynamics within the food webs were formulated as a multispecies consumer-resource model (Yodzis & Innes 1992; Williams & Martinez 2004; Brose *et al.* 2006; Bland *et al.* 2019). They were described by a set of ordinary differential equations (ODE)

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

$$\frac{dB_i}{\mathrm{dt}}_{\text{metabolic loss}} +_{\text{dietary intake}} -_{\text{loss to predation}}$$

where 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 1b for parameter values). The model deterministically simulated the biomass dynamics during growing seasons. F_{ij} was the functional response of consumer i when dealing with prey j

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

where ω_{ij} was the preference of consumeri toward prey j, $B_{0_{\mathrm{ij}}}$ was the half saturation density for consumer i eating prey j,c_{kj} was the predator interference competition coefficient of k eating j, and p_{ik} was the fraction of resources of consumer i shared with consumer k. The values of $B_{0_{\mathrm{ij}}}$ and c_{kj} varied among taxa and were taken from and Bland et al. (2019, their Figure 1) with modifications (Table 1; also see). The parameters for interspecific or between-stage interference competition were set to zero (i.e.,$c_{\mathrm{kj}} = 0$ for $k \neq i$) for simplicity (sensitivity to these assumptions were checked in the sensitivity analysis). Previous studies that used the ATN framework for aquatic systems (Brose et al. 2006, Boit et al. 2012, Bland et al. 2019) differentiated the assimilation rates of consumers between non-basal and basal species only. We added a rate for fish prey because fish is highly effective food for fish growth (Table 1, and lowered the assimilation rate for non-basal species (i.e., invertebrates) to have the average of the two rates remain the same.

We added an ecologically plausible assumption that fishes preferred to feed on fish over invertebrates and on invertebrates over autotrophs, if they were included in their diets, to quickly grow beyond a size vulnerable to predation and for higher fecundity. To achieve these preferences in the absence of such empirical data, we set the parameterω_{ij} such that fishes whose diets included both autotrophs and animals fed almost exclusively on fish, to a lesser extent on invertebrates, but not much on autotrophs (Table 1b). Similarly, we assumed that invertebrates preferred invertebrates the most, followed by fish, to autotrophs. Growth of fish depends on the quantity and quality of food they eat, and shifting to piscivory invariably increases fish growth rate . As fish grow, piscivory could be necessary to meet energetic demands (Juanes et al. 2002). Also, because optimal morphologies for different diets (e.g., planktivory, benthivory, piscivory) are quite different, tradeoffs often arise and a diet specializing on the most profitable is likely preferred (Persson 2002). Herbivory by fish occurs mostly in tropics and is much less common above 55° latitude because the enzyme to digest plant material is not active at low temperatures . If we assumed no preference of fish for prey items (consumption proportional to relative availability), the majority of fish would consume high proportions of autotrophs due to their high abundance, an unlikely scenario in temperate and northern systems. If prey taxa went extinct ($< 10^{-6}$), they were removed from preference calculation.

The Hill exponent q of the functional response was set to 1.8, higher than the value commonly used in previous ATN models (1.2–1.5), to ensure sufficient dynamical stability in large food webs (see Fig. A5 for sensitivity analysis; Williams & Martinez 2004). The high value of the exponent was desired especially because food preferences of consumers increased energy flow higher up in the food web and reduced stability of the food webs in the model

(Martinez *et al.* 2006). Higher values of q effectively converted the functional response closer to Holling type III($q = 2$), which implicitly incorporates prey refugia, other evasive behavior, or adaptive foraging .

Growth and reproduction: Growth and reproduction from surplus energy (dietary intake – metabolic loss – loss to predation; Eqn. 1) were accounted for at the end of the growing season when the ODE model was paused, which implicitly assumed that fishes all reproduced at the beginning of each growing season . The fraction of mature fish in each stage was determined by using a logistic function (Table 2). We assumed that 50% of individuals were mature halfway through to the terminal stage. For example, if the taxon had five stages, about 50% of individuals were mature in Stage 3. We further assumed that fish in immature stages invested all their surplus energy in somatic growth, while mature fish allocated surplus energy to both growth and reproduction (Kuparinen et al. 2016). The allocation to reproduction (I) linearly increased with stage, and the terminal stage allocated 20% of surplus energy to reproduction (Table 2). Therefore, the biomass of the first stage class produced through reproduction was surplus energy multiplied by the probability of being mature and reproductive investment. We used the Leslie matrix to shift somatic biomass to the stage above via growth and to convert it to new recruitment (Table 2). The model allowed phenotypic variability within a stage such that some individuals did not grow enough during the preceding growing season to be recruited to the higher stage. We assumed that fish in the terminal stage reproduced without having energy surplus in exchange for somatic mass (Wootton 1998). Each column added up to 1 in this formulation; therefore, there was no loss of biomass between consecutive growing seasons (i.e., fish did not gain or lose mass or die during winter).

Simulation design

We generated 30,000 networks of 60 nodes and connectance equal to 0.15 containing between 2 and 6 stage-structured fishes with at least 3 and up to 5 stages (Table 1a). We generalized the fixed numbers used by Bland et al. (2019; three fish species with three stages). Food web studies on northern temperate systems typically include two to three species of fish, each of which has two to four stages (e.g., The minimum overlap between feeding ranges to be qualified as consecutive stages of the same stage-structured fish species was 20% . We then ran the ATN on each network from random initial biomasses uniformly distributed between 0.1 to 100 $\mu gC/L$. We ran two sets of simulations on the same networks. In one set, stages were linked via growth and reproduction as described above ("linked"), while in the other set we removed the growth and reproduction links between stages ("unlinked") to examine the effects of the additional biomass flow on the resulting food web dynamics and persistence. The simulations were otherwise identical (including the seed for the random number generator). Taxa were considered extinct when the biomasses became $< 10^{-6}$ $\mu gC/L$, and if any of the taxon reached the biomass of 10^{12} $\mu gC/L$ the simulation was terminated (Table 1b). These values were many orders of magnitudes smaller and larger, respectively, to the mean total fish biomass ($10^{1.1}$ $\mu gC/L$). At the end of each generation, fishes that retained only older stages but not younger ones for more than 10 generations were removed as extinct. This happened in some simulations because the biomasses of older stages without younger ones lingered although they were to decay over time. Each year consisted of 90 time-steps, representing one growing season, followed by a non-growing season where reproduction and growth were accounted for. One time-step corresponded to the generation time of the autotrophic species the growth rates of other taxa were normalized to the time scale of the basal species, as typically done in the ATN models; Brose et al. 2006). Food webs were regarded as persistent if simulations lasted for 1000 growing seasons, which was sufficient for transient dynamics to die out, with all the nodes of persisting species connected in one network, no invertebrates without predators, no species without food (i.e., transients did not completely die out in a handful of webs), and at least one fish with 3 or more stages for the linked case or at least 3 fish taxa for the unlinked case. We note that we regarded food webs as persistent if they retained fishes and met other criteria we just stated (Fig. 3) to the end of the simulations, not by the proportions of taxa (nodes) persisted as typically reported by food web studies.

Analyzing model outputs

We first assessed various food web properties of the 30,000 networks ("original webs") to check whether the generated food webs were reasonable. Then, we identified the linked and unlinked food webs that persisted for 1000 growing seasons (i.e., years) and passed the abovementioned criteria (Fig. 3), and retained only persisting taxa in these webs ("ATN-filtered webs"). We then examined food web properties of the ATN-filtered food webs using the last 100 years of the simulations. We calculated the mean of the CVs of biomasses of fish stages to characterize dynamical stability of food webs and the number of nodes and link density to characterize food web complexity. We also compared the unlinked and the linked webs for total fish biomass, the mean body masses of fishes weighted by relative abundance, the number of fish stages, and the maximum trophic levels and median predator-prey body mass (PPMR) ratios for fish stages. We computed a surrogate of total interaction strengths by summing up all energy flows into fish stages from their resources, CVs and skewness of the energy flows, which were individually normalized by the total gain of the recipient fish , and the slopes of biomass spectra by fitting a linear model to estimate biomass at trophic levels as a function of body mass . The presence of weak interactions is theorized to stabilize food webs . Less negative slopes of biomass spectra indicate less bottom-heavy food webs (Treblico et al. 2013), which tend to be less stable than more bottom-heavy food webs . Some measurements were $\log_{10}$ transformed for interpretability. We computed 10000 bootstrap estimates of the mean effect sizes of a stage structure (linked – unlinked) for these metrics by taking the differences between the means of resampled values from persisting linked and unliked food webs.

We checked the sensitivity of the model outputs to major input parameters (Table 1). We ran 10000 simulations for each parameter variation (16 sets in total) using the same food web topologies as the baseline simulations. We computed 1000 bootstrap estimates of the mean effect sizes of a stage structure (linked – unlinked) for these metrics by taking the differences between the means of resampled values from persisting linked and unliked food webs and compared the mean effect sizes with those from the baseline simulations.

Results

Structural properties of the stage-structured food webs

The structural properties and characteristics of the 30000 original stage-structured food webs generated by the modified niche model were quantified on the unweighted networks (Fig. A3). The majority of the 60 nodes were invertebrates, followed by 8 to 30 life-history stages of fishes (2 to 6 species as specified) and 3-12 autotrophs. Between 6 and 30 fish stages were piscivorous (their diets included fish), while 3 to 28 of them had autotrophs in their diets. Fishes were almost all cannibalistic at some stage. Omnivores (feeding at 2 or more trophic levels) were abundant (45 to 50 species). Each fish stage had about 16 prey species and 7 predators on average. The mean maximum trophic level was near 5. Almost all interactions involved intermediate taxa (taxa with both prey and predators). About a half of the webs did not have a top predator (taxa without a predator), while the rest had one top predator. The sensitivity analysis showed that these patterns remained almost identical when $\mathrm{OL}_{\mathrm{min}}$ was reduced to 10 %, while the number of fish stages decreased along with other measures as a direct consequence of having fewer fish stages when$\mathrm{NStage}_{\mathrm{min}}$, and $\mathrm{NStage}_{\mathrm{max}}$ were decreased (Fig. A3).

The impact of a stage structure on the food webs

Out of 30,000 food webs, 5865 linked (19.6%) and 9099 unlinked webs (30.3%) persisted for 1000 growing seasons and passed the criteria, of which 2628 webs were shared. Assessed by a set of network structural metrics and characteristics quantified on the unweighted networks after removing extinct taxa ("ATN-filtered"; note that taxa that went extinct could be different between the linked and unliked webs), the persisting food webs in both scenarios largely overlapped in terms of the majority of the properties measured (Fig. A4). The number of persisting nodes ranged from 15 to 60, of which invertebrates comprised the majority and 3 to 30 nodes were life-history stages of fishes. The majority of the food webs did not have a top predator.

The distributions of measured food web properties between the linked and unlinked food webs overlapped substantially (Fig. 4a). Nonetheless, the bootstrap differences in means between the linked and unliked food webs (linked – unlinked webs) highlighted that some of the mean effect sizes were noticeable (Fig. 4b); the mean CVs of fish biomasses was about 3.3-orders of magnitude smaller, the number of nodes was greater by about 6, the slope of biomass spectra was 0.17 smaller, and the CV and skewness of normalized fish energy gain were 0.17 and 2.35 larger, respectively, in the linked webs than in the unlinked webs on average. These suggested that, when stages were linked relative to when unlinked, on average fish biomass dynamics were less variable, the biomass pyramids were more bottom-heavy, food webs sustained several more species or fish stages, and fish energy gain was more variable among links and dominated by small gains (indicated by the positive skews). Taken together, the results suggested that the life-history stage structure of fishes on average moderately promoted the stability of and diversity in these complex food webs, once they were able to persist. The sensitivity analysis showed that the patterns in the bootstrap differences in mean effect sizes remained in the same direction (negative or positive) as the baseline simulations across the sensitivity analysis simulations except several cases (Fig. A5). The bootstrap differences in mean effect sizes were qualitatively deviated from the baseline runs for a few measures when the maximum and minimum numbers of fish stages($\mathrm{NStage}_{\mathrm{max}}$, $\mathrm{NStage}_{\mathrm{min}}$) were smaller (#1), full interference competition was included (#13), or when q was reduced to 1.2 (#15). The number of persisting webs was markedly smaller (˜25%) when $q = 1.2$ (data not shown).

Discussion

The modified niche model

To introduce life-history stages into food webs, we developed additional algorithms that modified food webs from the niche model by Williams & Martinez (2000). Food web topologies generated by other food web structural models can also be used as long as they assign feeding hierarchies and ranges to every taxon, such as the variants of the niche model (generalized niche model ; the relaxed niche model ; the minimum potential niche model). Our method utilized the concepts of ontogenetic diet shifts and niche overlap among ontogenetic stages (Werner & Gilliam 1984; Werner 1986) to identify life-history stages and heuristically assembled the specified number of taxa with a stage structure. It can be adapted to other situations where, for example, stage-structured taxa feed higher in the trophic level (e.g., set the minimum trophic level > 3 to become a fish or exclude consumers feeding on autotrophs from the pool of fish candidates) or feeding range overlaps are smaller or larger. The outputs can be fed into the ATN framework or other dynamical models that can accommodate biomass flow via growth and reproduction.

We grouped trophic species created by the niche model to assemble a stage-structured fish taxon, unlike the previous models where a trophic species was split into stages (Rudolf & Lafferty 2010; Bland et al. 2019). As a result, our method generated food webs that largely preserved topologies (i.e., besides removing rare within-stage and reverse cannibalism) produced by the niche model, which has been shown to reproduce empirically observed food web properties (Williams & Martinez 2000, 2008). The previous methods introduced new nodes and links, likely compromising the merit of using the niche model. Our approach also agrees with the method employed by Williams & Martinez (2000, 2008) to evaluate the niche model's performance, where some of the empirical data they used distinguished different stages of the same species (e.g., larval/young-of-year and adult fish in Little Rock Lake, Ythan estuary, and Chesapeake data). Our approach hence followed from the definition of trophic species, a group of taxa sharing predators and prey, from the common phenomena of the ontogenetic diet shift, and from the fact that the niche model creates trophic species. What constitutes a trophic species should depend on the level of aggregation appropriate for a given study. Because we were interested in trophically distinct roles of ontogenetic stages on food web dynamics (Werner 1986), it was both convenient and reasonable to interpret trophic species as ontogenetic stages and group multiple trophic species into a stage structured species. It appears to be a great advantage to minimize alteration of food webs obtained from the niche model. As a by-product, we also eliminated the convoluted steps to assign niche values to newly created nodes in the method by Bland et al. (2019). We think that our approach improves and simplifies their method, making it more conceptually accessible to food web researchers.

In our results, a far greater number of food webs with unlinked stages persisted than those with linked stages. Linked stage-structured food webs were qualified with more stringent criteria (namely, higher stages cannot persist without lower stages for more than 10 generations vs. independent stages; at least one fish with 3 or more stages persisting vs. at least any 3 fish nodes persisting). Once the food webs were persisting, linked life-history stages stabilized food webs relative to when they were unlinked, as indicated by the lower variability of biomass dynamics (CV) and higher numbers of taxa (nodes) persisting in the food webs (Fig. 4). The relative frequency of food webs with oscillating biomass dynamics (i.e., higher CV) was higher when stages were unlinked. In contrast, the linked and unlinked food webs in Bland et al. (2019) behaved similarly in terms of these measures. Furthermore, the mean of the CVs of energy flow into fishes was modestly higher in the linked webs on average, mirrored by greater positive skewness, which indicated that the linked webs contained more weak links than the unlinked webs. A similar difference in CVs of energy influx resulted in approximately a 5% change (an increase in webs of 20 species, while a decrease in larger webs) in the proportion of stable webs in Gross et al. (2009). Having weak interactions is one of the key properties that can increase stability of food webs . Also, we observed that the linked webs had lower slopes of biomass spectra and hence exhibited more bottom-heavy biomass pyramids than did the unlinked webs. Bottom-heavy biomass pyramids tend to relate to dynamically stable consumer-resource dynamics, while top-heavy biomass pyramids tend to suggest unstable dynamics . Therefore, the stabilizing effects of life-history stages that we saw in our simulations appear in agreement with what current food web theories predict.

Our method and the method by Bland et al. (2019) also differed somewhat in modeling demographic shifts via growth and reproduction at the end of growing seasons. The differences were in how surplus energy were dealt with and in the proportion of the biomass of the terminal fish stage to be transferred to the first stage. Thus, the differences between our results and those of Bland et al. (2019) may not be attributable only to how life-history stages were constructed (grouping nodes vs. splitting a node). Further research should systematically explore how a life-stage structure can affect food web stability. Our method can serve as a tool to generate biologically justifiable stage-structured food web topologies to facilitate such explorations in future studies.

We noticed that the original niche model by Williams & Martinez (2000) produces many consumers that include autotrophs in their diets. In temperate and northern regions, fishes feeding on autotrophs are uncommon because of low activity levels of digesting enzymes . We added this realism through prey preferences in the dynamic model. In simulations, fishes consumed little autotrophic biomass as a consequence, despite including autotrophs in their diets. We also noticed that persisting webs often did not have a top predator based on their topologies (Fig. A4), which implied that food webs with top predators tended to be dynamically unstable. In natural systems, there may be no true top predators as even the adult stages of piscivorous fishes could be eaten by vertebrate and invertebrate predators (e.g., birds, octopuses) or parasitized (e.g., scale eaters, leeches, pathogens). Alternatively, we could have retained in the ATN filtered webs only interactions that were substantial enough to be observed in the fields. If we removed interactions that contributed a very small fraction to the consumers' total energy intake ($< 10^{-4}\%$) with the specified diet preference, 70% of persisting webs had at least one top predator (data not shown).

Life-history structure and food web stability

How a life-history structure may affect the stability and persistence of complex food webs has not been much studied. It is not immediately clear whether it is stabilizing or destabilizing based on existing theories. We can expect multiple aspects of stage-structured populations to contribute to instability. As discussed by Rudolf & Lafferty (2010), when stage classes have smaller subsets of the feeding range than the species as a whole, resources essentially become less substitutable, especially when the overlaps between feeding ranges are small. Thus, if resources for one stage become scarce, the persistence of the entire species is greatly endangered unless growth and reproduction can constantly replenish the dwindling stage. Similarly, as stages become more specialized, consumer-resource interactions may become less diffuse and some of the remaining interactions may strengthen. Because weak interactions tend to stabilize trophic interactions (McCann 2012; Gellner & McCann 2016), specialized stages likely reduce stability of food webs. Also, a stage structure introduces delays and asymmetry between stages into population models, both of which are known to often cause population instability in the forms of cohort cycles and alternative stable states . Therefore, the odds seem to be against increased food web stability by introducing life-history stages.

Stages in structured populations can subsidize dwindling stages through growth and reproduction, which is probably one of the main reasons why a stage structure in food webs could enhance the persistence of stage-structured populations and other dependent populations. Furthermore, biomass flow via growth or reproduction between competing stages with overlapping diet might moderate the destabilization effects of exploitative competition. showed that the exploitative competition module reduced food web persistence as it increased in frequency in dynamical models of complex food webs. This effect of diet overlap may appear contradictory to the result from Rudolf & Lafferty (2010), which showed that, when feeding niches were overlapping by more than about 30%, the inclusion of stages increased the robustness of food webs. Because they studied the robustness of static food webs (only topology, no dynamics), diet overlap reduced reliance of a stage-structured population on any particular resource, as the authors explained. In dynamic models, exploitative competition can ensue and drive one of the competitors and possibly other populations to extinction, but if the competitors are ontogenetic stages of the same species, biomass flow between the stages could alleviate competitive exclusion. In the study by Stouffer & Bascompte (2010), the frequency of the tritrophic food chain module had positive effects on persistence in large food webs. In a sense, life-history structured populations contain a biomass flow chain inside. We conjecture that this might also contribute to food web stability. In addition to the possible adverse effects on stability we discussed above, ontogenetic asymmetry may also help some populations persist in food webs. showed in stage-structured food web modules that persistence of consumers could be promoted in communities with stage-structured prey through emergent facilitation due to biomass compensation in the prey population. It seems reasonable to state that the effects of life-history stages on the stability of complex food webs are complex and contingent on the balance of the effects of different processes.

Conclusions

Life-history stages constitute part of biological diversity and increase complexity of food webs. As a large majority of organisms grow in size, often over orders of magnitude, during their lifetime and experience various degrees of ontogenetic diet shifts (Werner & Gilliam 1984), life-history structures are important to be considered in studies on the stability of complex food webs. In this study, we demonstrated a positive relationship between the complexity and stability of complex food webs; food webs with stage-structured taxa exhibited lower biomass variability and supported more taxa than did those with unlinked stages. These results are qualitatively in agreement with the findings by Mougi (2017). For aquatic systems and fishes in particular, ontogenetic stages are well recognized and studied so that including life-history stages explicitly in models can facilitate linking theory and data. Practically, including separate stages makes it more mechanistic and straightforward to implement allometrically scaled functions or parameters and differences in behaviors among stages. For example, simulating size-selective fishing and the evolutionary impacts of such fishing on the population dynamics of exploited species in food webs becomes more straightforward once a life-history structure is explicitly incorporated (e.g., Kuparinen et al. 2016). Moreover, our work contributes a way of incorporating another aspect of interaction diversity via life histories to the growing research on multi-layered networks . Biomass flow via growth and reproduction forms networks of energy transfer analogously to consumer-resource interactions. Research on multi-layered networks has so far revealed that non-trophic interactions (thus interaction diversity) can ameliorate or degrade the stability of trophic interactions and the persistence of species (reviewed by Kéfi *et al.* 2018). Interestingly, showed that network structures known to stabilize mutualistic interactions became less effective when combined with trophic interactions in a multi-layered network. Tritrophic food chain and omnivory modules have been shown to stabilize complex food webs (Stouffer & Bascompte 2010), and it will be instructive to examine if they still do so when embedded in complex food webs including ontogenetic biomass flow.

Literature cited

Box 1. The niche model by Williams & Martinez (2000)

The niche model requires the number of trophic species (the number of nodes, S_0) and connectance (the fraction of realized feeding interactions out of all potentially possible, C) as input parameters (Table 1). It hierarchically ranks species according to the "niche value," n_i, randomly drawn from a uniform distribution and assigns a feeding range to each species as follows. The range size,r_i (i is the index for taxa), is determined by first drawing a random variable, η_i, from a beta distribution calibrated to obtain the desired connectance and then multiplying η_i by the niche value for i ($r_i = \eta_i n_i$). The center of the feeding range, c_i, is randomly chosen from a uniform distribution in $\left[\frac{r_i}{2}, n_i\right]$, and the range is then determined as$\left[c_i - \frac{r_i}{2}, c_i + \frac{r_i}{2}\right]$. Therefore, species with larger niche values tend to have larger feeding ranges. The ranges are set such that cannibalism is allowed (i.e.,n_i can fall in the range of i). All the taxa whose niche values fall in the feeding range of another are regarded as the prey of the latter. The taxa with no prey are identified as basal taxa (i.e., autotrophs). The taxon with the lowest niche values is designated as an autotroph. We discard disconnected webs, webs with connectance beyond a given tolerance level (C_{error}), and webs with taxa not connected to a basal taxon.

Data accessibility statement

The Matlab code for the modified niche model and the ATN model used in this study is available in the Dryad Digital Depository https:/ XXX

Competing interests statement

The authors declare no competing interests.

Author contributions

A.K. and E.N. conceived the ideas. E.N. led the development of the model to generate life-history structured food webs, wrote the code, implemented and analyzed the models, interpreted model outputs, and wrote the manuscript. A.K. provided advice on the interpretation of outputs and critically commented on the manuscript. Both authors gave final approval of the version to be published.

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