# Incorporating Demographic Diversity into Food Web Models: Effects on Community Structure and Dynamics

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# Abstract

Life history strategies affect population dynamics; however, their effects on community dynamics remain poorly understood. A food web model with stage-structured populations (structured food web) and an equivalent model with unstructured populations (unstructured food web) were developed, and their structures and dynamics were compared. Both models incorporated energetic processes and allowed populations to go extinct and invade over time. The results from the two models shared some similarities. For example, all of the initial randomly-formed food webs were unstable, but the extinction and invasion rates of populations declined over time. However, there were also clear differences between them. For example, preventing trophic interactions among similar-sized organisms led to a large increase in the number of persisting consumer populations under the unstructured food web, but the number was almost unchanged under the structured food web. Furthermore, an increase in the carrying capacity of primary producers caused an increase in the population extinction rate of consumers under the structured food web, but the extinction rate declined under the unstructured food web. Finally, the average trophic level of consumers in the unstructured food web was often at 2, indicating the food web primarily consisted of herbivores. On the other hand, the average trophic level in the structured food web was significantly higher, indicating the existence of trophic interactions among consumers. These results suggest the importance of incorporating stage structures into food web models to bridge the current theories of food web dynamics and empirical observations because nature consists of structured populations. In particular, I conclude that if one wants to study trophic interactions beyond herbivory, it is crucial to incorporate structured populations into food web models.

**Keywords:** Competition, Diversity, Life history evolution, Predator-prey, Structured population, Trophic interactions

# 1. Introduction

Nature is a full of diversity in terms of their durations of developmental stages, which are defined by survival, reproduction, and developmental rates of individuals in a population (Cole, 1954). This type of diversity is herein termed demographic diversity. Demographic diversity plays an important role in determining population dynamics (e.g. Fujiwara, 2007; Jeppsson and Forslund, 2012; Neubert and Caswell, 2000; Tuljapurkar et al., 2009b), and its importance on community dynamics has been suggested (De Roos et al., 2003; Giacomini et al., 2013; Zhou et al., 2013). For example, Wollrab et al. (2013) demonstrated that a stage-structured predator can promote the diversity of its prey because a bottleneck in the life cycle of the predator can reduce predation pressure on some of its prey, which otherwise may be competitively excluded. Their study demonstrated the potential importance of demographic diversity on population interactions and motivated the current study to investigate how demographic diversity plays a role in determining the structure and dynamics of a food web consisting of a large number of structured populations.

Another set of recent studies also focused on how ontogenetic niche shifts affect food web dynamics (Nakazawa, 2015). Ontogenetic niche shifts occur partly because individuals in a population go through ontogenetic changes in their body size, which affects feeding relationships between consumers and resources (Werner and Gilliam, 1984). For example, Rudolf and Lafferty (2011) argued that a population as a whole may be a generalist, but each life stage within the population may be specialized in a certain resource, making a stage-structured population more vulnerable to resource losses than an unstructured population. This idea has been supported by a series of experimental studies (Rudolf and Rasmussen, 2013a, b). In the current study, the food web model that incorporates ontogenetic niche shifts and demographic diversity of consumers was developed. The model was motivated by the idea that populations can adjust their reproductive values and densities among stages, which can experience different niches, to optimize their life history strategies for their persistence (Fujiwara et al., 2011).

The current study also fits under a subset of ongoing studies investigating the relationships between species diversity (number of populations of different species) and the properties of ecological communities. Earlier studies argued that species diversity should increase the stability of a community because an increased number of interactions would attenuate population fluctuations reducing the chance of population explosions (Elton, 1927) or an increased number of energetic pathways to consumers would reduce the chance of their population extinction (MacArthur, 1955). On the other hand, a subsequent study using a mathematical model demonstrated that species diversity should reduce stability (May, 1972). Since these pioneering works, numerous studies, both empirical observations (e.g. Cohen et al., 1993; Gross et al., 2014; MacDougall et al., 2013; Martinson et al., 2012; Mora et al., 2011; Winemiller, 1990) and mathematical modeling (e.g. Allesina and Tang, 2012; DeAngelis, 1975; Ives and Carpenter, 2007; Lorrilliere et al., 2012; Otto et al., 2007; Petchey et al., 2008; Yodzis, 2000) were conducted, and these studies have been reviewed by a number of researchers (e.g. Hooper et al., 2005; McCann, 2000; Rooney and McCann, 2012). A majority of recent research has focused on attempting to understand the properties of communities with adapted populations (e.g. Otto et al., 2007; Rooney and McCann, 2012; Rooney et al., 2008) because natural communities are comprised of selected populations (May, 2006; Yodzis, 1981). However, the investigations of the dynamics of randomly assembled communities still continue (e.g. Allesina and Tang, 2012). Therefore, I also investigated how the dynamics of food webs change as they are assembled through a series of population extinctions and invasions.

Here, I investigated the properties of a food web model with stage-structured consumers (hereafter structured model/food web) and an equivalent model with unstructured consumers (hereafter unstructured model/food web). The models were formulated as a system of ordinary differential equations (ODEs), which were treated as semi-continuous time models. The continuous-time formulations allowed the incorporations of individual-level events occurring simultaneously within a population (i.e. birth, death, predation, and development). The discrete-time nature of the models allowed the simple incorporations of population-level events (i.e. extinctions and invasions). The food web models were built as a collection of interacting populations rather than individual-based models; this allowed fast simulations of the models, permitting multiple replications of the model simulations.

## 2. Methods

The food web models in this study included 10 primary producers and 15 consumers although some of the populations could go extinct (i.e. having a density of 0). The total number of populations was fixed so that the total number of equations in a model remained the same over time. Each of the consumer populations consisted of two stages under the structured food web and a single stage under the unstructured food web. Under both models, primary producers were unstructured (i.e. consisting of a single stage). Consumers fed on primary producers and/or other consumers (collectively referred to as resources), and feeding interactions were determined by the body sizes of potential consumer and resource stages (Fig. 1). The survival of individuals, development among stages, and reproduction were governed by energetic processes. The basic idea behind the energetic model in this study originated from the dynamic energy budget models (Nisbet et al., 2000) although the processes were substantially simplified to accommodate the complexity of food webs. For example, to reduce the number of state variables, the models in this study did not keep track of energy reserve within individuals.

A simulation of a model food web begun with populations with randomly selected individual body sizes (traits), but it experienced the extinctions of populations and resettlements of previously extinct populations. Furthermore, consumer populations with new traits (i.e. new species) invaded the system by replacing some of the extinct populations. Consequently, the composition of life history strategies, which were determined by individual body sizes, and the number of persisting populations in the food web changed over time. During this food web assembly process, changes in the properties of the food web were recorded; these properties included the number and biomass of persisting populations, rates of extinctions and invasions, number of population interactions, and mean trophic level of consumers. These properties were compared between the structured and unstructured food webs under five different scenarios that were different in the niche width of consumers (as determined by the range of resource body size that consumers can feed) and the carrying capacity for primary producers.

The food web models included three basic processes: population dynamics, population interactions, and energetics. These processes, along with the algorithm for simulating the models, are described in more detail.

## 2.1 Population Dynamics

A stage-structured consumer population consisted of juvenile and adult stages. Only adults could reproduce, and their offspring were assumed to become juveniles immediately. Individuals in each stage could die from three possible causes: being consumed by others (consumption death), starvation (starvation death), and other natural causes (natural death). Suppose $n_{i,s}$ was the density of individuals in stage $i$ (1: juveniles and 2: adults) of population $s$, then the dynamic equations were as following:

$$\begin{aligned}\frac{dn_{1,s}}{dt} &= b_s(N,W) - g_s(N,W)n_{1,s} - f_{1,s}(N,W)n_{1,s} - p_{1,s}(N,W)n_{1,s} - mn_{1,s},\\ \frac{dn_{2,s}}{dt} &= g_s(N,W)n_{1,s} - f_{2,s}(N,W)n_{2,s} - p_{2,s}(N,W)n_{2,s} - mn_{2,s},\end{aligned} \tag{1}$$

where $N$ was a vector of stage densities ($n_{i,s}$), $W$ was a vector of stage-specific individual mass ($w_{i,s}$), $b_s(N,W)$ was a per-population birth rate, $g_s(N,W)$ was a per-capita (per-juvenile) development rate from juvenile to adult, $f_{i,s}(N,W)$ was a per-capita starvation-death rate, $p_{i,s}(N,W)$ was a per-capita consumption-death rate, and $m$ was a per-capita "natural" death rate (Table 1). Because starvation- and predation-deaths were modeled separately, the natural deaths excluded these processes. The natural death rate was also independent of size and density; however, the two dependencies were incorporated into the starvation death rate $f_{i,s}(N,W)$ and the consumption death rate $p_{i,s}(N,W)$. The model was not individual-based; therefore, it did not keep track of the transitions of any particular individuals among stages. Instead, it modeled changes in the stage-specific densities of individuals. However, conceptually, the incorporation of the natural death rate reduced the possibility of individuals remaining in any one stage for perpetuity.

Under the unstructured food web, consumer populations consisted of only one stage (adults), and offspring were assumed to become adults immediately. Their dynamics were given by

$$\frac{dn_{3,s}}{dt} = b_s(N) - f_{3,s}(N)n_{3,s} - p_{3,s}(N)n_{3,s} - mn_{3,s}. \quad (2)$$

The notations were the same as those for the structured food web except $i = 3$ was used as a subscript to denote unstructured consumers.

Under both the structured and unstructured food webs, the dynamics of primary producers were given by the logistic equation with a consumption-death rate:

$$\frac{dn_{0,s}}{dt} = r_s n_{0,s}\left(1 - \frac{n_{0,s}}{k}\right) - p_{0,s}(N,W)n_{0,s}, \quad (3)$$

where $r_s$ was the intrinsic per-capita population growth rate, $k$ was the carrying capacity, and $p_{0,s}(N,W)$ was the per-capita consumption-death rate. The subscript $i = 0$ was used for denoting primary producers. The carrying capacity was set to an arbitrary value 10 for all primary producers as a reference case (Scenario 1; Table 2), and, for a comparison purpose, it was increased to 100 (Scenario 4) or allowed to fluctuate periodically (Scenario 5). This formulation assumed that each primary producer was limited by a different environmental resource so that they could co-exist when they did not experience consumption-deaths. Competitions among primary producers for an available resource were a potentially interesting factor to incorporate; however, they were omitted in the current study so that the investigation could be focused on the effect of the demographic diversity of consumers on food web structure and dynamics.

## 2.2 Population Interaction

Individuals in a consumer population could feed on individuals in other populations (both primary producers and other consumers). I assumed no cannibalism; therefore, adults and juveniles of the same population could not eat each other. I also assumed that all individuals in the same stage had the same body size. The existence of a feeding interaction was determined by the body sizes of potential consumer and resource stages. Suppose $l_{i,s}$ was the length of individuals in stage $i$ of population $s$. Then, individuals in stage $y$ of population $A$ (potential consumers) could feed on individuals in stage $x$ of population $B$ (a potential resource) if

$$c_1 l_{y,A} < l_{x,B} < c_2 l_{y,A}, \tag{4}$$

where $0 < c_1 < c_2$. Therefore, the fundamental niche width for a consumer was determined by the two parameters $c_1$ and $c_2$ along with the length(s) of the consumer. I explored different values of $c_1$ and $c_2$ to determine a potential role of niche width in determining the structure and dynamics of food webs (Scenarios 1-4; Table 2; Fig. 1).

The per-capita consumption-death rate of stage $x$ of population $B$ was given as

$$p_{x,B}(N) = \alpha_{x,B} \sum_{\{i,s\}\in\Omega_{consumer}} \beta_{i,s} n_{i,s} \tag{5}$$

where $\Omega_{consumer}$ was the set of stage and population indices ($i$ and $s$, respectively) of the consumers that satisfy inequality (4) for stage $x$ of population $B$ as a resource, and $\alpha_{x,B}$ and $\beta_{i,s}$ were the vulnerability of a resource and consumption efficiency of a consumer, respectively (Table 1). The vulnerability $\alpha_{x,B}$ was assumed to decline with the body size of a resource stage and asymptotes to 0, and the consumption efficiency was assumed to increase with the body size of a consumer stage. Choosing the simplest forms, I allowed $\alpha_{x,B}$ to change inversely with the length of a resource, and $\beta_{i,s}$ to change linearly with the length of a consumer.

## 2.3 Energetic Model

Development, birth, and starvation-death rates were based on the energy intake and expenditure of individuals. First, consumed energy was used for satisfying maintenance. The per-capita energetic requirement for stage $y$ of population $A$, denoted by $E_{y,A}$, was a function of mass-specific energy requirement ( $\mu$ ) and the mass of an individual ( $w_{y,A}$ ) as following:

$$E_{y,A} = \mu w_{y,A}^{3/4} . \tag{6}$$

This formulation assumed that the energy requirement scaled with the power of $3/4$ of body mass, which had been demonstrated with endotherms (Kleiber, 1947).

A per-capita intake rate $I_{y,A}$ was given as

$$I_{y,A} = \gamma \beta_{y,A} \sum_{\{i,s\} \in \Omega_{resource}} \alpha_{i,s} w_{i,s} n_{i,s} , \tag{7}$$

where $\gamma$ was the assimilation efficiency and $\Omega_{resources}$ was the set of stage and population indices ( $i$ and $s$ , respectively) of the resources that satisfy inequality (4) for stage $y$ of population $A$ as a consumer.

When the intake rate was smaller than the expenditure ( $I_{y,A} < E_{y,A}$ ), the mortality rate increased exponentially with the energy deficiency

$$f_{y,A}(N) = e^{0.1 \times (E_{y,A} - I_{y,A})} - 1 . \tag{8}$$

Because the energy expenditure exceeded the input, there was no development or birth (i.e. $g_s(N) = 0$ or $b_s(N) = 0$ ).

On the other hand, when the energy intake was greater than or equal to the energy expenditure ( $I_{y,A} \geq E_{y,A}$ ), the per-capita instantaneous mortality from starvation was 0 (i.e. $f_{y,A}(N) = 0$ ), and the excess energy was used for development or reproduction. The per-capita development rate from a juvenile to an adult was

$$g_s(N) = \frac{\delta \times \left(I_{1,s} - E_{1,s}\right)}{w_{2,s} - w_{1,s}}, \tag{9}$$

where $1-\delta$ was a proportion of the energy used for an overhead energetic cost for development. In this study, 50% of the energy ($\delta = 0.5$) was assumed to become available for development. The development rate was a function of the difference between the sizes of the two stages. The larger the size difference, the longer it took to develop from one stage to the next. These rates also depended on the energy intake. As more food became available, development from one stage to the next became faster. These were two of the important features of the model in this study. Consequently, the life history of a population was determined by the size distribution of individuals within a population (trait) as well as food availability (environment). Equation (8) was similar to the one derived from a detailed individual-based physiological model by De Roos et al. (2008) except that their model predicted depensatory non-linearity of the development rate with the available energy. I omitted the non-linear multiplier in De Roos et al. (2008) to make the model simpler on the basis that we still have uncertainty in how individuals' physiology and behavior compensate for starvation or excess energy availability.

Finally, the population birth rate was given as

$$b_s(N) = \frac{\delta\left(I_{2,s} - E_{2,s}\right)}{w_{1,s}} n_{2,s}. \tag{10}$$

Therefore, the birth rate was a function of the size of juveniles. In this study, 50% of the energy ($\delta = 0.5$) was also assumed to become available for reproduction. In two extreme cases, a large number of small offspring or a small number of large offspring could be produced. For an unstructured population, per-capita birth rate was given by equation (10) after replacing all of the stage indices (including that of the mass) with 3, indicating unstructured consumers.

## 2.4 Simulations

Each simulation consisted of solving the system of ODEs from time *t*=0 to 500, allowing existing populations to go extinct and new populations to invade, and iterating these processes 300 times (Fig. 2). Treating the system of ODEs as a semi-continuous time model alleviated a problem associated with numerical rounding errors when state variables were near 0. Although the equations were deterministic, they were used for simulations. Apart from the initial random assembly of the food web, the randomness in the simulation was introduced in the body sizes of invading consumers and initial population densities of invading consumers and resettled populations (Table 1). The process of simulating a food web is described in more detail below.

Initially, food web was randomly assembled. First, the intrinsic growth rates and body sizes of primary producers were assigned randomly (Table 1). In this simulation, the primary producers maintained the same intrinsic growth rates and body sizes over time. Then, the body sizes of consumer stages were randomly assigned (Table 1). Finally, the initial stage densities of both consumers and primary producers were randomly assigned by simulating uniform random distribution between 0 and 10.

Once the initial random food web was formed, the system of the ODEs was solved from *t*=0 to 1. At *t*=1, if stage densities were less than a quasi-extinction threshold ($1\times10^{-6}$, which was also the maximum tolerance level of the ODE solver used in this study), those densities were set to 0. Then, the processes of solving the ODEs and setting the densities of quasi-extinct stages to 0 at every integer time were continued until *t*=500.

After solving the system of ODEs from t=0 to 500, the extinctions of populations were determined, and new populations were introduced as invading populations. In this simulation, if the sum of the stage densities of a population was below $1\times10^{-6}$, the population was considered extinct. Although populations did not always reach the asymptotic dynamics, which were either stable at an equilibrium point or exhibiting periodic dynamics, I still considered all of the populations above the threshold to be persisting in the system because such populations would not be considered extinct under *in situ* observations. Then, among the extinct populations, five populations were randomly selected, and they were replaced with invading populations with randomly assigned body sizes. The rest of extinct populations were allowed to resettle into the system with the same body sizes as before. Under almost all occasions, more than five consumers were extinct. However, when less than five consumers were extinct, all extinct consumers were replaced with invading populations to maintain the maximum number of consumers rather than changing the number of equations. Stage densities of the invading and resettling populations received new randomly assigned small densities (uniformly distributed between $1\times10^{-6}$ and $1\times10^{-2}$). Then, the food web was solved from *t*=0 to 500 again, and this was iterated 300 times. This process was treated as if a food web was projected by one “time step” by solving ODEs from time *t*=0 to 500, and this projection was iterated over 300 time steps. The results were only evaluated at the end of each time step (i.e. at 300 time steps).

Finally, each scenario of each model was simulated independently 80 times to yield food web replicates. Unless otherwise noted, the means and associated standard errors were calculated over the 80 replicates under the same scenario. To reduce the effects of differences in the properties of primary producers, 80 sets of intrinsic population growth rates of primary producers were simulated once, and the same sets were used for structured and unstructured food webs of all scenarios.

All calculations were done with MATLAB (MATLAB, 2012). For pseudo-random number generations, command “rand” was used. A different seed for the random number generator was used each time the software was started in order to avoid using the same seed for the random number generations among replicates under the same scenario. For solving the system of ordinary differential equations, function “ode45” with the default options was used.

# 3 Results

The results under Scenario 1 are presented first as a reference case. These results are, then, compared with the results under other scenarios. Because a large number of results exist, selected results are presented in the main text, and additional results are provided online as Supplementary Material.

## 3.1 Reference Case (Scenario 1)

The initial randomly assembled food web consisting of 10 primary producers and 15 consumers, whether structured or unstructured, was unstable. It should be noted that, a food web (not a population) was considered stable in this study when the number of persisting populations remained steady; under a stochastic model, this was achieved when the mean number of extinctions was equal to the mean number of successful invasions over a window of time. The average number of persisting consumers at time step 1 (after the initial extinction process) was around 2 under the unstructured model and around 3 under the structured model. However, as they experienced a series of invasions and extinctions, the number of persisting consumers increased (Fig. 3a). The unstructured model reached stability faster than the structured model. Under this particular scenario, the number of persisting consumers under the structured food web was much greater than that under the unstructured food web. The total biomass of consumers under both models also increased quickly with time steps (Fig. 3b).

The average numbers of extinctions and invasions of consumers were greater at the beginning (e.g. time steps 1-50) than latter time steps regardless of whether the populations were structured or unstructured (Fig. 3c-d). This was true even though a food web consisted of a small number of persisting populations initially (Fig. 3a), indicating a high turnover rate of consumers. A large number of extinctions during the initial time steps were accompanied by an even larger number of successful invasions, increasing the number of persisting populations. As the number increases, both extinctions and successful invasions declined. Because the number of persisting populations was much greater under the structured food web than the unstructured food web, per-population rate of extinction (i.e. population extinction probability) was much lower under the structured food web than the unstructured food web.

Primary producers exhibited slightly different temporal dynamics (Fig. 4a-b) compared with consumers. Under both models, the initial randomly assembled food webs consisted of very small number of primary produces. Under the unstructured model, the number of persisting primary producers reached the maximum at time step 2 and declined thereafter, quickly reaching an asymptote. Under the structured model, the number of primary produces increased initially and started to decline after approximately 30 time steps. The total biomass of primary producers under both structured and unstructured food webs declined with time steps even though the biomass of consumers increased with time steps.

The mean trophic level of consumers (Fig. 5a) fluctuated widely under the structured model whereas it remained at a constant level under the unstructured model. The number of interactions per stage (Fig. 5b) rapidly reached stability under the unstructured food web whereas it took longer under the structured model. The increase in the trophic level along with the change in the mean biomass of consumers (Fig. 3b) indicated changing life history strategies of persisting consumers over time under the structured model. The trophic level of consumers under the unstructured model was approximately 2, indicating they were mostly herbivorous; on the other hand, it was higher under the structured model, indicating the consumptions of other consumers (predator-prey interactions) were occurring in the system. The mean number of interactions under the unstructured food web was less than 1. This was because a large number of persisting populations were primary producers and many of them persisted without being preyed upon by any consumers (i.e. no population interaction).

## 3.2 Comparisons of other scenarios with the reference case

An increase in $c_1$ (the relative minimum resource size that consumers can feed; Scenario 2) allowed more stages with a small body size to avoid consumption deaths. This had some similar effects on both structured and unstructured food webs. The number and total biomass of both persisting consumers (Fig. 6a, 6b) and primary producers (Fig. 6c, 6d) and the net primary production (Fig. 6e) increased significantly whereas the rate of extinction declined under both models (Fig. 6f). However, the average trophic level (Fig. 6g) increased significantly under the structured model, but it declined under the unstructured model. Similarly, the number of population interactions per stage (Fig. 6h) declined under the structured food web, but it remained the same under the unstructured food web.

A reduction in $c_2$ (the relative maximum resource size that consumers can feed; Scenario 3) meant multiple stages could co-exist at similar body size without eating each other (e.g. stages with length between 0.8 and 1.0 can co-exist without feeding interactions). The reduction in $c_2$ increased the number of persisting consumers (Fig. 6a); this effect was especially pronounced under the unstructured food web. On the other hand, the biomass of consumers was reduced under both models (Fig. 6b). This reflected the reduction in the net primary production (Fig. 6e). On the other hand, the number and biomass of primary produces changed only slightly (Fig. 6c, 6d). The average trophic level (Fig. 6g) declined whereas the number of interactions increased under both models (Fig. 6g, 6h). Finally, the rate of extinction increased under the structured food web whereas it declined substantially under the unstructured food web (Fig. 6f).

An increase in $k$ (the carrying capacity for primary producers; Scenario 4) resulted in different consequences between the structured and unstructured food webs. Under the structured model, the number of consumers (Fig. 6a) declined whereas the biomass of consumers (Fig. 6b) increased. On the other hand, under the unstructured model, the number of consumers remained approximately the same (Fig. 6a), but the total consumer biomass significantly increased (Fig. 6b). The number of primary producers significantly declined under both structured and unstructured models (Fig. 6c); however, the biomass of primary producers increased significantly under the structured food web whereas it remained almost unchanged under the unstructured food web.

Finally, the periodic fluctuation in the carrying capacity for primary producers had the least effect among the four scenarios when compared with the reference case. The major effect was in an increase in the trophic level of consumers under the structured model.

## 3.3 Comparison between structured and unstructured food webs

The number of persisting consumers was often higher under the structured food web compared with the unstructured food web. However, this relationship was reversed when $c_2$ (the relative maximum resource size that consumers can feed) was reduced. On the other hand, the biomass of consumers was almost always higher under the unstructured food web. The trophic level of consumers and the number of interaction per stage were higher under the structured food web than unstructured food web (Fig. 6).

## 4 Discussion

Nature consists of structured populations. Therefore, it is important to ask whether we can capture the caricatures of real food webs with the models consisting of unstructured populations or we need to include structured populations. For example, Rudolf and Lafferty (2011) investigated the potential effects of ontogenetic niche shifts on food web dynamics and argued for its importance. My study demonstrated that it is crucial to include stage structured populations because as simple as changing the carrying capacity ( $k$ ) for primary producers and how populations avoid consumptions ( $c_2$ ) could lead to conflicting results between the structured and unstructured food webs.

A reduction in $c_2$ (the relative maximum resource size that consumers can feed; Scenario 3) increased the number of persisting consumers under the unstructured food web, but it only had a small effect on the number of consumers under the structured food web. Under the unstructured model, a reduction in $c_2$ meant an increase in the number of populations with larger adults to co-exist without direct feeding interactions. Under the structured model, the effect was similar except that those populations also had juveniles, which could be eaten by the adults of other populations, and without juveniles, adults cannot be sustained. Consequently, the direct feeding interactions between populations were not necessarily reduced by reduction in $c_2$ under the structured food web.

In addition to ontogenetic niche shifts, demographic diversity plays an important role in food web structure and dynamics. For example, Fujiwara et al. (2011) showed that organisms can adjust their life history strategies to improve their competitive strength against other populations. In this study, poulations with large adults tended to have delayed maturation because the difference in sizes between adults and juveniles was large. Populations with large adults (i.e. delayed maturation) could exclude populations with small adults (i.e. early maturation) or *vice versa* when the competition increaseed between juvenile stages of the former and small adult stages of the latter. Therefore, simple partitioning of available resources is probably not enough to account for complex food-web dynamics.

Body size is closely associated with energetic processes (Nisbet et al., 2000); therefore, it is closely associated with life history strategy of populations. In this study, I also assumed that body size determines the existence and strength of feeding interactions. This probably produced very strong coupling of energetic process and feeding interactions. However, natural food webs vary greatly with regard to how feeding interactions are determined. For example, trophic interactions are thought to be structured more by body size under aquatic systems compared with terrestrial systems (Shurin et al., 2006). Other factors, such as behavior, morphology, physiology, and anatomy of organisms, probably play an important role in determining feeding interactions. In my model, consumers cannot feed on larger organisms, but in reality, many examples of small predators feeding on larger prey exist (e.g. wolf feeding on caribou). I suggest incorporating such variations is one of the important future directions of the study toward understanding the structure and dynamics of food webs. The current model allows a relatively easy incorporation of the complexity; it can be incorporated into vulnerability $\alpha_{i,s}$ and consumption efficiency $\beta_{i,s}$ by making them functions of both specific consumer and resource populations.

Determining the stability of randomly assembled food webs is still an active area of research (e.g. Allesina and Tang, 2012). My analysis showed that the initial, randomly assembled food webs were always unstable (Fig. 3), which is consistent with the results of May (1972). This is not surprising. For example, if we were to select populations randomly from the global pool of species and assembled a community, it would be very unlikely that the community is stable. Real-world food webs are, instead, comprised of selected populations (May, 2006; Yodzis, 1981). Therefore, it is more informative to investigate food webs consisting of selected populations. My model suggested such food webs have a much reduced extinction rate. At the same time, they also have a reduced invasion rate, suggesting the food webs consisting of selected populations can also resist invasions.

Fluctuations in environmental conditions are important mechanisms for the evolution of life history strategies (Tuljapurkar et al., 2009a). Therefore, I expected that the food webs with structured populations to become more stable compared with the ones with unstructured populations under fluctuating environment. On the contrary to this prediction, the model suggested periodic fluctuations in the carrying capacity of primary producers had only small effects on the structure and dynamics of food webs. It is plausible that amplitude of the fluctuation was not large enough or the deterministic (i.e. periodic) nature of the fluctuation made it easy for populations to adapt whether consumers were structured or not. I suggest future studies to investigate the effects of large amplitude and/or stochastic fluctuations in environmental conditions (e.g. Varughese, 2011) on food web structure and dynamics.

Because the purpose of this study was to show the difference between the structured and unstructured food webs, I attempted to make the parameters consistent between the two models. However, the actual values were not determined based on empirical studies, and the same parameter values were used for all populations except their body sizes. In reality, the types of consumers (e.g. ectotherms vs. endotherms, predators vs. herbivores) or the types of primary producers (e.g. terrestrial plants vs. phytoplankton) would affect the parameters substantially (Hairston and Hairston, 1993; Yodzis and Innes, 1992). Consequently, the use of any particular value for a parameter across all populations would have not satisfied the complexity of the natural food webs regardless of how carefully the parameter value was obtained, and incorporating population-specific parameters was beyond the scope of the study at this stage. I believe attempts to develop more realistic food web models and to estimate associated parameters empirically should be done in the future. The model in this study provides the basic structure of a model that is balanced between complexity to represent the reality and simplicity to allow multiple replications for accurate evaluations.

Under the unstructured models, consumers were almost always herbivores (i.e. the average trophic level was 2). On the other hand, the trophic level of the consumers was higher under the structured food web. Under the unstructured models, populations at a higher trophic level probably could not persist because trophic interactions were so strong that no animal populations could persist as a resource. On the other hand, under the structured models, if one of the stages could avoid being consumed, the population might be able to persist even though the other stage was consumed by other populations. This probably resulted in a higher average trophic level under the structured food webs. Nature consists of food webs with varying maximum trophic levels, and in order to understand the variation, it is important to investigate the balance between competition and consumer-resource interactions (Hairston and Hairston, 1993). My study suggested that understanding these interactions among structured populations is probably crucial for understanding the structure and dynamics of food webs. I speculate that the existence of complex life history strategies and the existence of high trophic levels are closely related with each other.

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Figure 1

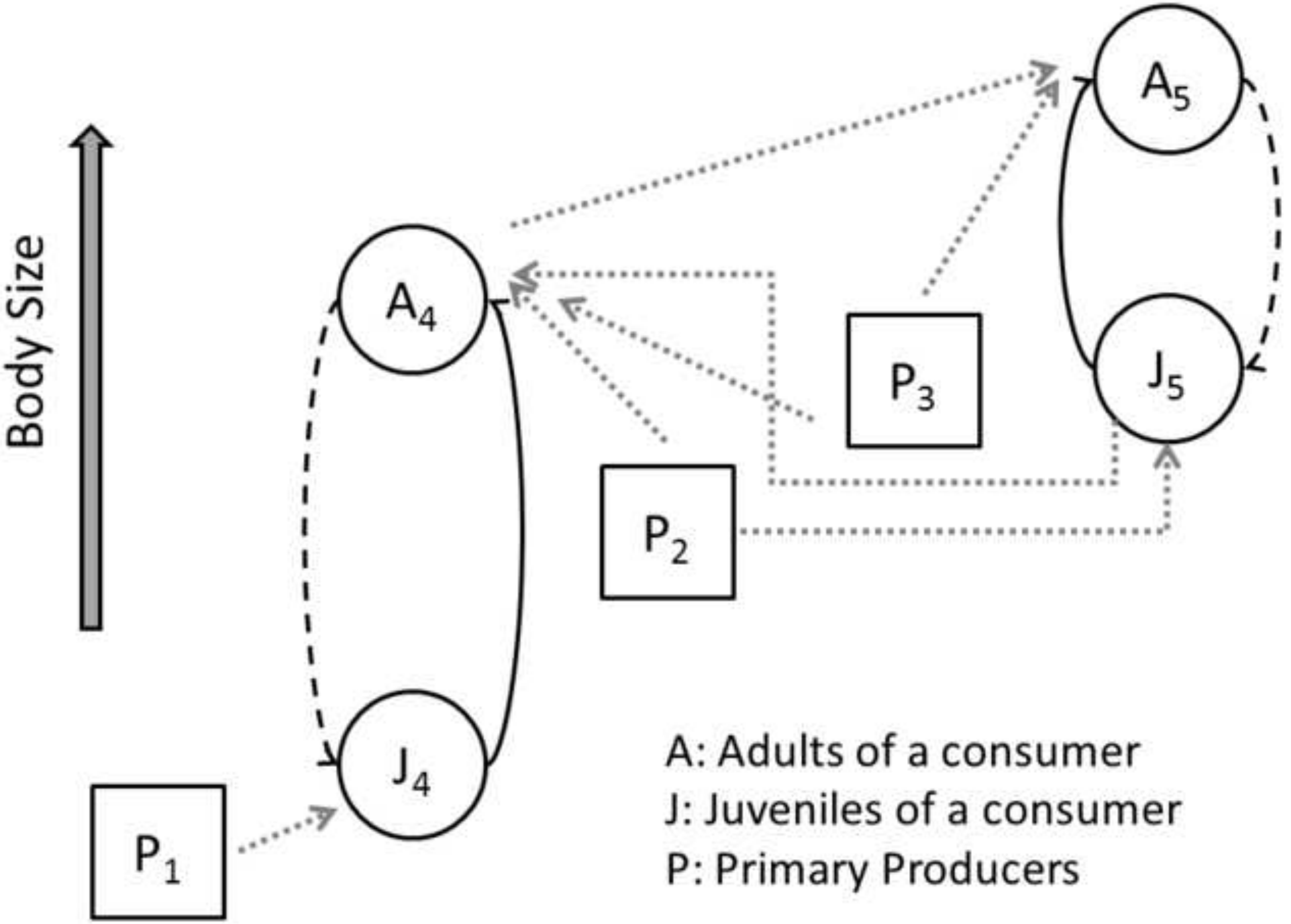
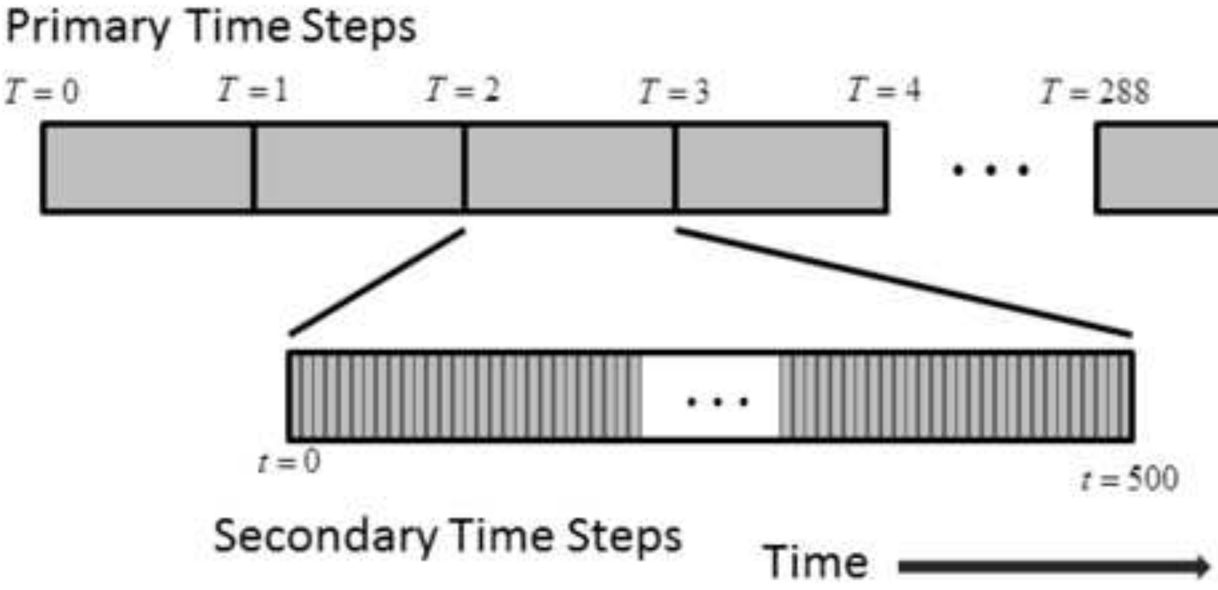

Body Size
A$_4$
J$_4$
A$_5$
J$_5$
P$_1$
P$_2$
P$_3$
A: Adults of a consumer
J: Juveniles of a consumer
P: Primary Producers

**Figure 2**



**Events**

$T$=0: Randomly assembled food web

$T$=1, 2, …, 299: Extinctions, invasions, and resettlement

$t$=1, 2, …, 500: Setting $n_{is}=0$ if $n_{is}<10^{-6}$

Figure 3

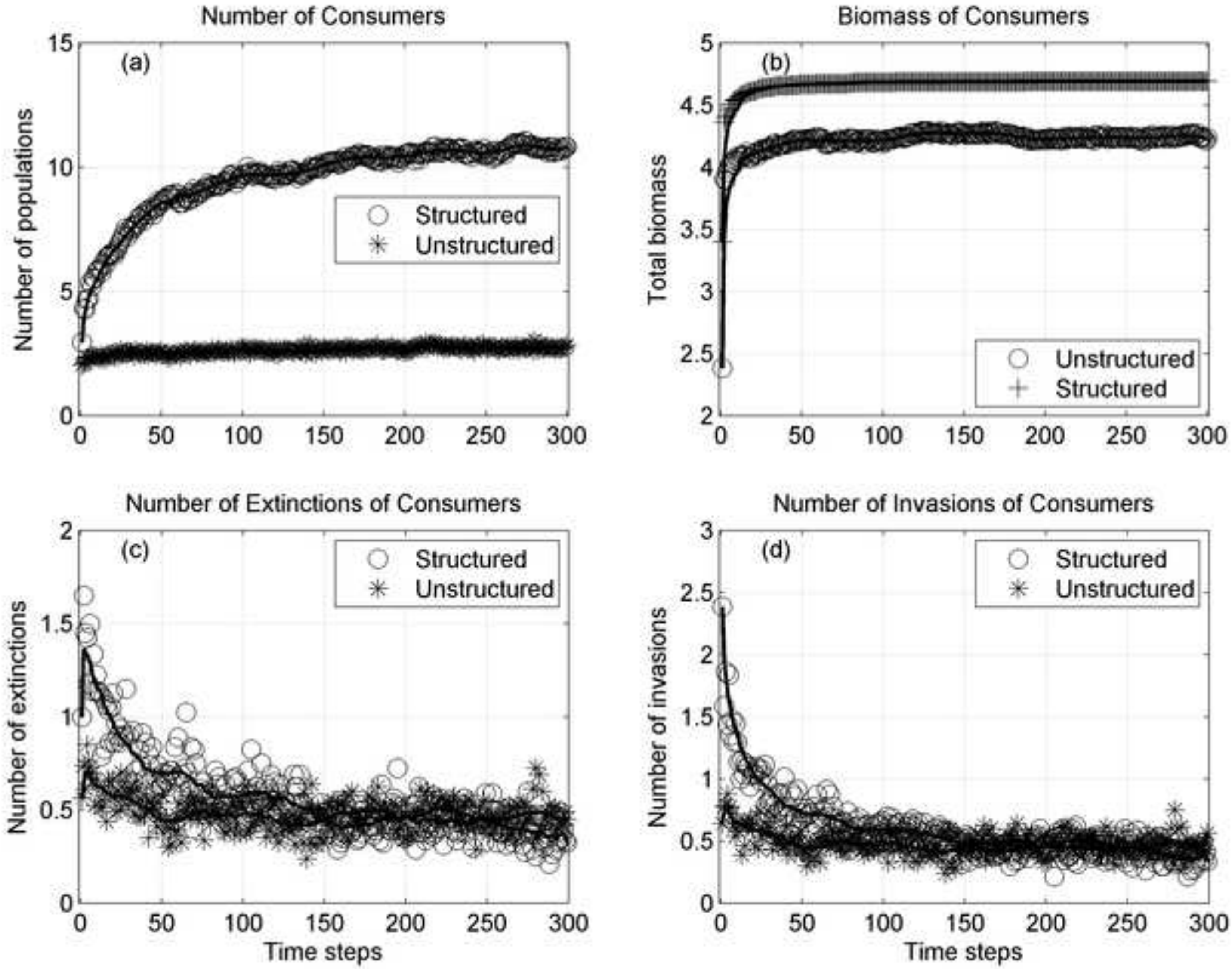

Number of Consumers
(a)
Number of populations
Structured
Unstructured
Biomass of Consumers
(b)
Total biomass
Unstructured
Structured
Number of Extinctions of Consumers
(c)
Number of extinctions
Time steps
Number of Invasions of Consumers
(d)
Number of invasions
Time steps
0
50
100
150
200
250
300
0
5
10
15
2
2.5
3
3.5
4
4.5
5
0.5
1
1.5
2
2.5
3

Figure 4

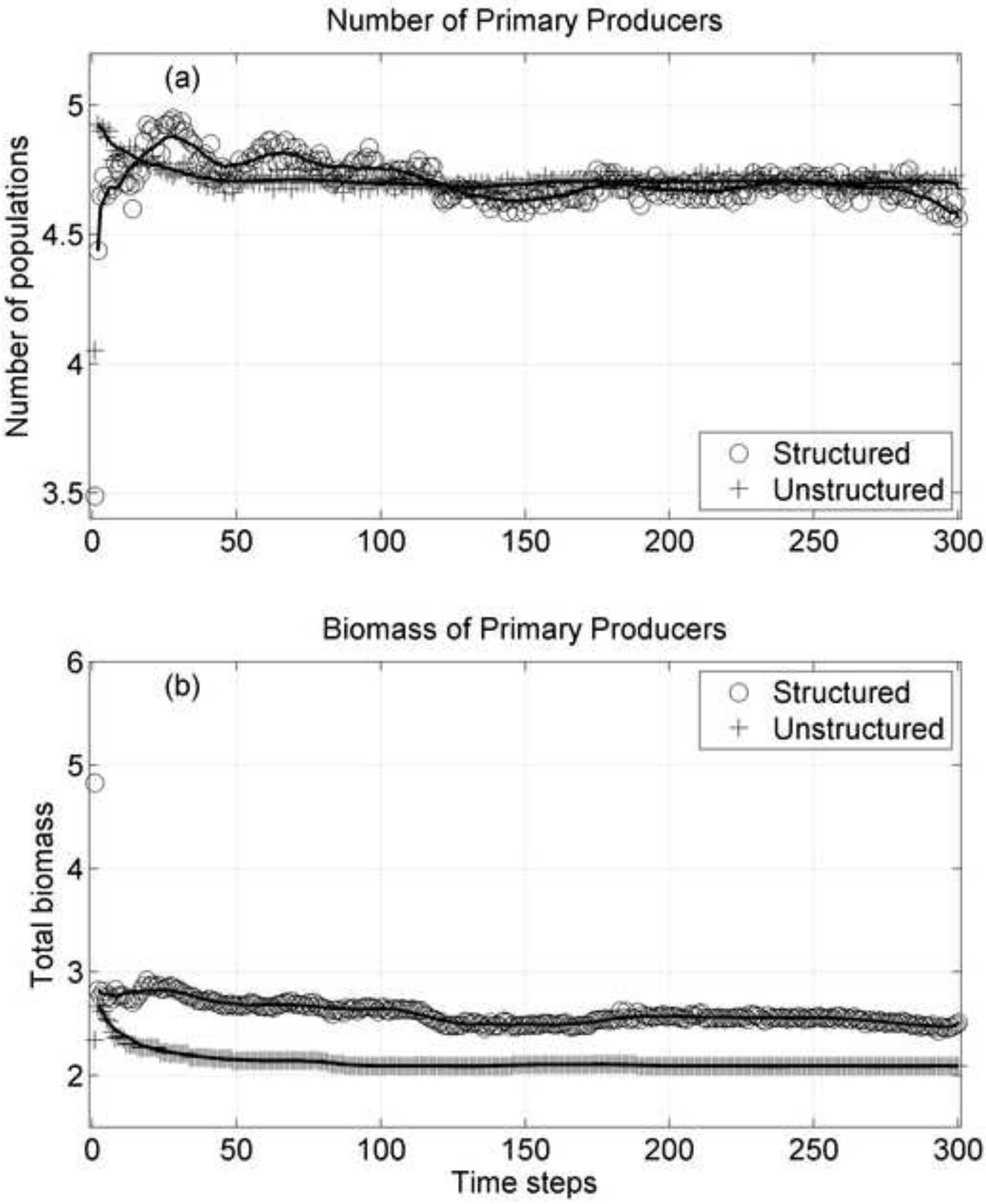

Number of Primary Producers
(a)
Number of populations
5
4.5
4
3.5
0
50
100
150
200
250
300
Structured
Unstructured
Biomass of Primary Producers
(b)
Total biomass
6
5
4
3
2
Structured
Unstructured
0
50
100
150
200
250
300
Time steps

**Figure 5**

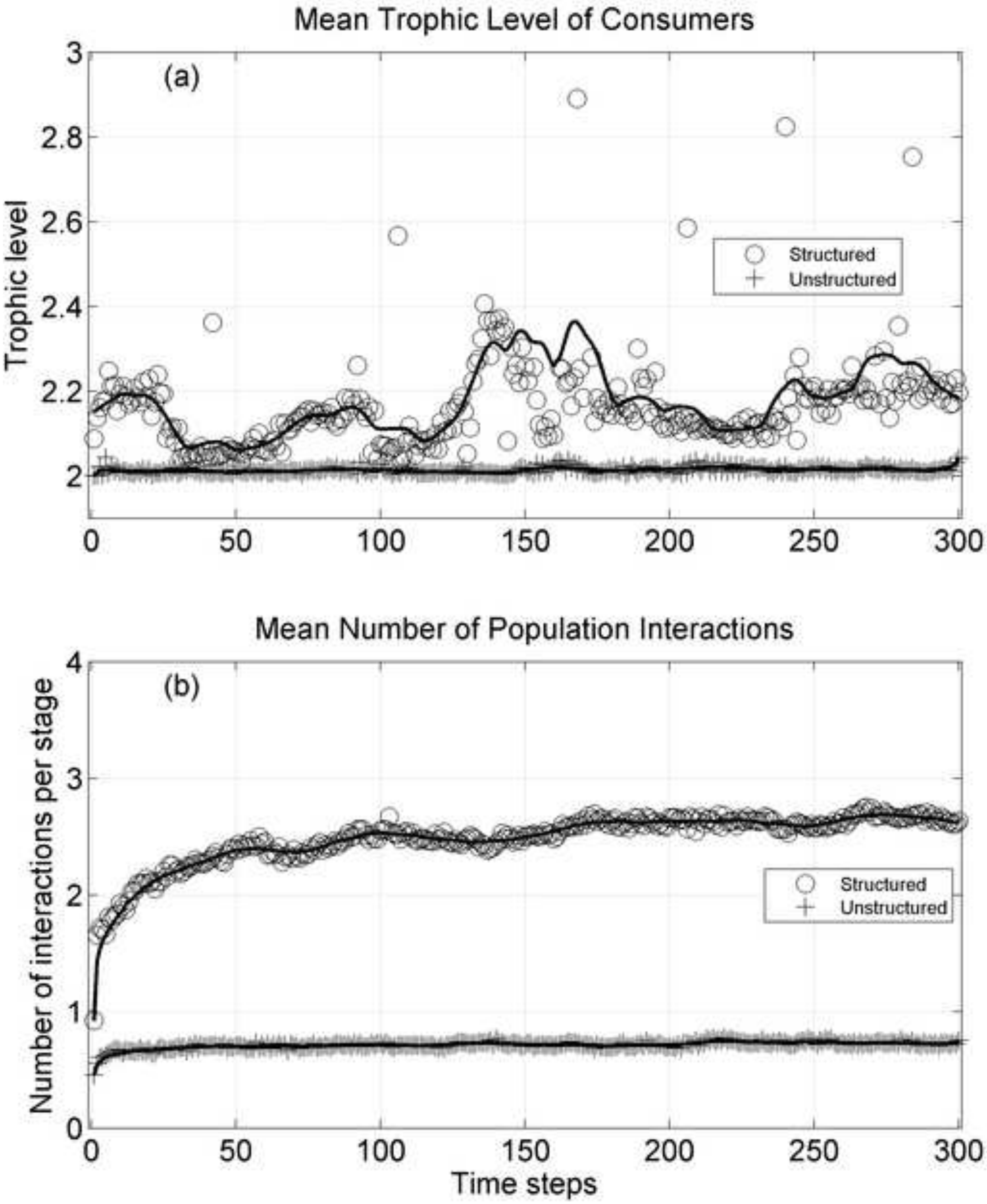

Mean Trophic Level of Consumers
(a)
Trophic level
3
2.8
2.6
2.4
2.2
2
0
50
100
150
200
250
300
Structured
Unstructured
Mean Number of Population Interactions
(b)
Number of interactions per stage
4
3
2
1
0
0
50
100
150
200
250
300
Time steps
Structured
Unstructured

Figure 6

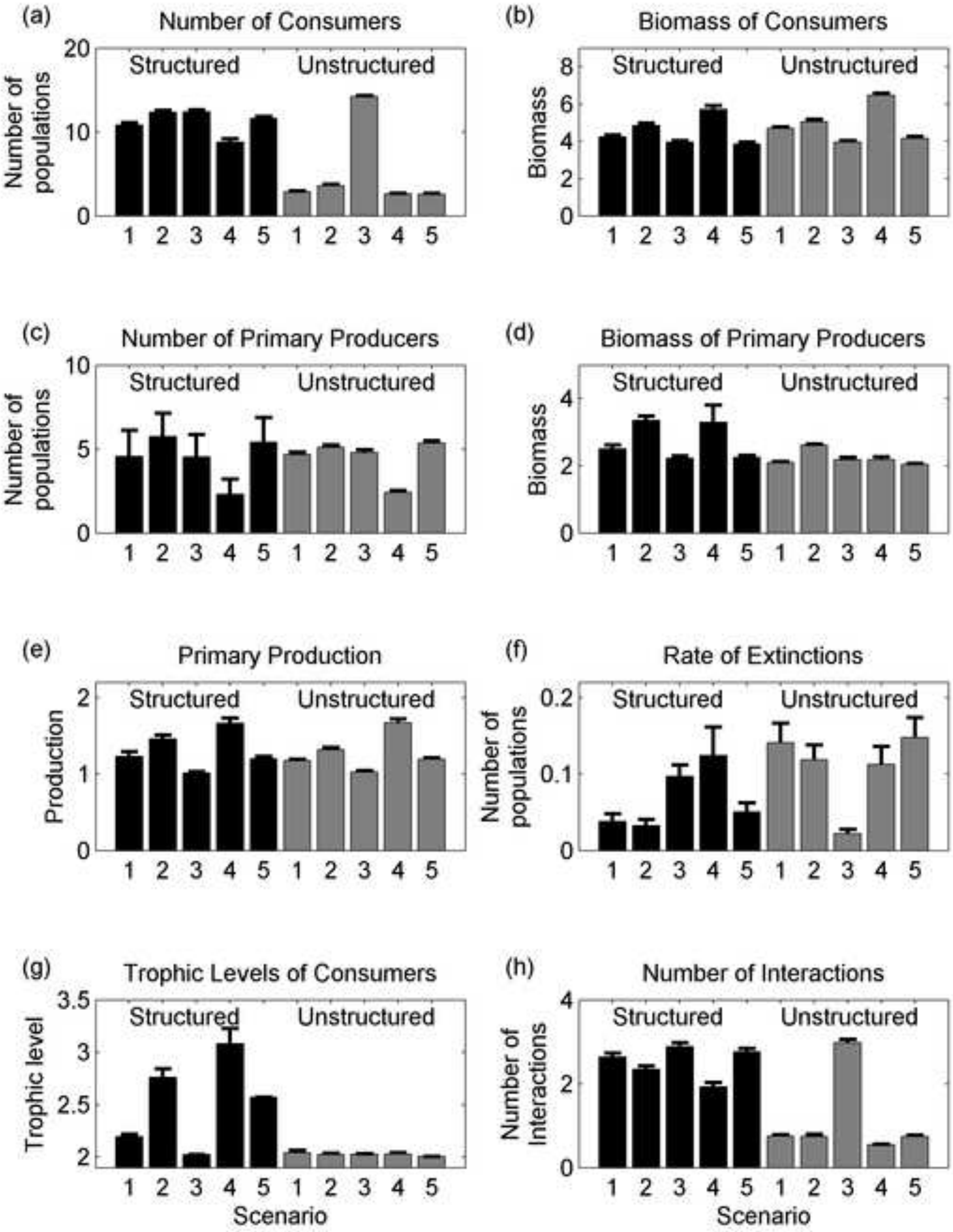

(a)
Number of Consumers
Structured
Unstructured
Number of populations
20
10
0
1 2 3 4 5 1 2 3 4 5
(b)
Biomass of Consumers
Structured
Unstructured
Biomass
8
6
4
2
0
1 2 3 4 5 1 2 3 4 5
(c)
Number of Primary Producers
Structured
Unstructured
Number of populations
10
5
0
1 2 3 4 5 1 2 3 4 5
(d)
Biomass of Primary Producers
Structured
Unstructured
Biomass
4
2
0
1 2 3 4 5 1 2 3 4 5
(e)
Primary Production
Structured
Unstructured
Production
2
1
0
1 2 3 4 5 1 2 3 4 5
(f)
Rate of Extinctions
Structured
Unstructured
Number of populations
0.2
0.1
0
1 2 3 4 5 1 2 3 4 5
(g)
Trophic Levels of Consumers
Structured
Unstructured
Trophic level
3.5
3
2.5
2
1 2 3 4 5 1 2 3 4 5
Scenario
(h)
Number of Interactions
Structured
Unstructured
Number of Interactions
4
2
0
1 2 3 4 5 1 2 3 4 5
Scenario

**Table 1. Parameters and variables in the food web models.**

| | Description | Value |
|---|---|---|
| **Index Variables** | | |
| $i$ | Stage | 0-3 |
| $s$ | Population | --- |
| **State Variable** | | |
| $n_{i,s}$ | Density of individuals in a stage | --- |
| **Fixed Parameters** | | |
| $m$ | Per capita natural mortality rate | 0.01 |
| $\delta$ | Efficiency for an individual to convert energy for development and reproduction. | 0.5 |
| $\mu$ | Energy required for maintenance per mass | 0.1 |
| $\gamma$ | Efficiency for converting consumed energy to usable energy | 0.5 |
| **Derived Parameters** | | |
| $\alpha_{i,s}$ | Vulnerability to consumption | $0.1 \times l_{i,s}^{-1}$ |
| $\beta_{i,s}$ | Efficiency of consumptions | $l_{i,s}$ |
| $w_{i.s}$ | Mass of individuals | $l_{i,s}^{3}$ |
| **Randomly Assigned Parameters** | | |
| $r_s$ | Intrinsic per-capita population growth rate | Uniform [0,1] |
| $l_{0,s}$ | Length of primary producers | Uniform [0,0.5] |
| $l_{2,s}$, $l_{3,s}$ | Length of adults | Uniform [0,1] |

| | | |
|---|---|---|
| $l_{1,s}$ | Length of juveniles | Uniform $[0, l_{2,s}]$ |

**Table 2. Scenarios investigated. Each scenario was applied to both structured and unstructured food webs.**

| **Scenario** | $c_1$ * | $c_2$ † | $k$ ‡ |
|---|---|---|---|
| **1** | 0.125 | 1 | 10 |
| **2** | 0.25 | 1 | 10 |
| **3** | 0.125 | 0.8 | 10 |
| **4** | 0.125 | 1 | 100 |
| **5** | 0.125 | 1 | $2.5\left(\cos\left(10\pi t\right)+3\right)$ |

| | |
|---|---|
| * | Proportion of minimum size relative to consumer |
| † | Proportion of maximum size relative to consumer |
| ‡ | Carrying capacity for primary producers. |