A matter of maturity: to delay or not to delay?

Continuous-time compartmental models of structured

populations in the literature 2000-2016

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Abstract

Structured compartmental models in mathematical biology track age classes, stage classes, or size classes of a population. Structured modeling becomes important when mechanistic formulations or intraspecific interactions are class-dependent. The classic derivation of such models from partial differential equations produces time delays in the transition rates between classes. In particular, the transition from juvenile to adult has a delay equal to the maturation period of the organism. In the literature, many structured compartmental models, posed as ordinary differential equations, omit this delay. We reviewed occurrences of continuous-time compartmental models for age- and stage-structured populations in the recent literature (2000-2016) to discover which papers did so. About half of the 249 papers we reviewed used a maturation delay. Papers with ecological models were more likely to have the delay than papers with disease models, and mathematically-focused papers were more likely to have the delay than biologically-focused papers.

Recommendations for Resource Managers:

• Interacting populations often are modeled with systems of ordinary differential equations in which the state variables are numbers of individuals of each species and interaction terms depend only on the current state of the system.

• Single-population continuous-time models with age- or stage-structure, in which state variables represent numbers of individuals in classes such as juveniles and adults, often but not always contain maturation time delays in the transition rates between classes. The exclusion of the delay typically changes the model dynamics.

• Managers should be aware of the maturation delay issue when considering the results of continuous-time models of structured populations.

• Discrete-time models have an inherent time delay, set by the census time step chosen by the modeler, and for that reason are convenient for modeling maturation and other biological delays.

Keywords: stage structure; age structure; maturation rate; continuous-time population

model; compartmental model; ordinary differential equation; delay differential equation; McKendrick-von Foerster partial differential equation

1 Introduction

Individuals in a population generally differ from each other in age, life cycle stage, size, and other physiological characteristics. Sometimes these differences play crucial roles in the dynamics of the population (Gurney and Nisbet, 1998). In 1911, F. R. Sharpe and A. J. Lotka posed integral equation models for age-structured populations (Sharpe and Lotka, 1911), and in 1926 A. G. McKendrick, in his classic paper "Applications of Mathematics to Medical Problems," developed a partial differential equation (PDE) model that accounted for the age structure of a population (McKendrick, 1926). H. von Foerster further developed this model in his seminal 1959 paper "Some Remarks on Changing Populations" (von Foerster, 1959). The model now known as the McKendrick-von Foerster equation is

$$\rho_t + \rho_a = -\mu\rho, \tag{1}$$

in which $\rho(t, a)$ is the age density of the population and satisfies conditions on the boundary that account for the generation of new individuals by births as well as the initial age distribution. The classic paper by Sinko and Streifer (1967) developed a similar model including both age and size structure.

In some circumstances it is helpful to "lump" together individuals having certain characteristics, for example into age classes or size classes (Gurney et al., 1983). Classes may require different mechanistic formulations, and dynamic interactions may occur between classes. In multiple-species models, life cycle stage classes of one species may differ in the nature of their interactions with the other species. Discrete-time structured Leslie matrix-type models are convenient if the classes have equal duration and if there is a natural discrete-time pulse in the life cycle, such as annual births (Cushing, 1998; Gurney and Nisbet, 1998). Discrete-time

models have inherent time delays determined by the actual biological delays as well as the census time step set by the modeler. In continuous time, one can obtain state variables for class abundances by integrating the structured PDE over the classes, for example by integrating $\rho(t, a)$ over age classes. This produces a compartmental model which is a system of differential equations having time delays in the transition rates between classes. For example, in a juvenile-adult model with maturation time τ, the transition rate from juvenile to adult at time t depends on the number of adults at time $t - \tau$. The resulting compartmental model is therefore a system of delay differential equations (DDEs) or functional differential equations (FDEs). In particular, the resulting model is not a system of ordinary differential equations (ODEs) in which transition rates depend only on the current state of the system.

A number of classic papers in the mathematical ecology literature derived age-structured DDEs or FDEs from PDEs in various settings (Metz and Diekmann, 1986; Nisbet and Gurney, 1982). Some of these used fixed maturation delays (Gurney et al., 1983; Sulsky et al., 1989), and some used distributed maturation delays (Blythe et al., 1984). The theory of the resulting FDEs is fairly complete (Smith, 1993, 1994a,b, 1995). A few papers have posed models with dynamically-varying, threshold-type maturation delays, for example models in which maturation is determined by the consumption of a threshold amount of resource, which is itself a dynamic variable (Nisbet and Gurney, 1983; Smith, 1993). Variation in age at maturity may also occur when development rates depend on physiological factors measured in degree-days rather than chronological time (Trudgill et al., 2005).

Some of the classic papers successfully linked DDE models to data. For example, Gurney et al. (1983) developed a detailed DDE model for Australian sheep-blowflies and fitted it to Nicholson's Blowflies data, and McCauley et al. (1996) tested whether a three-age-class DDE model could predict the dynamics of laboratory populations of herbivorous zooplankton *Daphnia galeata* and *Bosmina longirostris*.

The more recent literature contains numerous examples of ODE structured population models in which there is no time delay in the transition rates between classes. Although

some papers explicitly mention the lack of maturation delay, many do not, and in most cases the models are hypothesized directly as ODEs, with no connection to structured PDEs.

The goal of this paper is to review the mathematical biology literature from 2000-2016 in order to see how continuous-time age- and stage-structured compartmental population models are being derived and posed with respect to the issue of maturation delay. For the convenience of the reader, we begin by revisiting the classical derivation of compartmental structured models from the McKendrick von-Foerster PDE. For simplicity we consider a linear juvenile-adult system, while recognizing that the same issues arise in nonlinear age- and stage-structured models with two or more classes and also in size-structured models.

2   The McKendrick-von Foerster Age-Structured PDE

The linear first-order hyperbolic McKendrick-von Foerster PDE for an age-structured population is

$$\rho_t + \rho_a = -\mu\left(t, a\right)\rho \tag{2}$$

with nonstandard boundary conditions

$$\rho\left(t, 0\right) \;=\; \int_0^\infty \beta\left(t, a\right)\rho\left(t, a\right) da \tag{3}$$

$$\rho\left(0, a\right) \;=\; \varphi\left(a\right) \tag{4}$$

where $\rho\left(t, a\right)$ is the density of the population at time t and age a, $\beta\left(t, a\right)$ and $\mu\left(t, a\right)$ are the per capita birth and death rates at time t and age a, respectively, and $\varphi\left(a\right)$ is the initial age distribution. The total birth rate at time t is $\rho\left(t, 0\right)$. In this section we illustrate some ways in which differential equations can be derived for aggregated state variables, i.e. integrals (possibly weighted) of the density $\rho\left(t, a\right)$ over a range of ages a.

Let $\tau > 0$ be the maturation age of the juveniles. We begin by assuming that the death rates for juveniles and adults are μ_J and μ_A, respectively, and the birth rate of adults is

independent of time t and age a. The birth rate for juveniles is, by definition, equal to 0. Therefore, we have

$$\mu(t, a) = \begin{cases} \mu_J & \text{for } 0 \leq a < \tau \\ \mu_A & \text{for } \tau \leq a \end{cases} \tag{5}$$

$$\beta(t, a) = \begin{cases} 0 & \text{for } 0 \leq a < \tau \\ \beta & \text{for } \tau \leq a \end{cases} \tag{6}$$

where μ_J, μ_A and β are constants.

The numbers of juveniles and adults are

$$J(t) = \int_0^\tau \rho(t, a)\, da \tag{7}$$

$$A(t) = \int_\tau^\infty \rho(t, a)\, da, \tag{8}$$

respectively. By (3), (6), and (8), the total birth rate is

$$\rho(t, 0) = \beta A(t). \tag{9}$$

An integration along characteristics of (2)-(4) produces the general solution

$$\rho(t, a) = \begin{cases} \rho(t - a, 0) \exp\left(-\int_0^a \mu(t - a + s, s)\, ds\right) & \text{for } 0 \leq a \leq t \\ \varphi(a - t) \exp\left(-\int_{a-t}^a \mu(t - a + s, s)\, ds\right) & \text{for } t < a \end{cases} \tag{10}$$

For $a \leq \tau \leq t$, by (5), (9) and (10), we have

$$\begin{aligned} \rho(t, a) &= \rho(t - a, 0) \exp\left(-\int_0^a \mu_J ds\right) \\ &= \beta A(t - a) \exp(-\mu_J a). \end{aligned} \tag{11}$$

In particular, from (5), we obtain

$$\rho(t, \tau) = \beta A(t - \tau) \exp(-\mu_J \tau) \tag{12}$$

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for $t \geq \tau$. We note that if death rates depend on time as well as age, the exponential term $\exp(-\mu_J\tau)$ will be more complicated, involving an integral in the exponent.

Integration of (2) with respect to a over the juvenile stage ($a = 0$ to $a = \tau$) yields

$$J'(t) + \rho(t,\tau) - \rho(t,0) = -\mu_J J(t), \tag{13}$$

from which we obtain

$$J'(t) = \beta A(t) - \mu_J J(t) - \beta A(t-\tau)\exp(-\mu_J\tau) \tag{14}$$

for $t \geq \tau$. Integration of (2) with respect to a over the adult stage ($a = \tau$ to $a = \infty$) yields (assuming $\rho(t,\infty) = 0$)

$$A'(t) + 0 - \rho(t,\tau) = -\mu_A A(t), \tag{15}$$

from which we obtain

$$A'(t) = \beta A(t-\tau)\exp(-\mu_J\tau) - \mu_A A(t) \tag{16}$$

for $t \geq \tau$.

This yields a system of DDEs for J and A for $t \geq \tau$:

$$J'(t) = \beta A(t) - \mu_J J(t) - \beta A(t-\tau)\exp(-\mu_J\tau), \tag{17}$$

$$A'(t) = \beta A(t-\tau)\exp(-\mu_J\tau) - \mu_A A(t). \tag{18}$$

The transition rate between the juvenile and adult classes has a time lag τ, which is the age of maturation. The lag τ appears as a coefficient in both differential equations. Note that the A equation is uncoupled from the J equation.

If there is a nonlinear dependence in the death and/or birth rate, then the nature of the delay terms in the differential equations for J and A can be more complicated. For example,

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suppose μ_J, μ_A and β in (5) and (6) depend on the population sizes $J(t)$ and $A(t)$:

$$\mu_J(J(t), A(t)), \quad \mu_A(J(t), A(t)), \quad \beta(J(t), A(t)). \tag{19}$$

Then integration of (2) with respect to a over the juvenile stage ($a = 0$ to $a = \tau$) yields (assuming $\rho(t, \infty) = 0$)

$$J'(t) + \rho(t, \tau) - \rho(t, 0) = -\mu_J(J(t), A(t)) J(t) \tag{20}$$

from which, together with

$$\rho(t, \tau) = \rho(t - \tau, 0) \exp\left(-\int_0^\tau \mu_J(J(t - \tau + s), A((t - \tau + s))) \, ds\right)$$
$$= \beta(J(t - \tau), A(t - \tau)) A(t - \tau) \exp\left(-\int_{t-\tau}^t \mu_J(J(\sigma), A(\sigma)) \, d\sigma\right) \tag{21}$$

for $t \geq \tau$, we obtain

$$J'(t) = \beta(J(t), A(t)) A(t)$$
$$- \beta(J(t - \tau), A(t - \tau)) A(t - \tau) \exp\left(-\int_{t-\tau}^t \mu_J(J(\sigma), A(\sigma)) \, d\sigma\right) \tag{22}$$
$$- \mu_J(J(t), A(t)) J(t).$$

Similar calculations, utilizing an integration of (2) with respect to a over the adult stage ($a = \tau$ to $a = \infty$), yield

$$A'(t) = \beta(J(t - \tau), A(t - \tau)) A(t - \tau) \exp\left(-\int_{t-\tau}^t \mu_J(J(\sigma), A(\sigma)) \, d\sigma\right)$$
$$- \mu_A(J(t), A(t)) A(t). \tag{23}$$

The differential equations (22)-(23) for $J(t)$ and $A(t)$ have distributed delays in addition to the time lag τ.

The assumption (6) describes a simple dependence of the birth rate on age. A different assumption that has been widely used to derive ODE equations from the McKendrick PDE

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is

$$\beta\left(t,a\right) = k\left(t\right) a^{n} \exp\left(-ca\right) \tag{24}$$

with

$$k\left(t\right) = \beta_{0}\left(t\right) \tau^{-n} \exp\left(c\tau\right) \tag{25}$$

for a non-negative integer n and

$$c = \frac{n}{\tau} > 0 \tag{26}$$

(Busenberg and Travis, 1982; Metz and Diekmann, 1991). This age dependent distribution of birth rates assumes that maximal birth rate $\beta_{0}\left(t\right) > 0$ occurs at age $a = \tau > 0$. The integer n measures how closely birth rates are clustered around $a = \tau$, with larger values of n concentrating the birth rate near age τ. The total birth rate equation (3) is

$$\rho\left(t,0\right) = k\left(t\right) P_{n}\left(t\right) \tag{27}$$

where we have defined the weighted total population sizes

$$P_{n}\left(t\right) = \int_{0}^{\infty} a^{n} \exp\left(-ca\right) \rho\left(t,a\right) da. \tag{28}$$

If we assume the death rate $\mu = \mu\left(t\right)$ is independent of age, then from the McKendrick PDE

$$\rho_{t} + \rho_{a} = -\mu\left(t\right)\rho \tag{29}$$

we can derive ODEs for the quantities

$$P_{i}\left(t\right) = \int_{0}^{\infty} a^{i} \exp\left(-ca\right) \rho\left(t,a\right) da, \quad i = 0, 1, 2, ..., n. \tag{30}$$

For $i = 0$, we have

$$
\begin{aligned}
P_0'(t) &= \int_0^\infty \exp(-ca)\, \rho_t(t,a)\, da \\
&= \int_0^\infty \exp(-ca)\, [-\mu(t)\rho(t,a) - \rho_a(t,a)]\, da \\
&= -\mu(t)\, P_0(t) - \int_0^\infty \exp(-ca)\, \rho_a(t,a)\, da.
\end{aligned}
\tag{31}
$$

An integration by parts yields

$$
\begin{aligned}
P_0'(t) &= -\mu(t)\, P_0(t) - \left[0 - \rho(t,0) + c\int_0^\infty \exp(-ca)\, \rho(t,a)\, da\right] \\
&= -\left(\mu(t) + c\right) P_0(t) + k(t)\, P_n(t).
\end{aligned}
\tag{32}
$$

For $i = 1, 2, \ldots n$ we have

$$
\begin{aligned}
P_i'(t) &= \int_0^\infty a^i \exp(-ca)\, \rho_t(t,a)\, da \\
&= \int_0^\infty a^i \exp(-ca)\, [-\mu(t)\rho(t,a) - \rho_a(t,a)]\, da \\
&= -\mu(t)\, P_i(t) - \int_0^\infty a^i \exp(-ca)\, \rho_a(t,a)\, da
\end{aligned}
\tag{33}
$$

and, by an integration by parts

$$
P_i'(t) = -\left(\mu(t) + c\right) P_i(t) + i P_{i-1}(t).
\tag{34}
$$

In summary, we have the system of ODEs

$$
\begin{aligned}
P_0'(t) &= -\left(\mu(t) + c\right) P_0(t) + k(t)\, P_n(t) \\
\end{aligned}
\tag{35}
$$

$$
P_i'(t) = -\left(\mu(t) + c\right) P_i(t) + i P_{i-1}(t) \ \text{ for } i = 1, 2, \ldots, n.
\tag{36}
$$

In addition, an integration of the McKendrick PDE (29) with respect to a from $a = 0$ to ∞ yields

$$
P'(t) = k(t)\, P_n(t) - \mu(t)\, P(t)
\tag{37}
$$

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where

$$P\left(t\right) = \int_0^\infty \rho\left(t, a\right) da \qquad (38)$$

is the total population size.

If birth and death rates are density dependent, through a dependence of $\mu = \mu\left(P\left(t\right)\right)$ and $k = k\left(P\left(t\right)\right)$ on $P\left(t\right)$ (or any of the quantities $P_i\left(t\right)$), then the ODE system (35)-(36) is nonlinear.

Although the birth rate distribution (24) theoretically implies all ages are fertile, for large values of n both young and old age classes are essentially non-reproductive, since reproduction is focused tightly around age $a = \tau$. In this case, τ plays the role of a maturation period, and the system (35)-(36) models a population with a maturation period by means of a system of ODEs without delays. We also point out that for large n, the quantities $P_0\left(t\right)$ and $P_n\left(t\right)$ are weighted population sizes and are, in effect, the number of young non-reproducing and reproducing individuals respectively. Thus, they play roles analogous to the juveniles and adult classes $J\left(t\right)$ and $A\left(t\right)$ in the delay equations (22)-(23). This method is often called the linear chain trick and has been explored and utilized by many authors, including McDonald (1978), Metz and Diekmann (1991), and Busenberg and Travis (1982).

3 A Review of the Literature 2000-2016

We used Google Scholar and Web of Science to search for papers that appeared during the years 2000-2016 using the phrases *age structure model*, *age structured model*, *stage structure model*, and *stage structured model*. We considered only papers that proposed continuous-time compartmental models with age- or stage-class state variables. Some papers presented several models in the Introduction; we focused only on the model that was analyzed in the paper. We did not include papers that used size-structured models or models in which the state variable units were biomass. Some disease models assumed a time scale shorter than the duration of the age- or stage-classes and hence had no transitions between classes due to

maturation; we did not consider these papers.

We categorized relevant papers by type of structure (age or stage), whether there was a maturation delay in the transition between classes, whether the main focus of the paper was biological or mathematical (or both), whether the model was a disease model, and whether the model was derived from a PDE in the paper.

To determine the type of structure (age or stage), we categorized the paper according to the authors' terminology; most papers specified type of structure, often in the title. A few papers did not mention the type of structure. We called these age-structured if there was a clear reference to the age duration of the classes, and stage-structured otherwise.

We determined whether there was a maturation delay by looking at the transition rates between the classes. Transition rates were either a function of the current state of the previous class, for example $mJ(t)$ or $m(t)J(t)$ for transitions from a juvenile class J to an adult class A, or else they were functions of the the birth rate τ units of time ago, for example $e^{-m\tau}\beta A(t-\tau)$. In the first case we categorized the paper as "no maturation delay", and in the second case as "maturation delay." "No maturation delay" models sometimes contained other types of delays; most of these were structured predator-prey models with a gestational delay for the predator.

Papers that focused on model analysis through theorems and proofs or simulations were considered mathematics-focused, whereas papers that connected models to data or presented a thorough biological setting were considered biology-focused. If we felt that the papers were focused on both mathematics and biology, we classified them as having both foci.

We categorized papers as disease papers if the models tracked disease dynamics, for example, SIR models. Some papers contained population models of disease vectors, for example mosquitoes, that were developed in an epidemiological setting but had no disease dynamics. We did not classify these as disease models.

We found 249 relevant papers (Appendix A, Table 1). The most frequent years of publication were 2008, 2010, and 2016, with >20 papers in each of those years (Fig. 1). The year

Table 1: Papers found in the literature from 2000 to 2016 that contain continuous-time compartmental age- or stage-structured models.

	Number of Papers	Number with Maturation Delay	% with Maturation Delay	Total Papers
Age-structured	33	17	52%	249
Stage-structured	216	106	49%	
Biology-focused only	28	7	25%	249
Math-focused only	210	116	55%	
Both Bio- and Math-focused	11	2	18%	
Disease Model	38	15	39%	
Derived from PDE	12	12	100%	

Figure 1: Number of papers per year containing continuous-time compartmental age- or stage-structured models.
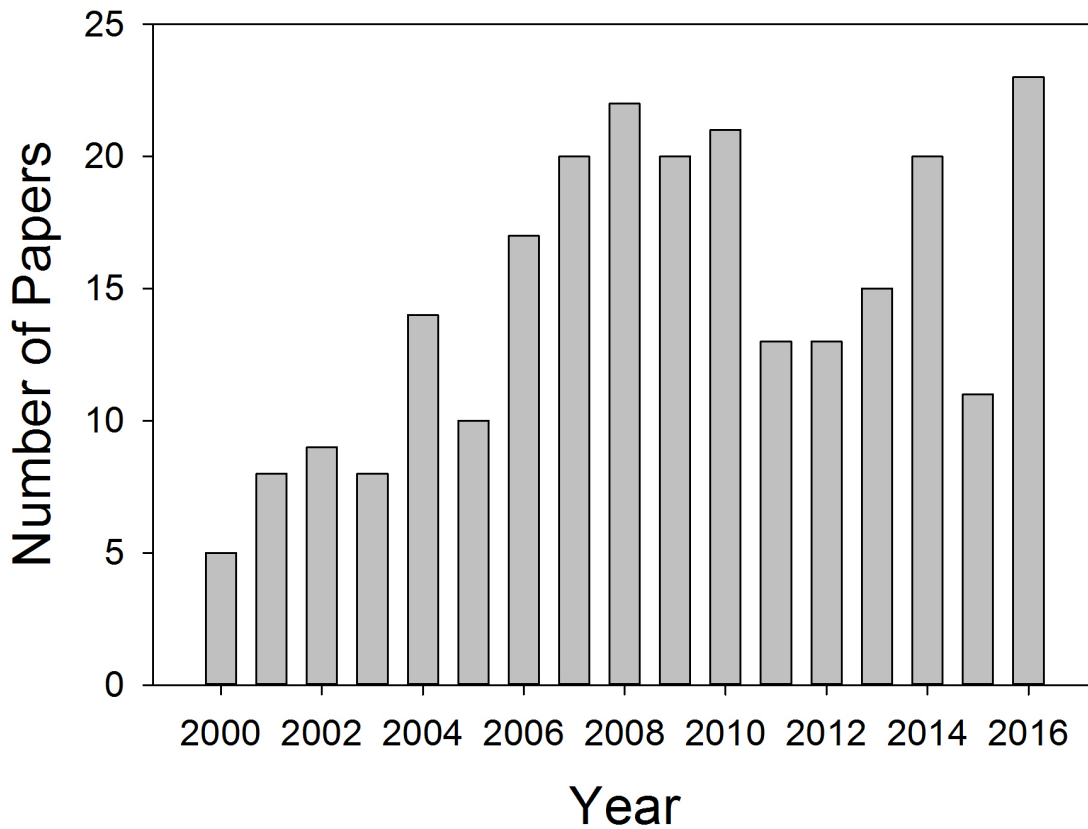
2000 was the least frequent, with 5 papers. Of the 249 papers, 33 (13%) were age-structured and 216 (87%) were stage-structured, and 49% of the papers had a maturation delay. Of age-structured models, 17 (52%) had a maturation delay; of stage-structured models, 106 (49%) had a maturation delay. Of the total number of papers, 210 were focused mainly on mathematics, 28 were focused mainly on biology, and we considered 11 papers to be focused on both mathematics and biology. Of the papers focused on mathematics, 55% contained a maturation delay; of those focused on biology, 25% contained a maturation delay. Of the 11 papers with dual focus, only 2 (18%) contained a maturation delay. 38 papers modeled disease dynamics. Most of the rest of the papers modeled ecological populations or communities, although a handful of papers modeled cell populations. Of the disease papers, 15 (39%) contained a maturation delay. 12 papers (5%) derived their models from a PDE within the paper, and, as expected, all of these models contained a maturation delay.

Table 2: Types of maturation rate terms.

	Maturation Rate Term	Papers
No maturation delay	Proportional to current number of juveniles	94
	Product of current number of juveniles and a time-dependent coefficient	22
Maturation delay	Proportional to number of adults delayed by constant maturation time	88
	More complex function containing number of adults delayed by constant maturation time	21
Varied	Other	24
	Total	249

The maturation rate terms found in the models of the collected papers can be loosely categorized into five categories (Table 2). The first category consists of papers that assumed that the maturation rate is proportional to the current state of the juvenile class, with the constant of proportionality equal to the mean maturation time of juveniles, for example $mJ(t)$ with mean maturation time $1/m$. The second category assumed that the maturation rate was

determined by the product of the current state of juveniles and a non-constant function of time, for example $m(t)J(t)$. In the third category, the maturation rate was proportional to the adult class delayed by a constant maturation time τ, for example $e^{-m\tau}\beta A(t-\tau)$. Many of these papers cited Aiello and Freedman (1990) as the motivation for their models. In the fourth category, the maturation rate contained a constant delay τ but was a more complicated function representing complex biological behavior. The third and fourth categories are not precisely defined and thus overlap somewhat. The final category includes types of models that are considered by only a handful of authors, such as a model with a density-dependent maturation delay.

In summary, about half of the papers in the recent literature that use continuous-time compartmental age- or stage-structured models had a maturation delay in the transition between classes. This "50-50" pattern held for both age-structured and stage-structured models. Papers with ecological models, however, were more likely to have a maturation delay than papers with disease models, and mathematically-focused papers were more likely to have a maturation delay than biologically-focused papers. Most papers did not derive the model from a PDE; those that did, however, invariably had a maturation delay. Papers that did not have a maturation delay typically did not mention the possibility of a maturation delay or explain the lack of such a delay, but rather posed an ODE model directly, with or without explicitly mentioning assumptions for the maturation rates. Papers in our study often clustered around seminal papers in the earlier literature, a notable example being the model of Aiello and Freedman (1990). This suggests that certain pivotal papers can greatly influence the form of models studied in later literature.

4   Discussion

Our review of the recent literature shows that multiple mathematical methodologies are being used to model structured populations in continuous time. The two most frequent approaches

are systems of ODEs with no time delay and DDEs with a constant maturation delay.

The former approach is used regularly in the epidemiology literature to account for transitions from exposed to infectious classes or infectious to recovered classes with the underlying assumption that residence times are exponentially distributed (Brauer, 2008). Analogous models for structured populations such as juvenile-adult systems assume an exponential distribution of residence times in the juvenile class, with a mean juvenile period equal to the reciprocal of the maturation rate. Although individuals within a species often exhibit significant variability in maturation times (Valpine et al., 2014), the assumption of exponentially distributed residence times is not biologically realistic in many cases because it allows some individuals to mature shortly after birth. Nonetheless, this assumption simplifies the analysis of the differential equations since it avoids time delays. By contrast, DDE model equations with a fixed time delay, such as those derived above, do not account for within-species variability in maturation time.

To our knowledge no derivation of an ODE model from the McKendrick-von Foerster PDE, under the assumption of an exponentially distributed maturation period, can be found in the literature. However, both the ODE and DDE models can be derived as special cases of a more general system of functional differential equations (Kostova et al., 1999). The degree to which the dynamics and predictions of these two types of models differ or agree is highly variable, and sometimes the differences are quite drastic. Abrams and Quince (2005) compared the dynamics of their ODE model to models with both fixed length and gamma distributed residence times, finding similar overall dynamics but differences in the size of stable and unstable regions. Hastings (1984) compared the dynamics of stage-structured predator-prey models (in which only adults interact) with and without a delay, again finding similarities and significant differences in model predictions. The ratio of the prey intrinsic growth rate to the adult predator natural growth rate was found to be important for stability in the DDE, whereas stability of the ODE was not as dependent on the growth rate of the prey. Both models found a short predator lifespan relative to the length of the prey juvenile

period to be necessary for stability, and the length of the predator juvenile period to be less important. Kostova et al. (1999) also compared ODE models with and without a delay for a single species with competition between juveniles and adults, finding similar conditions for stability of the extinction equilibrium and the existence of a positive equilibrium but different conclusions about the effects of intra-specific competition on the stability of the positive equilibrium. Wearing et al. (2005) found large differences in the dynamics of between-host transmission models assuming exponential versus gamma distributions for the duration of the latent or infectious periods (including fixed durations as a limiting case of the gamma distribution). Estimates of the basic reproduction number R_0 differ greatly depending on whether a latent class is included and the assumed distributions of the latent and infectious periods. Also see Getz and Dougherty (2018).

Under certain assumptions on birth rates, ODEs can be derived from the McKendrick-von Foerster PDE model by means of the linear chain trick as in Section 2. However, that method leads to a higher dimensional system of ODEs with new state variables; the sharper the delay kernel, the larger the resulting system becomes, with an instantaneous delay leading to an infinite system. These ODE models differ from the compartmental modeling method based on population structure. Models derived from the linear chain trick account for a time delay between newborns and adults by inventing an intervening sequence of alternative state variables between those two stages, so there is no direct flow between the juvenile class and the adult class. These new state variables are weighted population sizes with no obvious biological interpretations. While the linear chain trick has been well studied (Cushing, 1998, 2013; Kuang, 1993; McDonald, 1978; Metz and Diekmann, 1991; Smith, 2011), we encountered few uses in the recent literature in the context of structured populations (e.g. Bocharov and Hadeler, 2000).

Another approach seen in the literature, although less common, is the use of distributed delays to incorporate other distributions of maturation rates. Blythe et al. (1984) compared the dynamics of models with gamma distributions of maturation times starting after a min-

imum maturation age to models with a fixed delay. They find the results to depend on the ratio of the minimum maturation age to the mean of the subsequent distribution of maturation times. For large ratios the stability properties of the distributed delay model are found to be similar to those of a model with constant maturation period. When the ratio is smaller, such as for the case with a lower minimum maturation age and greater variability in subsequent maturation times, the shape of the distribution of maturation times becomes more important.

There are, of course, other important issues besides maturation delays that a modeler might want to address with regard to the validity of model equations, as based on some desired criterion or other. For example, the modeler might want to insure that solutions remain positive forward in time, so that the model does not predict population extinction in finite time (which, however, might be of interest to another modeler), or to insure that all solutions remain bounded in forward time, so that the model does not predict unlimited population growth, or to consider appropriate properties of initial conditions. Our focus here is not on the properties of solutions, desirable or undesirable, but on the derivation of the model equations and how a delay due to a maturation period might be formulated and expressed in the equations.

In summary, continuous-time age- and stage-structured models appear in the literature with multiple formulations, some with and some without a maturation delay. Managers should be aware of the issue of maturation delay when considering the results and predictions of continuous-time models of structured populations.

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