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Existence and stability of equilibria in age-structured population dynamics

J. M. Cushing

Department of Mathematics and Program in Applied Mathematics, University of Arizona, Building # 89, Tucson, AZ 85721, USA

Abstract. The existence of positive equilibrium solutions of the McKendrick equations for the dynamics of an age-structured population is studied as a bifurcation phenomenon using the inherent net reproductive rate n as a bifurcation parameter. The local existence and uniqueness of a branch of positive equilibria which bifurcates from the trivial (identically zero) solution at the critical value $n = 1$ are proved by implicit function techniques under very mild smoothness conditions on the death and fertility rates as functionals of age and population density. This first requires the development of a suitable linear theory. The lowest order terms in the Liapunov-Schmidt expansions are also calculated. This local analysis supplements earlier global bifurcation results of the author.

The stability of both the trivial and the positive branch equilibria is studied by means of the principle of linearized stability. It is shown that in general the trivial solution losses stability as n increases through one while the stability of the branch solution is stable if and only if the bifurcation is supercritical. Thus the McKendrick equations exhibit, in the latter case, a standard exchange of stability with regard to equilibrium states as they depend on the inherent net reproductive rate. The derived lower order terms in the Liapunov-Schmidt expansions yield formulas which explicitly relate the direction of bifurcation to properties of the age-specific death and fertility rates as functionals of population density.

Analytical and numerical results for some examples are given which illustrate these results.

Key words: Age-structured population dynamics — equilibria — stability — bifurcation

1. Introduction

If $\rho = \rho(t, a) \geq 0$ is the density of individuals of age a in a population at time t, then the equations

$$\partial\rho/\partial t + \partial\rho/\partial a + D(\rho)(a)\rho = 0, \qquad t > 0, \qquad 0 < a < A \leq +\infty$$
$$\rho(t, 0) = \int_0^A F(\rho)(a)\rho(t, a)\, da, \qquad t > 0 \tag{1.1}$$

describe respectively the removals and additions to the population, which is assumed closed to immigration and emigration, in terms of the (per unit density per unit time) death and fertility rates D and F. In general, D and F are functions of age a and functionals of the density ρ. For example, a frequently studied case is that when these vital rates are functions of the total population size $P(t) := \int_0^A \rho(t, a)\, da$. In this paper D and F will be left as quite general functionals of the density ρ which need only satisfy certain smoothness assumptions. The real A is the maximum age of any individual in the population, i.e. $\rho(t, A) = 0$ for all $t \geq 0$.

Coupled with an initial condition (1.1) constitutes a system of mathematical equations which determine the future time evolution of the age-specific population density. These equations have come to be called the McKendrick equations. In recent years (particularly since the seminal work of Gurtin and MacCamy [5]) there has been a rapidly growing literature dealing with various aspects of this model system of equations and its implications concerning age-structured population dynamics [6–12].

A great variety of types of modeling equations have been used to describe and study the growth dynamics of populations in spatially homogeneous habitats closed to immigration and emigration. These different types include integral equations, difference equations, ordinary differential equations and functional or integrodifferential equations. Of major concern in application to population dynamics is the long time, asymptotic behavior of solutions and in particular the existence and stability of equilibria. A very common scenario for the asymptotics of these types of model equations is the following. The asymptotics of the model equations are studied as a function of a selected parameter, usually an inherent per unit density birth (or net growth or net reproductive) rate. For small values of this parameter the population goes to extinction, i.e. the trivial zero solution is stable and either positive equilibria do not exist or are unstable. As the parameter is increased a critical value is reached at which a branch of positive equilibria bifurcates from the zero solution. If this bifurcation is supercritical these positive equilibria are stable although, as the parameter is further increased, it may lose its stability at a second (Hopf type) bifurcation point where time periodic solutions bifurcate from the positive equilibria branch. In some models, further increases of the parameter leads to further bifurcations and complicated dynamics (including "chaos"). The primary bifurcation point of positive equilibria can, on the other hand, also be subcritical and unstable. This phenomenon can lead to sudden population collapses and to hysteresis effects as the parameter is changed.

Virtually all model equations of all types can be derived, by means of appropriate assumptions on the fertility and death rates, from the fundamental McKendrick equations (1.1). It is natural then to ask how much of the above bifurcation scenario holds for the equations (1.1). Some of the fundamental components of this scenario have indeed been established under very mild conditions on the vital rates D and F. The primary bifurcation of a global branch of positive densities ρ was shown to occur at a critical value of the net reproductive rate in [4] and the secondary Hopf-type bifurcation to time periodic solutions was studied in [3].

The purpose of this paper is to contribute further to this bifurcation scenario for (1.1) by studying the local bifurcation behavior of positive equilibria near the primary bifurcation point. The goal is to study the stability of these branch equilibria (as well as the zero equilibrium) and to relate it to the direction of bifurcation. Lowest order terms in the Liapunov–Schmidt expansions will also be derived.

An equilibrium solution $\rho = \rho(a) \geq 0$ of (1.1) must satisfy the equations

$$\rho'(a) + D(\rho)(a)\rho(a) = 0, \qquad 0 < a < A \leq +\infty$$

$$\rho(0) = \int_0^A F(\rho)(a)\rho(a)\, da, \qquad \rho(A) = 0.$$

In order to study the existence and stability of solutions of these equilibrium equations by means of bifurcation techniques, a parameter must be selected to serve as the bifurcation parameter. This parameter will be chosen, as in [4], to be the *inherent net reproductive rate* n at low density (technically when $\rho \equiv 0$)

$$n := \int_0^A F(0)(a) \exp(-M(0)(a))\, da$$

$$M(\rho)(a) := \int_0^a D(\rho)(\alpha)\, d\alpha.$$

This number n is the expected number of offspring over an individual lifespan. In order to introduce n into the equations, the *normalized fertility rate* $f = f(\rho)(a)$ is defined to be the ratio of the per unit fertility rate at age a to the expected number of offspring per lifespan. Then $F = nf$ and the equilibrium equations can be written

$$\begin{aligned} &\text{(a)} \quad \rho'(a) + D(\rho)(a)\rho(a) = 0, \qquad 0 < a < A \leq +\infty \\ &\text{(b)} \quad \rho(0) = n \int_0^A f(\rho)(a)\rho(a)\, da \\ &\text{(c)} \quad \rho(A) = 0. \end{aligned} \tag{1.2}$$

Note that under this normalization

$$\int_0^A f(0)(a) \exp(-M(0)(a))\, da = 1. \tag{1.3}$$

Of fundamental interest in understanding the time evolution of an age-structured population whose dynamics are governed by equations (1.1) is a knowledge of the set of values of n for which the equilibrium equations (1.2) have a positive solution ρ and conditions under which this solution is stable. There are many recent papers which contain existence and stability results for positive equilibrium solutions (e.g. see [4, 6–12] and others cited in these papers), although none treat this problem from the point of view of bifurcation theory except [4] (which deals only with the existence question). Moreover the results here require only that D and f be smooth near $\rho = 0$; no special assumptions are made on the form of their functional dependence on ρ nor are monotonicity or boundedness restrictions needed as they usually are in the literature.

In [4] the global existence of a continuum C^+ of positive solutions (n, ρ), $\rho > 0$ on $[0, A)$, lying in a certain Banach space is proved under mild continuity assumptions on D and f. This continuum is global in the sense that it connects (i.e. bifurcates from) the trivial solution $(n, \rho) = (1, 0)$ to the boundary of the domain on which the problem is posed. The purpose of the present paper is to study in detail the structure of the bifurcating continuum C^+ near the critical point $(n, \rho) = (1, 0)$. Specifically, after the requisite linear theory in Sect. 2, a parametrization of the continuum C^+ near criticality is derived and the lowest order terms are calculated in Sect. 3. This will not only prove the existence and uniqueness of positive small amplitude equilibria near criticality, but will show exactly what properties of D and F determine the "direction of bifurcation". In Sect. 4 the stability of the trivial equilibrium $\rho \equiv 0$ and of those on the positive bifurcating branch is studied by means of a certain "characteristic equation" and the principle of linearized stability. It is shown that $\rho \equiv 0$ loses stability as n increases through $n = 1$, but that the positive equilibria on the bifurcating branch are stable if and only if the direction of bifurcation is supercritical. Thus in this case (whose occurrence depends on the nonlinearities in D and F in a manner precisely given in Theorem 1 below), the McKendrick model exhibits a standard "exchange of stability" as the inherent net reproductive rate n increases through the critical value $n = 1$. The critical value $n = 1$ of the inherent net reproductive rate represents exact per unit replacement. Conditions under which subcritical (and hence unstable) bifurcation occurs are also seen in Theorem 1.

The results given in Sects. 2–4 are for the case $A < +\infty$. This is done for simplicity. In Sect. 5 the changes necessary for the extension of these results to the technically more involved case when $A = +\infty$ are briefly described.

In Sect. 6 some general remarks are made concerning the direction of bifurcation and the normalized age distribution at equilibrium. Some examples are studied both analytically and numerically.

2. The linear theory when $A < +\infty$

Let R denote the set of reals and let Δ denote the set of continuous functions $\mu \in C^0([0, A); R)$ which satisfy

$$\lim_{a \to A^-} M(a) = +\infty \quad \text{where } M(a) := \int_0^a \mu(\alpha)\, d\alpha.$$

For $\mu \in \Delta$ define B_μ^0 to be the linear space of continuous functions $h \in C^0([0, A]; R)$ for which $h(a)\exp(M(a))$ is continuous on $[0, A]$ and B_μ^1 to be the space of those functions h for which, in addition, $h(a)\exp(M(a))$ is continuously differentiable on $[0, A]$. It is not difficult to show that these linear spaces are Banach spaces when endowed with the norms

$$\|h\|_0 := \sup_{[0, A]} |h(a)| \exp(M(a))$$

$$\|h\|_1 := \|h\|_0 + \sup_{[0, A]} |d/da(h(a)\exp(M(a)))|.$$

Also needed will be the Banach spaces $R\times B_\mu^0$ and $L_1([0,A]);R)$ endowed with the norms $\|(r,h)\|_+:=|r|+\|h\|_0$ and $\|h\|_L:=(\int_D^A|h|\,ds)$.

Note that $\rho\in B_\mu^0$ implies $\rho(A)=0$. Note also that $\rho_0\in B_\mu^1$ where

$$\rho_0(a):=\exp(-\mathrm{M(a)}).$$

Consider the nonhomogeneous linear system of equations

$$\begin{aligned}\rho'(a)+\mu(a)\rho(a)&=h_2(a),\qquad 0<a<A<+\infty\\ \rho(0)&=\int_0^A\beta(a)\rho(a)\,da+h_1\end{aligned}\tag{2.1}$$

and the associated homogeneous system

$$\begin{aligned}\rho'(a)+\mu(a)\rho(a)&=0,\qquad 0<a<A<+\infty\\ \rho(0)&=\int_0^A\beta(a)\rho(a)\,da\end{aligned}\tag{2.2}$$

with $\mu\in\Delta$, $\beta\rho_0\in L_1([0,A];R)$ and $(h_1,h_2)\in R\times B_\mu^0$. By a solution of (2.1) or (2.2) is meant a function $\rho\in B_\mu^1$ (which is then continuously differentiable on $[0,A)$). An integration of the differential equation in (2.2) easily shows that (2.2) has a nontrivial solution if and only if

$$\int_0^A\beta(a)\rho_0(a)\,da=1\tag{2.3}$$

in which case all solutions of (2.2) have the form $\rho(a)=c\rho_0(a)$, $c\in R$.

All solutions of the nonhomogeneous differential equation in (2.1) have the form

$$\rho(a)=\rho_0(a)\left(c+\int_0^a h_2(\alpha)/\rho_0(\alpha)\,d\alpha\right),\qquad c\in R$$

and lie in B_μ^1. Thus the nonhomogeneous system (2.1) is solvable in B_μ^1 if and only if the equation

$$\left(1-\int_0^A\beta(a)\rho_0(a)\,da\right)c=h_1+\int_0^A\beta(a)\rho_0(a)\int_0^a h_2(\alpha)/\rho_0(\alpha)\,d\alpha\,da$$

is solvable for $c\in R$.

These simple facts can be summarized in the following alternative: *either* (2.2) *has no nontrivial solution in* B_μ^1 *in which case* (2.1) *has a unique solution in* B_μ^1 *for each* $(h_1,h_2)\in R\times B_\mu^0$ *or* (2.2) *has a nontrivial solution in* B_μ^1 *in which case* (2.1) *has a solution in* B_μ^1 *if and only if* $(h_1,h_2)\in R\times B_\mu^0$ *satisfies*

$$h_1+\int_0^A\beta(a)\rho_0(a)\int_0^a h_2(\alpha)/\rho_0(\alpha)\,d\alpha\,da=0.\tag{2.4}$$

The following lemma is fundamental to the main results in the next Section 3. It concerns the linear operator $L\colon B_\mu^1\to R\times B_\mu^0$ defined by

$$L\rho:=\left(\rho(0)-\int_0^A\beta(a)\rho(a)\,da,\rho'(a)+\mu(a)\rho(a)\right).\tag{2.5}$$

Lemma 1. *Assume $\mu \in \Delta$, $\beta\rho_0 \in L_1([0, A]; R)$. The linear operator $L: B^1_\mu \to R \times B^0_\mu$ defined by* (2.5) *is bounded, has a closed nullspace $N(L)$ and range $R(L)$ with finite dimension and codimension respectively, both of which admit bounded projections. In fact,* $\dim N(L) = \operatorname{codim} R(L) = 1$ *if* (2.3) *holds and* 0 *otherwise.*

Proof: The inequalities

$$\begin{aligned}
\|L\rho\|_+ &= \left|\rho(0) - \int_0^A \beta(a)\rho(a)\,da\right| + \|\rho' + \mu\rho\|_0 \\
&\leq |\rho(0)| + \int_0^A |\beta(a)|\rho_0(a)|\rho(a)|/\rho_0(a)\,da + \sup_{[0,A]} |\rho' + \mu\rho|/\rho_0 \\
&\leq \|\rho\|_0 + \|\beta\rho_0\|_L \|\rho\|_0 + \sup_{[0,A]} |d/da(\rho/\rho_0)| \\
&= \|\beta\rho_0\|_L \|\rho\|_0 + \|\rho\|_1 \leq (\|\beta\rho_0\|_L + 1)\|\rho\|_1
\end{aligned}$$

imply the boundedness of L.

If (2.3) fails to hold, then $N(L) = \{0\}$ and $R(L) = R \times B^0_\mu$. In this case the Lemma is obvious.

If (2.3) holds, then $N(L)$ is the span of $\{\rho_0(a)\}$ and the projection $P_N: B^1_\mu \to N(L)$ defined by

$$P_N\rho := \rho_0(a) \int_0^A \rho(a)\rho_0(a)\,da \Big/ \int_0^A \rho_0^2(a)\,da$$

is clearly bounded. Also $B^1_\mu = N(L) \oplus N^\perp(L)$ where $N^\perp(L) := \{\rho \in B^1_\mu | \int_0^A \rho(a)\rho_0(a)\,da = 0\}$ is a closed subspace of B^1_μ. Thus $\rho \in B^1_\mu$ can be uniquely written $\rho = P_N\rho + (I - P_N)\rho$ where $I - P_N: B^1_\mu \to N^\perp(L)$ is a bounded projection.

If (2.3) holds, then the range $R(L)$ of L is the subspace of all $(h_1, h_2) \in R \times B^0_\mu$ for which (2.4) holds. As such $R(L)$ is clearly closed. Define the projection $P_R: R \times B^0_\mu \to R(L)$ by

$$P_R(h_1, h_2) := \left(-\int_0^A \beta(a)\rho_0(a) \int_0^a h_2(\alpha) \Big/ \rho_0(\alpha)\,d\alpha\,da,\ h_2(a)\right).$$

The inequalities

$$\begin{aligned}
\|P_R(h_1, h_2)\|_+ &= \left|\int_0^A \beta(a)\rho_0(a) \int_0^a h_2(\alpha) \Big/ \rho_0(\alpha)\,d\alpha\,da\right| + \|h_2\|_0 \\
&\leq A\|\beta\rho_0\|_L \|h_2\|_0 + \|h_2\|_0 \\
&\leq (A\|\beta\rho_0\|_L + 1)\|(h_1, h_2)\|_+
\end{aligned}$$

show that P_R is bounded. Also $R \times B^0_\mu = R(L) \oplus R^\perp(L)$ where $R^\perp(L) := \{(h_1, 0) | h_1 \in R\}$ is a closed subspace. In fact $(h_1, h_2) \in R \times B^0_\mu$ can be uniquely written

$$(h_1, h_2) = P_R(h_1, h_2) + (I - P_R)(h_1, h_2)$$
$$= \left(-\int_0^A \beta(a)\rho_0(a) \int_0^a h_2(\alpha) \Big/ \rho_0(\alpha)\, d\alpha\, da,\, h_2(a) \right)$$
$$+ \left(h_1 + \int_0^A \beta(a)\rho_0(a) \int_0^a h_2(\alpha) \Big/ \rho_0(\alpha)\, d\alpha\, da,\, 0 \right). \qquad \square$$

3. Bifurcation of positive equilibria when $A < +\infty$

In this section small amplitude positive solutions of the equilibrium equations (1.2) are constructed by a Liapunov–Schmidt procedure. The hypothesis needed on the death and fertility rates D and f are that they be defined and sufficiently differentiable in a neighborhood of $\rho \equiv 0$ in B^1_μ. Specifically, let $\Omega \in B^1_\mu$ denote an open neighborhood of $0 \in B^1_\mu$ and assume

$H1$: f and D can be written $f = \beta + r_1(\rho)$, $D = \mu + r_2(\rho)$ with $r_i(0) = 0$ where $\mu \in \Delta$, $\beta\rho_0 \in L_1([0, A]; R)$ and (2.3) holds and where the operators $r_1: \Omega \to L_1([0, A]; R)$, $r_2: \Omega \to C^0([0, A]; R)$ are $q \geq 1$ times continuously Fréchet differentiable.

In this hypothesis $C^0([0, A]; R)$ is endowed with the usual supremum norm. Note that $H1$ implies (by (2.3)) that (1.3) holds as required by the normalization in Section 1.

Let $r_i'(0)(\cdot)$ denote the first order Fréchet derivative of r_i at $\rho = 0$. These are linear operators defined on B^1_μ (mapping into L_1 for $i = 1$ and C^0 for $i = 2$). An ordered pair $(n, \rho) \in R \times B^1_\mu$ will be called a solution of (1.2) if ρ satisfies (1.2a, b) for the given value n ((1.2c) automatically holds for $\rho \in B^0_\mu$). Such a pair is a nontrivial (positive, etc.) solution if $\rho \not\equiv 0$ ($\rho > 0$ on $[0, A)$, etc.).

Theorem 1. (a) *If $H1$ holds then the equilibrium equations* (1.2) *have a unique branch of nontrivial solutions $(n, \rho) \in R \times B^1_\mu$ in a sufficiently small neighborhood of the critical solution $(n, \rho) = (1, 0)$ and these solutions have the form*

$$n_\varepsilon = 1 + \lambda(\varepsilon), \qquad \rho_\varepsilon = \varepsilon\rho_0 + \varepsilon z(\varepsilon), \qquad \rho_0 := \exp(-M(a))$$

for $|\varepsilon| < \varepsilon^*$ where $\lambda: (-\varepsilon^*, \varepsilon^*) \to R$ and $z: (-\varepsilon^*, \varepsilon^*) \to N^\perp(L)$ are q times continuously Fréchet differentiable and satisfy $z(0) = 0$, $\lambda(0) = 0$.

(b) *If $H1$ holds with $q \geq 2$ then*

$$n_\varepsilon = 1 + n_1\varepsilon + \gamma(\varepsilon), \qquad \rho_\varepsilon = \varepsilon\rho_0 + \varepsilon^2 z_1 + \varepsilon w(\varepsilon) \tag{3.1}$$

where $\gamma: (-\varepsilon^*, \varepsilon^*) \to R$ and $w: (-\varepsilon, \varepsilon^*) \to N^\perp(L)$ are continuous, $|\gamma(\varepsilon)| = O(\varepsilon^2)$ and $\|w\|_1 = O(\varepsilon^2)$ near $\varepsilon = 0$ and where

$$n_1 = \int_0^A \beta(a)\rho_0(a) \int_0^a D_\rho(0)(\rho_0)(\alpha)\, d\alpha\, da - \int_0^A \rho_0(a) f_\rho(0)(\rho_0)(a)\, da \in R$$

$$z_1 = \rho_0(a)\left(c - \int_0^a D_\rho(0)(\rho_0)(\alpha)\, d\alpha \right) \in N^\perp(L) \tag{3.2}$$

$$c = \int_0^A \rho_0^2(a) \int_0^a D_\rho(0)(\rho_0)(\alpha)\, d\alpha\, da \Big/ \int_0^A \rho_0^2(a)\, da \in R.$$

In part (b) of Theorem 1, $D_\rho(0)(\cdot) = r_2'(0)(\cdot)$ and $f_\rho(0)(\cdot) = r_1'(0)(\cdot)$ are the Fréchet derivatives of D and f with respect to ρ at $\rho = 0$.

Proof. The equilibrium equations (1.2) can be written in the operator form

$$L\rho = T(\lambda, \rho) \tag{3.3}$$

where $\lambda = n-1$, L is defined by (2.5) and $T: R\times\Omega \to R\times B_\mu^0$ is the operator $T(\lambda, \rho) := \lambda A\rho + N(\lambda, \rho)$ where

$$A\rho := \left(\int_0^A \beta(a)\rho(a)\,da, 0\right)$$

$$N(\lambda, \rho) := \left((\lambda+1)\int_0^A \rho(a)r_1(\rho)\,da, -\rho r_2(\rho)\right).$$

To the operator equation (3.3) can be applied straightforward implicit function techniques to obtain (a). To do this one can refer for example to Theorem 1 in [2]. Lemma 1 of Section 2 and (2.3) imply the necessary hypotheses on L (namely $H1$ and $H2$ in [2]) and the hypothesis $H1$ above implies the necessary hypotheses on T (namely $H3$ in [2]). All that remains to be verified for this application of Theorem 1 in [2] is that a certain nondegeneracy condition holds, namely $H4$ in [2]: $c_\lambda(0, 0, 0) \neq 0$ where $c = c(\lambda, z, \varepsilon)$ is the real coefficient of $(I - P_R)\bar{T}(\lambda, \rho_0 + z, \varepsilon) \in R^\perp(L)$. Here $\bar{T}$ is defined by $T(\lambda, \varepsilon\rho) = \varepsilon\bar{T}(\lambda, \rho, \varepsilon)$. A straightforward calculation shows that $c_\lambda(0, 0, 0) = \int_0^A \beta(a)\rho_0(a)\,da = 1$ by (2.3).

That n and ρ have the ε-expansions in part (b) follows again from Theorem 1 in [2] because $q \geq 2$. All that needs to be shown here is the validity of the formulas for the coefficients $n_1 \in R$ and $z_1 \in N^\perp(L)$. This can be done in the usual manner of substituting the ε-expansions into (1.2) and equating coefficients of like powers of ε on both sides of the resulting equations. The first order terms in ε result in the linear homogeneous system (2.2) which, by the assumption (2.3) in $H1$, is satisfied by $\rho = \rho_0(a)$.

The second order terms in ε result in a nonhomogeneous system of the form (2.1), namely

$$z_1'(a) + \mu(a)z_1(a) = -\rho_0(a)r_2'(0)(\rho_0)(a)$$

$$z_1(0) = \int_0^A \beta(a)z_1(a)\,da + \int_0^A \rho_0(a)r_1'(0)(\rho_0)(a)\,da + n_1$$

whose nonhomogeneous terms must satisfy the "orthogonality" condition (2.4). This leads immediately to the formula for n_1 in Theorem 1(b). Once (2.4) is satisfied by this choice of n_1, the above equations can be solved for z_1 as in Sect. 2 to obtain the one parameter family of solutions

$$z_1(a) = \rho_0(a)\left(c - \int_0^a r_2'(0)(\rho_0)(\alpha)\,d\alpha\right), \qquad c \in R.$$

The unique solution lying in $N^\perp(L)$ is obtained by choosing c as in Theorem 1(b). □

The solutions ρ_ε lying on the parameterized branch described in Theorem 1 are positive for $\varepsilon > 0$ (and negative for $\varepsilon < 0$) sufficiently small. This unique local branch of positive equilibria (n, ρ) for $n \sim 1$ is shown to exist globally in [4] in the sense that it is a subset of a continuum in $R \times B^1_\mu$ which intersects with the boundary of $R \times \Omega$. Locally near the critical value $n = 1$ the set of n values corresponding to positive solutions on the branch in Theorem 1 consists of n values less than or greater than $n = 1$ (that is to say the bifurcation is sub- or supercritical respectively) depending on the sign of $\lambda(\varepsilon) = n_\varepsilon - 1$ for $\varepsilon > 0$ small. When $q \geq 2$ this direction of bifurcation, which will be related to the stability of the positive equilibria in the next section, depends on the sign of the real coefficient n_1 (if it is nonzero) which in turn depends on the rates of change of D and f with respect to population density ρ at $\rho = 0$ as can be seen from the formula for n_1 in Theorem 1(b). Results concerning global properties of this spectrum can be found in [4].

4. Linearized stability when $A < +\infty$

In this section the stability of the trivial equilibrium $\rho \equiv 0$ and the positive equilibria in Theorem 1 is investigated using the principle of linearized stability. A characteristic equation will be derived for linearized versions of (1.2) and the stability analysis will be carried out by means of the location in the complex plane C of the roots of this equation. This procedure is of course standard and will not be rigorously justified here. A rigorous treatment of linearized stability for a similar problem by means of a semigroup approach can be found in [12].

(a) *The characteristic equation.* Consider the following linear problem:

$$\begin{gathered} \partial y/\partial t + \partial y/\partial a + c(a)y + \int_0^A K(a, \alpha) y(t, \alpha)\, d\alpha = 0 \\ y(t, 0) = \int_0^A k_1(\alpha) y(t, \alpha)\, d\alpha, \qquad y(t, A) = 0, \qquad t > 0. \end{gathered} \tag{4.1}$$

A system of this kind will result, under certain circumstances, when (1.1) is linearized around an equilibrium solution. Under the key assumption that the kernel K is multiplicatively separable

$$K(a, \alpha) = d(a) k_2(\alpha)$$

a relatively simple algebraic characteristic equation for (4.1) can be derived as follows. If $y = \phi(a) \exp(\zeta(t - a))$, $\zeta \in C$ and $\phi \in B^1_c$ is substituted into (4.1), the system of equations

$$\begin{aligned} &(a) \qquad \phi'(a) + c(a)\phi(a) + wd(a) \exp(\zeta a) = 0 \\ &(b) \qquad w = \int_0^A k_2(\alpha)\phi(\alpha) \exp(-\zeta\alpha) d\alpha \\ &(c) \qquad \phi(0) = \int_0^A k_1(a)\phi(a) \exp(-\zeta a)\, da \end{aligned} \tag{4.2}$$

for $\phi \not\equiv 0$ and complex numbers ζ, $w \in C$ results. Equation (4.2a) can be easily solved for ϕ and the result substituted into (b) and (c). This yields the equations

$$\begin{aligned}
&\text{(a)} \quad \phi(a) = y_0(a)(\phi(0) - wI(\zeta, a)) \\
&\text{(b)} \quad \left(\int_0^A k_2(a)Y(\zeta, a)\, da\right)\phi(0) + \left(-1 - \int_0^A k_2(a)Y(\zeta, a)I(\zeta, a)\, da\right) w = 0 \\
&\text{(c)} \quad \left(1 - \int_0^A k_1(a)Y(\zeta, a)\, da\right)\phi(0) + \left(\int_0^A k_1(a)Y(\zeta, a)I(\zeta, a)\, da\right) w = 0.
\end{aligned} \tag{4.3}$$

Solving this system for $\phi \not\equiv 0$ and ζ, $w \in C$ is equivalent to solving (4.2). Here $y_0(a) = \exp(-\int_0^a c(\alpha)\, d\alpha)$ and

$$Y(\zeta, a) := y_0(a)\exp(-\zeta, a), \qquad I(\zeta, a) := \int_0^a d(\alpha)/Y(\zeta, \alpha)\, d\alpha.$$

A necessary and sufficient condition for the solvability of (4.3) is the solvability of the homogeneous 2×2 algebraic system (4.3*b*, *c*) for a nontrivial solution $(\phi(0), w) \neq (0, 0)$. The solution of (4.1) is then given by $y = \phi(a)\exp(\zeta(t-a))$ where $\phi(a)$ is given by (4.3*a*). Thus we arrive at the following result.

Lemma 2. *Equations* (4.1) *have a solution of the form* $y = \phi(a)\exp(\zeta(t-a))$ *for* $\zeta \in C$ *if and only if* ζ *satisfies the characteristic equation*

$$\begin{aligned}
&\int_0^A k_2(a)Y(\xi, a)\, da \int_0^A k_1(a)Y(\zeta, a)I(\zeta, a)\, da \\
&\quad + \left(1 + \int_0^A k_2(a)Y(\zeta, a)I(\zeta, a)\, da\right)\left(1 - \int_0^A k_1(a)Y(\xi, a)\, da\right) = 0.
\end{aligned} \tag{4.4}$$

The linear homogeneous system (4.1) will be called *stable* if (4.4) has no roots satisfying $\operatorname{Re}\zeta \geq 0$. If (4.4) has a root satisfying $\operatorname{Re}\zeta > 0$ then (4.1) will be called *unstable.*

(b) *The stability of the trivial equilibrium solution.* If (1.1) with $F = nf$ is linearized at the trivial solution $\rho \equiv 0$ then a system of the form (4.1) results with

$$c(a) \equiv \mu(a), \qquad k_2(a) \equiv 0, \qquad k_1(a) \equiv n\beta(a)$$

where D and f are as in $H1$ ($d(a)$ is irrelevant). The characteristic equation is then

$$C(\zeta, n) := 1 - n\int_0^A \beta(a)\rho_0(a)\exp(-\zeta a)\, da = 0.$$

Clearly for $n < 1$ and $\operatorname{Re}\zeta \geq 0$

$$\left| n\int_0^A \beta(a)\rho_0(a)\exp(-\zeta a)\, da\right| < 1$$

by (2.3) and consequently $C(\zeta, n) = 0$ has no roots satisfying $\operatorname{Re}\zeta \geq 0$ when $n < 1$.

On the other hand, suppose that $n>1$ and consider real $\zeta=x$. Since $C(0, n)=1-n<0$ and $C(x, n)\to 1$ as $x\to+\infty$ (by the dominated convergence theorem) it follows that $C(\zeta, n)=0$ has at least one positive real root for $n>1$.

Theorem 2. *Assume* $H1$. *The trivial solution* $\rho\equiv 0$ *of* (1.1) *with* $F=nf$ *is stable if* $n<1$ *and unstable if* $n>1$.

(c) *Stability of the nontrivial branch equilibria* (3.1). We wish to investigate the stability of the equilibria (3.1) by studying the location of the complex roots ζ of the characteristic equation (4.4) arising from the linearization of (1.1) about the equilibrium (3.1) for small $\varepsilon>0$. To do this the linearization must take the form (4.1) and thus we assume that the functional dependencies of the vital rates D and f on ρ are of integral form. Specifically we assume that the Fréchet derivatives of the remainder terms r_i in $H1$ are of the integral form

$$r_i'(\rho)y=\int_0^A w_i(\rho)(a, \alpha)y(t, \alpha)\,d\alpha. \tag{4.5}$$

In order to obtain the multiplicative separability of K in (4.1) it is assumed that the kernel w_2 is separable:

$$w_2(\rho)(a, \alpha)\equiv k(\rho)(a)l(\rho)(\alpha). \tag{4.6}$$

In view of the Riesz representation theorem the assumption of the integral form (4.5) is not particularly restrictive. The main constraint here is the multiplicative separability (4.6). It is met for example when the density dependence and the age dependence are multiplicatively separable in the death rate term r_2.

Setting $y=\rho-\rho_\varepsilon$ and ignoring higher order terms in y in (1.1) one now arrives at (4.1) with

$$\begin{gathered} c(a)=\mu(a)+r_2(\rho_\varepsilon)(a), \qquad d(a)=\rho_\varepsilon(a)k(\rho_\varepsilon)(a), \qquad k_2(a)=l(\rho_\varepsilon)(a) \\ k_1(\alpha)=n_\varepsilon\left(\beta(\alpha)+r_1(\rho_\varepsilon)(\alpha)+\int_0^A w_1(\rho_\varepsilon)(s, \alpha)\rho_\varepsilon(s)\,ds\right). \end{gathered} \tag{4.7}$$

We are interested in the roots of the characteristic equation (4.4) for $\varepsilon\sim 0$. Denote the left hand side of (4.4) by $C(\zeta, \varepsilon)$. C depends on ε through the dependence of the coefficients and kernels (4.7) on ε. Note that $\rho_\varepsilon\equiv 0$, $n_\varepsilon=1$ when $\varepsilon=0$ and hence from (4.4) we see that

$$C(\zeta, 0)=1-\int_0^A \beta(a)\rho_0(a)\exp(-\zeta a)\,da \tag{4.8}$$

which is simply the characteristic function for the trivial solution at criticality $n=1$ (see (b) above). It is easy to see by (2.3) that the only purely imaginary root $\zeta=iy$ of $C(\zeta, 0)=0$ is $\zeta=0$. The following facts are straightforward to prove.

(i) Given any neighborhood N of $\zeta=0$ in the complex plane, there exists an $\varepsilon^*>0$ such that any roots ξ of $C(\zeta, \varepsilon)=0$ for $|\varepsilon|<\varepsilon^*$ satisfying $\operatorname{Re}\zeta\geq 0$ must necessarily lie in N;

(ii) $C_\zeta(0, 0)=\int_0^A a\beta(a)\rho_0(a)\,da>0$;

(iii) $C_\varepsilon(0, 0)=n_1$.

A proof of (iii) appears in the Appendix. From (ii), (4.8), (2.3) and the implicit function theorem it follows that

$$C(\zeta, \varepsilon)=0 \tag{4.9}$$

has a unique root $\zeta=\zeta(\varepsilon)$, $\zeta(0)=0$, for $\varepsilon \sim 0$. An implicit differentiation of (4.9) with $\xi=\xi(\varepsilon)$ together with (iii) shows that

$$\zeta'(0)=-n_1\Big/\int_0^A a\beta(a)\rho_0(a)\,da.$$

From (ii) it follows that the sign of Re $\zeta'(\varepsilon)$ is the negative of the sign of n_1 for $\varepsilon \sim 0$. This means that when $n_1>0$ (or <0) (4.9) has roots in the right half plane for small $\varepsilon<0$ (or >0). On the other hand, these roots $\zeta(\varepsilon)$ lie in the left half plane in the opposite case $\varepsilon>0$ (or <0) when $n_1>0$ (or <0). By (i) these are the only possible roots in the right half plane when $\varepsilon \sim 0$. We have arrived at the following theorem.

Theorem 3. *Assume $q \geq 2$ in $H1$. Assume that* (4.5) *and* (4.6) *hold. The positive nontrivial equilibria ρ_ε in* (3.1) *of Theorem* 1 *for small $\varepsilon \geq 0$ are stable if $n_1>0$ and unstable if $n_1<0$.*

5. The case when $A=+\infty$

Quite often the McKendrick system (1.1) is considered with $A=+\infty$. The reason for this is usually that in specific cases and applications certain calculations and formulas are thereby simplified (e.g. those for equilibrium solutions, the computation of stability criteria, etc.). It is possible to extend the results of the previous sections to the case when $A=+\infty$ by making suitable changes in the Banach spaces involved in a few of the assumptions. Specifically, the set Δ to which the inherent death rate $\mu(a)$ belongs is changed to the set Δ_∞^+ of nonnegative functions $0 \leq \mu \in C^0([0, +\infty); R)$ for which $\liminf_{a\to+\infty} \mu(a)>0$. For $\mu \in \Delta_\infty^+$ and $0<\nu\leq 1$ define $B_{\mu,\nu}^0$ to be the Banach space of continuous functions $h \in C^0([0,+\infty); R)$ under the norm

$$\|h\|_{\mu,\nu} := \sup_{[0,+\infty)} |\rho(a)|/\rho_{0,\nu}(a)$$

where $\rho_{0,\nu}(a) := \exp(-\nu\int_0^a \mu(\alpha)\,d\alpha)$. For $h \in B_{\mu,\nu}^0$ it follows that $h(+\infty)=0$. Similarly $B_{\mu,\nu}^1$ is the Banach space of continuously differentiable functions $h \in B_{\mu,\nu}^0$ under the norm

$$\|h\|_1 := |h\|_0 + \sup_{[0,+\infty)} |d/da(h(a)/\rho_{0,\nu}(a))|.$$

It is not difficult to show that the Fredholm alternative and Lemma 1 of Section 2 remain valid when $A=+\infty$ in (1.1) if Δ is replaced by Δ_∞^+, B_μ^0 and B_μ^1 are replaced by $B_{\mu,\nu}^0$ and $B_{\mu,\nu}^1$ and $\beta\rho_0 \in L_1([0, A]; R)$ is replaced by $\beta\rho_{0,\nu} \in L_1([0,+\infty); R)$ and if in addition $\mu(a)$ is assumed bounded on $[0, +\infty)$.

From this modified linear theory Theorems 1-3 and Lemma 2 can be justified when $A=+\infty$ provided these same substitutions and modified assumptions are made throughout. Details concerning these facts can be found in Section 4 of [4].

6. Some remarks and examples

Under the stated assumptions Theorems 1–3 show that the McKendrick equations (1.1) exhibit a standard bifurcation phenomenon with regard to the existence of positive equilibria as a function of the inherent net reproductive rate n. Namely, positive equilibria bifurcate from the trivial equilibrium $\rho \equiv 0$ at the critical value $n = 1$ and these equilibria are stable if and only if the bifurcation is supercritical, in which case there is an "exchange of stability" from the trivial equilibrium to the positive equilibria on the bifurcating branch as n increases through $n = 1$.

Subcritical (and hence unstable) bifurcation, on the other hand, relates to the concept of "depensation" in the theory of population dynamics and renewable resources [1]. Its occurrence implies the possibility of a hysteresis effect and the sudden "crash" or extinction of the population as the net reproductive rate n is decreased. Depensation is usually defined in terms of the nonlinear properties of the growth rate dependence on density for differential models involving total population size [1, Chapter 1]. Although we offer here no generalized definition of depensation for age structured populations nor study hysteresis effects in the McKendrick model equations (1.1), the formula for n_1 in Theorem 1 does provide a means of relating subcritical bifurcation to the nonlinear effects that changes in population density have on the age-specific death and fertility rates D and f.

One general conclusion that follows from Theorem 3 and the formula for n_1 in Theorem 1 is that if, for low population densities, the death rate D is nondecreasing and the fertility rate f is nonincreasing as functionals of density ρ for all age classes (i.e. if $D_\rho(0)(\rho_0)(a) \geqslant 0$ and $f_\rho(0)(\rho_0)(a) \leqslant 0$) then the bifurcation at criticality $n = 1$ is supercritical and stable. Such assumptions are typical in simple population growth models. These conditions are sufficient, but clearly are not necessary for supercritical bifurcation.

Consider the following illustrative example in which the death and fertility rates are simple linear functions of total population size $P = \int_0^A \rho(t, a)\, da$:

$$D = [1 + D_0 P]_+, \qquad f = [1 - f_0 P]_+, \qquad A = +\infty. \tag{6.1}$$

Here $[x]_+ = x$ for $x \geqslant 0$ and $[x]_+ = 0$ for $x < 0$. In this example $\mu(a) \equiv 1$ and $\beta(a) \equiv 1$ are constant, i.e. the inherent death and fertility rates are not age-specific. It is assumed that the coefficients D_0 and f_0 are nonnegative and $D_0 + f_0 > 0$. For this case the equilibrium equations (1.2) are easily found to have the unique nontrivial equilibrium solutions

$$\rho(a) = n(n-1)(D_0 + f_0)(D_0 + nf_0)^{-2} \exp(-n(D_0 + f_0)a/(D_0 + nf_0)).$$

One clearly sees here the bifurcating branch of positive equilibria for $n > 1$. Note that in this example $D_0 \equiv D_\rho(0)(\rho_0)(a) \geqslant 0$ and $-f_0 \equiv f_\rho(0)(\rho_0)(a) \leqslant 0$ so that $n_1 = D_0 + f_0 > 0$ as is consistent with supercritical bifurcation in Theorem 1.

Note also in this example when $D_0 > 0$ that as the net reproductive rate $n \geqslant 1$ increases the population "becomes younger" in the sense that the proportion of the total population taken up by younger age classes increases while that of older age classes decreases with increasing n. To see this observe that at equilibrium $P = (n-1)/(D_0 + nf_0)$ and

$$\rho(a)/P = n(D_0 + f_0)(D_0 + nf_0)^{-1} \exp(-n(D_0 + f_0)a/(D_0 + nf_0))$$

so that

$$\frac{\partial}{\partial n}(\rho(a)/P)\bigg|_{n=1} = D_0(1-a)e^{-a}/(D_0+f_0)\begin{cases}>0 & \text{for } a<1\\ <0 & \text{for } a>1.\end{cases}$$

This phenomenon in fact occurs more generally whenever supercritical bifurcation occurs and the death rate increases with density for all age classes. To see this consider the parameterized branch of equilibria (3.1) which, if $n_1 \neq 0$, can be parameterized by n in place of ε. Dropping the parameter subscript notation on the equilibrium solutions ρ, we calculate from (3.1)

$$\frac{\partial}{\partial n}\left(\frac{\rho(a)}{P}\right)\bigg|_{n=1} = \frac{\partial}{\partial \varepsilon}\frac{(\rho(a)/P)}{\partial n/\partial \varepsilon}\bigg|_{\varepsilon=0} = \frac{\int_0^A (\rho_0(\alpha)z_1(a) - \rho_0(a)z_1(\alpha))\, d\alpha}{n_1 P_0^2}$$

where $P_0 = \int_0^A \rho_0(a)\, da$. By (3.2) this expression can be written

$$\frac{\partial}{\partial n}\left(\frac{\rho(a)}{P}\right)\bigg|_{n=1} = \rho_0(a)\int_{\alpha=0}^{A}\int_{s=a}^{\alpha} D_\rho(0)(\rho_0)(s)\, ds\, \rho_0(\alpha)\, d\alpha / n_1 P_0^2. \tag{6.2}$$

If

$$n_1 > 0 \quad \text{and} \quad D_\rho(0)(\rho_0)(a) \geqslant 0 \quad (\not\equiv 0) \tag{6.3}$$

then the derivative (6.2) is positive when $a = 0$ and negative when $a = A$ and thus

$$\frac{\partial}{\partial n}\left(\frac{\rho(a)}{P}\right)\bigg|_{n=1}\begin{cases}>0 & \text{for } a \approx 0\\ <0 & \text{for } a \approx A.\end{cases} \tag{6.4}$$

For subcritical bifurcation ($n_1 < 0$) the inequalities reverse, but insamuch as the branch equilibria near bifurcation are in this case unstable this property of the normalized age distribution is probably of little interest.

If on the other hand $D_\rho(0)(\rho_0)(a)$ is not nonnegative for all a, (6.4) may no longer hold. To allow $D_\rho(0)(\rho_0)(a)$ to be negative for some a is to imply that increased population density *reduces* the death rate for these age classes. This could be caused by such things as enhanced predator protection due to schooling or herding or to improved survival rates of the young due to collective care. Such phenomena are at the heart of the concept of depensation and have, for example, been used to explain the dynamics of some fisheries [1].

As a simple example of this case suppose that the coefficient $D_0 = D_0(a)$ in the linear death rate functional (6.1) is age-specific and in particular that it is negative for younger age classes $a \approx 0$ and increases to positive values for older age classes $a \approx +\infty$. Since $D_\rho(0)(\rho_0)(a) = D_0(a)$, the one sign condition on D_ρ in (6.3) now fails to hold. To see the details of a specific example suppose D_0 is given by the exponential

$$D_0(a) = 1 - 2\exp(-\gamma a), \qquad \gamma = \theta^{-1}\ln 2. \tag{6.5}$$

In this case the effect of an increase in total population size P is a decrease in the death rate D for age classes $0 < a < \theta$ and an increase in D for $a > \theta$. From

(3.2) we find that

$$n_1 = f_0 + \frac{\gamma-1}{\gamma+1}, \qquad \frac{\partial}{\partial n}\left(\frac{\rho(a)}{P}\right)\bigg|_{n=1} = e^{-a}\Omega(a)/n_1$$

$$\Omega(a) := -a + \frac{2}{\gamma}(1-e^{-\gamma a}) + \frac{\gamma-1}{\gamma+1}.$$

This leads to three cases for this example:

$$\begin{aligned} &(a) && \theta < \ln 2 \\ &(b) && \theta > \ln 2 \quad \text{and} \quad f_0 > (\theta - \ln 2)/(\theta + \ln 2) \\ &(c) && \theta > \ln 2 \quad \text{and} \quad f_0 < (\theta - \ln 2)/(\theta + \ln 2). \end{aligned} \tag{6.6}$$

If (a) holds (i.e. if the range of young age classes whose death rates are decreased by population increases is sufficiently small), then $n_1 > 0$ and (6.4) holds. In this case supercritical stable bifurcation occurs and the normalized age distribution of the population becomes younger with increased $n \geq 1$ in the same sense as above for the case when D_0 was constant. This case is illustrated in Figs. 1 and 2 which show graphical results from numerically computed solutions of (1.2)–(6.1).

If (b) holds then $n_1 > 0$ and in place of (6.4) it turns out that

$$\frac{\partial}{\partial n}\left(\frac{\rho(a)}{P}\right)\bigg|_{n=1} \begin{cases} >0 & \text{for } a \approx \theta \\ <0 & \text{for } a \approx 0 \quad \text{and} \quad a \approx +\infty. \end{cases}$$

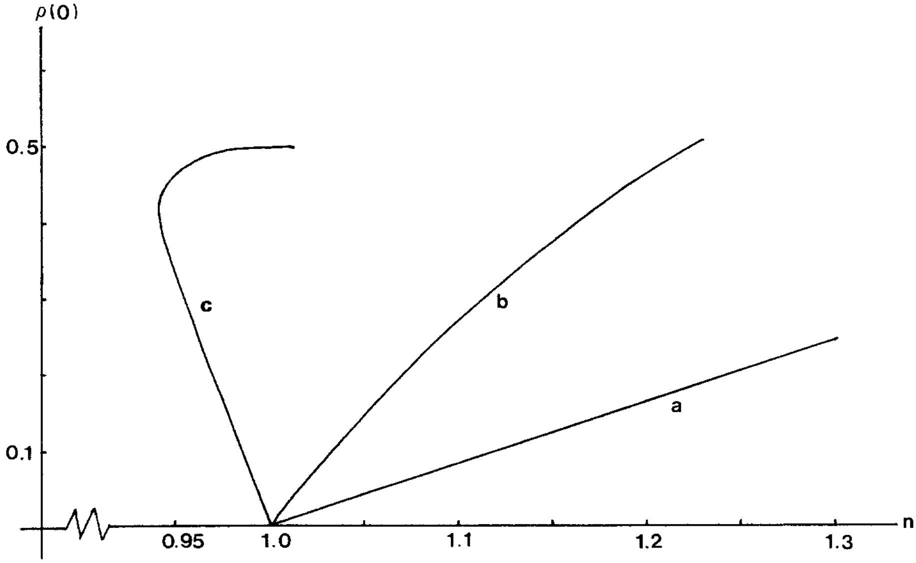

Fig. 1. Three branches of positive equilibrium solutions of (1.1) with death and fertility rates given by (6.1) and (6.5) were calculated numerically with $f_0 = 0.5$ for $\theta = 0.1$, 1.1 and 3.25. These cases correspond respectively to (a), (b) and (c) in (6.6)

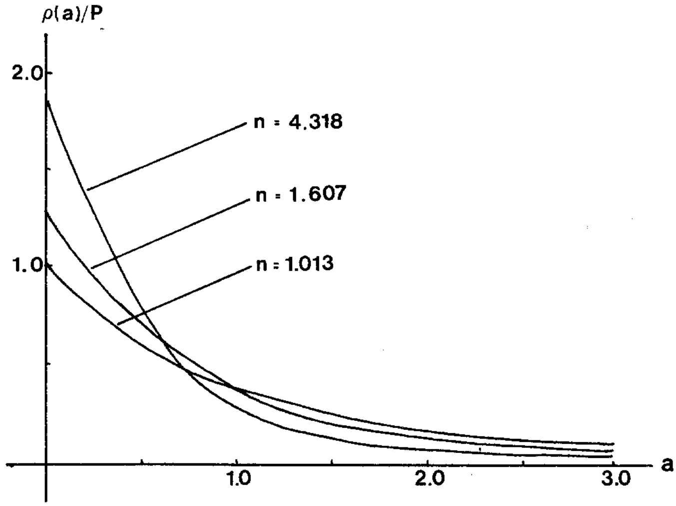

Fig. 2. Three normalized age distributions from branch (a) in Fig. 1 are plotted. As the inherent net reproductive rate n increases these distributions become younger

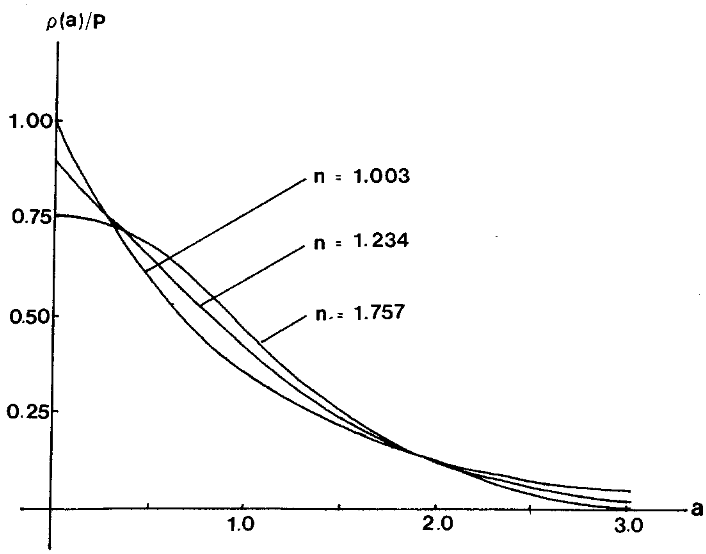

Fig. 3. Three normalized age distributions from branch (b) in Fig. 1 are plotted. As the inherent net reproductive rate n increases the proportion of young and of older age classes decreases while that of the middle age classes increases

In this case supercritical stable bifurcation still occurs but in the normalized age distribution both the proportion of younger and older age classes decrease as $n \geqslant 1$ increases. This case is illustrated by numerical results in Figs. 1 and 3.

Finally if (c) holds then $n_1 < 1$ and the bifurcation is subcritical and unstable. This case is also illustrated numerically in Fig. 1.

7. Concluding remarks

The existence of equilibrium solutions of the McKendrick equations (1.1) for the density ρ of an age-structured population has been studied here as a bifurcation problem using the population's inherent net reproductive rate n as a bifurcation parameter. Under general conditions Theorem 1 not only implies the local existence and uniqueness of a branch of positive equilibria which bifurcates from the zero density $\rho \equiv 0$ at the critical value $n = 1$, but gives the lower order terms in the Liapunov-Schmidt expansion of these equilibria. This local result is meant to supplement the more general global existence result in [4] in that it provides a means for studying the structure of the bifurcating branch near bifurcation, the age-distribution of the equilibrium density, the direction of bifurcation and the influence on these things of the density dependence of the death and fertility rates.

Theorems 2 and 3 deal with the stability properties of the zero density state and the positive branch equilibria of Theorem 1. Theorem 2 shows in general that $\rho \equiv 0$ is (locally) stable if and only if $n < 1$. Thus, for low density levels at least, it is necessary for the survival of the population that its inherent net reproductive rate exceed one. (This may not be true for large density levels.) Under slightly more restrictive conditions on the death and fertility rates as functionals of density, Theorem 3 utilizes linearized stability criteria to show that the positive equilibria in Theorem 1 are stable if and only if the bifurcation is supercritical.

The use of this local bifurcation analysis is illustrated in Section 6 where some general biological implications are derived and some examples are analysed. It is shown that the common case when an increase in population density causes an increase in the death rate and also a decrease in the fertility rate for all age classes always results in a stable supercritical bifurcation. Moreover, this case leads to a younger normalized age distribution in the equilibrium density as the inherent net reproductive rate is increased beyond the critical value of one. These assumptions are not always appropriate, however, and by means of examples it is shown in Section 6 that if they do not hold subcritical bifurcation can occur. These examples also show that the normalized age distribution of the equilibrium density is not always made younger by increasing the net reproductive rate.

This paper has concentrated on small amplitude equilibria lying in a neighborhood of the bifurcation point only. More global questions concerning the properties of solutions of (1.1) are not addressed. The global existence of the local branch investigated here is known [4], but the investigation of global stability properties remains a challenging problem. In general the stability of even a supercritical stable bifurcation may not be global nor persist globally along the branch [3] and even chaotic dynamics can occur. In the case of subcritical unstable bifurcation the dynamical properties of solutions are unclear. Many possibilities present themselves in this case, including for example a "turning back" of the bifurcating branch (as in Fig. 1(c)) with a resulting stable sub-branch of large amplitude stable equilibria (and a possible hysteresis effect) or the presence of multiple positive equilibrium states. That such phenomena can occur is clear from various special cases of (1.1), but a study of their occurrence, and that of other interesting dynamical behavior, related to general properties of the vital death and fertility rates and their density dependence, would be interesting.

Appendix

In this appendix the statement (iii) of Sect. 4(c) is proved. Using (4.7) we calculate

$$\frac{d}{d\varepsilon} y_0 \bigg|_{\varepsilon=0} = -\rho_0(a) \int_0^A l(0)(a)\rho_0(a) \int_0^a k(0)(\alpha)\, d\alpha\, da$$

$$\frac{d}{d\varepsilon} k_1 \bigg|_{\varepsilon=0} = n_1\beta(a) + \int_0^A w_1(0)(a, \alpha)\rho_0(\alpha)\, d\alpha + \int_0^A w_1(0)(\alpha, a)\rho_0(\alpha)\, d\alpha$$

where n_1 is given by (3.2) which turns out under (4.5)–(4.6) to equal

$$n_1 = \int_0^A \beta(a)\rho_0(a) \int_0^a k(0)(\alpha) \int_0^A l(0)(s)\rho_0(s)\, ds\, d\alpha\, da$$
$$- \int_0^A \int_0^A w_1(0)(a, \alpha)\rho_0(\alpha) d\alpha \rho_0(a)\, da.$$

This expression together with a differentiation of the left hand side of (4.4) with respect to ε at $\varepsilon = 0$ yields

$$C_\varepsilon(0, 0) = 2 \int_0^A l(0)(\alpha)\rho_0(\alpha)\, d\alpha \int_0^A \beta(a)\rho_0(a) \int_0^a k(0)(s)\, ds\, da - n_1$$
$$-2 \int_0^A \rho_0(a) \int_0^A w_1(0)(a, \alpha)\rho_0(\alpha)\, d\alpha\, da = 2n_1 - n_1 = n_1.$$

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