Nicholson’s blowflies differential equations revisited: Main results and open problems

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Abstract

This review covers permanence, oscillation, local and global stability of solutions for Nicholson’s blowflies differential equation. Some generalizations, including the most recent results for equations with a distributed delay and models with periodic coefficients, are considered.

Keywords:
Delay equations
Stability
Oscillation
Permanence
Nicholson’s blowflies equation
Periodic solutions

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1. Introduction

In biological applications [1] a recruitment-delayed model:

\[ \frac{dx}{dt} = B(x(t - \tau)) - D(x(t)) \]

(1)

is frequently used, where \( x(t) \) is a population size, the birth function \( B \) involves maturation delay \( \tau \), and the death rate \( D \) depends on the current population level only.

Eq. (1) is considered for given positive initial conditions:

\[ x(s) = \varphi(s) \quad \text{for} \quad s \in [-\tau, 0], \]

where \( \varphi \) is a continuous nonnegative function:

\[ \varphi \in C([-\tau, 0], \mathbb{R}^+), \quad \varphi(0) > 0. \]

Here \( x(t) \) is an adult population size and \( \tau > 0 \) is the maturation period. The birth and the death rates satisfy the following assumptions:

- \((A_1)\) \( B(0) = D(0) = 0, B(x) > D(x) \) for positive \( x \) small enough.
- \((A_2)\) there exists \( K > 0 \) such that \( B(K) = D(K) \).
- \((A_3)\) \( (z - K)[B(z) - D(z)] < 0 \) for \( z \in (0, \infty) \), \( z \neq K \).

Note that \((A_1)\) represents the fact that the population increases at low densities; \((A_2)\) guarantees the existence of a positive carrying capacity of the environment; \((A_3)\) indicates that this carrying capacity is unique and that in the absence of delay (\( \tau = 0 \)) there is a positive net growth below the carrying capacity, and a negative growth above it.

For example, the Ricker’s type function:

\[ B_1(x) = Pxe^{-\alpha x}, \]

or the Beverton–Holt function

\[ B_2(x) = \frac{px}{q + x^m}, \]

where \( m \) is a positive integer, together with the linear mortality term \( D(x) = \delta x, P > \delta > 0 \) or \( p/q > \delta > 0 \), respectively, satisfy all conditions \((A_1) - (A_3)\) and are widely used in fisheries [2].

Note that function \( B_1 \) was also used in [3] to model Chargas disease.

In this paper we consider Eq. (1) with \( B(x) = Pxe^{-\alpha x} \) and \( D(x) = \delta x \), which leads to the following model:

\[ \frac{dx}{dt} = P(x(t - \tau) \exp(-\alpha(x(t - \tau))) - \delta x(t)). \]

(2)

Here \( P > 0 \) is the maximum per capita daily egg production rate, \( \frac{1}{\alpha} > 0 \) is the size at which the population reproduces at its maximum rate, \( \delta > 0 \) is per capita daily adult mortality rate and \( \tau \) is the generation time, or the time taken from birth to maturity.

This equation was introduced by Nicholson [4] to model laboratory fly population. Its dynamics was later studied in [5] and [6], where this model was referred to as the Nicholson’s blowflies equation [5]. Over a period of nearly two years Nicholson recorded the population of flies and observed a regular basic periodic oscillation of about 35–40 days. Nicholson concluded that the basic cause of the oscillations was the time lag between stimulus and reaction of the density-related responses. Application of a classical logistic Hutchinson’s equation:

\[ \frac{dN}{dt} = rN(t) \left[ 1 - \frac{N(t - \tau)}{K} \right] \]

(3)

leads to some discrepancy in estimating the delay value. Eq. (3) was first studied in 1935 in the economic theory of the stability of business cycles. Later in 1948 this equation was used by Hutchinson to model herbivores grazing upon vegetation, which takes time \( \tau \) to recover. Eq. (3) represents an extremely crude first approximation, incorporating the minimum amount of essential biological information about the system. In [7] Eq. (2) was used to modify Hutchinson’s equation. It was shown in [6] that the fluctuations observed by Nicholson are quite clear of limit-cycle type; the period of the cycles is set mainly by the delay \( \tau \).

By letting \( N(t) = 2\alpha(t) \) Eq. (2) reduces to the equation:

\[ \frac{dN}{dt} = PN(t - \tau) \exp(-N(t - \tau)) - \delta N(t). \]

(4)
For a single species population with two-stage structure the following modification of Eq. (4) can be used:

$$\frac{dN}{dt} = Pe^{-\gamma t}N(t - \tau)e^{-\delta(t - \tau)} - \delta N(t),$$

(5)

where $\gamma$ is the juvenile through-stage mortality rate.

The theory of the Nicholson’s blowflies equation has made a remarkable progress in the past forty years with main results scattered in numerous research papers, see, for example, [8–23]. This paper presents, in a unified way, an overview of the results on the classical Nicholson’s model and some generalizations (in particular, to variable coefficients and delays). Emphasis is placed on the most important qualitative properties of the model such as existence of positive solutions, persistence, permanence, oscillation and stability. In any survey the authors must apologize for omissions; this case is no exception.

The paper is organized as follows. In Section 2 we present the results for the autonomous Eq. (4) in historical order from the earliest to the most recent and compare them. In Section 3 we consider several generalizations of Eq. (4): nonautonomous Nicholson’s equation with several delays, Nicholson’s equation with a distributed delay and Nicholson’s integro-differential equation. Theorem 3.6 of Section 3 on boundedness of solutions of the generalized Nicholson equation is a new result. Note that most of the results in this section were obtained by the authors of the present paper and have been published recently, see, for example, [24–26] and [27]. Finally, in Section 4 we formulate some relevant open problems and conjectures.

2. The autonomous model

2.1. Stability

In this section we study asymptotic properties, such as persistence, permanence and stability of solutions of Eq. (4).

We consider delay differential Eq. (4) for $t \geq t_0$ with the initial condition:

$$N(t) = \varphi(t), t \leq t_0,$$

(6)

where $\varphi \in C([t_0 - \tau, t_0], \mathbb{R}^+)$. The continuously differentiable function $N(t), t \geq 0$ is a solution of (4) if it is a solution of (4), (6) for some $t_0 \geq 0$. The initial value problem (4), (6) has a unique global solution on $[t_0, \infty)$ (see [8]). We note that the solution of (4), (6) is positive for any nonnegative initial function $\varphi(t)$ with $N(t_0) > 0$ (see Theorem 2.1 below).

Definition 2.1. We say that a solution $N'(t)$ of Eq. (4) is a global attractor or globally asymptotically stable (GAS) if for any positive solution $N(t)$

$$\lim_{t \to \infty} |N(t) - N'(t)| = 0.$$ 

Note that $N'(t)$ is either the trivial equilibrium $N_0 = 0$ of (4) or the nontrivial positive equilibrium:

$$N' = \ln \frac{P}{\delta}$$

which exists for $P > \delta$. We will use the same definition for the solution of nonautonomous equations with an equilibrium, if exists, and for a solution when there is a positive periodic solution rather than a constant equilibrium.

The following results were obtained in paper [8]:

Theorem 2.1 [8]. For all solutions of Eq. (4)

(i) $N(t) \geq 0$ for $t \geq 0$ provided $\varphi(s) \geq 0$ for all $-\tau \leq s \leq 0$;

(ii) $N(t) > 0$ for $t \geq \tau$ provided $0 \leq \varphi \neq 0$.

Theorem 2.2 [8]. Given positive initial data, all solutions of Eq. (4) remain positive for all $t \geq 0$ and

$$\lim_{t \to \infty} \sup N(t) \leq \frac{P}{\delta e}.$$

Theorem 2.3 [8]. Let $P \leq \delta$. Then $N(t) \to 0$ as $t \to \infty$ for any solution of (4).

From Theorem 2.3 it follows that $N_0 = 0$ is a global attractor independently of $\tau$ for $P \leq \delta$. If $P > \delta$, then the trivial solution of Eq. (4) is unstable, and a positive equilibrium point $N'$ appears.
Definition 2.2. We say that solutions of Eq. (4) are uniformly persistent if there exists $\eta > 0$ such that
\[ \liminf_{t \to \infty} N(t) > \eta \]
for every trajectory with positive initial values.

Theorem 2.4 [8]. Suppose $P > \delta$. There is no nontrivial solution $N(t)$ of (4) such that:
\[ \lim_{t \to \infty} N(t) = 0 \]
and all solutions of (4) are uniformly persistent.

Definition 2.3. We say that a function $y(t)$ is nonoscillatory about a number $K$ if the difference $y(t)/K$ is either eventually positive or eventually negative. Otherwise $y(t)$ is oscillatory about $K$.

Theorem 2.5 [8]. Suppose $P > \delta$. Let $N$ be a positive nonoscillatory about $N'$ solution. Then:
\[ \lim_{t \to \infty} N(t) = N' \]

The criteria of local asymptotical stability (LAS) (for the definition of local stability see [28]) of the nontrivial equilibrium $N'$ can be obtained by the direct computation of the roots of the characteristic equation:
\[ \lambda + \delta + e^{-\tau_1} \delta \left( \ln \frac{P}{\delta} - 1 \right) = 0, \]
associated with a linearized about the steady state solution of Eq. (4). For example, a delay-independent local stability condition was obtained in the following theorem:

Theorem 2.6 [29]. Assume that:
\[ 1 < \frac{P}{\delta} < e^2, \]
then a nontrivial steady state solution $N'$ is locally asymptotically stable.

Later we will prove that the same result is valid for some generalizations of Eq. (4), for example, for the equation with a variable delay.

Let $c = \ln \frac{P}{\delta} - 1$. In [14] the following result was obtained.

Theorem 2.7 [14]. If $\frac{P}{\delta} > e^2$, then the positive equilibrium $N'$ of (4) is LAS if
\[ \tau < \frac{1}{\delta} \ln \left[ \frac{c}{c - 1} \right]. \]
Moreover, there is a nonconstant periodic solution if
\[ \tau > \tau^* = \frac{\arccos(1/c)}{\delta \sqrt{c^2 - 1}}. \]

More general results on bifurcations of (4) can be found in [19].

Theorem 2.8 [19]. For Eq. (4), the following statements hold.

(i) If $\delta < P \leq \delta e^2$, then $N = N'$ is locally asymptotically stable.
(ii) If $P > \delta e^2$, then $N = N'$ is locally asymptotically stable for $\tau \in [0, \tau_0)$ and unstable for $\tau > \tau_0$, where
\[ \tau_0 = \frac{1}{\delta \sqrt{c^2 - 1}} \arcsin \sqrt{c^2 - 1} c. \]
(iii) If $P > \delta e^2$, Eq. (4) undergoes a Hopf bifurcation at $N'$ when $\tau = \tau_k$, where
\[ \tau_k = \frac{1}{\delta \sqrt{c^2 - 1}} \arcsin \left[ \sqrt{c^2 - 1} c + 2k\pi \right], \]
for $k = 0, 1, 2, \ldots$.

In paper [9] for the global attractivity or global asymptotic stability (see Definition 2.1) of the positive equilibrium, the set of all solutions of (4) was divided into those that oscillate about $N'$ and those that do not, and then the asymptotic behavior of each class was studied separately.
Theorem 2.9 [9]. If $P > \delta$ and

$$(e^{\tau - 1})\left(\frac{P}{\delta} - 1\right) < 1,$$ \hspace{1cm} (11)

then $N^*$ is a global attractor.

The meaning of condition (11) is that a “small” delay $\tau$ implies nice dynamics for Eq. (4), that is, the global attractivity of positive equilibrium $N^*$. So, in this case as we see, global attractivity can be controlled by this parameter. Condition (11) was updated to the case of the nonstrict inequality in [29]:

$$(e^{\tau - 1})\left(\frac{P}{\delta} - 1\right) \leq 1.$$ \hspace{1cm} (12)

Inequality (12) was improved in paper [8], where condition:

$$(e^{\tau - 1})\ln\frac{P}{\delta} < 1,$$ \hspace{1cm} (13)

guarantees GAS of the positive equilibrium. Some modifications of conditions (11) and (13) were presented in [23] and [30]. It was proved in [23] that each of the following conditions is sufficient for GAS of the positive equilibrium of Eq. (4):

$$(e^{\tau - 1})\ln\frac{P}{\delta} < 2e^{\tau} - 1$$ \hspace{1cm} (14)

or

$$(1 - \rho)\ln\frac{P}{\delta} < 1 - \rho + 0.5\left(1 + \sqrt{1 + 4\rho(1 - \rho)}\right),$$ \hspace{1cm} (15)

where $\rho = \exp(-\delta \tau)$. Clearly, the estimate (14) implies that inequalities (11)–(13) and $1 < \xi < e^2$ are sufficient for GAS.

In [32] more attempts were made to obtain new conditions for GAS in view of the Smith's conjecture. The authors observed that they obtained “the surprising closeness between the regions of local and global asymptotic stability”.

Theorem 2.10 [32]. The positive equilibrium $N^*$ of (4) is a global attractor if either:

1. $\frac{P}{\delta} \leq e$

or

2. $e^{\tau - 1} > c\ln\left(\frac{C^2 + C}{C^2 + 1}\right) \cdot c = \ln\frac{P}{\delta} - 1.$

Note that the first condition of Theorem 2.10 is a delay-independent condition. For convenience we summarize global stability results for Eq. (4) in Table 1.

<table>
<thead>
<tr>
<th>Author</th>
<th>Year</th>
<th>Global stability criterion</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kulevskić et al.</td>
<td>1992</td>
<td>$(e^{\tau - 1})(\frac{P}{\delta} - 1) &lt; 1$</td>
</tr>
<tr>
<td>Karakostas et al.</td>
<td>1992</td>
<td>$(e^{\tau - 1})(\frac{P}{\delta} - 1) \leq 1$</td>
</tr>
<tr>
<td>So and Yu</td>
<td>1994</td>
<td>$(e^{\tau - 1})\ln\xi &lt; 1$</td>
</tr>
<tr>
<td>Smith</td>
<td>1995</td>
<td>$\delta \tau &lt; P\tau &lt; \min{\exp(1 + \delta \tau), e^2}$</td>
</tr>
<tr>
<td>Győri and Trofimchuk (GT1)</td>
<td>1999</td>
<td>$(e^{\tau - 1})\ln\xi &lt; 2e^{\tau} - 1$</td>
</tr>
<tr>
<td>Győri and Trofimchuk (GT2)</td>
<td>1999</td>
<td>$(1 - \rho)\ln\xi &lt; 1 - \rho + 0.5\left(1 + \sqrt{1 + 4\rho(1 - \rho)}\right)$ where $\rho = \exp(-\delta \tau)$, $1 &lt; \xi &lt; e^2$, $e^{\tau - 1} &gt; c\ln\left(\frac{C^2 + C}{C^2 + 1}\right)$, $c = \ln\frac{P}{\delta} - 1$</td>
</tr>
<tr>
<td>Liz et al.</td>
<td>2003</td>
<td>$\frac{P}{\delta} &gt; e$, $(e^{\tau - 1})\ln\xi &lt; 1 - \rho + 0.5\left(1 + \sqrt{1 + 4\rho(1 - \rho)}\right)$ where $\rho = \exp(-\delta \tau)$, $1 &lt; \xi &lt; e$ or $\xi &gt; e$, $e^{\tau - 1} &gt; c\ln\left(\frac{C^2 + C}{C^2 + 1}\right)$, $c = \ln\frac{P}{\delta} - 1$.</td>
</tr>
</tbody>
</table>
Let us compare the results in Table 1.

**Remark 2.1.** It can be proven analytically that the GT2 stability result in Table 1 is an improvement over the previous ones.

For example, let us prove that GT1 is weaker than GT2. Firstly, both conditions of GT1 and GT2 can be reformulated as

\[
 c < \frac{1}{1 - \rho} \quad \text{and} \quad c < \frac{1 + \sqrt{1 + 4 \rho (1 - \rho)}}{2(1 - \rho)},
\]

respectively, where \( c = \ln(P/d) - 1 \) and \( \rho = e^{-\gamma \tau} \).

Clearly, \( \frac{1}{1 - \rho} < \frac{1 + \sqrt{1 + 4 \rho (1 - \rho)}}{2(1 - \rho)} \) for \( 0 < \rho < 1 \), thus the first inequality in (16) implies the second one.

To illustrate that LTT test is better than GT2 result, we note that for \( c < 1 \) all conditions of LTT are satisfied. Consider \( c > 1 \). Then function:

\[
 f(c) := c \ln\left(\frac{c^2 + c}{c^2 + 1}\right)
\]

is a monotone increasing function.

If the second condition of GT2 is satisfied, then monotonicity of \( f \) and inequality (16) yield:

\[
 f(c) < g(\rho) := f\left(\frac{1}{2(1 - \rho)} \left[1 + \sqrt{1 + 4 \rho (1 - \rho)}\right]\right), \rho \in (0, 1).
\]

In terms of function \( f \) the LTT condition has the form \( f(c) < \rho \). Assume \( \rho \in (0, 1) \) and compare two functions \( y = \rho \) and \( y = g(\rho) \). Fig. 1, left, demonstrates that \( g(\rho) < \rho \) for \( \rho > 0 \). Asymptotic expansion of function \( g \) around \( \rho = 0 \) yields \( g(\rho) = \rho - a \rho^3 \) with \( a > 0 \), thus in the neighborhood of zero \( g(\rho) < \rho \) (see Fig. 1, right). Hence \( f(c) < g(\rho) < \rho \), so \( f(c) < \rho \), and the second condition of GT2 implies LTT condition. Summing up, we conclude that the last result in Table 1 is the best one.

### 2.2. Oscillation

In [16] (see also [12], Theorem 2.5.1) the following oscillation criterion was obtained.

**Theorem 2.11**  [12,16]. If \( \xi > e \) and

\[
 \delta e^{\xi \tau} \left(\ln\frac{P}{\delta} - 1\right) > \frac{1}{e},
\]

then all solutions of Eq. (4) oscillate about \( N^* \).

If \( \xi > e^\gamma \) and

\[
 \delta e^{\xi \tau} \left(\ln\frac{P}{\delta} - 1\right) \leq \frac{1}{e},
\]

then there exists a nonoscillatory about \( N^* \) solution of (4).

---

![Fig. 1](image_url)

Since \( g(x) \) defined in (18) and (17) is less than \( x \), then the second condition by Györi, Trofimchuk implies the inequality of Liz, Tkachenko and Trofimchuk. Thus the latter result is sharper.
3.1. Existence, positiveness and permanence of solutions

Theorem 3.1. Otherwise we will say that

We say that a nonzero solution

Theorem 2.12[13].

3. Nonautonomous models and generalizations

The main purpose of this section is to study some generalizations of Nicholson’s Eq. (4) in variable environments.

3.1. Existence, positiveness and permanence of solutions

We introduce the following models:

(a) Nicholson’s model with a distributed delay:

(b) Nicholson’s model with several concentrated delays:

(c) the integro-differential Nicholson’s model

\[
\frac{\dot{N}}{N} = -\delta N(t) + P \int_{R(t)}^{t} K(t,s) e^{-N(s)} ds, \quad t \geq t_0.
\]

Note that in Eqs. (21), (23) the delay is not constant but is distributed around its expectancy value.

Remark 3.1. Note that (22) is a special case of (21) for \(R(t,s) = \sum_{k=1}^{m} a_k(t) x(t_{h_k(t)}),\) where \(x_i\) is the characteristic function of segment \(I;\) Eq. (23) is also a special case of (21) with \(R(t,s)\) differentiable in \(s\) and such that \(\frac{\partial R(t,s)}{\partial s} = K(t,s).\)

We assume that for Eqs. (21)–(23) and the initial function in (6) the following conditions hold:

(a1) \(a_k(t) \geq 0, k = 1, \ldots, m,\) are Lebesgue measurable functions, \(\sum_{k=1}^{m} a_k(t) = 1;\)

(a2) \(h, h_k : [0, \infty) \rightarrow \mathbb{R}, k = 1, \ldots, m,\) are Lebesgue measurable functions, \(\lim_{t \to \infty} h(t) = 1;\)

(a3) \(R(t,.)\) is a left continuous nondecreasing function for any \(t, R(.s)\) is locally integrable for any \(s, R(t, h(t)) = 0, R(t, t^+) = 1, \int_{h(t)}^{t} dR(t,s) = 1\) for any \(t > 0;\)

(a4) \(\varphi : (-\infty, t_0) \rightarrow \mathbb{R}^+\) is continuous, \(\varphi(0) > 0.\) For (23) condition (a3) has the form:

(a5) \(K(t,s)\) is a Lebesgue measurable locally essentially bounded function, \(K(t,s) \geq 0, \int_{h(t)}^{t} K(t,s) ds = 1\) for any \(t > 0,\) while for (22) conditions (a1)–(a2) imply (a3).

We will also consider Eq. (22) with variable coefficients \(\delta(t)\) and \(P(t).\)

Definition 3.1. An absolutely continuous function \(N : R \rightarrow R\) is called a solution of the problem (21), (6) (as well as (22), (6) and (23), (6)) if it satisfies these equations for almost all \(t \in [t_0, \infty)\) and the initial condition (6) for \(t \leq t_0.\)

Theorem 3.1. [24,25] There exists a unique positive global solution of the problem (21), (6) (as well as (22), (6) and (23), (6)) for \(t \geq t_0.\)
**Definition 3.2.** Positive solution $N(t)$ of an equation is permanent if there exist $t_0 \geq 0, A$ and $B, B > A > 0$ such that $A \leq N(t) \leq B$ for $t \geq t_0$.

**Theorem 3.2** [25]. Suppose $P > \delta$. Then the solution of the problem (21), (6) (as well as (22), (6) and (23), (6)) is permanent.

Note that explicit solution estimates depend on the initial function both for Nicholson’s blowflies model in [25], and for a more general class of the equations in [26]. In Section 3.2 we obtain estimates for lim inf and lim sup for all solutions of Eq. (21) which do not depend on initial functions and are also delay-independent. For autonomous equation (4) the solution estimates and attracting sets were studied in [33,34].

### 3.2. Stability and asymptotic estimates

We assume that $P > \delta$, so for all Eqs. (21)–(23) there exists the positive equilibrium $N^* = \ln(P/\delta)$. For a local stability analysis of the positive equilibrium we can apply the known stability conditions for linear differential equations with several delays. To illustrate application of such conditions, we consider the following equation with proportional coefficients:

$$\frac{dN}{dt} = r(t)[pN(h(t))e^{-N(h(t))} - \delta_0 N(t)],$$

(24)

where

$$r(t) > 0, \int_0^\infty r(s)ds = \infty, h(t) \leq t, u_{p(t-h(t))} < \infty.$$

For $P > \delta_0$, Eq. (24) has a positive equilibrium $N^* = \ln(P/\delta_0)$. After substitution $x(t) = N(t) - N^*$ Eq. (24) has the form:

$$x'(t) = \delta_0 r(t)[(x(h(t)) + N^*)e^{-x(h(t))} - N^* - x(t)].$$

(25)

Eq. (26) has the zero equilibrium. Linearization of (26) yields the following equation:

$$y'(t) = -\delta_0 r(t)[y(t) + \left(\ln \frac{P}{\delta_0} - 1\right)y(h(t))].$$

(27)

To obtain the following statement we apply to Eq. (27) the recent stability result [27] (Corollary 1.5).

**Theorem 3.3.** Suppose $P > \delta_0$, condition (25) and at least one of the following conditions holds:

1. $\frac{p}{\delta_0} < e^2$,
2. $\frac{p}{\delta_0} \geq e, \delta_0 \left[\ln \frac{p}{\delta_0} - 1\right]\limsup_{t \to \infty} \int_{h(t)}^t r(s)ds < 1$.

Then the positive equilibrium of Eq. (24) is LAS.

Multiple stability results for autonomous models are well-known, however there are only a few results for the global stability of nonautonomous equations. Delay-independent stability conditions of the positive equilibrium were obtained in [25] for $1 < p/\delta_0 < e$, and for $1 < p/\delta_0 < e^2$ in [26] for the equation:

$$\frac{dN}{dt} = r(t)\left[p\int_{h(t)}^t N(s)e^{-N(s)}dR(t,s) - \delta_0 N(t)\right].$$

(28)

**Theorem 3.4** [25,26]. Suppose (25) holds. If $1 < \frac{p}{\delta_0} < e^2$ then the positive equilibrium of Eq. (28) is GAS.

Delay-dependent stability condition was presented in [26].

**Theorem 3.5** [26]. Suppose (25) holds and

$$\limsup_{t \to \infty} \int_{h(t)}^t r(s)ds < \frac{1}{p/e^2 + \delta_0}.$$

(29)

Then Eq. (28) is GAS.

For autonomous Eq. (4) the latter result gives a sharper estimate than estimate (11) (here we can refer to the case $P/\delta > e$, since otherwise we have GAS independently of the delay).

In fact, inequality (29) for (4) gives the following bound for $\delta t$:

$$\delta t < \frac{de^2}{P + \delta e^2},$$

while (11) defines the bound (below we apply the fact that $P > \delta e$ and $\ln(x) < x - 1$ for $x > 1$)
\[ 0 < \delta t < \ln \left( \frac{P}{P - \delta} \right) < \frac{P}{P - \delta} - 1 = \frac{\delta}{P - \delta} \leq \frac{\delta e^2}{P + \delta e^2} \]

as far as \( \frac{\delta}{P} > \frac{2}{\delta e} \). Since the latter fraction is less than \( e \), then inequality (29) yields a sharper than (11) estimate for autonomous Eq. (4).

Nevertheless (29) is weaker than the corresponding results in [32].

In order to find the uniform estimates for the solutions, we introduce a reproduction function:

\[ f(x) = \frac{P}{\delta} xe^{-x}. \]  \((30)\)

Clearly, \( x = N^* \) is a fixed point of this function:

The following theorem extends and improves the result obtained in Theorem 2.4 for the autonomous Nicholson Eq. (4).

**Theorem 3.6.** All solutions of Eq. (21) (as well as (22), (23)) have the following uniform estimates:

1. If \( \delta < P < \delta e^2 \), then

\[ \liminf_{t \to \infty} N(t) = \limsup_{t \to \infty} N(t) = N^*. \]  \((31)\)

2. If \( P > \delta e^2 \), then

\[ \limsup_{t \to \infty} N(t) \leq M := \frac{P}{\delta e}, \quad \liminf_{t \to \infty} N(t) \geq m := f(M) = f\left( \frac{P}{\delta e} \right). \]  \((32)\)

**Proof.** It is sufficient to prove the theorem for Eq. (21). In part 1) the lower and the upper bounds coincide with the global attractor \( N^* \) since Eq. (21) is GAS.

Consider now the upper bound in part 2) which is the global maximum of function \( f \). Let \( N(t) \) be a solution of Eq. (21), then we have:

\[ \dot{N}(t) \leq -\delta N(t) + \frac{P}{e}, \]

since \( 1/e = \max_{x > 0} xe^{-x} \). Hence \( 0 < N(t) \leq c \exp(-\delta t) + \frac{P}{\delta e} \) which implies the upper bound estimation.

Moreover, \( M \) is not only the bound of the upper limit but is also the eventual bound of the solution. In fact, if \( N(t) > M \) for any \( t \) then:

\[ \dot{N}(t) \leq \delta(-M + f(M)) < 0, \]

which leads to the contradiction \( \lim_{t \to \infty} N(t) = -\infty \). Thus there exists \( t' \) such that \( N(t') \leq M \). Since \( \dot{N}(t) \leq 0 \) for any \( N(t) \geq M \), then \( N(t) < M \) for any \( t \geq t' \). Further we will assume without loss of generality that \( N(t) \leq M, t \geq 0 \).

To obtain the lower bound in part (2), we assume again that \( N(t) \) is a solution of Eq. (21). Firstly, we will prove that there exists a segment \([\tau_0, \tau_1] \subset [0, \infty)\) such that \( N(t) \geq m \) for any \( t \in [\tau_0, \tau_1] \) and \( h(t) \geq \tau_0 \) for any \( t \geq \tau_1 \). By condition (a2) there exists \( \tau_1 \geq 0 \) such that \( h(t) \geq 0 \) for \( t \geq \tau_1 \). Denote \( s_0 = \min_{t \in [0,1]} N(t) \). Since any solution is positive then \( s_0 > 0 \). We assume \( s_0 < m \), otherwise \( [\tau_0, \tau_1] = [0, t_1] \). Since \( f(x) > 0 \) for \( x < 0 \), then:

\[ s_1 = \min_{s < \frac{P}{\delta e}} f(s) = \min \left\{ \min_{s < \frac{P}{\delta e}} f(x), f(M) \right\} > s_0. \]

The solution \( N(t) \geq s_0 \) since:

\[ \dot{N}(t) = \delta \left[ -N(t) + \int_{h(t)}^{t} f(N(s)) dR(t, s) \right] \geq \delta (s_1 - s_0) > 0 \]

as far as \( N(z) \geq s_0 \) for \( z \in [h(t), t] \) and \( N(t) \leq s_0 \). Thus \( N(t) \) increases while \( N(t) < s_0 \).

If \( s_1 = m \), this confirms the lower bound. Indeed, either \( N(t) \) is always less than \( s_1 \) or there exists a point \( t' > t_1 \) such that \( N(t') \geq s_1 \). In the former case the solution is monotone increasing and has a limit \( d \leq m \). Since for some \( \varepsilon > 0 \) we have \( \max_{x \in [d - \varepsilon, d]} f(x) > d \), then \( N'(t) \) exceeds a certain positive number, which leads to a contradiction. In the latter case \( N'(t) \geq 0 \) for any \( N(t) \leq m \), thus \( N(t) \geq m \) for any \( t \geq t' \).

If \( s_1 < m \), then the same argument proves that there exists \( t' \) such that \( N(t) \geq s_1 \) for \( t \geq t' \). We continue the process until \( s_k = m \), which happens for some finite \( k \), since \( f(x) > x \) is increasing in \([0,1]\) and for any \( s < 1 \) and \( \varepsilon > 0 \) there exists a positive integer \( \kappa \) such that \( \kappa^\delta(\varepsilon) > s \). Thus we can find the segment \([\tau_0, \tau_1] \) such that \( N(t) \geq m \) for \( t \in [\tau_0, \tau_1] \).

Further, since:

\[ \dot{N}(t) \geq \delta \left[ -m + \int_{h(t)}^{t} f(N(s)) dR(t, s) \right] \geq \delta (m - m) = 0 \]
for any \( t \geq \tau_1 \) such that \( N(t) \leq m \) and \( N(\tau) \geq m \) in \([h(t), t]\), then \( N(t) \geq m \) for any \( t \geq \tau_0 \), which completes the proof.

\[ \square \]

**Remark 3.2.** Theorem 3.6 remains true for Eq. (28) if condition (25) for \( r(t) \) holds.

The following theorem gives the precise lower and upper bounds of the solution of Eq. (28). A similar result is true for (21)–(23).

**Theorem 3.7** [26]. Suppose for Eq. (28) \( P/\delta > e^2 \), condition (25) holds and number \( m \) is defined by (32).

Then for any \( a \in (m, 1) \) and any \( b \in (N^*, f(1)), f(b) < a \) there exist \( h(t) \) and distributed delay \( R(t, s) \) satisfying (a2)–(a3) such that there exists a positive solution \( N(t) \) of Eq. (28) with

\[
\liminf_{t \to \infty} N(t) = a, \limsup_{t \to \infty} N(t) = b.
\]

**Remark 3.3.** Theorem 3.7 illustrates that if we assume that this equation has an arbitrary variable delay, then condition \( P\delta \leq e^2 \) is necessary for GAS of Eq. (28).

3.3. Oscillation

**Theorem 3.8** [24]. Assume that \( \frac{P}{\delta} > e \).

If

\[
\delta \left( \frac{P}{\delta} - 1 \right) \liminf_{t \to \infty} \int_{h(t)}^{t} d\tau \int_{h(t)}^{\tau} e^{\delta(t-s)} dR(\tau, s) > \frac{1}{e},
\]

then all solutions of Eq. (21) are oscillatory about \( N^* \).

If \( \frac{P}{\delta} > e^2 \),

\[
\delta \left( \frac{P}{\delta} - 1 \right) \limsup_{t \to \infty} \int_{h(t)}^{t} d\tau \int_{h(t)}^{\tau} e^{\delta(t-s)} dR(\tau, s) < \frac{1}{e},
\]

then Eq. (21) has a nonoscillatory about \( N^* \) solution. All nonoscillatory solutions tend to \( N^* \) as \( t \to \infty \).

**Theorem 3.9** [24]. If \( P > \delta e \) and

\[
\delta \left( \frac{P}{\delta} - 1 \right) \liminf_{t \to \infty} \sum_{k=1}^{m} \int_{h(t)}^{t} a_k(s) e^{\delta(t-h(t)(s))} d\tau > \frac{1}{e},
\]

then all solutions of Eq. (22) are oscillatory about equilibrium \( N^* \). If \( P > \delta e^2 \) and

\[
\delta \left( \frac{P}{\delta} - 1 \right) \limsup_{t \to \infty} \sum_{k=1}^{m} \int_{h(t)}^{t} a_k(s) e^{\delta(h(t)(s))} d\tau < \frac{1}{e},
\]

then Eq. (22) has a nonoscillatory about \( N^* \) solution. For nonoscillatory solutions \( \lim_{t \to \infty} N(t) = N^* \).

It is interesting to note that for \( m = 1 \) oscillation and nonoscillation conditions in Theorem 3.9 coincide with the similar conditions obtained in [12,16] for the autonomous delay Eq. (4) (see Theorem 2.11).

**Theorem 3.10** [25]. If \( P > \delta e \) and

\[
\delta \left( \frac{P}{\delta} - 1 \right) \liminf_{t \to \infty} \int_{h(t)}^{t} d\tau \int_{h(t)}^{\tau} e^{\delta(t-s)} K(\tau, s) ds > \frac{1}{e},
\]

then all solutions of Eq. (23) are oscillatory about \( N^* \).

If \( \frac{P}{\delta} > e^2 \),

\[
\delta \left( \frac{P}{\delta} - 1 \right) \limsup_{t \to \infty} \int_{h(t)}^{t} d\tau \int_{h(t)}^{\tau} e^{\delta(t-s)} K(\tau, s) ds < \frac{1}{e},
\]

then Eq. (23) has a nonoscillatory about \( N^* \) solution. All nonoscillatory solutions tend to \( N^* \) as \( t \to \infty \).

Previously the definition of rapidly oscillating solutions was introduced for autonomous equations; below we adapt it to nonautonomous equations.

**Definition 3.3.** An oscillating solution \( N(t) \) of (21)–(23) is called slowly oscillating if for any \( t_0 > 0 \) there exist two points \( t_1, t_2, t_2 > t_1 > t_0 \), such that \( h(t) > t_1, t \geq t_2 \), and the difference \( N(t) - N^* \) preserves its sign in \([t_1, t_2]\) and vanishes at the point \( t_2 \).
Otherwise, the solution is rapidly oscillating.

The solution is rapidly oscillating if eventually the distance between adjacent zeros of the function does not exceed the delay.

**Theorem 3.11** [25].

1. If \( \delta < P < \delta e \), then Eq. (21) has no slowly oscillating about \( N^* \) solutions.
2. If \( P = \delta e \), then (21) has no oscillating about \( N^* \) solutions, other than identically equal to \( N^* \) for all \( t \geq t_0 \).

**Remark 3.4**. Theorem 3.11 claims that for \( \delta < P \leq \delta e \) there are nonoscillatory about \( N^*/C_3 \) solutions: in fact, any solution with a nonoscillating initial function does not oscillate.

### 3.4. Periodic solutions

The main method used in [21,23,35–40] is the upper-lower solution method where the existence of at least one positive periodic solution is obtained by constructing a pair of upper and lower solutions and application of a fixed point theorem in cones.

In [38] a nonautonomous model was studied:

\[
\frac{dN}{dt} = -\delta(t)N(t) + \sum_{i=1}^{m} P_i(t)N(h_i(t))e^{-\tau_i(h_i(t))},
\]

(33)

where \( P_i(t), \tau_i(t), \delta(t), t - h_i(t) \) are positive continuous \( \omega \)-periodic functions:

**Theorem 3.12** [38]. Assume that:

\[
\sum_{i=1}^{m} P_i(t) > \delta(t)
\]

for \( t \in [0, \omega] \). Then Eq. (33) has at least one positive \( \omega \)-periodic solution.

**Theorem 3.13** [38]. If

\[
\sum_{i=1}^{m} P_i(t) \leq \delta(t)
\]

for \( t \in [0, \omega] \), then every positive solution of Eq. (33) tends to zero as \( t \to \infty \).

Following [21] we consider a partial case of Eq. (33):

\[
\frac{dN}{dt} = -\delta(t)N(t) + P(t)N(t - n\omega)e^{-N(t - n\omega)}.
\]

(34)

Here \( P(t), \delta(t) \) are positive continuous \( \omega \)-periodic functions, \( n \) is a positive integer.

**Theorem 3.14** [21]. Assume that there exists a positive periodic solution \( \bar{N}(t) \) and

\[
\min_{t \in [0, \omega]} \bar{N}(t) > 1.
\]

Let \( N(t) \) be a positive solution of (34) which does not oscillate about \( \bar{N}(t) \). Then

\[
\lim_{t \to \infty} |N(t) - \bar{N}(t)| = 0.
\]

**Theorem 3.15** [21]. Assume that there exists a positive periodic solution \( \bar{N}(t) \) and

\[
\min_{t \in [0, \omega]} \bar{N}(t) > 1.
\]

Every positive solution of Eq. (34) oscillates about \( \bar{N}(t) \) if at least one of the following conditions holds:

\[
\liminf_{t \to \infty} \int_{t-n\omega}^{t} P(s)e^{-\bar{N}(s)}[\bar{N}(s) - 1] \exp \left( \int_{s-n\omega}^{s} \delta(u)du \right) ds > \frac{1}{\varepsilon}.
\]

(35)

\[
\limsup_{t \to \infty} \int_{t-n\omega}^{t} P(s)e^{-\bar{N}(s)}[\bar{N}(s) - 1] \exp \left( \int_{s-n\omega}^{s} \delta(u)du \right) ds > 1.
\]

(36)
Theorem 3.16 [21]. Assume that there exists a positive periodic solution \( \hat{N}(t) \) such that \( \min_{t \in [0,T]} \hat{N}(t) > 1 \). Further suppose that:
\[
\max_{t \in [0,T]} \frac{P(t)}{\delta(t)} e^{-\hat{N}(t)} \leq 1 \quad \text{and} \quad \limsup_{t \to \infty} \int_{t-m_0}^{t} P(s) \exp \left( \int_{s}^{t} \delta(v) dv \right) ds = \gamma < 1.
\]
Then for every positive solution of Eq. (34) we have \( \lim_{t \to \infty} |N(t) - \hat{N}(t)| = 0 \).

4. Open problems and conjectures

Finally, we formulate some open problems:

1. Obtain global stability results for nonautonomous Eqs. (21)–(23) which are similar to the best known results in the autonomous case.

Conjecture: All results in Table 1 are true for Eq. (21) (as well as (22), (23)) with any delay not exceeding \( \tau \), \( t - \tau \leq h(t) \leq t \).

Find necessary delay-dependent conditions for global stability of Eqs. (4), (21)–(23).

2. The oscillation conditions were obtained for Eqs. (4), (21)–(23) for \( P > \delta e \) and nonoscillation conditions were presented for \( P > \delta e^s \). If \( \delta < P < \delta e \) then by Theorem 3.11 Eq. (21) is nonoscillatory with no additional conditions. Describe oscillation behavior of solutions in the case \( \delta e < P < \delta e^s \).

3. For Eq. (4) inequality \( P < \delta e \) guarantees that there is an infinite set of rapidly oscillating solutions (Theorem 3.10). In [25] it was demonstrated that this result is, generally, not valid for Eq. (21), i.e., there exists Eq. (21) with \( P < \delta e \) such that it has no rapidly oscillating solutions. Find sufficient conditions on the parameters of Eq. (21) such that the condition \( P < \delta e \) implies existence of a rapidly oscillating solution.

4. Find global stability conditions for the positive periodic solution of Eq. (33) in terms of its coefficients.

5. Nicholson’s blowflies equations with linear impulsive perturbations \( x(t_k) = \alpha_k x(t_k) \) at fixed moments of time were studied in several papers, see, for example, [41,42]; most of publications are concerned with existence of a positive periodic solution and its global attractivity. To the best of our knowledge, all the results are obtained for constant delays. We propose to study the impulsive model with variable (generally, distributed) delay: existence of global positive solutions, permanence, stability and oscillation. In addition, the impulsive model can be considered as a perturbation of the equation without impulses. Let us assume that the positive equilibrium of the Nicholson’s blowflies equation is globally asymptotically stable. Find sufficient conditions on \( \alpha_k \) such that the zero solution of the impulsive equation is globally asymptotically stable. Biologically, this corresponds to the following problem: what should be the blowflies’ termination rate that would eventually lead to the extinction of the pest population (which is the desired outcome)?

6. Assume that a harvesting function is a function of the delayed estimate of the true population. Consider Eq. (2) with a linear harvesting term:
\[
\frac{dx}{dt} = Px(t - \tau) \exp \left( -x(t - \tau) \right) - h x(t) - H x(t - \sigma)
\]

or Eqs. (21)–(23) with a delayed harvesting strategy.

7. A new study indicates that a linear model of density-dependent mortality will be most accurate for populations at low densities, and marine ecologists are currently in the process of constructing new fishery models with nonlinear density-dependent mortality rates. Consider a Nicholson’s model with a nonlinear density-dependent mortality term, i.e.,
\[
\frac{dx}{dt} = -D(x) + Px(t - \tau) \exp \left( -x(t - \tau) \right),
\]

where function \( D \) might have one of the following forms: \( D(x) = ax/(x + b) \) or \( D(x) = a - be^{-x} \) with positive constants \( a, b > 0 \).

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References
