Article

About a non-parametric model of hermaphrodite population dynamics

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Received 22 November 2013; *Accepted 25 December 2013*; *Published online 1 March 2014*

Abstract

In current publication non-parametric model (model of Kolmogorov’s type) of hermaphrodite population dynamics is analyzed. It is assumed that there are four basic variables: number of individuals, number of pairs, and number of pregnant individuals. It is also assumed that number of pairs is fast variable: it allows decreasing of number of differential equations. For conditions of pure qualitative type for birth and death rates of individuals in population possible dynamic regimes are determined.

Keywords model of population dynamics; sexual structure; hermaphrodite; dynamic regimes.

Computational Ecology and Software
ISSN 2220-721X
URL: http://www.iaees.org/publications/journals/ces/online-version.asp
RSS: http://www.iaees.org/publications/journals/ces/rss.xml
E-mail: ces@iaees.org
Editor-in-Chief: WenJun Zhang
Publisher: International Academy of Ecology and Environmental Sciences

1 Introduction

Sex structure plays extremely important role in population dynamics (see, for example, Maynard, 1978; Bolshakov and Kubantsev, 1984; Geodakjan, 1965, 1981, 1991; Iannelli et al., 2005; Grechanii and Pogodaeva, 1996; Batlutskaya et al., 2010, and many others). We have to take into account existence of sex structure analyzing epidemiological situations with sexually-transmit diseases, some methods of population size management are based on input of sterile individuals into the system etc. Thus, constructing and testing of mathematical models of population dynamics with sex structure are among very actual problems of modern modeling.

In 1949 Kendall (Kendall, 1949) gave a description of model of population dynamics which contains individuals of two types: $F(t)$ and $M(t)$ are the numbers of females and males respectively in population at moment t,

$$\frac{dF}{dt} = -\mu F + \frac{1}{2}B(F,M) = P(F,M),$$

$$\frac{dM}{dt} = -\mu M + \frac{1}{2}B(F,M) = Q(F,M). \tag{1}$$

In model (1) coefficient μ is an intensity of death rate, $\mu = const > 0$, and function $B(F,M)$

describes a reproduction process:

$$\forall (F,M)\in R_+^2 \quad B(F,M)\ge 0,\ B(0,M)=B(F,0)=0,$$

$$\frac{\partial B}{\partial F}>0,\ \frac{\partial B}{\partial M}>0 \text{ for } F,M>0. \qquad (2)$$

In (2) $R_+^2=\{(F,M): F\ge 0, M\ge 0\}$. Conditions (2) are rather obvious: if number of males or females is equal to zero we have no reasons to talk about production process; increase of number of males or females leads to increase of the respective rates.

Model (1)-(2) has the following properties. If $F(0)=0$ or $M(0)=0$ then for all $t>0$ we have $F(t)\equiv 0$ or $G(t)\equiv 0$ respectively. At the same time other variable decreases monotonously. It means that origin is locally stable knot. From conditions (2) we get that isocline of vertical inclines $P=0$ is univocal with respect to F; isocline of horizontal inclines $Q=0$ is univocal with respect to M. For $F(0)=F_0$, $M(0)=M_0$ we have

$$F(t)-M(t)=(F_0-M_0)e^{-\mu t}.$$

It means that within the framework of model (1)-(2) initial difference between females and males converges to zero asymptotically. If $F_0=M_0$ then for all $t>0$ we have $F(t)\equiv M(t)$. For the situation when $F_0=M_0$ and $B(F,M)=FM$, we have

$$\frac{dF}{dt}=-\mu F+\frac{1}{2}F^2.$$

This equation has two stationary states: stable point $F_1=0$ and unstable point $F_2=2\mu$. If $F_0<F_2$ then population degenerates asymptotically, $F(t)\to 0$ when $t\to\infty$. If we have the inverse inequality, $F_0>F_2$, then population size becomes equal to infinity during the finite time t^*:

$$F(t)=\frac{2\mu}{1-Ce^{\mu t}},\ C=\frac{F_0-2\mu}{F_0},\ t^*=\frac{1}{\mu}\ln\left(\frac{F_0}{F_0-2\mu}\right).$$

If we don't want to have such dynamical effect within the framework of considering model when model can be applied to the description of population dynamics during finite time interval, we can assume, for example, that birth rate $B(F,M)$ is a linear function of population size (Kendall, 1949). But it looks more productive the following way: it is obvious that birth rate cannot increase up to plus infinity if number of males increases unboundedly at fixed value of females; it means that the following relation is truthful:

$$\lim_{M\to\infty} B(F,M)=aF,\ a=const>0.$$

It means that limit value of birth rate depends on number of females and coefficient a which characterizes maximum properties of females. The following relation must be truthful too: for fixed value of number of males unlimited increasing of females gives the following result:

$$\lim_{F\to\infty} B(F,M)=cM,\ c=const>0.$$

In this relation parameter c characterizes maximum possibilities of males. In most primitive case function $B(F,M)$ can be presented in the form:

$$B(F,M)=\frac{acFM}{1+cM+aF}. \qquad (3)$$

For particular case $F_0=M_0$ model (1)-(2) with function (3) has the form:

$$\frac{dF}{dt} = -\mu F + \frac{g_1 F^2}{1 + g_2 F}. \qquad (4)$$

In (4) $g_1 = ac/2 = const > 0$, $g_2 = a + c = const > 0$. Equation (4) is particular case of Bazykin' model (Bazykin, 1967, 1969, 1985) when self-regulation is absent in population ($\mu = const > 0$).

Further development of this scientific direction was connected with analysis of various modifications of model (1)-(2) (Ginzburg and Yuzefovich, 1968; Gimelfarb et al., 1974; Nedorezov, 1979, 1986; Kiester et al., 1981; Pertsev, 2000; Preece and Mao, 2009, and others), and in particular, with analysis of general properties of models of (1)-(2) type within the framework of non-parametric model (model of Kolmogorov' type; Nedorezov, 1978). A lot of publications were devoted to very actual problem of changing of population size at input of sterile males into the system (see, for example, Bazykin, 1967; Alexeev and Ginzburg, 1969; Brezhnev and Ginzburg, 1974; Costello and Taylor, 1975; Brezhnev et al., 1975; Nedorezov, 1979, 1983, 1986; Thome et al., 2010, and many others).

It is very important to point out the following problem of models of (1)-(2) type. For every fixed values of model variables F and M we have fixed value of function B that means that we have fixed value of pregnant females. This property of model doesn't correspond to reality, and number of pregnant females can vary from zero up to $F(t)$. Respectively, for every fixed values of model variables F and M we have to have a certain variety of values of function B. This problem can be solved in one way only if we have one or more additional variables which described dynamics of pregnant females or number of existing families.

Development of theory in this direction when models contain three or more variables (for families, pregnant females, with sex-age structures etc.) was provided in a lot of publications (see, for example, Kendall, 1949; Goodman, 1953, 1967; Pollard, 1973; Yellin and Samuelson, 1974, 1977; Nedorezov, 1979, 1986; Hadeler et al. 1988; Hadeler and Ngoma, 1990; Hadeler, 1992, 1993; Pertsev, 2000; Iannelli et al., 2005, and others). One more well-developed sub-direction contains models with discrete time (Hadeler et al. 1988; Hadeler and Ngoma, 1990; Hadeler, 1992, 1993; Castillo-Chaves et al., 2002; Frisman et al., 2011; Frisman, et al., 2010 a, b).

It is possible to point out some sub-directions which are not well-developed up to current moment but their further development look rather actual. Ginzburg (1969) analyzed model of predator-prey system dynamics in a situation when individuals in interacting populations were divided into two sexes. In our publications (Nedorezov, Utyupin, 2003, 2011) continuous-discrete model (system of ordinary differential equations with impulses) of bisexual population dynamics was analyzed. These models give more adequate description for insect population dynamics in boreal zone than models with continuous or discrete time.

In current publication we analyze non-parametric (model of Kolmogorov' type) dynamic model of hermaphrodite population. This sub-direction in modeling of population dynamics with sex structure is well-developed, and it is possible to point out models of various types (see, for example, Armsworth, 2001; Stewart, and Phillips, 2002; Cheptou, 2004; Alvarez et al., 2006; Harder et al., 2007; Kebir et al., 2010, and others) because of very important role hermaphrodites play in ecological processes, epidemiological processes etc. (Charnov et al. 1976; Maynard, 1978; Civeyrel and Simberloff, 1996; Barker, 2002).

2 Description of Model

Let $N(t)$ be a number of free individuals in population at moment t, $S(t)$ be a number of pairs, and $P(t)$ be a number of pregnant individuals. For every free individual N we will assume that it can die with intensity k_1 and can organize a pair S with other free individual with coefficient k_2. For coefficient k_1 we'll assume that it depends on total population size θ, where $\theta = N + P + 2S$, and the following conditions are truthful:

$$k_1 = k_1(\theta), \ \frac{dk_1}{d\theta} \ge 0, \ \exists \theta^*: \ \forall \theta \ge \theta^* \ \ k_1(\theta) = \infty. \tag{5}$$

Kendall (1949) had been analyzed the model with three variables - $F(t)$, $M(t)$, and $S(t)$, - assuming that speed of appearance of new pairs in system is proportional to the following function:

$$g(F,M) = 2\nu \min(F,M).$$

ν is positive coefficient. Pollard (1973) had been assumed that

$$g(F,M) = \frac{1}{2}(F+M).$$

Following the idea which is on the base of Bazykin' model (1967, 1969) we'll assume that speed of organizing of new pairs is proportional to N^2 when number of free individuals is rather small, and it is proportional to N when number of free individuals is rather big. Thus, function g can be presented in the following form:

$$g(N) = \frac{aN^2}{1+bN}. \tag{6}$$

In (6) $a,b = const > 0$. Respectively, it allows us concluding that coefficient of appearance of new pairs $k_2(N) = a/(1+bN)$ is monotonic decreasing function; in general case, we'll assume that following conditions are truthful:

$$k_2 = k_2(N), \ k_2(0) > 0, \ k_2(\infty) = 0, \ \frac{dk_2}{dN} \le 0, \ \frac{dg}{dN} \ge 0, \ \frac{d}{dN}\left(\frac{g}{N}\right) \ge 0. \tag{7}$$

Dynamics of free individuals can be described by the following equation:

$$\frac{dN}{dt} = -k_1(\theta)N - 2k_2(N)N^2 + k_5(m+1)P. \tag{8}$$

In (8) coefficient k_5 corresponds to time of staying of individuals in pregnant conditions, and it is naturally to assume that $k_5 = const > 0$. Function m is productivity of pregnant individuals. We'll assume that the next conditions are truthful for this function:

$$m = m(\theta), \ m(0) > 0, \ m(\infty) = 0, \ \frac{dm}{d\theta} \le 0. \tag{9}$$

Conditions (9) are rather obvious. Increasing of total population size θ leads to changing of food conditions for individuals (in a result of increasing of intensity of intra-population competition between individuals for food), and, finally, it leads to decreasing of productivity.

Pairs S can be organized in system in a result of interaction of free individuals with coefficient k_2 (7), and can be destroyed with coefficient k_3. We'll assume that in a result of destruction of complex S two pregnant individuals P appear in population; coefficient k_3 must be positive and constant, $k_3 = const > 0$. Taking it into account, dynamics of variable S can be described by the following equation:

$$\frac{dS}{dt} = k_2(N)N^2 - k_3 S. \tag{10}$$

It is obvious that S (10) is fast variable: time of existing of complex S is much less than time of living of free individuals and staying of individuals in pregnant condition. Thus, we can assume that $dS/dt \approx 0$,

$S = k_2(N)N^2 / k_3 \approx 0$, and $k_3 >> k_2(0)(\theta^*)^2$.

Every pregnant individual P can die with coefficient k_4 (we have no reasons to assume that coefficient k_4 is equal to k_1 but similar conditions to (5) are truthful for k_4) or can transforms into $m+1$ free individuals with coefficient k_5. Dynamics of variable $P(t)$ describes with following equation:

$$\frac{dP}{dt} = 2k_3 S - k_5 P - k_4(\theta)P . \qquad (11)$$

Taking into account that conditions (5) are truthful for coefficients k_1 and k_4, we can conclude that for $N(0) \le \theta^*$ and $P(0) \le \theta^*$ we have for all $t > 0$ variables $N(t) \le \theta^*$ and $P(t) \le \theta^*$. From (7) we obtain that for $S(0) \le S^*$ we have for all $t > 0$ following inequality:

$$S(t) \le S^* = \frac{k_2(0)(\theta^*)^2}{k_3}.$$

Thus, solutions of system of differential equations (8), (10), (11) belong to stable invariant compact

$$\Delta = [0, \theta^*] \times [0, S^*] \times [0, \theta^*].$$

Thus, we can decrease the order of system of differential equations, and determine the structure of phase space of system (8), (10), (11) analyzing properties of system

$$\frac{dN}{dt} = -k_1(\theta)N - 2k_2(N)N^2 + k_5(m+1)P ,$$

$$\frac{dP}{dt} = 2k_2(N)N^2 - k_5 P - k_4(\theta)P . \qquad (12)$$

Graphically all possible transitions of individuals in population are presented on Fig. 1. Note, that such kind of interactions is observed for various species, and, in particular, for earthworm (*Lumbricina*), for snails *Helix pomatia* and for other species. Such kind of interaction is normal for simultaneous (or synchronic) hermaphrodites.

3 Some Properties of Model (12)

1. For non-negative and finite initial values of variables solutions of the system (12) are non-negative and bounded.

2. Let

$$F_1(N,P) = -k_1(\theta)N - 2k_2(N)N^2 + k_5(m+1)P = 0 ,$$

$$F_2(N,P) = 2k_2(N)N^2 - k_5 P - k_4(\theta)P = 0 \qquad .$$

(13)

From (5), (7), and (9) we obtain the following inequality:

$$\frac{\partial F_1}{\partial N} = -k_1(\theta) - N\frac{dk_1}{d\theta} - 2\frac{d}{dN}(k_2(N)N^2) + k_5 P\frac{dm}{d\theta} < 0 .$$

It means that isocline of vertical inclines of system (12) $F_1(N,P) = 0$ is a single-valued function with respect to P. For isocline of horizontal inclines we have the following inequality:

$$\frac{\partial F_2}{\partial P} = -k_5 - k_4(\theta) - P\frac{dk_4}{d\theta} < 0 .$$

Thus, isocline of horizontal inclines (13) is a single-valued function with respect to N. Conditions (5), (7), (9) for coefficients k_j, $j = 1,...,5$, don't allow determining of signs for expressions $\partial F_1 / \partial P$ and $\partial F_2 / \partial N$.

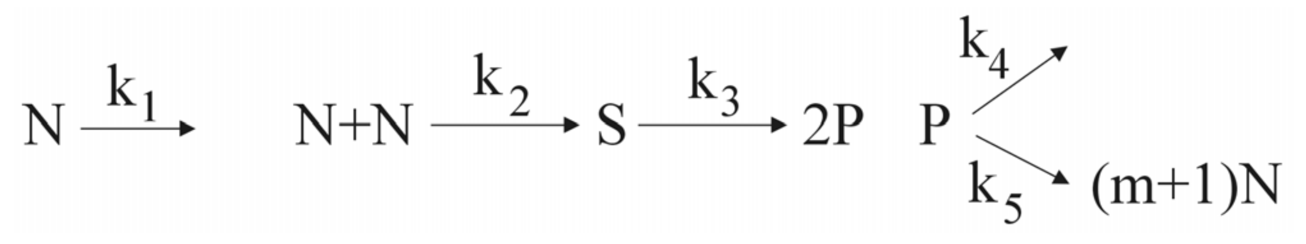

Fig. 1 All possible transformations of individuals in population. k_1 and k_4 are intensities of death rate. k_2 is coefficient of forming of pair S. k_3 is coefficient of destruction of pair S. k_5 is a coefficient of staying of individual in pregnant state. m is number of new free individuals which are produced by one pregnant individual.

3. Previous properties of model (12) give us the following inequality:

$$\frac{\partial F_1}{\partial N} + \frac{\partial F_2}{\partial P} < 0 .$$

Thus, there are no limit cycles in phase space (Bendixon' criteria; Andronov, Vitt, Khykin, 1959). Consequently, within the framework of model (12) there are the regimes of asymptotic stabilization of population size at any level only.

4. Origin $(0,0)$ is stationary state of system (12). This system in sufficient small vicinity of origin can be prersent6ed in following form:

$$\frac{dN}{dt} = -k_1(0)N + k_5(m(0)+1)P ,$$

$$\frac{dP}{dt} = -k_5 P - k_4(0)P .$$

Thus, characteristic values are negative: $\lambda_1 = -k_1(0)$ and $\lambda_2 = -k_5 - k_4(0)$. Consequently, in all situations origin is stable knot.

5. In a situation when we have a parametric model (model of Volterra type) we have the following main goal: we have to present a structure of a space of model parameters and to point out dynamical regimes which correspond to each determined part of space of parameters. When we have a non-parametric model (model of Kolmogorov type like in current publication) we have other main goal: in a result of provided analysis we have to present dynamical regimes which can be realized in model in principle, and their realization not in a contradiction with considering restrictions on the types of functions in right-hand sides of equations. Below we'll consider some simplest dynamic regimes of model (12) – restrictions (8)-(11) and (14) don't allow presenting all possible dynamic regimes which can be observed within the framework of model.

If algebraic system (13) has no solutions in positive part of phase plane, origin is global stable equilibrium. Population eliminates for all non-negative finite initial values (Fig. 2).

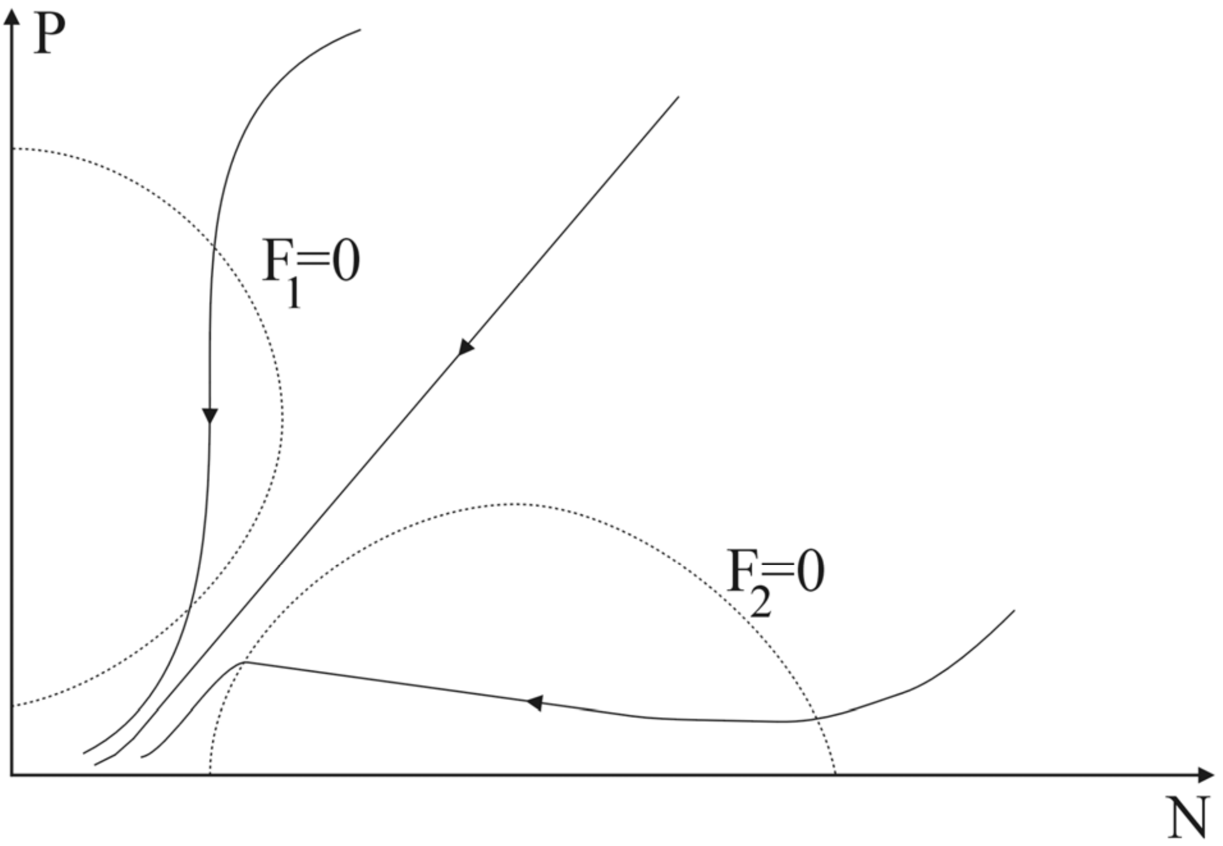

Fig. 2 Regime of population elimination for all initial values of variables. $F_1 = 0$ and $F_2 = 0$ are the main isoclines of vertical and horizontal inclines of model trajectories respectively.

If algebraic system (13) has two solutions in positive part of phase plane the trigger regime is realized for population: there are two stable attractors on phase plane (Fig. 3). Incoming separatrix y of saddle point W divides zones of attraction of origin and stable equilibrium V. If initial sizes of variables are rather small (within the limits of zone of elimination Ω_1; Fig. 3) population eliminates asymptotically. If initial values belong to another zone (zone of stabilization Ω_2) sizes of both variables stabilize asymptotically at unique level.

In general case within the limits of model (12) dynamic regimes with several stationary states in positive part of phase plane can be realized (see, for example, Fig. 4). When difference between total numbers of sizes which correspond to various stable stationary states are rather big, it can be considered as direct analog of the regime of fixed outbreak (Isaev et al., 1978, 1980; Isaev et al., 1984, 2001). Thus, we can conclude that big difference between pregnant individuals and free individuals can be a reason for population elimination or a reason for transmission of system from one stable level to another one (see Fig. 4). Such kind of changing of population size can be interpreted as unstable behavior of population within the limits of zone of population stability (Isaev et al., 1978, 1980; Isaev et al., 1984, 2001).

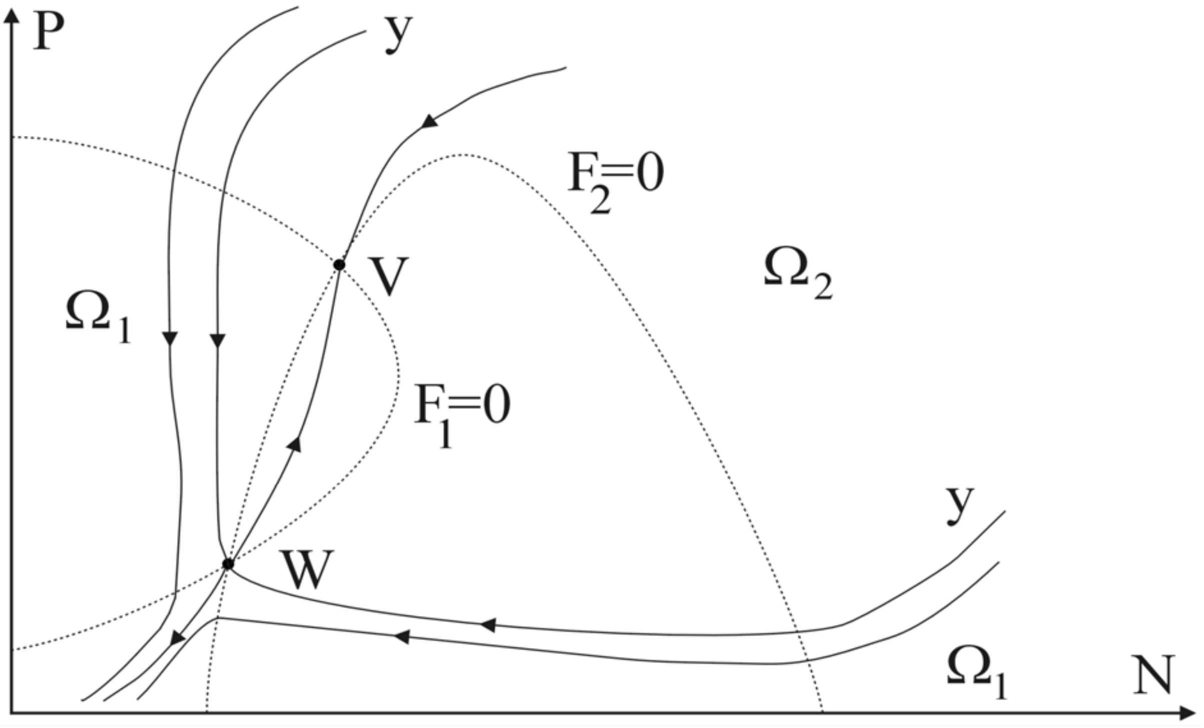

Fig. 3. Trigger regime of population dynamics. V is stable stationary state. W is saddle point. y is incoming separatrix of saddle point W. Ω_1 is zone of population elimination; Ω_2 is zone of population stabilization. $F_1 = 0$ and $F_2 = 0$ are the main isoclines of vertical and horizontal inclines of model trajectories respectively.

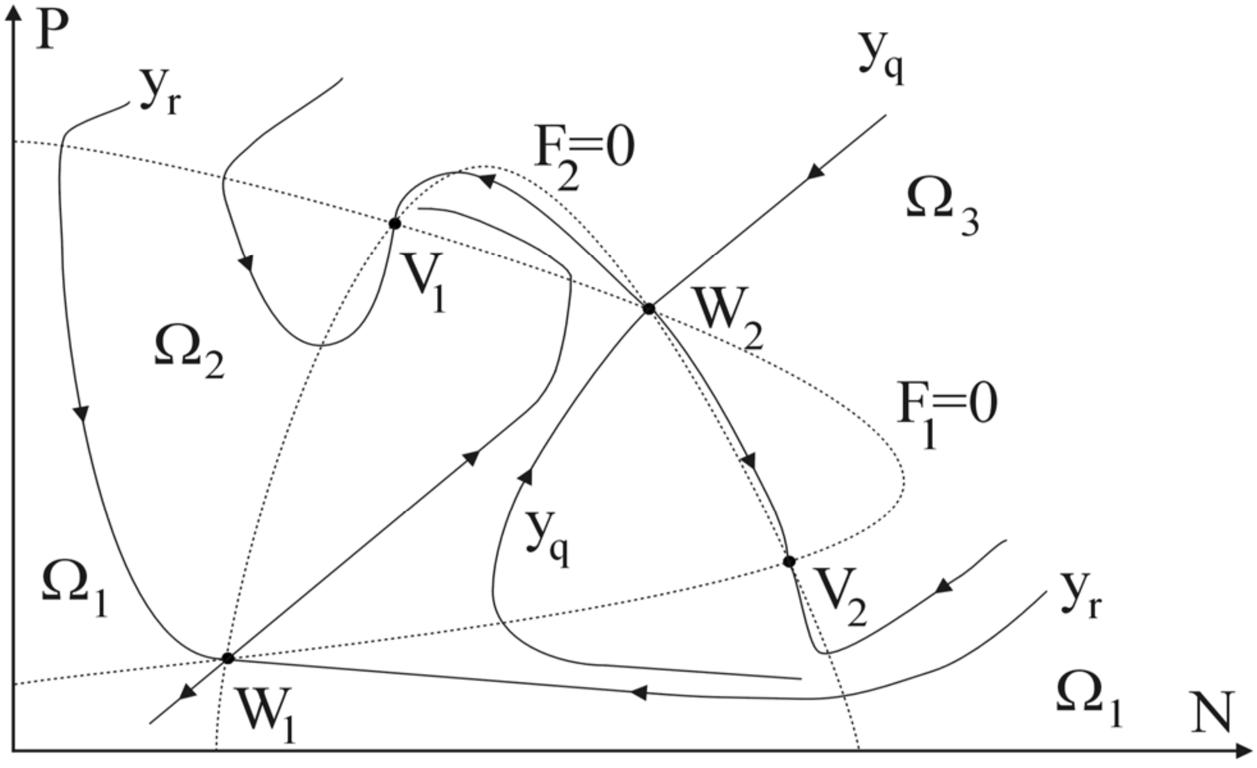

Fig. 4. Dynamical regime with three stable attractors: origin, V_1, and V_2. y_r is incoming separatrix of saddle point W_1, boundary of attraction zone of origin. y_q is incoming separatrix of saddle point W_2, boundary of attraction zones of V_1, and V_2. Ω_1 is zone of population elimination (attraction zone of origin); Ω_2 is zone of population stabilization at point V_1; Ω_3 is zone of population stabilization at point V_2. $F_1 = 0$ and $F_2 = 0$ are the main isoclines of vertical and horizontal inclines of model trajectories respectively.

4 Conclusion

Analysis of model of hermaphrodite population dynamics shows that in general case dynamic regimes with several non-trivial stationary states can be observed for the system. It means that changing of sizes of free and pregnant individuals (for example, under the influence of various management methods) can lead as to transaction of system from one stable level to another one, as to extinction of population. Existence of several stable levels in positive part of phase plane can be a reason of unstable behavior of system in zone of population stability (Isaev et al., 1978, 1980).

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