

Department
of
APPLIED MATHEMATICS

A description of daphnicle dynamics based on kinetic theory:
Attempts at analogue-modelling of swarming and behaviour of
Daphnia

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Alf H. Øien

Report no. 156

June 2001



UNIVERSITY OF BERGEN
Bergen, Norway

Department of Mathematics
University of Bergen
5008 Bergen
Norway

ISSN 0084-778X

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NB Rana
Depotbiblioteket

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Abstract:

Attempts are presented of an analogue modelling of *Daphnia* responses to various influences and stimuli, as distribution of food and of predators. The aim with the study is to examine to what extent a statistical-mechanical approach of swarms may be useful as a tool in modelling of *Daphnia* behaviour. In the modelling we follow a line close to test particle studies in physical sciences. A generalised kinetic equation of what we shall call *daphnicles* is derived. The modelling incorporates individual characteristics of daphnicles, as position, velocity and degree of food saturation and responses daphnicles have to say food- concentration and to threat. The daphnicles we model respond to some stimuli in ordered ways and to others in stochastic ways, and the degree or strength of reactions generally depends on the density and distribution of food available, the saturation level of daphnicles and the threat level in the environment, or background, the daphnicles are living on. Some fluid equations of daphnicle swarms are subsequently derived from the basic equation, and solutions are given of the model-equations in some particular cases and show peculiarities in reactions of daphnicles to food and to threat, when these are acting alone, and in combination. The results may have some relevance to certain laboratory experiments of *Daphnia* behaviour.

1 Introduction

The behaviour of *Daphnia pulex*, a zooplankton (size approximately 1-2 mm) has been extensively studied in recent year both under laboratory conditions and in the field. These studies have been focused on the response of individuals, as well as groups, to various external influences, as available food, food gradients and predator threat [1]-[4]. These studies among others have revealed and shown in particular mechanisms connected to swarming of groups of *Daphnia*. The density of *Daphnia* groups observed may to some extent seem to reflect the density of food available, but in such a way that individuals may take in food most efficiently. Thus individuals may seem to avoid high-density *Daphnia*/high density food locations to move to lower density locations for more effective food intake. Various working hypotheses of these mechanisms, that also question the ability of *Daphnia* to respond "reasonably", have been tested. Also the swarming due to predator threat, where a safety in number mechanism seems to play a role, has been investigated in laboratory and field experiments.

The author of the present work was inspired by these studies to use kinetic theory for making analogue modelling of what may resemble *Daphnia* dynamics and evolution, in particular swarming, related to food and to threat from predators. In the analogue modelling we shall replace "*Daphnia*" by what we shall call "daphnicles", to reflect the (physical) "particle" reasoning that the modelling uses. The author wants in this way to express the difference between the "real world" and the theory in the "model world" that is developed. At best the model may mimic trends in behaviour that really takes place, and hopefully give some new insight and ideas. In particular the daphnicles do not have the locomotion ability that *Daphnia* have, but move due to influences and "forces" they "feel". This movement in the modelling shall have both an ordered, or directed, component, and a stochastic component, and is meant to mimic among others the swarming of *Daphnia*, which seem to show both erratic behaviour and more directed behaviour, depending on for instance distribution of food patches or densities. Thus we shall incorporate several "forces", as attraction along food density gradients, and also a repulsion of individuals from daphnicle-accumulation regions to mimic the property the *Daphnia* seem to have to go for new food search other places where intake after all may be more efficient. However, in the modelling the repulsion may be turned off when high enough threat surrounds the daphnicles, say by "smell" of predators in natural environments. Gradients in light intensity and in threat are also incorporated as forces. The daphnicles are also embedded with a "food-saturation" property, and a food-saturation-decline force is incorporated, a force that is steadily on and leads for instance to particular behaviour when no food is available. The ordered behaviour of daphnicles will be coupled to stochastic behaviour, which in the present modelling is limited to a combination of

"microscopic" friction and erratic motion, or "temperature", and to stochastic intake of food. The degree of saturation of individuals in general varies, and we consider in particular that the strengths of the forces are dependent on this.

We start the description from a kinetic-theory point of view,[5], and a dynamical equation for a probability distribution function dependent on daphnicle position and velocity, as well as the degree of saturation, and time, is set up. The modelling is close to "test particle"- modelling in kinetic theory,[6], including an internal state variable, i.e. food saturation, where each particle responds to background influences. From this rather general point of view, equations that are more related to experiments in the laboratory and the field are successively derived, and some solved.

The paper is outlined as follows. Section 2 starts with the various forces giving rise to the ordered part of daphnicle motion. The one-daphnicle equations of ordered motion are set up. These equations are necessary when deriving the equation of ordered motion of the probability function. It is shown that in a 7 dimensional phase space, spanned by position, velocity and saturation of a single daphnicle, the probability function is conserved following the extended motion in this space. Then the erratic behaviour in movement and the stochastic intake of food are added as corrections to the equation of ordered motion. The resulting equation is our basic equation. In addition a dynamical equation for food density is necessary, and is set up. This equation is coupled to the basic equation. Ideally, we would prefer to solve these equations to obtain the best information and results of the model. However, this may not be possible at all, and from a practical point of view maybe not necessary. Therefore we look for approximations that may be sufficient for many purposes. Generally these approximations will contain some information from the detailed description. Thus in section 3 more coarse-grained equations are derived from the basic equation. These are obtained taking various moments of the basic equation, both velocity moments, [5], and saturation moments, and the two types of moments in combination. These equations include both an ordinary kinetic equation and a kinetic equation for food intake. However, these moment equations even in the simplest cases are coupled and therefore difficult to solve, and truncations are necessary for solutions to be found. Some examples of this are given. In section 4 fluid equations are derived from the truncated equations. An assumption of weak gradients is necessary to reduce the number of equations to 3, i.e., one equation for daphnicle density, one for mean saturation of daphnicles and one for the density of food. These are coupled, and generally non-linear. In section 5 some special states and solutions are studied. In particular the basic (kinetic) equation is solved when daphnicles are uniformly distributed and there is no food available, i.e. daphnicles are in a state of hunger. The solution shows how the distribution function of daphnicles depends on movement, saturation and threat as time goes on. Also a set of linearized equations for daphnicle- and food- densities is developed. These equations are valid around a static and

uniform state characterised by a steady input of food and a balance between food saturation and saturation decline. The equations are specialised for one space direction: In spite of being rather simple they may nevertheless have some relevance to a laboratory set up of Daphnia experiments,[1], namely Daphnia enclosed in a cylindrical shell region. In this case the region may be modelled as one-dimensional and periodic in space. These equations are solved for a number of cases in section 6 where the interplay between daphnic and food density perturbations are found when perturbed initial states, food input and threat gradients, both static and moving, are varied, and we consider reactions to various levels of uniform threat (stress) the daphnics may feel from the surroundings. The solutions show that higher densities of food attract daphnics and distribute them among humps of food in some sort of balance. When daphnics are stressed by higher uniform threat they accumulate more strongly. Daphnics also fly away from threat gradients and even more so when more stressed. Section 7 gives a short summary and conclusion. The paper ends with a figure section of 18 figures.

Modelling like this may serve as tools and give ideas of new laboratory experiments to be done.

2 Basic equation of daphnic evolution

By "daphnics" we shall mean small physical bodies, ideally particles, embedded with certain internal properties and being able to respond to external influences. The main internal property taken up here is their degree of fullfedness, or food saturation, connected to food intake, or, to lack of food intake. We shall denote this property by the variable ' m ' and measure it on a scale from $-\infty$ to $+\infty$, say. Positive m shall represent more and more fullfedness, while negative m represents more and more "hunger". $m=0$ may represent a degree of saturation the daphnics may 'feel well' in, but still too low for not going for more food. m may be compared to an internal state variable, say for atoms or molecules. The motion of daphnics shall be given as for physical particles by position and velocity, neglecting then for instance rotation, i.e. 6 variables in 3 dimensional space, denoted by \mathbf{r} (position) and \mathbf{v} (velocity). As for particles these variables describe the external state. Thus we shall consider the state of daphnics at time t to be given by 7 variables, $(\mathbf{r}, \mathbf{v}, m)$. The daphnics are responding to external influences. These influences are due to other daphnics, available food, light intensity and threat and threat gradients from predators. Threat feeling might be included among state variables, but will not be done so here, so all daphnics will feel the same threat in the following. We shall refer to influences due to food, light and predators as background influences analogous to influences on ordinary particles evolving on physical backgrounds. Thus our description to a large extent will follow a test-particle approach, often used in physical research, [6].

A probability distribution function of the 7 variables, $(\mathbf{r}, \mathbf{v}, m)$, of the extended phase space, plus time, $F(\mathbf{r}, \mathbf{v}, m, t)$, will be used to express the state of the daphnicles. If $d\mathbf{r}d\mathbf{v}dm$ denotes an infinitesimal volume element of the 7 dimensional space, then

$$F(\mathbf{r}, \mathbf{v}, m, t)d\mathbf{r}d\mathbf{v}dm \quad (1)$$

denotes the probable number of daphnicles in the volume element $d\mathbf{r}d\mathbf{v}dm$ at time t . The evolution of F will be determined by the influences. We shall distinguish between two types of influences of the dynamics of the daphnicles: Ordered ones and stochastic ones. In general the dynamics is a combination of the two. The ordered ones will be modelled by the following equations of motion, and will give rise to what we may refer to as ordered motion in the extended phase space:

$$\begin{aligned} \frac{d\mathbf{r}}{dt} &= \mathbf{v} \\ \frac{d\mathbf{v}}{dt} &= E(m, p, N) \frac{\partial n}{\partial \mathbf{r}} - K(m, p) \frac{\partial N}{\partial \mathbf{r}} + L(m) \frac{\partial l}{\partial \mathbf{r}} - V(m, p) \frac{\partial p}{\partial \mathbf{r}} \\ \frac{dm}{dt} &= -a \end{aligned} \quad (2)$$

The first equation gives the connection between position and velocity of a daphnicle. The second is an equation of motion, and on the right hand side are "forces". In the first term $n(\mathbf{r}, t)$ is the density of food available, and the term represents a force the daphnicle feels towards higher food density. $E(m, p, N)$ is a positive coefficient that may depend on m , the degree of fullfedness, the probable density N of daphnicles (that may be in whatever degree of saturation and have any velocity at position \mathbf{r} and time t),

$$N(\mathbf{r}, t) = \int F(\mathbf{r}, \mathbf{v}, m, t)d\mathbf{v}dm \quad , \quad (3)$$

and the level of a threat field $p(\mathbf{r}, t)$. The coefficient will be further specified below. The second term represents a force a daphnicle will feel away from high-density regions of other daphnicles, when the coefficient K is positive, which will be assumed in the following. However, we shall consider the coefficient to depend on the strength of the threat field so that the repulsion will die away when the threat is high enough, and we discuss this further below, together with the m -dependency. The third term represent a force the daphnicles will feel toward places of higher light intensity $l(\mathbf{r}, t)$, also depending on the degree of saturation through the positive coefficient $L(m)$. We note that many coefficients will also have some dependence on light intensity l , but we have suppressed this here since behaviour due to light is not taken up particularly in this report. The fourth term represents repulsion away from predators, being proportional to the gradient of the threat field. However, hungry daphnicles (negative m) may neglect the threat more than well-fed daphnicles, and the coefficient $V(m, p)$ shall reflect this dependency together with the property to increase when the threat level p increases. The third equation is a hunger equation: a is a positive constant, and the equation expresses that at any time there is a "drag" towards saturation decrease.

In addition to these ordered influences, the daphnicle state changes due to food intake when food is available. This intake will be modelled as a stochastic process. Also erratic motion of the daphnicles, different from ordered motion due to the forces discussed above, will be incorporated. However, we first discuss the coefficients $E(m,p,N)$, $K(m,p)$, $L(m)$ and $V(m,p)$.

2.1 Form of force-coefficients for ordered motion

The forms of the coefficients that follow have some backing from what is observed of *Daphnia* behaviour. Simple forms have been used for convenience and because even such forms may express trends in the evolution. However, changes and other assumption can be used instead or added, for instance, as mentioned above, that coefficients may depend on light intensity.

We shall let $E(m,p,N)$ be decreasing with higher m because higher m may in less degree direct daphnicles toward higher food concentrations. A simple form that may take care of this effect, and also threat and density effects, is

$$E(m, p, N) = E_0 e^{\alpha_0 p} (N_m - N)(m_0 - m) \quad (4)$$

Here E_0 is a positive coefficient and m_0 is another positive constant. m_0 represents a high degree of saturation that is very improbable to reach because of other influences. The exponential contains the threat field $p(\mathbf{r}, t)$ which may take values on a scale from 0 (no threat) to large values, say, and a positive constant α_0 . Hence we consider the movement of daphnicles towards higher food density regions to increase when threat is increasing. However, there is a limit for the accumulation of daphnicles, and a factor $(N_m - N)$, where N_m is an upper limit of density, may take care of such an effect. $E(m,p,N)$ turns negative only in exceptional cases.

$K(m,p)$, positive, shall be decreasing with increasing m to reflect a tendency of daphnicles to repulse each other less when they become more saturated. Hence we might set when no predator threat is present,

$$K(m) = K_0 e^{-\alpha m} \quad (5)$$

where K_0 and α are positive constants. When there is predator threat field $p(\mathbf{r}, t)$ (which takes values on a scale from 0 and upward), we may for instance set

$$K(m, p) = K_0 e^{-\alpha_2 p} e^{-\alpha_1 m} \quad (6)$$

where α_1 and α_2 are positive constants. Hence a threat will always have the effect of diminishing the repulsive effect of other daphnicles, and being high enough, will turn off the effect.

$L(m)$ may be modelled as

$$L(m) = L_0 e^{-\gamma m} \quad (7)$$

where γ and L_0 are positive constants to reflect a tendency to respond less to a light intensity gradient by increasing degree of saturation.

For $V(m, p)$ we take into account both an effect of hungry daphnicles to be more careless with respect to a threat gradient from predators than saturated ones, and also an effect of awareness and consequent response to a threat gradient when the threat level increases, using for instance

$$V(m, p) = V_0 e^{\tau_1 m + \tau_2 p} \quad (8)$$

where V_0, τ_1 and τ_2 are positive constants.

2.2 Dynamical equation of ordered evolution of F

When Eq.(2) determines the ordered dynamics of individual daphnicles on the influencing background, a Liouville theorem [6] is valid, such that the swarm of daphnicles behaves as an incompressible fluid in the 7 dimensional phase space. Two observations will lead to this conclusion:

1) Consider an infinitesimal volume element in the 7 dimensional phase space at time t , denoted by $dV = d\mathbf{r}d\mathbf{v}dm$. At time $t + \Delta t$ this volume element, following the motion of points according to the system of equations (2), transforms into $dV' = d\mathbf{r}' d\mathbf{v}' dm'$. The evolution of phase space points from time t to time $t + \Delta t$ may be considered as a co-ordinate transformation, and we have the relation

$$dV' = \left| \frac{\partial(\mathbf{r}', \mathbf{v}', m')}{\partial(\mathbf{r}, \mathbf{v}, m)} \right| dV, \text{ where the l.l term denotes the Jacobian of the transformation.}$$

Using the equations of motion ,Eq.(2), one derives that $\left| \frac{\partial(\mathbf{r}', \mathbf{v}', m')}{\partial(\mathbf{r}, \mathbf{v}, m)} \right| = 1 + O((\Delta t)^2)$,

where O is the order symbol.

2) The set of equations (2) has unique solutions. Hence the number of states within the volume element at time t and within the transformed volume element at time $t + \Delta t$, is the same. Therefore $F(\mathbf{r}', \mathbf{v}', m', t + \Delta t)dV' = F(\mathbf{r}, \mathbf{v}, m, t)dV$.

Using the results 1) above one obtains, letting $\Delta t \rightarrow 0$, that

$$\frac{dF}{dt} = 0 \quad (9)$$

i.e. the total time derivative following the motion of daphnicles is zero, and the daphnicles behaves as an incompressible fluid in the 7 dimensional phase space.

Written out in more detail, using the set of equations (2), one has for the ordered dynamics,

$$\frac{\partial F}{\partial t} + \mathbf{v} \cdot \frac{\partial F}{\partial \mathbf{r}} + \left(E(m, p, N) \frac{\partial n}{\partial \mathbf{r}} - K(m, p) \frac{\partial N}{\partial \mathbf{r}} + L(m) \frac{\partial l}{\partial \mathbf{r}} - V(m, p) \frac{\partial p}{\partial \mathbf{r}} \right) \cdot \frac{\partial F}{\partial \mathbf{v}} - a \frac{\partial F}{\partial m} = 0 \quad (10)$$

We make a remark concerning the $\partial N / \partial \mathbf{r}$ -force term: The term may be considered from a general point of view, namely as a non-correlated interaction term between

daphnicles, in contrast to correlated interaction terms, described later. It may be derived from the form

$$\frac{1}{M} \frac{\partial}{\partial \mathbf{v}_1} \cdot \int \mathbf{K}(|\mathbf{r}_1 - \mathbf{r}_2|) F(2,t) F(1,t) d\mathbf{r}_2 d\mathbf{v}_2 dm_2 = \frac{1}{M} \frac{\partial F(1,t)}{\partial \mathbf{v}_1} \cdot \int \mathbf{K}(|\mathbf{r}_1 - \mathbf{r}_2|) F(2,t) d\mathbf{r}_2 d\mathbf{v}_2 dm_2 \quad (11)$$

i.e. from a generalised "Vlasov term", see [6] for Vlasov's equation. M is the daphnicle mass, $\mathbf{K} = (\mathbf{r}_1 - \mathbf{r}_2) K(|\mathbf{r}_1 - \mathbf{r}_2|)$ represents an interaction force between daphnicle no.1 and daphnicle no 2, assumed directed along their relative position. Because of the product between the distribution functions, the term is named the uncorrelated part of interaction. When the integration is performed over the 7 dimensional phase space of daphnicle no. 2, the integral gives a force on daphnicle no. 1 due to all other daphnicles. For the special case of weak gradients we may approximate

$$F(2,t) \equiv F(\mathbf{r}_2, \mathbf{v}_2, m_2, t) \approx F(\mathbf{r}_1, \mathbf{v}_2, m_2, t) + (\mathbf{r}_2 - \mathbf{r}_1) \cdot \frac{\partial F(\mathbf{r}_1, \mathbf{v}_2, m_2, t)}{\partial \mathbf{r}_1} \quad (12)$$

and hence may write

$$\begin{aligned} & \int \mathbf{K}(|\mathbf{r}_1 - \mathbf{r}_2|) F(2,t) d\mathbf{r}_2 d\mathbf{v}_2 dm_2 \\ &= \int (\mathbf{r}_1 - \mathbf{r}_2) K(|\mathbf{r}_1 - \mathbf{r}_2|) \left(F(\mathbf{r}_1, \mathbf{v}_2, m_2, t) + (\mathbf{r}_2 - \mathbf{r}_1) \cdot \frac{\partial F(\mathbf{r}_1, \mathbf{v}_2, m_2, t)}{\partial \mathbf{r}_1} \right) d\mathbf{r}_2 d\mathbf{v}_2 dm_2 \\ &= \int K(|\mathbf{r}_1 - \mathbf{r}_2|) (\mathbf{r}_1 - \mathbf{r}_2) (\mathbf{r}_1 - \mathbf{r}_2) \cdot \frac{\partial F(\mathbf{r}_1, \mathbf{v}_2, m_2, t)}{\partial \mathbf{r}_1} d\mathbf{r}_2 d\mathbf{v}_2 dm_2 = K_0 \mathbf{I} \cdot \frac{\partial N(\mathbf{r}_1, t)}{\partial \mathbf{r}_1} \quad (13) \end{aligned}$$

On the far right here \mathbf{I} is an identity tensor. Using this result we have

$$\frac{1}{M} \frac{\partial}{\partial \mathbf{v}_1} \cdot \int \mathbf{K}(|\mathbf{r}_1 - \mathbf{r}_2|) F(2,t) F(1,t) d\mathbf{r}_2 d\mathbf{v}_2 dm_2 = K_0 \frac{\partial F(1,t)}{\partial \mathbf{v}_1} \cdot \frac{\partial N(\mathbf{r}_1, t)}{\partial \mathbf{r}_1} \quad (14)$$

which is the form in Eq.(10). However, when the assumption of weak gradients is not met one should consider using Eq.(11) instead.

2.3 Food intake and erratic motion

Both food intake and erratic motion will be modelled as stochastic processes.

Generally, the origin of stochasticity is connected to correlated parts of interactions.

Two terms representing these effects in sum will replace the zero on the right hand

side of Eq.(10). We shall assume that food intake, if allowed to go on alone,

eventually forces the distribution function towards a narrow normal distribution form

in the degree of saturation around the value $m=m_0$, and likewise, motion will turn

erratic if no influences are present, and force the distribution in velocity toward a

Maxwellian distribution. The form of the terms shall be the following:

2.3.1 Food intake:

Intake of food is related to daphnicle-food-density interaction, and a stochastic

modelling may be adequate. Therefore we assume a simple Fokker-Planck- term of

the form

$$\left(\frac{\partial F}{\partial t}\right)_{\text{food}} = \beta \frac{\partial}{\partial m} \left((m - m_0)F + \frac{q}{\beta} \frac{\partial F}{\partial m} \right) \quad (15)$$

Here β is a "collision frequency for food intake" between daphnicles and the background-food, and we model it simply as

$$\beta = \beta_0 n \quad (16)$$

where β_0 is a constant and n is the food density. The first term on the right hand side of Eq.(15) therefore represents a "drag" of daphnicle saturation towards m_0 as they take in food. The second term, the q/β -term, balances this drag and gives rise to saturation spread when food is taken in. The coefficient may be modelled as

$$q / \beta = k_0 e^{-h_0(t)n} \quad (17)$$

where k_0 is a positive constant and $h_0(t)$, also positive, may increase steadily in time. This will result in a saturation spread that is smaller for high food concentrations than for low, but eventually the spread will go to zero. For the case that h_0 is constant we observe that the food intake term will vanish when

$$(m - m_0)F + \frac{q}{\beta} \frac{\partial F}{\partial m} = 0$$

i.e. for

$$F = F_1(\mathbf{r}, \mathbf{v}) e^{-\frac{\beta(m-m_0)^2}{2q}} \quad (18)$$

when also the food concentration n is constant, both in space and time.

2.3.2 Erratic motion

A corresponding term as the one above may be used for the erratic motion of the daphnicles, even though a simple relaxation term would do for many purposes.

Corresponding to Eq.(15) we shall have

$$\left(\frac{\partial F}{\partial t}\right)_{\text{erratic}} = B \frac{\partial}{\partial \mathbf{v}} \cdot \left(\mathbf{v}F + \frac{Q}{B} \frac{\partial F}{\partial \mathbf{v}} \right) \quad (19)$$

B is a collision frequency reflecting a 'friction' between the daphnicles and the background, and we may assume it has a form

$$B = B_0 e^{\sigma n} \quad (20)$$

where B_0 and σ are positive constants. Hence we allow the friction to increase with increasing food density. We may assume the "temperature"-coefficient Q has a form

$$Q = Q_0 e^{-\rho_1 m - \rho_2 P} \quad (21)$$

where Q_0 , ρ_1 , and ρ_2 are positive constants such that the spread in velocity due to erratic motion will increase with hunger, i.e. with negative values of m , and decrease with increasing threat. However, a steady strong rise in Q and hence in velocity spread for daphnicles with lower and lower m is not to be expected due to weakening, so a decrease of Q for low m -values is probable. Hence a form like

$$Q = Q_0 \frac{\cosh \rho_1 m_1}{\cosh \rho_1 (m - m_1)} e^{-\rho_2 P} \quad (22)$$

where m_1 is some negative critical value of saturation where weakening sets in, may be used instead. However, for m -values around 0 the form Eq.(21) of Q will be used. We note that the erratic motion term will vanish when

$$\mathbf{v}F + \frac{Q}{B} \frac{\partial F}{\partial \mathbf{v}} = 0$$

i.e. when

$$F = F_2(\mathbf{r}, m) e^{-\frac{Bv^2}{2Q}} \quad (23)$$

for the case that food density (in B) is constant and threat p is constant (in Q).

However, the spread in velocity will vary with m and the constant levels of n and p .

2.4 Equation for distribution function including both ordered and stochastic evolutions, and equation for food density

Collecting results from the two foregoing paragraphs we have

$$\begin{aligned} \frac{\partial F}{\partial t} + \mathbf{v} \cdot \frac{\partial F}{\partial \mathbf{r}} + \left(E(m, p, N) \frac{\partial n}{\partial \mathbf{r}} - K(m, p) \frac{\partial N}{\partial \mathbf{r}} + L(m) \frac{\partial l}{\partial \mathbf{r}} - V(m, p) \frac{\partial p}{\partial \mathbf{r}} \right) \cdot \frac{\partial F}{\partial \mathbf{v}} - a \frac{\partial F}{\partial m} \\ = \beta \frac{\partial}{\partial m} \left((m - m_0) F + \frac{q}{\beta} \frac{\partial F}{\partial m} \right) + B \frac{\partial}{\partial \mathbf{v}} \cdot \left(\mathbf{v} F + \frac{Q}{B} \frac{\partial F}{\partial \mathbf{v}} \right) \end{aligned} \quad (24)$$

which takes into account both the ordered dynamics and the stochastic dynamics. The inclusion of stochastic terms in the equation has the general effect that the phase space density of daphnicles does not behave as an incompressible fluid any longer.

Coefficients have been discussed above. One may assume that the light intensity function $l(\mathbf{r}, t)$ is known. To simplify we shall also assume that $p(\mathbf{r}, t)$ is known.

However, the food density n in general has to be determined simultaneously as the above equation is solved. The equation for $n(\mathbf{r}, t)$ will be taken to be of the form

$$\frac{\partial n}{\partial t} + \mathbf{u}_0 \cdot \frac{\partial n}{\partial \mathbf{r}} = D \frac{\partial^2 n}{\partial \mathbf{r}^2} - n \int \lambda(m) F d\mathbf{m} d\mathbf{v} + S(\mathbf{r}, t) \quad (25)$$

where \mathbf{u}_0 is a drift of food in water, D is a diffusion coefficient, which may be assumed constant, $\lambda(m)$ is a consummation rate that depends upon the degree of saturation of daphnicles, and S is a source rate of food input. We shall assume the consummation rate increases with decreasing m , say as

$$\lambda(m) = \lambda_0 e^{-\varepsilon m} \quad (26)$$

where λ_0 and ε are constants, or more simply as,

$$\lambda(m) = -\varepsilon(m - m_0)$$

for $m < m_0$, which are the most probable values of m . Note that the consummation term is proportional to the product of the two densities. We also note that some link exists between this consummation term and the food intake term, Eq.(15), however, we shall not here elaborate any further on this connection in detail.

Eqs. (24) and (25) are a coupled set of equations for F and n and represent a rather detailed model description of daphnicles. We may refer to this description, in

particular Eq.(24), as a high level, or detailed, description. It is clear that some information resulting from this description may be difficult to observe directly in practise. One may therefore ask if a more coarse-grained description from the start could be adequate enough for practical purposes. However, derivations of more coarse grained or lower order level descriptions from the detailed description will contain some important high level effects. Such effects may be difficult to incorporate otherwise. In the next section we derive some lower level descriptions from the high level description developed till now.

3 Separate kinetic equations for saturation and velocity dependent densities. Warm and cold models

3.1 Equation of evolution for saturation dependent density

From Eq.(24) we here derive some lower level equations. These equations will arise when moments of velocity and saturation are taken. These new equations will be coupled, generally in infinite chains, and a central problem concerns how to truncate these chains to a few equations that may be solved.

The first of these low-level equations we discuss turn out when we integrate equation over velocity. We then have,

$$\frac{\partial f}{\partial t} + \frac{\partial}{\partial \mathbf{r}} \cdot (f\mathbf{U}(\mathbf{r}, m, t)) - a \frac{\partial f}{\partial m} = \beta \frac{\partial}{\partial m} \left((m - m_0)f + \frac{q}{\beta} \frac{\partial f}{\partial m} \right) \quad (27)$$

where

$$f = f(\mathbf{r}, m, t) = \int F(\mathbf{r}, \mathbf{v}, m, t) d\mathbf{v} \quad (28)$$

is the saturation dependent density and

$$f\mathbf{U}(\mathbf{r}, m, t) = \int F(\mathbf{r}, \mathbf{v}, m, t) \mathbf{v} d\mathbf{v} \quad (29)$$

gives the saturation dependent mean flow \mathbf{U} of daphnicles. The equation hence is coupled to an equation for \mathbf{U} . We derive an equation for \mathbf{U} multiplying Eq.(24) by \mathbf{v} and integrate over \mathbf{v} . Then the equation,

$$\begin{aligned} \frac{\partial (f\mathbf{U}(\mathbf{r}, m, t))}{\partial t} + \frac{\partial}{\partial \mathbf{r}} \cdot \langle F\mathbf{v}\mathbf{v} \rangle_{\mathbf{v}} - f \left(E(m, p, N) \frac{\partial n}{\partial \mathbf{r}} - K(m, p) \frac{\partial N}{\partial \mathbf{r}} + L(m) \frac{\partial l}{\partial \mathbf{r}} - V(m, p) \frac{\partial p}{\partial \mathbf{r}} \right) \\ - a \frac{\partial}{\partial m} (f\mathbf{U}(\mathbf{r}, m, t)) = \beta \frac{\partial}{\partial m} \left((m - m_0)f\mathbf{U}(\mathbf{r}, m, t) + \frac{q}{\beta} \frac{\partial (f\mathbf{U}(\mathbf{r}, m, t))}{\partial m} \right) - Bf\mathbf{U}(\mathbf{r}, m, t) \end{aligned} \quad (30)$$

turns out, where we have set

$$\langle F\mathbf{v}\mathbf{v} \rangle_v = \int \mathbf{v}\mathbf{v}F d\mathbf{v} \quad (31)$$

Thus the equation for fU introduces both a new unknown function $\langle F\mathbf{v}\mathbf{v} \rangle_v$ in addition to the ordinary density N which already appeared in Eq.(24). $\langle F\mathbf{v}\mathbf{v} \rangle_v$ expresses 'excitement', or the degree of erratic motion, of the daphnicles and is comparable to thermal motions of ordinary particles. $\langle F\mathbf{v}\mathbf{v} \rangle_v$ may be found taking the next higher velocity moment of Eq.(24). Instead of setting up such an equation for $\langle F\mathbf{v}\mathbf{v} \rangle_v$, which will contain even higher order velocity moments, we derive below an approximate expression for $\langle F\mathbf{v}\mathbf{v} \rangle_v$ that will truncate the set of coupled equations in this moment 'direction'. The equation for N will also be derived below.

3.2 Equations for evolution of velocity dependent density

First we consider moments in another direction from Eq.(24): Integrating equation over m we obtain

$$\begin{aligned} \frac{\partial g}{\partial t} + \mathbf{v} \cdot \frac{\partial}{\partial \mathbf{r}} g + \left(\frac{\partial \langle FE(m, p, N) \rangle_m}{\partial \mathbf{v}} \cdot \frac{\partial n}{\partial \mathbf{r}} - \frac{\partial \langle FK(m, p) \rangle_m}{\partial \mathbf{v}} \cdot \frac{\partial N}{\partial \mathbf{r}} + \frac{\partial \langle FL(m) \rangle_m}{\partial \mathbf{v}} \cdot \frac{\partial l}{\partial \mathbf{r}} \right. \\ \left. - \frac{\partial \langle FV(m, p) \rangle_m}{\partial \mathbf{v}} \cdot \frac{\partial p}{\partial \mathbf{r}} \right) = B(n) \frac{\partial}{\partial \mathbf{v}} \cdot (\mathbf{v}g) + Q_0 e^{-\rho_2 p} \frac{\partial^2}{\partial \mathbf{v}^2} \langle e^{-\rho_1 m} F \rangle_m \end{aligned} \quad (32)$$

where

$$g(\mathbf{r}, \mathbf{v}, t) = \langle F \rangle_m = \int F(\mathbf{r}, \mathbf{v}, m, t) dm \quad (33)$$

is the velocity distribution function. Eq.(32) corresponds to an ordinary kinetic equation. We have in general set,

$$\langle F\phi(m) \rangle_m = \int F(\mathbf{r}, \mathbf{v}, m, t) \phi(m) dm \quad (34)$$

for a function ϕ of m . Note that

$$N = \int g d\mathbf{v}. \quad (35)$$

The other form of $Q(m, p)$, Eq.(22), may equally well be used in Eq.(32). One observes in Eq.(32) the coupling to the various $\langle \cdot \rangle_m$ -moments. In general this coupling may rise a substantial problem. However, a study later will be done only for special cases where we only need the first order m -moment: Multiplying Eq.(24) by m and integrating we obtain

$$\frac{\partial G}{\partial t} + \mathbf{v} \cdot \frac{\partial}{\partial \mathbf{r}} G + \left(\frac{\partial \langle FE(m)m \rangle_m}{\partial \mathbf{v}} \cdot \frac{\partial n}{\partial \mathbf{r}} - \frac{\partial \langle FK(m, p, N)m \rangle_m}{\partial \mathbf{v}} \cdot \frac{\partial N}{\partial \mathbf{r}} + \frac{\partial \langle FL(m)m \rangle_m}{\partial \mathbf{v}} \cdot \frac{\partial l}{\partial \mathbf{r}} \right)$$

$$-\frac{\partial \langle FV(m, p)m \rangle_m}{\partial \mathbf{v}} \cdot \frac{\partial p}{\partial \mathbf{r}} + ag = -\beta G + m_0 g + B(n) \frac{\partial}{\partial \mathbf{v}} \cdot (\mathbf{v}G) + Q_0 e^{-\rho_2 p} \frac{\partial^2}{\partial \mathbf{v}^2} \langle e^{-\rho m} Fm \rangle_m \quad (36)$$

where

$$G(\mathbf{r}, \mathbf{v}, t) = \langle Fm \rangle_m = \int F(\mathbf{r}, \mathbf{v}, m, t) m dm \quad (37)$$

is connected to a mean saturation.

3.3 Equation for density $N(\mathbf{r}, t)$ of daphnicles - warm and cold models

In all the equations derived the density N appears. The equation for N is obtained integrating Eq.(24) over both velocity and saturation. Since integration over velocity gave Eq. (27) we need only integrate that equation over m . Thus we obtain

$$\frac{\partial N}{\partial t} + \frac{\partial}{\partial \mathbf{r}} \cdot (N\mathbf{U}_0(\mathbf{r}, t)) = 0 \quad (38)$$

where more precisely

$$N(\mathbf{r}, t) = \int F(\mathbf{r}, \mathbf{v}, m, t) d\mathbf{v} dm = \int f dm \quad (39)$$

is the probable observed number density of daphnicles and

$$N\mathbf{U}_0(\mathbf{r}, t) = \int F(\mathbf{r}, \mathbf{v}, m, t) \mathbf{v} d\mathbf{v} dm = \int f\mathbf{U}(\mathbf{r}, m, t) dm \quad (40)$$

gives the probable observed mean flow \mathbf{U}_0 . An equation for \mathbf{U}_0 we obtain integrating Eq.(30) over m ,

$$\frac{\partial (N\mathbf{U}_0(\mathbf{r}, t))}{\partial t} + \frac{\partial}{\partial \mathbf{r}} \cdot \langle F\mathbf{v}\mathbf{v} \rangle_{\mathbf{v}, m} - \left(\langle fE(m, p, N) \rangle_m \frac{\partial n}{\partial \mathbf{r}} - \langle fK(m, p) \rangle_m \frac{\partial N}{\partial \mathbf{r}} + \langle fL(m) \rangle_m \frac{\partial l}{\partial \mathbf{r}} - \langle fV(m, p) \rangle_m \frac{\partial p}{\partial \mathbf{r}} \right) = -B(n)N\mathbf{U}_0(\mathbf{r}, t) \quad (41)$$

3.3.1 Approximation of $\langle F\mathbf{v}\mathbf{v} \rangle_{\mathbf{v}}$ warm and cold models

In order to truncate the \mathbf{v} -moment equations we assume that the daphnicle distribution function to lowest order in the velocity variables may be approximated by a Maxwellian, i.e.

$$F(\mathbf{r}, \mathbf{v}, m, t) = f(\mathbf{r}, m, t) / (2\pi)^{3/2} (B/Q)^{3/2} e^{-\frac{B(\mathbf{v}-\mathbf{U})^2}{2Q}} \quad (42)$$

Then

$$\langle F\mathbf{v}\mathbf{v} \rangle_{\mathbf{v}} = f \frac{Q}{B} \mathbf{I} + f\mathbf{U}\mathbf{U} = f \frac{Q_0}{B_0} e^{-\sigma m - \rho_1 m - \rho_2 p} \mathbf{I} + f\mathbf{U}\mathbf{U} \quad (43)$$

where \mathbf{I} is the identity tensor. Using this approximation, Eq.(30) turns into

$$\frac{\partial (f\mathbf{U}(\mathbf{r}, m, t))}{\partial t} + \frac{Q_0}{B_0} \frac{\partial}{\partial \mathbf{r}} (f e^{-\sigma m - \rho_1 m - \rho_2 p}) + \frac{\partial}{\partial \mathbf{r}} \cdot f\mathbf{U}\mathbf{U} - f \left(E(m, p, N) \frac{\partial n}{\partial \mathbf{r}} - K(m, p) \frac{\partial N}{\partial \mathbf{r}} + L(m) \frac{\partial l}{\partial \mathbf{r}} - V(m, p) \frac{\partial p}{\partial \mathbf{r}} \right) = a \frac{\partial}{\partial m} (f\mathbf{U}(\mathbf{r}, m, t)) + \beta \frac{\partial}{\partial m} \left((m - m_0) f\mathbf{U}(\mathbf{r}, m, t) + \frac{q}{\beta} \frac{\partial (f\mathbf{U}(\mathbf{r}, m, t))}{\partial m} \right) - Bf\mathbf{U}(\mathbf{r}, m, t) \quad (44)$$

and the Eq.(41) for NU_0 into

$$\begin{aligned} & \frac{\partial(NU_0(\mathbf{r},t))}{\partial t} + \frac{Q_0}{B_0} \frac{\partial}{\partial \mathbf{r}} (e^{-\sigma n} e^{-\rho_2 p} \int f e^{-\rho_1 m} dm) + \frac{\partial}{\partial \mathbf{r}} \cdot \langle f \mathbf{U} \mathbf{U} \rangle_m \\ & - \left(\int E(m, p, N) f dm \frac{\partial n}{\partial \mathbf{r}} - \int K(m, p) f dm \frac{\partial N}{\partial \mathbf{r}} + \int L(m) f dm \frac{\partial l}{\partial \mathbf{r}} - \int V(m, p) f dm \frac{\partial p}{\partial \mathbf{r}} \right) = -BNU_0(\mathbf{r}, t) \end{aligned} \quad (45)$$

We shall refer to models including the Q_0 -term as 'warm' models, while 'cold' models means $Q_0=0$. In Eqs.(43), (44) and (45) we used Q from Eq.(21). We could of course equally well use Q from Eq.(22) instead.

4 Fluid equations of daphnicles

Eqs.(38) and (45) for N and U_0 , combined with Eq.(25) for n , comprise a set of fluid equations that could be used, when the force-coefficients are evaluated. This could most simply be done using f from Eq.(52) below. However, a simpler fluid model will be demonstrated and studied here.

4.1 Balance of forces-approximation, and approximations of m -moments

We assume NU_0 from Eq.(45) quite rapidly relaxes towards a quasi-stationary state, i.e. a state where the time-derivative term in Eq.(45) may be neglected. In this state we may solve the remaining equation with respect to NU_0 , and obtain

$$\begin{aligned} NU_0(\mathbf{r}, t) = \frac{1}{B} \left(\int E(m, p, N) f dm \frac{\partial n}{\partial \mathbf{r}} - \int K(m, p) f dm \frac{\partial N}{\partial \mathbf{r}} + \int L(m) f dm \frac{\partial l}{\partial \mathbf{r}} - \int V(m, p) f dm \frac{\partial p}{\partial \mathbf{r}} \right) \\ - \frac{Q_0}{BB_0} \frac{\partial}{\partial \mathbf{r}} (e^{-\sigma n} e^{-\rho_2 p} \int f e^{-\rho_1 m} dm) \end{aligned} \quad (46)$$

Here we also have neglected the $\frac{\partial}{\partial \mathbf{r}} \cdot \langle f \mathbf{U} \mathbf{U} \rangle_m$ -term, assumed relatively small, see below. Using this expression in Eq.(38) we have a continuity equation for daphnicle density N that take into account effects of various saturation moments,

$$\begin{aligned} \frac{\partial N}{\partial t} + \frac{\partial}{\partial \mathbf{r}} \cdot \left(\frac{1}{B} \left(\int E(m, p, N) f dm \frac{\partial n}{\partial \mathbf{r}} - \int K(m, p) f dm \frac{\partial N}{\partial \mathbf{r}} + \int L(m) f dm \frac{\partial l}{\partial \mathbf{r}} - \int V(m, p) f dm \frac{\partial p}{\partial \mathbf{r}} \right) \right. \\ \left. - \frac{Q_0}{BB_0} \frac{\partial}{\partial \mathbf{r}} (e^{-\sigma n} e^{-\rho_2 p} \int f e^{-\rho_1 m} dm) \right) = 0 \end{aligned} \quad (47)$$

We write the saturation moments more explicitly . We have

$$\int E(m, p, N) f dm = E_0 e^{\alpha_0 p} (N_m - N) \int (m_0 - m) f dm = E_0 e^{\alpha_0 p} (N_m - N)(m_0 N - P) \quad (48)$$

where we have written for the 1'st m -moment of m :

$$\int m f dm = P(\mathbf{r}, t) \quad (49)$$

Observe that

$$P = \int G dv \quad (50)$$

where G has been introduced above. The other m -moments in Eq.(47), however, generally introduce many new unknowns, beside P above, and rise a problem in the truncation process. If f were known one can of course calculate all these. But also a quite rough approximation of f may be useful: In particular, in cases where the $\frac{\partial}{\partial \mathbf{r}}$ -term in Eq.(27) for f is small, and may be neglected to lowest order, the remaining equation

$$\frac{\partial f}{\partial t} - a \frac{\partial f}{\partial m} = \beta \frac{\partial}{\partial m} \left((m - m_0) f + \frac{q}{\beta} \frac{\partial f}{\partial m} \right) \quad (51)$$

may be solved. If also condition for a quite fast relaxation of f towards a quasi-steady state, i.e. if relative much food is available, and the function f shows little spread in saturation, i.e. q/β is small, then f may be approximated by

$$f(\mathbf{r}, m, t) = N(\mathbf{r}, t) \delta(m - (m_0 - a / \beta(\mathbf{r}, t))) \quad (52)$$

where δ is the delta function. The t - and \mathbf{r} - variations here are relatively weak. Note that $\beta(\mathbf{r}, t) = \beta_0 n(\mathbf{r}, t)$. Using this approximation we may evaluate $\int f e^{\eta m} dm$ where η is some constant,

$$\int f e^{\eta m} dm = N(\mathbf{r}, t) e^{\eta(m_0 - a/\beta)} \approx N(\mathbf{r}, t) (1 + \eta(m_0 - a/\beta)) \quad (53)$$

where we also have written an approximation of the exact expression valid if $|\eta(m_0 - a/\beta)| \ll 1$. In the last approximation in Eq.(53) the first term is the 0'th order m -moment, the second the 1'st order m -moment, using the particular form of f , Eq.(52). We now assume that an approximation of integrals like $\int f e^{\eta m} dm$ may be obtained by these two m -moments, the 0.'th and the 1.'th, also for slightly more general functions f than the δ -function form above. However the inequality

$$|\eta(m_0 - a/\beta)| \ll 1 \quad (54)$$

must be fulfilled: Either η is very small. Then m_0 may be quite different from a/β . Or η may be relatively large, but then m_0 and a/β must be very close.

We shall assume these conditions to be fulfilled when approximating the remaining m -moments in Eq.(47): f is not far away from the distribution function Eq.(52), and each of α_1 , γ , τ_1 and ρ_1 fulfils the same inequality Eq.(54) as η above. We then may write:

$$\int K(m, p) f dm \approx K_0 e^{-\alpha_2 p} (N - \alpha_1 P) \quad (55)$$

$$\int L(m) f dm \approx L_0 (N - \gamma P) \quad (56)$$

$$\int V(m, p) f dm \approx V_0(N + \tau_1 P) e^{\tau_2 P} \quad (57)$$

$$\int f e^{-\rho_1 m} dm \approx N - \rho_1 P \quad (58)$$

In the equation for n , using the form λ from Eq.(26), we have when also the parameter ε fulfils the inequality Eq.(54),

$$\int \lambda(m) F dm d\mathbf{v} \approx \lambda_0 \int (1 - \varepsilon m) F dm d\mathbf{v} = \lambda_0 \int (1 - \varepsilon m) f dm = \lambda_0 (N - \varepsilon P) \quad (59)$$

Using these approximations, the equations for N and n turn into

$$\begin{aligned} \frac{\partial N}{\partial t} + \frac{\partial}{\partial \mathbf{r}} \cdot \left(\frac{1}{B} \left(E_0 (N_m - N) e^{\alpha_0 P} (m_0 N - P) \frac{\partial n}{\partial \mathbf{r}} - K_0 e^{-\alpha_2 P} (N - \alpha_1 P) \frac{\partial N}{\partial \mathbf{r}} + L_0 (N - \gamma P) \frac{\partial l}{\partial \mathbf{r}} \right. \right. \\ \left. \left. - V_0 (N + \tau_1 P) e^{\tau_2 P} \frac{\partial p}{\partial \mathbf{r}} \right) - \frac{Q_0}{BB_0} \frac{\partial}{\partial \mathbf{r}} e^{-\sigma m} e^{-\rho_2 P} (N - \rho_1 P) \right) = 0 \end{aligned} \quad (60)$$

and

$$\frac{\partial n}{\partial t} + \mathbf{u}_0 \cdot \frac{\partial n}{\partial \mathbf{r}} = D \frac{\partial^2 n}{\partial \mathbf{r}^2} - n \lambda_0 (N - \varepsilon P) + S(\mathbf{r}, t) \quad (61)$$

Thus we only need an equation for P , besides the equations for N and n , to have a closed system for N , P and n . Generally, we obtain the equation for P from Eq.(36) of G by integration over \mathbf{v} ,

$$\frac{\partial P}{\partial t} + \frac{\partial}{\partial \mathbf{r}} \cdot \left(\int f m \mathbf{U}(\mathbf{r}, m, t) dm \right) + aN = -\beta(P - m_0 N) \quad (62)$$

This is again coupled to an m -moment of Eq.(30), a mixed first order m - \mathbf{v} -moment of F . An equation for $\int f m \mathbf{U}(\mathbf{r}, m, t) dm = \mathbf{P}(\mathbf{r}, t)$ is obtained from Eq.(30) by multiplying it by m and integrating. The equation is of the form

$$\frac{\partial \mathbf{P}}{\partial t} + \left(\frac{\partial}{\partial \mathbf{r}} - \text{terms} \right) = -aN \mathbf{U}_0 - \beta \mathbf{P} + \beta m_0 N \mathbf{U}_0 - B \mathbf{P} \quad (63)$$

and generally introduces even higher order m -moments. However, in order to truncate these equations, we use assumptions that were used above: $\frac{\partial}{\partial \mathbf{r}} - \text{terms}$ are assumed

small, i.e. the state is nearly uniform, and furthermore, the state is nearly static, i.e.

$N \mathbf{U}_0$ from Eq.(46) is small. Since \mathbf{U}_0 mainly is driven by $\frac{\partial}{\partial \mathbf{r}}$, this last assumption is a

consequence of the first assumption. A similar "balance" of forces that gave Eq.(46) is

expected also in Eq.(63). The effect of the resulting \mathbf{P} on Eq.(62) for P then is very

small. Therefore in models where a uniform, static state exists and we look for small

deviations involving weak gradients, we may truncate the coupled equations by

assuming we have for P the simplified equation

$$\frac{\partial P}{\partial t} + aN = -\beta_0 n (P - m_0 N) \quad (64)$$

where we have written $\beta = \beta_0 n$. Hence, when the $l(\mathbf{r}, t)$ - and $p(\mathbf{r}, t)$ - functions are known,

Eqs.(60), (64) and (61) constitute a set of equations for N , P and n that may give a

particular 'fluid' evolution of the daphnicles when the assumptions used in the derivations are met.

5 Some special states and evolutions

5.1 Stationary and uniform state

Then $\frac{\partial}{\partial t} = 0$, $\frac{\partial}{\partial \mathbf{r}} = 0$. Since we assumed $\frac{q}{\beta} = k_0 e^{-h_0(t)n}$ such that

$\frac{q}{\beta} = k_0 e^{-h_0(t)n} \rightarrow 0$ as time increases, we have in the stationary state that $\frac{q}{\beta} = 0$, which

means all daphnicles are in a state of equal saturation.

To have a stationary state we furthermore must have a stationary and uniform source of food input, $S_0 > 0$, to obtain a stationary density n_0 : If food is not available starvation gives rise to a state that is not stationary, see below.

From Eq.(61) we have in the stationary and uniform state that the balance

$$-n_0 \lambda_0 (N_0 - \varepsilon P_0) + S_0 = 0 \quad (65)$$

must be fulfilled, furthermore, from the approximation Eq.(64)

$$aN_0 = -\beta_0 n_0 (P_0 - m_0 N_0) \quad (66)$$

In practice, a state like this may never be obtained. However, small deviations from such a state may be relevant from an observational point of view, and this is considered later. N_0 is the stationary and uniform density of daphnicles in this state, and P_0/N_0 the mean saturation. All ordered motions vanish, i.e. the state is static, and daphnicles show only erratic motion: From the equation for F we have

$$F(m, \mathbf{v}) = N_0 \left(\frac{B}{2\pi Q} \right)^{3/2} \delta\left(m - \left(m_0 - \frac{a}{\beta}\right)\right) e^{-\frac{Bv^2}{2Q}} \quad (67)$$

Here the δ -function expresses daphnicles of equal saturation, $m = \left(m_0 - \frac{a}{\beta}\right)$, a balance

between food intake and the starving process: If daphnicles take in food fast, i.e. β large, or, if starvation a is small, then they nearly obtain a saturation of m_0 . The daphnicles show erratic motion expressed by the Maxwellian factor. We have

$$\beta = \beta_0 n_0, \quad B = B_0 e^{\sigma n_0}, \quad Q = Q_0 e^{-\rho_1 \left(m_0 - \frac{a}{\beta}\right) - \rho_2 P_0} \quad (68)$$

if we use the Q -factor form from Eq.(21). The excitement of the daphnicles then is

$$\frac{Q}{B} = \frac{Q_0}{B_0} e^{-\rho_1 m_0 + \rho_1 \frac{a}{\beta_0 n_0} - \rho_2 P_0 - \sigma n_0} \quad (69)$$

According to this the excitement will increase with increasing hunger rate and decrease with increasing threat. Increase in food available, n_0 , will damp hunger excitement, and damp excitement in general.

5.2 Uniform state, no food available, hunger

We consider $\frac{\partial}{\partial \mathbf{r}} = \mathbf{0}$ and $\beta = \beta_0 n_0 = 0$. There is as in the state above no ordered movement. Starvation will dominate, and we shall in this state therefore use the form of Q from Eq.(22). The equation for F therefore reads

$$\frac{\partial F}{\partial t} - a \frac{\partial F}{\partial m} = B_0 \frac{\partial}{\partial \mathbf{v}} \cdot \left(\mathbf{v}F + \frac{Q_0}{B_0} \frac{\cosh \rho_1 m_1}{\cosh \rho_1 (m - m_1)} e^{-\rho_2 p_0} \frac{\partial F}{\partial \mathbf{v}} \right) \quad (70)$$

Introducing a new variable $\mu = m + at$, which transforms F to $F(\mu, \mathbf{v}, t)$, we have instead the equation

$$\frac{\partial F}{\partial t} = B_0 \frac{\partial}{\partial \mathbf{v}} \cdot \left(\mathbf{v}F + \frac{Q_0}{B_0} \frac{\cosh \rho_1 m_1}{\cosh \rho_1 (\mu - at - m_1)} e^{-\rho_2 p_0} \frac{\partial F}{\partial \mathbf{v}} \right) \quad (71)$$

which may be solved by the techniques used in [7]. For the case that movement is only back and forth in a z -direction, having averaged out movements in perpendicular directions, which is considered relevant for the experiments described in [1], the solution

$$F(v_z, m, t) = \frac{N_0}{(2\pi)^{1/2}} f_0(m + at) \frac{1}{\sqrt{\alpha(m, t)}} e^{-\frac{v_z^2}{2\alpha(m, t)}} \quad (72)$$

where

$$\alpha(m, t) = 2Q_0 e^{-\rho_2 p_0} \int_0^t \frac{\cosh \rho_1 m_1}{\cosh \rho_1 (m + as - m_1)} e^{-2B_0 s} ds, \quad (73)$$

is the particular one that obeys $F(v_z, m, t=0) = N_0 f_0(m) \delta(v_z)$. We may think of this initial state to represent a situation where all daphnicles are let into the experimental chamber uniformly distributed and simultaneously at time $t=0$, with different degree of saturation, given by $f_0(m)$, and all being immobile at that time, expressed by the δ -function. From then on they respond to the environment. More general solutions of the equations may be obtained from this fundamental solution. $f_0(m)$ is a quite arbitrary function obeying $\int f_0 dm = 1$. Figs.1-2 shows F for some increasing values of t , both for low threat $p_0=0$, and for some threat, $p_0=2$, when $f_0(m) = e^{-al \cdot m^2} (al / \pi)^{1/2}$, where al is constant.

5.3 Linearized fluid equations

Many of the equations derived in sections 2-4 are non-linear, in particular the low level (fluid) equations. They are generally difficult to solve by analytic procedures. However, solutions that deviate only little from stationary and uniform solutions like the ones derived earlier, may be found more easily since the equations for the small deviations are linear and hence more tractable.

In the discussion that follows we assume:

- 1) The daphnicles move back and forth in one dimension.

This may mimic laboratory experiments where *Daphnia* are confined to a cylindrical shell, [1], and we neglect the radial and vertical motions, assuming these may be averaged out. Hence,

2) We look for periodic, weak-gradient, smooth solutions in one dimension. For instance, for the density $N(z,t)$ we have $N(z+L,t)=N(z,t)$ where $L=2\pi R$, R being the mean radius of the cylindrical shell, and similarly for all other quantities involving space variation.

Accordingly, all quantities, for instance the density, will have a general form, $N=N_0+N_1$ where N_0 is z - and t -independent and $N_1(z,t)$ fulfils

$$\int_0^L N_1(z,t) dz = 0 \quad (74)$$

Thus we write,

$$\begin{aligned} N &= N_0 + N_1 \\ n &= n_0 + n_1 \\ P &= P_0 + P_1 \\ p &= p_0 + p_1 \\ l &= l_0 + l_1 \end{aligned} \quad (75)$$

The stationary, uniform parts of the solutions ('equilibrium' solution) are the ones discussed above, and subscript '1' refers to small perturbed z -oscillatory and time-dependent quantities: It is essential that these quantities are small, i.e. for instance $|N_1| \ll |N_0|$, for the linearization to work. The threat function p and light intensity function l are assumed known here. Also the food source shall be given in the same way,

$$S = S_0 + S_1 \quad (76)$$

The discussion and assumptions leading to the simplified Eq.(64) is now applicable, and to first order we have from Eq.(64)

$$\frac{\partial P_1}{\partial t} + aN_1 = -\beta_0 n_1 (P_0 - m_0 N_0) - \beta_0 n_0 (P_1 - m_0 N_1) \quad (77)$$

Assuming that $\frac{\partial}{\partial t} \rightarrow 0$ relatively fast in this equation, the first term may be neglected when only slow evolution is considered. Then the remaining terms in Eq.(77) give P_1 as a function of N_1 and n_1 ,

$$P_1 = (m_0 - \frac{a}{\beta_0 n_0}) N_1 - (P_0 - m_0 N_0) \frac{n_1}{n_0} = (m_0 - \frac{a}{\beta_0 n_0}) N_1 + \frac{a N_0}{\beta_0 n_0^2} n_1 \quad (78)$$

We note that the approximation of P_1 here also follows from using the f -approximation from Eq.(52). However, we could without difficulty have worked with the full Eq.(77), but follow this simpler procedure here.

The linearized food equation thus becomes

$$\begin{aligned}\frac{\partial n_1}{\partial t} + u_0 \frac{\partial n_1}{\partial z} &= D \frac{\partial^2 n_1}{\partial z^2} - n_1 \lambda_0 (N_0 - \varepsilon P_0) - n_0 \lambda_0 (N_1 - \varepsilon P_1) + S_1(z, t) \\ &= D \frac{\partial^2 n_1}{\partial z^2} - n_1 \lambda_0 N_0 (1 - \varepsilon m_0) - n_0 \lambda_0 N_1 (1 - \varepsilon m_0 + \varepsilon \frac{a}{\beta_0 n_0}) + S_1(z, t)\end{aligned}\quad (79)$$

or, for short,

$$\frac{\partial n_1}{\partial t} + u_0 \frac{\partial n_1}{\partial z} = D \frac{\partial^2 n_1}{\partial z^2} - C_1 n_1 - C_2 N_1 + S_1 \quad (80)$$

where we have written

$$\begin{aligned}C_1 &= \lambda_0 N_0 (1 - \varepsilon m_0) \\ C_2 &= n_0 \lambda_0 (1 - \varepsilon m_0 + \varepsilon \frac{a}{\beta_0 n_0})\end{aligned}\quad (81)$$

These constants are positive since we consider εm_0 to be smaller than 1.

Likewise, we may rewrite Eq.(60) for the perturbation N_1 . After some algebra it takes the form:

$$\frac{\partial N_1}{\partial t} + A \frac{\partial^2 n_1}{\partial z^2} - B \frac{\partial^2 N_1}{\partial z^2} = I_1 \frac{\partial^2 l_1}{\partial z^2} + I_2 \frac{\partial^2 p_1}{\partial z^2} \quad (82)$$

where we have for the coefficients,

$$\begin{aligned}A &= \frac{E_0 (N_m - N_0) e^{\alpha_0 p_0} a N_0}{B_0 \beta_0 n_0} + \frac{Q_0}{B_0^2} e^{-\sigma_0 - \rho_2 p_0} \rho_1 \frac{a N_0}{\beta_0 n_0^2} + \frac{Q_0}{B_0^2} e^{-\sigma_0 - \rho_2 p_0} N_0 (1 - \rho_1 m_0 + \frac{\rho_1 a}{\beta_0 n_0}) \sigma \\ B &= \frac{K_0 N_0}{B_0} e^{-\alpha_2 p_0} (1 - \alpha_1 m_0 - \alpha_1 \frac{a}{\beta_0 n_0}) + \frac{Q_0}{B_0^2} e^{-\sigma_0 - \rho_2 p_0} (1 - \rho_1 m_0 + \frac{\rho_1 a}{\beta_0 n_0}) \\ I_1 &= -\frac{L_0 N_0}{B_0} (1 - \gamma m_0 + \gamma \frac{a}{\beta_0 n_0}) \\ I_2 &= \frac{V_0 e^{\tau_2 p_0} N_0}{B_0} (1 + \tau_1 m_0 - \tau_1 \frac{a}{\beta_0 n_0}) - \frac{Q_0}{B_0^2} e^{-\sigma_0 - \rho_2 p_0} N_0 \rho_2 (1 - \rho_1 m_0 + \frac{\rho_1 a}{\beta_0 n_0})\end{aligned}\quad (83)$$

As in Eq.(80), Eq.(82) couples various parameter-effects in the coefficients. These coefficients therefore take different values when the parameters change. For instance, A and B may vary considerably when the threat level p_0 varies. Both of A and B are considered positive, and both simplify considerably for a 'cold' population ($Q_0=0$) of daphnics. I_1 is negative while I_2 is considered positive, however, less positive for warm models, $Q_0>0$. Note that I_2 may increase considerably when p_0 increases.

6 Some special solutions from linear fluid equations

We simplify the equation for n_1 somewhat neglecting the drift u_0 and the diffusion, such that only the essential interaction between the two densities remains, having

$$\frac{\partial n_1}{\partial t} = -C_1 n_1 - C_2 N_1 + S_1 \quad (84)$$

where C_1 and C_2 are given from Eq.(81). S_1 is considered known and periodic in z .

For various cases we solve the equation together with Eq.(82), i.e.

$$\frac{\partial N_1}{\partial t} + A \frac{\partial^2 n_1}{\partial z^2} - B \frac{\partial^2 N_1}{\partial z^2} = I_1 \frac{\partial^2 l_1}{\partial z^2} + I_2 \frac{\partial^2 p_1}{\partial z^2} \quad (82)$$

where coefficients are given from Eq.(83) and l_1 and p_1 also are considered known and periodic in z . Solutions are largely illustrated by figures, and we list at the start of the figure section at the end the parameter values used in Figs.4-18.

6.1 State of stationary balance

When all sources S_1 , l_1 and p_1 are time independent, a stationary solution for N_1 and n_1 is found when $\frac{\partial}{\partial t}$ -terms are neglected in Eqs.(82) and (84). Then we have

$$\begin{aligned} An_1 - BN_1 &= I_1 l_1 + I_2 p_1 \\ C_1 n_1 + C_2 N_1 &= S_1 \end{aligned} \quad (85)$$

and the steady solution

$$\begin{aligned} N_{1s} &= \frac{AS_1 - C_1(I_1 l_1 + I_2 p_1)}{AC_2 + BC_1} \\ n_{1s} &= \frac{BS_1 + C_2(I_1 l_1 + I_2 p_1)}{AC_2 + BC_1} \end{aligned} \quad (86)$$

is set up by the steady sources S_1 , l_1 and p_1 and hence is also oscillatory in z . These turn out to be 'end' solutions towards which time-dependent solutions evolve. We shall look at some particular situations:

6.2 The case $S_1=0$, $p_1=0$, $l_1=0$, i.e. the situations with no perturbed external influences

We have

$$\begin{aligned} \frac{\partial N_1}{\partial t} + A \frac{\partial^2 n_1}{\partial z^2} - B \frac{\partial^2 N_1}{\partial z^2} &= 0 \\ \frac{\partial n_1}{\partial t} &= -C_1 n_1 - C_2 N_1 \end{aligned} \quad (87)$$

The system lacks source terms and is homogeneous. Solutions will reflect intrinsic properties of the system. These properties are also important to tell how the system responds to sources. There is no steady state solution in this case, except $N_1=n_1=0$. We solve the equations subject to the initial perturbation,

$$\begin{aligned} N_1(z, 0) &= \sum_{m=1} N_{1m} \cos(2\pi m z / L) + \sum_{m=1} N_{2m} \sin(2\pi m z / L) \\ n_1(z, 0) &= 0 \end{aligned} \quad (88)$$

and we look for solutions of the form

$$\begin{aligned} N_1(z, t) &= \sum_{m=1} a_{1m}(t) \cos(2\pi m z / L) + \sum_{m=1} a_{2m}(t) \sin(2\pi m z / L) \\ n_1(z, t) &= \sum_{m=1} b_{1m}(t) \cos(2\pi m z / L) + \sum_{m=1} b_{2m}(t) \sin(2\pi m z / L) \end{aligned} \quad (89)$$

" m " is used for "azimuthal mode number", which is standard notation, (and must not be confused with food saturation). By insertion we find for each pair of the time dependent coefficients (a_{1m}, b_{1m}) and (a_{2m}, b_{2m}) , say (α_m, β_m) , the equations

$$\begin{aligned}\alpha'_m - A(2\pi m / L)^2 \beta_m + B(2\pi m / L)^2 \alpha_m &= 0 \\ \beta'_m + C_1 \beta_m + C_2 \alpha_m &= 0\end{aligned}\quad (90)$$

where ' means the time derivative. Using the initial conditions we obtain for the coefficients

$$\begin{aligned}\alpha_m &= \frac{N_m}{r_2 - r_1} \left((r_2 + B(2\pi m / L)^2) e^{r_1 t} - (r_1 + B(2\pi m / L)^2) e^{r_2 t} \right) \\ \beta_m &= \frac{1}{A(2\pi m / L)^2} \frac{N_m}{r_2 - r_1} (r_1 + B(2\pi m / L)^2)(r_2 + B(2\pi m / L)^2)(e^{r_1 t} - e^{r_2 t})\end{aligned}\quad (91)$$

Here N_m denotes either N_{1m} or N_{2m} depending on whether (α_m, β_m) denotes (a_{1m}, b_{1m}) or (a_{2m}, b_{2m}) . The roots r_1 and r_2 are given from the equation

$$r^2 + r(C_1 + B(2\pi m / L)^2) + (BC_1 + AC_2)(2\pi m / L)^2 = 0 \quad (92)$$

i.e.,

$$r = -(C_1 + B(2\pi m / L)^2) / 2 \pm \left[(C_1 + B(2\pi m / L)^2)^2 - 4(BC_1 + AC_2)(2\pi m / L)^2 \right]^{1/2} / 2 \quad (93)$$

and are either real or complex conjugates. In the last case we may write

$$r = \alpha \pm i\beta \quad (94)$$

where

$$\begin{aligned}\alpha &= -\frac{C_1 + B(2\pi m / L)^2}{2} \\ \beta &= \left[4(AC_2 + BC_1)(2\pi m / L)^2 - (C_1 + B(2\pi m / L)^2)^2 \right]^{1/2} / 2\end{aligned}\quad (95)$$

We write explicitly the solution for the case that

$$\begin{aligned}N_1(z, 0) &= N_{1m} \cos(2\pi m z / L) \\ n_1(z, 0) &= 0\end{aligned}\quad (96)$$

In the real root case we have

$$\begin{aligned}N_1(z, t) &= \frac{N_{1m}}{r_2 - r_1} \left((r_2 + B(2\pi m / L)^2) e^{r_1 t} - (r_1 + B(2\pi m / L)^2) e^{r_2 t} \right) \cos(2\pi m z / L) \\ n_1(z, t) &= \frac{1}{A(2\pi m / L)^2} \frac{N_{1m}}{r_2 - r_1} (r_1 + B(2\pi m / L)^2)(r_2 + B(2\pi m / L)^2)(e^{r_1 t} - e^{r_2 t}) \cos(2\pi m z / L)\end{aligned}\quad (97)$$

and in the complex conjugate root case

$$N_1(z,t) = N_{1m} \left(e^{\alpha} \cos \beta t - \frac{\alpha}{\beta} e^{\alpha} \sin \beta t - B(2\pi m / L)^2 e^{\alpha} \frac{\sin \beta t}{\beta} \right) \cos(2\pi m z / L) \quad (98)$$

$$n_1(z,t) = -\frac{N_{1m}}{A(2\pi m / L)^2} \left((\alpha + B(2\pi m / L)^2)^2 + \beta^2 \right) e^{\alpha} \frac{\sin \beta t}{\beta} \cos(2\pi m z / L)$$

We make the following distinctions:

$$1) AC_2 + BC_1 > 0 \text{ and } 4(BC_1 + AC_2)(2\pi m / L)^2 < (C_1 + B(2\pi m / L)^2)^2.$$

Both roots are real and have the same sign. Since $C_1 + B(2\pi m / L)^2 > 0$, both are negative.

$$2) AC_2 + BC_1 > 0 \text{ and } 4(BC_1 + AC_2)(2\pi m / L)^2 > (C_1 + B(2\pi m / L)^2)^2.$$

In this case the roots are complex conjugates, and since $C_1 + B(2\pi m / L)^2 > 0$ the real part of the roots is negative.

Some choices of parameters may also be investigated from Fig.3, showing two (A,B) diagrams, for fixed values of C_1 and C_2 (both set to 1), for $m=1$ (top) and $m=2$, bottom. The curves are the parabola $(C_1 - Bl^2)^2 = 4AC_2l^2$, where $l = 2\pi m / L$, and the straight lines $BC_1 + AC_2 = 0$ and $C_1 + Bl^2 = 0$. The regions for real and complex conjugate roots are indicated, together with the signs of the roots, or for their real parts. Note that only the region for $B > 0$ is relevant.

In both cases 1) and 2) the perturbed solutions N_1 and n_1 are damped away. As Figs.4-6 show the damping is dependent on the ground threat level p_0 which makes A increase and B decrease when it increases. We show solutions for a low level, an intermediate level and a high-level threat case. Though the response of daphnicles changes with threat, accumulation of daphnicles does not take place. In the complex conjugate case the solutions decay towards zero, showing also an oscillatory behaviour in time. The combined oscillatory behaviours in space and time may be considered as standing attenuated waves due to waves propagating in opposite directions, each with a phase velocity $v_\phi = L\beta / (2\pi m)$ where β here is given from Eq.(95).

6.3 Case of uniform light intensity, uniform threat, steady rate of non-uniform two-hump food input

This case may be more realistic concerning food input, since we allow the food input to vary from point to point, which will be the case in practise, even if we try to make the input uniform. We assume from $t=0$ and onwards,

$$S_1(z) = s_{11} \cos(2\pi z / L) + s_{12} \cos(4\pi z / L) \quad (99)$$

which corresponds to two different "humps" of steady food input, while at time $t=0$ we have

$$\begin{aligned}
 W_1(z) &= W_0 \left(z^n \cos \frac{Bz}{A} - B \sin \frac{Bz}{A} \right) \cos \frac{Bz}{A} \\
 W_2(z) &= \frac{W_0}{A} \left((z + B) \cos \frac{Bz}{A} + B \sin \frac{Bz}{A} \right) \cos \frac{Bz}{A}
 \end{aligned}
 \tag{98}$$

We make the following distinction:

- 1) $AC + BC > 0$ and $4(BC + AC)(A^2 + B^2) < (C + B)^2 A^2$
 Both roots are real and have the same sign. Since $C + B > 0$, both are negative.
- 2) $AC + BC > 0$ and $4(BC + AC)(A^2 + B^2) > (C + B)^2 A^2$
 In this case the roots are complex conjugates, and since $C + B > 0$ the real part of the roots is negative.

Some choices of parameters may also be investigated from Fig. 3, showing two (A, B) diagrams, for fixed values of C and B (first set in 1) for W_1 (top) and W_2 (bottom). The curves are the parabola $(C - B)^2 - 4AC^2$, where $C = 2A^2 B$, and the straight lines $BC + AC = 0$ and $C + B = 0$. The regions for real and complex conjugate roots are indicated, together with the signs of the roots, or for their real parts. Note that only the region for $B > 0$ is relevant.

In both cases 1) and 2) the perturbed solution W_1 and W_2 are damped away. As Fig. 4 shows the damping is dependent on the growth level μ , which makes A increase and B decrease when μ increases. We show solutions for a low level in intermediate level and a high-level limit case. Though the response or definition changes with these assumptions of definition does not take place in the complex conjugate case the solution decays towards zero, showing also an oscillatory behaviour in time. The combined oscillatory behaviour in space and time may be considered as standing resonant waves due to waves propagating in opposite directions, each with a phase velocity $v = \lambda B / 2\pi$, where λ is given from Eq. (95).

0.3.1. sec of uniform flow in a pipe, uniform shear, steady flow of non-Newtonian type

This case may be more realistic concerning food pipes, since we show the food pipes to vary from point to point, which will be the case in practice, even if we try to make the input uniform. We assume from the end onwards:

$$\dot{\gamma}(z) = \dot{\gamma}_0 \cos \frac{Bz}{A} \tag{99}$$

which corresponds to two distinct "waves" of steady flow pipes, while at any one we have

$$\begin{aligned} N_1(z,0) &= N_{11} \cos(2\pi z / L) \\ n_1(z,0) &= 0 \end{aligned} \quad (100)$$

i.e. initially a one-hump perturbation of the daphnic density. This corresponds therefore to a situation where we have an overall positive, oscillatory supply: The supply is split in two, $S = S_0 + S_1$. The constant part S_0 merely gives the uniform solution, i.e. the values n_0 , P_0 and N_0 from Eqs.(65) and (66), while the response to S_1 now follows.

The equations have in this case a stationary solution,

$$\begin{aligned} N_{1s} &= \frac{AS_1(z)}{AC_2 + BC_1} \\ n_{1s} &= \frac{BS_1(z)}{AC_2 + BC_1} \end{aligned} \quad (101)$$

Defining new variables,

$$\begin{aligned} N'_1 &= N_1 - N_{1s} \\ n'_1 &= n_1 - n_{1s} \end{aligned} \quad (102)$$

we have the problem to solve and find z -periodic solutions of

$$\begin{aligned} \frac{\partial N'_1}{\partial t} + A \frac{\partial^2 n'_1}{\partial z^2} - B \frac{\partial^2 N'_1}{\partial z^2} &= 0 \\ \frac{\partial n'_1}{\partial t} &= -C_1 n'_1 - C_2 N'_1 \end{aligned} \quad (103)$$

subject to initial conditions

$$\begin{aligned} N'_1(z,0) &= N_{11} \cos(2\pi z / L) - N_{1s}(z) \\ n'_1(z,0) &= -n_{1s}(z) \end{aligned} \quad (104)$$

The solution procedure follows the same lines as in the foregoing paragraph, and the listing of cases according to parameter values is the same. Results are shown in Figs.7-9 for three cases of threat levels. In all cases the solutions decay towards the steady-state solution as time goes on. Accumulation of daphnicles becomes stronger around food sources as the ground threat level p_0 rises, and the food distribution changes accordingly.

6.4 Case of uniform light intensity, uniform food input and non-uniform stationary threat

We now assume a small, steady gradient in the threat field,

$$p_1(z) = p_{1m} \cos(2\pi m z / L) \quad (105)$$

but we assume there is no variation in food input or in light intensity, i.e. $S_1=0$, $l_1=0$.

We take the initial state to be,

$$\begin{aligned} N_1(z,0) &= 0 \\ n_1(z,0) &= 0 \end{aligned} \tag{105}$$

We have

$$\begin{aligned} N_{1s} &= \frac{-C_1 I_2 p_1(z)}{AC_2 + BC_1} \\ n_{1s} &= \frac{C_2 I_2 p_1(z)}{AC_2 + BC_1} \end{aligned} \tag{106}$$

for the stationary solutions, and results for the full solution are shown in Figs.10-12, for the case $m=1$. As expected, daphnicles fly away from the threat gradient and settle in a state given by the steady state solution. However, since the parameters A , B and I_2 all depend on the ground threat level, the response to the same threat gradient is very different when the ground threat level changes.

6.5 Case of uniform light intensity, uniform food input and one-hump moving threat

We change the foregoing example to a threat gradient that is moving with a steady velocity v_0 ,

$$p_1(z,t) = p_{11} \cos(2\pi z / L - v_0 t) \tag{107}$$

still having $S_1=0$, $l_1=0$. Again we let

$$\begin{aligned} N_1(z,0) &= 0 \\ n_1(z,0) &= 0 \end{aligned} \tag{108}$$

No stationary solutions exist in this case. Eventually, as time goes on, a solution remains driven by the moving threat only. We have the results of Figs.13-15. Again the ground level threat p_0 is an important factor for the daphnicle response and evolution.

6.6 Case of uniform light intensity, steady two-hump food input and moving one-hump threat.

In this case we have

$$S_1(z) = s_{11} \cos(2\pi z / L) + s_{12} \cos(4\pi z / L) \tag{109}$$

$$p_1(z,t) = p_{11} \cos(2\pi z / L - v_0 t) \tag{110}$$

and

$$\begin{aligned} N_1(z,0) &= 0 \\ n_1(z,0) &= 0 \end{aligned} \tag{111}$$

Neither in this case there exists a stationary solution. As time goes on there remains a typical response and accumulation due to the combined influences of threat moving and steady food input. This is shown on Figs.16-18 for three cases of ground level threat.

7 Summary and conclusion

The purpose with the present investigation was to consider whether an analogue modelling parallel to physical modelling could qualitatively describe the behaviour of swarms of *Daphnia*, in particular their response to food and threat. It was assumed that the particle-like units, which we have called daphnicles, had only one internal state, which gave them some sort of individuality, namely their degree of food saturation. Due to this they showed individual responses to external influences. We assumed they responded uniformly to external threat, though also this property, connected to fright, might also be treated as an internal, individual property. A statistical-mechanical approach was used to follow in time the evolution in a 7 dimensional state space, spanned by velocity, position and saturation, of a density function, or distribution function, of daphnicles. A dynamic equation for the density function, i.e. an extended kinetic equation, was developed. The reasoning was close to test-particle reasoning in physical disciplines and gave the evolution in a statistical sense. From the basic equation eventually more ordinary kinetic equations and then fluid equations were developed. These had inherent properties that stemmed from the detailed equation first developed. In particular a line of derivation that lead towards fluid equations relying on balance of forces was followed, though there were other alternative lines of development. In some cases it was possible to solve these equations analytically when some conditions were met. These condition may to some extent be met in laboratory experiments [1] that have been done for some time and will be continued in the future. The results from the modelling may therefore be compared to matching experiments. The modelling can to some extent easily be modified to match new conditions, mechanisms and experimental findings. More elaborate solutions may be found by computer experiments, in particular when non-linearity must be included, or when the particular line we eventually followed must be modified, or new lines of development must be followed instead.

Acknowledgement:

The author wants to express his gratitude to Petter Larsson, Dept. of Zoology, Univ. of Bergen, for his seminar about experiments and research on *Daphnia* behaviour, and for informative and stimulating talks on the subject.

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Figure section

Parameter values used in Figures (4)-(18).

Spatial dimension, L :

$$L=2\pi, \text{ all figures}$$

Food intake rates C_1 and C_2 :

$$C_1 = C_2 = 1.$$

Amplitude of initial perturbation ($m=1$) of daphnicles:

$$N_{11}=0.2 \text{ or } N_{11}=0.$$

Amplitude of initial perturbation of food:

$$0, \text{ throughout.}$$

Food attraction and daphnicle repulsion coefficients A and B :

$$A=0.5, B=2, \text{ low threat level}$$

$$A=1, B=1, \text{ intermediate threat level}$$

$$A=5, B=0.2, \text{ high threat level}$$

Two-hump, perturbed food input amplitudes, $m=1, m=2$:

$$s_{11}=0.1, s_{12}=0.3.$$

Threat gradient coefficient I_2 :

$$I_2=0.5, \text{ low threat level}$$

$$I_2=1, \text{ intermediate threat level}$$

$$I_2=5, \text{ high threat level}$$

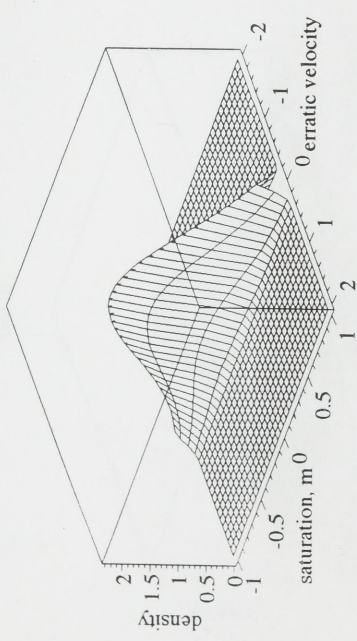
One-hump threat gradient amplitude, $m=1$:

$$p_{11}=0.2$$

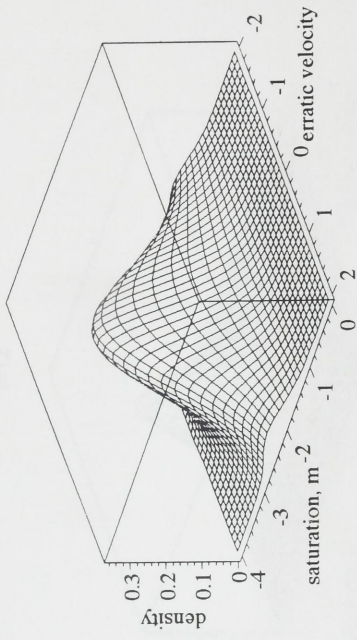
Velocity of moving threat gradient:

$$v_0=0.5$$

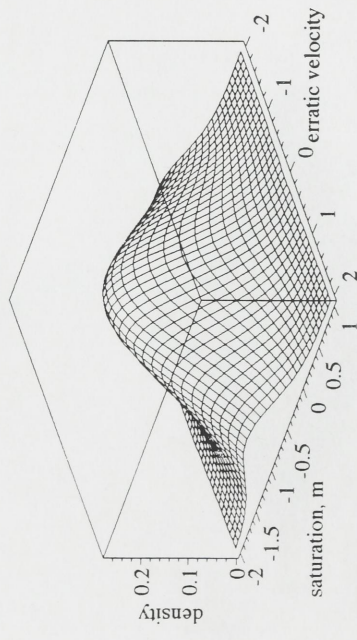
Distribution of daphnicles
no threat
t=0.01



Distribution of daphnicles
no threat
t=12



Distribution of daphnicles
no threat
t=3



Distribution of daphnicles
no threat
t=20

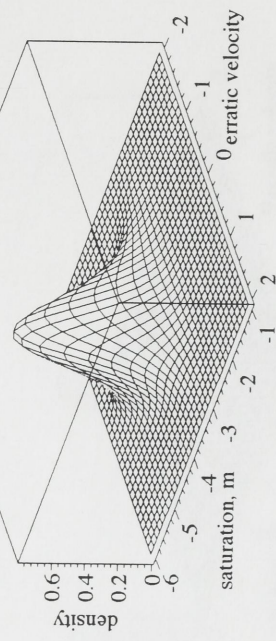
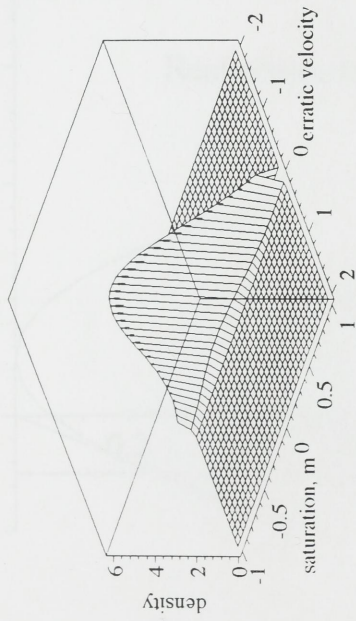


Fig.1: Distribution of daphnicles according to Eq.(72), "no threat"

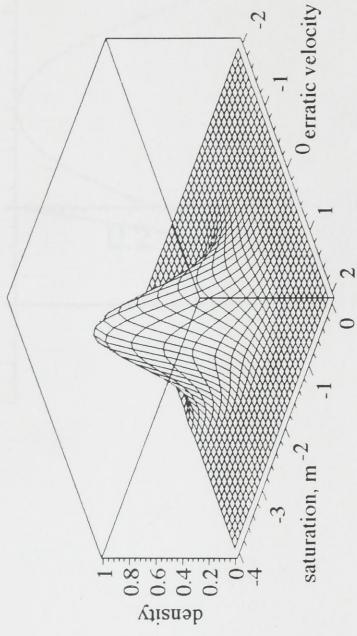
($\rho_0 = 0$), for 4 values of time . Parameter values used: $N_0 = 1$,
 $a = 0.2$, $Q_0 = 1$, $\rho_1 = 1$, $\rho_2 = 1$, $B_0 = 1$, $m_1 = -1$.

Function $f_0(m) = (aI/\pi)^{1/2} \exp(-aI \cdot m^2)$, $aI = 2$.

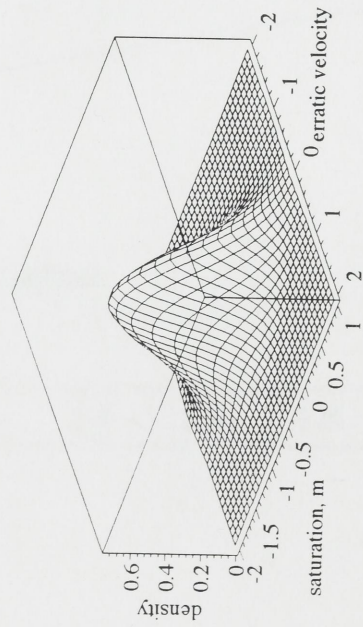
Distribution of daphnicles
some threat
 $t=0.01$



Distribution of daphnicles
some threat
 $t=12$



Distribution of daphnicles
some threat
 $t=3$



Distribution of daphnicles
some threat
 $t=20$

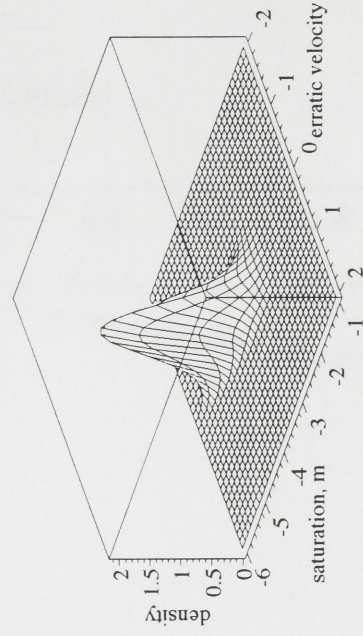
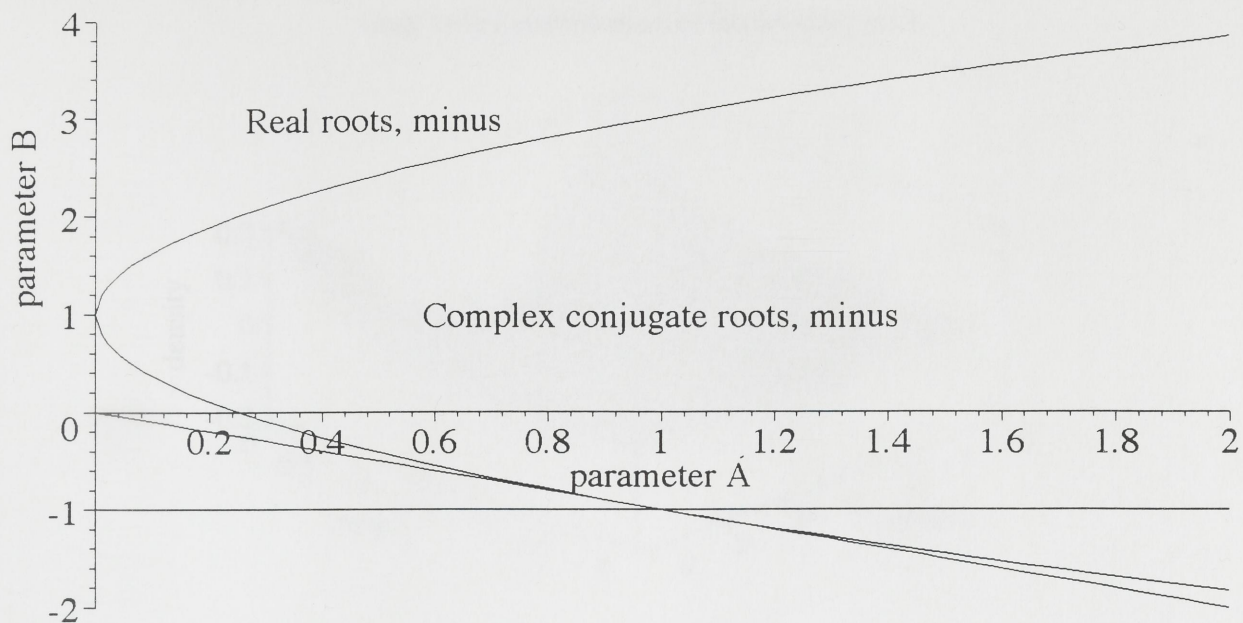


Fig.2: Same as Fig. 1, except that $p_0 = 2$ ("some threat").

$$m=1, L=2\pi, C_1=C_2=1$$



$$m=2, L=2\pi, C_1=C_2=1$$

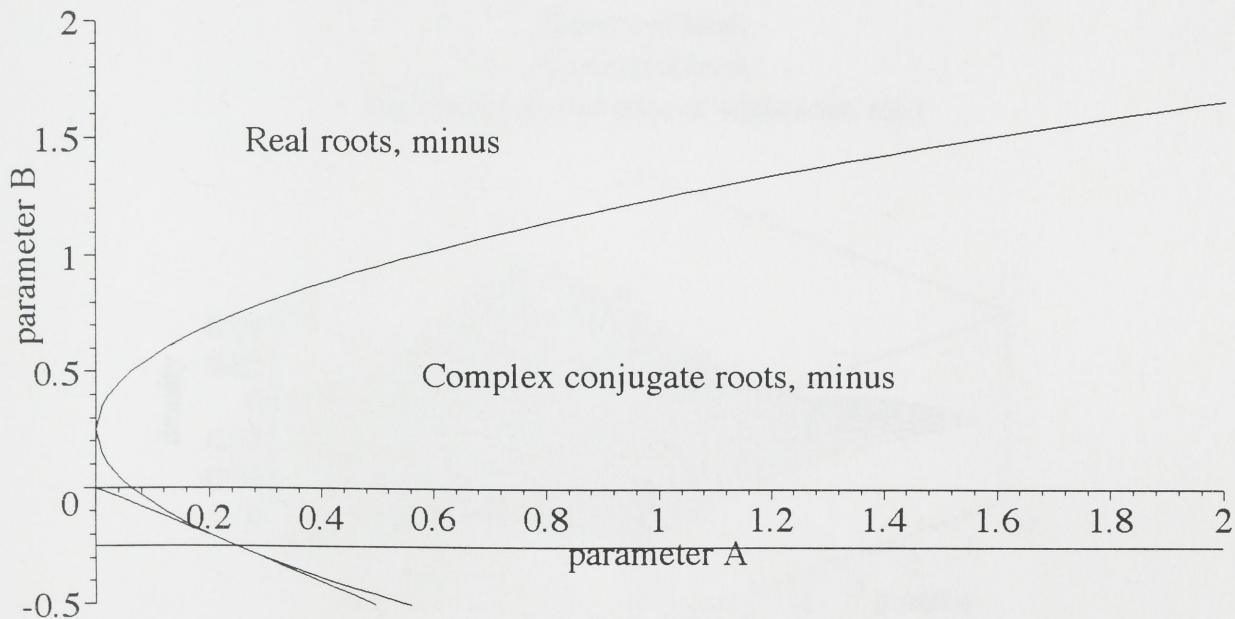
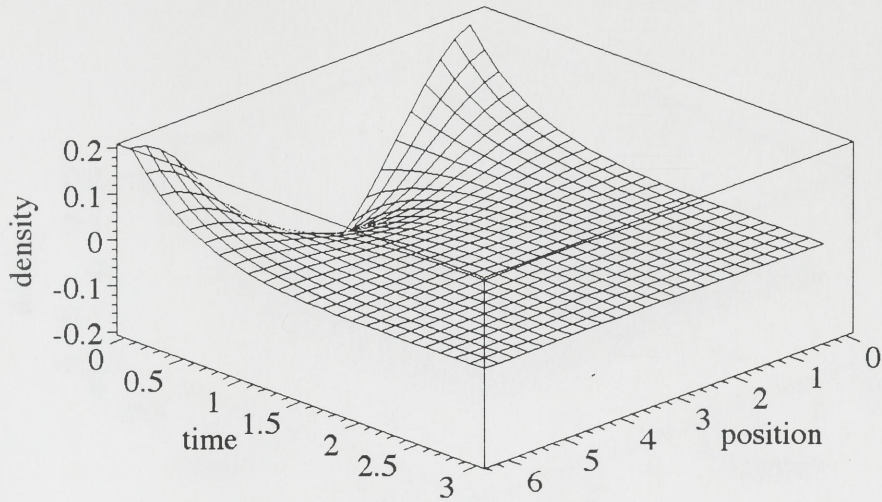


Fig.3: Regions in (A, B) - diagrams for real and complex conjugates roots of Eq.(93), when $L=2\pi$, $C_1=C_2=1$, for $m=1$ (top) and $m=2$ (bottom). Only $B \geq 0$ is relevant, sign of real part indicated.

Density of daphnicles,
Low threat level,
Only initial perturbation of daphnicles, $m=1$



Density of food,
Low threat level,
Only initial perturbation of daphnicles, $m=1$

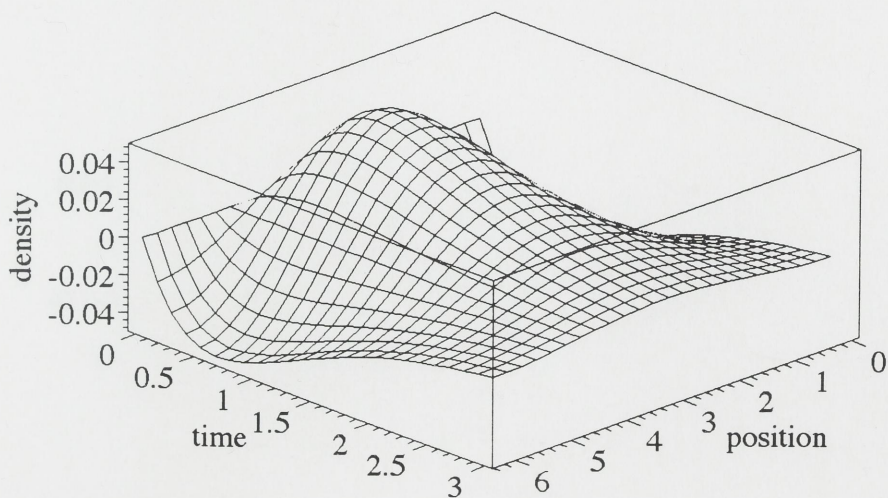
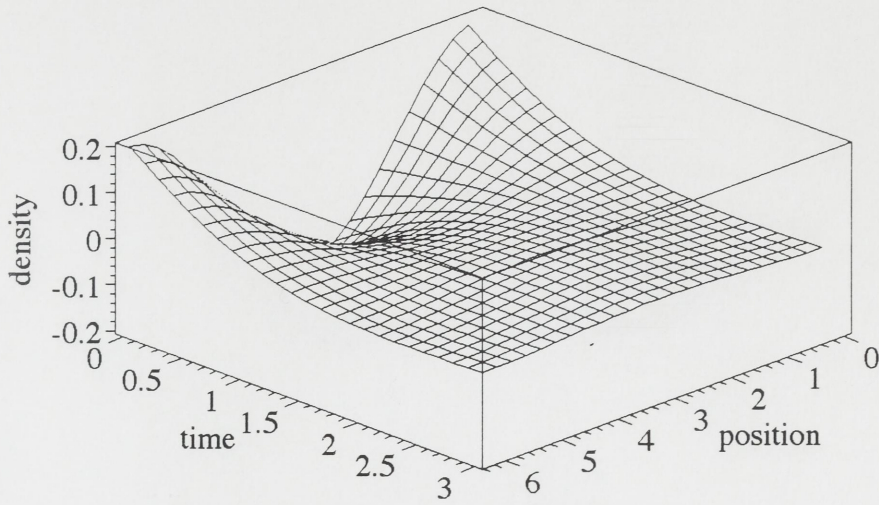


Fig.4: Space-time evolution of daphnicle density (top) and food density (bottom) in case of low ground-threat level, when daphnicles are perturbed at $t=0$, (Eq.(96), for $m=1$). For parameter values used, see start of figure section.

Density of daphnicles,
Intermediate threat level,
Only initial perturbation of daphnicles, $m=1$



Density of food,
Intermediate threat level,
Only initial perturbation of daphnicles, $m=1$

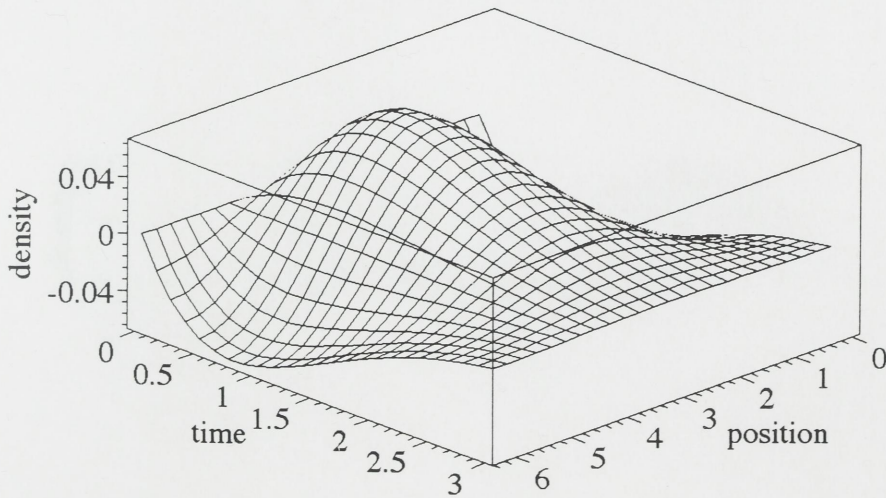
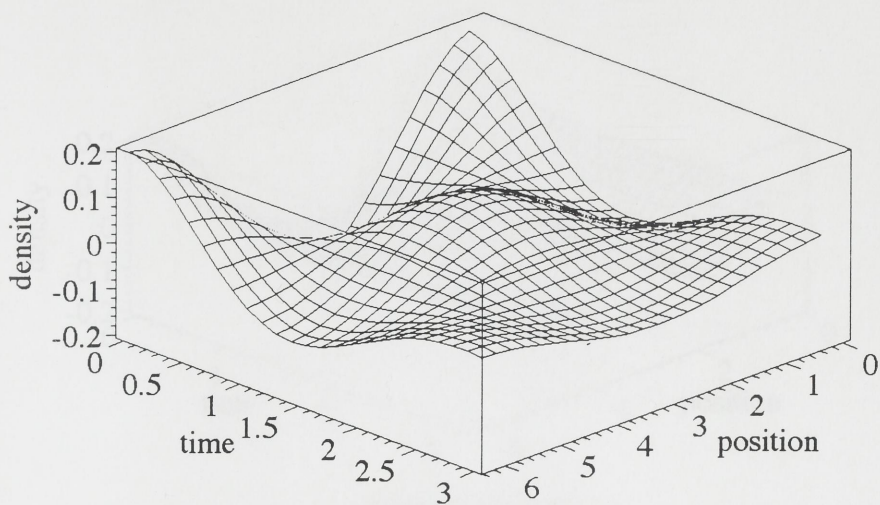


Fig.5: Same as Fig.4, except for intermediate ground-threat level instead, see start of figure section.

Density of daphnicles,
High threat level,
Only initial perturbation of daphnicles, $m=1$



Density of food,
High threat level,
Only initial perturbation of daphnicles, $m=1$

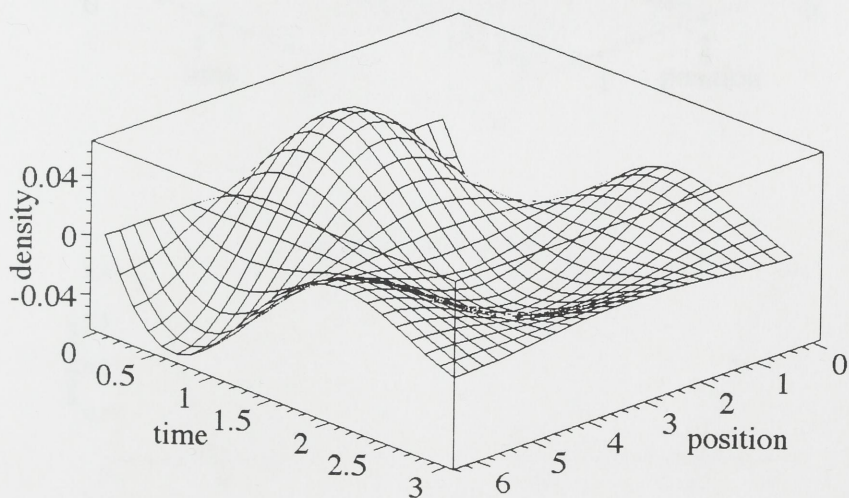
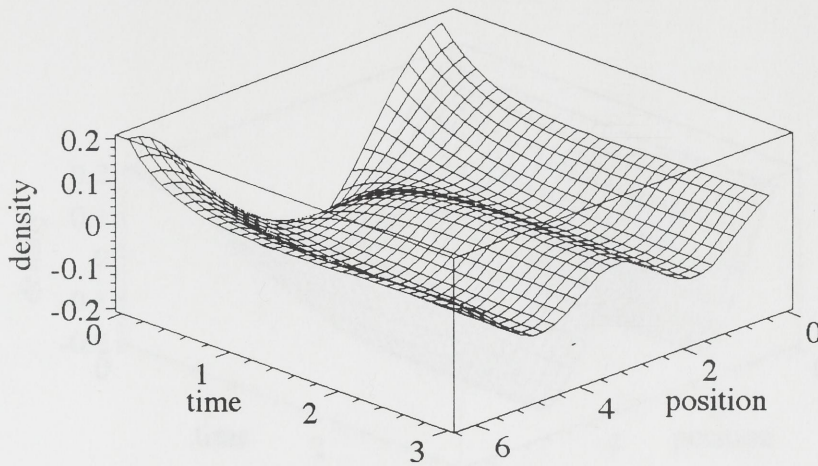


Fig.6: Same as Fig.4, except for high ground-threat level instead, see start of figure section.

Density of daphnicles,
 Low threat level,
 Initial one-hump perturbation of daphnicles, $m=1$,
 plus two-hump-perturbed steady food input, $m=1,2$.



Density of food,
 Low threat level,
 Initial one-hump perturbation of daphnicles, $m=1$,
 plus two-hump-perturbed steady food input, $m=1,2$.

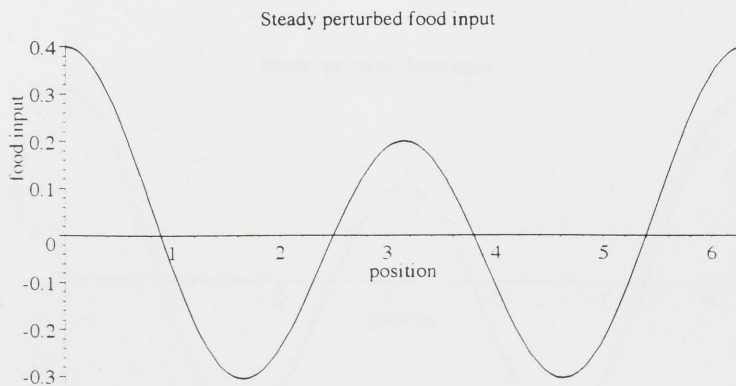
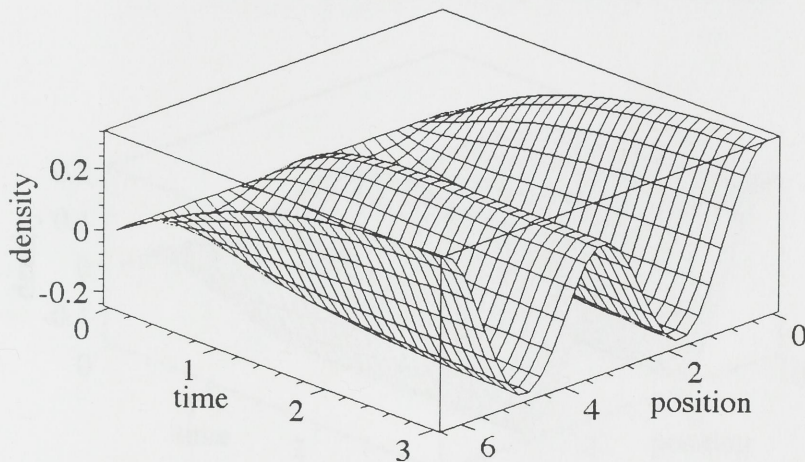
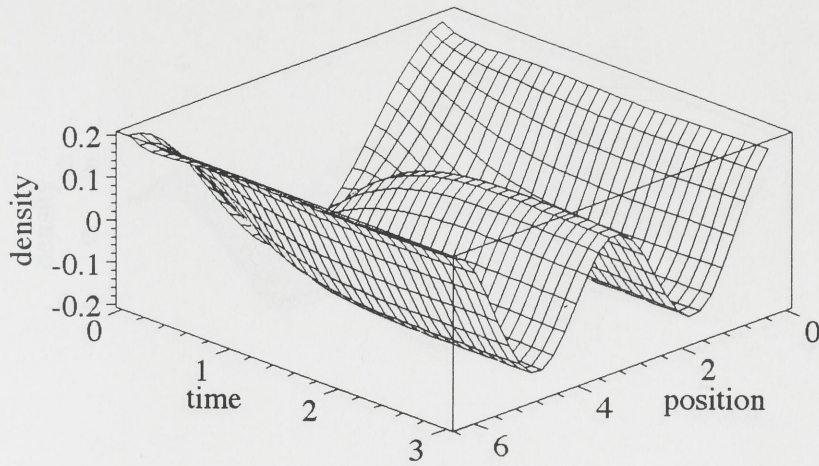


Fig.7: Space-time evolution of daphnicle density (top) and food density (middle) in case of low ground-threat level, when daphnicles are perturbed at $t=0$ as in Fig.4 and in addition a steady food input is given, bottom. For parameter values used, see start of figure section.

Density of daphnicles,
 Intermediate threat level,
 Initial one-hump perturbation of daphnicles, $m=1$,
 plus two-hump-perturbed steady food input, $m=1,2$.



Density of food,
 Intermediate threat level,
 Initial one-hump perturbation of daphnicles, $m=1$,
 plus two-hump-perturbed steady food input, $m=1,2$.

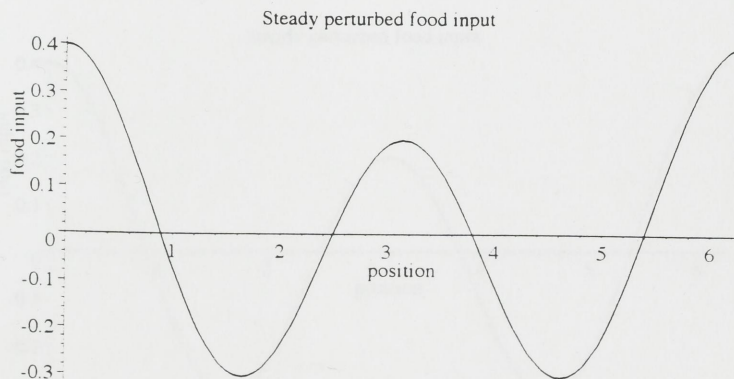
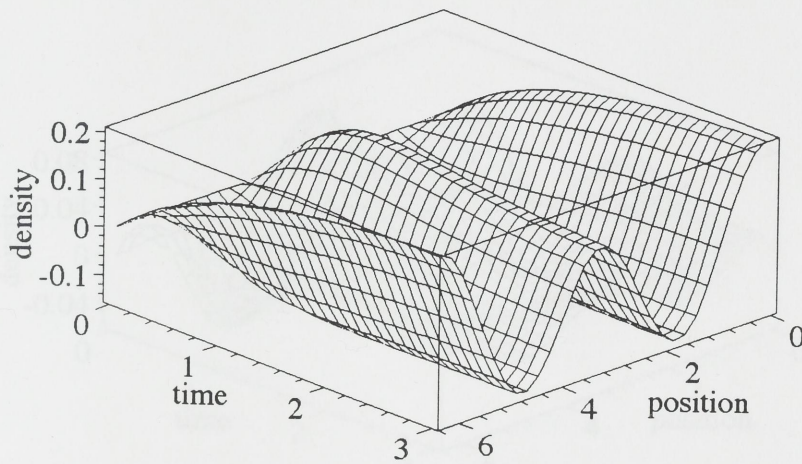


Fig.8: Same as Fig.7, except for intermediate ground-threat level instead, see start of figure section.

Density of diploids
 low-medium threat level
 Initial one-pump perturbation of diploids, level 1
 plus two-pump-perturbed steady food input, level 2

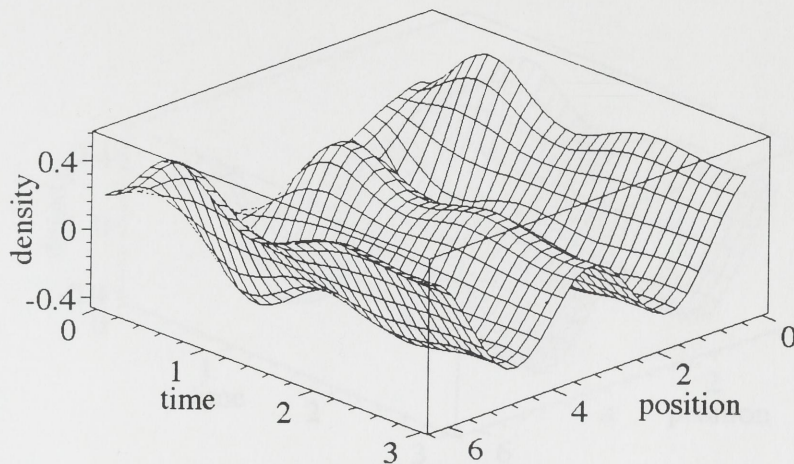


Density of food
 low-medium threat level
 Initial one-pump perturbation of diploids, level 1
 plus two-pump-perturbed steady food input, level 2

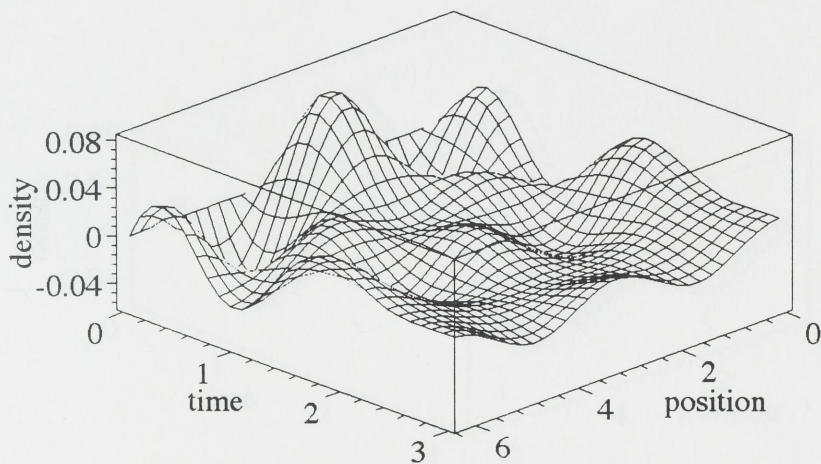


Fig. 8. Same as Fig. 7, except for intermediate growth-threat level instead, see text of figure caption.

Density of daphnicles,
High threat level,
Initial one-hump perturbation of daphnicles, $m=1$,
plus two-hump-perturbed steady food input, $m=1,2$.



Density of food,
High threat level,
Initial one-hump perturbation of daphnicles, $m=1$,
plus two-hump-perturbed steady food input, $m=1,2$.



Steady perturbed food input

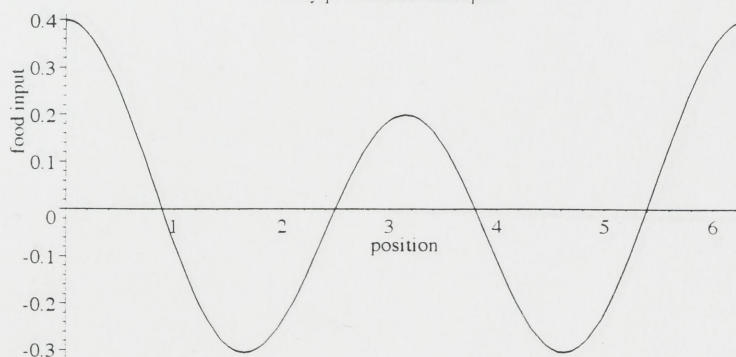


Fig.9: Same as Fig.7, except for high ground-threat level instead, see start of figure section.

Density of substrate
High input level
Initial one-bump perturbation of substrate level 1
plus two-bump perturbed steady food input level 2.

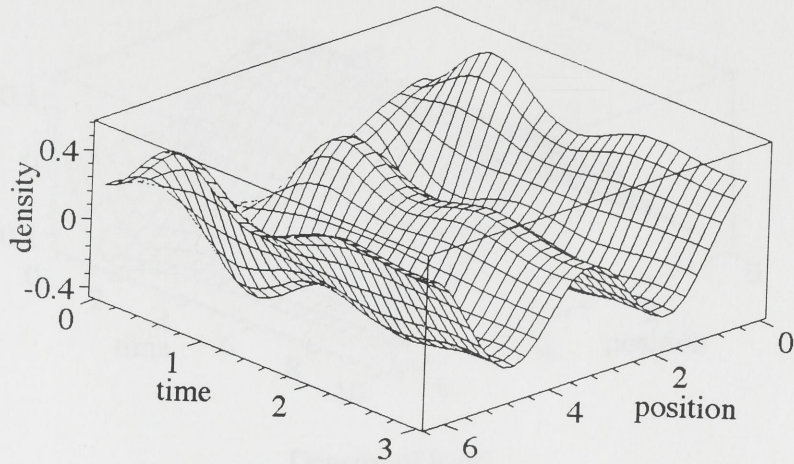


Density of food
High input level
Initial one-bump perturbation of substrate level 1
plus two-bump perturbed steady food input level 2.



Fig. 9. Same as Fig. 7, except for high ground-level input, see also Fig. 8.

Density of daphnicles,
High threat level,
Initial one-hump perturbation of daphnicles, $m=1$,
plus two-hump-perturbed steady food input, $m=1,2$.



Density of food,
High threat level,
Initial one-hump perturbation of daphnicles, $m=1$,
plus two-hump-perturbed steady food input, $m=1,2$.

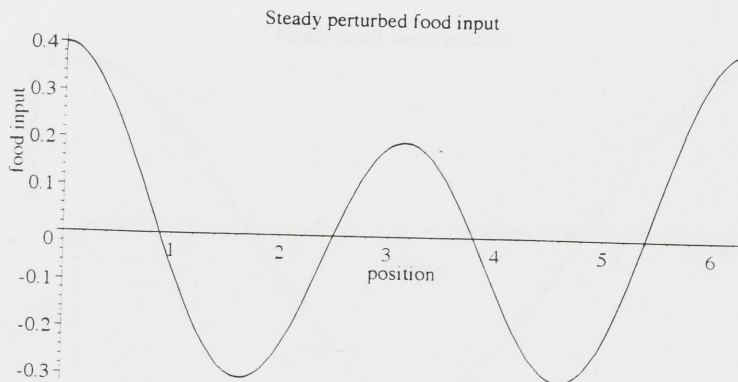
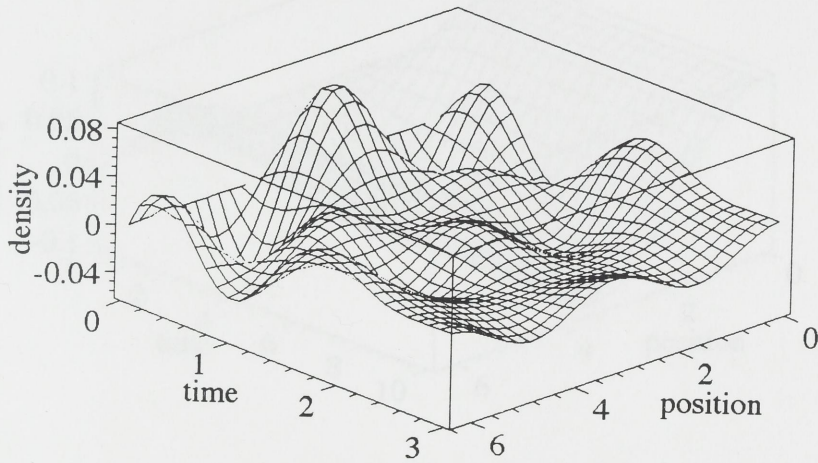


Fig.9: Same as Fig.7, except for high ground-threat level instead, see start of figure section.

Density of dustbins
 High thrust level
 Initial one-jump perturbation of dustbins, $m=1$
 plus two-jump perturbed steady state input, $m=1,2$

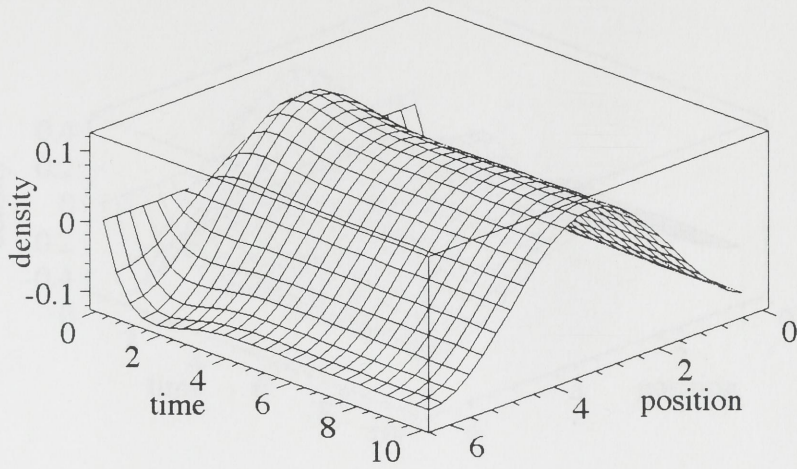


Density of food
 High-thrust level
 Initial one-jump perturbation of dustbins, $m=1$
 plus two-jump perturbed steady state food input, $m=1,2$



Fig. 8: Same as Fig. 7, except for high ground-thrust level input. Note that the position of the

Density of daphnicles,
Intermediate threat level,
No initial perturbations
Only small threat gradient



Density of food,
Intermediate threat level,
No initial perturbations
Only small threat gradient

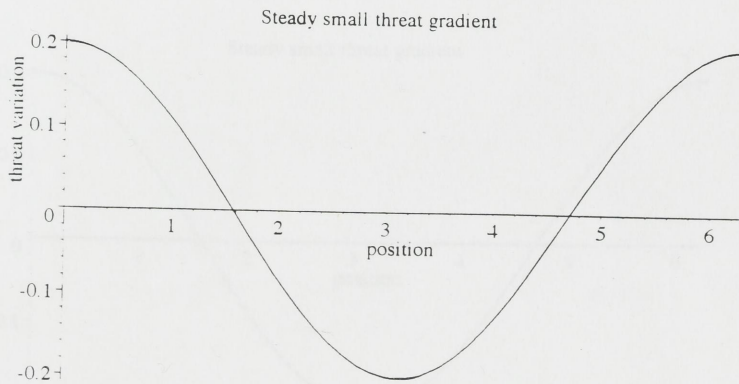
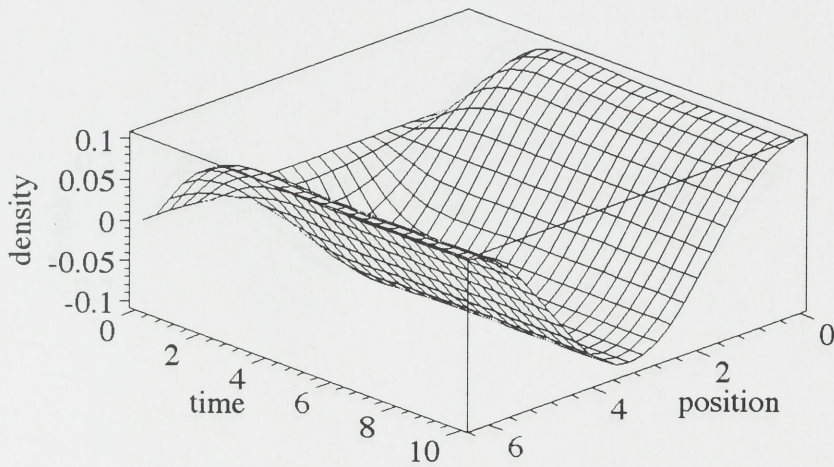
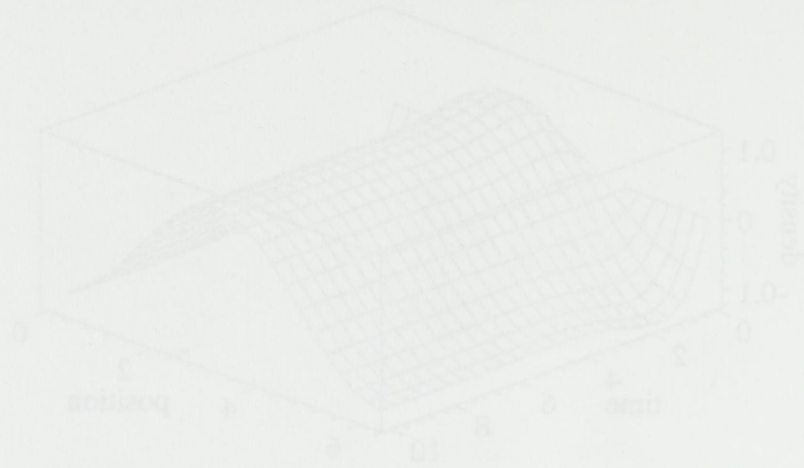


Fig.11: Same as Fig.10, except for intermediate ground-threat level instead, see start of figure section.

Density of bacteria
Intermediate front level
No initial perturbation
Only small front gradient



Density of food
Intermediate front level
No initial perturbation
Only small front gradient

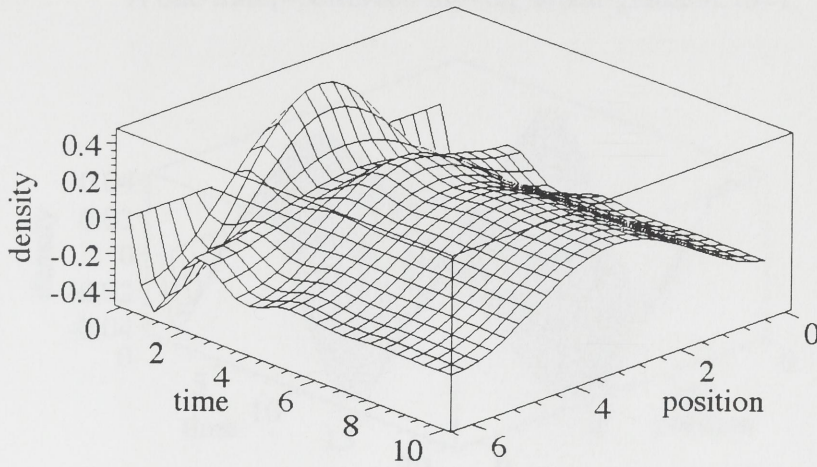


Density of bacteria



Fig. 11. Same as Fig. 10 except for intermediate front level instead of zero level.

Density of daphnicles,
 High threat level,
 No initial perturbations
 Only small threat gradient



Density of food,
 High threat level,
 No initial perturbations
 Only small threat gradient

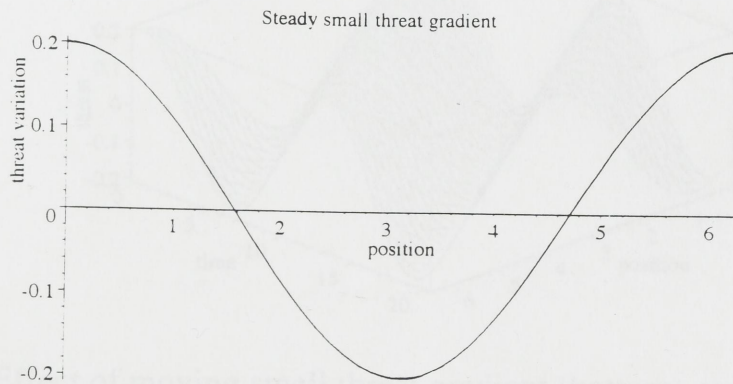
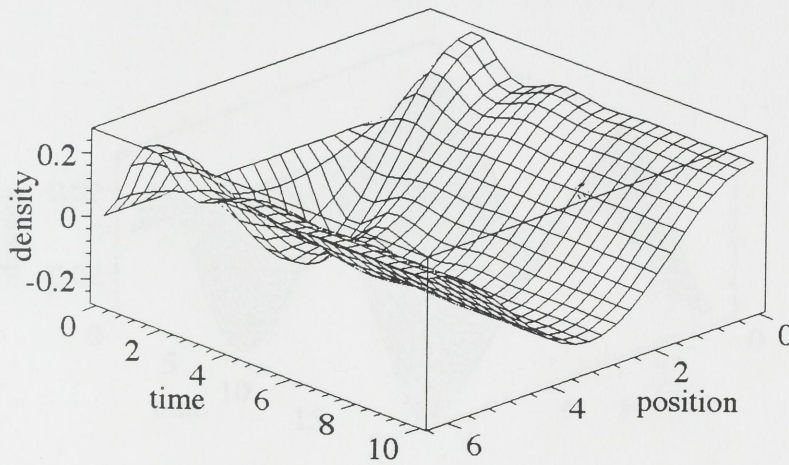


Fig.12: Same as Fig.10, except for high ground-threat level instead, see start of figure section.

Only small forest gradient
 No initial perturbations
 High forest level
 Density = 0.4



Only small forest gradient
 No initial perturbations
 High forest level
 Density of food

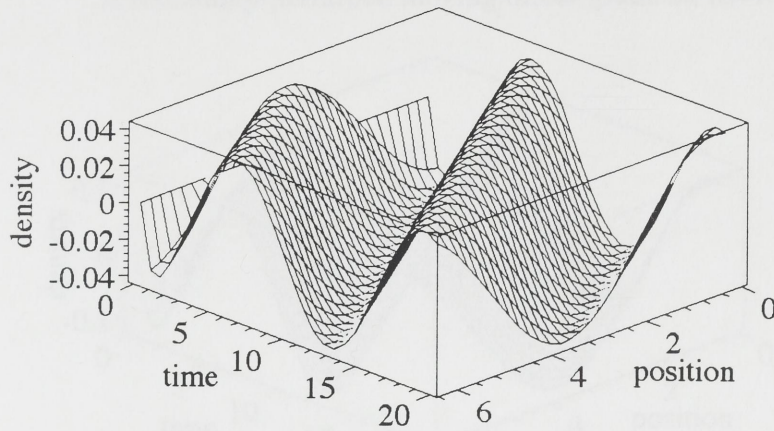


Substrate forest gradient

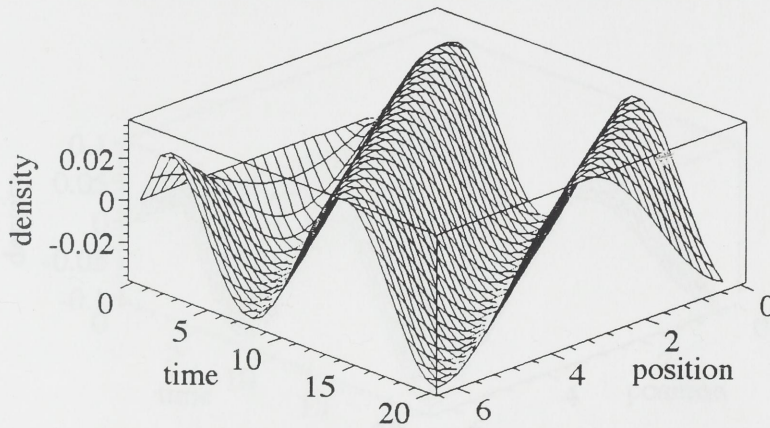


Fig. 12. Same as Fig. 10, except for high forest level instead, see also of figure

Density of daphnicles,
 Low threat level,
 No initial perturbation of daphnicles
 No perturbed food input.
 A one-hump-perturbed moving threat-gradient, $m=1$.



Density of food,
 Low threat level,
 No initial perturbation of daphnicles
 No perturbed food input.
 A one-hump-perturbed moving threat-gradient, $m=1$.



Moving threat density

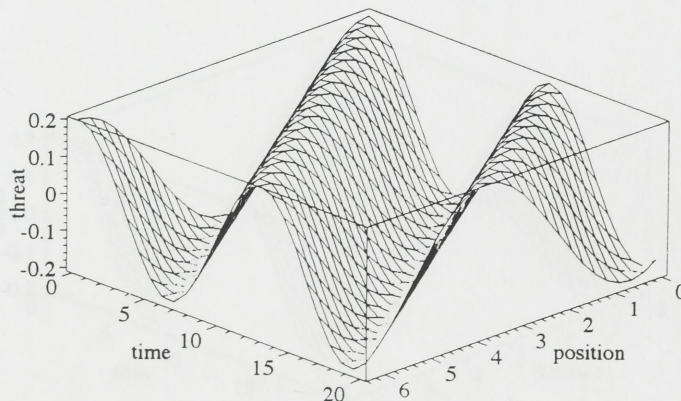
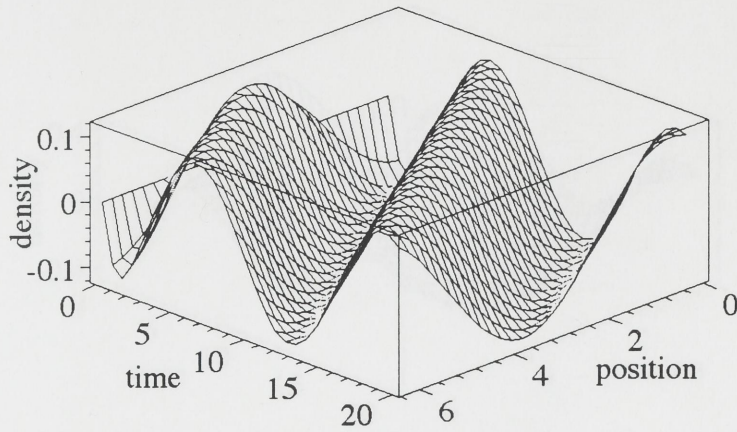
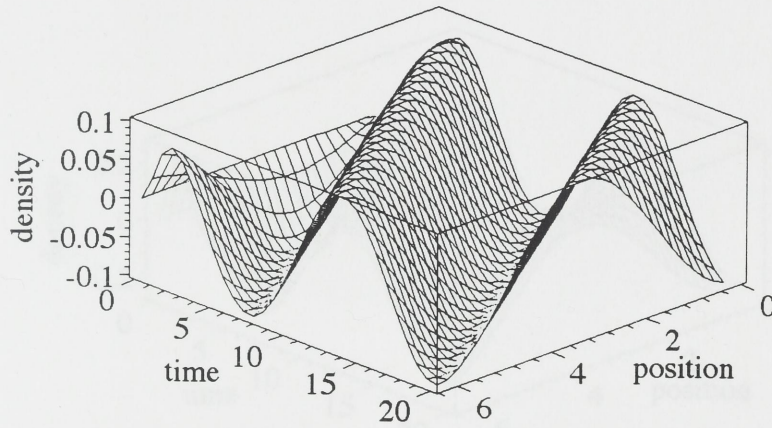


Fig.13: Effect of moving small threat gradient (bottom) on daphnicle density (top) and food density (middle) in case of low ground-threat level. For parameter values used, see start of figure section.

Density of daphnicles,
 Intermediate threat level,
 No initial perturbation of daphnicles
 No perturbed food input.
 A one-hump-perturbed moving threat-gradient, $m=1$.



Density of food,
 Intermediate threat level,
 No initial perturbation of daphnicles
 No perturbed food input.
 A one-hump-perturbed moving threat-gradient, $m=1$.



Moving threat density

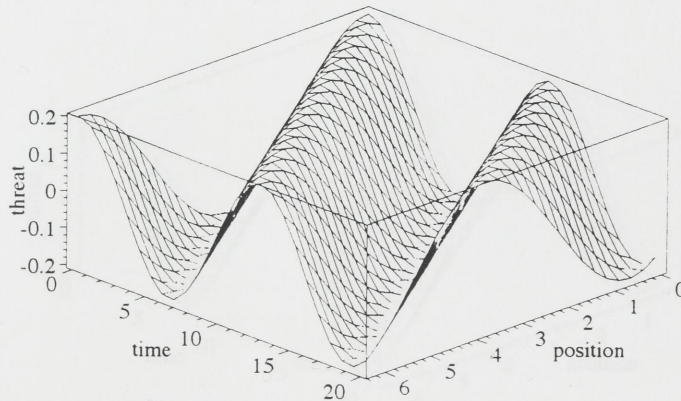
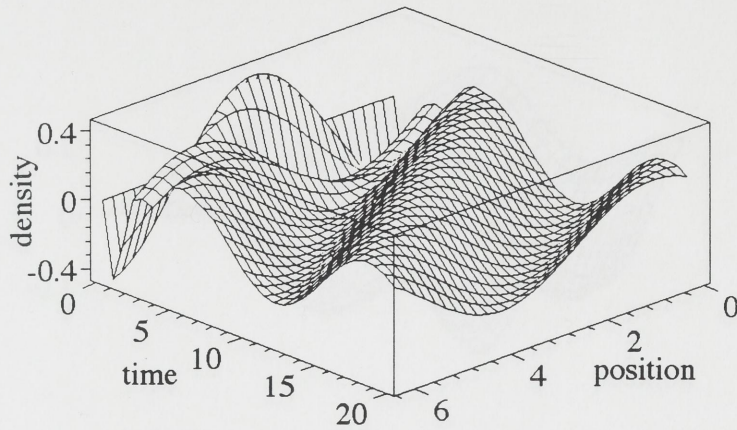
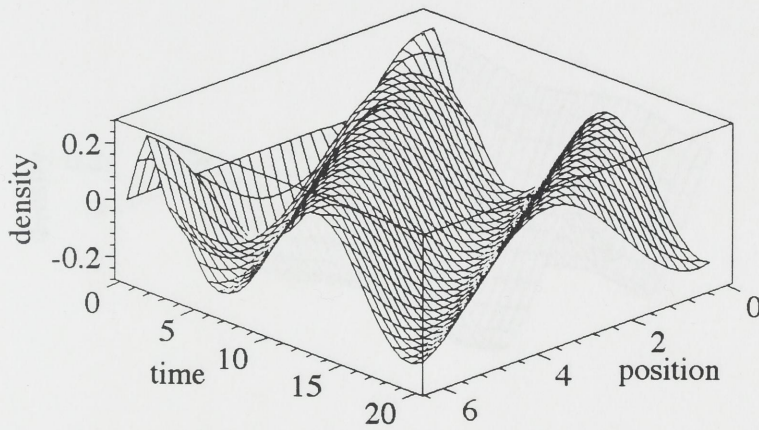


Fig.14: Same as Fig.13, except for intermediate ground-threat level instead, see start of figure section.

Density of daphnicles,
 High threat level,
 No initial perturbation of daphnicles
 No perturbed food input.
 A one-hump-perturbed moving threat-gradient, $m=1$.



Density of food,
 High threat level,
 No initial perturbation of daphnicles
 No perturbed food input.
 A one-hump-perturbed moving threat-gradient, $m=1$.



Moving threat density

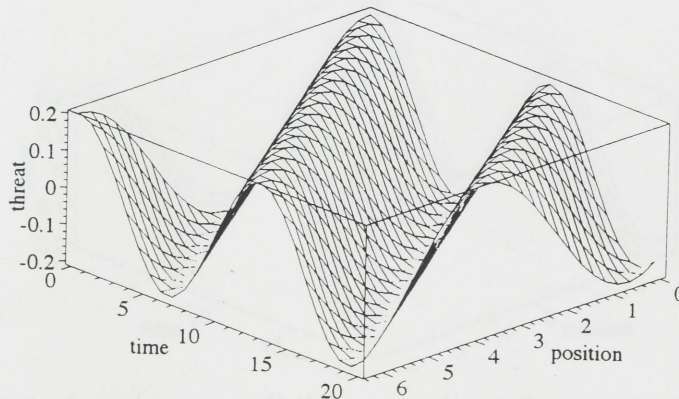


Fig.15: Same as Fig.13, except for high ground-threat level instead, see start of figure section.

A one-hour perturbed moving threat gradient, m^{-1}
 No perturbed food input
 No initial generation of daphnids
 High threat level
 Density of daphnids



A one-hour perturbed moving threat gradient, m^{-1}
 No perturbed food input
 No initial generation of daphnids
 High threat level
 Density of food

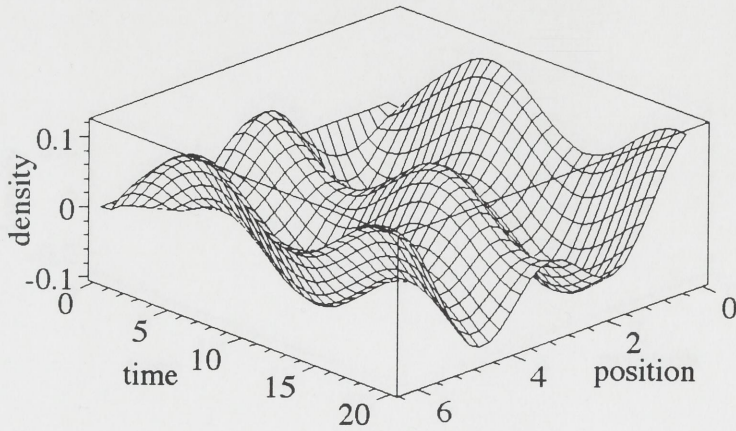


A one-hour perturbed moving threat gradient, m^{-1}
 No perturbed food input
 No initial generation of daphnids
 High threat level
 Density of daphnids

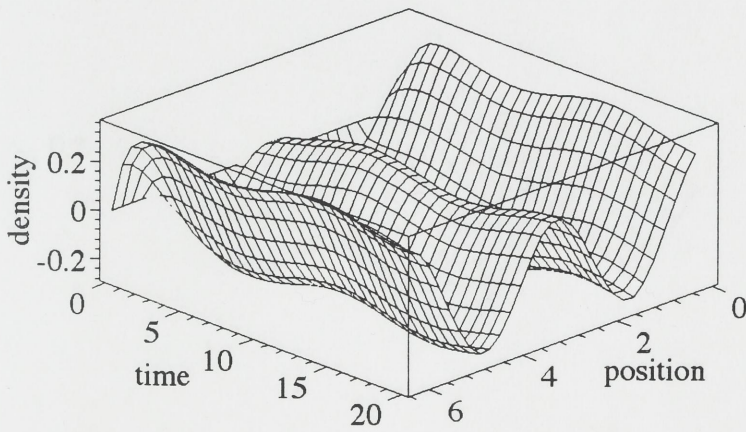


Fig. 15. Same as Fig. 13, except for high ground-threat level instead, constant of 0.1.

Density of daphnicles,
 Low threat level,
 No initial perturbation of daphnicles
 A two-hump-perturbed steady food input, $m=1,2$.
 A one-hump-perturbed moving threat-gradient, $m=1$.



Density of food,
 Low threat level,
 No initial perturbation of daphnicles
 A two-hump-perturbed steady food input, $m=1,2$.
 A one-hump-perturbed moving threat-gradient, $m=1$.



Moving threat density

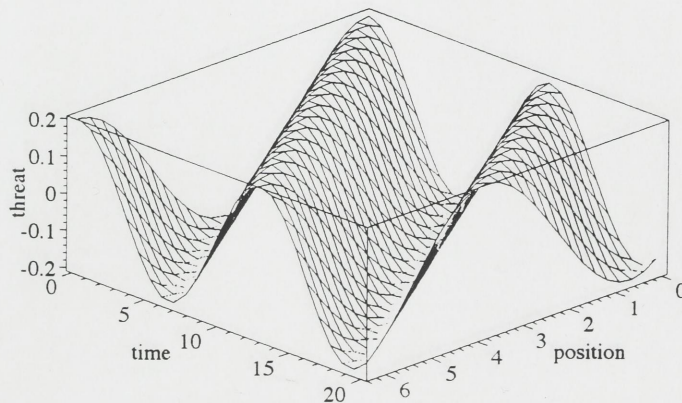
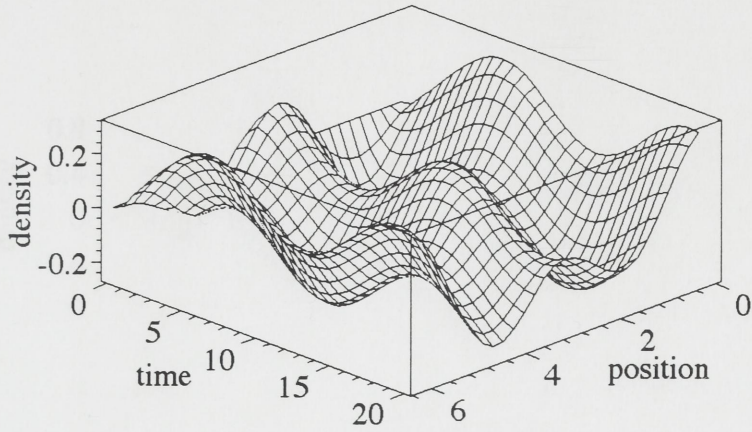
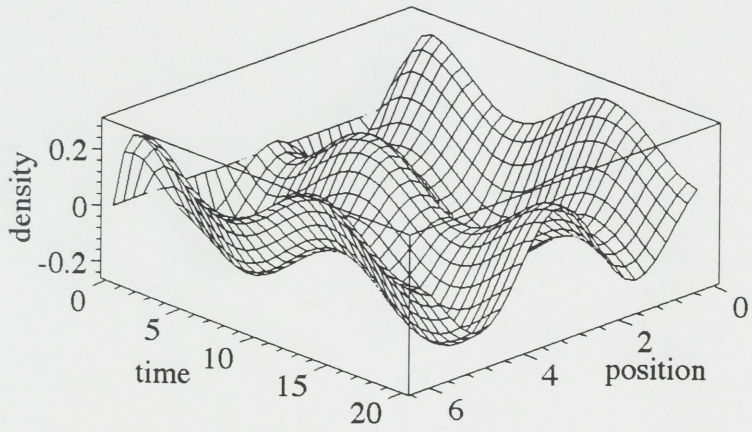


Fig.16: Effect of moving small threat gradient (bottom) on daphnicle density (top) and food density (middle) when a steady food input is given, as on bottom of Fig.7, when ground-threat level is low. For parameter values used, see start of figure section.

Density of daphnicles,
 Intermediate threat level,
 No initial perturbation of daphnicles
 A two-hump-perturbed steady food input, $m=1,2$.
 A one-hump-perturbed moving threat-gradient, $m=1$.



Density of food,
 Intermediate threat level,
 No initial perturbation of daphnicles
 A two-hump-perturbed steady food input, $m=1,2$.
 A one-hump-perturbed moving threat-gradient, $m=1$.



Moving threat density

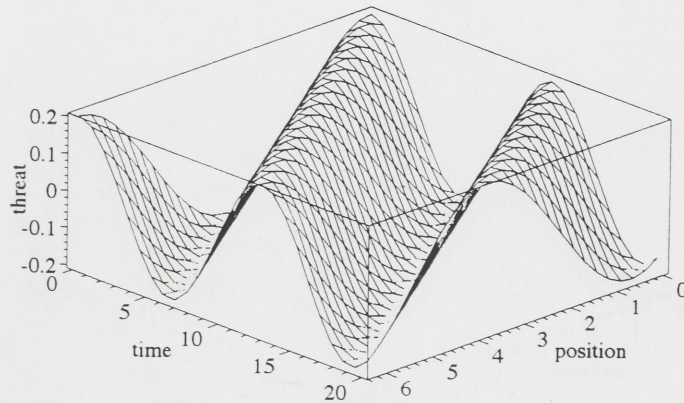
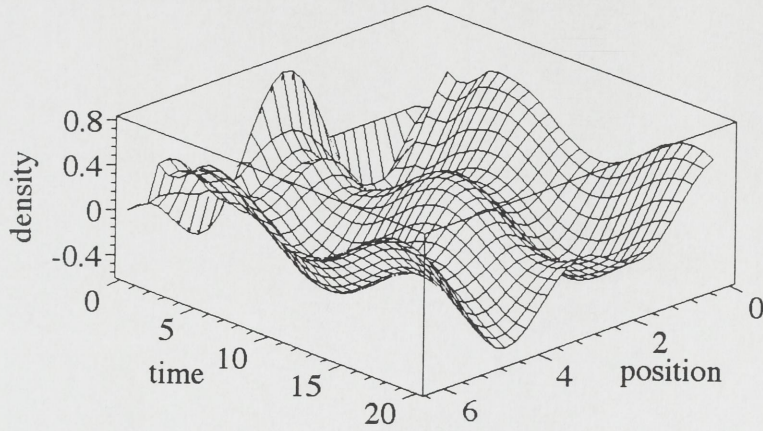
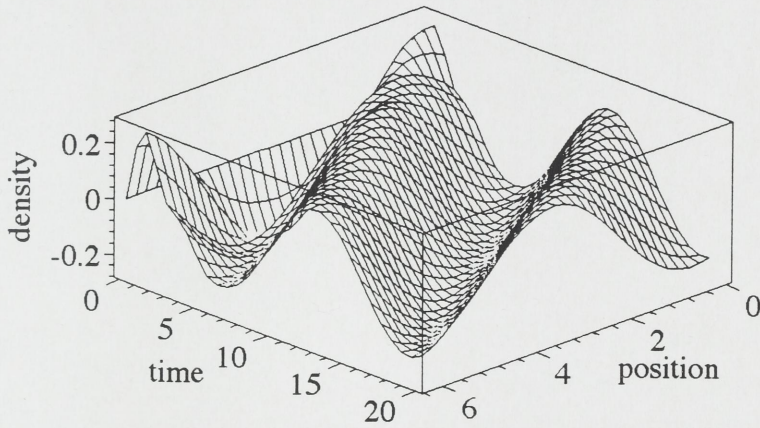


Fig.17: Same as Fig.16, except for intermediate ground-threat level instead, see start of figure section.

Density of daphnicles,
 High threat level,
 No initial perturbation of daphnicles
 A two-hump-perturbed steady food input, $m=1,2$.
 A one-hump-perturbed moving threat-gradient, $m=1$.



Density of food,
 High threat level,
 No initial perturbation of daphnicles
 A two-hump-perturbed steady food input, $m=1,2$.
 A one-hump-perturbed moving threat-gradient, $m=1$.



Moving threat density

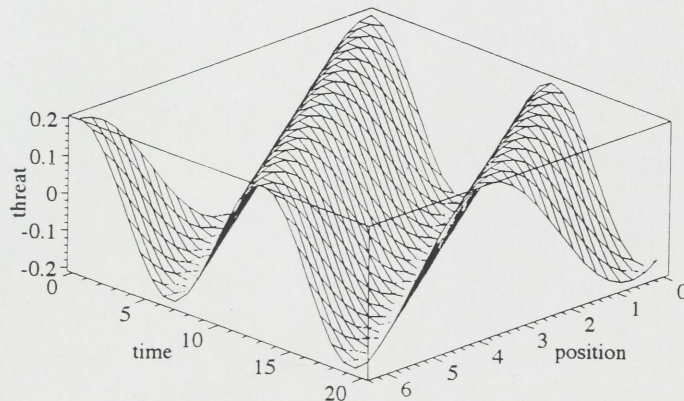


Fig.18: Same as Fig.16, except for high ground-threat level instead, see start of figure section.

Density of deerflies
 High initial level
 No initial perturbation of deerflies
 A two-hump perturbed steady food input, $w=1.2$
 A one-hump perturbed moving input, $w=1.2$



Density of deerflies
 High initial level
 No initial perturbation of deerflies
 A two-hump perturbed steady food input, $w=1.2$
 A one-hump perturbed moving input, $w=1.2$



Fig. 18. Same as Fig. 16 except for high ground level (see legend, see start of figure)



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