Department of APPLIED MATHEMATICS

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

by

Alf H. Øien

Report no. 156

June 2001



UNIVERSITY OF BERGEN Bergen, Norway



ISSN 0084-778X

Department of Mathematics University of Bergen 5008 Bergen Norway

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

by

Alf H. Øien

Report no. 156

June 2001

NB Rana Depotbiblioteket

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

by

Alf H. Øien

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

A description of daphnicle dynamics based on Einstie disory: Arecropts at analogue-modeling of systeming and beingviour of Daphnis

nalo HillA

angitad A

1 Introduction

The behaviour of Daphnia pulex, a zooplankton (size approximately1-2 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 daphnicleaccumulation 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

2

1 latroduction

The behaviour of Depining pulse, a couple should ge a upproximited viel must be a strained in the field extensively strained in recent year and made, is benating y conditions and in the field. These endes may be teen formaal of the trained of trained of trained of the trained of trained of trained of trained of the trained of tra

"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 daphnicleand food- densities is developed. These equations are valid around a static and

"microscopic" friction and excate (notion, or 'remperature', and to stochastic intalte of food. The degree of sutmation of individuals in gararal varies, and we cansider in particular that the strangths of the foreys are dependent on this

We stan the description from a Lincirc-discry point of view [5], and a dynamical equation for a probability distribution fraction dependent on depender position and velocity, as well at the depres of saturation, and virus, is set up. The modeling is close to "test particle" modeling in fraction theory. [b] a noluding an internal tract variable, i.e. food automized, wheth each particle responds to back ground infratence. From this raiser garend point of view, equations that are more related to at permittee in the the more virus in the decision of an area are more related to at permittee in the the states garend point of view equations that are more related to at permittee in the tests of the states are back and the states will be back at the states of the more states in the fact of the states and the states are not back at the states of the states of the tests of the states are back and the states are not back at the states of the states of the states of the tests of the states are back and the states are not be the states of the states of

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 daphnicle 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 daphnicles may feel from the surroundings. The solutions show that higher densities of food attract daphnicles are stressed by higher uniform threat they accumulate more strongly. Daphnicles 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 daphnicle evolution

By "daphnicles" 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 meassure 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 daphnicles 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 daphnicles 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 r (position) and v (velocity). As for particles these variables describe the external state. Thus we shall consider the state of daphnicles at time t to be given by 7 variables, (r, v, m). The daphnicles are responding to external influences. These influences are due to other daphnicles, 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 daphnicles 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].

mailtern state characterized by a closedy upper of technical existence however however staturation and saturation decline. The equations are specialized in a reconstruction for equicadimension. In spins of parine scalars starging they may nevertheless have write conservation of a laboratory set up of fairs case the region may be more their a conservation explination and multi targets. These equations are solved for a market begins on contraction where the interplay between destinates and food decary yeer relations are found writed multi targets. These equations are solved for a market of craces in ecclion of postaries and the food upper case there exists in a charter of the second varies, and we consider reactions to various hereis of uniform the higher depinicadepinic and the states food upper and these tracks of uniform the higher depinication of food actes depinicies and distributes them anone provide the states and of depinicies and the states food upper tracks and the states of the states of the states of depinicies and the states food upper tracks and the states of the states of the depinicies and the states food upper tracks and the states of the depinicies and the states food upper tracks and the states of the depinicies and the states food upper the states of the states of the depinicies and the states food upper the states and the states of the states of the states are states of the states and the states of the states of food actes of depinicies and destinates the states and the states of the states of the states food the states are states of the states and the states and the states of the states of the states were states of the states and the states of the states of the states are states of the states and the states of the states of the states are states of the states and the states of the states of the states are states of the states and the states and states are states of the states of the states are states of the states and the states and the states of the states are states are states of the

Modelling like this may serve as holis and give ideas of new isbastory experiments to be clone.

2 Basic equation of depletingle evolution:

By "displaying the "we shall mean and here a bie to repeat to establish minicipation and a source of minicipation and means the former service of minicipation and means the service depression of minicipation and means the mean service depression of minicipations, we shall demonst the former with the content of the weight of the mean means the mean service depression and the mean service is an available. We shall demonst the former with the former with the service of the mean means the mean service of the mean service of

A probability distribution function of the 7 variables, (r, 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 drdvdm denotes an infinitesimal volume element of the 7 dimensional space, then (1)

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

denotes the probable number of daphnicles in the volume element dr dv 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:

$$\frac{d\mathbf{r}}{dt} = \mathbf{v}$$

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

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 r and time t),

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

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.

A probability distribution function of the 7 veriables, or vant, of the extended phase space, plus time. F(t, r, r, r), will be used to appress the state of the daphnicles. If drababa denotes an infinite imal volusionisment of the 7 dimensional space, they F(t, v, meability)

denotes the probabile miniples of desiniteles in the voltage element deducts at these p. The evolution of F will be determined by the influences. We have discugated intrusces two types of influences of the dynamics of the dathcicles Ordered and and stochastic ones. In general the synamics to the dathcicles Ordered and and ones will be modelled by the following equations of metices, and well give size to what we may trajer to at ordered meticin in the extended class, contact, and well give size to what

The first equation gives the connection increases position and reflectly of a deplicitie. The second is an equation of motion, and on the right hand and a control of a deplicitie. (first term w(r,r) is the density of food evaluable, and the term represents a force that deplicitie feels towards higher food density. New w/V is a positive position as that may depend on an the depice of fulficiance, the probable density N of deplicities. (that may be in wherever degree of fulficiance, the probable density N of deplicities time 0.

and the level of a threat liefs (0.0). The coefficient will be further specified below. Thesecond term represents a first of densities will first a way, installing trends of in the following fibers or, we that densities the coefficient to depind on the strangh of the first first (1.0). The reputer will be used with the mediant on the strangh and we discuss the further is been allow, together will be mediant on the first near and we discuss the further is been allow. Together will be mediant on the strangh and we discuss the further is the strangent of the mediant on the first near and we discuss the further is the strangent of the rest of the mediant on the strangent of the further is the strangent of the strangent first of the strangent of the first strangent of the strangent of the strangent first of the strangent is the first strangent of the strangent of the strangent first of the strangent is the strangent of the strangent of the strangent is the strangent first of the strangent of the former strangent rest for the strangent first of the strangent is the strangent of the strangent of the strangent is the strangent densities from the strangent is the strangent of the strangent is the strangent densities from the strangent is the strangent of the strangent is the strangent densities from the strangent is the strangent of the strangent is the strangent densities from the strangent is the strangent of the strangent is the strangent densities from the strangent is the strangent of the strangent for the strangent densities from the strangent is the strangent of the strangent for the strangent densities from the strangent is the strangent of the strangent for the strangent densities from the strangent is the strangent of the strangent for the strangent densities from the strangent is the strangent of the strangent densities from the strangent is the strangent of the strangent for the strangent densities from the strangent is the strangent of the strangent densities from the strangent the strangent is the strangen 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

$$E(m, p, N) = E_0 e^{\alpha_0 p} (N_m - N)(m_0 - m)$$
(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 unprobable 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 $(N_{\rm m}-N)$, where $N_{\rm m}$ 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,

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

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

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

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

In addition to these ordered influences, the deployeds and dranges due to food bracks when food is available. This intake will be modelled as a stochastic process. Also erratio motion of the depinences, different from ordered intoion due to the forces discussed above, will be incorporated. However, we first discuss the conflorents. E(m.p.N), E(m.p.), L(m) and bim.p.).

2.1. Form of force-conflictents for maked method

The forme of the coefficients that follow must some bestering from what is observed of Daphnic behaviour. Simple forme have been used for coldeniation and occause even such forms may express treads 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 integrates.

We shall let E(m.p.N) be decreasing with bighes at radiated bighes in may in less degree direct depinistics toward higher food conscentions. A simple form that may take care of this effect, and she threat and density effects, is

Here E, is a positive coefficient and m, is unwhat positive constant, m, represent a high high degree of summary that is very unprobable to reach because of other collarences. The exponential terminary the field port of which may take values on a sense from 0 (no thread) to large values, say, and a positive constant of there we consule the field port of a terminary take values of other collarences in the terminary and a positive constant of the field is of the field port of t

K(m,p), positive, shall be decreasing with indenasing *m* to reflect a traitency of diphnicies to repulse each other less when they become more satisface we we might set when no predetor threat is present.

where K₀ and it are positive constants. When first is mailtain threat field sized (which takes values on a scale fibre () and appoint), we must for locance of

where d, and d, are positive constants Henry a thread will always italy a sector di diminishing the reputsive allow bi-other deployingly, and being inch anough, will then off the effect

L(m) may be modelled mi.

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

$$V(m,p) = V_0 e^{\tau_1 m + \tau_2 p}$$
(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 $dV' = \left| \partial(\mathbf{r}', \mathbf{v}', m') \right|_{dV}$ where the lattern denotes the Lember 1.5 for the state of the st

 $dV = \left| \frac{\partial(\mathbf{r}', \mathbf{v}', m')}{\partial(\mathbf{r}, \mathbf{v}, m)} \right| dV$, 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

$$\frac{dF}{dt} = 0 \tag{9}$$

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,

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

where γ and L_{γ} are positive constants to refer a least only to respond less in a light intensity gradient by increasing degrees of saturation.

For V(m,p) we take into account holds an effect of himery deplacence to be more careless with respect to a intrast gradient from predictors than categorie ones, and also an effect of awareness and coassoquent response non threat-gradient when the fractalevel increases, pare for iterative.

 $M_{\rm eff} = M_{\rm eff} = M_{\rm eff} = 1.2$

where Mart, and by the positive constants,

A2 Dynamical equation of codenal exclution of for the orderal exclution of a first departicles in the When Eq. (2) determines the orderal dynamics of introduct departicles in the influencing background, a Liozville theorem [5] is wild, such that the swerm of depinicles here to excern of depinicles to the compressible field in the 2-dimensional phase space. Two observations will lead to this compressible field in the 2-dimensional phase space. Two

1) Consider an infinitestruit volume element in the 7 dimensional phase space of time t, denoted by $dV = drebain At time <math>t + \Delta t$ this volume classics following the motion of points according to the system of equations (2), measiverus into dV = dr dv dist. The evolution of phase space points from time t to time $t + \Delta t$ may be considered as a co-ordinate transformation, and we neve size felaviou

 $dV = \frac{p(r, v, m)}{d(r, v, m)} dV$, where the Li star database the Jacobian of the manimum anon.

Using the equations of motion, Eq.(2), one derives mut $\begin{vmatrix} 362 & 7028 \\ 362 & 7028 \end{vmatrix} = 1 + 10(24)^{12}$.

where O is the order symbol.

2) The set of equations (2) has unique volutions. Hence the purpher of states whigh the volume elements at time t and within the relationed volume blemed at time $t + \Delta t$, is the sump. Transitors F(t', t', or (t'+ m))dN = E(t, t, m, t)dV.

i.a. the total time derivative tollowing the methon or daphneoles is zero, and the depinicles behaves as an histompressible fluid in the 2 dimensional phase space. Written out in more delait, using the set of consisting (2), one has for the ordered dynamics,

We make a related concerning the BN Car Index terms Tax term that he considered from a general point of view, namely as a not correlated but determine when

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

$$\frac{1}{M}\frac{\partial}{\partial \mathbf{v}_{1}} \cdot \int \mathbf{K}(|\mathbf{r}_{1}-\mathbf{r}_{2}|)F(2,t)F(1,t)d\mathbf{r}_{2}d\mathbf{v}_{2}dm_{2} = \frac{1}{M}\frac{\partial F(1,t)}{\partial \mathbf{v}_{1}} \cdot \int \mathbf{K}(|\mathbf{r}_{1}-\mathbf{r}_{2}|)F(2,t)d\mathbf{r}_{2}d\mathbf{v}_{2}dm_{2}$$
(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

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

and hence may write

$$\int \mathbf{K}(|\mathbf{r}_{1}-\mathbf{r}_{2}|)F(2,t)d\mathbf{r}_{2}d\mathbf{v}_{2}dm_{2}$$

$$=\int (\mathbf{r}_{1}-\mathbf{r}_{2})K(|(\mathbf{r}_{1}-\mathbf{r}_{2})|)\left(F(\mathbf{r}_{1},\mathbf{v}_{2},m_{2},t)+(\mathbf{r}_{2}-\mathbf{r}_{1})\cdot\frac{\partial F(\mathbf{r}_{1},\mathbf{v}_{2},m_{2},t)}{\partial\mathbf{r}_{1}}\right)d\mathbf{r}_{2}d\mathbf{v}_{2}dm_{2}$$

$$=\int K(|(\mathbf{r}_{1}-\mathbf{r}_{2})|)(\mathbf{r}_{1}-\mathbf{r}_{2})(\mathbf{r}_{1}-\mathbf{r}_{2})\cdot\frac{\partial F(\mathbf{r}_{1},\mathbf{v}_{2},m_{2},t)}{\partial\mathbf{r}_{1}}d\mathbf{r}_{2}d\mathbf{v}_{2}dm_{2}=K_{0}\mathbf{I}\cdot\frac{\partial N(\mathbf{r}_{1},t)}{\partial\mathbf{r}_{1}} \quad (13)$$

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

$$\frac{1}{M}\frac{\partial}{\partial \mathbf{v}_{1}} \cdot \int \mathbf{K}(|\mathbf{r}_{1}-\mathbf{r}_{2}|)F(2,t)F(1,t)d\mathbf{r}_{2}d\mathbf{v}_{2}dm_{2} = K_{o}^{'}\frac{\partial F(1,t)}{\partial \mathbf{v}_{1}} \cdot \frac{\partial N(\mathbf{r}_{1},t)}{\partial \mathbf{r}_{1}}$$
(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

daphniolas, in contrast to crenelated interaction rooms, described inten it may be derived from the form

(11)

i.e. from a generalised "Viscor term", see [6] for Viscor's equation. If is the daphnicle mass, $K = (r_1 - r_1)K\beta(r_2 - r_2)\beta$ nearestate calibratication force between daphnicle and 1 and daphnicle and 2, restricted directed along their relative position. Because of the product between the distribution functions, the form is merical ite uncorrelated part of interaction. When the integration is performed viscor the form is dimensional plane space of dephatels are located along the state the condimensional plane space of dephatels are located are along the state the no. I due to all other depinicles. For the special case of a rule gedemic water approximate

 $F(2, s) = F(s_1, s_1, m_1, s) = F(s_1, s_2, m_1, s) = (s_1 + s_2) = \frac{(s_1 + s_2)}{(s_1 + s_2)} \frac{(s_1 + s_2)}{($

and itence may write

$$= \int (a - a) \lambda \partial (a - a) \partial (a - a)$$

Af By, J and G - S, Dr C, Allant, Gr, and G, and F - A - Solution of the second state is not

et one should consider asing Eq.() () hadead.

3.3 Food intake and empire motion

Both food intake and erastic treatme will be modelled at stochtatic processes. Orenerally, the origin of stochtaticity is deprecent to constated parts of interactions. Two terms representing the erations in start will realized to constated parts of interactions. side of Eq.(10). We start contribute that food totates in allowed to up on nices. exemually forces the description factories in start will realized to up on nices. in the degree of saturation stored tot value many, and likewise, controls will targ eratic if no influences are present, and force the distribution in velocity forced to blacwelling distribution. The term of the target start to the distribution in the degree blacwelling distribution in the term of the target start better the distribution in the degree of saturation in the term of the terms and the degree of saturation in the term of the terms are influences are present and force the distribution in the degree of saturation in the term of the terms the terms in the degree of saturation in the term of the terms are influences are present and the terms are influences are present and the term of the terms in the terms in the terms in the terms of the terms in the terms of the terms of the terms in the term of the terms in the term of terms in ter

2.3.1 Food intaker

Intalize of food is related to dephetedo-load-density into action, and a sociality modelling may be adequate. Therefore we instance a simple Foldure Francie techn of the form

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

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

$$\beta = \beta_0 n \tag{16}$$

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

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

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

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

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

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

$$B = B_0 e^{\sigma n} \tag{20}$$

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

where
$$Q_0 \rho_1$$
, 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

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

$$\left(\frac{21}{57}\right)_{max} = B \frac{6}{100} \left((m - m_s) B - \frac{6}{100} \right)$$

Here β is a "collision frequency for from make" hereign depleticles and the background-food, and we model it simply as

$$(a_1) = a_1 a_2$$

where β_i is a constant and a to the base density. The first term on the right head side of Eq.(15) therefore represents a "deng" of duplicatic matricities towards m_i is they take in food. The second term, the $q_i \beta$ -term, bidences this drug and gives rise to sequence spread when food is taken in. The coefficient any he modelled as

where ke is a positive constant and helps ais's positive, why factores alcadily in their. This will result in a seturation spiced that is smaller for high food, concentrations deal for low, but eventually the specifi will go to tetric. For the case that h, is constant we

$$(1 - \frac{76}{16} + 7(\mu n - m))$$

not loc

when also the food septementation wils constant, hold in space and time

A conseptanding term as the and above stup harsed for the credic mation of the daphnicles, even though a simple refrastration term, weaking for many purposes. Correstruction to Fact 151 and 1000 areas

B is a collision frequency scheming a fuidillast between the databales and the background, and we may statute a form

where B_0 and ϕ are positive correlate. Hance we allow the friction to introduce with increasing food density W_0 may assume the "temperature" coefficient Q has a form $\phi = \partial_{10} \hat{P}_{0000}$

where $Q_{n} \rho_{n}$ and ρ_{n} are positive constants such that the spread in velocity due to entric motion will measure emphasized, i.e. with necesive values of m and the reside with increasing thesis, itoricites a steppy along mas in Q and hence m referring equal for depictives with inner and lowers in to not to be expected due to need mingation a decrease of Q for low metalens is provide the finance from the methods. 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

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

$$Bv^{2}$$

(23)

i.e. when

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 .

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

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

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

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

where 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

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

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

$$\lambda(m) = -\mathcal{E}(m - m_0)$$

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

where m₁ is some negative critical value of anutation where well-ching sets in, may be used instead. However, for m-values mouth 0 the form Eq.(21) of (2 will be used. We note that the creatic realizes well, while we have

 $vE + \frac{Q}{B} \frac{\partial F}{\partial x} = 0$

i.c. when

 $F = F_{i}(x,m)e^{-2\theta}$

for the case that food density (i.e. 3) is constant and during a is accessent (is, Q). However, the spread in velocity will vary with a and the constant levels of a and a

> 2.4 Equation for distribution function including both ordered and specifical evolutions, and equation for food density Collection result from the two forencess results on the terms

 $\frac{37}{37} + \pi \cdot \frac{37}{37} + \left(E(m,p,N) \frac{36}{37} - E(m,p) \frac{37}{37} + E(m,p) \frac{37}{37} - \frac{37}{37} - \frac{37}{37} - \frac{37}{37} - \frac{37}{37} - \frac{37}{37} + \frac{37}{37} +$

which takes into necount both the oniered dynamics and the stochastic dynamics. The inclusion of stochastic terms is the quantum the grant of the plane space density of depleticles does not believe as an incompressible fluid any inner $d_{\rm eff}$. Coefficients have been directed above. One may assert that the light intensity of depleticles does not believe as an incompressible fluid any inner $d_{\rm eff}$. Coefficients have been directed above. One may assert that we light intensity for the context of the plane dependent of the terms of the term of the terms of the terms of the terms of terms o

where n_e is a dult of food in water. D is a diffusion coefficient, which may be assured consistal. A(m) is a consumention rate that depende upon the degree of saturation of dephylicles, and D is a constant rate of food input. We shall assume the colourprination rate increases with decreasing at cap as

where A, and E are constraint, or more simply ds.

Alma - alla - alla -

for means, which are the most product of the two densities of m Nove that the experimentation term is proportional to the product of the two densities. Second contract and that serve the exists between this computation term and the food backs term, Eq.(15), have term, Eq.(16), not have elaborate any factors on this connection in detail. Eqs. (24) and (25) are a coupled set of equations for F and a child recesses a faller detailed model description of declarations for a set of equations for F and a child recesses a faller 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

<u>3.1 Equation of evolution for saturation dependent density</u>

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,

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

where

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

is the saturation dependent density and

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

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

$$\frac{\partial (f\mathbf{U}(\mathbf{r},m,t))}{\partial t} + \frac{\partial}{\partial \mathbf{r}} \cdot \langle F\mathbf{v}\mathbf{v} \rangle_{\mathbf{v}} - f \left(E(m,p,N) \frac{\partial n}{\partial \mathbf{r}} - K(m,p) \frac{\partial N}{\partial \mathbf{r}} + L(m) \frac{\partial l}{\partial \mathbf{r}} - V(m,p) \frac{\partial p}{\partial \mathbf{r}} \right)$$
(30)

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

turns out, where we have set

particular fiq (24), as a high forei, or detailed, dawerginen. It is clean that genes information resulting from this description may be difficult to discrete directions practice. One may fluctions ask if a more source grained description from the gran could be adequate newspir for practical purposes. However, derivations of more could be adequate newspir for practical energies as However, derivations of more contain some important high level descriptions from the difficult is treatparent otherwise. In the rest section we derive must larger into the difficult is treatparent level description develored all years

3 Separate kindik equations for attaccion and velocity dependent dominies. Warm and cold models

3.1 Equation of evalution for estumtion dependent descent

From Eq.(24) we have derive some hower level appartone. These equations will adde when anotheras, of velocity and saturation are micer. These new exactions will be coupled, generally in infinite chains, and a central problem concerns how to quacante these chains to a new equations that may be solved:

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

$$\frac{\partial f}{\partial t} + \frac{\partial}{\partial t} \cdot (f_{t})(r_{t}, m'_{t})(r_{t} - \frac{\partial f}{\partial m} = f_{t} \frac{\partial}{\partial m} \left((r_{t} - r_{m})f_{t} + \frac{\partial}{\partial t} \frac{\partial f}{\partial t} \right), \dots$$
(12)

where

$$= f(a_{m,1}) = f(a_{m,2},a_{m,2}) dx$$

is the saturation dependent density under

gives the saturation dependent mean flow E of daphatches. The equation before is coupled to an equation for U. We derive an equation for E multiplying Eq.(C4) by a and integrate over b. Then the equation.

the shell an shelly also about

$$\langle F\mathbf{v}\mathbf{v}\rangle_{\mathbf{v}} = \int \mathbf{v}\mathbf{v}Fd\mathbf{v} \tag{31}$$

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

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

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

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

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

for a function ϕ of *m*. Note that

$$N = \int g d\mathbf{v}.$$
 (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 $\langle . \rangle_m$ -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

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

$$f(Free)_{i} = free Freet$$

Thus the equation for /C introducer both a new orknown function (Fwe), maddition to the ordinary density M which already append to Eq.(24). (Fwe), expresses excitational, or the degree of cirulic moment, of the deprinistics and is comprovide to thermal motions of ordinary particles. (Fwe), may be found inling the next higher velocity moment of Eq.(24). Instead of setting up such an equation for (Fwe), which will contain even higher order velocity moments, we derive below an approximate expression for (Fwe), that will monents the set of crimpled equations in this measure 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): Integrates equiddat over m we obtain

$$\frac{16}{26} = \frac{1}{26} + \frac{1}{26}$$

where

$$g(\mathbf{x}, \mathbf{v}, 0) = \langle \mathcal{E} \rangle_{\mathbf{v}} = \langle \mathcal{E} \langle \mathbf{x}, \mathbf{v}, \mathbf{u}, \mathbf{v} \rangle du_{\mathbf{v}} \quad (33)$$

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

$$F_0(m))_{\mu} = \left\{ F(x, y, m, x) \phi(m) dn_{\mu} \right\}$$
(34)

for a function (nof m Note that

The other form of Q(m,e), Eq.(22), may actually well be used in Eq.(32). One obscives in Eq.(32) the coupling to the variance () - moments in general this coupling may dise a substantial problem. However, a suide interval be done only for special cases where we only need the first order re-moment. Maintolying Eq.(24) by a suid integrating we obtain

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

where

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

is connected to a mean saturation.

3.3 Equation for density N(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

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

where more precisely

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

is the probable observed number density of daphnicles and

$$N\mathbf{U}_{0}(\mathbf{r},t) = \int F(\mathbf{r},\mathbf{v},m,t)\mathbf{v}d\mathbf{v}dm = \int f\mathbf{U}(\mathbf{r},m,t)dm$$
(40)

gives the probable observed mean flow U_0 . An equation for U_0 we obtain integrating Eq.(30) over m,

$$\frac{\partial (N\mathbf{U}_{0}(\mathbf{r},t))}{\partial t} + \frac{\partial}{\partial \mathbf{r}} \cdot \langle F\mathbf{v}\mathbf{v} \rangle_{\nu,m} - \left(\langle fE(m,p,N) \rangle_{m} \frac{\partial n}{\partial \mathbf{r}} - \langle fK(m,p) \rangle_{m} \frac{\partial N}{\partial \mathbf{r}} + \langle fL(m) \rangle_{m} \frac{\partial l}{\partial \mathbf{r}} - \langle fV(m,p) \rangle_{m} \frac{\partial p}{\partial \mathbf{r}} \right) = -B(n)NU_{0}(\mathbf{r},t) \quad (41)$$

<u>3.3.1 Approximation of</u> $\langle Fvv \rangle_v$ warm and cold models In order to truncate the *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.

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

Then

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

where **I** is the identity tensor. Using this approximation, Eq.(30) turns into

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

$$\frac{\partial (FV(m,p)m)_{n}}{\partial v} = \frac{\partial p}{\partial r} + ag = -\beta G + m_{0}g + \beta (n) \frac{\partial}{\partial r} (nG) + Q_{0}e^{-m} \frac{\partial}{\partial r} (r-r,p_{0})_{g}$$

where

$$G(\mathbf{r}, \mathbf{v}; t) = \{t, m\}_{t} = \{S_{t}, t, u, m, t\}$$
 makes

is connected to a mean saturation.

3.3 Equation for density West of daphaidles - Swam and cold goods!

In all the equinions derived the density N appears. The equi-ten for N is obtained integrating Eq.(24) over both velocity and saturation. Since integration ever, velocity give Eq. (27) we need only integrats that expansion everys. Thus we obtain

$$(30) = (30) + \frac{1}{32} + \frac{1}{3$$

where more precisely

$$N(\mathbf{r},t) = \int F(\mathbf{r},\mathbf{v},m,t)d\mathbf{r}d\mathbf{n} = \int g(\mathbf{n} \mathbf{r}, \mathbf{v}, \mathbf{r}, \mathbf{r},$$

the probable observed an initial density of daplanicles and

$$(01) \qquad \text{mig}(1, m, \pi)(P) = \min \min(1, m, \pi, \pi) + \left[= (1, \pi)_{\pi} \text{Ov} \right]$$

gives the preliable observed mean flow file. An equation for the we obtain integraling Eq.(30) over m.

3.1. Approximation of (PVR) is and cold models.

In order to truncate the r-monical equations we assume that the daphatele distributed finited function function to lowest tador in the velocity variables may be approximated by a Maxwellian, i.e.

$$F(x, x, m, t) = f(x, m, t) I(2\pi)^{-2} (B I (t)^{-2} = \frac{2}{2}$$
(4.2)

and the Eq.(41) for NU_0 into

$$\frac{\partial(N\mathbf{U}_{0}(\mathbf{r},t))}{\partial t} + \frac{Q_{0}}{B_{0}}\frac{\partial}{\partial\mathbf{r}}(e^{-\sigma_{1}}e^{-\rho_{2}p}\int fe^{-\rho_{1}m}dm) + \frac{\partial}{\partial\mathbf{r}}\cdot\left\langle f\mathbf{U}\mathbf{U}\right\rangle_{m} - \left(\int E(m,p,N)fdm\frac{\partial n}{\partial\mathbf{r}} - \int K(m,p)fdm\frac{\partial N}{\partial\mathbf{r}} + \int L(m)fdm\frac{\partial l}{\partial\mathbf{r}} - \int V(m,p)fdm\frac{\partial p}{\partial\mathbf{r}}\right) = -BN\mathbf{U}_{0}(\mathbf{r},t)$$

$$(45)$$

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

$$N\mathbf{U}_{0}(\mathbf{r},t) = \frac{1}{B} \left(\int E(m,p,N) f dm \frac{\partial n}{\partial \mathbf{r}} - \int K(m,p) f dm \frac{\partial N}{\partial \mathbf{r}} + \int L(m) f dm \frac{\partial l}{\partial \mathbf{r}} - \int V(m,p) f dm \frac{\partial p}{\partial \mathbf{r}} \right)$$

$$-\frac{Q_0}{BB_0}\frac{\partial}{\partial \mathbf{r}}(e^{-\sigma_n}e^{-\rho_2 p}\int f e^{-\rho_1 m}dm)$$
(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,

$$\frac{\partial N}{\partial t} + \frac{\partial}{\partial \mathbf{r}} \cdot \left(\frac{1}{B} \left(\int E(m, p, N) f dm \frac{\partial n}{\partial \mathbf{r}} - \int K(m, p) f dm \frac{\partial N}{\partial \mathbf{r}} + \int L(m) f dm \frac{\partial l}{\partial \mathbf{r}} - \int V(m, p) f dm \frac{\partial p}{\partial \mathbf{r}} \right)$$

$$\frac{Q_0}{BB_0}\frac{\partial}{\partial \mathbf{r}}(e^{-\sigma_1}e^{-\rho_2 p}\int f e^{-\rho_1 m}dm)\bigg)=0 \quad (47)$$

We write the saturation moments more explicitly . We have

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

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

and the Eq.(41) for NE, into

$$\frac{\partial(NU_{n}(x,x))}{\partial x} + \frac{Q_{n}}{B_{n}} \frac{\partial}{\partial x} (e^{-m}e^{-m}f_{n}x) + \frac{Q_{n}}{B_{n}} \cdot (RU)_{n}}{\int E(m,p,k) \int dm \frac{\partial R}{\partial x} - \int E(m)pm \frac{\partial R}{\partial x} - \int E(m)pm \frac{\partial R}{\partial x} + \int U(m,p) \int dm \frac{\partial R}{\partial x} = -\frac{R}{M} \int E(m,p) \int dm \frac{\partial R}{\partial x} + \int E(m,p) \int dm \frac{\partial R}{\partial x} = -\frac{R}{M} \int E(m,p) \int dm \frac{\partial R}{\partial x} + \int E(m,p) \int dm \frac{\partial R}{\partial x} +$$

We shall refer to models including the Q_i term as water models, while cold models means $Q_i=0$. In Eqs.(43), (4-2) and (4.5) we used Q from Eq.(24). We could at course equally well use Q from Eq.(25) instead

4 Fluid equations of dayshirider

Eqs. (38) and (42) for Wand W, combined with Eq. (25) for a computed a we of flaid equations that could be used, when the force to fluients are evaluated. This could most simply be done using r thoto Eq. (52) below. However, a simpler that model will be demonstrated and studied note.

4.1. Bahmee of forest-controls instain, and argenta instained at a monetary We assume NC, from Eq.(45) quite analys relaxer towards a quasi-stationary wate, i.e. a state where the time-derivative term in Eq.(45) may be neglicited. In this state we may solve the remaining equation with respect to AU, and obtain AT, c. o. - 1 (From A), and by form a state respect to AU, and obtain

and an even provide a car

tere we also have begreated the error party detail, databased relatively shall be of or lenow. Using this expression in Eq.(38) we have a continuity equation for daphaic level of the second of the second se

(CP) 0= (man a,) 1 - 5 - 5 - 6 - 12 - -

Verwige the astronation company materies exploring. We have $\int E(m, p, N) pins = E_{\mu} e^{2\pi i} (N_{\mu} - N) \int (m_{\mu} - m) ddu = E_{\mu} e^{2\pi i} (N_{\mu} - N) (m_{\mu}N - N) - 48)$ where we have written for the first moment of m:

$$\int mfdm = P(\mathbf{r}, t) \tag{49}$$

Observe that

$$P = \int G d\mathbf{v} \tag{50}$$

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

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

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

where δ is the delta function. The *t*- and *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,

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

where we also have written an approximation of the exact expression valid if $\eta(m_0 - a \mid \beta) \mid < 1$. 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 $\int fe^{\eta m} dm$ 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

$$|\eta(m_0 - a / \beta)| < 1 \tag{54}$$

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:

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

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

$$\int n f d d m = P(\mathbf{r}_{*} \mathbf{r})$$

$$(39)$$

Observe that

$$P = \int Gdy \qquad (20)$$

where G has been mireduced above. The other in moments in Eq.(4.7), however, generally introduce many new unknowns, beside F above, and the g problem in the transation process. If f were known one can of course calculere all these. But also a quite rough approximation of f may be useful: In particular, in clares where the $\frac{3}{2T}$ -term in Eq.(27) for f is small, and may be neglected to lowest order, the

$$\frac{\partial f}{\partial t} = \frac{\partial f}{\partial t} = f \frac{\partial f}{\partial t} \left(e^{ith} - e_{ith} M + \frac{e_{ith}}{\partial t} \frac{\partial f}{\partial t} \right)$$
(51)

may be solved. If also condition for a quite fast relatedian of flowords a quasi-steady state, i.e. if relative much food is available, and the fast fastion / shows fittle spread in saturation, i.e. o/B is small, then f nov be approximated by

$$I(r, m, t) = h(r, t)\delta(m + On_{0} - m) [He_{1}(0)]$$
(52)

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

$$\int \partial^{2m} dm = \mathcal{H}(\mathbf{r}, t) e^{\mathcal{H}(\mathbf{r}, t) \cdot \mathbf{r}} = \mathcal{H}(\mathbf{r}, t) (t) + \mathcal{H}(\mathbf{n}_{0} - \mathbf{r}_{0}) (t)$$
(53)

where we also have written as approximation of the exact expression which iff $\eta(m_0 - q/\beta) \ge 1$. In the last approximation in Eq.(53) the first term is the 0th order *m*-moment, the second the list approximation in Eq.(53) the first term is the 0th Eq.(52). We now assume that an approximation of integrals first $\int d^2 dm$ may be obtained by these two *m*-moments, the first the and the 1th, also for similarly more general functions first the *E*-function from above. First respectively, more

must be fulfilled: Either η is very small. Then m_0 may be quite different that eqf. (3) η may be relatively increased in the way and references in very close We shall assume draw conditions to be infilled when approximating the remaining memoments in Eq.(47): f is not for it of form the distribution function E (5), and each of z_0 , χ , η and ρ_0 fulfils the same inequality Eq.(54) as η above. We can may write:

Let
$$M$$
 be $M = M - M$

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

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

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

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

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

$$\frac{\partial N}{\partial t} + \frac{\partial}{\partial \mathbf{r}} \cdot \left(\frac{1}{B} \left(E_0 (N_m - N) e^{\alpha_0 p} (m_0 N - P) \frac{\partial n}{\partial \mathbf{r}} - K_0 e^{-\alpha_2 p} (N - \alpha_1 P) \frac{\partial N}{\partial \mathbf{r}} + L_0 (N - \gamma P) \frac{\partial l}{\partial \mathbf{r}} \right) \right)$$
(60)

$$-V_0(N+\tau_1 P)e^{\tau_2 p}\frac{\partial p}{\partial \mathbf{r}}\right) - \frac{Q_0}{BB_0}\frac{\partial}{\partial \mathbf{r}}e^{-\sigma_0}e^{-\rho_2 p}(N-\rho_1 P)\right) = 0$$

and

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

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

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

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

and generally introduces even higher order *m*-moments. However, in order to truncate these equations, we use assumptions that were used above: $\frac{\partial}{\partial \mathbf{r}}$ - terms are assumed small, i.e. the state is nearly uniform, and furthermore, the state is nearly static, i.e. NU_0 from Eq.(46) is small. Since 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 P on Eq.(62) for P then is <u>very</u> 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

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

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

$$N(m;p))dm = N_{1}(N + \pi_{1}P)p^{(m)}$$

$$\int d^{n} r^{n} dn = N + g_{1} P.$$
(58)

In the equation for n, using the form X from Eq.(26), we have when alog the parameter ε fulfils the inequality Eq.(34).

$$\int A(m) F dmax = \lambda_0 \int (1 - e^m)^2 dmax = \lambda_0 \int (1 - e^m) f dm = \lambda_0 (2 - e^n)$$
(59)

$$\frac{16}{36}(26-31)x^{2}+\frac{36}{36}(24x-31)x^{2}-3x^{2}-\frac{36}{37}-3x^{2}-3$$

$$\frac{\partial n}{\partial t} + n_0 = \frac{\partial n}{\partial t} = D_{0} \frac{\partial n}{\partial t} - n_0 (n - D_{0} + S(n, n))$$
 (61)

Thus we only need an equation for P. besides the equations for M and n. to have a closed system for M. P and n. Generally, we obtain the equation for P fram Eq.(26) of G by integration over v.

This is again coupled to an re-moment of Eq.(30), a mixed first order m-a-maintent of F. An equation for $\int \beta(d)(r, m, t)dn = P(r, t)$ is obtained from Eq.(30) by tabilitying it by m and integrating. The consistent is of the form

$$\frac{35}{5} - \left(\frac{5}{5} - 19779 \right) = -6NO_0 - 6N = 900, NO_0 - 200$$

where we have written \$=5,0. Hance, while the first- and plact- hencebils are written. Eqs. (60), (64) and (61) constitute a set of canadacia for M. P and c dust may give a

(53)
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 $\frac{q}{\beta} = k_0 e^{-h_0(t)n} \to 0$ 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

$$-n_0\lambda_0(N_0 - \mathcal{E}P_0) + S_0 = 0$$
(65)

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

$$aN_0 = -\beta_0 n_0 (P_0 - m_0 N_0) \tag{66}$$

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

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

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

$$\beta = \beta_0 n_0, \ B = B_0 e^{\sigma n_0}, \ Q = Q_0 e^{-\rho_1 (m_0 - \frac{-}{\beta}) - \rho_2 p_0}$$
(68)

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

$$\frac{Q}{B} = \frac{Q_0}{B_0} e^{-\rho_1 m_0 + \rho_1 \frac{a}{\beta_0 n_0} - \rho_2 p_0 - \sigma n_0}$$
(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.

particular 'fluid' evolution of ibe daphaicles whon the securations used in the derivations are met.

5 Some special states and evaluation

5.1 Stationary and uniform state

Then
$$\frac{\partial}{\partial t} = 0$$
, $\frac{\partial}{\partial t} = 0$. Since we assumed $\frac{\partial}{\partial t} = t_1 e^{-t_1 t_1 t_2}$ and that

 $\frac{1}{\beta} = k_0 e^{-\gamma m} \rightarrow 0$ as thing increasing, we have in the staticnery same that $\frac{1}{\beta} = 0$, which

To have a stationary state we furthermore must have a stationary and uniform source of food input, 5,>0, to obtain a stationary density at 11 food is not available sharenford gives fixe to a state that is not stationary, see below.

an Eq.(0.1) we have in the stationary and indicate state that the balance
$$-\infty \xi_n(N_n - \xi P_n) + \xi_n = 0$$

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

$$(33) = -\beta_{1}\alpha_{1}(\beta_{1} - \alpha_{2}\beta_{1}) + (\beta_{1} - \alpha_{2}\beta_{1}) + (\beta$$

In practice, a state life this may never to obtained. However, angli deviation's from such a state may he relevant from an observational point of view, and this is considered lines. N_c is the stationary and uniform density of depinicies in this state, and P_0/N_0 the mean actuation. All ordered monimum variant, i.e. the state is static, and depinicies show only emitte motions: from the sequention for F we have

$$F(n, n) = N_0 \left(\frac{n}{2\pi c}\right) \quad S(n) = In_0 + \frac{1}{\beta} N_0^{-\frac{1}{2}}$$

Here the δ -function expresses depinteless of equal sammation, $m = (m_0 - \frac{1}{\sqrt{2}})$, a related between food intoles and the marving process. If depinteles take in food fast, i.e. β is large, or, if starvation α is small, then they nearly obtain a submation of m_0 . The dipinicles show emain matter contains expressed by the black dipinicles show emain matter β .

if we uso the Q-fitcher form Eq.(21). The excitement of the diplomotor than is:

According to this the excitement will increase with increasing langer site hore decrease with increasing treast. Increase in food available, e., will doing himge excitement, and doma excitation of increased in second

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

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

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

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

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

where

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

5.2 Uniform state, no food available. huseers

We consider $\frac{\partial}{\partial r} = 0$ and $\beta = \beta_0 n_0 = 0$. There is as in the state above we erdered

movement. Starvation will dominate, and we shall in this state (sightlers use the form of Q from Eq.(22). The equation for F therefore reads

$$\left(\frac{36}{36} - \frac{36}{36}\right) = \frac{6}{36} \left(\frac{36}{37} - \frac{36}{36}\right) \left(\frac{36}{36} - \frac{36}{36}\right) = \frac{36}{36} - \frac{36}{36} = \frac{36}{36}$$

Introducing a new variable $\mu = m + at$, which transforms F to $F'(\mu, \nu, t)$, we have instead the equation

$$\frac{36}{36} = 8_{\frac{3}{20}} \left(\sqrt{2} + \frac{9}{8}_{\frac{1}{2}} \cos \left(\frac{1}{2} - \frac{1}{2$$

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

$$f(v_{i},m,t) = \frac{N_{i}}{(2\pi)^{1/2}} f_{i}(m+\alpha) \frac{1}{\sqrt{\alpha(m,t)}} e^{\frac{1}{1+\alpha(m,t)}} dt$$

vitere

$$\alpha(m, n) = 2Q_n e^{-nnn} \left[\frac{1}{2\pi m (n+1)} \frac{\alpha(m)}{\alpha(m+1)} \frac{\alpha(m)}{\alpha(m+1)} e^{-nnn} \frac{\alpha(m)}{\alpha(m+1)} \right]$$

is the particular one that oney $F(u, m, t = 0) = N_{c} f_{c}(y_{1}v_{1})$. We near their of the initial state to represent a simulation where all dephasics are lest into the extrementation chamber uniformly distributed and simultaneously at time teol, with different degree of saturation, given by $f_{c}(n)$, and all being immobile at time teol, with different degree of saturation. From then on they respond to the environment, there general semilars of the equations may be obtained from this foldamental saturation, $f_{c}(n)$ is a obtained from this foldamental semilars of a staturation of saturation of the environment. More general semilars of the equations may be obtained from this foldamental solution, $f_{c}(n)$ is a quite a thirtrary function obeying $\int f_{c}(n) = 1$. Figs.1-2 shows F for some incatable, $n = 1^{-2}$, both for low these incatables $f_{c}(n) = e^{-h^{-1}}$ (all x).

5.3 Lincorized 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 andytic procedures. However, solutions that device only little from stanogary and uniform selations like the case derived earlier, may be found more easily since the equations for the multideviations are linear and based more metable.

The discussion cost rollows we assume

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

$$\int_{0}^{2} N_{1}(z,t)dz = 0$$
(74)

$$N = N_{0} + N_{1}$$

$$n = n_{0} + n_{1}$$

$$P = P_{0} + P_{1}$$

$$P = p_{0} + p_{1}$$

$$l = l_{0} + l_{1}$$
(75)

Thus we write,

The stationary, uniform parts of the solutions ('equilibrium' solution) are the ones discussed above, and subscript '1' refers to <u>small</u> perturbed *z*-oscillatory and time-dependent quantities: It is essential that these quantities are small, i.e. for instance $|N_1| << |N_0|$, 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,

$$S = S_0 + S_1 \tag{76}$$

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

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

Assuming that $\frac{\partial}{\partial t} \to 0$ 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 ,

$$P_{1} = (m_{0} - \frac{a}{\beta_{0}n_{0}})N_{1} - (P_{0} - m_{0}N_{0})\frac{n_{1}}{n_{0}} = (m_{0} - \frac{a}{\beta_{0}n_{0}})N_{1} + \frac{aN_{0}}{\beta_{0}n_{0}^{2}}n_{1}$$
(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

This may mimic laboratory experiments, where Daphres 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(2,1) we have N(2+1, D=N(2,1) where L=2n0, N being the mean radius of the cylindrical shell, and simplarly for all other quantities involving source variation.

Accordingly, all quantities, for instance the density, will have a general form. $N=N_r+N_r$ where N_r is z_r and r-independent and $N_r(z,s)$ for $R_r(z)$.

 $\left[\partial f_{1}(c_{1})\partial dc = 0\right] = 0$

Thus we write,

nen, en Pessen Pessen Pessen Leber

The stationary, uniform parts of the solutions (requilibrium relation) are the own discurated above, and autoentys II refers to graff perturbed cooldinary and timedependent quantities. It is essential that there against as are small, i.e. for instance Wylee Wyl, for the linearization to work. The stream part light manners function I are assumed known bere. Also the food powers shall be given in the state way.

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

 $\frac{1}{2n} + eN_1 = -P_0 e_1 Q_0^2 + e_0 N_0^2 - P_0 e_0 (P_1 - e_0 N_1) = \frac{1}{2n}$

Assuming that $\frac{2}{3t} \rightarrow 0$ relatively fast in this equation, the first term may be neglected by here only slow evolution is considered. Then the remaining terms in Eq.(7), give P_{i}

a = long - the - the - man = from and - the - man = a

We note that the approximation of P₁ have and follows from using the *J* approximation from Eq.(32). However, we could wishout during the verticed with the full Eq.(77), but follow this marging percenture sere. The functorized feed equation thus becomes

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

or, for short,

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

where we have written

$$C_{1} = \lambda_{0} N_{0} (1 - \varepsilon m_{0})$$

$$C_{2} = n_{0} \lambda_{0} (1 - \varepsilon m_{0} + \varepsilon \frac{a}{\beta_{0} n_{0}})$$
(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:

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

where we have for the coefficients,

$$A = \frac{E_0(N_m - N_0)e^{\alpha_0\rho_0}aN_0}{B_0\beta_0n_0} + \frac{Q_0}{B_0^2}e^{-\sigma n_0 - \rho_2 p_0}\rho_1\frac{aN_0}{\beta_0n_0^2} + \frac{Q_0}{B_0^2}e^{-\sigma n_0 - \rho_2 p_0}N_0(1 - \rho_1 m_0 + \frac{\rho_1 a}{\beta_0 n_0})\sigma$$

$$B = \frac{K_0N_0}{B_0}e^{-\alpha_2 p_0}(1 - \alpha_1 m_0 - \alpha_1\frac{a}{\beta_0 n_0}) + \frac{Q_0}{B_0^2}e^{-\sigma n_0 - \rho_2 p_0}(1 - \rho_1 m_0 + \frac{\rho_1 a}{\beta_0 n_0})$$

$$I_1 = -\frac{L_0N_0}{B_0}(1 - \gamma m_0 + \gamma\frac{a}{\beta_0 n_0})$$

$$I_2 = \frac{V_0e^{\tau_2 p_0}N_0}{B_0}(1 + \tau_1 m_0 - \tau_1\frac{a}{\beta_0 n_0}) - \frac{Q_0}{B_0^2}e^{-\sigma n_0 - \rho_2 p_0}N_0\rho_2(1 - \rho_1 m_0 + \frac{\rho_1 a}{\beta_0 n_0})$$
(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 daphnicles. 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

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

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.

$$\frac{dn}{dt} + m \frac{dn}{dt} = D \frac{d^2n}{dt} - n \delta_{1}(M - 68) - n \delta_{2}(M - 67) + \delta_{1}(2,0)$$

$$= D \frac{d^2n}{dt} - n \delta_{1}(M - 68) - n \delta_{1}(M - 67) + \delta_{1}(2,0)$$

$$= D \frac{d^2n}{dt} - n \delta_{1}(M - 68) - n \delta_{1}(M - 67) + \delta_{1}(2,0)$$
(39)

.1018 101 ,10

$$\frac{1}{22} + a_{\alpha} \frac{2}{22} = D \frac{d}{dz} - q_{\alpha} - q_{\alpha} - q_{\alpha} + q_{$$

where we have written

$$C_{i} = n_{0}\lambda_{0}(1 - \alpha n_{0}) + \alpha \frac{1}{\alpha_{i}}$$
(B1)

These constants are positive since we consider era, to be smaller data 1. Likewise, we may rewrite Eq.(60) for the participation N₀. After some algebra it takes the form:

where we have for the coefficients

As in Eq.(80), Eq.(82) complex variants 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, variat. Both of A and B are considered positive, and hold simplify considerably for a 'cold population' (2,2-0) of daphnicles, *I*, is negative while *I*, is considerably for a 'cold population' (2,2-0) of warm models. (2,5-0. Now that *I*, may increase considerably when a bowever, test positive for

6 Some special coincions from linear fluid constitues

We simplify the equation for *n*, socreywhat neglecting the that us and the difference, such that only the essential relaxed with relevabelies has fired scholing having

where C₁ and C₂ are given from Eq.(61). S₁ is considered budwe and participe [#'s J. For various cases we solve the equation rogether with Eq.(57) (i.e.

$$\frac{\partial N_1}{\partial t} + A \frac{\partial^2 n_1}{\partial z^2} - B \frac{\partial^2 N_1}{\partial z^2} = I_1 \frac{\partial^2 l_1}{\partial z^2} + I_2 \frac{\partial^2 p_1}{\partial z^2}$$
(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 S₁, 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

$$An_{1} - BN_{1} = I_{1}l_{1} + I_{2}p_{1} + I_{2}p_{2} + I_{2}p_{1} + I_{2}p_{2} + I_{2}p_{1} + I_{2}p_{2} + I_{2}p_{2}$$

and the steady solution

$$N_{1s} = \frac{AS_1 - C_1(I_1I_1 + I_2p_1)}{AC_2 + BC_1}$$

$$n_{1s} = \frac{BS_1 + C_2(I_1I_1 + I_2p_1)}{AC_2 + BC_1}$$
(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:

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

We have

$$\frac{\partial N_1}{\partial t} + A \frac{\partial^2 n_1}{\partial z^2} - B \frac{\partial^2 N_1}{\partial z^2} = 0$$

$$\frac{\partial n_1}{\partial t} = -C_1 n_1 - C_2 N_1$$
(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,

$$N_{1}(z,0) = \sum_{m=1} N_{1m} \cos(2\pi mz / L) + \sum_{m=1} N_{2m} \sin(2\pi mz / L)$$

$$n_{1}(z,0) = 0$$
(88)

and we look for solutions of the form

$$N_{1}(z,t) = \sum_{m=1}^{\infty} a_{1m}(t) \cos(2\pi mz/L) + \sum_{m=1}^{\infty} a_{2m}(t) \sin(2\pi mz/L)$$

$$n_{1}(z,t) = \sum_{m=1}^{\infty} b_{1m}(t) \cos(2\pi mz/L) + \sum_{m=1}^{\infty} b_{2m}(t) \sin(2\pi mz/L)$$
(89)

where coefficients are given from Eq.(8.3) and f_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 and the parameter values used in Figs.4-18.

6.1 State of stationary balance

When all sources S_1 , I_1 and p_1 are time independent, a spacenery solution for N_1 and n_1 is found when $\frac{3}{2}$ -terms are neglected in Eqs.(S2) and (84). Then we have

$$A_{N_1} = B_{N_2} = f_1 + f_2 p_1$$
(85)

and the steady solution

$$M_{ij} = \frac{M_i - C_{ij}(M_i + M_{ij})}{M_i}$$

is set up by the steady sources S₁, I, and p₁ and hence is also escillatory in z. There then cut to be bud solutions towards which time-dependent adminent coolee. We shall look at some particular situations:

The system lacks source terms and is homogeneous. Soletions will enflore instance properties of the system. These properties are debimpertain to bell how the system tesponds to sources. These is no standy sets relating in this case, except N, ex, e0. We solve the equations subject to the initial remarkation.

$$N_{1}(z,0) = \sum_{i=1}^{n} N_{1,i} \exp\{2\pi i m z + \sum_{i=1}^{n} N_{1,i} \exp\{2\pi i m z + z\}$$

 $n_{1}(z,0) = 0$

and we look for solutions of the form

$$M_{1}(z,t) = \sum_{i=1}^{n} a_{ii}(t) de al 2 \pi arr (2) + \sum_{i=1}^{n} a_{ii}(t) alm 2 \pi arr (2)$$

"*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 $\alpha'_m - A(2\pi m / L)^2 \beta_m + B(2\pi m / L)^2 \alpha_m = 0$

$$\beta'_m + C_1 \beta_m + C_2 \alpha_m = 0 \tag{90}$$

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

$$\alpha_{m} = \frac{N_{m}}{r_{2} - r_{1}} \left((r_{2} + B(2\pi m / L)^{2})e^{r_{1}t} - (r_{1} + B(2\pi m / L)^{2})e^{r_{2}t} \right)$$

$$\beta_{m} = \frac{1}{A(2\pi m / L)^{2}} \frac{N_{m}}{r_{2} - r_{1}} (r_{1} + B(2\pi m / L)^{2})(r_{2} + B(2\pi m / L)^{2})(e^{r_{1}t} - e^{r_{1}t})$$
(91)

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

$$r^{2} + r(C_{1} + B(2\pi m / L)^{2}) + (BC_{1} + AC_{2})(2\pi m / L)^{2} = 0$$
(92)

i.e.,

$$r = -(C_1 + B(2\pi m / L)^2) / 2 \pm \left[(C_1 + B(2\pi m / L)^2)^2 - 4(BC_1 + AC_2)(2\pi m / L)^2 \right]^{172} / 2$$
(93)

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

$$r = \alpha \pm i\beta \tag{94}$$

where

$$\alpha = -\frac{C_1 + B(2\pi m / L)^2}{2}$$

$$\beta = \left[4(AC_2 + BC_1)(2\pi m / L)^2 - (C_1 + B(2\pi m / L)^2)^2 \right]^{1/2} / 2$$
(95)

We write explicitly the solution for the case that

$$N_{1}(z,0) = N_{1m} \cos(2\pi mz / L)$$

$$n_{1}(z,0) = 0$$
(96)

In the real root case we have

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

$$n_{1}(z,t) = \frac{1}{A(2\pi m / L)^{2}} \frac{N_{1m}}{r_{2} - r_{1}} (r_{1} + B(2\pi m / L)^{2})(r_{2} + B(2\pi m / L)^{2})(e^{r_{1}t} - e^{r_{2}t}) \cos(2\pi m z / L)$$
(97)

and in the complex conjugate root case

"a" is used for "azimuthil mode number", which is standard paration. (and must not be confused with food saturation). By insertion we fitted for each pair of the time dependent coefficients (a_1, b_2) and (a_2, b_3) . Sup (a_2, β_2) , the equations dependent coefficients (a_1, b_2) and (a_2, b_3) . Sup (a_2, β_2) , the equations

$$p_1 + c_1 p_1 + c_2 q_2 = 0$$

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

$$\alpha_{n} = \frac{N_{n}}{2^{-n}} \left((q + M(2\pi m) LF) e^{c} - (q + B(2\pi m) LF) e^{c} \right)$$

$$\beta_{n} = \frac{1}{2^{-n}} \left((q + M(2\pi m) LF) e^{c} - (q + B(2\pi m) LF) e^{c} \right)$$

$$\beta_{n} = \frac{1}{4(2\pi m)(L)} \frac{N_{n}}{q - q} \left(q + B(2\pi m) LF \right) \left(q + B(2\pi m) LF \right) \left(e^{c} - e^{c} \right)$$
(91)

Here M_{n} denotes either N_{1n} or N_{2n} depending on whether (a_{n}, β_{n}) denotes (a_{n}, b_{1n}) is or (a_{n}, b_{2n}) . The roots r_{1} and r_{2} are given from the equation

$$^{2} + r(C_{1} + B(2\pi m / L)^{2}) + (BC_{1} + AC_{2})(2\pi n / L)^{2} = 0$$
 (22)

r=-(C+B(2mm/L))/2±[(C+B(2mm/L)))-4(BC+AC)(2mm/L)]²/2

and are either real or complex conjugates. In the last case we may write r = r + r + i f

onoriw'

$$\alpha = \frac{C_1 + M(2\pi ms/L)^2}{2}$$

(623)

 $\beta = [4(AC_1 + BC_2)(2\pi m I L)^2 - (C_1 + B(2\pi m I L)^2)^2]^2 / 25]$

We write explicitly the solution for the case man

$$N_{1}(z,0) = N_{10} \cos(2\log_{10} 1)$$

$$n_{1}(z,0) = 0$$
(96)

in the real root case we have

$$M_{(2,i)} = \frac{M_{i}}{2 - 4} \left((z_{i} + B_{i}^{2} z_{i} + L)^{2} \right) e^{-(z_{i} + B_{i}^{2} z_{i} + L)^{2} e^{-2}} \left((z_{i} + B_{i}^{2} z_{i} + L)^{2} e^{-2} \right) e^{-(z_{i}^{2} + B_{i}^{2} z_{i} + L)^{2} e^{-2}} \right) e^{-(z_{i}^{2} + B_{i}^{2} z_{i} + L)^{2} e^{-2}} e^{-2} e^$$

and in the complex conjugate real case

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

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

We make the following distinctions:

1) $AC_2 + BC_1 > 0$ 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) $AC_2 + BC_1 > 0$ 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 $v_{\varphi} = L\beta / (2\pi m)$ where β here is given from Eq.(95).

<u>6.3 Case of uniform light intensity, uniform threat, steady rate of non-uniform twohump food input</u>

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,

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

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

 $N_{1}(z,t) = N_{1} \left\{ e^{it} \cos \beta_{1} - \frac{2}{3} e^{it} \sin \beta_{1} - B(2mn+1)^{2} e^{it} \frac{\sin \beta_{1}}{3} \left[\cos(2mn+1) e^{it} \frac{1}{3} e^{it} \right] \right\}$ $n_{1}(z,t) = \frac{N_{1}}{A(2mn+1)^{2}} \left\{ (\alpha + B(2mn+1)^{2})^{2} + B^{2} \right\} e^{it} \frac{\sin \beta_{1}}{3} \cos(2mn+1) e^{it}$ (93)

We make the following distinctions:

1) $AC_{i} + BC_{i} > 0$ and $4(BC_{i} + AC_{i})(2\pi m/L)^{2} < (C_{i} + B(2\pi m/L)^{2})^{2}$. Both roots are real and have the second sign. Since $C_{i} + B(2\pi m/L)^{2} > 0$, both are require.

2) $AC_1 + BC_2 > 0$ and $A(BC_1 + AC_2)(2 \tan t A)^2 > (C_1 + B(2\pi t M A)^2)^2$. In this case the roots are complex conjugates, and since $C_1 + B(2\pi t n A A)^2 > 0$ the real part of the roots is negative.

Some choices of parameters may size be investigated from Fig.3, showing two (4, 8) diagrams, for fixed values of C₁ and C₂ (carb set to 1) for me i (top) and me², bottom. The curves are the parabola $(C_1 - Bt^2)^2 = 4AC_1t^2$, where $t = 2\pi to 1$, and the straight lines BC + AC = 0 and C₂ + Bt² = 0. The regions for real and complex conjugate roots are indicated, together with the signs of the regions for teal and complex conjugate roots are indicated, together with the signs of the roots of the regions for teal and complex conjugate roots are indicated, together with the signs of the roots of the regions for teal and complex conjugate roots are indicated, together with the signs of the roots of the roots of the roots of the roots of the root of the root of the roots of the roots of the roots of the roots of the root of the roots of the root of the roots of the roots of the root of the roots of the roots of the roots of the root of the roots of the roots of the root of the roots of the roots of the roots of the root of the roots of the root of the roots of the root of the roots of

In both cases 1) and 2) the perturbed solutions N_{1} and n_{2} we decrease the set 1) and 2) the perturbed solutions N_{2} and n_{1} we decrease the set 2) and 2 the set 2 the

6.3.Crae of uniform light intensity, uniform threat, storty rate of non-uniform (with

This case way be more realistic concerning fred inper, since we allow the food injert to vary from point to point, which will be the case at practice, even if we up to make the input uniform. We assume from tell and brownes,

which corresponds to two different "humps" of steady food lepter, while at time test we have

$$N_1(z,0) = N_{11} \cos(2\pi z / L)$$

$$n_1(z,0) = 0$$
(100)

i.e. initially a one-hump perturbation of the daphnicle 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,

$$N_{1s} = \frac{AS_{1}(z)}{AC_{2} + BC_{1}}$$

$$n_{1s} = \frac{BS_{1}(z)}{AC_{2} + BC_{1}}$$
(101)

Defining new variables,

$$N_{1} = N_{1} - N_{1s}$$

$$n_{1} = n_{1} - n_{1s}$$
(102)

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

$$\frac{\partial N_1'}{\partial t} + A \frac{\partial^2 n_1'}{\partial z^2} - B \frac{\partial^2 N_1'}{\partial z^2} = 0$$

$$\frac{\partial n_1'}{\partial t} = -C_1 n_1' - C_2 N_1'$$
(103)

subject to initial conditions

$$N_{1}(z,0) = N_{11}\cos(2\pi z / L) - N_{1s}(z)$$

$$n_{1}(z,0) = -n_{1s}(z)$$
(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,

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

$$M_1(z,0) = N_1 \cos(2\pi z / E)$$

 $\pi (z,0) = 0$

i.e. initially a one-hump perturbation of the depindence density. This corresponds therefore to a situation where we have an oriently 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_1 and N_0 from Eqs (65) and (56), while the response to S_1 now follows.

The equations have in this case a stationary solution.

$$M_{\mu} = \frac{AS(c)}{ASC} + BSC$$

$$M_{\mu} = \frac{BS(c)}{ASC} + BSC$$

$$M_{\mu} = \frac{BS(c)}{ASC} + BSC$$

Defining new variables

$$M = M_{\rm e} - M_{\rm e}$$
 (102)

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

subject to initial constituents

$$N_{1}(z,0) = N_{12} \cos(2\pi z + L) - N_{2}(z)$$

$$G(z,0) = -\kappa_{2}(z)$$

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 time cases of threat levels, in all cases the solutions decay towards the steady-state solution as time goes of Accordination of deckinizes becomes stanges through the troud food sources as the ground threat fevel or times, and the food flattribution is the ground threat fevel or times, and the food flattribution cases as the ground threat fevel or times, and the food flattribution can be ground threat fevel or times, and the food flattribution can be ground threat fevel or times, and the food flattribution can be ground threat fevel or times, and the food flattribution can be ground threat fevel or times, and the food flattribution can be caused to be accordingly.

6.4 Case of uniform light intensity, uniform lood many and not millions subjergent threat

We now assume a sould, standy gradient in the threat faith

$$(c_1) = (c_1) + (c_2) + (c_3) + (c_4) + (c_4$$

but we assume there is no variation in lood inpottor in light intensity, i.e. $S_i=0$, $f_i=0$. We take the initial state to be:

(001)

$$N_1(z,0) = 0$$

$$n_1(z,0) = 0$$
(105)

We have

$$N_{1s} = \frac{-C_1 I_2 p_1(z)}{A C_2 + B C_1}$$

$$n_{1s} = \frac{C_2 I_2 p_1(z)}{A C_2 + B C_1}$$
(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.

<u>6.5 Case of uniform light intensity, uniform food input and one-hump moving threat</u> We change the foregoing example to a threat gradient that is moving with a steady velocity v_0 ,

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

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

$$N_1(z,0) = 0$$

 $n_1(z,0) = 0$
(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.

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

In this case we have

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

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

and

$$n_1(z,0) = 0 \tag{111}$$

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.

 $N_1(z,0) = 0$

We have

for the stationary solutions, and results for the full solution are shown in Figs. 10-32, for the case mal. As expected, depinides fly every from the linest gradient and soule in a state given by the steady state solution. However, sized the parameters A, B and A all depend on the ground threat level, the tespense to the same threat gradient is very different when the strong threat level chapters.

6.5 Case of undered fait intensity, uniform load incatand mediumo netwing threat. We change the foragoing exemple to a filmal gradient that is moving with a steady. velocity is,

$$(z_{1}) = p_{0} \cos(2\pi z I L - y_{0})$$

still having 5,=0, 4=0. Again we let

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 dreat or is an important factor for the depintile response and evolution.

5.6 Case of untions liefs intensity, steady two-insus food input and akeying one-

n this case we have

$$\mathcal{L}(z) = z_0 \cos(2\pi z / L) + z_0 \cos(4\pi z / L)$$
 (109)

$$p_1(z,t) = p_0 \cos(2\pi z/L - z_0)$$

0 (0) = (0,5) = D = (0,5) =

Nelther in this case there exists a stationary solution. As time great on table temains a typical response and accumulation due to the construction due to the construction of a station of a table of the state of t

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 nonlinearity 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.

References

[1] Larsson, P, 1997. Ideal free distribution in *Daphnia*? Are daphnids able to consider both the food patch quality and the position of competitors? Hydrobiologia **360**: 143-152.

[2] Kleiven, O.T., Larsson, P. and Hobæk, A., 1996. Direct distributional response in *Daphnia pulex* to a predator kairomone. J.Plankton Res., 18, 1341-1348.
[3] Larsson, P. and Kleiven, O.T., 1996. Food search and swimming speed in

Daphnia. Zooplankton: Sensory Ecology and Physiology. Red. Lenz, P.H.,

7 Summary and conclusion

Acknowledgement:

The author wants to express my gravitade to Pener Lingen, Dept. of Zeelegy 4 mixof Bergen, for his seminar about experiments and resourch on Depinia behavious, and for informative and stimulating talks on we appled

References

[1]-Lansson, P. 1997. Ideal free distribution in *Dephated Inv.* dephates sole to consider both the food patch quality and the position of annethal NH deblic logic. 360: 143–152.

24 Kielven, O. L., Larsson, C. and Sanors, A., 1996. Christ databaliadat responses a Dophula puler to a produtor fairmance. J.Phaneuri Res. 10, 1241-1245 [3] Larsson, P. and Kleiven, O.T., 1996. Food search and swampling speed in Daphula. Zooplanitton: Sensory Ecchery and Physiology, Red. Larsson, P. 4 Hartline, J.E., Purcelle, J.E., Macmillane, D.L. Gordon and Breach Publishers, Amsterdam 375-387.

[4] Jensen, K.H.M., 2000, Gregariousness in *Daphnia*: Significance of food distribution and predator evasion. Dr.scient thesis, Department of Zoology, University of Bergen, Norway.

[5] Chapman, S. and Cowling, T.G, 1939. The mathematical theory of non-uniform gases. Cambridge University Press.

[6] Montgomery, D.C. and Tidman, D.A., 1964. Plasma kinetic theory. McGraw-Hill.
[7] Øien,A.H. 1999. Transition from collision-dominated to collisionless regions in a plasma: a global distribution function for outflowing light ions in polar regions of the ionosphere - an analytical approach, J.Plasma Physics, 61, 735-760.

Figure section

Parameter values used in Figures (4)-(18). Spatial dimension, L: $L=2\pi$, 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, throughout. Food attraction and daphnicle repulsion coefficients A and B: A=0.5, B=2, low threat level A=1, B=1, intermediate threat level A=5, B=0.2, 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 : $I_2=0.5$, low threat level $I_2=1$, intermediate threat level $I_2=5$, high threat level One-hump threat gradient amplitude, m=1: $p_{11}=0.2$ Velocity of moving threat gradient: $v_0 = 0.5$

Hardine, I.B., Purcelle, I.B., Macmillano, D.I., Gorden and Breach Publishers, Amsterdam 375-387

[4] Jenson, K.H.M.: 2000, Gaeganonaness in Daphata: Significance of food distribution and predator evasion. Draciant thesis, Department of Zoology, University of Bergen, Norway.

[5] Chapman, S. and Cowling, T.G. 1939. The mathematical theory of son-onligingases. Cambridge University Press.

[6] Montgomery, D.C. and Tidanna, D.A., 1964. Plasma kmette theory: McGraw-Hill, [7] Gien, A.H. 1999. Transition from collision-dominated as collisionless regions in a plasma: a global distribution function for outflowing light lons in polar regions of the ionosphere - an analytical approach, J.Plasma Physics, 61, 735-760.

Figure scotion -

meter values used in Highweek (-f)-(18).

L=2π, all figures

Amplitude of initial perturbation of feeds

O, throughout

A=0.5, B=2, low threat level

A=1, B=1, Internicalistic Bread lavel

A=5, B=0.2, high through terral

wo-hump, perturbed food input emplifiedes, m=1, mm.

cat gradient coofficient /,:

The set in a station we have a station of the

re-f--5, high fluxes lovel

no-many threat gradient amplituda, need th

Velocity of moving threes employed



Fig.1: Distribution of daphnicles according to Eq.(72), "no threat" ($p_0 = 0$), for 4 values of time . Parameter values used: $N_0 = 1$, a=0.2, $Q_0 = 1$, $p_1 = 1$, $p_2 = 1$, $B_0 = 1$, $m_1 = -1$. Function $f_0(m) = (al / \pi)^{1/2} \exp(-al \cdot m^2)$, al=2.

1.





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



m=1,L=2*π*,C1=C2=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.



0.2 0.4 0.6 0.8 1 1.2 1.4. 1.6 1, 1.8 2

Fig.3: Regions in (*A*, *B*)- diagrams for real and consplex conjugters roots b(Eq.(93), when $L=2\pi$. $C_1=C_2=1$. for m=1 (rep) and m=2 (bour m). Only *ReD* is relevant, sign of real part indicated.

Density of daphnicles, 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 food, Low threat level, Oaly initial partnehation of depirateles, met



Fig.4: Space-time evolution of dapinicle density ((up) and rood density (betweet in case of low ground-threat level, when depinicles are parenthed at r=0. (Eq.(90), for m=1). For parameter values used, see start of figure section.







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





Danator of tood, Internations threat level, Only initial pararrhetion of daphaicles, med.



Pig.5: Sume as Fig.4, except for intermediate fround-thirod. level instead: ele start of intre-section









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

Density of daphnicles Figh threatlevel. Only initial perturbation of daphnicles, m=1



Laneny of food, High threat level, Unit while certarhabits of darberides, mut



Fig.6: Same as Fig.4, except for high grannd-threat level batend, say stort of figure



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.



DETERMENT SECTION


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



ever partie is right, except for intermediate ground-threat level instaud, see shar o



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.





Exercity of food, Flight threat lovel. Initial one-kump perturbation of depinicies, m=1, plus two-humo-perturbed meady food input, m=1,2.



section

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.





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





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





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 depinicies, Low threat lovel No initial perterbution of depinicies No perturbed food tiput.



Evenity of Inod. Low-theat ferel. No initial permitation of depheteles No permited food input.



vaire to up odd a cloudd



Pig.13: Effect of moving small threat gradient (bonom) on dephasele density (top) and food density (middle) in case of low ground threat level. For parageter vidnes used, see)that of figure service





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.

Dennity of daphinicies, Intermediate Uncat is wi, No initial perturbation of dephnicles No perturbad food input. A one-hump-perturbed moving threat-gradient, see I.



Dansity of food, internecient times farel, No initial perturbation of dephateles No perturbed food input, one-huttur to surphed avoying timest conduct sec.



Service of real density



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.





Density of food, Fligh threat level, No initial perturbation of daphuicles No perturbation of daphuicles due hormo-controlocd food input.



symmetry through the second



Fig.15: Same as Fig.13, except for hurb ground-direct fevel instead, and start of figure

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.



-0.2

5 time¹⁰



0

³ position

4

Dennicy of daphilicles Low firmat level No initial perturbation of dephainles A two-bing-perturbed meady food input, me1,2. A one-bing-perturbed moving firmat-gradient, me1



Density of food. Low threat level, No initial perturbation of daphricles A two-inrup-perturbed steady food input, m=1,2. A one-iump-perturbed moving threat-predient, m=1.



Montaing Gireat dennity



Fig.16: Effect of moving small threat gradicat (bottom) on doptimicle density ((60)) and food density (middle) when a steady tood input is given, as for bottom of Fig.7, when ground-threat level is fow. For parameter values used, see start of figure 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.





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

Dausity of daphaicies, laternadiate thrant 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.



Internationa threat level. No luitial perturbation of daphnicles A two-hump-perturbed aready food input, m=1.2. A one-hump-perturbed area ing threat-gradient, m=1



After the distant distantly



Fig.17: Same as Fig.16, except for intermediate ground-firmatics for instead, sob start of figure section



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



Fig.13: Same is Fig.16, except for high around these facet in the set in the set of the





