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Abstract

Plankton patchiness in homogeneous physical environments is studied in this paper assuming that all involved populations disperse diffusively. A recent but powerful sufficient condition for the emergence of spatial patterns in models with any number of species is systematically applied to all food chain and food web plankton models and the result is rather sharp: All models explicitly containing phytoplankton, zooplankton and planktivorous fish suggest zooplankton patchiness, while models not containing phytoplankton or fish populations do not. The results are in agreement with many previous but particular theoretical studies on plankton patchiness and Turing instability, and testable prediction of the models satisfying the sufficient predictions is that zooplankton should be more patchy then phytoplankton, a property that is often seen in natural settings. An application to a complex model with five compartments (nutrient, phytoplankton, zooplankton, planktivorous fish, carnivorous fish) highlights the predictive power of the method.

Keywords: plankton patchiness, plankton models, diffusive instability, Turing instability, dispersal, spatial pattern

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1. Introduction

Plant and animal populations are often not uniformly distributed in space, in particular when turbulent flows are controlling their dispersal. In aquatic ecosystems, the paradigmatic example is plankton patchiness that has attracted the attention of many researchers since the very beginning of spatial ecology (Levin and Segel, 1976, Steele, 1978, Okubo, 1992). In general, when populations interact demographically in media that vary in time and space one is, at least in principle, forced to study the problem through the use of two distinct submodels connected in cascade as sketched in Fig. 1. This makes the problem rather complex, because population samples not only contain information on demography but also on the characteristics of the physical environment, at the point of being sometimes dominated by them. For example, all techniques used for extracting the Liapunov exponent (the most popular indicator of chaos) from a plankton time series (Sugihara and May, 1990, Ascioti, Beltrami, Carroll and Wirick, 1993, Pascual, Ascioti and Caswell, 1995) would give an estimate (actually an upper bound) of the Liapunov exponent of the environmental submodel (Rinaldi and Solidoro, 1998, Colombo, Dercole and Rinaldi, 2008). That is to say, the plankton community plays the role of an instrument that measures a characteristic parameter of the environment, as noted by Pascual et al. (1995), who discovered that the Liapunov exponent extracted from plankton time series was actually very close to the Liapunov exponent emerging from the analysis of purely oceanographic time series.

Only a few studies have been carried out on complete models of the
kind shown in Fig. 1 (Vilar, Solé and Rubí, 2003, Abraham, 1998, Hillary and Bees, 2004b, Colombo et al., 2008). These studies confirm that the characteristics of the environment can be dominant, but that in some cases plankton demography may add extra complexity.

In order to simplify the study of plankton, one can restrict the analysis to only one of the two submodels in Fig. 1. The first extreme approach consists of studying the spatio-temporal dynamics of the flows and deduce from them the population patterns by considering plankton, as well as other species, as inert particles (see Gower (1980) for an early support of this idea). In this way, the problem is reduced to a relatively standard problem of hydrodynamics where only the sinking, floating or swimming characteristics of the populations are taken into account. This approach can explain numerous plankton patterns, observed at various spatial scales, like vortices that turn on and off alternatively (Aref, 1984), multiple bands of dense organisms lumped into swaths (Shanks, 1983), and long single stripes of swimming or floating plankton parallel to shore (Franks, 1997). Conversely, the second extreme approach, simply rules out the hydrodynamics by assuming that all flows are constant in time and space, so that the model becomes a classical population model with a dispersal mechanism controlling the movement of the individuals in a spatial domain. This approach has a long scientific tra-
dition and emphasizes the role of biology by pointing out that demography has the power of creating surprisingly complex spatial patterns, like spots and stripes of abundances, even in perfectly homogeneous environments.

Segel and Jackson (1972) were the first to show that the theory developed by Turing (1952) in his celebrated study on the origin of morphogenesis could be applied in ecology to check if density dependent mechanisms could promote spatial pattern formation in perfectly homogeneous environments. Their study was limited to models with two populations and diffusive dispersal, because these were Turing’s assumptions. A few years later, Levin and Segel (1976) conjectured that Turing’s theory was potentially the most appropriate tool for supporting the idea that plankton patchiness could be the consequence of demographic characteristics of the populations. However, the phytoplankton-zooplankton model they used is not credible (phytoplankton in the absence of zooplankton increases unboundedly) and suggests that the so-called “activator” (a key notion in Turing’s theory) is phytoplankton. This implies that phytoplankton should be more patchy than zooplankton, a property which is in contrast with observations (Levin, 1992, Vilar et al., 2003). Here we show that Levin and Segel could not do any better, given the constraint of using a model with only two populations. In fact, all standard ditrophic food chain models with zooplankton at the top or at the bottom of the chain can not have zooplankton as activator (we consider as non-standard not only the models with unboundedly growing phytoplankton (Levin and Segel, 1976), but also those with predator with ratio-dependent functional responses which are known to be prone to degeneracies (Yodzis, 1994, Abrams, 1994). By contrast Levin and Segel were right in making
their conjecture because, as shown in this paper, a recently derived sufficient condition for pattern formation (Satnoianu, Menzinger and Maini, 2000, Satnoianu and van den Driessche, 2005, Della Rossa, Fasani and Rinaldi, 2012), is structurally satisfied in all realistic models where zooplankton feeds on phytoplankton and is predated by fish.

The paper is organized as follows. In the next section we briefly report the sufficient condition implying pattern formation in models with more than two populations. Then, we show that under very general assumptions such a condition is satisfied in models with (one or more groups of) phytoplankton, zooplankton and planktivorous fish. This is done by distinguishing between zooplankton and phytoplankton patchiness. Finally, we highlight the power of our condition by simulating a model with five compartments, namely nutrient, phytoplankton, zooplankton, planktivorous fish, and carnivores. A final section presents the conclusions and discusses possible extensions.

2. A simple sufficient condition for pattern formation

Assume that $n$ populations with densities $x_i$, $i = 1, \ldots, n$ depending upon time and space interact in a spatial domain in accordance with a standard reaction-diffusion PDE

$$\frac{\partial x_i}{\partial t} = f_i(x) + d_i \nabla^2 x_i \quad i = 1, \ldots, n$$

(1)

where $d_i$ is dispersal of $i$-th population. In general, zero-flux or periodic conditions are imposed at the boundary of the spatial domain. If $d_i$ and $f_i$ do not depend on time and space, then a uniform solution $\bar{x} = (\bar{x}_1, \ldots, \bar{x}_n)$ of
(1) (satisfying $\partial x_i / \partial t = \nabla^2 x_i = 0$) is an equilibrium of the lumped model

$$\frac{dx_i}{dt} = f_i(x) \quad i = 1, \ldots, n$$

(2)

In his famous paper on morphogenesis, Turing (1952) discovered that $\bar{x}$
can be stable in model (2) but unstable in model (1) for suitably unbal-
anced dispersal rates. This somehow counterintuitive phenomenon, called
diffusive (or Turing) instability, has been extensively used in ecology in the
last 40 years to discuss the problem of pattern formation in spatially ex-
tended ecosystems (see, for instance, Segel and Jackson (1972), Levin and
Segel (1976), Chakraborty, Singh, Lucy and Ridland (1996), Bartumeus,
Alonso and Catalan (2001), Alonso, Bartumeus and Catalan (2002), Bau-
and Xue (2009), Sun, Zhang and Jin (2009), Banerjee (2010), Fasani and Ri-
naldi (2011, 2012), Della Rossa et al. (2012)). Also the problem of plankton
patchiness has been studied in terms of diffusive instability (Levin and Segel,
1976, Malchow, 1993, 1994), even if it has more often been dealt with through
the analysis of power spectra (see, for example, Steele and Henderson (1992),
Powell and Okubo (1994), Abraham (1998), Vilar et al. (2003)).

Necessary and sufficient conditions for diffusive instability have first been
obtained by Turing for the particular case $n = 2$ and then by Satnoianu et al.
(2000), Satnoianu and van den Driessche (2005) for the general case. In this
paper, we only use the following sufficient condition for diffusive instability
that can be easily derived (see Della Rossa et al. (2012)) from the general
results of Satnoianu and coauthors.

A sufficient condition for diffusive instability. If a population, say
the $i$-th one, is an activator, in the sense that $\partial f_i / \partial x_i > 0$ at a positive stable
equilibrium $\bar{x}$ of (2), then the uniform solution $\bar{x}$ of (1) is unstable provided the activator disperses sufficiently less than the other populations. The existence of an activator is only a sufficient condition for diffusive instability, in the sense that there are systems with three or more species in which diffusive instability can emerge even if there are no activators. In contrast, this is not possible in systems with only two species, where the existence of an activator is a necessary and sufficient condition of diffusive instability, again under the assumption of unbalanced dispersals.

In the case $n = 2$, there can be only one activator because, $\bar{x}$ being stable, the trace of the Jacobian ($\partial f_1/\partial x_1 + \partial f_2/\partial x_2$) must be negative. By contrast, when $n > 2$, we can have multiple activators, in which case the dispersals of the activators required to guarantee spatial patterns do not need to be unbalanced.

The spatial patterns that emerge when the sufficient condition is satisfied (typically spot-like patterns) are particularly sharp for the activators and depend upon demographic parameters and dispersal, as shown in the application described in Sect. 4.

3. Patchiness in plankton models

Phytoplankton ($P$) and zooplankton ($Z$) populations are central components of the aquatic food web going from nutrient ($N$) to fish ($F$). They are usually present in a high number of groups characterized by different size, mobility and life strategies. Each phytoplankton group is limited by light and nutrients (typically, nitrogen and phosphorous) and is predated by a few zooplankton groups, which, in turn, are the food sources of a number
of fish species. Some demographic characteristics of the various components of the food web are influenced by periodic (or almost periodic) exogenous factors (daily cycle for light, weekly cycle for nutrient production, moon cycle for predator efficiency, yearly cycle for light and water temperature) that can have relevant impacts on plankton dynamics (see, for example, May (1974), Harris (1986), Berryman and Millstein (1989), Sugihara and May (1990), Scheffer (1991b), Steele and Henderson (1992), Hastings, Hom, Ellner, Turchin and Godfray (1993), Ascioti et al. (1993), Pascual et al. (1995)). Depth is also an important independent variable that, in principle, should be included in any model in order to carefully describe the impact of self-shading on phytoplankton growth.

Models used to mimic spatio-temporal plankton dynamics are much more simple than reality. In particular, in order to apply our sufficient condition for diffusive instability we rule out exogenous periodicities and depth. Thus, the models we will consider are, in the most complex case, food webs with constant demographic parameters and dispersal. But, more often, they simply mimic food chains going from nutrients to fish or segments of this food chain.

The aim of our analysis is to show that, under general and standard assumptions, zooplankton populations are activators, in the sense specified in the previous section. This occurs with almost no exception if the model includes explicitly (as it should!) phytoplankton and fish. By contrast, if preys or enemies of zooplankton are missing, then there is no chance that the model predicts zooplankton patchiness. In order to support these statements, we first show that in food chain models ending with zooplankton
(e.g. phytoplankton-zooplankton \((P-Z)\) models or nutrient-phytoplankton-zooplankton \((N-P-Z)\) models), or starting with zooplankton (e.g. zooplankton-fish \((Z-F)\) models), zooplankton can not be an activator. Then, we prove that food chain models including prey and enemies of zooplankton, like \(N - P - Z - F\) models, satisfy our sufficient condition for the emergence of zooplankton patchiness. Finally, we show that the result remains valid also in food webs, i.e., when the model includes multiple groups of phytoplankton and/or zooplankton.

### 3.1. Zooplankton patchiness

Food chain models with zooplankton at the top of the chain are either \(P - Z\) models (Levin and Segel, 1976, Steele and Henderson, 1992, Vilar et al., 2003) or \(N - P - Z\) models (Steele and Henderson, 1992, Abraham, 1998, Hillary and Bees, 2004a,b). They all share the same equation for zooplankton, namely

\[
\frac{dZ}{dt} = f_Z(P, Z) = e_Z \Psi_Z(P, Z)Z - m_Z(Z)Z = Z \left[ e_Z \Psi_Z(P, Z) - m_Z(Z) \right]
\]

(3)

where \(e_Z\), \(m_Z\) and \(\Psi_Z\) are efficiency, per-capita mortality and functional response of zooplankton. If we assume, that the stable equilibrium \((\bar{N}, \bar{P}, \bar{Z})\) is strictly positive (zooplankton patchiness in the absence of zooplankton makes no sense) then

\[
\frac{\partial f_Z}{\partial Z} = \bar{Z} \left[ e_Z \frac{\partial \Psi_Z}{\partial Z} - \frac{\partial m_Z}{\partial Z} \right]
\]

(4)

because the term in the brackets in (3) is zero at a positive equilibrium. If the functional response \(\Psi_Z\) and the per-capita mortality \(m_Z\) of zooplankton
do not depend on zooplankton density, then $\partial f_Z/\partial Z = 0$ so that zooplankton is not an activator (even if our sufficient condition is ‘almost satisfied’).

If zooplankton individuals interfere when predating ($\partial \Psi_Z/\partial Z < 0$) and/or suffer some kind of intraspecific competition ($\partial m_Z/\partial Z > 0$), then $\partial f_Z/\partial Z$ is negative and the sufficient condition for pattern formation is not satisfied.

In order to obtain the opposite result, one should imagine that zooplankton is cooperative in searching for food ($\partial \Psi_Z/\partial Z > 0$) or in activating survival mechanisms ($\partial m_Z/\partial Z < 0$), but these assumptions are not sensible and in fact they have never been reported in the literature.

Food chain models with zooplankton at the bottom of the chain (never discussed in the literature so far) should be $Z - F$ models with the fish equation of the form

$$\frac{dF}{dt} = f_F(Z, F) = e_F\Psi_F(Z, F)F - m_F(F)F = F[e_F\Psi_F(Z, F) - m_F(F)]$$

so that, at a positive equilibrium $(\bar{Z}, \bar{F})$,

$$\frac{\partial f_F}{\partial F} = \bar{F} \left[ e_F \frac{\partial \Psi_F}{\partial F} - \frac{\partial m_F}{\partial F} \right]$$  \hspace{1cm} (5)

The standard assumption in studies of fish stocks (Walters and Martell, 2004) is that the functional response $\Psi_F$ and the per-capita mortality $m_F$ do not depend on $F$ (notice that this rules out the case of ratio-dependency), so that from (5) $\partial f_F/\partial F = 0$. Since, by assumption, the equilibrium $(\bar{Z}, \bar{F})$ is stable, the trace of the Jacobian ($\partial f_Z/\partial Z + \partial f_F/\partial F$) must be negative, and hence $\partial f_Z/\partial Z < 0$, i.e. our sufficient condition is not satisfied for zooplankton. This conclusion is reinforced if $\partial \Psi_F/\partial F > 0$ and/or $\partial m_F/\partial F < 0$, i.e. if fish are cooperative and/or predated by Holling type II carnivores. Thus, in
conclusion, even $Z - F$ models do not suggest zooplankton patchiness under very general and realistic assumptions.

Let us now consider $P - Z - F$ and $N - P - Z - F$ models where both prey and predator of zooplankton appear explicitly. Models of this kind have been proposed in the literature with $N$ and $F$ fixed at constant values and used as control parameters (in order to still obtain a model with only two differential equations) (Scheffer, 1991b,a, Malchow, 1993, 1994, Medvinsky, Petrovskii, Tikhonova, Malchow and Li, 2002) or with $N$ and $F$ varying in time in accordance with a differential equation (Doveri, Scheffer, Rinaldi, Muratori and Kuznetso, 1993, Rinaldi and Solidoro, 1998). In all these cases, the zooplankton equation is still eq. (3) but with the addition of an extra mortality due to fish, namely

$$
\frac{dZ}{dt} = f_Z(P, Z, F) = e_Z\Psi_Z(P, Z)Z - m_Z(Z)Z - F\Psi_F(Z, F) = Z\left[e_Z\Psi_Z(P, Z) - m_Z(Z) - F\frac{\Psi_F(Z, F)}{Z}\right] (6)
$$

In the absence of interference and cooperation in the zooplankton population ($\partial\Psi_Z/\partial Z = \partial m_Z/\partial Z = 0$) we obtain from (6) that at a positive equilibrium $Z$

$$
\frac{\partial f_Z}{\partial Z} = -ZF\frac{\partial (\Psi_F/Z)}{\partial Z} \quad (7)
$$

To evaluate the sign of $\partial f_Z/\partial Z$ in (7) we can consider the two standard cases of fish functional response

$$
\Psi_F = \begin{cases} 
  aZ/(b + Z) & \text{Holling type II} \\
  aZ^2/(b^2 + Z^2) & \text{Holling type III}
\end{cases}
$$

where $b$ is the half-saturation constant, namely the density of zooplankton
at which fish predation is half maximum. After some algebra, we obtain

\[
\frac{\partial f_Z}{\partial Z} = \begin{cases} 
  a\bar{Z}/(b + \bar{Z})^2 \\
  a\bar{Z}(\bar{Z}^2 - b^2)/(b^2 + \bar{Z}^2)^2
\end{cases}
\]

and the conclusion is that if the fish has a Holling type II functional response the zooplankton is always an activator, while in the case of Holling type III functional response the zooplankton is an activator if \( \bar{Z} > b \), i.e. if the equilibrium \((\bar{N}, \bar{P}, \bar{Z}, \bar{F})\) is a so called zooplankton dominated equilibrium (Malchow, 1993). In the opposite case, namely when the equilibrium is a phytoplankton dominated equilibrium (i.e. \( \bar{P} \) large and \( \bar{Z} \) small) zooplankton is not an activator and its patchiness can not be inferred from our sufficient condition. This is not a great deal because knowing if a population with low abundance is patchy or not is only a futile curiosity.

The results obtained so far are valid also in food web models characterized by multiple phytoplankton and zooplankton groups (see, for example, Rose, Swartzman, Kindig and Taub (1988)). In these models each zooplankton group \( i \) is described by an equation similar to (6)

\[
\frac{dZ^{(i)}}{dt} = e_{Z}^{(i)}\Psi_{Z}^{(i)}Z^{(i)} - m_{Z}^{(i)}(Z)Z^{(i)} - F_{F}\Psi_{F}^{(i)}
\]

where the \( i \)-th functional response \( \Psi_{Z}^{(i)} \) depends upon the phytoplankton groups that are in the diet of the \( i \)-th zooplankton group but not upon \( Z^{(i)} \), while the fish functional response \( \Psi_{F}^{(i)} \) depends upon \( Z^{(i)} \) but also upon the other zooplankton groups. More precisely, \( \Psi_{F}^{(i)} \) takes the form

\[
\Psi_{F}^{(i)} = \frac{aZ^{(i)}}{b_0 + b_1Z^{(1)} + b_2Z^{(2)} + \ldots + b_iZ^{(i)} + \ldots}
\]

in the case of a generalized type II fish functional response, or a similar form in the case of a generalized type III fish functional response. Substituting
(9) into (8) one obtains

$$\frac{dZ^{(i)}}{dt} = Z^{(i)} \left[ e_{Z}^{(i)} \Psi_{Z}^{(i)} - m_{Z}^{(i)} - \frac{aF}{b_{0} + b_{1}Z^{(1)} + b_{2}Z^{(2)} + \ldots + b_{i}Z^{(i)} + \ldots} \right]$$

that gives

$$\frac{\partial f_{Z}^{(i)}}{\partial Z^{(i)}} = \frac{aFb_{i}Z^{(i)}}{(b_{0} + b_{1}Z^{(1)} + b_{2}Z^{(2)} + \ldots + b_{i}Z^{(i)} + \ldots)^{2}}$$

which is always positive, thus indicating that each zooplankton group is an activator. As in the case of food chain models, the analysis of model (8,9) with type III fish functional response brings to the conclusion that zooplankton groups are activators in zooplankton dominated regimes. However, not all zooplankton groups have the same chance to be patchy, because some of them might not satisfy the condition of sufficiently low dispersal. This result might be of some interest for interpreting the dependence of patchiness upon individual size recently pointed out in a study on field data (Decima, Ohman and De Robertis, 2010).

3.2. Phytoplankton patchiness

The analysis performed for zooplankton can be repeated to check if also phytoplankton is an activator in $N - P - Z$ or $N - P - Z - F$ models. In these models the phytoplankton equation is

$$\frac{dP}{dt} = f_{P}(N, P, Z) = e_{P}\Psi_{P}(P, N)P - m_{P}(P)P - Z\Psi_{Z}(P, Z) = P \left[ e_{P}\Psi_{P}(P, N) - m_{P}(P) - Z\frac{\Psi_{Z}(P, Z)}{P} \right]$$

where $\Psi_{P}$ is nutrient uptake of phytoplankton. Thus,

$$\frac{\partial f_{P}}{\partial P} = P \left[ e_{P} \frac{\partial \Psi_{P}}{\partial P} - \frac{\partial m_{P}}{\partial P} - Z \frac{\partial (\Psi_{Z}/P)}{\partial P} \right]$$
and even in the simplest case of constant mortality ($\partial m_P/\partial P = 0$) and type II functional response of zooplankton ($\Psi_Z = aP/(b + P)$) we can not obtain a unique answer. In fact

$$\frac{\partial f_P}{\partial P} = \bar{P} \left[ e_P \frac{\partial \Psi_P}{\partial P} + \frac{aZ}{(b + P)^2} \right]$$

(11)

and the first term in brackets is negative because self-shading is depressing the nutrient uptake of phytoplankton. Actually, eq. (11) shows that phytoplankton has higher chances to be an activator when its density is low and $\bar{Z}$ is high, i.e. in zooplankton dominated regimes. But this result, as shown in the next section, is not always guaranteed.

3.3. Unbalance of dispersals

We conclude this section with a comment on a somehow delicate point, namely that of the required unbalance of dispersals. Since zooplankton is in general an activator, its patchiness is guaranteed by our sufficient condition provided it disperses sufficiently less than phytoplankton and fish, i.e.

$$d_Z < d_P \quad d_Z < d_F.$$

While there is no doubt on the latter condition, the first poses some problems. The most common opinion on this matter, in particular when phytoplankton and zooplankton are considered as inert traces, is that $d_P$ and $d_Z$ are roughly comparable (see, for instance, Medvinsky et al. (2002)). But the inequality $d_Z < d_P$ can, in principle, be supported by noticing that many zooplankton species are capable of resisting to currents by grasping, while phytoplankton is not. In reality, the mobility of zooplankton can be used to say that when there is no turbulence the opposite inequality can hold (see, for
instance, Malchow (1994)). However, this issue is of no relevance when also phytoplankton is an activator, because in that case the only unbalance that matters is $d_Z < d_F$. From the above discussion it follows that this should often be the case in zooplankton dominated regimes.

4. Analysis of a particular plankton model

In this section we study in some detail a spatially extended food chain model with 5 components: Nutrient ($N$), Phytoplankton ($P$), Zooplankton ($Z$), Planktivorous fish ($F$), and Carnivores ($C$). The zooplankton is the central compartment of the chain and we therefore expect zooplankton patchiness for suitably low zooplankton dispersal. The model, derived from Doveri et al. (1993), has been selected for three reasons: First, it has performed quite well in explaining the emergence of chaotic plankton dynamics in the presence of seasonalities (Rinaldi and Solidoro, 1998); second, realistic parameter ranges are available for it (Doveri et al., 1993); third it is much more detailed than the simple $P - Z$ or $P - Z - F$ models used until now for testing pattern formation due to Turing instability.

The model equations, obtained from Doveri et al. (1993) by eliminating
all seasonalities, are:

\[
\frac{dN}{dt} = \delta(N_0 - N) - \beta_P \frac{PN}{k_P + N} \frac{l}{\gamma + l} + \rho_{Pm}P + \rho_{Zm}Z + \rho_{Fm}F + \\
+ \rho_{Cm}C + \xi_{Z}\beta_{Z} \frac{ZP}{k_{Z} + P} + \xi_{F}\beta_{F} \frac{ZF}{k_{F} + Z}
\]

\[
\frac{dP}{dt} = e_{\beta_P} \frac{PN}{k_P + N} \frac{l}{\gamma + l} - \beta_{Z} \frac{ZP}{k_{Z} + P} - m_{P}P - \delta P
\]

\[
\frac{dZ}{dt} = e_{Z}\beta_{Z} \frac{ZP}{k_{Z} + P} - \beta_{F} \frac{ZF}{k_{F} + Z} - m_{Z}Z - \delta Z
\]

\[
\frac{dF}{dt} = e_{F}\beta_{F} \frac{ZF}{k_{F} + Z} - \beta_{C} \frac{CF}{k_{C} + F} - m_{F}F - \delta F + V_{0}\bar{I}
\]

\[
\frac{dC}{dt} = e_{C}\beta_{C} \frac{CF}{k_{C} + F} - m_{C}C
\]

(12)

Notice that the nutrient uptake per unit of phytoplankton decreases with phytoplankton density in order to take the effect of self-shading into account. Thus, phytoplankton is not guaranteed to be an activator.

The reference parameter values used in all simulations are reported in Table 1. They have been fixed in the feasible ranges proposed in Doveri et al. (1993) except the parameter \(l\) which has been selected in order to enhance the self-shading effect.

For these reference parameter values the model has a strictly positive stable equilibrium

\[
\bar{N} = 0.356 \ [mg_{P} \ l^{-1}]
\]

\[
\bar{P} = 0.075 \ [mg_{dC} \ l^{-1}]
\]

\[
\bar{Z} = 0.565 \ [mg_{dC} \ l^{-1}]
\]

\[
\bar{F} = 0.024 \ [mg_{dC} \ l^{-1}]
\]

\[
\bar{C} = 0.099 \ [mg_{dC} \ l^{-1}]
\]

which is a zooplankton dominated equilibrium. The Jacobian matrix evalu-
Table 1: Parameter values for model (12)

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<th>Value</th>
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</tr>
<tr>
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<tr>
<td>$\rho_P$</td>
<td>$mg P (mg dw)^{-1}$</td>
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<td>$\rho_Z$</td>
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<td>0.0031</td>
</tr>
<tr>
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<td>0.00465</td>
<td>$\rho_C$</td>
<td>$mg P (mg dw)^{-1}$</td>
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<tr>
<td>$\xi_Z$</td>
<td>$mg P (mg dw)^{-1}$</td>
<td>0.007</td>
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<td>0.006</td>
</tr>
<tr>
<td>$\delta$</td>
<td>$day^{-1}$</td>
<td>0.025</td>
<td>$l$</td>
<td>$cal m^{-2}day^{-1}$</td>
<td>4</td>
</tr>
<tr>
<td>$\gamma$</td>
<td>$cal l m^{-2} (day mg dw)^{-1}$</td>
<td>150</td>
<td>$V_0$</td>
<td>$mg dw l^{-1}$</td>
<td>2</td>
</tr>
<tr>
<td>$N_0$</td>
<td>$mg P l^{-1}$</td>
<td>0.37</td>
<td>$I$</td>
<td>$day^{-1}$</td>
<td>0.00027</td>
</tr>
</tbody>
</table>

and the sign of its central element confirms that zooplankton is an activator.

The negativity of the second diagonal element shows, as observed in the previous section, that in a zooplankton dominated equilibrium there is no guarantee that phytoplankton is an activator.

Thus, on the basis of the results obtained with our sufficient condition
we expect zooplankton patchiness if zooplankton dispersal is sufficiently low.

To confirm this guess we have performed extensive simulations of the PDE model (1,12) on 51.2 km × 51.2 km square spatial domains with periodic boundary conditions. The initial conditions have been randomly selected, in order to avoid the formation of special patterns. Significant parts of the simulation results are reported in Fig. 2 (see captions for details) and confirm all our expected results. They point out that the zooplankton spatial patterns are typically spot-like patterns, where the spots become more numerous and irregular when the zooplankton dispersal decreases.

Figure 2: Stationary solutions of model (1,12) obtained through simulations on 51.2 km × 51.2 km square spatial domains with periodic boundary conditions and randomly selected initial conditions. In order to show more details on the shape and dimension of zooplankton spots, only parts of the solutions are shown, by zooming on 3.2 km × 3.2 km squares. Parameter values are as in Table 1 and dispersal coefficients are \( d_N = d_P = 2 \, \text{km}^2 \, \text{day}^{-1} \), \( d_F = d_C = 10 \, \text{km}^2 \, \text{day}^{-1} \) and, from left to right, \( d_Z = 1, 0.5, 0.1 \, \text{dm}^2 \, \text{day}^{-1} \). Simulations have been performed using GRIND for Matlab, \url{http://www.aew.wur.nl/UK/GRIND/}. 
5. Concluding remarks

We have studied in this paper the problem of plankton patchiness due to diffusive instability. For this we have used a very simple but powerful sufficient condition for pattern formation that can be applied when a diagonal element of the Jacobian matrix is positive. First we have systematically discussed all possible zooplankton models and discovered that the sufficient condition is satisfied if and only if the model contains both the prey (phytoplankton) and the predator (planktivorous fish) of zooplankton. The discovery that the impact of fish on zooplankton, a problem rarely considered in the technical literature, is the key for understanding pattern formation, gives a new value to old contributions in aquatic sciences (Rose, Swartzman, Kindig and Taub, 1975, Leah, Moss and Forrest, 1980, Cronberg, 1982, Shapiro and Wright, 1984, Reinertsen and Olsen, 1984, Levitan, Kerfoot and De Mott, 1985). Then, we have studied models involving phytoplankton and discovered that patchiness emerges if the effect of self-shading is not too strong and the equilibrium is zooplankton dominated. In conclusion, we have pointed out subtle but relevant differences between phytoplankton and zooplankton in the role they play in promoting patchiness.

The present study has been carried out under the assumption of diffusive dispersal of all populations, which is rigorously justified if all automotive individuals (like planktivorous fish and carnivores) undergo unbiased random walks. In contrast, if individuals of some species are also actively moving, it is, in principle, important to add to the diffusive term a second term (called cross-emigration) interpreting the tendencies of individuals to escape from predator and/or pursuit prey. In general this second dispersal mechanism
is assumed to depend on the gradient of prey and predator abundances, (see, for example, Murray (1990), Arditi, Tyutyunov, Morgulis, Govorukhin and Senina (2001), Huang and Diekmann (2003), Li, Gao, Hui, Han and Shi (2005)) and the conclusion is that cross-emigration can either increase or decrease spatial complexity (Huang and Diekmann, 2003). It would therefore be interesting, though certainly not trivial, to apply Huang and Diekmann approach to the case in which planktivorous fish and carnivores have relevant cross-emigration responses.

Obviously, the present study could also be extended in other directions, for example by looking at the effect of depth, seasons and multiplicity of attractors. But certainly more attractive is the idea of checking if what we have discovered here can be extended up to the point of formulating a sort of general ecological principle, namely that populations that disperse less than their prey and enemies tend to be patchy under very general conditions.

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References


