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Conditions for patchiness in plankton models

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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 than 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 **1. Introduction**

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

24 Only a few studies have been carried out on complete models of the

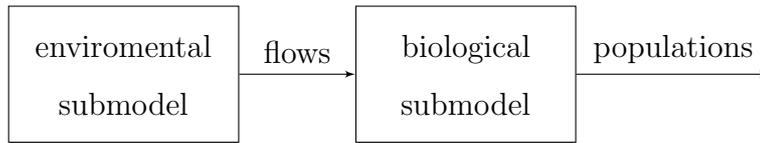


Figure 1: Two submodels connected in cascade.

25 kind shown in Fig.1 (Vilar, Solé and Rubí, 2003, Abraham, 1998, Hillary
26 and Bees, 2004b, Colombo et al., 2008). These studies confirm that the
27 characteristics of the environment can be dominant, but that in some cases
28 plankton demography may add extra complexity.

29 In order to simplify the study of plankton, one can restrict the analysis
30 to only one of the two submodels in Fig. 1. The first extreme approach
31 consists of studying the spatio-temporal dynamics of the flows and deduce
32 from them the population patterns by considering plankton, as well as other
33 species, as inert particles (see Gower (1980) for an early support of this idea).
34 In this way, the problem is reduced to a relatively standard problem of hy-
35 drodynamics where only the sinking, floating or swimming characteristics of
36 the populations are taken into account. This approach can explain numer-
37 ous plankton patterns, observed at various spatial scales, like vortices that
38 turn on and off alternatively (Aref, 1984), multiple bands of dense organisms
39 lumped into swaths (Shanks, 1983), and long single stripes of swimming or
40 floating plankton parallel to shore (Franks, 1997). Conversely, the second
41 extreme approach, simply rules out the hydrodynamics by assuming that all
42 flows are constant in time and space, so that the model becomes a classical
43 population model with a dispersal mechanism controlling the movement of
44 the individuals in a spatial domain. This approach has a long scientific tra-

45 dition and emphasizes the role of biology by pointing out that demography
46 has the power of creating surprisingly complex spatial patterns, like spots
47 and stripes of abundances, even in perfectly homogeneous environments.

48 Segel and Jackson (1972) were the first to show that the theory devel-
49 oped by Turing (1952) in his celebrated study on the origin of morphogenesis
50 could be applied in ecology to check if density dependent mechanisms could
51 promote spatial pattern formation in perfectly homogeneous environments.
52 Their study was limited to models with two populations and diffusive dis-
53 persal, because these were Turing’s assumptions. A few years later, Levin
54 and Segel (1976) conjectured that Turing’s theory was potentially the most
55 appropriate tool for supporting the idea that plankton patchiness could be
56 the consequence of demographic characteristics of the populations. However,
57 the phytoplankton-zooplankton model they used is not credible (phytoplank-
58 ton in the absence of zooplankton increases unboundedly) and suggests that
59 the so-called “activator” (a key notion in Turing’s theory) is phytoplankton.
60 This implies that phytoplankton should be more patchy than zooplankton,
61 a property which is in contrast with observations (Levin, 1992, Vilar et al.,
62 2003). Here we show that Levin and Segel could not do any better, given
63 the constraint of using a model with only two populations. In fact, all stan-
64 dard ditrophic food chain models with zooplankton at the top or at the
65 bottom of the chain can not have zooplankton as activator (we consider as
66 non-standard not only the models with unboundedly growing phytoplankton
67 (Levin and Segel, 1976), but also those with predator with ratio-dependent
68 functional responses which are known to be prone to degeneracies (Yodzis,
69 1994, Abrams, 1994). By contrast Levin and Segel were right in making

70 their conjecture because, as shown in this paper, a recently derived sufficient
71 condition for pattern formation (Satnoianu, Menzinger and Maini, 2000, Sat-
72 noianu and van den Driessche, 2005, Della Rossa, Fasani and Rinaldi, 2012),
73 is structurally satisfied in all realistic models where zooplankton feeds on
74 phytoplankton and is predated by fish.

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

84 **2. A simple sufficient condition for pattern formation**

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

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

88 where d_i is dispersal of i -th population. In general, zero-flux or periodic
89 conditions are imposed at the boundary of the spatial domain. If d_i and f_i
90 do not depend on time and space, then a uniform solution $\bar{x} = (\bar{x}_1, \dots, \bar{x}_n)$ of

91 (1) (satisfying $\partial x_i / \partial t = \nabla^2 x_i = 0$) is an equilibrium of the lumped model

$$\frac{dx_i}{dt} = f_i(x) \quad i = 1, \dots, n \quad (2)$$

92 In his famous paper on morphogenesis, Turing (1952) discovered that \bar{x}
93 can be stable in model (2) but unstable in model (1) for suitably unbal-
94 anced dispersal rates. This somehow counterintuitive phenomenon, called
95 diffusive (or Turing) instability, has been extensively used in ecology in the
96 last 40 years to discuss the problem of pattern formation in spatially ex-
97 tended ecosystems (see, for instance, Segel and Jackson (1972), Levin and
98 Segel (1976), Chakraborty, Singh, Lucy and Ridland (1996), Bartumeus,
99 Alonso and Catalan (2001), Alonso, Bartumeus and Catalan (2002), Bau-
100 rmann, Gross and Feudel (2007), Wang, Liu and Jin (2007), Zhang, Wang
101 and Xue (2009), Sun, Zhang and Jin (2009), Banerjee (2010), Fasani and Ri-
102 naldi (2011, 2012), Della Rossa et al. (2012)). Also the problem of plankton
103 patchiness has been studied in terms of diffusive instability (Levin and Segel,
104 1976, Malchow, 1993, 1994), even if it has more often been dealt with through
105 the analysis of power spectra (see, for example, Steele and Henderson (1992),
106 Powell and Okubo (1994), Abraham (1998), Vilar et al. (2003)).

107 Necessary and sufficient conditions for diffusive instability have first been
108 obtained by Turing for the particular case $n = 2$ and then by Satnoianu et al.
109 (2000), Satnoianu and van den Driessche (2005) for the general case. In this
110 paper, we only use the following sufficient condition for diffusive instability
111 that can be easily derived (see Della Rossa et al. (2012)) from the general
112 results of Satnoianu and coauthors.

113 **A sufficient condition for diffusive instability.** If a population, say
114 the i -th one, is an activator, in the sense that $\partial f_i / \partial x_i > 0$ at a positive stable

115 equilibrium \bar{x} of (2), then the uniform solution \bar{x} of (1) is unstable provided
116 the activator disperses sufficiently less than the other populations. The exist-
117 tence of an activator is only a sufficient condition for diffusive instability, in
118 the sense that there are systems with three or more species in which diffusive
119 instability can emerge even if there are no activators. In contrast, this is not
120 possible in systems with only two species, where the existence of an activator
121 is a necessary and sufficient condition of diffusive instability, again under the
122 assumption of unbalanced dispersals.

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

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

132 **3. Patchiness in plankton models**

133 Phytoplankton (P) and zooplankton (Z) populations are central compo-
134 nents of the aquatic food web going from nutrient (N) to fish (F). They
135 are usually present in a high number of groups characterized by different
136 size, mobility and life strategies. Each phytoplankton group is limited by
137 light and nutrients (typically, nitrogen and phosphorous) and is predated by
138 a few zooplankton groups, which, in turn, are the food sources of a number

139 of fish species. Some demographic characteristics of the various components
140 of the food web are influenced by periodic (or almost periodic) exogenous
141 factors (daily cycle for light, weekly cycle for nutrient production, moon
142 cycle for predator efficiency, yearly cycle for light and water temperature)
143 that can have relevant impacts on plankton dynamics (see, for example, May
144 (1974), Harris (1986), Berryman and Millstein (1989), Sugihara and May
145 (1990), Scheffer (1991b), Steele and Henderson (1992), Hastings, Hom, Ell-
146 ner, Turchin and Godfray (1993), Ascioti et al. (1993), Pascual et al. (1995)).
147 Depth is also an important independent variable that, in principle, should be
148 included in any model in order to carefully describe the impact of self-shading
149 on phytoplankton growth.

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

157 The aim of our analysis is to show that, under general and standard
158 assumptions, zooplankton populations are activators, in the sense specified
159 in the previous section. This occurs with almost no exception if the model
160 includes explicitly (as it should!) phytoplankton and fish. By contrast, if
161 preys or enemies of zooplankton are missing, then there is no chance that
162 the model predicts zooplankton patchiness. In order to support these state-
163 ments, we first show that in food chain models ending with zooplankton

164 (e.g. phytoplankton-zooplankton ($P-Z$) models or nutrient-phytoplankton-
165 zooplankton ($N-P-Z$) models), or starting with zooplankton (e.g. zooplankton-
166 fish ($Z-F$) models), zooplankton can not be an activator. Then, we prove
167 that food chain models including prey and enemies of zooplankton, like
168 $N-P-Z-F$ models, satisfy our sufficient condition for the emergence of
169 zooplankton patchiness. Finally, we show that the result remains valid also
170 in food webs, i.e., when the model includes multiple groups of phytoplankton
171 and/or zooplankton.

172 3.1. Zooplankton patchiness

173 Food chain models with zooplankton at the top of the chain are either
174 $P-Z$ models (Levin and Segel, 1976, Steele and Henderson, 1992, Vilar
175 et al., 2003) or $N-P-Z$ models (Steele and Henderson, 1992, Abraham,
176 1998, Hillary and Bees, 2004a,b). They all share the same equation for
177 zooplankton, namely

$$\begin{aligned} \frac{dZ}{dt} = f_Z(P, Z) &= e_Z \Psi_Z(P, Z)Z - m_Z(Z)Z \\ &= Z [e_Z \Psi_Z(P, Z) - m_Z(Z)] \end{aligned} \quad (3)$$

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

$$\frac{\partial f_Z}{\partial Z} = \bar{Z} \left[e_Z \frac{\partial \Psi_Z}{\partial Z} - \frac{\partial m_Z}{\partial Z} \right] \quad (4)$$

182 because the term in the brackets in (3) is zero at a positive equilibrium. If
183 the functional response Ψ_Z and the per-capita mortality m_Z of zooplankton

184 do not depend on zooplankton density, then $\partial f_Z/\partial Z = 0$ so that zooplank-
185 ton is not an activator (even if our sufficient condition is ‘almost satisfied’).
186 If zooplankton individuals interfere when predated ($\partial\Psi_Z/\partial Z < 0$) and/or
187 suffer some kind of intraspecific competition ($\partial m_Z/\partial Z > 0$), then $\partial f_Z/\partial Z$
188 is negative and the sufficient condition for pattern formation is not satisfied.
189 In order to obtain the opposite result, one should imagine that zooplankton
190 is cooperative in searching for food ($\partial\Psi_Z/\partial Z > 0$) or in activating survival
191 mechanisms ($\partial m_Z/\partial Z < 0$), but these assumptions are not sensible and in
192 fact they have never been reported in the literature.

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

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

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

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

197 The standard assumption in studies of fish stocks (Walters and Martell, 2004)
198 is that the functional response Ψ_F and the per-capita mortality m_F do not
199 depend on F (notice that this rules out the case of ratio-dependency), so that
200 from (5) $\partial f_F/\partial F = 0$. Since, by assumption, the equilibrium (\bar{Z}, \bar{F}) is stable,
201 the trace of the Jacobian ($\partial f_Z/\partial Z + \partial f_F/\partial F$) must be negative, and hence
202 $\partial f_Z/\partial Z < 0$, i.e. our sufficient condition is not satisfied for zooplankton.
203 This conclusion is reinforced if $\partial\Psi_F/\partial F > 0$ and/or $\partial m_F/\partial F < 0$, i.e. if
204 fish are cooperative and/or predated by Holling type II carnivores. Thus, in

205 conclusion, even $Z - F$ models do not suggest zooplankton patchiness under
 206 very general and realistic assumptions.

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

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

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

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

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

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

222 where b is the half-saturation constant, namely the density of zooplankton

223 at which fish predation is half maximum. After some algebra, we obtain

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

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

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

$$\frac{dZ^{(i)}}{dt} = e_Z^{(i)}\Psi_Z^{(i)}Z^{(i)} - m_Z^{(i)}(Z)Z^{(i)} - F\Psi_F^{(i)} \quad (8)$$

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

$$\Psi_F^{(i)} = \frac{aZ^{(i)}}{b_0 + b_1Z^{(1)} + b_2Z^{(2)} + \dots + b_iZ^{(i)} + \dots} \quad (9)$$

241 in the case of a generalized type II fish functional response, or a similar form
 242 in the case of a generalized type III fish functional response. Substituting

243 (9) into (8) one obtains

$$\frac{dZ^{(i)}}{dt} = Z^{(i)} \left[e_Z^{(i)} \Psi_Z^{(i)} - m_Z^{(i)} - \frac{aF}{b_0 + b_1 Z^{(1)} + b_2 Z^{(2)} + \dots + b_i Z^{(i)} + \dots} \right]$$

244 that gives

$$\frac{\partial f_Z^{(i)}}{\partial Z^{(i)}} = \frac{aF b_i \bar{Z}^{(i)}}{(b_0 + b_1 Z^{(1)} + b_2 Z^{(2)} + \dots + b_i Z^{(i)} + \dots)^2}$$

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

254 3.2. Phytoplankton patchiness

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

$$\begin{aligned} \frac{dP}{dt} = f_P(N, P, Z) &= e_P \Psi_P(P, N)P - m_P(P)P - Z \Psi_Z(P, Z) \\ &= P \left[e_P \Psi_P(P, N) - m_P(P) - Z \frac{\Psi_Z(P, Z)}{P} \right] \end{aligned} \quad (10)$$

258 where Ψ_P is nutrient uptake of phytoplankton. Thus,

$$\frac{\partial f_P}{\partial P} = \bar{P} \left[e_P \frac{\partial \Psi_P}{\partial P} - \frac{\partial m_P}{\partial P} - Z \frac{\partial (\Psi_Z/P)}{\partial P} \right]$$

259 and even in the simplest case of constant mortality ($\partial m_P/\partial P = 0$) and type
 260 II functional response of zooplankton ($\Psi_Z = aP/(b + P)$) we can not obtain
 261 a unique answer. In fact

$$\frac{\partial f_P}{\partial P} = \bar{P} \left[e_P \frac{\partial \Psi_P}{\partial P} + \frac{a\bar{Z}}{(b + \bar{P})^2} \right] \quad (11)$$

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

267 3.3. *Unbalance of dispersals*

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

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

272 While there is no doubt on the latter condition, the first poses some problems.
 273 The most common opinion on this matter, in particular when phytoplank-
 274 ton and zooplankton are considered as inert traces, is that d_P and d_Z are
 275 roughly comparable (see, for instance, Medvinsky et al. (2002)). But the
 276 inequality $d_Z < d_P$ can, in principle, be supported by noticing that many
 277 zooplankton species are capable of resisting to currents by grasping, while
 278 phytoplankton is not. In reality, the mobility of zooplankton can be used to
 279 say that when there is no turbulence the opposite inequality can hold (see, for

280 instance, Malchow (1994)). However, this issue is of no relevance when also
281 phytoplankton is an activator, because in that case the only unbalance that
282 matters is $d_Z < d_F$. From the above discussion it follows that this should
283 often be the case in zooplankton dominated regimes.

284 **4. Analysis of a particular plankton model**

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

296 The model equations, obtained from Doveri et al. (1993) by eliminating

297 all seasonalities, are:

$$\begin{aligned}
\frac{dN}{dt} &= \delta(N_0 - N) - \beta_P \frac{PN}{k_P + N} \frac{l}{\gamma P + l} + \rho_P m_P P + \rho_Z m_Z Z + \rho_F m_F F + \\
&\quad + \rho_C m_C C + \xi_Z \beta_Z \frac{ZP}{k_Z + P} + \xi_F \beta_F \frac{FZ}{k_F + Z} \\
\frac{dP}{dt} &= e_P \beta_P \frac{PN}{k_P + N} \frac{l}{\gamma P + l} - \beta_Z \frac{ZP}{k_Z + P} - m_P P - \delta P \\
\frac{dZ}{dt} &= e_Z \beta_Z \frac{ZP}{k_Z + P} - \beta_F \frac{FZ}{k_F + Z} - m_Z Z - \delta Z \\
\frac{dF}{dt} &= e_F \beta_F \frac{FZ}{k_F + Z} - \beta_C \frac{CF}{k_C + F} - m_F F - \delta F + V_0 \bar{I} \\
\frac{dC}{dt} &= e_C \beta_C \frac{CF}{k_C + F} - m_C C
\end{aligned} \tag{12}$$

298 Notice that the nutrient uptake per unit of phytoplankton decreases with
299 phytoplankton density in order to take the effect of self-shading into account.

300 Thus, phytoplankton is not guaranteed to be an activator.

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

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

$$307 \quad \bar{N} = 0.356 \quad [mg_P l^{-1}]$$

$$308 \quad \bar{P} = 0.075 \quad [mg_{dw} l^{-1}]$$

$$309 \quad \bar{Z} = 0.565 \quad [mg_{dw} l^{-1}]$$

$$310 \quad \bar{F} = 0.024 \quad [mg_{dw} l^{-1}]$$

$$311 \quad \bar{C} = 0.099 \quad [mg_{dw} l^{-1}]$$

312 which is a zooplankton dominated equilibrium. The Jacobian matrix evalu-

Parameter	Units	Value	Parameter	Units	Value
m_P	day^{-1}	0.2	m_Z	day^{-1}	0.15
m_F	day^{-1}	0.02	m_C	day^{-1}	0.01
k_P	$mg_P l^{-1}$	0.02	k_Z	$mg_{dw} l^{-1}$	0.075
k_F	$mg_{dw} l^{-1}$	0.5	k_C	$mg_{dw} l^{-1}$	1.2
β_P	day^{-1}	0.1	β_Z	day^{-1}	0.6
β_F	day^{-1}	0.2	β_C	day^{-1}	0.5
e_P	$mg_{dw}(mg_P)^{-1}$	100	e_Z	-	0.6
e_F	-	0.6	e_C	-	1
ρ_P	$mg_P(mg_{dw})^{-1}$	0.003	ρ_Z	$mg_P(mg_{dw})^{-1}$	0.0031
ρ_F	$mg_P(mg_{dw})^{-1}$	0.00465	ρ_C	$mg_P(mg_{dw})^{-1}$	0.0054
ξ_Z	$mg_P(mg_{dw})^{-1}$	0.007	ξ_F	$mg_P(mg_{dw})^{-1}$	0.006
δ	day^{-1}	0.025	l	$cal m^{-2} day^{-1}$	4
γ	$cal l m^{-2} (day mg_{dw})^{-1}$	150	V_0	$mg_{dw} l^{-1}$	2
N_0	$mg_P l^{-1}$	0.37	\bar{I}	day^{-1}	0.00027

Table 1: Parameter values for model (12)

313 ated numerically at this equilibrium is

$$\begin{pmatrix} -0.0252777 & 0.00199401 & 0.00257325 & 0.000729839 & 0.000054 \\ 0.0277658 & -0.70517 & -0.299329 & 0 & 0 \\ 0 & 0.681537 & 0.00243975 & -0.10614 & 0 \\ 0 & 0 & 0.00129449 & -0.0212353 & -0.01 \\ 0 & 0 & 0 & 0.0399192 & 0 \end{pmatrix}$$

314 and the sign of its central element confirms that zooplankton is an activator.
315 The negativity of the second diagonal element shows, as observed in the
316 previous section, that in a zooplankton dominated equilibrium there is no
317 guarantee that phytoplankton is an activator.

318 Thus, on the basis of the results obtained with our sufficient condition

319 we expect zooplankton patchiness if zooplankton dispersal is sufficiently low.
 320 To confirm this guess we have performed extensive simulations of the PDE
 321 model (1,12) on $51.2 \text{ km} \times 51.2 \text{ km}$ square spatial domains with periodic
 322 boundary conditions. The initial conditions have been randomly selected,
 323 in order to avoid the formation of special patterns. Significant parts of the
 324 simulation results are reported in Fig. 2 (see captions for details) and confirm
 325 all our expected results. They point out that the zooplankton spatial patterns
 326 are typically spot-like patterns, where the spots become more numerous and
 327 irregular when the zooplankton dispersal decreases.

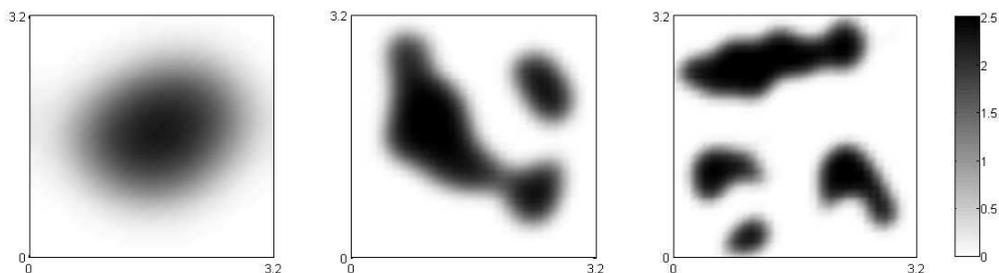


Figure 2: Stationary solutions of model (1,12) obtained through simulations on $51.2 \text{ km} \times 51.2 \text{ km}$ square spatial domains with periodic boundary conditions and randomly selected initial conditions. In order to show more details on the shape and dimension of zooplankton spots, only parts of the solutions are shown, by zooming on $3.2 \text{ km} \times 3.2 \text{ km}$ 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, $d_Z = 1, 0.5, 0.1 \text{ km}^2 \text{ day}^{-1}$. Simulations have been performed using GRIND for Matlab, <http://www.aew.wur.nl/UK/GRIND/>.

328 5. Concluding remarks

329 We have studied in this paper the problem of plankton patchiness due
330 to diffusive instability. For this we have used a very simple but powerful
331 sufficient condition for pattern formation that can be applied when a diago-
332 nal element of the Jacobian matrix is positive. First we have systematically
333 discussed all possible zooplankton models and discovered that the sufficient
334 condition is satisfied if and only if the model contains both the prey (phyto-
335 plankton) and the predator (planktivorous fish) of zooplankton. The discov-
336 ery that the impact of fish on zooplankton, a problem rarely considered in the
337 technical literature, is the key for understanding pattern formation, gives a
338 new value to old contributions in aquatic sciences (Rose, Swartzman, Kindig
339 and Taub, 1975, Leah, Moss and Forrest, 1980, Cronberg, 1982, Shapiro and
340 Wright, 1984, Reinertsen and Olsen, 1984, Levitan, Kerfoot and De Mott,
341 1985). Then, we have studied models involving phytoplankton and discov-
342 ered that patchiness emerges if the effect of self-shading is not too strong and
343 the equilibrium is zooplankton dominated. In conclusion, we have pointed
344 out subtle but relevant differences between phytoplankton and zooplankton
345 in the role they play in promoting patchiness.

346 The present study has been carried out under the assumption of diffusive
347 dispersal of all populations, which is rigorously justified if all automotive
348 individuals (like planktivorous fish and carnivores) undergo unbiased random
349 walks. In contrast, if individuals of some species are also actively moving, it
350 is, in principle, important to add to the diffusive term a second term (called
351 cross-emigration) interpreting the tendencies of individuals to escape from
352 predator and/or pursuit prey. In general this second dispersal mechanism

353 is assumed to depend on the gradient of prey and predator abundances,
354 (see, for example, Murray (1990), Arditi, Tyutyunov, Morgulis, Govorukhin
355 and Senina (2001), Huang and Diekmann (2003), Li, Gao, Hui, Han and
356 Shi (2005)) and the conclusion is that cross-emigration can either increase or
357 decrease spatial complexity (Huang and Diekmann, 2003). It would therefore
358 be interesting, though certainly not trivial, to apply Huang and Diekmann
359 approach to the case in which planktivorous fish and carnivores have relevant
360 cross-emigration responses.

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

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