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SYSTEMS BIOPHYSICS

## Microscale Patchiness of the Distribution of Copepods (Harpacticoida) as a Result of Trophotaxis

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**Abstract**—A minimal conceptual model has been built that is capable of explaining the microscale heterogeneity observed in the benthic trophic system of harpacticoid copepods grazing on diatom microalgae. Alternative models of trophotaxis in predator–prey systems are considered in which the stimulus for predator movement is prey density, attractant secreted by the prey, or predator satiation. The model in which taxis is determined by predator satiety proves the most suitable for describing the harpacticoid–diatom dynamics.

*Key words:* predator–prey model, taxis, trophotaxis, reaction–diffusion–taxis, pattern formation, spatiotemporal heterogeneity

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### INTRODUCTION

The distribution of populations of harpacticoids (Harpacticoida: Copepoda), a major constituent of marine benthos, is a vivid example of spatiotemporal heterogeneity in natural trophic communities. The aggregations of these copepods vary in size from speckles of 0.5–1 cm<sup>2</sup> to large patches of several square meters [1–6]. The disposition of micro-patches can change markedly over a day though the mean size of the aggregation remains the same [2, 5]. The mosaic distribution of separate biotopes over tens or hundreds of meters is relatively stable. The causes of small-scale heterogeneity in quite homogeneous biotopes are still obscure. Most researchers concur in that primarily biotic factors operate on the centimeter scale, such as food distribution, propagation, and competition [7–11].

Harpacticoids graze on bacteria and unicellular algae, mainly diatoms, and are markedly selective for algae of certain size. In the available estimates, the daily grazing impact of harpacticoids ranges from a few percent to 2/3 of the total algal biomass [12–14]; on account of the size selectivity, this impact (and hence the possible food limitation) may be substantially heavier [15]. It has thus been hypothesized that harpacticoid migrations are due to their grazing behavior, and the stable existence of a community with such tense local trophic relations depends on the high spatiotemporal heterogeneity [15, 16].

The present study aimed to:

- (i) build, with the example of the copepod–microalgae community, a minimal conceptual model of the spatiotemporal dynamics of a predator–prey system;
- (ii) consider alternative mechanisms giving rise to dynamic structures in such communities, and discern those that can most adequately describe the clustering in the harpacticoid–diatom system.

### MATHEMATICAL MODEL

The model of a harpacticoid–diatom community in a closed habitat is a predator–prey model

$$\begin{cases} \frac{\partial R}{\partial t} = rR \left(1 - \frac{R}{K}\right) - aRN + \delta_R \frac{\partial^2 R}{\partial x^2}, \\ \frac{\partial N}{\partial t} = \frac{\partial}{\partial x} \left( -\chi(S)N \frac{\partial S}{\partial x} + \mu(S) \frac{\partial N}{\partial x} \right), \end{cases} \quad (1)$$

$$\left. \frac{\partial R}{\partial x} \right|_{x=0, L} = 0, \quad (2)$$

$$J_N|_{x=0, L} = \left( -\chi(S)N \frac{\partial S}{\partial x} + \mu(S) \frac{\partial N}{\partial x} \right) \Big|_{x=0, L} = 0,$$

where  $R(x, t)$  and  $N(x, t)$  are population densities for the prey (algae) and the predator (copepods);  $r$  is prey increment coefficient;  $K$  is habitat capacity;  $a$  is search efficacy coefficient;  $\chi(S)$  is taxis coefficient;  $S(x, t)$  is

stimulus concentration;  $\delta_R$ ,  $\mu(S)$  are prey and predator density diffusion coefficients. Predator movements are described with the Patlak–Keller–Segel flux  $J_N$  [17, 18], which we have validated and derived for a harpacticoid population elsewhere [19–21]. Since the density of microalgae of preferred size is not large enough to saturate the harpacticoid diet [15], the predator trophic function is approximated by the Lotka–Volterra function  $aR$ , as typical of many crustaceans [22] including harpacticoids [23]. The model includes no terms for predator birth and death, because the demographic processes in the predator population are far slower than in the prey population.

In model (1), (2), the space-average predator density is time-independent and is a parameter of the system:

$$\langle N \rangle = \frac{1}{L} \int_0^L N(x, t) dx = \text{const},$$

$$\frac{d\langle N \rangle}{dt} = \frac{1}{L} \left( -\chi(S) N \frac{dS}{dx} + \mu(S) \frac{dN}{dx} \right) \Big|_{x=0, L} = 0.$$

Elsewhere [19–21] we have substantiated the relationship of  $\mu(S)$ ,  $\chi(S)$ , and the frequency of copepod egress into water,  $f(S)$ :

$$\begin{aligned} \mu(S) &= \bar{l}^2 \tau / 2 f(S), \\ \chi(S) &= -d\mu(S)/dS. \end{aligned} \quad (3)$$

Here  $\tau$  is a time interval setting the minimal temporal resolution of the model;  $\bar{l}^2$  is mean squared length of movement executed by an individual within  $\tau$ .

Taking this into account, we can formulate hypotheses concerning  $\mu(S)$ ,  $\chi(S)$  that ensure a positive chemotactic response: (i)  $\mu(S) > 0$  for any  $S \geq 0$ ; (ii)  $\mu(S)$  declines with increasing stimulus,  $d\mu(S)/dS < 0$ , and  $\chi(S) > 0$  for any  $S > 0$ . Hence  $\chi(S) \xrightarrow{S \rightarrow 0} 0$ , which agrees nicely with the Weber–Fechner law.

Since  $\mu(S) > 0$  and we consider a closed habitat,  $\partial S / \partial x|_{x=0, L} = 0$ , the boundary conditions (2) are equivalent to

$$\frac{\partial R}{\partial x} \Big|_{x=0, L} = \frac{\partial N}{\partial x} \Big|_{x=0, L} = 0. \quad (4)$$

## THE NATURE OF THE STIMULUS FOR TAXIS

Proceeding to the main goal of this study, let us check with which hypothetical tactic stimulus the system (1), (4) can have a heterogeneous dynamic regime.

### Prey Density

Consider a case when predator taxis is stimulated by prey density:  $S(x, t) = R(x, t)$ . Then model (1), (4) appears as

$$\begin{cases} \frac{\partial R}{\partial t} = rR \left( 1 - \frac{R}{K} \right) - aRN + \delta_R \frac{\partial^2 R}{\partial x^2}, \\ \frac{\partial N}{\partial t} = -\frac{\partial}{\partial x} \left( \chi(R) N \frac{\partial R}{\partial x} \right) + \frac{\partial}{\partial x} \left( \mu(R) \frac{\partial N}{\partial x} \right), \end{cases} \quad (5)$$

$$\frac{\partial R}{\partial x} \Big|_{x=0, L} = \frac{\partial N}{\partial x} \Big|_{x=0, L} = 0. \quad (6)$$

This set has two equilibria. The first one is trivial, corresponding to complete wipe-out of diatoms by copepods, and is of little biological interest, as its inhomogeneous perturbation obligatorily includes the region of negative prey density. For the second equilibrium, corresponding to predator and prey co-existence, linear analysis of stability against spatially inhomogeneous perturbations showed that if the equilibrium is positive it is always locally stable. This means that no heterogeneous regimes evolve in model (5), (6) at any admissible parameter values. Such a property obviously contradicts the naturally observed mosaicism of harpacticoid distribution. Thus, the stimulus must be not the diatom density but something else.

### Attractant Release

Now consider a case when the stimulus for taxis is the concentration of some chemical substance  $S(x, t)$  that is an exometabolite of the prey and an attractant for the predator. The model (1), (4) converts to

$$\begin{cases} \frac{\partial R}{\partial t} = rR \left( 1 - \frac{R}{K} \right) - aRN + \delta_R \frac{\partial^2 R}{\partial x^2}, \\ \frac{\partial N}{\partial t} = -\frac{\partial}{\partial x} \left( \chi(S) N \frac{\partial S}{\partial x} \right) + \frac{\partial}{\partial x} \left( \mu(S) \frac{\partial N}{\partial x} \right), \\ \frac{\partial S}{\partial t} = \kappa R - \nu S + \delta_S \frac{\partial^2 S}{\partial x^2}, \end{cases} \quad (7)$$

$$\frac{\partial R}{\partial x} \Big|_{x=0, L} = \frac{\partial N}{\partial x} \Big|_{x=0, L} = \frac{\partial S}{\partial x} \Big|_{x=0, L} = 0, \quad (8)$$

where the coefficients are  $\kappa$  for the intensity of substance release by the prey,  $\nu$  for its chemical breakdown,  $\delta_S$  for diffusion.

Model (7), (8) can be interpreted as follows. The prey releases an attractant that decomposes with  $\nu$  and spreads with  $\delta_S$ . The reaction of predators to attractant level  $S$  depends on their egress frequency according to (3),  $\mu(S)$  pertaining to random movements and  $\chi(S)$  to those along the gradient of  $S$ . Replacement of variables and parameters  $\tilde{x} = x/L$ ,  $\tilde{t} = rt$ ,  $\tilde{R} = R/K$ ,  $\tilde{N} = aN/r$ ,  $\tilde{S} = S/\kappa K$ ,  $\tilde{\chi}(\tilde{R}) = \kappa K \chi(\kappa K \tilde{S}/r)/r^2 L^2$ ,  $\tilde{\mu}(\tilde{R}) =$

$\mu(\kappa K \tilde{S}/r)/rL^2$ ,  $\tilde{\delta}_R = \delta_R/rL^2$ ,  $\tilde{\delta}_S = \delta_S/rL^2$ ,  $\tilde{v} = v/r$  brings set (7), (8) to dimensionless form

$$\begin{cases} \frac{\partial \tilde{R}}{\partial \tilde{t}} = \tilde{R}(1 - \tilde{R}) - \tilde{R}\tilde{N} + \tilde{\delta}_R \frac{\partial^2 \tilde{R}}{\partial \tilde{x}^2}, \\ \frac{\partial \tilde{N}}{\partial \tilde{t}} = -\frac{\partial}{\partial \tilde{x}} \left( \chi(\tilde{S}) \tilde{N} \frac{\partial \tilde{S}}{\partial \tilde{x}} \right) + \frac{\partial}{\partial \tilde{x}} \left( \mu(\tilde{S}) \frac{\partial \tilde{N}}{\partial \tilde{x}} \right), \\ \frac{\partial \tilde{S}}{\partial \tilde{t}} = \tilde{R} - \tilde{v}\tilde{S} + \tilde{\delta}_S \frac{\partial^2 \tilde{S}}{\partial \tilde{x}^2}, \end{cases} \quad (9)$$

$$\left. \frac{\partial \tilde{R}}{\partial \tilde{x}} \right|_{x=0,L} = \left. \frac{\partial \tilde{N}}{\partial \tilde{x}} \right|_{x=0,L} = \left. \frac{\partial \tilde{S}}{\partial \tilde{x}} \right|_{x=0,L} = 0. \quad (10)$$

The tilde sign is omitted henceforth.

Set (9), (10) has two homogeneous stationary regimes:

$$\begin{aligned} (R_1^*, N_1^*, S_1^*) &= (0, \langle N \rangle, 0), \\ (R_2^*, N_2^*, S_2^*) &= \left( 1 - \langle N \rangle, \langle N \rangle, \frac{1 - \langle N \rangle}{v} \right). \end{aligned}$$

As above, we do not consider the trivial equilibrium  $(R_1^*, N_1^*, S_1^*)$ . Equilibrium  $(R_2^*, N_2^*, S_2^*)$  is stable against small spatially homogeneous perturbations at  $\langle N \rangle < 1$  and unstable at  $\langle N \rangle > 1$ . In the stability region  $0 < \langle N \rangle < 1$  we examine  $(R_2^*, N_2^*, S_2^*)$  for stability against small spatially inhomogeneous perturbations. Linearizing (9), (10) on  $(R_2^*, N_2^*, S_2^*)$ , we obtain a set of equations for the dynamics of inhomogeneous spatial perturbations,

$$\begin{cases} \frac{\partial r}{\partial t} = (1 - 2R_2^* - N_2^*)r - R_2^*n + \delta_R \frac{\partial^2 r}{\partial x^2}, \\ \frac{\partial n}{\partial t} = -N_2^* \chi(S_2^*) \frac{\partial^2 s}{\partial x^2} + \mu(S_2^*) \frac{\partial^2 n}{\partial x^2}, \\ \frac{\partial s}{\partial t} = r - vs + \delta_S \frac{\partial^2 s}{\partial x^2}, \end{cases} \quad (11)$$

$$\left. \frac{\partial r}{\partial x} \right|_{x=0,1} = \left. \frac{\partial n}{\partial x} \right|_{x=0,1} = \left. \frac{\partial s}{\partial x} \right|_{x=0,1} = 0, \quad (12)$$

where  $r(x, t)$ ,  $n(x, t)$ ,  $s(x, t)$  are small deviations from equilibrium. We seek the solution of linearization (11), (12) as a Fourier series

$$\begin{aligned} r(x, t) &= \sum_{k=1}^{\infty} r_k \cos(k\pi x) e^{\lambda_k t}, \\ n(x, t) &= \sum_{k=1}^{\infty} n_k \cos(k\pi x) e^{\lambda_k t}, \\ s(x, t) &= \sum_{k=1}^{\infty} s_k \cos(k\pi x) e^{\lambda_k t}. \end{aligned} \quad (13)$$

Substitution of (13) into (11) gives the eigenvalue problem for the  $k$ -th mode ( $k = 1, 2, \dots$ ):

$$\mathbf{A}_k \mathbf{u}_k = \lambda_k \mathbf{u}_k,$$

$$\mathbf{u}_k = \begin{pmatrix} r_k \\ n_k \\ s_k \end{pmatrix},$$

$$\mathbf{A}_k = \begin{pmatrix} R_2^* - \delta_R(k\pi)^2 & -R_2^* & 0 \\ 0 & -\mu(S_2^*)(k\pi)^2 & \langle N \rangle \chi(S_2^*)(k\pi)^2 \\ 1 & 0 & -v - \delta_S(k\pi)^2 \end{pmatrix}.$$

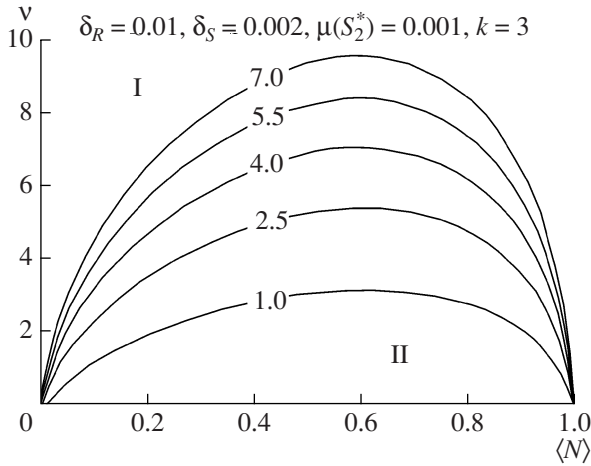
Eigenvalues  $\lambda_k$  are solutions of

$$\begin{aligned} (\lambda_k)^3 + a_1(\lambda_k)^2 + a_2\lambda_k + a_3 &= 0, \\ a_1 &= R_2^* + v + (k\pi)^2(\delta_R + \delta_S + \mu(S_2^*)), \\ a_2 &= (k\pi)^4(\mu(S_2^*)(\delta_R + \delta_S) + \delta_R\delta_S) + \\ &+ (k\pi)^2(\delta_R v + \mu(S_2^*)v + \delta_S R_2^* + \mu(S_2^*)R_2^*) + vR_2^*, \\ a_3 &= (k\pi)^6\delta_R\delta_S\mu(S_2^*) + (k\pi)^4\mu(S_2^*)(\delta_S R_2^* + \delta_R v) + \\ &+ (k\pi)^2(vR_2^*\mu(S_2^*) + R_2^*\langle N \rangle\chi(S_2^*)). \end{aligned} \quad (14)$$

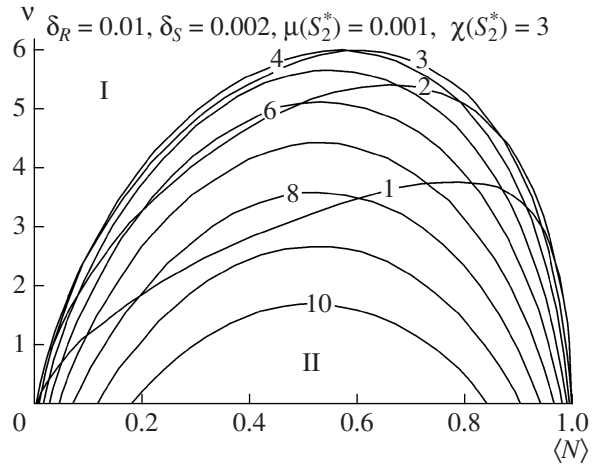
By the Lyapunov theorem,  $(R_2^*, N_2^*, S_2^*)$  is stable against spatially inhomogeneous perturbations when the real parts of the eigenvalues for any mode are negative,  $\forall k \text{Re}(\lambda_k) < 0$ . By the Lienard–Chipart criterion [24], all roots of (14) have a negative real part if the even minor is positive:

$$T_2 = \begin{vmatrix} a_1 & 1 \\ a_3 & a_2 \end{vmatrix} > 0. \quad (15)$$

Thus, equilibrium  $(R_2^*, N_2^*, S_2^*)$  is unstable against spatially inhomogeneous perturbations if the taxis coefficient exceeds a critical value  $X$ :



**Fig. 1.** Lines of the 3rd mode level  $T_2 = 0$  corresponding to the specified values of taxis coefficient  $\chi(S_2^*)$ ; (I) region of positive  $T_2$  where  $k = 3$  fades, (II) region of negative  $T_2$  where  $k = 3$  is excited.



**Fig. 2.** Lines of the level  $T_2 = 0$  for specified modes; (I) region of positive  $T_2$  where the  $k$ -th mode fades, (II) region of negative  $T_2$  where the  $k$ -th mode is excited.

$$\begin{aligned} \chi(S_2^*) > X(\langle N \rangle, v, k, \delta_R, \mu(S_2^*), \delta_S) > 0, \\ X(\langle N \rangle, v, k, \delta_R, \mu(S_2^*), \delta_S) = \\ = (\langle N \rangle R_2^*)^{-1} [(k\pi)^4 (\delta_R + \delta_S) (\delta_R \mu(S_2^*) + \\ + \delta_S \mu(S_2^*) + \delta_R \delta_S + \mu^2(S_2^*)) + \\ + (k\pi)^2 ((R_2^* + v) (\mu^2(S_2^*) + 2\mu(S_2^*) (\delta_R + \delta_S) + \delta_R \delta_S) + \\ + (\delta_R + \delta_S) (\delta_S R_2^* + \delta_R v)) + ((R_2^* + v)^2 \mu(S_2^*) + \\ + (R_2^* + v) (\delta_S R_2^* + \delta_R v) + (\delta_R + \delta_S) R_2^* v)] + \\ + \langle N \rangle^{-1} (k\pi)^{-2} (R_2^* + v) v. \end{aligned} \tag{16}$$

Figure 1 shows how the border between stability region I and instability region II for the 3rd mode changes with varied  $\chi(S_2^*)$ .

By the rule of signs, (14) has no positive real root  $\lambda_k$  at  $T_2 > 0$ . Thus, upon transition from the region of positive  $T_2$  to that of negative  $T_2$ , the imaginary axis is intersected by a complex-conjugate pair  $\lambda_k, \bar{\lambda}_k$  transiting from the left to the right half-plane. Therewith we have a Poincare–Andronov–Hopf bifurcation: in the vicinity of an oscillatorily destabilized stationary homogeneous regime  $(R_2^*, N_2^*, S_2^*)$  there arises a periodic spatially heterogeneous wave regime. The emerging regime can be quite complicated if it is the small-scale mode that first loses stability (e.g.  $k = 2, 3$  or 4 in Fig. 2).

Consider an important asymptotic case of infinitely great diffusion coefficients  $\delta_R, \mu(S_2^*), \delta_S$ . In this case condition (16) is not fulfilled, and the system cannot

develop spatially heterogeneous regimes. Such a situation may arise when the attractant spreads quickly enough ( $\delta_S$  is large). Since this is likely to be so in the water medium, the hypothesis of an algal exometabolite being the stimulus for predator taxis also appears implausible, though model (7), (8) in principle can yield spatially heterogeneous solutions.

### Predator Satiation

Finally, model (7), (8) admits a somewhat different interpretation. Specifically, assume that the frequency of copepod egress into water  $f(S)$  and accordingly  $\mu(S)$  and  $\chi(S)$  depend on the satiety of the animal, which is determined by the mean filling of its stomach  $S(x, t)$ . Then the predator–prey dynamics is described as

$$\begin{cases} \frac{\partial R}{\partial t} = rR \left(1 - \frac{R}{K}\right) - aRN + \delta_R \frac{\partial^2 R}{\partial x^2}, \\ \frac{\partial N}{\partial t} = -\frac{\partial}{\partial x} \left( \chi(S) N \frac{\partial S}{\partial x} \right) + \frac{\partial}{\partial x} \left( \mu(S) \frac{\partial N}{\partial x} \right), \\ \frac{\partial S}{\partial t} = eaR - vS \end{cases} \tag{17}$$

$$\left. \frac{\partial R}{\partial x} \right|_{x=0, L} = \left. \frac{\partial N}{\partial x} \right|_{x=0, L} = \left. \frac{\partial S}{\partial x} \right|_{x=0, L} = 0. \tag{18}$$

Here  $e$  is the food uptake coefficient,  $eaR$  is the amount of food ingested per unit time;  $v$  is the digestion coefficient,  $vS$  is the amount of food digested per unit time. In contrast to (7), (8), here it is reasonable to take  $\delta_S = 0$ , because the amount of food in the stomach of a predator at point  $x$  does not depend on the satiety of predators at neighboring points.

Since set (17), (18) is equivalent to (7), (8) at  $\kappa = ea$  and  $\delta_s = 0$ , the results of linear analysis given above are also valid. Thus, on condition (16),  $\delta_s = 0$ , via the Poincaré–Andronov–Hopf bifurcation the dimensionless system evolves into complicated spatially heterogeneous regimes.

## DISCUSSION

We have presented a predator–prey population model describing interactions in the benthic harpacticoid–diatom system. The mobility of copepods is determined by how often they go out into water, which depends on the level of the stimulus. As the latter factor, we have evaluated the diatom density (5), (6); the concentration of an exometabolite attractant (7), (8); and the satiety of grazers (17), (18). Linear analysis of the nontrivial homogeneous regime has been conducted for each model.

There is little sense in considering prey density as a stimulus because in (5), (6) the homogeneous regime is locally stable at any biologically reasonable parameters, and there are no spatially heterogeneous regimes consistent with the mosaic distributions of harpacticoids observed in nature. Models (7), (8) and (17), (18) take into account the inertia in the predator response to variation in prey density: the predators react to a change in the level of a stimulus that is conditioned by the gradient of prey distribution. It is owing to this delay that spatially heterogeneous regimes may arise under certain conditions (16). Comparing these two models, we can conclude that the dynamics of the system under study is best described by model (17), (18) where the taxis of predators is determined by their satiety. Indeed, the real values of the attractant diffusion coefficients in (7), (8) must be too high (in view of the modest scale of events and rapid propagation of compounds in water) to admit microscale heterogeneity.

Notably, at small supercriticalities the satiety model (17), (18) proves equivalent to a simpler model of trophotaxis [25–28] which also realizes the mechanism of overcoming prey shortage observed in harpacticoids [15, 16].

To our knowledge, there are no field data whereby harpacticoid satiation could be directly linked to their motility. However, there is indirect evidence in favor of our idea. Thus the frequency and the distance of copepod saltation drop with increasing food concentration [29]. Active migration has been shown to play a leading part in the formation of benthic communities [30]: within a few hours most of the species proved several-fold more abundant in containers with much food than in those with little food, which has been attributed to different rates of active emigration from the containers.

Our field experiments also show that the rate of harpacticoid migration from foodless sediment is about four times higher than from diatom-containing sediment.

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