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Turbulence, diffusion and patchiness in the sea

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SUMMARY

We explore the role that biological processes play in the patchiness of plankton populations in the sea. We ask how population interactions modify the variance in plankton density as a function of spatial scale (i.e. the variance spectrum) from that expected if the biota were merely passive tracers. Using an approximate model for two limiting cases of turbulence – the inertial subrange and two-dimensional turbulence – we consider a simple predator – prey formulation for interacting populations in a turbulent ocean. No simple generalizations emerge. The interacting populations 'redden' (i.e. more variance at large scale) the spectrum of the passive tracers in the inertial subrange. Conversely, the interaction 'whitens' (i.e. less variance at large scale) the passive tracer spectrum for two-dimensional turbulence. This mirrors results in terrestrial environments.

INTRODUCTION

The vast majority of marine organisms are planktonic. By definition, then, they are largely at the mercy of the motions in the sea. For many decades investigators have known that the planktonic organisms are neither uniformly nor randomly distributed in the ocean (Hardy & Gunther 1935; Cassie 1963; Steele 1978; Mackas *et al.* 1985). Rather, they exist in clumps, or in patches; and, commonly, one speaks of patchiness, or plankton patchiness. Planktonic organisms are, of course, not mere passive tracers of the flows in the sea. They grow, reproduce, are preyed upon (and, in turn, prey upon other plankton), compete for resources, die, etc., in the moving marine environment. It is still unclear, after several decades of intense study, in what situations either the physical processes of concentration (convergence) and dispersion (divergence), or the many biological processes (growth, reproduction, even behavior) control the spatial distribution of plankton in the sea.

How can one understand the coupling of biological and physical processes in order to explain the patchiness of plankton in the sea? Consider some measureable quantity, q: temperature, salinity, nitrate concentration, chlorophyll concentration or zooplankton biomass. In any segment of the water column one can write

$$\mathrm{d}q/\mathrm{d}t = F_\mathrm{I} - F_\mathrm{O} + P - C. \qquad (1)$$

Equation (1) is a budget for the rate of change of the quantity q; F_I (F_O) is an input (output) flux of q; P is the rate at which q is produced within the control volume, and C is the rate at which q is consumed. Budgets cannot be constructed for all quantities. One calls those important quantities for which budgets can be written down 'conserved'; familiar examples of conserved quantities include momentum, energy, and mass. The traditional emphasis in biological investigations has been on P and C, the production and consumption terms. But in many situations budgets may be dominated by the physical transport fluxes, F_I and F_O. In even more situations the relative importance of physical transport processes (F_I,F_O) compared to biological processes (P,C) is not known. The evaluation of a budget almost always demands understanding of the coupling between biology and physics in the ocean. And spatial distribution, i.e. patchiness, is just one example of this general consideration.

The study of patchiness in plankton populations has a long history. The 1970s saw a sharp upswing in interest in this topic. Perhaps the earliest and most influential of such studies was that of Platt (1972) who investigated the fluctuations in chlorophyll concentration in the Gulf of the St Lawrence. Platt found that the power spectrum (or variance spectrum) of the chlorophyll fluctuations followed closely the $k^{-5/3}$ shape predicted for high Reynolds number turbulence in the inertial subrange (Kolmogorov 1941). k is a wavenumber, with units of inverse length; the power spectrum describes the functional dependence of the variance on k (and hence upon spatial scale). The sum of the power spectral estimates for all k (i.e. the integral of the power spectrum over all k) equals the total variance in the record of the fluctuating quantity under study (Bendat & Piersol 1986). Subsequent studies found similar results for chlorophyll in lakes (Powell *et al.* 1975) and estuaries (Lekan & Wilson 1978). In an elegant study Denman (1976) showed (and interpreted) the difference between the chlorophyll variance spectrum (i.e. a biologically controlled quantity) and temperature variance spectrum (i.e. a physically controlled quantity) in the coastal ocean.

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A summary statement of such studies might be that all the power spectra seem to have a region where they follow a $k^{-5/3}$ shape (often statistically difficult to distinguish from a k^{-2} shape). Some exceptions are worth noting. At lower wavenumbers (larger spatial scale) the spectra may become less steep than k^{-2}, i.e. 'whiter' (Denman 1976); n.b. a 'white' spectrum is flat, that is, no dependence upon k. Spectra for higher trophic level organisms (e.g. zooplankton) seem to be less steep than k^{-2}, i.e. 'whiter' (e.g. Mackas & Boyd 1979; Weber *et al.* 1986). Physical, chemical, or topographic discontinuities can modify the slopes of these spectra (Leigh-Abbott *et al.* 1978; Abbott *et al.* 1982), but, in general, biologically interesting quantities are spatially distributed as though they were distributed solely by 'the physics'.

Although a number of significant papers on patchiness and spatial distribution continue to appear, the intense interest of the early to mid-1970s seems to have waned with the appearance of Steele's (1978) review volume. Interest in this field turned to the exciting developments in satellite oceanography. Satellite images of very detailed surface patterns for both chlorophyll and temperature at scales never imagined by previous generations of oceanographers soon become a staple in many articles published in oceanography. And the 'physical–biological coupling' questions that had driven patchiness investigators began to be asked of individual surface features seen at 'satellite' scales (Abbott & Zion 1985, 1987; Denman & Abbott 1988). Moreover, with the rapid increase in computing power and sophistication investigators began to construct detailed 'process models' of such coupled biological–physical features (see Hofmann 1988; Werner *et al.* 1993). It can be argued that, with some notable exceptions, recent investigations have turned away from the search for broad generalities about spatial patterns. Indeed, numerical modelling results seem to indicate that even very minor changes in parameter values lead to vastly different spatial distributions (Werner *et al.* 1993); accordingly, the search for generalities could, in principle, be fruitless.

In this paper we return to this question of generalities about spatial patterns in plankton communities. We ask a more modest question: how do biological interactions modify the patchiness that physical processes by themselves generate? Can one find any generalities here? One answer to these questions has three parts. First, one must have a 'general' model of physical processes. Toward this end we sketch an approximation to turbulent diffusion (a more complete exposition of this approximate turbulence model will appear in a more specialized publication). Second, we show how the addition of biological interactions might modify the spatial patterns that result from this simple model of turbulent diffusion. Finally, we conclude by discussing how our results compare to those one might find in terrestrial environments.

2. THE PHYSICS OF DIFFUSION

One can represent diffusion processes in the sea through the Navier–Stokes (N.–S.) equation(s) for an incompressible, non-rotating fluid.

$$\frac{\partial \boldsymbol{u}}{\partial t} + \boldsymbol{u} \cdot \nabla \boldsymbol{u} = -\frac{1}{\rho} \nabla p + \nu \nabla^2 \boldsymbol{u} + \boldsymbol{f}, \qquad (2)$$

$\boldsymbol{u}$ is the velocity, p is the pressure, ρ is the density, and ν is the kinematic viscosity. We have added an additional (random) force, $\boldsymbol{f}(\boldsymbol{x},t)$, that is assumed to be non-divergent. Thus, $\nabla \cdot \boldsymbol{u} = \nabla \cdot \boldsymbol{f} = 0$. $\boldsymbol{f}$ is necessary to generate and maintain a turbulent velocity field in an infinite fluid. $\boldsymbol{f}$ might arise from, say, wind stress fluctuations at the ocean surface. Incorporating rotational (Coriolis) effects in our formulation would be an important addition, but would take us unnecessarily far from the points we wish to present (but see Holloway 1986).

The pressure can be eliminated by taking the divergence of equation (2) and writing down the particular solution of the resulting Poisson equation (see Batchelor 1953, Chapter 5; or McComb 1991, Appendix D). Equation (2) now involves only components of the velocity. To proceed we take Fourier components of the velocity, $\tilde{\boldsymbol{u}}$, and the (random) force, $\tilde{\boldsymbol{f}}$ substitute into the N.–S.equations (2), and make a suitable definition for a scale-dependent (i.e. wavenumber-dependent) turbulent viscosity, $D(\boldsymbol{k})$. The result is

$$\tilde{u}_i(\boldsymbol{k},\omega) = \frac{\tilde{f}_i(\boldsymbol{k},\omega)}{i\omega + k^2(D(\boldsymbol{k}) + \nu)}, \qquad (3a)$$

where

$$-D(\boldsymbol{k})k^2\,\tilde{u}_i(\boldsymbol{k},\omega) =$$

$$\int \mathrm{d}^3k' k_j \tilde{u}_j(\boldsymbol{k} - \boldsymbol{k}',\omega)\left[-\tilde{u}_i(\boldsymbol{k}',\omega) + \frac{k_i}{k^2} k_l \tilde{u}_l(\boldsymbol{k}',\omega)\right]. \qquad (3b)$$

One can integrate over all directions in wavenumber ($\boldsymbol{k}$) space, and over all frequencies, ω, to obtain an expression that relates the power spectrum $[F(k)]$ of the random force ($\boldsymbol{f}$), to the energy spectrum $[E(k)]$ for the fluid flow ($\boldsymbol{u}$).

$$E(k) = F(k)/k^2(D(k) + \nu). \qquad (4)$$

The units for $F(k)$ are (L^3T^{-3}) and for $E(k)$ are (L^3T^{-2}). Furthermore, note that $E(k)$ falls off much more rapidly as a function of k than $F(k)$ because of the factor of k^2 in the denominator of equation (4).

(*a*) *Two examples*

No general solution of the nonlinear N.–S. equations (2) is known. Much of what investigators of turbulence have determined about the phenomenon has been learned from careful laboratory experimentation and field observation, as well as numerical simulation of subsets (or, increasingly, the full set) of the N.–S. equations. One deceptively simple, but extremely powerful technique, dimensional analysis, has yielded much insight. Using dimensional results we will present here two special cases that apply to many oceanographic conditions. The first is Kolmogorov's inertial subrange; the second is strictly two-dimensional turbulence. In this article we can only briefly describe a few of the details of turbulence in these two régimes. The reader is directed to texts such as Tennekes & Lumley (1972), Hinze (1975), McComb (1991); or the review literature (e.g. Gargett 1989) for further exposition.

(i) *Kolmogorov's inertial subrange*

At high Reynolds numbers the energy-containing eddies are almost always large in size. It is in this large-scale realm where the turbulent kinetic energy is generated. Conversely, turbulent kinetic energy is dissipated (to heat) at small scales (say, a centimeter or less) by viscosity. As long as the Reynolds number is sufficiently high these two realms are widely separated in scale. The régime between the generation realm and the dissipation realm is called the inertial subrange. In the inertial subrange the turbulence is completely characterized by one number, the energy dissipation rate, ε (units: L^2T^{-3}) at wavenumber k. (Note: at equilibrium ε is also the rate of transfer of turbulent kinetic energy from large to small scales via vortex stretching.)

Accordingly, on dimensional grounds alone

$$F(k) \propto \varepsilon\, k^{-1} \qquad \text{(units: } L^3T^{-3}\text{)}, \tag{5a}$$

$$D(k) \propto \varepsilon^{1/3}\, k^{-4/3} \qquad \text{(units: } L^2T^{-1}\text{)}. \tag{5b}$$

Substituting these expressions into equation (4) and using $\nu \ll D$ one obtains Kolmogorov's famous $-5/3$ law.

$$E(k) \propto \varepsilon^{2/3} \cdot k^{-5/3} \qquad \text{(units: } L^3T^{-2}\text{)}. \tag{6}$$

(Note: a particularly clear version of Kolmogorov's original paper (1941) has recently appeared in English (Hunt *et al.* 1991).)

(ii) *Two-dimensional turbulence*

When the turbulence is completely two dimensional one finds a conservation law for the square of the component of vorticity perpendicular to the plane of the motion. The square of the vorticity is called the enstrophy (when considering turbulent flows the enstrophy is the mean squared vorticity). And in this two-dimensional régime the turbulence is completely characterized by one number, the enstrophy dissipation rate, θ (units: T^{-2}) at wavenumber k.

As above, on dimensional grounds alone

$$F(k) \propto \theta^{3/2}\, k^{-3} \qquad \text{(units: } L^3T^{-3}\text{)}, \tag{7a}$$

$$D(k) \propto \theta^{1/2}\, k^{-2} \qquad \text{(units: } L^2T^{-1}\text{)}. \tag{7b}$$

Substituting these expressions into equation (4), and using $\nu \ll D$ one finds the familiar -3 power law (Kraichnan 1967).

$$E(k) \propto \theta\, k^{-3} \qquad \text{(units: } L^3T^{-2}\text{)}. \tag{8}$$

In summary, our simple diffusion approximation model for turbulence regards the nonlinear transport terms for the Fourier components of the velocity as a diffusion process, with a wavenumber-dependent viscosity. To maintain an energy cascade we drive the turbulent fields by a random force, $\boldsymbol{f}$, whose Fourier components in general also depend upon wavenumber. Appropriate dimensional arguments reveal that the diffusion model gives results consistent with both the '$-5/3$' energy spectra in the Kolmogorov inertial subrange and the '-3' spectra in the two-dimensional, 'enstrophy cascade', régime.

We now proceed to use this model in our discussion of plankton spectra and patchiness.

3. COUPLING BIOLOGY AND PHYSICS: PLANKTON SPECTRA AND PATCHINESS

We now consider plankton species embedded in a turbulent environment. We ignore the motility of the organisms, assuming they are passive in the ambient flow. The plankton populations are reactive, interacting with themselves and other species (i.e. intra- and interspecific interactions). Thus, fluctuations in the population densities may arise from both the turbulence in the environment (the 'diffusion'), as well as the species interactions (the 'reaction').

Our approach is to derive the variance spectrum of the fluctuations in interacting plankton populations using the approximate diffusion model of turbulence sketched in the previous section. One starts from the general formulation

$$\mathrm{D}S_j(\boldsymbol{x},t)/\mathrm{D}t = \text{INTERACTION}, \tag{9}$$

where $\mathrm{D}/\mathrm{D}t$ is the material derivative, and $S_j(\boldsymbol{x},t)$ the concentration of the jth species as a function of position ($\boldsymbol{x}$) and time (t). In the usual fashion (McComb 1991), analogous to the Reynolds decomposition for the velocity, one expresses S_j and $\boldsymbol{u}$ in terms of their mean and fluctuating values (we assume that the mean values for all the components of $\boldsymbol{u}$ vanish). Again, in the usual fashion, one defines a diffusivity, D_j for the jth species in terms of a mean gradient of S_j and the correlation between S_j and components of $\boldsymbol{u}$. Most importantly, referring to equations (5b) and (7b), the diffusivity thus defined is assumed to have the same dependence upon k (and ε and θ) as the eddy viscosity in our approximate diffusion model of turbulence of the previous section. Thus,

$$\partial S_j/\partial t = D_j \nabla^2 S_j + F_j(S_l) + P_j, \tag{10}$$

$$j = 1, \ldots, n \qquad l = 1, \ldots, n$$

where $S_j(\vec{x},t)$ = concentration of jth species; D_j is the diffusivity of jth species; F_j is the reaction term (population dynamics) for the jth species; and P_j is the random environmental fluctuation (forcing) of the jth species not associated with 'diffusion' or population dynamics

Note that we have expressed the INTERACTION term of equation (10) as the sum of two terms. The first, F_j, is the 'reaction' term that arises from the intra- and interspecific interactions between species: it is the effect of 'population dynamics' upon the jth species. The second, P_j, is a (random) environmental fluctuation (or forcing) of the jth species. It is not associated with either the 'diffusion' or the 'reaction' (the population dynamics). Such a term might arise from a fluctuating resource field, perhaps due to fluctuating nutrient conditions, that an organism experiences in the fluid environment. Alternatively, it might arise from differing growth conditions controlled by the rapidly varying temperature seen by planktonic organisms in the sea.

We next decompose S_j and P_j into their mean and fluctuating components: $S_j = \bar{S}_j + S_j'$, and $P_j = \bar{P}_j + P_j'$. $F_j(\bar{S}_j)$ and $\bar{P}_j$ are assumed to vanish. We substitute into (10), and linearize around the mean values of S_j and P_j, which leads to

$$\partial \mathrm{S}_j'/\partial t = D_j \nabla^2 S_j' + a_{jl} \mathrm{S}_j' + P_j', \tag{11}$$

$$a_{jl} = \frac{\partial \mathrm{F}_j}{\partial \mathrm{S}_l}\bigg|_{\bar{S}_l}.$$

Proceeding as in the previous section we take Fourier components (denoted by $\sim$) of S_j' and P_j'. This leads to a matrix equation, analogous to equation (3), for S_j' in terms of P_j'.

$$\boldsymbol{A}\tilde{\boldsymbol{S}} = \tilde{\boldsymbol{P}} \qquad \text{or} \qquad \tilde{\boldsymbol{S}} = \boldsymbol{A}^{-1}\tilde{\boldsymbol{P}}, \tag{12}$$

where

$$\boldsymbol{A} = \begin{pmatrix} -i\omega + D_1k^2 - a_{11} & -a_{12} & \cdots & -a_{1n} \\ -a_{21} & -i\omega + D_2k^2 - a_{22} & & \vdots \\ \vdots & \vdots & & \vdots \\ -a_{n1} & \cdot & & -i\omega + D_nk^2 - a_{nn} \end{pmatrix}$$

$$\tilde{\boldsymbol{S}} = \begin{pmatrix} \tilde{\boldsymbol{S}}_1 \\ \tilde{\boldsymbol{S}}_2 \\ \vdots \\ \tilde{\boldsymbol{S}}_n \end{pmatrix}, \qquad \tilde{\boldsymbol{P}} = \begin{pmatrix} \tilde{\boldsymbol{P}}_1 \\ \tilde{\boldsymbol{P}}_2 \\ \vdots \\ \tilde{\boldsymbol{P}}_n \end{pmatrix},$$

and primes have been dropped.

The $n \times n$ matrix equation arises because the n species may interact with one another. In equation (12) the off-diagnonal elements of $\boldsymbol{A}$ contain only biological ('reaction') terms. The diagonal elements have both 'reaction' and 'diffusion' effects.

Again, one can integrate over all directions in wavenumber ($\boldsymbol{k}$) space, and over all frequencies, ω, to obtain an expression that relates the power spectrum $[Q_l(k)]$ of the random environmental fluctuation, or forcing (P_l), to the power spectrum $[E_{S_j}(k)]$ of the jth species concentration (S_j).

$$E_{Sj}(k) = \int \mathrm{d}\omega \sum_l \boldsymbol{A}_{jl}^{-1*}(k,\omega)\boldsymbol{A}_{jl}^{-1}(k,\omega)\, Q_l(k). \tag{13}$$

The units for $Q_l(k)$ are (C^2LT^{-1}) and for $E_{S_j}(k)$ are (C^2L), where C denotes concentration of planktonic species. Furthermore, note that $E_{S_j}(k)$ is no longer proportional to a single $Q_l(k)$ as in the analogous expression (4). Rather, $E_{S_j}(k)$ is a linear combination of all the $Q_l(k)$s, $l = 1, \ldots, n$, due to species interactions. Moreover, it is no longer possible to make even approximate statements about the relative rates of falloff with wavenumber of $E_{S_j}(k)$ and the $Q_l(k)$s. This is because each $Q_l(k)$ enters equation (13) with a different coefficient, each of which can have different k-dependence, as the individual components of $\boldsymbol{A}$ have different dependence upon wavenumber (see equation (12)).

(*a*) ***Two cases***

We will restrict our attention to two cases: a single species in a turbulent environment, and two interacting species. Our single species results are consistent with those from previous studies; accordingly, we devote more space to our two species results.

(i) *A single species ($j = 1$)*

The matrix $\boldsymbol{A}$ in equation (12) reduces to one element. Substitution into equation (13) gives

$$E_{S_1}(k) = \frac{Q_1(k)}{|D_1k^2 - a_{11}|}. \tag{14}$$

One additional parameter must be introduced to proceed with dimensional arguments, namely, the dissipation rate of concentration fluctuations (or dissipation rate of plankton density fluctuations), χ_1. This quantity is completely analogous to ε of the previous section. It is the rate at which concentration fluctuations are dissipated at small scale (ultimately) by molecular processes. Its units are (C^2T^{-1}), where C is concentration. Hence quantities like $Q_1(k)$ and $D_1(k)$ (and $E_{S_1}(k)$) will now depend on k, ε, and χ.

The inertial subrange

Dimensional arguments lead to

$$Q_1 \propto \chi_1\, k^{-1}, \tag{15a}$$

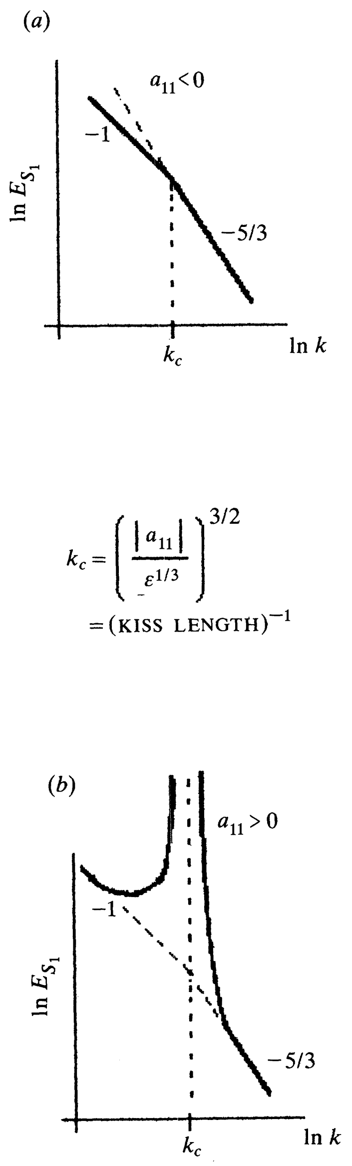
$$D_1 \propto \varepsilon^{1/3}\, k^{-4/3} = \alpha\, \varepsilon^{1/3}\, k^{-4/3}, \tag{15b}$$

where α is merely a dimensionless constant of proportionality. Substitution of (15a,b) into (14) gives

$$E_{S_1} \propto \frac{\chi_1\, k^{-1}}{|\alpha\varepsilon^{1/3}\, k^{-2/3} - a_{11}|}. \tag{16}$$

Note that when a_{11} vanishes (i.e. non-reacting) then $E_{S_1}(k) \propto \chi_1\varepsilon^{-1/3}k^{-5/3}$, consistent with the results of early investigators (e.g. Corrsin 1951).

When a_{11} does not vanish two cases arise: a_{11} negative (figure 1*a*), and a_{11} positive (figure 1*b*). In both cases when $k \gg k_c$ (i.e. small scale), then $E_{S_1}(k) \propto k^{-5/3}$ where $k_c = (\text{KISS LENGTH})^{-1} = (a_{11}/\varepsilon^{1/3})^{3/2}$. (The KISS LENGTH) is the minimum size patch which can maintain itself in the face of diffusion (Okubo 1980).) Moreover, in both cases, when $k \ll k_c$ (i.e. large scale), then $E_{S_1}(k) \propto k^{-1}$. Thus, at small scales, the distribution of 'patchiness' has the same shape as environmental turbulence, i.e. it is controlled solely by turbulence;



$$k_c = \left(\frac{|a_{11}|}{\varepsilon^{1/3}} \right)^{3/2} = (\text{KISS LENGTH})^{-1}$$

Figure 1. (*a*) $a_{11} < 0$. The power spectrum of concentration fluctuations of a single species in the inertial subrange of a turbulent velocity field. Note the change in slope at the KISS LENGTH. (*b*) $a_{11} > 0$. The power spectrum of concentration fluctuations of a single species in the inertial subrange of a turbulent velocity field. There is a singularity at the KISS LENGTH indicating high variance, i.e. large patchiness, at this length scale.

and the 'reaction' terms play no role in the spatial distribution of planktonic organisms. However, at large scales the power spectrum of plankton density fluctuations is flatter (i.e. 'whiter') than the energy spectrum; i.e. the intensity of patchiness is less than that of environmental turbulence fluctuations. Put another way, large scale structures in plankton distribution have less power than structures found at the same scale for a non-reacting, passive quantity found in the same aquatic environment. Denman & Platt (1976) first described these relations (also see Denman *et al.* 1977); their theoretical curves are identical to figure 1*a*. For the case $a_{11} > 0$, there is a singularity at $k = k_c$ (i.e. at length scale = (KISS LENGTH); see figure 1*b*). Here the patchiness should be strong within the range of length scales close to k_c^{-1} = (KISS LENGTH). This perhaps explains the peak in the observations of Powell *et al.* (1975), and it is analogous to the (Fickian diffusion) calculations of Fasham (1978).

Two-dimensional turbulence

Again, on dimensional grounds

$$Q_1 \propto \chi_1 k^{-1}, \qquad (17a)$$

$$D_1 \propto \theta^{1/2} k^{-2} = \alpha\, \theta^{1/2} k^{-2}, \qquad (17b)$$

where α is again a dimensionless constant of proportionality. Substitution of (17a,b) into (14) gives

$$E_{S_1} \propto \frac{\chi_1 k^{-1}}{|\alpha\theta^{1/2} - a_{11}|}, \qquad (18)$$

$$\propto k^{-1} \qquad (\neq k^{-3}; \text{ i.e. 'whiter'}).$$

In this case $E_{S_1}(k) \propto k^{-1}$ for all wavenumbers (length scales). Thus, for the entire two-dimensional range in k, the slope of the power spectrum of plankton density fluctuations ($\propto k^{-1}$) is less than that for environmental turbulence fluctuations ($\propto k^{-3}$). These results are identical to those given by Bennett & Denman (1985). Parenthetically, Denman (1983) (and Bennett & Denman (1985)) makes the important point that to have any differences between 'the physical spectrum' and 'the plankton spectrum' (i.e. any modification to 'the physics' due to 'the biology') the growth rates for plankton populations must vary in space. In our formulation that is equivalent to the existence of the power spectrum $[Q_1(k)]$ due to the random environmental fluctuation, or forcing (P_l); i.e. $[Q_l(k)]$ cannot vanish for all l species, $l = 1, \ldots, n$.

(ii) *Two interacting species*

The matrix $\boldsymbol{A}$ in equation (12) reduces to a 2×2 matrix.

$$\boldsymbol{A} = \begin{pmatrix} i\omega + D_1 k^2 - a_{11} & -a_{12} \\ -a_{21} & i\omega + D_2 k^2 - a_{22} \end{pmatrix}. \qquad (19)$$

The power spectrum of plankton fluctuations must depend on several more variables than in the single species case. That is, $E_{S_{i,j}}(k) = E_{S_{i,j}}(Q_1, Q_2; D_1, D_2; a_{ij}; \omega, k)$. Space does not permit us to display the manipulations that arise when the expressions in equation (19) are substituted into equation (13). We merely quote the results for the non-reacting case ($a_{ij} = 0$). In the inertial subrange the power spectra for both (non-interacting) species are $\propto k^{-5/3}$; for the two-dimensional turbulence case, the power spectra are $\propto k^{-1}$. This is, of course, what one would expect for non-interacting, passive tracers: they follow the non-reacting, single species cases (see equations (16) and (18))!

Now consider interacting species. We explore a simple case: $a_{11} = a_{22} = 0$; $a_{12} \neq 0$, $a_{21} \neq 0$. This is the Lotka–Volterra predator–prey model. Equation (20) gives the results for $E_{S_1}(k)$ and $E_{S_2}(k)$ (where we have left out the details of the calculations arising from substitution into equation (13)).

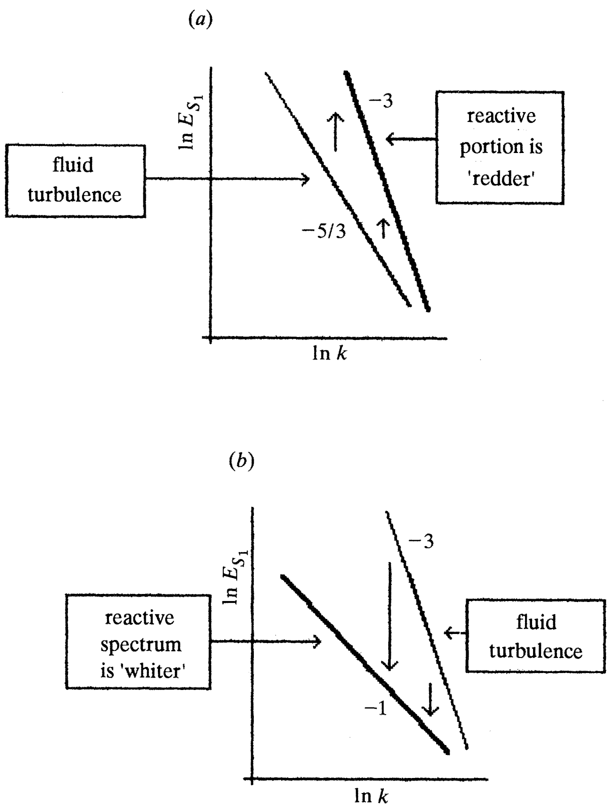


Figure 2. (*a*) The power spectrum of concentration fluctuations of two interacting species (i.e. Lotka–Volterra predator–prey) in the inertial subrange of a turbulent velocity field. The population interaction leads to more intense patchiness at large scales (i.e. the spectrum is 'redder' than that for passive particles in turbulence in the inertial subrange). (*b*) The power spectrum of concentration fluctuations of two interacting species (i.e. Lotka–Volterra predator–prey) in a two-dimensional turbulent velocity field. The population interaction leads to less intense patchiness at large scales (i.e. the spectrum is 'whiter' than that of two-dimensional fluid turbulence).

$$E_{S_1}(k) = \frac{\pi Q_1}{D_1\, k^2} + \frac{\pi a_{12}^2\, Q_2}{(D_1 + D_2) D_1 D_2\, k^6}, \qquad (20a)$$

$$E_{S_2}(k) = \frac{\pi Q_2}{D_2\, k^2} + \frac{\pi a_{21}^2\, Q_1}{(D_1 + D_2) D_1 D_2\, k^6}. \qquad (20b)$$

$$\underset{\text{reacting}}{\text{non-}} + \underset{\text{biological interactions}}{\text{modifications due to}}$$

We note (without proof) that the first two terms of (20a) and (20b) are identical to $E_{S_1}(k)$ and $E_{S_2}(k)$ in the non-reacting ($a_{ij} = 0$) case. The second terms in (20a) and (20b) arise solely from the biological interactions between species (in this case predator–prey interactions). (Note, our analysis assumes that $|a_{12}a_{21}|/(D_1 D_2)] \ll k^4$.) Note further that in the 'biological interaction' terms the square of a_{12} (and a_{21}) appears; the sign is immaterial.

The inertial subrange

Following (15a,b)

$$Q_1 \propto \chi_1\, k^{-1}, \qquad Q_2 \propto \chi_2\, k^{-1}, \qquad (21a)$$

$$D_2, D_1 \propto \varepsilon^{1/3} k^{-4/3}, \qquad (21b)$$

so that substitution into (20a,b) leads to

$$E_{S_1}(k) = \lambda_1\, \chi_1\, \varepsilon^{-1/3}\, k^{-5/3} + \beta_1\, a_{12}^2 \chi_2\, \varepsilon^{-1}\, k^{-3}, \qquad (22a)$$

$$E_{S_2}(k) = \underset{\text{(passive)}}{\lambda_2\, \chi_2\, \varepsilon^{-1/3}\, k^{-5/3}} + \underset{\text{(reactive)}}{\beta_2\, a_{21}^2 \chi_1 \varepsilon^{-1}\, k^{-3}}. \qquad (22b)$$

The λs and βs are constants. Note that the reactive term has a steeper slope (i.e. k^{-3}, it is 'redder') than the $k^{-5/3}$ behaviour that is characteristic of passive transport by turbulence in the inertial subrange (see figure 2*a*). Thus, this simple Lotka-Volterra predator-prey system develops more variance at large length scales (i.e. has more intense, large 'patches') than a system of merely passive particles (see Steele and Henderson 1977).

Two-dimensional turbulence.

Following (17a) and (17b)

$$Q_1 \propto \chi_1\, k^{-1}, \qquad Q_2 \propto \chi_2\, k^{-1}, \qquad (23a)$$

$$D_2, D_1 \propto \theta^{1/2}\, k^{-2}, \qquad (23b)$$

and substitution into (20a,b) gives

$$E_{S_1}(k) = \sigma_1\, \chi_1\, \theta^{-1/2}\, k^{-1} + \sigma_2\, a_{12}^2\, \chi_2\, \theta^{-3/2}\, k^{-1}, \qquad (24a)$$

$$E_{S_2}(k) = \underset{\text{(passive)}}{\sigma_2\, \chi_2\, \theta^{-1/2}\, k^{-1}} + \underset{\text{(reactive)}}{\sigma_1\, a_{21}^2 \chi_1\, \theta^{-3/2} k^{-1}}. \qquad (24b)$$

The σs are constants.

Here both the passive and the reactive terms exhibit k^{-1} behaviour. This slope is less (i.e. flatter, or 'whiter') than that for the environmental turbulence (see equation (8)). That is, the intensity of patchiness is weak, with less tendency toward large, intense patches, than the turbulent behaviour that is dominated by large, intense eddying motion.

4. CONCLUSION

Do any generalities emerge from our studies of the modifications that biological processes make to the patchiness imposed solely by physical processes? We answer no. Specifically, does any general behaviour emerge from the alterations that biological 'reactions' make on the slopes of the straight lines found in the log–log spectral plots of figures 1 and 2? Again, we answer no. Depending upon the diffusion model, biological interactions can either 'redden' the physically derived spectrum (see figure 2*a*), or 'whiten' the physically derived spectrum (see figure 2*b*); and which occurs might well depend upon the length scale under observation (e.g. greater (or less) than the KISS LENGTH, see figure 1). Careful statistical description of the spatial distribution of plankton populations by itself is unlikely to give much information about the biological mechanisms at work. The recent emphasis on understanding detailed mechanisms that determine each individual feature has much to recommend it. Indeed, the small details do count!

Our general conclusions mirror those for terrestrial environments. In a thorough study Roughgarden (1978) considered the effect of competition between species on patchiness. The dispersal process used by Roughgarden (a 'geometric dispersal model' (Roughgarden 1977), although a 'stepping stone' model could also be utilized) differs greatly from the turbulent diffusion formulation we employ. None the less, the details of Roughgarden's (1978) calculations are remarkably similar to our own (the results are even phrased in spectral terms!), and lead to similar conclusions. Depending on the specific values of model parameters Roughgarden finds that competition may lead to '. . . more distinct and longer patches . . .', or '. . . reduce patch distinctiveness and patch length . . .'. That is, biological interactions (in this case competition) can either flatten ('whiten') plankton variance spectra, thus decreasing patch distinctiveness and increasing patch length, or steepen ('redden') spectra by increasing patch distinctiveness and shortening patch length. These are identical to our own conclusions; i.e. biological interactions may either 'redden' or 'whiten' the spectrum of fluctuations that is due to the 'physical' process of diffusion alone. One should expect no general results that describe in all (or most) cases how 'the biology' modifies a spatial pattern that has arisen solely from the dispersal of species in a terrestrial habitat.

Inasmuch as one should expect biological interactions to modify 'the physics' in various ways, one might also expect that several biological mechanisms might lead to the same (or very similar) spatial patterns in the plankton. One example is the flattening of the spectrum (i.e. 'whitening') for higher trophic levels. That is, several examples exist of spectra that describe the spatial distribution of zooplankton that are significantly flatter than the spectra for phytoplankton collected simultaneously (Mackas & Boyd 1979; Weber *et al.* 1986). One explanation for this observation is that aggregation behavior at small scale leads to higher variance at large k. But Steele & Henderson (1992) present a model study in which Fickian diffusion, plus the nonlinear coupling of phytoplankton to their zooplankton predators, is sufficient to 'flatten' the spectrum. No data presently exists to distinguish between these two explanations. Again, the small details do count.

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