TOWARDS DEVELOPING A GENERAL FRAMEWORK FOR MODELLING VERTICAL MIGRATION IN ZOOPLANKTON

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ABSTRACT. Diel vertical migration (DVM) of zooplankton is a widespread phenomenon in both oceans and lakes, and is generally considered to be the largest synchronized movement of biomass on Earth. Most existing mathematical models of DVM are based on the assumption that animals maximize a certain criterion such as the expected reproductive value, the venturous revenue, the ratio of energy gain/mortality or some predator avoidance function when choosing their instantaneous depth. The major shortcoming of this general point of view is that the predicted DVM may be strongly affected by a subjective choice of a particular optimization criterion. Here we argue that the optimal strategy of DVM can be unambiguously obtained as an outcome of selection in the underlying equations of genotype/traits frequency dynamics. Using this general paradigm, we explore the optimal strategy for the migration across different depths by zooplankton grazers throughout the day. To illustrate our ideas we consider four generic DVM models, each making different assumptions on the population dynamics of zooplankton, and demonstrate that in each model we need to maximize a particular functional to find the optimal strategy. Surprisingly, patterns of DVM obtained for different models greatly differ in terms of their parameters dependence. We then show that the infinite dimensional trait space of different zooplankton trajectories can be projected onto a low dimensional space of generalized parameters and the genotype evolution dynamics can be easily followed using this low-dimensional space. Using this space of generalized parameters we explore the influence of mutagenesis on evolution of DVM, and we show that strong mutagenesis allows the coexistence of an infinitely large number of strategies whereas for weak mutagenesis the selection results in the extinction of most strategies, with the surviving strategies all staying close to the optimal strategy in the corresponding mutagenesis-free system.

1. INTRODUCTION

One of the most intriguing features of marine and freshwater zooplankton is the phenomenon of regular diel vertical migration (DVM) which is often considered to be the largest collective movement of biomass on our planet [31, 36]. DVM plays a major role in

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the carbon exchange between the surface waters and deeper layers and potentially has a strong influence on the Earth's climate [14, 5]. A typical DVM pattern consists in ascending to food rich surface waters for feeding on phytoplankton at night, then descending to deep layers and remaining there during the day [52, 31]. Currently, the most supported explanation for DVM in the literature is that it is an adaptive behavioral response allowing animals to both feed in food rich shallow waters and escape from visual predators such as planktivorous fish, which are more efficient in the day time [3, 52, 45, 20, 54]. It has also been pointed out that zooplankton may perform DVM for some other reasons, such as saving energy in deep waters due to the low temperature, avoiding solar radiation or increasing genetic exchange [48, 6, 54]. Despite the fact that the phenomenon of DVM in zooplankton has been extensively studied both empirically and theoretically, there is still a rather poor understanding of the key factors which shape this migration behaviour [6, 54, 57, 50].

Various mathematical models have been proposed in the literature which explain the emergence of DVM as a trade-off between food consumption and predator avoidance. A number of models use elements of game theory, assuming that organisms maximise their gain based on a certain pay-off matrix which can differ from model to model [35, 21, 22]. Other related approaches are based on the idea that organisms should maximize some fitness function, for instance the expected individual reproductive value [16, 17, 6], the 'venturous revenue' [46, 47], the ratio of energy gain/mortality [11] or minimize instantaneous changes in some particular types of predation pressure [28, 29]. Models using different optimization criteria generally predict similar patterns of migration, in the sense that the optimal strategy is to stay in deep waters during the day and feed at night near surface, as is widely observed in real plankton systems. However, when more specific features are considered, for instance, the optimal choice of the instantaneous depth by animals through the day, or the dependence of the amplitude of migration and the average depth on the key parameters (e.g. the amount of predators, food, light intensity, etc), the implementation of different models can predict different outcomes [16, 29, 46].

One of the main shortcomings of the existing models of DVM, as in many other models of animals' optimal strategies, is that the choice of optimization criterion is often subjective and based on conventional wisdom or even individual preference of the researcher (cf. [6]). As a result, the fact that the optimal behaviour predicted can be strongly affected by the choice of optimization criterion is a serious shortcoming. As an alternative approach, we can make a natural assumption that the organisms follow Darwin's idea of the survival of the fittest [10, 60], which can be formalized by means in mathematical modeling. In the case where we have model equations adequately describing the given biological system, we can expect that the fittest genotypes will be those which will persist in the system whereas the others will go extinct. Mathematically, this would signify that the relative frequency of unsuccessful genotypes should vanish compared with the that of better fitted individuals [26, 37, 43]. In the long run, the best animal strategies will dominate less

efficient strategies. Note that a similar concept is the basis of the adaptive dynamics paradigm, where evolution of genotypes/strategies is the result of consecutive invasions by small amounts of genetically close mutants, and the eventual outcome is a strategy which cannot be invaded by nearby mutants [12, 24, 53, 33].

In this paper, we explore the patterns of optimal zooplankton DVM obtained from the dynamics of the genotype/ functional trait distribution in the strategy space. Unlike earlier models, the optimal strategy of DVM is now an emerging property of the given model, i.e. it is independent of any the optimization criterion. Here we are interested in finding the optimal trajectory of an animal in terms of the instantaneous depth $x(t)$ of a zooplankter in the water column throughout the day. The choice of a particular strategy $x(t)$ will automatically determine the population dynamics of the given zooplankton cohort and its eventual evolutionary outcome. Each strategy can be considered as a function-valued trait, and so mathematically the space of available genotypes is infinite-dimensional. We demonstrate how the optimal strategy of DVM can be found in such a space, and how we can follow the dynamics of strategy distributions across the space of genotypes/ functional traits. Unlike some previous works considering function-valued traits [53, 13], we do not implement the adaptive dynamics formalism here. This allows us to consider a system with long-range mutation (strong mutagenesis) in the genotype space as well as the possibility of invasion by individuals with any possible genotype structure.

As insightful examples, we derive the optimal DVM for three zooplankton models: three single-species models (one of which explicitly includes developmental stages) and a predator-prey model. In each case, we unambiguously define a generalized fitness function R , maximisation of which gives the optimal strategy of migration $x(t)$; all other genotypes eventually go extinct. We consider the effects of key parameters such as predation pressure, food abundance, metabolic cost of migration, etc, on the optimal strategy of DVM. We demonstrate that although the models predict broadly qualitatively similar patterns (i.e. feeding at upper layers at night and staying in deeper layers during the day), variation of food availability may affect the response of optimal strategy differently, both in terms of the amplitude and the average depth. Finally, we show that the infinite dimensional space of DVM strategies can be projected onto a low dimensional space of generalized traits. Considering such a space allows us to model evolution of strategies both for a weak and a strong mutagenesis. In particular, we show that a weak mutagenesis results in extinction most of strategies, except for those in the vicinity of the optimal strategy in the mutagenesis-free scenario.

The paper is organized as follows. Section 2 introduces the generalized variational principle of biological selection. In Section 3, four basic models of zooplankton dynamics are introduced and the expression for the generalized fitness is derived in each case. In Section 4, the optimal strategies of DVM for all models are analyzed and then compared and the role of mutagenesis in the on selection process is investigated. In the Discussion

(Section 5), the main results are summarized and further ideas are considered for finding optimal DVM strategies in more complex models.

2. GENERAL VARIATIONAL PRINCIPLE OF NATURAL SELECTION

Here we discuss the generic mathematical framework of modelling a process of natural selection which will be further applied to modelling DVM of zooplankton.

Let us assume that the behavioural strategy v of an organism is genetically inherited and belongs to a certain space V of genotypes or functional traits (finite or infinite dimensional). In terms of DVM, V can include the amplitude of migration, the average depth throughout the day or the instantaneous spatial location of organisms as a function of time. The distribution of the genotype/trait density over the space V is determined by ρ . The temporal dynamics of ρ is governed by the evolution operator $\rho'_t(v, t) = \phi[\rho, v, t]$. Using this general equation it is possible to compare efficiency of different genotypes in the space V . Mathematically, we make an important assumption that the density ρ continuously depends on v . We state that the genotype/trait v is more advantageous, or fitter, than genotype w if

$$\lim_{t \rightarrow \infty} \frac{\rho(w, t)}{\rho(v, t)} = 0. \quad (2.1)$$

In the case where the biomass of species is bounded in the model, condition (2.1) signifies that the organisms with genotypes belonging to w will be eventually replaced by those belonging to v [26, 43].

It can be shown [44] that the natural selection criterion (2.1) is equivalent to the following

$$\left\langle \frac{\rho'_t(v, t)}{\rho(v, t)} \right\rangle = \lim_{t \rightarrow \infty} \frac{1}{t} \int_0^t \frac{\rho'_t(v, t)}{\rho(v, t)} > \left\langle \frac{\rho'_t(w, t)}{\rho(w, t)} \right\rangle = \lim_{t \rightarrow \infty} \frac{1}{t} \int_0^t \frac{\rho'_t(w, t)}{\rho(w, t)}. \quad (2.2)$$

In other words, the genotype v with a higher average per capita growth rate will over-compete a genotype w with a lower average per capita growth rate [26, 43].

In a number of biological applications, equation the initial population model can be transformed to the following form (see examples from this paper)

$$\rho'_t(v, t) = r(v, t)\rho(v, t) - \rho(v, t) \int_V h(w, t)\rho(w, t)dw, \quad (2.3)$$

where $r(v, t)$ describes the per capita growth rate of the genotype v , h takes into account the limitation due to competition with other genotypes. Note that in this section we do not consider the process of mutagenesis, i.e. we assume that each organism inherits the genotype of its parent. We shall briefly address the role of mutagenesis in Section 4.

In the case where dynamics in V is described by (2.3), it can be shown (see [44]) that the selection criterion (2.2) is equivalent to maximization of the average value of the functional $r(v, t)$, i.e.

$$\langle r(v, t) \rangle > \langle r(w, t) \rangle. \quad (2.4)$$

The biological meaning of condition (2.4) is that natural selection will eventually result in genotypes with the highest average value of $\langle r(v, t) \rangle$, which can be interpreted as the generalized fitness. These genotypes will be stable to invasion by any other strategies (mutants), and so maximization of $\langle r(v, t) \rangle$ will give us an evolutionary stable strategy (ESS) [4].

Note that although equation (2.3) may seem to be too simplistic, a large number of practically important models can be transformed into this form, including some predator-prey models. In next section we shall show few examples of how this can be done. We shall then implement condition (2.4) to derive the optimal strategy for zooplankton vertical migration. In this case, the genotype/functional trait v will correspond to the choice of vertical location $x(t)$ in the water column; for simplicity we re-scale time so that a 24h period corresponds to the interval $t \in [0, 1]$, and assume that due to periodicity of the function we have $x(0) = x(1)$. Thus, formally our space of genotypes V is the infinite dimensional space $V = C_1[0, 1]$ of smooth functions on the interval $[0, 1]$.

3. MODELS FORMULATION AND DERIVING THE GENERALIZED FITNESS

3.1. Model 1.

We start with the basic model. We assume that the age structure of the zooplankton population is always constant, i.e. the proportion of the size of any developmental stage always stays the same relative to the overall population size. This assumption implies that the percentage ϵ of reproductive females within the population is constant.

The population growth occurs due to consumption of food (phytoplankton) which is described by E_0 . The losses in population growth are due to predation M and metabolic costs of migration described by E_1 . Approaching the limits of the habitat (i.e. the surface of the ocean and deep waters) causes extra mortality of animals which is described by the term G . We assume that intraspecific competition is given by the logistic term. The overall density of predators (carnivorous zooplankton or planktivorous fish) is suggested to be constant. Then the dynamics of the population density $\rho(v, t)$ of the genotype implementing behavioral strategy v is described by the following equation (we assume quadratic mortality due to intraspecific competition with the kernel $h(v, t)$)

$$\rho'_t(v, t) = (E_0 - E_1 - S - G)\epsilon\rho(v, t) - \rho(v, t) \int_V \rho(v, t)h(v, t)dv. \quad (3.5)$$

The outcome of the competition will be determined by averaging the growth rate $r(v, t)$, where the strategy v will correspond to the choice of vertical location $x(t)$

$$r(v, t) = (E_0 - E_1 - S - G)\epsilon. \quad (3.6)$$

The strategy with maximal average $r(v, t)$ will be the optimal strategy as shown in Section 2.

To calculate the optimal strategy we need to specify the functions in equation (3.6). We assume that the consumption of phytoplankton at depth x can be described by the

following law

$$E_0 = \alpha(\tanh \sigma x + 1),$$

where a positive parameter σ characterizes the steepness of the vertical gradient in phytoplankton distribution; α is proportional to the overall abundance of phytoplankton. The function $\tanh \sigma x + 1$ mimics the general distribution of phytoplankton in the water: it is highest in surface waters (provided there is enough nutrient supply) and vanishes in deep waters. The coordinate $x = 0$ corresponds to the middle of the euphotic zone of the ocean.

For simplicity, we assume that the vertical distribution of the predators consuming zooplankton follows the same relationship as (3.1), however this assumption is not crucial. Here we consider visual predators of zooplankton, whose efficiency is determined by the light intensity, which varies throughout the day. The overall predation term (assuming a Holling type I functional response) is given by

$$S = \gamma(\tanh \sigma x + 1)(\sin 2\pi t + 1),$$

where the coefficient γ is the product of the constant predator density and the attack rate.

The metabolic costs of vertical migration are proportional to the losses due to resistance forces, or drag, given by

$$E_1 = \beta(x'_t)^2,$$

where β is a positive parameter, taking into account the viscosity and resistance of water as well as the average size of animals [16].

Finally, we consider the following form of the extra mortality of zooplankton when they approach the ocean surface or deep depths (recall that the level $x = 0$ corresponds to the middle of the water column)

$$G = \delta \frac{\exp(\xi x) + \exp(-\xi x)}{2} = \delta \cosh \xi x,$$

where the positive constant ξ characterizes the width of the habitat. Note that the assumption about the functional form of G is not crucial for the main results.

We substitute the parameterizations of E_0 , E_1 , S and G into $r(v, t)$ and integrate over the day. This gives

$$R = \epsilon \int_0^1 (\alpha(\tanh \sigma x + 1) - \gamma(\tanh \sigma x + 1)(\sin 2\pi t + 1) - \beta(x'_t)^2 - \delta \cosh(\xi x)) dt \quad (3.7)$$

According to condition (2.4), the outcome of competition between the genotypes will be determined by the generalized fitness R : the strategy which maximises the fitness will outcompete all other strategies.

Technical details of solution of the above optimization problem are discussed in Appendix.

3.2. Model 2.

Consider now a more complicated model, where mature zooplankton have two alternating states: (i) a long-term non-reproductive state and (ii) a short-term reproductive state. During the non-reproductive state, zooplankton accumulate energy and changes in the population are only determined by losses due to predation. We assume that during the reproductive state all individuals produce the same number of offspring, but to be able to reproduce it is required that the energy accumulated during the non-reproductive state should not drop below a certain fitness threshold I_0 .

The instantaneous per capita growth rate $r(x, t)$ during the non-reproductive stage will be given by the predation losses

$$r = -\gamma(\tanh \sigma x + 1)(\sin 2\pi t + 1)$$

and during the reproductive stage by

$$\begin{cases} r = r_0, \text{ if } \int_0^1 \alpha(\tanh \sigma x + 1) - \beta(x'_t)^2 - \delta \cosh(\xi x) dt \geq I_0; \\ r = 0, \text{ otherwise.} \end{cases}$$

The integral term in the above expression describes the accumulated energy due to food consumption and metabolic losses due to migration.

The average value of r (the generalized fitness R) will be given by

$$\begin{cases} R = \langle r \rangle = \left(T \left(\int_0^1 -\gamma(\tanh \sigma x + 1)(\sin 2\pi t + 1) dt + \tau r_0 \right) / (T + \tau); \right. \\ \text{if } \int_0^1 \alpha(\tanh \sigma x + 1) - \beta(x'_t)^2 - \delta \cosh(\xi x) dt \geq I_0 \\ R = \langle r \rangle = \left(T \left(\int_0^1 -\gamma(\tanh \sigma x + 1)(\sin 2\pi t + 1) dt \right) / (T + \tau), \right. \\ \left. \text{otherwise.} \right. \end{cases}$$

Thus, the optimal strategy of DVM will be the one which maximises the generalized fitness R , which results in the following optimization problem

$$\int_0^1 (\tanh \sigma x + 1)(\sin 2\pi t + 1) dt \rightarrow \min, \quad \int_0^1 (\alpha(\tanh \sigma x + 1) - \beta(x'_t)^2 - \delta \cosh(\xi x)) dt \geq I_0. \quad (3.8)$$

Technical details of solution of the above optimization problem are discussed in Appendix.

3.3. Model 3.

In the following model, we take into account zooplankton-predator interactions, so the fish (or carnivorous zooplankton) density $F(t)$ is now a dynamical variable. In the simplest case, the system can be described by the Lotka-Volterra predator model [2]

$$z'_t(v, t) = b(v)z(v, t) - F(t)a(v)z(v, t), \quad (3.9)$$

$$F'_t(t) = F(t) \int_V a(v)z(v, t) dv - mF(t), \quad (3.10)$$

where $z(v, t)$ is the density of zooplankton implementing behavioral strategy v ; $F(t)$ is the total biomass of fish; V is the space of the existing strategies. The growth rate $b(v)$ and the attack rate $a(v)$ by the predator are day time averages:

$$b = \int_0^1 \alpha(\tanh(\sigma x) + 1) - \beta(x'_t)^2 - \delta \cosh(\xi x) dt, \quad (3.11)$$

and

$$a = \int_0^1 \alpha(\tanh(\sigma x) + 1)(\sin(2\pi t) + 1) dt, \quad (3.12)$$

where the meaning of the model parameters is the same as in the previous models.

We make the following change of variables: $y(v, t) = (z(v, t))^{1/a(v)}$. Next we introduce a new variable (having the meaning of the genotype frequency)

$$\rho(v, t) = \frac{y(v, t)}{\int_V y(w, t) dw}.$$

After some calculation we obtain

$$\rho'_t(v, t) = \frac{b(v)}{a(v)} \rho(v, t) - \rho(v, t) \int_V \frac{b(w)}{a(w)} \rho(w, t) dw, \quad (3.13)$$

which coincides with the basic equation (2.3). Thus the generalized fitness R for this model is given $R = \frac{b(v)}{a(v)}$. Therefore, the best behavioral strategy is the one which maximises the following functional

$$R = \frac{\int_0^1 ((\alpha(\tanh \sigma x + 1) - \beta(x'_t)^2 - \delta \cosh(\xi x) dt))}{\int_0^1 (\tanh \sigma x + 1)(\sin 2\pi t + 1) dt} \rightarrow \max, \quad (3.14)$$

and the other strategies will eventually vanish.

Technical details of solving optimization problem (3.14) are discussed in Appendix.

3.4. Model 4.

Finally, we consider a model of a zooplankton population with explicit dynamics for different developmental stages. For simplicity, we assume that the whole population consists of adults and juveniles with the densities (in terms of numbers) $\rho(v, t)$ and $\zeta(v, t)$, respectively. As before, V describes the space of strategies. The dynamics of $\rho(v, t)$ and $\zeta(v, t)$ is given by [42]

$$\rho'_t(v, t) = b_0(v)\zeta(v, t) - p(v)\rho(v, t) - q(v)\rho(v, t) - \rho(v, t) \int_V (\theta\rho(v, t) + \kappa\zeta(v, t)) dv, \quad (3.15)$$

$$\zeta'_t(v, t) = p(v)\rho(v, t) - s(v)\zeta(v, t) - \zeta(v, t) \int_V (\theta\rho(v, t) + \kappa\zeta(v, t)) dv, \quad (3.16)$$

where $b_0(v)$ is the reproduction coefficient of adults; $q(v)$ and $s(v)$ are the mortalities of juveniles and adults, respectively, caused by predation; $p(v)$ describes the rate of

transition from juveniles to adults. The coefficients θ and κ describe the contribution of adults and juveniles into the overall carrying capacity.

Interestingly, system (3.15)-(3.16) can be transformed to an equation which is equivalent to (2.3) (see Supplementary Material S3 for details) with the generalized fitness being

$$R = -s(v) - p(v) - q(v) + \sqrt{4b_0(v)p(v) + (p(v) + q(v) - s(v))^2} \rightarrow \max. \quad (3.17)$$

One can see that the expression for generalized fitness (3.17) involves all functions controlling the dynamics of both the juvenile and adult cohorts. Also, the particularity of the given two-stage model is that each strategy v of the population comprises two trajectories $x_A(t)$ and $x_J(t)$ describing vertical migration of adults and juveniles.

The reproduction rate of adults $b_0(v)$ is proportional to the daily net food gain (similar to (3.11))

$$b_0 = \epsilon_A \int_0^1 (\alpha_A(\tanh \sigma x_A + 1) - \beta_A(x'_A)^2 - \delta_A \cosh(\xi x_A)) dt, \quad (3.18)$$

where ϵ_A describes the conversion of the food gain into the newly produced juveniles (we can have $\epsilon_A > 1$ since $\rho(v, t)$ and $\zeta(v, t)$ express the numbers of individuals). Note that here the index A (or J) corresponds to the parameters related to adults (or juveniles).

The mortalities $q(v)$ and $s(v)$ are parameterized by the same expression as in (3.12) with all parameters corresponding to juveniles and adults, respectively. We parameterize $p(v)$ - the inverse time of transition from juveniles to adults - using the following Monod-like equation

$$p = \frac{\eta L}{L + K}, \quad (3.19)$$

where L is the energy gain per day by the juveniles. Note that L is described by the same functional as (3.18) with $x_A(t)$ being replaced with $x_J(t)$ (the corresponding parameters for adults should be replaced with those of juveniles). K is the saturation constant, indicating that the maturation time $1/p$ should not approach zero even if the amount of food consumed is very high; η is the upper boundary of p .

Optimisation of (3.17) composed of 4 functionals is a non-trivial problem; it is briefly described in Appendix.

4. RESULTS

Based on the optimization techniques described in Appendix, we have numerically computed the optimal patterns of DVM for the four above models. The optimal trajectories $x(t)$ are shown in Figs.1,2,3,4 where $t = 0$ and $t = 0.5$ correspond, respectively, to 6 a.m. and 6 p.m in terms of the absolute time of the day. In all figures the vertical coordinate is dimensionless, where $x = 0$ corresponds to the centre of the euphotic zone. One can see from the figures that the general pattern of all optimal trajectories $x(t)$ is such that zooplankton spend the night feeding in upper layers and stay in deeper waters

during the day time, i.e. as observed empirically [54]. The amplitude and the average depth of migration depend on the key model parameters α, β and γ .

In Model 1 an increase of the overall amount of predator (described by γ) results in an increase in the amplitude of migration and a decrease of the average depth of zooplankton (see Fig.1A). However, in the case where the predator is almost absent (e.g. $\gamma = 0.3$), zooplankton mostly stay in the upper layer, and DVM is not observed (except for small amplitude oscillations). An increase in the metabolic costs of migration (described by β) results in a drop of the amplitude of migration and an ascend of the average depth of animals (Fig.1B), i.e. movement across the column becomes costly compared to staying and feeding near a fixed depth.

In Model 2, the optimal strategy is sensitive to the minimal fitness threshold I_0 (see Fig.2A). A small variation in I_0 can trigger a substantial shift of the average depth and the amplitude of DVM: vertical migration is more pronounced for smaller I_0 . This signifies that when large energetic requirements are needed for reproduction, organisms cannot afford DVM and preferentially stay in the upper layers, even if this entails extra losses from predation. This corresponds to the strategy ‘better dead than unfed’, which has been observed empirically in both oceans and lakes [34, 18]. On the other hand, a smaller value of I_0 results in a deeper average depth of zooplankton. As in Model 1, an increase in the metabolic costs of migration (β) causes a decrease of the amplitude of migration (Fig.2(B)).

Typical patterns of the optimal DVM in Model 3 are represented in Fig.3, constructed for various β . As in the previous models, an increase in the cost of migration β reduces the strength of DVM.

Investigation of Model 4 shows that patterns of DVM for juveniles and adults are different both in terms of the amplitude and average depth as well as the response to variation of the key parameters (see Fig.4). In particular, a gradual increase in β_J results in a gradual decrease in the amplitude of DVM of juveniles with the average depth being slightly below $x = 0$ (i.e. slightly below the middle of the euphotic zone). On the other hand, a gradual increase in β_A causes a sharp discontinuous jump in the behaviour of adults: the amplitude of DVM suddenly collapses and the organisms move to surface waters where they stay throughout the whole day. Mathematically, a sharp transition in the behaviour of adults is related to the existence of more than one local maxima of the generalized fitness R , the largest one being the global maximum which defines the optimal strategy. Variation of parameters results in the situation, where one of the previous local maxima becomes a new global maximum and the optimal trajectory abruptly switches to this new global maximum.

It is interesting to compare how the behavioral strategies $x(t)$ in each model respond to a gradual increase of the amount of available food for zooplankton, which is described by the parameter α . Fig.5,6 shows the optimal patterns of DVM in the four models for small, intermediate and large values of α , which describe, respectively, oligotrophic, mesotrophic

and eutrophic waters. As can be seen from this figure, the models demonstrate rather different behaviour.

In Model 1 (Fig.5a), an increase in available food results in shallower average depths and the migration almost ceases. Despite the high losses via predation, it is beneficial for organisms to stay near the surface and consume more food, because the number of predators in Model 1 is fixed. In Model 2 (Fig.5b), an increase in the food supply results in deepening of the average depth and an increase in the amplitude of migration. This can be explained by the fact that zooplankton should minimize the predation pressure and that any high food consumption in upper layers beyond the value of the minimal fitness threshold I_0 is not rewarded, while causing extra mortality. In Model 3 (Fig.5c) an increase in the amount of food triggers large amplitude DVM, but the shallowest depths are almost independent of the amount of food (Fig.5c), whereas in Model 2 those depths decrease with α . Finally, in Model 4, an increase in the food supply has little effect on the migration of juveniles, which do not stop their migration even if the food density is very high (Fig.6b). This can be explained by the assumption that the maturation rate is a saturated function of the consumed food (see (3.19)): staying mostly in surface waters and consuming there a large amount of food will not result in a substantial increase in the maturation rate of juveniles, but will cause their high mortality. On the other hand, a supercritical amount of food would result in a sharp change in DVM of adults which should cease their migration and stay in the surface layers (Fig.6a).

The largest migrations observed in Model 3 (when compared with the other models) can be explained by the fact that the organisms are rewarded for feeding near the surface in food rich layers, unlike Model 2. At the same time, the number of predators in Model 3 is no longer constant as in Models 1,4 and is instead proportional to the consumption of food by zooplankton. Thus staying most of time in the upper layers for a long time will result in an increase in the biomass of predator and cause severe losses. Then zooplankton should exhibit a high amplitude DVM as a result of these two features. Thus, we should emphasize again that the optimal DVM in the four models greatly differ in their parameters dependence.

Visual analysis of the optimal strategies shown in Fig.1-5 allows us to assume that $x(t)$ can be approximated by the sum of few first functions of the Fourier series. Computation shows that a reasonably good approximation can be obtained even with only two terms with the coefficients A and B_1 standing for the average depth and the amplitude of migration: using other terms provides only a small improvement ($< 1-2\%$). The observed closeness between the approximation and the true solution (i.e. obtained via Pontryagin's method) allows us to conduct optimization by directly searching for the leading Fourier coefficients which maximize the generalized fitness R . More importantly, the possibility of approximating the optimal trajectories by the few first terms of Fourier approximation signifies that we are now able to project the initial infinitely dimensional space $V = C_1[0, 1]$ of strategies $x(t)$ into a low-dimensional space of generalized parameters of Fourier

coefficients. Using this low-dimensional space we can follow the evolution of distribution of strategies across the population in the course of time.

For simplicity, we consider just two first leading terms A and B_1 . In the case where we can assume that all possible values of these generalized parameters belong to some rectangular domain Ω . The equation for the genotype density dynamics is given by (2.3). This equation can be solved analytically under the assumption that the evolutionary timescale is much larger than the timescale of daily variations (see Supplementary Material S2). The distribution of the relative frequencies of genotypes/functional traits as a function of time is described by

$$\rho(A, B_1, t) = \frac{\rho(A, B_1) \exp(tR(A, B_1))}{\int_{\Omega} \rho(A, b_1) \exp(tR(A, b_1)) d\Omega / R(A, b_1)}. \quad (4.20)$$

One can see from (4.20) that the optimal strategy maximizing R will eventually overcome the other strategies and the distribution will converge to the Dirac's delta function centred at the ESS. In terms of practical applications, by using (4.20) we can estimate the characteristic evolution time of approaching the optimal strategy, for instance fixing the time when the standard error of the frequency distribution drops to 1%. Note that estimating of the characteristic evolution time in the original infinite dimensional space of traits $V = C_1[0, 1]$ would be a mathematical challenge.

The possibility of projecting the infinite-dimensional trait space into a finite-dimensional space allows us to easily describe the effects of mutagenesis in the strategies, by modelling the role of mutations. The probability of mutated strategy w of DVM arising in the offspring of a parental genotype with strategy v can be described by the kernel $k(w, v)$. We suggest $k(w, v)$ should be a monotonically decreasing function of the distance $\|v - w\|$ in the genotype space V . In general, the equation describing the evolutionary dynamics of the distribution of strategies (2.3) across the space V is given by [40, 51]

$$\rho'_t(v, t) = \int_V k(v, w) r(w) \rho(w, t) dw - \rho(v, t) \int_V \rho(w, t) dw. \quad (4.21)$$

This equation can be re-written in terms of relative densities of the genotypes by introducing $\tilde{\rho} = \rho(v, t) / \int_V \rho(v, t) dv$. We further omit the 'tilde' over ρ for simplicity and arrive at (see Supplementary Material S3)

$$\rho'_t(v, t) = \int_V k(v, w) r(w) \rho(w, t) dw - \rho(v, t) \int_V \int_V k(v, w) r(w) \rho(w, t) dw dv. \quad (4.22)$$

The above equation can be integrated numerically by considering, for instance, the subspace A and B_1 .

Let us consider two cases of mutations: (i) strong mutagenesis, allowing large-distance mutations in V and (ii) weak mutagenesis where only small mutations are possible. As an example, we use the parametrisation of the kernel k described by the Gaussian law with the standard error ω .

Fig.7A,B,C show a typical pattern of the evolution of DVM strategies in Model 1 with a strong mutagenesis ($\omega = 40$). The initial distribution of strategies is homogeneous. One can see that the distribution $\rho(A, B_1)$ has a pronounced maximum, which approximately corresponds to the maximal value of the generalized fitness (3.7). However, the density distribution does not vanish at any point of space even for large times. In other words, the selection processes does not hold and an infinite number of strategies can coexists in the system for $t \rightarrow +\infty$: high rate of mutations can compensate the selection process. In the case of weak mutagenesis ($\omega = 0.003$) the evolution of strategies is completely different (Fig.7D,E,F). Indeed, although the selection process is not well pronounced at some intermediate times, the density of most suboptimal strategies will eventually vanish and the surviving strategies will be grouped in the vicinity of the strategy corresponding to the optimal R in the system without mutation. The principle of survival of the fittest still holds in this case. As an important conclusion, small mutations will not affect the selection process resulting in a single optimal strategy of DVM, whereas larger mutations will result in coexistence of a continuum of migration strategies.

5. DISCUSSION AND SUMMARY OF RESULTS

In this paper, we revisit the fundamental principles of modelling zooplankton diel vertical migration (DVM). We are particularly interested in finding the optimal instantaneous depth $x(t)$ of the grazer in the water column throughout the day as a function of key parameters such as predation, food and swimming cost. In earlier models, the optimal strategy of DVM was obtained by maximization or minimization of some criterion (e.g. reproductive value, venturous revenue or some effective predation pressure, etc), but here we argue that the choice of such criteria is often subjective or based on conventional wisdom [16, 17, 28, 29, 6, 11, 46]. Here, we use a different paradigm of DVM modelling, where optimisation of a functional - the generalized reproductive value R - emerges directly from the underlying model for the density of the strategies in the genotype space. In other words, after the underlying model of genotype dynamics is fixed, we have no ambiguity in the choice of the optimization function(al) and suboptimal genotypes will eventually go extinct as a result of selection, which is a mathematical formulation of Darwin's principle of survival of the fittest [10, 60]. We should stress that here we do not claim that all earlier models of DVM are necessarily wrong: under some assumptions each of those models might be correct. For instance, the idea of maximisation of the energy gain/mortality ratio in Model 3 is the same as in [11, 6]. The major difficulty with earlier frameworks is that it is hard to say under which conditions we should implement a particular optimization criterion. For instance, our study shows that for four different population dynamics models we should maximize different expressions for the generalized reproductive value R . As a result, maximisation of the energy/mortality gain ratio should make sense only if we can assume a dynamical adjustment of the amount of predator as response to variation in the zooplankton biomass. On the other hand, considering a relatively simple two-stage Model 4 shows that R may be a complicated

function of intermingled parameters: considering more developmental stages will make this function even more complex.

The general idea to replace maximization of arbitrary chosen characteristics with direct modelling of the selection process from the underlying dynamics of genotype frequency is not completely new. Similar ideas have been suggested, for instance, in the well-developed theory of adaptive dynamics, where the resultant evolutionary stable strategy is unambiguously found via repeated introduction of close mutant strategies [12, 24, 53]. However, we believe that our approach is somewhat broader since it is not only limited to small mutations and it also allows us to consider the evolution of various initial distributions in the space of strategies (Fig.7).

Although we consider four generic models with somewhat abstract parameters, these simple models allow us to reveal different responses of DVM to environmental changes. For instance, a gradual eutrophication of the environment (corresponding to an increase in α) results in the cessation of vertical migration in Model 1 and Model 4 (adults) when the overall amount of predator is fixed, whereas in Model 3, with a dynamical predator, a high food density amplifies DVM (Fig.5c). It has been reported in some field studies that vertical migration is not observed when the ambient food is not high enough: such a strategy is known as ‘better dead than unfed’ [9, 34], and Models 2 and 3 predict such behaviour. On the other hand, other field studies have found that abundant food causes a reduction of DVM [25, 23]. In Model 1, this fact can be explained by assuming a relatively constant amount of predators in the system (see Fig.5A): predation losses can be potentially compensated by high food consumption and fast reproduction.

An important finding of this study is that the original space V of function-valued traits, which is infinite-dimensional, can be accurately projected onto the low dimensional space of generalized parameters given by the leading Fourier coefficients. In our case these parameters represent the average depth and the amplitude of migration. This approach allows us to directly follow the transitional process of selection and estimate the time of extinction of a particular genotype. Considering a finite dimensional space also makes it possible to model evolution in the case of mutagenesis. The existing framework of modelling evolution of infinite-dimensional traits is usually based on the canonical equation of adaptive dynamics [13, 53], and approach is a complementary one since it allows us to take into account an arbitrary mutagenesis process as well as the evolution of a complex initial distribution of strategies which are not close each other, which cannot be represented by the canonical equation. Also, this approach allows us to model fast evolution in physiologically structured populations, which has so far been done only for a single trait value [51]. Using equation (4.22) in the generalized parameter space we demonstrate that only high mutation rates can affect the eventual selection process: a weak mutagenesis still results in a strong selection where only a narrow distribution of strategies can survive in the long run (see Fig.7). This confirms previous theoretical findings on the role of mutagenesis in selection [26].

It is important to note that considering a low-dimensional subspace of generalized parameters is not only a mathematical trick to avoid working with infinite-dimensional spaces: in the case of zooplankton DVM this idea has a clear biological interpretation. It is well known that light intensity is one of the key stimuli of the timing of migration and its amplitude - when performing DVM pelagic organisms often follow the depth with a certain constant light intensity which is known as the ‘isolume’ [30, 56, 15, 58]. The daily variation of the isolume is described by a harmonic-like function, for instance the sinusoidal relationship. As the simplest strategy of DVM, organisms can only control two parameters: the amplitude and the average depth. In the case of a sudden change in the environment, organisms can change the intensity level at value which they follow in the isolume, while still performing qualitatively similar vertical movement as before. Having a large number of independent ‘degrees of freedom’ in the space of strategies, on the other hand might generally be a shortcoming for adaptation to changes in the environment since it makes such adaptation less robust to eventual errors which can be amplified due to the phenomenon known as structural sensitivity [7, 1].

When specifying model functions describing the resource distribution, predation pressure or natural mortality across the water column, we used rather generic parameterizations. However, one can easily include in this framework more realistic functions, for instance, taking into account the influence of vertical variation of temperature, oxygen, salinity, etc (cf. [16, 17, 29, 46]). Also, the temporal variation of predator activity can be more accurately described by considering more complicated functions (see Fig. 5.3 in [6]). For instance, we can consider the following parametrization of the daily variation in predator activity: $J = 1 + \text{sgn}(\sin(2\pi t)) \sqrt[4]{|\sin(2\pi t)|}$. We should say that, interestingly, our computation shows that the use of this new parametrization or some other similar parameterizations does not greatly affect the results constructed for the simplest term $1 + \sin(2\pi t)$. We find that the most important issue is not the exact parametrization of J , but its daily periodicity. This strengthens our conclusion on the key role of light in the shaping of the optimal trajectory of DVM [30, 56, 15, 58].

Our framework makes it possible to consider some other scenarios of the metabolic cost of displacement of animals across the water column. For instance, we can assume that it is proportional to the absolute value of the velocity, i.e. that $G = \beta|x'_t|$. The optimal trajectories under this assumption are investigated in Supplementary Material S1. The main difference from the previous results is that $x(t)$ is now given by a piecewise linear function, which is shown in S1. This accords with previous reports that in some zooplankton species migration between the upper and the lower depths occurs at a constant speed [54]. For an example of modelling zooplankton migration based on piecewise functions, see [32]. Interestingly, the main outcomes regarding the dependance of the average depth and the amplitude on the model parameters remain the same as in the case with $G = \beta(x'_t)^2$. In particular, the response of the amplitude and the average depth to an increase in the available food is qualitatively similar to that shown in Fig.5,6. Note that again the infinite-dimensional space of strategies V can be projected into the space

consisting of small number of parameters: the average depth, the amplitude of migration and the speed of animal movement.

Finally, we should stress that apart from relatively simple models of zooplankton dynamics, we can apply the same ideas to more complex models, by including more than two different developmental stages, for instance. In the most general case, one can even consider continuous age structuring of animals, which will require the use of a hyperbolic PDE of Foerster's type [8]. Some theoretical results on selection in equations with continuous age structuring have been obtained in [41] and other works, but due to the high complexity of the underlying equations, only numerical methods of optimization are available at the moment. Exploring selection in continuously structured zooplankton populations will be one of the directions of our future research.

6. APPENDIX

Here we briefly consider mathematical and computational techniques to solve optimization problems arising in Models 1,2,3 and 4.

Model 1

Mathematically, maximization of the functional R in (3.7) is equivalent to minimization of $-R$, for which we can implement Pontryagin's maximum principle [55]. We denote $u = x'_t$ and introduce the adjoined variable ψ which satisfies the equation

$$\psi'_t = -\frac{\sigma((\alpha - \gamma) - \gamma(\sin 2\pi t))}{\cosh^2 \sigma x} + \delta \xi \sinh \xi x$$

along with the boundary conditions

$$\psi(0) = \psi(1), x(0) = x(1).$$

The Hamiltonian of this optimal control problem is given by

$$H = \psi u + \beta u^2.$$

According to the Pontryagin's maximum principle, the optimal control is achieved for u , for which the Hamiltonian $H(u)$ has its minimum. This gives the solution

$$u = x'_t = -\frac{\psi}{2\beta}.$$

The obtained boundary problem for the unknowns x and ψ needs to be solved numerically. This has been done using the shooting method combined with Newton's method of solving nonlinear equations in MATLAB package [49].

Model 2

We can solve optimization problem (3.8) using the Lagrange multipliers technique. The corresponding Lagrange multiplier can be taken as $-1/\gamma$, where γ is unknown, and for a fixed γ the solution of the problem will be the same as when minimizing the

functional $-R$ in Model 1. We need to chose the value of $-1/\gamma$ such that

$$\int_0^1 (\alpha(\tanh \sigma x + 1) - \beta(u)^2 - \delta \cosh(\xi x)) dt = I_0.$$

The numerical computation has been done using MATLAB.

Model 3

To solve optimization problem (3.14) one can consider the following auxiliary problem

$$J = \int_0^1 (\alpha(\tanh \sigma x + 1) - \beta(u)^2 - \delta \cosh(\xi x)) dt \rightarrow \max,$$

$$\int_0^1 (\tanh \sigma x + 1)(\sin 2\pi t + 1) dt \leq C = \text{const},$$

where the constant C is fixed at the moment. Let $J^*(C)$ be the maximal value of the considered functional under the given constraint. Then the initial optimization problem can be solved by finding the constant C which gives the maximal ratio of $J^*(C)/C$, which can be solved using the Lagrange multiplier technique. As in Model 2, we can denote the Lagrangian multiplier by $-1/\gamma$, then mathematically we need to find the minimum of the functional $-R$ in Model 1 given by (3.7). The numerical computation has been done using MATLAB.

Model 4

We maximize the functional R given by (3.16) which is a function of the following functionals s , q , b_0 , and L (note that $p = p(L)$) We assume that $r > 0$ and $L > 0$ as well as $b_0 + q - s > 0$ (see Supplementary Material S3 for detail). Let us introduce auxiliary constants C_2 and C_3 and consider the optimisation of R with $s = C_2$ and $q = C_3$.

It is easy to check that the partial derivatives of (3.16) with respect to b_0 and p are positive, which signifies that the maximum of R will be achieved at the maximal values of r and p . Note that b_0 and p are independent since they are determined by $x_A(t)$ and $x_J(t)$, respectively. Thus, optimization of (3.16) is equivalent to two optimization problems: (i) maximization of $b_0(v)$ and (ii) maximization of $p(v)$. Both optimization problems can be solved using the Lagrange multipliers technique.

Let us consider first maximisation of b_0 which is equivalent to minimisation of $-b_0$. We introduce a Lagrange multiplier λ_2 , corresponding to the constraint $s = C_2$. We need to find the minimum of the Lagrange function $-b_0 + \lambda_2 s$. We implement Pontryagin's maximum principle. As in Model 1, we denote $u = x'_A$ (here and further differentiation should be understood with respect to time) and introduce the adjointed variable ψ_A which satisfies the equation

$$\psi'_A = -\frac{\sigma(\alpha_A - \lambda_2 \gamma_A (\sin 2\pi t + 1))}{\cosh^2 \sigma x_A} + \delta_A \xi \sinh \xi x_A$$

along with the boundary conditions

$$\psi_A(0) = \psi_A(1), x_A(0) = x_A(1).$$

The Hamiltonian of this optimal control problem is given by

$$H_A = \psi_A u + \beta_A u_A^2.$$

According to the Pontryagin's maximum principle, the optimal control is achieved for u , for which the Hamiltonian has its minimum. This gives

$$u_A = x' = -\frac{\psi_A}{2\beta_A}.$$

We substitute the value of u_A to obtain

$$x'_A = -\frac{\psi_A}{2\beta_A}, \psi'_A = -\frac{\sigma(\alpha_A - \lambda_2 \gamma_A (\sin 2\pi t + 1))}{\cosh^2 \sigma x_A} + \delta_A \xi \sinh \xi x_A$$

The above boundary value problem should be solved for a fixed value of λ_2 ; its actual value can be found under condition $s = C_2$. As a result, the optimal trajectory becomes a function of the constant C_2 , i.e. $x_A(t, C_2)$.

The second optimization problem (maximization of p) is equivalent to to maximization of the functional L , or minimization of $-L$.

We introduce a new Lagrange multiplier λ_3 , corresponding to the constraint $q = C_3$. We need to find the minimum of the Lagrange function $-L + \lambda_3 q$. We implement Pontryagin's maximum principle and obtain (omitting some calculations) that the optimal trajectory is determined as the solution of the following boundary value problem

$$x'_J = -\frac{\psi_J}{2\beta_J}, \psi'_J = -\frac{\sigma(\alpha_J - \lambda_3 \gamma_J (\sin 2\pi t + 1))}{\cosh^2 \sigma x_J} + \delta_J \xi \sinh \xi x_J$$

with

$$\psi_J(0) = \psi_J(1), x_J(0) = x_J(1).$$

The above boundary value problem should be solved for a fixed value of λ_3 ; its actual value can be found under condition $q = C_3$. As a result, the optimal trajectory becomes a function of the constant C_3 , i.e. $x_J(t, C_3)$.

Finally, the obtained optimal trajectories $x_A(t, C_2)$ and $x_J(t, C_3)$ should be substituted in the expression for the fitness (3.16). We get

$$f(C_2, C_3) = -C_2 - p(C_3) - C_3 + \sqrt{4b_0(C_2)p(C_3) + (p(C_3) + C_3 - C_2)^2}.$$

Now the unknown values of C_2 and C_3 can be derived as the point of the global maximum of f ; this can be done numerically using any standard method (e.g. gradient descent).

For all above problems, numerical computation has been done using MATLAB.

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7. FIGURE CAPTIONS

1. Optimal trajectories $x(t)$ of DVM obtained in Model 1. (A) The dependence of $x(t)$ on the amount of predator γ : a decrease in γ results in an attenuation of the migration amplitude and an increase of the average depth. Curves 1-5 are constructed for $\gamma=1, \gamma=0.8, \gamma=0.6, \gamma=0.4, \gamma=0.3$, respectively, $\beta=0.04$. (B) The dependence of $x(t)$ on the metabolic cost of migration described by β : a high cost of migration results in a disappearance of DVM. Curves 1-5 are constructed for $\beta=0.005, \beta=0.01, \beta=0.03, \beta=0.07, \beta=0.15$, respectively, $\gamma=0.8$. The other model parameters are $\alpha=1, \sigma=1, \delta=0.1$ and $\xi=1$.

2. Optimal trajectories $x(t)$ of DVM obtained in Model 2. (A) The dependence of $x(t)$ on the minimal fitness threshold I_0 : a decrease in I_0 results in an attenuation of the DVM amplitude and an increase in the average depth. Curves 1-5 are constructed for $I_0=0.7, I_0=1.15, I_0=1.5, I_0=1.95, I_0=2.15$, respectively, $\beta=0.03$. (B) The dependence of $x(t)$ on the metabolic cost of migration described by β : a high cost of migration results in a disappearance of DVM. The curves 1-5 are constructed for $\beta=0.005, \beta=0.01, \beta=0.03, \beta=0.07, \beta=0.15$, respectively, $I_0=1.5$. The other model parameters are $\alpha=1, \sigma=1, \delta=0.1$ and $\xi=1$.

3. Optimal trajectories $x(t)$ of DVM obtained in Model 3. The figure shows the dependence of $x(t)$ on the metabolic cost of migration described by β : a high cost of migration results in the disappearance of DVM. Curves 1-5 are constructed for $\beta=0.005, \beta=0.01, \beta=0.03, \beta=0.07, \beta=0.15$, respectively. The other model parameters are $\alpha=1, \sigma=1, \delta=0.1$ and $\xi=1$.

4. Optimal trajectories $x(t)$ of DVM obtained in Model 4 for adults (A) and juveniles (B). The figure shows the dependence of $x(t)$ on the metabolic cost of migration described by β_A and β_B . One can see a discontinuous change in the optimal trajectories for adults at high values of β (curve 5 in (A)). The curves 1-5 are constructed for $\beta_A=0.01, \beta_A=0.03, \beta_A=0.07, \beta_A=0.1$ and $\beta_A=0.15$. The other model parameters are $\alpha_A=10, \alpha_J=1.1, \gamma_A=0.8, \gamma_J=0.8, \beta_J=\beta_A/5, \delta_A=0.1, \delta_J=0.1, \sigma=1, \xi=1, \eta=1/20, K=0.5$ and $\epsilon_A=3$.

5. The dependence of DVM in the models on the amount of the available food α . (A) Model 1, curves 1-4 are constructed for $\alpha=0.7, \alpha=1.0, \alpha=1.5, \alpha=2.0$, respectively, $\gamma=0.7$. (B) Model 2, curves 1-4 are constructed for $\alpha=0.7, \alpha=1.0, \alpha=1.5, \alpha=2$, respectively, $I_0=1$. (C) Model 3, curves 1-4 are constructed for $\alpha=0.3, \alpha=0.7, \alpha=1.0, \alpha=1.5, \alpha=2.0$, respectively. The other parameters are the same for all models: $\beta=0.01, \sigma=1, \delta=0.1$ and $\xi=1$.

6. The dependence of DVM in the two-stage Model 4 on the amount of the available food α_A for adults (A) and juveniles (B). One can see a discontinuous change in the optimal trajectories for adults at high values of α (curves 4 and 5 in (A)). The curves 1-5 are constructed for $\alpha_A=3, \alpha_A=7, \alpha_A=15, \alpha_A=17$ and $\beta_A=20$. The other model parameters are $\alpha_J=1.1, \beta_A=0.05, \beta_J=\beta_A/5, \gamma_A=0.8, \gamma_J=0.8, \delta_A=0.1, \delta_J=0.1, \sigma=1, \xi=1, \eta=1/20, K=0.5$ and $\epsilon_A=3$.

7. Evolution of the genotypes in the space of strategies in Model 1 in the case of mutagenesis. Strong mutagenesis (A-C) does not result into selection: all strategies with non-zero initial densities can coexist for an infinitely long period of time. Weak mutagenesis (D-E) eventually results in selection of an optimal strategy and other strategies having a large distance from the optimal strategy go extinct. The model parameters are $\alpha = 1.0$, $\gamma = 0.8$, $\beta = 0.01$, $\sigma = 1$, $\delta = 0.1$ and $\xi = 1$. In each column the graphs are constructed for $t_1 = 10$, $t_2 = 100$, $t_3 = 1000$.

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(A)

(B)

Figure 1

(A)

(B)

Figure 2

Figure 3

(A)

(B)

Figure 4

(A)

(B)

(C)

Figure 5

(A)

(B)

Figure 6

Figure 7

Figure 7