

Recognition of patterns of optimal diel vertical migration of zooplankton using neural networks

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Abstract—Here we apply artificial neural networks to facilitate recognition of regular diel vertical migrations (DVM) of zooplankton in the ocean and lakes, the phenomenon which is considered to be the most significant synchronous biomass movement on Earth. The underlying mathematical framework of finding the optimal (i.e. evolutionarily stable) strategies of DVM of zooplankton is based on the generic idea of maximization of fitness of many competing subpopulations each of which uses a particular strategy. To be able to recognize patterns of DVM from data, we have created novel software which technically consists of two interconnected complexes. The first complex is required to find the evolutionarily stable behaviour using the principle of optimality and its implementation produces training samples for the neural network. The second complex provides recognition of evolutionarily stable DVM taking into account a few key characteristics of the aquatic environment and this also allows for some uncertainty (only partial information available) in the input data. In our work, we use a four-layer neural network. Extensive testing of our method demonstrates its efficiency in revealing the presence of detectable regular DVMs as opposed to a random vertical movement of zooplankton.

Index Terms—zooplankton, diel vertical migration, evolutionarily stable strategy, fitness, calculus of variations, recognition, neural network, learning, training set.

I. INTRODUCTION

Methods of patterns recognition and neural networks technologies are now widely implemented in various research areas (see [1] for a short review), in particular, in life sciences, and an important current application area is the recognition of evolutionarily stable behaviour of living organisms.

In evolutionary biology, we are generally interested in determining a certain behavioural strategy (or a life trait) that would persist within the population (community) under given environmental conditions for a relatively long period of time [2]. Such a strategy would persist in the population even if some mutants with other different behavioural strategies are occasionally introduced: in this case, the strategy is called evolutionarily stable. The knowledge of an evolutionarily stable strategy in the biological system generally allows us to understand and predict outcomes of long-term biological evolution.

Darwin's idea of "survival of the fittest" is often used as the methodological basis for predicting evolutionarily stable strategies in various biological systems [3]. This idea suggests,

in particular, that the strategy remaining in the population after a long time is the one that should have the highest fitness. This paradigm is often used to formulate different variational principles in mathematical modelling in biology [4]–[9], which eventually allow us to derive equations predicting optimal behaviours in a similar way as fundamental equations of motion in theoretical mechanics can be obtained from Euler-Lagrange's variational principles.

To practically implement the fundamental idea of Darwin, it is necessary to be able to compare the values of fitness of different hereditary strategies with each other and to numerically express fitness as a functional of hereditary strategies. Proceeding in this way, we first need to select some key characteristics of hereditary strategies that determine fitness. For example, this may be the reproduction or mortality rates of species depending on the biotic or/and abiotic factors. Each hereditary strategy will determine a set of life traits under given environmental conditions. Then, it is necessary to find a fitness function that would link all significant characteristics based on available information on long-term population dynamics. The above concept of fitness reflects the selective advantages of each hereditary strategy within the population. Thus, predicting the evolutionarily stable strategy consists of finding the optimal fitness (e.g. by using calculus of variations or other methods) for the abiotic/biotic parameters describing the environment.

However, our available information about environmental factors often contains uncertainty, for example, we are not aware of accurate instantaneous spatial distributions of temperature, predators, food, light, etc. Moreover, there can always be effects of stochasticity due to both external and internal factors which would cause fluctuations in the individual behaviour. Therefore, it is more important to find some key qualitative characteristics of a strategy rather than its precise quantitative description. On the other hand, such key qualitative characteristics of an optimal strategy will be determined by the environment (we assume that after long-term evolution the observed strategy becomes optimal). Thus, the second problem consists in recognition of qualitative characteristics of the evolutionarily stable strategy in the given environment. To tackle this problem, we may use pattern recognition algorithms and artificial neural networks. Obviously, the implementation

of neural networks requires their initial training which can be done using patterns of optimal behaviour predicted via optimization procedure in population dynamics models. Then we can use the existing efficient neural networks algorithms to solve the problem of qualitative characteristics recognition of patterns in biological systems [10]–[13].

In this study, we implement artificial neural networks to a particularly important problem of recognition of patterns of evolutionarily stable diel vertical migrations (DVM) of zooplankton in the ocean and lakes.

II. DIEL VERTICAL MIGRATION OF ZOOPLANKTON

The phenomenon of diel vertical movements of aquatic organisms was discovered almost two hundred years ago [4], [14], [15] and it consists of regular ascending and descending of zooplankton in the water column. Diel vertical movements of zooplankton play an important role in the dynamics of the organic matter of the ocean, they are the most significant synchronous movement of biomass on Earth [15], [16] and can potentially have an influence on the planet climate [17], [18]. Identifying the causes and mechanisms of DVM is an important problem in modern ecology. The study of zooplankton migration is also significant for the fishing industry.

The effect of diel vertical movements of zooplankton has been studied by many scientists both empirically and theoretically. Various mathematical models of DVM were considered in the literature, however many aspects of this phenomenon are still poorly understood [19]–[27]. In particular, this is due to the wide variety of patterns of DVM observed in nature [4].

Mathematical models and empirical data suggest that the evolutionary stable movement of plankton is determined by various environmental factors: spatial distributions across the depth x of food $E(x)$, predator density $S_x(x)$, temperature $G(x)$, radiation level, the overall predator activity $S(t)$ during the day, etc. [4], [19]–[24]. All of these factors can be considered as mathematical functions of the vertical coordinate x (measured in meters) or time of day t (measured as a fraction of the day).

The complexity of the problem of identifying the evolutionarily stable DVM is aggravated by the inaccuracy of environmental knowledge of the above functions and stochasticity of different nature. From this point of view, determining the qualitative characteristics of DVM is more important than finding the exact mode of oscillations. For example, it may be the presence or absence of detectable vertical oscillations against the background of random movements of individuals. It is known that some species of zooplankton carry out detectable vertical movements, but for others, this is not typical [4]. In addition, certain species of zooplankton make detectable movements only when they reach a certain age. Some recent results of the long-term observations of DVM are available on <http://www.oceannetworks.ca/zap-data-saanich-inlet> and <http://hdl.handle.net/1828/4630>.

The purpose of this work is to propose a methodology of recognizing the evolutionarily stable DVM, in particular,

reporting the presence or absence of detectable vertical movements of organisms using partial information on the observable environmental conditions as input data.

III. METHODOLOGY

The first step in our methodology is constructing and maximizing population fitness using a suitable theoretical model. Deriving fitness in population models is based on considering long-term dynamics of the population density distribution in the space of hereditary strategies [7], [9], [28], [29], [31]. The construction of fitness implements the so-called ranking order reflecting selective advantages of strategies in the considered space of strategies [9], [29], [31]. Below we provide a brief description of the framework (for more details see [31]).

Consider v to be a hereditary strategy from some set V of hereditary strategies of the population; $\rho(v, t)$ is the number of individuals realizing strategy v or the density distribution of population over V ; $\rho'(v, t)$ - rate of change of $\rho(v, t)$ over time. Then fitness $J(v)$ has the following form

$$J(v) = \lim_{T \rightarrow \infty} \frac{1}{T} \int_0^T \frac{\rho'(v, t)}{\rho(v, t)} dt \equiv \left\langle \frac{\rho'(v)}{\rho(v)} \right\rangle$$

or we can use any other function equivalent to $J(v)$.

Note that fitness can be expressed analytically for a number of relevant population models (Verhulst, von Foerster, Volterra, etc.), determining the dynamics of the zooplankton population [8], [9], [30], [31]. For example, consider the following equation of population dynamics

$$\rho' = k(v)\rho - \rho R(v)P(t). \quad (1)$$

where $k(v)$ is the reproduction coefficient corresponding strategy v , P is the result of the action of some limiting factors (predators, interspecific competition, etc.) on the population, $R(v)$ is the degree of the influence of the limiting factors. In this model, k and R are the main significant characteristics of strategy v . It is easy to show [31] that in (1) fitness is given by

$$J(v) \sim k(v)/R(v). \quad (2)$$

Consider x as the vertical coordinate of the position of zooplankton; t is the time of day varying from 0 to 1; $v = x(t)$ is the hereditary strategy of plankton behaviour, $V = C_1[0, 1]$ is the set of continuously differentiable functions on the segment $[0, 1]$, satisfying condition $x(0) = x(1)$, $v \in V$; $E(x)$ is the amount of food depending on the depth; $S(x, t) = S_x(x)S_t(t)$ is the effect of a predator depending on the depth and time of day, $G(x)$ is the temperature distribution depending on the depth. In this case

$$k(v) = \int_0^1 (\alpha E(x) - \gamma S(x) - \beta(x')^2 - \delta G(x)) dt. \quad (3)$$

Here we assume that the energetic cost of the vertical movement is proportional to the square of its velocity $x'(t)$. The weighting coefficients $\alpha, \gamma, \beta, \delta$ quantify the relative contribution of the corresponding environmental factors.

However, fitness function J can also be directly constructed by observing the selection processes taking place in the system under certain conditions (e.g. via long-term time series).

In this work, we developed an algorithm for the approximate construction of fitness as a function of the model parameters which are determined by a strategy. We can observe long-term dynamics $\rho(v_i, t)$ for some hereditary strategies v_1, \dots, v_n with known values of corresponding significant characteristics, then approximately calculate $J(v_i) = \langle \rho'(v_i) / \rho(v_i) \rangle$. Comparing them with each other allows us to introduce ranking order in the set of strategies (and their corresponding significant characteristics). If this order does not change with initial condition changing, then we can introduce a function of these characteristics reflecting the order. This function is an approximation of fitness. It is most convenient to find this function in the class of linear or quadratic functions. The resulting function is actually Taylor's approximation of fitness.

For example, assume $k(v_i)$ and $R(v_i)$ to be the only parameters determined by competing strategies $v_i, i = \overline{1, n}$. We can approximate fitness by, for example, a quadratic function F of k and $1/R$:

$$F(k, 1/R) = \lambda_1 k + \lambda_2 / R + \lambda_{11} k^2 + \lambda_{12} k / R + \lambda_{22} / R^2.$$

In the case where we know (from either a mathematical model or some empirical time series) that $J(v_i) > J(v_j)$, then we should take coefficients to satisfy the inequality

$$\begin{aligned} & \lambda_1 k_i + \lambda_2 / R_i + \lambda_{11} k_i^2 + \lambda_{12} k_i / R_i + \lambda_{22} / R_i^2 > \\ & > \lambda_1 k_j + \lambda_2 / R_j + \lambda_{11} k_j^2 + \lambda_{12} k_j / R_j + \lambda_{22} / R_j^2. \end{aligned}$$

Thus the problem of the fitness approximation is reduced to solving the system of linear inequalities with respect to coefficients λ .

As an illustrative example, we apply the above algorithm to model (1). We considered six and nine different strategies and corresponding values of k and R . We simulated the dynamics of a number of individuals realizing these strategies and calculated $J(v_i)$. Then we solved the system of linear inequalities. As a result we obtained $\lambda_1 \approx \lambda_2 \approx \lambda_{11} \approx \lambda_{22} \approx 0$; $\lambda_{12} \approx 1$. The result almost coincides with (2). The approach can be also used to find a priory unknown coefficients $\alpha, \gamma, \beta, \delta$ in (3).

In the case where the fitness function is known, it is possible to find the evolutionary stable behaviour by methods of calculus of variations or the optimal control theory. The fitness function will be considered as the objective functional [8], [9].

For some cases, it is analytically possible to solve the corresponding problem of calculus of variation. For example, consider the model (1), (3) with $E(x) = x + C$, $S_x(x) = x + C$, $G = -(x + C/2)^2$, where C is a constant; $S_t(t) = \cos 2\pi t + 1$, $R(v) = 1$. One can prove that the optimal strategy is given by

$$x = A + B \cos 2\pi t; A = \frac{\alpha - \delta C - \gamma}{2\delta}; B = \frac{-\gamma}{8\beta\pi^2 + 2\delta}.$$

This result can be used as a test to check the accuracy of the approximation of fitness.

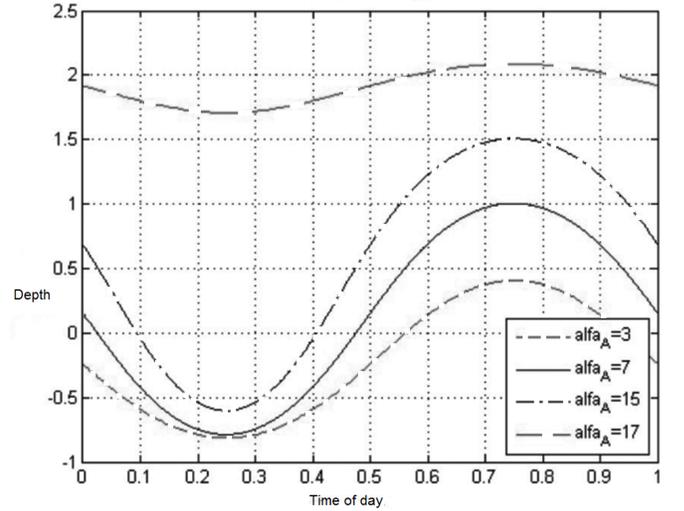


Fig. 1. Various patterns of zooplankton vertical migrations for different values of impact of the food factor ($\text{alfa}_A = \alpha$).

The numerically obtained solution can be analyzed with respect to the presence of an important qualitative feature: the appearance of detectable vertical migrations against the background of random interference. For this, a threshold value of the oscillation amplitude is set and the range of depth variation in the found strategies is compared with it.

For example, the graphs in fig. 1 show different behaviour of optimal curves of DVM obtained as a solution of the variational problem for different values of parameter α (fig.2, $\text{alfa}_A = \alpha$). If the threshold value is equal to 1 (meter), then we have detectable vertical migrations for $\alpha = 7, \alpha = 15, \alpha = 17$ and we have not them for $\alpha = 3$.

The second important step is to recognize the presence or absence of detectable DVM on the base of the approximate characteristics of the environment. In this case, the key characteristics of the environment (the amount of food, the predator pressure depending on the depth and the time of day) are not specified precisely. Only the ranges of their values are known for a discrete set of arguments corresponding to the location of the sensors registering these quantities.

To cope with this challenge, a learning multilayered neural network was implemented and we used previous patterns of optimal DVM as a training sample. Based on the recognition, each considered case was assigned to one of two classes of images - the absence or the presence of detectable vertical movement corresponding to predicted evolutionarily stable DVM.

IV. SOFTWARE IMPLEMENTATION

The software for recognition of evolutionarily stable vertical migrations of zooplankton was developed as a system of two interconnected complexes. The first complex provides the possibility of calculating the evolutionarily stable movement for the given exact functions describing the environment. The second complex allows one to recognize the presence or

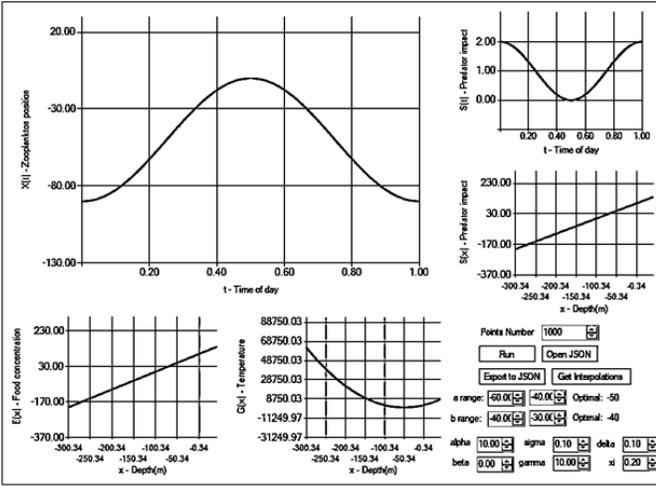


Fig. 2. The result of the numerical solution of the variational problem for the test case.

absence of oscillations of zooplankton using only approximate characteristics of the environment.

The first software complex uses as its input, analytical functions describing the current state of the environment (vertical profiles of food and predator, predator activity, the temperature, etc) or the input of arrays of their values corresponding to a discrete set of arguments. The input data are visualized. Experimental values are given in tabular form (as discrete sets of input functions values). This data is interpolated. This data set can be quickly corrected by a visual display of the interpolation function graph on the screen. As a result simulation, the theoretical optimal trajectory of DVM can be constructed.

The efficiency of the first complex was checked using the above test case. The outcome is shown in fig. 2 constructed for $\alpha = 10, \gamma = 10, \beta = 0.01, \delta = 0.1$. One can see that the numerical result coincides with the corresponding analytical result.

We can compare our results with some empirical data. For example, in accordance with the recent data provided at <http://www.oceanetworks.ca/zap-data-saanich-inlet>, zooplankton were located at a depth of 10 meters for one-half day and at a depth of 100 meters for the second half of the day. If we expand the depth function in a Fourier series and take into account the first two terms, we get the following harmonic approximation $x = -55 - 70 \cos 2\pi t$. In accordance with [19], the amount of food $E(x)$ varies from 20 in the upper water layers ($x = -10m$) to 0 in the lower ($x = -100m$), the predator pressure $S_x(x)$ varies from 70 to 0, respectively. We use a linear approximation of these quantities and a quadratic approximation of negative factors $G(x) = -(x - 50)^2$ when approaching the border. If $\alpha = 100\Delta = 0.1, \beta = 0.001, \gamma = 29$, then we numerically get the following solution $x = -51.5 - 72.7 \cos 2\pi t$. This is in a good agreement with the Fourier approximation of real behaviour.

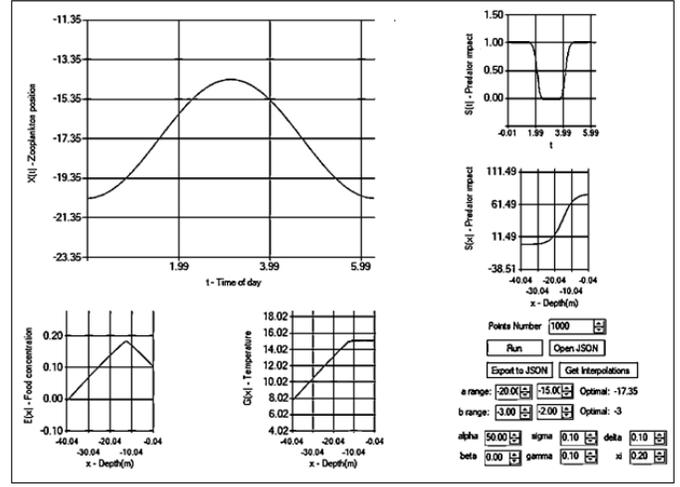


Fig. 3. The input data of the food, predator and temperature distribution, predator activity and the result of the numerical solution.

Then we used some other empirical data on the food, predator and the temperature distribution from [19], data on the predator activity according to [4]. The input data and result are shown in fig. 3.

The base of samples was created using the results of the work of the first software complex. It contains exact solutions to the problem of finding evolutionally stable behaviour. They are used further as training samples. A training sample is formed as follows: a series of four functions of the environment is specified, the optimal migration is found and then the amplitude of the found oscillations is compared with a predetermined threshold value. If the amplitude is greater than the threshold, then this precedent is considered as a case of the presence of the detectable oscillation. If the amplitude is less than the threshold, it is considered that the oscillation is not detectable against the background of constant random noise. Each series of the four external factors is assigned the logical value of "yes/no" – the presence/absence of detectable oscillations. Accordingly, the series of the four external factors are divided into two non-intersecting classes.

The second software complex is the multilayer neural network. The four-layer neural network is built using the Keras library software (<https://keras.io/>) on the Python Tensorflow framework (www.tensorflow.org).

The input data for the second complex is a discrete set of values of four external functions of the environment state. First of all, the glueing of four arrays corresponding to four input functions is carried out. Then, to use the Keras library software, the input array is converted into a list of the Numpy library format (feature vector).

At first, the input list passes through two convolution layers, after that the max-pooling is applied to reduce dimensionality (see fig. 4). Finally, the fully-connected layer is applied to obtain the resulting value that will be compared with the threshold. The output information of the second complex is the answer regarding the presence/absence of DVM under the

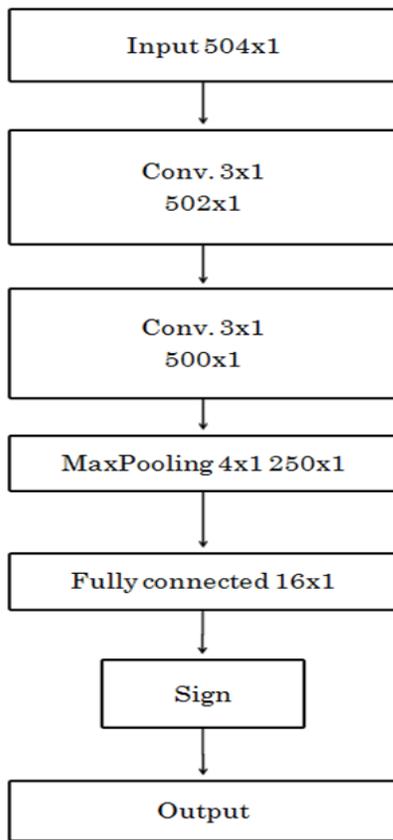


Fig. 4. The architectur of the neural network.

given environmental conditions.

We found that the main difficulty of the implementation of the method consists in teaching the network. The current accuracy is estimated as the proportion of correctly guessed answers from the training set. To improve the settings, the Adam optimizer of Keras library with Cross Entropy loss is used. It is possible to replenish the base of comparison samples adding information about new precedents.

The work of the network was checked for some test cases. For example, we took $E(x) = \tanh(x) + 1$; $S_x(x) = \tanh(x) + 1$; $S_t(t) = \sin(2\pi t) + 1$; $G(x) = -\cosh(x)$; the threshold value 1. In this case, we got the following results:

$$\alpha = 0.7, \beta = 0.01, \gamma = 0.7, \delta = 0.1 \rightarrow NO;$$

$$\alpha = 1, \beta = 0.01, \gamma = 0.7, \delta = 0.1 \rightarrow NO;$$

$$\alpha = 1.5, \beta = 0.01, \gamma = 0.7, \delta = 0.1 \rightarrow YES;$$

$$\alpha = 2, \beta = 0.01, \gamma = 0.7, \delta = 0.1 \rightarrow YES;$$

$$\alpha = 1, \beta = 0.005, \gamma = 0.8, \delta = 0.1 \rightarrow YES;$$

$$\alpha = 1, \beta = 0.01, \gamma = 0.8, \delta = 0.1 \rightarrow YES;$$

$$\alpha = 1, \beta = 0.03, \gamma = 0.8, \delta = 0.1 \rightarrow NO;$$

$$\alpha = 1, \beta = 0.07, \gamma = 0.8, \delta = 0.1 \rightarrow NO.$$

The above results show the report on the absence/presence of DVM provided by the first complex. Then we took functions $E(x)$, $S_x(x)$ and $G(x)$ with accordance to [19], function $St(t)$ with accordance to [4] and the threshold value of DVM of 3m. In this case, we got the following results:

$$\alpha = 50, \beta = 0.001, \gamma = 0.1, \delta = 0.1 \rightarrow YES;$$

$$\alpha = 10, \beta = 0.001, \gamma = 0.5, \delta = 100 \rightarrow YES;$$

$$\alpha = 10, \beta = 0.001, \gamma = 50, \delta = 0.5 \rightarrow NO;$$

$$\alpha = 10, \beta = 0.001, \gamma = 100, \delta = 0.1 \rightarrow NO;$$

$$\alpha = 1, \beta = 0.001, \gamma = 1000, \delta = 0.1 \rightarrow NO;$$

In the above outcomes, we can see a mistake in the third example (line) because the observed amplitude of DVM is equal to 3.1m. However, the difference between the threshold and the observed amplitude is relatively small. This is the actual cause of the mistake.

SHORT SUMMARY

In this study, we develop a novel method and software to explore evolutionary stable strategies of diel vertical migration (DVM) of zooplankton. The method combines the theoretical approach to reveal evolutionary fitness in models and the computational approach using artificial neural networks to recognize the presence or absence of detectable DVM based on the existing base of reference samples. Our straightforward tests of the new software demonstrated great potential of the proposed methodology in revealing DVM in the case of partial information about environmental conditions.

As future extensions, we are planning to analyse a large number of empirical cases of DVM and include more complicated theoretical models of zooplankton population growth to better train neural networks.

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