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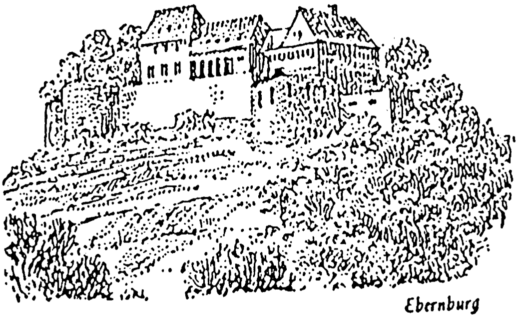

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Contents

Interaction Analysis and Stability Concept as a means for Understanding Complex Systems-Application to Vertical Migration of Zooplankton

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Zusammenfassung. Die Vertikalwanderung von Zooplankton stellt ein recht komplexes Phänomen dar, bei dem verschiedenartige physiologische und ökologische Bedingungen gleichermaßen eine wichtige Rolle zu spielen scheinen. Es wird gezeigt, wie die empirischen Befunde und möglichen Determinanten dieses Verhaltens eine Reihe von Modellansätzen zu deren Untersuchung nahelegen. Es zeigt sich, daß ein umfassender Ansatz letzlich auf evolutionäre Gesichtspunkte führen muß. Dieser basiert auf einer Interaktionsanalyse und der Anwendung von Methoden der Evolutionären Spieltheorie.

Summary. Vertical migration in zooplankton species is a phenomenon of considerable complexity, since many different physiological and ecological aspects appear to be of importance. It is shown how experimental findings and possible determinants of this behaviour lead to a succession of approaches to analyse and understand this behaviour. It turns out that a comprehensive discussion becomes feasible from an evolutionary point of view, applying methods of evolutionary game theory.

1. Introduction: Some facts and implications on vertical migration

Diurnal vertical migration is observed in many marine and freshwater zooplankton species (e.g. Daphnia). At sunrise, they start leaving the upper water layers where they have been feeding during the night, and remain in considerable dephts until dusk, when they ascend again for the night. There are also other species, even closely related ones living at the same place, that do not migrate (see e.g. [6]).

This behaviour has puzzled limnologists since long and many facts have been gathered from observations and experiments. It is known that many zooplankton species feed on phytoplankton (green algae) and suffer from predation by visual hunters (fish). With respect to these facts, upper water layers provide good feeding conditions on the one hand, whereas there is practically no visibility even during daytime in the deeper layers on the other hand. Also, temperature differs between layers, with considerable effect on zooplankton development rates and offspring production. Low temperatures reduce metabolic turnover and prolong egg production and release intervals.

Thus, questions arose for the reasons and determinants that make zooplankton leave rich food sources during the day. If it is predator evasion, what makes some species remain stationary (and feed fish instead)? Are there metabolic or demographic reasons, effects of density regulation? What does coexistence of migrating and stationary populations tell us? Which among several conceivable determinants are predominant?

In the past, mainly mono-causal explanations have been tested and discussed (see references in [3]). An attempt to analyse the significance of the various known effects in a comprehensive, albeit complex, system has recently been made by Gabriel and Thomas ([1]). By means of a modelling and analysis technique from evolutionary game theory (see [5] for an introduction) they derived an understanding of vertical migration as an adaptive character in a complex setting of physiological constraints and selective forces.

It is the intention of this paper to demonstrate how the analysis of the zooplankton system and the questions posed by limnologists quite naturally lead to an approach based on interaction models and evolutionary stability analysis. Whereas primary results of the model have been described elsewhere ([1],[2]), the companion paper ([3]) demonstrates the usefulness of this type of model as a tool for deriving testable predictions and a ranking of causes.

2. Descriptive models: Migrating individuals

Vertical migration (v.m.) is a periodical event, and since it is known that the descent can be triggered as a phototactical reaction in migrating species, it is easy to design a stochastic, random walk type of model for individual migration behaviour. With a time dependent probability p_t, giving the tendency for an individual to descend (and $1-p_t$ to ascend, resp.) for another unit of depth, periodicity of movement can easily be generated by a 24-hour periodic p_t. Being somewhat more elaborate, $p_t(d)$ might reflect periodic light conditions as experienced in different depths d. Trivial (depth > 0) and physiological (maximal depth) constraints will have to be incorporated to reconstruct a given pattern of zooplankton density distribution over various depths as measured at different times of a day/night cycle.

From this, the answer to the questions of vertical migration is mainly that, yes, v.m. is a direct response to light conditions - with a possible alternative interpretation introducing light as a key for (visibility dependent) predation pressure. Posed as an inverse problem, experimental data could be used to derive estimate values for the individual migration tendency and to obtain some further intricate information about $p_t(d)$. Note however that not much is really known empirically about the *individual* migration behaviour.

3. Optimization models: Problem solving individuals

The migrating individual model does not address questions that are typically related to food availability, temperature, retarding development conditions, metabolic costs and the like. Nor does it consider the diversity of migrating and non-migrating populations. Given an idea about their interrelations, a compound parameter, or function, as $p_t(d)$ above could be derived to incorporate these effects explicitly, which makes it a model with a lot more independent parameters to be adjusted.

Alternatively, such a relation between counter-effective parameters can be used directly to understand v.m. as a solution to an optimization problem, e.g. minimizing visibility - and thus, predation pressure - subject to the constraints given by food availability, metabolic costs etc. Here, the results may well give more detailed answers to why diel vertical migration occurrs and what the relevance of the different parameters is. Moreover, it may explain why some populations migrate and others don't: for a given population constraints might not leave room for any minimization. Still, the model strongly focusses on predation avoidance as the main cause.

4. Optimization models: Optimizing natural selection

Another, even more refined approach leads to an optimization model as typically considered in behavioural ecology (see [4] for an introduction) and already introduces adaptive aspects of v.m.

Here, it is assumed that a common measurement can be found that relates such diverse issues as food availability, temperature, visibility etc. in an appropriate magnitude. A widely used measure in behavioural ecology is in terms of energy (cost or gain), implying that optimizing the energy balance means optimal survival conditions. So far, however, the effects of food-to-egg conversion and prolonged egg development and release times have not been included. If they are to be included "energy" might be a poor concept. The measure must rather be related to something like the reproductive output, which is open to incorporate egg production as well as developmental and metabolic conditions as well as predation risk.

The answers obtained from this approach now attains a different flavour. Vertical migration is no longer explained as a mere response to one cause, e.g. minimizing predation - physiological constraints being included or not. Rather, the understanding is that the migration behaviour optimizes the reproductive output (or *fitness)* and thus is a feature of an optimal phenotype that has evolved under the given conditions. This might include predator avoidance as a side result for one population but may as well dictate for another one to stay at richer food sources and benefit from shorter egg development times instead.

5. Models from evolutionary game theory: Interaction and stability

Given certain physiological and ecological conditions, the "performance" or fitness of a phenotype may also depend on how other members of the population behave. Vertical migration might be an optimal solution for an individual in a non-migrating population but might become a poor strategy if all do v.m. Likewise, coexistence of stationary and migratory populations add a new flavour to the mere optimality consideration. That is, optimality might not be an appropriate concept if e.g. competition and other types of direct or indirect interaction among individuals have to be considered. A trait being optimal when rare might become disadvantageous with increasing frequency in the population.

Here evolutionary game theory introduces the concept of *evolutionary stability* instead, which in some sense means that a trait or behaviour must be optimal given that all or almost all individuals behave this way. More generally, evolutionary game theory provides a method to analyse questions of the type raised for the migration complex, which can be outlined in 4 steps:
(i) Specify a model of the interactions, leaving room for different alternatives of behaviour (*strategies* in a formal sense) and including all the elements that are felt to be important for the system.
(ii) Specify a set of strategies that represent behavioural alternatives in the interaction model.
(iii) In terms of a suitable measure (formally called *payoff*) evaluate competing strategies with respect to the interaction. This is very much like setting up a strategic model in (economic) game theory but might be much more involved (see e.g. [7]). Also there is no need to provide a global optimality criterion.
(iv) Instead, a formal criterion is applied to identify *evolutionarily stable strategies* (ESS) or population mixtures (ES states).

In the following we will shortly present a model of the ESS-theoretical type which incorporates the necessary complexity as arising from the zooplankton system and reflects the limnologists' questions. It includes:

- Daily period governed by the light cycle.
- Dynamics of food ressources available at upper water level.
- Predation pressure in upper layers, possibly depending on zooplankton density.
- Food competition among zooplankton.
- Temperature (and thus depth) dependent rates of metabolic turnover, development, egg production and release intervals.
- Main behavioural alternatives (migrating vs stationary).

The shortest reasonable period over which interacting strategies will have to be considered is a 24-hour interval, taken as time unit and divided into a dark and a light phase of length T_n and $(1-T_n)$, resp. The evaluation of strategies (payoff) will be in terms of food converted to successfully released eggs per time unit, and allows for a separation of contributions during night and day phase:

$$F = F^n + F^d$$

The essential contributions to F are derived from individual food uptake during either phase and the total loss of converted food in case of predation. These of course differ with light conditions, i.e. with day and night as well as water depth.

In [1] algal growth dynamics and grazing activities of the zooplankton have been modelled and terms for the total food uptake per animal during daylight a_d and nighttime a_n have been derived explicitly. Conversion of food uptake into hatching eggs is expressed by a parameter β which mainly reflects the fact that food is also needed for metabolism and somatic growth. Obviously, β depends on temperature, and thus changes with water conditions as particularly experienced by migrating individuals. The model also takes into account temperature- (or depth-) dependent egg release intervals t by deriving a suitable normalization factor w.

Finally predation during the day phase in the upper water layer is assumed to occur with (possibly density dependent) probability p. In case of predation the loss is calculated from the material already stored in eggs and in the ovaries since the last molting (release of juveniles).

We consider a single population model with two possible strategies, reflecting stationary (near water surface) and vertical migration behaviour (maximum depth during day; surface level during night). Let their relative frequencies be represented by $x=(x_s, x_v)$, $x_v=1-x_s$. Then strategy dependence of the terms introduced above will become explicit and interactions will be found in the fact that the effect and success of grazing depends on the number of feeding zooplankter (food competition). Hence $a_d=a_d(x)$, $a_n=a_n(x)$ incorporating night length T_n as another important parameter. Also, predation risk p may depend on the abundance of zooplankton in the upper layer, which implicitly introduces further interaction of zooplankton phenotypes. (The relevant formulae of the model are explicitly mentioned in the companion paper [3].)

We finally arrive at payoff terms for the two strategies considered:

$$F_s(x) = \beta_s a_n(x) + (1-p(x))\, \beta_s a_d(x) - 1.5 p(x) (a_n(x) + a_d(x)) \beta_s t_s$$

$$F_v(x) = \beta_v a_n(x) w_{v,s}$$

where the first term gives the night phase contribution. Note that for strategy v we set the contribution during the day phase to zero.

F_s and F_v , or the difference $\Delta F = F_s - F_v$, can now be subjected to the criteria of evolutionary stability to find out which strategy, or strategy mix, might be evolutionarily stable under what conditions. Here, the general criteria simply yield

s is an ESS if $\Delta F(x) > 0$ for $x_s = 1$.
v is an ESS if $\Delta F(x) < 0$ for $x_v = 1$.
A mixture $\hat{x}$ is an ES state if $\Delta F(\hat{x}) = 0$ and $\frac{d}{dx_s} \Delta F(\hat{x}) < 0$.

6. Results from stability analysis

Within this context vertical migration can be explained by assuming physiological and environmental conditions that make v an ESS, i.e. $\Delta F(x) < 0$ near $x_v = 1$. Evolutionary stability states that if v.m. is a behaviour commonly used in a population then an alternative strategy, i.e. non-migrating, is disadvantageous and will ultimately vanish from the scene.

Likewise, conditions might as well turn out to stabilize s , i.e. a non-migrating population. Finally, coexistence of fixed portions of migrating and stationary individuals could be explained by an evolutionarily stable x.

In fact, the model analysis in [1] showed that all three types of results can emerge, with conditions and parameters ranging within reasonable bounds. A typical "reasonable" parameter set was derived from the data of [6] on Daphnia populations in Lake Constance (W. Germany).

Parameter studies have also been conducted [2] showing the impact of particular conditions. From this, typical questions could be answered as to why zooplankton populations do or don't leave warm, rich food source layers in spite of predation and/or prolonged development times. Tolerance levels e.g. opposing predation pressure to metabolic and developmental factors have also been investigated. Further investigations concerning the predictive value of the model and a ranking of selective forces are presented in the companion paper [3].

We will not repeat these results here in detail, as the aim of this contribution was mainly to show how a complex of facts and the questions discussed by experimental biology can direct the modelling and analysis of the system gradually but almost inevitably towards an appropriate level. It appears that the evolutionary approach will probably be the ultimate level, given that facts and data reflect important, but rather diverse aspects of the system. Interaction analysis and stability considerations as suggested by evolutionary game theory appear to provide a method both powerful and flexible enough to make this a feasible approach.

References

[1] Gabriel, W. and B. Thomas, 1988a. Vertical migration of zooplankton as an evolutionarily stable strategy. Am. Nat. (in press).
[2] Gabriel, W. and B. Thomas, 1988b. The influence of food availability, predation risk and metabolic costs on the evolutionary stability of diel vertical migration in zooplankton. Verh. Internat. Verein Limnol. 23 (in press).
[3] Gabriel, W. and B. Thomas, 1988c. Predictive value of evolutionary game theory for vertical migration in zooplankton. (this volume).
[4] Krebs, J.R. and N.B. Davies, 1981. An introduction to behavioural ecology. Blackwell Scientific Publications, Oxford.
[5] Maynard Smith, J., 1982. Evolution and the theory of games. Cambridge University Press, Cambridge.
[6] Stich, H.-B. and W. Lampert, 1981. Predator evasion as an explanation of diurnal vertical migration by zooplankton. Nature 293: 396-398.
[7] Thomas, B., 1984. Evolutionary stability: States and strategies. Theor. Popul. Biol. 26:49-67.