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Models on diel vertical migration

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With 3 figures and 3 tables in the text

Abstract

To clarify what can be expected from models the role of modelling in the scientific process in relation to experiments and field studies is addressed. Hypotheses to explain vertical migration are reviewed with respect to the selection mechanism assumed; it is asked whether group selection instead of individual selection arguments are used explicitly or implicitly. Models which are formulated more precisely than verbal arguments are listed; one conceptual, evolutionary model (GABRIEL & THOMAS 1988) and one ecological simulation model (SCHEERER 1991) are discussed in detail. Perspectives and directions for improvements and further development of models are given.

Introduction

What makes models so fashionable? What are the essential differences between models and experiments? In which respect can models be wrong? Such questions will be asked in the first chapter to give a framework for judgement of principal potentials and limitations of models. After a review of hypotheses and explicit models on diel vertical migrations I describe in more detail one descriptive and one conceptual model to contrast the goals of such different approaches. At the end I give some outlook on improvements and further modelling which would be helpful for deeper insight into problems connected with diel vertical migration.

Field studies, experiments and models: in which respect are they similar?

To clarify the special aims of a modelling approach, I will first discuss some general aspects of the scientific process and ask in which respect models, experiments, and field studies are similar. One possible view of the scientific process is visualized in Fig. 1. All questions we ask are strongly dependent on current theories, concepts, beliefs, and agreements within the scientific community. Our perception and selection of phenomena can be heavily biased by cultural influences which are important parts of historical and current science. Therefore, the data and facts which are known to us are obtained by a very complex filtering process which also influences the kind of questions we are able to ask. Besides such processes which determine e.g., how facts are isolated and which

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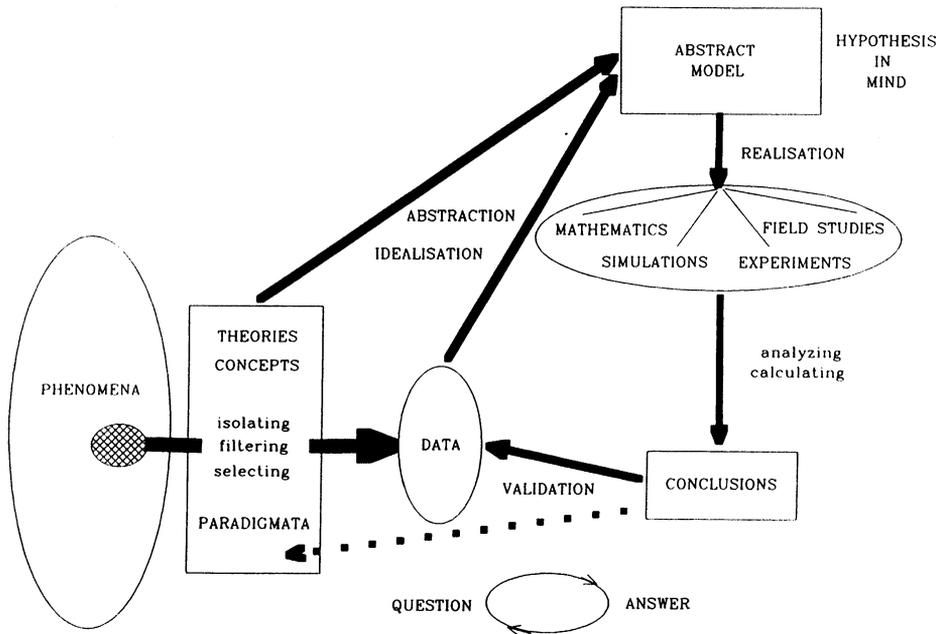


Fig. 1. The modelling process.

conditions are specified, a further process of abstraction and idealization takes place any time we ask a question in a precise way that enables us to design a scientific investigation. Doing science we all have an abstract “ideal model” in mind which is related to the hypothesis under test or to the specific question asked. Only such an abstract model enables us to design and to perform experiments, field studies or models; the accuracy and complexity of such abstract models vary drastically with the object of investigation and may differ extremely between researchers. All studies are performed by “realizations” of such abstract models. The common denominator is that one starts with some (more or less) well-defined assumptions and tries to gain conclusions. The realization of an abstract model in the form of field studies, experiments, and mathematical or simulation models and the following analysis of the emerging results are, therefore, the instruments used to obtain answers to the questions posed. The possible answers are constrained by the underlying assumptions. The final results are just logical consequences of the given implicit and explicit assumptions including mechanisms that range from well-defined to unknown. In this respect, there is nothing special about model studies when compared to field studies or experiments; the process from assumptions to conclusions is the same. It is important to note that model results are also just logical consequences of the assumptions. Therefore, in this context, a model cannot be wrong if it is free of logical and technical errors. It can be unrealistic – like many experiments – because of the underlying assumptions. If the results of a scientific investigation disagree with other known data, then there are at least three possible explanations for the discrepancy. First, a logical or technical error might have occurred in the “real model”: program errors in a model, mathematical mistakes, experimental artifacts, systematic errors in sampling of

field data etc. But if this can be ruled out with a high probability, then there might be, as a second source of errors, an underlying mistake during the process of building the abstract model; such errors are often quite hard to detect. The contradiction might be caused by undetected implicit assumptions or wrong abstractions. But even if we also assume that in this process everything is correct, we have the third possibility that we are misled by our preconceptions and current theories. Then we have the seldom but important case that we can solve the contradictions only by changing a scientific paradigm. Without keeping in mind that the current paradigm might be wrong, we are always in danger of getting only answers to already biased questions; we are then unable to escape from a self-sustaining circular process producing a consistent but incomplete scientific reality.

What is now unique to models in this scientific process? I would like to point out one special feature which might help to better illuminate the differences between descriptive and conceptual models in the following chapter. In experiments and in field studies it is helpful to know the underlying assumptions. The problem is that quite often after an experiment or a field study has been performed, one detects further underlying implicit and explicit assumptions or one realizes that certain conditions were very constraining. The experiment was successfully performed without this knowledge, but when writing down a model, it is essential to know all assumptions explicitly. Furthermore there is another striking difference between models and experiments or field studies: to make a model one has to specify all mechanisms. For example one has to know how filtration or assimilation rates change in relation to a variation in food concentration. For each variable, one must specify its interdependence among all other variables. All these mechanisms are part of the assumptions. A conceptual model often concentrates on evaluating the consequences of certain selected mechanisms and is not designed to be a mirror of the whole complexity of the real world. The more realistic a model is the more mechanisms there are which have to be specified. Quite often it is impossible to get all the information necessary to build a realistic model. Then the analysis of alternative (sub-) models may help to decide which processes are important to study experimentally. In such cases, the results of the model itself might be of minor interest, but the attempt to build a model helps to clarify and specify the questions asked and helps one to become more conscious of the underlying assumptions. The main value of such models is not in developing new insights but in stimulating further experiments to study unknown or missing but relevant mechanisms.

Review of models

In the following I do not intend to add another paper to the list of reviews on diel vertical migration (BOWERS 1979, PEARRE 1979, KERFOOT 1956, BAYLY 1986, LAMPERT 1989), but I will first look to the proposed hypotheses from (my personal and biased!) point of view of evolutionary biology. I will categorize the hypotheses according to the assumed selection process, in particular I will point to the often implicitly used arguments of group selection. In the second part of this paragraph I will characterize some models which are more explicitly given – by usage of equations or simulation algorithms.

Table 1. Hypotheses on vertical migration of zooplankton.

Authors	Hypothesis	Selection	
		Group	Individual
MCLAREN 1963	metabolic; energy bonus for increased fecundity and storage capacity		x
MCALLISTER 1969, 1970	metabolic; feeding strategy better utilization of food resources	x	
RUDJAKOV 1970	not adaptive; by-product due to circadian rhythm of locomotory activity hunger migration	-	-
KERFOOT 1970	metabolic; light adaptation, pathway analysis, isolume movement	x	
MCLAREN 1974	demographic; size and fecundity advantage at low temperatures		x
LANE 1975	demographic; reduction of interspecific competition by niche segregation	(x)	(x)
ZARET & SUFFERN 1976 (and many authors before)	demographic; predation avoidance		x
ENRIGHT 1977 (as suggested by CONOVER 1968)	metabolic; interaction with algae, net energy gain, control of timing	x	x
HAIRSTON 1980	photo-damage		x
GELLER 1986	demographic and metabolic; starvation avoidance	x	(x)

Hypotheses

Table 1 gives in chronological order the proposed hypotheses together with their main ideas and the kind of selection arguments used. In contrast to individual selection which acts within populations and changes the relative frequencies of inherited behavioral, somatic, metabolic and other traits according to the associated relative fitness, group selection acts mainly via population characteristics. The differences among populations must be related to extinction and recolonization rates to let group selection work. I am not opposed to group selection and I have no doubt that group selection can efficiently operate under certain conditions, e.g. in rock pools. But I can hardly imagine that these conditions are usually fulfilled in situations where selection for or against diel vertical migration takes place. In most cases group selection is easily overpowered by individual selection because of the different time scales involved. Therefore, group selection could be important only if selection on the individual level is very weak and popula-

tion sizes are very small. Assume for example that in a large *Daphnia* population the food resources recover better from grazing if the population performs vertical migration and that at the population level the available food is more abundant if the whole population migrates. This might perhaps allow a larger population size with reduced extinction probability. If it would still be advantageous for an individual daphnid not to migrate – having more food than a migrating ethotype in addition to being exposed to higher temperature resulting in shorter developmental time – then group selection could never prevent the invasion of non-migrating ethotypes. It would be even harder to think about a mechanism which could enhance the frequency of migrating ethotypes in a non-migrating population. Individual selection would act against a migrating mutant orders of magnitude faster than would the occurrence of the extinction of a population. Therefore, if in planktonic communities group selection acts in opposite direction to individual selection, group selection would always be easily overpowered by individual selection. If group selection and individual selection act in the same direction, the contribution of group selection would be negligible. Therefore, group selection arguments should be avoided to explain diel vertical migration (DVM).

Now some comments on the proposed hypotheses (see Table 1). MCALLISTER (1969, 1970) gives consequences of different grazing schemes on the estimate of secondary production. The consequences might be correctly described. One should, however, never misuse the consequences of DVM as explanation for DVM without proving the selection argument. MCALLISTER's arguments hold only under group selection. (Astonishingly, it is quite a common mistake even in the scientific literature to use correctly derived consequences as an explanation. It is like changing the direction of logical implication $A \rightarrow B$ often observed in every day life; if B follows from A nothing can be told about A if B has been found to be fulfilled. An implication is still logically true if B is true but A is wrong; the implication is false only if A is true and B is false.)

RUDIJKOV (1970) argues that DVM might not be the result of adaptation to planktonic mode of life. DVM is assumed to be a by-product of consequence of locomotory activity modified by temperature, food supply, hydrostatic pressure and biological clocks. Therefore, DVM is not selected for. KERFOOT (1970) performs a pathway analysis in marine situations at high latitude and argues for a selective advantage of isolume-behavior of light-orienting populations by adaptation to specific light ranges and by nocturnal food exploitation. He does not argue how such populations can be selected, but obviously only group selection could work in this way. LANE (1975) argues with interspecific competition and niche segregation but does not show that these mechanisms are strong enough to explain DVM without usage of group selection arguments. ENRIGHT (1977) argues against group selection – but his arguments of timing and his algae dynamics assumed to calculate available food are valid only under the implicit assumptions of group selection. Further he uses energy for a fitness measure which is incorrect because he neglects developmental time. It seems possible to reformulate GELLER's (1986) hypothesis at least partly without invoking group selection.

It should be mentioned that some authors argue for multiple causes of DVM. I think it is reasonable to assume that the selective forces for DVM may change in their relative importance during a season and may differ considerably between lakes – but this does not preclude the formulation of a theory which is generally quite valid.

Table 2. Explicit models.

PEPITA & MAKAROVA 1969	formulas; dependence of phytoplankton production on rhythm and rate of zooplankton grazing
MCALLISTER 1969, 1970	formulas, simulation model; effects of vertically migrating zooplankton on marine production
ENRIGHT 1977	formulas; metabolic expenditures for intermittent and continuous grazers
WRIGHT et al. 1980	demographic simulation model; conditions under which reduced predation risk can offset the disadvantage of reduced temperature and slowed growth rate
IWASA 1982	predator-prey-game-model ¹
GLIWICZ & PIJANOWSKA 1988	correlation model; depth distribution of predation and resources
CLARK & LEVY 1988	dynamic-programming; DVM of juvenile salmon, trade-off between food intake and predation risk, antipredation window
GABRIEL & THOMAS 1988a, b, c, 1989	ESS-model; static model for fixed situation, evaluation of various selective forces and their interactions
SCHEERER 1991	dynamic model with differential equations; biomass oriented

¹The proposed stable equilibria are unstable and, therefore, useless (see critique in GABRIEL & THOMAS 1988a).

Explicit models

Table 2 contains only such models which are formulated more explicitly than by verbal description. The models are given by explicit or numerically solvable formulas, algorithms for simulations, statistical correlation between observable variables, game theory, theory of evolutionarily stable strategies, mathematical analysis, and numerical solution of systems of differential equations. It is astonishing that more model studies have not been performed for such a well-known and controversial phenomenon like DVM. The models differ not only in the methods applied but also in the leading questions under which they have been designed. As two extremes one might distinguish between models which try to reproduce real data as closely as possible and models which are purely conceptually designed. Conceptual means that the model is not primarily designed to fit given data sets but to get a better principal understanding of the assumed relevant mechanisms and their interactions. To exemplify and to compare these different approaches, one more conceptual and one more simulation oriented model are discussed in the next chapter.

Simulation and conceptual models: two examples

Both models are centered around the same phenomenon observed in Lake Constance. There coexist two physiologically and morphologically very similar *Daphnia* species which differ in DVM-behavior: *Daphnia hyalina* performs DVM but *Daphnia galeata* does not (STICH & LAMPERT 1981, STICH 1985, GELLER 1986).

Conceptual model by GABRIEL and THOMAS

The approach by GABRIEL & THOMAS (1988a, b, c, 1989) starts from an evolutionary point of view and asks the question whether this coexistence can be understood within the framework of "evolutionarily stable strategies (= ESS)" (MAYNARD SMITH & PRICE 1973, MAYNARD SMITH 1974, 1982). Roughly speaking, an ESS is a strategy such that, if the members of a population adopt it, there is no "mutant" strategy that would give higher reproductive fitness. Therefore, ESS means a strategy which cannot be invaded by a rare mutant once it has become established in a population. With this definition one can ask under which conditions vertical migration is an ESS. To analyze the possibility of coexistence, the analysis is more complicated because one has to look for a stable polymorphism or strategy mixture as an ESS (for details see GABRIEL & THOMAS 1988a). With only two strategies present, there is an easy graphical interpretation of the payoff differences so that the analysis for a stable polymorphism can be performed quite easily as soon as the payoff functions are known. It is a big advantage of an ESS-approach that this payoff comparison is possible without explicit simulation of complicated population dynamics. Such an approach can be very powerful: without explicit fitting of data, the models allow quite general predictions and conclusions from first principles. All parameters of the model are measurable and by estimating its values for a given field of experimental situation, the model could also give rough specific predictions. But it is not the intention of the model to describe a certain data set; the emphasis is on principal understanding of the mechanisms and its possible interactions. Consequently, one tries to simplify reality as far as possible and concentrates on essential components – or components which the modelers believed to be important. GABRIEL & THOMAS reduced the problem by distinguishing only the four situations made up by the combinations of day or night and upper or lower water column. It is clear that such a simplified system does not allow precise data fitting, but to answer principal questions, simplicity is quite often a crucial keystone.

The model concept, its underlying assumptions and the derivation of the payoff functions including the zooplankton-algae interaction are described in detail in GABRIEL & THOMAS (1988a). Model parameters used are food concentration of algae, growth rate of algae, maximal filtration rate of zooplankton, predation risk for zooplankton during the day in the upper water layers, density of zooplankton, and length of the night; the strategy dependent parameters used are egg developmental time and conversion efficiency of food into successful reproduction. The main results are:

- Both the migrating and non-migrating strategy can be an ESS.
- Stable coexistence of both ethotypes is possible but only at low food concentrations (i.e., below the incipient limiting level, for details see GABRIEL & THOMAS 1988a).
- For the non-migrating strategy: a maximum tolerable predation risk is predicted (see GABRIEL & THOMAS 1988b). A general upper limit exists which only depends on the day-length and the egg-developmental time of the non-migrating ethotype (which is mainly determined by the temperature in the upper water layer).

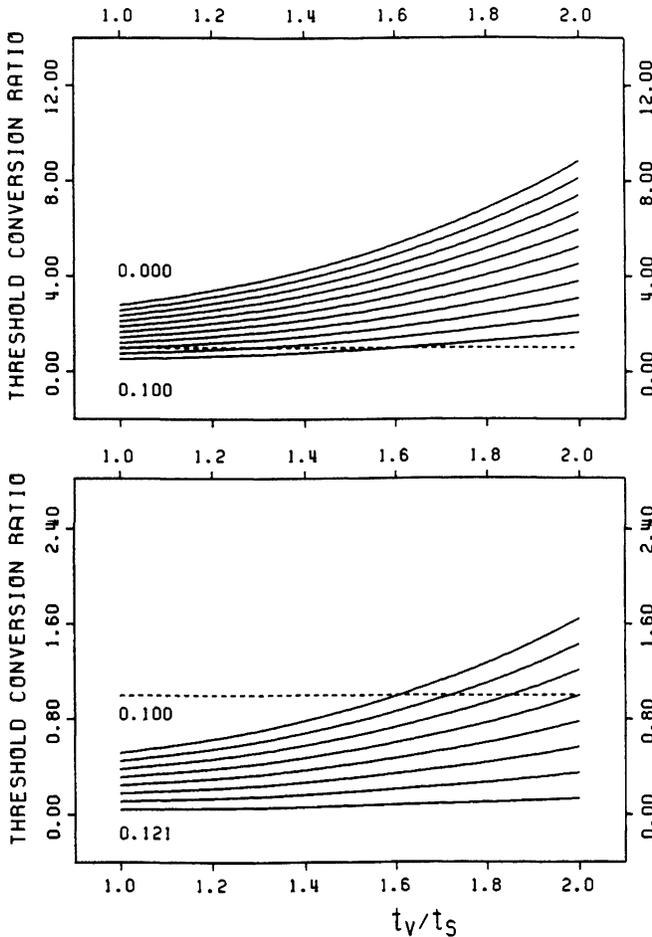


Fig. 2. Threshold ratio of the conversion efficiency β_v/β_s of food into successful reproduction depending on the ratio of egg developmental time of both strategies. The predation risk is varied from 0 to 0.1 in the upper panel and from 0.1 to 0.121 in the lower panel. The broken line indicates equal conversion efficiencies for both strategies.

- For the migrating strategy: below a critical value of the ratio of strategy dependent reproductive efficiencies migrating can never be an ESS (see GABRIEL & THOMAS 1988c).
- Metabolic advantage alone cannot be an ultimate reason for vertical migration.

Because the results on metabolic advantage and reproductive efficiency are published in an inaccessible symposium volume, its graphs are given in Fig. 2.

An important model parameter is the efficiency at which the assimilated food is converted into successful reproduction. This efficiency is strategy dependent. Let us assign β_v and β_s the conversion efficiencies for the migrating (v) and non-migrating (s) ethotype. Using ESS-arguments (GABRIEL & THOMAS 1988c) it can be concluded from the model equation that there exists a threshold for the ratio β_v/β_s ; below this threshold, vertical migration can never be an ESS. Its dependence on the ratio t_v/t_s of the egg-developmental time of both strategies is shown for several values p of the predation risk during the day in the upper water layers (see Fig. 2). For $t_v/t_s = 1$ there would be no

Table 3. Selection direction of the model parameters. If an increase of a parameter value is in favor of vertical migration this is indicated by v, in the opposite case by n.

strategy independent parameters:			
A	food concentration (algae density)		n
r	intrinsic growth rate of algae		n
g	maximal filtration rate of zooplankton		n
p	predation risk during day (upper water)	v	
N	density of zooplankton	v	(n)
T_n	length of night	v	n
strategy dependent parameters:			
t_v	egg development time of migrating zooplankton		n
t_s	egg development time of non-migrating zooplankton	v	
β_v	conversion efficiency of migration zooplankton	v	
β_s	conversion efficiency of non-migration zooplankton		n

difference in the egg developmental time i.e., the different strategists experience the same temperature as it would be in non-stratified lakes. With increasing thermal stratification the ratio t_v/t_s increases. As shown in Fig. 2, the threshold conversion ratio increases with increasing t_v/t_s but decreases with increasing predation risk p . The broken reference line gives $\beta_v/\beta_s = 1$. If the temperature difference between epi- and hypolimnion becomes larger, the conversion efficiency of the migrating type has to become better and better relative to the non-migrating type in order to allow migration to be an ESS. This works as long as the additional predation risk for non-migrating individuals is high enough. For high p migration is an ESS even if $\beta_v < \beta_s$. But for small predation risks β_v must be very large compared to β_s . This could never be achieved by a metabolic advantage alone, but a high juvenile mortality under non-migration (e.g., by high invertebrate predation) could account for the demanded β_s -value in some parameter regions.

In highly non-linear systems, it is difficult to perform a sensitivity analysis because the results would change drastically depending on the parameter values chosen. Therefore, a special sensitivity analysis of the system has been designed by GABRIEL & THOMAS (1989). In a realistic parameter space combinations of parameter values are chosen randomly. If for such parameter settings a stable polymorphism exists, a sensitivity analysis is performed by changing each parameter by 1%. Also a relative sensitivity is calculated weighing absolute values of the payoff differences with the mean values over all absolute values of payoffs at the parameter setting selected for the sensitivity analysis. Table 3 gives the parameter and its selection direction. Its relative sensitivities are given as Box-and-Whisker plots in Fig. 3. The three most important parameters are the two strategy dependent egg developmental times and the predation risk for non-migrating ethotypes. Grazing rate, algae density, and algal growth rate are of minor importance. This sensitivity analysis might help to avoid one-dimensional thinking by looking for one single ultimate reason of vertical migration.

The ESS approach has the advantage that conclusions can be drawn without calculating in detail the underlying complex population dynamics. The selective forces can be determined without knowing how fast the selection process goes or when assumed equilibria are reached. This is justified if one asks evolutionary questions and tries to find

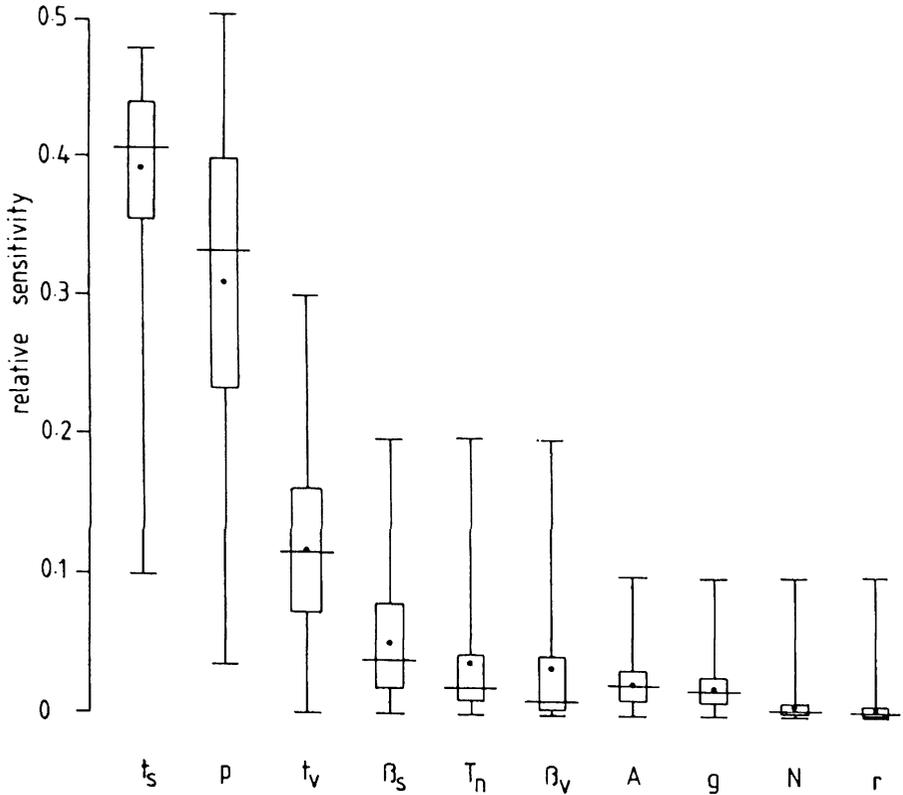


Fig. 3. Relative sensitivity of the model parameters. Mean values are given by points, median values by long horizontal bars. Short horizontal bars indicate maximum and minimum values, the central box covers the middle 50% of the data between the lower and upper quartiles. For description of the parameters see Table 3.

ultimate reasons for DVM. In principal, an ESS analysis can also be performed with implemented complex dynamics, but this has not yet been done.

To get information on the population dynamics during a season, one has to analyze a dynamic model as given in the next chapter.

Simulation model by SCHEERER

SCHEERER (1991) describes the dynamics of the *Daphnia galeata* and *D. hyalina* populations and their predator-prey interaction with algae using a system of four differential equations. Two equations describe the algae biomass in the epilimnion and in the hypolimnion, and two equations represent the biomass of *D. galeata* and *D. hyalina*; time dependent coefficients regulate growth and mortality. SCHEERER performs a sophisticated stability analysis of this system and also of reduced forms of this system. He looks for conditions of stable periodic solutions of the system and by using such a procedure extracts information on equilibrium conditions. He argues that from this procedure he also gets insight into the selective forces driving the system. The whole approach is biomass (or energy) oriented.

It might be quite a naive assumption that such a simple model can fit exactly to real data. But nevertheless, SCHEERER's approach can give at least some hints. One valuable contribution is the attempt to check whether the population dynamics of *D. hyalina* is consistent with the assumption of clonal replacement. Let us assume that *D. hyalina* consists of two clones: one clone switches its behavior to migration in spring and the other never migrates. The questions are: can the migrating clone build up a large population fast enough and is the non-migrating one eliminated by selection. Then clonal replacement would be a possible explanation for the build-up of the migrating *D. hyalina* population in June. SCHEERER's analysis shows that a migrating clone can grow fast enough but that the non-migrating *D. hyalina* do not disappear due to selection. SCHEERER points to the possibility that the non-migrating clone switches to sexual reproduction, produces resting eggs and then reproduction stops. Such speculations are sometimes hard to disprove, but in my opinion, there is no evidence from field data to support such a possibility. Therefore, we can conclude, that clonal replacement is unlikely to appear according to the model calculations.

Besides this investigation on clonal replacement, there is another biologically interesting result in SCHEERER's analysis. He claims that the role of invertebrate predation is under-estimated in previous analyses. The first hint comes from re-analyzing published data. His second argument results from his model studies. With his system of differential equations, SCHEERER tries to fit the monthly data of STICH (1985). The only free parameters of these fits are for vertebrate and invertebrate predation. From the stability analysis one can deduce a band of parameter combinations which allows stable coexistence of *D. hyalina* and *D. galeata*. The corresponding parameter combinations vary from month to month. This could be interpreted as a reflection of changing selective forces. SCHEERER then argues that at least in special parameter settings invertebrate predation affects the competition between *D. hyalina* and *D. galeata* more than vertebrate predation. This analysis of SCHEERER has several weak points, but nevertheless it seems worthwhile to take his conclusions seriously and to test more carefully the impact of invertebrate predation.

It is always easier to criticize a model than to build a better one. The following critique is not given to discredit SCHEERER's model but to make the reader cautious and to avoid over-interpretations of the results. A more realistic approach would be an age and size structured model; then the egg developmental time would be incorporated and a biomass could then be converted into a reliable fitness measure. Without age and size structure, there is no time delay i.e., the consumed algae are immediately converted into biomass of zooplankton. In such a context, energy is not a sufficient variable to measure the impact of selective forces. Because net energy gain still seems to be an attractive variable even when neglecting the time component, I would like to point out that the release of two eggs every two days results in a lower fitness than the production of one egg every day (see GABRIEL & THOMAS 1988a). Only under very restrictive conditions like stable age distribution and constant population size (not growing, not declining) can net energy gain be a good fitness measure. But in plankton populations most selection occurs during non-stable conditions.

SCHEERER criticizes the model of GABRIEL & THOMAS and then says "the objections shall be overcome by using the second, even more established common measurement for the impact of selective forces: energy". SCHEERER not only uses the wrong measure for the selective forces but probably also misunderstood the aim of the model of GABRIEL & THOMAS. SCHEERER uses the simple approach of GABRIEL & THOMAS – simplicity was an important feature for the design of the conceptual model – and extends it by adding

dynamics. By switching to a wrong fitness measure, however, he loses most of the explanatory power of the conceptual model. SCHEERER's model cannot be used to answer questions addressing the ultimate reasons for DVM, but the model is still valid to gain some insight into the populations dynamics.

Toward better models

One prerequisite for building predictive models is a detailed understanding of life history, energy budget and population dynamics of the involved species. But the knowledge of the ecological processes are probably not sufficient because, especially in algae and daphnids, the time scale of ecological and evolutionary changes might be similar. Therefore, a combination of evolutionary and ecological models is desired even if this might be very difficult to perform.

The possible improvements of existing models are quite obvious – but such improvements need quite a lot of laborious work. One problem not yet attacked is a prediction of the vertical distribution – instead of the oversimplified picture of migrating and non-migrating ethotypes. Such a model approach should try to distinguish between phenotypic plasticity in the reaction to the stimuli and clonal diversity in the type of reaction (e.g., genetically determined thresholds and intensities in response to stimuli). Besides phenotypic plasticity and clonal diversity, it would be very important to implement age and size structure to describe behavioral changes with regard to age, size and the actual number of eggs in the brood chamber. Also to study the influence of invertebrate predation in contrast to vertebrate predation, it would be necessary to have the size structure built into the model.

With the new data based on individual observations and chemical communications, it seems feasible to build more individual-based models for specific questions and to test the model predictions experimentally. For many questions it might be essential to also implement genetically determined plastic responses that vary between clones. Recent developments in the theory of reaction norms (e.g., GABRIEL & LYNCH 1992) should be connected with behavioral, physiological and morphological responses associated with DVM.

In my opinion, we are still far from being able to build a complete model which adequately describes the population dynamics over a whole season, because we do not yet have enough precise data on many parameters. However, the population dynamics under relatively controlled conditions like in plankton towers should be accessible. Modelling would be worthwhile only if one expects a deeper understanding of the processes from the model's results (or from the process of model building as described in chapter II). This would depend on the specific question being asked and there is no doubt that there are still many open and interesting questions to be answered.

To give an example I would like to come back to the problem of coexistence which does not yet appear to be fully solved. The model of GABRIEL & THOMAS predicts and gives conditions under which the coexistence of migrating and non-migrating ethotypes is possible. It also gives some quite general conditions for evolutionary stability of these behavioral patterns. But the static ESS-approach does not allow for the prediction of specific population dynamics during a season. SCHEERER's model is designed to describe the dynamics of the populations but it has in its present form no explanatory and no predictive power. The parameter values for the coexistence of both ethotypes like in Lake Constance are restricted to quite narrow bands (in both models). It seems plausible that

the variability of the environment within and between years enhances the possibility of coexistence; but this has to be checked – otherwise something very essential is missing in the approaches of both models. In my opinion, the model approaches to DVM are accurate enough (at least after some non-essential modifications) to predict DVM in an experimental setting. But we are still unable to quantify the selective forces and its temporal changes in nature. Therefore, there is a large demand for further experimental, field and modelling investigations in order to predict DVM behavior under natural conditions.

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References

- BAYLY, I.A.E. (1986): Aspects of diel vertical migration in zooplankton, and its enigma variations. In: P. DE DECKKER & W.D. WILLIAMS: *Limnology in Australia*. – pp. 349–368. CSIRO Aust, Melbourne. W.J. Junk, Dordrecht.
- BOWERS, J.A. (1979): Zooplankton grazing in simulation models: the role of vertical migration. In: D. SCAVIA & A. ROBERTSON (eds.): *Perspectives on lake ecosystem modelling*. – pp. 53–73. Ann Arbor Science, Ann Arbor, Michigan.
- CLARK, W.C. & LEVY, D.A. (1988): Diel vertical migration by juvenile sockeye salmon and the antipredation window. – *Amer. Nat.* **131**: 271–290.
- CONOVER, R.J. (1968): Zooplankton-life in a nutritionally dilute environment. – *Amer. Zoologist* **8**: 107–118.
- ENRIGHT, J.T. (1977): Diurnal vertical migration: adaptive significance and timing. Part 1. Selective advantage: a metabolic model. – *Limnol. Oceanogr.* **22**: 856–872.
- GABRIEL, W. & LYNCH, M. (1992): The selective advantage of reaction norms for environmental tolerance. – *J. evol. Biol.* **5**: 41–59.
- GABRIEL, W. & THOMAS, B. (1988a): Vertical migration of zooplankton as an evolutionarily stable strategy. – *Amer. Nat.* **132**: 199–216.
- (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**: 807–811.
- (1988c): Ultimate causes of vertical migration in zooplankton: An evaluation by evolutionary game theory. – In: W. WOLFF, C.J. SOEDER & F.R. DREPPER (eds.): *Ecodynamics, contributions to theoretical ecology*. – pp. 127–134. Springer, Heidelberg.
- (1989): Predictive value of evolutionary game theory for vertical migration in zooplankton. – In: D.P.F. MÖLLER (ed.): *System Analysis of Biomedical Processes. Advances in System Analysis, Vol. 5*. – pp. 173–180. Vieweg, Braunschweig.
- GELLER, W. (1986): Diurnal vertical migration of zooplankton in a temperate great lake (L. Constance): a starvation avoidance mechanism? – *Arch. Hydrobiol. Suppl.* **74**: 1–60.
- GLIWICZ, Z.M. & PIJANOWSKA, J. (1988): Predation and resource depth distribution in shaping behaviour of vertical migration in zooplankton. – *Bull. Mar. Sci.* **43**: 695–709.
- HAIRSTON, N.G. jr. (1980): The vertical distribution of diaptomid copepods in relation to body pigmentation. In: W.C. KERFOOT (ed.): *Evolution and Ecology of Zooplankton Communities*. – pp. 98–110. University Press of New England, Hanover, New Hampshire.
- IWASA, Y. (1982): Vertical migration of zooplankton: a game between predator and prey. – *Amer. Nat.* **120**: 171–180.
- KERFOOT, W.B. (1970): Bioenergetics of vertical migration. – *Amer. Nat.* **104**: 529–546.
- KERFOOT, W.C. (1985): Adaptive value of vertical migration: comments on the predation hypothesis and some alternatives. – In: M.A. RANKIN (ed.): *Migration: mechanisms and adaptive significance*. pp. 91–113. *Contrib. Mar. Sci.* **27**, Univ. Texas, Port Aransas.

- LAMPERT, W. (1989): The adaptive significance of diel vertical migration of zooplankton. – *Functional Ecology* 3: 21–27.
- LANE, P.A. (1975): Dynamics of aquatic systems – Comparative study of 4 zooplankton communities. – *Ecol. Monogr.* 45: 307–336.
- MAYNARD SMITH, J. (1974): The theory of games and the evolution of animal conflicts. – *J. Theor. Biol.* 47: 209–221.
- (1982): *Evolution and the theory of games.* – Cambridge University Press, Cambridge.
- MAYNARD SMITH, J. & PRICE, G.R. (1973): The logic of animal conflicts. – *Nature* 246: 15–18.
- MCALLISTER, C.D. (1969): Aspects of estimating zooplankton production from phytoplankton production. – *J. Fish. Res. Board Can.* 26: 199–220.
- (1970): Zooplankton rations, phytoplankton mortality and the estimation of marine production. In: J.H. STEELE (ed.): *Marine food chains.* – pp. 419–457. Univ. California Press, Berkeley, California.
- MCLAREN, I.A. (1963): Effect of temperature on growth of zooplankton and the adaptive value of vertical migration. – *J. Fish. Res. Board Can.* 26: 199–220.
- (1974): Demographic strategy of vertical migration by a marine copepod. – *Amer. Nat.* 108: 91–102.
- PEARRE, S. jr. (1979): Problems of detection and interpretation of vertical migration. – *J. Plankton Res.* 1: 29–42.
- PETIPA, T.S. & MAKAROVA, N.P. (1969): Dependence of phytoplankton production on rhythm and rate of elimination. – *Mar. Biol.* 3: 720–730.
- RUDJAKOV, J.A. (1970): The possible causes of diel vertical migration of planktonic animals. – *Marine Biol.* 6: 98–105.
- SCHEEERER, U. (1991): Coexistence of vertically migrating and non-migrating daphnids in Lake Constance. – PhD-thesis (in English), University of Heidelberg.
- STICH, H.B. (1985): Untersuchungen zur tagesperiodischen Vertikalwanderung planktischer Crustaceen im Bodensee. Ph.D. Thesis. University Freiburg (BrsG.), Freiburg, Germany.
- STICH, H.B. & LAMPERT, W. (1981): Predator evasion as an explanation of diurnal vertical migration by zooplankton. – *Nature* 293: 396–398.
- WRIGHT, D., O'BRIEN, W.J. & VINGARD, G.L. (1980): Adaptive value of vertical migration: a simulation model argument for the predation hypothesis. – In: W.C. KERFOOT (ed.): *Evolution and Ecology of Zooplankton Communities.* – pp. 138–147. University Press of New England, Hanover, New Hampshire.
- ZARET, T.M. & SUFFERN, J.S. (1976): Vertical migration in zooplankton as a predator avoidance mechanism. – *Limnol. Oceanogr.* 21: 804–813.

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