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Contents

Part I	Evolution	
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Evolution: Why the Whole is Greater Than the Sum of the Parts By P.M. Allen (With 11 Figures)	2
The Evolution of Spatially Inhomogeneous Populations By J.M. McGlade	31
Intraspecific Competition and Evolution By F. Bugge Christiansen (With 4 Figures)	40
Fundamental Components in Ecology and Evolution: Hierarchy, Concepts and Descriptions By S.H. Cousins (With 3 Figures)	60
Simulated Evolution of Primitive Organisms By G. Duchateau, J.A. Meyer, P. Tarroux, P. Vincens, and G. Weisbuch (With 4 Figures)	69
Dynamics of Developmentally Constrained Populations By M. Kerszberg (With 3 Figures)	77
Differential Evolution of Pesticide Resistance in Predators and Prey By J.D. van der Laan and P. Hogeweg (With 4 Figures)	86
Collective Intelligence in Evolving Systems By H.-P. Schwefel	95

Part II	Marine and Lake Ecodynamics	
----------------	------------------------------------	--

Biological-Physical Interactions in the Sea: Marine Ecodynamics By A. Okubo (With 1 Figure)	102
Understanding the Baltic Sea: Systems Ecology in Theory and Practice By F. Wulff (With 7 Figures)	113
Ultimate Causes of Vertical Migration in Zooplankton: An Evaluation by Evolutionary Game Theory By W. Gabriel and B. Thomas (With 2 Figures)	127

Trophy-Balanced Turnover Velocities in a Two-Species System of Competing Daphnids: A Test of the "Energy Residence Time" Concept
 By W. Geller (With 1 Figure) 135

Ecodynamic Changes in Suburban Lakes in Berlin (FRG) During the Restoration Process After Phosphate Removal
 By G. Klein (With 6 Figures) 138

A Comparison of Fish Size-Composition in the North Sea and on Georges Bank
 By J.G. Pope, T.K. Stokes, S.A. Murawski, and S.I. Idoine (With 3 Figures) 146

Generic Models of Continental Shelf Ecosystems
 By W. Silvert (With 1 Figure) 153

Part III Ecosystems Analysis

On Quantifying the Effects of Formal and Final Causes in Ecosystem Development
 By R.E. Ulanowicz and A.J. Goldman (With 3 Figures) 164

Avoidance of Ecological Risk in Optimal Exploitation of Biological Resources
 By C. Wissel (With 7 Figures) 181

Deterministic Modelling of the Combined Action of Light and Heat Stress on Microbial Growth
 By E. Fiolitakis, J.U. Grobbelaar, C.J. Soeder, and E. Hegewald (With 2 Figures) 202

Different Responses in Ecosystems to Environmental Stress
 By E. Gutiérrez, R. Guardans, and M.A. Canela (With 2 Figures) 211

An Example of Modelling in Ecotoxicology
 By K. Mathes, V.M. Schulz-Berendt, and G. Weidemann (With 4 Figures) 220

Spatial Simulation of Population Dynamics in the Evaluation of Foraging Theory in Complex Ecological Systems
 By F. Perez-Trejo (With 2 Figures) 229

Models for the Management of Renewable Resources Embedded in Complex Marine Systems
 By P.A. Shelton (With 4 Figures) 235

Part IV Forest Ecosystems

Ecodynamics as a Function of Ecosystem Structure: Forest Dieback as an Example
 By H. Bossel (With 14 Figures) 244

Ecosystem Theory Required to Identify Future Forest Responses to Changing CO₂ and Climate
 By A.M. Solomon (With 4 Figures) 258

Part V Modelling Approaches

The Role of Theoretical Research in the Design of Programmes for the Control of Infectious Disease Agents
 By G.F. Medley (With 2 Figures) 276

Microinteractive Predator-Prey Simulations
 By W.F. Wolff (With 5 Figures) 285

Biological Attractors, Transients, and Evolution
 By S.P. Blythe and T.K. Stokes (With 9 Figures) 309

Unstable Determinism in the Information Production Profile of an Epidemiological Time Series
 By F. Drepper (With 4 Figures) 319

Random Elements in a Population Model Based on Individual Development
 By N. van der Hoeven (With 4 Figures) 333

Measures of Spatio-Temporal Irregularity
 By A.V. Holden, J. Brindley, and R.M. Everson 343

Index of Contributors 351

Ultimate Causes of Vertical Migration in Zooplankton: An Evaluation by Evolutionary Game Theory

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INTRODUCTION

Diel vertical migration is a widespread but not well understood behaviour in freshwater and marine zooplankton (Pearre 1979a and 1979b). Many taxa avoid the warm and food rich upper waters during day, but at dusk they swim long distances upward and stay in the upper water layers during night. Around sunrise they descend again and stay in colder and food scarce waters during day. At least cladocerans can not compensate for the food shortage during day by increasing feeding rates and by storing food during night (Lampert and Taylor 1985). The extra swimming for migration seems not to be very costly in terms of energy consumption. Most zooplankters carry their eggs with them. As egg development time is inversely proportional to temperature, a lowered temperature increases generation time drastically but may reduce metabolic costs.

To find ultimate causes for the migratory behaviour, the mentioned disadvantages have to be offset by fitness components, which increase because of vertical migration. Several hypotheses have been proposed: metabolic advantages or better utilization of resources (McLaren 1963 and 1974, Kerfoot 1970, Enright 1977, Enright and Honegger 1977), avoidance of starvation (Geller 1986), and avoidance of visual predators (Zaret and Suffern 1976, Wright et al. 1980). The validity and relative importance of these arguments can be tested only by quantifying the relative strength of the various selective forces. There are good reasons to assume migratory behaviour has a strong genetic component (Weider

1984, Gliwicz 1986). Therefore, a most promising framework for such a problem is the concept of evolutionarily stable strategies (=ESS) (Maynard Smith and Price 1973, Maynard Smith 1982, Thomas 1984).

Gabriel and Thomas (1988a) developed an ESS-model on vertical migration of zooplankton which is able to explain the observed coexistence of two similar *Daphnia* species, one migrates while the other does not migrate (Stich and Lampert 1981). After a short description of the model parameters we will derive equations for a discussion of the ultimate causes of vertical migration of zooplankton.

MODEL PARAMETERS

A detailed discussion and description of the model is given in Gabriel and Thomas (1988a). Migrating and non-migrating behaviour are treated as two distinct strategies. The model calculates the food uptake and its conversion into successful reproductive output for both strategies. Fitness is calculated in terms of intrinsic growth rate on a time scale of 24 hours. The interaction of zooplankton with its algae food is considered in detail according to the well studied feeding physiology of zooplankton. The payoffs depend on the following parameters which all are known from laboratory experiments and field studies:

- t : egg development time,
- A : algal density,
- N : population density of zooplankton,
- p : predation risk for zooplankton by optically orientated predators like fish,
- r : partial intrinsic growth rate of algae,
- T_n : relative length of night (in parts of 24 hours),
- β : conversion efficiency of food uptake to successful reproductive output (mortalities other than considered under p are taken into account),
- g : maximal grazing rate of zooplankton.

Some of these parameters, especially t and β , vary strongly for the different strategies.

Due to self-interaction through food competition and frequency depen-

dent predation risk, the payoff to the two strategies is dependent on their relative frequencies. In fact, the payoff difference is a non-linear function.

BASIC EQUATIONS TO STUDY ULTIMATE CAUSES

To study the ultimate causes of vertical migration let us assume that a population consists only of non-migrating ethotypes and let us ask for conditions allowing a successful invasion of migrating ethotypes. This is only possible when the payoff for migrating ethotypes is larger than for non-migrating ones. Therefore, we can derive a minimal condition for vertical migration by setting the payoff difference equal to zero (at relative frequency of non-migrating zooplankton arbitrarily close to $x_s=1$). From the payoff equations given by Gabriel and Thomas (1988b), we have

$$(1) \quad 0 = (1 - p)\beta_s a_d - 1.5p\beta_s(a_n + a_d)t_s + \beta_s a_n - \beta_v a_n w .$$

Subscript s is used for the (stationary) strategy of non-migrating zooplankton and subscript v for the strategy of vertical migration. The food-uptake during night (=n) and day (=d) in the upper water layers is denoted as a_n and a_d , respectively, and is a function of zooplankton density, daylength, algal growth rate, maximal filtration rate of zooplankton, and availability of algal food. A slow-breeding correction factor w has to be applied to measure the fitness disadvantage of prolonged generation time (for detailed discussion see Gabriel and Thomas 1988):

$$(2) \quad w = (1 + \beta_v a_n t_v) / (1 + \beta_v a_n t_s)^{t_v/t_s} .$$

The food uptake is calculated from the interaction of zooplankton and algae. At low food levels the ingested food is proportional to the actual food concentration. This results in a food uptake during day of

$$(3) \quad a_d = gA[\exp\{(r_p - gx_s N)(1 - T_n)\} - 1]/(r_p - gx_s N) ,$$

and during night (for non-migrating zooplankton) of

$$(4) \quad a_n = A \exp\{(r_p - gx_s N)(1 - T_n)\} [1 - \exp\{-gNT_n\}]/N .$$

At algal concentrations above a certain limit (A_{lim}) the food uptake during day ($= a_d$) and night ($= a_n$) is independent of the actual algal density but only a function of this limiting concentration level. For high food concentrations a_d and a_n are then simply given by

$$(5) \quad \begin{aligned} a_d &= gA_{lim}(1 - T_n) && (\text{for } A > A_{lim}) \\ a_n &= gA_{lim}T_n && (\text{for } A > A_{lim}). \end{aligned}$$

For any situation, viz. for any given parameter set, we can now solve equation (1) in order to calculate threshold values. Whether these threshold values are maximal or minimal values depends trivially on the derivative of the payoff difference with respect to the parameter in question. To discuss ultimate causes we solve equation (1) for the ratio between the strategy dependent conversion efficiencies β . From the model equations, it follows that β_s is always positively correlated with the non-migration strategy and any increase in β_v is in favour of vertical migration. Therefore, the threshold ratio β_v/β_s is a minimum value: vertical migration can never be an ESS for values below this threshold. In the following we will discuss the consequences of this threshold ratio which can be calculated from equation (1) :

$$(6) \quad (\beta_v/\beta_s)_{thres} = [1 + a_d/a_n - p(a_d/a_n + 1.5 t_s(1 + a_d/a_n))] / w .$$

RESULTS AND DISCUSSION

Lets first consider the simplest case of very low mortality caused by visually orientated predators like fish; i.e. $p=0$. The threshold ratio (6) then gives the value that compensates for the lower food uptake and the prolonged development time of vertically migrating zooplankton. The value for this threshold ratio is then

$$(\beta_v/\beta_s)_{thres} = [1 + a_d/a_n] / w \quad (\text{for } p=0)$$

and is reduced further in the case of high food concentration to the simple expression

$$(\beta_v/\beta_s)_{thres} = (T_n w)^{-1} \quad (\text{for } p=0 \text{ and } A > A_{lim})$$

because of $a_d/a_n = T_n^{-1} - 1$. At lower food concentrations ($A < A_{lim}$) this

is also a valid approximation under the condition that $gNT_n \ll 1$ and $(r-gN)(1-T_n) \ll 1$; this means biologically that the interaction of algae and zooplankton is not too far from a steady-state condition and that the mortality imposed on the algae by zooplankton is not too large.

The necessary advantage for vertically migrating zooplankton in β_v , the efficiency of converting food uptake into successful reproduction, can be lowered drastically for $p > 0$. For high food concentrations we get from equations (6) and (5)

$$(\beta_v/\beta_s)_{\text{thres}} = [1 - p(1 - T_n + 1.5 t_s)]/wT_n.$$

This is again approximately true also at low food concentrations under the above mentioned conditions.

If predation pressure is high enough, vertical migration is favoured even for $\beta_v < \beta_s$. For further increasing p , the necessary β_v -value to establish vertical migration as an ESS becomes smaller and smaller. From equation (6) it can be seen that there is an upper limit for p

$$p_{\text{tol}} = (a_d + a_n(1 - \beta_v w/\beta_s)) / (a_d(1 + 1.5t_s) + 1.5a_n t_s)$$

above which the threshold ratio would become negative. This means that at predation pressure above this value the strategy of non-migrating zooplankton can never be an ESS irrespective of the value for β_v , the conversion efficiency for migrating ethotypes. (This limit on p is discussed by Gabriel and Thomas (1988b) as the tolerable predation pressure for the non-migratory strategy.) In Figures 1 and 2 the threshold ratios are shown for values of p varying from $p=0$ to $p=p_{\text{tol}}$. They are plotted as functions of t_v/t_s , and reflect various mean temperature differences between upper and lower water strata which are experienced by migrating and non-migrating zooplankton. From the figures it is immediately clear that it would be very difficult to compensate for the disadvantage of vertical migration without the added advantage of predation avoidance. It seems to be impossible to overcome this disadvantage simply by invoking a more favourable metabolic state. But there might be a chance to compensate for the disadvantage of vertical migration even at low predation pressure (small p) if juvenile mortality for non-migrating zooplankton is very high compared to migrating ones.

Another interesting aspect arises from the attempt to quantify the

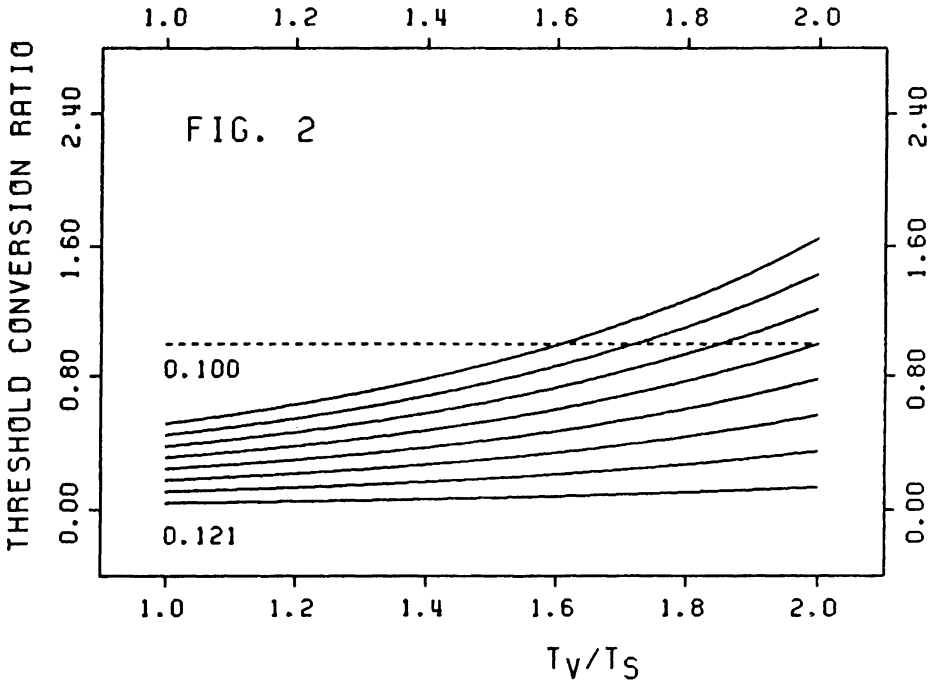
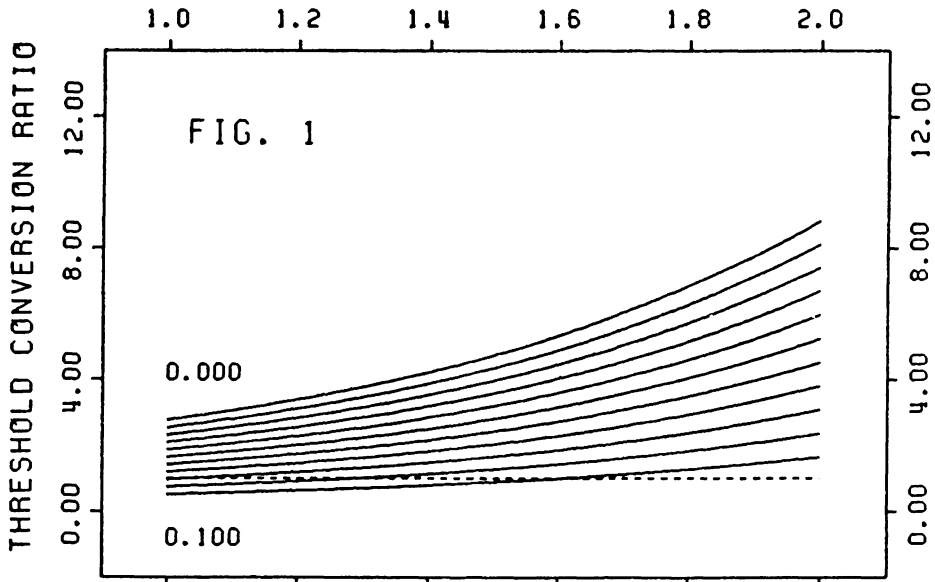


Fig. 1 and Fig. 2 :
 Threshold ratio of the conversion efficiency β_V/β_S of food into successful reproduction depending on the ratio t_V/t_S of egg development time of both strategies. The predation pressure is varied from 0 to 0.1 in Fig.1 and from 0.1 to 0.121 in Fig.2. The broken lines indicate equal conversion efficiencies $\beta_V=\beta_S$. (The following parameter values are used : $g = 0.55$, $r = 0.35$, $N = 1$, $T_n = 0.4$, $t_s = 5$, $A = 0.5 A_{lim}$.)

necessary compensation just for the reduced food uptake during vertical migration. Let us assume equal conversion efficiencies for this purpose. Therefore, we put $(\beta_v/\beta_s)_{\text{thres}} = 1$. Furthermore let us assume equal developmental time for both strategies which is equivalent to a negligible temperature difference between upper and lower water strata. Therefore, let us put $t_s = t_v$ which implies $w=1$. With equation (6) we can now calculate a predation pressure p_{com} that compensates only for the lower food uptake of migrating ethotypes:

$$P_{\text{com}} = (1 + 1.5(a_n/a_d + 1)t_s)^{-1} .$$

For high food concentrations (and also approximately for low food concentrations) we get

$$P_{\text{com}} = (1 + 1.5t_s/T_n)^{-1} \quad (\text{for } A > A_{\text{lim}}).$$

It may be counterintuitive that this value is still dependent on t_s , the egg development time for non-migrating zooplankton. But the energy stored in the eggs and ovaries is lost in the case of predation and this energy is a function of the moulting period which is roughly equivalent to t_s . Therefore, at lower temperatures in the upper waters, fish predation can compensate more easily for the reduced food supply due to vertical migration. This is completely independent of the temperature in the bottom waters.

SUMMARY

The model equations demonstrate that it is extremely unlikely that metabolic advantages by themselves are the ultimate causes of diel vertical migration in zooplankton. Various selective forces interact in a complex way to select this behaviour, which only seems to be disadvantageous at the first glance. Relative strength and interaction of single components of these selective forces can be quantified by applying evolutionary game theory. This concept allows one to calculate boundary conditions for the invasion of vertically migrating ethotypes into a population consisting only of non-migrating zooplankton. A most useful quantity to study ultimate causes of this behavioural phenomenon is the threshold ratio of conversion efficiency of food into reproduction. From this analysis, we suggest that the reduction of predator-induced mortality is one of the most important selective forces influencing vertical migration.

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