

EVALUATION OF SYSTEM PERFORMANCE THROUGH OPTIMIZING ASCENDENCY IN AN AQUATIC ECOSYSTEM MODEL

SANTANU RAY^{*,†}, LUDEK BEREČ[†], MILAN STRAŠKRABA[†]
and ROBERT E. ULANOWICZ[‡]

[†]*Department of Theoretical Biology, Institute of Entomology,
Academy of Sciences of the Czech Republic,
and*

*Faculty of Biological Sciences, University of South Bohemia,
Branišovská 31, 37005 České, Budějovice, Czech Republic*

[‡]*University of Maryland System, Chesapeake Biological Laboratory,
Solomons, MD 20688-0038, USA*

**santanu_5@yahoo.com*

Received 2 January 2001

Revised 2 March 2001

We develop a six-compartment model consisting of phosphorus, detritus, phytoplankton, zooplankton, planktonivorous fish and pisciphagous fish. In this model, we study the implications that the body sizes of phytoplankton and zooplankton have on the system dynamics. We use ascendancy as a goal function or indicator of system performance. Ascendancy quantifies growth and development of an ecosystem as a product of total system throughflow and the mutual information inherent in the pattern of internal system flows. Different physiological rate parameters of phytoplankton and zooplankton are assessed by means of allometric relationships applied to their body sizes. We let the phytoplankton body size range from $10 \mu\text{m}^3$ to $10^7 \mu\text{m}^3$ and the zooplankton body size range from $10 \mu\text{m}^3$ to $10^4 \mu\text{m}^3$ in volume. We also investigate the effects of phosphorus input conditions, corresponding to oligotrophic, mesotrophic and eutrophic systems on system dynamics. Ascendancy (to be maximized over phytoplankton and zooplankton sizes) was computed after the system had reached a steady state. Since it always was a seasonal cycle, and the ascendancy followed this behavior, we averaged the ascendancy over 365 successive days (duration of one year) in the oscillatory phase. Under all types of nutrient conditions, the smallest phytoplankton size yielded the maximal values of the ascendancy, while the corresponding zooplankton size varied. Under oligotrophic conditions, a phytoplankton size of $10 \mu\text{m}^3$ combined with a zooplankton size of $10^{1.25} \mu\text{m}^3$ to give the maximum value of the ascendancy. Under mesotrophic and eutrophic conditions, maxima were obtained for zooplankton sizes $10^{2.26} \mu\text{m}^3$ and $10^{3.20} \mu\text{m}^3$, respectively.

Keywords: Ascendancy; phytoplankton; zooplankton; phosphorus; fish; body size; allometry.

*Corresponding author. Present address: Visva Bharati University, Siksha Bhaban (Science Faculty), Department of Zoology, Santiniketan, Birbhum, India.

1. Introduction

The size of an organism affects virtually all aspects of its physiology and ecology [36]. The works of Hemmingsen and Schmidt-Nielsen on the physiology of body size [26, 27, 62], Gould on its phylogenetic ramifications [22], and a general theoretical model by McMahon [43] have collectively served to bring the importance of body size as a biological variable forcibly to the attention of biologists. The recent explosive growth of both theoretical and empirical studies on the influence of size on all aspects of biology and evolution, and the extension of such studies from a focus on physiology and functional morphology to broader ecological characteristics have resulted in a spate of books on the subject [7, 56, 63]. As a result, the field of allometry — the study of relationships between organism size and function — has become rather suddenly a prominent focus in ecology and evolutionary biology.

The size distributions of the various organisms comprising an ecosystem provide a holistic description that facilitates comparisons of distinct ecosystems in time and space [16]. Gliwicz and Umana proposed that, out of different morphological, behavioral and life history comparisons, body size appears to be the factor most responsible for the vulnerability of any system dynamic [21]. Biomass size spectra provide an important tool with which to search for generalizations in pelagic ecosystems [15]. The allometric relationships of physiological processes of living organisms with their respective body sizes are cast as algebraic statements that often include logarithms [56, 57]. System dynamics are regulated mainly by the physiological rate parameters of all living state variables, and body size contributes significantly to the control of these parameters [28, 75].

Usually, planktonic ecosystems are described by compartmental models, wherein each compartment represents a trophic level or taxonomic group. In most such cases the models are primarily descriptive, because the most important components and their interactions relate to the links among the compartments [45]. The use of these models carries with it numerous problems, however. Unrealistic lumping of various plankton sizes having vastly different physiological rate parameters is a common practice in many dynamical models [44]. To overcome this problem, Anderson *et al.* have suggested to increase the number of compartments [3], but this approach seems only to add to the complexity of the model and lead, in most cases, to unrealistic results. Thus, an alternative approach has been developed for planktonic systems: incorporating rate processes that vary according to the body sizes of plankton explicitly into the model dynamics. Lebedeva first used this approach for phytoplankton [38] and was followed by Radtke and Straškraba [60], Platt *et al.* [58] and Moloney and Field [45]. Ray *et al.* applied the same approach to both phytoplankton and zooplankton [61]. This is also the modelling approach we follow in this paper.

Ecological (and biological) growth and development have very much to do with the evolution of order in organized matter, and work must be done to create this order out of the background (reference state) that is less ordered. Purpose is frequently

brought into discussions on the origins of order in the form of “objective functions”, “goal functions”, “optimization criteria”, “extremal principles” or “orienters” [48]. Various authors have proposed various concepts to serve as goal functions. Lotka suggested the “maximum power principle”: systems become organized to maximize their energy throughput, or power [41, 42]. Prigogine and Stengers proposed the “maximum production of entropy” [59], and later Schneider and Kay suggested an extended version of the second law of thermodynamics as an organizing principle for systems (the “maximum dissipation of exergy” principle) [64, 65]. (“Exergy” is defined as the work a system can perform as it is brought into equilibrium with the environment or with another well defined reference state.) Morowitz considered that energy flow caused cycling, which in its turn produced organization, implying “maximum cycling” as a goal function [46]. Cheslak and Lamarra proposed that ecological systems self organize so as to maximize the retention time of acquired energy (the “maximum residence time” principle) [8]. Odum introduced another goal function, “embodied energy”, which was later contracted to “emergy” [53]. Jørgensen also considered exergy to be key to the development process [31, 32], but unlike Schneider and Kay, he proposed that systems maximize their storage of exergy [64]. Straškraba described this idea in cybernetic terms: the goal function is transmitted to an optimizer, which is also provided with relevant information about the process [72]. Information signals are used in conjunction with the goal function to select for the optimal species from among an existing set. Ulanowicz proposed the principle of “maximum ascendancy”, where ascendancy quantifies network organization of the system as the product of throughflow and the mutual information inherent in the pattern of flows [77].

In the current work, we couple the cybernetic viewpoint of Straškraba [72] with the ascendancy goal function of Ulanowicz [77] to examine what might be the best pattern of growth and development of a system under different levels of available nutrients. Oligotrophic, mesotrophic and eutrophic conditions are provided to an ecosystem model, and different size classes of phytoplankton and zooplankton are examined to see which will yield the greatest ascendancy value. Such a cybernetic approach was first used by Radtke and Straškraba to maximize algal biomass in a size-structured phytoplankton model [60], and later Ray *et al.* followed the same procedure to optimize exergy in a size-structured model containing both phytoplankton and zooplankton [61].

2. The Model

We employ empirically established allometric relationships between the (logarithm of) individual cell or body volume and rates of physiological processes of phytoplankton and zooplankton. Cell or body volume has been used as a measure of organism size by many authors [34, 60, 66, 75]. We surveyed the literature thoroughly and selected appropriate ranges for cell or body volumes of phytoplankton (from 10 to $10^7 \mu\text{m}^3$) and zooplankton (from 10 to $10^4 \mu\text{m}^3$). We shall denote

phytoplankton and zooplankton volumes by V_p and V_z , respectively, where $V_p i$ and $V_z i = \log(10^i \mu\text{m}^3)$. All rates involved have the unit day^{-1} .

2.1. Physiological Parameters of Phytoplankton

Williams, Eppley and Sloan, Tilzer, Findlay, Archambault *et al.* and Smith *et al.* experimentally studied the dependence of phytoplankton growth rate upon organism size in different environments [4, 12, 14, 68, 76, 80]. On the basis of their observations on maximal gross photosynthetic activity (P_{\max}), we estimate that

$$P_{\max}(V_p) = 3.0 - 0.3 \log V_p.$$

Photosynthesis depends upon temperature, and the above formula holds true for the temperature of 20°C. The dependence on temperature (T) becomes exponential,

$$P_{\max}(V_p, T) = (P_{\max}(V_p)/6.05) \exp(0.09 T).$$

The respiration rate of phytoplankton (Resp) depends upon its body size [82] too. For smaller species of phytoplankton the respiration rate is four times higher than for larger species. The result is an approximately logarithmic dependence of the respiration rate upon size:

$$\text{Resp}(V_p) = 0.02 - 0.002 \log V_p.$$

Referring to the work of Kiefer and Austin [35], Radtke and Straškraba proposed the following equation for size-dependent self-shading (Ext) among phytoplankton [60]:

$$\text{Ext}(V_p) = 0.12 V_p^{-0.33} = 0.12 \exp(-0.33 \log V_p).$$

Findlay observed that the natural rate of phytoplankton mortality (Mort) also depends upon size [14], being high in smaller phytoplankton but low in larger organisms. We choose to estimate the mortality rate as

$$\text{Mort}(V_p) = 0.043 - 0.006 \log V_p.$$

Eppley *et al.* suggested a logarithmic increase with size of the half-saturation constant (K_s) of nitrogen uptake by phytoplankton [11]. We assume a similar relationship for phosphorus uptake, with values ranging between 5 and 65 mg Phos m^{-3} . We therefore propose that

$$K_s(V_p) = 10 \log V_p - 5.$$

2.2. Physiological Parameters for Zooplankton

The growth rate of zooplankton also varies according to the body size, with the maximum recorded for smaller species and the minimum among larger species [1, 5, 19]. On this basis and according to the calculations by Peters [56], we propose that

$$\text{Growth}(V_z) = 0.715 - 0.13 \log V_z.$$

In a similar fashion, the respiration rate of zooplankton also depends upon size, achieving its maximum among smaller species and its minimum for larger species [1, 2, 5, 8]. Again, following Peters [56], we assume that

$$\text{Resp}(V_z) = 0.033 - 0.008 \log V_z.$$

Blueweiss *et al.* reported much the same qualitative dependency of zooplankton mortality rate on size [5], and we have calculated the rate as

$$\text{Mort}(V_z) = 0.054 - 0.012 \log V_z.$$

Lehmann and Blueweiss *et al.* reported that the half saturation constant of zooplankton grazing on phytoplankton (K_s) increases logarithmically with body size [5, 39]. Working with phosphorus, Straškraba and Gnauck suggested that the constant ranges from 10 to 55 mg Phos m^{-3} [73], and we therefore propose the relation

$$K_s(V_z) = 15 \log V_z - 5.$$

2.3. Model Equations

All of the above allometric dependencies have been incorporated into a dynamic model of phosphorus (N), phytoplankton (P), zooplankton (Z), planktonivorous fish (F_1), pisciphagous fish (F_2) and detritus (D); see Fig. 1. The model equations are presented below, and the description of the parameters, their values and the corresponding dimensions are given in Table 1. This model may pertain to the well-mixed epilimnion of a temperate lake.

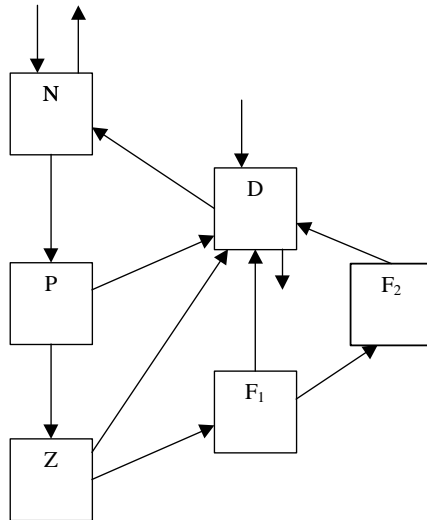


Fig. 1. Conceptual diagram of the six-compartment model. The compartments include phosphorus (N), phytoplankton (P), zooplankton (Z), planktonivorous fish (F_1), pisciphagous fish (F_2), and detritus (D).

$$\begin{aligned}
dN/dt &= (Q/V)(\text{Fin} - N) + d_D D - P_{\max}(V_p, T) \text{Le}PN/(N + K_s(V_p)) \\
&\quad \text{Le} = \text{light effect on photosynthesis} = (I/I_{\text{opt}}) \exp(1 - I/I_{\text{opt}}) \\
&\quad I = I_s \exp[(-E_c + \text{Ext}(V_p)ze)] \\
dP/dt &= P_{\max}(V_p, T) \text{Le}PN/(N + K_s(V_p)) - \text{Resp}(V_p)P \\
&\quad - \text{Growth}(V_z)ZP/(P + K_s(V_z)) - \text{Mort}(V_p)P \\
&\quad \text{Growth}(V_z)ZP/(P + K_s(V_z)) = \text{grazing of } Z \text{ on } P \\
dZ/dt &= a_{rz} \text{Growth}(V_z)ZP/(P + K_s(V_z)) - \mu_{zf}F_1Z/(Z + K_{sf1}) \\
&\quad - \text{Mort}(V_z)Z - \text{Resp}(V_z)Z \\
&\quad \mu_{zf}F_1Z/(Z + K_{sf1}) = \text{predation of } F_1 \text{ on } Z \\
dF_1/dt &= a_{rf1}\mu_{zf}F_1Z/(Z + K_{sf1}) - m_{rf1}F_1 - r_{rf1}F_1 \\
&\quad - \mu_{ff}F_2s_{f1f2}F_1/(s_{f1f2}F_1 + s_{f2f2}F_2 + K_{sf2}) \\
&\quad \mu_{ff}F_2s_{f1f2}F_1/(s_{f1f2}F_1 + s_{f2f2}F_2 + K_{sf2}) = \text{predation of } F_2 \text{ on } F_1 \\
dF_2/dt &= a_{rf2}\mu_{ff}F_2s_{f1f2}F_1/(s_{f1f2}F_1 + s_{f2f2}F_2 + K_{sf2}) - m_{rf2}F_2 - r_{rf2}F_2 \\
&\quad - (1 - a_{rf2})\mu_{ff}F_2s_{f2f2}F_2/(s_{f1f2}F_1 + s_{f2f2}F_2 + K_{sf2}) \\
dD/dt &= (Q/V)\text{Din} + (1 - a_{rz})\text{Growth}(V_z)ZP/(P + K_s(V_z)) \\
&\quad + \text{Mort}(V_p)P + \text{Resp}(V_p)P + (1 - a_{rf1})\mu_{zf}F_1 \\
&\quad Z/(Z + K_{sf1}) + \text{Mort}(V_z)Z + \text{Resp}(V_z)Z \\
&\quad + (1 - a_{rf2})\mu_{ff}F_2s_{f1f2}F_1/(s_{f1f2}F_1 + s_{f2f2}F_2 + K_{sf2}) + m_{rf1} \\
&\quad F_1 + r_{rf1}F_1 + (1 - a_{rf2})\mu_{ff}F_2s_{f2f2}F_2/(s_{f1f2}F_1 + s_{f2f2}F_2 + K_{sf2}) \\
&\quad + m_{rf2}F_2 + r_{rf2}F_2 - d_S D - d_D D
\end{aligned}$$

2.4. Ascendency

The ascendency concept aims at quantitatively describing the growth and development of an ecosystem as a whole [77]. Growth is defined as an increase in the total system throughflow, while development is taken to be a rise in the average mutual information inherent in the network flow structure. According to Ulanowicz, as an ecosystem matures and goes through a series of successional stages, its ascendency exhibits a propensity to increase [78]. It follows that if a system is affected by pollution or other disturbance the flows of energy and materials through the system will change, and with them the ascendency. This was demonstrated experimentally by Ray *et al.* [61]. Formally, the ascendency can be computed as follows [55, 79]:

$$A = T \sum_{i,j=0}^n \frac{f_{ij}}{T} \log \left[\frac{f_{ij}T}{T_i T_j} \right]$$

Table 1. Parameter symbols, their description, values and units.

| Symbol | Description | Value | Unit |
|-------------------|--|---------------------------|--|
| Iopt | Optimum surface radiation for photosynthesis | 300 | cal cm ⁻² day ⁻¹ |
| Is | Surface solar radiation | 280 + 210 sin (58.1 Time) | cal cm ⁻² day ⁻¹ |
| Time | | | day |
| Ec | Extinction coefficient | 0.2 | m ⁻¹ |
| T | Temperature | 12 + 10 sin (58.1 Time) | °C |
| ze | Depth of epilimnion | 4 | m |
| Q | Discharge rate of water | | m ³ day ⁻¹ |
| V | Volume of epilimnion | | m ³ |
| Q/V | | 10 ⁻² | |
| Fin | Concentration of the inflow of Phosphorus in mesotrophic/oligotrophic/eutrophic conditions | 20/5/100 | mg m ⁻³ |
| a _{rz} | Assimilation rate of Z | 0.6 | day ⁻¹ |
| μ _{zf} | Maximum predation rate of F ₁ on Z | 0.14 | day ⁻¹ |
| μ _{ff} | Maximum self-predation rate of F ₂ | 0.08 | day ⁻¹ |
| r _{rf1} | Respiration rate of F ₁ | 0.0015 | day ⁻¹ |
| m _{rf1} | Mortality rate of F ₁ | 0.001 | day ⁻¹ |
| a _{rf1} | Assimilation rate of F ₁ | 0.5 | day ⁻¹ |
| r _{rf2} | Respiration rate of F ₂ | 0.0001 | day ⁻¹ |
| m _{rf2} | Mortality rate of F ₂ | 0.001 | day ⁻¹ |
| a _{rf2} | Assimilation rate of F ₂ | 0.4 | day ⁻¹ |
| s _{f1f2} | Predation preference of F ₂ on F ₁ | 2/3 | dimensionless |
| s _{f2f2} | Self-predation preference of F ₂ | 1/3 | dimensionless |
| K _{sf1} | Saturation constant of F ₁ | 70 | mg Phos m ⁻³ |
| K _{sf2} | Saturation constant of F ₂ | 80 | mg Phos m ⁻³ |
| Din | Concentration of D in inflow | 20 | mg m ⁻³ |
| d _S | Settling rate of D | 0.01 | day ⁻¹ |
| d _D | Remineralization rate of D to N | 0.3 | day ⁻¹ |

where T is the total system throughflow, n is the number of compartments, f_{ij} is the flow from compartment i to compartment j (zeroth compartment is the environment), T_i is the total flow leaving compartment i ,

$$T_i = \sum_{j=0}^n f_{ij}, \quad j \neq i,$$

and T_j the total flow entering compartment j ,

$$T_j = \sum_{i=0}^n f_{ij}, \quad i \neq j.$$

We computed the ascendancy after the system had reached a steady state. Since it always was a seasonal cycle (after a transient phase), and since the ascendancy always tracked this behavior, we decided to average the ascendancy over 365 successive days (duration of one year) after the model had reached the oscillatory period. In order to speed up computations and to avoid being trapped in local maxima, maximization was performed in two steps. During the first exploratory step, a square lattice with the edge length $0.2 [\log \mu\text{m}^3]$ was superimposed upon the region of admissible phytoplankton and zooplankton sizes. The average ascendancy was computed at each node to get a rough picture of the behavior of the optimized function. Then a small region was delineated around the expected maximum and inserted into the maximization procedure, being the *fmincon* procedure from the MATLAB 5.3 software package (The Math Works Inc., USA). This procedure solves the constrained optimization problems via the technique of sequential quadratic programming [18].

3. Results

As the size classes of phytoplankton and zooplankton varied, the results of the model varied accordingly. Body sizes of phytoplankton and zooplankton were considered to range from V_p1 to V_p7 and from V_z1 to V_z4 , respectively. Identical initial conditions were applied to all runs. The model was tested under three different phosphorus input rate scenarios: the oligotrophic conditions (input rate 5 mg Phos m^{-3}), the mesotrophic conditions (input rate $20 \text{ mg Phos m}^{-3}$) and the eutrophic conditions (input rate $100 \text{ mg Phos m}^{-3}$). The simulations were intended to pertain to a through-flowing temperate mesotrophic lake with an average retention time of 100 days, an inflow phosphorus concentration of 20 mg m^{-3} , and an extinction depth [70] equal to 4 m. These conditions could apply equally well to the shallow epilimnion of a very cloudy (e.g. bog like) pond or to a deeply mixed but transparent lake. The dependencies of photosynthesis on light and temperature and the influence of self-shading by phytoplankton on photosynthesis were all incorporated into this model.

The annual water temperature and surface solar radiation vary from 2°C to 22°C and $70 \text{ cal m}^{-2}\text{d}^{-1}$ to $490 \text{ cal m}^{-2}\text{d}^{-1}$, respectively. We incorporated a sine function to simulate these variations. Maximum photosynthetic rate of phytoplankton is thus recorded in summer while it reaches its minimum in the winter, and the annual cycle in this rate is observed for all phytoplankton size classes. The growth rate of zooplankton depends mainly on phytoplankton, planktonivorous fish depend on zooplankton, and pisciphagous fish on planktonivorous fish. Thus, we observed annual cycles (simulations suggest that they are stable limit cycles) in all non-zero state variables for all size combinations of phytoplankton and zooplankton.

The annual average biomass of all living state variables and ascendancy values, corresponding to different combinations of phytoplankton size (ranging from V_p1 to V_p7) and zooplankton size (ranging from V_z1 to V_z4) with a unit step in both P and

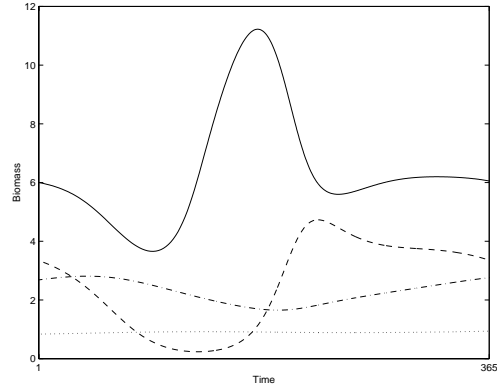
Z , are listed in Table 2 (under the mesotrophic conditions). We used the software package STELLA 6.0 Research (High Performance Company) to run the model for all these size combinations. Table 2 shows that the biomass of phytoplankton increases with its cell size, but this brings decrease in biomass of both types of fish for small and medium V_z . Also, larger-bodied zooplankton are not well-adapted to small-celled phytoplankton. Zooplankton are eliminated from the system when V_z4 is combined with V_p1 , but zooplankton and fish biomasses gradually increase with V_z4 as phytoplankton size increases.

The phytoplankton population increases at high V_p in spite of its slow growth rate. Many authors have pointed out that this slow growth rate is commonly observed in spring, as V_p increases, because it takes more time for the phytoplankton to take advantage of the improved light and temperature conditions, even in the face of increasing phosphorus concentration and weak control by zooplankton. The retarded phytoplankton pulse occurs as a steep exponential increase, which reaches a higher density for larger V_p because there is less control by both nutrients and zooplankton. At V_p7 , there is only a small, late peak in biomass, and zooplankton is unable to reproduce at an adequate rate. The phosphorus concentration in the water column nearly reaches the inflow concentration. For low V_p , the phytoplankton growth rate remains high, which results in the rapid utilization of phosphorus and also causes an increase in zooplankton and fish biomasses. In turn, these mechanisms control phytoplankton, zooplankton and both fish levels in such a way that the fluctuations in all living state variables are smoothed, and the peak does not attain a very large value.

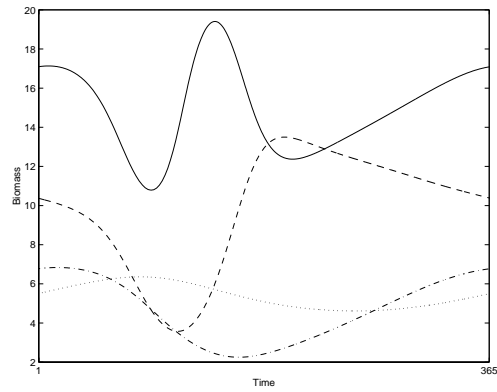
Next, we optimized ascendancy under each of the three nutrient scenarios — mesotrophic, oligotrophic and eutrophic. During optimization, size classes of phytoplankton and zooplankton were free to take on any value within the specified intervals. Under oligotrophic conditions, the combination of the smallest phytoplankton (V_p1) and a small zooplankton ($V_z1.25$) yielded the highest ascendancy value (Fig. 3a). The biomasses of phytoplankton, zooplankton, planktonivorous fish and pisciphagous fish under these conditions are displayed in Fig. 2a. Under mesotrophic conditions, the highest ascendancy value occurred for the smallest phytoplankton size V_p1 and the intermediate zooplankton size $V_z2.26$ (Fig. 3b). The corresponding biomasses of all living state variables are shown in Fig. 2b. Under eutrophic conditions, comparatively larger zooplankton ($V_z3.20$) combined with the smallest phytoplankton (V_p1) to give the maximum ascendancy value (Fig. 3c). The biomasses of all living state variables for this combination are shown in Fig. 2c. We may generalize from these results that, under all nutrient conditions, the system attains its maximum ascendancy whenever phytoplankton are as small as possible; the optimal zooplankton size increases with increasing nutrient load. The physiological rate parameters of phytoplankton and zooplankton corresponding to maximum ascendancy values under various nutrient conditions are given in Tables 3 and 4, respectively.

Table 2. Average biomasses (over a period of 365 days) of phytoplankton (P), zooplankton (Z), planktonivorous fish (F_1), and pisciphagous fish (F_2), and the corresponding ascendancy values (A) under mesotrophic phosphorus conditions.

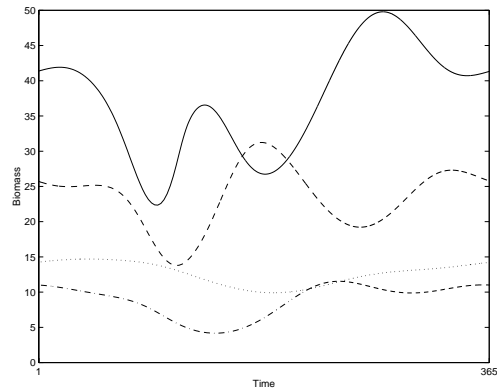
| | | V_z1 | V_z2 | V_z3 | V_z4 |
|--------|-------|--------|--------|--------|--------|
| V_p1 | P | 8.13 | 10.46 | 16.21 | 22.26 |
| | Z | 5.30 | 4.15 | 2.24 | 0.00 |
| | F_1 | 2.28 | 2.43 | 1.32 | 0.00 |
| | F_2 | 1.81 | 2.01 | 0.82 | 0.00 |
| | A | 7.98 | 9.12 | 8.79 | 6.56 |
| V_p2 | P | 10.42 | 12.78 | 17.22 | 20.75 |
| | Z | 6.32 | 3.82 | 2.64 | 0.82 |
| | F_1 | 2.15 | 1.73 | 1.84 | 0.00 |
| | F_2 | 1.81 | 1.07 | 0.82 | 0.00 |
| | A | 5.74 | 6.94 | 7.15 | 5.84 |
| V_p3 | P | 12.32 | 13.87 | 18.61 | 22.97 |
| | Z | 6.58 | 3.84 | 2.64 | 1.78 |
| | F_1 | 1.62 | 1.78 | 1.81 | 0.23 |
| | F_2 | 1.03 | 1.08 | 0.90 | 0.00 |
| | A | 4.46 | 5.49 | 5.97 | 4.95 |
| V_p4 | P | 13.14 | 13.03 | 18.53 | 28.68 |
| | Z | 6.46 | 3.69 | 2.76 | 1.87 |
| | F_1 | 1.75 | 1.58 | 1.98 | 0.81 |
| | F_2 | 1.23 | 1.31 | 0.90 | 0.11 |
| | A | 3.72 | 4.45 | 4.38 | 4.83 |
| V_p5 | P | 15.92 | 12.98 | 19.77 | 30.32 |
| | Z | 6.46 | 4.11 | 3.26 | 1.97 |
| | F_1 | 1.69 | 1.65 | 1.58 | 1.30 |
| | F_2 | 1.13 | 1.30 | 0.82 | 0.10 |
| | A | 3.53 | 3.93 | 5.41 | 4.08 |
| V_p6 | P | 12.74 | 13.13 | 21.86 | 32.63 |
| | Z | 6.81 | 4.87 | 4.12 | 2.35 |
| | F_1 | 0.76 | 2.03 | 1.37 | 1.81 |
| | F_2 | 0.41 | 1.75 | 0.66 | 0.83 |
| | A | 2.68 | 2.73 | 2.85 | 3.26 |
| V_p7 | P | 14.89 | 22.88 | 22.93 | 35.97 |
| | Z | 3.92 | 5.04 | 5.34 | 4.07 |
| | F_1 | 0.00 | 1.62 | 0.63 | 1.46 |
| | F_2 | 0.00 | 0.00 | 0.34 | 0.90 |
| | A | 2.58 | 3.57 | 2.92 | 3.72 |



(a)

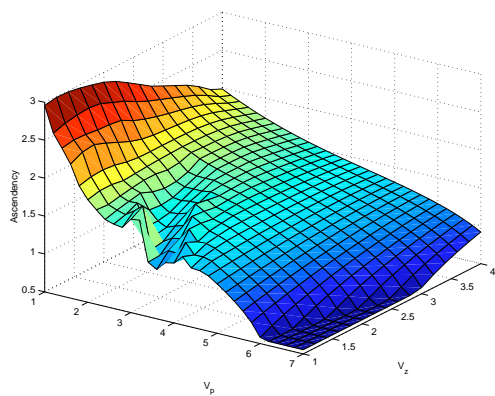


(b)

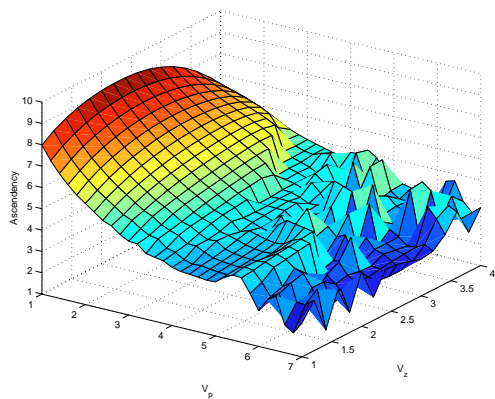


(c)

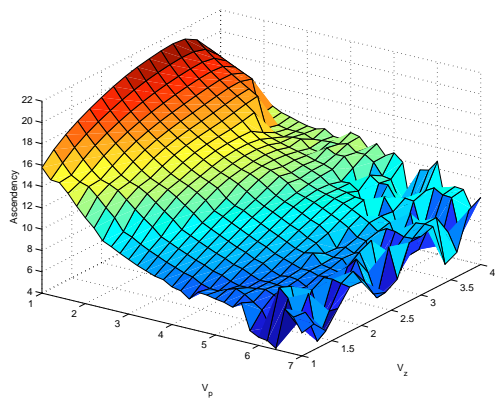
Fig. 2. Biomasses of phytoplankton (solid line), zooplankton (dashed line), planktonivorous fish (dash-dot line) and pisciphagous fish (dotted line) under (a) oligotrophic conditions, (b) mesotrophic conditions, and (c) eutrophic conditions. The horizontal axis represents a period of 365 days, while the vertical axis depicts the concentrations of biomass (mg Phos m^{-3}) of phytoplankton, zooplankton, planktonivorous fish, and pisciphagous fish.



(a)



(b)



(c)

Fig. 3. Plot of average ascendency values for various size classes of phytoplankton and zooplankton over a period of 365 days under (a) oligotrophic conditions, (b) mesotrophic conditions, and (c) eutrophic conditions.

Table 3. Physiological rate parameters of phytoplankton corresponding to the maximum ascendency values obtained under various phosphorus conditions.

| | Under all nutrient conditions: $V_p 1$ |
|--|---|
| Phytoplankton growth rate | 2.40 (at 22°C) d^{-1} 1.31 (at 12°C) d^{-1} 0.22 (at 2°C) d^{-1} 1.31 (average) d^{-1} |
| Phytoplankton respiration rate | 0.018 d^{-1} |
| Phytoplankton mortality rate | 0.037 d^{-1} |
| Phytoplankton self-shading | 0.12 |
| Phytoplankton half-saturation constant | 5 |

Table 4. Physiological rate parameters of zooplankton corresponding to the maximum ascendency values obtained under various phosphorus conditions.

| | Oligotrophic conditions 5 mg Phos m^{-3} : $V_z 1.25$ | Mesotrophic conditions 20 mg Phos m^{-3} : $V_z 2.26$ | Eutrophic conditions 100 mg Phos m^{-3} : $V_z 3.20$ |
|--------------------------------------|---|---|--|
| Zooplankton growth rate | 0.552 d^{-1} | 0.421 d^{-1} | 0.299 d^{-1} |
| Zooplankton respiration rate | 0.023 d^{-1} | 0.015 d^{-1} | 0.007 d^{-1} |
| Zooplankton mortality rate | 0.039 d^{-1} | 0.027 d^{-1} | 0.016 d^{-1} |
| Zooplankton half-saturation constant | 13.80 | 28.93 | 43.00 |

4. Discussion

Evolutionary ecology portends that not only will the organisms best fitted to their environment survive, but that they will also become dominant under those conditions. The environment of an organism includes both its biotic and abiotic components. The abiotic environment for plankton is characterized mainly by temperature, light and nutrients; and these are determined largely by solar radiation, chemical inputs and the activities of organisms. The biotic environment consists mainly of the other organisms present in the pelagic system. Optimal structure theory informs us that selection will favor those organism sizes whose physiological rate parameters are best adapted to the system. Evolutionary system ecology strives not simply to take into account the fitness of each individual organism, but the mutual fitness of all organisms living in the community. By applying system theory to ecological systems, Lebedeva first showed the role of phytoplankton size in aquatic system dynamics [38], and later Straškraba and Radtke and Straškraba extended this work [60, 72]. Ray *et al.* described the effects of phytoplankton and zooplankton size upon the performance of aquatic ecosystems [61]. It has long been recognized that the rates of physiological functions of an organism are quantitatively related to its body size [26].

Progress towards understanding the implications of body size to community functioning followed from empirical measurements of the size structure of aquatic and other communities. Such progress was particularly accelerated by the appearance of automatic sizing machines. Sprules, among others, studied organism size distributions among freshwater plankton systematically and demonstrated that the size spectrum of plankton biomass and/or abundance exhibits distinct peaks at those sizes that correspond to the average sizes of the individual plankton groups [69]. A theoretical explanation of why such peaks of spectra might occur when the underlying relationship of the determining parameters is smooth was presented by Han and Straškraba [24]. They demonstrated that the peaks arose because the slope of the size relationships for individual organism groups is less than the slope across different groups. Other studies presented examples of flatter spectra (on a logarithmic scale) for marine plankton [57], and have indicated how the spectral shape changes with geographical differences. The re-analysis of size spectra models by Han and Straškraba showed that, to avoid massive confusion, it is necessary to distinguish carefully the units of measurement and to exercise great care in how one groups classes of organisms [24]. The size structure of pelagic ecosystems is not constant, but shifts dynamically in response to growth and mortality of individual organisms [23]. What is missing from these empirical investigations is any demonstration of the degree to which the presence of various organisms with different dependencies on size might affect the dynamics of the ecosystem, particularly if representatives of different groups should mutually interact and modify the abiotic environment. In this paper we have attempted to investigate but one aspect of these complex interactions.

In our model we have attempted to express the size dependent qualities of plankton by means of linear functions of the logarithm of cell or body volume. A number of investigators [12, 25, 47, 68, 74] considered how different parameters for phytoplankton and zooplankton depend upon size and have suggested that considerable improvement might be achieved by incorporating this recent knowledge into dynamic models. Inherent in the body size of an organism is an interplay between its physiological properties and the overall community structure. Relationships between body size and physiological rates in plankton are more or less linear on a logarithmic scale, but it should be stressed that in most instances the curves are highly nonlinear when viewed on a non-logarithmic scale. At low V_p and V_z one often observes a steep drop in the parameter values. At higher V_p and V_z changes in the rate parameters level out. Therefore, a change in V_p or V_z by a single order of magnitude when they are large might induce only a small effect on process rates, but it could have a pronounced effect when V_p and V_z are low.

Recent data on rates of growth and photosynthesis suggest no changes to our basic idea. Observations in nature using ^{14}C autoradiography tend to support ideas derived from the analysis of cultures [9, 49]. One problem concerns the need for a more exact specification of the interactions between growth, respiration and the effects of nutrient limitation. Most experiments are not adequately designed to

address these process interactions, and the isolated treatment of variables related to size could lead to serious errors in estimation. For example, the marked dependence of growth rates on size might be a consequence of the other two factors (respiration and nutrient limitation), so that their additive inclusion would be superfluous.

An approach to self-shading similar to what we have used in the present model was treated by Steele and Frost [71]. Detailed theoretical analyses suggest, however, that size exerts a much less pronounced effect on Ext (V_p) than was modelled here, because we ignored changes in the optical properties of phytoplankton of different volumes. (Steele and Frost also did not account for these changes.) In addition to optical properties, differently shaped phytoplankton cells containing different proportions of photosynthetic pigments give rise to different mathematical expressions for attenuation.

Nutrient uptake is strongly limited by transport, and thus depends upon cell or body volume [13, 17, 40, 54]. Nyholm obtained the proportionality factor relating K_s values (phosphorus) to cell or body diameter [50]. Radtke and Straškraba, however, showed that the half-saturation constant is not the ideal parameter for comparing the nutrient dynamics of different species under various conditions, because it depends upon all variables affecting photosynthesis or growth of organisms at higher trophic levels [60]. The index called the “affinity” [6], which is related to the initial slope of the photosynthesis — nutrient curve, should provide a more reliable basis for comparison, but few estimates of this quantity have been made to date. A key factor in transport limitation theory is how transport depends upon the gradient between the external and internal nutrient concentrations. Therefore, two stage internal pool models provide a more adequate description of nutrient uptake and growth limitation, particularly for non-steady-state solutions [30, 50, 51].

Our expressions for the dependency of respiration on body size yield almost the same values for respiration (when recalculated to 10°C) as the formulae used by Steele and Frost [71]. On the other hand, the equation by Laws predicts an extremely steep drop in respiration rate with size [37]; their absolute magnitudes are not comparable to those of Steele and Frost [71]. Smith studied the effect of motility on respiration losses [67]. The photosynthesis-to-respiration ratio was studied by Humphrey for eleven species of marine phytoplankton [29], but it is difficult to isolate the size dependence of these processes from his data, because such effect is confounded by changes in pH and population sizes. From studies of the effects of light intensity upon phytoplankton, one concludes that light sensitivity should also be a function of V_p , although the functionality could also be a consequence of other effects [60].

It seems hardly necessary to point out that size-dependent phytoplankton and zooplankton properties that are driven by physical processes should be supplemented by biotic processes understanding of which remains very limited at present. It is probable that inclusion of such differences in contemporary models would at least reduce the scatter between predictions and observations that is found in most direct comparisons and might even increase our understanding of the processes

themselves. In our model, we can distinguish between those size-dependent processes that we were able, more or less, to base adequately upon the framework of contemporary ideas [$P_{\max}(V_p, T)$, Growth (V_z), Resp (V_p), Resp (V_z), Mort (V_p), Mort (V_z)] and those for which considerably more detail would be desirable [Ext (V_p), $K_s(V_p)$, $K_s(V_z)$]. It might also be desirable to include some additional processes, such as filtration rate of zooplankton or the sinking rate of phytoplankton, into the model.

Different types of goal functions were discussed in the introduction. In this paper we use ascendancy as our gauge of system organization. Ascendancy is a measure of the whole system size and organization, so that an increase in ascendancy can be identified with system growth and development [77, 78]. Ascendancy was tailored to encapsulate numerous phenomenological observations into a single quantitative variable. According to Odum, there are four major groups of attributes that help to identify more “mature” ecosystems: (a) more speciation, (b) finer specialization, (c) longer retention and (d) more cycling [52]. An improvement in any of these generic network properties tends to augment system ascendancy. It is a quantitative tool for diagnosing ecosystem change at the level of whole system. Early in system development the rise in ascendancy is due mostly to the rate at which resources are sequestered by the system, while later the continuing rise is caused mostly by the ever-finer articulation that results from competition between parallel pathways. A decrease in ascendancy is almost always indicative of a stress acting on the system. A small subclass of perturbations, however, can actually serve to increase the overall ascendancy. For example, a sudden increase in exogenous inputs can actually increase the ascendancy by disproportionately raising the total throughflow (T), while at the same time decreasing the mutual information factor. Such a configuration of changes is usually recognized as eutrophication, which always leaves its characteristic signature on the rise in ascendancy [77].

According to the ascendancy theory, in the absence of overwhelming external disturbances, living systems exhibit a propensity to increase in an “ascendent” direction. Increased cycling at a steady state increases both the throughflow and the storage that can be derived from boundary inputs [33]. One is traded for the other, depending on the compositions of components, which affects the turnover rate. Rapid turnover decreases storage and increases throughflow, and vice-versa. Because ascendancy is dominated by its extensive factor, throughflow, whenever this attribute is maximized, storage must be sacrificed accordingly (in the steady state). But, as throughflow and storage are closely coupled, any increase in throughflow is likely to induce a consequent increase in the storage. Conversely, the greater the storage in a system, the more of it is available to be converted to throughflow as circumstances warrant. The idea behind the use of ascendancy as a goal function in models with dynamic structure is expressed as follows: the combination of properties of all the organisms in the ecosystem that gives the highest ascendancy is hypothesized to contribute to the best system performance under the prevailing conditions and provide the most resistance to change from within the system [77,

78]. (Resistance and vulnerability to external stress is another matter entirely.)

We discovered that under all types of nutrient conditions the smallest-sized phytoplankton always gave the maximum ascendancy value, in association with increasing sizes of zooplankton as increasing nutrient loading. It can be concluded that to maintain the best system performance, small phytoplankton should be cropped by small to gradually large-sized zooplankton, as nutrient inputs are increased.

From the experimental observations of many authors [10, 20], it was found that in the small-sized phytoplankton reproduction rate is very high, predation pressure on them by zooplankton is low and in spite of a high mortality rate, these phytoplankton grow successfully under all types of nutrient conditions and their biomass increases proportionally to the increase of the nutrient load. These observations also showed that the grazing efficiency of small-to-large-sized zooplankton increases with their size. Under low nutrient conditions (oligotrophic conditions), minimum phytoplankton biomass is recorded which can only support survival of small zooplankton. The large-sized zooplankton by their higher grazing rate rapidly exhaust the low biomass of phytoplankton and cannot survive. Due to an increase in nutrient load the biomass of phytoplankton also increases and subsequently larger-sized zooplankton are adapted to the changing environment with their increasing grazing efficiency. Our optimization giving maximum ascendancy corroborates the same phenomenon of this experimentally observed phenomenon. It is conceivable that the maximum ascendancy always corresponded with minimum phytoplankton size, because the level of activity of the whole system is driven by the gross primary production, which is maximal for the smallest organisms. Under oligotrophic conditions, there are probably insufficient resources to pass on to higher trophic levels, so the activity of the zooplankton compartment is maximized via small organisms. As more resources (nutrients) are made available to the system, a greater fraction can be passed up the food chain and stored at the higher levels.

Last of all we want to mention that some questions concerning system behavior under certain parameter combinations remain unsolved. It appears that the proper combination of parameters affects model outcome more than the exact representation of the various size dependencies. Obviously, we are unable to a priori reproduce in the model all competitive mechanisms at work (although the optimization process might help to pinpoint the lacunae). Recent theoretical concern over "structural" problems in aquatic ecosystems has centered at size structure [82]. In their simulation results, Steele and Frost observed no profound changes in the proportions of different size groups (or at least the changes were far less than those observed in nature where some species of both phytoplankton and zooplankton were seen to disappear completely from the system, which did not happen in the simulations) [71]. There are possible two reasons behind the discrepancy. First, the competitive mechanisms tending to reduce populations at lower frequencies may be different from those considered in the model. Secondly, the simulation interval may have been too short to allow such profound differences to arise, and asymptotic stability

was not achieved starting from the arbitrary initial conditions we employed. Clearly, some additional work is necessary to improve the correspondence of model results with the natural observations:

- It is important to modify the model runs to correspond to different types of water bodies, so as to allow for direct comparison with observed data on process rates and size distributions.
- The functional relationships of individual process rates to phytoplankton and zooplankton body volumes (and their combinations) have to be updated in accordance with the latest research.
- A comparative study using several different goal functions to gauge system performance should be undertaken to check reliability of the theoretical results.

Acknowledgements

Most unfortunately, Prof. Milan Straškraba passed away while this work was being completed. The other authors hope that this finished work will pay tribute to him and his manifold talents, and they offer their sincere condolences to his family. We are thankful to Prof. Vera Straškrabová for her valuable comments on the early version of this manuscript. Santanu Ray and Luděk Berec acknowledge the support from the Ministry of Education, Youth and Sports of the Czech Republic (Projects VS 96086 and MSM 123100004). Luděk Berec also acknowledges the support by the Grant Agency of the Czech Republic (Grant 201/98/P202) and the Academy of Sciences of the Czech Republic (Grant Z5007907). Robert Ulanowicz was supported in part by the US Environmental Protection Agency's Multiscale Experimental Ecosystem Research Center (MEERC, Contract R819640).

References

- [1] Ahrens A. M. and Peters R. H., Plankton community respiration: Relationships with size distribution and lake trophy, *Hydrobiologia* **224** (1991a) pp. 77–87.
- [2] Ahrens A. M. and Peters R. H., Patterns and limitations in limnoplankton size spectra, *Can. J. Fish. Aquat. Sci.* **48** (1991b) pp. 1967–1978.
- [3] Anderson V., Nival P. and Harris R., Modelling of a planktonic ecosystem in an enclosed water column, *J. Mar. Biol. Assoc. U.K.* **67** (1987) pp. 407–430.
- [4] Archambault P., McKindsey C. W. and Bourget E., Large scale shoreline configuration influences phytoplankton concentration and mussel growth, *Estuarine Coastal and Shelf Science* **49** (1999) pp. 193–208.
- [5] Blueweiss L., Fox H., Kudzma V., Nakashima D., Peters R. H. and Sams S., Relationships between some body size and some life history parameters, *Oecologia (Berl.)* **37** (1978) pp. 257–272.
- [6] Button D. K., Rates of growth, respiration, and photosynthesis of unicellular algae as related cell size: A review, *J. Phycol.* **12** (1976) pp. 135–140.
- [7] Calder W. A. III, *Size, Function and Life History* (Harvard University Press, Cambridge, 1984).

- [8] Cheslak E. F. and Lamara V. A., The residence time of energy as a measure of ecological organization, *Energy and Ecological Modelling*, ed. by Mitsch W. J., Bosserman R. W. and Klopatek J. M. (Elsevier, Amsterdam, 1981) pp. 591–600.
- [9] Desortová B., Productivity of individual algal species in natural phytoplankton assemblage determined by means of autoradiography, *Arch. Hydrobiol. Suppl. 49, Algal. Stud.* **17** (1976) pp. 415–449.
- [10] Duncan A., Food limitation and body size in the life cycles of planktonic rotifers and cladocerans, *Hydrobiologia* **186/187** (1989) pp. 11–28.
- [11] Eppley R. W., Rogers J. N. and McCarthy J. J., Half-saturation constants for uptake of nitrate and ammonium by marine phytoplankton, *Limnol. Oceanogr.* **14** (1969) pp. 912–920.
- [12] Eppley R. W. and Sloan P. R., Growth rate of marine phytoplankton: Correlation with light-absorption by cell chlorophyll a, *Physiol. Plant* **19** (1966) pp. 17–59.
- [13] Falco J. W., Kerr P. C., Barron M. B. and Brockway G. L., The effect of mass transport on bio-stimulation of algal growth, *Ecol. Model.* **1** (1975) pp. 117–131.
- [14] Findlay I. W. O., Effects of external factors and cell size on the cell division rate of a marine diatom *Coscinodiscus pavillardii* Forti, *Int. Rev. Ges. Hydrobiol.* **57** (1992) pp. 523–533.
- [15] Gaedke U., The size distribution of plankton biomass in a large lake and its seasonal variability, *Limnol. Oceanogr.* **37** (1992) pp. 1202–1220.
- [16] Gaedke U., Ecosystem analysis based on biomass size distribution: A case study of a plankton community in a large lake, *Limnol. Oceanogr.* **38** (1993) pp. 112–127.
- [17] Gavis J., Munk and Riley, Nutrient diffusion transport and rates of phytoplankton growth (revised), *J. Mar. Res.* **34** (1976) pp. 161–179.
- [18] Gill P. E., Murray W. and Wright M. H., *Practical Optimization* (Academic Press, London, 1981).
- [19] Gillooly J. F., Effect of body size and temperature on generation time in zooplankton, *J. Plankton Res.* **22** (2000) pp. 241–251.
- [20] Gliwicz Z. and Lampert W., Body-size related survival of cladocerans in a trophic gradient: An enclosure study, *Arch. Hydrobiol.* **129** (1993) pp. 1–23.
- [21] Gliwicz Z. and Umana G., Cladoceran body size and vulnerability to copepod predation, *Limnol. Oceanogr.* **39** (1994) pp. 419–424.
- [22] Gould S. J., Allometry and size in ontogeny and phylogeny, *Bio. Res.* **41** (1966) pp. 587–640.
- [23] Han B. P. and Straškraba M., Size dependence of biomass spectra and population density. I. The effects of size scale and size intervals, *J. Theor. Biol.* **191** (1998) pp. 259–265.
- [24] Han B. P. and Straškraba M., Reanalysis of models and improved model of biomass size spectra, *Int. Rev. Hydrobiol.* **83** (1999) pp. 207–231.
- [25] Harris G. P., *Phytoplankton Ecology: Structure, Function, and Fluctuation* (Chapman and Hall, 1986).
- [26] Hemmingsen A. M., The relation of standard (basal) energy metabolism to total fresh weight of living organisms, *Rep. Steno. Mem. Hos.* **4** (1950) pp. 1–58.
- [27] Hemmingsen A. M., Energy metabolism as related body size and respiration surfaces, and its evolution, *Rep. Steno. Mem. Hos.* **9** (1960) pp. 7–110.
- [28] Hrbáček J., Species composition and amount of the zooplankton in relation to fish stock, *Rozpr. Česk. Akad. Ved., Rada. Mat. Přír. Ved.* **10** (1962) pp. 1–116.
- [29] Humphrey G. F., The photosynthesis: Respiration rate of some unicellular marine alga, *J. Mar. Biol. Ecol.* **18** (1975) pp. 111–119.
- [30] Jørgensen S. E., A eutrophication model for a lake, *Ecol. Model.* **2** (1976) pp. 155–212.

- [31] Jørgensen S. E., *Integration of Ecosystem Theories: A Pattern* (Kluwer Academic Publishers, Dordrecht, 1992a).
- [32] Jørgensen S. E., Parameters, ecological constraints and energy. In *Ecol. Model.* **62**, ed. by Jørgensen S. E. (1992b) pp. 163.
- [33] Jørgensen S. E., Patten C. and Straškraba M., Ecosystem emerging: 4. growth, *Ecol. Model.* **126** (2000) pp. 249–284.
- [34] Kerr S. R., Structural analysis of aquatic communities, *Proc. Ist. Int. Cong. Ecol.* (1974) pp. 69–84.
- [35] Kiefer D. A. and Austin R. W., The effect of varying phytoplankton concentration upon submarine light transmission in the Gulf of California, *Limnol. Oceanogr.* **19** (1974) pp. 55–64.
- [36] La Barbera M., The evolution and ecology of body size. In *Patterns and Process in the History of Life*, ed. by Ranp M. and Jablonsky D. (Springer-Verlag, Berlin, Heidelberg, 1986) pp. 69–98.
- [37] Laws E. A., The importance of respiration in controlling the size distribution of marine phytoplankton, *Ecology* **56** (1975) pp. 419–426.
- [38] Lebedeva L. P., A model of the latitudinal distribution of the numbers of species of phytoplankton in the sea, *J. Cons. Int. Explor. Mer.* **34** (1972) pp. 341–350.
- [39] Lehman J., The filter feeder as an optimal forager and the predicted shapes of feeding curves, *Limnol. Oceanogr.* **21** (1976) pp. 501–516.
- [40] Liu S. H., Oxygen diffusion in a spherical cell with nonlinear oxygen — uptake kinetics, *J. Theor. Biol.* **60** (1976) pp. 449–457.
- [41] Lotka A. J., Contribution to the energetics of evolution, *Proc. Natl. Acad. Sci. USA* **8** (1921) pp. 147–150.
- [42] Lotka A. J., *Elements of Physical Biology* (Williams and Wilkins, Baltimore, Maryland, 1925), pp. 460.
- [43] McMahon T. A., Size and shape in biology, *Science* **179** (1973) pp. 1201–1204.
- [44] Moloney C. L., Bergh M. O., Field J. G. and Newell R. C., The effect of sedimentation and microbial nitrogen regeneration in a plankton community: A simulation investigation, *J. Plankton Res.* **8** (1986) pp. 427–445.
- [45] Moloney C. L. and Field J. G., Modelling Carbon and nitrogen flows in a microbial plankton community. In *Protozoa and their Role in Marine Processes*, ed. by Reid P. C., Burkhill P. H. and Turley C. M. (NATO ASI Series, Springer-Verlag, New York, 1991) pp. 443–474.
- [46] Morowicz H. J., *Energy Flow in Biology, Biological Organization as a Problem in Thermal Physics* (Academic Press, New York, 1968) pp. 179.
- [47] Mostajir B., Simengando T., Demers S., Belzile C., Roy S., Gosselin M., Chanut J. P., Demora S., Fauchot J., Vidussi F. and Levasseur M., Ecological implication of changes in cell size and photosynthetic capacity of marine Prymnesiophyceae induced by ultraviolet – β – radiation, *Marine Ecol. Prog. Ser.* **187** (1999) pp. 89–100.
- [48] Muller F. and Leupelt M. (eds.), *Eco Targets, Goal Function, and Orientors* (Springer, Berlin, 1998).
- [49] Nikulina B. N. and Gutelmacher B. L., Photosynthetic activity of individual species of algae in Lake Krivoe, *Ekologia Moskva* **4** (1974) pp. 101–104 (in Russian).
- [50] Nyholm N., Kinetic studies of phytoplankton limited algal growth, PhD Thesis, Dept. Appl. Biochem., Technical University, Copenhagen, 1975.
- [51] Nyholm N., A simulation model for phytoplankton growth and nutrient cycling in eutrophic, shallow lakes, *Col. Modelling* **4** (1978) pp. 279–310.
- [52] Odum E. P., The strategy of ecosystem development, *Science* **164** (1969) pp. 262–270.
- [53] Odum H. T., *System Ecology* (Wiley Interscience, New York, 1983).

- [54] Pasciak W. J. and Gavis J., Transport limitation of nutrient uptake in phytoplankton, *Limnol. Oceanogr.* **19** (1974) pp. 881–888.
- [55] Patten B. C., Network integration of ecological extremal principles: Exergy, emergy, power, ascendancy, and indirect effects, *Ecol. Model.* **79** (1995) pp. 75–84.
- [56] Peters R. H., *The Ecological Implications of Body Size* (Cambridge University Press, Cambridge, 1983).
- [57] Platt T., Structure of the marine ecosystem: Its allometric basis. In *Ecosystem Theory for Biological Oceanography*, ed. by Ulanowicz R. E. and Platt T. (Can. Bull. Fish. Aquat. Sci., 1985) **213** (1985) pp. 55–64.
- [58] Platt T., Mann K. H. and Ulanowicz R. E., *Mathematical Models in Biological Oceanography* (The Unesco Press, Paris, 1981).
- [59] Prigogine I. and Stengers I., *Order Out of Chaos: Man's New Dialogue with Nature* (Bantam Books, New York, 1984) pp. 349.
- [60] Radtke E. and Straškraba M., Self-optimization in phytoplankton model, *Ecol. Model.* **9** (1980) pp. 247–268.
- [61] Ray S., Ulanowicz R. E., Majee N. C. and Roy A. B., Network analysis of a benthic food web model of a partly reclaimed island in the Sundarban mangrove ecosystem, India, *J. Biol. Syst.* **8** (2000) pp. 263–278.
- [62] Schmidt-Nielsen K., Scaling in biology: The consequences of size, *J. Exp. Zool.* **194** (1975) pp. 287–308.
- [63] Schmidt-Nielsen K., *Scaling: Why is Animal Size So Important?* (Cambridge University Press, Cambridge, 1984).
- [64] Schneider E. D. and Kay J. J., Life as a manifestation of the 2nd law of thermodynamics, *Math. Comput. Model.* **19** (1994a) pp. 25–48.
- [65] Schneider E. D. and Kay J. J., Complexity and thermodynamics: Towards a new ecology, *Futures* **24** (1994b) pp. 626–647.
- [66] Sheldon R. W., Prakash A. and Sutcliffe W. H. Jr., The size distribution of particles in the ocean, *Limnol. Oceanogr.* **17** (1972) pp. 327–340.
- [67] Smith W. O. Jr., The respiration of photosynthetic carbon in eutrophic areas of the ocean, *J. Mar. Res.* **35** (1977) pp. 557–565.
- [68] Smith W. O. Jr., Nelson D. M. and Mathot S., Phytoplankton growth rate in Ross Sea determined by independent methods: Temporal variations, *J. Plankton Res.* **21** (1999) pp. 1519–1536.
- [69] Sprules W. G., Effects of trophic interaction on the shape of pelagic size spectra, *Verh. Int. Verein. Limnol.* **23** (1988) pp. 234–240.
- [70] Steel J. A., Reservoir algal productivity. In *The Use of Mathematical Models in Water Pollution Control*, ed. by James A. (University of Newcastle-upon-Tyne Symp., 1973) pp. 107–135.
- [71] Steele J. H. and Frost B. W., The structure of plankton communities, *Phil. Trans. R. Soc. London, Ser. B.* **280** (1977) pp. 485–534.
- [72] Straškraba M., Natural control mechanisms in models of aquatic ecosystem, *Ecol. Model.* **6** (1979) pp. 305–321.
- [73] Straškraba M. and Gnauck A. H., *Freshwater Ecosystem, Modelling and Simulation* (Elsevier, Amsterdam, 1985) pp. 309.
- [74] Taguchi S., Relationship between photosynthesis and cell size of marine diatoms, *J. Phycol.* **12** (1976) pp. 185–189.
- [75] Tang E. P. Y., The allometry of algal growth rates, *J. Plankton Res.* **17** (1995) pp. 1325–1335.

- [76] Tilzer M., Dynamik and produktivitat von phytoplankton and pelagischen bakterien in einem Hochgebirgeseesee (Vorderer Finstertaler Sec. Osterreich), *Arch. Hydrobiol. Suppl.* **40** (1972) pp. 201–273.
- [77] Ulanowicz R. E., *Growth and Development, Ecosystem Phenomenology* (Springer-Verlag, New York, 1986).
- [78] Ulanowicz R. E., *Ecology, The Ascendent Perspective* (Columbia University Press, New York, 1997) pp. 201.
- [79] Ulanowicz R. E., Life after Newton: An ecological metaphysic, *Biosystems* **50** (1999) pp. 127–142.
- [80] Williams R. B., Division rates of salt marsh diatoms in relation to salinity and cell size, *Ecology* **45** (1965) pp. 877–880.
- [81] Wetzel R. G., *Limnology* (Saunders, Philadelphia, 1975).
- [82] Yurista P. M., A model for temperature correction of size specific respiration in *Bythotrephes cederstroemi* and *Daphnia middendoffiana*, *J. Plankton Res.* **21** (1999) pp. 721–734.