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Pelagic foodweb analysis: hypothesis testing by simulation

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Abstract

Energy flow and material cycling in aquatic environments can be conceptualized in terms of food webs, linking various taxonomic or functional biological compartments and their physical environment. Interpretation of empirical data and finally a functional understanding of the system studied requires a high degree of abstraction and aggregation. The complexity and variability of environmental systems, the scarcity of appropriate observations and experiments, and the lack of a well established theoretical background make it difficult to test any possible conceptualization, or hypothesis, describing a given system. A formal approach to hypothesis testing, based on numerical simulation, which explicitly considers the above constraints, is proposed. Based on a data set from the North Sea, a series of hypotheses on the structural relations and the dynamic function of the pelagic food web is formulated in terms of numerical models. Hypotheses of various degrees of aggregation and abstraction are tested by comparing singular statements (predictions) deduced from the proposed hypotheses (the models) with the observations. The basic processes of primary production, consumption, and remineralization, driven by light, temperature, and advection/diffusion, are described in systems models ranging in complexity from two compartments to many compartments and species groups. With each of the proposed models, a yearly cycle of the systems behavior is simulated. The comparative analysis of the response of each of the models allows conclusions to be drawn on the adequacy of the alternative hypotheses. This analysis also allows one to reject inadequate constructs, and provides some guidance on how to improve a certain hypothesis, even in the presence of a high degree of uncertainty.

Introduction

Hypothesis testing and simulation modeling

Environmental systems are generally large, diverse, and complex. Variability in space and time and an extremely high number of interacting components, which themselves are subject to changes in time, make their observation and understanding an extremely difficult, though challenging, scientific task of increasing socio-economic importance. This is especially true for marine systems, where in addition to all other problems the logistics of the research pose major difficulties.

The very high number of interactions between the numerous elements of ecological systems requires conceptual simplifications, aggregation, and abstraction of the systems under study, to make the theories one can formulate about the structural properties and the function of a system traceable.

Universal statements, describing those properties of a system which are invariant in space and time, may be called models, whether they are of an informal verbal or mental, or a formalized mathematical structure. Such models, viewed as scientific theories, have to be testable, that is to say, when one puts a set of specific singular statements (the initial conditions, which, in the case of a mathematical model also include the model parameters in a general sense, (cf. FEDRA et al. 1980, FEDRA 1981 a) into the model, it must be possible to deduce or predict testable singular statements (observations or experimental results). Disagreement between the prediction deduced from the hypothesis or model and the available observations would then require rejection of the given hypothesis, its modification and improvement or looking for alternative hypotheses, to be subjected to the same procedure. This method, which would basically represent the strategy of scientific research proposed by POPPER (e.g. 1959), however, has a major drawback when applied to complex simulation models or dynamic hypotheses describing ecological systems, in that the so-called initial conditions to be used with the basic structure of the theory, to deduce the testable predictions are not exactly known. This certainly could be seen as the result of two basic shortcomings, one in the available measurement techniques, another in the formulation of the models themselves: if the models require unknowns as inputs, they are not well formulated. The latter is certainly a generic shortcoming of ecological models, or ecological theory in general.

The same line of argument can be followed with regard to the observations used for model-output comparison in hypothesis testing. The degree of abstraction and aggregation is quite different in the measurements and in the model conceptualisation, so that the measurements can only serve as samples of the properties of the units conceptualized. As these units are generally heterogeneous (in terms of their measurable properties), and are generally characterised by a high degree of variability, i.e. the repeatable part of the observations is only a certain range, further uncertainty has to be dealt with in the hypothesis testing procedure. For a more detailed discussion of issues of uncertainty in ecosystems modeling see FEDRA et al. 1980 and FEDRA 1981 a, b.

But whatever the objective of a formal approach to the analysis of a complex, dynamic environmental system may be, the testability of the models involved is an essential criterion to make them a useful scientific tool.

Method

The empirical background: describing the environmental system

Considering the above constraints, the direct use of the raw data available on any ecosystem seems to be rather difficult for the testing of complex and highly aggregated dynamic hypotheses. Consequently, we have to derive, from the available data, a description of the system and the processes we want to study at an appropriate level of abstraction and aggregation. This description, which already has to be formulated in the terms of the hypothesis to be tested, should take advantage of all the available information, and at the same time provide an estimate of the reliability of this information at the required level of abstraction.

As an example to illustrate the approach, a data set from the southern North Sea was used. Most of the information utilized stems from the yearly reports of the Biological Station Helgoland, and describes physico-chemical as well as biological variables at the sampling station "Helgoland-Reede" for the period 1964–1979 (HAGMEIER 1978, LUCHT and GILLBRICHT 1978, Biologische Anstalt Helgoland, yearly reports 1964–1979, including unpublished data of HAGMEIER, HICKEL, MANGELSDORF,

TREUTNER, GASSMANN, GILLBRICHT). However, various other sources have been used for additional information (e.g. STEELE 1974, NIHOUL 1975) to compile a data set typical for an arbitrary location representative for the German Bight, southern North Sea.

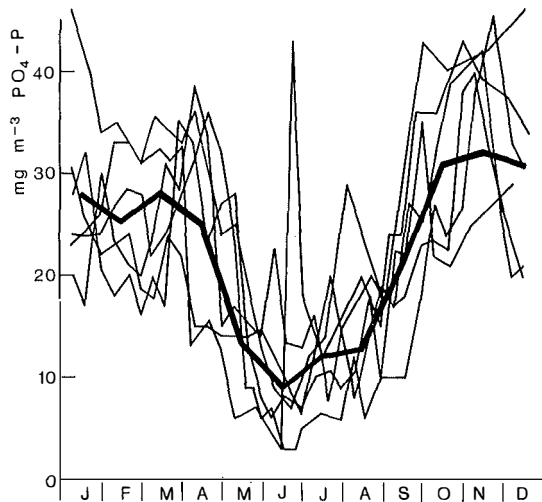


Figure 1

Phosphorus dynamics ($P-PO_4$) for selected years from 1964 to 1979. Thick line indicates monthly averages for the years 1965 to 1975. After unpublished data from WEIGEL and MANGELSDORF; HARMS; HARMS and HAGMEIER; HARMS, MANGELSDORF and HAGMEIER; MANGELSDORF

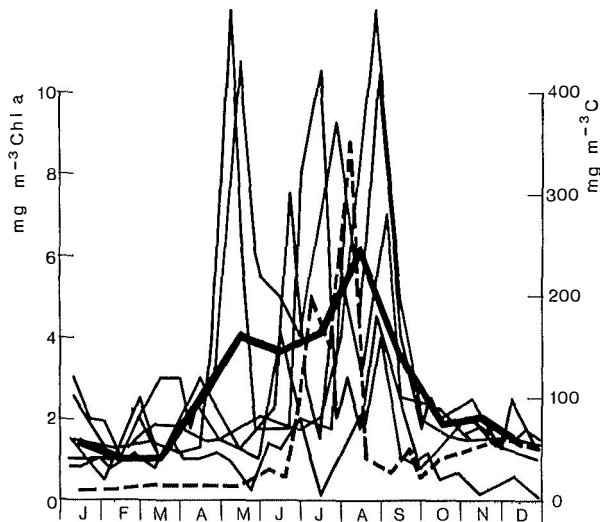


Figure 2

Chlorophyll dynamics for selected years from 1964 to 1979. Thick line indicates monthly averages for the years 1965 to 1975; broken line shows micro-zooplankton carbon for the year 1975. After unpublished data from WEIGEL, HAGMEIER and TREUTNER; HAGMEIER, KANJE and TREUTNER

Figures 1, 2 and 3 summarize the data used. The driving environmental variables water temperature and radiation were found to be smooth and regular enough for a direct utilization of the long-term averages, approximated by simple sine waves. Data for nutrients ($P-PO_4$) and algae (measured as chlorophyll as well as in terms of carbon, recalculated from counts) showed consistent yearly patterns. However, when including the year-to-year variations (as well as the implicit sampling errors), the high variability of the observations as well as the difficulty in averaging over time (several years) becomes obvious. Although the average phytoplankton dynamics show a single, but extended peak around July/August, the individual years exhibit at least two peaks in the summer, which, due to their variable timing, are averaged out when looking at the long-term mean (Fig. 2). Also, the long-term mean is about one order of magnitude below the spiky peaks of the individual year's data. Little information was available on zooplankton biomass values. However, some additional information from independent experimentation, mainly on primary production, was also found. For example, estimates of monthly primary production for three years are shown in Figure 3 b. Also, the (time-variable) ratio of phytoplankton carbon to chlorophyll was used for the models described below, approximated by a simple exponential curve (Figure 3 a).

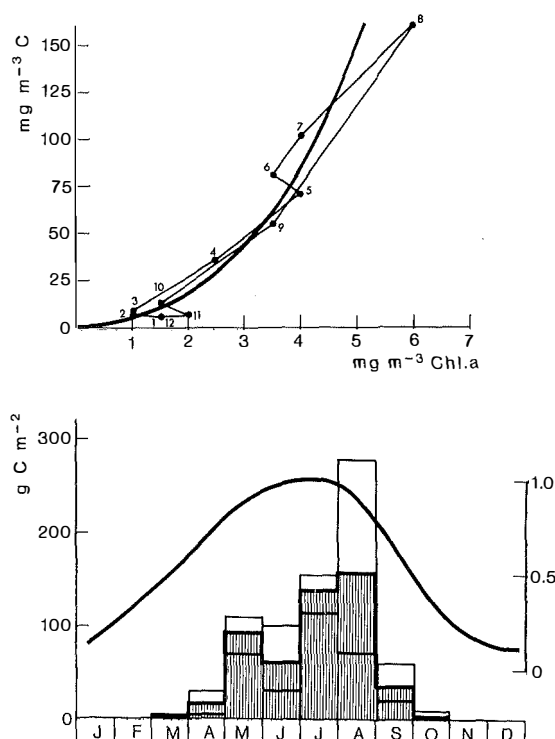


Figure 3a

Relationship between phytoplankton carbon and chlorophyll, approximated by an exponential curve (monthly averages for 11 years). Numbered dots indicate data point of individual months

Figure 3b

Estimates of monthly sums of primary production for the years 1966–1968. After HAGMEIER; smooth curve shows the light- and temperature-dependent relative productivity used in the models

Among the invariable generalizable features derived from the observations are the following:

1. Primary producers are below a level of $4\text{mg}\cdot\text{m}^{-3}$ chlorophyll during the first three months of the year;
2. between Julian day 120 and day 270 there is an at least twofold increase in biomass;
3. there have to be at least two peaks within that period, with a more than 25 % reduction of the first peak value in between the two peaks;
4. after day 270, biomass must be below $4\text{mg}\cdot\text{m}^{-3}$ chlorophyll again;
5. the higher of the two peak values must not exceed $25\text{mg}\cdot\text{m}^{-3}$ chlorophyll;
6. yearly primary production must be above 300 and below $700\text{ g C}\cdot\text{m}^{-2}$;
7. herbivorous consumers (zooplankton) reach their first biomass peak value (defined as an at least twofold increase of their initial biomass before a consecutive decline) after the phytoplankton;
8. the maximum density of herbivorous consumers must not exceed $1\,000\text{ mg C}\cdot\text{m}^{-3}$;
9. $\text{PO}_4\text{-P}$ has to be above $20\text{mg}\cdot\text{m}^{-3}$ between day 1 and 90;
10. the average between day 120 and 240 has to be below $20\text{mg}\cdot\text{m}^{-3}$;
11. P-PO_4 has to be above $20\text{mg}\cdot\text{m}^{-3}$ after day 270;
12. it must never exceed $50\text{mg}\cdot\text{m}^{-3}$; and it must never be below $2\text{mg}\cdot\text{m}^{-3}$;
- 13.–17. all state variables must be cyclically stable ($\pm 25\%$ tolerance level).

This description of the observed systems features, defining a region in the behavior hyperspace of the system, has to be understood as a semi-quantitative description of persistent patterns rather than a quantitative description of the system for any specific period in time. Certainly, more resourceful analysis of the available data and the incorporation of additional information would allow this description to be refined.

The description so far is little more than a summary of the more persistent patterns in the data. To make that a description of the system we want to study, we have to define what that system shall be, its elements and its boundary conditions. This, however, is already part of the hypothesis generation, as the assumptions used here are no longer directly deduced from the data. Also, to make this potentially misleading point more explicit, the kind of data collected and the way they are collected is of course already part or rather consequence of a (generally implicit) conceptualization or model of the system. Measuring a few selected variables out of the very large number of potentially measurable items already requires an implicit definition of the system under study and the assumption that whatever is measured is an important and meaningful attribute of the system in the light of the objective of the respective study. Also, measurement strategies, i.e. the distribution of samples in time and space, imply numerous assumptions (as a rule untested assumptions) on the spatio-temporal behavior of the system.

Hypotheses generation: designing alternative models

These relations might well lead to a circular argument: given a certain (implicit) hypothesis about the system structure or function, information is collected according to this hypothesis, which is then in turn used to "proof" the initial hypothesis, now made explicit. It therefore seems to be very important to make all these implicit assumptions based on a priori information explicit, to make all of them subject to critical, independent tests and to explore the consequences in terms of future testability of any complex hypothesis. Also, there are several implicit assumptions

hidden in the way the data are interpreted and the description is derived. Ignoring the short-term spatio-temporal variations (e.g. caused by tide) and looking at average features instead, implies that we are considering a hypothetical body of water, not absolutely fixed in space. The horizontal extension of this water-body is rather arbitrarily limited by the requirement of homogeneity within this spatial element. On the vertical plane, the water-body considered is defined by the extent of the measurements used, but again homogeneity has to be assumed.

Another crucial step to be made is the specification of boundary conditions: we assume the system as it will be described in the subsequent models to have no material exchange at its upper boundary, i.e. with the atmosphere; we also assume that there are no lateral flows, which implies that for the element concerned the surrounding area is big enough and unified enough to make flows due to advection/diffusion negligible; and finally we have to specify the conditions at the lower boundary, where we will assume an "endless sink" of constant chemical properties, that is to say, very large as compared to the productive upper layer we are studying, and the exchange between the upper layer and this sink will be controlled by eddy diffusivity.

All these assumptions are more or less unrealistic whenever we think in terms of specific physical units in time and space; however, this is not what we attempt to model, and the basic idea behind all these assumptions is that the simplified process, rather than the ignored processes, largely dominates the behavior of the conceptual system.

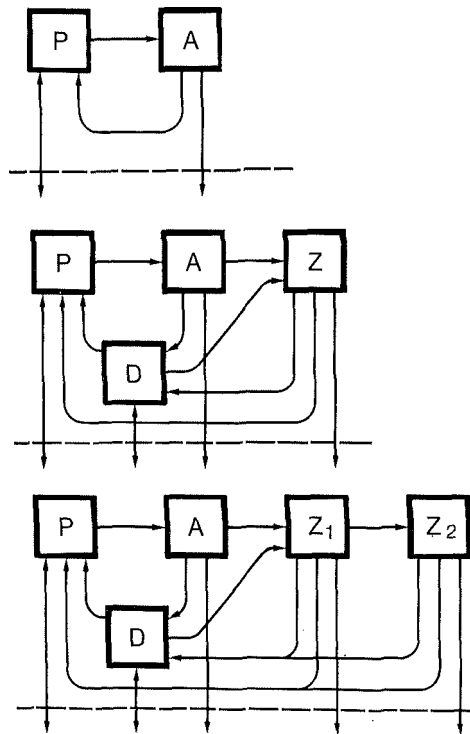


Figure 4

Flow diagrams for the models compared. P: phosphate; A: phytoplankton; D: detritus; Z: zooplankton; Z₁: herbivores; Z₂: carnivores

Hypothesis No. 1: two compartments in a simple physical framework

Let me now try to formulate one very simple hypothesis about the pelagic food web described in the data set above. The system is conceptualized as consisting of only two compartments, namely particulate, photosynthesizing organic matter, and mineral nutrients, which are coupled by the processes of primary production and nutrient uptake, mortality, and respiration/mineralization; the system is driven by light and temperature, and by turbulent mixing (eddy diffusivity). Controlling mechanisms are light and nutrient limitation of primary production, self-shading of algae, and temperature dependency of all the biological processes. Fig. 4 gives a diagrammatic representation of this system.

The model description uses Monod-kinetics to describe nutrient limitation of primary production, using a constant half-saturation concentration; maximum growth rate is described as an exponential function of temperature, with a Q_{10} of about 2; light limitation is described using the double time-depth integral of DITORO et al. (1971) of STEELE's (1962) equation; (for a discussion of the implications of this formulation see KREMER and NIXON 1978). Mortality is described as a nonlinear, concentration-dependent function of algae biomass, and is directly coupled to remineralization, without any time lag or further control. Mixing with a "deep layer" is described as the exchange of a constant fraction of the upper layer's (10 m) volume, where the $P-PO_4$ concentration of the deep layer equals the initial (winter) concentration of the upper layer, and the algae concentration is zero, that is to say, algae can only get lost. The rate of mixing is changed by a step function, triggered by temperature, such that the initial high (January) value is set to one tenth as soon as the surface temperature reaches three times its starting value; mixing rate is reset to the high value, as soon as the surface temperature drops below the trigger-level. The governing model equations are summarized in the Appendix, part 1.

This model requires only six parameters to be estimated, given that the initial conditions and the driving variables are "known". For each of these parameters or rate coefficients, a possible, allowable range can be specified, depending on the available knowledge. In the worst case, a mortality rate, for example, has to be greater than zero and smaller than one. To circumvent the problem of uncertain initial conditions, a set of likely values (estimated from the available data) was taken and allowed to adjust by letting the model run for three years. This strategy (using the results of the third year after arbitrarily specifying the initial condition for year one instead of adding more dimensions to the input search space) was followed with all the models described below. The model is formulated in terms of phosphorus, with constant stoichiometric conversions to carbon and a time-variable carbon-chlorophyll ratio (compare Figure 3). A discussion of the description of the major biological processes can be found in FEDRA 1979.

Testing hypothesis No. 1

To test the hypothesis formulated in model 1, the model was incorporated into a Monte Carlo framework, which randomly sampled a set of model parameters from the allowable ranges (see Table 1), ran the model for a period of three years – to allow the arbitrary initial values of the state variables to adjust – and finally tested for violations of the constraint conditions. This process was repeated for a sufficiently high number of trials (in fact, more than 100,000 model runs were performed with each of the models). Since 100,000 runs of even a comparatively simple simulation model produces a large amount of almost incomprehensible information, several auxiliary programs for the automatic analysis of the simulation results were used. Table 1

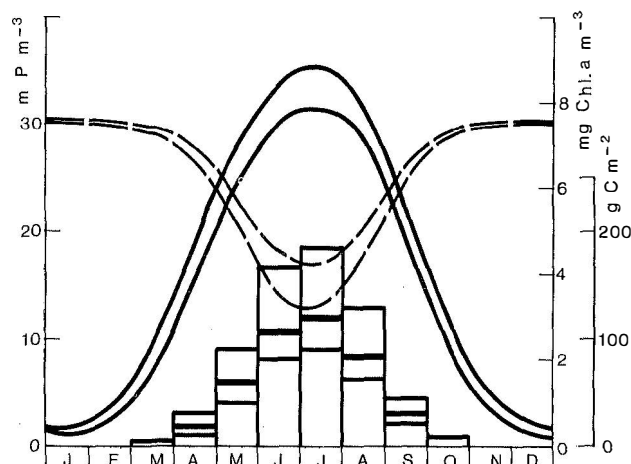


Figure 5

Sample output from model 1, showing an envelope for the state variables phosphate and phytoplankton for a set of runs which only violate the condition of two phytoplankton peaks; histogram shows monthly sums (minimum, mean, maximum) of primary production

shows an example of the output of one of these analysis programs, which includes the parameter ranges sampled and the basic statistics of the parameter ensemble used to generate the model response shown in Figure 5.

Summarizing, model 1 could fulfill all of the constraint conditions but one: it was not possible to reproduce two algae peaks during the summer period (without violating several other conditions), Fig. 5 shows a sample output from model 1.

Hypothesis No. 1 consequently had to be rejected. To build an improved hypothesis, the distributions and correlation structure of parameters and output variables from those runs violating only condition 3 (the two algae peaks) were analyzed. The technical details of this analysis are described elsewhere (FEDRA et al. 1980, FEDRA 1981 a, b). However, the analysis indicates that phytoplankton mortality is a critical process, and consequently deserves refinement. This can be deduced from the significant correlations between the mortality rate coefficient and the other parameters as well as different output variables in groups of simulations violating different constraint conditions.

Hypothesis No. 2: a four-compartment web

As a slightly more realistic alternative to model 1, a second version was formulated which incorporates detritus and omnivorous zooplankton. The description of primary production as well as the physical framework are essentially the same as in the first version. Model two, however, splits the phytoplankton mortality into a natural background mortality, which is described as concentration-dependent, and losses due to grazing. Background mortality as well as zooplankton mortality now feed into the detritus pool, which in turn feeds (temperature-dependent) back into the nutrient pool; detritus is also available for zooplankton, for which, however, a certain preference for living algae is assumed. Zooplankton respiration also feeds into the nutrient pool. Figure 4 shows the flow chart for this model. Grazing was described based on a simple encounter theory. The resulting model performance was not

satisfactory either: for low values of the grazing rate constant, the zooplankton did not survive phytoplankton lows in winter, and died away. For high values of the feeding rate, in contrast, phytoplankton was removed very quickly, as soon as it started to grow in the spring, with a consequent collapse of the zooplankton population itself.

After consequently rejecting the encounter theory, description of grazing was based on a saturation curve, similar to Michaelis-Menten kinetics, using a temperature-dependent maximum feeding rate coefficient, with the same temperature dependency as for respiration and remineralisation. The governing equations are given in the Appendix, part 1 a and 2 b respectively.

Again this version was subjected to the simulation procedure described above, and the resulting response was analyzed (see Table 2 a). The introduction of a second trophic level in model 2 now allowed reproduction of the well-known oscillatory behavior of predator-prey systems, and thus fulfilment of condition 2, requiring two

Table 1

Automatic parameter estimation analysis program, parameter statistics for MOD 1.mc – output run selection: violation of condition 3 only

31 runs evaluated	mean	minimum	maximum	S.D.	range	sampled
Parameter values:						
1 Michaelis constant	6.08	2.23	13.84	3.33	2.00	15.00
2 Phytoplankton mortality	0.36	0.25	0.50	0.07	0.05	0.50
3 Light optimum	410.10	301.51	497.40	63.15	300.00	500.00
4 Mixing coefficient	0.18	0.11	0.23	0.03	0.05	0.50
5 Maximum growth coeff.	1.03	0.70	1.42	0.18	0.50	2.50
6 Temperature trigger	3.24	2.56	3.86	0.29	2.00	4.00
Output-constraint variables: (all concentrations in $\text{mg} \cdot \text{m}^{-3}$)						
7 Chl. high 1–90	0	0	0	0	(not violated)	
8 Chl. summer peak	8.16	7.84	8.72	0.24		
9 Chl. first	8.16	7.84	8.72	0.24		
10 Chl. low between peaks	3.89	3.49	4.09	0.13		
11 Day of first peak	189.81	188.00	191.00	0.83		
12 Chl. second peak	0	0	0	0		
13 Day of second peak	270.	270.	270.	0		
14 Chl. high after 270	0	0	0	0		
15 Chl. maximum	8.16	7.84	8.72	0.24		
16 PO_4 maximum	30.00	30.00	30.00	0		
17 PO_4 minimum	15.47	12.86	16.87	1.07		
18 PO_4 low before day 90	29.92	29.67	29.99	0.092		
19 PO_4 low after day 270	27.84	27.56	28.36	0.18		
20 PO_4 average day 120–240	19.02	17.27	19.93	0.73		
21 Primary prod. $\text{g C} \cdot \text{m}^{-2}$	406.20	303.05	625.44	86.58		
Correlation matrix of parameters						
	1	2	3	4	5	
2	– 0.2					
3	0.1	– 0.6				
4	0.1	0.7	– 0.5			
5	0.5	0.6	– 0.0	0.7		
6	– 0.2	0.5	– 0.2	0.2	0.3	

phytoplankton peaks. However, this version was incapable of producing enough algae carbon over the year, thus violating condition 6 (see Table 2 b). This is simply due to the fact that only at comparatively low primary productivity levels was the system stable enough to stay within the behavioral bounds specified. The output or constraint variable of yearly primary production showed a strong positive correlation with the zooplankton grazing coefficient (parameter 6 in Tables 2) and zooplankton respiration (parameter 7), which is a major source of nutrient recycling. This directly points at the positive feedback loop in these processes, and the resulting stability problems in this version of the model.

Consequently, model 2 was used as the basis for yet another modification, namely the introduction of another trophic level of carnivorous zooplankton, to explore its importance in controlling the herbivores (GREVE and REINERS, in press). A sample output of this version 3 is shown in Figure 6, and the equations are given in the

Table 2a

Automatic parameter estimation analysis program, parameter statistics for MOD2.mc – output run selection: 3123 runs numerically stable over 3 years of simulation

3123 runs evaluated	mean	minimum	maximum	S.D.	range	sampled
Parameter values:						
1 Michaelis constant	9.17	6.00	11.99	1.72	6.00	12.00
2 Phytoplankton mortality	0.047	0	0.10	0.025	0.00	0.10
3 Light optimum	386.07	300.05	499.84	57.03	300.00	500.00
4 Mixing coefficient	0.07	0.05	0.13	0.01	0.05	0.15
5 Max. growth coefficient	1.88	0.50	2.50	0.44	0.50	2.50
6 Zooplankton grazing	0.38	0.05	1.00	0.20	0.05	1.00
7 Zoopl. detritus uptake	0.07	0	0.15	0.04	0.00	0.15
8 Zoopl. respiration	0.06	0.01	0.15	0.04	0.01	0.15
9 Zoopl. mortality	0.27	0.05	0.50	0.13	0.05	0.50
10 Remineralization	0.14	0.05	0.25	0.06	0.05	0.25
11 Temperature trigger	2.95	2.50	3.50	0.29	2.50	3.50
12 Grazing half-saturation	13.02	0.55	20.00	4.98	0.50	20.00
Output-constraint variables: (all concentrations in mg ' m ⁻³)						
13 Chl. high day 1–90	7.73	0	9.65	0.93		
14 Chl. summer peak	7.33	3.36	10.08	1.16		
15 Chl. first peak	7.10	0.94	10.08	1.34		
16 Chl. low between peaks	5.29	0.03	9.52	1.62		
17 Day of first peak	122.74	120.00	250.00	10.58		
18 Chl. second peak	5.59	0	9.61	1.62		
20 Chl. maximum	8.19	6.29	10.08	0.62		
21 PO ₄ maximum	22.23	8.41	25.36	2.32		
22 PO ₄ minimum	1.17	0.001	7.14	0.87		
23 PO ₄ low until day 90	3.26	0.66	24.36	1.74		
24 PO ₄ low after day 270	6.29	0.32	21.86	2.85		
25 PO ₄ average day 120–240	3.26	0.12	15.39	2.02		
26 Primary production	240.92	41.51	442.56	66.92		
27 Day of zoopl. peak	180.29	110.00	325.00	32.33		
28 Zoopl. at algae peak	5.76	0	19.89	4.43		
29 Zoopl. peak value	9.29	0.006	21.37	4.04		

Appendix. Another 5 additional parameters had to be introduced for the additional detail in model 3, leading to further problems in the estimation and analysis. For example, the proportion of runtime aborted runs (due to the violation of some runtime-checks on the state variables, confining them within certain plausible ranges or numerical instabilities in solving the system of differential equations) grew dramatically to almost 99.9 % of the trial runs when sampling the broad initial parameter intervals given in Table 3.

The second trophic level of carnivorous zooplankton feeds on the herbivores in the (structurally) same way as the herbivores feed on the phytoplankton; herbivores however, have the additional source of detritus available. Due to its higher complexity, model 3 was able to generate a broad spectrum of behavioural features (compare Table 3); it could not, however, fulfill all of the test conditions imposed on its behaviour at the same time. Obviously, the simple inclusion of a structurally similar additional

Table 2b

Automatic parameter estimation analysis program, parameter statistics for MOD2.mc – output run selection: 43 runs violating condition 6 only (primary production)

43 runs evaluated	mean	minimum	maximum	S.D.	range	sampled
Parameter values:						
1 Michaelis constant	9.88	5.06	14.88	3.17	5.00	15.00
2 Phytoplankton mortality	0.07	0.03	0.10	0.02	0.00	0.10
3 Light optimum	429.54	317.58	499.78	52.08	300.00	500.00
4 Mixing coefficient	0.05	0.01	0.10	0.02	0.01	0.10
5 Max. growth coefficient	1.53	0.82	2.35	0.41	0.50	2.50
6 Zooplankton grazing	1.01	0.19	1.87	0.48	0.01	2.00
7 Zoopl. detritus uptake	0.10	0.005	0.20	0.06	0.01	0.50
8 Zoopl. respiration	0.09	0.02	0.28	0.06	0.01	0.25
9 Zoopl. mortality	0.11	0.012	0.28	0.07	0.01	0.50
10 Remineralisation	0.25	0.015	0.49	0.13	0.01	0.50
11 Temperature trigger	3.04	2.51	3.49	0.29	2.50	3.50
12 Grazing half-saturation	13.80	3.94	23.44	5.07	0.00	25.00
Output-constraint variables: (all concentrations in mg ' m ⁻³)						
13 Chl. high day 1–90	0.56	0.20	1.07	0.23		
14 Chl. summer peak	7.60	5.86	9.05	0.69		
15 Chl. first peak	7.60	5.86	9.05	0.69		
16 Chl. low between peaks	1.35	0.06	3.91	1.00		
17 Day of first peak	155.37	138.00	192.00	13.07		
18 Chl. second peak	3.13	1.00	4.45	0.72		
19 Day of second peak	270.	270.	270.	0		
20 Chl. maximum	7.60	5.79	9.05	0.69		
21 PO ₄ maximum	25.76	24.76	26.72	0.433		
22 PO ₄ minimum	4.83	2.16	11.97	2.19		
23 PO ₄ low until day 90	25.36	24.73	25.91	0.23		
24 PO ₄ low after day 270	22.19	20.06	25.11	1.12		
25 PO ₄ average day 120–240	17.11	13.70	19.86	1.67		
26 Primary production	40.60	19.08	75.76	14.08		
27 Day of zoopl. peak	165.63	145.00	220.00	16.20		
28 Zoopl. at algae peak	0.69	0	3.48	0.92		
29 Zoopl. peak value	14.33	7.66	18.74	3.00		

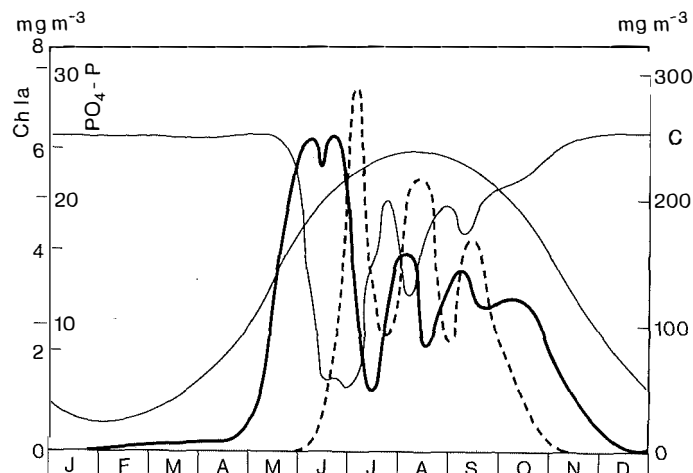


Figure 6

Sample output from model 3, run violating only the condition of yearly primary production above 300 g C m^{-2} . Solid thick line: phytoplankton (chlorophyll a); broken line: zooplankton carbon; solid thin line: phosphate; smooth curve: surface temperature

compartment did not resolve the basic problem; since the process rates of both zooplankton compartments are only determined by external driving variables (temperature, food availability) but not by internal control mechanism (e.g. developmental stages, size and age classes, etc.), the resulting zooplankton response was not adequate over the whole of driving conditions for a yearly cycle. The model does well for part of the year, or part of the required behavioural features over a full year; if, however, the model behaves well during the productive season, zooplankton will starve and collapse during the winter. Or, alternatively, if all plankton groups survive the winter well, the onset of high primary productivity will quickly lead to explosive growth and consequent collapse of the planktonic groups.

To test the importance of the (size and age class dependent) internal control mechanisms in the zooplankton compartment, STEELE's (1974) model was incorporated into the same Monte Carlo framework as the above models. Several modifications had to be made, since the model describes the pelagic system in terms of nitrogen and zooplankton numbers and individual size. The model incorporates nutrients (nitrogen), phytoplankton, herbivorous zooplankton numbers, individual size, and eggs produced (which translates into number of larvae released through the specification of an initial size). Egg production starts as soon as a certain individual size is reached. Zooplankton dynamics are all related to individual size by a simple allometric relation. To summarize, the model which was originally designed for the period of summer stratification only does well during this period. When extended over a whole yearly cycle however, it suffers from the same (generic?) shortcomings as the other models discussed. Either the zooplankton population collapsed over the winter, or explosive growth and consequent collapse was observed during the summer. This is, at least in part, attributable to the fact that the model does not consider temperature dependency of the biological processes (since it was designed for the summer period in the northern part of the North Sea only); also, phytoplankton production is described as a function of nutrient concentrations only, and the model does not include detritus. However, a more likely conclusion seems to be that there are qualitative differences

Table 3

Automatic parameter estimation analysis program, parameter statistics for MOD 3. mc
– output

250000 trial runs made 219 runs evaluated	mean	minimum	maximum	S.D.
Michaelis constant	11.131	2.306	19.816	4.818
Phytoplankton mortality	0.192	0	0.496	0.136
Light optimum	419.037	300.647	548.945	74.599
Mixing coefficient	0.050	0.001	0.197	0.045
Maximum growth coefficient	7.097	0.764	9.977	2.110
Zooplankton grazing	1.012	0.003	1.995	0.573
Zooplankton detritus uptake	0.508	0.044	0.799	0.191
Zooplankton respiration	0.180	0	0.722	0.169
Zooplankton mortality	0.206	0	0.779	0.184
Remineralisation	0.205	0	0.497	0.143
Temperatur trigger	2.943	2.502	3.493	0.289
Grazing rate carnivores	1.152	0.038	1.989	0.532
Mortality rate carnivores	0.146	0.001	0.787	0.111
Respiration carnivores	0.067	0	0.620	0.085
MM constant algae	16.417	0.431	29.995	7.902
MM constant detritus	10.770	0.002	29.803	8.802
MM constant herbivores	15.066	0.109	29.653	8.821
parameter ranges sampled:				
parameter No.: 1	2.000	20.000		
parameter No.: 2	0	0.500		
parameter No.: 3	300.000	550.000		
parameter No.: 4	0	0.200		
parameter No.: 5	0.500	10.000		
parameter No.: 6	0	2.000		
parameter No.: 7	0	0.800		
parameter No.: 8	0	0.800		
parameter No.: 9	0	0.800		
parameter No.: 10	0	0.500		
parameter No.: 11	2.500	3.500		
parameter No.: 12	0.020	2.000		
parameter No.: 13	0	0.800		
parameter No.: 14	0	0.800		
parameter No.: 15	0	30.000		
parameter No.: 16	0	30.000		
parameter No.: 17	0	30.000		
Output-constraint variables: (all concentrations in $\text{mg} \cdot \text{m}^{-3}$)				
chl. high 1–90	4.049	0.058	9.492	2.293
chl. summer peak	6.149	2.385	10.111	1.589
chl. first peak	5.867	1.686	10.111	1.687
day of first peak	131.416	120.000	182.000	17.468
chl. low between peaks	4.227	0.539	8.306	1.840
chl. second peak	4.675	0	8.551	1.739
chl. high after day 270	4.678	1.039	9.112	1.689
chl. maximum	6.423	2.385	10.111	1.488
PO ₄ maximum	23.616	6.541	27.994	3.250
PO ₄ minimum	1.975	0.062	18.797	2.098
PO ₄ low until day 90	15.387	1.351	25.170	8.266

250000 trial runs made 219 runs evaluated		mean	minimum	maximum	S.D.
PO ₄ low after day 270		6.457	0.531	23.395	5.126
zooplankton peak value		132.307	0.001	1 259.682	229.683
carnivores peak value		402.631	8.680	1 422.003	272.741
PO ₄ average day 120–240		3.791	0.294	21.827	3.490
primary production		142.038	6.016	374.074	74.652
pp January		0.207	0	3.976	0.528
pp February		0.932	0	12.258	1.892
pp March		5.218	0	23.553	5.450
pp April		15.463	0	38.713	8.502
pp May		19.989	0.239	46.851	10.749
pp June		26.289	1.038	76.145	15.214
pp July		23.977	0.842	71.133	14.238
pp August		20.277	0.698	63.635	12.717
pp September		18.847	0.557	59.717	12.386
pp October		8.838	0.114	32.067	6.462
pp November		1.735	0.003	7.953	1.697
pp December		0.266	0	3.600	0.480
secondary production		82.737	1.284	571.125	91.024
tertiary production		3.745	– 0.001	23.717	4.149
algae carbon end		11.608	0.001	241.564	32.676
algae carbon start		11.610	0.001	241.525	32.676
phosphate end		22.584	4.600	26.336	3.870
phosphate start		22.584	4.600	26.336	3.870
zooplankton end		8.470	0.002	221.002	23.783
zooplankton start		8.459	0.002	219.280	23.701
zoopl. 2 end		1.139	0	41.086	3.933
zoopl. 2 start		1.140	0	41.051	3.931
detritus end		32.840	1.217	473.174	60.060
detritus start		32.850	1.253	472.995	60.078
total P end		23.94	5.14	33.26	3.30
total P start		23.09	4.96	28.68	3.58

between summer and winter periods in the dynamics of the planktonic systems. This would require yet another reformulation of the models.

Quite obviously, none of the models discussed above is entirely satisfactory in the light of the constraint conditions defined. However, this paper does not attempt to propose an elaborated dynamic model of the pelagic food web of the southern North Sea, but rather attempts to demonstrate (using the example of admittedly quite simplistic models) a formal approach to model or hypothesis testing.

Discussion

The generalizable lesson

To build complex hypotheses, used to describe and explain the structural and behavioural features of ecological systems, a formal approach and rigorous testing procedures are required. As has been demonstrated, parts of the observed behaviour of the system may easily be reproduced. This however, goes parallel with unrealistic behaviour in other parts of the system. A complex hypothesis or model, however, can only be accepted as a valuable working tool with explanatory value and predictive

capabilities if it fulfills all the constraints one formulates as defining the observed system's behaviour. Violation of one single condition necessitates the rejection of such a model, which should be just one step in an iterative process of analysis.

One basic idea of the approach is to use the available information according to its relevance on the models' (this is the theory's) level of abstraction. Obviously, the description of the states of a system can be done much more easily on the appropriate level than the description of process rates and controls (just think in terms of phytoplankton biomass versus production rate). Consequently, we turn the argument of the hypothesis testing process around: instead of putting the "known" initial conditions (the rates, among others) into the model structure and deriving the response for comparison, we use the allowable response as a constraint to identify possible initial conditions. In other words, we map a given region in the response hyperspace of a model back into the input hyperspace.

The test is then as follows: whether or not this region in the input space exists within the specified possible or plausible bounds. In addition, several other features of the input space can be used as a basis for either rejecting or corroborating a given hypothesis; for example, the uniqueness of the input space region, whether it is closed or not, and its structure, which is determined by the interdependencies of the individual input values. In addition, all these features, including the relationship or correlation of input and output space, allow us to learn something about the way the proposed systems' structure functions. The method facilitates an understanding of the systems behaviour on the appropriate level of abstraction, which is the input and output of the model, and it also provides diagnostic information for hypothesis generation.

And above all, the approach emphasizes testability. Any rigorous scientific approach to the study and analysis of complex, hard-to-handle systems which are no longer easily understandable and traceable, requires that all the individual elements of the systems' conceptualization, all the assumptions that are necessary, are made explicit – and thus testable.

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Appendix: model equations

Parameter numbers (pmetr(i)) correspond to the numbers in the Tables above. The equations are given in FORTRAN code.

Variable names and meanings:

alg	algae biomass, expressed in nutrient units
chl	chlorophyll a, $\text{mg} \cdot \text{m}^{-3}$
death	mortality/mineralisation of phytoplankton
depth	depth of productive layer in meters
Dt*	time derivatives
eps	extinction coefficient in m^{-1}
fotop	photoperiod in fraction of a day (24 h)
gmax	maximum growth rate of algae
growth	actual growth rate of algae
plim	nutrient limitation factor
po4	limiting nutrient (phosphorus)
rad	radiation in $\text{cal} \cdot \text{cm}^{-2}$
radlim	light limitation factor
sink	algae losses due to sinking/mixing
temp	water temperature in Centigrade
tfact	temperature factor
xmix	ratio of volume exchanged
zo	omnivorous zooplankton
zo2	carnivorous zooplankton

```

c food-chain simulation model:
c two compartment versions 1:
c for parameter ranges compare Table 1
c
c primary production:
c
c self shading:
c

      chl = .64 * (40. * alg)**.4
      eps = .04 + .054 * chl **.67 + .009*chl
      zk  = eps * depth

c
c light limitation:
c
      ratio = 0.9 * rad / pmeter(3)
      x1    = ratio * exp (-zk)
c
      part1 = exp ( -x1)
      part2 = exp ( -ratio)
      part3 = (part1 - part2) / zk
c
      radlim = part3 * fotop * 2.7
c
c nutrient limitation:
c
      plim   = po4/(po4 + pmeter(1))
c
c temperature dependent max. growth rate:
c
      gmax   = pmeter(5) * exp (.065*temp)
c
      growth = alg * gmax * radlim * plim
      sink   = alg * xmix
      death  = alg **1.25 *pmeter(2)
c
      Dtalg  = growth -sink -death
c
c nutrients:
c
      vmix   = (po4-po4) * xmix
c
      Dtpo4  = -growth + death + vmix

c
c MOD2: four compartment web
c for parameter ranges compare Table 2
c
c herbivorous grazing:
c
c temperature factor:
c      tfact = exp(-2.3 * abs(temp-16.5)/15.)
c

```

```

c      saturation and threshold:
          fph = max(0.,(alg-alg0)/(alg + pmeter(12)))
          rate = pmeter(6) * fph * tfact
c
          graz = alg * zo * rate
c
c      algae loss due to sinking/mixing:
          sink = alg * xmix
c
c      detritur remineralization:
          rem = det * pmeter(10) * exp(.065*temp)
c
c      zooplankton detritus uptake
          dgraz = det * zo * pmeter(7)
c
c      zooplankton respiration
          resp = zo * pmeter(8) * exp(.06*temp)
c
c      zooplankton mortality
          zmort = zo**1.2 * pmeter(9)
c
c      losses from upper layer due to mixing
          zloss = zo * xmix
c
c      detritus exchange with deep water
          dmix = (detlow-det) * xmix
c
          Dtalg    = growth - death - graz - sink
          Dtpo4    = - growth + rem + resp + vmix
          Dtzo     = graz + dgraz - resp - zmort - zloss
          Dtdet    = death + zmort - dgraz + dmix - rem
c

c
c      MOD3: five compartment foodweb
c
c      for parameter ranges compare Table 3
c
c      herbivorous grazing
          graz = (alg/(alg + pmeter(15))) * pmeter(6) * tfact * zo
c
c      assimilation
          ass = min(graz,zo)
c
c      phytoplankton removal
          remo = graz - ass
c
c      detritus uptake
          dgraz = (det/(det + pmeter(16))) * zo * pmeter(7)
c
c      respiration, mortality and losses due to mixing
          resp = zo * pmeter(8) * tfact
          zmort = zo**1.2 * pmeter(9)
          zloss = zo * xmix/4.

```

```

c  carnivorous grazing, mortality and respiration
    zgraz = (zo/(zo + pmeter(17))) * zo2 * pmeter(12) * tfact
    z2mort = zo2**1.2 * pmeter(13)
    zresp = zo2 * pmeter(14) * tfact
c
c  algae
    Dtalg = growth -death -graz -aloss
c  nutrients (phosphorus)
    Dtpo4 = -growth + rem + resp + zresp + vmix
c  omnivorous zooplankton
    Dtzo = ass + dgraz -zgraz -resp -zmort -zloss
c  carnivorous zooplankton
    Dtzo2 = zgraz -zresp -z2mort
c  organic detritus
    Dtdet = death + remo + zmort2 + zmort -dgraz + dmix -rem
c

```