

Steady-State Models

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6.1. Introduction

Steady-state models presume a condition in which the values of the model state variables do not change over time. A steady-state model corresponds to a dynamic model where all the derivatives dx/dt , dy/dt , and so forth are equal to zero. Observations, giving the time variations of the ecological components, are therefore not needed. Instead, average values are sufficient. Average values (e.g., annual average values) often correspond to steady-state values because they are only changed on a longer time basis. The model is only able to give information about average values of the modelled components or about specific steady-state conditions.

This chapter presents three different approaches to develop steady-state models:

1. Chemostat models, which are often used for aquatic ecosystems with a moderate to long retention time such as ponds, lakes, estuaries, lagoons, and the open sea
2. Using downloadable software Ecopath, which has been widely used to develop steady-state models of aquatic ecosystems
3. Using steady-state models to analyze ecological networks

These three approaches illustrate the advantages and disadvantages of steady-state models and how they can be used to obtain a good picture of the interactions among ecological components in an ecosystem.

6.2. A Chemostat Model to Illustrate a Steady-State Biogeochemical Model

A chemostat model is a mixed flow reactor, which implies that the concentrations of all the components are the same in the entire reactor. Physical, chemical, and biological processes take place in the reactor, but the reactor is sufficiently well mixed to maintain the same concentration throughout the entire reactor so there are no gradients. A well-mixed aquatic ecosystem can be considered a mixed flow reactor or a chemostat (Figure 6.1). The concentrations of the various components can be found as a function of time using a developed system of equations. It is easy to find the steady-state concentrations that adequately describe the conditions in the aquatic ecosystem.

Let us consider one component in a chemostat with the concentration, C . The following differential equation is valid:

$$\bullet dC/dt = (\text{input} - \text{output} - \text{decomposition} - \text{settling} - \text{evaporation})/V \quad (6.1)$$

where V is the volume (m^3). The processes can be expressed by algebraic equations, which change the differential equation to:

$$\bullet dC/dt = (I - Q * C)/V - k * C - sr * C - A * v * C/V \text{ mg}/(\text{m}^3/24\text{h}) \quad (6.2)$$

where I is the input in $\text{mg}/24\text{h}$, Q is the flow rate ($\text{m}^3/24\text{h}$), k is the first-order decomposition rate coefficient for the component, sr is the settling rate ($1/24\text{h}$), A is the surface area (m^2), and v is the evaporation

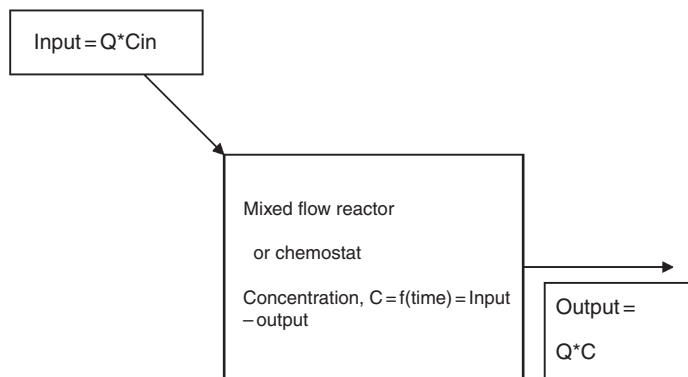


FIGURE 6.1 The principle for a mixed flow reactor or chemostat is shown.

rate (m/24h) of the component. At steady state, the following equation is valid:

$$\begin{aligned} \bullet \text{Steady state : } dC/dt &= 0, \text{ which implies that} \\ \bullet I &= (Q * C + V * k * C + V * sr * C + A * v * C) \end{aligned} \quad (6.3)$$

If I, Q, V, A, k, sr, and v are known, C can be expressed as function of time and the steady-state value can be found:

$$C = (I - Q * C) / V - k * C - sr * C + A * v * C / V \quad (6.4)$$

The solution of Eq. (6.2) or (6.3) will give C as a function of time. The steady state is, in principle, never reached, but C approaches asymptotically the steady-state value. A typical and possible plot of $C = f(\text{time})$ is shown in Figure 6.2.

It is possible to follow the concentration of a toxic substance in an organism as a function of time by a similar simple model, which will yield a similar result: The toxic substance concentration as $f(\text{time})$ is approaching the steady state asymptotically as shown in Figure 6.2. The applied equations are:

$$dTx/dt = (\text{daily})\text{intake} - kTx \quad (6.5)$$

At steady state:

$$\begin{aligned} dTx/dt &= 0 \\ kTx &= \text{input or } Tx = \text{input}/k \\ \text{Concentration} &= Tx/\text{biomass} \end{aligned} \quad (6.6)$$

where Tx is the total amount of toxic substance in the organism, k is the excretion coefficient (units 1/24h), which is very dependent on the toxic

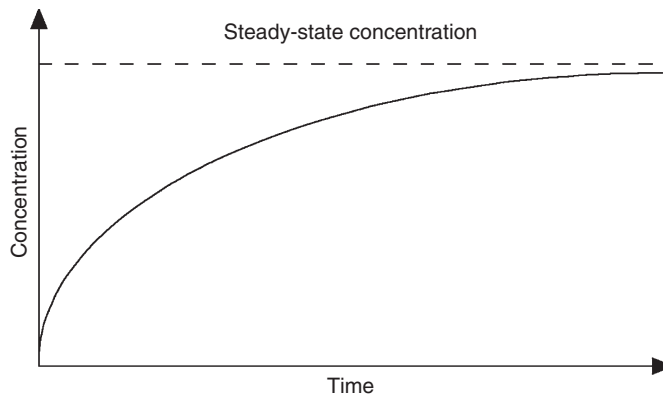


FIGURE 6.2 C as function of time. C is approaching asymptotically the steady-state concentration.

compounds and the organism. The daily intake may consist of uptake from the medium (air or water) and uptake from the food.

Illustration 6.1

A pesticide, Pz, is discharged to a lake that can be considered a mixed flow reactor. 400 m³ of wastewater with a Pz concentration of 4 mg/L is discharged to the lake per 24 hours. The natural inflowing stream has a rate of 1000 m³/24h. The pesticide has a biological half-life of 40 days. The settling and evaporation are negligible. The volume of the lake is 200,000 m³. What is the steady state concentration of Pz?

Solution

The specific decomposition rate k can be found from the first-order differential equation for the decomposition:

$dPz/dt = k \cdot Pz$, which means since the half-life is 40 days:

$\ln 2 = 0.693 = k \cdot 40$ or $k = 0.0173$ (1/24h)

The differential equation: $dPz/dt = (\text{input} - \text{output} - \text{decomposition})/V$, which implies that:

$dPz/dt = (400 \cdot 4 - Pz \cdot 1400)/200,000 - 0.0173 \cdot Pz =$ (at steady state)

or

$0.008 - 0.007 \cdot Pz - 0.0173Pz = 0$; or $Pz = 0.329$ mg/m³

6.3. Ecopath Models

Ecopath was designed to help the user construct trophic network models of aquatic ecosystems. Ecopath is downloadable, public domain software (see www.ecopath.org). Several hundred Ecopath models have been developed, and it has been extensively applied for marine ecosystems and fishery models; see and Christensen and Pauly (1992, 1993). Many Ecopath models have been published in the journal *Ecological Modelling*. This software also provides useful procedures for parameter estimation and for balancing the system of equations for mass and energy conservation. The latest versions, which have been accessible for more than a decade, have introduced accumulation and depletion of biomass by any organisms during the considered time period. This addition allows us to refrain from the restrictive steady-state conditions.

The required input data can be different types depending on the available data set. The software accepts as input biomass values (standing stock at presence or means of the period considered) and flow values. The latter should be given together with metabolic parameters (food uptake, respiration, excretion rate, etc.). The eventually unknown parameters are automatically determined by means of energy balance equations. An estimation of the diet composition of the various organisms is always asked for as input. The necessary input ratios of fundamental metabolic parameters are:

- Production/biomass ratio (P/B)
- Consumption/biomass ratio (Q/B)
- Gross efficiency, $GE = \text{production}/\text{consumption} = (P/B) \cdot (Q/B)$
- Unassimilated part of the food

It is sufficient to know two out of the three ratios (P/B), (Q/B), and GE.

Figure 6.3 shows an example of an Ecopath model. As seen from the figure, the model provides the quantitative information about the trophic network, including flows between compartments and storages within the compartments. Note that all inflows are balanced by outflows so that the model is at steady state.

6.4. Ecological Network Analysis

Ecological network analysis (ENA) is a methodology used to study objects as part of a larger system. It starts with the assumption that a system can be represented as a network of nodes (compartments, components, etc.) and the connections between them (flows of energy or matter). Network analysis, by design, provides a systems-oriented perspective because it is based on uncovering patterns and influence among all the objects in a system. Therefore, it illustrates how system components are tied to a larger web of interactions. Ecological network analysis is included in this chapter because the current methodologies are developed for models in which input and output are balanced for each compartment, but the approach is not conceptually limited to steady-state models as time-varying methodologies are being considered and developed (Hippe, 1983; Shevtsov et al., 2009).

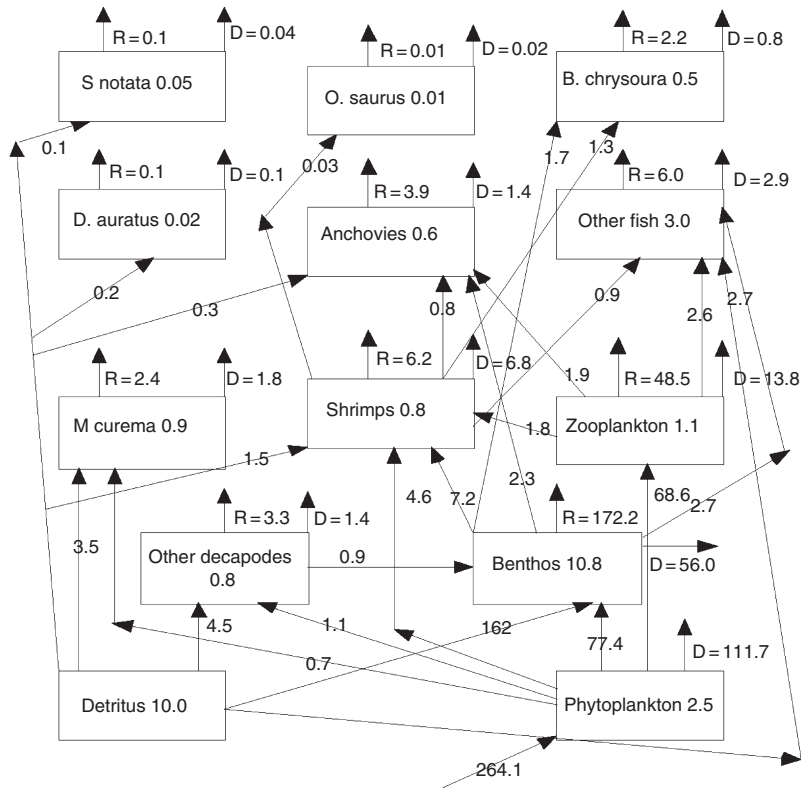


FIGURE 6.3 Example of a marine Ecopath model, taken from Christensen and Pauly (1993). R means respiration and D the transfer to detritus. Notice that all the components are in steady state: input = output.

Ecological network analysis is based on economic input-output analysis (Leontief, 1951) and was first introduced into ecology by Hannon (1973). His models were linked by the energy flow through the food web to determine interdependence of organisms in an ecosystem based on their direct and indirect energy flows. In ecological systems, the connections are often based on the flow of conservative units such as energy, matter, or nutrients between the system compartments. If such a flow exists, then there is a direct transaction between the two connected compartments. These direct transactions give rise to both direct and indirect relations between all of the objects in the system. Several formulations of ENA have arisen including embodied energy analysis (Herendeen, 1981), ascendancy analysis (Ulanowicz, 1980, 1986, 1997, 2009), and network

environ analysis (Fath & Patten, 1999; Patten, 1978a, 1981, 1982a). There are several available software packages that carry out the network analysis, such as NETWRK (Ulanowicz, 1982), WAND (Allesina & Bondavalli, 2004), NEA (Fath & Borrett, 2006), EcoNet (Kazanci, 2007), and R.ENA (Scotti & Bondavalli, 2010).

An ecological network flow model is essentially an ecological food web (energy–matter flow of who eats whom), which also includes nonfeeding pathways such as dissipative export out of the system and pathways to detritus. The first step is to identify the system of interest and place a boundary (real or conceptual) around it. Energy–matter transfers within the system boundary comprise the network; transfers crossing the boundary are either input or output to the network; and all transactions starting and ending outside the boundary without crossing it are external to the system and are not considered. Once the system boundary has been established, it is necessary to compartmentalize the system into the major groupings. The most aggregated model could have only two compartments: producers and consumers (where decomposers are included in consumers). A slightly more disaggregated model could have the following functional groups: producers, herbivores, carnivores, omnivores, decomposers, and detritivores (Fath, 2004). Most ecological network models will have many more compartments.

Mathematically, network analysis is built on the formalisms of graph theory and matrix algebra. The most basic realization of network analysis consists of a graph in which an edge or arc links two or more nodes together. An isomorphic mapping allows for representation of the graph as a matrix, which is called an adjacency matrix (Figure 6.4). When the edges are directed, that is, flow in a particular direction, the model can

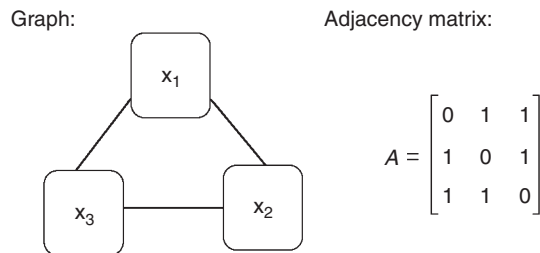


FIGURE 6.4 Graph and adjacency matrix for simple network.

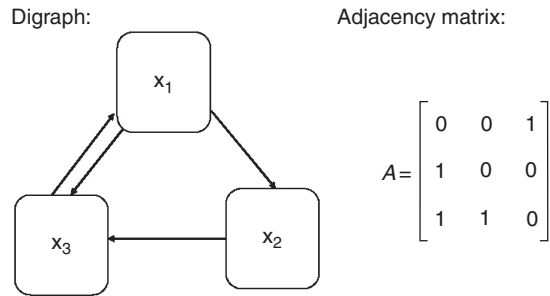


FIGURE 6.5 Digraph and adjacency matrix for simple network.

be considered as a directed graph or digraph (Figure 6.5). A digraph-based adjacency matrix can be used for investigating the structural properties of the network such as number of pathways, connectivity, and rate of path proliferation (Borrett et al., 2007). The next level of analysis occurs when weighted flow values can be determined for each arc including (since an ecosystem is an open environmental system) the input and output boundary exchanges (Figure 6.6). This should also include information regarding the storage values, in which case the full suite of network analysis properties can be investigated and calculated.

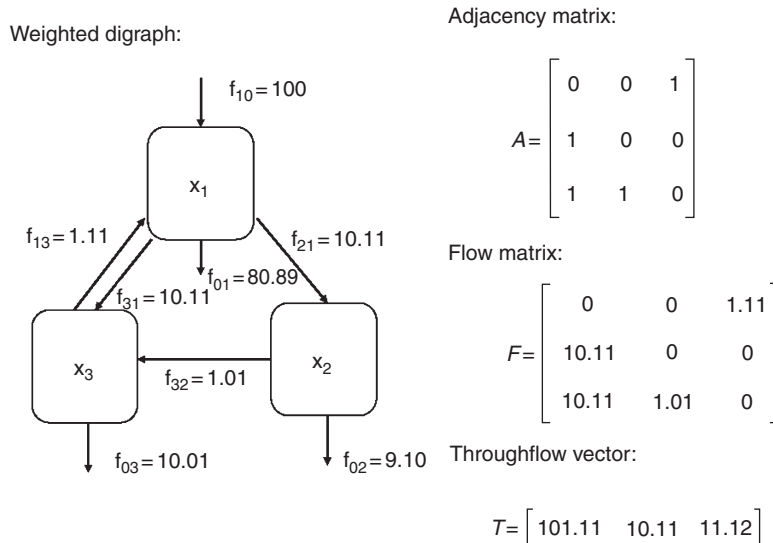


FIGURE 6.6 Weighted digraph, adjacency, and flow matrix.

Lastly, it is useful to normalize and nondimensionalize the flows between compartments relative to a reference condition, typically, using the component's throughflow or storage values (Figure 6.7). These values are used in the network environ analysis. This involves the power series analysis and subsequent transitive closure matrix, which yield the combined direct and indirect flows in the network.

An adjacency matrix element, $a_{ij} = 1$ if a direct arc from j to i exists and zero if no arc exists (note that some authors orient the adjacency matrix from rows to columns $a_{ij} = 1$ if there is a direct arc from i to j). In other words, the A matrix gives the direct connectivity of a model. A row sum would give the total number of arrows emanating out of the compartment (called out degree), and a column sum gives the total number of arrows entering the compartment (called in degree). In ecological models, the interpretation is clear and relevant because the in degree is the number of diet sources (prey items) and the out degree is the number of predators or sinks for the compartment. Whereas the adjacency matrix indicates the presence or absence of a direct connection, matrix A^2 gives the number of pathways that take exactly two steps between two compartments, and matrix A^3 gives the number of pathways that take exactly two steps, and so forth. Therefore, A^m gives the

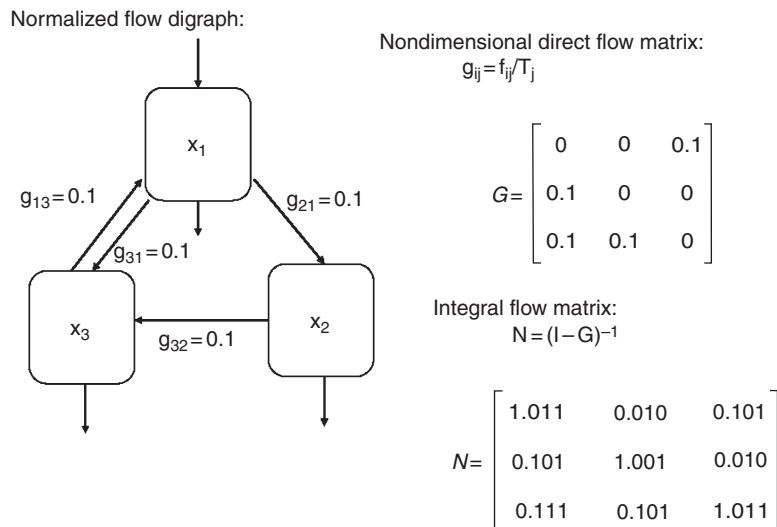


FIGURE 6.7 Normalized flow digraph, nondimensional flow matrix, and integral flow matrix.

number of pathways of length m . For example, A^2 , A^3 , and A^4 for Figure 6.7 are given as:

$$A^2 = \begin{bmatrix} 1 & 1 & 0 \\ 0 & 0 & 1 \\ 1 & 0 & 1 \end{bmatrix} A^3 = \begin{bmatrix} 1 & 0 & 1 \\ 1 & 1 & 0 \\ 1 & 1 & 1 \end{bmatrix} A^4 = \begin{bmatrix} 1 & 1 & 1 \\ 1 & 0 & 1 \\ 2 & 1 & 1 \end{bmatrix}$$

The reachability matrix $A^{[R]}$ is given by:

$$A^{[R]} = A + A^2 + \dots + A^{n-1}$$

Two nodes are reachable if and only if all elements of $A^{[R]} \geq 1$, and not reachable if it is 0. In this example, all compartments are reachable to each other. Furthermore, by A^4 we see that there are multiple pathways from compartment 1 to compartment 3 ($a_{31} = 2$). These are: $1 \rightarrow 2 \rightarrow 3 \rightarrow 1 \rightarrow 3$ and $1 \rightarrow 3 \rightarrow 1 \rightarrow 2 \rightarrow 3$, which are distinct paths carrying energy through the network. Note that in this case the elements will continue to increase as the path length increases. In fact, the rate of increase in the limit for each pairwise combination is equal to the magnitude of the maximum eigenvalue:

$$\frac{a_{ij}^{(m+1)}}{a_{ij}^m} = \lambda_{\max}$$

as $m \rightarrow \infty$

Not all networks have this property of increasing pathways with increasing path length, referred to as path proliferation, in which the pathways increase without bound. It depends on the connectivity and is an important feature for ecological systems that cycle material and energy. Three classes of connectivity and therefore cycling, can be defined using the eigenvalues as follows (Fath and Hynes, 2007):

$$\lambda_{\max} = 0; \text{ no cycling}$$

$$\lambda_{\max} = 1; \text{ weak cycling}$$

$$\lambda_{\max} > 1; \text{ strong cycling}$$

As previously stated there are several ENA approaches applied. Here, for illustrative purposes, we present an example using EcoNet software for a common network model of an oyster reef community (Dame & Patten, 1981, see Fig. 3.7). EcoNet 2.1 is an online, user-friendly, interactive domain that allows the easy calculation of many of the network properties (<http://eco.engr.uga.edu/>). The Web site provides sufficient background information for new users, including modelling information, theoretical background, and preloaded examples. The user is prompted to enter the model structure in the provided window, which will include flows, flow types, coefficients, initial conditions, and comments. The

model is currently set up to accept three types of flow: donor controlled, donor-recipient controlled, and Michaelis-Menten taking the following forms, respectively, for a flow from compartment A to compartment B:

Donor controlled : Flow $A \rightarrow B = c * A$

Donor – recipient controlled : Flow $A \rightarrow B = r * A * B$

Michaelis – Menten flow : Flow $A \rightarrow B = A * B / (v + A)$

The symbols c , r , and v for the coefficient values indicate the type of flow used in the model. Multiple flow types are permissible in this model.

The oyster reef is one of the examples preloaded in the EcoNet software, and is formulated as follows:

```
# Intertidal Oyster Reef Ecosystem Model, by Dame and
Patten.
# Model flows are in kcal mo-2 day-1; storage data is
# kcal mo-2.
# This model is based on the Matlab model written by Fath
# and Borrett (2004).
# Dame, R. F., and B. C. Patten. 1981. Analysis of energy
# flows in an intertidal oyster reef. Marine Ecology
Progress
# Series 5:115-124.
# Patten, B. C. 1985. Energy cycling, length of food
chains,
# and direct versus indirect effects in ecosystems. Can.
# Bull. Fish. Aqu. Sci. 213:119-138.
* -> Filter_Feeders c=41.4697
Filter_Feeders -> Dep_Detritus c=0.0079
Filter_Feeders -> Predators c=0.0003
Dep_Detritus -> Microbiota c=0.0082
Dep_Detritus -> Meiofauna c=0.0073
Dep_Detritus -> Dep_Feeders c=0.0006
Microbiota -> Meiofauna c=0.5
Microbiota -> Dep_Feeders c=0.5
Meiofauna -> Dep_Detritus c=0.1758
Meiofauna -> Dep_Feeders c=0.0274
Dep_Feeders -> Dep_Detritus c=0.1172
Dep_Feeders -> Predators c=0.0106
Predators -> Dep_Detritus c=0.0047
Filter_Feeders -> * c=0.0126
```

```

Dep_Detritus -> * c=0.0062
Microbiota -> * c=2.3880
Meiofauna -> * c=0.1484
Dep_Feeders -> * c=0.0264
Predators -> * c=0.0052
Filter_Feeders = 2000; Dep_Detritus = 1000;
Microbiota = 2.4121; Meiofauna = 24.121;
Dep_Feeders = 16.274; Predators = 69.237
# Model flows are in kcal mo-2 day-1; storage data is
# kcal mo-2.

```

The model diagram is given in [Figure 6.8](#). This model can be run using four numerical methods: (1) adaptive time-step, Runge-Kutta-Fehlberg is the default, and also allows for (2) fixed time step, 4th order Runge-Kutta;

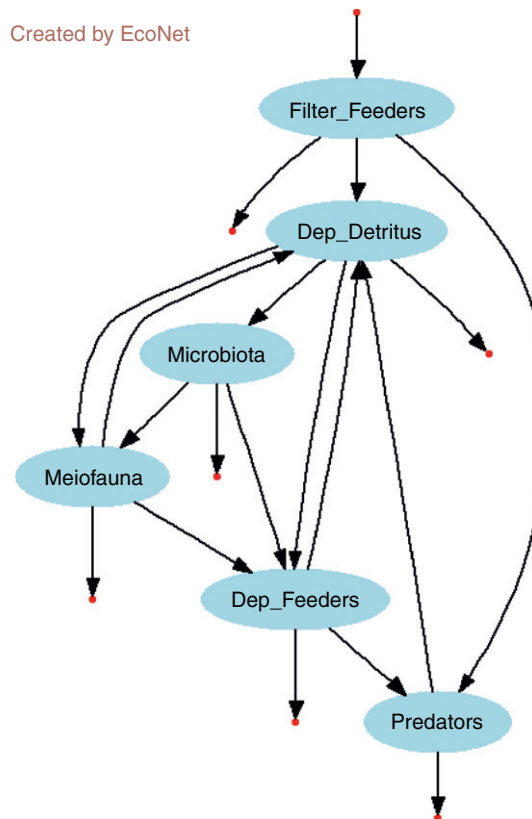


FIGURE 6.8 Flow diagram for oyster reef model constructed from EcoNet software.

(3) stochastic, fixed time step, Langevin equation which generates different solutions at each run, and (4) stochastic, adaptive time step, Gillespie's method, which is a variety of a dynamic Monte Carlo method. The default approach has maximum time and sensitivity as parameters. The sensitivity is related to the amount of error between the actual and numerical solution, which provides a trade-off between accuracy and computational time.

After the model is run, the results are presented, starting with the diagram, followed by a plot of the state variables during the simulation (called the time course figure). For the oyster reef example, which is balanced, there is no change in any of the state variables during the duration of the simulation. Next, the compartmental properties are provided including the initial and final storage values (essentially the same in this case) as well as the boundary input and output from each compartment. Also included in the compartmental properties are the input throughflow (and equivalently the output throughflow) and the residence time for energy in each compartment. Input throughflow is the amount of flow through each compartment that arrives from boundary flow without cycling. This is also referred to as first passage flow in the literature (Higashi et al., 1993; Fath et al., 2001). Values for input throughflow and residence time are given in [Table 6.1](#).

Next the analysis gives results for a suite of system-wide properties that are described in [Box 6.1](#) and the values given in [Table 6.2](#).

Lastly, in the “short” version of the output, the software completes the throughflow, storage, and utility analyses. As these are the key environment analysis results, they are presented here in full.

Table 6.1 Values for Input Throughflow and Residence Time

	Input Throughflow	Residence Time
X1- Filter_feeders	41.4697	48.0769
X2-Dep-Detritus	22.2257	44.843
X3-Microbiota	8.1779	0.2952
X4-Meiofauna	8.4872	2.8441
X5-Dep_Feeders	2.4667	6.4851
X6-Predators	0.7679	101.01

Notes: This is also referred to as first passage flow in the literature

Source: Fath et al., 2001; Higashi et al., 1993.

BOX 6.1 DESCRIPTION OF THE SYSTEM-WIDE PROPERTIES CALCULATED IN ECONET SOFTWARE

1. **Link Density:** Number of intercompartmental links (d) per compartment: $d/(\text{number of compartments})$.
2. **Connectance:** Ratio of the number of actual intercompartmental links (d) to the number of possible intercompartmental links: $d/(\text{Number of compartments})^2$.
3. **Total System Throughflow (TST):** The sum of throughflows of all compartments: $TST = T_1 + T_1 + \dots + T_n$.
4. **Finn's Cycling Index:** Measures the amount of cycling in the system by computing the fraction of total system throughflow that is recycled.
5. **Indirect Effects Index:** Measures the amount of flow that occurs over indirect connections versus direct connections. When the ratio is greater than one, indirect flows are greater than direct flows.
6. **Ascendency:** It quantifies both the level of system activity and the degree of organization (constraint) with which the material is being processed in ecosystems.
7. **Aggradation Index:** Measures the average path length. In other words, it is the average number of compartments a unit flow quantity (e.g., an N atom, unit biomass, energy quanta, etc.) passes through before exiting the system: $TST/(z_1 + z_2 + \dots + z_n)$.
8. **Synergism Index:** Based on utility analysis, it provides a system-wide index for pairwise compartment relations. Values larger than 1 indicate a shift toward quantitative positive interactions (synergism). It is computed as the ratio of the sum of positive entries over the sum of negative entries in the utility analysis matrix U .
9. **Mutualism Index:** Similar to synergism index, mutualism index provides a system-wide index for pairwise compartment relations. Values larger than 1 indicate a shift toward qualitative positive interactions (mutualism). It is computed as the ratio of number of positive entries over the number of negative entries in the mutual relations matrix.
10. **Homogenization Index:** Quantifies the action of the network making the flow distribution more uniform. Higher values indicate that resources become well mixed by cycling in the network, giving rise to a more homogeneous distribution of flow.

Source: EcoNet Web site: <http://eco.engr.uga.edu/DOC/econet4.html#scalar>

Nondimensional, direct flow matrix:

$$G = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ 0.38 & 0 & 0 & 0.5 & 0.76 & 0.475 \\ 0 & 0.367 & 0 & 0 & 0 & 0 \\ 0 & 0.327 & 0.148 & 0 & 0 & 0 \\ 0 & 0.027 & 0.148 & 0.0779 & 0 & 0 \\ 0.014 & 0 & 0 & 0 & 0.0687 & 0 \end{bmatrix}$$

Table 6.2 Analysis Gives Results for a Suite of System-wide Properties Described in [Box 6.1](#) and the Values Given in [Table 6.2](#).

Link density	2
Connectance	0.3333
Total system throughflow	83.5959
Finn's cycling index	0.1097
Indirect effects index	1.5297
Ascendency	115.329
Development capacity	188.573
Aggradation index	2.0158
Synergism index	6.5379
Mutualism index	2
Homogenization index	1.8905

Integral flow matrix:

$$N = \begin{bmatrix} 1.000 & 0 & 0 & 0 & 0 & 0 \\ 0.536 & 1.386 & 0.277 & 0.779 & 1.01 & 0.658 \\ 0.197 & 0.510 & 1.102 & 0.286 & 0.404 & 0.242 \\ 0.205 & 0.529 & 0.253 & 1.297 & 0.419 & 0.251 \\ 0.059 & 0.154 & 0.190 & 0.164 & 1.122 & 0.073 \\ 0.0185 & 0.0106 & 0.013 & 0.0113 & 0.077 & 1.005 \end{bmatrix}$$

Partial turnover rate matrix:

$$C = \begin{bmatrix} -0.0208 & 0 & 0 & 0 & 0 & 0 \\ 0.0079 & -0.0223 & 0 & 0.1758 & 0.1172 & 0.0047 \\ 0 & 0.0082 & -3.388 & 0 & 0 & 0 \\ 0 & 0.0073 & 0.5 & -0.3516 & 0 & 0 \\ 0 & 0.0006 & 0.5 & 0.0274 & -0.1542 & 0 \\ 0.0003 & 0 & 0 & 0 & 0.0106 & -0.0099 \end{bmatrix}$$

Integral storage matrix:

$$S = \begin{bmatrix} 48.0769 & 0 & 0 & 0 & 0 & 0 \\ 24.0392 & 62.172 & 12.423 & 34.929 & 49.283 & 29.516 \\ 0.0582 & 0.150 & 0.325 & 0.0845 & 0.119 & 0.071 \\ 0.582 & 1.505 & 0.721 & 3.690 & 1.193 & 0.714 \\ 0.386 & 0.997 & 1.231 & 1.066 & 7.276 & 0.473 \\ 1.870 & 1.068 & 1.318 & 1.141 & 7.790 & 101.517 \end{bmatrix}$$

Mutualism relations:

$$\text{sgn}(U) = \begin{bmatrix} + & - & + & + & - & - \\ + & + & - & - & + & - \\ + & + & + & - & - & + \\ + & + & + & + & - & + \\ - & + & + & + & + & - \\ + & - & + & + & + & + \end{bmatrix}$$

Utility analysis:

$$U = \begin{bmatrix} 0.832 & -0.221 & 0.0699 & 0.0126 & -0.027 & -0.014 \\ 0.424 & 0.599 & -0.193 & -0.0357 & 0.065 & -0.0012 \\ 0.394 & 0.547 & 0.741 & -0.200 & -0.061 & 0.0071 \\ 0.208 & 0.287 & 0.0014 & 0.946 & -0.056 & 0.0054 \\ -0.0035 & 0.065 & 0.446 & 0.169 & 0.911 & -0.0615 \\ 0.473 & -0.449 & 0.251 & 0.066 & 0.156 & 0.975 \end{bmatrix}$$

The software does have extended results that include control analysis and an eco-exergy calculator. The analysis data may be downloaded in Matlab format (.m file) or in spreadsheet format (.csv file). Overall, the EcoNet software provides a very easy to use application for researchers or students interested in conducting network analysis.

Problems

1. Construct the adjacency matrix of the oyster reef model in Figure 6.8.
2. How can you determine if the compartments are at steady state in a network model?
3. What are typical units of flow in a network model? Why is it necessary to normalize the flow values by the throughflows before taking the powers of the matrix?
4. How could one conduct a network analysis for time-varying data?
5. What is network mutualism? What role do indirect influences play in determining it?