Pond S and Pickard GL (1983) *Introductory Dynamical Oceanography*. Oxford: Pergamon.

Thomsen L and McCave IN (2000) Aggregation processes in the benthic boundary layer at the Celtic Sea continental margin. *Deep Sea Research I*, 47: 1389–1404.

Thorndike EM (1975) A deep sea, photographic nephelometer. *Ocean Engineering* 3: 1–15

Tucholke BE and Eittreim SL (1974) The western boundary undercurrent as a turbidity maximum over the Puerto Rico Trench. *Journal of Geophysical Research* 79: 4115–4118.

Zaneveld JRV, Roach DM and Pak H (1974) The determination of the index of refraction of oceanic particulates. *Journal of Geophysical Research* 79: 4091–4095.

NEPHELOMETRY

See **TRANSMISSOMETRY AND NEPHELOMETRY**

NETWORK ANALYSIS OF FOOD WEBS

J. H. Steele, Woods Hole Oceanographic Institution, Massachusetts, USA

doi:10.1006/rwos.2001.0291

Introduction

Photosynthesis transforms energy from sunlight into calories within marine plants, predominantly phytoplankton and seaweeds. The plants use this energy to take up carbon and essential nutrients, such as nitrogen and phosphorus, from sea water to produce organic materials. This organic matter forms the base for the food web composed of herbivores that eat those plants and the carnivores that prey on the herbivores. There can be several trophic levels of carnivores, including all the fish species that we harvest.

In the open sea, away from the coast and the seabed, microscopic single-celled phytoplankton dominate the plant life, so the organisms tend to get bigger as each trophic level feeds on the one below: from small herbivorous crustaceans to larger invertebrates, to small and large fish, and finally to human beings and marine mammals.

When any animal consumes food, most of the energy in that food is used for metabolism; some of the remainder is excreted as waste products and only a small fraction goes to growth. In young, cold-blooded animals in the sea, growth can be relatively efficient: 20–30% of energy intake. In older animals growth is replaced by reproduction, which, after all, is the whole point of the life cycle. As an approximate overall figure we usually assume that the energy converted into growth and reproduction is about 10% of the total energy intake. Thus, in a simple trophic pyramid, the energy in successive trophic levels would be 100:10:1:0.1. From this one can see why we are encouraged to eat plants on land, and why fish from the sea are energetically expensive in terms of plant calories.

In practice it is very difficult to measure directly the energy content of marine organisms and, especially the energy transfers between trophic levels. However, carbon is the essential building block for organic matter, being taken up from inorganic form at photosynthesis and returned to sea water during respiration. The carbon content of organisms and the rates of uptake of inorganic carbon can be measured using radioactive carbon, carbon-14, as a tracer; transfers through the food can then be measured. Carbon is therefore frequently used as a proxy for the more elusive concept of energy flow.

All organisms also require many essential elements, and many of these are in short supply in sea water. In particular, inorganic nitrogen and phosphorus, as nitrate and phosphate, are regarded as limiting factors in photosynthesis and thus in the rate at which energy and carbon are supplied to the food web. Since organic carbon, nitrogen and phosphorus have a roughly constant ratio in marine organisms (the Redfield ratio), nitrogen can also be used as a proxy for energy flow; it will not, however be considered here.

Carbon and nitrogen fluxes are also important in relation to other issues concerning marine food webs. The biologically mediated flux of carbon to deeper water is important for the calculation of global carbon budgets and climate change.

Eutrophication in coastal waters produces imbalance in the food webs of these regions.

Units

Ideally, all presentations would be in units of energy but, as discussed, the actual measurements are often in carbon or, for fisheries, in biomass (wet weight). Conversion from one unit to another will vary with the organism but, as an approximation:

$$10\,\text{kcal} = 1\,\text{g carbon} = 10\,\text{g biomass}. \qquad [1]$$

History

The first attempt to produce an energy budget for an aquatic food web was made by Lindeman in 1942, for a freshwater lake. In 1965 a budget for the North Sea (**Figure 1**), showed possible pathways from primary production to commercial fisheries. The main conclusion was that the ecological efficiencies needed to be quite high for the budget to balance. This conclusion depends on the number of pathways introduced; for example, the category 'other carnivores' is put in to account for the presence of gelatinous invertebrate predators, such as ctenophores, that are ubiquitous but the biomass of which is difficult to estimate. Without this box, the herbivore efficiency could be less than 20%.

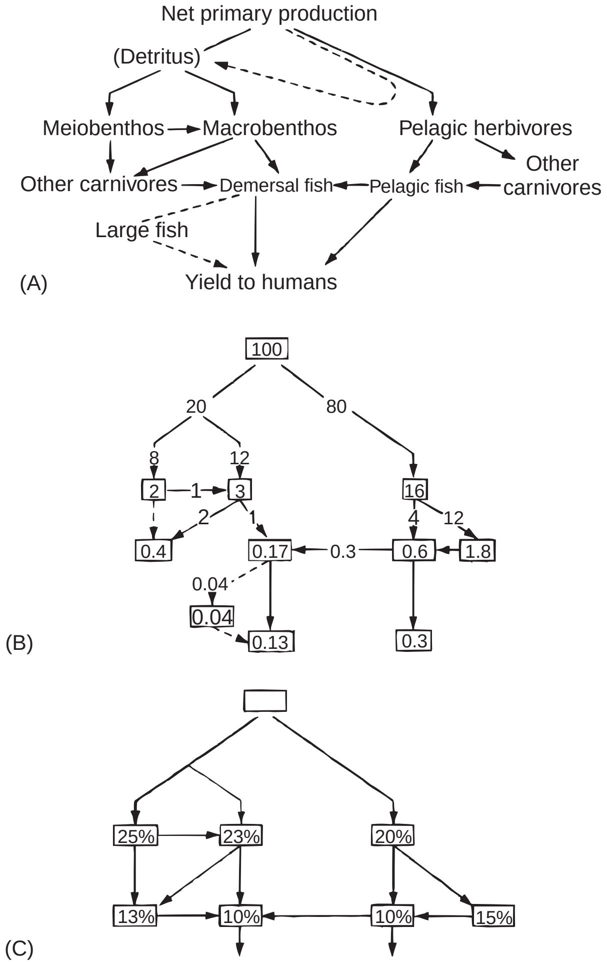

Figure 1 Energy or carbon fluxes in the food web for the North Sea. (A) A simplified food web. (B) Transfers of particulate organic carbon assuming a primary production of 100 gC m^{-2} per year. Each box indicates the production by that component available to its predators, including humans. (C) The transfer or ecological efficiencies calculated from the output as percentage of input.

In 1969 Ryther wrote a seminal paper that outlined the pathways at the global scale, by dividing the marine ecosystems into three types, upwelling, continental shelf, and open ocean (**Table 1**). The major implication of Ryther's calculations was that there were no great untapped fish resources in the open ocean. He estimated that the potential sustained yield of fish to humans was unlikely to be greater than 100 million tons. In 1998, the yield was about 90 million tons.

The reason for the low open-ocean yield of fish – and the controversial part of Ryther's calculation – is his estimate of five trophic levels from primary production to fish. This choice was based on the very small size of open-ocean phytoplankton. In the intervening years, research on the base of open-ocean food webs has shown that much of the primary production is recycled through the smallest sized categories in the food web – the microbial loop. For the intermediate trophic levels, such as the gelatinous predators, there is still relatively little quantitative information on biomass and production; this has led to an extensive development of mathematical treatments to infer energy or carbon flows.

Quantitative Methods

Early calculations, such as those illustrated in **Figure 1**, were put together by a very informal series of iterations until all the flows balanced and the

Table 1 Primary production, number of trophic levels to commercial fish species, efficiency of transfer of energy (or carbon) between trophic levels and resultant ratios of fish to primary production for three major marine categories

	Ocean	*Coastal*	*Upwelling*
Primary production (gC m^{-2} year^{-1})	50	100	300
Trophic levels	5	3	1.5
Ecological efficiency (%)	10	15	20
Fish production: primary production (%)	0.01	0.3	12

ecological efficiencies were not unreasonable. The major advance has been the development of numerical methods to make more objective estimates of best fit. Essentially, the ecosystem is considered to be at steady state, so that, for any box, such as those in **Figure 1**, there has to be a balance between rates of energy flow or carbon flux entering and leaving:

$$\text{consumption} = \text{predation} + \text{metabolism} + \text{export (input)} \qquad [2]$$

The information for each of these terms for each box can be qualitatively different. In particular, for animals:

$$\text{consumption} = \text{growth} + \text{reproduction} + \text{metabolism}. \qquad [3]$$

These complexities are eliminated if it is assumed that, for each box, there is a constant ecological efficiency, e_i:

$$\mathrm{e}_i = \frac{(\text{growth} + \text{reproduction})}{\text{consumption}}. \qquad [4]$$

Generally, for the system to be soluble, the terms in eqn [2] for all boxes must be expressed as a set of linear equations. For this purpose the variables are usually taken to be the energy, carbon or biomass flux through each box, T_i, that is available to higher trophic levels. Linearity requires that the rate processes in eqn [2] are constants independent of T_i.

$$\frac{T_i}{\mathrm{e}_i} = \sum b_{ij} \cdot T_j + c_i \quad i = 1, n, \qquad [5]$$

where b_{ij} is the fraction of T_j consumed by T_i and c_i is the constant rate of external input to T_i; c_i would be, for example, the rate of primary production. Note that, as in **Figure 1**, all the variables are rates of throughput in the food web and the parameters are non-dimensional. These matrix inversion techniques can also be used with nutrient flows that involve recycling.

An alternative top-down approach is often used for flow calculations where emphasis is on the higher trophic levels, and fish yields are the defining input. For these situations, consumption, C_i, is expressed as:

$$\text{consumption} = \frac{(\text{consumption})}{\text{biomass}} \cdot \text{biomass} = \left(\frac{C_i}{B_i}\right) \cdot B_i. \qquad [6]$$

Then the biomass in each box, B_i, becomes the state variable. The rate process C_i/B_i is assumed constant, for each box. Then:

$$\mathrm{a}_i \cdot B_i = \sum p_{ij} \cdot B_j + \mathrm{d}_i, \qquad [7]$$

where a_i represents production per unit biomass, the 'P/B' ratio, assumed constant for any box; p_{ij} is the unit consumption rate of B_j on B_i, assumed to be independent of the magnitude of B_j or B_i; d_i is the export, assumed constant for each box.

If all the parameters are known for either eqns [2] or [7] then the set of equations can be solved for T_i or B_i. In practice it is never as simple as that. Usually a number of parameters are unknown or ill defined; for example, as upper or lower bounds. Then iterative procedures can be used to obtain best fits. The selection of the number of boxes and the content of each box is the critical process. The assumption of a linear, steady-state ecosystem is the critical constraint for this type of analysis involving a large number of boxes. This approach is complemented by the highly nonlinear analysis used for modelling of fisheries and plankton dynamics.

Examples of Carbon and Biomass Networks

The emergence of the microbial loop as a significant feature of pelagic food webs, together with the availability of computer based inverse methods, resulted in a focus on flow analysis of the lower levels of the pelagic ecosystem; levels that were represented simply as phytoplankton-to-zooplankton in **Figure 1**. The results of analyses (**Figure 2**) illustrate how this part of the system is expanded into seven boxes with 19 links. Two examples in **Figure 2**, from the continental shelf around Britain, show the kinds of patterns that arise from these calculations. The authors point out differences between the English Channel and the Celtic Sea. The former puts 85% of primary production through the microbial loop, whereas the latter has 40% going directly to the mesoplankton (predominantly copepods). However, for both examples, the exports from this part of the food web are very similar: 3% to higher trophic levels via the mesoplankton, and 30% to the benthos as detritus. The major change from the earlier calculations is the dominant role of the microbial loop, involving recycling of most of the primary production. Only the 'new' production from nitrate (NO_3) in **Figure 2A** fuels the export

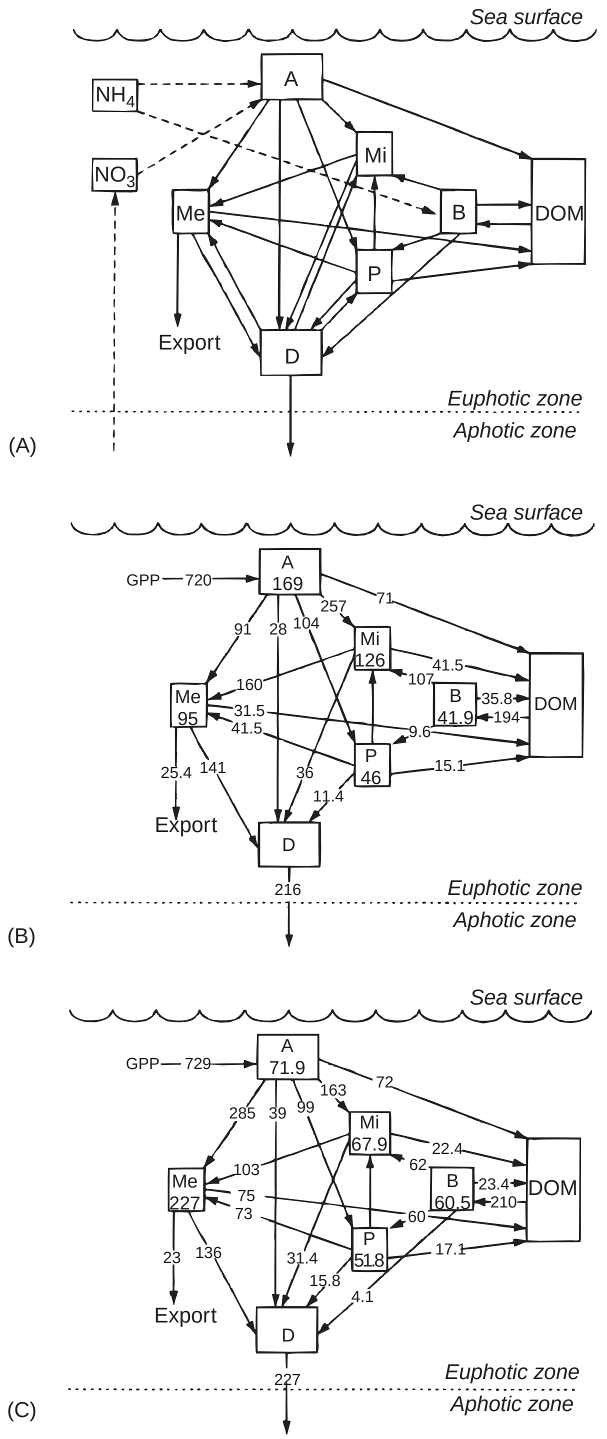

Figure 2 (A) Generic model of a plankton food web in the upper layer of a stratified water column. (B) The inverse solution for carbon fluxes in summer at a station in the English Channel. Values inside the boxes are respiration flows (mgC m^{-2} per day). (C) Flows at a station in the Celtic Sea. A, autotrophs; B, bacteria; D, detritus; DOM, dissolved organic matter; solid arrows denote intercompartmental transfer of carbon; dashed arrows indicate flows of inorganic nitrogen into the system; Me, mesozooplankton; Mi, microzooplankton; P, Protozoans. (Vezina and Platt, 1988.)

of detritus and mesoplankton to higher trophic levels.

The alternative approach (eqn [7]) has been used for a wide range of aquatic ecosystems, including lakes and coral reefs as well as ocean systems. One example (**Figure 3**) shows calculations for the continental shelf around the Gulf of Mexico. There is no microzooplankton box and the general flow patterns are not dissimilar to those of **Figure 1**; 30% of primary production goes directly to detritus, as does 40% of zooplankton food, presumably as fecal material. Detritus then feeds the demersal fish through the benthos. Note, however, that once again detritus is the dominant biomass (85% of the total).

It would appear that all the solutions of these linear systems – whether as energy or biomass, for lower or higher trophic levels – require a major role for detritus. Detritus is a difficult variable to define and measure. This box can contain phytoplankton cells, zooplankton feces, marine snow and other residues. It is assumed that detritus is broken down by bacteria but the a_i or e_i values are not well known. It is rarely sampled directly, either as biomass or for rate processes, and so is an empty box that can be used to balance flows.

Discussion

In terrestrial ecosystems most of our food comes directly from plants, with the remainder from herbivores – animals that eat plants. In the sea, the fish we eat are nearly all carnivores. Many feed on the small herbivorous crustaceans, such as krill, but some – the most highly prized, like tuna – themselves feed on carnivores, such as smaller fish. So what we hope to take from the sea, the potential fishery yield, depends very much on the patterns and magnitudes of the flow of energy or carbon from primary production. Our understanding of these patterns can therefore provide valuable estimates on the limits of what we can take from the sea, as well as increasing our insight into the ecological processes.

The selection of boxes and the arrows between them depends on our knowledge of which prey–predator interactions are quantitatively significant. It is obvious from the examples here that there is a considerable compaction into large, often heterogeneous groups, such as mesoplankton or pelagic fish. Thus the level of organization is very different from that for biodiversity studies, or even for descriptions of the full complexity of the food web. However, in producing a manageable number of

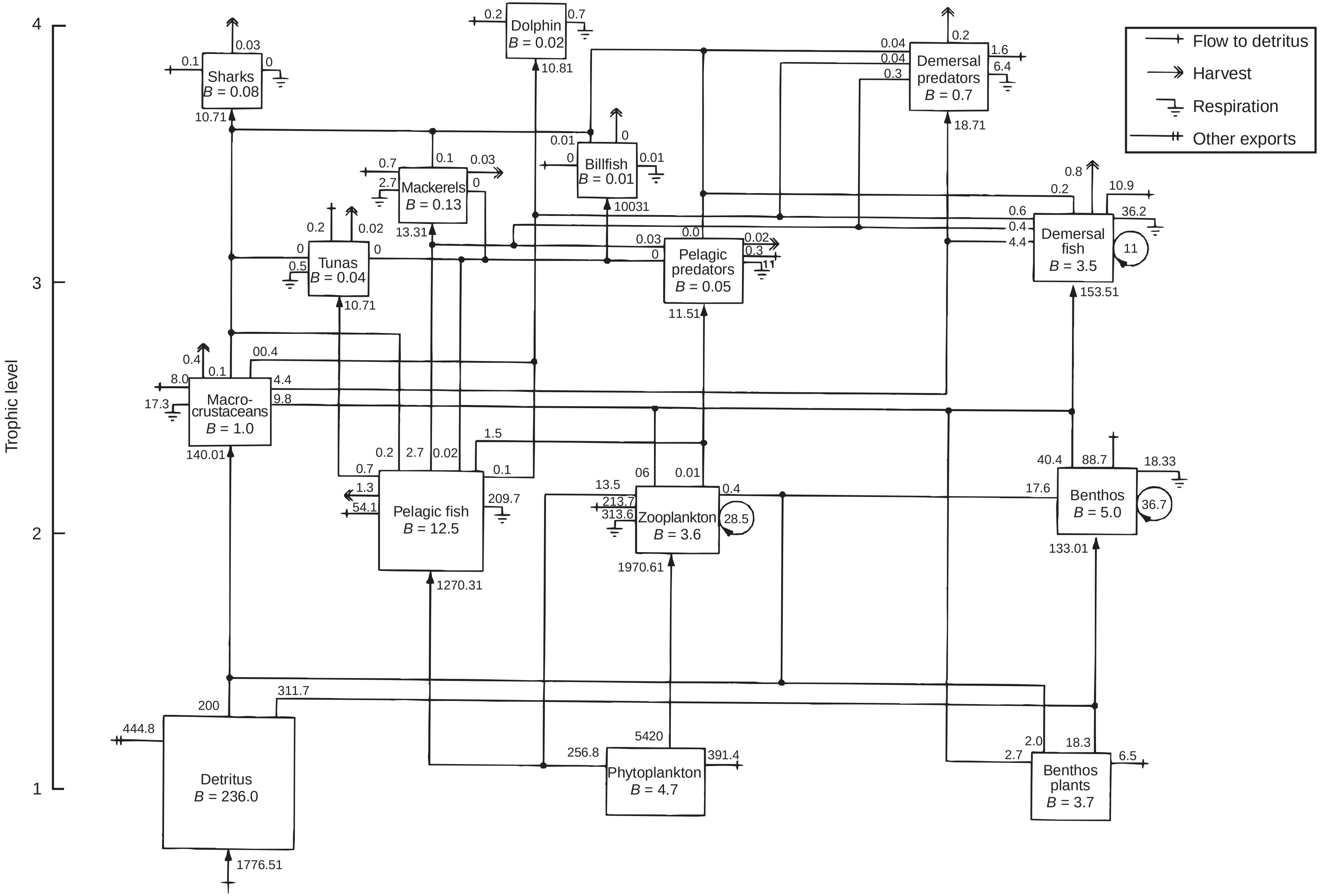

Figure 3 Gulf of Mexico ecosystem model: trophic compartments with values for biomass (g m^{-2}) and connecting flows (g m^{-2} per year^{-1}). (Christensen and Pauly, 1993.)

boxes, it is important not to fold significant prey–predator interactions into the same box. Thus, in **Figure 1**, prey–predator interactions at the microbial scale were ignored. On the other hand, it has been pointed out that, for the North Sea, the inclusion of both the detrital box and the invertebrate carnivores does not provide enough energy flow for the fishery yield. The definition of boxes will remain a central problem, but this is also the great strength of this approach: it requires attention to all aspects of the food web.

The major limitation is that the method assumes that the system is in steady state. This is usually achieved by taking yearly averages and ignoring shorter seasonal variability and longer decadal trends. For the former, several researchers have constructed dynamic plankton models of the nonlinear interactions between nutrients and detritus based on the seven boxes or variables in **Figure 2**.

The longer term changes are especially important for fisheries. It is possible to transform the linearized eqn [7] for equilibrium states into a time varying system by writing:

$$\frac{\mathrm{d}B_i}{\mathrm{d}t} = \mathrm{a}_i \cdot B_i - \sum p_{ij} \cdot B_j - \mathrm{d}_i. \qquad [8]$$

This linearized approximation to an essentially non-linear system can be used to indicate the directions that changes may take when the system departs from a previous steady state, but is unlikely to be adequate for the very large switches, or regime shifts, that occur in the relative abundance of different fish stocks. An alternative is to assign very different values to the boxes for the fish stock biomass and then recalculate the network. This technique can be used to estimate the status of ecosystems before the impact of human predation on fish or marine mammals. As an example, the Gulf of Mexico flows were recalculated, with the biomass of the top predators increased by a factor of 10. The major change was that the utilization of detritus within the ecosystem increased from 11% to 70%. Thus the ‘detritus’ box appears to act as a reservoir for over-exploited systems.

Conclusions

Calculations of the overall energy, or carbon, fluxes through a marine ecosystem provide a valuable check on estimates for the potential productivity associated with each component of the food web. These calculations can set limits on expected yields to humans; they can act as links between detailed, but necessarily static, descriptions of biodiversity, and models of the dynamics of individual populations.

It is necessary to bear in mind that our knowledge of the food webs used in these calculations are provisional and the outcome of the calculations is dependent on the specification of this structure; thus the full benefits from this approach depend on further studies of each ecosystem.

See also

Carbon Cycle. Copepods. Diversity of Marine Species. Eutrophication. Krill. Large Marine Ecosystems. Marine Snow. Microbial Loops. Photochemical Processes. Upwelling Ecosystems.

Further Reading

Christensen V and Pauly D (eds) (1993) Trophic models of aquatic ecosystems. *ICLARM Conf. Proc.* 26: 390pp.

Christensen V and Pauly D (1998) Changes in models of aquatic ecosystems approaching carrying capacity. In: Ecosystems management for sustainable marine fisheries. *Ecol. Appl* 8 (suppl).

Fasham MJR (1985) Flow analysis of materials in the marine euphotic zone. In: Ulanowicz RE and Platt T (eds) Ecosystem theory for biological oceanography. *Can. Bull. Fish Aquat. Sci.* 213: 260pp.

Lindeman RL (1942) The trophic-dynamic aspect of ecology. *Ecology* 23: 399–418.

Ryther JH (1969) Photosynthesis and fish production in the sea. *Science* 166: 72–76.

Steele JH (1974) *The Structure of Marine Ecosystems*. Boston: Harvard University Press.

Vezina AF and Platt T (1988) Food web dynamics in the ocean. I. Best-estimates of flow networks using inverse methods. *Mar. Ecol. Prog. Ser.* 42: 269–287.

Wulff F, Field JG and Mann KH (eds) (1989) *Network Analysis in Marine Ecology*. Berlin: Springer-Verlag.