

## Potential Trophic Biomasses and Trace-Substance Concentrations in Unstructured Marine Food Webs

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### Abstract

It is proposed that unstructured food webs may more closely resemble real marine food webs than does the conventional, structured model. An unstructured food-web model leads to a set of very simple expressions for the potential partition of matter in the food web in steady state, including the potential fluxes of material and biomasses of trophic types and the concentration of trace substances in the members and materials of such a food web. The approach may explain some anomalies of relative predator-prey biomasses and of trace-element distribution, and may be of further use for analyzing and predicting (a) the tropho-dynamic parameters of marine systems, (b) the trophic positions, and the steady-state fluxes and biomasses of marine organisms, (c) the distribution of trace materials in marine biota; and for relating findings among these areas. Other matters, such as limitations of food conversion, indicated by concentration factors of trace substances, the possibilities of non-causal association of anomalously high levels of trace substances (including pollutants) with diseased or otherwise abnormal marine creatures, and an inverse relationship of early concentrations of newly introduced trace substances and their eventual concentrations in various organisms, are also developed in this approach.

### Introduction

In a classical food-web model, the major developmental stages of each species of heterotrophs are considered to occupy relatively well-defined positions within a finite sequence of trophic steps. I will refer to such a model as a structured food web. It is increasingly apparent, however, that in much of the marine environment, most creatures feed on whatever available food is broadly suitable as to size, and accessible to their mode of feeding. For example, the stomach contents of tunas and salmon differ in no important regard from the catch of nekton nets towed in the immediate waters that they occupy (Allen and Aron, 1957; Alverson, 1963). Similarly, both filter and particulate feeders consume a heterogeneity of zooplankton, eggs and larvae, detritus, and phytoplankton, and may themselves become food for the organisms whose eggs, larvae, and detritus they consume.

Considering the many such alternate pathways, and "downward" and "upward" flow of energy and material in the food web, it is prudent to explore

the implications of the sort of food web to which I refer as unstructured, in which each moiety of food material merely passes through an infinite series of steps and conversions (with associated losses), partly and successively converted into living material, and partly and successively into non-living but recoverable material.

In such a system, the composition of any creature, excepting strict herbivores, is a broad mixture of material ranging from food freshly introduced into the system to some disappearingly small quantity of material that has been recycled a great number of times. Such penultimate material will, of course, not be of important quantity from the standpoint of food material or energy, but for content of some chemical materials that are concentrated at each step, such remnants may dominate.

The maximum steady-state biomass of a population of a single trophic type in any food web is limited by the available total material that it can convert into its own biomass. However, in an unstructured web, there are no *a priori* restrictions on the relative biomasses of trophic types. For example, the biomasses of predators and of detrital feeders can be much less or much greater than that of herbivores in a steady state, depending upon the values of the coefficients of the system, as will be seen later.

Both structured and unstructured food webs may be looked upon as trophic pyramids. The pyramid of a structured food web is comprised of relatively few (4 to perhaps 7) steps, with specific groups of organisms rather closely restricted to a specific step. Unstructured food webs, on the other hand, can be viewed as composed of a pair of interwoven pyramids, each of an infinite number of steps. Each successive step is occupied only by material and energy remaining from the preceding step, with living material in one pyramid and non-living but recoverable material in the other. Organisms in the unstructured food web do not occupy a small number of steps, but rather occupy broad regions that always extend to infinity (except for strict herbivores), and that differ principally in the point at which they begin in respect to the autotrophic

level, and in the degree to which they are restricted to one or the other of the living or recoverable pyramids.

Clearly, both structured and unstructured food webs are highly idealized and somewhat opposed models of reality. Thus, more complexly formulated expressions of either model will ordinarily converge toward the other, and possibly also toward reality.

### Description and Discussion of the Model

In a previous paper (Isaacs, 1972), I showed that the characteristics of an unstructured steady-state food web can be represented by two doubly-infinite series of terms that are exactly solvable to yield extremely simple expressions for the potential partition and flux of matter (or energy) in any distinct trophic members or materials of the web. Reasonable values of conversion coefficients in the web lead to a reasonable explanation of some observations on relative biomasses of herbivores and predators, as will be discussed later. Similarly reasonable values of conversion yield a compatible explanation of the highly anomalous levels of the trace element Cs found in the flesh of fishes in the Gulf of California (Mexico) in comparison with the same several species of fish in the Salton Sea (USA), where a relatively simple, almost linear, food chain exists (Young, 1970).

These equations for potential fluxes and biomasses of trophic types are extended and evaluated below, along with the related equations for the concentration of trace elements. They suggest that: (a) realistically measured coefficients of conversion in experiments may allow the calculation of meaningful trophic biomass limits for various trophic types in the sea; (b) conversely, measured values of trophic biomasses or trace-element concentrations in marine populations may yield insight into coefficients of conversion and other natural tropho-dynamic parameters; (c) the carefully determined concentration of certain trace elements in specific marine organisms may constitute indices of their trophic positions; (d) the specific radioactivity of certain elements in distinct trophic types of organisms may permit insight into the time scales involved in tropho-dynamic systems; (e) the steady-state distribution of certain potential pollutants in a food web may be predictable.

The construction of a doubly-infinite unstructured food-web matrix and its solutions are described in a previous paper (Isaacs, 1972). Briefly, the highly simplifying assumptions are:

(a) All significant members of a food web feed broadly from the total contents of the web, subject only to gross limitations from feeding structures and habits of the organisms. (These gross limitations define trophic types and are indicated in the descriptions of Eqs 2 through 11 below.)

(b) The food web is in steady state and, unless separately considered, all steps are considered to be equally probable.

(c) The consumer steps in the food web for a specific component, introduced only by autotrophs, can be specified by any two of three coefficients ( $K_i$ ), which unless separately defined<sup>1</sup>, are constant for all types of food and for all consumer organisms, for each single component of the food. An equivalent general assumption is that the food web can be epitomized by single average values of its major parameters and coefficients.<sup>1</sup> These coefficients are defined as:  $K_1$ : the coefficient of net steady-state conversion of the material or energy in food into living material resulting from a single consumer step;  $K_2$ : the coefficient of loss in the immediate conversion and subsequent metabolism that is not recovered by consumers; and  $K_3$ : the coefficient of loss during and subsequent to the step that is recovered by consumers, where

$$K_1 + K_2 + K_3 = 1 \quad (1)$$

and

$$0 < K_i < 1, \quad (1a)$$

where

$$i = 1, 2, \text{ or } 3.$$

### Potential Fluxes and Biomasses

Defining a term,  $M_o$ , as the total quantity of autotrophic matter or energy introduced successively into a food web over each period of time ( $\Delta t$ ), which is equal to the time required for an average consumer step (that is, the average time for a quantity of material equal to all of the non-autotrophic material in the web to progress one trophic step), the potential steady-state flux and biomass distribution of matter (or energy) in the food web is:

<sup>1</sup> More complex unstructured food webs can be constructed and solved. For example, different coefficients for the recoverable-to-living versus living-to-living steps can be employed, leading to a quadruply-infinite web. Also time-rate differences for different types of steps can be incorporated. Such higher-order, unstructured webs may be shown to be necessary to explain features of marine food webs. A simple and perhaps necessary complication is to assume different coefficients for the first consumer step (namely that of herbivorous feeding) than for the remainder of the web, since the consumption of plant material may be subject to different coefficients than that of other subsequent material. Examples of equations expressing this assumption are:

Total in heterotrophic living material

$$M_{t,*} = M_o \left\{ \frac{K_1^* K_2 + K_1 (K_1^* + K_3^*)}{K_2} \right\} \quad (3)^*$$

Herbivores

$$M_n^* = M_o K_1^* \quad (5)^*$$

Predators

$$M_p^* = K_1 M_{t,*} = M_o K_1 \left\{ \frac{K_1^* K_2 + K_1 (K_1^* + K_3^*)}{K_2} \right\}, \quad (9)^*$$

where the asterisk denotes the symbols pertinent to special coefficients for the first consumer step. Similar use of coefficients  $K_i^*$  can take account of a direct autotroph-to-detrital step.

Total non-autotrophic and net autotrophic material,

$$M = \frac{M_o}{K_2} \quad (2)^2$$

Total non-autotrophic material in the web,

$$M_t = M_o \frac{1 - K_2}{K_2} \quad (2a)$$

Total in heterotrophic living material,

$$M_{l'} = M_o \frac{K_1}{K_2} \quad (3)$$

Total in non-living recoverable material,

$$M_{l''} = M_o \frac{K_3}{K_2} \quad (4)$$

Strict herbivores (feeding on  $M_o$ ),

$$M_m = M_o K_1 \quad (5)$$

Omnivores (feeding on  $M$ ),

$$M_v = M_o \frac{K_1}{K_2} \quad (6)$$

Particle feeders (feeding on  $M_o + M_{l''}$ ),

$$M_{\mu} = M_o \frac{K_1(1 - K_1)}{K_2} \quad (7)$$

Detrital feeders (feeding on  $M_{l''}$ ),

$$M_d = M_o \frac{K_1 K_3}{K_2} \quad (8)$$

Full predators<sup>3</sup> (feeding on  $M_{l'}$ ),

$$M_p = M_o \frac{(K_1)^2}{K_2} \quad (9)$$

Non-herbivorous omnivores (feeding on  $M_t$ ),

$$M_n = M_o \frac{K_1(1 - K_2)}{K_2} \quad (10)$$

Feeders on a detrital milieu (feeding on  $M_{l''} + M_d$ ),

$$M_{dt} = M_o \frac{K_1 K_3 (1 + K_1)}{K_2} \quad (11)^4$$

<sup>2</sup> Quantity  $M_o$  as defined, is not a standing biomass, but rather a flux — the net autotrophic input integrated over the time interval ( $\Delta t$ ) and successively introduced over each such time interval. Unlike the quantities expressed by Eqs. 2a through 10, where potential standing biomasses are also expressed, the standing crop of autotrophs and, in part, total material in the web ( $M$ ), are dependent upon productivity and grazing rates, which are not assumed to be related to the coefficients ( $K_i$ ) for the heterotrophs. Integrated steady-state losses over the interval  $\Delta t$ , from the entire system are, of course, equal to  $M_o$ : the series expressing integrated losses ( $\Sigma L$ ) is:

$$\Sigma L = M_o K_2 [1 + (K_1 + K_3) + (K_1 + K_3)^2 + \dots + (K_1 + K_3)^n + \dots] \quad (1b)$$

or

$$\Sigma L = M_o \frac{K_2}{1 - (K_1 + K_3)} = M_o.$$

The potential values of biomasses, absolute and relative, are also absolute or relative potential fluxes through the trophic type during the time interval  $\Delta t$ . These fluxes can exceed  $M_o$ , since part of the flux results from recycled material.

With the exception of Eqs. 2 and 11, these expressions can be evaluated to yield the potential absolute fluxes and biomasses, if the input,  $M_o$ , is known. However, if the input is not known, the potential relative organic flux and biomass of each trophic type for various values of the coefficients may be evaluated, nevertheless, by employing unit values of autotrophic input of organic material for  $M_o$ , ( $M_{of}$ ). These steady-state biomasses and fluxes, absolute or relative, may be considered limits for any type, but not for all types simultaneously, as the total biomass of living heterotrophic forms cannot exceed the expression for the total (Eq. 3) under the assumptions of the derivation. Some subsets, however, are fully utilizing (e.g.  $M_m + M_d + M_p = M_{l'}$ ) and non-competing (see Fig. 1), and hence might mutually approach their potential biomasses.

Within the range of apparently realistic lower values for the conversion coefficients for organic material (subscript  $f$ ) [e.g.  $0.1 \leq (K_{1f}$  and  $K_{3f}) \leq 0.4$ ;  $0.2 \leq K_{2f} \leq 0.8$  (for examples and summary, see Lowman *et al.*, 1971)], rather surprising alterations of the potential relative abundance of trophic types occur. Fig. 1 shows these potential relative organic biomasses for the non-competing, fully-utilizing subset consisting of herbivores, detrital feeders, and full predators. As can be seen in Fig. 1, in steady state, the potential relative biomass of such predators may range from

<sup>3</sup> Several other strictly predaceous types are possible. Most parasites, for example, must be considered strict predators. Among free-living types, limited predators ( $M_{pi}$ ) might feed principally on herbivores ( $M_m$ ) and detrital feeders ( $M_d$ ), viz:

$$M_{pi} = K_1 (M_m + M_d) \\ M_{pi} = M_o \frac{K_1^2}{K_2} (1 - K_1) \quad (9a)$$

However, secondary predators ( $M_{ps}$ ), which include full predators in their diet, are necessarily indistinguishable from full predators, viz:

$$M_{ps} = K_1 (M_m + M_d + M_p) \\ M_{ps} = M_o \frac{K_1^2}{K_2} \\ M_{ps} \equiv M_p \quad (9b)$$

However, secondary predators ( $M_{ps'}$ ), other than parasites, feeding only on predators ( $M_p$ ), are possible in some systems:

$$M_{ps'} = M_o \frac{K_1^3}{K_2}, \text{ etc.} \quad (9c)$$

The consumption of gametes and embryos, which may represent a sizeable food flux, is a predatory step on adult populations in this model.

<sup>4</sup> Expressions for such more specialized trophic types can be generated, but are not useful for calculating flux or biomass limits, as these types compete with their prey for food. Additionally, any substantial biomass dominance of highly specialized trophic types is, of course, characteristic of the assumptions of a structured rather than of an unstructured food web. However, such expressions may be used to derive expressions for concentrations of trace substances despite their lack of validity as indicators of their total biomass.

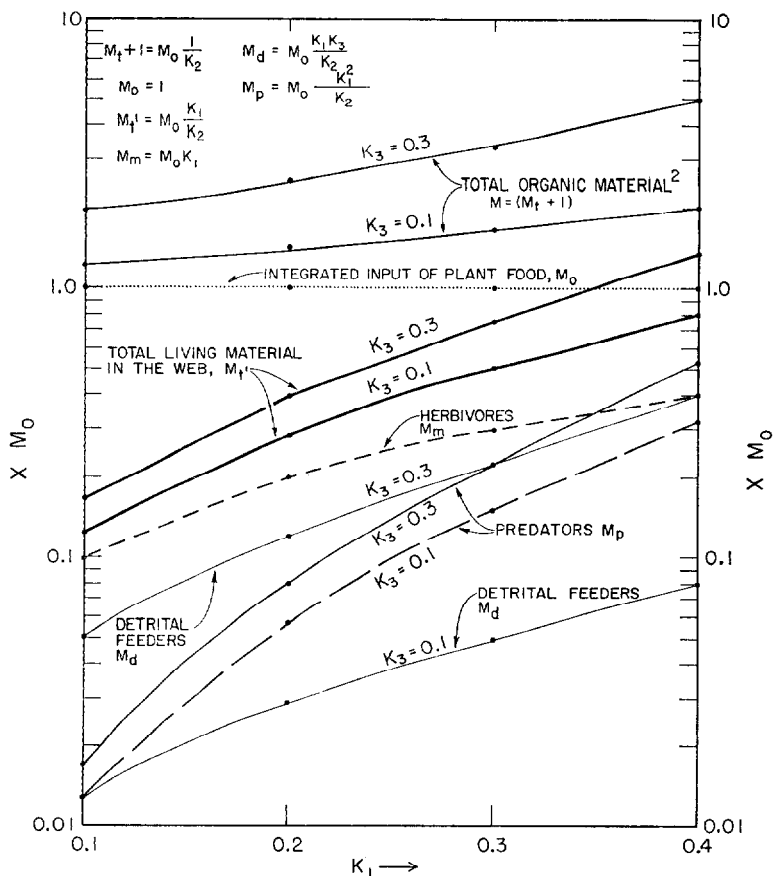


Fig. 1. Comparison of potential biomass levels in 3 trophic types. A non-competing, fully-utilizing set (i.e.,  $M_m + M_d + M_p = M_f$ )

very much less to twice that of herbivores for reasonable values of the coefficients. A similar range exists also between predators and detrital feeders. Other comparisons yield similarly widely ranging relationships. Despite the simplified assumptions, these results qualitatively yield an alternative explanation of the persistent findings of a number of field studies<sup>5</sup> (namely, that the biomasses of predators and other heterotrophic forms are of the same order or larger than those of the herbivorous types with which they are in an apparent steady-state balance), without invoking extremely rapid herbivore turn-over rates or inadequate sampling or mass advection of herbivores.

Thus, these expressions may have some qualitative validity for comparative organic biomasses. More challenging tests would be their validity in expressing absolute biomasses from known inputs, and their prediction of trace-substance concentrations.

<sup>5</sup> For example, in the Eastern Tropical Pacific Ocean, Blackburn (1966) p. 38; in the North Pacific Central Gyre, J. A. McGowan, personal communication (1972); in the Pacific and Indian Oceans, Vinogradov and Voronina (1963).

### Trace Substances

These equations can also be employed to generate simple expressions for the passage of chemical trace-substances through a food web and their steady-state concentration with respect to organic material in the several trophic types and material reservoirs.

I will define two additional coefficients,  $j$  and  $p$ , that express the relationship between the net transfer of the specific chemical substance and the food material in single consumer steps within a steady-state food web, where

$$j = \frac{K_{1c}}{K_{1f}}, \quad (12)$$

$$p = \frac{K_{3c}}{K_{3f}}, \quad (13)$$

and subscripts  $c$  and  $f$ , above and following, refer to the coefficients applicable to the chemical substance and food material, respectively. These two coefficients, and  $K_1$ , crudely subsume factors of residence times, metabolic rates, uptakes, losses, etc., unless specifically expressed. Linearity of all of these rates with concentration for trace elements is also implicitly assumed.

Some substances (e.g., lipids, Na, Si, Ca, Sr, V) probably cannot be handled so simply, because they violate the assumptions of the model by entering the food web at positions other than the autotrophs, are much differently metabolized or discriminated in various heterotrophs, or for other reasons. However, ranges of the coefficients  $j$  and  $p$  for Cs and for some other possible appropriate substances (e.g., DDT, Zn, P, Pb) are available from various sources.

With these simplifications, steady-state concentrations,  $C$ , can then be expressed for several trophic components in a fashion similar to the following example from Eq. 7 for particle feeders:

$$C_{\mu} = \frac{M_{\mu c}}{M_{\mu f}} = \frac{M_{oc} \frac{jK_{1f}(1-jK_{1f})}{1-jK_{1f}-pK_{3f}}}{M_{of} \frac{K_{1f}(1-K_{1f})}{1-K_{1f}-K_{3f}}}; \quad (14)$$

where  $\frac{M_{oc}}{M_{of}}$  is the concentration,  $C_o$ , of the chemical substance with respect to organic material in the primary autotrophic plants.

For simplicity of expression, allowing

$$K_1 \equiv K_{1f}, K_2 \equiv K_{2f}, K_3 \equiv K_{3f}, \text{ and } K_4 \equiv K_{2c},$$

the expressions for concentration of a chemical trace substance in the organic material of the non-autotrophic components are:

Total material in the web,

$$C_t = C_o \frac{K_2(1-K_4)}{K_4(1-K_2)} \quad (15)$$

Total living material,

$$C_l = C_o \frac{jK_2}{K_4} \quad (16)$$

Total non-living recoverable material,

$$C_{ln} = C_o \frac{pK_2}{K_4} \quad (17)$$

Strict herbivores,

$$C_m = C_o j \quad (18)$$

Omnivores,

$$C_o = C_o \frac{jK_2}{K_4} \quad (19)$$

Particle feeders,

$$C_{\mu} = C_o \frac{jK_2(1-jK_1)}{K_4(1-K_1)} \quad (14)$$

Detrital feeders,

$$C_d = C_o \frac{j p K_2}{K_4} \quad (20)$$

Full predators,

$$C_p = C_o \frac{j^2 K_2}{K_4} \quad (21)$$

Limited predators,

$$C_{pl} = C_o \frac{j^2 K_2(1-jK_1)}{K_4(1-K_1)} \quad (21a)$$

Secondary predators (from Eq. 9c),<sup>3</sup>

$$C_{ps} = C_o \frac{j^2 K_2}{K_4} \quad (21b)$$

Non-herbivorous omnivores,

$$C_n = C_o \frac{jK_2(1-K_4)}{K_4(1-K_2)} \quad (22)$$

Feeders on a detrital milieu,

$$C_{dt} = C_o \frac{j p K_2(1-jK_1)}{K_4(1-K_1)} \quad (23)^4$$

A number of features of the above treatment of concentrations should be noted. For example, with the exception of strict herbivores, the concentration in all types increases without limit as  $K_4$  ( $\equiv K_{2c}$ )  $\rightarrow 0$ , that is, as losses of the chemical substance from the web become small.

Less obvious, perhaps, from Eq. 12, is that  $j \gg \frac{1}{K_{1f}}$  since  $K_{1c} \gg 1$ . As the relevance of this limit depends upon dilution of the retained chemical substances by new tissues,  $j$  is no longer limited by this effect as  $K_{1f} \rightarrow 0$ . Under these circumstances, the concentrations of trace substances will then be determined solely by the intake and residence times in the organism. Certain individual marine creatures that are non-growing or only slowly growing because of disease, abnormality, age, definitive size, or other reasons, will have a higher upper limit of concentration. Thus they may show much higher levels of trace substances than their healthy growing associates.<sup>6</sup> Conclusions as to cause and effect relationships of abnormalities and trace substances must consider this toxomimetic possibility. There also may be non-linear feedback effects on growth or residence time, when the trace substances in the organism approach toxic levels, and the trace substances may then be subject to greater concentrative or eliminative effects.

The converse limits also hold. Hence, when  $j$  and  $p$  are known, and either or both are greater than unity, the upper values of the possible coefficients of conversion of food may be further constrained, since  $jK_1 + pK_3 \gg 1$ .<sup>6</sup> These are shown in the example in Fig. 2 where, for  $j = 3$ ,  $p = 1$ , the upper limits for  $K_1$  are 0.30 and 0.233, when  $K_3 = 0.1$  and 0.3, respectively. When the concentration in some trophic type is also known, as in Young's work, the range of possible trophic coefficients may become very narrowly limited. A treatment of this nature brings most of Young's

<sup>6</sup> The validity of these particular results are not dependent upon the validity of the total general thesis. A general mathematical treatment of the effect of growth of an organism on its trace element content, particularly radioisotopes, is published by the National Academy of Sciences (1962) p. 57. For uptake of radiospecies with high physical decay rates and low biological decay rates (i.e., short half-lives and long retention times) rapidly growing organisms will, of course, show higher levels than their slower growing associates.

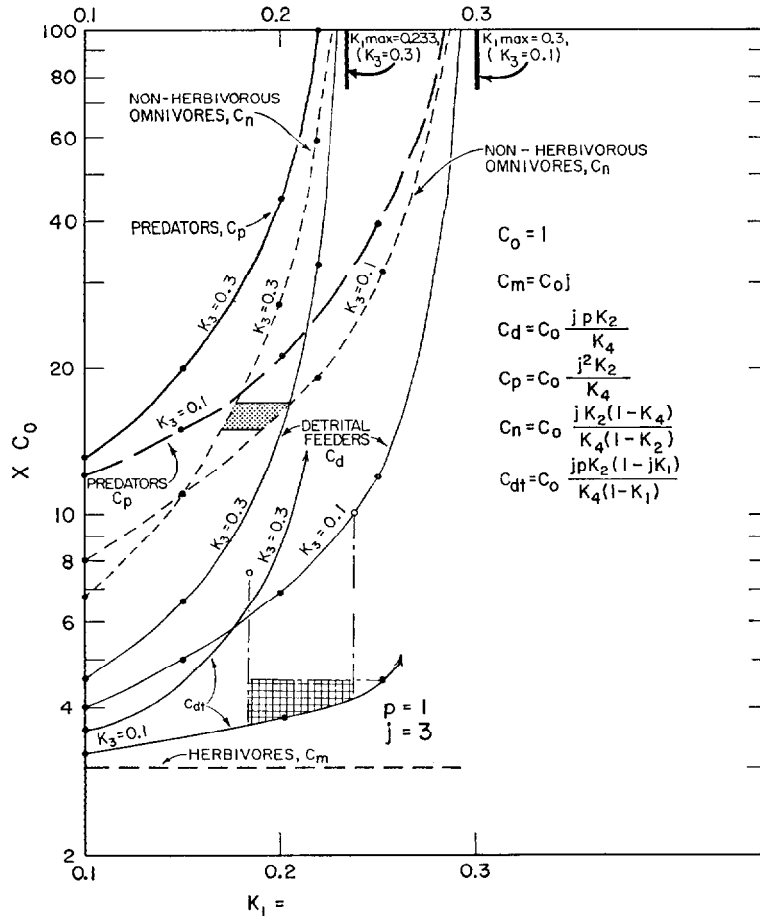


Fig. 2. Comparison of trace-substance concentration in 5 trophic types. Shaded area: limits for  $C_n = 16 \pm 1$ ; cross-hatched area: limits for  $C_{dt} = 3.8 \pm 0.5$ , when  $C_v = C_d = 8.4 \pm 1.2$ . When  $p = 1.0$ ,  $C_v = C_d$

anomalous results on cesium in the fishes of the Gulf of California versus those of the Salton Sea (Young, 1970) into reasonable agreement with values of the order of  $0.1 < K_3 < 0.3$  and  $0.16 < K_1 < 0.20$ , where it was known that  $C_n \approx 16$  (for Gulf fish),  $j \approx 3.0$  and  $p \approx 1.0$ , for Cs (normalized to potassium, K) in the organisms. As shown in the shaded area of Fig. 2,  $K_1$  is very narrowly limited.

Using the only other suitable data on Cs and other trace elements that apparently is available (Robertson *et al.*, 1972), the flesh of three species of flatfish and one species of shrimp all taken in the same area off the Oregon-Washington coast, show consistent concentrations of Cs (in respect to K) of  $3.8 \pm 0.5$  over the water. The flesh of a fifth species, a flatfish, however, shows a concentration of  $8.4 \pm 1.2$ . These results are plotted on Fig. 2. The most reasonable absolute fit is obtained by considering the four species in the first group to be feeders on a detrital milieu, and the fifth species to be an omnivore or detrital feeder. As shown, the range of coefficients common to both is

$K_1 = 0.18$  to  $0.23$ , and  $K_3 = 0.1$  to  $0.2$ . The ranges are undoubtedly broadened by my employment of a single value of  $0.016$  gK/g dry weight for normalization, as the published related concentrations of K are highly variable and appear faulty. The data reported for other trace elements in these species are also highly variable, and although Rb, Ag and Hg show trends related to the Cs results, the trends are not quite statistically defensible.

Further comparisons of the concentrations of several trophic types from single webs may further refine limits and determine consistent ranges for the coefficients.

It should be noted that several of the possible comparisons eliminate the need for estimating some of the coefficients. For example, in the ratio of the concentration of appropriate trace substances in predators versus particle feeders,

$$\frac{C_p}{C_\mu} = \frac{j(1 - K_1)}{(1 - jK_1)}, \tag{24}$$

only two coefficients are involved.

### Time Scales

Should these expressions be found to have further general validity, it will be interesting and important to evaluate the time scales of events in marine environments. One approach to time should be available from the comparative specific activity of suitable substances between trophic types where both the stable and radiospesies can be assumed to be in similarly steady input and tropho-dynamic state, and for which entry into the food web is via the autotrophs only.

It is not clear that suitable elemental species exist. Some fission isotopes may be in a meaningful steady state, and of the natural isotopes,  $Pb^{210}$ ,  $H^3$  (in organic material),  $Ra^{228}$  or  $Ac^{227}$  are perhaps possible candidates.

Should such radioactive species be discernible, time scales may be approached by the following treatment. Expressing the periodic input as  $M_o = \Delta t P$ , where  $P$  is the net rate of autotrophic plant input and  $\Delta t$  is the time period of the average trophic step, the comparison of specific activities of an element in several well-defined trophic types should yield estimates of the time scale of the processes. The expressions will be similar to the following example for full predators versus autotrophs:

$$\Delta t - \ln \left\{ \frac{2R_o K_1 c^2}{-R_p(1 - K_{2c}) \pm (R_p^2(1 - K_{2c})^2 + 4R_p R_o K_1 c^2)^{1/2}} \right\} \frac{1}{\alpha} \quad (25)$$

where  $R_o$  and  $R_p$  are the specific activities in the autotrophs and the predators, respectively, and  $K$  is the physical decay constant of the radiospesies. By a more thorough analysis of specific activities for several suitable isotopes in several trophic types, further penetrations of food web coefficients and other parameters are perhaps possible, including those in webs in non-steady-state conditions.

No adequate data appear to exist for examining the time scales in a free marine food web by this approach. In the nearly linear food chain of the Salton Sea, however, the specific activity of the water is about  $3.00 \times 10^{-7}$  CiCs<sup>137</sup>/g Cs, and the top predator,  $2.78 \times 10^{-7}$  CiCs<sup>137</sup>/g Cs (Young, 1970). This yields  $\Delta t \approx 240$  to 300 days for each of the presumed 4 to 5 intervening trophic steps. There is no assurance that Cs<sup>137</sup> is in steady state in this environment, and the specific activities of some of the intermediate organisms are not in agreement with this interpretation. However, the result is very similar to the period of emergence of the top predator following its first successful spawning (i.e.,  $\sim 3$  years) (Whitney, 1961), hence the calculation lends some credence to the specific activity approach to time scales, which will be the subject of further study.

Further study will also be made of the unsteady-state dynamics, and especially to concentrations in organisms in secularly increasing inputs of trace substances. Certain dynamics of the system can be

expressed by the preceding treatment on concentrations. I have not yet developed expressions for unsteady states. For cases involving the sudden initiation of a new continuous input, the approach of the system to a new equilibrium will follow equations of the general type:

$$M = \frac{p\Delta t f(K_i^n) e^{-n\Delta t/t}}{e^{\Delta t/t} - (K_1 + K_3)}$$

or

$$M = \frac{p\Delta t f(K_i^n) (1 - e^{-t/\Delta t})^{n+1}}{1 - (1 - e^{-t/\Delta t}) (K_1 + K_3)}$$

where  $f(K_i^n)$  is an  $n$ th order polynomial of the  $K_i$ 's and where  $t$  is time following initiation of a new continuous input. Qualitatively, it is clear that the rate at which equilibrium is approached in the various trophic components may be very sensitive to the values of the factors that are related to conservation and build-up of the substance in the web. Thus if  $K_4$  ( $\equiv K_{2c}$ ) be very small, equilibrium may be approached slowly for all components excepting herbivores. Additionally, powers above unity or products of the coefficients in the expressions for concentration generally imply a slower approach to equilibrium, but in general these are also the same features in the expressions that lead to high equilibrium levels of the trace materials.

It thus appears that those trophic components which eventually will show the highest concentrations, due to an increasing input of a trace substance, may be the slowest to approach the equilibrium values, and in some cases, the slowest to show any detectable effect. Surveys of the distribution of non-equilibrium trace substances in the biota, may be seriously misinterpreted if high and low concentrations in various species are respectively equated to high and low ultimate vulnerability of the species.

### Summary

1. An unstructured food-web model may emulate real marine food webs with greater veracity than does a structured model.

2. An unstructured steady-state doubly-infinite marine food-web model yields extremely simple expressions for the potential relative and absolute flux, biomass, and chemical composition of specific trophic types and materials.

3. Despite the highly simplified assumptions, these expressions qualitatively permit the high level of predaceous and other types versus herbivores observed in many field surveys, and quantitatively explain some anomalous results of concentration of the trace element Cs in marine forms.

4. The treatment shows how findings in one area of marine research may yield insight into another. For example, concentration factors of trace substances set

meaningful strict limits on coefficients of food conversion, and vice versa.

5. The treatment also points out some peripheral matters, such as possible non-causal association of high trace-substance concentrations in abnormal organisms, and possible inverse relationship of the early concentrations of recently introduced trace-substances to ultimate steady-state levels in various organisms.

6. Suitable data for further quantitative testing of the model does not now appear to exist, and only data carefully collected to test the model can be expected to be adequate. Should such data show that the approach possesses any further substantial and general validity to natural marine tropho-dynamic systems, it should be possible to estimate a number of fundamental features, parameters, and rates of a system, to estimate the trophic positions and potential relative and absolute biomasses of its members, and to predict the potential steady-state distribution and levels of trace substances in these members and the systems in general.

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