

# UNSTRUCTURED MARINE FOOD WEBS AND "POLLUTANT ANALOGUES"

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## ABSTRACT

The several species of fish living in the Gulf of California have been shown to possess quite different concentrations of cesium (and cesium in respect to potassium) than the same species of fish living in the Salton Sea. The Salton Sea fish display simple trophic steps of concentration, whereas those in the Gulf all show about the same levels. These differences are reasonably well explained by simplified trophic models of the two environments. The concentration factor found in the known and describable *food chain* of the Salton Sea, applied to a model of an assumed unstructured *food web* in the Gulf, leads to reasonable results. This suggests that study of the concentrations in marine organisms of such natural trace substances as cesium may lead to an understanding of the trophic position of the organisms, and hence constitute "pollutant analogues" that may yield a better understanding of the existing or potential distribution of pollutants in marine organisms.

Young (1970) found that the cesium content of the muscle of the several species of fish in the Salton Sea (California) increased by about a factor of 2 (average 2.15) in each of the successive steps in the simple linear food chain existing in that isolated marine environment and that the cesium/potassium (Cs/K) ratio similarly increased by about a factor of 3 (average 3.1). Results both for normal and radioactive cesium were in agreement. Young further demonstrated that the entry of the cesium into the food chain was via the phytoplankton, only. However, Young found that the same several species of fish in the Gulf of California displayed no such successive steps of increase, but rather, that the muscle tissue of all contained about the same concentration of cesium (with the supposedly more primary feeding mullets surprisingly having a somewhat greater than average concentration of cesium). Young's results are summarized in Table 1, where it can be seen that the Cs/K ratio is elevated by about a factor of

16 between the primary food and the fish in the Gulf of California.

Young suggested that these differences might be the result of a complex food web in the Gulf of California, and reported some evidence for this in the stomach contents of these Gulf fish.

## DEVELOPMENT OF AN UNSTRUCTURED FOOD WEB MATRIX AND EQUATIONS

The following is an attempt to develop a highly simplified model of a generalized food web, to discuss some of its implications, and to test its validity by using real data.

Let us first assume that in a food web each transfer of organic material (or energy), or of individual elements such as cesium, from one component of the web to another can be characterized by the following quantities:

$K_1$  = a coefficient of conversion of matter (or energy) in food into living tissue

$K_2$  = a coefficient of conversion of matter (or energy) in food into irretrievable form (e.g., by respiratory combustion or mineralization)

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TABLE 1.—Summary of Young's results.

Item	Salton Sea		Gulf of California	
	Cs/K ratio $\times 10^6$	Concentration factor relative to food	Cs/K ratio $\times 10^6$	Concentration factor relative to food
Water	3.5 $\pm$ 0.1		0.823 $\pm$ 0.047	
Algae	4.0 $\pm$ 1.0		0.823 $\pm$ 0.047	
Invertebrate <sup>2</sup>	3.8 $\pm$ 8.5	1.0 — 2.1		
Mullet	9.0 $\pm$ 1.1	2.3 $\pm$ 0.7	(algae) 15.2 $\pm$ 1.7	18.5 $\pm$ 2.0
Shad	14.8 $\pm$ 3.1	2.7 $\pm$ 0.7	(invertebr.) <sup>2</sup>	
Sargo-croaker	26.0 $\pm$ 2.7	5.5	(invertebr.) <sup>2</sup>	13.2 $\pm$ 1.0
Corvina	57.7 $\pm$ 7.7	2.0 $\pm$ 0.3	(croaker) 10.4 $\pm$ 0.8	12.7 $\pm$ 1.0
	Average	3.1 $\pm$ 0.8	12.8 $\pm$ 1.1	15.6 $\pm$ 1.3

<sup>1</sup> Cs/K for algae taken as Cs/K for water.

<sup>2</sup> Concentration factor involves values for specific invertebrates within the range shown.

$K_3$  = a coefficient of conversion of matter (or energy) in food into nonliving but retrievable form (e.g., organic detritus or dissolved organic matter)

For each component

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

$$0 < K_i < 1, \text{ where } i = 1, 2, \text{ or } 3.$$

These coefficients are assumed to apply to the nutrient processes of all heterotrophs in the system, microorganisms, invertebrates, and vertebrates alike. Further they are assumed to have constant mean values for each ingested component of a food web in which plant production is the only primary source.

Under these assumptions, some of the principal characteristics of a generalized food web can be represented by a matrix such as Figure 1. Each division along an abscissa represents the conversion of a fraction,  $K_1$ , of any arbitrary unit of food into living tissue. Therefore, the numbers on the horizontal axis are powers of  $K_1$ . Each division along an ordinate similarly represents the conversion of a fraction,  $K_3$ , of any arbitrary unit of food into retrievable but nonliving organic matter, and the numbers on the vertical axis are, thus, powers of  $K_3$ . These numbers can be used to name points in the matrix as in any set of cartesian coordinates. One use of the matrix can be illustrated by considering a unit of food,  $M_m$ , (e.g., in a copepod or in an edible nonliving particle) at 2, 3. If it is consumed by a heterotroph, the fraction  $K_1$  is converted into tissue and the fraction  $K_3$  into nonliving retrievable matter. The sum of these two fractions  $M_m (K_1 + K_3)$  is now found at 3, 4.

Its trajectory in the matrix is always to the right and down.<sup>2</sup> All points on a line at right angles to this trajectory (e.g., a diagonal line) can be considered to represent organic matter that has undergone the same number of steps of conversion from its origin as tissue of autotrophic organisms. The expression at the end of each diagonal line in Figure 1 is the sum of all fractions of an original unit of organic matter along that diagonal.

The number of possible paths from the origin to each point in the matrix is easily counted and is the sum of the two numbers of units shown at the point, the lower right-hand number being the number of paths resulting in living matter (or energy) at that point, and the upper left-hand number being the number of paths resulting in nonliving but recoverable matter (or energy) at the point.

It will be seen that this doubly infinite matrix is composed of two superimposed binomial (Pascal) triangles, and can be summed along diagonals resulting in two infinite series of binomials of the form:

$$a + a(a + b) + a(a + b)^2 + a(a + b)^3 \dots \\ a(a + b)^n.$$

The sum of such a series is

$$\frac{a}{1 - (a + b)} \quad (2)$$

and for the sum of living matter (or energy),

<sup>2</sup> Cases may be considered in which either  $K_1$  or  $K_3 = 0$  and motion is either only to the right or only down.  $K_1 = 0$  is, of course, not a permanently viable condition.

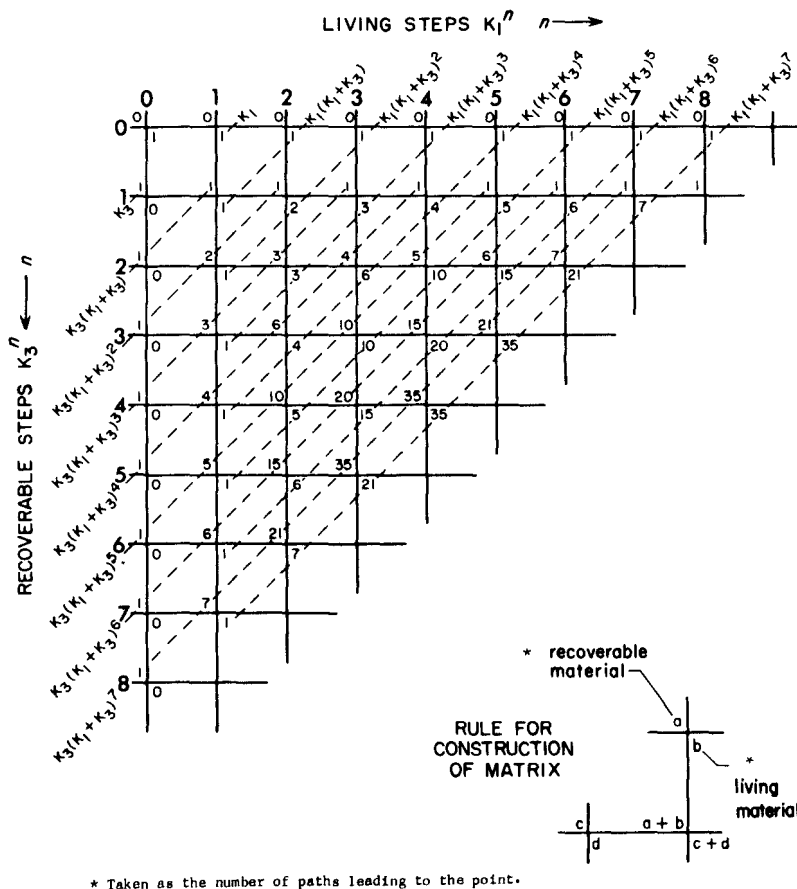


FIGURE 1.—Matrix representing principal characteristics of a generalized food web.

$a = K_1$ ,  $b = K_3$ , and for the sum of recoverable matter (or energy),  $a = K_3$ ,  $b = K_1$ .

These series can be further modified and summed in several ways. We will define a term,  $M_0$ , where  $M_0$  is an increment of initial input periodically introduced into the system at intervals equal to the time taken by one average step in the food web. Under the assumption that all steps are equally probable, the diagonals along which the matrix has been summed mark equal intervals of time. Thus, allowing the quantity  $M_0$  to be successively introduced at the origin of the matrix, the total quantity of material in the entire web, above the phytoplankton level, ( $M_t$ ) for steady state becomes:

$$M_t = M_t' + M_t'' \tag{3}$$

where  $M_t'$  = total in living material, and

$M_t''$  = total in nonliving recoverable material;

$$M_t' = M_0 \frac{K_1}{1 - (K_1 + K_3)} = \frac{M_0 K_1}{K_2} \tag{4}$$

$$M_t'' = M_0 \frac{K_3}{1 - (K_1 + K_3)} = \frac{M_0 K_3}{K_2} \tag{5}$$

$$M_t = \frac{M_0 (K_1 + K_3)}{K_2} \tag{6}$$

### FURTHER VARIATIONS OF THE FOOD WEB MATRIX ANALYSIS

Later I will delete earlier steps in the matrix series. In this case, a more general solution of equation (4) involves a summation of the matrix above any step. Here the partial sum,

$$M_p' = \frac{M_0 K_1 (K_1 + K_3)^p}{1 - (K_1 + K_3)} \quad (7)$$

where  $p$  is the number of steps of the series eliminated.

Other types of formulations and summations are, of course, possible. For example, differences in the time for living-to-living and recoverable-to-living steps may be incorporated by multiplying the constant appropriate to the slower step by another constant representing the inverse ratio of the times of the two respective processes.

As another example, the average content of each point in time in the matrix can be derived by dividing each term of the series by the number of points along the particular diagonal.

Other manipulations of this matrix will be suggested later.

### CALCULATION OF THE COEFFICIENTS OF THE PREDACEOUS FOOD WEB

For the purpose of examining Young's results on cesium, we will proceed with equations (4), (5), and (7) and test the hypothesis that the carnivorous fishes of the Gulf of California are members of an unstructured food web. That is to say that they randomly draw from the mean composition of the food web above the plant level.

Since, from the Salton Sea results, the Cs/K ratio increases by a factor of about 3 for each living step, we can say that

$$K_{1c} \cong 3K_{1f}, \text{ for organic food material} \quad (8)$$

and since the invertebrates in the Salton Sea which feed partially on detritus show no substantially different increase in Cs/K ratio, I will assume that a double step from living to recoverable to living material also results in an increase in the Cs/K ratio of only about 3, and, hence, that

$$K_{3c} \cong K_{3f} \quad (9)$$

where subscript  $c$  denotes the coefficients  $K_1$  and  $K_3$  applicable to the Cs/K ratio, and subscript  $f$  those applicable to food.

For the conditions in the Gulf of California, it is clear that, with the exception of the mullet, the fish do not consume plant material directly, and we can eliminate the first step in the series, and thus, for non-herbivorous omnivores,  $p = 1$ , and equation (7) becomes

$$M_p = M_0 \frac{K_1 (K_1 + K_3)}{1 - (K_1 + K_3)} \quad (10)$$

Let us also define the Cs/K ratio in the plant material as:

$$q_c = \frac{M_{oc}}{M_{of}}$$

$$\text{then } \frac{M_{pc}}{M_{pf}} = \frac{q_c \frac{K_{1c} (K_{1c} + K_{3c})}{1 - (K_{1c} + K_{3c})}}{\frac{K_{1f} (K_{1f} + K_{3f})}{1 - (K_{1f} + K_{3f})}} = 16q_c \quad (11)$$

where the coefficient 16 is approximately the mean increase in the Cs/K ratio from algae to predaceous fish in the Gulf (Table 1), and subscripts are as in equations (8) and (9).

Substituting (8) and (9), equation (11) for food<sup>3</sup> becomes

$$39K_1^2 + K_1(52K_3 - 7) - 13K_3(1 - K_3) = 0. \quad (12)$$

Assumption of a range of reasonable values of  $K_3$  results in the following:

$K_3$	$K_1$	$M_t'/M_0$	$M_t''/M_0$	$M_t'/M_t''$
0.0	0.18	0.22	0.0	--
0.1	0.20	0.29	0.14	2.10
0.2	0.19	0.31	0.33	0.94
0.3	0.18	0.35	0.58	0.60
0.4	0.16	0.36	0.91	0.40

Values of ratios  $M_t'/M_0$  (living material to input),  $M_t''/M_0$  (recoverable to input) and  $M_t'/M_t''$  (living to recoverable) are derived, but it is not known what values of these ratios might exist in nature.

The values of  $K_1$ , however, are within the range of values of conversion commonly found in laboratory experiments and culture operations involving growing animal populations.

We can thus conclude that the assumption of

<sup>3</sup> In the remainder of this paper,  $K_1 \equiv K_{1f}$ , and  $K_3 \equiv K_{3f}$ .

an unstructured food web in the Gulf of California in explanation of Young's findings on *predaceous* fish leads to reasonable estimates of the coefficient of conversion of food.

## PELAGIC VERSUS SHALLOW WATER POPULATIONS

Other variations or testable conclusions or manipulations of these equations can be undertaken. For example, we can derive the relative biomass of two similar environments where, in one, the recoverable matter approaches zero. These might be a near-surface population over deep water where  $K_3 \rightarrow 0$  because of rapid sinking of inert particles compared with a similar population over shallow water where  $K_3$  could have any of the values shown in the table above.

From equation (4)

$$\frac{M'_i \text{ pelagic}}{M'_i \text{ shallow}} = \frac{M_0 \text{ pelagic}}{M_0 \text{ shallow}} \times \left(1 - \frac{K_3}{1-K_1}\right). \quad (13)$$

For the range of values found in the Gulf

$K_3 = 0.0$	$K_1 = 0.18$	$\left(1 - \frac{K_3}{1-K_1}\right)$	$= 1.00$
$K_3 = 0.1$	$K_1 = 0.20$	"	$= 0.88$
$K_3 = 0.2$	$K_1 = 0.19$	"	$= 0.75$
$K_3 = 0.3$	$K_1 = 0.18$	"	$= 0.62$
$K_3 = 0.4$	$K_1 = 0.16$	"	$= 0.52$

## THE MULLET ANOMALY

The high Cs/K ratio of the mullet is difficult to explain. It is generally thought that the mullet is largely herbivorous. Three possible factors may give rise to the anomalous levels: First, the mullet in the Gulf of California may ingest far more organisms with the detrital material than is generally supposed, and these organisms may be part of a microscopic multistep food web that generates a high Cs/K ratio. No such effect was apparent in the Salton Sea, however, possibly because of the paucity and simplicity of invertebrate infauna in the detrital mat. Secondly, some members of the detrital community

in the Gulf may take up inorganic cesium from the sediment, unlike those of the Salton Sea. Third, the high fat level of the mullet results in their possessing a caloric level, as related to organic material, that is 1.6 that of the other fish. This argues that it might be more significant to normalize cesium to calories than to dry organic weight, since more food intake (and hence more cesium) possibly is required for a given increment of growth in a fish with high fat content, with the potassium better normalized to fat free dry weight. This latter assumption would bring the Cs/K ratio in the mullet into the lower ranges of that in predaceous fish.

Pursuing this latter possibility, the adjusted Cs/K ratio for Gulf mullet can be set at about 10, and considering that the composition of the detrital feeding creatures ( $M_d$ ) should be [from food represented by equation (5)]

$$M_d = M_0 \frac{K_1 K_3}{1 - (K_1 + K_3)}; \quad (14)$$

then the Cs/K ratio should be

$$\frac{M_{dc}}{M_{df}} = \frac{q_c \frac{K_{1c} K_{3c}}{1 - (K_{1c} + K_{3c})}}{\frac{K_{1f} K_{3f}}{1 - (K_{1f} + K_{3f})}} = 10q_c. \quad (15)$$

Substituting equations (8) and (9), as before, this becomes

$$K_3 = 1 - \frac{27}{7} K_1 \quad (16)$$

which is within the range of values for these constants previously derived (e.g.,  $K_3 = 0.30$ ,  $K_1 = 0.18$ ). In simultaneous solutions of equations (12) and (16) values of  $K_3$  are extremely sensitive to the values of concentration. The values of  $K_1$ , however, are essentially stable.

## CONCENTRATION FACTORS

It should be noted in this discussion that the high concentration of cesium in the mullet may be a specific case of a more general principle, which is that the concentration factor ( $f_c$ ) of a trace substance in a single step may be inversely

related to the coefficient of conversion of food (in terms of material). Certainly the upper value of  $f_c$  is limited to the total trace substance intake "diluted" by the new growth and hence,

$$f_c \not\geq \frac{1}{K_{1f}} \quad (17)^4$$

This argues that a creature with a low coefficient of conversion for food can show high concentrations of trace elements or pollutants for this reason alone.

Such lower coefficients of conversion and high concentration of trace elements may result from definitive growth, sickness or abnormality or, as probably in the case of the mullet, when food is converted into a more energetic form. Conclusions as to cause and effect of pollutant trace element concentrations in creatures with abnormalities must thus be considered with caution.

## CONCLUSIONS

The assumption and analysis of an unstructured food web is reasonably consistent with findings on the concentration of the element cesium (in respect to potassium) in the Gulf of California. It suggests that unstructured marine food webs may be common and that the distribution of natural trace elements, such as cesium, may give insight into food webs in gen-

<sup>4</sup> This can be derived more formally as follows: let  $C_f$  be the concentration in the food; then

$$C_f = \frac{q_c}{q_f}$$

where  $q_c$  is quantity of the substance and  $q_f$  is total quantity of food material.

Then the concentration in the organism,

$$C_o = \frac{q_c K_{1c}}{q_f K_{1f}} = C_f \times \frac{K_{1c}}{K_{1f}}$$

since

$$f_c = \frac{C_o}{C_f} = \frac{K_{1c}}{K_{1f}} \quad , \text{ and}$$

$$K_{1c} \not\geq 1 \quad , \text{ then}$$

$$f_c \not\geq \frac{1}{K_{1f}} \quad .$$

eral, and hence into the existing or potential distribution of pollutants.

## ADDENDUM

Several reviewers of this paper have suggested that I expand the treatment of trophic types in an unstructured food web. Dominance of any highly complex trophic types is incompatible with an unstructured food web hypothesis. However, the following may be considered compatible (from equations 4, 6, or 7 as appropriate):

Strict herbivores

$$M_h = M_0 K_1 \quad (19)$$

Omnivores

$$M_o = M_0 \frac{K_1}{1 - (K_1 + K_3)} \quad (20)$$

Particle feeders

(detritus + phytoplankton)

$$M_u = M_0 \frac{K_1 (1 - K_1)}{1 - (K_1 + K_3)} \quad (21)$$

Detrital feeders

$$M_d = M_0 \frac{K_1 K_3}{1 - (K_1 + K_3)} \quad (14)$$

Feeders on the detrital

milieu (detritus and detrital feeders)

$$M_{d+t} = M_0 \frac{K_1 K_3 (1 + K_1)}{1 - (K_1 + K_3)} \quad (22)$$

Strict predators

$$M_p = M_0 \frac{K_1^2}{1 - (K_1 + K_3)} \quad (23)^5$$

Non-herbivorous omnivores

$$M_v = M_0 \frac{K_1 (K_1 + K_3)}{1 - (K_1 + K_3)} \quad (10)$$

<sup>5</sup> Equation 23 could well have been employed instead of equation (10) in the previous treatment. Differences in results would be small, however.

These expressions can be employed to generate expressions for the coefficient  $R$ , or the increase in the concentration of any component passing through the food web and introduced only via plants. The derivation follows that of equation (11) above, where  $j$  is the coefficient of increase over the conversion of food, as in

equation (8) above, where  $j \cong 3$ . Also, for interest, is shown the coefficient  $N$ , which is the limiting or maximum increase in the biomass of each trophic type resulting from a unit input into the food web (i.e.  $M_0 = 1$ ), evaluated from the above equations.

	$R$	Equation No.	$R^*$	$N^*$
Strict herbivores	$j$	(24)	3.0	0.18
Omnivores	$\frac{jK_2}{1 - jK_1 - K_3}$	(25)	9.7	0.35
Particle feeders	$\frac{jK_2(1 - jK_1)}{(1 - K_1)(1 - jK_1 - K_3)}$	(26)	5.5	0.28
Detrital feeders	$\frac{jK_2}{1 - jK_1 - K_3}$	(27)	9.7	0.10
Feeders on the detrital milieu	$\frac{jK_2(1 + jK_1)}{(1 + K_1)(1 - jK_1 - K_3)}$	(28)	12.7	0.12
Strict predators	$\frac{j^2K_2}{1 - jK_1 - K_3}$	(29)	10.4	0.06
Non-herbivorous omnivores	$\frac{jK_2(jK_1 + K_3)}{(K_1 + K_3)(1 - jK_1 - K_3)}$	(30)	15.0	0.17

\* for  $K_1 = 0.18$ ,  $K_3 = 0.30$ ,  $j = 3$

It should be noted that the coefficient  $N$  indicates only the potential increase of the biomass of each trophic type, as related to productivity input. The potential population (standing crop) depends upon how closely this maximum is approached, and the fecundity, mortality, etc. of the appropriate organisms.

It should also be noted that the usefulness of the total assumptions of this model can be tested by the determination of  $R$  for an appropriate

trace element, such as Cs, in samples of well defined trophic types.

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