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ASSIGNING TROPHIC LEVELS TO MARINE ANIMALS

The concept of using trophic steps to represent the feeding relationships between a succession of prey and predators has long been established (Odum 1971). There is a general understanding among marine biologists that these steps are approximately as follows: Trophic Level I for primary producers (plants), II for herbivores (plant consumers), III for primary carnivores that feed on herbivores, IV for secondary carnivores, and V for the tertiary or top carnivores in the ocean. As the generally larger animals at the top eat the successively smaller ones below, the energy in foods flows upwards to the top predators. Because animals often feed on whatever is available, as well as several kinds of preferred prey (all of which may be at different trophic levels), an orderly succession, or "chain," is rare. This lateral spreading makes it preferable to refer to the structures as a food "web."

In recent years there has been much speculation about whether contaminants in the sea, including metals and synthetic organic chemicals, also move upwards thru the food web and, if like energy, are concentrated or biomagnified at higher levels. Therefore, this Project, under a grant from NSF, undertook to study a series of ocean food webs in contaminated regions, as well as the open ocean. It became apparent at once that refinements would have to be made to the broad trophic level assignments given above so that the question of contaminant magnification could be tested. Therefore, the objective of the work described here was to produce an objective and repeatable means of assigning values to each species. This paper describes how those assignments were made.

Although the principles of establishing trophic levels are simple, there are problems when they are put into practice. For example, some marine animals change diets and thus pass thru several trophic levels as they increase in size. Fish with swim bladders have the stomach contents forced out as they are brought to the surface so it is hard to determine what they have been eating. Little is known about what some very small animals eat; other mascerate their food so thoroughly it is unidentifiable.

In spite of these and other difficulties, I believe that the method described here is generally valid and can be used by scientists elsewhere.

THEORY

By definition, a predator occupies a position in a food web one trophic step higher than the trophic level of its prey. Thus, the trophic level of a predator may be defined as the trophic level of its prey plus 1.0. Marine predators commonly consume prey representing several trophic levels or even intermediate trophic levels; thus, to make this definition operational, a method is needed whereby one can compute the "average" trophic level of a predator's suite of prey using data from stomach content analyses or direct observations of feeding. Several steps are required to accomplish this, including,(a) identifying prey and ranking them in terms of their relative "importance" (such as nutritional content, abundance, size, etc.), (b) re-classifying the most "important" prey by **their** trophic levels, and (c) computing a single "importance-weighted" average prey trophic level. Thus, the trophic level assignment (TLA) is equal to 1 plus the sum of the prey values.

$$\text{TLA} = 1 + \Sigma\ (k_n \cdot I_n) \qquad (1)$$

where TLA = trophic level assignment of the predator (range $1 \geq 5$)

k_n = trophic level assignment of prey item "n" (range 0 to = 5)

I_n = fractional importance of prey item "n" (range 0 to 1.0)

PRACTICE

Use of this formula begins with thoughtful selection of target species suspected to represent the major components of a food web. It ends with computation of each species' TLA and presentation of the results in a fashion appropriate for further analysis and comparison. The actual computations require information sufficient to compute some measure of prey importance and the prey TLA's. If such information is readily available, the method is straight-forward. In practice, however, the needed information is not easily acquired.

The first step - enumerating prey and computing some measure of "importance" of each prey item (I_n in equation 1) - is relatively simple. Biologists have developed a variety of methods for estimating the relative importance of prey to predators. These range from a simple ranking by numbers, weight, volume or frequency of occurrence of each prey type to estimating the contribution which each prey type makes to the total nutrition of the predator. I chose to replace I_n in the equation (1) with the currently popular Index of Relative Importance (IRI) developed by Pinkas *et al.* (1971) to compare food habits of tunas:

$$\text{IRI}_n = \%F_n(\%N_n + \%V_n) \qquad (2)$$

where:

IRI_n = Index of Relative Importance of prey item "n"

$\%F_n$ = frequency of occurrence of prey item "n" among all predators sampled.

$\%N_n$ = number of prey "n" in the collection of predators expressed as a precentage of total number of prey items.

$\%V_n$ = volume or weight (cm^3 or gm) or prey item "n" expressed as a percentage of the total volume or weight of all prey items.

Single predator specimens rarely contain sufficient numbers and kinds of prey to represent what the population as a whole is eating. Therefore, the IRI is usually used to assess important prey in a large collection or sub-sample of each predator. The IRI, which ranges up to a value of 20,000, is computed for each prey item. To make the numbers useful for computing TLA, all IRI's must be transformed to fractions of the total IRI for each predator. These fractions replace I_n in Equation (1).

The second step, determination of prey trophic level (k_n), requires tracing important food of the prey to primary producers (phytoplankton, seaweeds,or bacteria) or detritus. The most objective approach is to first collect the predators of interest and determine their prey items of highest "importance" (eg., IRI's). Then, it is necessary to take additional samples to fill in details until all lines lead to primary producers or detritus. In a simple ecosystem, such as the Salton Sea (Young *et al.*, 1980), this is a simple task, but, in the ocean it is not. One may spend years attempting to elucidate diets of the myriads of small crustaceans, worms,and molluscs that appear in the diets of larger fishes and invertebrates. There is, however, an extensive, if sometimes controversial, literature on feeding habits of small invertebrates (eg;. Fauchald and Jumars, 1979 and Simenstad *et al.* 1979). An example shows how the literature can be used: certain copepods are found to be important (high IRI) prey of a small fish species; several references suggest the copepod feeds exclusively on phytoplankton which has a TLA of 1. Thus, the TLA for the copepod is 2.0 (conventional trophic level II), a value that will replace one k_n in equation (1) as part of the complete TLA computation for the small fish.

The third step, computing a single "importance-weighted" average prey trophic level, is accomplished as in equation (1) by summing the products of the prey trophic level assignments (k_n) and the prey IRI's (expressed as fractions, I_n). This results in solution of the term $\Sigma(k_n I_n)$ with values in the range of 1.0 to about 5.0. To this number we then add 1.0 to obtain the predator's TLA (the importance-weighted average trophic level assignment of the predator).

As described in more detail in the following section, I applied the method to determine TLA's of 32 species of invertebrates, fishes, sharks,and mammals representing three Pacific Ocean food webs. Our research team attempted to identify food items to the species level, but often only genus, family, or order could be determined. In several species, stomachs and intestines were empty in all specimens examined; in others the amount and number of prey items were too low to justify computation of IRI's and TLA's using only our data. In these cases, it was necessary to search for, find, and use quantitative food habits data from other reports and publications. Furthermore, if one of the variables required for computation of IRI was missing (eg., frequency or abundance or volume), it was necessary to substitute a different measure of "importance," such as the modified IRI used by Karpov and Cailliet *et al.* (1978). Sometimes I relied on a single variable, such as the frequency of occurrence.

Likewise, assignment of prey, especially small prey, to a TLA was not always straightforward. We were unable to determine the food of a variety of small worms, crustaceans,and clams common in the diets of several shrimp and fishes; in this, I relied on literature sources. Our best estimates of the TLA's for these small prey are shown in Table 1.

In conducting the computations, I found it useful to compile tables showing for each predator the number, weight, or volume, and frequency of occurrence of each prey in each specimen. These data were then reduced, in the same table, to computations of the IRI and fraction of IRI for each prey item. An example is shown in Table 2. I also found it useful to enter the

Table 1. Assumed trophic levels and origin or food of small prey items identified from stomachs of predators from the three ecosystem collections cited in this report. Data on food or diets from various literature sources and textbooks, but primarily from a compilation prepared by Simenstad et al., 1979.

Assumed Trophic Level	Organism(s)	Comments Origin or food
1.0	diatoms, dinoflagellates, leafy and filamentous algae, vascular plants.	primary producers
1.5	detritus, bacteria	dead plant and animal material
	debris, "mush," fecal pellets.	
2.0	radiolarians, foraminifera, tintinnids, unidentified copepods, calanoid copepods, cyclopoid copepods, nauplii, cyprids, zoea, unidentified small crustacea, insect pupae, oikopleura, siphonophores.	phytoplankton feeders
2.25	sponges and remains, unidentified mysis and mysids, unidentified euphausiids, unidentified pelecypods.	mixed diets of bacteria, phytoplankton, small protozoans
	isopods.	algae, kelp, detritus
2.5	gastropods, nematodes.	microalgae, detritus, small metazoans
	echiuroids, brittlestars, harpacticoid copepods, ostracods, cumaceans, unidentified amphipods.	detritus
	decapod larvae, megalops, fish larvae, unidentified molluscs.	mixed phytoplankton, zooplankton
2.8	rotifers	phytoplankton, protozoa, other rotifers
3.0	tanaids, shrimp, techtibranch *Pleurobranchaea*, unspecified polychaetes.	detritus, small benthic invertebrates
	cladocerans, stomatopod larvae, insect *Halobates*, pteropods, heteropods, myctophids, eggs, unspecified tissue, fish and crabs.	copepods or other zooplankters (small)
3.3	nemerteans.	polychaetes, clams, crustaceans
3.5	argonauts.	large zooplankton
	chaetognaths.	zooplankton, small and larval fish
3.75	unidentified cephalopods (squid, cotopods).	invertebrates and small fish.

fractional (or per cent) IRI's into a complete predator-prey matrix (food spectrum table) for each ecosystem surveyed. This allowed rapid identification and tracking of the major prey items through the food web.

APPLICATION

Equation (1) was used to compute trophic level assignments (TLA's) for 32 species of marine organisms sampled as part of an NSF sponsored study of pollutant flow through marine food webs. The food webs included (a) the benthic macrofaunal community of the Palos Verdes Shelf near a large municipal outfall, (b) the coastal pelagic fauna of the Southern California Bight, and (c) the remote ocean pelagic fauna of the Eastern Tropical Pacific.

Table 2. Example of calculations used to compute trophic level assignment for the Pacific mackerel, *Scomber japonicus*. Fifty-four stomachs were examined, 37 contained prey. F = frequency of prey in predator; N = total number of prey items; V = weight (g) of prey type, and; IRI = Index of relative importance (Pinkas et al, 1971).

(A) CALCULATION OF IRI'S:

	F		N		V		
PREY	#	%	#	%	g	%	IRI
anchovy	8	21.6	32	0.52	242.0	61.09	1331.0
fish, uid.	19	51.4	19	0.31	36.9	9.31	494.5
mysids	3	8.1	5782	94.05	110.0	27.77	987.4
crustaceans, uid.	3	8.1	113	1.84	0.9	0.23	16.8
polychaetes	4	10.8	7	0.11	2.7	0.68	8.5
nematodes	6	16.2	15	0.24	0.2	0.06	4.9
tissue, uid.	2	5.4	2	0.03	1.1	0.28	1.7
eggs	2	5.4	16	0.26	0.2	0.05	1.7
copepods	1	2.7	45	0.73	0.5	0.13	2.3
copepod parts	1	2.7	25	0.41	0.1	0.03	1.2
mush	2	5.4	2	0.03	1.5	0.38	2.2
TOTAL	-	-	6148	100.0	396.1	100.0	2852.2

(B) CALCULATION OF WEIGHTED AVERAGE PREY TLA:

PREY	(1) IRI	(2) % IRI	(3) Prey TLA	(4) Source	(5) Weighted TLA (2) * (3)/100
anchovy	1331.0	46.7	2.82	Table 4	1.317
fish, uid.	494.5	17.3	3.00	Table 1	0.519
mysids	987.4	34.6	2.00	Table 1	0.692
crustaceans, uid.	16.8	0.6	2.00	Table 1	0.012
polychaetes	8.5	0.3	3.00	Table 1	0.009
nematodes	4.9	0.2	2.50	Table 1	0.005
tissue, uid.	1.7	0.1	3.00	Table 1	0.003
eggs	1.7	0.1	3.00	Table 1	0.003
copepods	2.3	0.1	2.00	Table 1	0.002
copepod parts	1.2	0.1	2.00	Table 1	0.002
mush	2.2	0.1	1.50	Table 1	0.002
TOTAL	2852.2	100.0	-	-	2.563 (Prey TLA)

(C) CALCULATION OF PREDATOR TLA:

TLA (Pacific Mackerel) = 1 + 2.563

= 3.56

Results concerning the behavior of pollutants in each of these food webs is summarized in an accompanying article (Schafer *et al.*, this report). Below, I have summarized some of what we learned about each of these ecosystems as a result of making the trophic level assignments. Information is presented to convey both the opportunities and problems associated with determining the trophic levels of these marine organisms.

Sampling Sites and Methods

The soft-bottom region on the Palos Verdes peninsula coastal shelf was sampled for demersal invertebrates and fishes between 22 July 1980 and 29 July 1981. Trawl sampling was conducted along two transects within 1 kilometer of the Los Angeles County outfalls . Ridgeback prawn (*Sicyonia ingentis*), Dover sole (*Microstomus pacificus*), white croaker (*Genyonemus lineatus*) and California scorpionfish (*Scorpaena guttata*) were taken from 60-m deep hauls on 22 July 1980. To broaden the range of predators, we returned on 4 January 1981 and 2 June 1981 to capture spiny dogfish (*Squalus acanthias*) and again on 6 July 1981 and 29 July 1981 to capture epibenthic mysids and shrimp. The spiny dogfish were taken by trawl at the previously sampled stations, but the mysids and shrimp were captured using a benthic sled fitted with 0.5 mm mesh cod end and towed at a station approximately 5 km west of the outfall stations.

Organisms representing the southern California pelagic ecosystem were sampled during 1979 and 1980. We made collections of zooplankton and 16 species of larger animals from the portion of the Southern California Bight roughly bounded by San Miguel Island, San Nicholas Island, San Clemente Island and San Diego. Zooplankton were sampled with a net of 0.3 mm mesh from three stations in Santa Monica Bay and at two sites near Catalina Island. Some fish were taken by hook and line, but 11 species of squid, fishes,and sharks were taken by commercial fishermen and transferred directly to us with catch data. In addition, we were able to sample, or subsample, tissues from five California sea lions (*Zalophus californianus*), a blue whale (*Balenoptera musculus*), a basking shark (*Cetorhinus maximus*), and a white shark (*Carcharodon carcharias*).

All of the biological samples of the ocean pelagic ecosystem were taken during several tuna tagging cruises in the eastern tropical Pacific in 1978, 1980, and 1981. These cruises were sponsored and conducted by the Inter-American Tropical Tuna Commission (IATTC). Species captured included zooplankton, flying fish (*Exocoetus moncirrhus*), squid (*Symplectoteuthis oulaniensis*), frigate tuna (*Auxis* sp.), young skipjack tuna (*Euythunnus pelamis*), young and adult yellowfin tuna (*Thunnus albacares*), and silky shark (*Carcharhinus falciformis*).

Trophic Level Assignments and Food Web Structure

The Palos Verdes Benthic Ecosystem

The food habits study of this ecosystem involved seven predators and nine sets of supportive data from the literature and from other SCCWRP data sets (Table 3). Over 50 types of prey items were recorded from these samples and references. The most important items ranged from sediments, seeds, hair, and diatoms to remains of larger items such as crabs, squid, and fish.

Table 3 shows considerable dietary overlap between the mysids and shrimp, as well as among the apparently more predaceous ridgeback prawn, Dover sole, and white croaker. In contrast, diets of the California scorpionfish and the spiny dogfish were clearly distinct from each other and from the other fish and invertebrate predators indicating predaceous feeding (i.e., on crabs, squid, etc.).

The computed TLA's for these predators reflect dietary differences and overlap ranging from 2.78 for the mysids to 4.53 for the scorpionfish, with an extremely narrow range of values (3.33 to 3.54) for the ridgeback prawn, decapod shrimp, Dover sole, and white croaker.

Some doubts remain because we were unable to conduct a quantitative analysis of the food habits of the Palos Verdes mysids, shrimp and prawn. Neither did we analyze, quantitatively, the dorvelleid polychaete that dominates the diet of Dover sole, nor that of the crabs *Mursia quadichaudii* and *Cancer* spp. that dominate the food habits of the California scorpionfish. Thus, Table 3 includes data from several references selected in an attempt to fill these gaps.

Table 3. Trophic level assignments (TLA's) and food habits spectrum for seven prominent marine animals from the Palos Verdes Shelf. Numerical values are IRI's unless noted otherwise in footnotes.

TLA (Trophic Level)	2.78	3.35	3.33	3.37	3.54	4.16	4.53
PREDATOR	Mysid[1]	Shrimp[2]	Prawn[3]	White Croaker[7]	Dover Sole[4]	Spiny Dogfish[5]	California Scorpionfish[6]
No. Examined	0	0	3	25	30	5	18
No. Positive	0	0	3	24	29	4	15
Avr. Weight (g)	0.006	1	5	129	70	2864	256
PREY							
diatoms	11 - 12.5		X				
dinoflagellates	4.1 - 7.0						
algae	11 - 12.5	20 - 25					
vascular plants	15 - 18.8						
detritus	12.6 - 25.5		X				
fecal pellets				11.4			
rotifers	8 - 25						
sponge parts	6 - 8.2		X				
nematodes				<0.1			0.9
nemerteans					0.5		
polychaetes	2.5	<1	X	30.8	67.4		30.8
crustaceans, unident.	25 - 42		X	<0.1	0.4		
copepods	8.2 - 26	1 - 20	X	<0.6			
harpacticoids				22.3			
cyclopoid				1.5			
cladocerans	2.0						
mysids		40 - 55		<0.1	<0.1		
cumaceans					<30.0		
isopods					0.1		
amphipods	7.1 - 11.3	1	X	0.1	2.2		
decapod larvae		5 - 10		<0.1			
decapod shrimp			31.8	<0.1			
euphausiids			X	<0.1	<0.1	4.4	
crabs			31.8		0.4		99.1 (97.4)[6]
insects	9 - 12.3	<1		<0.1			
molluscs, unident.	2.5 - 10.7						
gastropods			34.7	0.5		4.4	
techtibranchs		1		1.2			
cephalopods						69.7	
tissue, unidentified	2.0 - 8.0	65 - 80		30.3			
fish, unidentified			1.8				0.1
anchovy						5.2	
white croaker						8.2	
northern midshipman						8.2	

FOOTNOTES

[1]Target species is *Neomysis kadiakiensis* but food data is frequency of occurrence among several mysid species cited by Mauchline (1980).

[2]Target species is *Heptacarpus stimpsoni* but food data is from two species, *Crangon* and *Palaemon*, which co-exist with and feed on *Neomysis mercedis* in San Francisco Bay (Sitts and Knight, 1979).

[3]Target species is the ridgeback prawn, *Sicyonia ingentis*; "X" denotes item observed by us; numerical values are IRI's computed from data for *Penaeus monodon* reported by Marte (1980).

[4]*Microstomus pacificus*; data are from reanalysis of samples cited by Kleppel et al (1980) from Palos Verdes.

[5]*Squalus acanthias*.

[6]*Scorpaena guttata*. Number in parentheses is from an earlier collection (unpublished data).

[7]*Genyonemus lineatus*.

The case of the Dover sole represents an example of how uncertainties about prey feeding habits can affect the TLA's. Palos Verdes Dover sole were preying mainly upon polychaetes and cumaceans. These groups of organisms were considered mixed plant and animal feeders in a review conducted by Simenstad *et al* (1979). However, there is controversy about the food of dorvelleid polychaetes, the Dover sole's major polychaete prey at Palos Verdes. Some consider *Schistomeringus*, a dominant Palos Verdes dorvelleid, a herbivore (eg., Word 1980; TLA = 2.0); others consider dorvelleids to be carnivores (eg., Fauchald and Jumars, 1979; TLA = at least 3.0). I chose a median value (TLA = 2.5) which results in a Dover sole TLA = 3.54. However, the value could range from 3.29 to 3.81 depending on the true nature of dorvelleid food habits.

California scorpionfish also presented a problem. It is obviously a crab-eater at Palos Verdes (Table 3), but we were unable to complete a quantitative analysis of the food habits of the prime crab prey *Mursia quadichaudi* and *Cancer anthonyi*. We therefore turned to Warner (1977) who concluded that callipid and cancrid crabs (the families to which, respectively, *Mursia* and *Cancer* belong) are carnivores, consuming gastropods and bivalves; callipids also consume other crabs. In any case, our computed scorpionfish TLA = 4.53 is a value in full agreement with the conventional trophic level IV-V we assigned in an earlier study (Young *et al.*, 1980).

Finally, the computed TLA = 4.16 for the spiny dogfish, a shark, was surprisingly low, especially when compared to the much smaller California scorpionfish (TLA = 4.53, above). The predominantly pelagic nature of these food items suggests that the spiny dogfish were not closely linked to the benthic ecosystem of Palos Verdes at the time of capture.

A summary of the Palos Verdes Benthic Ecosystem food web is shown diagrammatically in Figure 1. This figure indicates the lack of clarity in the food chains and trophic levels of the Palos Verdes shelf demersal fauna. Based on these data, one would expect to have difficulty in distinguishing pollutant/trophic level relationships among these species.

The Southern California Pelagic Ecosystem

Our study of the coastal pelagic ecosystem of southern California involved sampling zooplankton, 17 species of prominent invertebrates, fish, mammalian predators, and locating several dozen food habits data sets in the literature. The data was reported, in part, in Mearns *et al.*, 1981.

A scan of this food spectrum table (Table 4) reveals considerable dietary overlap among several groups of predators, but also a generally uniform progression from small predators and prey in the upper left to large predators and prey in the lower right. In fact, there appears to be considerable opportunity for dietary and trophic distinctness among the predators sampled.

The computed TLA's for these predators reflect this pattern of distinctness and progression. As shown across the top of Table 4, the TLA's ranged from 2.0 for the zooplankton to 5.02 for great white shark, corresponding to a range in traditional trophic level assignments of II to V (herbivores to tertiary carnivores). Nevertheless, there are obvious clusters of species with nearly indistinguishable TLA's.

The first cluster includes species that can be classified as primary carnivores with TLA's that center about a value of 3.00. The eight species in this group include northern anchovy, Pacific sardine, market squid, jack mackerel, Pacific hake, blue whale and basking shark. Despite the wide range in sizes (from 10 g anchovy to 50 m ton blue whale), all feed on zooplankton, especially copepods (TLA = 2.00), crab or shrimp zoea (TLA = 2.00) or euphausiids (TLA = 2.25, from Table 1).

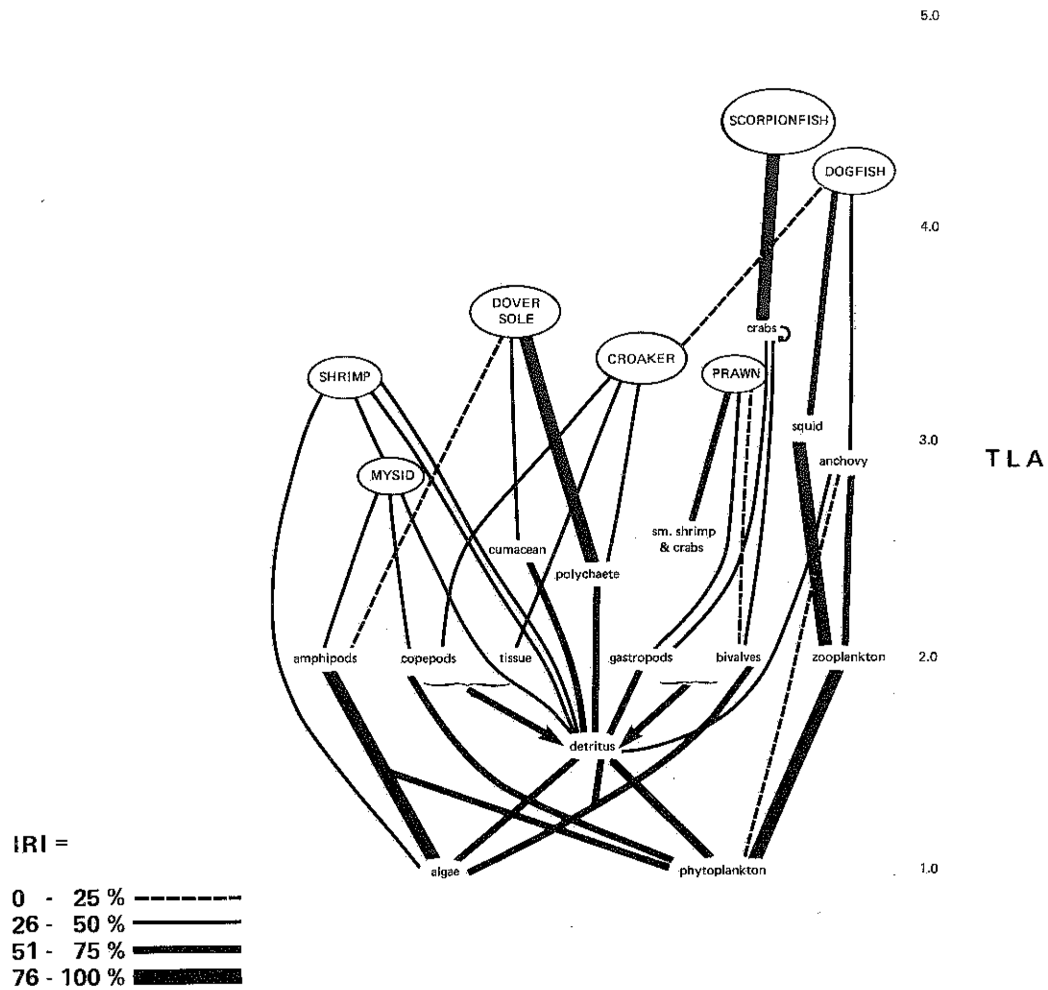

Figure 1. Summary of trophic relationships between target organisms (bold-type and circled) and their major prey sampled on the Palos Verdes coastal shelf, 1980 and 1981. Width of connecting lines proportional to % Indices of Relative Importance (IRI's) from stomach content analysis. Vertical position approximates Trophic Level Assignments (TLA's) computed from IRI's or as suggested in the literature.

The second cluster includes species that are almost, but not quite, secondary carnivores ie., species with TLA's that center about a mean value of 3.73. This group includes Pacific mackerel, California barracuda, Pacific bonito, and thresher shark. Northern anchovy with a TLA of 2.82 was the most important single prey item (IRI's range from 46.7% in Pacific mackerel to 97.9% in Pacific bonito). Mysids with an IRI of 34.6% were nearly as important as anchovies in the Pacific mackerel diets, thus contributing to the low TLA for this species.

A third cluster includes animals that are secondary carnivores since their TLA's center about a value of 4.00. These include swordfish, blue shark, and California sea lion (TLA's range from 3.97 to 4.02). The absence of zooplankton and the relatively larger importance of squid appears to explain the difference of one-quarter trophic step between this and the previously mentioned group of predators. Curiously, one blue shark's stomach contained the remains of a western meadowlark.

	HERBIVORES			PRIMARY CARNIVORES						INTERMEDIATE (III - IV) CARNIVORES		SECONDARY CARNIVORES					INTERMED-IATE CARNI-VORES	TOP CARNI-VORES
TLA (Trophic Level)	2.00	2.82	2.94	3.00	3.00	3.01	3.04	3.05	3.09	3.56	3.74	3.80	3.82	3.97	4.00	4.02	4.40	5.02
PREDATOR	Zoo-plankton	Northern Anchovy	Pelagic Red Crab	Basking Shark	Blue Whale	Pacific Sardine	Jack Mackerel	Market Squid	Pacific Hake	Pacific Mackerel	California Barracuda	Pacific Bonito	Thresher Shark	Swordfish	Blue Shark	California Sea Lion	Mako Shark	White Shark
No. Examined	3	19	100	1	(38)	24	50	50	16	49	28	29	14	17	16	(29)	5	1
No. Positive	-	19	100	1	(34)	24	21	0	14	34	12	16	9	15	15	(27)	5	1
Avg. Weight (g)	0.001	10.8	5.0	10^6	29×10^6	213	154	46.8	314	357	1250	921	61,400	145,000	28,800	35,000	16,800	1.36×10^6
PREY																		
detritus/mush		34.0			P		7.8	11.1	7.1	0.1	27.4	0.8						
diatoms		0.25	20.7															
dinoflagellates		0.04	1.6															
radiolarians			14.8															
tintinnids			15.4															
foraminifera			25.5															
copepods, unid.		55.0	3.6				52.0			0.2								
calanoid	94.0	9.8		100	P	98.9												
harpacticoid		0.5																
cyclopoid	<1.0	0.2																
nauplii/cypris		<0.1																
ostracods	0.3	<0.1																
amphipods					P			0.6										
mysids								3.1		34.6								
zoea/megalopa	5.0					1.0		61.2										
euphausiids	0.3				100				77.6	0.6								
pelagic red crabs									4.5						25.2			
crustaceans, unid.			0.1				24.9	5.4		0.6				0.01				
invertebrates, misc. small	0.3	0.1				<0.1				0.3					0.3			
gastropods			1.4					16.6										
polychaetes							5.2	1.4		0.3								
squid, unid.							1.2						0.1	0.4	64.3	14.5		
market squid												0.5				10.8		
fish, tissue						<0.1	8.2	0.6	2.4	17.4	5.9	0.8	2.0	6.7	8.0	49.7	27.2	
Northern anchovy										46.7	66.7	97.9	97.2	42.6	2.1	14.3		
Pacific argentine									1.2									
mesopelagic, unid.														P				
Pacific hake									7.2				0.8	41.9		10.7		
Jack mackerel																	25.8	
Pacific mackerel																	47.1	
Western meadolark															0.4			
California sea lion																		50.0
Northern elephant seal																		50.0

Table 4. Trophic Level Assignments (TLA) and food habits spectrum for 18 prominent marine animals of the Southern California coastal pelagic ecosystem. Numerical values for zooplankton are % abundance; all other numerical values are % IRI's; p = item present, but not enumerated. Complete documentation including data obtained from the literature is reported in Mearns et al. 1981.

The mako shark (TLA = 4.40) stands alone as a predator, intermediate between secondary and tertiary carnivores. Interestingly, it was the only predator observed consuming both Pacific mackerel and jack mackerel, two of the most abundant pelagic fish in southern California.

The white shark (TLA = 5.02) is the only tertiary carnivore taken. Apparently, pinnipeds, such as California sea lions (TLA = 4.02), are a normal and important part of its diet.

A diagram of the southern California pelagic ecosystem food web is given in Figure 2. For contaminant, which indeed are expected to undergo biomagnification, one would predict a clear increase in chemical concentrations with an increase in TLA's in this ecosystem.

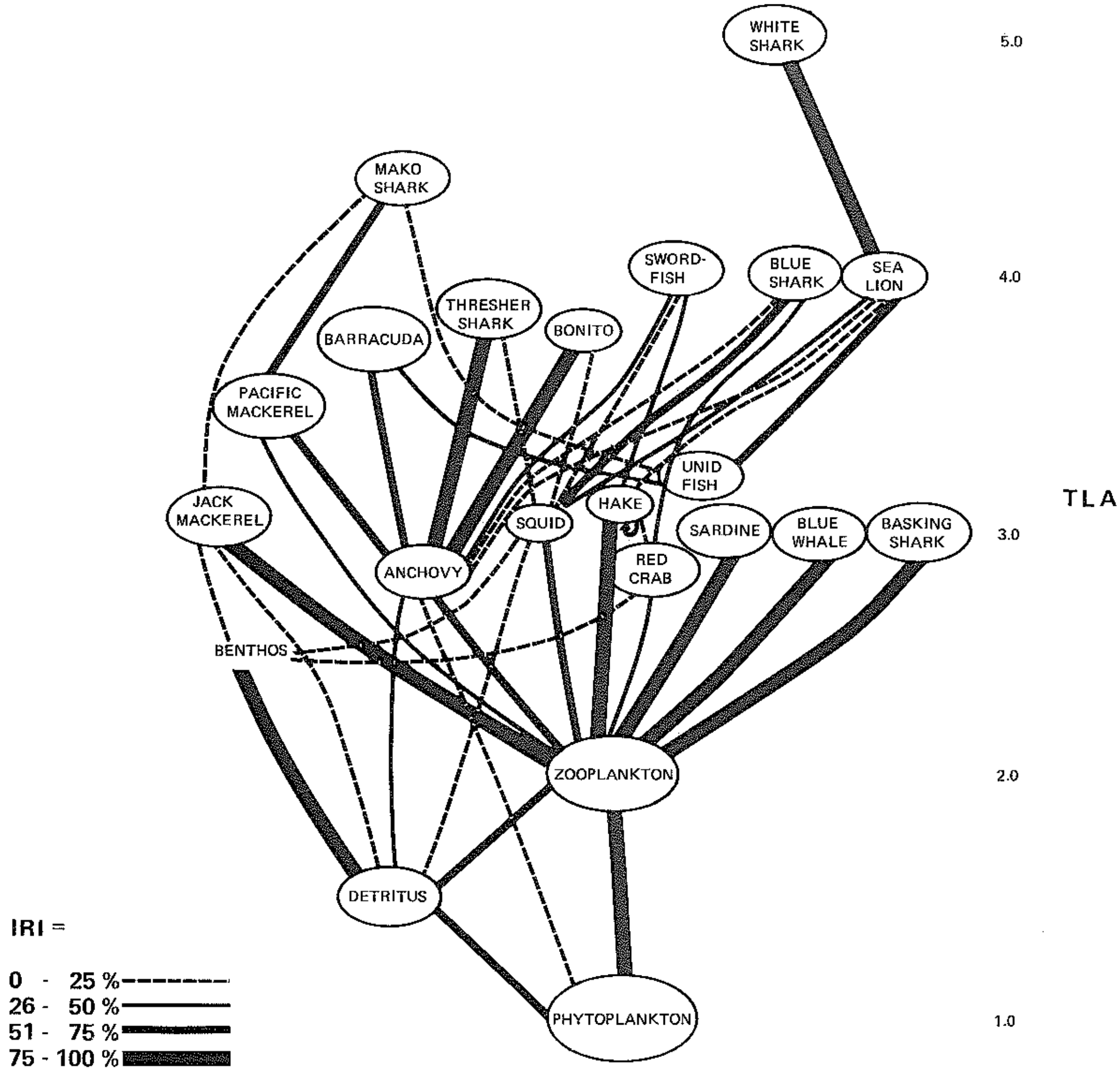

Figure 2. Summary of trophic relationships between organisms and their major prey sampled from the Southern California Bight coastal pelagic ecosystem, 1978 - 1981. Width of connecting lines approximately proportional to % Indices of Relative Importance (IRI's) computed from stomach content analyses. Vertical position approximately equivalent to computed Trophic Level Assignments (TLA's).

The Ocean Pelagic Ecosystem

This ecosystem was represented in our survey by samples of zooplankton, six species of prominent invertebrates, fishes and shark and several food habits data sets from the published literature. Although some of these results have been reported elsewhere (Mearns *et al.*, 1981), this version includes addition of new data for large yellowfin tuna.

Nearly 50 groups or species of actual or potential prey items were identified from this ocean pelagic ecosystem collection. Table 5 reveals little dietary overlap and rather clear separation of trophic levels among the seven species or species groups. TLA's range from 2.0 to about 4.8 corresponding to conventional trophic levels II through about V. Nevertheless, the diets of the large (30.7 kg) yellowfin tuna and the silky shark were such that their TLA's were practically indistinguishable. Frigate tuna (*Auxis* spp.) and skipjack were important prey for both. Flyingfish were moderately important in the diets of small (3.3 kg) yellowfin tuna and skipjack. Relative to the coastal pelagic food web, noted above, top predators of the oceanic food web took a larger variety of small fishes and squid in their diets.

The TLA computations for this food web required assumptions about the trophic levels of several important prey including flyingfish, argonauts (squid-like molluscs) and portunid (swimming) crabs. Based on remarks in several references (cited in Mearns *et al.*, 1981), I assumed that flyingfish fed mainly on zooplankton. Finding no references at all, I had to assume that argonauts also fed mainly on zooplankton. I also assumed that the portunid crab, *Euphylax dovi*, important in the food of large yellowfin tuna, fed on small fish as well as planktonic crustaceans (as noted in Warner 1977). Thus, flyingfish and argonauts were assigned TLA = 3.0 and the crab TLA = 3.75.

The TLA's for zooplankton (2.00), flyingfish (3.00) and squid (3.52) remain unchanged from values reported earlier (Mearns *et al.*, 1981). However, since that report, additional data has come to my attention that increases the published TLA's of the small yellowfin tuna, skipjack, and silky shark. Only one of our frigate tuna, an important food of these predators, contained prey (a small jack mackerel). Uchida (1981) cites data from Kumaran (1964) on the closely related *Auxis rochei* which feeds largely on megalops larvae, predaceous squid, and chaetognaths. Use of these data increases the published frigate tune TLA by 0.36 units, which in turn increases the TLA's for small yellowfin tuna by 0.03 units, for skipjack by 0.19 units, and for silky shark by 0.26 units (Table 5, bottom).

The animals sampled are generally well linked together in this food web. As shown in Figure 3, there is a strong link (high IRI) between the squid (prey) and young yellowfin tuna (predator), between frigate tuna and each of the three large predators (large yellowfin tuna, skipjack and silky shark) and between zooplankton and flyingfish. However, links between flyingfish and upper trophic levels are weak in this survey.

DISCUSSION AND CONCLUSION

This method produces results that make sense and the assignments generated by it compare favorably with more subjectively derived assignments for these and similar species used in previous studies. The method reported here produced values in the range 1 to 5 (Table 6), but is not limited to this range. This is important in view of the fact that the open oceans and other ecosystems may contain more than five trophic levels (Ryther 1969 and Wyatt 1979). Finally, as noted in the introduction, marine biologists recognize that individual species can feed from a range of trophic levels, including intermediate levels, their own level, or even higher trophic levels (e.g., parasites). The method also allows for intermediate assignments that result from any or all of these possibilities (Table 6).

Table 5. Trophic level assignments and food habits spectrum for eight prominent animals from the ocean pelagic ecosystem of the Eastern Tropical Pacific Ocean. Numbers for zooplankton are % relative abundance; all others are % IRI's. IRI's for frigate tuna are for the related *Auxis rochei* from date of Kumaran (1964) cited in Uchida (1980); see Mearns et al. (1981) for other important notes and qualifications.

TLA (Trophic Level)	2.00	3.00	3.52	3.92	4.29	4.49	4.81	4.82
PREDATOR	Zooplankton	Flyingfish	Squid	Frigate tuna	Yellowfin tuna	Skipjack tuna	Silky shark	Yellowfin tuna
No. Examined	4	35	78	2	36	44	4	50
No. Positive	-	35	15	2	27	18	2	59
Prey Weight (g)	0.001	51.0	209	774	3315	2487	25.8×10^3	30.7×10^3
Detritus, debris, mush		P	8.2					
polychaetes				0.32				
Copepods, unid.		100						
calanoid	55.8							
cyclopoid	4.0							
Ostracods	0.4							
isopods								0.04
amphipods	1.8			1.05		0.8		
mysis of shrimp				0.84				
zoea/megalopa decapod	2.7			47.76	0.1			
stomatopod larvae	0.7					0.3		
euphausiids	16.5							
portunid crabs								43.86
Alima larvae				0.68				
unid. crustaceans	0.1	+	+	0.22				
Insects-Halobates				0.99				
Molluscs								
gastropods	0.9							
pteropods	2.3				0.8			
heteropods	1.3							
bivalves	0.1							
cephalopods				13.24				0.03
argonauts					17.4	0.8		1.34
squid					55.9			3.04
octopods			13.9		0.3		26.9	0.01
Siphonophores	0.8							
Oikopleura	0.1							
Chaetognatus	6.1			8.85				
Fishes								
unid., tissue, larvae	0.2	tr	77.8	14.76	2.4	3.2		0.05
eggs	1.6							
engraulids (anchovy)			+	3.09	0.3	1.6		
clupeids (herring)				2.25				
myctophids (lanternfish)			+	0.68	0.2			
exocoetids (flyingfish)					22.6	39.0		0.60
leiognathids				3.53				
sygnathids (sea horse)					0.5	9.2		
frigate tune (*Auxis*)					0.1	53.1	73.1	50.2
scombersodidae (saury)			+			110.6		
coryphaenids (dolphinfish)								0.24
balcstids (trigger file fish)					0.1			
tetradontids (pufferfish)					0.2			0.60
sphyraenids (barracuda)				0.28				
carangids (Jacks)				0.55	0.2			

P = Present but not quantified

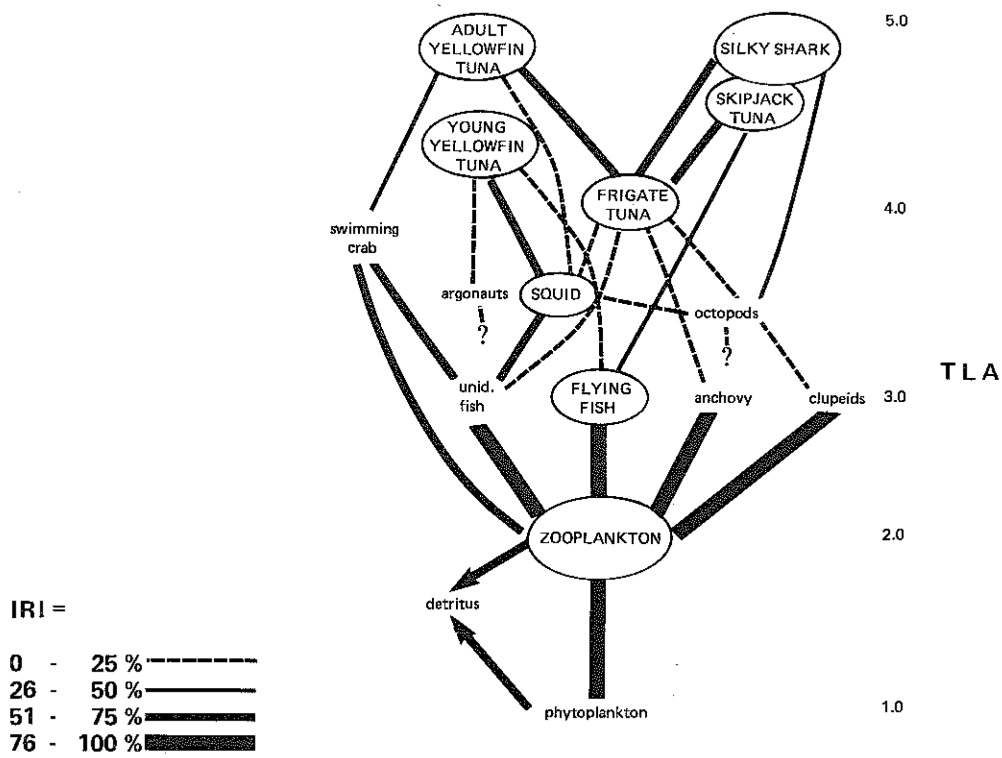

Figure 3. Summary of trophic relationships between target organisms (bold-type and circled) and their major prey sampled from the Eastern Tropical Pacific Ocean, 1980 and 1981. Width of connecting lines proportional to % Indices of Relative Importance (IRI's) from stomach content analyses. Vertical position approximates Trophic Level Assignments (TLA's) computed from IRI's.

Yang (1981), who recently used a method similar to this one to compute trophic levels of North Sea commercial shellfish and fishes, has kindly allowed us to cite some of his unpublished results. Comparison of our two data sets reveals one species, five genera, and four families in common between the two studies (Tables 6 and 7). Relative to Yang's numbers, I have overestimated TLA's of three invertebrates by 0.1 to 0.4 TLA units and underestimated TLA's of zooplankton and six carnivorous fishes by 0.1 to 0.5 units.

Many questions remain to be answered. The accuracy and variability of this method has not been determined, although comparison with Yang's data offers some clues. Demonstration of accuracy rests on comparison with some other independent method of estimating trophic levels. Chemical tracers such as methyl mercury, stable isotope ratios, and the cesium-potassium ratio have been proposed.

It would be instructive to compute confidence limits for TLA's derived from a large number of replicate samples or composites of stomach contents from single species or populations. Marine animals also change diet with size and the effect of this on trophic level assignments needs to be explored. Finally, more data is obviously needed on the feeding habits of small planktonic and benthic invertebrates that are important prey for the region's shrimp, prawns, bottomfish, small pelagic fish, and whales.

Table 6. Summary of Trophic Level Assignments (TLA's) for plankton, invertebrates, fishes, sharks, and mammals from three ecosystems sampled 1978-1981.

PREDATOR	TLA Conventional	TLA Numerical	COMPARISON
Palos Verdes Benthic Ecosystem			
Mysid	II — III	2.78	2.4[1]
Shrimp	II — III	3.35	3.2[1]
Prawn	III — IV	3.33	3.2[1], III-IV[2]
Dover sole	III — IV	3.54	3.7[1]
White croaker	III — IV	3.37	
Spiny dogfish	IV ← V	4.16	4.4[1]
California scorpionfish	IV — V	4.53	IV-V[2]
Southern California Coastal Pelagic			
Zooplankton	II	2.00	2.1[1]
Northern anchovy	III	2.82	-
Blue whale	III	3.00	-
Basking shark	III	3.00	-
Pacific sardine	III	3.01	3.5 (herring)[1]
Market squid	III	3.05	-
Jack mackerel	III	3.04	3.5 (scad)[1]
Pacific hake	III	3.09	4.6 (hake)[1]
Pacific mackerel	III — IV	3.54	3.5 (mackerel)[1]
California barracuda	III — IV	3.74	-
Pacific bonito	III → IV	3.80	-
Thresher shark	III → IV	3.82	-
Swordfish	IV	3.97	-
Blue shark	IV	4.00	-
California sea lion	IV	4.02	-
Mako shark	IV — V	4.40	-
White shark	V	5.02	
Eastern tropical Pacific Ecosystem			
Zooplankton	II	2.00	2.00[3]
Flyingfish	III	3.00	3.0[3]
Squid	III — IV	3.52	3.52[3]
Frigate tuna	III → IV	3.92	3.56[3]
Yellowfin tuna (small)	IV ← V	4.29	4.23[3]
Skipjack tuna	IV — V	4.49	4.30[3]
Silky shark	IV → V	4.81	4.55[3]
Yellowfin tuna (large)	IV → V	4.82	-

[1]TLA's from similar North Sea fishes as reported by Yang (1981)

[2]Subjectively derived TLA's as reported in an earlier study (Young et al., 1980)

[3]TLA's computed previous to discovery of more relevant data on feeding habits of frigate tunas (i.e. Mearns et al., 1981 prior to Uchida, 1981, report).

Trophic level, a useful concept in ecology, has been poorly quantified in the past. Perhaps this contribution will lead to use of the concept with more confidence and better numerical assignments when it is used.

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Table 7. Comparison of Trophic Level Assignments (TLA's) made by SCCWRP for 10 Southern California organisms with TLA's made by Yang (1981) for similar or related species from the North Sea.

Southern California (Mearns) Name			North Sea (Yang)			Deviation from Yang
Common	Scientific	TLA	Common	Scientific	TLA	
mysid	*Neomysis* spp.	2.8	mysids	-	2.4	+0.4
shrimp	*Crangon* sp.	3.4	shrimp	*Crangon* sp.	3.2	+0.2
prawn	penaeid	3.3	prawn	pandalid	3.2	+0.1
Pacific mackerel	*Scomber japonicus*	3.5	mackerel	*Scomber scomber*	3.5	0
zooplankton	calanoid dominated	2.0	copepods	calanoids but not *Calanus finnmarchichus*	2.1	-0.1
Dover sole	*Microstomus pacificus*	3.5	Lemon sole	*Microstomus kitt*	3.7	-0.2
Spiny dogfish	*Squalus acanthias*	4.1	Spurdog	*Squalus acanthias*	4.4	-0.3
Pacific sardine	*Sardinops sagax*	3.0	Spratt	*Sprattus sprattus*	3.3	-0.3
Jack mackerel	*Trachurus symmetricus*	3.0	Scad	*Trachurus trachurus*	3.5	-0.5
Pacific hake	*Merluccius productus*	3.1	hake	*Merluccius merluccius*	4.5	-1.5

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REFERENCES

Fauchald, K. and P. A. Jumars. 1979. The diet of worms: a study of polychaete feeding guilds. Ocean. Mar. Biol. Ann. Rev., 17: 193-284.

Karpov, K. A., and G. M. Cailliet. 1978. Feeding dynamics of *Loligo opalescens*. pp. 45-65. *In* C. W. Recksiek and H. W. Frey, eds. Biological, oceanographic, and acoustic aspects of the market squid, *Loligo opalescens* (Berry) Fish Bull. 169, Calif. Dept. Fish and Game. 185 pp.

Kleppel, G. S., J. Q. Word, and J. Roney. 1980. Demersal fish feeding in Santa Monica Bay and off Palos Verdes. In SCCWRP Bien. Rep. 1979-1980; Bascom, W., ed.; Long Beach, CA, pp. 309-318.

Marte, C. L. 1980. The food and feeding habits of *Penaeus monodon* Fabricus collected from Makato River, Aklan, Philippines. Crustaceana, 38(3): 225-236.

Mauchline, J. 1980. The biology of mysids and euphausiids. Adv. Mar. Biol., 18: 1-681. New York: Academic Press.

Mearns, A. J., D. R. Young, R. J. Olson, and H. A. Schafer. 1981. Trophic structure and the cesium-potassium ratio in pelagic ecosystems. CalCOFI Rep., 22: 99-110.

Mearns, A. J., and D. R. Young. 1978. Trophic structure and pollutant flow in a harbor ecosystem. In SCCWRP Bien. Rep. 1979-1980; Bascom, W., ed.; Long Beach, CA pp. 287-308.

Odum, E. P. 1971. Fundamentals of ecology. Third edition. W. B. Saunders Co. Philadelphia. 574 pp.

Pinkas, L., M. S. Oliphant, and I. L. K. Iverson. 1971. Food habits of albacore, bluefin tuna and bonito in California waters. Fish Bull. Calif. Fish and Game. 152: 1-105.

Rau, G. H., A. J. Mearns, D. R. Young, R. J. Olson, H. A. Schafer, and I. R. Kaplan. Animal $^{13}C/^{12}C$ correlates with trophic level in pelagic food webs. In Prep. (submitted to **Ecology**, June, 1982).

Ryther, J. H. 1969. Photosynthesis and fish production in the sea. Science 166: 72-76.

Simenstad, C. A., B. S. Miller, C. F. Nyblade, K. Thornburgh, and L. J. Bledsoe. 1979. Food web relationships of Northern Puget Sound and the Strait of Juan de Fuca: A synthesis of available knowledge. Rep. EPA-600/7-79-259. Off. Res. Dev., US E.P.A., Washington, DC, 335 pp.

Sitts, R. M., and A. W. Knight. 1979. Predation by the estuarine shrimps *Crangon franciscorum* Stimpson and *Palaemon macrodactylus* Rathbun. Biol. Bull. 156: 356-368.

Uchida, R. M. 1981. Synopsis of biological data on frigate tuna, *Auxis thazard*, and bullet tuna, *A. rochei*. NOAA Tech. Reps. NMFS 436, 63 pp.

Warner, G. F. 1977. The biology of crabs. New York: Van Nostrand Reinhold Co.

Wyatt, T. 1976. Food chains in the sea. 341-358. In D. H. Cushing and J. J. Walsh, eds., The ecology of the seas. W. B. Saunders Co. Philadelphia.

Word, J. Q. 1980. Classifications of benthic invertebrates into infaunal trophic index feeding groups. In SCCWRP Bien. Rep. 1979-1980; Bascom, W., ed.; Long Beach, CA pp. 103-121.

Yang, J. 1981. Trophic levels of North Sea fishes. ICES Rep. CM 1981/G: 17. Demersal Fish Committee. Inter. Coun. Explor. Seas., Woods Hole, Mass., Oct., 1981. Copenhagen, Denmark.

Young, D. R., A. J. Mearns, T- K. Jan, T. C. Heesen, M. D. Moore, R. P. Eganhouse, G. P. Hershelman, and R. W. Gossett. 1980. Trophic structure and pollutant concentrations in marine ecosystems of southern California. CalCOFI Reps. 21: 197-206.