TROPHIC STRUCTURE AND THE CESIUM-POTASSIUM RATIO IN PELAGIC ECOSYSTEMS[1]

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ABSTRACT

Collections of plankton and of pelagic squid, fishes, and marine mammals from the Southern California Bight and the eastern tropical Pacific were made to determine what, if any, relationships exist between trophic level and the cesium-potassium (Cs/K) ratio. Numerical trophic level assignments were computed independently from stomach content analysis data and were then compared to concentrations of Cs and K, as determined by atomic absorption spectrometry of muscle tissues, and to the Cs/K ratio, which was found to increase by a factor of 2.4 per trophic step. This increase is higher than that found in inshore food webs, suggesting that pelagic food webs may be more highly structured than those inshore. The need for more rigorous methods for making trophic level assignments is discussed.

RESUMEN

Se hicieron colecciones de plancton y de calamares pelágicos, peces y mamíferos marinos de la Bahía del Sur de California y del Pacífico oriental tropical para determinar qué relaciones, si las hay, existen entre el nivel trófico y la proporción de cesio a potasio (Cs/K). Asignaciones numéricas de niveles tróficos fueron computadas independientemente de los datos de análisis de contenidos estomacales, y después se compararon con concentraciones de Cs y K determinadas por espectrometría de absoación atómica de los tejidos musculares, y también con la proporción Cs/K, que aumentaba por un factor de 2.4 por etapa trófica. Este incremento es más alto que aquel que se ha encontrado en redes alimenticias cercanas a la costa, lo que sugiere que las redes alimenticias pelágicas pueden ser más estructuradas que las que se encuentran cerca de la costa. Se discute la necesidad de desarrollar métodos más rigurosos para hacer asignaciones de niveles tróficos.

INTRODUCTION

It is not in the terrestrial experience continuously to inhale the young, eggs, sperm, food and excreta of all of our fellow creatures . . . Although it may seem repulsive to us, it, nevertheless, is the way of marine life. John D. Isaacs, Testimony before House Hearings, U.S. 92nd Congress, 24-25 May 1978.

The goal of this study was to determine the degree to which increased structure of pelagic marine food webs can lead to increasing concentrations of pollutants in marine animals. It is commonly assumed that marine food webs are as highly structured as those in terrestrial and freshwater ecosystems, an assumption that has led to public apprehension that pollutants will accumulate in seafood organisms via the feeding process. However, Isaacs (1972, 1973, 1976) proposed that with the exception of terrestrial expatriates (birds and mammals), marine food webs are largely unstructured, i.e. that they are composed of opportunistic, multidirectional feeders, and thus are not amenable to concentration of trace contaminants via the feeding process. Studies by Young (1970), Young et al. (1980), and Mearns and Young (1980), which included determination of cesium (Cs), potassium (K), and the ratio Cs/K in several coastal ecosystems and the Salton Sea, have given conflicting results. In the Salton Sea, Cs and the Cs/K ratio increased 2- to 3-fold per trophic step; in contrast, Cs and the Cs/K ratio in nearshore coastal ecosystems either did not increase with increase in trophic level (Gulf of California) or increased only slightly. Young et al. (1980) also included determination of Cs/K in a small group of fishes caught offshore in the San Pedro Channel; these data suggested that pelagic organisms produce trophic

step increases in Cs/K ratios higher than those in the nearshore ecosystems.

METHODS

In this study we conducted a new survey of pelagic ecosystems. Our primary objective was to determine to what extent Cs/K ratios are related to trophic level assignments when those assignments are derived from food habits analyses of a suite of representative pelagic organisms. In addition, we felt that it would be useful to identify trophic relationships among major fishery species of the region—mainly anchovy, mackerel, bonito, tuna, and billfish.

A chemically independent quantitative method for assigning trophic levels to target species was developed. This is a simple numerical method based on the Index of Relative Importance *(IRI)* of food items (Pinkas et al. 1971).

To make sure the patterns we found were not unique to the Southern California Bight or its particular fauna, we decided to also make collections from a different ecosystem—the eastern tropical Pacific food web of tunas and pelagic sharks.

Field Sampling

In the Southern California Bight, collections of zooplankton, squid, teleosts, elasmobranchs, and mammals were taken during 1979 and 1980 from an area 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 south of Point Dume. Some fish were taken by hook-and-line, but most of the fish specimens were taken by commercial fishermen and transferred directly with catch data to the Southern California Coastal Water Research Project (Table 1). In addition to the major pelagic fishes and invertebrates, we were able to collect tissues from five California sea lions *(Zalophus californianus)*, a blue whale *(Balenoptera musculus)*, and a white shark *(Carcharodon carcharias*, Table 1).

Quantities (25-50 g) of zooplankton, taken from each of three surface horizontal tows south of Point Dume on 21 August 1980, were quickly frozen in glass containers for chemical analyses; subsamples were fixed in formalin for taxonomic identification. Small and medium-sized fishes and the squid were returned on ice to the laboratory where they were frozen for later dissection. The mackerels and bonito were measured, weighed, and eviscerated and their stomach contents examined immediately or fixed in formalin for later examination. Eviscerated bodies were then frozen for later tissue dissection. Large fishes were identified, measured, and where possible, weighed in the field or at dockside. Then one or more 0.5- to 1.0-kg chunks of muscle tissue from the anterior dorsal area were removed, returned to the laboratory on ice, and frozen for later tissue dissection.

Collections from the eastern tropical Pacific region were taken during Cruise 1089 aboard the M/V *Sarah Ann* under charter to the Inter-American Tropical Tuna Commission (IATTC) between 11 and 29 April 1980 (Table 1). Additional collections of flying fishes *(Exocoetus moncirrhus)*, taken aboard the M/V *Enterprise* on Cruise 1083 during October and November 1978, were used in the chemical analyses.

As soon as possible after capture, the tunas, sharks, and other large fish were weighed to the nearest half-pound, measured to the nearest millimeter (fork length), and placed on a clean plastic-covered work area. A 0.5- to 1.0-kg chunk of white muscle was then cut from the dorsal area behind the head with a clean stainless steel knife and frozen in a clean labeled plastic bag. The entire stomach was removed from each fish, and individual bait fishes (consumed by the tunas during the fishing operation) were removed and discarded. If food organisms in the stomachs were found to be in very fresh condition, they were removed and frozen separately in clean plastic bags. Stomachs containing partially digested organisms were frozen intact in plastic bags. The whole squids, flying fishes, and frigate mackerels were also frozen in plastic bags.

Stomach Content Analysis

Stomach contents were analyzed in detail sufficient to compute one of several Indices of Relative Importance *(IRI)*. Our requirements were (a) minimum of 15 positive stomachs, (b) a taxonomic description of each item in each stomach, (c) number of each item in each stomach, and (d) total volume or weight of each type of item in each stomach. For most fish, stomach contents were completely sorted by eye with aid of a dissection microscope. Contents of anchovy intestines and stomachs required use of a compound microscope in order to estimate the proportions of zooplanktonic and phytoplanktonic taxa. In general, then, organisms and other material were removed from the stomachs, rough sorted, identified to the lowest possible taxonomic level, and weighed by lowest taxonomic category to the nearest 0.1 g (squid beaks and small

TABLE 1

Common and Scientific Names, Months, Years, Locations and Methods of Capture of Zooplankton and Pelagic Squid, Elasmobranchs, Teleosts, and Mammals from the Southern California Bight and Eastern Tropical Pacific Ocean, 1978-80.

Common name	Scientific name	Month(s) captured	Location(s)	Method(s)
SOUTHERN CALIFORNIA BIGHT (32°40'-34°20'N; 118°20'-120°40'W)				
Zooplankton		August 1980	3-5 km S. of Pt. Dume	0.3-mm mesh net
Northern anchovy	*Engraulis mordax*	August-October 1980	Off Orange County and Port Hueneme	Commercial and bait seine
Market squid	*Loligo opalescens*	December 1979	Isthmus, Catalina Island	Commercial hoop net
Pacific sardine	*Sardinops sagax caeruleus*	May 1980	S. of Pt. Dume, Los Angeles County	Commercial seine
Jack mackerel	*Trachurus symmetricus*	January and June 1980	San Pedro Channel, Catalina Is.	Commercial seine, gill net
Pacific mackerel	*Scomber japonicus*	January 1980-January 1981	San Pedro Channel, Dago Bank, Catalina Is., Newport Beach	Commercial seine, gill net, jigging.
Pacific bonito	*Sarda chiliensis*	January and June 1980	King Harbor, Huntington Beach, Newport Beach	Hook and line, gill net
California barracuda	*Sphyraena argentea*	June 1980	Newport Beach, Orange County	Commercial gill net
California sea lion	*Zalophus californianus*	March-April 1980	Beaches, Los Angeles and Orange Counties	Taken by Los Angeles Co. Dept. Health Services.
Swordfish	*Xiphias gladius*	October-December 1980	San Miguel Is., San Clemente Is., Catalina Is., Oceanside	Commercial gill net
Blue shark	*Prionace glauca*	May 1980	Newport Beach, Avalon Bank	Commercial gill net
Thresher shark	*Alopias vulpinus*	September-October 1980	San Nicholas Is., Santa Barbara Is., Catalina Is., Oceanside	Commercial gill net
Mako shark	*Isurus oxyrinchus*	May-June 1980	San Pedro Channel, Avalon Bank, Newport Beach	Commercial gill net
White shark	*Carcharodon carcharias*	February 1980	Catalina Island	Commercial gill net
Blue whale	*Balenoptera musculus*	July 1980	140 km SW of San Diego	Collided with tanker, recovered in L.A. Harbor
EASTERN TROPICAL PACIFIC (5°-13°N; 81°-89°W, IATTC Cruise 1089)				
Zooplankton		April 1980	5°34'-12°27'N; 85°12'-89°32'W	0.6-mm mesh
Squid	*Symplectoteuthis oualaniensis*	April 1980	5°56'-12°00'N; 81°45'-88°35'W	Rod and reel, dipnet
Flyingfish	*Oxyporhamphus micropterus*	April 1980	11°48'-12°18'N; 88°29'-89°34'W	Landed on deck, regurgitated
Frigate tuna	*Auxis thazard*	April 1980	11°14'-12°30'N; 87°52'-89°38'W	Jig line
Skipjack tuna	*Katsuwonus pelamis*	April 1980	5°39'-11°16'N; 81°42'-88°06'W	Live bait and pole, jig line
Yellowfin tuna	*Thunnus albacares*	April 1980	5°52'-11°16'N; 81°56'-88°06'W	Live bait and pole, jig
Silky shark	*Carcharhinus falciformis*	April 1980	6°31'N; 85°01'W	Rod and reel
EASTERN TROPICAL PACIFIC (3°-4°S; 78°-84°W, IATTC Cruise 1086)				
Flying fish	*Exocoetus moncirrhus*	October-November 1978	3°-4°S; 78°-84°W	Dip net

items) or 1.0 g (whole organisms).

Stomachs of some of our specimens were empty (See RESULTS section for details.). Therefore we turned to the literature for additional data that could be used to compute *IRI* or otherwise help in making trophic level assignments. These data are included in the RESULTS section.

Assignments of Trophic Levels

Five trophic levels were used in this study:

I. Primary Producers

II. Herbivores (feed on I)

III. Primary Carnivores (feed on II)

IV. Secondary Carnivores (feed on III)

V. Tertiary Carnivores (feed on IV)

This system (see Lindeman 1942; Odum 1971) was sometimes modified in order to permit intermediate assignments of trophic level.

For our calculations we assigned trophic levels to prey items, computed a weighted average prey trophic

level, and then assigned the predator to the next highest full trophic step. In order to assign prey trophic levels, we made some assumptions about the feeding habits of several kinds of organisms; for example, that both diatoms and dinoflagellates are primary producers (Trophic Level I) and that all small crustacea, including copepods, ostracods, mysids, amphipods, and euphausiids, are herbivores (Trophic Level II), even though there are many predatory forms in these groups.

In order to weight the data we computed the Pinkas et al. (1971) Index of Relative Importance:

$$IRI = \%F (\%N + \%V)$$

where $\%F$ = percent frequency of occurrence of prey item, $\%N$ = percent by numerical abundance of prey item, and $\%V$ = percent by weight or volume of prey item. By convention the resulting numbers, in terms of percent of total *IRI*, are hereinafter referred to in terms of their relative importance.

Dissection and Chemical Analysis

White muscle, sufficient to make 10 g or more of tissue, was dissected and placed in acid-washed vials (Jan et al. 1977) for determination of Cs and K (Young et al. 1980; Jan and Young, unpublished manuscript). For some species represented by large specimens (sea lions, mako shark, silky shark, and blue shark), we analyzed one tissue sample from each of four or five specimens. For the white shark and blue whale, we analyzed three replicate muscle samples from each. For all other teleosts, elasmobranchs, and squid we attempted to analyze five samples, each containing a composite of tissue dissected from ten different individuals taken largely from the same sites and dates. This approach was not always possible or sufficient, so that samples ranged from three to five and individuals (per final sample) from two (swordfish) to 35 (northern anchovy).

Cesium was reported in micrograms per wet kg (μg/wet kg) and K in units of milligrams per wet g (mg/wet g). The Cs/K ratio is therefore expressed as Cs/K $\times$ 10^{-6} and is compared with trophic level assignments and other biological and chemical variables.

RESULTS

Zooplankton Composition

The Southern California (Point Dume) zooplankton samples were numerically dominated by calanoid copepods, namely *Acartia tonsa* (75%), *Calanus pacificus* (10%), and the genus *Paracalanus* (8%, Table 2); less abundant (1% or less) were euphausiids and their young, cyclopoid copepods, the calanoid *Labidocera*, ostracods, and bryozoan larvae. The dominance of *Acartia* and the absence of forms such as chaetognaths suggested that we sampled a near-shore zooplankton community.

Zooplankton from the night tows in the eastern tropical Pacific collection area were also numerically dominated by calanoid copepods (55.8%, Table 3). Euphausiids were abundant (16.5%), and there was a wide variety of other oceanic zooplankton including chaetognaths, pteropods, heteropods, cyclopoid copepods, and decapod larvae and zoea.

Feeding Habits

Stomachs of pelagic organisms from both collection areas contained a wide variety of items ranging from phytoplankton to remains of fish, a bird, and marine mammals (Tables 2 and 3). In several species, stomachs were either completely empty (market

squid), unavailable (California sea lions and blue whale), or contained totally unrecognizable material (flying fish). We therefore used data from the literature, which are noted in footnotes to Tables 2 and 3.

Important items in stomachs of pelagic organisms from the Southern California Bight collections (Table 2) included zooplankton, northern anchovy, market squid, pelagic red crab, Pacific hake, Pacific mackerel, and pinnipeds. Plankton were important items, as defined by percent of total *IRI*, in the stomachs of several species of small fish. Northern anchovy stomachs contained, in order of importance, zooplankton (66% of total *IRI*; mainly *Acartia tonsa*) and unidentifiable matter (34% of total *IRI*); phytoplankton were relatively unimportant (less than 0.3% of total *IRI*) except in a few fish from Port Hueneme which contained diatoms *(Coscinodiscus, Thallasiosira,* and *Rhizosolenia)* and dinoflagellates *(Gymnodinium* and *Gonyaulax).* Zooplankton were also the most important items in stomachs of Pacific sardine (99.9% of total *IRI*) and jack mackerel (76.9% of total *IRI*). In the Pacific sardine, the zooplankton were mainly calanoid copepods *(Calanus pacificus* and *Labidocera)* and zoea. Stomachs from some of the jack mackerel also contained numerous scales and remains of a few polychaetes and squid.

Northern anchovy was the most important prey in stomachs of a group of larger fishes; in terms of percent of total *IRI*, anchovy accounted for 97.9% in Pacific bonito, 97.2% in thresher shark, 66.7% in California barracuda, 46.7% in Pacific mackerel, and 42.6% in swordfish. Food items of secondary importance in the last of these predators included zooplankton in Pacific mackerel (mysids, 35%), Pacific hake in swordfish (41.9%) and unidentifiable material in California barracuda (27.4%).

Blue shark stomachs contained squid as the most important item (64.3% of total *IRI*) and pelagic red crab *(Pleuroncodes planipes)* as the second most important item (25.2%). One blue shark also contained remains of a western meadowlark *(Sturnella neglecta).* In contrast, mako shark stomachs contained Pacific mackerel as the most important item (47.1% of total *IRI*) and unidentifiable fish remains and jack mackerel as the second and third most important items (27.2% and 25.8%, respectively). The white shark contained only two items, a young California sea lion and the remains of another pinniped, possibly a northern elephant seal *(Mirounga angustiriotris).*

Stomachs of several species were either completely

TABLE 2

Trophic Spectrum for Some Pelagic Organisms[1] from the Southern California Bight.

PREDATOR / PREY	Zooplankton	Pelagic red crab	Northern anchovy	Pacific sardine	Market squid	Jack mackerel	Pacific mackerel	Pacific bonito	Pacific hake	California barracuda	Blue shark	Swordfish	Mako shark	Thresher shark	California Sea lion	White shark	Blue whale
Number examined	3[2]	100[3]	19	24	50[4]	50	49	29	16	28	16	28	16	14	(29)[5]	1[6]	(38)[7]
Number positive	—	100	19	24	0	21	34	16	14	12	15	15	5	9	(27)	1	(34)
Weight (g)	0.001 (est.)	5.0 (est.)	10.8	213	46.8	154	357	921	314	1250	28.8×10^3	145×10^3	16.8×10^3	61.4×10^3	35×10^3	1.36×10^6	28.6×10^6
Detritus/debris/mush			34.0		11.1	7.8	0.1	0.8	7.1	27.4							
PHYTOPLANKTON																	p
diatoms		20.7	0.25														
dinoflagellates		1.6	0.04														
ZOOPLANKTON																	
radiolarians		14.8															
foraminifera		25.5															
copepods, unidentified	94.0	3.6															p
calanoid			55.0	98.9		52.0	0.2										
harpacticoid			9.81														
cyclopoid	<1.0		0.47														
nauplii/cypris	<1.0		0.21														
ostracods			0.04														
amphipods			0.06		0.6												
mysids	5.0				3.1												p
zoea/megalops				1.0	61.2		34.6										
pelagic red crabs																	100
unidentified crustaceans		0.1			5.4	24.9	0.6		4.5		25.2						
gastropods		1.4			16.6							0.01					
other small invertebrates	<1.0	15.4		<0.1			0.3				0.3						
tintinnids	<1.0		0.06		1.4	5.2	0.3										
POLYCHAETES																	
CEPHALOPODS																	
squid, unidentified											64.3	0.4		0.1	14.5		
market squid						1.2		0.5							10.8		
FISH																	
fish eggs																	
tissue, unidentified parts				<0.1	0.6	8.2	17.4	0.8	2.4	5.9	8.0	6.7	27.2	2.0	49.7		
Northern anchovy							46.7	97.9		66.7	2.1	42.6		97.2	14.3		
Pacific argentine									1.2								
mesopelagic, unidentified																	
Pacific hake									7.2			p					
Jack mackerel												41.9	25.8	0.8	10.7		
Pacific mackerel													47.1				
BIRDS																	
Western meadowlark																	
MAMMALS																	
California sea lion											0.4					50.0	
Elephant seal																50.0	

[1] Data are % of total Indices of Relative Importance (% IRI) unless otherwise noted (see below). Data are from our own zooplankton and stomach content analyses except as noted in footnotes 3 and 7. Samples from all except pelagic red crab and Pacific hake were analyzed for Cs and K; food habits for these species were included in order to compute trophic level assignments for their predators.

[2] Data represent percent numerical abundances estimated from samples at three sites south of Point Dume, August 1980.

[3] Data are percent numerical abundances observed by Aleman and Martinez (1976) from specimens trawled by the A. de Humbolt presumably off Baja California; they note that 20.7% of the food items were phytoplankton and 79.3% were zooplankton (including some dinoflagellates).

[4] All of our squid from Catalina had empty stomachs. Data are from Karpov and Cailliet (1978) from 52 Loligo opalescens taken in Monterey Bay spawning grounds between September 1975 and March 1976; numbers are "modified IRI" as described by these authors.

[5] Gut contents not available from our specimens; data combined from examinations by Scheffer and Neff (1948). Fiscus and Baines (1966), and Morejohn et al. (1978); Morejohn et al. (1978) list other fish and cephalopod species in addition to those cited in this table. These data are in general agreement with a recently published account by Antonellis and Fiscus (1980).

[6] White shark (Carcharodon carcharius) over 3.7 m (12 feet) prey on seals according to Snow (1980). They also consume other sharks, large and small fish, turtles, squid, crab, dead animals and other items such as potatoes, coal, dogs, a horse, and man according to D'Aubry (1964) and Walford (1935).

[7] Data are from Thompson (1940) from 38 blue whales (Balenoptera musculus) received at Akutan, Alaska, in 1937; whales averaged 22.6 m. All specimens contained euphausiids; some had trace amounts of copepods. Of 268 whales reported by Nemoto (1959), 266 contained only euphausiids (Thysanoessa spp. and Euphausia pacifica) and two had a mixture of euphausiids and copepods (Calanus spp.).

TABLE 3

Trophic Spectrum of Squid and Fishes from the Eastern Tropical Pacific Collected in 1978 (Flying fish) and in 1980 (Others).[1]

PREY	PREDATOR	Zooplankton	Flying fish	Squid	Frigate tuna	Skipjack tuna	Yellowfin tuna	Silky shark
	Number examined	11	35	78	2	44	36	4
	Number positive	—	35	15	2	18	27	2
	Weight(g)	0.001	51.0	209	774	2,487	3,315	25.8 × 10³
Detritus/debris/mush			p	8.2				
PHYTOPLANKTON								
ZOOPLANKTON								
foraminifera		<0.1						
copepods, unidentified			100²					
calanoid		55.8						
cyclopoid		5.0						
ostracods		0.4						
amphipods		1.8				0.8		
zoea/megalops		2.7					<0.1	
stomatopod larvae		0.7				0.8		
euphausiids		16.5						
unidentified crustaceans		<0.1	+²	+				
oikopleura		<0.1						
gastropods, unidentified		0.9						
pteropods		2.3				0.8		
heteropods		1.3						
bivalves		<0.1						
siphonophores		0.8						
chaetognaths		6.1						
CEPHALOPODS								
argonautidae						0.8	17.4	
squid				13.9+			55.9	
octopods							0.1	26.9
FISH								
unidentified fish/tissue/parts		0.2	tr²	77.8		3.15	2.4	
eggs		1.6						
anchovy (unidentified)				+		1.6	0.3	
myctophids				+			0.2	
flying fish						39.0	22.6	
seahorse							0.5	
jacks							0.2	
frigate tuna						53.1	0.1	73.1
jack mackerel					p			
triggerfish							0.1	
nomeidae							0.2	

[1]Numbers for zooplankton are per cent relative abundance; all others are per cent of total Indices of Relative Importance (IRI).
[2]Material in stomachs of our flying fish was unidentifiable. Data based on qualitative observations cited in Breder (1938), Parin (1950), and Parin (1960).

empty (market squid) or unavailable to us (California sea lions, pelagic red crabs, and the blue whale). Therefore, we used data from the literature (cited in Table 2). Karpov and Cailliet (1978) reported that crustaceans (mainly zoea) were the most important items in stomachs of squid on winter spawning grounds in Monterey Bay (61.2% of their total IRI, Table 2); euphausiids were most important elsewhere and at other times of the year.

California sea lions apparently prey on a large variety of fishes and invertebrates; pooled data from several sources (cited in Table 2) indicate that unidentified fish, market squid, northern anchovy, and Pacific hake were important food items (49.7%, 14.5%, 14.3%, and 10.7% of total IRI respectively). Blue whale in the North Pacific were reported by

Thompson (1940) and Nemoto (1959) to feed on large euphausiids and incidentally on copepods (Table 2). Finally, Aleman and Martinez (1976) reported that small zooplankton occurred frequently in intestines of pelagic red crab from Baja California (Table 2).

Important items in the stomachs of organisms from the eastern tropical Pacific collections included crustaceans, squid, flying fish, argonauts, and frigate tuna (Table 3). Squid and argonauts were the most important items in stomachs of yellowfin tuna (55.9 and 17.4% of total IRI) whereas frigate tuna was the most important item in the stomachs of skipjack tuna (53.1% of total IRI). Flying fish were of secondary importance in yellowfin tuna (22.6%) and skipjack tuna (39.0%).

Frigate tuna and octopods were the most important

TABLE 4

Summary of Weights, Lengths,[1] Number of Samples Analyzed, Resulting Concentrations of Cs and K, and the Cs/K Ratios in Specimens from Southern California Bight Collected in 1979 and 1980.

Predator	Number collected	Weight (g) $\bar{x}$	Weight (g) R	Length (cm) $\bar{x}$	Length (cm) R	Number of Chemical Samples	Cs (μg/wet kg) $\bar{x}$	Cs (μg/wet kg) R	K (mg/wet g) $\bar{x}$	K (mg/wet g) R	Cs/K $\times$ 10^{-6} $\bar{x}$	Cs/K $\times$ 10^{-6} R
Zooplankton	3 (tows)	—		—		3(r)	3.29(2.22-4.11)		1.58 (1.48-1.73)		2.07 (1.50-2.67)	
Northern anchovy	177	10.8 (5.7-14.9)		10.0 (8.7-11.3)		5(c,35)	7.62 (5.0 -11.7)		4.11 (3.88-4.33)		1.86 (1.29-2.96)	
Market squid	33	46.8 (37.9-53.5)		13.3 (12.7-14.3)		3(c,11)	<3.7 (<2.3-5.1)		1.63 (1.11-2.60)		<2.39(1.96-<3.14)	
Pacific sardine	40	213 (190-220)		25.2 (22-3-26.0)		4(c,10)	16.9 (16.0-17.8)		4.22 (3.58-4.58)		4.82 (3.65-4.47)	
Jack mackerel	50	154 (59-215)		24.0 (17.4-26.9)		5(c,10)	25.6 (15.2-30.9)		4.24 (3.67-4.60)		5.73 (4.14-6.72)	
Pacific mackerel	49	357 (139-675)		29.7 (23.5-36.1)		5(c,10)	33.2 (28.3-37.5)		4.58 (4.43-4.82)		7.23 (6.14-8.28)	
Pacific bonito	29	921 (887-949)		41.9 (41.7-42.1)		2(c,10)	37.7 (25.6-49.8)		4.65 (4.48-4.82)		8.01 (5.71-10.3)	
Calif. barracuda	28	1250 (1060-1313)		58.0 (41.9-62.4)		5(c,3.2)	20.7 (15.0-28.9)		5.37 (5.0 -5.80)		4.20 (3.00-5.17)	
Calif. Sea lion	5	20 to 50 × 10^3 est.		100-150 est.		5(s)	32.8 (16.0-44.6)		3.03 (2.21-4.30)		10.7 (7.24-14.2)	
Swordfish	10	145 (125-165)10^3		N.M.		5(c,2)	58.4 (50.2-76.8)		4.80 (4.39-5.54)		12.3 (9.66-17.4)	
Blue shark	16	28.8 (23-35) 10^3		173 (150-185)		4(s)	43.9 (38.4-53.4)		3.33 (2.77-3.62)		13.2 (10.6-15.3)	
Mako shark	5	16.8 (11.2-25.0)10^3		108 (91-120)		5(s)	91.8 (74.0-118)		4.65 (4.56-4.80)		19.7 (16.2-25.1)	
Thresher shark	14	61.4 (49.1-83.2)10^3		229 (213-244)		4(c,3)	92.5 (57.3-129)		3.85 (3.50-4.28)		24.0 (16.3-27.3)	
White shark	1	1.36 × 10^6		512		1(r)	105.0 (84.4-123)		3.30 (3.05-3.51)		31.7 (27.7-35.0)	
Blue whale	1	28.6 × 10^6		1737		1(r)	41.7 (36.5-45.6)		3.81 (3.75-3.89)		11.0 (9.38-12.1)	

[1]Weights and lengths are sample grand means with ranges (in parentheses; n = 1 to 5; see footnote 2).
[2]Each sample includes tissue from one or more specimens of the same species; number in parentheses is average number of specimens in a sample; s = single specimens only; r = replicates from a single specimen; c = composites.

items in stomachs of the silky sharks (73.1% and 26.9% of total *IRI*, respectively). Flying fish from both of our collections contained material, but it was totally unidentifiable; several reports (Table 3) suggest that copepods may be important food items.

Cesium, Potassium, and Cs/K Ratios

There were considerable variations in the concentrations of Cs and K and the Cs/K ratio in organisms from southern California (see Table 4). Cesium (sixth column, Table 4) varied approximately 32-fold from 3.29 μg/wet kg in zooplankton to 105 μg/wet kg in the white shark. In contrast, potassium (K) varied only about 3.4-fold from 1.58 mg/wet g in zooplankton and squid to 5.37 mg/wet g in barracuda. The Cs/K ratio varied about 17-fold from 1.86 × 10^{-6} in northern anchovy to 31.7 × 10^{-6} in the white shark.

Chemical variations similar to those of the Southern California Bight occurred in the eastern tropical Pacific fauna (Table 5). Cesium ranged 26-fold from an average of 4.35 μg/wet kg in zooplankton to 114.5 μg/wet kg in the silky shark. Potassium ranged 3.5-fold from 1.45 mg/wet g in the zooplankton to 5.01 mg/wet g in the silky shark. The Cs/K ratio varied 12-fold from 1.94 × 10^{-6} in the squid to 22.8 × 10^{-6} in the silky shark. In general, then, both ecosystems produced a variety of organisms that were similar with respect to the distribution in Cs/K.

Trophic Level Assignments and Relation to Cs/K Ratios

Table 6 presents three samples of trophic level assignments computed according to the steps indicated in the METHODS section. As indicated in A of Table

TABLE 5

Summary of Weights, Lengths,[1] Number of Samples Analyzed, Resulting Concentrations of Cs and K, and the Cs/K Ratios in Specimens from the Eastern Tropical Pacific Collected in 1978 and 1980.

Predator	Number collected	Weight (g) $\bar{x}$	Weight (g) R	Length (cm) $\bar{x}$	Length (cm) R	Number[2] of Chemical Samples	Cs (μg/wet kg) $\bar{x}$	Cs (μg/wet kg) R	K (mg/ wet g) $\bar{x}$	K (mg/ wet g) R	Cs/K $\times$ 10^{-6} $\bar{x}$	Cs/K $\times$ 10^{-6} R
Zooplankton	11	—		—		5(s)	4.35 (2.77-6.15)		1.45 (0.80-1.98)		3.30 (1.54-5.35)	
Flyingfish	35	51.0 (29.0 - 71.7)		16.3 (14.1-18.2)		5(c,7)	20.2 (16.9-24.3)		2.91 (2.54-3.51)		7.00 (5.58-8.47)	
Squid	78	209 (162 - 275)		19.7 (19.0-21.5)		5(c,5)	4.89 (2.35-6.41)		3.12 (2.50-3.73)		1.94 (0.95-2.34)	
Frigate tuna	2	774 (757 - 791)		36.5 (36.0-37.0)		2(s)	32.5 (30.0-34.9)		3.67 (3.49-3.85)		8.90 (7.79-10.0)	
Skipjack tuna	44	2487 (2398-2675)		49.1 (48.0-51.5)		5(c,9)	37.5 (34.4-43.3)		4.38 (4.25-4.59)		8.59 (7.49-10.2)	
Yellowfin tuna	36	3315 (2757 -4219)		54.4 (50.5-59.2)		5(c,7)	60.5 (42.5-74.8)		4.79 (4.56-5.03)		12.7 (8.84-16.6)	
Silky shark	4	25.8 (7.72-31.8)×10^3		131 (93.0-168)		4(s)	114.5 (96.3-126)		5.01 (4.43-5.33)		22.8 (13.8-30.6)	

[1]Weights and lengths are sample grand means with ranges (in parentheses; n = 1 to 5; see footnote 2).
[2]Each sample includes tissue from one or more specimens of the same species; number in parentheses is average number of specimens in a sample; s = single specimens only; c = composites.

6, the composite prey of northern anchovy resulted in a computed trophic level of 1.82, resulting in a computed trophic level assignment of 2.82 for the anchovy. This is equivalent to the conventional trophic level expression II → III, i.e. almost, but not quite, a primary carnivore. We made similar calculations for the remaining species of macroorganisms using our own *IRI* or *IRI* derived from literature sources (as reported in Tables 2 and 3).

These computed trophic levels are compiled together with the assumed trophic levels of the zooplankton in Table 7. As indicated, computed trophic level assignments ranged from 2.82 for northern anchovy to 5.02 for the white shark. The data cluster into several groups that each center about one of the conventional trophic level assignments. One group centers around Trophic Level III (or computed trophic level 3.00, i.e. primary carnivores) and includes northern anchovy, the blue whale, flying fish, Pacific sardine, market squid, and jack mackerel (range, 2.82 to 3.05; mean, 2.99). Several animals, including the larger squid *(Symplectoteuthis)*, Pacific mackerel, and frigate tuna, are distinctly higher (range, 3.52 to 3.56; mean, 3.54) but midway between primary and secondary carnivores (Trophic Level III - IV). A third group centers about Trophic Level IV, i.e. secondary carnivores: California barracuda, Pacific bonito, two coastal sharks, swordfish, and pinnipeds (range 3.74 to 4.02; mean, 3.89). At a level intermediate between

full secondary and full tertiary carnivores (i.e. Trophic Level IV - V) are the yearling tunas, mako and silky sharks (4.23 to 4.55; mean, 4.37). Finally, because it contained nothing other than pinnipeds (centered around Trophic Level IV) in its stomach, the white shark produced a computed trophic level of 5.02 and thus centered on conventional Trophic Level V (tertiary carnivore).

The scatter diagram in Figure 1 shows that the Cs/K ratios generally increase with trophic level assignments (assumed and computed). The trend occurs irrespective of the source of the organisms (Southern California Bight or eastern tropical Pacific). Accordingly all data were combined for further statistical analysis.

Untransformed, these data produce a high correlation coefficient $(r = 0.753, p<0.001,$ Table 8). However, the regression line (dashed line, Figure 1) intercepts the Y-axis above Trophic Level 2.00 and thus predicts negative Cs/K ratios at lower trophic levels (i.e. Cs/K $= -10.1 \times 10^{-6}$ at computed Trophic Level I and -17.99 at the Cs/K intercept, Table 8). In contrast, $\log_e$ transformation of the Cs/K ratio produces both a stronger correlation coefficient $(r = 0.776, p<0.001,$ Table 8) and a more realistic fit to the data points (no negative Cs/K ratios). This line (solid line in Figure 1) predicts a Cs/K ratio of 0.83 $\times$ 10^{-6} for computed Trophic Level I (primary producers), a value in close agreement with a mean Cs/K

TABLE 6

Computation of Trophic Level Assignments for Northern Anchovy, Jack Mackerel, and Mako Shark.

Predator/prey	(1) Assumed or computed prey trophic level	(2) % IRI	(3) (1) × (2)/100	(4) Computed trophic level = (3) + 1	(5) Traditional trophic level assignment
A northern anchovy					
copepod	2.0	65	1.30		
detritus	1.5	34	0.51		
phytoplankton	1.0	1	0.01		
			1.82	2.82	II → III
B jack mackerel					
copepods	2.0	52	1.04		
Unidentified crustacean	2.0	24	0.48		
Unidentified matter	1.5	8	0.12		
Unidentified fish	3.0	8	0.24		
polychaetes	2.5	5	0.13		
squid	3.06	1	0.03		
			2.04	3.04	III
C mako shark					
Pacific mackerel	3.54	65	2.30		
jack mackerel	3.04 (from above)	19	0.58		
Unidentified fish	3.0	17	0.51		
			3.39	4.40	IV—V

TABLE 7
Summary of Locations of Capture, Cs/K Ratios, Assigned Trophic Levels (Assumed or Computed) and Conventional Expression of Assigned Trophic Levels for 22 Species of Pelagic Animals from the Southern Califorña Bight and the Eastern Tropical Pacific, 1978 and 1980.

Species number[1]	Common Name	Location[2]	Cs/K × 10^{-6}	Assigned trophic level	Conventional trophic level
HERBIVORES (II)					
1	Coastal zooplankton	SCB	<2.07	2.00[3]	II
2	Oceanic zooplankton	ETP	3.30	2.00[3]	II
PRIMARY CARNIVORES (III)					
3	Northern anchovy	SCB	<1.86	2.82	II→III
4	Blue whale	SCB	11.0	3.00	III
5	Flying fish	ETP	7.00	3.00	III
6	Pacific sardine	SCB	4.02	3.01	III
7	Market squid	SCB	2.39	3.05	III
8	Jack mackerel	SCB	5.73	3.04	III
INTERMEDIATE (PRIMARY-SECONDARY) CARNIVORES (III-IV)					
9	Squid	ETP	1.94	3.52	III-IV
10	Pacific mackerel	SCB	7.23	3.54	III-IV
11	Frigate tuna	ETP	8.90	3.56	III-IV
SECONDARY CARNIVORES (IV)					
12	California barracuda	SCB	4.20	3.74	III→IV
13	Pacific bonito	SCB	8.01	3.80	III→IV
14	Thresher shark	SCB	24.0	3.82	III→IV
15	Swordfish	SCB	12.3	3.97	IV
16	Blue shark	SCB	13.2	4.00	IV
17	California sea lion	SCB	10.7	4.02	IV
INTERMEDIATE (SECONDARY-TERTIARY) CARNIVORES (IV-V)					
18	Yellowfin tuna	ETP	12.7	4.23	IV←V
19	Skipjack tuna	ETP	8.59	4.30	IV-V
20	Mako shark	SCB	19.7	4.39	IV-V
21	Silky shark	ETP	22.8	4.55	IV-V
TERTIARY CARNIVORE (V)					
22	White shark	SCB	31.7	5.02	V

[1]Refers to numbers in Figure 1.
[2]SCB = Southern California Bight and adjacent waters; ETP = Eastern Tropical Pacific (oceanic)
[3]Assumed trophic level; all others computed from stomach contents data according to method described in text.
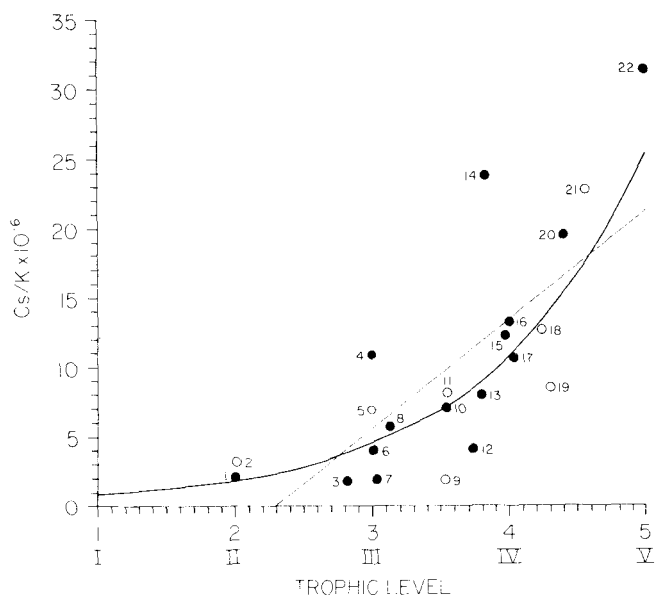

Figure 1. Scatter plot of mean Cs/K ratios against computed (arabic numerals) and traditional (Roman numerals) trophic level assignments. Data are for 22 species of coastal (closed circles) and oceanic (open circles) pelagic organisms. Refer to Table 7 for species identifications (numbered 1 through 22 above). Also shown are regression lines for raw (dashed line) and log 10-transformed (solid line) data; statistics for these lines are listed in Table 8.

ratio of 0.71 measured in giant kelp (Macrocystis pyrifera, Mearns and Young 1980).

The equation for the solid line in Figure 1 also predicts constant Cs/K increase factor of 2.35 per whole trophic step. This increase factor is similar to a value of 2.39 computed by grouping data around traditional trophic and intermediate trophic levels, calculating mean Cs/K ratios, and then computing Cs/K increase factors for whole trophic steps (Table 9). As shown in the last column in Table 9, these increase ratios vary from 1.98 between Trophic Levels III and II to 2.65 between Trophic Levels IV-V and III-IV. The average of the four increase ratios is 2.39±0.32 SD, a value in close agreement with that predicted from the curvilinear fit to all 22 data points (2.35).

DISCUSSION AND CONCLUSIONS

In animal tissues, the biological half-life of Cs is two to three times that of K (see Young 1970). Young (1970) has also shown that under equilibrium conditions food appears to be the major source of Cs to

TABLE 8

Regression Statistics for Cs/K versus Trophic Level Computed Using Mean Values for Cs/K and All 22 Pelagic Organisms.

Comparison	r	df	p	m	b	$Cs/K \times 10^{-6}$ Prediction for trophic level 1
Cs/K vs. trophic level	0.753	20	<0.001	7.890	−17.99	−10.10
Log$_e$ Cs/K vs. trophic level	0.776	20	<0.001	0.85430	−1.04078	−0.18648
Inverse Log$_e$ Cs/K[1]	—	—	—	2.3497	0.3532	0.830

[1]Log$_e$ Cs/K returned to untransformed values.

TABLE 9

Average Computed Trophic Levels, Weights, and Cs/K Ratios for Each of Six Intermediate or Full Trophic Levels, Together with Calculated Step Increases between Trophic Levels for Cs/K.

Trophic level		N	Computed trophic level $\bar{x}$	SD	Weight (g) $\bar{x}$	SD	$Cs/K \times 10^{-6}$ $\bar{x}$	SD	Calculated Increase[1]
II	Herbivores	2	2.00	—	1×10^{-3}	0	2.69 ± 0.89		—
III	Primary Carnivores	6	3.00 ± 0.10		$4.77 \pm 11.7 \times 10^6$		5.33 ± 3.39		1.98/step
III-IV	Interm. Carnivores	3	3.54 ± 0.02		$4.47 \pm 2.93 \times 10^2$		6.02 ± 3.63		—
IV	Secondary Carnivores	6	3.89 ± 0.12		$4.54 \pm 5.38 \times 10^4$		12.07 ± 6.69		2.29/step
IV-V	Interm. Carnivores	4	4.37 ± 0.14		$1.21 \pm 1.13 \times 10^4$		15.95 ± 6.47		2.65/step
V	Tertiary Carnivore	1	5.02	—	1.36×10^6		31.7	—	2.63/step

Average step increase in Cs/K = 2.39
± Standard deviation = 0.32

[1]Computed only where there is data for a whole step: e.g. III/II = 5.33/2.69 = 1.98.

marine fish; a similar conclusion is reached when the argument is applied to K (D.R. Young, unpublished manuscript). On the assumption that this is also true for other types of marine organisms, this implies that the ratio of Cs to K in a marine predator should be two to three times higher than the ratio in its prey when both are in equilibrium. Thus in a linear food chain, such as once noted of the Salton Sea (Young 1970; Young et al. 1980), the Cs/K ratio should increase two to three-fold per trophic step. In fact, Young (1970) found the ratio to increase 2.5-fold in the Salton Sea. However, Isaacs (1972, 1973, 1976) postulated that marine food webs are not so structured; rather, they are composed of opportunistic, multidirectional feeders. A lack of increase in Cs/K ratio in several trophic steps in representatives of a nearshore food web in the Gulf of California (Young 1970; Young et al. 1980) was taken by Isaacs as evidence in support of this hypothesis.

In the present study, the Cs/K ratio in pelagic organisms from the eastern Pacific Ocean clearly increases with increase in trophic levels derived independently from gut content analysis. The Cs/K ratio increases by a factor of about 2.4 between trophic levels. In addition, a median increase factor of 2.3, computed from an earlier pilot study of representative pelagic fishes from the Southern California Bight (Young et al. 1980) agrees with the new data. Together or separately, these data do not support the hypothesis that pelagic food webs are unstructured.

However, we have also reported that considerably smaller increases in the ratio occur in nearshore and benthic food webs of the southern California mainland shelf (Young et al. 1980). As summarized in Table 10, the average increases in Cs/K were 1.52 in a benthic food web on the Palos Verdes Shelf, 1.40 in Los Angeles Harbor, and 1.23 in Upper Newport Bay. These data suggest that structure amenable to biomagnification of Cs increases as one leaves nearshore (detritus-based) food webs and enters offshore pelagic food webs.

Although the increase in Cs/K ratio with increase in trophic level is evident in our data, there are some

TABLE 10

Comparison Cs/K Ratios and Step Increases in Cs/K Ratios (parentheses) in Four Marine Ecosystems.

Trophic level	Upper Newport Bay 1978[1]	Los Angeles Harbor 1979[2]	Palos Verdes 1976[1]	Pelagic 1980[3]
I	NA	0.71	NA	NA
II	NA	NA	NA	2.69
II-III	3.64	1.97	6.50	NA
III	NA	NA	NA	5.28 (1.98)
III-IV	5.53 (1.52)	3.05 (1.55)	9.93 (1.53)	6.02
IV	NA	NA	NA	12.07 (2.29)
IV-V	5.22 (0.94)	3.82 (1.25)	15.1 (1.52)	15.95 (2.65)
V	NA	NA	NA	31.7 (2.63)
Average increase	1.23	1.40	1.52	2.39

[1]Young et al. 1980.
[2]Mearns and Young 1980.
[3]This study; Young et al. (1980) also reported a mean predator/prey increase factor of 2.42 for a small separate group of coastal pelagic fishes.

important deviations. Northern anchovy (primary carnivores) and both species of squid (primary to secondary carnivores) produced Cs/K ratios no higher than zooplankton (herbivores), whereas elasmobranchs (secondary and tertiary carnivores) produced high values when compared to fish of similar size (e.g. swordfish). It is possible the northern anchovy were feeding on phytoplankton for several months prior to capture; they are certainly capable of doing so, as noted by Miller (1976). Moreover, we have previously measured somewhat higher Cs/K ratios (mean 2.08 × 10^{-6}) in anchovy from Los Angeles Harbor (Young et al. 1980). The low Cs/K ratios in both squid species are also difficult to explain. It is possible we did not sample a tissue equivalent to the muscle in fish; however, the mantle is sufficiently active to be involved in propulsion of squid. Alternatively, the biological half-life of Cs may be much shorter in molluscs than in teleosts. Likewise, the biological half-life of Cs may be different (higher?) in elasmobranchs than in molluscs or teleosts. Although we have yet to fully investigate these possibilities, we can point out that we arrive at substantially the same general conclusions when we exclude all but the teleosts from our correlations. For example, regression of fish-only log-transformed Cs/K ratios with computed trophic levels significant ($r = 0.737$, $0.01 > p < 0.001$) and results in a Cs/K ratio increase of 2.23 per trophic step (Table 11).

Tables 3 and 4 suggest there may be some relation between the Cs/K ratio and size. Linear regression of untransformed data do not support this ($r = 0.054$, $p > 0.1$, Table 11); the lack of correlation is also obvious considering the six-order of magnitude range in weight between northern anchovy (10 g) and the blue whale (28.6 × 10^6 g), both of which are primary carnivores Trophic Level III. However, there is a significant correlation ($r = 0.741$, $p < 0.001$) when $\log_e$-transformed Cs/K ratios are regressed against $\log_e$-transformed weight data (Table 11). This

suggests there may be some connection between size (or size-related conditions such as growth rate or metabolic rate) and the Cs/K ratio. However, it can also be pointed out that this regression predicts a Cs/K ratio that is already too high for the blue whale (23.4 versus 11.0).

This study and a similar study in Los Angeles Harbor (Mearns and Young 1980) differ from most other studies on marine food webs in that an attempt has been made to objectively assign numerical values to trophic levels based on quantitative feeding habits data. There are hazards in doing this: for example, setting a numerical value for a trophic level disregards the omnivorous nature of some predators (as evident in Tables 2 and 3). Thus, we prefer to view the "computed trophic level" as an indicator of central tendency of food sources. Moreover, assigned prey trophic levels range 0.5 "trophic steps" around their central tendency for some predators. Thus, if this approach is to be used, we recommend reporting some measure of trophic dispersion such as that observed in true trophic spectra (e.g. Cailliet et al. 1979; Darnell 1961).

The studies done to date raise many questions that have yet to be thoroughly investigated. Factors such as growth rates, undiscovered food sources, (including seasonal variations), phylogenetic differences in biological half-lives of alkali metals (which may explain obvious deviations in squid and the three-fold range in K concentrations) have yet to be thoroughly explained. Nevertheless, the present study provides a new kind of focus on pelagic food webs and on some possible relationships among economically important species of pelagic fishes, their prey, and their predators. At present, we conclude that pelagic organisms live under conditions that are sufficient to promote accumulation of Cs in a pattern that is related to our concept of trophic structure. However, if relative change in the Cs/K ratio is indeed a measure of trophic structure, as proposed by Isaacs (1972, 1973, 1976), then these data support the hypothesis that pelagic

TABLE 11

Regression Statistics for Cs/K versus Trophic Level for Teleosts only and for Cs/K versus Weight for all 22 Pelagic Organisms (Including Log$_e$—transformed Data).

Comparison	r	df	p	m	b	Cs/K × 10^{-6} Prediction
Log$_e$ Cs/K vs. trophic level, teleosts only	0.737	9	$0.01 > < 0.001$	0.80050	−0.97255	−0.17205
Inverse for Log$_e$ Cs/K	—	—	—	2.227	0.378	0.845 for trophic level I
Cs/K vs. weight (g), all data	0.054	20	n.s.[1]	7.1 × 10^{-8}	10.05	—
Log$_e$ Cs/K vs. Log$_e$ weight (g), all data	0.741	20	< 0.001	0.11048	1.25613	3.15296
Inverse for Log$_e$ Cs/K	—	—	—	1.117	3.512	23.4 for 38.6 mt blue whale

[1]not significant ($p > 0.1$)

food webs are structured. However, we also note that Cs/K ratios increase in nearshore, harbor, and bay ecosystems much less than in pelagic ecosystems (factors of 1.52, 1.40, and 1.23 versus 2.35, respectively). In fact, the present data suggest that the ability of marine food webs to "biomagnify" Cs decreases with proximity to shore. Thus, it is possible that nearshore systems are indeed more like the "unstructured" food webs proposed by Isaacs (1972), whereas the pelagic systems are more like simplified, well-structured food webs such as noted of the Salton Sea (Isaacs 1972; Young 1970). Analyses are now in progress to determine which, if any, trace contaminants (metals and chlorinated hydrocarbons) also increase with trophic level.

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