

# GILL RAKER APPARATUS AND FOOD SELECTIVITY AMONG MACKERELS, TUNAS, AND DOLPHINS

JOHN J. MAGNUSON AND JEAN G. HEITZ<sup>1</sup>

## ABSTRACT

Gill raker morphology and fork length were measured from 411 fish, representing eight species of scombrids and two species of coryphaenids (dolphin). For each species linear regressions passing through the origin were determined relating mean gill raker gap in millimeters (first gill arch) with fork length in centimeters ( $l$ ), and log filtering area (first gill arch) with log fork length. Mean gill raker gaps equaled: *Auxis rochei*—0.0144 $l$ , *Katsuwonus pelamis*—0.0211 $l$ , *Auxis thazard*—0.0213 $l$ , *Thunnus albacares*—0.0344 $l$ , *Thunnus alalunga*—0.0365 $l$ , *Euthynnus affinis*—0.0386 $l$ , *Thunnus obesus*—0.0391 $l$ , *Sarda chiliensis*—0.0509 $l$ , *Coryphaena hippurus*—0.0650 $l$ , *Coryphaena equisetis*—0.0655 $l$ , and *Acanthocybium solanderi*—no gill rakers. Among the species gill raker gap was directly proportional to the number of gill rakers, but no relation occurred between mean gap and filtering areas. Gill raker gap differed markedly among species and lengths of fish. A 50-cm *K. pelamis*, a 30-cm *T. albacares*, and a 10-cm *Sarda orientalis* all had an estimated mean gap of 1 mm. Conversely the gaps of a 50-cm fish of each species were estimated to be ca. 1.0, 1.7, and 4.5 mm respectively.

Mean gill raker gaps from this study were compared with the percentage of crustaceans in stomachs of Central Pacific fishes based on literature records. Body sizes of fishes and squids in the stomachs were larger than crustaceans. Percent volumes that crustaceans contributed to the stomach content were inversely related to mean gaps (Kendall rank correlation coefficient,  $\tau = -0.59$ ,  $n = 16$ ,  $P < 0.001$ ). Partial correlation indicated that gap was more important than fork length in predicting the quantity of crustaceans. Thus, the gill raker gap was related functionally with the quantity of smaller organisms in the stomachs. Presence of euphausiids in stomachs of *K. pelamis* and their absence in *T. albacares* from the eastern tropical Pacific may result from the small size of euphausiids and the smaller gill raker gaps of *K. pelamis* relative to *T. albacares*. Gill raker gap and the maximum distensibility of the esophagus would set physical limits on the size of food eaten. The diverse fauna assemblage of crustaceans, fishes, and squids within this size range has masked to a great extent the selective feeding that does occur among scombrids and coryphaenids on the basis of food size.

Most scombrid fishes have a varied diet that includes numerous crustaceans, cephalopod molluscs, and fishes. The Indian mackerel, *Rastrelliger kanagurta* (Cuvier), even eat phytoplankton (Bhimachar and George, 1952). The high diversity of organisms in their stomach contents has generated the opinion that scombrids are nonselective feeders, preying upon anything they encounter. Coryphaenid fishes, dolphins, eat fish predominantly.

Yet selectivity does exist in food habits of scombrids. Within a species, larger fish contain relatively fewer crustaceans and more fishes. Crustaceans constituted 44% of the stomach volume of skipjack tuna, *Katsuwonus pelamis* (Lin-

naeus), shorter than 50-cm fork length but only 1.5% of the volume for fish longer than 60 cm (Yuen, 1959). Similarly, crustaceans constituted 35% of the stomach volume of yellowfin tuna, *Thunnus albacares* (Bonnaterre), shorter than 130 cm but only 1% for those longer than 130 cm (Reintjes and King, 1953). Reintjes and King suggested that these differences might result, as the fish grew, from a change in food preference or a change in the ability to search out and capture larger, more mobile prey (fishes). Another consideration, in our view, is that larger predators have a reduced ability to catch small prey (crustaceans).

Prevention of food loss through the opercular gap is generally recognized as the primary function of gill rakers. Species with more closely

<sup>1</sup> Laboratory of Limnology, Department of Zoology, University of Wisconsin, Madison, Wis. 53706.

spaced gill rakers are more likely to feed on plankton than those with more widely spaced rakers (Suyehiro, 1942; Yasuda, 1960a; Brooks and Dodson, 1965; Kliewer, 1970).

This paper (1) quantitatively describes the gill raker apparatus of certain scombrids and coryphaenids with respect to the gap between gill rakers and the filtering area of the first gill arch, (2) compares differences in gill raker gap among species and lengths of fish, and (3) considers the proposition that observed inter- and intraspecific variations in the diet are associated functionally with the morphometrics of the gill raker apparatus.

### MORPHOMETRY OF GILL RAKER APPARATUS

Gill raker morphometry and fork length were measured from 411 fish, representing eight species of scombrids and two species of coryphaenids. Albacore, *Thunnus alalunga* (Bonnaterre), were from the commercial longline fishery operated from American Samoa, the Pacific bonito, *Sarda chiliensis* (Cuvier), were from waters off Palos Verdes, Calif., and chub mackerel, *Scomber japonicus* Houttuyn, were from the Honolulu fish market. All other specimens were from Hawaiian waters and were caught with pole and line or longline by commercial fishermen or on numerous cruises of the research vessel *Charles H. Gilbert* of the Bureau of Commercial Fisheries Biological Laboratory, Honolulu (now National Marine Fisheries Service Hawaii Area Fishery Research Center).

Measurements were from the first right gill arch of fresh or thawed specimens. The arch was removed from the fish and extended by pulling the upper and lower branches apart until the rakers were stiffly erect. Gaps between adjacent rakers (Figure 1) were measured at the base of the rakers by expanding a vernier caliper until the two gill rakers began to spread apart. Arch length and gill raker length were also measured with the caliper (Figure 1). Depending on the species, six to nine gaps and six to eight gill raker lengths spaced along the arch

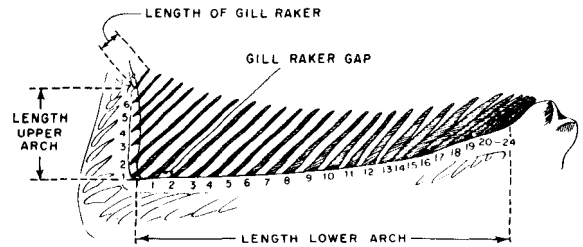


FIGURE 1.—Diagram of the first right gill arch of a scombrid as viewed from oral chamber showing the morphometric measurements. Numbers indicate particular rakers.

were obtained from scombrids and three gaps and five gill raker lengths from coryphaenids. Mean gap was the average of those measured along the arch. A gap near the middle of the lower arch was also used to represent gap width in the primary filtering area. Filtering area was calculated from average length of gill rakers and length of the arch. Lower and upper arch filtering areas were computed separately and summed.

### DESCRIPTION

Gill rakers of the first arch of most scombrids were conspicuous and well developed. Inner edges of the rakers of most species were covered with numerous short, spiny protuberances. For *S. japonicus*, these spines were thin, about as long as the gill raker gap, and evenly spaced to form a finer sieve between adjacent gill rakers. The other three arches of scombrids lacked gill rakers, but smaller rakerlike processes on the inner faces of the all arches projected posteriorly to the adjacent arch forming a sieve. Inner edges of these processes had short, spiny protuberances similar to the gill rakers.

Rakers were articulated so that they became stiffly erect forming a parallel row of blade-shaped rakers when the acute angle between the upper and lower arch was expanded toward 90 degrees. In the branchial chamber the tips of the rakers extended to the inner surface of the flared gill cover.

The wahoo, *Acanthocybium solanderi* (Cuvier), has no gill rakers, but most scombrids have more than 20 elongated rakers—*K. pelamis* in

our samples had 53 to 64. Longest rakers were near the joint between the upper and lower branches of the arch. They became progressively shorter toward the ends of the arch. For example, a *K. pelamis* 50 cm long had gill rakers 21 mm long at the joint but only 2 and 8 mm at the ends of the upper and lower branches, respectively. The largest gap (1.8 mm) was near the center of the lower branch. Gaps were smaller on the upper branch than lower branch and were most narrow at the ends of the arch (0.2 mm and 0.9 mm for the upper and lower branches). Often the gap between the first raker of the upper and the first raker of lower

arch was as great as the widest gap on the lower arch.

Most of the filtering area of scombrids was confined to the lower branch of the gill arch. The lower branch comprised 73 to 80% of the total. The filtering area of coryphaenids was essentially restricted to the lower arch. Dolphin, *Coryphaena hippurus* Linnaeus, had no rakers on the upper arch, pompano dolphin, *Coryphaena equisetis* Linnaeus, had only one.

Gill rakers of the two coryphaenids were shorter and more uniform in length than those of scombrids. The longest gill raker from a 55-cm *C. equisetis* was only 9 mm contrasted

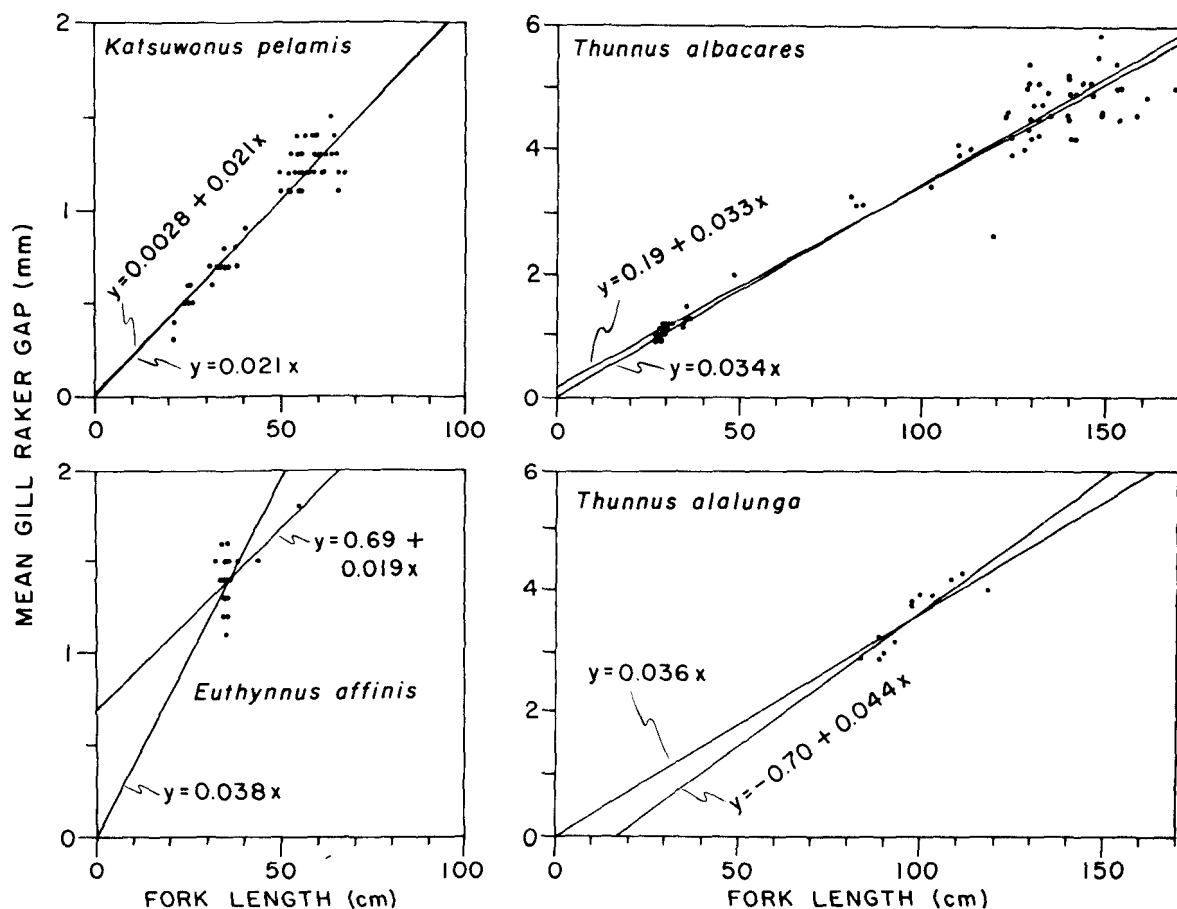


FIGURE 2.—Relation between mean gill raker gap and fork length showing the advantage of using regression through the origin for predicting mean gill raker gap especially when sample sizes are small and restricted in length range.

to 21 mm from a 50-cm *K. pelamis*. Even the longest raker of a 125-cm *C. hippurus* was only 16 mm—shorter than that of a 50-cm *K. pelamis*.

## SIZE AND SPECIES COMPARISONS

### METHODS

Linear regressions relating gill raker gap to fork length and log filtering area to log fork length were computed for each species. Regressions were computed once about the mean, and a second time, were forced to pass through the origin. The latter procedure was used because the ranges of fork lengths of some species were not sufficient to obtain reasonable equations (Figure 2).

Both *K. pelamis* and *T. albacares* were represented by large samples that included small and large specimens. Their regressions of gill raker gap on fork length passed close to the origin even when not forced to do so; the  $y$ -intercept was 0.00 mm for *K. pelamis* and 0.19 mm for *T. albacares* (Figure 2). In contrast, kawakawa, *Euthynnus affinis* (Cantor), and *T. alalunga* were represented by small samples that did not include small specimens. Regressions

extrapolate outside the size ranges represented in our samples, the regressions forced to pass through the origin were used for all computations of gill raker gap.

The same reasoning was used for the relations between log filtering area and log fork length. In this case, the zero-zero intercept was equivalent to 1 cm fork length and 1 mm<sup>2</sup> filtering area rather than zero fork length and zero filtering area. Since most comparisons made later were for fish at least 35 cm long with filtering areas near 100 mm<sup>2</sup>, errors owing to the position of the intercept were believed negligible.

### SIZE AND SPECIES COMPARISONS

Linear regressions passing through the origin that relate gill raker gap to fork length and log filtering area to log fork length are presented in Table 1 along with the numbers and lengths of fishes measured.

Mean gill raker gap increased with fork length and was equal to 1.4 and 6.6% of fork length for frigate mackerel, *Auxis rochei* (Risso), and *C. hippurus*, respectively. Gill raker gap in the middle of the lower branch was usually 1.0 to 1.2 times the mean gill raker gap except for

TABLE 1.—Linear regressions passing through the origin that relate mean gill raker gap to fork length and log filtering area to log fork length and the number and length of fish measured.

Species	Number of fish measured	Regressions of gap ( $G$ ) and fork length ( $l$ )	Fork length		$G$ (mm)	Standard error of estimate for $G$ (mm)	Regressions of log filtering area (log $A$ ) and log fork length (log $l$ )	Mean		Standard error of estimate for Log $A$ (mm <sup>2</sup> )
			Mean (cm)	Range (cm)				Log $l$ (cm)	Log $A$ (mm <sup>2</sup> )	
<i>Sarda chiliensis</i>	8	$G = 0.0509 l$	50.13	38.7- 58.8	2.56	0.27	log $A = 1.73$ (log $l$ )	1.7001	2.9246	0.0584
<i>Auxis thazard</i>	16	$G = 0.0213 l$	31.40	25.1- 35.7	0.67	0.10	log $A = 1.79$ (log $l$ )	1.4969	2.6730	0.0393
<i>Auxis rochei</i>	11	$G = 0.0144 l$	30.24	29.2- 32.9	0.44	0.06	log $A = 1.78$ (log $l$ )	1.4706	2.6291	0.0192
<i>Euthynnus affinis</i>	25	$G = 0.0386 l$	36.29	33.4- 54.6	1.41	0.29	log $A = 1.82$ (log $l$ )	1.5598	2.8421	0.0234
<i>Katruwonus pelamis</i>	63	$G = 0.0211 l$	47.60	21.0- 67.5	1.00	0.10	log $A = 1.83$ (log $l$ )	1.6776	3.0135	0.0697
<i>Thunnus alalunga</i>	12	$G = 0.0365 l$	98.56	84.0-118.8	3.59	0.25	log $A = 1.81$ (log $l$ )	1.9937	3.6088	0.0343
<i>Thunnus albacares</i>	74	$G = 0.0344 l$	94.86	27.1-166.9	3.31	0.36	log $A = 1.78$ (log $l$ )	1.9771	3.3468	0.0405
<i>Thunnus obesus</i>	82	$G = 0.0391 l$	132.96	75.2-175.3	5.26	0.60	log $A = 1.85$ (log $l$ )	2.1236	3.9058	0.0449
<i>Coryphaena equisetis</i>	38	$G = 0.0655 l$	94.90	30.8- 58.7	6.16	0.54	log $A = 1.39$ (log $l$ )	1.9773	2.7339	0.0704
<i>Coryphaena hippurus</i>	68	$G = 0.0650 l$	40.52	63.2-126.4	2.69	0.34	log $A = 1.36$ (log $l$ )	1.6077	2.1716	0.0727

of gill raker gap on fork length for these two species did not closely approach the origin (Figure 2); we believe these equations would also have had  $y$ -intercepts near 0.0 mm if lengths of our specimens had been more evenly distributed. Since some comparisons were made that

*A. rochei* (1.3) and *K. pelamis* (1.4). Mean gap increased in direct proportion to fish length; i.e., if length doubled, gap also doubled.

Filtering area increased as the 1.4 to 1.8 power of fork length. When these regressions were not forced to pass through the origin, the filter-

ing area increased as the 2.2 power of fork length for *K. pelamis* and the 1.9 power for *T. albacares*. Forcing the regressions to pass through the origin may have decreased the slope.

To facilitate comparison of different species, the mean gap and filtering area were computed from the regression in Table 1 for fish with a fork length of 35 cm. These are listed in Table 2 in order of decreasing number of gill rakers, increasing gap, and decreasing filtering area.

As expected, the number of rakers and gill raker gap were closely related (Table 2). Lack of complete correspondence may have resulted from differences in the thickness of gill rakers, differences in the length of the gill arch, or both.

Among scombrids no relation was evident between filtering area and number of rakers or between filtering area and mean gill raker gap (Table 2). Apparently, the length of raker was an important variable determining differences

TABLE 2.—Scombrid and coryphaenid species (35-cm fork length) listed in order of increasing numbers of gill rakers, and decreasing mean gill raker gap and filtering area. (Data on *S. orientalis* from one fish, *S. japonicus* from two fish.)

Rank	Mean number of rakers (n)	Species	Mean gill raker gap (mm)	Species	Filtering area (mm <sup>2</sup> )	Species
12	8	<i>Coryphaena hippurus</i>	3.3	<i>Sarda orientalis</i>	--	<i>Scomber japonicus</i>
11	10	<i>Coryphaena equisetis</i>	2.3+	<i>Coryphaena equisetis</i>	685	<i>Thunnus obesus</i>
10	11	<i>Sarda orientalis</i>	2.3-	<i>Coryphaena hippurus</i>	650	<i>Euthynnus affinis</i>
9	25	<i>Sarda chilensis</i>	1.8	<i>Sarda chilensis</i>	620	<i>Thunnus alalunga</i>
8	26	<i>Thunnus obesus</i>	1.4	<i>Thunnus obesus</i>	530	<i>Katsuwonus pelamis</i>
7	29	<i>Thunnus alalunga</i>	1.4	<i>Euthynnus affinis</i>	570	<i>Auxis thazard</i>
6	30	<i>Thunnus albacares</i>	--	<i>Scomber japonicus</i>	550	<i>Auxis rochei</i>
5	31	<i>Euthynnus affinis</i>	1.3	<i>Thunnus alalunga</i>	450	<i>Sarda chilensis</i>
4	37	<i>Scomber japonicus</i>	1.8	<i>Thunnus albacares</i>	410	<i>Thunnus albacares</i>
3	40	<i>Auxis thazard</i>	0.74	<i>Auxis thazard</i>	--	<i>Sarda orientalis</i>
2	45	<i>Auxis rochei</i>	0.74	<i>Katsuwonus pelamis</i>	135	<i>Coryphaena hippurus</i>
1	58	<i>Katsuwonus pelamis</i>	0.51	<i>Auxis rochei</i>	120	<i>Coryphaena equisetis</i>

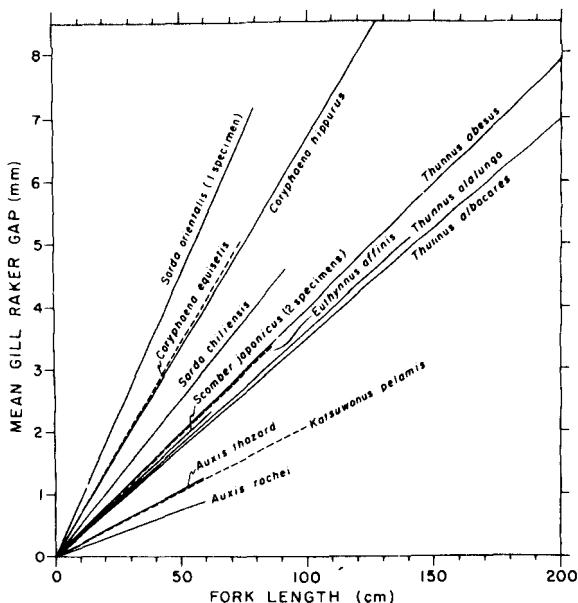


FIGURE 3.—Comparison of the mean gill raker gap and fork length relationship for various scombrid and coryphaenid fishes. Lengths shown approximate ranges known for each species.

in filtering area among species. Coryphaenids had a larger gill raker gap and smaller filtering area than any scombrid except striped bonito, *Sarda orientalis* (Temminck and Schlegel).

Among scombrids 35 cm long, *Sarda* had the largest gaps (1.8-3.3 mm) and *Auxis* and *Katsuwonus* the smallest (0.51-0.74 mm). *Thunnus*, *Euthynnus*, and *Scomber* had intermediate gap widths (1.2-1.4 mm). Among *Sarda*, *Auxis*, and *Thunnus* represented in our samples, species within genera had more similar gill raker gaps than those in different genera. On this basis alone food habits for fish of the same length would be expected to be more similar within genera than among genera.

Mean gill raker gap differed markedly with species and length of fish (Figure 3). For example, a 50-cm *K. pelamis*, a 30-cm *T. albacares*, and a 10-cm *S. orientalis* all had a mean gill raker gap of approximately 1 mm. Conversely, gill raker gaps of these three species differed markedly at the same fork length. Gaps of 50-cm *K. pelamis*, *T. albacares*, and *S. orientalis* were ca.

TABLE 3.—The average size of individual crustaceans, squids, and fishes in the stomachs of scombrids from the central Pacific.

Species	Volume of individual organisms (ml)			Volume of food analyzed (ml)	Source
	Crustaceans	Squids	Fishes		
<i>Thunnus albacares</i>	0.3	4.8	6.4	44,680	King & Ikehara (1956)
<i>Thunnus obesus</i>	0.6	9.5	8.2	22,297	King & Ikehara (1956)
<i>Thunnus albacares</i>	0.2	3.8	4.6	52,336	Reintjes & King (1953)
<i>Katsuwonus pelamis</i>	0.2	4.3	3.7	13,974	Waldrón & King (1963)
Mean (unweighted)	0.3	5.6	5.7		

1.0, 1.7, and 4.5 mm, respectively. Selectivity of the gill raker apparatus would vary with gill raker gap, a function of both species and length of the fish. Thus, a small *T. albacares* and a large *K. pelamis* should have more similar diets than a small and a large *T. albacares*. Any number of such predictions can be generated from Figure 3. A fish with smaller mean gap, regardless of its species or length, would be expected to be more planktivorous.

#### RELATION BETWEEN GILL RAKER GAP AND DIET

Stomach-content data from published literature from the central Pacific were compared with the mean gill raker gaps reported here to test the hypothesis that fish with a finer gill raker gap have a greater proportion of smaller organisms (crustaceans) in their diet.

Crustaceans in the diet of scombrids from the central Pacific were smaller than were the other major food organisms (squids and fishes) (Table 3). The volume of individual, partially digested crustaceans in the stomachs of five species averaged 0.3 ml whereas individual, partially digested squids and fishes averaged 5.6 and 5.7 ml, respectively. The much smaller body size of the crustaceans was not likely the result of differential digestion, especially since the exoskeleton of crustaceans, if anything, might be expected to slow, rather than accelerate, digestion (Pandian, 1967).

For comparison with gill raker data, the percent volumes of the stomach content comprised by crustaceans, squids, or fishes are presented in Table 4 for five scombrids and one coryphaenid. Only stomach data from the central Pacific were used because differences in typical body size of crustaceans in scombrid stomachs from other regions would have invalidated these

TABLE 4.—Food of scombrid and coryphaenid fishes from the central Pacific divided into the percentages of the stomach volume that were crustaceans, squids, or fishes. The median fork length of fishes in the sample is also given along with the literature source for the data.

Species	Stomach content (percent volume)			Fork length		Number of stomachs	Literature source
	Crustaceans	Squids	Fishes	Median (cm)	Range (cm)		
<i>Acanthocybium solanderi</i>	0	0	100	111	104-123	3	Tester & Nakamura (1957)
<i>Acanthocybium solanderi</i>	0	--	--	--	54-198	235	Iversen & Yoshida (1957)
<i>Euthynnus affinis</i>	8	0	92	49	31-67	32	Tester & Nakamura (1957)
<i>Katsuwonus pelamis</i>	44	--	40	44	39-49	>25	Yuen (1959)
<i>Katsuwonus pelamis</i>	4.0	23	72	47	33-60	305	Waldrón & King (1963)
<i>Katsuwonus pelamis</i>	67	7	26	50	40-61	67	Tester & Nakamura (1957)
<i>Katsuwonus pelamis</i>	25	--	70	55	50-60	>25	Yuen (1959)
<i>Katsuwonus pelamis</i>	3.7	19	74	73	60-89	254	Waldrón & King (1963)
<i>Katsuwonus pelamis</i>	1.5	--	91	73	62-84	>25	Yuen (1959)
<i>Thunnus albacares</i>	45	14	33	80	53-100	544	Reintjes & King (1953)
<i>Thunnus albacares</i>	39	9	49	115	100-130	205	Reintjes & King (1953)
<i>Thunnus albacares</i>	1.7	29	65	135	85-140	188	King & Ikehara (1956)
<i>Thunnus albacares</i>	3	4	93	140	130-168	26	Reintjes & King (1953)
<i>Thunnus albacares</i>	0.8	30	60	148	140-175	251	King & Ikehara (1956)
<i>Thunnus obesus</i>	2.3	26	70	128	75-140	63	King & Ikehara (1956)
<i>Thunnus obesus</i>	1.4	36	58	158	140-200	103	King & Ikehara (1956)
<i>Coryphaena hippurus</i>	1.6	2	97	81	42-121	52	Tester & Nakamura (1957)

TABLE 5.—Percent crustaceans by volume in the stomachs, median fork length, mean gill raker gap, and species of fish. (Ranks are from smallest to largest and ordered by the percentage of crustaceans in the stomachs.)

Species	Crustacea		Median fork length		Mean gill raker gap	
	%	Rank	(cm)	Rank	(mm)	Rank
<i>Acanthocybium solanderi</i>	0	1	111	10	0	16
<i>Thunnus albacares</i>	0.8	2	148	15	5.2	13
<i>Thunnus obesus</i>	1.4	3	158	16	6.3	15
<i>Katsuwonus pelamis</i>	1.5	4	73	6	1.5	5
<i>Coryphaena hippurus</i>	1.6	5	81	9	5.3	14
<i>Thunnus albacares</i>	1.7	6	135	13	4.7	10
<i>Thunnus obesus</i>	2.3	7	128	12	5.1	12
<i>Thunnus albacares</i>	3	8	140	14	4.9	11
<i>Katsuwonus pelamis</i>	3.7	9	73	6	1.5	5
<i>Katsuwonus pelamis</i>	4.0	10	47	2	0.99	2
<i>Euthynnus affinis</i>	8	11	49	3	1.9	7
<i>Katsuwonus pelamis</i>	25	12	55	5	1.2	4
<i>Thunnus albacares</i>	39	13	115	11	4.0	9
<i>Thunnus albacares</i>	44	14	80	8	2.8	8
<i>Katsuwonus pelamis</i>	45	15	44	1	0.92	1
<i>Katsuwonus pelamis</i>	67	16	50+	4	1.0	3

analyses. The galatheids and portunids dominating the crustaceans found in *T. albacares* stomachs in the eastern tropical Pacific (Alverson, 1963) are much larger (Longhurst, 1967; Jerde, 1967b) than the typical crustaceans from the stomachs of central Pacific scombrids given in Table 3. Also, data were not used if fewer than 25 stomachs had been examined. None of the 238 *A. solanderi* contained crustaceans and 0% crustaceans in the stomach was considered a reasonable estimate for any larger *A. solanderi*. The median or midrange fork length of fish was determined for each set of stomach data. Then mean gill raker gaps for fish of those species and length were estimated with the regressions from Table 1. Data on median fork length, mean gill raker gap, and percent crustaceans by volume in the stomach are presented in numerical and ranked form in Table 5.

Percent volumes that crustaceans contributed to the stomach content were inversely related to mean gill raker gap (Figure 4a) (Kendall rank correlation coefficient,  $\tau = -0.59$ ;  $n = 16$ ;  $P < 0.001$ ) and to fork length (Figure 4b) (Kendall rank correlation coefficient,  $\tau = -0.45$ ;  $n = 16$ ;  $P < 0.01$ ). Several notable exceptions occurred in the relation with fork length (Table 5, Figure 4b). *C. hippurus*, 81 cm long, contained 2% crustaceans while *T. albacares*, 80 cm long, contained 45% crustaceans. *T. albacares*, 135 cm long, also contained 2% crus-

taceans. Not unexpectedly, *C. hippurus*, 81 cm long, and *T. albacares*, 135 cm long, both had mean gill raker gaps near 5 mm whereas the 81-cm *T. albacares* had a smaller mean gill raker gap near 3 mm. The somewhat closer correspondence of percentage of crustaceans to gill raker gap than to fork length can be observed by comparing Figures 4a and 4b or by comparing the associated probabilities of no correlation ( $< .01$  versus  $< .001$ ).

Kendall partial rank correlation coefficients were computed to determine the association between percent crustaceans in the stomach and gill raker gap, with the effect of fork length held constant. The partial correlation coefficient between percent crustaceans and gap, independent of variation in fork length, was  $-0.43$  while the partial correlation between percent crustaceans and fork length independent of variations in gap, was only  $-0.05$ . Thus, although fork length was correlated with the percent crustaceans, this correlation resulted from the association between gill raker gap and fork length. Gill raker gap was the important variable correlated to percent crustaceans in the diet.

Data on percent crustaceans in the stomach by volume were also presented for *K. pelamis* and *T. albacares* of various size by Alverson (1963) and for *K. pelamis* and blackfin tuna, *Thunnus atlanticus* (Lesson), by Suarez Caabro

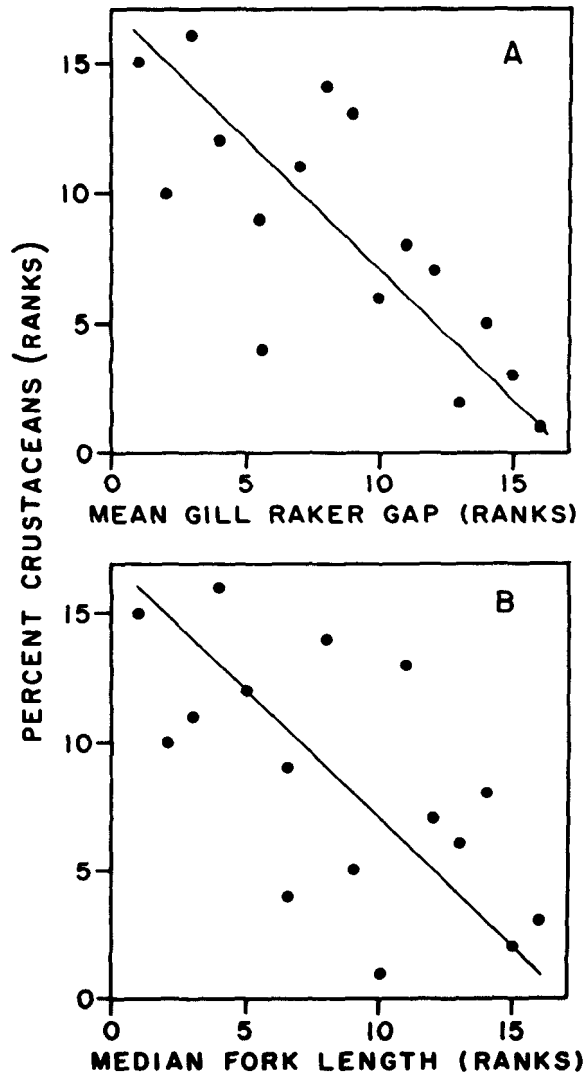


FIGURE 4.—Relation between percentage crustaceans by volume of diet (ranked) and the (a) mean gill raker gap of a fish (ranked) and (b) fork length of fish (ranked). The diagonal line depicts a perfect inverse relationship.

and Duarte Bello (1961). These were not used in the present analysis because sample sizes were fewer than 25 fish or because the size of the individual crustaceans was unavailable. Regardless, larger *K. pelamis* in both studies contained less crustaceans. However, larger *T. albacares* in Alverson's study tended to eat more crustaceans than did smaller specimens. This

may have been because the crustaceans in their diet were relatively large.

Alverson's paper also presents a good example of selectivity among crustaceans that may be based on size of gill raker gaps. *K. pelamis* and *T. albacares* from the same areas had markedly different diets. Crustaceans contributing the greatest volume to the stomachs were galatheids and portunids for *T. albacares* but euphausiids for *K. pelamis*. Euphausiids were rare in stomachs of *T. albacares* even when common in the micronekton (Blackburn, 1968). Galatheids and portunids (Longhurst, 1967; Jerde, 1967b) are typically larger in size than euphausiids (Jerde, 1967a). The small euphausiids were not important in stomachs of *T. albacares* (i.e., 1% of the volume) in any of the areas of the eastern tropical Pacific studied by Alverson (1963), but the larger galatheids and portunids were important in the stomachs of *K. pelamis* from certain areas. The above observations would be the predictions from gill raker gaps—*T. albacares* have broader gaps than *K. pelamis* and would not be expected to capture the smaller crustaceans.

The major hypothesis under investigation in the present study was that the quantity of smaller organisms (crustaceans) eaten should be related to the selectivity of the gill raker apparatus. The above correlations on central Pacific data, although only crude in nature, lend support to this idea. A more definitive test would require extensive data on the size of food organisms and the diet of scombrids over more narrow length ranges than are available from the published literature.

Even though the structure of the gill raker apparatus ultimately determines the smallest size of prey, it is possible that actual selection of fishes is made prior to ingestion (Ivlev, 1961; Galbraith, 1967). Galbraith believed that the gill rakers of yellow perch, *Perca flavescens* (Mitchill), and rainbow trout, *Salmo gairdneri* Richardson, could have retained smaller zooplankton than were typically found in their stomachs. These species ate only larger *Daphnia* even though numerous smaller ones were in the zooplankton.



Several authors have pointed out that fish tend to select the largest food organisms available to them (Hayashi, 1956, as cited in Yasuda, 1960b; Ivlev, 1961; Brooks, 1968). The large mouth of larval scombrids facilitates capture of large copepods at first feeding and contributes to their rapid early growth rates (Shirota, 1970). The responsiveness of at least one scombrid to food is influenced by the size of the food organism—*K. pelamis* ate whole shrimp and squid at the beginning of a feeding, but as they became sated, they would only eat cut-up pieces of smaller size (Nakamura, 1962). Feeding behavior of Atlantic mackerel, *Scomber scombrus* Linnaeus, (Sette, 1950) and northern anchovy, *Engraulis mordax* Girard, (Leong and O'Connell, 1969) changes with the size of food. When small food is present, they open the mouth wide and flare the opercles in a filter feeding mode, but with larger food they make individual biting attacks. *S. japonicus* eats food smaller than would be predicted by gill raker gap (Hiyama and Yasuda, 1957). The spiny process we observed on the rakers of *S. japonicus* probably form an even finer sieve than is formed by the rakers themselves. Regardless of the mode of selection (anatomical, behavioral, or perceptual), the selective capabilities of scombrids and coryphaenids would appear to be correlated with the anatomy of the gill raker apparatus.

An individual scombrid is able to prey on organisms differing greatly in size. It is capable of engulfing and retaining crustaceans, small fishes, and squid by means of a well-developed gill raker apparatus. It is also capable of pursuing, capturing, and ingesting fast-moving fishes and squids, provided they are not too large to be swallowed whole. The gill raker gap and maximum distensibility of the mouth and esophagus then would be expected to set limits on the range of food sizes eaten by scombrids. Within this size range a diverse faunal assemblage exists in the sea that includes numerous species of crustaceans, fishes, and molluscs. The diversity of species in the size range consumed by an individual scombrid has, to a great extent, masked the selectivity that does occur. The present paper provides some evidence for selection of or-

ganisms above a minimum size determined by the magnitude of gill raker gaps.

## ACKNOWLEDGMENTS

We thank Reginald Gooding for assistance with collection of data, Marian Yong and Betty Ann Keala for computer processing the data, and William H. Neill and Dr. James F. Kitchell, Laboratory of Limnology, Madison; Witold L. Klawe, Inter-American Tropical Tuna Commission, and Dr. Maurice Blackburn, Scripps Institution of Oceanography, who critically reviewed the manuscript. This project was supported entirely by the Bureau of Commercial Fisheries Biological Laboratory, Honolulu.

## LITERATURE CITED

- ALVERSON, F. G.  
1963. The food of yellowfin and skipjack tunas in the Eastern Tropical Pacific Ocean. Inter-Amer. Trop. Tuna Comm., Bull. 7: 293-396.
- BHIMACHAR, B. S., AND P. C. GEORGE.  
1953. Observations on the food and feeding of the Indian mackerel, *Rastrelliger canagurta* (Cuvier). Proc. Indian Acad. Sci., Sect. B 36: 105-118.
- BLACKBURN, M.  
1968. Micronekton of the eastern tropical Pacific Ocean: family composition, distribution, abundance, and relations to tuna. U.S. Fish Wildl. Serv., Fish. Bull. 67: 71-115.
- BROOKS, J. L.  
1968. The effects of prey size selection by lake planktivores. Syst. Zool. 17: 272-291.
- BROOKS, J. L., AND S. I. DODSON.  
1965. Predation, body size, and composition of plankton. Science (Washington) 150: 28-35.
- GALBRAITH, M. G., JR.  
1967. Size-selective predation on *Daphnia* by rainbow trout and yellow perch. Trans. Amer. Fish. Soc. 96: 1-10.
- HIYAMA, Y., AND F. YASUDA.  
1957. The methods of utilization of plankton by fishes. Rec. Oceanogr. Works Jap., Spec. No. [1] March 1957: 67-70.
- IVERSEN, E. S., AND H. O. YOSHIDA.  
1957. Notes on the biology of the wahoo in the Line Islands. Pac. Sci. 11: 370-379.
- IVLEV, V. S.  
1961. Experimental ecology of the feeding of fishes. (Translated from the Russian by Douglas Scott.) Yale Univ. Press, New Haven, 302 p.

- JERDE, C. W.  
1967a. A comparison of euphausiid shrimp collections made with a micronekton net and a one-meter plankton net. *Pac. Sci.* 21: 178-181.  
1967b. On the distribution of *Portunus (Achelous) affinis* and *Euphyllax dovii* (Decapoda Brachyura, Portunidae) in the eastern tropical Pacific. *Crustaceana* 13: 11-22.
- KING, J. E., AND I. I. IKEHARA.  
1956. Comparative study of food of bigeye and yellowfin tuna in the central Pacific. *U.S. Fish Wildl. Serv., Fish Bull.* 57: 61-85.
- KLIEWER, E. V.  
1970. Gill raker variation and diet in lake whitefish, *Coregonus clupeaformis*, in northern Manitoba. In C. C. Lindsey and C. S. Woods (editors), *Biology of coregonid fishes*, p. 147-165. Univ. of Manitoba Press, Winnipeg.
- LEONG, R. J. H., AND C. P. O'CONNELL.  
1969. A laboratory study of particulate and filter feeding of the northern anchovy (*Engraulis mordax*). *J. Fish. Res. Bd. Can.* 26: 557-582.
- LONGHURST, A. R.  
1967. The pelagic phase of *Pleuroncodes planipes* Stimpson (Crustacea, Galatheidae) in the California Current. *Calif. Coop. Oceanic Fish. Invest., Rep.* 11: 142-154.
- NAKAMURA, E. L.  
1962. Observations of the behavior of skipjack tuna, *Euthynnus pelamis*, in captivity. *Copeia* 1962: 499-505.
- PANDIAN, T. J.  
1967. Transformation of food in the fish *Megalops cyprinoides*. I. Influence of quality of food. *Mar. Biol.* 1: 60-64.
- REINTJES, J. W., AND J. E. KING.  
1953. Food of yellowfin tuna in the central Pacific. *U.S. Fish Wildl. Serv., Fish. Bull.* 54: 91-110.
- SETTE, O. E.  
1950. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America, Part II—migrations and habits. *U.S. Fish Wildl. Serv., Fish Bull.* 51: 251-358.
- SHIROTA, A.  
1970. Studies on the mouth size of fish larvae. [In Japanese, English abstract.] *Bull. Jap. Soc. Sci. Fish.* 36: 353-368.
- SUAREZ CAABRO, J. A., AND P. P. DUARTE BELLO.  
1961. Biología pesquera del bonito (*Katsuwonus pelamis*) y la albacora (*Thunnus atlanticus*) en Cuba. *I. Inst. Cubano Invest. Tecnol. Ser. Estud. Trab. Invest.* 15, 150 p.
- SUYEHIRO, Y.  
1942. A study of the digestive system and feeding habits of fish. *Jap. J. Zool.* 10: 1-303.
- TESTER, A. L., AND E. L. NAKAMURA.  
1957. Catch rate, size, sex, and food of tunas and other pelagic fishes taken by trolling off Oahu, Hawaii, 1951-55. *U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish.* 250, 25 p.
- WALDRON, K. D., AND J. E. KING.  
1963. Food of skipjack in the central Pacific. In H. Rosa, Jr. (editor), *Proceedings of the world scientific meeting on the biology of tunas and related species*, p. 1431-1457. *FAO (Food Agr. Organ. U.N.) Fish. Rep.* 6.
- YASUDA, F.  
1960a. The relationship of the gill structure and food habits of some coastal fishes in Japan. *Rec. Oceanogr. Works Jap., New Ser.* 5(2): 139-152.  
1960b. The feeding mechanism in some carnivorous fishes. *Rec. Oceanogr. Works Jap., New Ser.* 5(2): 153-160.
- YUEN, H. S. H.  
1959. Variability of skipjack response to live bait. *U.S. Fish Wildl. Serv., Fish. Bull.* 60: 147-160.