

STOMACH CONTENTS OF ALBACORE, SKIPJACK, AND BONITO CAUGHT OFF SOUTHERN CALIFORNIA DURING SUMMER 1983

HANNAH J. BERNARD, JOHN B. HEDGEPEETH, AND STEPHEN B. REILLY
National Marine Fisheries Service
Southwest Fisheries Center
P.O. Box 271
La Jolla, California 92038

ABSTRACT

Three species of scombrids were troll-caught off southern California for a food habits study during Cruise 166 of NOAA research vessel *David Starr Jordan* in August 1983, to examine effects of the anomalous oceanography (El Niño) of that period. The stomachs of 94 albacore (*Thunnus alalunga*), 31 skipjack (*Katsuwonus pelamis*), and 42 bonito (*Sarda chiliensis*) were examined. Chi-square analysis for homogeneity showed highly significant differences in types of prey and proportions consumed by the three species. Albacore consumed 96.8% fish, 35.1% cephalopods, and 52.1% crustaceans by frequency of occurrence, and 82.4% fish, 1.7% cephalopods, and 15.9% crustaceans by numerical frequency. Skipjack consumed 19.4% fish, 12.9% cephalopods, and 54.8% crustaceans (45.2% euphausiids) by frequency of occurrence, and 11.1% fish, 2.6% cephalopods, and 86.3% crustaceans (76.5% euphausiids) by numerical frequency. Bonito consumed 71.4% fish and 26.2% crustaceans (11.9% euphausiids) by frequency of occurrence, and 32.1% fish and 67.9% crustaceans (63.4% euphausiids) by numerical frequency. A comparison to historical data during similar and dissimilar environmental conditions suggests that the scombrids are opportunistic predators, and that prey availability was partly a function of the oceanographic conditions. The index of relative importance and mean volumetric ratio measurement of northern anchovy (*Engraulis mordax*) in the diet of albacore is presented.

RESUMEN

Con el fin de examinar los efectos oceanográficos anómalos (El Niño) en el período de agosto de 1983, durante la campaña 166 del buque de investigación de la NOAA "David Starr Jordan" para un estudio de hábitos alimentarios, se capturaron con línea tres especies de escómbridos a la altura del sur de California. Se examinaron 94 contenidos estomacales de albacora (*Thunnus alalunga*), 31 de listado (*Katsuwonus pelamis*), y 42 de bonito (*Sarda chilensis*). Análisis de chi-cuadrado para homogeneidad demostraron diferencias altamente significativas en los tipos y

proporciones de presas consumidas por las 3 especies. Por frecuencia de registro, la albacora consumió un 96.8% de peces, 35.2% de cefalópodos, y 52.1% de crustáceos; mientras que por frecuencia numérica los valores fueron, peces: 82.4%, cefalópodos: 1.7%, y crustáceos: 15.9%. El listado consumió 19.4% de peces, 12.9% de cefalópodos, y 54.8% de crustáceos (45.2% de eupáusidos) por frecuencia de registro; en frecuencia numérica los valores fueron, peces: 11.1%, cefalópodos: 2.6%, y crustáceos: 86.3% (76.5% de eupáusidos). El bonito consumió 71.4% de peces, y 26.2% de crustáceos (11.9% de eupáusidos) por frecuencia de registro, y 32.2% de peces y 67.9% de crustáceos (63.4% de eupáusidos) por frecuencia numérica.

La comparación con datos históricos similares durante condiciones ambientales semejantes y diferentes sugiere que los escómbridos son predadores oportunistas, y que la disponibilidad de presas era, parcialmente, el resultado de las condiciones oceanográficas. Se presentan el índice de importancia relativa y medidas de la tasa volumétrica media de la anchoveta del norte (*Engraulis mordax*) en la dieta de la albacora.

INTRODUCTION

The limitations of single-species models in fisheries management have been recognized and well documented (Anderson and Ursin 1977; Laevastu and Larkins 1981; and Livingston MS¹). That predation mortality can control year-class strength of a given prey species has been established and deserves further examination (Laevastu and Larkins 1981; Rothschild and Forney 1979). We conducted a multispecies comparison by examining stomach contents of three species of scombrids—skipjack (*Katsuwonus pelamis*), albacore (*Thunnus alalunga*), and Pacific bonito (*Sarda chiliensis*)—collected in the California Current during the 1983 El Niño. Food habits studies from El Niño and other periods are also reviewed here.

¹Livingston, P.A. MS. Marine fishery management demands on fish food habits data: a discussion of alternative uses of food habits data for management purposes. NMFS, Resource Ecology and Fishery Management Division, 7600 Sand Point Way, N.E., Bldg. 4, Bin c15700, Seattle, Washington, 98115, 16 p.

We found significant amounts of young-of-the-year anchovies, *Engraulis mordax*, in the diet of these scombrids, especially albacore. A number of animals prey on the northern anchovy, including at least 33 species of fish, seabirds, marine mammals, and man (Radovich 1979). The impact of predation and adverse environmental conditions on a commercially important fish like the northern anchovy could have far-reaching economic repercussions.

Prior to Iversen's (1962) study on albacore in the central and northeast Pacific Ocean, food habits studies on albacore were largely nonquantitative (Clemens and Iselin 1963; McHugh 1952; Powell and Hildebrand 1949; Hart 1942; and Hart and Hollister 1947). In the 1970s, more quantitative studies were undertaken, including those by Pinkas et al. (1971) and Iversen (1962). Both studies were conducted when El Niño events were mild or absent.

Most food habits studies on skipjack have taken place in the central and eastern tropical Pacific Ocean (Alverson 1963; Nakamura 1965; and Waldron and King 1963). However, Alverson's study in the eastern tropical Pacific Ocean includes the region between Point Conception and 20°N, between 123° to 115°W during another strong El Niño (1957-59).

There is a paucity of literature on bonito's food habits in the California Current. One other study, spanning two years of collection (1968 and 1969—mild El Niño years), was available for comparison (Pinkas et al. 1971).

METHODS

The three scombrid species (94 albacore, 41 Pacific bonito, and 21 skipjack) were caught by hand-operated jig lines with artificial lures trolled at an average speed of 6 knots, during Cruise 166 of NOAA research vessel *David Starr Jordan*. In addition, 1 bonito and 10 skipjack were caught in gill nets deployed at night. Size of fish caught was fairly homogeneous within each species (Table 1). The albacore and bonito were caught in water approximately the same temperature (17.8°C and 17.3°C); the skipjack were caught in the warmer water (21.2°C) of the Southern California Bight (Table 1).

The albacore and bonito were caught in close association with each other, within 100 miles of shore, between 33°59' to 36°44'N and 121°19' to 122°30'W. The skipjack were all taken south of Point Conception in the Southern California Bight between 32°38' to 33°46'N and 117°57' to 119°16'W (Figure 1).

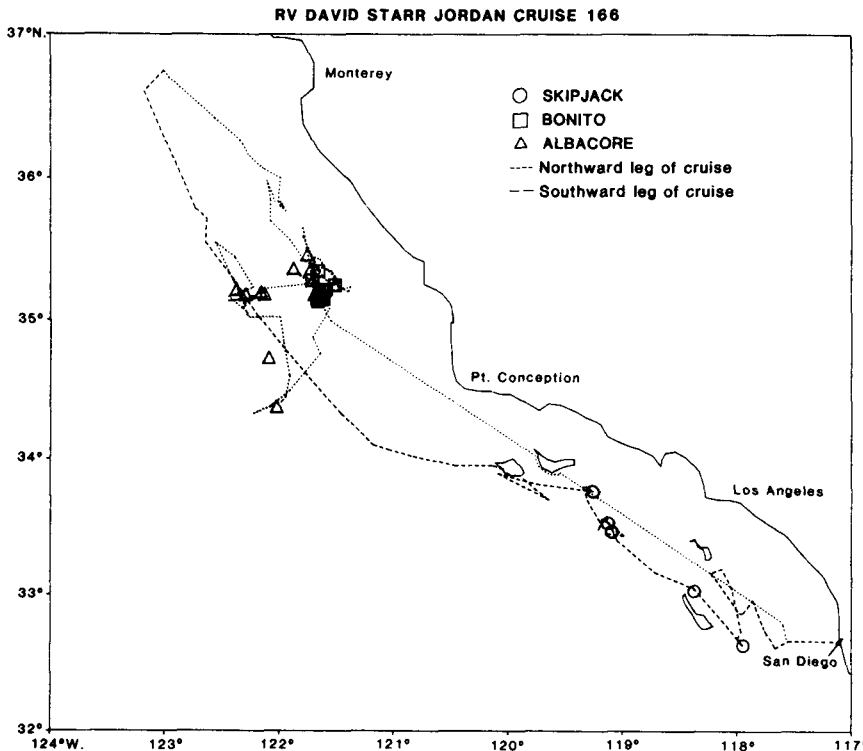


Figure 1. Capture locations of albacore, skipjack, and bonito during Cruise 166 of R/V *David Starr Jordan*, August 15-September 1, 1983.

TABLE 1
**Mean Fork Lengths and Standard Deviations, and
 Mean Water Temperatures at Time of Catch**

		Albacore (n=94)	Skipjack (n=31)	Bonito (n=42)
FL. (cm)	\bar{x}	69.3	48.7	59.9
	(s)	(8.817)	(2.031)	(1.902)
Temp. (°C)	\bar{x}	17.77	21.17	17.32
	(s)	(0.624)	(0.442)	(0.252)

Stomachs were removed aboard the ship and frozen. Contents were thawed in the laboratory and rough-sorted. Because many prey items in the stomachs in this study have not yet been identified, they were pooled into gross taxonomic categories, usually at the class level, except where otherwise indicated. In order to compare our data with previous studies, we pooled (whenever possible) the data from those studies to correspond to our fewer categories.

Percent frequency of occurrence (number of stomachs in which a particular prey occurred as a percentage of the total number of stomachs = %FO) and percent numerical frequency (%NF) were determined for all three species. Additionally, anchovies were separated from the other fish found in the albacore stomachs. The percent volumes of anchovies and other fish prey were determined.

We calculated a measure of relative importance (Pinkas et al. 1971) for the fish consumed by 85 albacore. This value, termed index of relative importance (IRI), is the product of the sum of the numerical plus volumetric percentages of a given prey item and percent frequency of occurrence of that prey [IRI = %FO(%NF + %VF)]. It is used here for comparison of anchovies consumed relative to all other fish prey combined and not as a total IRI for all prey items.

The data from the 85 albacore stomachs that contained fish were also examined individually to determine the importance of a given prey to an individual predator. Individual stomach analysis is similar in principle to an IRI calculation; however, instead of pooling prey from all of the stomachs of a given predator, one evaluates the distribution of fractional volumes and numbers of prey for each stomach. In contrast to the IRI, these data make it possible to determine the variance, mean, and standard deviation, and to perform statistical tests. The mean volumetric or numerical ratio measurement (MVRM, MNRM) was based on the percentages or proportions of prey in relation to total stomach volume or total numbers of all prey in individual stomachs (Ankenbrandt, in press). We calculated the MVRM for anchovies in the

diet of albacore by the following equation (and MNRM can be calculated similarly):

$$\bar{r}_j = \frac{\sum_{i=1}^N r_{ij}}{N} = \text{mean volumetric ratio of prey } j \text{ to the total volume of } N \text{ stomachs}$$

where N = number of stomachs examined

$$r_{ij} = \frac{V_{ij}}{\left[\sum_{j=1}^n V_{ij} \right]} = \text{ratio of prey } j \text{ to the total volume of stomach } i$$

and where V_{ij} = volume of prey type j in stomach i

n = number of prey items

In an attempt to determine if the albacore were consuming anchovies at random, we performed a runs test (Sokal and Rohlf 1969) to test the null hypothesis that the frequency of occurrence of anchovies within the albacore stomachs is random.

It appeared that the three predator species were not eating the same kinds of prey items in the same proportions. We used Crow's (1982) suggestion for showing differences in feeding habits by analysis of stomach contents using a 2-way, $R \times C$, contingency table, where R is the number of prey categories and C is the predator species.

RESULTS

Scombrid Feeding Habits

Chi-square analysis for homogeneity showed highly significant differences in types of prey and proportions consumed by the three scombrid species (Table 2).

TABLE 2
Observed Frequency

Prey	Predator			Total
	Skipjack	Albacore	Bonito	
Unident. Crust.	6	71	13	90
<i>Pleuroncodes</i>	4	84	0	88
Amphipods	8	20	19	47
Hyperiididae	1	18	0	19
Euphausiids	148	916	449	1513
Fish	22	5741	228	5991
Cephalopods	5	117	0	122
Total	194	6967	709	7870

Minimum estimated expected value is 0.47

Independence of prey occurrence was tested, and the null hypothesis of homogeneity was rejected. Chi-square value = 1,641.721, probability <0.0001.

PERCENT FREQUENCY OF PREY

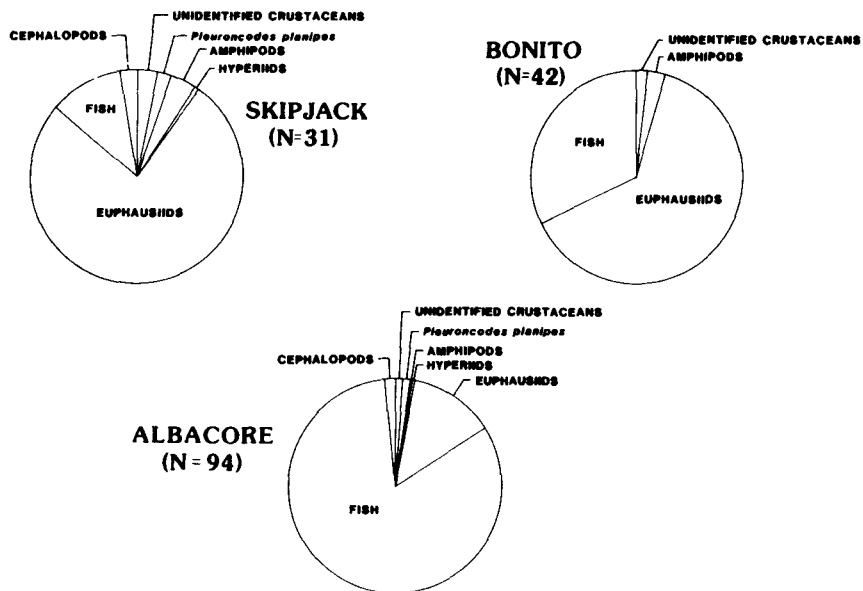


Figure 2. Percent numerical frequency of prey consumed by three scombrids (skipjack, albacore, and bonito) caught during Cruise 166.

Skipjack consumed crustacea most frequently (FO = 54.8%) and in greatest numerical frequency (NF = 86.3%). Bonito consumed fish most frequently (FO = 71.4%), but crustacea were highest in numerical frequency (NF = 67.0%) (Figures 2 and 3). The

crustacean most important to both skipjack and bonito was the euphausiid *Nyctiphanes simplex*.

The primary prey of albacore was fish (FO = 96.8%, NF = 82.4%) (Figures 2 and 3). The IRI for anchovies in the diet of albacore was 7,630; for all

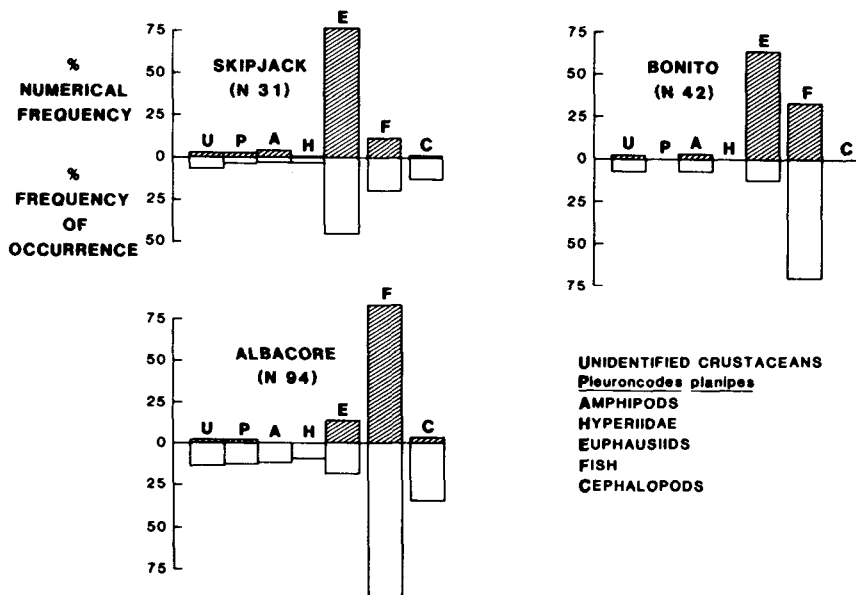


Figure 3. Percent numerical frequency and percent frequency of occurrence of prey consumed by skipjack, albacore, and bonito caught during Cruise 166.

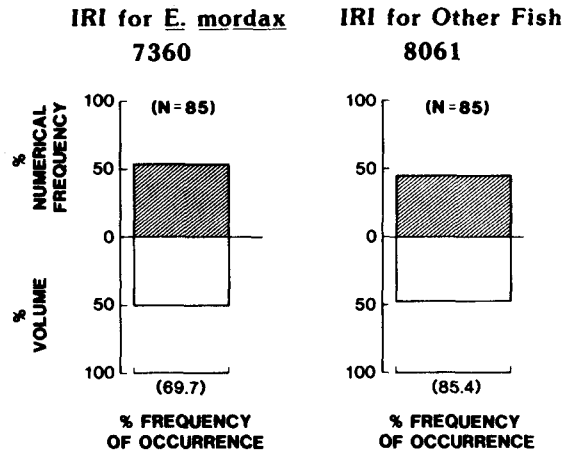


Figure 4. Index of relative importance and percent numerical frequency, percent volumetric frequency, percent frequency of occurrence for anchovies and other fish consumed by albacore caught during Cruise 166.

other fish combined, the IRI was 8,061 (Figure 4). The anchovies found in the albacore stomachs were young-of-the-year, from 22-47 mm SL, with a mean of 33.6 mm and a standard deviation of 4.97 (Figure 5). Albacore stomachs can be a source for verifying the existence or abundance of the anchovy size classes that are underrepresented in the California reduction fishery sampling program used for anchovy population studies (Mais 1981).

The presence of *Pleuroncodes planipes*, pelagic red crab, in the diets of skipjack and albacore is notable because the crab's northern limit in most years appears to be 28°N, in Sebastian Viscaino Bay (Longhurst 1967).

Individual Stomach Analysis

The mean volumetric ratio measurement for anchovies in albacore stomachs (0.092) was only a little less

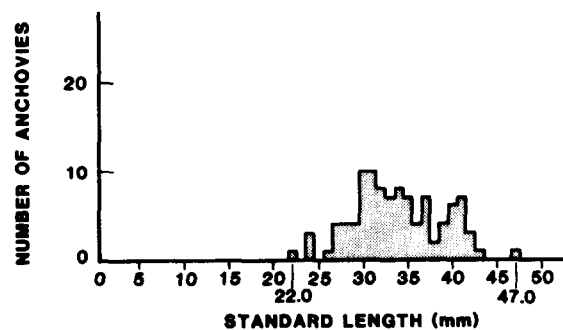


Figure 5. Length-frequency distribution of anchovies found in albacore stomachs caught during Cruise 166.

TABLE 3
 Mean Volumetric Ratio Measurements (MVRM) and Standard Deviations of Anchovies and All Other Fish Consumed by 85 Albacore

	<i>E. mordax</i>	Other fishes
MVRM	0.092	0.110
(s)	0.144	0.207

than the mean volumetric ratio measurement for all other fish combined (0.11) (Table 3).

The mean numerical percentage of anchovies in albacore stomachs is somewhat less ($\bar{x} = 42.4\%$) than all other fish combined ($\bar{x} = 57.6\%$), as was the mean volumetric percentage of anchovies ($\bar{x} = 44.1\%$) to all other fish combined ($\bar{x} = 55.9\%$) (Table 4).

The mean volumetric and numerical percentages of anchovies from individual stomach analyses were also less than the numerical and volumetric percentages of anchovies in the IRI calculation (Table 5).

Cumulative frequency plots showing the proportions of percent numerical and volumetric frequencies of anchovies in albacore stomachs (Figures 6 and 7) demonstrate that there were more albacore stomachs containing fish other than anchovies than stomachs containing anchovies alone.

The runs test resulted in rejection of the null hypothesis of random distribution of anchovies in albacore stomachs at the 5% significance level. Ancho-

TABLE 4
 Mean Volumetric and Numerical Percentages and Standard Deviations of Anchovies and Other Fish Consumed by 85 Albacore

	<i>E. mordax</i>	Other fishes
Numerical percentage		
\bar{x}	42.4%	57.6%
(s)	39.7	39.7
Percent volume		
\bar{x}	44.1%	55.9%
(s)	41.2	41.2

TABLE 5
 Percentages Used in IRI Calculation

	<i>E. mordax</i>	Other fishes
Numerical percentage	53.9%	46.1%
Percent volume	51.7%	48.3%
Frequency of occurrence	69.7%	85.4%

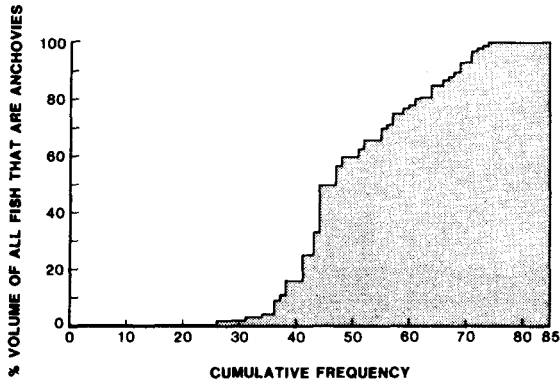


Figure 6. Cumulative frequency plot of volumetric percentage of all anchovies in 85 albacore stomachs.

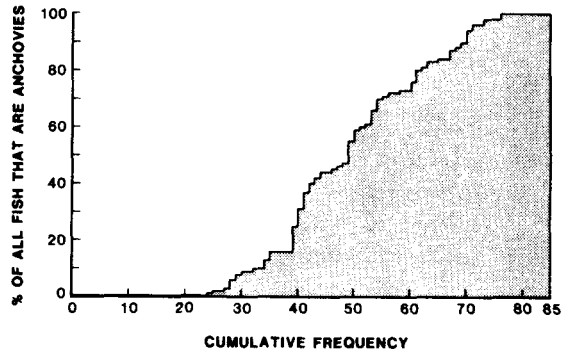


Figure 7. Cumulative frequency plot of numerical percentage of all anchovies in 85 albacore stomachs.

vies were present in some of the albacore stomachs in large quantities; and some stomachs did not contain any anchovies. This finding is not necessarily a reflection of active selection, but more likely an indication of the patchy distribution of the anchovy schools.

DISCUSSION

There are significant differences in types of prey and proportions consumed among the three scombrids. Bonito and skipjack consumed more euphausiids than any other type of prey. Albacore consumed more fish than any other prey, and the northern anchovy, *Engraulis mordax*, was consumed nearly as much as all other fish combined.

The 1983 El Niño event resulted in, among other things, a marked decrease in the southward transport of the California Current. The decreased transport

correlates with a decrease in zooplankton biomass (Chelton et al. 1982) and a decrease in the occurrence of cephalopods off the California coast. In addition, fauna endemic to more southerly ranges (e.g., *Pleuroncodes planipes* and *Nyctiphanes simplex*) were transported northward and incorporated into the diets of the scombrid predators. A comparison of this study with other food habits studies during El Niño periods showed similar trends.

Pacific Bonito

In 1968 and 1969 (Pinkas et al. 1971), fish were the primary prey for bonito, with cephalopods next in importance (in 1968, NF for cephalopods = 13.9% and FO = 21.3%; in 1969, NF = 5.8% and FO = 28.2%). However, in our study, the importance of crustacea is about the same as fish (Figure 8). No

BONITO

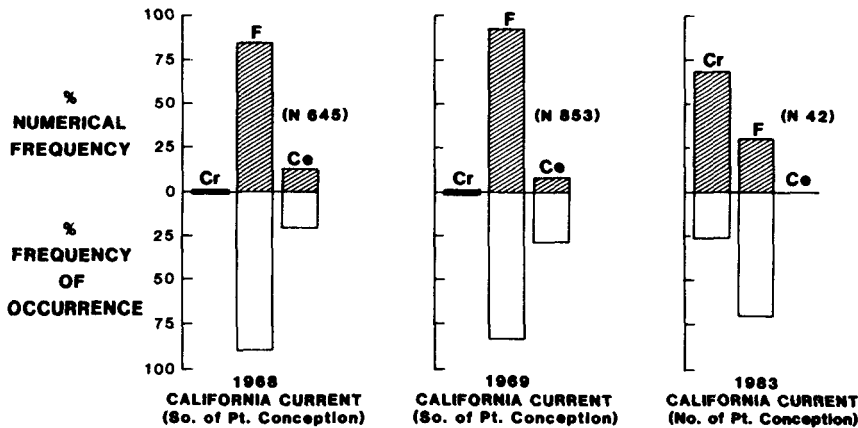


Figure 8. Comparison of percent numerical frequency and percent frequency of occurrence of prey consumed by bonito caught in 1968 and 1969 (Pinkas et al. 1971) and those caught from August 15-September 1, 1983. Cr = crustaceans, Ce = cephalopods, and F = fish.

SKIPJACK

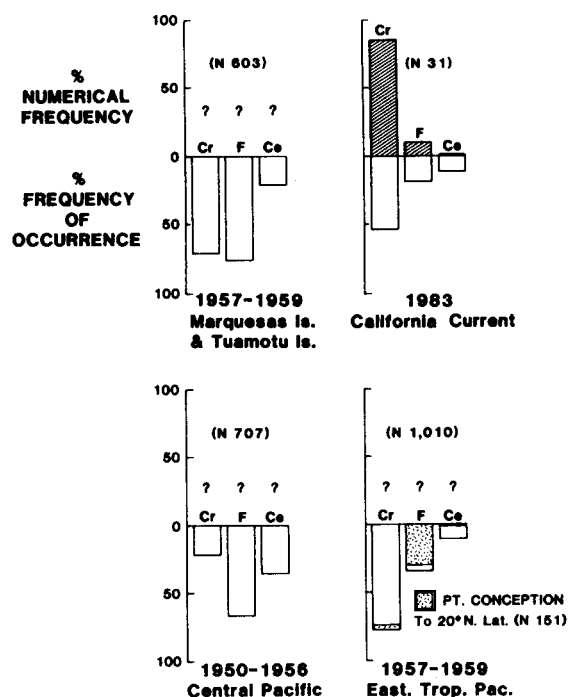


Figure 9. Comparison of percent numerical frequency and percent frequency of occurrence of prey consumed by skipjack in several studies. On left are studies from central and south Pacific: 1957-59 (Nakamura 1965), and 1950-56 (Waldron and King 1963). On right are studies from the eastern tropical Pacific and California Current: 1983 (this study) and 1957-59 (Alverson 1963). Question marks represent unavailable data. Cr = crustaceans, Ce = cephalopods, and F = fish.

cephalopods were found in the bonito stomachs collected during the 1983 cruise. This suggests that cephalopods were not available to the bonito we sampled during the 1983 El Niño.

Skipjack

In Alverson's (1963) study conducted in the region between Point Conception and 20°N during the 1957-59 El Niño, crustacea were consumed most frequently, as in 1983 (Figure 9). In contrast to 1983, when euphausiids were the most important crustacean, the pelagic red crab was the most important crustacean in 1957-59.

Albacore

We used Pinkas et al. (1971) for a detailed comparison to our study because of the similar location (Iversen's 1962 data from the equatorial and northeastern Pacific were pooled together). Fish were the primary prey in 1968 and 1969, with anchovies the most important species in 1968, and sauries (*Cololabis*

ALBACORE

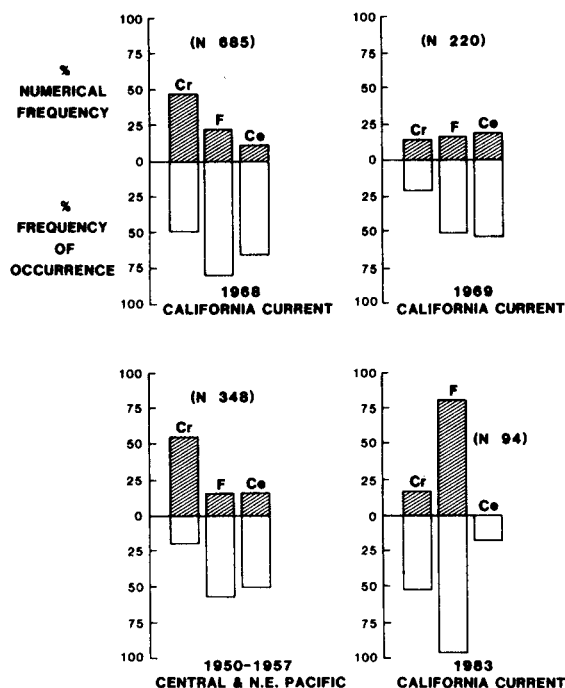


Figure 10. Comparison of percent numerical frequency and percent frequency of occurrence of prey consumed by albacore in 1968 and 1969 (Pinkas et al. 1971), 1950-57 (Iversen 1962), and 1983 (this study). Cr = crustaceans, Ce = cephalopods, and F = fish.

saira) the most important species in 1969 (Figure 10). In 1983, anchovies were almost equal in importance to all other fish combined.

MVRM versus IRI

The MVRM and the numeric and volumetric proportions (used in IRI calculations) gave similar results: anchovies were consumed almost as much in volume and numbers as all other fish combined. The mean numerical and volumetric percentages of anchovies consumed by albacore were slightly less (42.4% and 44.1%, respectively) than the numerical and volumetric percentages used for the IRI calculation (53.9% and 51.7%). This reflects the difference between establishing a measurement based on a pooled average (volumetric and numerical proportions) and a weighted average (MVRM and MNRM). The fact that numerical and volumetric proportions based on pooled (IRI-type) data are greater than the means of volumetric and numerical frequency shows that some albacore were primarily consuming anchovies, whereas, at other times, other albacore were consuming more of some other fish species. This suggests that the com-

plementary use of the MVRM and volumetric frequency and the MNRM and the numerical frequency will provide insight into the feeding habits of fishes.

The MVRM calculation enabled us to perform statistical tests on these data and resulted in the conclusion that the distribution of anchovies as prey among individual albacore was not random. That is, it appears that some albacore encountered and fed on anchovy schools, while other albacore encountered and fed on schools of other fish, a possible reflection of the inherently patchy distribution of anchovy schools.

Gill-Raker Gap and Prey Size

In a previous study (Magnuson and Heitz 1971), the gill-raker gap (space between the first two gill rakers of the first gill arch) was measured or estimated by linear regression in tunas, mackerels, and dolphinfish. The results showed a positive correlation between gill-raker gap and fork length, and gill-raker gap and prey size—i.e., the predators with smaller gill-raker gaps consumed smaller prey.

We determined the mean gill-raker gaps for the scombrids in our study by linear regression (fork length vs gill-raker gap). Although bonito had a larger gill-raker gap (ca. 3.05 mm) than both skipjack (ca. 1.03 mm) and albacore (ca. 2.50 mm), we found that the proportion of prey items in bonito stomachs more closely resembled the contents of skipjack stomachs (mostly euphausiids) than albacore stomach contents.

Our findings were contrary to those of Magnuson and Heitz: most of the bonito prey were smaller than most of the albacore prey, even though albacore had a smaller gill-raker gap than bonito and they were caught in the same area on the same days. This information, added to the evidence that scombrids in previous studies have diverse and opportunistic feeding habits during similar and dissimilar environmental conditions, underscores the complexities of food-web dynamics.

ACKNOWLEDGMENTS

We wish to thank Norman Bartoo, Lisa Ankenbrandt, Earl Weber, Dave Holts, John Michno, and Robert Pitman for collecting the scombrid stomachs during Cruise 166. Tim Smith, Gary Sakagawa, and Patricia Livingston read an earlier version of the manuscript and gave helpful suggestions for its improvement.

Ken Raymond, Roy Allen, and Henry Orr provided their excellent illustrative services.

LITERATURE CITED

- Alverson, F.G. 1963. The food of yellowfin and skipjack tunas in the eastern tropical Pacific Ocean. IATTC Comm. Bull. VII (5):295-459.
- Andersen, K.P., and E. Ursin. 1977. A multispecies extension to the Beverton and Holt theory of fishing with accounts of phosphorus circulation and primary production. Meddr Danm. Fisk-og Havunders. N.S. 7:319-435.
- Ankenbrandt, L.G. In press. Food habits of bait-caught skipjack tuna (*Katsuwonus pelamis*) from the southwestern Atlantic ocean. Fish. Bull., U.S.
- Chelton, D.B., P.A. Bernal, and J.A. McGowan. 1982. Large-scale interannual physical and biological interaction in the California Current. J. Mar. Res. 40(4):1095-1125.
- Clemens, H.B., and R.A. Iselin. 1963. Food of Pacific albacore in the California fishery (1955-1961). FAO Fish. Rep. Exp. paper (30) 3(6):1523-1535.
- Crow, M.E. 1982. Some statistical techniques for analyzing the stomach contents of fish. In G.M. Cailliet and C.A. Simenstad (eds.), GUT-SHOP '81 Fish Food Habits Studies Proc. Third Pac. Workshop. Wash. Sea Grant Pub., Univ. Wash, Seattle.
- Hart, J.L. 1942. Albacore food. Fish. Res. Board Can., Prog. Rep. Pac. Coast Stn. (52):9-10.
- Hart, J.L., and H.J. Hollister. 1947. Notes on the albacore fishery. Fish. Res. Board Can., Prog. Rep. Pac. Coast Stn. (71):3-4.
- Iverson, R.T.B. 1962. Food of albacore tuna, *Thunnus germon* (Lacepede), in the central and northeastern Pacific. U.S. Fish Wildl. Serv., Fish. Bull. 62(214):459-481.
- Laevastu, T., and H.A. Larkins. 1981. Marine fisheries ecosystem: its quantitative evaluation and management. Fishing News Books, Ltd. Farnham, Surrey, England, 162 p.
- Longhurst, A.R. 1967. The biology of mass occurrences of Galatheid crustaceans and their utilization as a fisheries resource. Proc. World Scientific Conf. on the Biol. and Culture of Shrimps and Prawns. FAO Fish Rep. 2(57):95-110.
- Magnuson, J.J., and J.G. Heitz. 1971. Gill raker apparatus and food selectivity among mackerels, tunas and dolphins. Fish. Bull., U.S. 69(2):361-370.
- Mais, K.F. 1981. Age-composition changes in the anchovy, *Engraulis mordax*, central population. CalCOFI Rep. 22:82-87.
- McHugh, J.L. 1952. The food of albacore (*Germo alulunga*) off California and Baja California. Scripps Inst. Oceanogr., Bull. 6(4):161-172.
- Nakamura, E.L. 1965. Food and feeding habits of skipjack tuna (*Katsuwonus pelamis*) from the Marquesas and Tuamotu Islands. Trans. Am. Fish. Soc. 94(3):236-242.
- Pinkas, L., M.S. Oliphant, and I.L.K. Iverson. 1971. Food habits of albacore, bluefin tuna, and bonito in California waters. Calif. Dept. Fish Game, Fish Bull. 152, 84 p.
- Powell, D.E., and H.A. Hildebrand. 1949. Albacore tuna exploration in Alaskan and adjacent waters—1949. U.S. Fish Wildl. Serv., Fish. Leaflet 376, 33 p.
- Radovich, J. 1979. Managing pelagic schooling prey species. In R.H. Stroud (compiler) and H. Clepper (ed.), Predator-prey systems in fisheries management. Sport Fishing Inst., Wash. D.C., p. 365-375.
- Rothschild, B.J., and J.L. Forney. 1979. The symposium summarized. In R.H. Stroud (compiler) and H. Clepper (ed.), Predator-prey systems in fisheries management. Sport Fishing Inst., Wash. D.C., p. 487-496.
- Sokal, R.R., and F.J. Rohlf. 1969. Biometry: the principles and practice of statistics in biological research. W.H. Freeman and Co., San Francisco, 776 p.
- Waldron, K.D., and J.E. King. 1963. Food of skipjack in the central Pacific. FAO Fish. Rep. Exp. Paper (26),6(3):1431-1457.